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# Tide-dependent Predation Patterns of Piscivorous Fishes in Shallow Estuarine Creeks

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TIDE-DEPENDENT PREDATION PATTERNS OF PISCIVOROUS FISHES IN SHALLOW  
ESTUARINE CREEKS

By

Matthew Ross Helms

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Submitted in Partial Fulfillment of the  
Requirements for the Degree of Master of Science in  
Coastal Marine and Wetland Studies in the  
School of Coastal and Marine Systems Science  
Coastal Carolina University  
2015

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To my father and mother, Hank and Suzanna; and my sister, Sarah: I am forever grateful for your unwavering support and encouragement.

This thesis is dedicated to the memory of Sue Deaton Ross.

## **Abstract**

The distribution and foraging behavior of predatory salt marsh fishes is shaped by the movements of prey, many of whom seek shelter in shallow and tributary creeks. I hypothesized that the distribution of piscivorous fishes in marsh creek channels would differ with proximity to the mouths of intertidal creeks and with tidal stage. Custom-built trotlines baited with live minnows were deployed during four discrete tidal stages at two microhabitats in main creek channels: (1) adjacent to intertidal creek mouths, and (2) along straight banks in North Inlet estuary, South Carolina. Catch-per-unit-effort of predatory fishes was significantly higher (Wilcoxon signed-rank tests,  $p < 0.05$ ) near creek mouths during all tidal blocks except the period between slack high tide and mid-ebb. I infer that these predators were attempting to intercept prey species that enter and leave small creeks that offer refuge during high tides. A total of 176 animals representing 14 species were captured, with Atlantic sharpnose sharks, Atlantic stingrays, ladyfish, and red drum composing 88.7% of the catch. The ability to predict spatial and temporal distributions for these and other piscivores improves our understanding of trophic and ecosystem function and may aid in the management of recreational fisheries.

## **Preface**

This dissertation is original, unpublished, independent work by the author, Matthew Ross Helms. It is submitted in partial fulfillment of the requirements for the degree of Master of Science in Coastal Marine and Wetland Studies in the School of Coastal and Marine Systems Studies at Coastal Carolina University. The research described herein took place between August 2010 and September 2013.

This manuscript is formatted following the style of the journal *Estuaries and Coasts*.

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## **Introduction**

As stocks of large nekton continue to be threatened by overexploitation and habitat destruction (Worm et al., 2006), the need for greater understanding of nekton life histories and niche utilization has become critically important (Bacheler et al., 2009) to the persistence of these animals. Salt marshes and tidal creek habitats are some of the most valuable yet vulnerable ecosystems on the planet (Lotze et al., 2006) and house critical life stages of many economically important fish species (Able et al., 2009; Beck et al., 2001; Boesch and Turner, 1984; Bozeman and Dean, 1980; Weinstein et al., 1980). Fluctuating hydrology and limited access to these important habitats make them difficult to study, particularly with regard to the animals which use them (Kneib, 1991). Despite the importance of larger (>20 cm) predatory fishes to trophic and ecosystem functions such as intertidal migration and nutrient transfer (Gibson, 1992; Gibson, 2003; Rountree and Able, 2007), as well as to commercial endeavors (Smith et al., 1984), these animals have largely been disregarded in efforts to quantify fish assemblages and habitat use across the entire tidal cycle.

While disparate and contradictory conclusions often exist regarding the presence of predatory nekton in shallow-water estuarine habitats, it is generally accepted that these areas provide refuge for juvenile and larval fishes (Bozeman and Dean, 1980; Kneib, 1997; Gibson, 2003). The ephemeral nature of these habitats results in a cyclical relationship between predator, prey, and suitable habitat—as the tides change along with the habitats they provide, so too do the animals which use them, including larger piscivorous fishes more commonly seen in larger bodies

of water (Rountree and Able, 2007). Cyclical habitat usage is especially evident in small rivulets which appear at higher tidal stages, allowing smaller prey species access to the marsh surface (Rozas et al. 1988). Lower-order (headwater) streams exhibit a greater density and abundance of nekton than larger, higher-order channels (Rozas and Odum, 1988; Allen et al. 2007; Granados-Dieseldorff and Baltz, 2008).

Odum (1984) expanded on the non-biological characteristics of stream order and habitat selection, showing that physiochemical properties differed significantly along the stream order continuum. In an expansive study, Allen et al. (2007) reported that nekton use of tidal salt marsh creeks is highly dependent on geomorphological features, particularly water depth, flow, steepness, and location. In contrast with active predators adapted for open-water hunting, prey species (such as minnows, killifish, and juveniles of several species) were found in greater abundance in shallower, slower-moving intertidal or subtidal creeks. Christian and Allen (2014) built upon these findings to establish that geomorphology also affects habitat selection by predators at higher trophic levels.

It stands to reason that aquatic predators would still exploit these habitats (and the conduits to access them) whenever possible. Sheaves (2001) concluded that the perception that few piscivores utilize intertidal creeks is in fact severely lacking in evidence. Rountree and Able (2007) identified the “marsh gradient,” a concept involving several components of salt marsh habitat use by predatory nekton that are affected by tidal, diel, and seasonal shifts in abiotic parameters (e.g., water depth and volume, light availability, and water quality) and biotic interaction



(e.g., refuge suitability, crowding, foraging opportunities, and abundances of young-of-year and prey fishes). While the authors explored the concept of predation pressure affecting prey concentrations throughout the marsh, they repeatedly acknowledge that the influence of tidal cycles and habitat selection by large nektonic predators comprises a portion of this marsh gradient that has not yet been thoroughly examined *in situ*.

Some previous studies of intertidal fish movement in salt marshes have primarily focused on small larval and juvenile fishes. Bozeman and Dean (1980) and Shenker and Dean (1979) targeted small fishes by blocking an intertidal creek at high tide with a 3 mm mesh channel net at a location within North Inlet, a relatively pristine coastal plain estuary in South Carolina. The authors did not report on adult fish capture, and acknowledge that large fishes were capable of avoiding the nets and probably persisted and successfully foraged in pools left by the receding tide. Furthermore, the presence of large nekton was likely reduced because the two studies cited above took place in the late fall, winter, and early spring, during which nekton abundance and diversity in North Inlet is significantly lower because of colder temperatures (Ogburn et al., 1988; Lehnert and Allen, 2002).

Other netting studies have included large nekton species but retain the same issue of blocking or ignoring the tide-based movement of predators. One of the earliest and most inclusive examinations of fish communities in North Inlet creeks was performed by Cain and Dean (1976). Their study resulted in incidental catches of piscivores, including bluefish, stingrays, jacks, grouper, and flounder, migrating within the creeks proper. However, their methods involved blocking off the mouth

of an intertidal creek at high tide and introducing a fish toxin upstream, not only resulting in a high rate of mortality but also preventing any potential upstream migration by predators and neglecting the possibility of tide-dependent predator movements. The geomorphology of the creek sampled (South Clambank Causeway Creek; see Figure 1) has changed significantly since it was dredged in 1954, and is currently much shallower and less conducive to use by larger migratory predators than it was at the time of the study (Allen, personal communication), suggesting the need for an immediate and comprehensive examination of North Inlet piscivore fauna.

Hettler, Jr. (1989) used a block net to compare nekton usage of the banks of first-order ("rivulet marsh") and third-order ("channel marsh") streams in a North Carolina salt marsh, and also confirmed the presence of transient piscivores such as seatrout, barracuda, and flounder in both habitat types. However, like Cain and Dean, he sampled only during the falling tide. Bretsch and Allen (2006) investigated the tidal component by utilizing a sweep flume to sample a shallow subtidal North Inlet creek throughout the tide, revealing that the majority of resident animals entered early in the rising tide and exited late in the ebbing tide while transient animals moved in and out of the creek while the water level was higher. In contrast to Cain and Dean's work, the only large piscivore they encountered in the creek was the summer flounder *Paralichthys dentatus*, suggesting that creeks are indeed refugia for small fishes and shrimps (Bretsch and Allen, 2006; Paterson and Whitfeld, 2000) .

Able et al. (2009) undertook a focused sampling effort using multi-mesh gillnets at multiple tidal stages in Delaware Bay and successfully confirmed the presence of large nektonic species, many of which also occur in marsh subtidal creek habitats of South Carolina. Rountree and Able (1992) experienced similar results when extensively sampling subtidal creeks using weirs and seines in southern New Jersey. Piscivores were caught using both types of gear, but no attention was given to the catch's proximity to intertidal habitats, despite the authors noting a tremendous amount of variety in creeks in the area of sampling.

These studies indicate large predators are present in estuarine systems, including areas around the smaller channels of North Inlet (Ogburn et al., 1988; Abel et al., 2007), but researchers have focused mainly on large creeks and little attention has been given to assessing catch rates throughout all tidal stages. Therefore, there exists a gap in our scientific knowledge regarding predator assemblages among various habitats throughout the tidal cycle. This is despite anecdotal and experimental indications that predator movement does occur around, and may in fact depend upon, intertidal habitats (Baker and Sheaves, 2005; Paterson and Whitfield, 2000; Sheaves, 2001), particularly with regard to their juncture with shallow subtidal habitats. This study attempts to directly address the issue of piscivore tidal movements with targeted sampling of piscivorous fishes (any species of fish whose diet has been identified in scientific literature as comprising mostly other fish species) that are in the immediate vicinity of intertidal creek mouths throughout the tidal cycle. These large piscivores focused upon in this study likely

exert a significant top-down trophic influence in the largest tidal creeks, and are also of greatest interest to anglers and fisheries managers (Bacheler et al., 2009).

It is reasonable to propose that concurrent with small intertidal creeks themselves providing a temporary refuge for smaller nekton, the adjoining subtidal creeks play host to significant and cyclical movements of their predators. Logically, it makes sense for piscivorous fish to target the mouths of smaller intertidal creeks during the late ebb tide when prey species are forced to leave these creeks, or during the early flood tide when intertidal creeks begin to become available as refugia for smaller fishes. I hypothesize that either of these two tidal periods surrounding low tide will be when the capture rate of fishes at the mouths of intertidal creeks will be highest relative to areas away from the creek mouths. In addition, I submit a null hypothesis that the relative capture rate will not vary significantly depending on the tidal stage.

## Methods & Materials

### Study Area

The study area comprised sites within North Inlet Estuary, an ocean-dominated coastal plain estuary and salt marsh system covering approximately 28 km<sup>2</sup> and located roughly six kilometers east of Georgetown, South Carolina (Ogburn et al., 1988). North Inlet and Winyah Bay to the south are designated by the National Oceanic and Atmospheric Association as part of the National Estuarine Research Reserve System (NERRS). The estuary and adjacent areas are monitored and maintained for research purposes by the Belle W. Baruch Institute for Marine Biology and Coastal Research, and are classified as relatively pristine due the lack of nearby anthropogenic development or agricultural or industrial influence (Nelson, 2005). Salinity in the major creeks ranges between 30-35 psu for most of the year, and the mean tidal range is around 1.4 m (Ogburn et al., 1988). Roughly 55% of high tide water is flushed out of the estuary during each ebb tide (Dame et al., 1986). During low tide, the estuary consists of exposed *Spartina alterniflora* (71%), open water and subtidal creeks (16%), and oyster reefs, mud flats, and intertidal creeks (13%) (Potthoff and Allen, 2003).

### Sampling Methodology

Custom-built trotline rigs were deployed at various times during the tidal cycle to assess predator densities in subtidal marsh channels both adjacent to and away from the confluence of smaller, intertidal creeks throughout North Inlet.

Sampling occurred between May 1st and October 1st of 2011 through 2013, when the water temperature was consistently greater than 21.1°C and the abundance of predatory teleost fishes and sharks was high (Cain and Dean, 1976; Hueter and Tyminski, 2007; Lehnert and Allen, 2002).

Fifteen replicate locations were identified, each comprising a section of subtidal creek with two paired sampling sites: an intertidal creek mouth and an open creek bank (Figure 1). The intertidal creeks associated with the creek mouth sampling sites were treated as replicates and were selected for this study by having a mouth no more than 7 meters wide, a depth at the mouth between 0.9 and 2 meters at bank full tide, and a total linear creek distance between 280 and 340 meters as determined from aerial photography. More importantly, as small intertidal creeks which largely drain at low tide and provide corridors to the marsh surface at high tide, these creeks all share a similar ecological role as prey refugia and feeding corridors for juvenile and small nekton species.

At each sampling location, two baited trotlines were simultaneously deployed at the intertidal creek and creek bank sites during four different tidal stages. The creek mouth rig was deployed at the site perpendicular to the adjacent intertidal creek and centered across the creek mouth at a depth of approximately 2.4 meters as measured at high tide, the average depth at which the sill begins to drop off into the central portion of the subtidal channel. The creek bank line was set at the same depth along a straight bank of the subtidal creek at least 100 meters away from the intertidal creek mouth and 50 meters away from any other intertidal creek mouths (Figure 2, Plate 1).

The tidal cycle was divided into four distinct segments during which sampling occurred: Early ebb (slack high falling to mid-ebb), late ebb (mid-ebb falling to slack low), early flood (slack low rising to mid-flood), and late flood (mid-flood rising to slack high). In order to help ensure that sampling occurred discretely in each of the four portions of the tide, no sampling took place during a twenty-minute buffer at the start and end of each tidal segment. Thus, at each of the 15 intertidal creek locations, paired trotlines (creek mouth and bank) were deployed at each of the four tidal segments, yielding a total of 60 paired samples (120 lines and 1,440 hooks) over the course of the study.

Each bottom trotline rig consisted of a braided 90.7 kg test mainline, 15 meters long, suspended roughly 0.6 m off the bottom and attached at each end by tuna clips to hard-laid poly rope serving as anchor lines which could be adjusted for depth. Twelve 30.5 cm gangions were attached to the mainlines via loops spaced 1 m apart, with 2 m of space between the last gangion and anchor line at each end. Each gangion consisted of 22.7 kg test monofilament line connecting a 45.4 kg test swivel clip to a 4/0 aluminum circle hook (Figure 3). Hooks were baited with live mummichogs (*Fundulus heteroclitus*).

Each line was left to soak for 30 minutes (from last anchor in to first anchor out), during which time researchers maintained visual contact with the rigs. Hooked fishes were removed as the lines were retrieved and temporarily placed into livewells prior to handling. Each individual was identified to the species level. Total and standard/precaudal lengths, as well as sex when applicable, were recorded prior to returning the fish to the water. Disk width was recorded for stingray

species. Water temperature, air temperature, and salinity were recorded at the beginning of each sampling session using either a portable handheld sampling meter (Yellow Springs Instrument Model 85) or boat-mounted device, or from the National Oceanic and Atmospheric Association water and atmospheric monitoring station located at the reserve's Oyster Landing (33° 20' 57.66" N, -79° 11' 19.97" W).

Data pertaining to the status of each baited hook was logged. Each hook was given a number based on its position in the sequence of deployment, and the condition of each bait was assessed upon retrieval and assigned to one of six categories: "bitten" (clearly severed but not entirely removed from the hook, indicating predation by a toothed animal), "crushed" (one or more body segments flattened to the point of mutilation, indicating predation by animals with pharyngeal teeth such as red drum or by stingrays, who have rough hardened plates in their mouths rather than biting teeth [Tee-Van et al., 1953]), "chewed" (chunks of flesh removed), "cut" (ganglion was severed above the hook, indicating a large predator either snapped or bit through the monofilament), "missing" (bare hook), or "intact" (bait was untouched and/or still living).

### Statistical Analysis

For each of the four segments in the tidal cycle, the catch-per-unit-effort (CPUE) at creek mouth sites was compared to that of bank sites. Each CPUE index was calculated using the combined samples at creek mouth and bank sites for each tidal stage. The overall comparisons were accomplished by comparing the CPUE values using the non-parametric equivalent to the paired-sample t-test, the



Wilcoxon signed rank test. The non-parametric equivalent to the ANOVA test, the Kruskal-Wallis  $H$  test, was used to determine if a significant difference existed among the 15 creek mouth CPUE means or among the 15 bank CPUE means and thus reinforce that the chosen sites in each category were acceptably similar to one another. Chi-square tests were utilized to compare observed versus expected (1:1) sex ratios in animals where external sex characteristics were identifiable (sharks and stingrays).

Several basic ecological indices were also calculated to portray and compare community structure. In addition to basic richness (or total number of encountered species,  $S$ ), species diversity at creek mouth and bank sites during each tidal block was statistically compared between treatments using the Shannon-Wiener diversity ( $H'$ )  $t$ -test, following Magurran (1988). Pielou's evenness index  $J'$  is derived from the Shannon-Wiener diversity index and was calculated to illustrate the species evenness in each sampling set. Wilcoxon signed rank tests were used to determine significance for each of the obtained richness, diversity, and evenness values.

SPSS (Version 17) was used for statistical analyses and an *a priori* 95% confidence interval ( $\alpha = 0.05$ ) was established for tests of significance.

## Results

Between August 2011 and September 2013, 176 predatory fishes representing 14 species were collected in total (Table 1). Four species accounted for 88.73% of the catch: juvenile Atlantic sharpnose sharks, *Rhizoprionodon terraenovae*, (55.78% of the total catch); Atlantic stingrays, *Dasyatis sabina* (18.75%); ladyfish, *Elops saurus* (9.09%); and red drum, *Sciaenops ocellatus* (5.11%).

*R. terraenovae* were all young-of-the-year juveniles and exhibited a male to female ratio of 1:0.78, which was not significantly different than the expected 1:1 ratio ( $\chi^2$  test,  $p > 0.22$ ). The ratio of male to female *D. sabina* captured was 1:2.08, which was slightly biased towards females but was also not statistically different ( $p > 0.08$ ). All three southern stingrays (*D. americana*) were female.

Catch-per-unit-effort was not significantly different between creek mouth and bank sites during the early ebb period between slack high and mid-falling tide ( $p > 0.05$ ). However, during the remaining three tidal stages (i.e., late ebb, early flood, and late flood), CPUE for predatory fishes was significantly greater at creek mouth sites (Figure 4). The most significant difference between the two treatments occurred during the time between slack low and mid-flood, where the mean CPUE for creek mouth samples ( $2.13 \pm 0.45$ ) was significantly higher ( $Z = -2.64$ ;  $p < 0.01$ ) than the mean CPUE of the bank samples ( $1.47 \pm 0.40$ ). More animals were caught during this tidal period than any other. No significant differences were found among the CPUEs of creek mouth samples, or among the CPUEs of bank samples (Kruskal-Wallis  $H$  test).

Because Atlantic sharpnose sharks accounted for over half of the total catch, the above calculations were repeated with that species excluded in order to assess whether they disproportionately influenced the results. The mean CPUE excluding *R. terraenovae* did not significantly differ between creek mouth and bank samples during the falling tide nor during early flood. During late flood, the mean CPUE for creek mouth samples was significantly higher ( $Z = -2.64$ ;  $p < 0.01$ ) than the mean CPUE of the bank samples (Figure 5a). The mean CPUE for *R. terraenovae* alone was not significantly different between creek mouth and bank samples for any portion of the tidal cycle (Figure 5b).

CPUE was calculated for baited hooks showing evidence of predation even though no animals were caught on these hooks. No significant difference was detected between creek mouth and bank sites during any tidal segment for baits designated as "bitten," "crushed," "chewed," "missing," or "cut." When these data were combined with the catch data, no significant difference was found between creek mouth and bank sets at any point during the tidal cycle (Table 2).

Of the 1,440 hooks deployed during the course of this study, the majority of impacted baits (i.e. those not intact, missing, or holding a captured animal) were "bitten" (106 hooks or 7.4% of the total). Hook status that could not be defined in any of these categories was designated as "other" and accounted for 17 (1.2%) of all baits. This category included anomalies such as twisted hooks, gangions completely removed from their swivels, and crabs. The remaining three categories of impacted hooks ("chewed," "crushed," and "cut") combined to make up 1.6% of all deployed baits (Figure 6).

Species richness, diversity, and evenness were significantly greater ( $p < 0.05$ ) at creek mouth sites during the late flood period (between mid-flood and slack high). The values were not significantly different between creek mouth and bank sites during any other part of the tidal cycle. The results of diversity index calculations are shown in Table 3.

During this study's sampling periods, the air temperature ranged from 22.3 to 36.0°C with a mean temperature of 29.1°C (standard deviation of 3.0°C), and the water temperature ranged from 22.7 to 34.8°C with a mean of  $28.8 \pm 2.5$ °C. The mean salinity was  $32.8 \pm 2.7$  psu and ranged between 23.4 and 36.2 psu.

## Discussion

As predicted, large predatory fishes deliberately targeted tidal creek mouths during late ebb and early flood tides; i.e., the two tidal periods immediately before and after low tide. However, this pattern was broader than expected and included late flood as well. Predatory fish catch-per-unit-effort was significantly higher at creek mouth sites during the period leading up to low tide, then during the entire rising portion of the tidal cycle (Figure 4). As the tide began falling, the distribution of predatory fishes at creek mouths was not significantly different than their distribution at banks away from the creek mouth.

Due to the novel and relatively selective sampling methods used in this study, direct comparisons with composition and abundance of fishes at a similar trophic level in other South Carolina estuary studies is difficult. However, these data suggest a significant cyclical pattern of predator distribution relative to the mouths of shallow tidal creeks, in support of the previous findings of others (e.g., Bretsch and Allen, 2006) that report clear patterns of nekton distribution based on changes throughout the tidal cycle.

There are a variety of potential explanations for the significantly higher numbers of predators at creek mouths at all stages of the tide other than early ebb. The primary reasoning centers on the function of prey refuge. It was not anticipated that piscivores would concentrate on creek mouths in the tidal stages surrounding high tide (i.e., late flood and early ebb), since the majority of resident prey species, including *F. heteroclitus* and other killifishes, have been repeatedly shown to migrate into shallow creek edges during the early rising tide and out of the creeks

towards subtidal waters during late ebb (Weisberg et al., 1981; Kneib and Wagner, 1994; Bretsch and Allen, 2006). Cattrijsse et al. (1994) showed that the goby *Pomatoschistus microps*, which in European marshes occupies a comparable niche to *F. heteroclitus*, exhibits this same pattern. This is because when the water level is high enough it provides refuge for small prey items among the marsh grasses where it is difficult, though not impossible, for large predatory fishes to travel (Montague and Wiegert, 1990; Peterson and Turner, 1994; Kneib, 1997). Even when the water level is not high enough to inundate the grassy marsh surface, common prey fishes will continue to exhibit this pattern of tidal migration due to the increased abundance of food sources and the greater volume of water in which to seek refuge (Weisberg et al., 1981).

Refuge is one of many attributes of lower-order streams like intertidal creeks (Boesch and Turner, 1984; Odum, 1984; Allen et al., 2007). The intertidal creeks in this study were selected as replicates because they serve similar ecological functions as prey refuge corridors from the adjacent subtidal channel in which sampling occurred. The physical similarities between intertidal creeks studied as well as the lack of statistical difference among creek mouth and among bank CPUEs (Kruskal-Wallis  $H$  test) reinforce that these sites were appropriate replicates.

Interestingly, a significantly higher catch rate of predators at creek mouth sites also occurred during late flood (Figure 4). One explanation for this difference revolves around temperature. As the water level falls during early ebb, warm water that is retained in the intertidal creeks during high tide is flushed out. In North Inlet, this water is often 3-5°C warmer than the water flowing through the subtidal

channels. Predators may have been hesitant to cross this relatively steep temperature gradient, preferring instead to remain in areas with more well-mixed waters (Allen, personal communication). During the flood tide, by contrast, the water flowing from the inlet mouth is closer to the temperature within the subtidal channels, providing an environment more conducive to predation activities.

A thought experiment based upon basic animal energetics may reveal another reasoning for this curiosity. During the early ebbing tide, prey fishes with well-developed locomotive abilities are forced to either remain behind in shallow pools and risk desiccation or predation from non-aquatic animals, or exit the creeks. Predators may be focusing on creek mouths at this time in an attempt to intercept prey fishes choosing to migrate outwards with the tide, as many fishes use the prevailing current to change their positions (Gibson, 1980). However, the amount of energy expended by predators remaining in position at the creek mouth while fighting against the outgoing tide may cause such endeavors to not be worthwhile. This may explain why we observed significant differences in predation during both early and late rising portions of the tide but not early ebb. Predators intercepting prey items entering the creek while the water level rises have to worry less about being swept "out of position," as the most the current can do is push them into the same creeks as the prey items they are pursuing. They can then swim back out and resume their hunting in the main channel, if necessary, or even remain in the creeks and wait for prey animals to wash "downstream."

This is not to say, however, that large predators will not routinely fight against strong tidal currents in these creeks. Preliminary research with gill nets

across the mouths of intertidal creeks (8.89 and 7.30 cm stretch) deployed during the early falling tide in these same sites was carried out in 2010 and 2011. Despite the water level dropping, these previous experiments resulted in the capture of several species traveling upstream into the creeks, most notably *E. saurus* and adult female bonnethead sharks, *Sphyrna tiburo* (Helms, unpublished data). Curiously, though, no bonnetheads were collected during the trotlining studies despite their known presence in the sampling areas. It is likely that their size (mean TL = 110 cm) and sharp teeth exceeded the holding capacity of the gangions, making them possible culprits behind some of the rare cut lines recorded during this study. Alternatively, they may simply have been uninterested in the mummichogs used as bait, since the diet of *S. tiburo* typically consists primarily of invertebrates such as blue crabs (Cortés et al., 1996). Female bonnetheads from these collections occasionally showed evidence of bite marks, possibly from mating attempts, and even though gravid bonnetheads have been routinely captured in South Carolina estuaries, to date no primary pupping location is known in coastal South Carolina (Ulrich, 2007).

Atlantic sharpnose shark pups, on the other hand, are commonly found in South Carolina estuaries (Castro, 1993; Loefer and Sedberry, 2003; Abel et al., 2007; Ulrich, 2007), with North Inlet noted as a primary nursery location for this species (Abel et al., 2007). Because these animals were so abundant in the samples, the possibility existed that this single dominant species was driving the pattern of significance observed. However, when *R. terraenovae* was removed from CPUE calculations, the general pattern remained similar to those found in the CPUE data



for all animals combined (relative predator abundances were higher at creek mouths especially during late ebb, early flood, and late flood) (Figure 5a). This difference was significant during late flood. The fact that the relative abundance patterns were very similar yet only significantly different during one tidal block as opposed to three means it is unlikely the high abundance of the sharks was primarily responsible for inducing the differences in predator abundances at creek mouth and bank locations, but removing the sharks from the data made it more difficult to achieve statistical significance primarily due to the smaller sample size used in calculating CPUE.

Comparing CPUE values for *R. terraenovae* alone showed no significance at any tidal stage, indicating that distributions of Atlantic sharpnose sharks were roughly equal throughout the tide at creek mouth and bank locations. This could be due to their young age—all sharks caught were within the published parameters (320-630 mm TL) to be considered young of the year (Castro, 1993) and may not have yet developed a regular temporal pattern of hunting compared to older animals of other species. These results follow the findings of Carlson et al. (2008), who, despite not focusing on movement relative to tidal creeks specifically, also failed to find consistent patterns of diel movement in juvenile *R. terraenovae* in a Florida lagoon where the animal had the highest CPUE of all species present in the study.

Many stingrays of the genus *Dasyatis* are known to be successful benthic predators, feeding on crustaceans, polychaete worms, molluscs, and other demersal invertebrates. While the southern stingray *Dasyatis americana* is known to

incorporate small teleosts into its diet (Gilliam and Sullivan, 1993; Michael, 2005), the diet of the closely-related Atlantic stingray *Dasyatis sabina* consists mainly of small demersal worms, crustaceans, and other small invertebrates, and is not typically known to feed on fishes (Michael, 2005). The high frequency with which *D. sabina* was caught in this study indicates that, at least in this area, they will in fact readily act as piscivores when presented with the opportunity.

A particularly unusual catch was that of the pinfish, *Lagodon rhomboides*. This abundant nearshore member of the porgy family is more often associated with being used as bait than acting as a predator of fishes, and feeds primarily on algae, vascular plants, zooplankton and small benthic invertebrates. Past studies of pinfish diets have found fish remains in stomach content analyses, primarily in adults between 76 and 173 mm SL (Hansen, 1969). However, the total percentage of the overall diet composed of fish was roughly between 1.7% and 6.6%, and in terms of chordate food sources, fishes were described as secondary at best (Bowman et al., 2000; Hansen, 1969). The mummichogs used as bait in this study appeared to be out of the diet range of *L. rhomboides* and to be physically too large for them to consume. Inexplicably, however, the single 152 mm SL pinfish collected was in good health and cleanly hooked through the mouth in the same fashion as the much larger piscivores captured on hooks.

All three ecological indices (i.e., richness  $S$ , Shannon-Wiener diversity  $H'$ , and Pielou's evenness  $J'$ ) were significantly higher at creek mouth sites only during the late flood period immediately preceding high tide. Eight different species were caught at creek mouth sites during this tidal block, including the only specimens of

the northern sea robin *Prionotus tribulus* and the northern sennet *Sphyræna borealis*. Specimens of the gafftopsail catfish *Bagre marinus* were collected only during this period and during early flood (also at a creek mouth site). By contrast, only two types of animals were caught at bank sites during late flood, *R. terraenovae* and *E. saurus*. Both were among the four most commonly encountered animals in the study. This stark difference in species richness alone could partially account for the significantly higher diversity and evenness at creek mouths during late flood, as both values are derived partially from the number of species present at each habitat being compared. The possibility also exists that transient prey animals entering the creeks late in the flood tide (Bretsch and Allen, 2006) were being pursued by a wider variety of predatory fishes from elsewhere in the marsh system, leading to an increase in piscivore diversity as the tide neared slack high.

It should be noted that hooks showing evidence of predation (missing, crushed, chewed, bitten, and cut) but not holding a captured animal were slightly more numerous at bank sites throughout the tide. However, none of these comparisons were significant (Wilcoxon signed rank tests, minimum  $p > 0.2$ ). “Bitten” baits were the most numerous of baits showing distinct predation damage. The animals most likely responsible for these were Atlantic sharpnose sharks, bluefish (*Pomatomus saltatrix*), and southern flounder (*Paralichthys lethostigma*), all of which are toothed predators common to North Inlet but, with the exception of the sharks, were relatively uncommonly encountered in this study. On many occasions the animal could have darted in, grabbed a bite of the bait, and fled without ever being hooked.

This type of study helps to clarify the diel cycles of movement and predation within salt marsh creeks, and it is worth exploring and expanding upon this work in the future. The types of sampling gear used here were carefully chosen because they were anticipated to be the most efficient on this scale, and it is unlikely that other common types of large fish collection techniques would be appropriate for this research. Gill nets are frequently used in shark surveys, which sometimes comprise thousands of individual organisms (Ulrich et al., 2007; e.g., Able et al., 2009), but often result in fairly high mortality and are very size-selective (Hubert, 1996). The South Carolina Department of Natural Resources typically uses trammel nets for their research in similar environments, as they are effective in capturing a wide variety of large nekton with a relatively low mortality rate. However, trammel nets do not specifically target predatory fishes and do not perform well in strong currents such as those found at creek mouths during flowing tides, though it could conceivably be a technique to explore in future studies. Longlines can directly target predators and are often used to sample shark populations (Abel et al., 2007), but again they are mainly suited for larger-scale research in deeper water. More importantly, however, longlining often utilizes chopped-up fish or dead baits. This study aimed to analyze the temporal movement of predators based on their natural rhythm; this could potentially be disrupted by adding a smell component which attracts piscivores that may not be present naturally. The equipment and methodology used in this study was essentially a scaled-down version of longlining using live baits. A thorough understanding of large piscivore movements in environments similar to North Inlet would likely be best achieved with a

combination of multiple sampling techniques, but the core objectives of this research (namely, to sample common predatory fishes in their natural cyclical movements, with minimal mortality, in size classes ranging from 20 cm to the sizes frequently targeted by game fishermen) were well satisfied with the sampling procedures used.

## **Conclusion**

One of the most pressing environmental issues in modern times is the current state of our oceans, and, in particular, our fisheries. Dramatic increases in technology and catch efficiency, coupled with a consequential reduction in biodiversity, greatly threaten marine environments and sensitive areas such as salt marshes. A greater understanding of the behavior and community structure of fishes is vital to the effective management of these critical resources, particularly in tidal creeks and salt marshes which are heavily affected by non-point source pollution and runoff in coastal areas. Large piscivores, the focus of this study, have been hit especially hard by overfishing, and many commercially and recreationally important species can be found in inshore areas such as North Inlet. By analyzing patterns of movement based on the tidal cycle, we may be able to more accurately and efficiently identify critical habitats and potential protected areas for species targeted by both recreational anglers and commercial fishermen. This will greatly benefit not only fisheries management policies by groups such as the National Marine Fisheries Service but the integrity of the greater estuarine ecosystem as well.

## Tables

Table 1. Total number (total N = 176), relative abundance, and minimum, maximum, and mean size measurements (in mm), including standard deviation, of predatory fishes caught in this study. Also included are male-to-female ratios (M:F) for elasmobranchs. TL = Total Length, DW = Disk Width (for rays), SL = Standard Length (for teleosts), PCL = Pre-Caudal Length (for sharks).

Species	N	% of total	Mean TL/DW	Min	Max	SD	Mean SL/PCL	Min	Max	SD	M:F
<i>Rhizoprionodon terraenovae</i>											
Atlantic sharpnose shark	98	55.68%	391.53	321	508	36.36	291.20	240	380	28.73	1:0.78
<i>Dasyatis sabina</i>											
Atlantic stingray	33	18.75%	305.48	232	398	43.54	N/A	N/A	N/A	N/A	1:1.91
<i>Elops saurus</i>											
Ladyfish	16	9.09%	472.64	292	563	83.56	380.86	243	455	65.22	N/A
<i>Sciaenops ocellatus</i>											
Red drum	9	5.11%	498.56	290	762	187.93	413.11	231	637	158.45	N/A
<i>Paralichthys lethostigma</i>											
Southern flounder	7	3.98%	343.83	249	400	60.71	290.17	202	342	55.78	N/A
<i>Dasyatis americana</i>											
Southern stingray	3	1.70%	645.33	551	760	105.97	N/A	N/A	N/A	N/A	0:3
<i>Bagre marinus</i>											
Gafftopsail catfish	3	1.70%	461.67	450	474	12.01	342.00	322	368	23.58	N/A
<i>Prionotus tribulus</i>											
Bighead sea robin	1	0.57%	199.00	199	199	N/A	150.00	150	150	N/A	N/A
<i>Pomatomus saltatrix</i>											
Bluefish	1	0.57%	292.00	292	292	N/A	246.00	246	246	N/A	N/A
<i>Caranx hippos</i>											
Jack crevalle	1	0.57%	213.00	213	213	N/A	174.00	174	174	N/A	N/A
<i>Sphyraena borealis</i>											
Northern sennet	1	0.57%	Fish escaped; no measurements taken								N/A
<i>Opsanus tau</i>											
Oyster toadfish	1	0.57%	270.00	270	270	N/A	239.00	239	239	N/A	N/A
<i>Lagodon rhomboides</i>											
Pinfish	1	0.57%	189.00	189	189	N/A	152.00	152	152	N/A	N/A
<i>Menticirrhus americana</i>											
Southern kingfish	1	0.57%	342.00	342	342	N/A	298.00	298	298	N/A	N/A

Table 2. Mean CPUE (catch-per-unit-effort) values for mouth and bank samples, Wilcoxon  $Z$  values,  $p$  values, and significance for each of the four tidal stages ( $N = 60$ , 15 paired samples for each tidal block). Calculated values are shown for "impacted" hooks; i.e., hooks where bait was missing or showing evidence of predation but not actually holding a captured animal; and "impacted" hooks combined with true CPUE values from collected fishes. Mean CPUE values shown in **bold** are the greater of each pair. All Wilcoxon  $Z$  values are reported as negative regardless of whether they were based on positive or negative rankings. Significance is based on an  $\alpha$  level of 0.05.

Analysis	Tidal Stage	Mean CPUE		$Z$	$p$	Significant
		Creek Mouth	Bank			
Impacted hooks	Early ebb	3.867	<b>5.200</b>	-1.140	>0.25	No
	Late ebb	5.933	<b>6.267</b>	-0.457	>0.64	No
	Early flood	4.267	<b>5.933</b>	-1.826	>0.06	No
	Late flood	2.333	<b>2.867</b>	-1.031	>0.30	No
Impacted hooks combined with fishes caught	Early ebb	5.000	<b>6.600</b>	-1.390	>0.16	No
	Late ebb	<b>7.667</b>	7.600	-0.223	>0.82	No
	Early flood	6.400	<b>7.333</b>	-1.084	>0.27	No
	Late flood	<b>3.867</b>	3.667	-0.200	>0.84	No



Table 3. Ecological diversity index values for creek mouth and bank samples, Wilcoxon  $Z$  values,  $p$  values, and significance for each of the four tidal stages ( $N = 60$ , 15 paired samples for each tidal block). Included are species richness (total number of species  $S$  in each sample group), Shannon-Wiener diversity ( $H'$ ), and Pielou's evenness ( $J'$ ). All Wilcoxon  $Z$  values are reported as negative regardless of whether they were based on positive or negative rankings. Significance is based on an  $\alpha$  level of 0.05.

Index	Tidal Stage	Creek Mouth	Bank	$Z$	$p$	Significant
Richness ( $S$ )	Early ebb	6	4	-0.577	>0.56	No
	Late ebb	5	6	-1.667	>0.95	No
	Early flood	6	6	-1.571	>0.11	No
	Late flood	8	2	-2.373	<0.02	Yes
Diversity ( $H'$ )	Early ebb	1.316	0.912	-0.271	>0.78	No
	Late ebb	1.163	1.330	-0.365	>0.71	No
	Early flood	1.452	1.210	-1.577	>0.11	No
	Late flood	1.642	0.429	-2.232	<0.03	Yes
Evenness ( $J'$ )	Early ebb	0.734	0.658	-0.271	>0.78	No
	Late ebb	0.723	0.742	0.000	1.00	No
	Early flood	0.810	0.675	-1.787	>0.07	No
	Late flood	0.790	0.619	-2.232	<0.03	Yes

## Figures

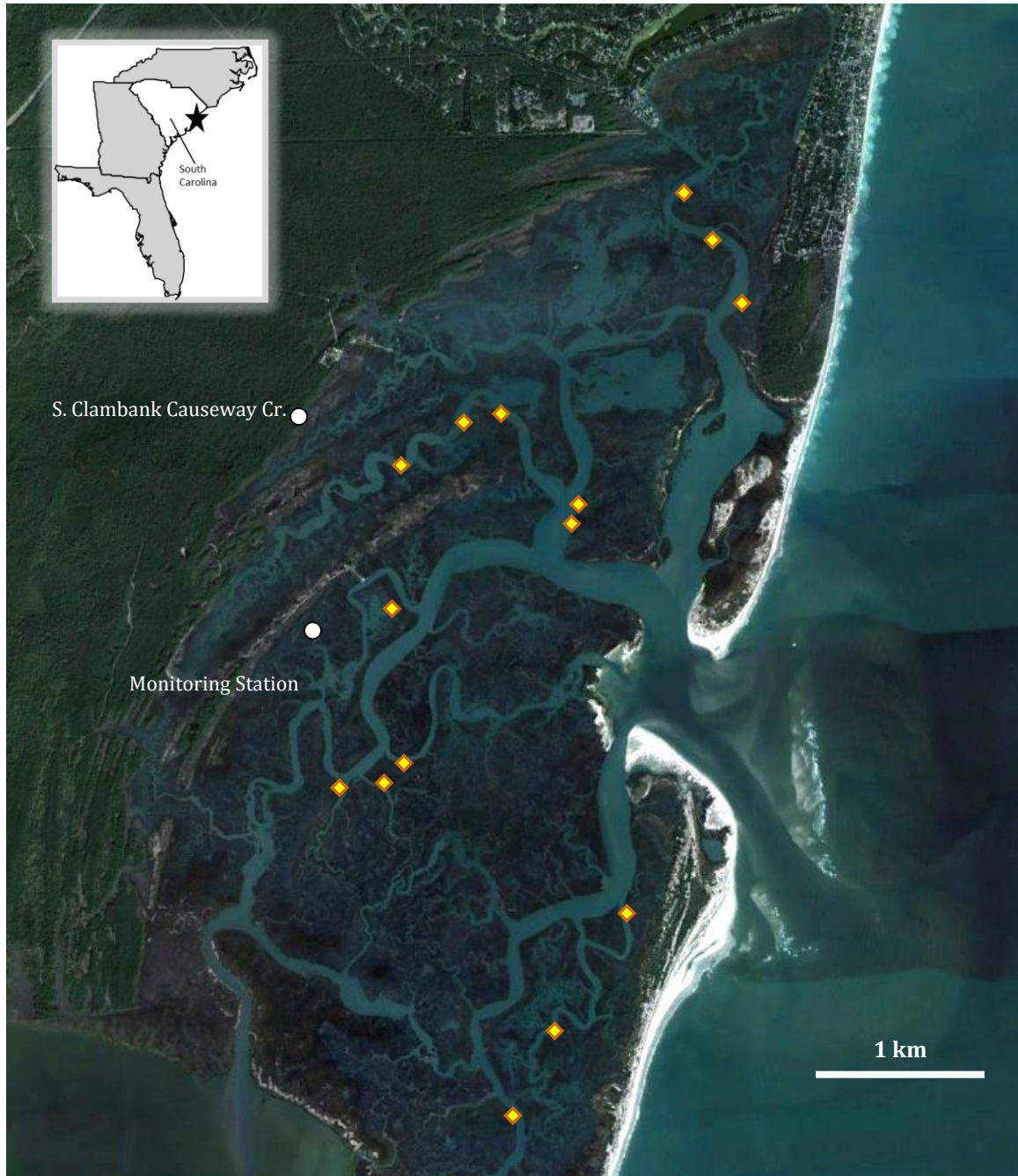


Figure 1. Sampling locations (15) within North Inlet Estuary, South Carolina. Each location consists of a sampling site adjacent to an intertidal creek mouth and a

nearby sampling site along a subtidal bank. The inset map shows the location relative to the southeastern United States. Also shown are the launch site (South Clambank Causeway Creek) and chemical monitoring station.

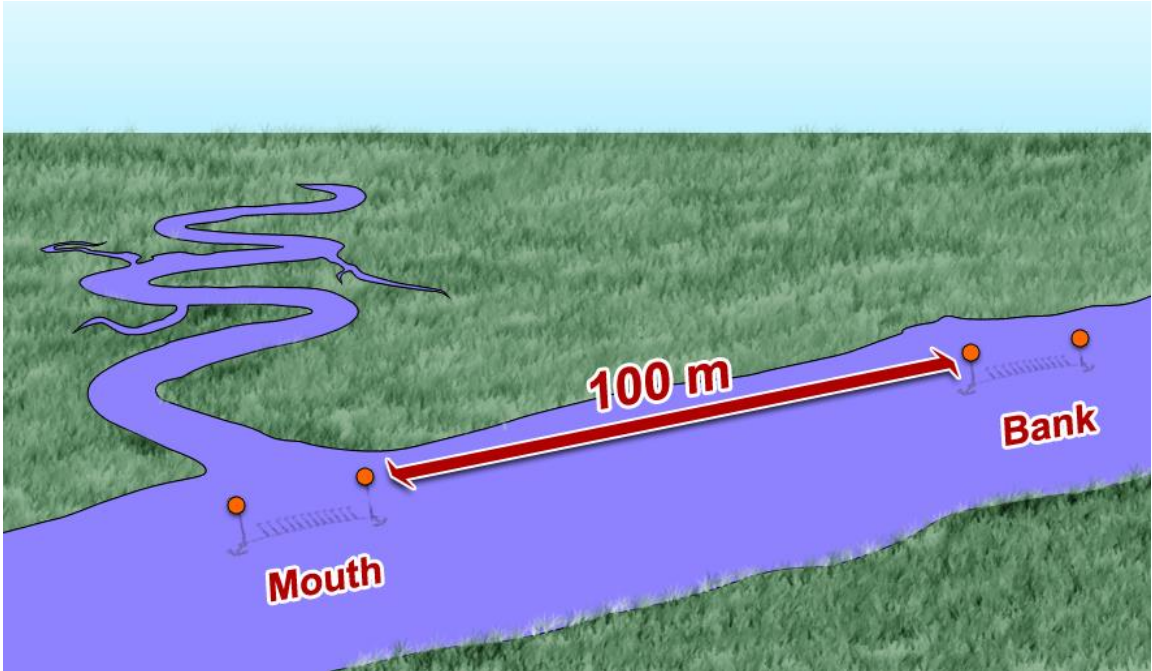


Figure 2. Typical deployment of trotlines for a single sampling session. A 15-meter long line is deployed in a subtidal channel perpendicular to an intertidal creek, while a second line is simultaneously deployed away from any creeks along the same bank at an identical depth at least 100 m away.

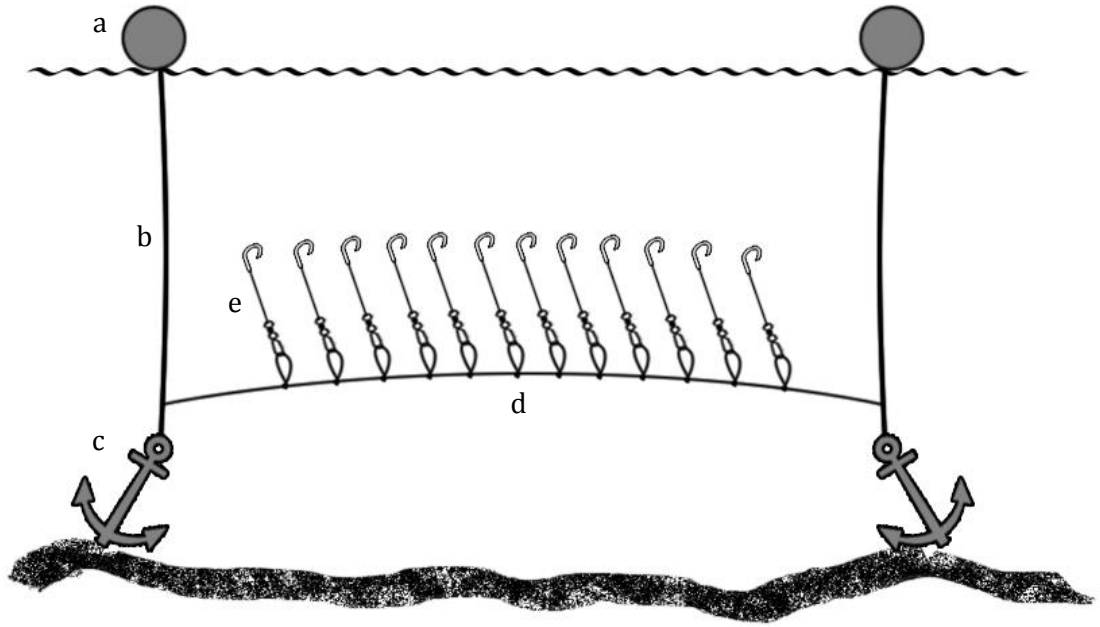


Figure 3. Diagram of trotline rig. a) surface floats; b) anchor lines; c) anchors; d) mainline; e) gangions

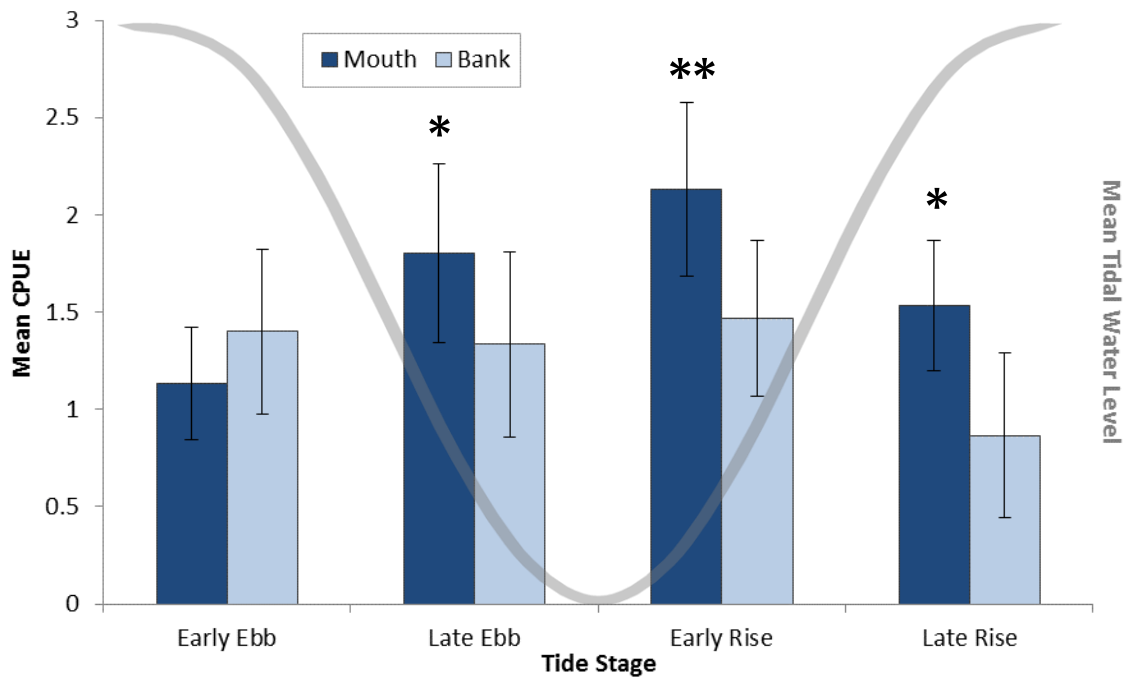


Figure 4. Mean CPUE  $\pm$  standard error for creek mouth and bank sampling sites (N = 60; 15 paired samples for each tidal block) during slack high tide falling to mid (H-M), mid falling to low (M-L), low rising to mid (L-M), and mid rising to high (M-H). \* denotes a significance level of  $p < 0.05$  and \*\* denotes a significance level of  $p < 0.01$ . The mean tidal water level during a complete tidal cycle (slack high to slack high) is also shown for reference.

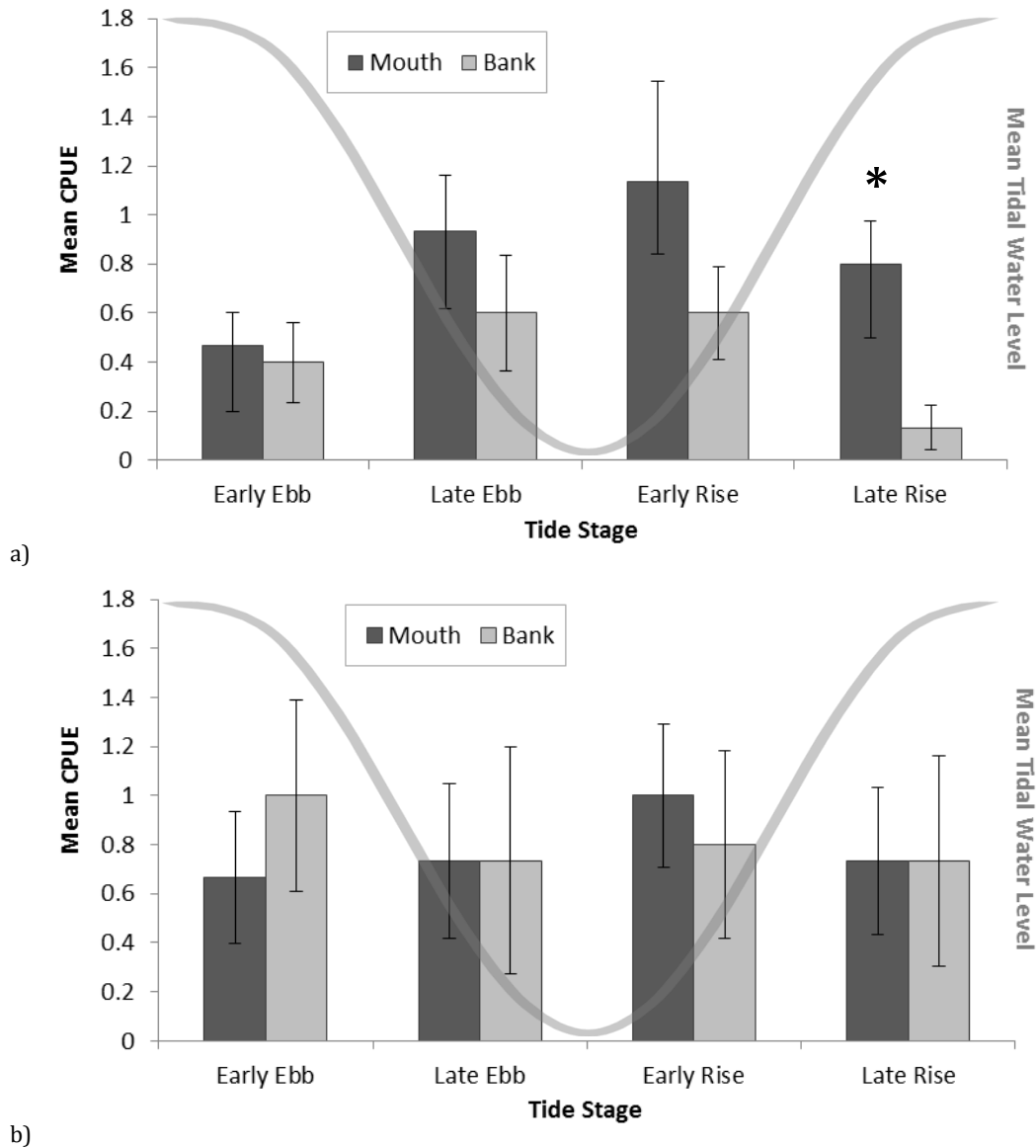


Figure 5. Mean CPUE  $\pm$  standard error for creek mouth and bank sampling sites (N = 60; 15 paired samples for each tidal block) with various restrictions applied to catch data relating to the highly abundant Atlantic sharpnose sharks *Rhizoprionodon terraenovae*. \* denotes a significance level of  $p < 0.05$ . a) Mean CPUE for all animals excluding *R. terraenovae*. b) Mean CPUE for *R. terraenovae* alone. The mean tidal water level during a complete tidal cycle (slack high to slack high) is also shown for reference.

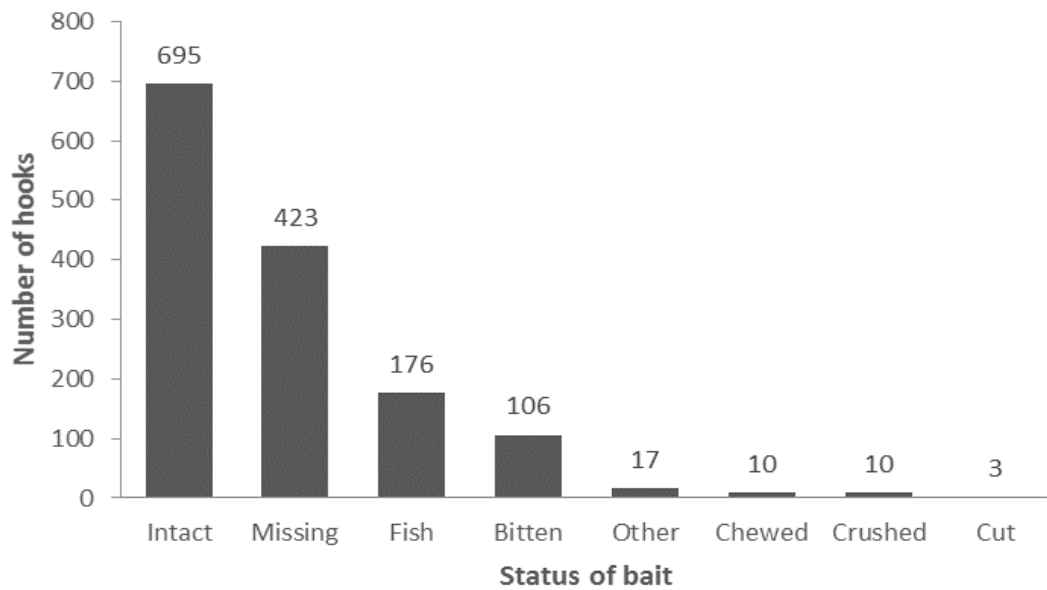


Figure 6. Status of individual mummichog baits deployed throughout this study (N = 1,440). “Intact” refers to baits that were untouched and/or still alive, “Missing” indicates the retrieved hooks were bare, and “Fish” denotes hooks that were holding a captured fish. The remaining categories describe the status of the baits themselves. “Other” refers to baits that did not fall into any other category (e.g., a hook holding a crab, or an event where the gangion had been removed completely).



## Plates



Plate 1. Photograph of a typical creek mouth deployment (site "Old Man 1"). Surface floats (see Fig. 3) shown in the foreground are 15 meters apart.

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