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Osmoregulation and Salinity Preference in Juvenile Sandbar Sharks (*Carcharhinus plumbeus*) in Winyah Bay, SC, USA

By

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Dedication

This thesis is dedicated first and foremost to my Grannie, Ann Wingar. She passed away during the Summer of 2018 as data were being collected for this thesis. She was the most determined person I have ever met, and I hope I am as half as determined as she was throughout her whole life. Grannie Annie loved the ocean and was always supportive of my dreams and goals. I miss our weekly phone calls about my progress that always ended with her saying *good luck and I love you.*

This thesis is also dedicated to my incredibly hardworking and special parents, Geoff and Caroline. They have worked their whole lives to give me the best education that they could and for that I will be forever grateful. This thesis would not have been possible without their endless encouragement and phone calls that made me laugh until I cried.

I'd also like to dedicate this thesis to my numerous friends, Elise Pullen, Kathryn Greiner-Ferris, Daniel Coward, Charlotte Pechtl, Emily Rose Nelson, Claudia Mazur, David Fertitta, Andrea Szabo, Chris Huebler, and Charlotte Newman, for their constant support and listening ears.

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Abstract

Juvenile sandbar sharks (*Carcharhinus plumbeus*) have been caught in salinities ranging from 7 – 40. In Winyah Bay, a partially mixed estuary in Northeast SC, juvenile sandbar sharks tidally alternate between higher tides in middle bay and lower tides in lower bay. To assess salinity preference and duration in eight acoustically-tagged juvenile sandbar sharks in different salinities, acoustic receivers with salinity loggers were placed throughout Winyah Bay. Juvenile sandbar sharks were caught in salinities from 17.2 to 36.1 and acoustic detections were recorded from 11.5 to 24.7 by salinity loggers in middle bay. Smaller juvenile sandbar sharks used lower salinities, presumably to decrease osmoregulatory costs and predation, and used tidal currents to move throughout the bay, which also decreased energy expenditure. Acoustically tagged sharks spent most of their time in middle Winyah Bay at high tide or tidal phases immediately before or after high tide, whereas when these sharks were present at the mouth of the bay, they spent more time at tides related to low tide. To test whether duration spent in lower salinities was sufficient to change plasma osmolality and osmolyte concentrations, we measured sodium, chloride, urea, TMAO, and potassium concentrations and total osmolality in plasma of juvenile sandbar sharks caught on longlines set at either flood or ebb tide from May-August, 2018. All variables differed significantly ($p < 0.05$; ANOVA) between salinity groups (17 – 21.9; n = 14, 22 – 26.9; n = 9, 27 – 31.9; n = 9, and > 32; n = 11). Sodium and chloride concentrations in the lowest salinity group (LSG) were 243.15 ± 2.82 and 241.91 ± 2.86 mM, respectively, and increased to 279.84 ± 2.06 and 280.73 ± 1.72 mM, in the highest salinity group (HSG). Between the LSG and the HSG, urea increased from 269.34 ± 5.97 mM to 352.25 ± 5.95 mM, and TMAO increased from 49.69 ± 2.59 mM to 81.15 ± 3.92 mM. Potassium increased from 4.35 ± 0.21 mM (LSG) to 5.09 ± 0.10 mM (HSG). Total osmolality in the HSG was 998.73 ± 12.61 mOsm/kg and 822.24 ± 11.62 mOsm/kg in the LSG. Post-hoc Tukey tests of all variables revealed that the HSG was significantly different than the other three salinity groupings in all osmotic components except potassium, whose contribution to osmoregulation is minimal. This study further supports that juvenile sandbar sharks seek out brackish salinities and that salinity becomes a smaller factor in movement as they grow. It is the first to suggest that juvenile sandbar sharks can partially osmo- and ionoconform in a similar manner to juvenile bull sharks.

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Introduction

Sandbar shark habitat

Sandbar sharks (*Carcharhinus plumbeus*) are highly migratory along global temperate and subtropical coastlines (Bigelow and Schroeder, 1953; Springer, 1960; Kohler *et al*., 1998). On the US East Coast, adult female sandbar sharks use near-shore and estuarine environments as primary nurseries, where they give birth and offspring spend their first year of life, and secondary nurseries, where the offspring return as juveniles (Bigelow and Schroeder, 1953; Springer, 1960; Castro, 1993; Merson and Pratt, 2001; Abel *et al.*, 2007; Grubbs *et al.*, 2007; Grubbs and Musick, 2007; McCandless *et al.*, 2007; Ulrich *et al.*, 2007; Gary, 2009; Bangley, 2016). These nursery habitats are critical because they provide shelter from predators and have abundant food sources (Castro, 1993). Nurseries are particularly important for sandbar sharks as their populations are still recovering from overfishing (Grubbs and Musick, 2007; SEDAR, 2011). As sharks reach adulthood, they leave nurseries and move to nearshore communities, whereas the juveniles remain in estuarine nurseries. Protecting nurseries and understanding how they are used by both these sharks and their prey species are central for the stock to rebuild.

Female adult sandbar sharks move into East Coast estuaries in early summer to birth their young (Castro, 1993). The two main US East Coast nurseries for sandbar sharks are Delaware Bay and Chesapeake Bay (Carlson, 1998; Grubbs and Musick, 2007). Estuarine and nearshore areas of South Carolina, notably Bulls Bay and Winyah Bay, are also potential primary nurseries for sandbar sharks, with juveniles being found more in estuarine than nearshore environments (Abel *et al.*, 2007; Ulrich *et al.*, 2007; Collatos, 2018). After pups are born, the female adult sandbar sharks leave the nursery (Castro, 1993). During early summer adult male sandbar sharks reside offshore, but are occasionally seen in more coastal environments during late fall. After the female adults leave the nursery, they typically mate the following summer, and will give birth the summer after that (Castro, 1993). Populations of adult sandbar sharks are not well known in estuaries; however, gillnet and longline methods may not be effective in targeting larger, adult sandbar sharks and thus they may be underrepresented in surveys (Thorpe *et al.*, 2004; Ulrich *et al.*, 2007).

Within their primary and secondary nursery estuarine habitats, juvenile sandbar sharks have the highest likelihood of being present near the mouth of the estuary more so than in the low salinity, higher reaches (Abel *et al.*, 2007; Grubbs *et al.*, 2007; Grubbs and Musick, 2007; Collatos, 2018), primarily in shallow and nearshore environments in the estuary (Medved and Marshall, 1983; Castro, 1993; Wetherbee and Rechisky, 2000; Grubbs and Musick, 2007; McCandless *et al.*, 2007; Ulrich *et al.*, 2007; Collatos, 2018). Even though juvenile sandbar sharks reside more in the lower reaches of estuaries, they move within these estuaries, primarily using tidal currents, presumably to save energy and position themselves in locations better suited for foraging and protection (Medved and Marshall, 1983; Wetherbee and Rechisky, 2000).

Juvenile sandbar sharks inhabiting estuaries along the US East Coast leave these estuaries from September through November and migrate (Springer, 1960; Grubbs *et al.*, 2007; Grubbs and Musick, 2007; McCandless *et al.*, 2007; Conrath and Musick, 2008; Bangley, 2016; Collatos, 2018). When temperature in their over summering habitats drops below 18-20°C in late fall, juvenile sandbar sharks occupying NE US estuaries such as Chesapeake and Delaware Bay move as far south as the Gulf of Mexico, but most overwinter in North Carolina, in places like Raleigh Bay and Cape Hatteras (Castro, 1993; Merson and Pratt, 2001; Grubbs *et al.*, 2007; McCandless *et al.*, 2007; Bangley, 2016; Collatos, 2018). Recently, juvenile sandbar sharks inhabiting Winyah Bay, along the NE coast of South Carolina, were found to migrate south and not to nearer North Carolina water in September through November (Collatos, 2018).

Evidence for migration of juvenile sandbar sharks until recently has depended heavily on tag-recapture studies. These studies rely on voluntary reporting of recaptures by both commercial and recreational fishers. However, these studies have low rates of recapture, ranging from 1.2 – 6.4% (Kohler *et al*., 1998; Merson and Pratt, 2001; McCandless *et al*., 2007; Grubbs *et al.*, 2007; Collatos, 2018) and thus require long-term monitoring involving large numbers of sharks. In the last thirty years, acoustic telemetry has provided a more robust method of understanding movements of sharks without relying on recaptures (Conrath and Musick, 2008; Bangley, 2016; Collatos, 2018).

Salinity Ranges

Most elasmobranchs are restricted to high salinity environments, with notable exceptions that include the bull shark (*Carcharhinus leucas*), potamotrygonid rays, some dasyatid rays, and sawfish (Compagno, 1995; Martin, 2005). Only 10% of elasmobranch species reside in estuaries, only 2% are euryhaline, and 1% are stenohaline in freshwater (Martin, 2005; Hammerschlag, 2006). In the family Carcharhinidae, only two species are known to tolerate low salinities for extended periods, the bull shark and the Ganges River shark (*Glyphis gangeticus*) the latter of which is considered extinct (Martin, 2005). Sandbar sharks are listed as a “marginal” species, which means that they are, “common in inshore marine habitats” and “marginal in brackish or freshwater” (Martin, 2005). Their salinity ranges (see below) along the US East Coast support the occupancy of brackish environments.

Several studies along the Eastern US have reported that juvenile sandbar sharks inhabit brackish environments (Carlson, 1998; Merson and Pratt, 2001; Abel *et al*., 2007; Grubbs and

Musick, 2007; McCandless *et* al., 2007; Ulrich *et* al., 2007; Gary, 2009; Bangley *et* al., 2018; Collatos, 2018) and the species has been found in salinities as low as 7 (Gary, 2009). Along Florida's northern Gulf of Mexico coastline, neonate and juvenile sandbar sharks were caught in salinities from 13 – 36; however, there was no significant relationship between salinity and shark abundance (Carlson, 1998). In Delaware Bay, juvenile sandbar sharks were caught in salinities ranging from 22.8 – 30.3, and salinity also did not correlate significantly with abundance (Merson and Pratt, 2001). Also in Delaware Bay, McCandless *et al*. (2007) caught juvenile sandbar sharks in a salinity range of 18.3 – 31. In Chesapeake Bay, the greatest number of juvenile sandbar sharks were found in salinities higher than 20.5, but they were caught in salinities as low as 15.4 (Grubbs and Musick, 2007). Unlike previous studies (Carlson, 1998; Merson and Pratt, 2001; McCandless *et al*., 2007), Grubbs and Musick (2007) found that higher salinity was significantly correlated with higher catch per unit effort (CPUE).

In North Carolina, juvenile sandbar sharks were found in salinities between 31 and 37 from Long Beach south to Shallotte Inlet (Thorpe, 2004), and between 18 and 32.3 in Pamlico Sound (Bangley *et al*., 2018). In SE South Carolina estuaries and nearshore environments from Bulls Bay south to Port Royal Sound, Ulrich *et al*. (2007), in a study that did not report salinity data by life stage, caught mostly juvenile and some adult sandbar sharks in salinities from 13 to 37. In Winyah Bay, South Carolina, juvenile and adult sandbar sharks were found in salinities ranging from 7 – 40, with means of approximately 28 (Abel *et al.*, 2007; Gary, 2009; Collatos, 2018). Abel *et al*. (2007) found that salinity was significantly correlated with CPUE in this species in Winyah Bay. Gary (2009) also found that top and bottom salinity were significantly correlated with CPUE. Although Gary's finding was based on all sharks caught in Winyah Bay, 49% of the catch was sandbar sharks. Collatos (2018) did not find a significant correlation between the CPUE for juvenile sandbar sharks and salinity, but did find a positive significant correlation between CPUE and high tide.

Osmoregulation in Elasmobranchs

In saltwater, elasmobranchs (sharks, skates, and rays) maintain extracellular osmolality at around the same concentration or slightly higher than the surrounding environment by retaining urea (Pang *et al*., 1977). For bull sharks, the ability to be euryhaline depends heavily on the organism lowering their urea concentration in lower salinities (Thorson *et al.*, 1983). Urea is toxic, but when paired with the osmolyte trimethylamine oxide (TMAO), its protein-disrupting effects are counteracted (Yancey and Somero, 1979). By being isosmotic, or slightly hyperosmotic, with seawater, energy is conserved because there is no need to expend energy drinking to help decrease dehydration (Mandrup-Poulsen, 1981). As sodium and chloride salts from the environment move into the animal in accordance with Fick's Laws of Diffusion, they are removed by the energy-requiring rectal gland and are excreted from the body through the cloaca (Pang *et al*., 1977).

The only true freshwater elasmobranchs are the family Potamotrygonidae, about 37 species of freshwater stingrays (Fricke *et al*., 2019). This family has evolved to retain virtually no urea, since the osmotic pressure of freshwater is much lower than seawater (Appendix Table 2). In a lab experiment, it was found that potamotrygonids cannot survive in water with a salinity greater than 3 (Wood *et al.*, 2002). In addition, these rays have smaller rectal glands because they need to conserve, and not excrete, salts (Thorson *et al*., 1978).

Among euryhaline elasmobranchs, the best-studied is the bull shark. Populations of bull sharks are found in freshwater systems, including Lake Nicaragua and Rio San Juan in Nicaragua (Urist, 1962a; Thorson *et al*., 1973), Lake Bayano in Panama (Montoya and Thorson, 1982), and Wenlock and Brisbane Rivers in Queensland, Australia (Pillans and Franklin, 2004; Pillans *et al*., 2005; Reilly *et al*., 2011). In brackish waters, bull sharks decrease their total osmolality by lowering their sodium, chloride, urea, and TMAO concentrations (Appendix Table 1), but do not completely iono- and osmoconform to their environment. Bull sharks that spend more time in freshwater than seawater were shown to have fewer tubules for salt excretion in their rectal glands, consistent with there being a decreased demand for salt excretion (Pillans and Franklin, 2004). In these environments osmolyte components and total osmolality decrease (Appendix Table 1) and sometimes become negligible, as is the case in Lake Nicaragua and the Rio San Juan (Urist and Van de Putte, 1967).

In the estuarine environments of the Caloosahatchee River, San Carlos Bay, and Pine Island Sound in SW Florida, juvenile bull sharks segregate by size along a salinity gradient, with smaller sharks occurring in lower salinities and adults occurring in higher salinities (Simpfendorfer *et al*., 2005; Heupel and Simpfendorfer, 2008). For juveniles in lower salinities, the likelihood of predation decreases, since many larger sharks, their primary predators, are stenohaline and thus do not inhabit lower salinities (Pillans and Franklin, 2004; Pillans *et al*., 2005). In studies on juvenile bull sharks, osmolyte concentrations and total osmolality decreased in lower salinities; urea had the largest decrease (Urist, 1962b; Urist and Van de Putte, 1967; Thorson *et al.*, 1973; Manire *et al.*, 2001; Pillans and Franklin, 2004; Pillans *et al.*, 2005; Pillans *et al.*, 2008; Reilly *et al.*, 2011). Moreover, defending intracellular osmotic conditions found in bull sharks in full-strength seawater is energetically costly for smaller bull sharks, as they have a higher surface area to volume ratio. In lower salinities, these juveniles avoid the additional energetic costs of osmoregulation and these energy "savings" may be allocated to growth (Simpfendorfer *et al*., 2005; Heupel and Simpfendorfer, 2008).

Despite the evidence of sandbar sharks in lower salinities, no studies of their blood chemistry and osmolality have been conducted. Bull sharks have been caught in the same areas as sandbar sharks in nearshore and estuarine communities throughout North and South Carolina (Castro, 1993; Abel *et al.*, 2007; Ulrich *et al.*, 2007; Gary 2009; Bangley *et al.*, 2018; Collatos, 2018). None of these studies has documented how long juvenile sandbar and bull sharks spend in lower salinities. Since juvenile sandbar sharks reside in similar habitats and have the similar surface area to volume constraints and natural predation as juvenile bull sharks, it is pertinent to know whether the plasma osmolyte concentration and total osmolality of juvenile sandbar sharks exhibit some degree of iono- and osmoconformity in lower salinities, like juvenile bull sharks (Castro, 1993; Abel *et al.*, 2007; Ulrich *et al.*, 2007; Gary 2009; Bangley *et al.*, 2018; Collatos, 2018).

Objectives

The specific objectives of this study were to assess the duration that juvenile sandbar sharks spend in lower salinities and to determine whether osmolyte concentrations and total osmolality change in lower salinities. To determine when and for how long juvenile sandbar sharks were using lower salinities, passive acoustic telemetry and salinity loggers at acoustic receiver stations were used. To examine osmolyte concentrations and total osmolality, these values were measured from blood plasma in juvenile sandbar sharks.

Materials and Methods

The Study Site: Winyah Bay, SC

Winyah Bay has an area of about 65 km^2 (Abel *et al.*, 2007). The bay is a partially-mixed estuary during periods of average river flow and rainfall, but behaves as a salt wedge when river flow into the bay increases during higher than normal rainfall in the watershed. Saltwater input occurs during high tide when salty water from the Atlantic Ocean floods into the bay (Patchineelam *et al*., 2004). Riverine freshwater input into the estuary originates from the Black, Waccamaw, Pee Dee, and Sampit Rivers (Abel *et al*., 2007). Rainfall in late summer is typically higher than earlier in the summer. Thus, mean Winyah Bay salinity is higher in early summer than late summer. Salinity difference between surface and bottom waters of Winyah Bay mostly varies between 0 and 15; however, differences can be > 30 (Abel *et al*., 2007).

Experimental Protocol

Longlines targeting juvenile sandbar sharks for acoustic telemetry and blood plasma analysis were set at three reference stations in Winyah Bay using boats from the CCU fleet (R/V Coastal Research and R/V Brooks McIntyre). These sampling stations included Harvest Moon in upper Middle Bay (~ 33.29° N, ~ 79.25° W), “Sandbar City (SBC)” in lower Middle Bay (~ 33.25° N, ~ 79.23° W), and Mother Norton Shoals (MNS) in Lower Bay (~ 33.21° N, ~ 79.19° W). These sites were selected because of historically larger catches of juvenile sandbar shark in previous studies (Abel *et al.*, 2007; Gary, 2009; Collatos, 2018) and from captain input (Jayroe, W, pers comm).

At each station, two 50-hook bottom longlines were deployed, one with 16/0-hook gangions to target larger juvenile sandbar sharks and the other with 12/0-hook gangions for smaller juveniles. Gangions were one meter long with a tuna clip attached to monofilament, swivel, leader wire, and a hook, as described by Abel *et al.*, 2007. Longlines soaked for 45 - 60 minutes, followed by a reset at a different location if weather permitted. Boston mackerel (*Scomber scombrus*) was used as bait. Longlines were set within one hour preceding either high or low tide based on the NOAA tide prediction for the Georgetown Lighthouse. In addition, juvenile sandbar sharks caught by other ongoing CCU Shark Project studies using the same collection techniques were utilized for this study.

Salinity monitoring

Before each longline was set, a YSI Pro 2030 was used to measure bottom and top salinity, temperature, and dissolved oxygen. These abiotic measurements were also measured after the longline was set and before and after the longline was hauled. The four bottom salinities were averaged to account for variation during the time that the longline was soaking.

Bottom salinity was continuously monitored using U-24 HOBO conductivity loggers on the MNS and both SBC acoustic receivers and the NERRS (National Estuarine Research Reserve System) acoustic receiver utilized the bottom salinity logger already present on the station.

Shark processing

Juvenile sandbar sharks caught on longlines were brought onboard and precaudal length (PCL), fork length (FL), and total length (TL) were measured. Either a Casey tag (for sharks > 110 cm TL) or a roto tag (for sharks < 110 cm TL) was inserted into the dorsal side under the first dorsal fin of the animal or in the first dorsal fin, respectively. Sandbar sharks were considered juveniles if their PCL was < 136 cm (Springer, 1960; Sminkey and Musick, 1995).

Tonic immobility was induced in each shark, after which 3 mL of blood was drawn from the hemal canal using an 18-gauge needle. Additionally, eight juvenile sandbar sharks (> 110 cm total length and PCL < 136 cm) had acoustic tags surgically implanted into their body cavity after blood was taken. These lengths were selected for acoustic implantation because sharks were large enough that the threat of predation had decreased, but the sharks were still within the juvenile size range (Springer, 1960; Sminkey and Musick, 1995).

Acoustic telemetry

The FACT (Florida Atlantic Coast Telemetry) Network and the SCDNR (South Carolina Department of Natural Resources) were used to obtain detections along the US East Coast. Four Vemco (VR2W) acoustic receivers were also deployed around Winyah Bay fishing sites in addition to collecting detections from the SCDNR's acoustic array deployed in and immediately outside of Winyah Bay (Fig. 1). The receivers deployed by the CCU Shark Project were deployed on the NERRS Station (33.30945° N, 79.28882° W), on a cement mount on the western side of SBC (33.25613° N, 79.23322° W), on a piling on the eastern side of SBC (33.25788° N, 79.21435° W), and on a piling just inside the mouth of the bay at MNS (33.20148° N, 79.18693° W). The receiver on the western side of "Sandbar City" was placed in a concrete receiver mount provided by SCDNR. The other three CCU Shark Project receivers were attached to pilings using industrial zip ties, chain, and a weight. Every two months, data were downloaded and batteries were changed from the four CCU Shark Research Project receivers. Acoustic data were sent from SCDNR and the FACT Network as these organizations downloaded data from their receivers.

To get an estimate of the range of acoustic tags in Winyah Bay, range testing was conducted using a specialized range testing acoustic tag from Vemco. The stated maximum range of the V16-4H tags is 400 m, so the tag was deployed in 100 m increments for ten-minute time periods to determine the efficiency at different distances. The efficiency of the tags in this environment was calculated by dividing the number of recorded detections by the number of expected detections (Welsh *et al.*, 2012).

Blood processing

Three mL of blood were taken from the hemal canal of juvenile sandbar sharks and was placed into two 1.5 mL Eppendorf microcentrifuge tubes, and stored on ice in a cooler. At the dock, blood was centrifuged for five minutes at 10000 rpm to separate red blood cells from plasma. Plasma was removed and was frozen (0°C) until analysis. Samples were overnighted on dry ice to Dr. Paul Yancey's lab at Whitman College (Walla Walla, WA) where sodium, chloride, TMAO, urea, and potassium concentrations, and total osmolality were measured. Sodium concentration was measured with a sodium electrode made by Hanna Instruments (Woonsocket, RI) and chloride and potassium concentrations were measured with ion specific electrodes made by Pasco Scientific (Roseville, CA). Urea concentration was measured with a PerkinElmer 200 pump, Sugarpak-1 column, and a BioRad refractive index detector. TMAO concentration was measured using a Beckman spectrophotometer, and total osmolality was measured using a Wescor 550, a vapor pressure osmometer. Forty-three plasma samples were analyzed.

Statistics and Analysis

Normal distribution was tested by conducting a Shapiro-Wilkes test (Appendix *Shapiro-Wilkes Normality Tests*). Precaudal lengths of all juvenile sandbar sharks were log transformed because the raw values were not normal, and the resulting data set was determined to be normal by a Shapiro-Wilkes test. Salinity was split up into four salinity groups based on the lowest salinity in which a juvenile sandbar shark was caught on a longline (1: 17 - 21.9; 2: 22 – 26.9; 3: 27 – 31.9; 4: > 32). To compare blood osmolyte and total osmolality values and precaudal length between the varying salinity conditions, an ANOVAs were conducted in R. Post-hoc Tukey tests were conducted in R to reveal significant differences between the salinity groups. Individual detections were compressed into detection events, which were defined as detections within 20 minutes of each other at the same receiver. Tide times were correlated to detection events, and salinity measurements from the loggers were correlated to individual detections. To determine whether ebb and flood tides were associated more with high or low tide, they were split into high and low ebb and high and low flood. Detections events were categorized as high ebb if the tide was outgoing, ebb tide, and the event occurred within three hours of high tide, and were categorized as low ebb if the tide was outgoing, ebb tide, and the event occurred within three hours of low tide. The same divisions were used for high and low flood; however, the tide was incoming, flood tide, instead of outgoing, ebb tide. If the detections fell between within three hours of high and low tide, the time was either labeled as flood if the tide was incoming or ebb if the tide was outgoing. A visual analysis of time spent at each tidal stage by receiver location was conducted through QGIS.

Results

Length vs. Salinity

PCL increased with salinity for both the juvenile sandbar sharks utilized in the plasma study and of all juvenile sandbar sharks caught in this study (Tables 1 and 2; Fig. 2). The subset of juvenile sandbar sharks used for the plasma study was representative of all juvenile sandbar sharks caught during the study period. PCL had significant differences between salinity groups for all juvenile sandbar sharks caught in this study (Table 3; All Juveniles: $p < 0.001$). Post-hoc Tukey tests revealed that there were significant differences in PCL of all juveniles caught between the LSG and HSG, the second salinity group (SSG) and the HSG, and the TSG and HSG (Table 4; All Juveniles: HSG x LSG, $p < 0.001$; HSG x SSG, $p < 0.001$; HSG x TSG, $p < 0.05$).

Winyah Bay Acoustic Telemetry

Out of the three juvenile sandbar sharks tagged in August, 2018, only transmitter #9042 had detections for more than three days. This juvenile sandbar shark had a total of 2032 detections totaling 3891 minutes from August 10, 2018 to September 24, 2018 in Winyah Bay, SC and utilized eight of the thirteen receivers in and immediately outside of Winyah Bay (Table 5). Most of the detection events within Winyah Bay occurred within three hours before or after high tide, but detection events related to low tide became more prominent the more seaward the receiver (Tables 6 and 7; Fig. 3). As high tide came in the animal moved from the mouth of Winyah Bay up through to SBC and then as the tide started to ebb, the animal moved back out through the bay to the mouth at low tide.

Out of the eight acoustic transmitters, six of them had detection events that lasted over 90 minutes (Table 8). There were a total of 16 detection events that lasted over 90 minutes (Table 8). Transmitters #9043 and #9044 didn't have any detection events over 90 minutes, and transmitter #9042 had the most detection events (6) over 90 minutes (Table 8).

Five juvenile sandbar sharks were fitted with acoustic transmitters in May, 2019. High tide comprised one of the top two percentages of time for all five transmitters and high flood or high ebb were often the second highest percentage at the MNS receiver (Fig. 4). The least amount of time for all five transmitters was spent at the SBC Piling receiver (Fig. 4). Transmitter #9037 spent 0.2% of total time at this receiver, #9038 spent 0.78% of total time, #9039 spent 0% of total time, #9040 spent 0.3% of total time, and #9041 spent 1.1% of total time at the SBC Piling receiver (Fig. 4). These juvenile sandbar sharks were detected at the South Island Dock and Across South Island SCDNR receivers and spent more time at the South Island Dock compared to the Across South Island receiver (Fig. 4). Other receivers were unavailable for data retrieval at the time of writing.

Hurricane Florence hit on 9/14/18 and the last Winyah Bay detection was on that day, and there was not a detection in Winyah Bay until 9/17/18. After which there was only a single detection event (48 minutes) on only one of the SBC receivers. The salinity profile from the HOBO logger on the SBC Piling receiver from 9/01/18 through 10/12/18 displays how bottom salinity decreased to zero as the Waccamaw River flooded into Winyah Bay. The last detection of 2018 in Winyah Bay was from transmitter #9043 in the early hours of September 29, 2018 (Fig. 6).

Blood plasma

Sodium, chloride, urea, TMAO, potassium, and total osmolality all declined as salinity declined (Table 9; Figs. 7 - 19). TMAO had the greatest percent decrease as salinity decreased (39.01%) followed by urea (23.54%) and sodium and chloride decreased least with percentages of 13.11% and 13.83%, respectively (Table 9). There were significant differences between salinity groups for each osmotic component and total osmolality (Table 10; $p < 0.001$ for all components apart from potassium ($p = 0.03$)). Potassium had the fewest significant differences between groups as there was only a significant difference between the LSG and TSG (Table 11; Fig. 12). Whereas, urea and total osmolality had the most significant differences because only the TSG and SSG weren’t significantly different than each other (Table 11; Figs. 10 and 13). Total osmolality had the highest positive correlation to salinity ($R^2 = 0.7401$) and potassium had the lowest positive correlation to salinity ($R^2 = 0.1891$) (Figs. 18 and 19).

Discussion

This study was not only the first to reveal the extent of how juvenile sandbar sharks utilize lower salinity environments, but was also the first to reveal osmoregulatory changes with decreasing salinity that are comparable to juvenile bull sharks. In this study, juvenile sandbar sharks exhibited ecological and physiological adaptations within lower salinity environments that could potentially lead to energy savings, decreased predation, and increased prey items. Before this study, it was unknown whether a shark species other than the bull shark could partially iono- and osmoconform in less than marine conditions.

Ecological Use of Winyah Bay

Based on longline surveys and acoustic detections, juvenile sandbar sharks in this study were found in salinities as low as 11.5 and as high as 36.1. Juvenile sandbar sharks were caught on longlines in salinities ranging from 17.2 to 36.1, and an acoustically-tagged shark was detected at the SBC receivers with fixed salinity loggers at salinities from 11.5 to 24.7. The acoustic telemetry salinity range represented the middle to top range of the salinity range within SBC because both SBC salinity loggers did not record a value higher than 26. Acoustic receivers with salinity loggers revealed a larger salinity range than conventional longlining methods because conventional longlining trips are often scheduled during times when sharks are more numerous, high tide, and depend on the sharks being hungry and biting the bait. Whereas, the acoustic receivers with salinity loggers passively monitored shark movement with regards to salinity. These salinity ranges are comparable to previous studies on juvenile sandbar sharks (Carlson, 1998; Merson and Pratt, 2001; Thorpe, 2004; Abel *et al.*, 2007; Grubbs and Musick, 2007; McCandless *et al.*, 2007; Gary, 2009; Bangley *et al.*, 2018; Collatos, 2018). However, only one previous study described a salinity as low as 11.5 (Gary, 2009). Due to malfunctioning salinity loggers at MNS in 2018 and 2019 and at SBC during 2019, a more complete salinity range for juvenile sandbar sharks within Winyah Bay could not be determined.

Salinity played a role in how juvenile sandbar shark size classes partitioned themselves within Winyah Bay. Our data demonstrate that different size classes of juvenile sandbar sharks utilize different salinities. Smaller juvenile sandbar sharks (PCL < 70 cm) in Winyah Bay were caught mostly in salinities < 28 and larger juvenile sandbar sharks (PCL > 70 cm) were more frequently caught in salinities > 30. Juvenile bull sharks in the Caloosahatchee River, San Carlos Bay, and Pine Island Sound area of southwest Florida were more likely to be located within the Caloosahatchee River when the stretched TL was less than 95 cm. If their stretched TL was greater than 95 cm, however, they were more likely to be caught in the more saline San Carlos Bay (Simpfendorfer *et al.,* 2005). In addition, in Chesapeake Bay, smaller juvenile sandbar sharks were caught more in the upper, less saline, reaches of the bay and larger juvenile sandbar sharks were caught more frequently at the lower, more saline, reaches of the bay (Grubbs and Musick, 2007). The use of salinities of less than 28 by smaller juvenile sandbar sharks could be beneficial for this size class as energy used in osmoregulation decreases in lower salinities, especially for smaller animals (Ballantyne, 1997; Simpfendorfer *et al.,* 2005; Abel *et al.,* 2007; Heupel and Simpfendorfer, 2008; Ortega *et al.,* 2009; Schlaff *et al.,* 2014), the predation risk is decreased (Pillans and Franklin, 2004, Pillans *et al.,* 2005), and preferred prey items, like spot (*Leiostomus xanthurus*), may be inhabiting these lower salinities (Abel *et al.,* 2007; Collatos, 2018). The energy saved, could be allocated to growth instead of osmoregulation or feeding, and the juveniles have a higher likelihood of surviving. Although the correlation coefficient between salinity and PCL was low in this study, there was still a significant difference between the PCL in the HSG and the three other lower salinity groups. Length and salinity data from juvenile sandbar sharks from previous years and further sampling seasons could further determine the salinity preferences of each size class.

Acoustic telemetry detection events correlated to tidal phase revealed that six acoustically tagged juvenile sandbar sharks shifted locations within Winyah Bay with tidal currents. By moving the same direction as the tides, juvenile sandbar sharks are using less energy to move and thus allocate more energy to growth and survival. Previous studies on juvenile sandbar sharks have also shown movement with tides (Medved and Marshall, 1983; Wetherbee and Rechisky, 2000). These studies were conducted by actively acoustically tracking the sandbar sharks in real time. Thus, these comparable studies are based on shorter time periods than this study. We were able to actively track two juvenile sandbar sharks and they moved with tidal currents; however, we were able to track them for only two hours. Movement with tidal currents is also supported by the fact that for the 2019 transmitters and transmitter #9042, receivers in Middle Bay had little to no detections at or near low tide compared to the receivers located at the mouth and outer channel of Winyah Bay, which had more detections events at or near low tide. The receiver that was most used by transmitter #9042, the SBC Channel receiver, was vandalized, and was not available for acoustic telemetry analysis for the five transmitters deployed in 2019. If this receiver had been available, percentage at high or low tide usage could be better understood within Middle Bay for the 2019 animals, instead of for only one acoustically-tagged juvenile in 2018. Detection ranges of acoustic tags within Winyah Bay were variable for this study and did not have 100% detection success at any distance tested, so many detections may have not been received (Appendix *Range Testing*). In addition, the SBC Channel receiver was unable to be tested for range during high tide because the receiver went missing before we had the opportunity to range test, so an accurate count of high-tide detections at this site was not possible.

When detections were correlated with salinity measured by salinity loggers, salinity preference was determined by the duration spent during certain salinities. Salinity loggers within SBC during 2018, revealed that the single juvenile sandbar shark tagged in 2018, spent the majority of their time in brackish salinities between 16 and 25.9. Previous studies, suggest that juveniles occupying lower than fully seawater (~35) environments use less energy to osmoregulate and therefore can create a less stressful environment (Ballantyne, 1997; Simpfendorfer *et al.,* 2005; Heupel and Simpfendorfer, 2008; Dowd *et al.,* 2010; Froeschke *et al.,* 2010; Schlaff *et al.,* 2014). In a lab study on the euryhaline killifish, *Fundulus heteroclitus,* it was proposed that as the osmotic gradient is lower in freshwater than saltwater that freshwater environments are less stressful than saltwater environments, with brackish environments being the least osmotically stressful (Kidder *et al.,* 2006). Duration in brackish salinities for juvenile sandbar sharks would be better defined if all the salinity loggers had functioned over the entire study period and at all receiver locations.

Flooding from Hurricane Florence resulted in a large influx of freshwater into Winyah Bay and caused salinity to decrease. Hurricane Florence made landfall on September 14, 2018 and no detections from transmitters 9042, 9043, and 9044, were recorded in Winyah Bay until the 17th. The only transmitter that had detections on the 17th was transmitter 9042, which is also the only acoustic tag deployed in 2018 that had detections over more than three days. During that time salinity decreased because of increased freshwater input from the flooding Waccamaw River and low tide had lower salinities (< 3) up until the salinity logger stopped recording on 10/12/18. The last detection in Winyah Bay was at 0:05 on September 29th, 2018 at high tide.

However, this detection occurred at the SBC Piling receiver and with transmitter #9043, which only had four detection events. The other transmitter (#9042) that was more active during this time of 2018 was last detected on 9/24/18 and was detected only as far in the Bay as the South Island Dock receiver after Florence made landfall. These last detections occurred at the beginning of juvenile sandbar sharks southerly seasonal migration out of Winyah Bay. This migration period starts in September and goes through November (Collatos, 2018). Despite that this is the beginning of their migration period, high tide longline fishing trips after Hurricane Florence only resulted in two juvenile sandbar sharks being caught, which suggests that juvenile sandbar sharks were less common in the Bay after Florence and may have emigrated slightly earlier from Winyah Bay than in previous years. Freshwater input, similar to the results from Florence, has been shown to cause bull sharks, pigeye sharks (*Carcharhinus amboinensis*), and cownose rays (*Rhinoptera bonasus*) to move more towards marine inputs in estuarine systems, and large storms have caused blacktip sharks (*Carcharhinus limbatus*) to change their short-term movements (Heupel *et al.,* 2003; Simpfendorfer *et al.,* 2005; Collins *et al.,* 2008; Heupel and Simpfendorfer, 2008; Froeschke *et al.,* 2010; Knip *et al.,* 2011). Some climate change models have indicated that large storms, like Hurricane Florence, will become stronger and more frequent with time, so it will be crucial to understand how the subsequent environmental effects, like increased freshwater input and large changes in barometric pressure, impact sandbar shark movement (Heupel *et al.,* 2003; Chin *et al.,* 2014).

Osmoregulatory Changes

All osmolyte concentrations in juvenile sandbar sharks, in this study, were negatively correlated with salinity (> 32 to 17) and sodium, chloride, urea, and TMAO concentrations had a significant difference between the HSG and all other lower salinity groups. In a study on the small-spotted catshark (*Scyliorhinus canicula*), 10 – 15% of their standard metabolism was spent on osmoregulation and this species is more sluggish than sandbar sharks (Kirschner, 1993). Therefore, any osmoregulatory adaptation, i.e., decreasing concentrations of osmolytes in lower salinity, could potentially save some osmoregulatory energy and allocate that energy to growing into an adult. By decreasing sodium and chloride concentration in a less saline environment, juvenile sandbar sharks are creating a lower concentration gradient between themselves and their environment, and thus are decreasing the energy used to continually pump these ions into the rectal gland to be excreted (Ballantyne, 1997). Energy expenditure is decreased because for every three sodium ions pumped, one ATP is used, and for every six chloride ions pumped, one ATP is used (Kirschner, 1993; Pillans *et al.,* 2005). The decrease in urea production at lower salinities could also potentially lead to energy-savings that can be allocated towards growth (Simpfendorfer *et al.*, 2005; Heupel and Simpfendorfer, 2008). Potassium is a very minor osmotic constituent and therefore, there was no significant change with salinity. Since, all major osmoregulatory components declined with declining salinity, total osmolality also significantly declined with declining salinity.

Urea and TMAO both had the highest percent increase, 17.69% and 26.51%, respectively, between the TSG and HSG and a small percent increase between the SSG and TSG. There may be a salinity threshold at which it is energetically advantageous to start producing more urea for osmoregulation. Although there was a large percent increase in both urea and TMAO between the SSG and TSG to the HSG in this study this finding could be a result of the salinity groups chosen and further divisions of salinity groups would be able to demonstrate whether the percent increase in urea and TMAO is constant over the range of the middle two salinity groups. A larger sample size with more intermediate salinity samples could help to determine if a true urea threshold exists. A similar urea trend was observed in juvenile and sub-adult bull sharks. In this study, urea increased by 1.54% per salinity unit from freshwater through a salinity of 24, but that increase grew to 5.2% increase in urea per salinity unit from 27 – 33 (Pillans and Franklin, 2004). Potassium is a very minor osmotic constituent and therefore, there was no significant change with salinity. Since, all major osmoregulatory components declined with declining salinity, total osmolality also significantly declined with declining salinity.

Other studies on euryhaline bull sharks and Atlantic stingrays have shown that sodium, chloride, and urea concentrations were lower in freshwater than saltwater (Urist, 1962b; Piermarini and Evans, 1998; Pillans *et al.*, 2004). Although juvenile sandbar sharks, in this study, were not found in freshwater, the sodium, chloride, and urea concentrations from this study did exhibit a decrease with decreasing salinity. This study was mostly compared to bull sharks because bull sharks are a sister taxon to sandbar sharks and juveniles of both species utilize varying salinity environments in similar ways. Reilly *et al.* (2001) studied bull sharks caught in salinities from 21 to 32, and found overlap between the sodium (247.5 ± 4.1 mM), chloride (242.8 ± 4.5 mM), urea (278.1 ± 12.2 mM), and potassium (4.5 ± 0.4 mM/L) values found in similar salinity juvenile sandbar sharks in this study. Estuarine adult bull sharks in 50% seawater in Florida had similar sodium (233 ± 37 mM) and urea (220 ± 68 mM) concentrations to juvenile sandbar shark values found in this study at similar salinities (Thorson *et al*., 1973). Adult bull sharks in full seawater in Florida had similar sodium (288 ± 12 mM), chloride (288 ± 21 mM), and urea (356 ± 67 mM) concentrations to the juvenile sandbar sharks in the HSG in this study (Thorson *et al*., 1973). Similar osmoregulatory studies on juvenile bull sharks had significant differences in potassium concentrations with salinity (Thorson *et al.*, 1973; Pillans and Franklin, 2004), whereas there were other studies that did not have significant difference in potassium

(Pillans *et al.*, 2005; Coelho and Erzini, 2006). With a larger sample size, variation within potassium concentrations would decrease. Similar osmoregulatory components, in the same salinities seen in this study, outside of the family Carcharhinidae are emboldened in Table 2 in the Appendix. Even though this study has shown that juvenile sandbar sharks do decrease the concentration of their osmotic components in lower salinities, these values are not equal to their environment, and further laboratory experiments could determine the extent to which juvenile sandbar shark osmotic components can decrease.

Conclusions

Future research to quantify plasma components for more blood samples in addition to seawater samples to compare osmolyte concentrations to the animal's environment would help to determine to what extent juvenile sandbar sharks iono- and osmoconform to their environment. Observing acoustically tagged juvenile sandbar sharks for longer periods of time, with functioning salinity loggers, would reveal more information about juvenile sandbar shark movement through varying salinities.

From the acoustic telemetry and salinity data, it is concluded that juvenile sandbar sharks move with tides in search of brackish salinities from 16 to 26 in middle bay and utilize the lower range of the salinity range in MNS and the channel outside of Winyah Bay. Juvenile sandbar sharks decrease organic and inorganic osmoregulatory components to be more similar to their environment and smaller juveniles use brackish salinities to potentially conserve osmoregulatory energy for growth and to avoid some predation risk. More research needs to be done to determine the rate a which juvenile sandbar sharks lower their osmolality, the energetic benefits of partial iono- and conforming, and to determine more completely what the salinity range and preference are for sandbar sharks in this system.

Tables

Table 1: Salinity and precaudal length measurements by salinity group for juvenile sandbar sharks from which plasma samples were taken (n=43).

Salinity Group	**Salinity Range (Mean ± S.E.)**	**n**	**Precaudal Length, cm (Mean ± S.E.)**
1	17 – 21.9 (20.1 ± 0.3)	14	76.1 ± 3.3
2	22 – 26.9 (24.8 ± 0.5)	9	85.7 ± 3.3
3	27 – 31.9 (29.9 ± 0.5)	9	83.3 ± 3.9
4	> 32 (33.7 ± 0.2)	11	98.3 ± 2.8

Table 2: Salinity and precaudal length measurements by salinity group for all juvenile sandbar sharks caught in this study (n=118).

Salinity Group	**Salinity Range (Mean ± S.E.)**	**n**	**Precaudal Length, cm (Mean ± S.E.)**
1	17 – 21.9 (20 ± 0.2)	34	79.6 ± 3.3
2	22 – 26.9 (25 ± 0.2)	38	80.6 ± 2.2
3	27 – 31.9 (29.3 ± 0.4)	18	84.4 ± 3.5
4	> 32 (33.8 ± 0.2)	28	96.8 ± 1.9

Table 3: ANOVA statistical results for precaudal lengths for juvenile sandbar sharks utilized in the plasma study and for all juvenile sandbar sharks caught in this study.

Length measurement	**p-value (plasma study juveniles)**	**p-value (all juveniles)**
PCL	0.000177*	< 0.001*

*Indicates significant difference ($p < 0.05$)

Table 4: Post-hoc Tukey test p-values for precaudal lengths of juvenile sandbar sharks utilized in the plasma study and for all juvenile sandbar sharks caught in this study.

Interaction	**Precaudal Length (Plasma Juveniles)**	**Precaudal Length (All Juveniles)**
1 x 4	0.0000673*	0.0000130*
2 x 4	0.0673617	0.0000807*
3 x 4	0.0211358*	0.0266684*
2 x 1	0.1878833	0.9321876
3 x 1	0.4250909	0.4901103
3 x 2	0.9666081	0.7770312

*Indicates significant difference ($p < 0.05$)

Table 5: Percentage of detections at each of the Winyah Bay receivers for transmitter #9042. These percentages are based on the number of detections and not the duration of detections. Detections occurred from 8/10/18 – 9/24/18. The receivers are listed from the mouth of Winyah Bay up through to the head of Winyah Bay.

Acoustic Receiver	**Number of Detections**	**Percentage of Detections**
LB4*	10	0.5
LB5*	188	9.3
LB7*	463	22.8
MNS	157	7.7
South Island Dock*	434	21.4
SBC Piling	84	4.1
SBC Channel	671	33
Near Mud Bay*	25	1.2
Total	2032	

*SCDNR Receiver

Table 6: Duration (minutes) at specific Winyah Bay receivers for transmitter #9042 by tidal phase. Time events were compiled of detections that were less than 20 minutes apart at the same acoustic receiver. Ebb and flood tides were determined to be high if the detections occurred within three hours of high tide and low if the detections occurred within three hours of low tide. If detections didn’t fall within three hours of either high or low tide, detections were named either ebb or flood tide. Detections occurred from 8/10/18 – 9/24/18. The receivers are listed from the mouth of Winyah Bay up through to the head of Winyah Bay.

	Duration (minutes)								
Acoustic Receiver	**Total**	**Low Ebb Tide**	**High Ebb Tide**	**Ebb Tide**	**Low Flood Tide**	**High Flood Tide**	**Flood Tide**	**Low Tide**	**High Tide**
LB4[*]	12	0	7	0	0	0	0	5	0
LB5[*]	392	66	0	0	63	0	0	263	0
LB7[*]	758	19	0	0	292	8	0	439	0
MNS	249	11	59	0	74	71	7	17	10
South Island Dock[*]	647	98	118	8	19	204	0	66	134
SBC Piling	193	8	32	0	0	78	0	0	75
SBC Channel	1610	49	507	0	0	224	0	0	830
Near Mud Bay[*]	30	0	30	0	0	0	0	0	0
Total	3891	251	753	8	448	585	7	790	1049

[*] SCDNR Receiver

Table 7: Percentage of time spent at specific Winyah Bay receivers for transmitter #9042 by tidal phase. Percentages at each tide represent the proportion of total time at that specific receiver. Ebb and flood tides were determined to be high if the detections occurred within three hours of high tide and low if the detections occurred within three hours of low tide. If detections didn't fall within three hours of either high or low tide, detections were named either ebb or flood tide. Detections occurred from 8/10/18 – 9/24/18. The receivers are listed from the mouth of Winyah Bay up through to the head of Winyah Bay.

	Percentage of Time								
Acoustic Receiver	**Total**	**Low Ebb Tide**	**High Ebb Tide**	**Ebb Tide**	**Low Flood Tide**	**High Flood Tide**	**Flood Tide**	**Low Tide**	**High Tide**
LB4*	0.31	0	58.3	0	0	0	0	41.7	0
LB5*	10.1	16.8	0	0	16.1	0	0	67.1	0
LB7*	19.5	2.5	0	0	38.5	1.1	0	57.9	0
MNS	6.4	4.4	23.7	0	29.7	28.5	2.8	6.8	4
South Island Dock*	16.7	15.1	18.2	1.2	2.9	31.5	0	10.2	20.7
SBC Piling	5	4.1	16.6	0	0	40.4	0	0	38.9
SBC Channel	41.5	3	31.5	0	0	13.9	0	0	51.6
Near Mud Bay*	0.77	0	100	0	0	0	0	0	0
Total	100	6.5	19.4	0.21	11.5	15	0.18	20.3	27

*SCDNR Receiver

Table 8: Detection events lasting over 90 minutes for all transmitters in chronological order. 90 minutes was chosen as the threshold for a long detection because it is about a quarter of a tidal cycle.

Date	Transmitter Number	Time Span	Total Time (Minutes)	Number of Detections	Receiver Location	Salinity Range	Tidal Stage
8/12/18-8/13/18	9042	23:01-1:02	121	52	SBC Mount	24.7-24.6	High/High Ebb
8/17/18	9042	7:04-8:47	103	50	LB 7*	[a]	Low
8/26/18	9042	21:29-23:32	123	33	SBC Mount	20.3-22.3	High/High Ebb
8/27/18	9042	14:10-15:52	102	33	LB 5*	[a]	Low Ebb/Low
8/28/18-8/29/18	9042	22:43-0:33	110	32	SBC Mount	18.4-20.1	High/High Ebb
8/30/18-8/31/18	9042	23:00-2:21	201	115	SBC Mount	12.1-13.8	High Flood/High/High Ebb
5/11/19	9040	13:37-15:58	141	83	MNS	[b]	High/High Ebb
5/12/19	9040	15:01-17:04	123	55	MNS	[b]	High/High Ebb
5/15/19	9037	19:13-20:43	90	41	South Island Dock	[a]	High/High Ebb
5/24/19	9039	0:15-2:38	143	73	MNS	[b]	High/High Ebb
5/24/19	9040	0:43-2:20	97	56	South Island Dock	[a]	High
5/25/19	9039	14:44-18:04	200	37	MNS	[b]	High/High Ebb
5/25/19	9039	21:05-23:09	124	76	MNS	[b]	Low/Low Flood
5/26/19	9040	14:03-16:22	139	66	MNS	[b]	High/High Ebb
5/27/19	9038	3:57-6:10	133	76	South Island Dock	[a]	High/High Ebb
5/29/19	9041	0:28-2:04	96	31	MNS	[b]	Low Flood/Slack Flood

*SCDNR Receiver

[a] Salinity values not available as salinity loggers are not present on SCDNR receivers

[b] Salinity values not available as salinity logger malfunctioned

Table 9: Plasma osmolyte concentrations and total osmolality values with samples sizes divided by salinity group.

Salinity Group	Salinity Range	Sodium Concentration (mM) Mean ± S.E. (n)	Chloride Concentration (mM) Mean ± S.E. (n)	Urea Concentration (mM) Mean ± S.E. (n)	TMAO Concentration (mM) Mean ± S.E. (n)	Potassium Concentration (mM) Mean ± S.E. (n)	Total Osmolality (mOsm/kg) Mean ± S.E. (n)
1	17-21.9	243.15 ± 2.82 (14)	241.91 ± 2.86 (14)	269.34 ± 5.97 (14)	49.69 ± 2.59 (14)	4.35 ± 0.21 (12)	822.24 ± 11.62 (14)
2	22-26.9	251.44 ± 3.53 (9)	251.92 ± 4.52 (9)	299.49 ± 11.46 (9)	56.07 ± 4.45 (9)	4.72 ± 0.2 (8)	889.44 ± 18.10 (9)
3	27-31.9	264.20 ± 4.51 (9)	262.01 ± 4.05 (9)	299.30 ± 6.14 (9)	59.64 ± 3.49 (9)	5.21 ± 0.32 (6)	921.89 ± 14.89 (9)
4	>32	279.84 ± 2.06 (9)	280.73 ± 1.72 (10)	352.25 ± 5.95 (11)	81.15 ± 3.92 (10)	5.09 ± 0.10 (7)	998.73 ± 12.61 (11)

Table 10: Statistical ANOVA F and p-values for plasma osmolyte concentrations and total osmolality.

Plasma component	**F value**	**P value**
Sodium	24.34	< 0.001*
Chloride	26.62	< 0.001*
Urea	24.66	< 0.001*
TMAO	15.7	< 0.001*
Potassium	3.347	0.0326*
Total osmolality	31.38	< 0.001*

*Indicates significant difference ($p < 0.05$)

Table 11: Post-hoc Tukey test p-values for plasma osmolyte concentrations and total osmolality.

Interaction	**Sodium**	**Chloride**	**Urea**	**TMAO**	**Potassium**	**Total Osmolality**
1 x 4	0^*	0^*	0^*	0.0000004^*	0.0899073	0^*
2 x 4	0.0000088^*	0.0000057^*	0.0001038^*	0.0001398^*	0.6863160	0.0000266^*
3 x 4	0.0163056^*	0.0028843^*	0.0000983^*	0.0010905^*	0.9831615	0.0032091^*
2 x 1	0.2712104	0.1505741	0.0273640^*	0.5594059	0.5740450	0.0073652^*
3 x 1	0.0002170^*	0.0005237^*	0.0286337^*	0.1886019	0.0488093^*	0.0000527^*
3 x 2	0.0657662	0.2086030	0.9999983	0.9095421	0.4862368	0.4445851

*Indicates significant difference ($p < 0.05$)

Figures

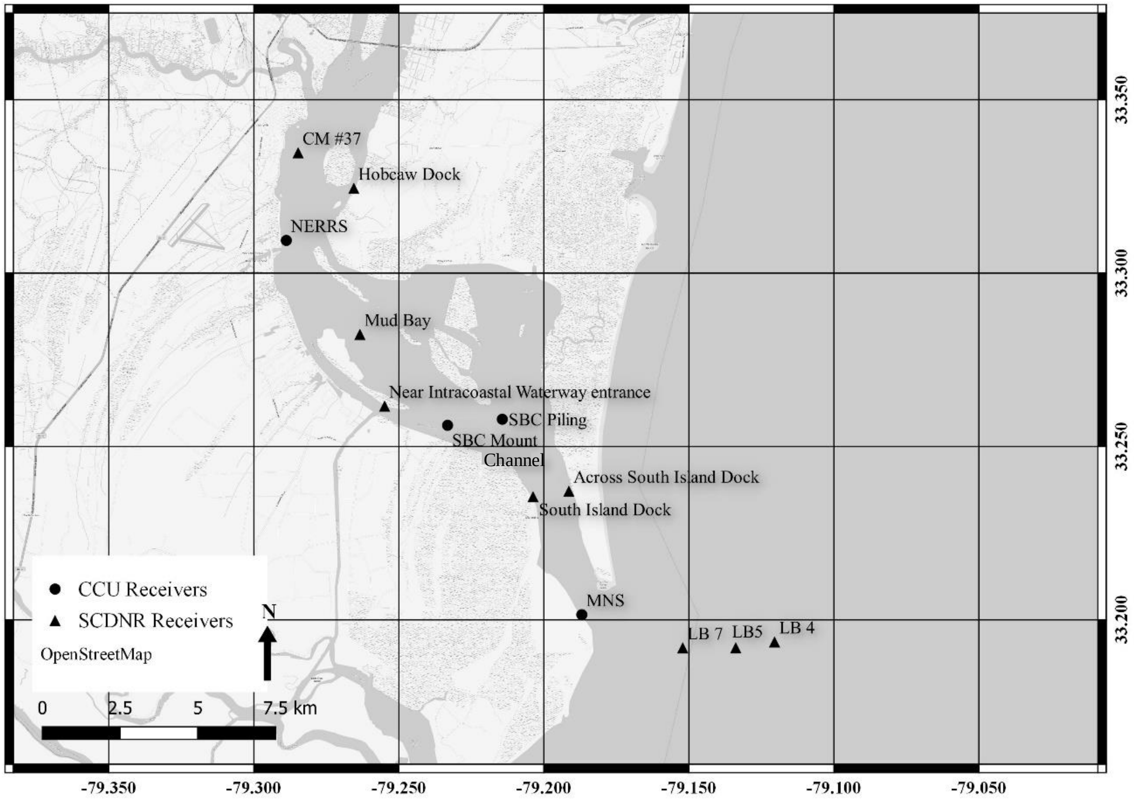

Figure 1: Map of acoustic receiver locations in Winyah Bay, SC. All SCDNR receivers are labelled with the name given to the receiver by SCDNR.

NERRS: National Estuarine Research Reserve System
SBC: Sandbar City
MNS: Mother Norton Shoals

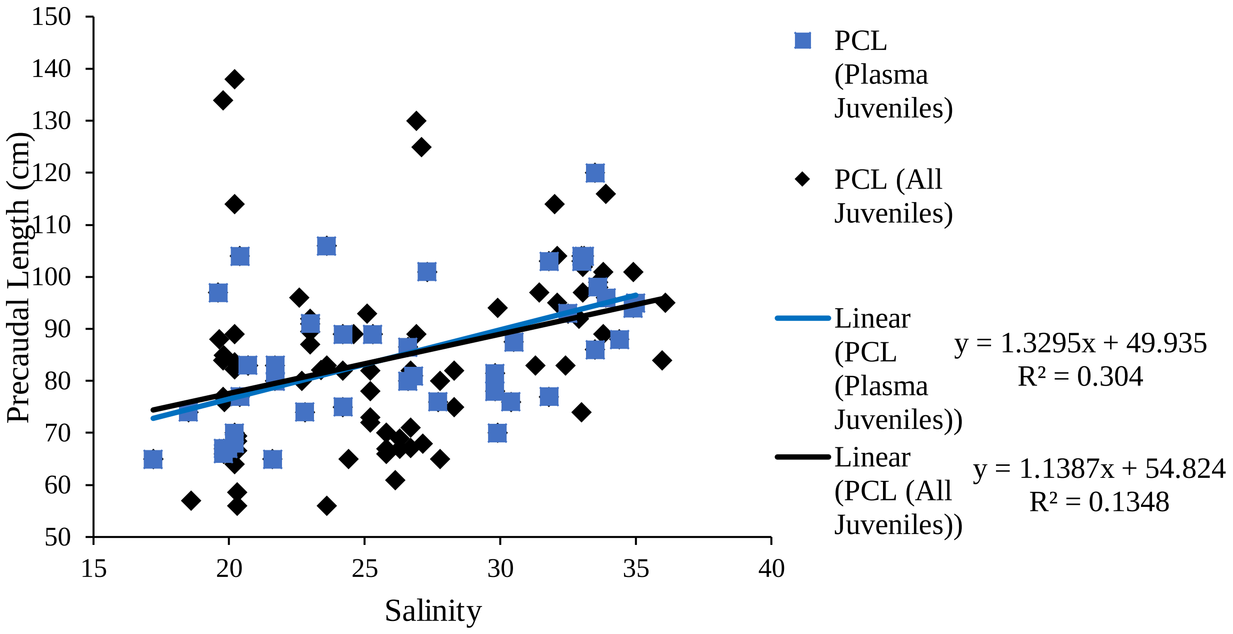

Figure 2: Precaudal lengths (cm) vs. salinity for both the juvenile sandbar sharks in the plasma study and all juvenile sandbar sharks caught.

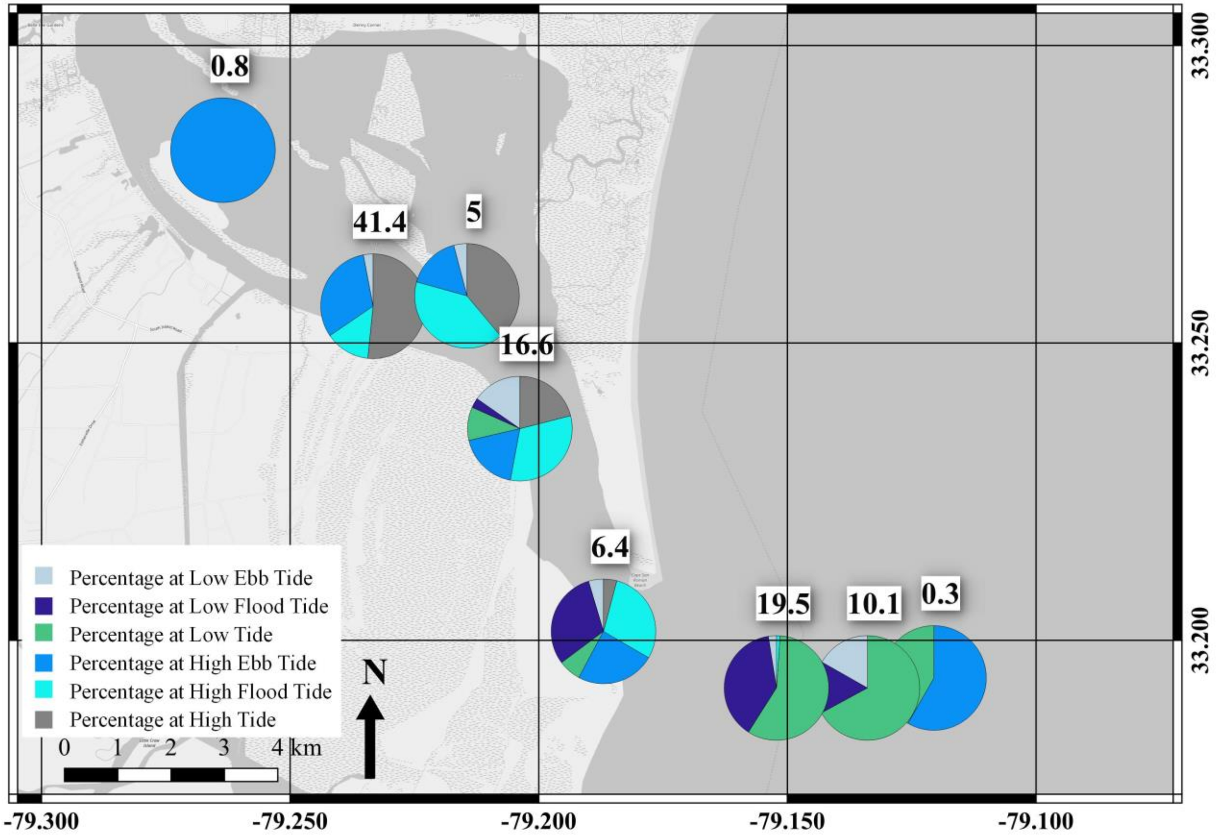

Figure 3: Percentage of time at each tidal phase for each acoustic receiver visited by transmitter #9042 in Winyah Bay, SC (8/10/18 – 9/24/18). The size of pie charts does not reflect the proportion of total time duration spent at each these Winyah Bay acoustic receivers. The percentages in white boxes represent the percentage of total time duration spent at each of these Winyah Bay acoustic receivers.

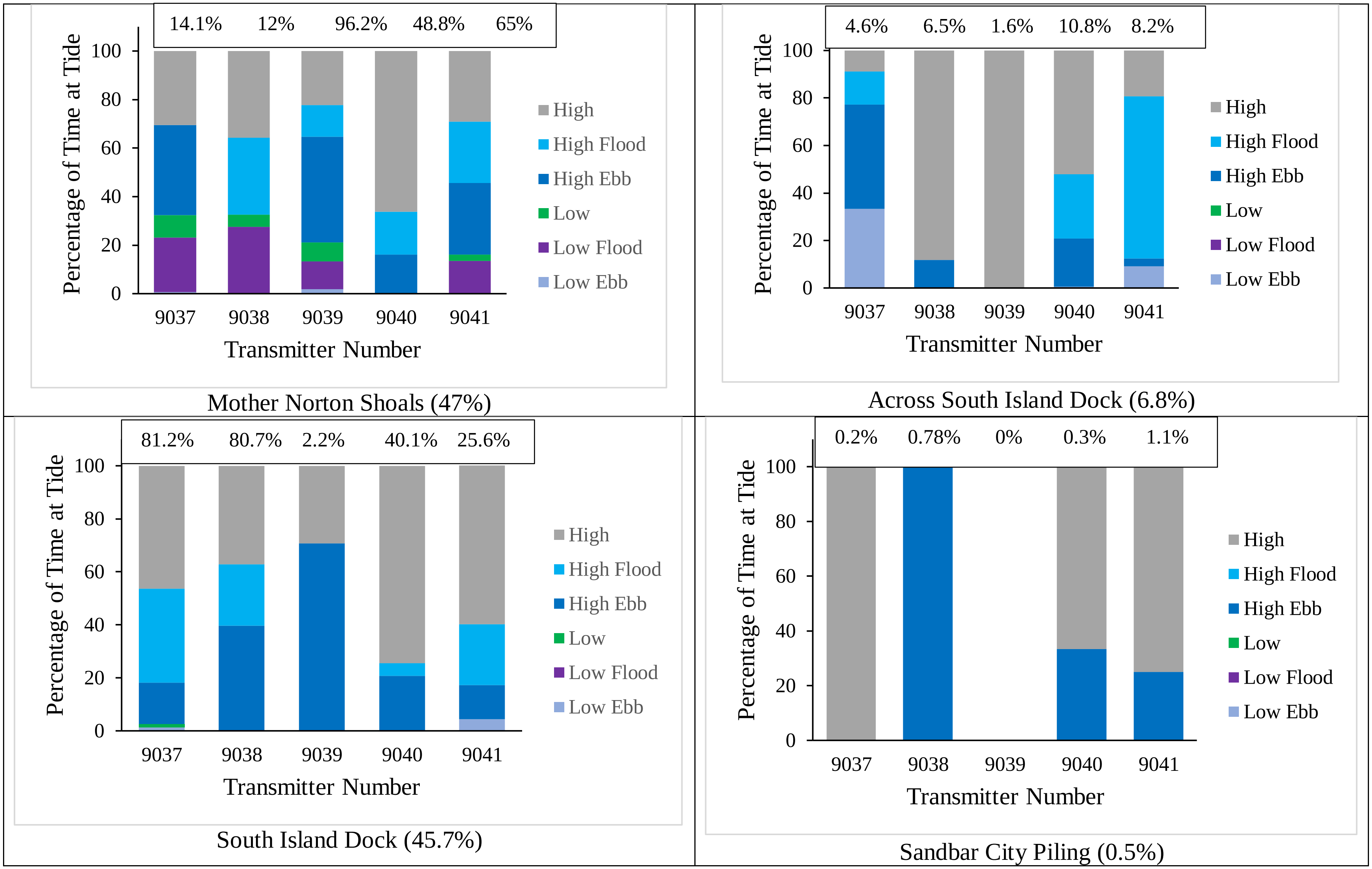

Figure 4: Percentage of time at each tidal phase for transmitters deployed in 2019 (05/08/19 – 05/29/18). Receivers are arranged from the mouth of Winyah Bay to Middle Bay. The percentage next to the receiver name represents the percentage of total time spent at each receiver for all five receivers. The percentage above the bars represent the percentage of time spent at that specific receiver for that transmitter.

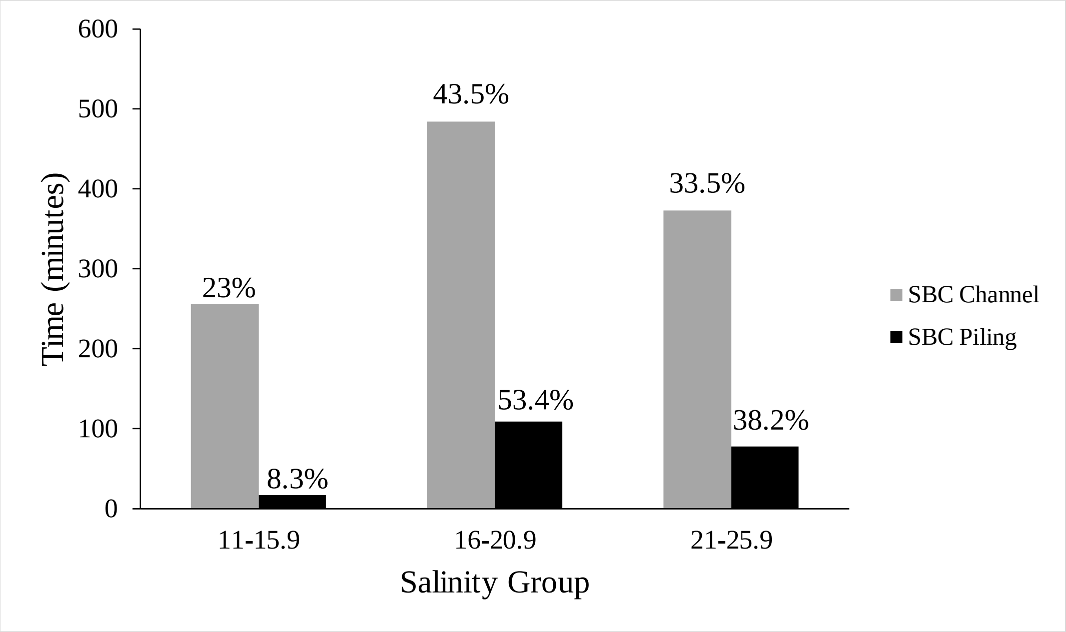

Figure 5: Duration as a function of salinity group for transmitter #9042 at the two Sandbar City receivers. Percentage of time spent at each salinity is shown above the salinity group.

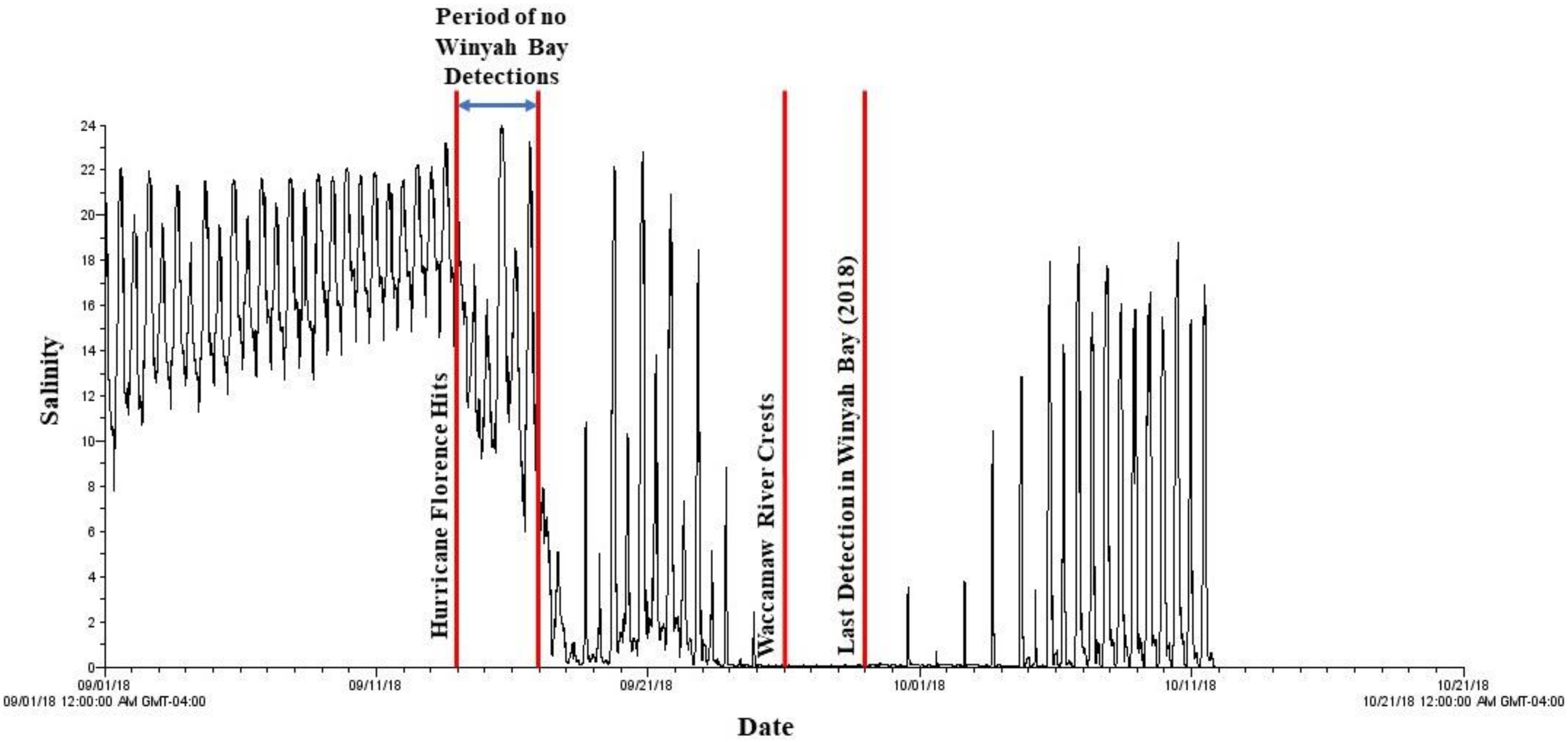

Figure 6: Salinity profile from the Sandbar City Piling HOBO conductivity logger from 9/01/18 – 10/12/18. The profile represents the time from when Hurricane Florence made landfall (9/14/18) through when the Waccamaw River was flooding into Winyah Bay.

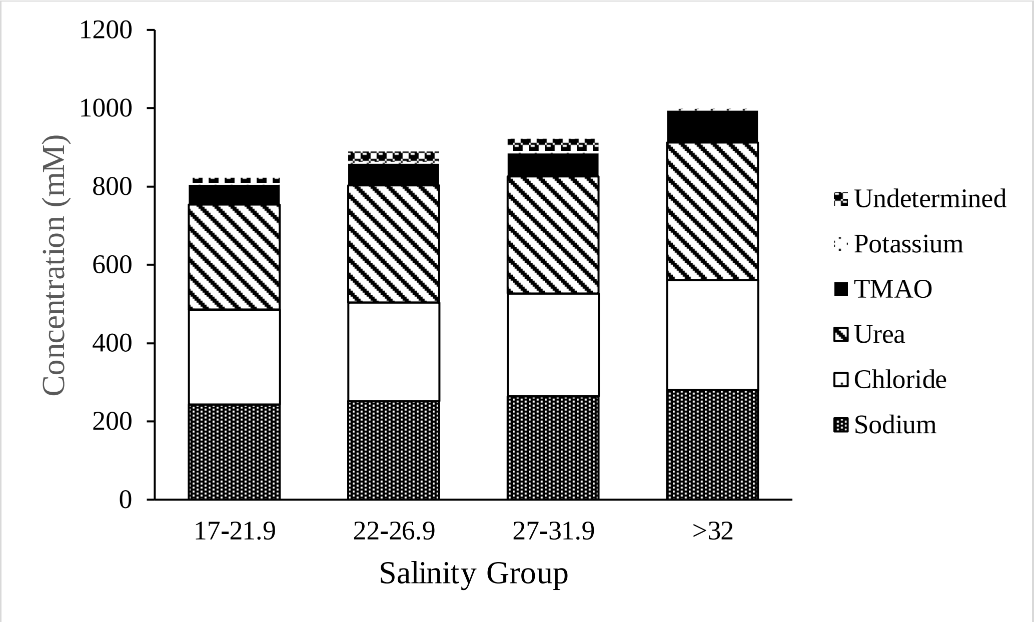

Figure 7: Mean concentrations for all osmolyte components measured for each salinity group (17 – 21.9, 22 – 26.9, 27 – 31.9, >32).

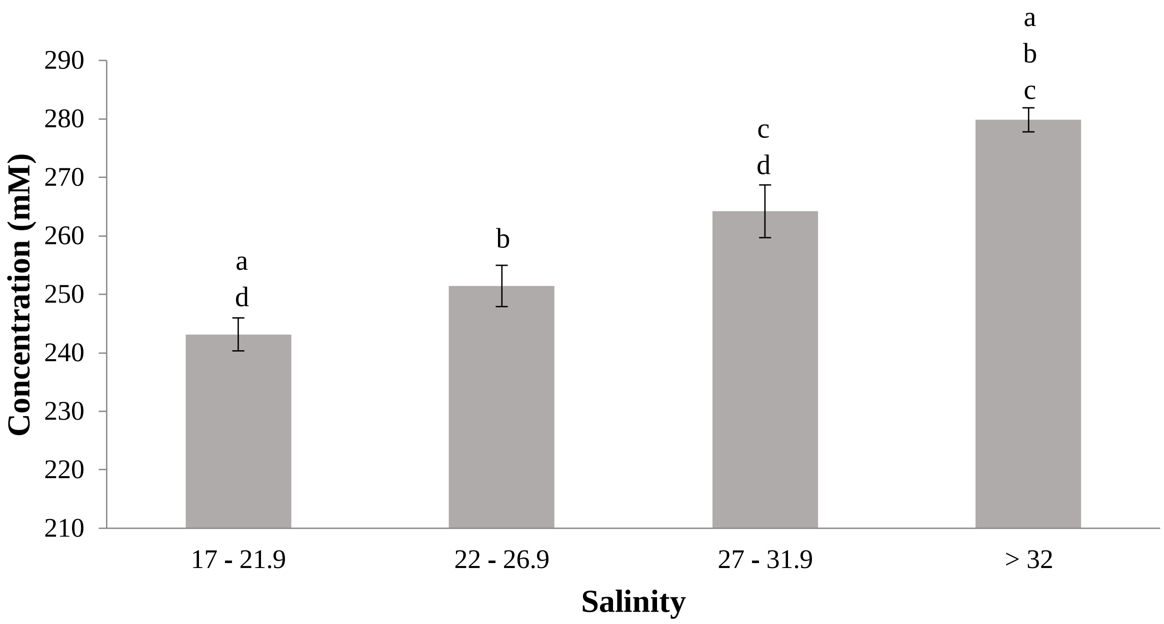

Figure 8: Sodium concentrations (Mean ± S.E.) for each salinity group (17 – 21.9, 22 – 26.9, 27 – 31.9, >32). Letters indicate significant differences between salinity groups based on the post-hoc Tukey tests.

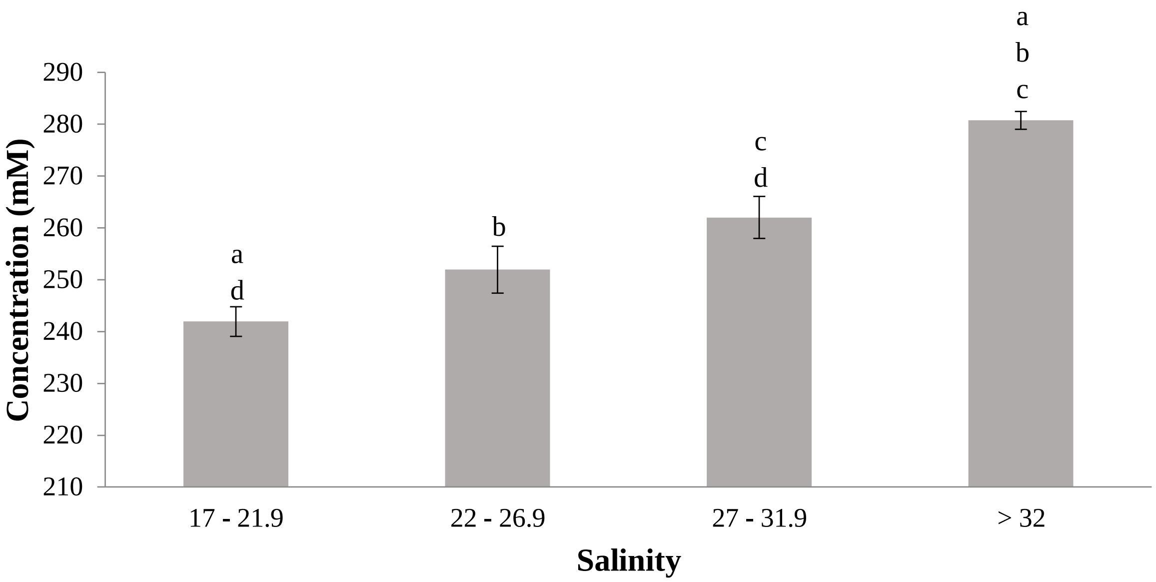

Figure 9: Chloride concentrations (Mean ± S.E.) for each salinity group (17 – 21.9, 22 – 26.9, 27 – 31.9, >32). Letters indicate significant differences between salinity groups based on the post-hoc Tukey tests.

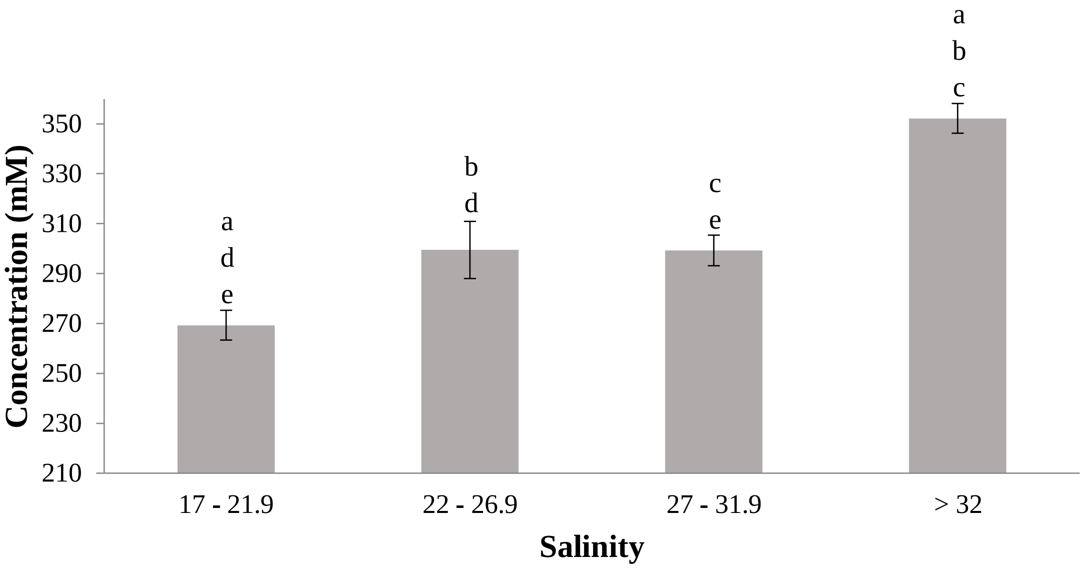

Figure 10: Urea concentrations (Mean ± S.E.) for each salinity group (17 – 21.9, 22 – 26.9, 27 – 31.9, >32). Letters indicate significant differences between salinity groups based on the post-hoc Tukey tests.

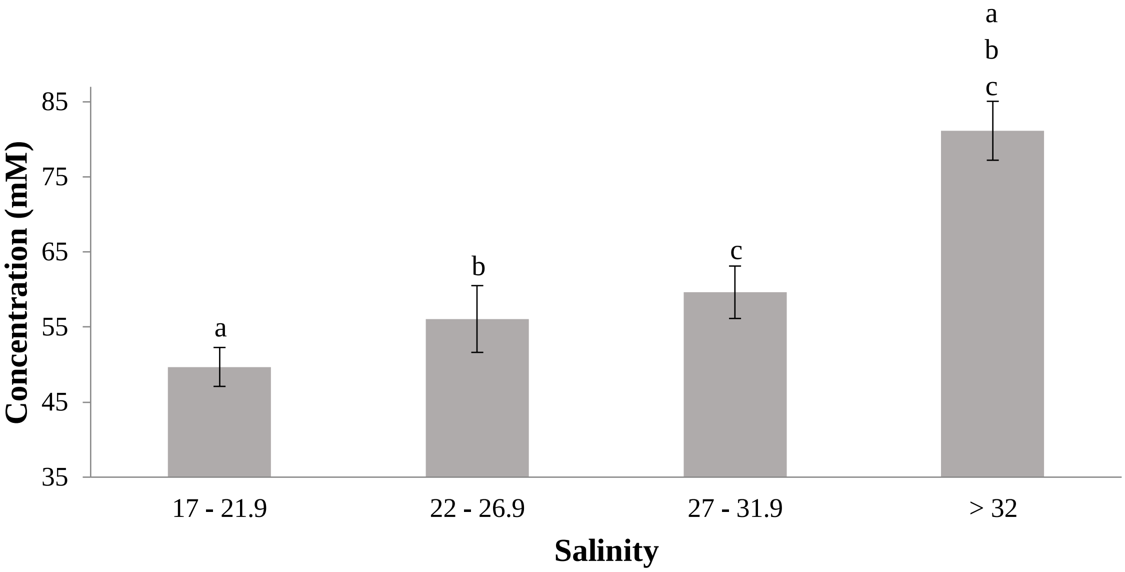

Figure 11: TMAO (trimethylamine oxide) concentrations (Mean ± S.E.) for each salinity group (17 – 21.9, 22 – 26.9, 27 – 31.9, >32). Letters indicate significant differences between salinity groups based on the post-hoc Tukey tests.

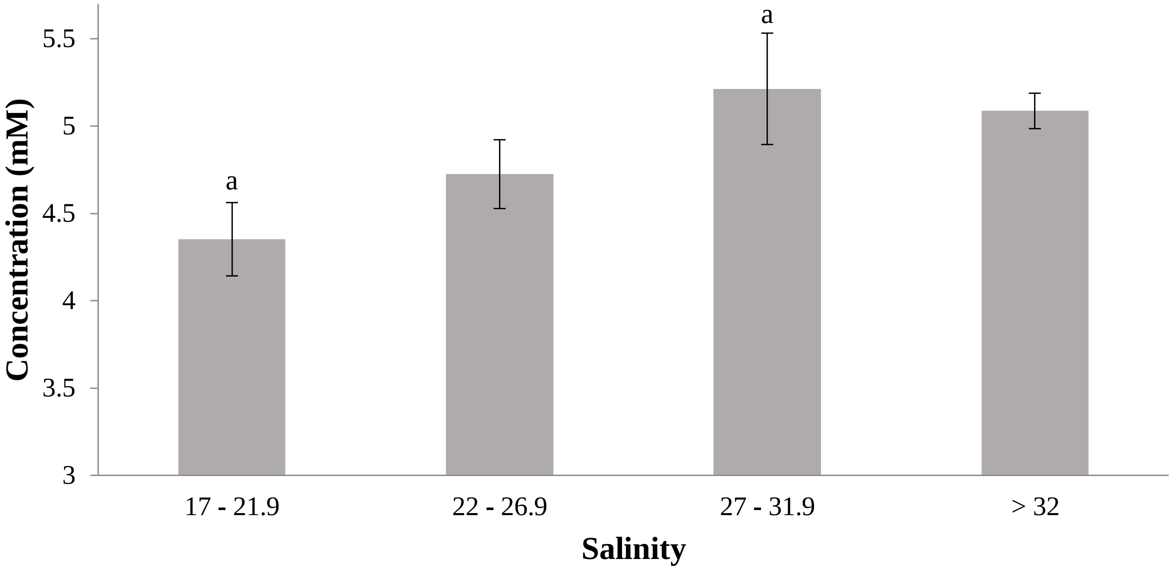

Figure 12: Potassium concentrations (Mean ± S.E.) for each salinity group (17 – 21.9, 22 – 26.9, 27 – 31.9, >32). Letters indicate significant differences between salinity groups based on the post-hoc Tukey tests.

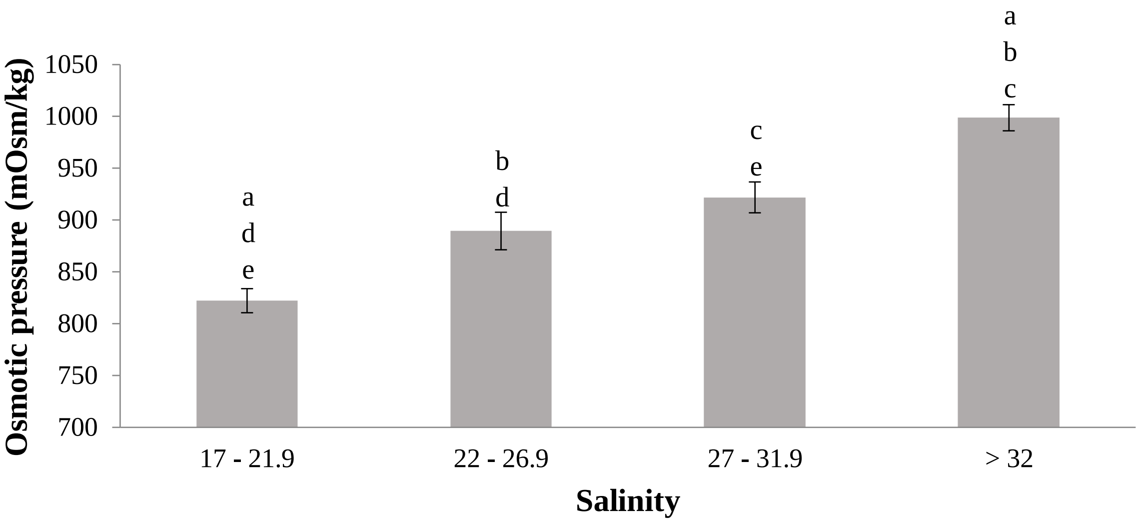

Figure 13: Total osmolality (Mean ± S.E.) for each salinity group (17 – 21.9, 22 – 26.9, 27 – 31.9, >32). Letters indicate significant differences between salinity groups based on the post-hoc Tukey tests.

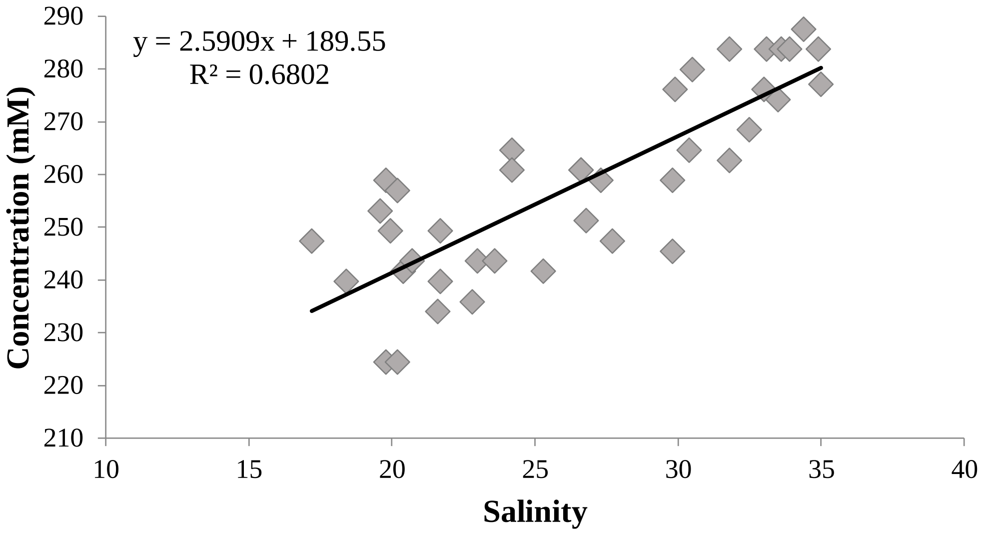

Figure 14: Plasma sodium concentration vs. environmental salinity.

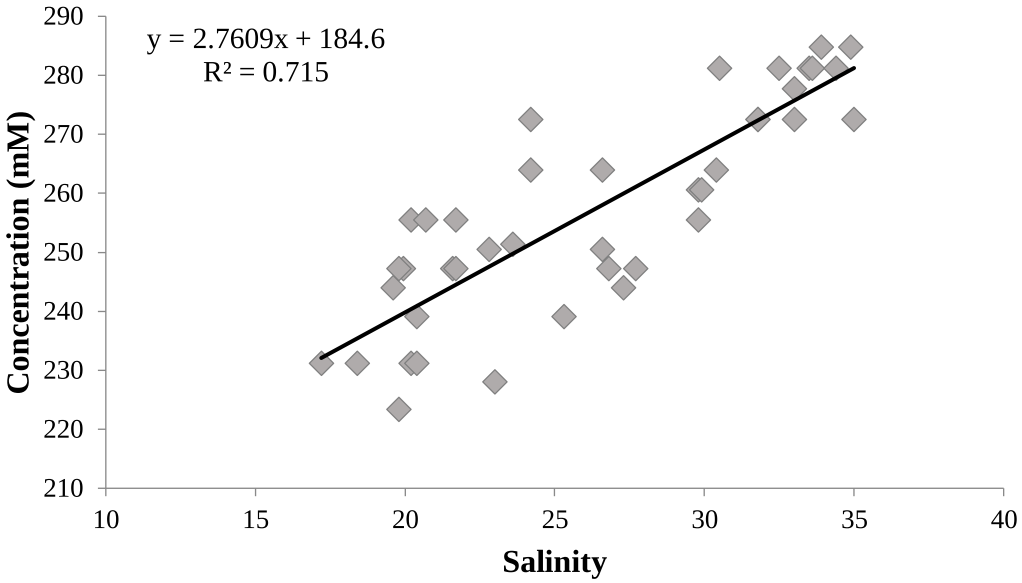

Figure 15: Plasma chloride concentration vs. environmental salinity.

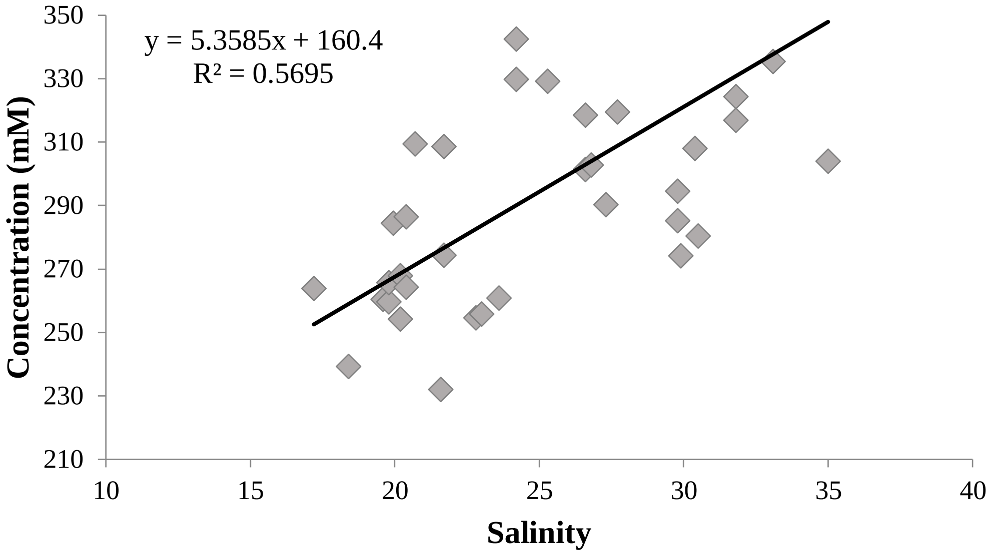

Figure 16: Plasma urea concentration vs. environmental salinity.

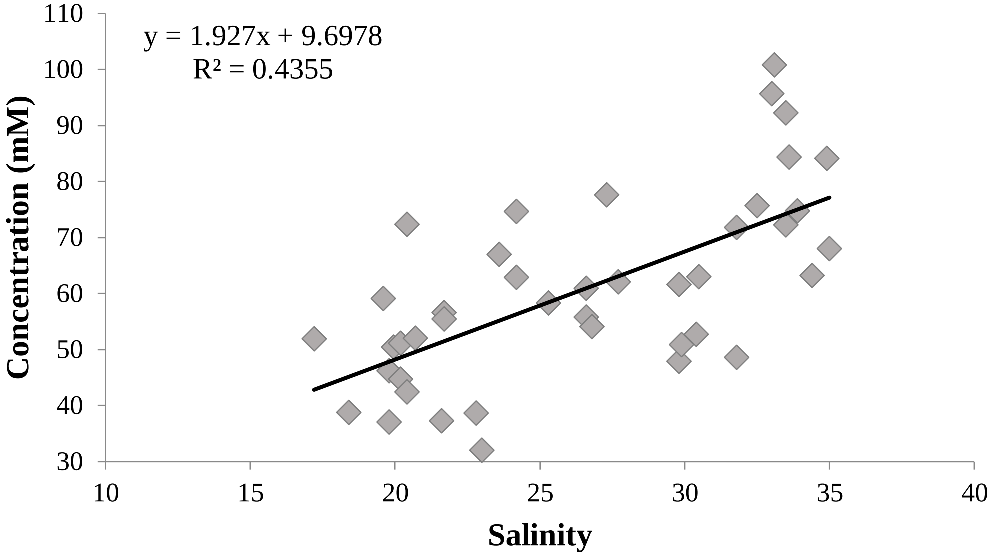

Figure 17: Plasma TMAO concentration vs. environmental salinity.

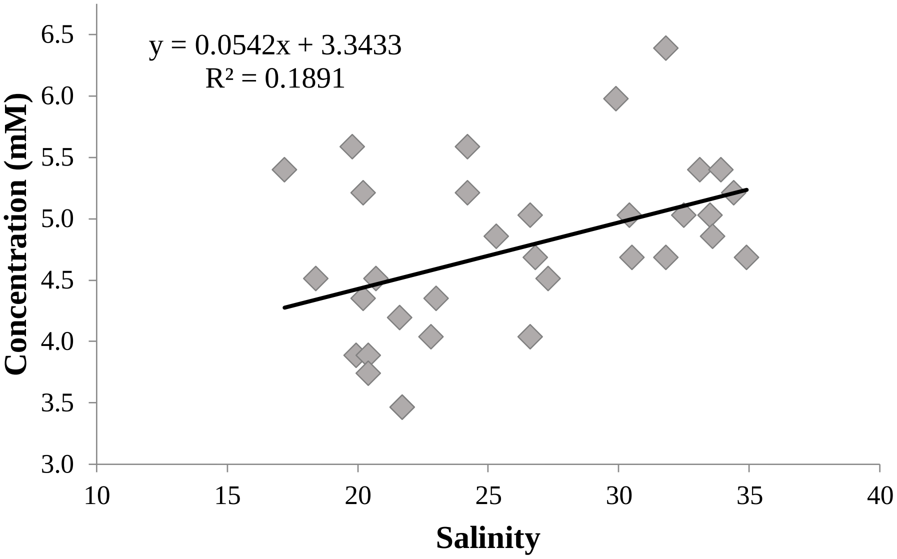

Figure 18: Plasma potassium concentration vs. environmental salinity.

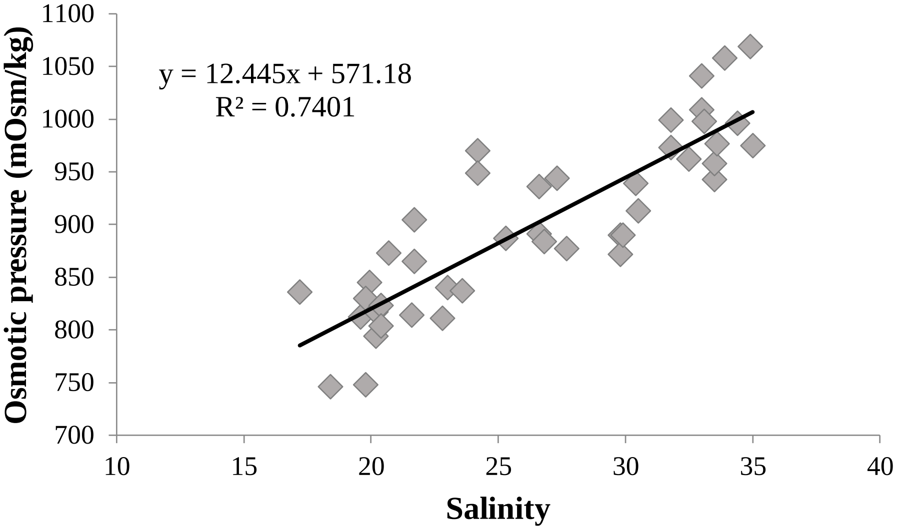

Figure 19: Plasma total osmolality vs. environmental salinity.

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Appendix

Literary Review of Osmoregulatory Values

Table 1: Osmolyte concentrations and total osmolality for members of the Family Carcharhinidae

Species	Environment	Na^+ (mM/L)	Cl^- (mM/L)	Urea (mM/L)	TMAO (mM/L)	Potassium (mM/L)	Total osmolality (mOsm/kg)	Source
Carcharhinus isodon	SW	238	270					Sulya *et al*., 1960
Carcharhinus leucas	SW	223.4[a]	236[a]	333[a]		9.0		Urist, 1962b
Carcharhinus leucas	SW	223.4 ± 20.1	236 ± 21					Urist and Van de Putte, 1967
Carcharhinus leucas (FL adults)	SW	288 ± 12	288 ± 21	356 ± 67	30.7 - 53.6	6.1 ± 0.47		Thorson *et al*., 1973
Carcharhinus leucas	SW	285 – 294[b]	201 - 204[b]			5.7 – 6.7[b]		Manire *et al*., 2001
Carcharhinus leucas	SW	289 ± 3[a]	296 ± 6[a]	370 ± 9.5[a]				Pillans and Franklin, 2004
Carcharhinus leucas	SW	304 ± 3	315 ± 3	293 ± 10	47.3 ± 4.5	5.8 ± 0.3	940 ± 10[c]	Pillans *et al*., 2005
Carcharhinus leucas	SW	305 ± 6	315 ± 5	292 ± 13	24.8 ± 2.1		947 ± 17	Pillans *et al*., 2008
Carcharhinus leucas	SW (21-32 ppt)	247.5 ± 4.1	242.8 ± 4.5	278.1 ± 12.2		4.5 ± 0.4	797.5 ± 15.6	Reilly *et al*., 2011
Carcharhinus leucas (Estuarine adults)	50% SW	233 ± 37	233 ± 60	220 ± 68	8.9 - 23.3	5.9 ± 0.37		Thorson *et al*., 1973
Carcharhinus leucas	FW	200.12[a]	180.5[a]	132[a]		8.2		Urist, 1962b
Carcharhinus leucas	FW	245.8	219.3	180				Thorson, 1967
Carcharhinus leucas	FW (Lake Nicaragua)	1.3	1.8					Urist and Van de Putte, 1967
Carcharhinus leucas	FW (San Juan River, CA)	0.7	0.8					Urist and Van de Putte, 1967
Carcharhinus leucas (Adults)	FW	245 ± 31	219 ± 40	169 ± 48		6.4 ± 0.29		Thorson *et al*., 1973
Carcharhinus leucas (Juveniles)	FW	228 ± 24	207 ± 28	138 ± 24		6.3 ± 0.43		Thorson *et al*., 1973
Carcharhinus leucas	FW	208 ± 3[a]	203 ± 3[a]	192 ± 21.7[a]				Pillans and Franklin, 2004
Carcharhinus leucas	FW	221 ± 4	220 ± 4	151 ± 5	19.1 ± 1.5	4.2 ± 0.2	595 ± 11[c]	Pillans *et al*., 2005
Carcharhinus leucas	FW	233 ± 3	233 ± 4	159 ± 8	13.2 ± 1.5		613 ± 17	Pillans *et al*., 2008
Carcharhinus leucas	FW (0-5 ppt)	234 ± 1.7	230.7 ± 1.6	168 ± 6.9		4.1 ± 0.1	639.7 ± 14.1	Reilly *et al*., 2011
Carcharhinus leucas nicaraguensis	SW	200.12 ± 21	180.5 ± 24.1					Urist and Van de Putte, 1967
Carcharhinus leucas nicaraguensis	FW	200.1	180.5	132			404.3	Urist, 1961
Carcharhinus littoralis	SW	267	235	381				Smith, 1929

Carcharhinus limbatus	SW	313 - 329[b]	207 – 212[b]			3 – 4.3[b]		Manire *et al*., 2001
Carcharhinus obscurus	SW					3.3	1027	Cliff and Thurman, 1984
Carcharhinus melanopterus	FW		158	103			484	Smith, 1931
Negaprion brevirostris	SW	307	277					Oppelt *et al*., 1966
Negaprion brevirostris	SW		310 ± 5	421 ± 2	76 ± 4			Goldstein *et al*., 1968
Negaprion brevirostris	50% SW		252 ± 2	191 ± 4	31 ± 2			Goldstein *et al*., 1968
Rhizoprionodon terraenovae	SW					4.9 – 7.6	1013 – 1300[d]	Haman *et al*., 2012

[a] mM

[b] mEq/L

[c] mOsm/L*kg

[d] mOsm

Table 2: Osmolyte concentrations and total osmolality for Elasmobranchs not in the Family Carcharhinidae

Species	**Environment**	**Na^{+} (mM/L)**	**Cl^{-} (mM/L)**	**Urea (mM/L)**	**TMAO (mM/L)**	**Potassium (mM/L)**	**Total osmolality (mOsm/L)**	**Source**
Raja clavata (Females)	SW		285				1095	Pora, 1936c
Raja clavata	SW	289^{d}	311^{d}	444^{d}			995	Murray and Potts, 1961
Raja clavata	SW	285	240					Enger, 1964
Raja diaphenes	SW	237	227	377				Smith, 1929
Raja eglanteria	SW	243	249	366				Price, 1967
Raja eglanteria	SW		222	368			844	Price and Creaser, 1967
Raja erinacea	SW	254	355	320				Hartman *et al.*, 1941
Raja erinacea	SW	260	253	285			917	Maren *et al.*, 1963
Raja erinacea	SW		287 ± 4^{a}	396 ± 1^{a}	48 ± 3^{a}			Goldstein and Forester, 1971
Raja erinacea	50% SW		202 ± 9^{a}	220 ± 9^{a}	35 ± 5^{a}			Goldstein and Forester, 1971
Raja ocellata	SW	285	255				928	Maren *et al.*, 1963
Raja stabuloforis	SW	255	241	453				Smith, 1929
Raja undulata (Males)	SW						1097	Pora, 1936b
Raja undulata (Females)	SW						1125	Pora, 1936b
Zapteryx brevirostris	35ppt	227^{a}		406-458^{a}		8 – 10^{a}	980 - 985^{c}	Wosnick and Freire, 2013
Zapteryx brevirostris	25ppt	195^{a}						Wosnick and Freire, 2013
Zapteryx brevirostris	15ppt					4^{a}	795^{c}	Wosnick and Freire, 2013
Zapteryx brevirostris	5ppt	168^{a}		266^{a}		4^{a}	713^{c}	Wosnick and Freire, 2013
Dasyatis americana	SW	251	256	351			864	Bernard *et al*., 1966
Dasyatis americana	SW	315	342	444		**5**	1065^{g}	Cain *et al*., 2004
Dasyatis sabina	SW	310 ± 5	300 ± 4.5	394.5 ± 5.5			1034 ± 7.5^{c}	De Vlaming and Sage, 1973
Dasyatis sabina	SW	**279 ± 13**	**289 ± 7**	**346 ± 17**			891 ± 4^{i}	Janech *et al.*, 2006
Dasyatis sabina	50% SW	216 ± 6	**235 ± 6**	327 ± 16			741 ± 13^{i}	Janech *et al.*, 2006
Dasyatis sabina	FW	212 ± 2.8	208 ± 3.4	196 ± 7.9		6.95 ± 0.7	621.4 ± 10.8^{c}	Piermarini and Evans, 1998
Dasyatis sabina (Lake Jesup)	FW (Lake)	3 ± 1.4	3.7 ± 1.5			5.2 ± 0.25	38 ± 0.5^{c}	Piermarini and Evans, 1998
Dasyatis saj	SW	256	262	382			840	Bernard *et al*., 1966
Dasyatis uarnak	FW		212^{a}	104^{a}			548^{c}	Smith, 1931
Himantura signifer	15ppt			153 ± 4^{a}				Chew *et al.*, 2006
Himantura signifer	1 ppt			74 ± 2^{a}				Chew *et al.*, 2006
Narcine brasiliensis		134	159	209				Pereira and Sawaya, 1957
Platyrhinoidis triseriata	SW	234	208					Urist, 1961
Potamotrygonidae sp.	14.5 ppt	198.3 ± 2.7^{b}	183.1 ± 2^{b}	2.31 ± 0.77				Griffith *et al.*, 1973

Potamotrygonidae sp.	FW	164 ± 5.6[b]	151.7 ± 5[b]	1.08 ± 0.13				Griffith *et al.*, 1973
Potamotrygonidae sp.	FW	178 ± 4.8[a]	146 ± 2.1[a]	1.2 ± 0.185[a]			319.6 ± 8.5[c]	Wood *et al.*, 2002
Potamotrygon garouaensis	FW	153		212				Thorson and Watson, 1975
Potamotrygon motoro	13 ppt	166 ± 7	180 ± 5	1.28 ± 0.07			378 ± 9[c]	Tam *et al.*, 2003
Potamotrygon motoro	0.7 ppt	157 ± 16	163 ± 14	0.65 ± 0.17			349 ± 16[c]	Tam *et al.*, 2003
Pristis microdon	FW		170	130			548	Smith, 1931
Pristis microdon	FW			130[a]				Holmes and Donaldson, 1969
Pristis perotteti	FW	216.6	193.1					Thorson, 1967
Rhinoptera bonasus	SW	**276 ± 36**	**255 ± 33**			1.5 ± 0.4		Ferreira *et al.*, 2010
Rhinobatus percellens		143	144	349				Pereira and Sawaya, 1957
Torpedo marmorata (Males)	SW		369				1098	Pora, 1936c
Urolophus jamaicensis	SW	301 ± 5	325 ± 4	384 ± 5		4.27 ± 0.2	**1010 ± 5[c]**	Sulikowski and Maginniss, 2001
Urolophus jamaicensis	82% SW	260 ± 6	**279 ± 4**	307 ± 12		3.9 ± 0.09	851 ± 8[c]	Sulikowski and Maginniss, 2001
Urolophus jamaicensis	74% SW	233 ± 7	247 ± 5	295 ± 12		3.84 ± 1.5	773 ± 6[c]	Sulikowski and Maginniss, 2001
Urolophus jamaicensis	66% SW	**240 ± 12**	**265 ± 16**	168 ± 44		3.77 ± 0.19	704 ± 12[c]	Sulikowski and Maginniss, 2001
Ginglymostoma cirratum	SW	291	287					Oppelt *et al.*, 1966
Chiloscyllium punctatum	25 ppt	**251.56 ± 13.8**	218.67 ± 11.81	**301.70 ± 59.56**		**4.98 ± 0.46**	787 ± 6[c]	Cramp *et al.*, 2015
Chiloscyllium punctatum	34 ppt	**290.74 ± 10.98**	255.56 ± 17.72	448.63 ± 55.34		6.52 ± 2.69	**1019 ± 10[c]**	Cramp *et al.*, 2015
Chiloscyllium punctatum	40 ppt	309.44 ± 15.9	**262.22 ± 18.32**	675.06 ± 63.4		**5.44 ± 0.81**	1153 ± 6[c]	Cramp *et al.*, 2015
Heterodontus francisci	SW	235 ± 6.9	230 ± 9.8	338				Urist and Van de Putte, 1967
Heterodontus portusjacksoni	SW	359 ± 4[a]	310 ± 3[a]	269 ± 16[a]	57 ± 12[a]		**987 ± 13[g]**	Cooper and Morris, 1998
Heterodontus triseriata	SW	235	230	338				Urist and Van de Putte, 1967
Hypolopus sephen	FW		146	81				Smith, 1931
Mustelis canis	SW						1011	Garrey, 1905
Mustelis canis	SW	270	234	381				Smith, 1929
Mustelis canis	SW		275[d]				970	Davson and Grant, 1960
Mustelis canis	SW	288[d]	270[d]	342[d]	97[d]		962	Doolittle *et al.*, 1960

Mustelis canis	SW						981.3	Bloete *et al.*, 1961
Mustelis canis (Males)	SW	255.4 ± 2	253 ± 3.5	981.1 ± 12.7[f]		4.3 ± 0.5	838.6 ± 5.6[c]	Persky *et al.*, 2012
Mustelis canis (Females)	SW	255.3 ± 3.8	254.6 ± 6.1	993.8 ± 23.1[f]		4.0 ± 0.5	843.1 ± 12.7[c]	Persky *et al.*, 2012
Scyliorhinus canicula (Males)	SW	156	299				1107	Pora, 1936a
Scyliorhinus canicula (Females)	SW	192	277				1098	Pora, 1936a
Scyliorhinus canicula	140% SW	378.2 ± 19.3	383 ± 15.6	467.7 ± 7.1			1341 ± 6.7	Hazon and Henderson, 1984
Scyliorhinus canicula	120% SW	352.6 ± 9.8	363.4 ± 5.4	376.4 ± 7.4			1168 ± 4.4	Hazon and Henderson, 1984
Scyliorhinus canicula	100% SW	**278.8 ± 8.9**	297.6 ± 5.6	311.4 ± 5.5			970.3 ± 4.4	Hazon and Henderson, 1984
Scyliorhinus canicula	90% SW	223.4 ± 2.8	238.6 ± 3.8	280.1 ± 4.4			845.9 ± 6.8	Hazon and Henderson, 1984
Scyliorhinus canicula	80% SW	211.1 ± 2.9	212.9 ± 3.7	208.7 ± 3.9			754.3 ± 2.9	Hazon and Henderson, 1984
Scyliorhinus canicula	70% SW	198.8 ± 4.3	202 ± 4.4	160.7 ± 2.3			684 ± 4	Hazon and Henderson, 1984
Scyliorhinus canicula	60% SW	197 ± 8.4	198.5 ± 5.2	120.1 ± 3.4			600.2 ± 3.3	Hazon and Henderson, 1984
Scyliorhinus canicula	50% SW	184 ± 5.2	186.4 ± 5.6	82.2 ± 4.4			503.3 ± 3.8	Hazon and Henderson, 1984
Sphyrna tiburo	SW	289	254					Sulya *et al.*, 1960
Sphyrna tiburo	40ppt	319 ± 14.2	354 ± 24	**354.3 ± 24.3**	**95.2 ± 13.9**	7.2 ± 1.5		Mandrup-Poulsen, 1981
Sphyrna tiburo	30ppt	258.3 ± 3.3	279.1 ± 8.1	289.6 ± 30.3	67.1 ± 17.3	**6 ± 1.8**		Mandrup-Poulsen, 1981
Sphyrna tiburo	20ppt	**241.6 ± 4.1**	264.1 ± 6	178.8 ± 32.8	**45.3 ± 14.2**	4.8 ± 0.2		Mandrup-Poulsen, 1981
Sphyrna tiburo	SW	306 – 317[b]	206 - 209[b]			6 – 7.1[b]		Manire *et al.*, 2001
Sphyrna tiburo	SW	**273 - 292**	**277 - 304**	**337 - 381**		5.7 – 9.2	1056 - 1139	Harms *et al.*, 2002
Sphyrna tiburo	SW					**5 – 7.8**	**997 – 1329[g]**	Haman *et al.*, 2012
Squalus acanthias	SW				71			Cohen *et al.*, 1958
Squalus acanthias	SW	286	246	**351**			1018[g]	Burger and Hess, 1960
Squalus acanthias	SW	255	239				973[h]	Maren, 1962
Squalus acanthias	SW	240	259					Robin *et al.*, 1964
Squalus acanthias	SW	234.6					997	Burger, 1965
Squalus acanthias	SW	250		330			980	Boylan, 1967

Squalus acanthias (wild plasma)	SW	233 - 240	228 - 245				**996 - 1030**	Burger, 1967
Squalus acanthias (Live-car plasma)	SW	253 - 262	222 - 262				**948 - 1036**	Burger, 1967
Squalus acanthias	SW			343	84.7			Forster, 1967
Squalus acanthias	SW	263	249	**357**			**1007**	Murdaugh and Robin, 1967
Squalus acanthias	SW	**296 ± 24.4**^{e}	**276 ± 21.6**^{e}	308 ± 31.3^{e}	**72.4 ± 15**^{e}	7.2 ± 1.8^{e}	**993 ± 5.6**^{c}	Robertson, 1975
Squalus acanthias	SW					3.2 – 4.8	**699 – 1210**^{g}	Haman *et al.*, 2012
Squatina angelus (Males)	SW		255				1102	Pora, 1936c
Triakis semifasciatus	SW	235	230	333				Urist, 1962b

[a] mM
[b] mEq/L
[c] mOsm/kg
[d] mM/kg
[e] mM/kg H_2O
[f] mg/dl
[g] mOsm
[h] mOsm/L*kg
[I] mOsm/kgH_2O

Shapiro-Wilkes Normality Tests

Precaudal lengths for juvenile sandbar sharks utilized in the plasma study
Shapiro Wilkes Test
W=0.96149
p=0.1571

Precaudal lengths (log transformed) for all juvenile sandbar sharks caught for this study
Shapiro Wilkes Test
W=0.98647
p=0.2884

Sodium
Shapiro Wilkes Test
W=0.95338
p=0.09203
Chloride
Shapiro Wilkes Test
W=0.95523
p=0.09953
Urea
Shapiro Wilkes Test
W=0.95708
p=0.1083
TMAO
Shapiro Wilkes Test
W=0.97032
p=0.3384
Potassium
Shapiro Wilkes Test
W=0.98449
p=0.9071
Total osmolality
Shapiro Wilkes Test
W=0.97672
p=0.5229

Range Testing
From Collatos, 2018

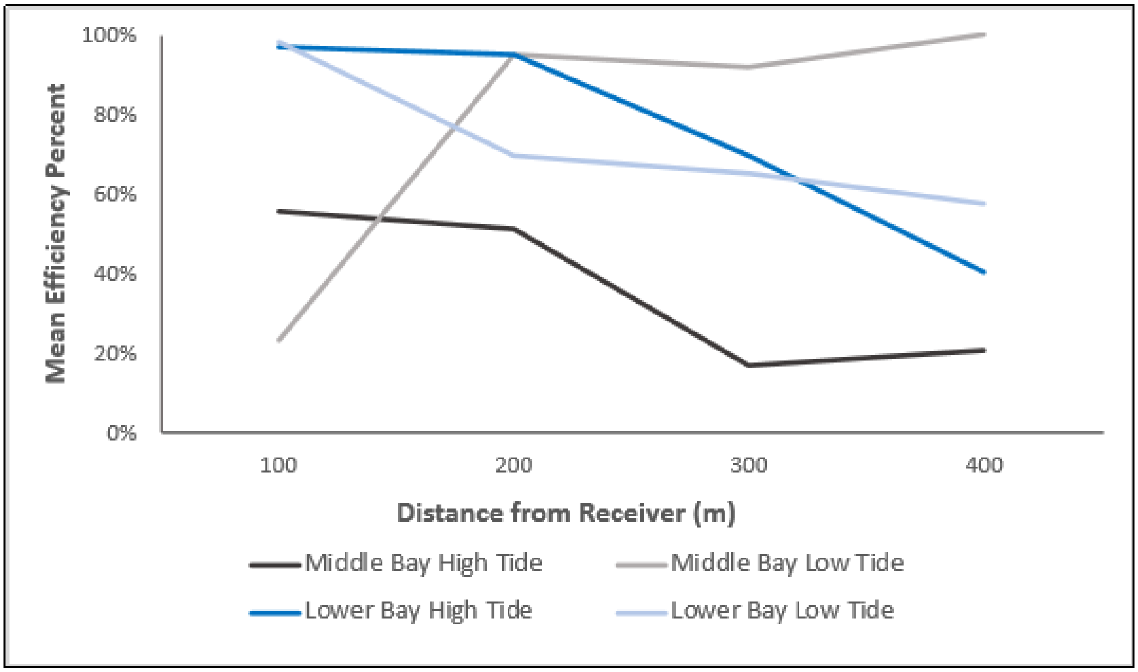
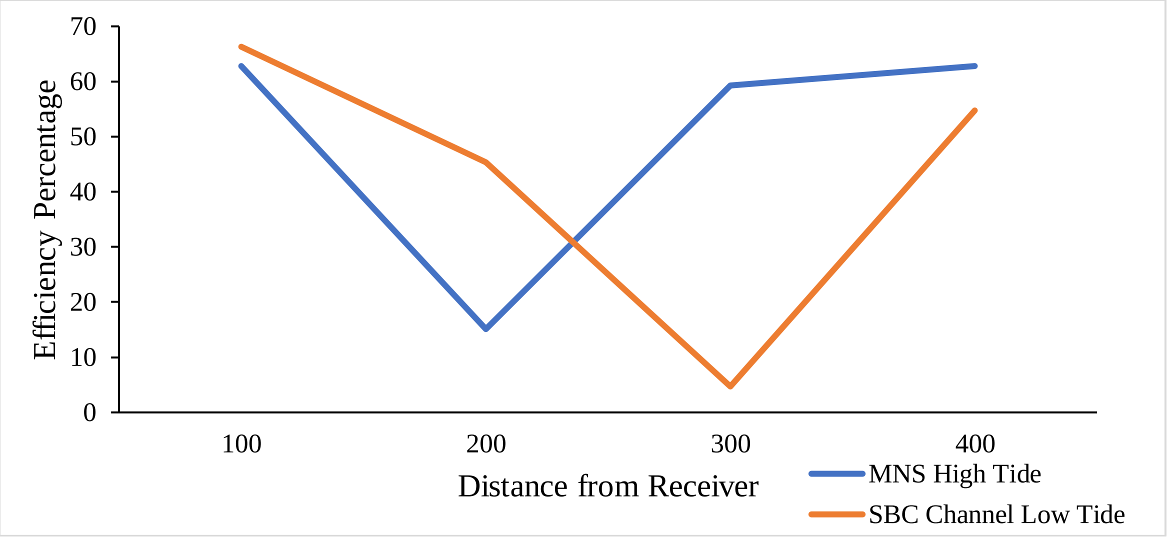


Figure 2. Range testing results for both low and high tide in middle and lower bay.

From this study



Detection efficiency percentages were very variable. Low tide was unable to be measured at Mother Norton Shoals as the receiver was moved and High tide was unable to be measured at the Sandbar City Channel receiver because the receiver was lost