12-4-2020

Residency, Diel Movement, and Tidal Patterns of Large Juvenile Bull Sharks (*Carcharhinus leucas*) in Winyah Bay, SC

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Residency, Diel Movement, and Tidal Patterns of Large Juvenile Bull Sharks (*Carcharhinus leucas*) in Winyah Bay, SC

By

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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

2020

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Acknowledgments

First and foremost, I would like to thank my thesis committee and their tireless advice, commitment, and support throughout my thesis development. Additionally, I liked to thank my funding agencies, Coastal Carolina University and the United States Air Force Aim High program funding. I want to also thank Steve Luff for his strenuous work recovering data and committing numerous hours to equipment recovery.

Dr. Abel's role in my thesis design, implantation, and execution cannot be understated. I am eternally grateful for him giving me the opportunity to study at Coastal Carolina University and developing me as a scientist. I consider him to be a trusted friend and mentor with whom I have the utmost respect. I would also like to thank Dr. Gallagher and Mr. Fraser, who were crucial in developing methods and ideas to form the basis of my research and their contribution was critical to capturing Bull Sharks for implantation. I want to thank Dr. Crane for serving on my committee and his critical insights on thesis development and statistical advice adding to Bull Shark research. Additionally, I want to thank Dr. Boneillo for his sage council and assistance in developing this thesis.

I would also like to acknowledge the contributions of the Winyah Bay-North Inlet NERR, OTN, FACT, DNR, and ACT networks, who donated equipment, time, and patience to this study. Without the coordination of these agencies this study would not have been possible. I want to specifically thank both the Diadromous fish group and Coastal Shark Survey group who contributed telemetry data and assistance with methodology. Additionally, I would like to thank all my fellow graduate students and volunteers contributing to this project.

Finally, I would like to thank my family for their tireless devotion to supporting my goals at great personal sacrifice, specifically my wife Andrea Arnt for scrambling to watch my children and working while assisting with a plethora of work. She also went above and beyond enduring my absence, whether it was because of writing, to sampling trips, or for anything else I needed. Lastly, I would like to thank my son and daughter Jeremy Arnt Jr. and Nataly Arnt for their support and motivation in everything that I do.

Abstract

Winyah Bay, South Carolina is a large, partially-mixed estuary that provides an annual habitat for juvenile and adult bull sharks (*Carcharhinus leucas*). From July 15, 2019 until October 31, 2019 I deployed drumlines targeting bull sharks within Winyah Bay. Seven large juvenile bull sharks were implanted with VEMCO (V16-4H) acoustic transmitters and monitored with eight VEMCO (VR2W) receivers to study bull shark residency, diel, and tidal movements in Winyah Bay. Additionally, abiotic factors contributing to presence were analyzed to determine factors affecting bull shark presence.

Data analysis was performed using 10,805 detections spanning 108 days inside Winyah Bay. Residency indices indicated repeated use of the Winyah Bay habitat and these varied by month (July – October). Furthermore, Rao's spatial statistics demonstrated bull sharks were detected at distinct temporal periods dependent on bay area. Additionally, the linear mixed model of tidal data suggested bull sharks altered their duration-of-stay depending on the interaction of tide and bay region. Abiotic detection data showed that bull sharks were more likely to be present in warm (27.10 °C), normoxic (4.12 mg/L), and brackish waters (13.31 ppt) based on the binomial GLM in the middle bay area.

Our telemetry data suggest that the Winyah Bay ecosystem may be more important to large juvenile bull shark populations than previously thought. Residency data indicated that bull sharks use Winyah Bay repeatedly throughout the late summer, and duration-of-stay of large juvenile bull sharks varied within bay area dependent on tidal stage. Additionally, like previous studies, I observed that while capable of inhabiting a wide range of habitats, bull sharks preferred specific abiotic conditions. Finally, qualitative analysis of bull shark presence outside Winyah Bay during Hurricane Dorian suggested bull sharks temporarily left Winyah Bay.

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Introduction

Bull sharks (*Carcharhinus leucas*) are a large (> 2 m) coastal species that inhabit tropical and sub-tropical waters circumglobally (Ballie *et al*. 2004; Simpfendorfer & Burgess 2009). In the western Atlantic Ocean, bull sharks range from New England to southern Brazil, inhabiting fresh, brackish, and marine habitats (Castro 1993). In the eastern United States, bull sharks inhabit lagoons, estuaries, and mangroves as juveniles for nursery habitat but emigrate from these habitats as they increase in length (Castro 1993; Curtis 2011). Adult bull sharks incorporate additional areas including neritic habitats but still frequent estuarine environments (Castro 1993; Werry 2010). However, data concerning estuarine habitat use is limited in large juveniles and adult bull sharks.

Several bull shark nurseries have been identified and defined along the US eastern coastline, with the largest habitat located in the Indian River Lagoon in Florida and the northernmost found in Pamlico Sound, North Carolina (Castro, 1993; Bangley, 2018). Nursery sites are habitats that neonate and juvenile shark density and site-fidelity are greater than other locations and are used across years (Heupel *et al*. 2007; Heupel *et al*. 2018). Nurseries also provide areas of high productivity and low predation to young sharks, which reduce mortalities and increase prey availability (Heupel *et al*. 2007; Heupel *et al*. 2018).

Prior to 2018, the northernmost bull shark nursery in the United States was considered the Indian River Lagoon in Florida (Castro 1993; Simpfendorfer & Burgess 2009). However, Bangley (2018) discovered increasing populations of young-of-year and small juvenile bull sharks within Pamlico Sound over a thirteen-year gillnet study. These population increases were correlated with higher temperature and salinity in the system (Bangley 2018). Traditionally, the northern limit of bull shark nurseries was considered restricted by temperature, since low temperatures are associated with high juvenile bull shark mortality (Snelson & Bradley 1978; Castro 1993; Simpfendorfer & Burgess 2009). Increased water temperature is not isolated to Pamlico Sound and temperatures in the western Atlantic Ocean are increasing due to global climate change (Cheung *et al*. 2009; Portner & Peck 2010; Hare *et al*. 2016). The increasing marine temperatures are likely to alter bull shark habitat use and distribution and warrant further study (Cheung *et al*. 2009).

Prior studies on movement and residency of bull sharks have focused on neonate and juveniles in nurseries (Yeiser *et al*. 2008; Ortega *et al.* 2009; Heupel *et al.* 2010; Drymon *et al*. 2014). Small juvenile bull sharks reside in brackish salinities year-round in Florida and these have been extensively researched (Heupel *et al.* 2010). However, larger juvenile bull shark movement and residency have not been as extensively researched. Large juvenile bull sharks can inhabit a wide range of salinities, but smaller juveniles prefer brackish salinities (Castro 2010). Werry (2010) noted that bull sharks partition habitat in eastern Australia according to salinity, with young individuals occupying low salinity environments and larger conspecifics preferring more saline environments. Werry (2010) postulated the habitat partitioning in eastern Australia most likely occurs due to cannibalism in the species, with smaller individuals avoiding predation from larger conspecifics in lower salinity waters. While spatial data of juvenile bull sharks is known for numerous locations in the U.S. and beyond, similar information in South Carolina's estuaries is lacking.

Bull sharks inhabit coastal South Carolina and the Winyah Bay estuary (Abel *et al*. 2007; Gary 2009). Winyah Bay is a 65 km^2 partially mixed estuary in northeast South Carolina whose shark fauna has been extensively studied by the Coastal Carolina University's (CCU) Shark Research Project and the South Carolina Department of Natural Resources (SCDNR) (Gary

2009; Peterson *et al*. 2017). During summer months sandbar sharks (*Carcharhinus plumbeus*), Atlantic sharpnose sharks (*Rhizoprionodon terraenovae*), blacktip sharks (*Carcharhinus limbatus*), finetooth sharks (*Carcharhinus isodon*), bull sharks, lemon sharks (*Negaprion brevirostris*), spinner sharks (*Carcharhinus brevipinna*), bonnetheads, (*Sphyrna tiburo*), blacknose sharks (*Carcharhinus acronotus*), and scalloped hammerheads (*Sphyrna lewini*) are captured in Winyah Bay (Abel *et al*. 2007; Gary 2009; Castro 2010). The most abundant species caught in Winyah Bay by researchers, who use bottom longlines baited with Boston mackerel (*Scomber scombrus*), are all life stages of sandbar sharks (Gary 2009; Collatos 2018).

The CCU Shark Research Project captured few bull sharks on longlines over its 20-year survey (Gary 2009; Collatos 2018). However, anecdotal evidence suggests that this low bull shark capture rate may be due to gear biases or bait type (Boston mackerel) (Snelson *et al*. 1984; Cliff & Dudley 1991). A study by Cortes (1999) show bull shark occupy relatively high trophic levels and chondrichthyans account for 35% of their diet. Since employing previous standardized capture methods and baits have limited success, prioritizing novel capture methods and bait may increase bull shark capture.

Numerous shark species, including scalloped hammerheads, common thresher sharks (*Alopias vulpinus*), blacktip sharks, lemon sharks, and blue sharks demonstrate foraging area expansion, contraction, and shifts based on diel cycles (Klimley & Nelson 1984; Cartamil *et al*. 2010; Heard *et al*. 2018; Legare *et al*. 2018). For instance, juvenile lemon sharks actively tracked in Bimini Lagoon showed a shift in nocturnal activity space when compared to diurnal movements (Gruber *et al*. 1988). Moreover, lemon sharks exhibited increased rates of movement during crepuscular and nocturnal diel periods, suggesting foraging behavior (Gruber *et al*. 1988). Similarly, longline data in the southeastern U.S. shows bull sharks are more likely to be caught on longlines nocturnally then diurnally (Driggers III *et al*. 2012). Driggers III *et al*. (2012) suggested nocturnal captures of bull sharks are indicative of nocturnal foraging behavior, like lemon sharks (Gruber *et al*. 1988). Since bull sharks and lemon sharks share similar ecological niches, bull sharks may exhibit similar diel changes in movement (Heupel *et al*. 2010; Drymon *et al*. 2014; Legare *et al*. 2015; Gallagher *et al*. 2017).

The objectives of this study are to use longlines, drumlines, and acoustic telemetry to (1) Determine how bull sharks utilize Winyah Bay spatially and temporally; (2) correlate this use with abiotic factors (salinity, temperature, etc.); (3) determine if bull sharks in Winyah Bay alter their movement based on diel cycles?; (4) Elucidate residency patterns of bull sharks in Winyah Bay.

Methods

Site Description

Winyah Bay is a 22 km long, 65 km^2 coastal estuary located adjacent to Georgetown, SC, U.S. and is formed by five rivers, the Black, Pee Dee, Great Pee Dee, Waccamaw and Sampit (Goni *et al*. 2003). Under low river flow conditions, Winyah Bay is a partially mixed estuary (Bloomer 1973). However, the upper and middle bay act as a salt wedge estuary under high river flow conditions (Bloomer 1973). Tidal flow is semi-diurnal (mean amplitude =1.4 m) with salinities along the Winyah Bay axis ranging from freshwater to 34 ppt (Goni *et al*. 2003). The influx of saltwater under normal conditions penetrates just north of the US-17 highway bridge. Winyah Bay is surrounded by 160 km^2 of coastal intertidal marshlands and is 1.2 km across at the mouth and 6.4 km at its widest point.

The substrate of Winyah Bay consists of mud, silt, clay, and sand, with sand dominating the upper bay area. The average depth is 4 m with an 8 m central shipping channel (Patchineelam & Kjerfve 2004), which is not maintained and is currently silting in (Edwin Jayroe, pers comm). The deepest portion of Winyah Bay is located near the mouth of the estuary, with depths > 10 m. Water temperature varies seasonally from 9 ^{o}C during the winter to 30 ^{o} C during the peak of summer.

Abel *et al.* (2007) and Gary (2009) considered Winyah Bay as divided into three regions along the long axis: the upper bay, middle bay, and lower bay. These regions corresponded to the ecosystem's salinity gradient varying from freshwater, brackish, and marine respectively (Abel *et al*. 2007, Gary 2009). I used Abel *et al.* (2007) and Gary's (2009) delineation criterion and sampled the lower bay, middle bay, and upper bay regions. Additionally, I added a coastal area using South Carolina's Department of Natural Resources receivers for diel and tidal analysis but not residency statistics.

Capture techniques

Bull sharks were captured using bottom longlines and drumlines at sites in middle and lower Winyah Bay. Each 150-m longline consisted of 25 one-meter gangions with 0.5 m steel braided leader and 0.5 m mono-filament line attached to 18/0 carbon steel circle hooks. Bottom longlines were baited with Boston mackerel and soaked for 60-minutes. Soak times were determined when the final gangion was deployed until the first hook was retrieved.

Bottom drumlines were deployed by attaching a surface line tethered to a buoy at the surface and anchored in the substrate. A 23 m monofilament gangion line (~540 kg test) was attached via snap swivel and tuna clip to the anchor. An additional 2 m of leader line consisting of a six-strand monofilament line (250 kg test) was attached via swivel and terminated with an 18/0 circle hook. Additionally, the proximal end of the mainline had hook timers attached using monofilament line (250 kg test). Drumlines were set at high and low slack tide according to the local NOAA tidal predictions and soaked for ~2 hours. Soak times began when the hook entered the water and ended when it was removed.

Captured bull sharks were either brought onboard to be processed and implanted with an acoustic transmitter or were moved alongside the vessel, secured via tail rope and pectoral fin ropes, and inverted to induce tonic immobility. Once the shark was positioned, an onboard hose was inserted in the animal’s mouth to provide oxygen to the gills. Any sharks showing advanced signs of stress based on nictitating reflex and general appearance were released at this point. For sharks considered healthy, pre-caudal length (PCL), fork length (FL), total length (TL), maturity and sex were measured. Maturity was determined based on the degree of clasper calcification in males and FL (189 cm) for females. If male bull sharks had hardened elongated claspers, they were considered mature. If their claspers were partially hardened or flaccid, they were categorized as immature. Any bull sharks deemed healthy underwent surgery to implant acoustic tags, as described below. After implantation, the hook, and for sharks processed in the water, securing ropes, were removed and the shark was released.

Acoustic Tagging Surgery

Bull sharks were surgically implanted with V16 acoustic coded transmitters (VEMCO Ltd Halifax, Canada). Prior to implantation acoustic transmitters were enveloped in a mix of 70% paraffin and 30% beeswax coating to reduce the immune response of the sharks (Holland *et al*. 1999; Lowe *et al*. 2006; Bond *et al*. 2012). A 4-5 cm incision was made along the abdominal wall and the coded transmitter was activated then inserted into the peritoneal cavity. All incisions were closed using absorbable polyester surgical sutures through muscle and skin tissue. All transmitters operated in high-power mode with a 60-second delay (Range: 30-90 seconds) at 69 kHz. The estimated life for acoustic transmitters with these specifications is 1613 days and covered the entire study period.

Telemetry and Receivers

Nine VR2W (VEMCO Ltd Halifax, Canada) acoustic receivers owned by the South Carolina Department of Natural Resources (SCDNR) at permanent locations in Winyah Bay data were incorporated in analyses. Additionally, CCU and the Ocean Tracking Network receiver array consisted of eight VR2W acoustic receivers. Two of CCU's receivers were attached to existing moorings within Winyah Bay. To secure the receivers, a 1-inch galvanized steel chain was bolted to moorings with the VR2W receiver attached via plastic zip ties approximately 1 m above the substrate. The remaining receivers were deployed by attaching the receiver to a PVC housing enveloped in cement to secure it above the substrate. Range testing was conducted during July 2019 and tested at 100 m, 200 m, 300 m, and 400 m distances. Receiver detection ranges were tested using the V16-4x (VEMCO Ltd Halifax, Canada) range testing tag on a 7-second delay. Range testing tags were attached to a 1-m rigid mounted pole anchor by a cement block and lowered into the water to simulate a bull shark's benthic behavior. Detection data from receivers was downloaded every three to four months and receivers were cleaned before being redeployed. Receivers had HOBO loggers attached to the apparatus approx. 0.5m below the receiver to sample the bottom water salinity and temperature at five-minute intervals for abiotic analysis. The receiver located at the National Estuary Research Reserve (NERRs) station in Winyah Bay used the open source data from NERRs to sample temperature and salinity.

Residency/Telemetry Data analysis

All raw detection data was processed through VEMCO's VUE false detection algorithms to minimize erroneous detections. After processing detections, the individual tags were broadly categorized as either resident or non-resident for each day of the study. Resident categorization was determined daily whenever an animal was initially captured or any day it was detected more than once by the receiver array. Individuals were categorized as non-resident if 1 or no detections were received to reduce false detections.

Raw residency data was converted into a residency indices (RI) for further analysis. Residency indices for monthly and overall values were calculated by dividing the number of days considered resident by the total number of days monitored for each month and overall. The RI data conversion allowed us to standardize the data irrespective of an individual's period monitored since some individuals would have more days monitored than others. Variation of RI values compared to TL of individuals was analyzed using a linear regression.

During September of 2019 I had the opportunity to observe presence data following Hurricane Dorian from receivers connected to the ACT/FACT network and used these detections to compare presence in Winyah bay to the Santee river system following the disturbance. I gathered 1088 detections of telemetered bull sharks in the Santee river system over the course of the study, these data were not statistically analyzed but used to compared usage between Winyah Bay and the Santee river system.

I used ANOVA to analyze the total number of detections of individual bull sharks for each binned period (day, night, sunrise, sunset). Sunrise and sunset detections were considered one hour before and after their respective local time base on NOAA sunrise/sunset times. All other detections were considered day or night based on sunlight. Additionally, I binned raw detection data into hourly periods and the number of detections within each hour were analyzed to determine any temporal directedness of detections using the Oriana software package (version 4, Kovach Computing Services). Since circular data cannot be analyzed using conventional linear statistics, I used a Rao's spatial analysis to investigate the null hypothesis that bull shark detections were evenly distributed throughout a 24-hour period (Batschelet 1981). Furthermore, I grouped detection data by bay area to investigate any statistical significance between habitats.

I investigated bull shark duration-of-stay data based on tide cycle and bay area to determine spatiotemporal use of Winyah Bay. The duration-of-stay metric allowed us to determine the temporal use during specific tide periods and bay areas. Duration-of-stay was calculated by the time elapsed from initial detection from a single receiver until the final detection without a time gap larger than 30 minutes. To determine differences of receiver detections based on tide cycle, I grouped detections into four categories (high tide, low tide, ebb, flood). Durations of stays were categorized as high or low tide if the first detection was within 1.5 hours of the respective tide. Ebb tide was categorized if the first detection was following a high tide but before the next low tide. Additionally, flood tides were categorized if the first detection was following a low tide but prior to high tide. Any duration-of-stays that spanned multiple tides were binned into the period that had majority of time. All tide times were determined using the closest available NOAA tide site to the receivers (Georgetown Lighthouse ID: 8662447, Frazier Point ID: TEC 2937).

I used a linear mixed effect model (LMM) to determine differences in the duration-of-stay of bull sharks based on bay area and tidal stage described above. Bay area and tidal stage were considered fixed effects with tag identification number as a random effect to meet the assumption of independence in our LMM. We fit three models to predict the duration-of-stay of bull sharks by bay area, tide stage, and the interaction of bay area and tide stage (Table 1). Models were then compared using Akaike's information criterion, corrected for a small sample size (AICC) to determine the most likely model. Akaike weights were used to determine the likelihood of the model's accuracy. Additionally, I used odds ratios to estimate how changes in the predictor variable effects the odds of sharks being detected. The model with the lowest AICC value and highest Akaike weight was used for the final analysis and parameter estimates (Brewer *et al*. 2016).

Water Quality data

Receiver detection data were used in combination with Hobo logger data and NERRs sampling stations to investigate abiotic factors related to presence of bull sharks near receivers. For individual receivers, bull sharks were considered present if receivers detected an individual >1 time during a thirty-minute period. Bull shark detection data were then binned into thirty-minute periods and linked with water quality data to determine the influence of temperature, salinity, dissolved oxygen, and month on bull shark presence. I used a generalized linear model (GLM) with a binomial probability distribution to assess the influence of water quality on bull shark detections. I also used AICC and weights to compare individual models to determine the best fit model for the parameters analyzed (Brewer *et al*. 2016). Lastly, I calculated coefficient estimates (95% CI) and odds ratios for variables included in the most probable model.

Results

Range Testing

All bay areas demonstrated a distinct pattern of decreasing detection efficiency with increased distance from the receivers (Figure 15). Range test sampling was conducted over five days in the middle of July 2019 in the upper, middle, and lower bay habitats. Transmitter detections occurred at ranges up to 400 m from the receivers' location. Hypothetically all locations and scenarios should have resulted in a 100% detection efficiency. However, due to local environmental conditions (turbidity, substrate type, benthic morphology etc.) range tests were below the receiver's ideal detection efficiency. During high tide, the middle bay receiver had the highest detection efficiency (77.0 %) followed by upper bay (68.5 %) and lower bay (64.0 %). During low tides, detection efficiency was highest in lower bay (87.0 %) followed by middle bay (75.8 %) and upper bay (67.3%; Figure 14).

Residency data

Seven large juvenile bull sharks, four males (mean TL 196.25 ± 6.33 cm) and three females (mean TL 204.33 ± 7.31 cm), were monitored in Winyah Bay for a total of 108 days spanning from July 15th to October 31st, 2019 (Table 1). Of the 17 receivers deployed by CCU, SCDNR, and the Ocean Tracking Network, five were either vandalized, stolen, or otherwise unable to gather data. Remaining acoustic receivers recorded 10,805 detections from implanted transmitters over the study period (mean 1,543 ± 136). All sharks were detected in Winyah Bay at least one day following deployment. Total number of days detected between tags ranged from 29 to 80 days (61.43 mean ± 6.27) over the study period. Consecutive days resident ranged from a single day to 33 days from detected receivers (Fig 1.; Fig 2.). Overall bull shark RIs ranged from 0.58 to 0.76 (mean 0.67 ± 0.02) and showed no significant differences between sizes (n = 7, df = 1, p > 0.05). ANOVA revealed a significant difference between RI and month with high RI values in July and August with a decrease in RI values in September and October ($F_{3,21} = 35.98$, $p < 0.001$) (Figure 3). Additionally, linear regression analysis of RI compared to bull shark FL was not significant (n = 7, df = 1, $p > 0.05$).

Hurricane Dorian

The eye of Hurricane Dorian made landfall as a category 2 storm in South Carolina on September 5th, 2019, inundating Winyah Bay with 10 inches of rainfall in one day. Our analysis of RI in Winyah Bay showed a distinct absence of bull sharks from September 5th until September 9th. I also found novel detections from bull sharks in the adjacent Santee estuarine systems. During the four-day absence of detections of telemetered bull sharks in Winyah Bay, bull sharks were detected only in coastal regions or the Santee river system. Additionally, prior to Hurricane Dorian's arm reaching South Carolina, only a single individual (tag # 25908) was detected in the Santee river receiver array on September 2, 2019 (Figure 12; Figure 13).

Diel data

Binned diel detection ANOVA was not significantly different between all bull sharks across diurnal, nocturnal, and crepuscular periods based on raw detection data ($F_{3, 24} = 1.24$, $p > 0.05$). However, circular data analysis showed bull shark detections within Winyah Bay had non-uniform distribution depending on bay area. All bay areas had detections across the 24-hour period. Rao's spatial analysis revealed a non-homogenous detection distribution and received detections clustered during early morning within Winyah Bay and coastal detections during midmorning (Figure 3-6; Table 2).

Linear Mixed Model

The most likely model included variables for bay area and tidal stage to determine the duration-of-stay (W_i=0.99; Table 4; Figure 11). The model was based on 1370 observations from bull sharks in Winyah Bay. Bull sharks had the longest duration-of-stay in middle bay during high tide (21.14 minutes) and the shortest in lower bay during ebb tide (6.50 minutes).

Abiotic Data

Temperature, salinity, and dissolved oxygen measurements were recorded in upper bay and middle bay only due to equipment failures in lower bay. Mean temperature when bull sharks were absent was 27.10 °C (± 0.02 SE) over the sampling period ranging from 16.25 °C to 33.90 °C. During bull shark presence the mean temperature was slightly higher at 27.84 °C (± 0.07 SE) and ranged from 21.10 °C to 33.70 °C. Mean salinity during bull shark absence was 13.31 ppt (± 0.07 SE) and ranged from 0.50 ppt to 24.80 ppt. The mean salinity during bull shark presence was 13.10 ppt (± 0.17 SE) and ranged from 1.85 ppt to 22.65 ppt. DO concentrations during bull shark absence was a mean of 5.00 mg/L (± 0.02 SE) and varied from 0.45 mg/L to 11.10 mg/L. DO measurements in the presence of bull sharks was a mean of 4.12 mg/L (±0.05 SE) and varied from 0.60 mg/L to 10.40 mg/L. Telemetered bull sharks in Winyah Bay were not detected across the entire range of water quality perimeters measured in this study. In middle and upper bay bull sharks were present in 40% of the interquartile range of available temperatures in relatively warm water (Figure 8). Additionally, bull sharks in this study were detected in low DO concentrations relative to their available habitat at 40% of the interquartile ranges (Figure 9). Lastly, presence of bull sharks regarding salinity varied based on individual month with interquartile ranging broadly from 8 ppt to 19 ppt (Figure 10).

The best fit binomial GLM based on AICC included dissolved oxygen, temperature, and the interaction of month and salinity (W_i 0.99; Table 3). The model results showed that bull shark presence was positively associated with salinity depending on month and temperature (Table 6). Conversely, bull shark presence was negatively associate with dissolved oxygen increases. Odds ratios indicated an interaction between month and salinity with a positive correlation with September having the great odds ratio value and July the least. Similarly, the odds of bull shark presence were positively correlated with increased temperature, in C°, based on odds. Finally, bull sharks had a negative association of presence for every 1 mg/L increase is dissolved oxygen.

Discussion

The results from this study reveal new information on the presence, behavior, and movements of bull sharks within Winyah Bay. Acoustic data from July through October 2019 suggest that large juvenile bull sharks inhabit Winyah Bay over extended periods and are present in specific bay area’s according to diel periods. High (>0.5) RI indicate that Winyah Bay may be an important seasonal migratory habitat for large juvenile bull sharks over the late summer months. Tidal data suggests that bull sharks remain present, at high tide, longer in middle and upper bay. Conversely, bull sharks were present for shorter periods at high, flood, and ebb tides in lower bay. However, relative receiver efficiency based on bay area and tidal stage may be biased. Receivers in upper and middle bay had similar efficiency between high and low tides. However, lower bay was more likely to detect signal during low tide than high tide. The discrepancy of duration-of-stay between bay area and tide period may be variability of receiver detections rather than shark presence. Additionally, abiotic data suggest bull sharks show preferences to warm, normoxic, mesohaline environments.

Winyah Bay usage

Bull Sharks tracked in Winyah Bay remained present and resident throughout the study period. While mean RI remained high throughout the late summer, these data likely underrepresent the true residency of these individuals because the receiver coverage in Winyah Bay was sparse and incomplete. RI values indicate large juvenile bull shark presence is like neonate and small juveniles in nurseries that reside continuously until reaching larger sizes or are forced away by extreme environmental events (Snelson 1977; Matich & Heithaus 2012;). Winyah Bay is a productive estuary which is habitat for numerous bull shark prey species, including striped mullet, red drum (*Sciaenops ocellatus*), ladyfish (*Elops saurus*), Atlantic stingray, arriid catfish, tarpon (*Megalops atlanticus*) and numerous small shark species (bonnethead, Atlantic sharpnose shark, etc.) or juveniles of larger species, such as sandbar sharks (Muncy & Wingo 1983; Snelson *et al*. 1984; Hammerschlag *et al*. 2012). Residency in Winyah Bay is likely high due an abundance of prey species and populations.

Bull sharks in the western Atlantic Ocean are believed to transition into adult offshore habitat at ~180 cm TL (Simpfendorfer *et* al. 2005; Blackburn *et* al. 2007; Wiley &

Simpfendorfer 2007; Curtis 2011). In contrast, all bull sharks acoustically tracked in this study were >185 cm TL and remained in Winyah Bay from July throughout October. While offshore transitions from nursery habitats occur, our data indicate that Winyah Bay bull sharks, in this size group, still utilize estuaries extensively during the late summer months. Additionally, offshore receivers show that bull sharks will enter coastal habitat regularly, which is not a documented behavior of smaller juvenile bull sharks (Ortega *et al*. 2009; Heupel *et al*. 2010; Werry *et al*. 2010). Small juvenile bull sharks demonstrate coastal and offshore habitat use almost exclusively during extreme barometric and temperature changes and remain in estuarine habitats under normal conditions in nursery habitats (Curtis *et al*. 2011; Strickland *et al*. 2020). The larger bull sharks tracked in this study likely have a reduced predation risk due to their larger size relative to neonate and small juvenile conspecifics. The reduced risk of predation may enable large juvenile bull sharks to forage in coastal habitats that are high risk to smaller conspecifics.

Coastal habitats may offer additional benefits to large juvenile bull sharks. Large bull sharks require increased food consumption relative to smaller conspecific to offset the additional energy cost of their higher body mass (Carrier *et al*. 2012). By utilizing coastal habitats, bull sharks can forage when estuarine forage is reduced in availability without high predation risk. Supplementary foraging area would likely increase prey capture, offsetting the metabolic cost of higher body mass of large juveniles (Werry 2010). Ontogenetic shifts and expansions of bull sharks have been documented over small and large spatiotemporal scales in Pacific and Atlantic populations and the regular inclusion of coastal habitat in Winyah Bay may be the result of this behavior (Simpfendorfer *et al*. 2005; Werry 2010).

Bull sharks and blacktip sharks have demonstrated movement away from nursery habitats in response to relative hydrostatic pressure drops associate with hurricanes (Heupel & Simpfendorfer 2003; Strickland *et al*. 2020). We believe our bull sharks showed similar behavior as a result of the effect of Hurricane Dorian. Before Hurricane Dorian bull sharks remained in the middle bay area of Winyah Bay consistently with brief forays into coastal habitats. However, just prior to Hurricane Dorian making landfall, bull sharks emigrated Winyah Bay to offshore receivers. The emigration of bull sharks was likely cause by barometric pressure decreases and not salinity changes caused by rainfall since shark were absent prior to Hurricane Dorian's rain. During the days following Hurricane Dorian, bull sharks continued to remain in coastal habitat or the adjacent Santee river system likely to avoid aftereffects of hurricanes including increased river flow, salinity changes, prey absence, turbidity, and temperature changes.

Diel/tidal activity

The analysis of diel detections based on bay area showed bull sharks were present in lower, middle, and upper bay at early morning periods and coastal receivers at mid-morning. Circular statistical analysis showed detections were clustered around nocturnal early morning periods. Bull sharks may be foraging for prey in this area while light conditions are low and predator detection by prey is decreased. Bull shark vision is less effective nocturnally; however, it is unlikely that vision is the primary sensory modality in turbid Winyah Bay water (Lisney & Collins 2007). The bull shark's small eyes in relation to body size suggest lesser use of photoreception, compared to other shark species (Lisney & Collins 2007). Additionally, lemon sharks, which are confamilials, show a duplex retina with an extreme sensitivity to nocturnal vision, which may offer some degree of sensory input at night (Gruber 1977; Gruber & Cohen

1978). The low light conditions may offer bull sharks a foraging advantage by allowing them to remain undetected while using their remaining sensory modalities for prey capture.

Previous research shows bull sharks consume Atlantic stingrays (*Hypanus sabinus*) and ariid catfishes as a large portion of their diet (Snelson 1981; Snelson *et al.* 1984). Earlier work on Atlantic stingray ecology in Winyah bay shows distributions of this species based on salinity regimes, favoring mesohaline environment typical of the middle bay region (Klien-Majors 2006; Abel *et al*. 2007). Foraging in middle bay, where favored prey species are abundant, could reduce energy expenditure by minimizing time spent foraging (Klien-Majors 2006; Abel *et al*. 2007). The high prey abundance and reduced foraging period might offset any costs associate with energy expended by swimming against tidal and river currents.

Diel periodicity of bull shark detections suggests tidal stage was not a contributing factor of bull shark presence, contrary to the LMM results. Similarly, the diel relationship of bull shark presence also indicates salinity was not a contributing factor since salinity changes in response to tide. The most probable explanation of LMM results is the dissimilar efficiency of receivers in Winyah Bay. Receiver detection efficiency during low and high tide in bay areas were different and likely skewed detection and duration-of-stay data in favor of tidal periods with the highest receiver efficiency. While previous studies show bull shark movement in response to tidal transport, additional data need to be collected before determining tidal movement behavior of bull sharks in Winyah Bay. Further studies on tidal influences on bull shark presence should incorporate robust receiver array designs, center of activity models using kernel density estimates, or active acoustic telemetry to reduce biases present in this study’s design.

Abiotic factors

Large juvenile bull shark presence in Winyah Bay was affected by the concentration of DO in their environment followed by temperature and then by monthly salinity. DO, temperature, and salinity have all been shown to control spatiotemporal use of habitat in various Atlantic bull shark populations (Gulf of Mexico, western Atlantic) to varying degrees (Heithaus *et al*. 2009; Drymon *et al*. 2014; Bangley *et al*. 2018). However, many of these studies focused on small bull sharks (< 1m) whose habitat preference is affected by predator avoidance controlled by conspecifics based on salinity (Werry 2010). The large juvenile Winyah Bay bull sharks are not likely to alter behaviors based on predator avoidance since they are the apex predator in this system. The reduced predator avoidance pressure may allow large juvenile bull sharks to utilize reduced DO habitats that are more advantageous in some manner. However, DO concentrations in estuaries can vary on small spatial scales and are affected by numerous abiotic (temperature, tide, turbidity, diel period, nutrient loading) and biotic factors (photosynthesis, respiration) (Du & Shen 2015). The multiple factors contributing to dissolved oxygen levels and the broad DO tolerance of bull sharks make clear conclusions of spatiotemporal use enigmatic.

A preference for higher temperature in estuaries is a well-documented behavior in Atlantic bull sharks, and we corroborated this in Winyah Bay (Heupel & Simpfendorfer 2008; Bangley *et al*. 2018). Bull sharks are ectotherms and require warm temperatures to maintain their physiological functions (Carrier *et al*. 2012). Bull sharks are likely present during warmer temperature to maintain their physiological requirements at optimum efficiency. Additionally, large numbers of bull shark kills have been reported when temperatures decreased below about 20 °C in Florida (Snelson & Bradley 1978).

The detection of bull sharks in higher temperatures also suggests that bull sharks are using Winyah Bay as foraging habitat. Numerous studies on ectothermic elasmobranch species show behavioral thermoregulation by foraging in relatively warm environments and digesting prey in cooler temperature to conserve energy (Matern *et al*. 2000; Sims *et al*. 2006; Carrier *et al*. 2012). Bull sharks may be foraging in Winyah Bay when temperature is high and move offshore to digest prey during the morning to conserve energy. The temperature reduction would decrease digestive efficiency, but also reduce energy expenditure for other functions providing a net energy surplus (Matern *et al*. 2000; Sims *et al*. 2006). The cluster of coastal detections may be bull shark leaving Winyah Bay to thermoregulate by moving into cooler deeper water. However, this is purely speculative since temperature and direction of movement could not be determined in this study. Bull sharks are likely using the upstream habitats when temperatures are high and remain offshore where temperature decreases. Bull sharks may enter Winyah bay only during this period when temperatures are high, which would explain low relative RI values. Further, studies should use annual periods to analyze abiotic factors contributing to presence and RI to determine seasonal effects on bull sharks.

Bull shark presence was affected by monthly salinity, and sharks showed preferences within the available salinity range. The subtle preferences were likely caused by the large influx of freshwater by Hurricane Dorian after September 5, 2019. Bull sharks in prior studies show preferences for salinities from 10 ppt to 20 ppt depending on length (Heupel *et al*. 2010; Werry 2010). The drastic salinity change in September cause by Hurricane Dorian likely changed the "normal" salinity range experienced in middle bay in September. Again, since samples were measured in middle and upper bay bull sharks probably still prefer mesohaline environment, but Hurricane Dorian changed the typical salinity regime.

Conclusions

This study concludes that bull sharks within upper and middle Winyah Bay are present in response to abiotic factors including temperature, dissolved oxygen, and salinity. However, temperature preference is likely a response to seasonal temperature changes rather shorter temporal periods (days, hours). Additionally, large juvenile bull sharks are resident in Winyah Bay over extended periods from July to September 2019 and presence in described bay areas is linked to diel periods. Bull shark residency is likely a response to Winyah Bay’s abundant prey species, and Winyah Bay is an important foraging habitat for large juvenile bull sharks during warm summer months. Hurricane Dorian had a distinct effect on bull shark residency and behavior at least temporarily following its landfall in South Carolina. Further studies on bull shark residency in Winyah Bay should focus on long term study concerning bay residency to determine annual and seasonal bull shark presence.

Figures and Tables

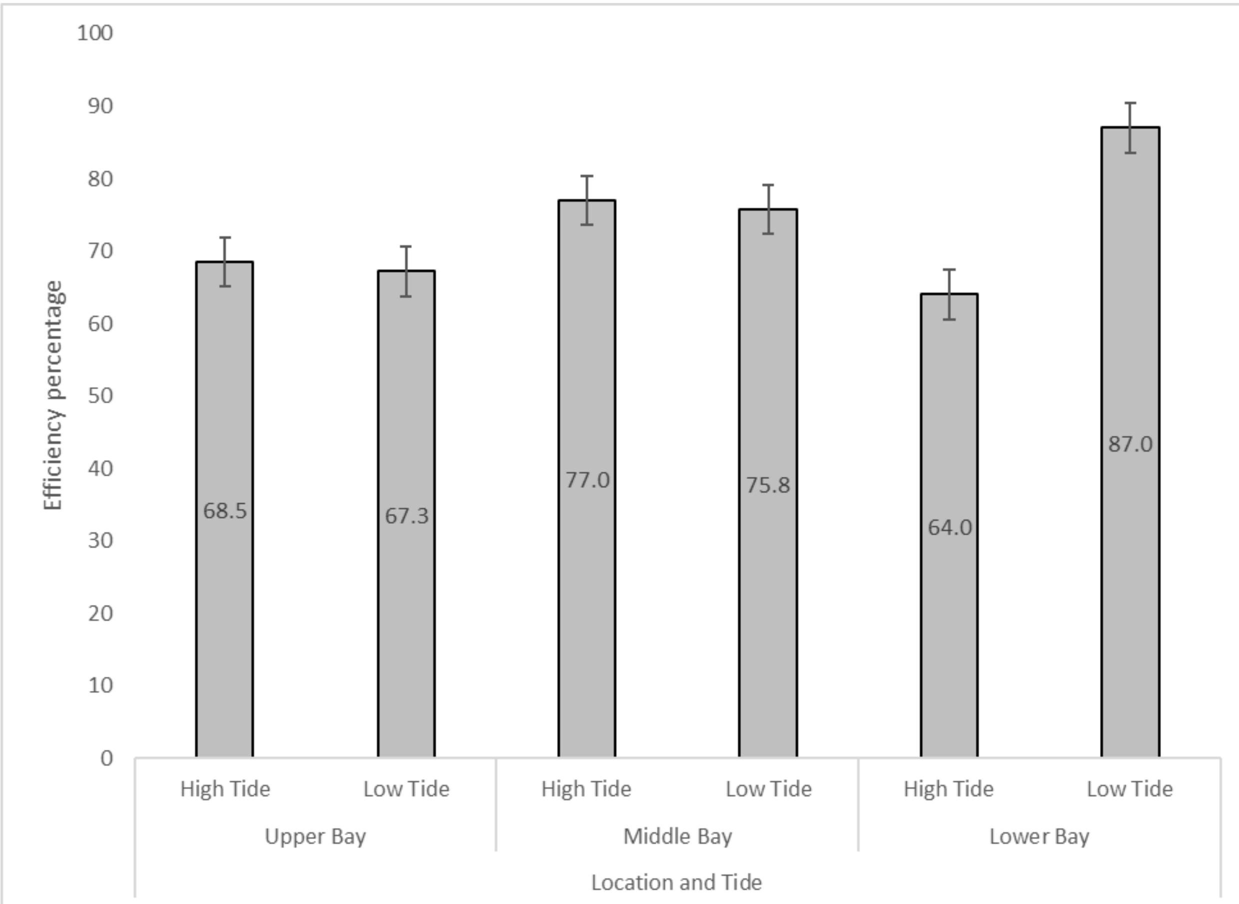

Figure 1. Bar graph of receiver efficiency based on bay area and tidal stage. All receiver efficiency measurements were assessed during July 2019 at each receiver during high and low tide.

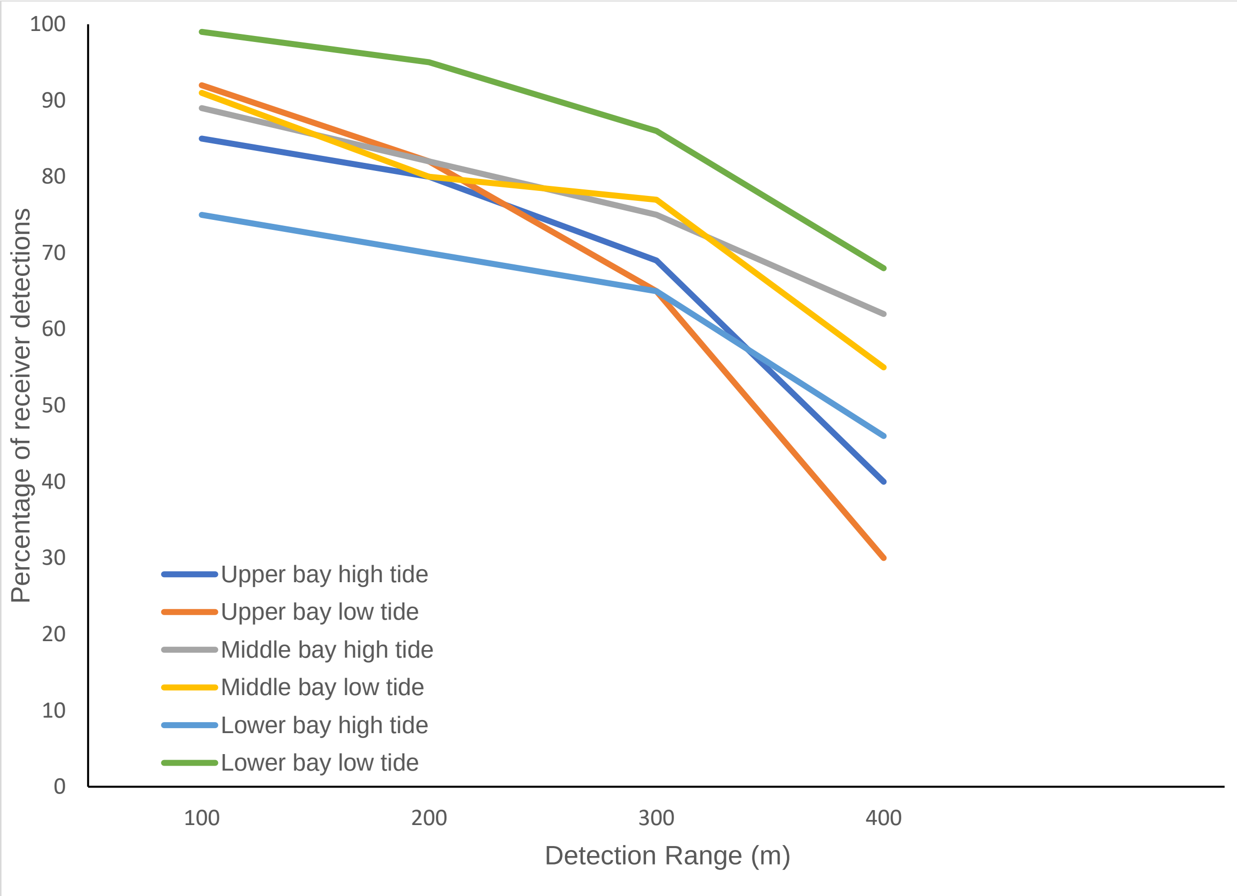

Figure 2. Line graph of mean receiver efficiency of bay area by distance. Percentage were divided to their respective bay area and tidal stage.

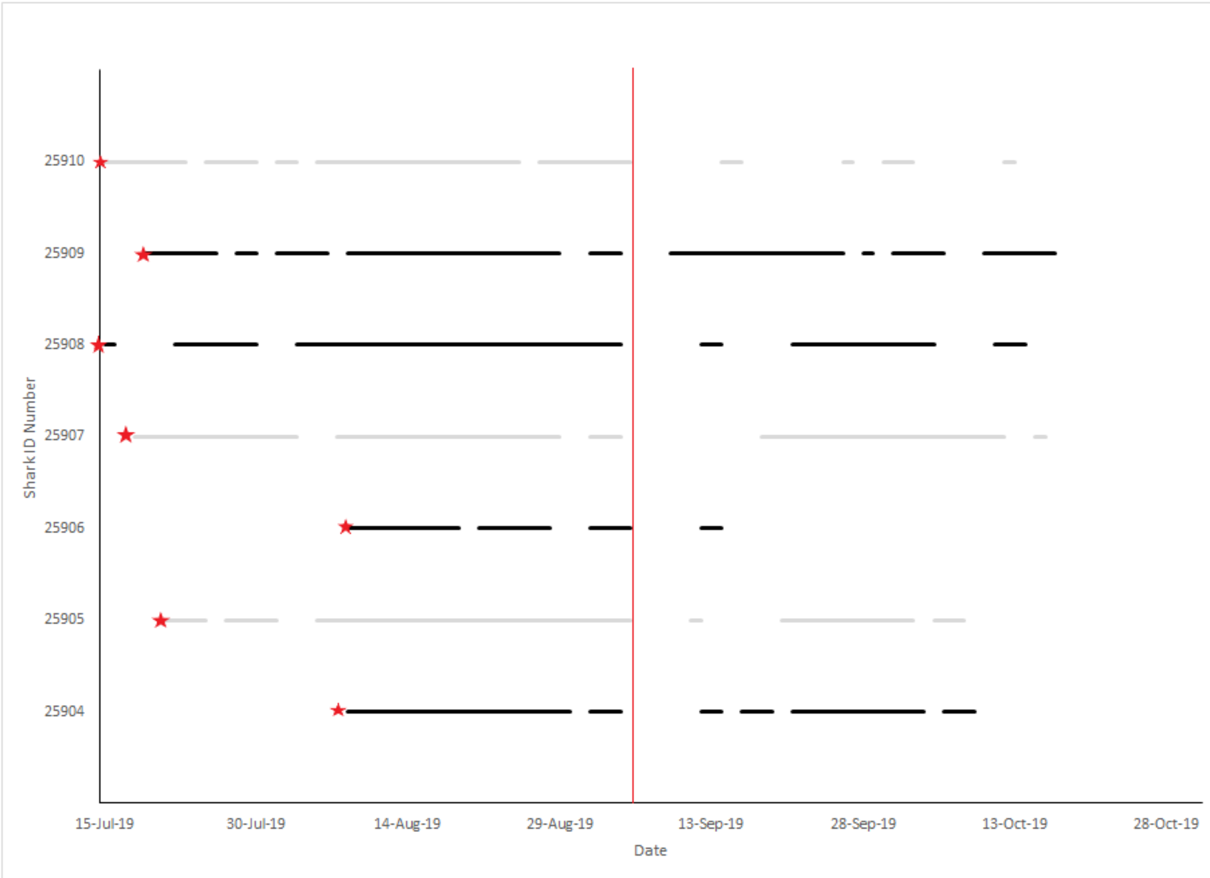

Figure 3. Residency for all bull sharks at the study site from July 15, 2019 until October 31, 2019. Male bull sharks are indicated by solid black lines and females by light grey lines. Red stars indicate the initial date of capture of the animals except for tag 25908 which was caught in a previous season. The red vertical line indicates the date that Hurricane Dorian made landfall in South Carolina.

Figure 4. Map of Winyah Bay showing delineations of bay areas, and all receivers with acoustic detections. The number adjacent to receivers indicates the distance (km) upstream the estuary inlet. Dashed lines indicate delineations of bay areas for receiver categorizations.

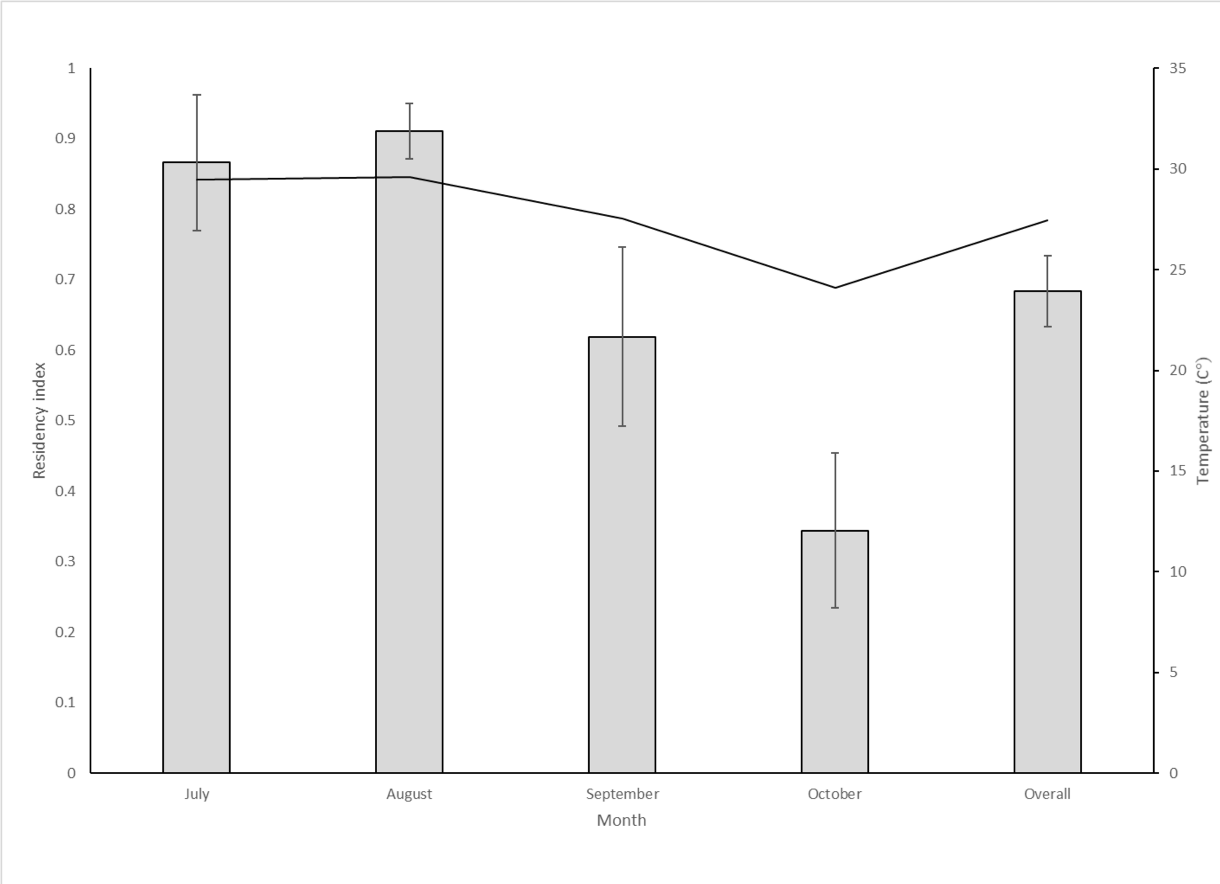

Figure 5. Residency indices (±SE) of bull sharks and mean water temperature within Winyah Bay by month and over the sampling period. The line indicates the mean water temperature (°C) of Winyah Bay during the relative time period.

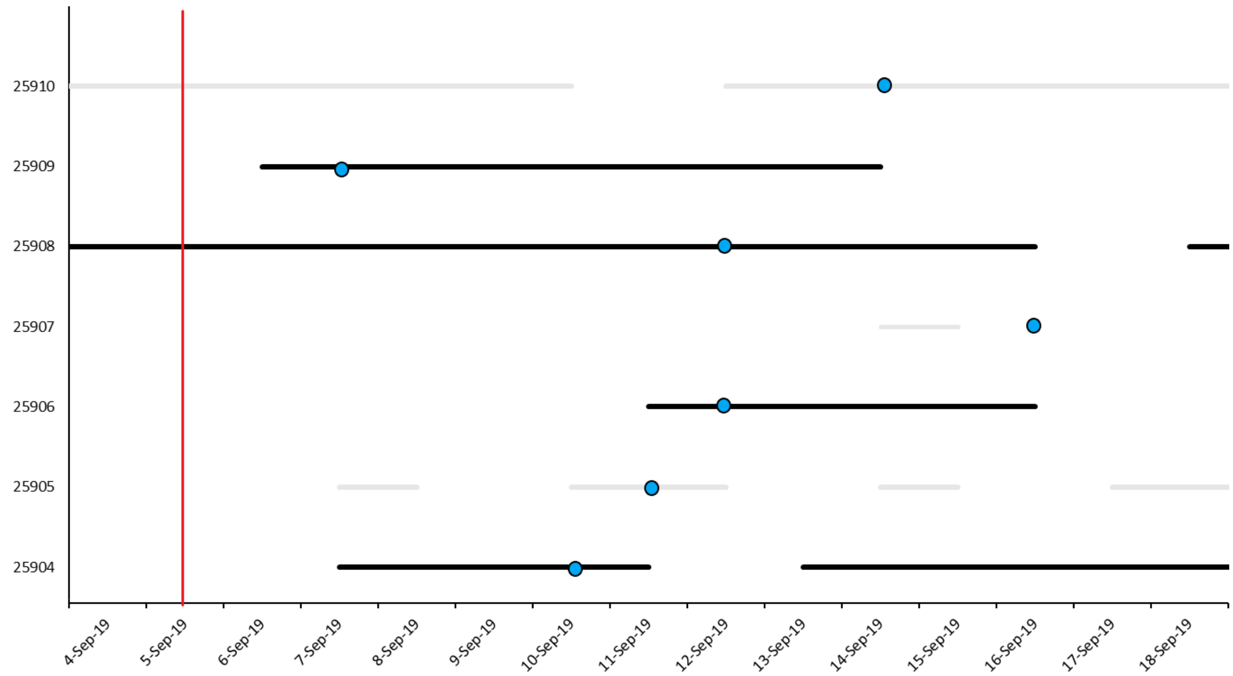

Figure 6. Bull shark residence in the nearshore area and Santee river system after Hurricane Dorian. Male bull sharks are indicated by solid black lines and females by light grey lines. The red vertical line indicates the date that Hurricane Dorian made landfall in South Carolina. Blue circles indicate the day that bull sharks returned and were detected in the Winyah Bay.

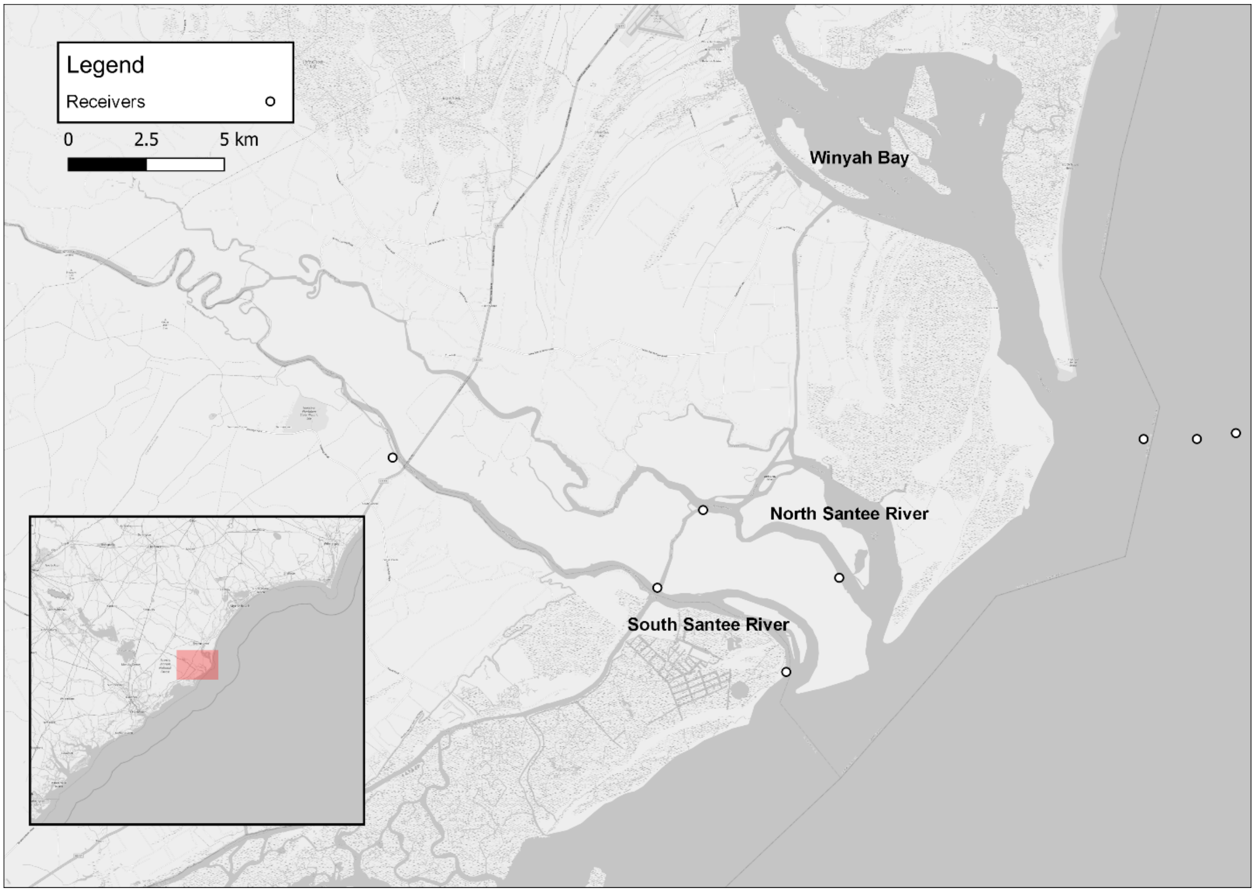

Figure 7. Map of Winyah Bay and the Santee river systems and surrounding areas showing receivers managed by SCDNR that detected acoustically tagged bull sharks from this study.

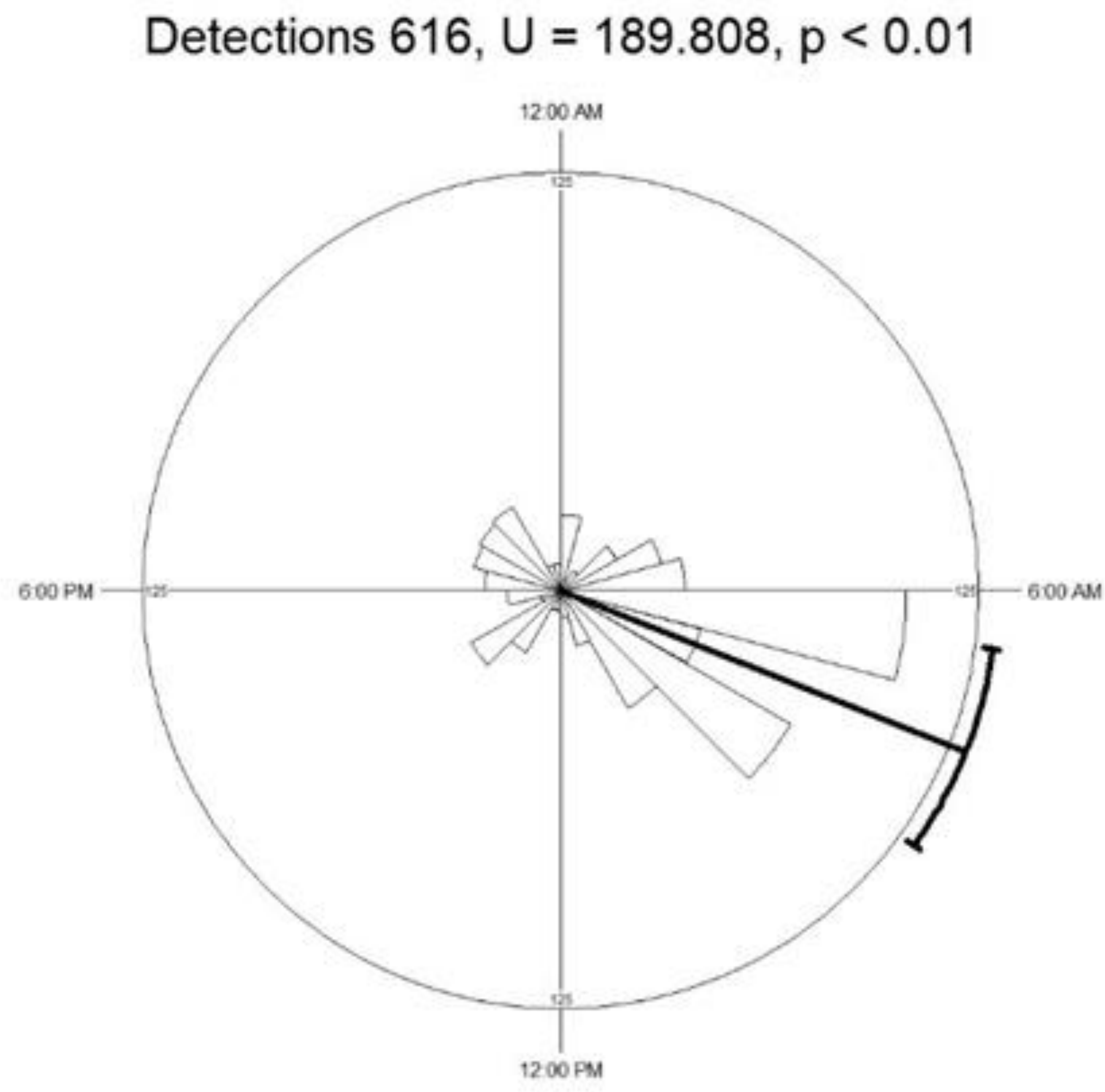

Figure 8. Rose diagram of bull shark detections by all upper bay receivers by time of day. The total number of detections, U-statistic, and *p*-value are displayed. Mean vector is indicated by the bold line extending from the center of the diagram and the error bar represents the 99% confidence interval.

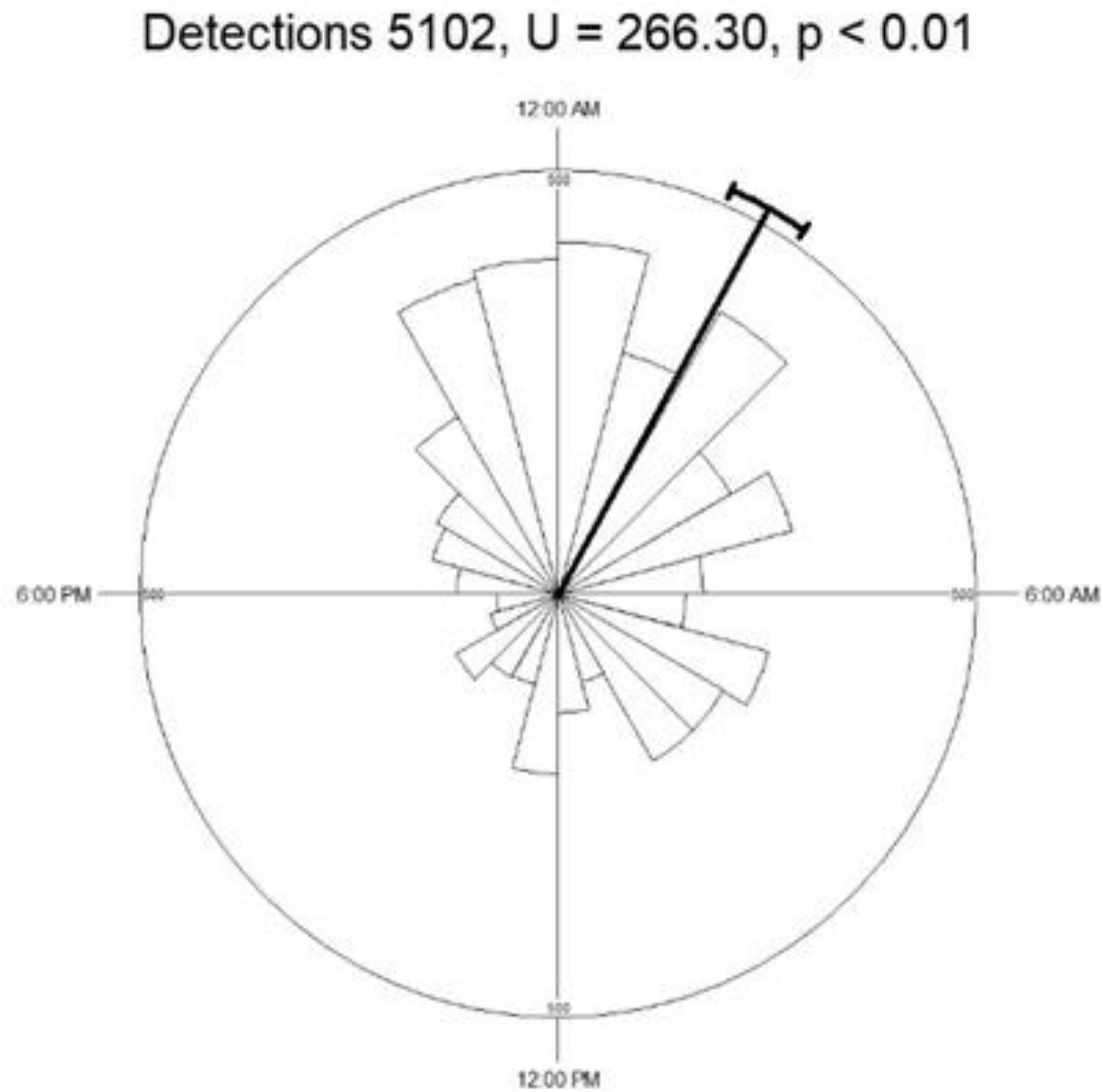

Figure 9. Rose diagram of bull shark detections by all middle bay receivers by time of day. The total number of detections, U-statistic, and *p*-value are displayed. Mean vector is indicated by the bold line extending from the center of the diagram and the error bar represents the 99% confidence interval.

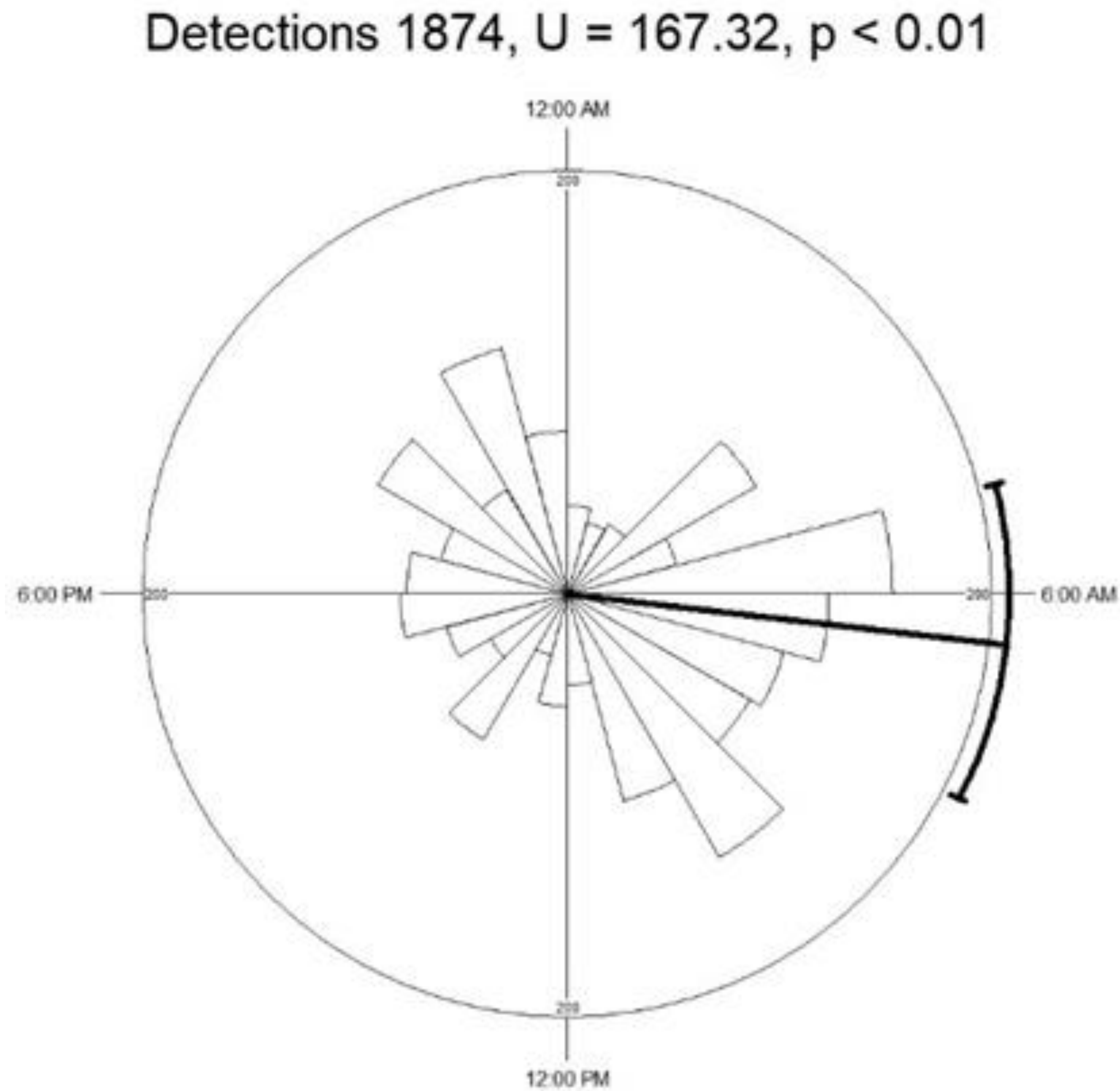

Figure 10. Rose diagram of bull shark detections by all lower bay receivers by time of day. The total number of detections, U-statistic, and *p*-value are displayed. Mean vector is indicated by the bold line extending from the center of the diagram and the error bar represents the 99% confidence interval.

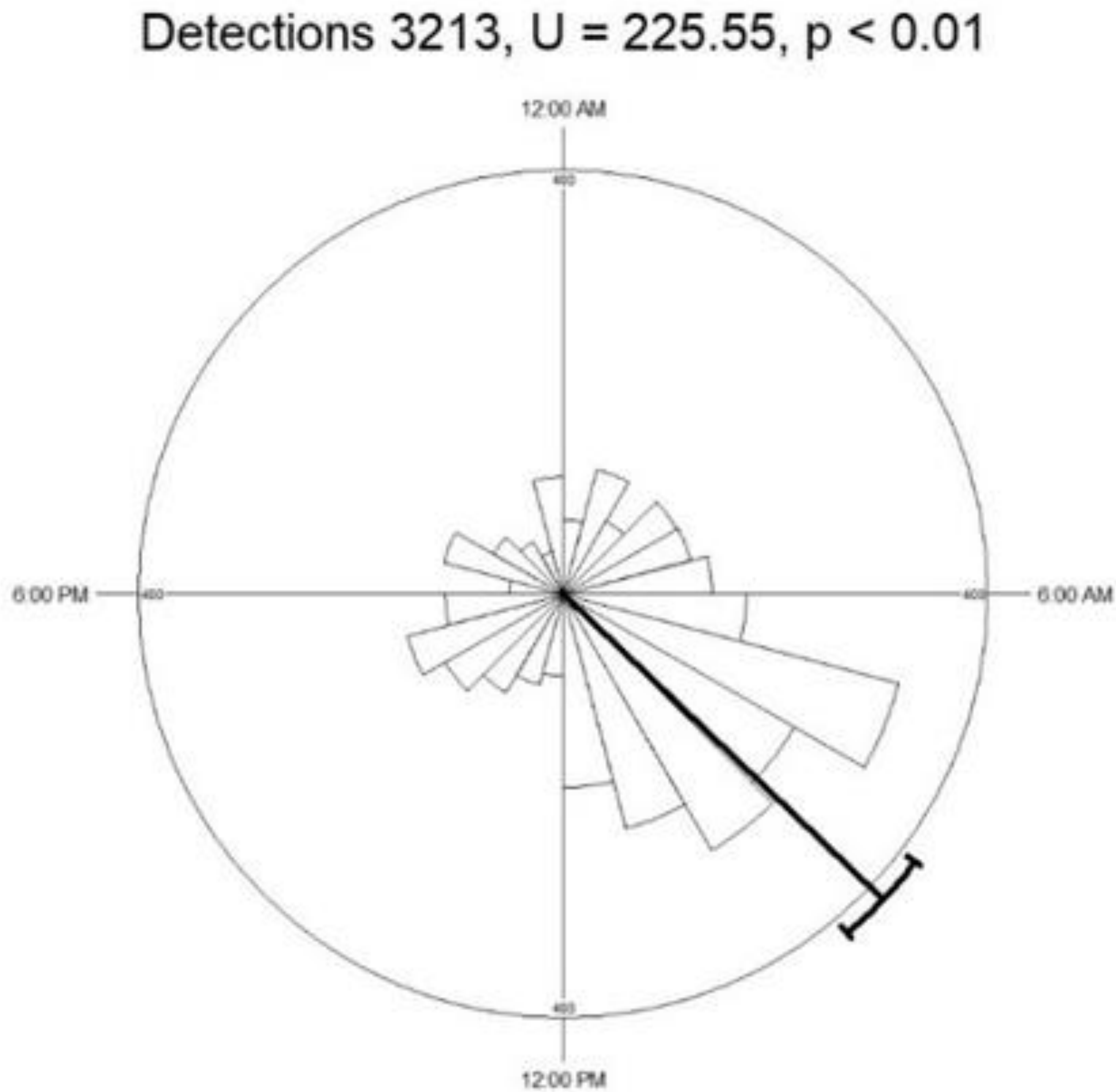

Figure 11. Rose diagram of bull shark detections by all coastal receivers by time of day. The total number of detections, U-statistic, and *p*-value are displayed. Mean vector is indicated by the bold line extending from the center of the diagram and the error bar represents the 99% confidence interval.

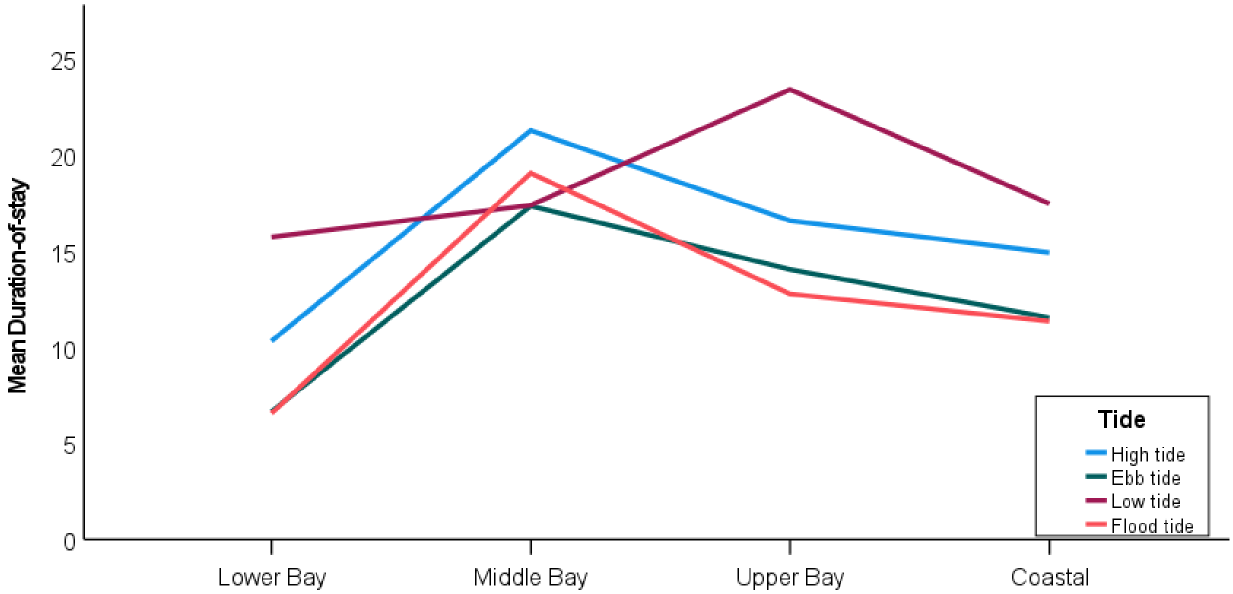

Figure 12. Interaction plot of bull shark duration-of-stay as functions of bay area and tidal stage.

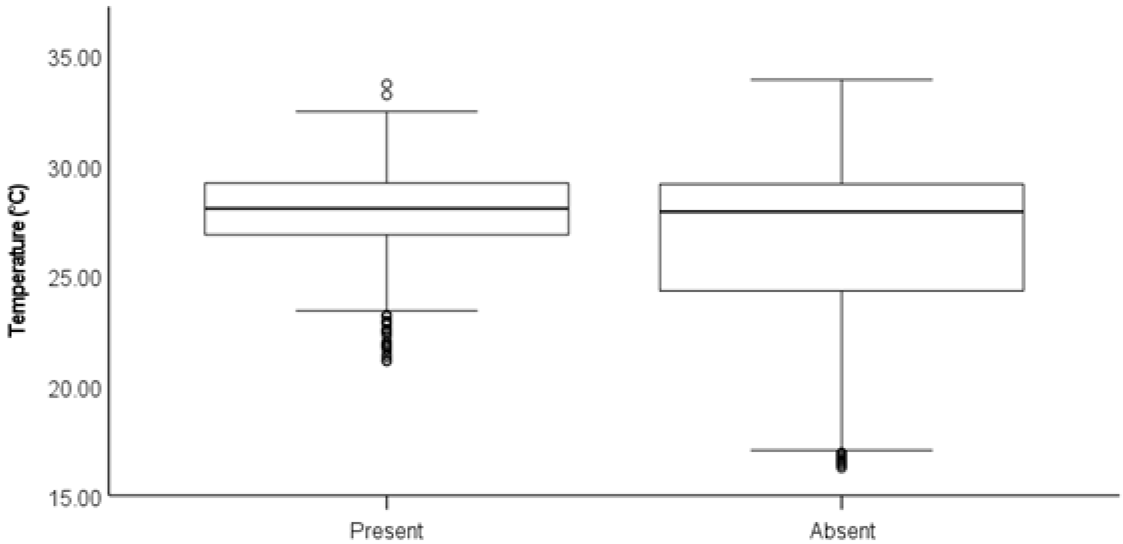

Figure 13. Box-and-whisker plot of bull shark presence/absence as a function of temperature. Open circles and asterisks indicate outlier presence/absence detections.

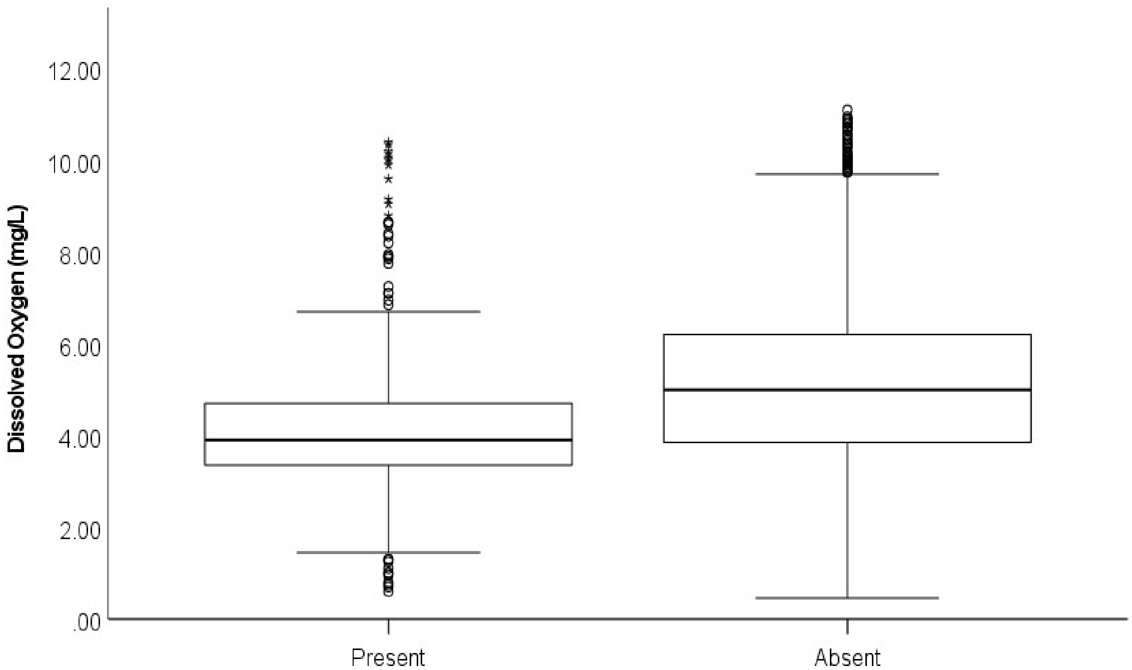

Figure 14. Box-and-whisker plot of bull shark presence/absence as a function of dissolved oxygen. Open circles and asterisks indicate outlier presence/absence detections.

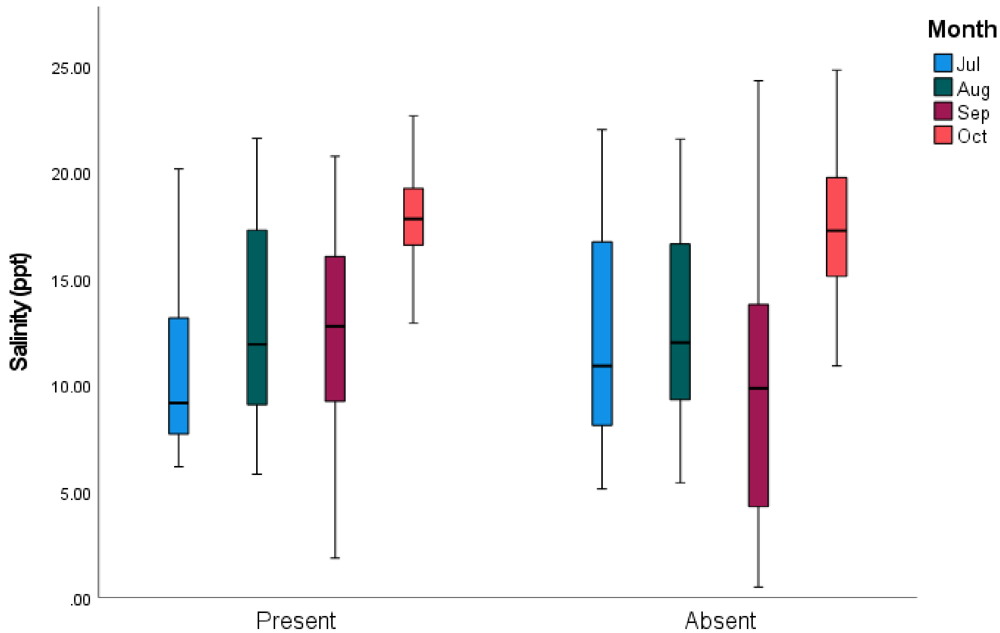

Figure 15. Box-and-whisker plot comparing bull shark presence/absence to salinity by month.

Model	AICC	ΔAICC	W
Bay * Tide (Transmitter ID)	4318.50	0	0.99
Bay (Transmitter ID)	4363.18	44.68	< 0.001
Tide (Transmitter ID)	4433.97	115.47	< 0.001

Table 1. Linear mixed effects model AICC values and weights. Transmitter identification number for individual bull sharks was used as the random variable for all models.

Tag ID #	Length (cm)			Sex	Date deployed	First detection	Days resident	Days-at-liberty	Residency indices (RI)
	PCL	**FL**	**TL**						
25904	139	151	186	M	Aug-08-2019	Aug-09-2019	55	85	0.64
25905	154	172	214	F	Jul-21-2019	Jul-21-2019	67	103	0.65
25906	148	167	201	M	Aug-08-2019	Aug-09-2019	29	40	0.73
25907	153	169	209	F	Jul-18-2019	Jul-18-2019	72	106	0.68
25908	124	140	186	M	Aug-29-2018	Aug-30-2018	68	109	0.62
25909	153	166	212	M	Jul-19-2019	Jul-19-2019	80	105	0.76
25910	139	158	190	F	Jul-15-2019	Jul-15-2019	63	109	0.58

Table 2. Residency indices, sex, and length of bull sharks from this study.

Area	Mean vector	Detections	U-statistic	r^2	*p* value
Upper bay	0721	616	189.81	0.64	< 0.001
Middle bay	0145	5102	266.30	0.55	< 0.001
Lower bay	0532	1874	167.32	0.26	< 0.001
Coastal	0824	3213	225.55	0.45	< 0.001

Table 3. Results from the Rao's spatial analysis grouped by bay area. The table includes the mean vector (local time), number of total detections, U-statistic, r squared, and *p*-values.

Model	AICC	ΔAICC	W
Bay * Tide (Transmitter ID)	4318.50	0	0.99
Bay (Transmitter ID)	4363.18	44.68	< 0.001
Tide (Transmitter ID)	4433.97	115.47	< 0.001

Table 4 Linear mixed effects model AICC values and weights. Transmitter identification number for individual bull sharks was used as the random variable for all models.

Model Parameters	AICC	ΔAICC	W
DO + Temp + Month*Salinity	3684.57	0.00	0.99
Salinity + Month * DO	3693.09	8.52	< 0.001
Month + Temp + Salinity + DO	3702.00	17.43	< 0.001
Month + DO + Salinity * Temp	3708.22	23.65	< 0.001
Salinity + DO + Month * Temp	3711.79	27.22	< 0.001

Table 5. Binomial generalized linear model AICC values and weights. The transmitter identification number for individual bull sharks was used as the random variable for all models.

Parameter	Coefficient Estimate (95% CI)	Odds Ratio (95% CI)
Intercept	-3.95 (-5.39 to -2.61)	0.02 (0.01 - 0.08)
Dissolved Oxygen (mg/L)	-0.45 (-0.52 to -0.39)	0.64 (0.60 - 0.68)
Temperature (°C)	0.13 (0.07 - 0.17)	1.13 (1.08 - 1.19)
July * Salinity (ppt)	0.01 (-0.01 - 0.17)	1.02 (0.99 - 1.04)
August * Salinity (ppt)	0.07 (0.05 - 0.09)	1.07 (1.05 - 1.09)
September * Salinity (ppt)	0.80 (0.06 - 0.10)	1.09 (1.06 - 1.11)
October * Salinity (ppt)	0.03 (0.01 - 0.05)	1.03 (1.01 - 1.05)

Table 6. Parameter estimates from the best fit binomial generalized linear mixed model.

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