Acoustic telemetry of shark movements and residency near artificial habitats in the northern Gulf of Mexico

by

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Abstract

In the present study, acoustic telemetry was used to monitor the movements and residency of seven Sandbar Sharks *Carcharhinus plumbeus,* five Atlantic Sharpnose Sharks *Rhizoprionodon terraenovae,* four Bull Sharks *Carcharhinus leucas* and two Nurse Sharks *Ginglymostoma cirratum* around artificial reefs in the northern Gulf of Mexico. Sharks were tracked for periods of one to 449 days. Residency indices (RIs) were not significantly different among species (GLMM: $F_{3,14} = 2.29$, $P > 0.05$), however there was a significant effect of season on residency for *C. plumbeus* (GLMM: $F_{3,83} = 7.54$, $P < 0.001$), with greater residencies in fall. In addition, there was a significant, positive relation between temperature and residency for *C. plumbeus* (MLM: $F_{1,82} = 12.90$, $R^2 = 0.41$, $P < 0.001$), *C. leucas* (MLM: $F_{1,53} = 5.42$, $R^2 = 0.12$, $P < 0.05$) and *G. cirratum* (MLM: $F_{1,20} = 12.19$, $R^2 = 0.35$, $P < 0.01$). A significant negative relation was also detected between dissolved oxygen and residency for *C. leucas* (MLM: $F_{1,53} = 12.08$, $R^2 = 0.22$, $P < 0.001$). Minimum convex polygon (MCP) areas (ANOVA: $F_{3,14} = 1.81$, $P > 0.05$) and spatial evenness indices (ANOVA: $F_{3,14} = 0.67$, $P > 0.05$) were not significantly different among species.

One *C. plumbeus* and one *G. cirratum* showed long-term (repeated over 3 years) preferences for specific sites. When detected within the present study area, mean distance traveled was 5.5 km day^{-1}for *R. terraenovae,* 6.3 km day^{-1} for *C. leucas,* 8.8 km day^{-1} for *G. cirratum* and 8.1 km day^{-1} for *C. plumbeus*. Long-distance migrations away from the study area were observed for one *C. leucas* (843 - 858 km), one *G. cirratum* (230 - 856 km) and three *C. plumbeus* (229 – 1,894 km). Specifically, one *C. leucas* was detected in the present study area in the summer after two annual winter migrations to the Florida Keys. One *G. cirratum* made three migrations (February - April) to the Florida Keys and returned each year to the northern Gulf of Mexico in late summer and stayed through fall. One female *C. plumbeus* was detected off Tampa, Florida one spring (May), and one male *C. plumbeus* was detected over three winters (January, February) along the Florida panhandle and further south to Tampa, Florida. Interestingly, one additional female *C. plumbeus* migrated around the southern tip of Florida and up the Atlantic coast and was detected in May 2017 off the South Carolina coast. All of these sharks subsequently returned to the study area after each migration.

The long-term residencies and homing behavior observed in the present study indicate that the artificial reefs off coastal Alabama provide important habitat for shark species, with foraging as their most probable function. These homing behaviors, combined with the occurrence of regular long-distance migrations, indicate that the artificial reefs off coastal Alabama may have far-reaching effects that extend as far as the northwestern Atlantic Ocean.

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List of Abbreviations

IUCN	International Union for the Conservation of Nature
TL	Total Length
DO	Dissolved Oxygen
PCL	Pre-Caudal Length
FL	Fork Length
iTAG	Integrated Tracking of Aquatic Animals in the Gulf of Mexico
RI	Residency Index
GLMM	Generalized Linear Mixed Model
ANOVA	Analysis of Variance
MLM	Multilevel Model
MCP	Minimum Convex Polygon

Introduction

The Sandbar Shark *Carcharhinus plumbeus* is a large coastal shark common in subtropical and warm-temperate waters ranging from 15 - 30ºC (Springer, 1960; Ulrich et al., 2007). The species is distributed across the globe in coastal and continental shelf habitats including those in the Hawaiian Pacific and western Atlantic Oceans, the Gulf of Mexico and the Caribbean Sea (Springer, 1960; Wass, 1973). *Carcharhinus plumbeus* have slow growth rates, low fecundity and late age at maturity (15 - 16 years, Sminkey & Musick, 1995). They have been heavily exploited in recent decades and are a major component of the finning market (Clarke et al., 2006). Their drastic population decline (Myers et al., 2007) resulted in a total moratorium on the capture of the species since 2008 (50 C.F.R. § 635.24 2017). The population has more recently shown signs of recovery (Peterson et al., 2017), however they remain listed as vulnerable by the International Union for the Conservation of Nature (IUCN; Musick et al., 2009) and are still considered overfished as of the 2017 stock assessment (SEDAR, 2017).

The average lengths at maturity for *C. plumbeus* are approximately 110 cm for males and 131 cm for females (Wass, 1973). *Carcharhinus plumbeus* are viviparous with a yolk sac placenta and give birth to eight to nine young per litter. Maximum mating activity likely occurs in summer and reproduction occurs every two to three years (Springer, 1960; Merson, 1998; Baremore & Hale, 2012). Adult females are known to give birth in shallow estuaries along the western Atlantic coast from Long Island, New York to Cape Canaveral, Florida, U.S.A. (Springer, 1960; Castro, 1993), and some individuals in the Gulf of Mexico originate from these Atlantic stocks (Heist et al., 1995). However, the presence of juvenile and neonate *C. plumbeus* in the eastern Gulf of

Mexico, and full-term and postpartum females in the Florida Keys, suggest additional nursery sites (Carlson, 1999; Baremore & Hale, 2012).

The Bull Shark *Carcharhinus leucas* is widely distributed in United States waters including both the western Atlantic and the Gulf of Mexico (Compagno, 1984). *Carcharhinus leucas* inhabit tropical to warm-temperate marine habitats and are common in coastal and shelf habitats in the northern Gulf of Mexico (Drymon et al., 2010). Like *C. plumbeus*, they also have slow growth rates, low fecundity and late age at maturity (210 - 220 cm TL, 14 - 15 years for males; > 225 cm TL, 18+ years for females; Branstetter & Stiles, 1987). *Carcharhinus leucas* are viviparous and give birth to six to eight young per litter (Compagno, 1984). Parturition occurs in early summer after a gestation period of approximately 10 - 11 months (Clarke & Von Schmidt, 1965). A unique ecological aspect of *C. leucas* is that they frequently venture into freshwater habitats for extended periods of time (Thorson, 1971). They also use estuarine habitats as nurseries from central Texas to the east coast of Florida, U.S.A. (Caillouet Jr. et al., 1969; Snelson et al., 1984; Hueter & Tyminski, 2007; Parsons & Hoffmayer, 2007; Ortega et al., 2009; Froeschke et al,. 2010; Drymon et al., 2014). Juveniles leave the nursery areas when they reach around 160 cm TL (Curtis et al., 2011).

Nurse Sharks *Ginglymostoma cirratum* reside in shallow, hard-bottom marine habitats along the eastern Gulf of Mexico coast (Clark & Von Schmidt, 1965) and the Atlantic coast from the Carolinas to Brazil (Bigelow & Schroeder, 1948). They are opportunistic predators that feed on small reef fishes, cephalopods, mollusks, crustaceans and even corals (Castro, 2000). Female *G. cirratum* reach maturity at 223 - 231 cm and males reach maturity at about 214 cm (Castro, 2000). *Ginglymostoma cirratum* are known to aggregate in shallow water of the lower Florida Keys and Dry Tortugas to mate (Carrier et al., 1994). Mating occurs around mid-June and parturition occurs in November to December of the same year. Brood sizes are large, ranging from 21 to 50 young (mean = 34; Castro, 2000).

Atlantic Sharpnose Sharks *Rhizoprionodon terraenovae* are common to the northwestern Atlantic and the Gulf of Mexico (Castro, 1983; Branstetter, 1990). Their prey items are diverse, and include teleosts, crustaceans, mollusks and elasmobranchs (Hoffmayer & Parsons, 2003). *Rhizoprionodon terraenovae* are considerably smaller and shorter-lived than *C. plumbeus*, *C. leucas* and *G. cirratum*, with theoretical maximum lengths (L_∞) of 95.62 cm TL for females and 91.95 cm TL for males (Carlson & Baremore, 2003). The median size at maturity is 75.8 cm TL (1.6 years) for females and 72.6 cm TL (1.3 years) for males (Carlson & Baremore, 2003). Parsons & Hoffmayer (2005) suggested that *R. terraenovae* show sexual segregation with males mostly inhabiting inshore waters, while females reside offshore after maturation, with both mating and pupping occurring offshore. They also may be particularly sensitive to thermal and hypoxic stress and leave inshore waters during summer most likely due to extreme environmental conditions, reproduction or a combination of both (Parsons & Hoffmayer, 2005).

Shark populations and distributions have been monitored throughout the northern Gulf of Mexico primarily through yearly bottom longline surveys since 1995 (Ingram et al., 2005; Drymon et al., 2010, 2013; Powers et al., 2013; Pollack et al., 2017). Some of the most common sharks in the northern Gulf of Mexico include the Blacknose Shark *Carcharhinus acronotus*, Blacktip Shark *Carcharhinus limbatus, C. leucas, C. plumbeus,* *R. terraenovae*, Spinner Shark *Carcharhinus brevipinna* and Scalloped Hammerhead Shark *Sphyrna lewini* (Drymon et al., 2010). Most of these species are large apex predators (length > 2 m) that may consume other elasmobranchs and perciform fishes (Hoffmayer & Parsons, 2003; McElroy et al., 2006).

Large, apex predatory sharks are important in maintaining balance of marine communities through top-down trophic effects (Myers et al., 2007). However, they have been highly exploited in both the directed fisheries and as bycatch (Bonfil, 1994) and many species have suffered major declines since the 1960's (Baum et al., 2003; Myers & Worm, 2003; Baum & Myers, 2004; Robbins et al., 2006; Myers et al., 2007). Shark surveys in the northwestern Atlantic coastal waters have estimated an 87% - 99% decline in the large shark (length > 2 m) populations from 1972 to 2004 (*C. plumbeus* 87%, *C. limbatus* 93%, tiger shark *Galeocerdo cuvier* 98%, *S. lewini* 98%, *C. leucas* 99%; Meyers et al., 2007). Shark populations have also shown evidence of decline in the Gulf of Mexico, including *C. leucas*, Oceanic Whitetip *Carcharhinus longimanus*, Silky Shark *Carcharhinus falciformis* and Dusky Shark *Carcharhinus obscurus* (O'Connell et al., 2007; Heithaus et al., 2007; Baum & Myers, 2004). However, several shark species have shown some signs of recovery since the early 1990's (Carlson et al., 2012; Peterson et al., 2017). Observer data in the northwest Atlantic indicated relative abundance increases of 14% for *C. brevipinna*, 12% for *C. leucas*, 6% for Lemon Sharks *Negaprion brevirostris*, and 3% for *G. cuvier* from 1994 to 2009 (Carlson et al., 2012). In addition, surveys along the southwestern Atlantic coastal waters have indicated preliminary recoveries of all large coastal shark species since the late 2000's (Peterson et al., 2017).

Shark populations are slow to recover from population declines due to their slow growth rates and low fecundity, which highlights the importance of their proper management (Springer, 1960; Branstetter & Stiles, 1987; Castro, 2000). One critical aspect of species management is proper knowledge of movement patterns and distributions in relation to habitat. However, much of this is presently unknown for large coastal shark species, because tracking studies on adults are very limited. All fishery management plans are required to describe essential fish habitat for managed fisheries. Essential fish habitats are defined as "those waters and substrates necessary to fish for spawning, feeding or growth to maturity" (NOAA, 1996). The continental shelf off coastal Alabama presently has the largest artificial reef program in the United States with an estimate near 10,000 privately and publicly deployed structures (Szedlmayer S.T., & Mudrak P. A., 2017 unpublished side-scan sonar surveys). These artificial reefs offer increased habitat complexity compared to the surrounding seafloor and provide habitat for structure-oriented epibenthos and reef fishes (Lingo & Szedlmayer, 2006; Redman & Szedlmayer, 2009). However, no studies at the present time have examined shark movement patterns in relation to these artificial reefs. Since their rise in popularity, these reefs have affected the feeding ecology (Ouzts & Szedlmayer, 2003; Szedlmayer & Lee, 2004), movements (Topping & Szedlmayer, 2011) and population size (Gallaway et al., 2009) of perciform reef fishes in the northern Gulf of Mexico. If these artificial reefs provide habitat for large coastal sharks, they may also help in the recovery of these exploited species.

Acoustic telemetry is a widespread method of quantifying area use in aquatic environments. It is one of the most effective methods for spatial analysis due to its ability to track movements on a continual basis over multiple years (Szedlmayer & Able, 1993; Szedlmayer, 1997; Heupel et al., 2006; Topping & Szedlmayer, 2011). Depending on project design, telemetry methods can produce fine-scale individual positions (m) as well as large-scale movement patterns (km). Acoustic telemetry has been used extensively in the northern Gulf of Mexico to track movements of Red Snapper *Lutjanus campechanus* and Gray Triggerfish *Balistes capriscus* in relation to artificial reefs (Piraino & Szedlmayer, 2014; Herbig & Szedlmayer, 2016; Williams-Grove & Szedlmayer, 2016). It has also been used to track long-term horizontal migrations, vertical migrations and quantify habitat use for sharks in locations throughout the world (Nakano et al., 2003; Heupel et al., 2004; Heupel et al., 2010a,b; Papastamatiou et al., 2010; Bessudo et al., 2011; Daly et al., 2014; Espinoza et al., 2015; Lea et al., 2016; Shipley et al., 2017). However, at the present time acoustic telemetry has not been reported in movement studies of large shark species around artificial reefs in the northern Gulf of Mexico.

In general, telemetry studies on shark species common to the Gulf of Mexico are limited. For example, only two telemetry studies have been reported on *R. terraenovae*, and the studies were limited to juveniles or by short study durations (Gurshin & Szedlmayer, 2004; Carlson et al., 2008). Therefore, present knowledge of adult *R. terraenovae* habitat use and distribution patterns in the Gulf of Mexico is based on survey and recapture data (Ingram et al., 2005; Parsons & Hoffmayer, 2005; Drymon et al., 2010). In addition, few telemetry studies have been reported on *G. cirratum*, with earlier studies indicating seasonal changes in detections (Chapman et al., 2005; Ferreira et al., 2013) and a more recent study off Florida reporting *G. cirratum* migrations of up to 335 km (Pratt et al., 2018). Previous tag-recapture data has also indicated long-distance *G. cirratum* movements (541 km), yet little is known about the timing, location and frequency of these migrations (Kohler & Turner, 2001).

In contrast, it is well known that *C. plumbeus* and *C. leucas* are highly migratory species. Pop-up satellite tags have shown large movements for *C. leucas* over short time scales (i.e. 1,506 km; Carlson et al., 2010) and *C. plumbeus* tag-recapture data has indicated movements of 3,776 km (Kohler & Turner, 2001). *Carcharhinus plumbeus* and *C. leucas* have been monitored in acoustic telemetry studies, but nearly all of these studies were limited to juveniles and neo-nates (Rechisky & Wetherbee, 2003; Heupel & Simpfendorfer, 2008; Ortega et al., 2009; Conrath & Musick, 2010; Heupel et al., 2010b), with a few exceptions (Papastamatiou et al., 2010; Daly et al., 2014; Espinoza et al., 2015). Although they are highly migratory, adult *C. plumbeus* have also shown long term residency indices of up to 0.71 (mean ± SD = 0.23 ± 0.28, days detected divided by days monitored) around fish-farming cages in Hawaii (Papastamatiou et al., 2010). Similarly, *C. leucas* have also shown long term site fidelity with residency indices of up to 0.67 (mean ± SD = 0.14 ± 0.15) on reefs off the coast of Africa (Daly et al., 2014) and up to 0.69 (mean ± SD = 0.19 ± 0.19) on the Great Barrier Reef (Espinoza et al., 2015). Conventional mark recapture studies have also indicated high site fidelity for *C. leucas*, with short dispersal distances in relation to other species (Kohler & Turner, 2001).

In the present study, acoustic telemetry was used to estimate the movement and residency patterns of *C. plumbeus, G. cirratum, C. leucas* and *R. terraenovae* around artificial reef structures in the northern Gulf of Mexico. Tracking data was used to estimate home ranges, habitat preferences and assess potential use of artificial reef habitats. Movement patterns were compared among species, seasons and environmental conditions. The movement patterns obtained in the present study were also used to identify a ‘predator movement pattern’ that can be used in future studies to distinguish shark movements from other acoustically tracked species such as *L. campechanus* and *B. capriscus*. The present shark habitat use patterns provide a more comprehensive understanding of artificial reef ecology in the northern Gulf of Mexico and can assist in the future management of these important apex predator shark species.

Methods

Study Area

The northern Gulf of Mexico is a subtropical ocean basin with annual mean bottom-temperatures ranging from 24 to 28ºC (Turner et al., 2017). Environmental variables such as dissolved oxygen and salinity are influenced by riverine influxes into the northern Gulf of Mexico, including the Mississippi River to the northwest and the outflow from Mobile Bay. The northern Gulf of Mexico continental shelf is considered a naturally flat-bottom habitat composed of sand and mud substrate, with exceptions near the west coast of Florida (Parker et al., 1983). The region is also intermittently affected by hurricanes in the late summer months.

The present study monitored shark movements from 9 November 2012 to 9 July 2018. The study area included 26 monitoring sites within the Hugh Swingle General Permit Area in the northern Gulf of Mexico (Figure 1). Sites were positioned 1.4 - 1.9 km apart and covered an area of approximately 64 km^2 located 23 - 35 km south of Dauphin Island, Alabama, U.S.A. Twenty-four receivers were each placed next (< 20 m) to a steel cage artificial reef (2.5 x 1.3 x 2.4 m; Syc & Szedlmayer, 2012), one receiver was next (< 20 m) to a barge artificial reef and one receiver was over open habitat.

Receivers were positioned 4.5 m above the seafloor on individual mooring lines attached to the sea floor with ground anchors. Floats attached to the mooring lines kept the receivers suspended in the water column at a constant depth. Mooring floats and receivers were painted with copper-based antifouling paint to prevent biofouling (Williams-Grove & Szedlmayer, 2016).

Each of the 26 sites contained a single receiver (VEMCO® VR2W) that provided presence-absence data within 800 m of the known receiver locations. This design allowed for the estimation of km-scale movements (Szedlmayer & Schroepfer, 2005; Topping & Szedlmayer, 2011). Considering that large sharks tagged in the present study may migrate long distances (e.g., out of the entire Gulf of Mexico and up the east coast of the United States; Carlson et al., 2010), an accuracy of 800 m was considered adequate for these shark species. Receivers were downloaded and replaced every 6 - 9 months to avoid reaching memory capacity. Greater distance migrations outside of the study area were identified through the Integrative Tracking of Aquatic Animals in the Gulf of Mexico (iTAG) network. In 2014, the iTAG network was developed (Lowerre-Barbieri et al., 2017; http://myfwc.com/research/saltwater/telemetry/itag/). This network is building large marine ecosystem scale tracking capacity through data sharing of detections across all members' study arrays and the strategic deployment of long-term monitoring arrays in collaboration with the Ocean Tracking Network. This data-sharing network allowed the identification of much greater distance migrations compared to the receivers deployed in the present study.

Environmental Monitoring

Temperatures were recorded at four receiver sites with Onset HOBO® U22-001 meters at 1-hr intervals and data were downloaded every 3 to 6 months (Figure 1). At each of these four sites, two temperature loggers were attached to the receiver lines, with one 5 m above the seafloor and one at the seafloor.

A YSI EX02 environmental recorder (YSI Inc., Yellow Spring, Ohio) was deployed 3 m above the seafloor at one site near the center of the receiver array to continuously monitor temperature, salinity and dissolved oxygen (DO) from August 2016 through December 2016 (Figure 1). A different DO meter (Onset HOBO® U26-001) was deployed at the same site 0.5 m above the seafloor starting in December 2016 to the end of the study in July 2018.

Shark tagging

All shark species were caught with hook-and-line (hooks: Eagle Claw 13/0 Circle Sea) and tagged and released within the receiver study area. To increase shark tagging survival, dissolved oxygen was measured throughout the water column prior to fishing (YSI Model 6920, YSI Incorporated), and a different tagging site was chosen if levels were < 3.5 mg l^{-1}. For transmitter implantation, captured sharks were kept in the water, inverted to induce tonic immobility and secured to the stern of the research vessel. Once tonic immobility was established, a 5 cm incision was made on the ventral side and an acoustic transmitter inserted into the peritoneal cavity (Vemco Ltd, V16-6x, 69 kHz, 20-69 s transmission delay, 1825 d battery life). The incision was closed with 3 - 4 interrupted sutures (ETHICON® LR; reverse cutting; 75 mm; 3/8c; ETHIBOND*EXCEL) and disinfected with BETADINE® solution. After surgery, fish were measured (PCL, FL, TL), gender recorded, externally tagged in the dorsal fin then released. Time from capture to release did not exceed 10 minutes.

Detection validation

False detections can sometimes cause difficulties in acoustic telemetry. Transmitter signals can be interrupted by collision with other transmitter signals, which may cause receivers to record a false tag identification (Pincock, 2012; Simpfendorfer et al., 2015). To filter out these false detections, an individual was considered "present" at a site only if there were at least two detections on the same receiver within a 24-hr period.

Residency

A residency index (RI) was used to quantify individual residency to the study area (Espinoza et al., 2015). Residency indices were calculated by dividing the number of days an individual was present in the study area, divided by the number of days monitored (days between release and end of study). If the estimated battery life was less than the days monitored, the denominator was set equal to the battery life (1825 d). Monthly, yearly, seasonal and cumulative RIs were calculated for each individual. Residency indices were compared among seasons by species with generalized linear mixed models (GLMMs). For the GLMMs, data were modeled with a binomial distribution and subject was a random factor. Cumulative RIs were compared among species with Analysis of Variance (ANOVA). Multilevel Models (MLMs) were used to compare environmental data to residency, with dissolved oxygen or temperature set as continuous predictor variables (Kwok et al., 2008). All statistics were calculated in SAS®.

Habitat Use

Sites with valid detections were used to create minimum convex polygons (MCPs) of each individual's area use within the 64 km^2 study area. The minimum convex polygon method of estimating home range area provides an estimation of an individual's least-possible spatial extent by connecting all outer positions into a single convex polygon (Mohr, 1947). These MCPs were compared among species with ANOVA. Mean positions were also calculated for each individual with the ArcMap® Mean Center tool and averaged for each species.

Mean distance traveled per day was calculated to examine movement within the study area. This mean distance was calculated by summing the distances among all positions for each day that an individual shark was detected within the study area. Shark positions were based on the positions of the receivers. The daily distance values were then averaged among species (Least Squared Means) and the mean distance was reported for each species. Spatial evenness was also calculated for each shark to assess the spread of its detections among the 26 sites, where R = 26 (the number of total receivers in the

$$Spatial\ Evenness\ (E) = \frac{-\sum_{i=1}^{R}[\rho_i \ln(\rho_i)]}{\ln(R)}$$

study area), and ρ_i = the number of detections at the i^{th} receiver (Pielou, 1966; TinHan et al., 2014). A spatial evenness index value of one indicates even shark detection counts among all sites, while values closer to zero indicate site preference. Spatial evenness was compared among species using ANOVA.

In addition, a mean length of time for each site visit was calculated to quantify how long sharks remained at a site before moving. This time was based on the difference in time between the last detection and the first detection for each site visit and averaged for each species.

Results

Eight *C. plumbeus*, five *R. terraenovae*, four *C. leucas* and two *G. cirratum* were tagged with transmitters and released from 9 November 2012 to 22 September 2017 (Table 1). One *C. plumbeus* suffered a tagging-induced mortality and was removed from further analyses. Based on known size at maturity, all *R. terraenovae* were adult females (Carlson & Baremore, 2003). Among *C. plumbeus*, seven were adult females and one was an adult male (Wass, 1973). Among *C. leucas*, one was a juvenile male, one was a juvenile female and two were adult females (Branstetter & Stiles, 1987), and the two *G. cirratum* were both adult males (Castro, 2000).

Spatial evenness (ANOVA: $F_{3,14} = 0.67$, $P > 0.05$) and MCP areas (ANOVA: $F_{3,14} = 1.81$, $P > 0.05$) were not significantly different among species (Table 1). Wide variations were observed in RIs and no significant differences were detected among species (ANOVA: $F_{3,14} = 2.29$, $P > 0.05$; Table 2).

Carcharhinus plumbeus

Carcharhinus plumbeus had the highest number of detections (*n* = 132,082) and accounted for 84% of all shark detections. These high detections of *C. plumbeus* were mostly (69.5% of total detections) due to one individual (S6; Table 1). Among the seven tagged *C. plumbeus*, most (*n* = 5) were detected regularly throughout the present study (RI = 0.004 - 0.432, mean ± S.D. = 0.150 ± 0.160; Table 2). Low-residency individuals (*n* = 2, RI ≤ 0.01) were only detected on a few days during their entire time monitored (Table 2; Figure 2a). Medium-residency individuals (*n* = 3, RI = 0.01 - 0.20) showed repeated patterns of intermittent presence for a few months, followed by absence for a few months (Figure 2b). The high-residency individuals (*n* = 2, RI ≥ 0.30) had high monthly residencies for multiple months (Figure 2c). These two high-residency individuals also had periods of absence, however their residencies increased to their previous levels after returning.

On days that *C. plumbeus* were present, mean distance traveled was 8.13 km day^{-1} within the study area. When *C. plumbeus* were detected at a site, mean time present (± S.D.) was 71.3 ± 150.7 minutes and ranged from 0.4 – 2093.8 minutes. Also, *C. plumbeus* had the largest range in spatial evenness from 0.11 to 0.94, with a mean (± S.D.) of 0.68 ± 0.33 (Table 1). Among the *C. plumbeus* that were regularly detected in the study area (*n* = 5), most (*n* = 4) used the entire study area evenly (spatial evenness index ≥ 0.70). Hence, the calculated mean position for *C. plumbeus* was located near the center of the study area (Figure 3d). However, the shark with the greatest number of detections (*C. plumbeus* S6) had a lower spatial evenness index (*E* = 0.11), with 94.5% of its detections recorded at the same site throughout all three years it was monitored.

The maximum yearly residency index for any *C. plumbeus* was 0.595, corresponding to 217 days detected out of the year (S6; Table 2). Among the seven *C. plumbeus,* four were detected regularly from their tagging date through the end of the study period (July 2018): shark S8 tagged in July 2017 was detected for one year, shark S6 tagged in September 2015 was detected for three years, and sharks S3 and S5 tagged in August 2013 were detected for all five years of the study. One additional shark (S1) tagged in November 2012 was also detected regularly for seven months after tagging, but likely suffered a mortality before the end of the study period (transmitter was located on a beach in Mexico). The remaining two *C. plumbeus* showed lower residency than the other five and were detected on only a few occasions throughout the study period. Despite their low residency, these individuals were both detected in the study area up to sixteen months after tagging: shark S7 tagged June 2016 was detected up to October 2017, and shark S2 tagged July 2013 was detected up to November 2014.

A similar residency pattern among *C. plumbeus* was decreased presence in winter. Two *C. plumbeus* (S3, S8; females) had long 3 to 5 month absences in winter, and S6 (female) also showed monthly residency declines in January. *Carcharhinus plumbeus* residency showed a significant positive relation with temperature (MLM: $F_{1,82} = 12.90$, $R^2 = 0.41$, $P < 0.001$), and was significantly less in summer, spring and winter than in fall (GLMM: $F_{3,83} = 7.54$, $P < 0.001$; Figure 4d). No significant dissolved oxygen effects were detected (MLM: $F_{1,82} = 2.57$, $R^2 = 0.34$, $P > 0.05$).

Three female *C. plumbeus* also had long absences from the study area in the spring and summer months. Two of these individuals performed confirmed migrations during these absences. For example, after remaining highly resident to the study area for over one year, S6 left the study area for five months, leaving in the beginning of March 2017 and then returning in August 2017 (Figure 2c). This absence was later confirmed as a long-distance migration when S6 was detected off the coast of South Carolina, U.S.A., in May of 2017 (Figure 5). This migration event from coastal Alabama to coastal South Carolina was 1,894 km one way and took 76 days. Shark S6 then returned to coastal Alabama after 79 additional days. Another female *C. plumbeus* (S2) performed a long-distance migration in the spring and summer of 2014. Shark S2 was detected off Tampa, Florida, U.S.A. in May 2014 (509 km; Figure 5). Although this shark showed low residency to the present receiver area, it was detected both before (April 2014) and after (August 2014) its migration to Tampa (Figure 2a). Based on these detections, shark S2 traveled from coastal Alabama to Tampa in 23 days and returned to Alabama after 92 additional days. A third female *C. plumbeus* (S3) also had long absences (3-5 months) in late spring and summer of 2014, 2016 and 2017, however, its locations during those absences were undetermined (Figure 2b).

One male *C. plumbeus* (S5) also made long-distance migrations in the present study (Figure 5). Shark S5 showed two residency peaks in the study area each year, with the first in June-July and the second in November (Figure 2b). Shark S5 showed complete absences from the study area off Alabama during winter of all five years that it was monitored. However, shark S5 was detected off Tampa, Florida in January 2015 (512 km), and in the Madison Swanson Marine Protected Area off Panama City, Florida in February of 2017 and 2018 (229 km; Figure 5).

Ginglymostoma cirratum

Two *G. cirratum* were captured and released with transmitters and they were detected frequently in the present study (19,643 detections; 12.6% of total detections). Residency indices ranged from 0.021 to 0.096 (mean ± S.D. RI = 0.058 ± 0.053; Table 2). *Ginglymostoma cirratum* spatial evenness ranged from 0.48 to 0.68 (mean ± S.D. *E* = 0.58 ± 0.14; Table 1), with both individuals being detected more often in the northern, shallower sites (Figure 3c). Compared to the other shark species, *G. cirratum* showed the longest mean time at a site (mean ± S.D. time = 84.3 ± 378.3 minutes) that ranged from 0.5 to 7843.4 minutes. One of the *G. cirratum* was present at a site for five consecutive days before moving. *Ginglymostoma cirratum* mean distance traveled within the study area was 8.81 km day^{-1}.

Ginglymostoma cirratum were only detected in the study area in late summer through fall (Figures 4c, 6). *Ginglymostoma cirratum* S18 (male) was monitored for five years and showed a repeated high residency pattern for 3 to 5 months in late summer through fall, followed by complete absence the rest of the year (Figure 6). When absent from coastal Alabama, shark S18 made long-distance migrations in three of the five years that it was monitored (Figure 7). Shark S18 was detected in the Florida Keys in late March and April of 2016 and 2017 and as early as February in 2018 (856 km). It was also detected off the coast of Apalachicola, Florida (324 km) in summer 2017 during its migration north, and in the Madison Swanson Marine Protected Area (230 km) in January 2018 during its migration south to the Florida Keys.

The other tagged *G. cirratum* provided less information and was tagged only one year prior to the end of the study period. This individual was tagged in the fall and was detected for several days after tagging followed by complete absence. Residency indices were not statistically compared among seasons due to low sample size for this species. However, *G. cirratum* residency showed a significant positive relation with temperature (MLM: $F_{1,20} = 12.19$, $R^2 = 0.35$, $P < 0.01$), but did not show relation with dissolved oxygen (MLM: $F_{1,20} = 0.14$, $R^2 = 0.12$, $P > 0.05$) .

Carcharhinus leucas

Compared to the other shark species in the present study *Carcharhinus leucas* had a lower number of detections (1319 detections; 0.8% of total detections) and lower residency indices (RI = 0.001 – 0.024, mean ± S.D. = 0.012 ± 0.010; Table 2). *Carcharhinus leucas* spatial evenness ranged from 0.33 to 0.83 (mean ± S.D. $E = 0.54 \pm 0.26$; Table 1), and their mean positions were spread throughout the study area (Figure 3b). Mean time at a site (± S.D.) was 20.4 ± 31.1 minutes and ranged from 0.6 to 211.9 minutes, which was less time than other species in the present study. *Carcharhinus leucas* traveled an average of 6.26 km day^{-1} when they were detected within the study area.

Two *C. leucas* (S15, S16; females) were tagged in July 2016 and both briefly returned to the study area each summer over two years until the end of the study period. The other female (S17) did not return to the study area, however it was tagged only one year before the end of the study period. One male *C. leucas* (S14) was tagged July 2013, but only detected for one day after tagging. Among all *C. leucas* individuals, annual residencies never exceeded 0.02 (7 days detected out of 365; Table 2).

Carcharhinus leucas were only detected in the study area in the late spring and summer months. The earliest *C. leucas* detections occurred in late April and the latest in

August. *Carcharhinus leucas* residencies were not compared among seasons due to the low number of detections. However, *C. leucas* residency showed significant positive relation with temperature (MLM: $F_{1,53} = 5.42$, $R^2 = 0.12$, $P < 0.05$) and significant negative relation with dissolved oxygen (MLM: $F_{1,53} = 12.08$, $R^2 = 0.22$, $P < 0.001$).

Long-distance migrations (843 - 858 km) were detected for *C. leucas* S15 (female) that had moved to the Florida Keys in February of 2017 and 2018. This shark returned to the northern Gulf of Mexico in the summer months after each of these migrations (Figure 8).

Rhizoprionodon terraenovae

Rhizoprionodon terraenovae were detected 3,361 times during the present study (2.1% of total detections). Most (80%) *R. terraenovae* showed lower residencies to the study area compared to *C. plumbeus* and *G. cirratum* (RI = 0.001 – 0.049, mean ± S.D. = 0.013 ± 0.020; Table 2). However, one individual showed longer residencies than the other *R. terraenovae*, and returned to the study area in all five years that the transmitter was active (Figure 9). The maximum yearly residency index for this individual was 0.12 (43 of 365 days; Table 2). All other transmitter tagged *R. terraenovae* showed only a few detections during the first few months after tagging, followed by complete absence for the remaining battery life of the transmitters.

Rhizoprionodon terraenovae spatial evenness ranged from 0.35 to 0.69 (mean ± S.D. $E = 0.54 \pm 0.13$; Table 1). *Rhizoprionodon terraenovae* detections were predominantly in the southern portion of the study area, thus the mean position of *R. terraenovae* was located in the southeast portion of the study area (Figure 3a). When *R.*

terraenovae visited a site they stayed for a mean (± S.D.) of 57.81 ± 73.60 minutes with a range of 0.53 to 487.67 minutes. *Rhizoprionodon terraenovae* traveled an average of 5.46 km day^{-1} when they were detected in the study area.

Rhizoprionodon terraenovae residency showed no significant seasonal effect (GLMM: $F_{3,97} = 1.30$, $P > 0.05$; Figure 4a). *Rhizoprionodon terraenovae* residency also did not show a significant relation with temperature (MLM: $F_{1,57} = 0.68$, $R^2 = 0.20$, $P > 0.05$) or dissolved oxygen (MLM: $F_{1,57} = 0.04$, $R^2 = 0.19$, $P > 0.05$). Long-distance migrations were not recorded for any *R. terraenovae.*

Discussion

Carcharhinus plumbeus

Carcharhinus plumbeus showed high residencies to the study area between long-distance migrations. The significant season effect and significant positive relation with temperature indicates that *C. plumbeus* had greater presence in the study area in fall (September through November) during times of increased water temperatures. Two individuals (S3, S8) showed long (3 to 5 months) absences during the cooler winter months, and even S6 with high residencies for several months had decreased presence every year in January. Although water temperatures did not drop below the biological range for *C. plumbeus* (Springer, 1960; Ulrich et al., 2007), rapid decreases in temperatures may have caused *C. plumbeus* to move farther offshore in winter to more stable, warmer temperatures in deeper water. Previous movement studies have indicated temperature-directed winter movements in juvenile *C. plumbeus* in the western north

Atlantic (Merson & Pratt, 2001; Grubbs et al., 2007; Conrath & Musick, 2008). For example, satellite tracking studies have shown juvenile *C. plumbeus* overwintering near the edge of the continental shelf off North Carolina, where water temperatures are warmed by the Gulf Stream (Conrath & Musick, 2008). Mark-recapture studies have also shown that juvenile *C. plumbeus* in Chesapeake Bay leave the estuary in fall to overwinter in waters off North Carolina, with older juveniles (7 - 10 y) being recaptured up to 60 km offshore (Grubbs et al., 2007). Even juveniles tagged off New Jersey have been recaptured in the warmer waters offshore North Carolina in winter (Merson & Pratt, 2001). It is well-known that temperature has a positive effect on metabolic rate, and that ectotherm growth rates increase with increasing temperatures (Gillooly et al., 2001; Dowd et al., 2006). *Carcharhinus plumbeus* have very slow growth rates (Sminkey & Musick, 1995), therefore thermoregulatory behaviors such as seeking more stable water temperatures in winter may be an important tactic for maximizing growth.

A possible explanation for the greater residencies observed in fall could be increased feeding during that time. Metabolic rates generally increase as temperatures rise, which increases the need for food items (Gillooly et al., 2001; Dowd et al., 2006). Also, fall is the postpartum recovery season for *C. plumbeus,* which is likely a time of increased food consumption (Baremore & Hale, 2012). The need for food may be especially heightened in fall for females after their long-distance migrations that occur for parturition in summer. For example, *C. plumbeus* S6 showed its greatest monthly residency (RI = 0.80) in September 2017 when it returned from its 1,894 km migration. These artificial reefs are highly productive habitats in a region with little natural structured reef habitat and harbor large numbers of potential shark prey items (Lingo &

Szedlmayer, 2006; Redman & Szedlmayer, 2009). Since *C. plumbeus* residency at the reefs was highest during these times of increased need for food, it is likely that they were using the artificial reefs to forage. This is also supported by the increased prey availability on the artificial reefs in fall (Jaxion-Harm et al., 2018). Thus, the productive artificial reefs of the northern Gulf of Mexico may be important foraging habitats for *C. plumbeus* and possibly help them to endure their long-distance migrations.

Although *C. plumbeus* residency was positively associated with temperature, there were also long-term absences (4 – 5 months) during the warm summer months. *Carcharhinus plumbeus* of the northwestern Atlantic and the eastern Gulf of Mexico give birth in May and June (Baremore & Hale, 2012) every two years, allowing one year to recover following a 12 month-long pregnancy. In the present study, three females (S2, S3, S6) showed long absences in the spring and summer during peak *C. plumbeus* parturition time. Shark S6 was also detected off the coast of South Carolina during this absence, which is one of many Atlantic coast states with well-known *C. plumbeus* pupping grounds (Springer, 1960; Castro, 1993; Carlson, 1999; Baremore & Hale, 2012). In addition, *C. plumbeus* S2 was detected off Tampa, Florida in May 2014, which also coincides with parturition time. Therefore it is possible that summer migrations were due to parturition occurring away from the study area.

It was difficult to make gender comparisons, but still worth noting that the only male *C. plumbeus* in the present study showed a seasonal pattern that differed from the four females that were regularly detected. This male *C. plumbeus* showed complete absence for most of the year interrupted by brief presence nearly every summer (June and July) and fall (October and November). This distinct residency pattern occurred every year from tagging until the end of the study period. Peak mating time for *C. plumbeus* of the northwestern Atlantic and the eastern Gulf of Mexico occurs from May to July (Baremore & Hale, 2012), therefore male *C. plumbeus* presence in the summer may be related to mating behavior. This male's residency pattern was in contrast to the greater residencies observed for most (67%) females in the present study. This repeated pattern may support the claim that *C. plumbeus* segregate by gender, and that males are found in deeper and cooler water than females except when they venture inshore to mate (Springer, 1960). However, an increased sample size and a larger study area are necessary to confirm this pattern.

Although some *C. plumbeus* made long-distance migrations, they showed philopatry to the artificial reefs over many years. *Carcharhinus plumbeus* have been monitored in previous telemetry studies, yet nearly all studies were limited to juveniles (Medved & Marshall, 1983; Wetherbee et al., 2001; Rechisky & Wetherbee, 2003; Conrath & Musick, 2010). However, one comparable acoustic telemetry study monitored adult *C. plumbeus* movements around fish farms off Hawaii (Papastamatiou et al., 2010). In some ways these farms were similar to artificial reef habitats due to their large numbers of fish and ability to aggregate wild fishes, thus providing potential foraging opportunities for predators (Uglem et al., 2009). Papastamatiou et al. (2010) determined that the fish farms aggregated *C. plumbeus* and observed high site fidelities that were similar to those observed in the present study. Some individuals even returned to the fish farms for up to 2.5 years after tagging. However, in the present study *C. plumbeus* showed even longer term philopatry, with some individuals returning to the study area for up to five years. Interestingly, shark S6 showed homing behavior to one particular site that persisted for multiple years, even after returning from a 1,894 km migration. This philopatry to the general study area and even particular reefs indicates that these reefs provided important habitat for *C. plumbeus*. It also shows that even wide-ranging species such as *C. plumbeus* can show high site fidelity to specific locations, which can have important implications for management.

Ginglymostoma cirratum

The two *G. cirratum* tagged in the present study showed localized movements specifically within the northern portion of the study area. This pattern was unlikely due to chance, because both individuals showed a preference for the same sites. One *G. cirratum* (S18) showed these localized movements for five consecutive years. *Ginglymostoma cirratum* are common to shallow, coastal habitats from 3 to 75 m depths (Castro, 2000), but the individuals in the present study rarely visited sites over 25 m. Thus, the *G. cirratum* concentrated area use around the northern sites may be attributed to their shallow depth preference. This area use pattern may also have been due to these sites' closer proximity to one of the few natural reefs off coastal Alabama.

A remarkable behavior seen in one of the *G. cirratum* individuals (S12) was the occurrence of long-distance annual migrations from the northern Gulf of Mexico to the Florida Keys. *Ginglymostoma cirratum* were never detected in the study area in winter or spring, yet one individual (S18) was consistently detected from late summer through fall in every year that it was monitored. This highly seasonal residency pattern indicates that some *G. cirratum* from the Florida Keys make directed migrations in summer to the northern Gulf of Mexico off Alabama and remain resident to the region until late fall.

The absence of detections in winter and positive relation with temperature indicated that lower water temperatures caused *G. cirratum* to migrate south to warmer latitudes to overwinter.

The behavior shown by shark S18 in the present study suggested that *G. cirratum* from the Florida Keys may seek out this region of the northern Gulf of Mexico as seasonal foraging habitat. Although previous studies have indicated large (541 km) *G. cirratum* movements (Kohler & Turner, 2001), seasonal changes in residency (Chapman et al., 2005; Ferreira et al., 2013) and partial migrations up Florida's west coast (up to 335 km; Pratt et al., 2018), very little has been reported about the ecology of these migrations. A recent telemetry study reported both male and female *G. cirratum* migrating up to 330 km, from the Dry Tortugas to off Tampa Bay, Florida (Pratt et al., 2018). Although both genders migrated, the timing of migration was gender-specific. Migrating females departed from the Dry Tortugas in the spring and early summer and returned after the summer mating season ended (Pratt et al., 2018). In contrast, male *G. cirratum* monitored by Pratt et al. (2018) were first detected at the northern sites in late July, and last detected in November. The male *G. cirratum* in the present study (S18) showed the same seasonal migration pattern as the males observed by Pratt et al. (2018), with consistent presence in the study area beginning as early as July and lasting until around November. Therefore, *G. cirratum* of the Florida Keys may commonly migrate even farther north than Tampa Bay.

Pratt et al. (2018) concluded that *G. cirratum* displayed partial migration, with only a portion of the population conducting large-scale migrations and others remaining in the Dry Tortugas year-round. Pratt et al. (2018) suggested that the ecosystems around the Florida Keys and the Dry Tortugas may have limited resources, so individuals with greater fitness may make the decision to migrate north to the rich estuarine habitats of Florida's Gulf of Mexico coast. The repeated migrations of S18 to the present study area off the Alabama coast lend support to the conclusions of Pratt et al. (2018). If *G. cirratum* migrate for increased access to food, the highly productive artificial reef zone of the northern Gulf of Mexico may attract such migrants. Pratt et al. (2018) also suggested that temperature may be a secondary factor governing *G. cirratum* migration. A temperature effect was also observed in the present study, as both *G. cirratum* left the study area in fall before temperatures dropped substantially, and their residency showed a significant positive relation with temperature. The repeated migrations to coastal Alabama suggest that these artificial reefs provide important seasonal foraging habitat for *G. cirratum*.

Carcharhinus leucas

Carcharhinus leucas showed lower residencies to the study area off coastal Alabama than either *C. plumbeus* or *G. cirratum*. However, there were significant temperature effects on residency, with higher residencies occurring when temperatures were higher. Although seasonal residencies could not be compared for *C. leucas*, detections were only recorded for this species in spring and summer months (April through August). A possible explanation for increased *C. leucas* presence during this time of the year may be the warmer temperatures compared to those in winter. Previous studies have shown that *C. leucas* presence was positively related to temperature and this species rarely occurred in water temperatures below 20ºC (Carlson et al., 2010;

Froeschke et al., 2010; Matich & Heithaus, 2012; Daly et al., 2014). In the present study, water temperatures typically did not exceed 20ºC until June, which may explain why *C. leucas* were only detected in spring and summer. However, the highest temperatures were recorded in the study area during September and October, but *C. leucas* were not detected during these months. Therefore, *C. leucas* residency in the present study may have been influenced by other factors in addition to temperature.

A second possible explanation for *C. leucas* detections occurring only in the spring and summer may be related to reproduction. *Carcharhinus leucas* in the northern Gulf of Mexico give birth in late spring and early summer, and many locations along the Gulf of Mexico coast are considered nursery sites for this species including Mobile Bay, Alabama located just north of the study area (Parsons & Hoffmayer, 2007). The *C. leucas* females were only detected in the study area during peak parturition time, and stayed for only a few days, which may indicate a transient movement pattern typical of a reproduction-related migration (Carlson et al., 2010; Lea et al. 2015).

Interestingly, one *C. leucas* (S15; female) made repeated migrations from the study area to the Florida Keys over two years and returned to the study area off Alabama in the summer of both years. The occurrence of long-distance migrations to the northern Gulf of Mexico from the Florida Keys over multiple years indicated that the region provides important habitat for the species. The present study migration pattern was similar to a pattern in an earlier study, i.e., a female *C. leucas* tagged with a pop-off satellite transmitter made a migration to the northern Gulf of Mexico from the Florida Keys in summer over the course of just one month (Carlson et al., 2010).

Previous tracking studies are limited for adult *C. leucas*. Some studies have indicated large *C. leucas* movements of up to 1,506 km from south Florida to Texas (Carlson et al., 2010), and a pregnant female tracked off the east coast of Africa migrated 1,960 km from the Seychelles to Madagascar and back again for parturition (Lea et al., 2015). Despite reports of long-distance movements, most studies have reported greater site fidelity and more limited movements than observed in the present study (Brunnschweiler et al., 2010; Carlson et al., 2010; Daly et al., 2014; Espinoza et al., 2015). For example Carlson et al. (2010) also reported small movements by *C. leucas* (as low as 2 km), as did another study off Fiji and the Bahamas (Brunnschweiler et al., 2010), yet those movement patterns were limited due to the short study durations (< 85 d). However, in long term studies *C. leucas* also showed high residencies of up to 0.67 on a reef site off the southern coast of Africa (mean RI ± SD = 0.14 ± 0.15; Daly et al., 2014) and up to 0.69 in the Great Barrier Reef (mean RI ± SD = 0.19 ± 0.19; Espinoza et al. 2015). The differences in residencies between the present study and these previous studies may be differences in geographical location and habitat types, but indicate a need for additional acoustic telemetry studies on adult *C. leucas.*

There are a few possible explanations for the lower *C. leucas* residences observed in the present study. The positive relation with temperature, increase in detections in summer and repeated winter migrations of S15 to the Florida Keys indicate that *C. leucas* residency was linked to warmer temperatures. Therefore, *C. leucas* may have shown lower residencies to the present study area due to the lower water temperatures compared to other nearby locations like those off southern Florida.

A second possible explanation for lower *C. leucas* residencies may be the depth of the present study area. Previous studies have indicated that *C. leucas* spent most of their time in shallow water (< 20 m; Carlson et al., 2010; Drymon et al., 2010), however the sites in the present study ranged from 20 m to 30 m. Thus, the transmitter-tagged *C. leucas* may have favored shallower locations further inshore, resulting in lower residency to the study area.

Despite the low residencies seen in *C. leucas* in the present study, their philopatry over multiple years after long absences indicate that the northern Gulf of Mexico was still an important habitat for this species. However, additional studies are necessary to further quantify *C. leucas* artificial reef habitat use.

Rhizoprionodon terraenovae

Low residencies were observed for most (80%) *R. terraenovae* in the present study, however one individual showed regular visits to the study area. No significant relations were detected among *R. terraenovae* residency and environmental variables or season. However, an interesting observation was the localization of *R. terraenovae* detections in the southeast portion of the study area. This may be indicative of a preference for deep water, which has also been observed in previous studies (Drymon et al., 2010). Female *R. terraenovae* in the northern Gulf of Mexico have been shown to prefer deeper waters, evident by greater catch per unit effort in depths ≥ 30 m (Drymon et al., 2010). This depth preference may also explain their low residencies in the present study. The maximum depth for any site in the present study area was approximately 30 m, therefore the tagged female *R. terraenovae* may have remained in deeper waters that occur south of study area.

One individual *R. terraenovae* (S13) showed long-term philopatry to the study area, returning all five years that its transmitter was active. Very little is known about the site fidelity and movement patterns of adult *R. terraenovae,* as previous tracking studies on the species are limited to either juveniles (Carlson et al., 2008) or short time periods (Gurshin & Szedlmayer, 2004). However, conventional tag-recapture data has indicated long-distance movements for adult *R. terraenovae* (up to 298 km; SEDAR, 2007), and juveniles have been recaptured up to 400 km from their tagging location (Carlson et al., 2008). Although it is unknown whether *R. terraenovae* S13 made long-distance movements away from the study area, its philopatry to the study area every year indicates that the artificial reefs off Alabama may be important habitat for this species. However, additional studies are necessary to further quantify *R. terraenovae* residency to these artificial reefs.

Homing Behavior and Implications

In the present study, one *C. leucas,* one *G. cirratum* and three *C. plumbeus* showed homing behavior to the study area after long-distance migrations (229 to 1,894 km). *Carcharhinus leucas* S15 returned to the study area after migrating to the Florida Keys (> 860 km) over two consecutive years. *Ginglymostoma cirratum* S18 traveled between the study area and the Florida Keys for at least three consecutive years, each year returning to the same sites. *Carcharhinus plumbeus* S6 was resident to one particular site for over three consecutive years, and even returned to the same site after migrating 1,894 km away.

Homing behavior, the ability to return to a specific place after migrating away, is a common phenomenon in many marine fishes (Dittman & Quinn, 1996; Marnane, 2000; Thorrold et al., 2001; Kaunda-Arara & Rose, 2004; Loher, 2008). Homing behavior is well-known for its ties to reproduction, as many fishes return to their birthplace to reproduce in a process known as natal homing. Many species of shark have shown natal homing behaviors and reproductive philopatry, including *N. brevirostris* (Feldheim et al., 2014), *C. leucas* (Tillett et al., 2012), Blacktip Reef Sharks *Carcharhinus melanopterus* (Mourier & Planes, 2013) and *C. limbatus* (Keeney et al., 2005). However this behavior is not limited to reproduction, and philopatry to other locations such as feeding sites has been observed in fishes ranging from Pacific Halibut *Hippoglossus stenolepis* (Loher, 2008) to White Sharks *Carcharodon carcharias* (Jorgenson et al., 2009).

Many species of shark are geographically widespread and thus included in large-scale regional and international management programs. However, philopatry over a long period of time can render local regulations extremely important, and can have direct effects on population size, particularly in locations frequently visited for feeding or reproductive purposes. For example, temporary longline closures of a Striped Marlin *Kajikia audax* aggregation area off Baja California, Mexico in 1977 - 1980 and 1984 - 1985 led to rapid 6 to 22% population recoveries in the region (Jensen et al., 2010).

There have been many efforts by NOAA Fisheries to gather information on the distributions and essential fish habitats for shark species. For example, the Cooperative Atlantic States Shark Pupping and Nursery (COASTSPAN) and Cooperative Gulf of

Mexico States Shark Pupping and Nursery (GULFSPAN) programs are intended to define shark nursery habitats along the Atlantic and Gulf of Mexico United States coasts. Increases in shark research efforts have led to stricter regulations since 2005 for a location off the coast of North Carolina (Mid-Atlantic Shark Area) that comprises important breeding and migratory grounds for many large coastal shark species (50 C.F.R. § 600, 2003). Thus, a better understanding of philopatric behaviors and identification of important habitats can lead to improved regulations for many wide-ranging shark species.

The high site fidelities and repetitive homing behaviors observed in the present study indicate that the artificial reefs off coastal Alabama are important feeding habitats for these shark species. Therefore, with proper regulations these artificial reefs may help in the recovery of depleted shark populations by providing increased access to prey. However, a high degree of site fidelity can make populations more susceptible to fishing pressure (Hueter et al., 2005), indicating the complicated task for fishery management strategies and the need for further movement studies on these species.

Conclusions

The present study was the first to quantify shark movements around the artificial reefs off coastal Alabama. Prior to this study, nearly all tracking studies for *C. plumbeus, G. cirratum, C. leucas* and *R. terraenovae* were limited to juveniles or had short study durations (Medved & Marshall, 1983; Wetherbee et al., 2001; Rechisky & Wetherbee, 2003; Gurshin & Szedlmayer, 2004; Carlson et al., 2008; Heupel & Simpfendorfer, 2008; Ortega et al., 2009; Brunnschweiler et al., 2010; Conrath & Musick, 2010; Heupel et al., 2010b), with a few exceptions (Chapman et al., 2005; Papastamatiou et al., 2010; Ferreira et al., 2013; Daly et al., 2014; Espinoza et al., 2015; Pratt et al., 2018). However, the present study focused mainly on adults, with some monitored for up to five years. *Carcharhinus plumbeus*, *G. cirratum* and *C. leucas* are long-lived species (Branstetter & Stiles, 1987; Sminkey & Musick, 1995; Castro, 2000), therefore long-term telemetry studies are important and provide a more dynamic understanding of life history.

Carcharhinus plumbeus and *G. cirratum* showed the highest residencies in the present study. Higher residencies for *C. plumbeus* and *G. cirratum* occurred in the fall during a time of likely increased feeding due to high temperatures, reproductive cycles and recently completed long-distance migrations. *Carcharhinus plumbeus* and *G. cirratum* migrations away from the study area were likely due to low winter temperatures and to reproductive processes such as mating and parturition occurring in other locations. *Carcharhinus leucas* were only detected during summer and spring months which was likely influenced by higher temperatures as well as parturition occurring along the northern Gulf of Mexico coast. *Rhizoprionodon terraenovae* residency patterns were distinguished by a returning pattern for one fish over five years, but the other four tagged fish were detected few times after tagging.

One important advance of the present study was the ability to track long-distance migrations away from the study area in *C. plumbeus*, *G. cirratum* and *C. leucas*. These data provided an expansion of known *G. cirratum* migrations (up to 856 km), which prior to this study have not been recorded over 541 km. Also notable was the occurrence of a 1,894 km migration in the same *C. plumbeus* individual that also showed the greatest residency to the study area. Although *C. plumbeus* are well known to migrate between the Gulf of Mexico and northwestern Atlantic, the present study indicated that the individuals that make long-distance migrations can also show high site fidelity to specific reefs between migrations.

The philopatry and high residencies between migrations observed in the present study indicated that the artificial reefs in the northern Gulf of Mexico provide important foraging habitats for *C. plumbeus* and *G. cirratum*. In addition, the philopatry of some *C. leucas* and *R. terraenovae* individuals to the study area suggest that the reefs were also important habitats to these species. Perhaps the most notable observation in the present study was the occurrence of homing behaviors not only to the general region, but even to an individual artificial reef. This homing occurred for multiple consecutive years and even after long-distance migrations. The combination of long-term residencies between long-distance migrations in the present study indicate that the beneficial effects of artificial reefs may be far more wide ranging than previously considered. With three of the tracked shark species showing these patterns, these artificial reefs in the northern Gulf of Mexico may be affecting fish stocks as far away as the Florida Keys or even up the eastern coast of the U.S.A., and may be helping in efforts to rebuild wide ranging depleted shark populations.

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Table 1. Shark species tagged and released with transmitters in the present study. Fish number, TL = total length, F = female, M = male, MCP = Minimum convex polygon area, *E* = spatial evenness, N = not detected outside of the study area and Y = detected outside study area.

ID	Date Tagged	Species	TL (cm)	Gender	MCP (km^2)	*E*	Migration
S1	9-Nov-2012	*Carcharhinus plumbeus*	198	F	45.09	0.84	N
S2	8-Jul-2013	*Carcharhinus plumbeus*	217	F	40.29	0.72	Y
S3	15-Aug-2013	*Carcharhinus plumbeus*	206	F	51.11	0.89	N
S4	15-Aug-2013	*Carcharhinus plumbeus*	196	F	n/a	n/a	n/a
S5	15-Aug-2013	*Carcharhinus plumbeus*	204	M	51.11	0.93	Y
S6	3-Sep-2015	*Carcharhinus plumbeus*	225	F	51.11	0.12	Y
S7	22-Jun-2016	*Carcharhinus plumbeus*	195	F	0.12	0.34	N
S8	27-Jul-2017	*Carcharhinus plumbeus*	194	F	51.11	0.39	N
S9	23-Nov-2012	*Rhizoprionodon terraenovae*	96	F	8.98	0.46	N
S10	23-Jan-2013	*Rhizoprionodon terraenovae*	97.5	F	30.43	0.59	N
S11	23-Jan-2013	*Rhizoprionodon terraenovae*	98	F	2.35	0.34	N
S12	24-Jan-2013	*Rhizoprionodon terraenovae*	97	F	33.58	0.69	N
S13	24-Jan-2013	*Rhizoprionodon terraenovae*	98	F	9.12	0.60	N
S14	8-Jul-2013	*Carcharhinus leucas*	199	M	0.00	0.20	N
S15	19-Jul-2016	*Carcharhinus leucas*	237	F	49.95	0.63	Y
S16	20-Jul-2016	*Carcharhinus leucas*	200	F	25.54	0.46	N
S17	9-Jun-2017	*Carcharhinus leucas*	256	F	6.11	0.33	N
S18	17-Oct-2013	*Ginglymostoma cirratum*	221	M	51.11	0.67	Y
S19	22-Sep-2017	*Ginglymostoma cirratum*	231	M	5.94	0.10	N

Table 2. Residency index table for all sharks. Days present = number of days detected, total days = number of days between release and end of study period, RI = cumulative residency index, and year RI = RI for each year. Residency Index values of zero indicate that a shark was monitored during that period but was not detected. An RI value of "n/a" indicates that the shark was not monitored for that period.

ID	Species	Sex	Days Present	Total Days	RI	Year 1 RI	Year 2 RI	Year 3 RI	Year 4 RI	Year 5 RI
S1	*Carcharhinus plumbeus*	F	32	234	0.137	0.137	n/a	n/a	n/a	n/a
S2	*Carcharhinus plumbeus*	F	7	1825	0.004	0.011	0.008	0	0	0
S3	*Carcharhinus plumbeus*	F	229	1789	0.128	0.107	0.137	0.071	0.121	0.213
S4	*Carcharhinus plumbeus*	F	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a
S5	*Carcharhinus plumbeus*	M	83	1789	0.046	0.055	0.036	0.041	0.058	0.043
S6	*Carcharhinus plumbeus*	F	449	1040	0.433	0.595	0.290	0.411	n/a	n/a
S7	*Carcharhinus plumbeus*	F	8	747	0.011	0.019	0.003	0	n/a	n/a
S8	*Carcharhinus plumbeus*	F	102	347	0.300	0.300	n/a	n/a	n/a	n/a
S9	*Rhizoprionodon terraenovae*	F	4	1825	0.002	0.011	0	0	0	0
S10	*Rhizoprionodon terraenovae*	F	18	1825	0.010	0.049	0	0	0	0
S11	*Rhizoprionodon terraenovae*	F	2	1825	0.001	0.005	0	0	0	0
S12	*Rhizoprionodon terraenovae*	F	6	1825	0.003	0.016	0	0	0	0
S13	*Rhizoprionodon terraenovae*	F	89	1825	0.049	0.033	0.060	0.008	0.118	0.025
S14	*Carcharhinus leucas*	M	1	1825	0.001	0.003	0	0	0	0
S15	*Carcharhinus leucas*	F	12	720	0.015	0.014	0.017	n/a	n/a	n/a
S16	*Carcharhinus leucas*	F	5	719	0.007	0.008	0.006	n/a	n/a	n/a
S17	*Carcharhinus leucas*	F	3	395	0.008	0.008	0	n/a	n/a	n/a
S18	*Ginglymostoma cirratum*	M	165	1726	0.096	0.156	0.088	0.090	0.099	0.026
S19	*Ginglymostoma cirratum*	M	6	290	0.021	0.021	n/a	n/a	n/a	n/a

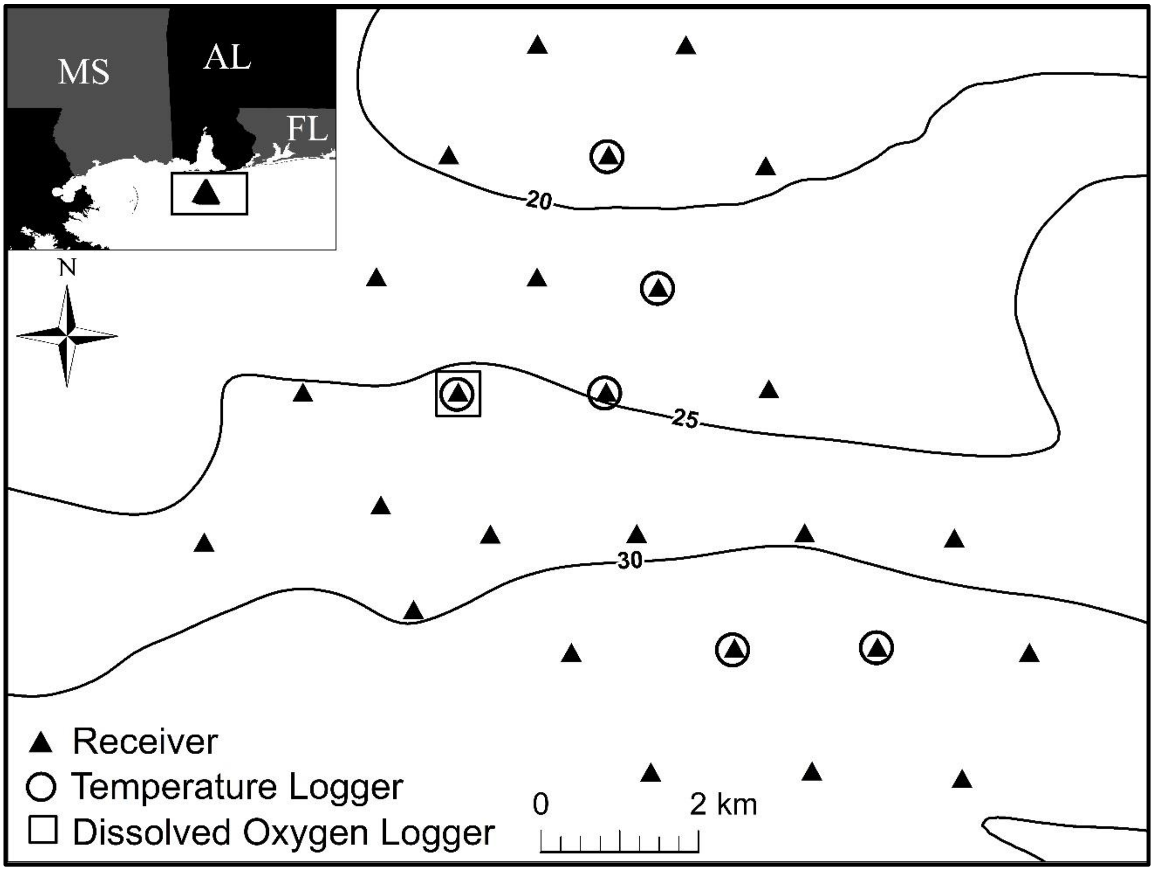

Figure 1. Locations of receivers, temperature loggers and dissolved oxygen logger within the study area. Four sites contained temperature loggers at any given time, however they were rotated among the six sites throughout the study period. Depth contours = m.

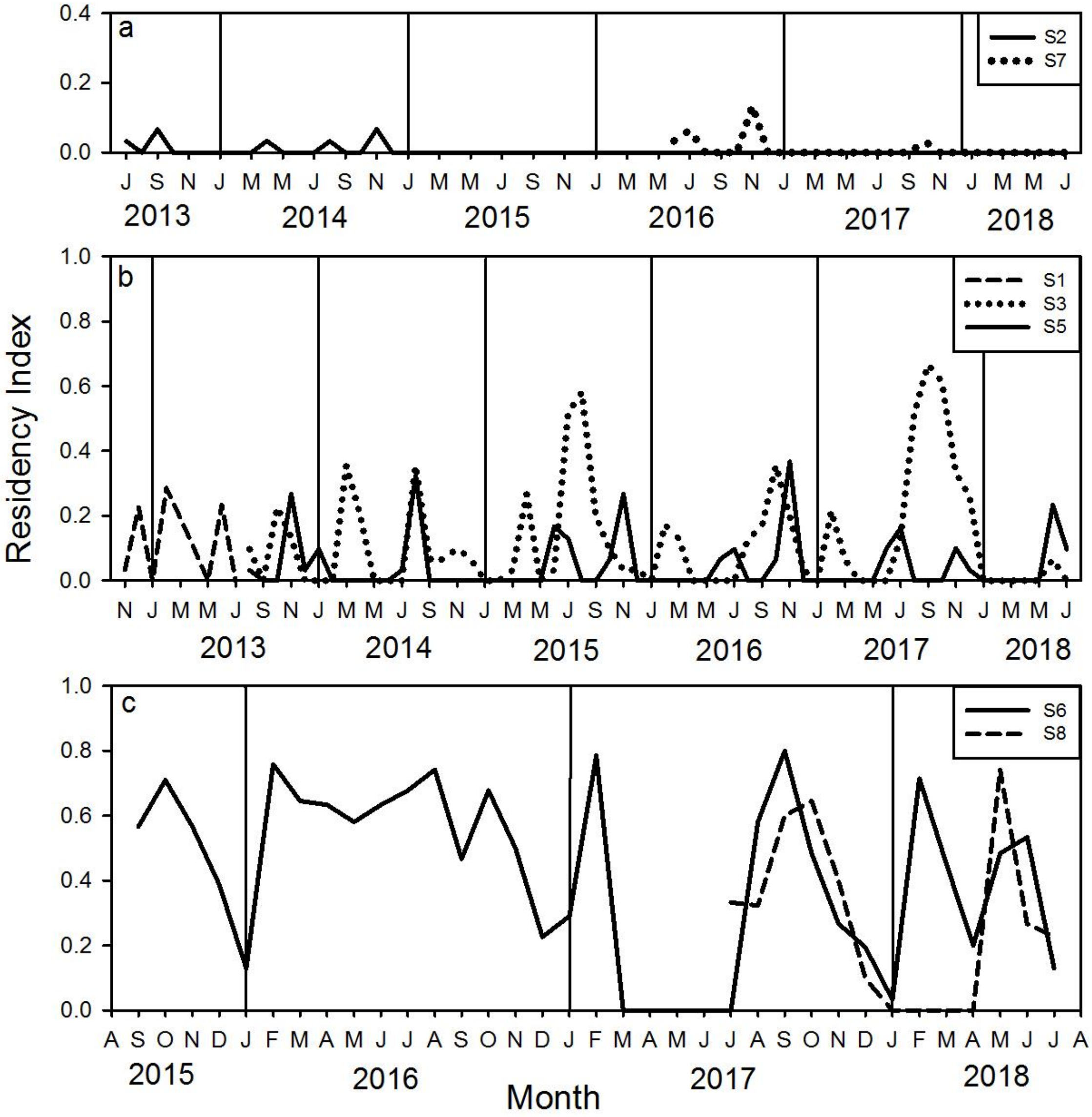

Figure 2. Monthly residency indices for *Carcharhinus plumbeus* from their tagging dates until the end of the study period. Sharks were separated by their residency patterns with low residencies in the top graph (a), medium residencies in the middle graph (b), and high residencies in the bottom graph (c).

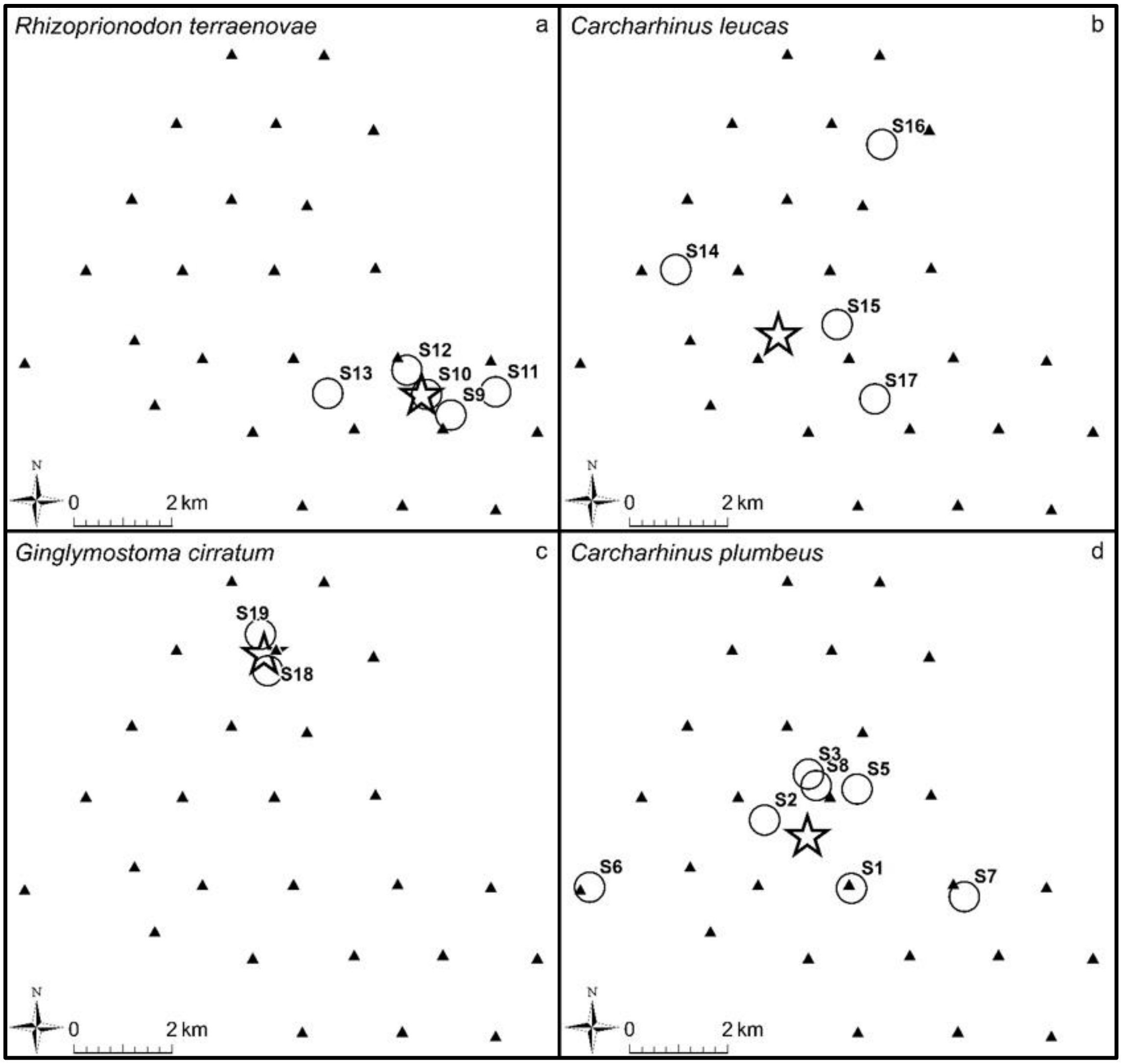

Figure 3. Mean positions for *Rhizoprionodon terraenovae* (a), *Carcharhinus leucas* (b), *Ginglymostoma cirratum* (c) and *Carcharhinus plumbeus* (d). Circles = mean positions for each individual shark and stars = overall mean position for a species.

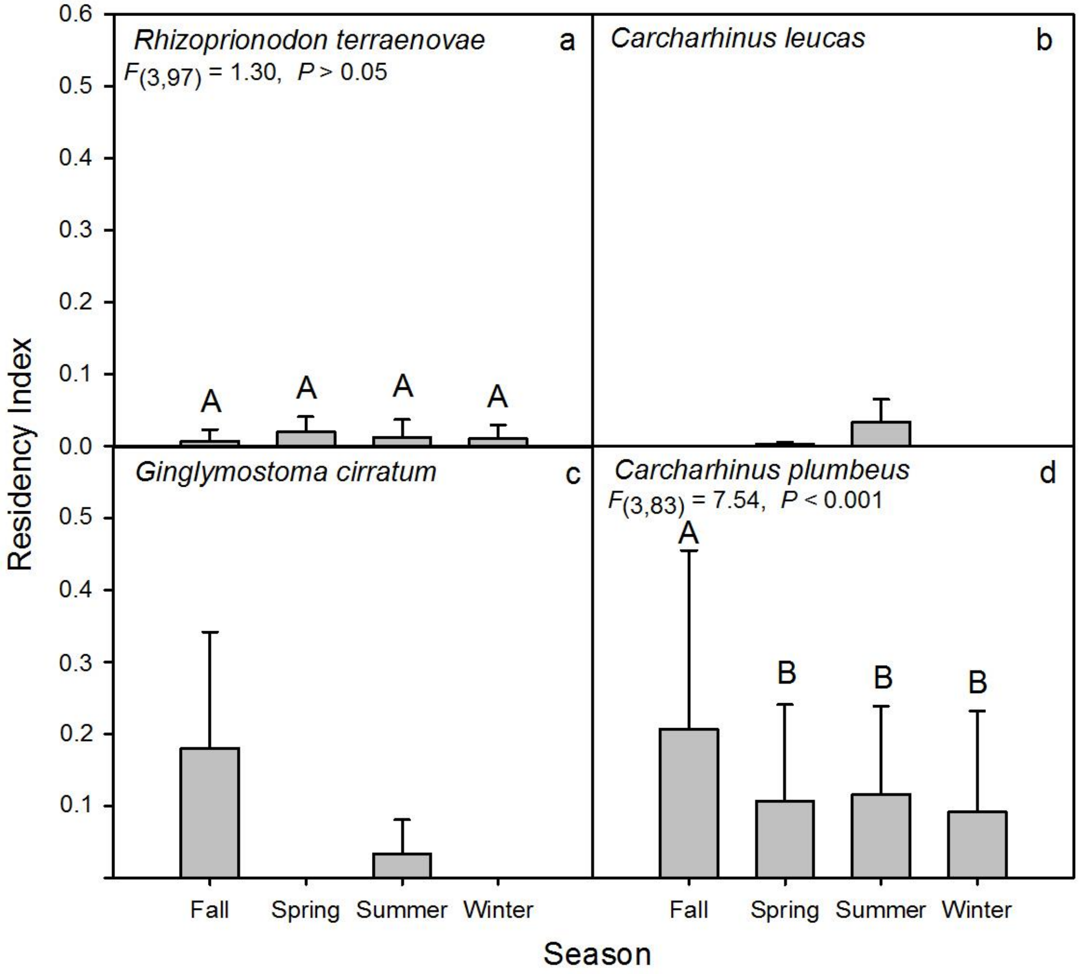

Figure 4. Comparison of seasonal residency indices for *Rhizoprionodon terraenovae* (a), *Carcharhinus leucas* (b), *Ginglymostoma cirratum* (c) and *Carcharhinus plumbeus* (d). Significant differences among seasons are represented by different letters. A significant effect of season was seen in *Carcharhinus plumbeus*.

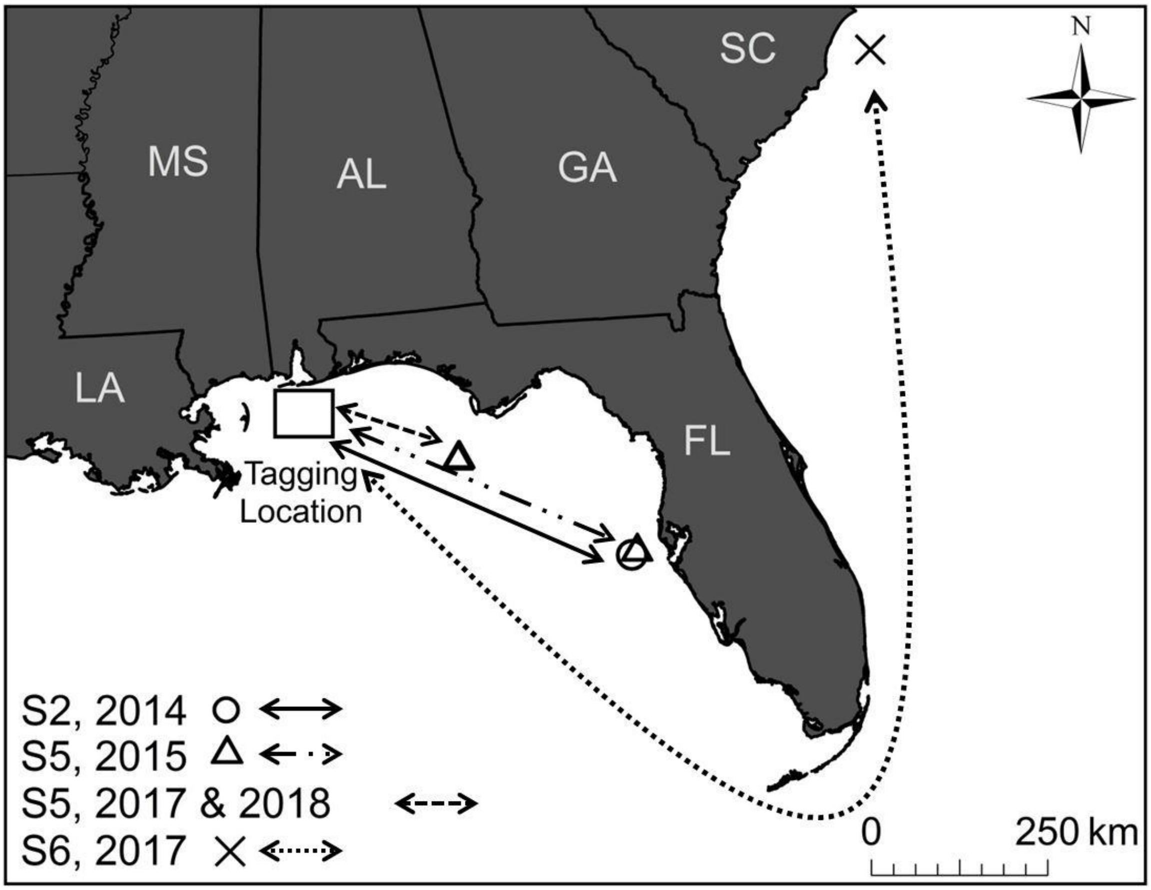

Figure 5. Observed migrations of three *Carcharhinus plumbeus*. The maximum distance recorded away from the study area was 509 km for shark S2, 512 km for shark S5 and 1,894 km for shark S6. Directional arrows indicate that all three sharks returned to the study after each of their recorded migrations.

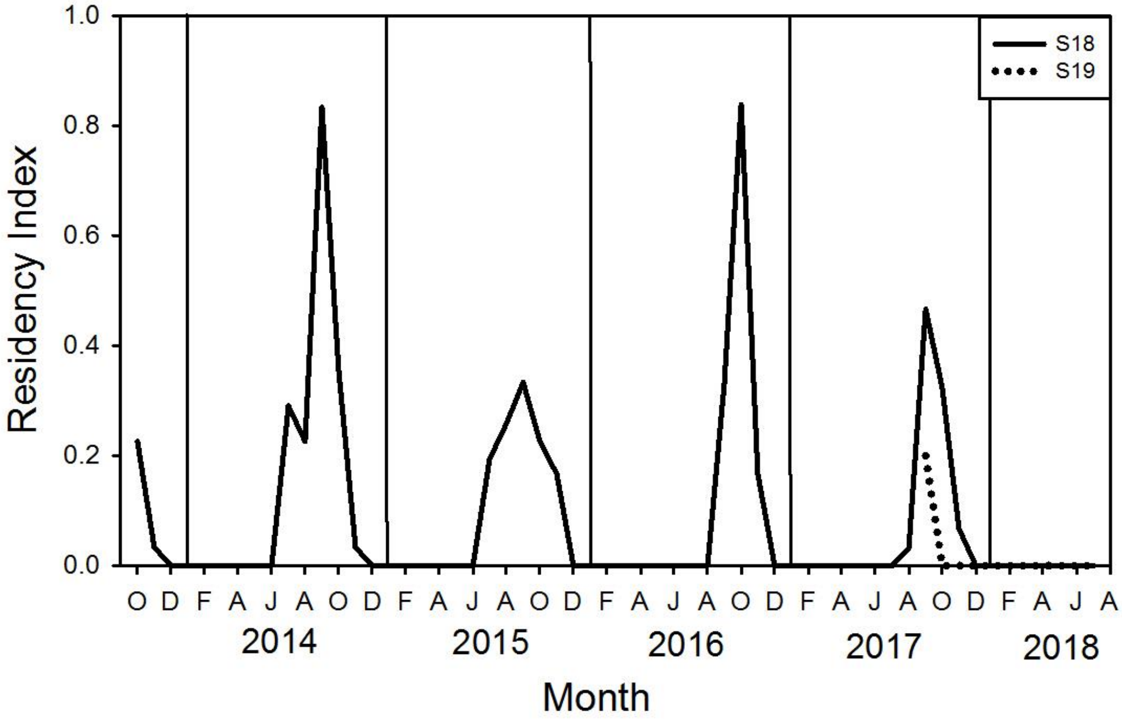

Figure 6. Monthly residency indices for *Ginglymostoma cirratum*. Line connects monthly residency indices (RIs) for each month from their tagging month to the end of the study period.

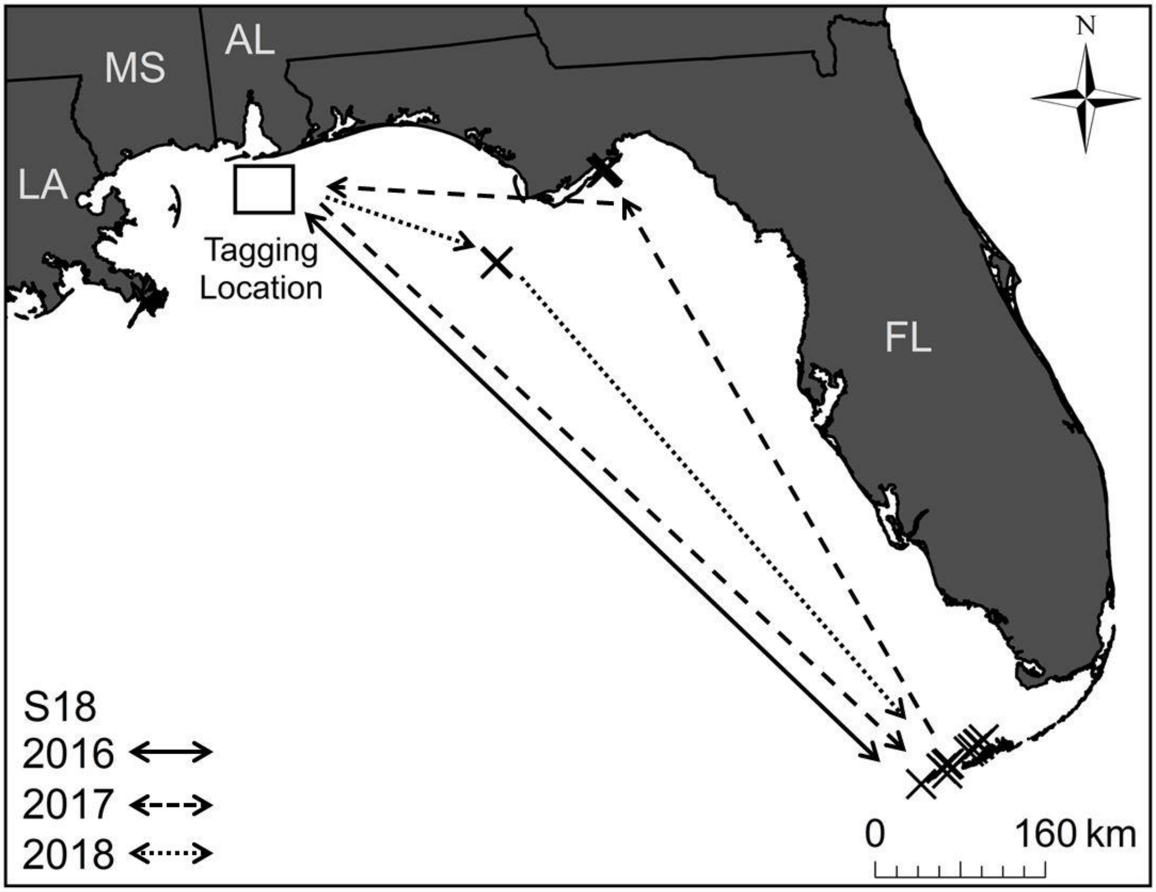

Figure 7. Observed migrations for *Ginglymostoma cirratum* S18. The maximum distance recorded away from the study area was 856 km. Directional arrows indicate that shark S18 traveled to the Florida Keys from the study area and back in three separate migrations.

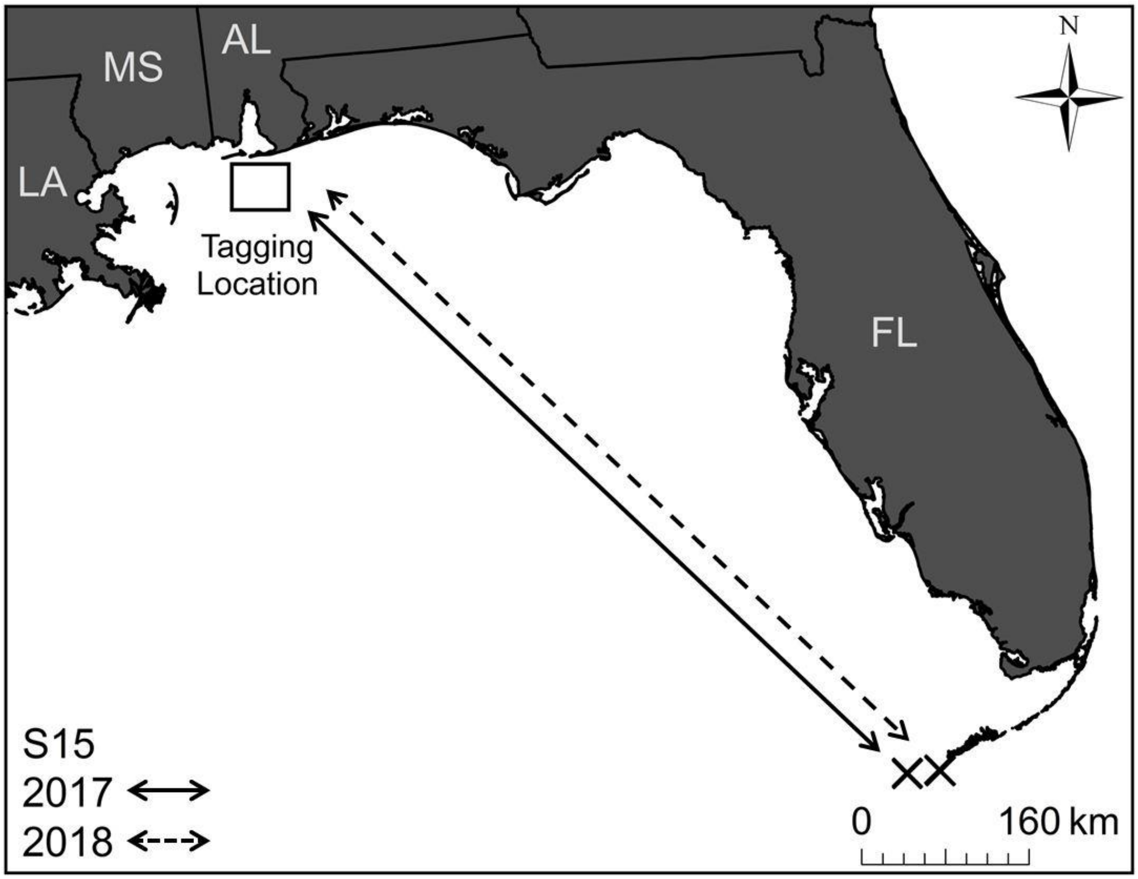

Figure 8. Observed migrations of *Carcharhinus leucas* S15. The maximum distance recorded away from the study area for shark S15 was 858 km. Directional arrows indicate that shark S15 traveled to the Florida Keys and back to the study area in two migrations.

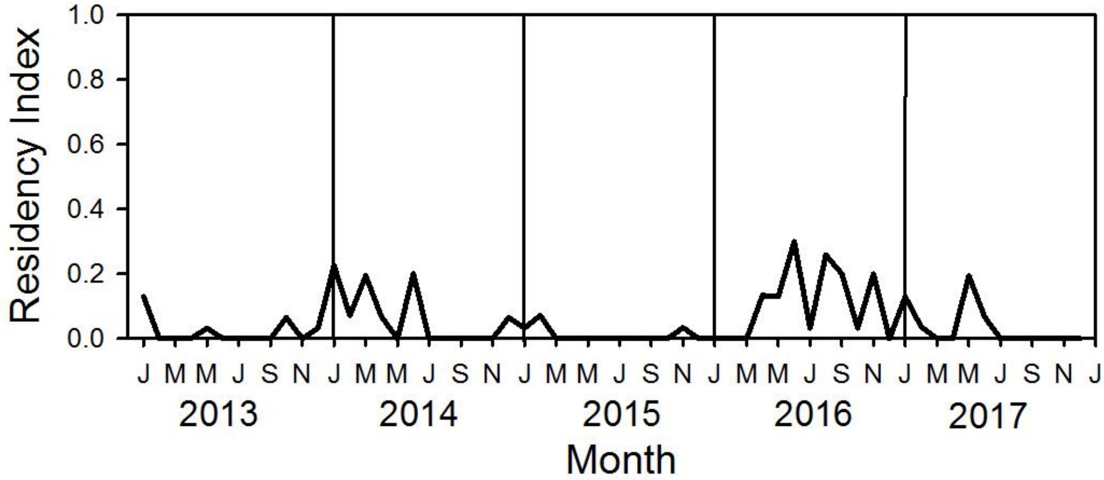

Figure 9. Monthly residency indices for *Rhizoprionodon terraenovae* S13. Shown are the residency indices (RIs) for each month from its tagging month to the end of the study period.