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Article type : Regular Paper

After the nursery: regional and broad-scale movements of sharks tagged in the Caribbean.

Running head: After the Nursery broad-scale shark movements

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Key words: Coastal Sharks, Regional Management, Acoustic Telemetry, Data Sharing, Broad-scale movements.

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Abstract: Broad-scale movements (10s-100s km) of highly migratory species, such as sharks, present unique management challenges as fish migrate across international boundaries, thereby exposing them to different levels of anthropogenic pressure. Lemon sharks and blacktip sharks are well-studied throughout their range in the western North Atlantic, but broad-scale movements in the Caribbean region are largely unknown. Utilizing 10 years (2004-2014) of acoustic and conventional tagging data, this study presents the post-nursery movements of young of the year (YOY) and juvenile blacktip (n = 198) and lemon (n = 130) sharks tagged in the United States Virgin Islands (USVI). A total of five (2.5%) blacktip sharks were recaptured by recreational and commercial fishers in the greater Caribbean and as far north as the southeastern coast of the United States, moving between 2-2200 km and crossing a minimum of six international boundaries. Of the acoustically-tagged blacktip (n= 88) and lemon (n=45) sharks, 28 (32%) and 16 (24%), respectively, were detected outside the boundaries of the nursery area in which they were tagged, dispersing throughout the USVI territory; blacktip sharks were acoustically detected beyond territorial waters as far as Florida, US (1881 km). Both species transited through local marine protected areas but did not establish residency resulting in little protection. This is the first study to examine connectivity between blacktip shark populations of the USVI and the east coast of the United States.

Introduction

A thorough understanding of migration and movement patterns is essential for the sampling, monitoring, and sustainable management of fish populations (Musick, Burgess, Cailliet, Camhi, & Fordham, 2000). For species with high residency in a specific management zone, migration across political boundaries is limited. However, fish that cross political, jurisdictional, and/or management boundaries (e.g., marine protected areas [MPAs]; national, state, or territorial boundaries) can be exposed to varying and often conflicting management regimes and levels of enforcement (Dulvy et al., 2014; Pittman, Monaco, et al., 2014). The greater Caribbean region presents a challenging management scenario as it contains numerous small island nations and territories, each with different management goals and capacities in very close proximity. As a result, the management areas of each country are, for many fish species, smaller than their potential movements (Dwyer et al., 2020; Pittman, Monaco, et al., 2014). To manage highly migratory species (HMS) effectively and equitably, it is imperative that common resources be identified through research on the broad-scale movements (10s-100s km), and levels of connectivity, of fish populations between management regions.

In the western North Atlantic (WNA), a number of studies have examined the movements of blacktip and lemon sharks off the southeast coast of the US (SE-US; (Carlson, Sulikowski, & Baremore, 2006; Castro, 1996; Reyier et al., 2014), in the Gulf of Mexico (GOM; (MR Heupel & Hueter, 2002; M. Heupel & Simpfendorfer, 2005; Passerotti & Baremore, 2012), and in The Bahamas (Feldheim, Gruber, & Ashley, 2001; Gledhill et al., 2015; Gruber, De Marignac, & Hoenig, 2001). While both species have been shown to move between The Bahamas and the SE-US (Reyier et al., 2014), connectivity between these regions and the Caribbean remains poorly studied. Although there are limited data about the broad-scale movement of both species, much has been inferred from genetics and life history characteristics (Ashe et al., 2015; Carlson et al., 2006; Gledhill et al., 2015). For example, differences in life history traits between blacktip sharks in the GOM and those off the SE-US are indicative of separate stocks (Carlson et al., 2006), yet blacktips in Belize and Yucatan are genetically similar to those in The Bahamas (Gledhill et al., 2015). For the lemon shark, genetic analyses indicate fine-scale population structure and limited exchange within the WNA (Ashe et al., 2015). To strengthen our understanding of stock structure in these two species, and the subsequent implications for international management, additional movement data are warranted from the Caribbean region,

which supports small, more isolated nurseries (DeAngelis, 2006; DeAngelis et al., 2008; Legare et al., 2015; Legare et al., 2018).

Collecting broad-scale movement data on HMS, such as sharks, is difficult as habitat use and migratory paths can be distinctly different, often hundreds or thousands of kilometers apart, at different life stages (Musick et al., 2000). Monitoring efforts need to be spatially complete to avoid population hyperstability, which produces stable catch indices while the population declines and results in an overestimation of the total population (Erisman et al., 2011). Hyperstability is particularly a problem in fish species that form aggregations or perform long distance migrations (Erisman et al., 2011), which has been demonstrated in blacktip and lemon sharks during different life stages (Castro, 1996; Kajiura & Tellman, 2016; Reyier et al., 2014).

In the Caribbean, a handful of studies have examined the abundance and habitat use of elasmobranchs in the coastal waters of the United States Virgin Islands (B. DeAngelis, 2006; B. M. DeAngelis, McCandless, Kohler, Recksiek, & Skomal, 2008; Legare, Kneebone, DeAngelis, & Skomal, 2015; Legare, Skomal, & DeAngelis, 2018). This work has identified important shark nursery habitat for blacktip and lemon sharks in the USVI and the spatiotemporal movements of these species while utilizing these nurseries (B. DeAngelis, 2006; Legare et al., 2015; Legare et al., 2018). On a broader scale, Kohler and Turner (2019) provided a recent summary of conventional tag and recapture data for these two species, but acknowledged the need to complement this information with electronic tagging methods.

In this study, we supplemented conventional tagging data (Kohler and Turner, 2019) with acoustic telemetry data to examine the regional and broad-scale movements of blacktip and lemon sharks when they emigrate from nurseries. In doing so, we examined population connectivity among and between regions of the WNA while also relating these movements to the complex political matrix of the region.

Materials and Methods

Region

In this study, the Caribbean region included the political boundaries of the following: Puerto Rico and the United States Virgin Islands (USVI), which are unincorporated territories of the United States; the independent nations of the Dominican Republic, the British overseas

territories of the Turks and Caicos Islands (TCI), and the British Virgin Islands (BVI); and the British constitutional monarch of The Bahamas (Figure 1).

The broad-scale movements of blacktip and lemon sharks in this region were derived from conventional tagging and acoustic telemetry data collected over the period of 2004-2014. Sharks were captured, tagged, and released on the islands of St. Thomas (51.5 km^2) and St. John (32 km^2), which comprise two of three major islands of the USVI (Figure 1). The coasts of both islands are characterized by long-shore bays with extensive coral reef assemblages on narrow shelves (Zitello et al., 2009). Conventional tagging was conducted throughout both islands from 2004-2012, while acoustic tagging was conducted exclusively in Fish Bay and Coral Bay during 2006-2012. These embayments provide important nursery habitat for blacktip and lemon sharks on the island of St. John (Legare et al., 2015); both contain extensive seagrass meadows, fringing mangroves, and coral reefs (Costa, Kendall, Edwards, Kagesten, & Battista, 2013).

Shark tagging methods, locations, and dates are summarized by DeAngelis (2006), DeAngelis et al. (2008), and Legare et al. (2015). In short, intense sampling was conducted in 2004 (22 days from June to August) and 2005 (38 days in January, March, May, July, and December). Annual trips were then conducted from 2006-2012 between May and August for a total of 26 sampling days. An additional three sampling days were conducted in January of 2011. The demersal longline gear and sampling procedures were modeled after the methodology of the Cooperative Atlantic States Shark Pupping and Nursery (COASTSPAN) survey (Nancy E. Kohler & Turner, 2001). Longline gangions comprised 25-50 circle hooks (size 12/0, O. Mustad & Son, Gjøvik, Norway) with barbs depressed attached to 50 cm of 0.16 cm stainless cable and 100 cm of 0.64 cm braided nylon line, which was clipped to the mainline and baited with Atlantic mackerel (*Scomber scombrus*), Atlantic bonito (*Sarda sarda*), little tunny (*Euthynnus alleratus*), and/or barracuda (*Sphyraena barracuda*); soak time was 30-60 minutes. In addition, opportunistic rod-and-reel, seine, and hand-line sampling was conducted to increase sample size when appropriate. Upon haulback, sharks were removed from the line and sex, fork length (FL), and total length (TL) were recorded. Small sharks (< 1 m FL) were tagged through the dorsal fin with a blue rototag (Dalton-Henly, Nettlebed, Oxford, England) and larger sharks were tagged with a M-tag inserted at the base of the dorsal fin using standard methods (Kohler and Turner, 2001).

A brief summary of recaptures of these sharks is reported in Kohler and Turner (2019) and, following their recommendations, this paper provides more extensive analysis supplemented with electronic acoustic tags. For sharks that were acoustically tagged in Fish Bay and Coral Bay (Figure 1), individually coded transmitters (models V9-2L, V13-1L, V13-H, Vemco Ltd., Nova Scotia) were surgically implanted using the methodology of Heupel and Hueter (2001) these sharks were also conventionally tagged. Shark movements were monitored using 8-12 passive acoustic receivers (Models VR2, VR2W, Vemco, Nova Scotia, Canada) placed in Fish Bay from 2006-2013 and 5-32 in Coral Bay from 2008-2013 (See Legare et al., 2015). In addition, data were also collected by >100 receivers placed and maintained on the islands of St. John, St. Thomas, St. Croix, Vieques, and Culebra by the University of the Virgin Islands, National Oceanic and Atmospheric Administration Biogeography, National Marine Fisheries Service (Galveston, Texas), the University of Massachusetts, Amherst, and the Florida Atlantic Coast Telemetry Network (FACT). These receivers were deployed for varying durations during this study (Brownscombe, Cooke, & Danylchuk, 2017; Doerr & Hill, 2013; Kendall, Monaco, & Winship, 2016; Pittman & Legare, 2010).

Broad-scale movements were defined as any movement beyond the nursery areas in which the sharks established residency, as quantified by previous studies (B. DeAngelis, 2006; B. M. DeAngelis et al., 2008; Legare et al., 2015; Legare et al., 2018). These movements were calculated as the linear distance between the initial capture location and the recapture or detection location. Time at liberty and size at capture were used to estimate age and maturity stage at time of final detection and/or recapture based on previously published estimates (Baremore & Passerotti, 2013; Carlson et al., 2006; Freitas, Rosa, Gruber, & Wetherbee, 2006). For the blacktip shark, median age at maturity was assumed to be 6.7 and 5.0 years for females and males off the SE-US and 5.7 and 4.5 years for females and males in the GOM, respectively (Baremore & Passerotti, 2013; Carlson et al., 2006). Total days present and number of visits (a single visit is defined as a period of residency without a day absent) to areas outside the nursery and specific MPAs. When data were sufficiently available, residency indices for areas beyond the nursery area were calculated by taking the number of days present by the number of days monitored (Knip, Heupel, & Simpfendorfer, 2012).

Results

Tagging

Between June 2004 and May 2012, 198 blacktip sharks ranging from 43-92 cm FL (mean = 52 ± 6 cm) were tagged and released on St. Thomas and St. John (Table 1); 108 (55%) were captured in Fish Bay and 77 (39%) in Coral Bay. All were fitted with conventional tags and 88 were also fitted with acoustic tags. In total, 195 (98%) were less than 75 cm FL (n = 95 females; n = 100 males), representing young of the year (YOY) individuals (Carlson et al., 2006). A total of three blacktips (1.5%) were captured in a MPA including one within the National Park (Mary's Creek) and two in the St Thomas East End Reserve at Cas Cay (Table1; Figure 1). These represent the only blacktip sharks that were captured within a MPA boundary.

During the same period, 130 lemon sharks ranging from 48-139 cm FL (mean = 62 ± 14 cm) were tagged including 68 (52%) in Fish Bay and 42 (32%) in Coral Bay (Table 1); 45 were tagged with acoustic transmitters. In total, 115 (88%; n = 59 female, n = 56 male) were YOY sharks less than 73 cm FL (Freitas et al., 2006). The remaining 12% (15 sharks) represent sharks between 1-5 years of age, thereby providing evidence of a small number of individuals using these areas for multiple years after birth. A total of 16 lemon sharks (13%) were captured in a MPA including six within the National Park (Mary's Creek) and 10 in the St Thomas East End Reserve at Cas Cay and Lagoon Point (Table1; Figure 1). These represent the only lemon sharks that were captured within a MPA boundary.

Recaptures

A total of five (2.5%) blacktip sharks and no lemon sharks were recaptured outside of the embayment in which they were tagged. These sharks, which were all tagged in Fish Bay, were recaptured 2.5-2207.0 km away after 177- 2471 days at liberty (Table 2; Figure 2, 3). Two of these sharks were recaptured off the island of St. John: B1 in Enigh Pond (3.5 km) after 177 days and B2's dorsal fin, which was found 213 days post release on the shore of Chocolate Hole about 2.5 km from the tagging location (Table 2, Figure 2). Both of these recaptured sharks traveled west and away from the Virgin Islands National Park or Virgin Islands National Coral Monument (Table 3, Figure 2).

Three blacktip sharks were recaptured outside the territorial waters of the USVI (Table 2, Figure 3). One of these sharks (B3) was acoustically tagged in Fish Bay on 7/11/2009 and

subsequently recaptured and released in Fish Bay on 6/9/2010. This shark was tracked in Fish Bay until 5/27/2012 (1051 days; 2.9 yrs post release). B3 was then detected on 15 different days along the south coast of St John until its last detection in Coral Bay on 1/24/2013 (1293 days; 3.5 yrs post release possibly due to battery life; Figure 3). B3 was ultimately recaptured 21 km from Fish Bay by a fisher in the British Virgin Islands after 1635 days (4.5 yrs) at liberty (Figure 3). The fisher processed the shark, discovered the acoustic transmitter, and reported the recapture to the British Virgin Islands Department of Natural Resources. The remaining two recaptured blacktip sharks were caught off the SE-US and reported to the Cooperative Shark Tagging Program (N. E. Kohler & Turner, 2019). B4 was a male recaptured off Cape Canaveral Florida, 1970 km from the tagging location, by a commercial gillnetter after 745 days (2 yrs) at liberty (Table 2; Figure 3). B5 was a male caught 2207 km from the tagging location on Jekyll Island, Georgia by a surf fisher after 2471 days at liberty (Table 2; Figure 3). Based on published growth curves (Baremore & Passerotti, 2013; Carlson et al., 2006) and time at liberty, B5 was the only recaptured blacktip shark that was mature at the time of capture after 6.8 years at liberty.

At a minimum, the two blacktip sharks (B4, B5) recaptured off the SE-US must have moved from the US territorial waters of the USVI and Puerto Rico through the jurisdictions of the Dominican Republic, the Turks and Caicos, The Bahamas, and the US, and ultimately landed in the state waters of Florida and Georgia (Figure 3).

Acoustic Detections

A total of 88 blacktip sharks was acoustically tracked for a total of 1,868,901 detections. Of the 88 blacktip sharks acoustically tagged, 87 were a maximum of 1 year old based on growth estimates (Baremore & Passerotti, 2013; Carlson et al., 2006). Twenty-eight blacktip sharks (32%) were acoustically detected outside the boundaries of the embayment in which they were tagged (Table 1, Figure 2). These sharks were tracked from 1-1881 km from Fish Bay or Coral Bay and were at liberty for 1-960 days (Figure 2); all were still immature at the time of last detection. Of these fish, all but one moved into MPAs for 1-10 days (mean = 4.2 ± 3.0 days): 19 were detected in the Virgin Islands National Park, 14 detected in the National Monument, and one within the Hind Bank Marine Conservation District (MCD) south of St Thomas (Figure 2, Table 3). Three males and no females were detected beyond the waters of the USVI: two on receivers around Culebra and one on a receiver off the coast of Port St Lucie Florida (Figures

2,3). Four blacktip sharks tagged in Fish Bay were also detected in Coral Bay, but only for a limited time (days/hours); no blacktip sharks tagged in Coral Bay moved into Fish Bay (Figure 1). Considering both acoustic and manual recaptured fish, male blacktip sharks were tracked between 0.7 – 2207 km (n=13; mean = 472 ± 884 km), whereas female blacktip sharks were tracked between 0.8 -21 km (n= 21; mean = 8 ± 13 km).

A total of 45 lemon sharks was acoustically tracked for a total of 278,507 detections. Of the 45 lemon sharks acoustically tagged, 42 were a maximum of 1 year old based on growth estimates (Freitas, Rosa, Gruber, & Wetherbee, 2006). Sixteen lemon sharks (24%) were detected 1-28 km from Fish Bay or Coral Bay and were at liberty for 1- 624 days (Table 2; Figure 2); no sex-specific patterns were identified. Eleven of the twelve lemon sharks were detected within the Virgin Islands National Park (Table 2, Figure 2) for time periods ranging from 1-17 days (mean = 3.2 ± 4.5 days). The remaining shark (L12) was the largest lemon shark acoustically tagged in this study at 103 cm FL. L12, a male tagged in Fish Bay on 5/10/2011, was monitored for 624 days and, during this time, was detected in Fish Bay 25 times for a total of 39 days. This equals a residency index in Fish Bay of 0.07 8 with an average stay of 1.5 ± 1.1 days (mean ± sd). When outside Fish Bay, L12 was also detected for 67 days in National Park waters, which results in a residency index of 0.10. L12 remained in National Park waters between 1-8 days (1.7 ± 1.7 days) each visit. Two lemon sharks exhibited connectivity between nursery areas as one shark tagged in Coral Bay was detected in Fish Bay and one shark tagged in Fish Bay moved into Coral Bay, but neither remained for more than one day.

Discussion

This study is the first to examine the movements of YOY and juvenile lemon and blacktip sharks when they leave nursery areas in the USVI. These efforts identified broad-scale regional movements within the territory, into adjacent MPAs, and into the waters of adjacent nations, as well as connectivity with populations off the SE-US. In this study, three (1.5%) of the tagged blacktip sharks moved over minimum (straight-line) distances up to 2207 km and passed through the jurisdictional waters of at least six countries. Of the 198 blacktip and 130 lemon sharks tagged, only blacktip sharks were detected beyond the waters of the USVI.

As suggested by Kohler and Turner (2019), this study combines conventional tag/recapture data with acoustic tagging data to better understand the broader movements of two

tropical shark species over a period of ten years. The use of both datasets strengthens our findings by not only increasing our sample size, but also through the incorporation of fisheries-independent (acoustic) data. It is impractical to place acoustic receivers throughout the entire range of any highly migratory species. Therefore, the coupling of multiple datasets is essential, and should be a priority of fisheries agencies and researchers (Hazen et al., 2012; N. E. Kohler & Turner, 2019; Pittman & Legare, 2010). Moreover, while the number of blacktip sharks acoustically detected outside the nursery areas speaks to the general movement of sharks throughout the USVI, the recapture of a shark in the BVI provided additional data from areas that lack acoustic receivers. The creation of data sharing networks between researchers helps to fill in spatial gaps (Crossin et al., 2017; Donaldson et al., 2014; Pittman & Legare, 2010). Dense receiver arrays in the USVI provide detail within the territory, with the high priority of understanding movements between spawning aggregations, nursery habitats, and MPAs. The exchange of data between the Caribbean Acoustic Telemetry Network (Pittman & Legare, 2010) and others along the SE-US have shown to be a valuable partnership in this study.

After birth, neonatal blacktip and lemon sharks spend most of their time (average 73-95%) within the confines of the nursery areas during the first months to a year (Legare et al., 2015). It is believed these nurseries are refuges providing protection from larger predators and ample food resources that enhance survival (B. M. DeAngelis et al., 2008; A. C. Henderson, Jourdan, & Bell, 2016; Michelle R. Heupel, Carlson, & Simpfendorfer, 2007; Legare et al., 2015). Neither species studied here exhibited similar residency or site fidelity to any monitored area once outside the nursery areas (Fish Bay or Coral Bay). As previously reported, the majority of sharks (blacktip and lemon) vacated the nursery areas within the first year of life, dispersing throughout late summer to early winter (Legare et al., 2015). The movements described in this study were indicative of transitory behavior over a broader scale (M.R. Heupel & Hueter, 2001) and not associated with establishing residency in adjacent areas or gradually expanding their home range beyond the bounds of their initially established nursery areas (Legare et al., 2015). Even fish that transited from one nursery area to another (i.e., Fish Bay to Coral Bay or vice versa) did not remain more than one consecutive day.

Blacktip Movements

In this study, we examined the movement of blacktip sharks between the USVI and the SE-US, which is a minimum distance of 1800-2200 km. Of the 10,293 blacktip sharks tagged in the WNA by the Cooperative Shark Tagging Program from 1962-2013, these were the only two sharks to demonstrate connectivity between these two regions (N. E. Kohler & Turner, 2019), and this study identified a third using acoustic telemetry. Despite the significantly lower effort associated with our conventional tagging, our recapture rate of 2.5% was very similar to that reported by Kohler and Turner (2.6%; 2019). These broad-scale movements were not seemingly associated with size/age/maturity (Figure 2), as these blacktip sharks ranged from 1.0-6.7 years and included juveniles and one adult.

Blacktip shark movements along the SE-US and GOM have been characterized as seasonal migrations driven by water temperature (Heithaus et al., 2007; Michelle R. Heupel, Simpfendorfer, Olsen, & Moland, 2012). Nursery areas in these regions are known to be vacated by winter, but conventional tag recaptures and the return of up to 50% of acoustically tagged fish during the first two years suggests some degree of philopatry (Hueter, Heupel, Heist, & Keeney, 2004). Similarly, previous work has shown that most, but not all, blacktip sharks emigrate from nurseries in the USVI by winter, however none of them return to re-establish residency in these bays (Legare et al., 2015). The longest continuously tracked blacktip in the current study was a female that remained in Fish Bay for 2.9 years. That individual was captured by a fisher in the BVI 1.6 years after departing the nursery. Twice the number of females were detected in USVI waters than males, and none were detected or captured farther than 57 km away. This is consistent with movement patterns suggested by genetic analyses (mtDNA data) conducted on YOY and juveniles sampled off the SE-US and GOM, which indicates that females have higher site fidelity to their natal region, while males make larger migrations among regions (Hueter et al., 2004). Indeed, in this study, all three long distance movements (1881-2207 km) to the SE-US were males and females were not tracked beyond the 21 km.

Lemon Shark Movements

In this study, we found that post-nursery movement patterns of lemon sharks varied from other studies conducted throughout the region (Casselberry et al., 2020; A. Henderson, Katherine, & Calosso, 2010; Newman, Handy, & Gruber, 2011; Reyier et al., 2014). While lemon sharks in these other areas establish secondary nurseries and long-term residency adjacent

to primary nursery areas (Chapman et al,. 2009; Kessel et al., 2016), we found that the areas immediately adjacent to the nursery areas of Fish Bay and Coral Bay are not heavily utilized by lemon sharks. Mature lemon sharks in the USVI exhibit long-term (110-1339 days) residency on reefs south of St. Thomas (Pickard et al., 2016) and immature lemon sharks have been shown to establish long-term residency (350-1427 days) around St. Croix (Casselberry et al., 2020; Pickard et al., 2016). The lemon sharks in the nursery areas of Fish Bay and Coral Bay have a seasonal residency pattern of highest abundance in the summer and the majority are absent during the winter (Legare et al., 2015). No lemon sharks were recaptured outside of their respective tagging bay and those that were acoustically detected were in the area outside of the habitat for days, not months. The exception in this study, L12 (the largest acoustically tagged lemon shark), exhibited similar residency to that found by Casselberry et al. (2019) and Pickard et al. (2016), suggesting long-term residency in the region. In comparison, the residency L12 exhibited (Residency index 0.06) within the nursery area it was captured in is much lower than the YOY sharks tagged in Coral Bay or Fish Bay with an average residency of 0.73 ± 0.33 and 0.86 ± 0.20 (average ± sd) respectively reported in Legare et al. (2015). This indicates that L12 is using a bigger area than was monitored. Given the behavior of L12 and the limited movements of our lemon sharks (maximum distance of 28 km), these findings support the genetic analyses conducted by (Ashe et al., 2015), who found restricted female-mediated gene flow within the Northern Hemisphere. When considering the limited movement described here, the strong site fidelity identified in adult (Pickard et al., 2016), immature (Casselberry et al., 2020) and YOY lemon sharks (Legare et al., 2015), and limited genetic flow (Ashe et al., 2015), lemon sharks would benefit greatly from local protection. To better put this into perspective, population size and estimates of mortality are needed to understand post-nursery area movement.

The significance of these results are further highlighted when mortality is considered. Although mortality has not been estimated for blacktip or lemon sharks in the Virgin Islands, high mortality has been estimated in nursery areas throughout their range (Gruber et al., 2001; M. R. Heupel & Simpfendorfer, 2002). We did not attempt to measure mortality in this study, but some inferences can be made because at least 32% of the blacktip and 24% of lemon sharks survived long enough to be detected outside of the nursery area in which they were tagged. This infers maximum mortality rates of 68% and 76%, respectively, in nursery areas. The mortality rate of YOY lemon sharks ranges from 35-65% in The Bahamas (Gruber et al., 2001) and from

61-92% for blacktip sharks within nurseries along the west coast of Florida (Gruber et al., 2001; M. R. Heupel & Simpfendorfer, 2002). If blacktip mortality in USVI nurseries is consistent with Florida nurseries, the three blacktip sharks that traveled >1800 m represent 4-15% of surviving sharks. Nursery areas are expected to provide protection from predation suggesting that once they vacate, sharks are exposed to greater predation pressures. During capture, several sharks had predatory wounds suggesting that even while in the nursery area, predators are a threat. Predation could explain why none, but the largest lemon shark (L12), established long-term monitoring in any adjacent waters.

Trans-jurisdictional Movement and Management

As these fish move within and away from the boundaries of the USVI, they are subject to recreational and commercial fishing pressure. As they travel throughout the greater Caribbean, the sharks are only afforded protection when crossing into territorial waters of the British Virgin Islands and The Bahamas (Table 3). Although the Turks and Caicos Islands prohibits commercial export of shark products, both the TCI and the Dominican Republic have no restrictions on take (Table 3). In federal and state waters of the SE-US, GOM, and US Caribbean, blacktip and lemon shark landings are controlled by a minimum size, bag limit, and commercial quotas; in addition, the state of Florida prohibits the landing of lemon sharks, but has no minimum size for blacktips (Table 3). Although regulations in the USVI are consistent with those in US federal waters, enforcement in the region remains a problem (Legare et al., 2015).

The MPAs around St. Thomas and St. John were established to protect essential habitat, such as coral reefs or mangroves, and commercially important species such as Nassau grouper (*Epinephelus striatus*) or Red Hind (*Epinephelus guttatus*; Pittman, Bauer, et al., 2014); none were established to protect sharks and only one of the five prevents harvest. For an MPA to be effective, it must encompass the movements of the species at risk (Pittman, Monaco, et al., 2014). The MPAs transited in this study offered little protection to the sharks that used Fish Bay and Coral Bay as nursery areas. The MCD (Figure 2) is ~ 12 x 4.5 km and ~ 45 km^2, which is smaller than the movements described herein (Table 2) and for most (4 of 6) of lemon sharks tracked in Pickard et al. (2016) and Casselberry et al. (2020). To better protect sharks in the USVI, larger areas would be required to prohibit shark fishing. A recent analysis conducted by Dwyer et al. (2020) estimated the minimum size of 50 km wide for a MPA designed to protect

mobile sharks, which is approximately the longitudinal distance from the BVI to Puerto Rico. To protect sharks from fishing pressure in the Virgin Islands, the entire territory would need to be considered.

Three of the five blacktip sharks recaptured in this study were killed and only one was mature at the time, based upon existing age and growth estimates (Carlson et al., 2006). Although both blacktip and lemon sharks are monitored by fisheries-independent and dependent surveys in state and federal waters along the SE-US and in the GOM, no long-term monitoring exists for the territorial waters of the US Caribbean. As nursery areas of the USVI are producing blacktip sharks that migrate to the SE-US, population hyperstability could be established as catches remain stable along the SE-US and the population declines in the USVI. Unfortunately, such a situation would not be detected unless monitoring efforts are established in the US Caribbean and additional genetic analyses are performed. The results of this study further emphasize the need for broad regional monitoring of shark populations to fully understand the health and status of the blacktip and lemon shark populations throughout their range.

Acknowledgments

This research was supported by funding from grants from: NOAA Coral Reef Conservation Program (award NAO4NMF46330 343), University of Puerto Rico Sea Grant PD-259 and (Project No. R-31-1-10), New England Biolabs Foundation, NOAA Center for Sponsored Coastal Ocean Research, University of Puerto Rico (award NA17OP2919), Project AWARE, NMFS Highly Migratory Species Management Division, Silver Spring, MD, Peter and Carol Bouyoucos, and Federal Aid in Sportfish Restoration. We thank the following: Sharon Coldren and the Coral Bay Community Council for support and logistics; Phil Strenger (R/V GEV) for vessel time and local expertise; Maho Bay Camps, Inc. for housing; Randy Brown, Randy Fish, and Jamie Irving of the Virgin Islands Environmental Research Station for the use of their equipment and field logistics; Dr. Richard Nemeth (University of the Virgin Islands), Dr. Andy Danylchuk (University of Massachusetts, Amherst), Dr. Simon Pittman (NOAA Biogeography Branch), and Dr. Joy Young from the FACT array for data sharing. This is Massachusetts Division of Marine Fisheries Contribution Number YYY.

At the time this field work (animal handling) was performed, the University of the Virgin Islands did not have an Animal Welfare Committee and an institutional permit was not required.

Rather, all animal handling procedures were conducted using guidelines established by the American Fisheries Society and American Society of Ichthyology and Herpetology, and all efforts were made to minimize animal stress and suffering. Surgical procedures were approved by the University of the Virgin Islands Center for Marine and Environmental Science policies and guidelines. Permission to capture fish and conduct experiments including tagging and tracking inside waters managed by the Department of Planning and natural Resources fell under PERMIT NO. STT 025-11.

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Figure legends:

Figure 1. The southeastern US and Caribbean region showing national jurisdictional boundaries (grey lines). Inset: the United States Virgin Islands of St. Thomas and St. John with tagging locations for blacktip and/or lemon sharks, numbered as (1) Brewer's Bay, (2) Lindberg Bay, (3) Water Island, (4) Cas Cay, (5) Lagoon Point, (6) Megan's Bay, (7) Water Bay, (8) Grass Cay, (9) Chocolate Hole, (10) Mary's Creek, (11) Fish Bay, and (12) Coral Bay. Marine protected areas are indicated by (A) Hind Bank, (B) Grammanik Bank, (C) Virgin Islands Coral Monument, (D) Virgin Islands National Park, and (E) St Thomas East End Reserve.

Figure 2. Acoustic detections of blacktip (X) and lemon sharks (●) tagged in Fish Bay (A) and Coral Bay (B) showing movement along the north and south coasts of St. John to the shelf edge and to the Spanish Virgin Island of Culebra, Puerto Rico to the West. Each symbol represents the final location of an individual shark. Marine Protected Areas are shaded grey.

Figure 3. Long distance movements of blacktip sharks that left Fish Bay and were recaptured (red) or acoustically detected (black). Area disputed between United States Federal Waters (US-FED) and the Dominican Republic denoted by (●).

Table 1. Tagging data for blacktip and lemon sharks tagged and released from 2003-2012 around St. Thomas and St. John, USVI; (N) indicates number of acoustically tagged individuals.

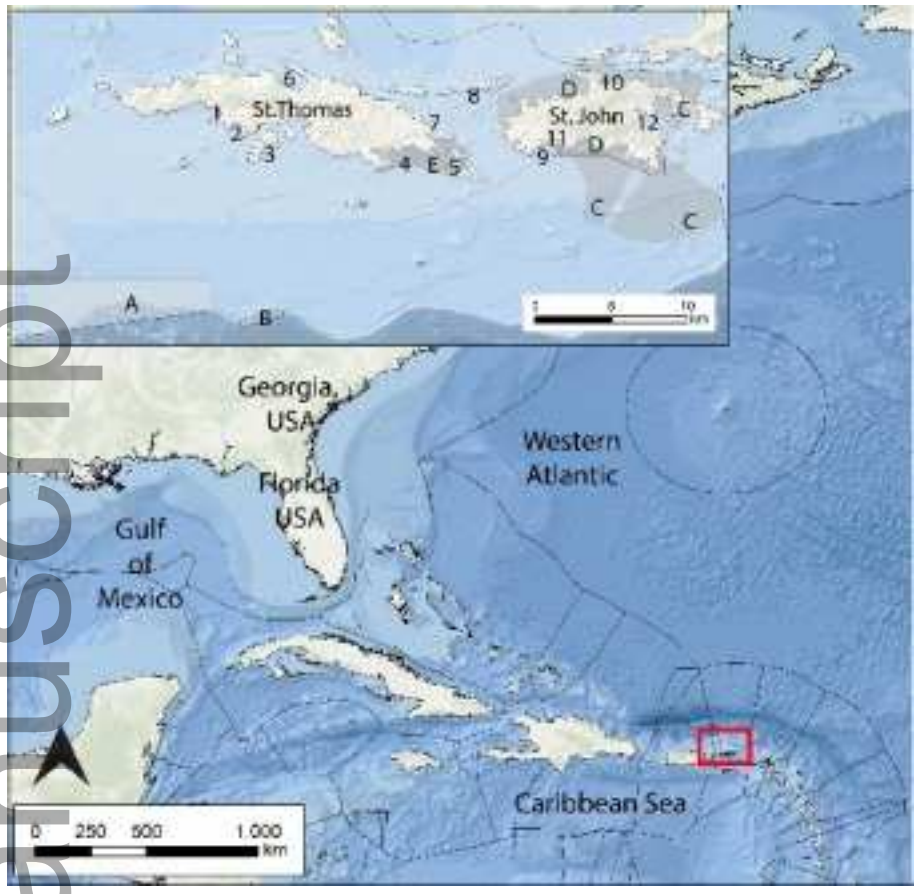
	Location	Fork Length (cm)				
		n	Mean	Max	Min	SD
Blacktip	Brewers Bay, St Thomas	1	55	55	55	-
	Cas Cay, St Thomas	2	51	51	51	0.0
	Coral Bay, St John	77 (58)	51	66	44	4.3
	Fish Bay, St John	108 (30)	51	77	43	5.3
	Lindberg Bay, St Thomas	1	57	57	57	-
	Mary's Creek, St John	1	54	54	54	-
	Megans Bay, St Thomas	5	60	68	45	11.0
	Water Bay, St Thomas	2	88	91	84	4.9
	Water Island, St Thomas	1	50	50	50	-
	Total	**198**	**52**	**91**	**43**	**14.0**
Lemon	Brewers Bay, St Thomas	2	73	91	54	26.2
	Cas Cay, St Thomas	2	72	75	69	4.5
	Coral Bay, St John	42 (23)	58	70	48	5.4
	Fish Bay, St John	68 (22)	61	103	51	10.6
	Grass, St Thomas	2	124	130	119	7.4
	Lagoon Point, St Thomas	8	65	139	52	29.8
	Mary's Creek, St John	6	61	78	51	10.5
	Total	**130**	**62**	**139**	**48**	**11.2**

Table 2. Summary of straight line distances traveled by blacktip and lemon sharks tagged and released from 2003-2012 around St. Thomas and St. John, including number of sharks observed entering a MPA and minimum number of national boundaries crossed; bold indicates mature at time of capture.

	Recaptured Sharks				
	Shark ID	Distance (km)	Days at Liberty	MPA (n)	Boundaries (n)
Blacktip	B1	2	177	0	0
	B2	3	213	0	0
	B3	21	1635	2	1
	B4	1969	745	0	6
	B5	2207	2471	0	7
	Acoustically Tracked Sharks				
	Sharks (n)	Distance (km)	Days at Liberty	MPA (n)	Boundaries (n)
Blacktip	2	0-1	6	2	0
	18	1-5	98	18	0
	4	5-10	261	4	0
	1	10-50	41	1	1
	2	50-100	734	1	1
	1	1881	321	0	6
	Sharks (n)	Distance (km)	Days at Liberty	MPA (n)	Boundaries (n)
Lemon	1	0-1	8	0	0
	13	1-5	109	11	0
	2	5-10	15	2	0

Table 3. Summary of blacktip and lemon shark fishing regulations in each jurisdiction transited during this study. Gray indicates areas in which both blacktips and lemon sharks are protected.

Jurisdiction	Regulations	Minimum Size (FL)	Commercial Quota	Recreational Bag Limit	Source
United States Federal waters	Federal permit required	137 cm	YES	1	(NMFS, 2018)
USVI Territory	Federal permit required	137 cm	YES	1	(DNR, 2016)
Virgin Islands National Park	Rod and Reel federal permit required	137 cm	NA	1	(DNR, 2016
Virgin Islands Coral Monument	Rod and Reel federal permit required	137 cm	NA	1	(DNR, 2016
St. Thomas East End Reserve	Rod and Reel federal permit and local permit	137 cm	NA	1	(NMFS, 2018)
Grammanik Bank	Seasonal Rod and Reel federal permit required	137 cm	YES	1	(CFMC, 2016)
Hind Bank Conservation District	No fishing of any kind	NA	NA	NA	(CFMC, 2016)
Puerto Rico	Federal permit	137 cm	YES	1	(CFMC, 2016)
British Virgin Islands	Only sustenance shark fishing allowed.	NA	NA	NA	(MNRL, 2014)
Dominican Republic	Permit required	None	No limit	No limit	(Herrera et al. 2011)
Turks and Caicos	Permit required	None	X	No limit	(DCR 2019)
The Bahamas	Shark sanctuary	NA	NA	NA	(Techera & Klein 2014)
Florida, USA	No minimum size for blacktip, lemon prohibited	None	YES	1	(FWC, 2018)
Georgia, USA	Federal permit required	137 cm	YES	1	(GADNR, 2019)



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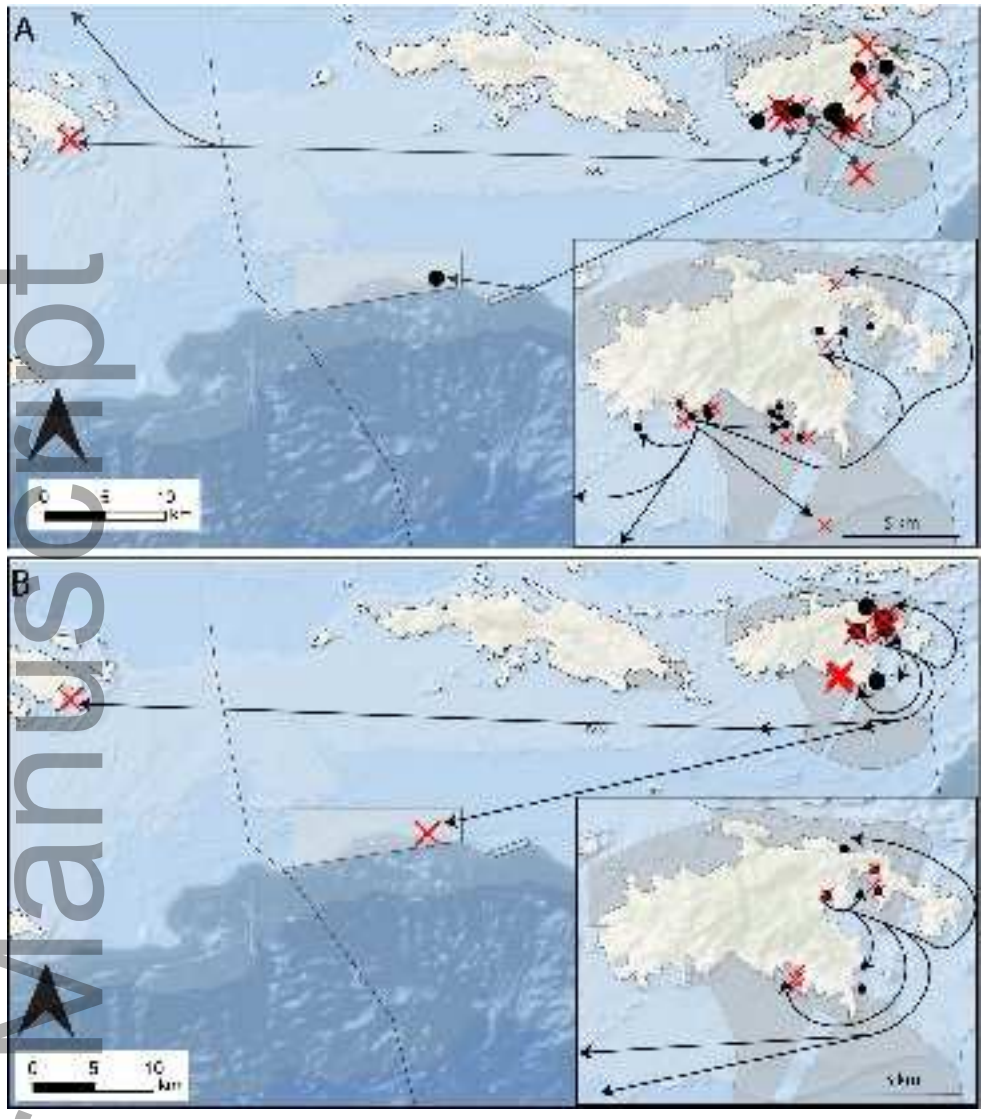

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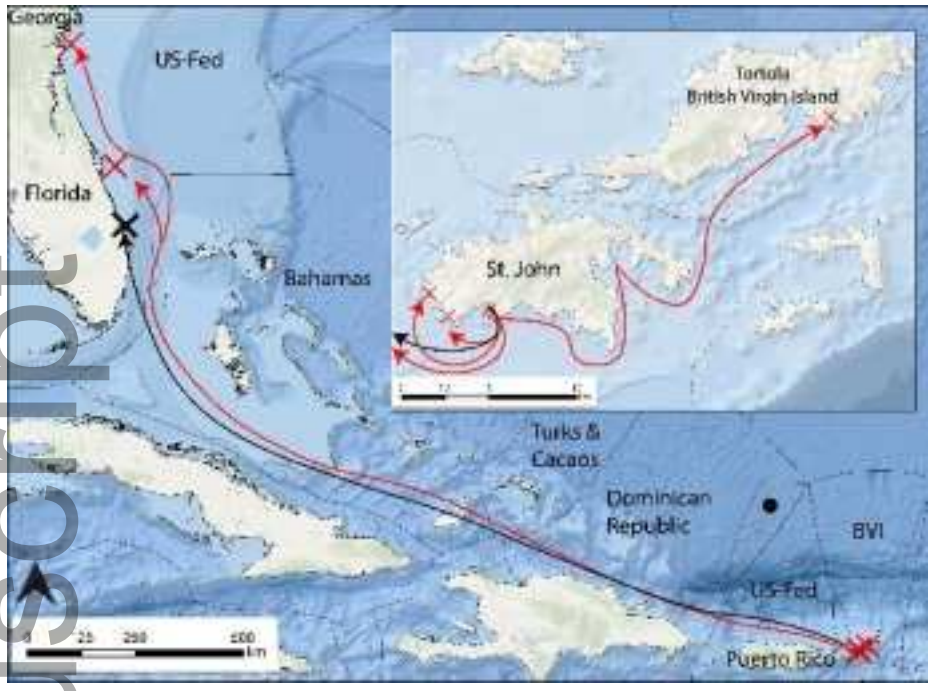

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