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Insights into the Relative Abundance, Life History, and Ecology of Oceanic Sharks in the Eastern Bahamas

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Abstract: Fisheries-independent data on the diversity, relative abundance, and demographic structure of poorly studied, threatened oceanic sharks are absent from much of the western North Atlantic Ocean, where multiple oceanic shark species have experienced significant population declines. Resource-limited management approaches require the identification of critical habitats or aggregation sites worthy of protection and enforcement. Data were collected on oceanic sharks using pelagic longline surveys, targeted baiting, and opportunistic encounters in oligotrophic open-ocean habitats of north-eastern Exuma Sound (NES), The Bahamas. The oceanic epipelagic shark community was also characterized using targeted baiting off Columbus Point, Cat Island (CI), a seamount north of San Salvador (SSSM), and the northwestern tip of Mayaguana. Pelagic longline surveys suggested that the relative abundance of sharks at NES was low (shark catch-per-unit-effort: 0.0007 sharks hook^{-1} h^{-1}; 2.3 sharks per 1000 hooks). Silky sharks *Carcharhinus falciformis*, particularly juveniles (134 ± 39 cm stretched total length; mean ± SD STL), were the most common. Targeted baiting suggested oceanic whitetip sharks *C. longimanus* were abundant at CI, where large adults (245 ± 23 cm STL), most of which were females (83.8%, $n = 98$ of 117) that were gravid (65.7%; $n = 46$ of 70 assessed for pregnancy), dominated the aggregation. Many (20.5–26.5%, $n = 24$–31 of 117 depending on assumptions regarding tag loss) were recaptured or resighted at CI for up to five years. Silky sharks dominated catches at SSSM. Oceanic sharks, particularly adults, were sometimes caught or observed alongside short-finned pilot whales *Globicephala macrorhynchus* or tunas. Although The Bahamas offers threatened oceanic sharks refuge from fishing across its entire jurisdiction, these data suggest that some fixed features, including sites such as CI and potentially SSSM, are important aggregation sites with high regional conservation value and should be prioritized by fisheries managers and enforcement officials.

Keywords: oceanic sharks; oceanic whitetip shark; silky shark; open ocean; pelagic; The Bahamas

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1. Introduction

Understanding the distribution, relative abundance, and demographic structure of oceanic shark populations across space and time is essential for effective fisheries management. In the western North Atlantic Ocean, these data have been primarily collected through the region's artisanal- (e.g., [1,2]) and industrial-scale pelagic fishing fleets (e.g., [3]). For example, fishery-dependent (i.e., sourced from fishers) logbook and observer data from the U.S. pelagic longline fleet suggested declines in the relative abundance of some oceanic sharks in this region, including the oceanic whitetip shark *Carcharhinus longimanus* and silky shark *C. falciformis* [4,5] (Figure 1), mirroring a 71% decline in the global abundance of oceanic sharks and rays from 1970 to 2018 [6].

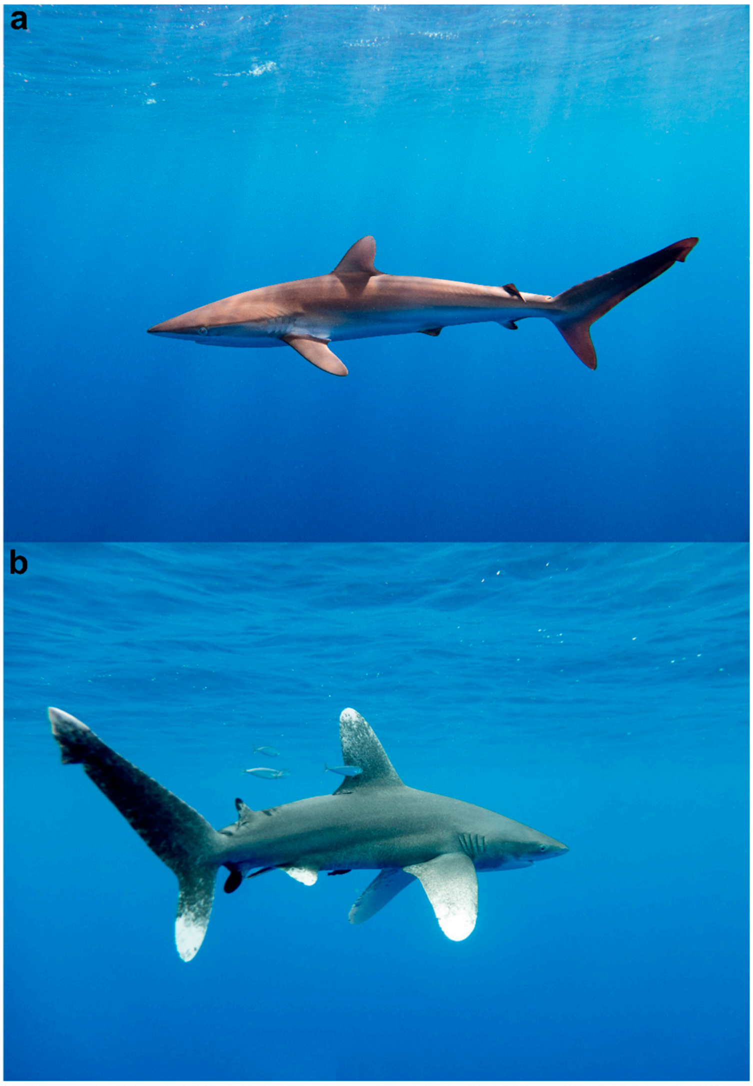

Figure 1. Images of the two primary study species, (**a**) silky shark *Carcharhinus falciformis* and (**b**) oceanic whitetip shark *Carcharhinus longimanus* in the eastern Bahamas. Photos: B. Talwar.

Despite oceanic sharks being highly vulnerable to pelagic longline fisheries [7], their management is limited by poor fisheries catch and effort data [8,9], high uncertainty in some stock assessment inputs (e.g., basic biology and ecology [10]) and outputs [11], and a lack of international cooperation required to manage populations that span multiple jurisdictions and the high seas [12]. Some oceanic shark species, such as the oceanic whitetip shark and silky shark, are commonly caught as bycatch in the Atlantic Ocean but lack stock assessments [10,13]. Robust fisheries management frameworks require more information on the fisheries interactions and life histories of these species [14–16], whereas resource-limited management approaches require the identification of critical habitats or aggregation sites worthy of protection or restoration [17]. For migratory oceanic sharks, those sites can include areas where individuals exhibit mating and/or feeding site fidelity [18], which are important life-history criteria for designating important shark and ray areas (ISRAs) [19].

Some shelf-edge open-ocean habitats in the eastern Bahamas may serve as these habitats for wide-ranging oceanic and semi-pelagic sharks (as defined by [20]). For example, Critically Endangered (IUCN Red List of Threatened Species [15]) adult oceanic whitetip sharks aggregate off Columbus Point, Cat Island, The Bahamas (CI) in April–May, with at least 20% of individuals exhibiting multi-year site fidelity that may be motivated by abundant pelagic teleost prey in late spring [21] and/or mating in summer [22]. Satellite telemetry data revealed that oceanic whitetip sharks tagged at CI spent considerable time (24–100% of 31–245-day tag durations) within the Bahamian Exclusive Economic Zone (EEZ) [23], but sample size and inherent limitations of light-level based geolocation estimates precluded the fine-scale identification of high-use areas. Similarly, the Vulnerable (IUCN Red List of Threatened Species [16]) silky shark may be common in some open-ocean habitats in The Bahamas [24,25], but remains poorly studied throughout the western Atlantic Ocean [26]. Data from elsewhere in the silky shark's circumtropical distribution suggest that areas of high primary productivity and/or biophysical coupling, such as upwelling areas [27] and seamounts [28], are strongly associated with its presence [29]. Both oceanic whitetip sharks and silky sharks may also associate with other species in mixed-species groups (i.e., in close association within the same group) or aggregations (i.e., drawn to a shared resource or environmental cue) [8,30–32], which could improve their foraging efficiencies. These associations may be particularly beneficial in oligotrophic, food-limited, open-ocean habitats [33].

The Bahamas protected oceanic sharks from large-scale fishing by prohibiting longlining in 1993 and shark fishing in 2011 [34]. The Bahamas also participated in the international management of trade in oceanic shark species by supporting proposals that successfully listed the oceanic whitetip shark and silky shark on Appendix II of the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES; CoP16 Prop. 42, CoP17 Prop. 42). However, the open ocean tends to be overlooked in The Bahamas' spatial management plans [35] despite being the country's largest marine habitat type. Similarly, most shark research in The Bahamas has focused on coastal and, to a lesser extent, deep-water species. Fishery-independent longline surveys have been particularly useful in providing data on shark diversity and relative abundance [36–40], but none have occurred in the open ocean. Their absence from this habitat type is unsurprising; it is challenging to sample highly mobile fishes that forage on patchily distributed prey [41] in a seemingly featureless, but highly dynamic, environment [42].

Data on the diversity, relative abundance, and demographic structure of shark populations in The Bahamas' open-ocean habitats are required to assess the impacts of disturbance (e.g., fishing, climate change), appropriately site open-ocean and shelf-edge protected areas, and prioritize areas for enforcement. These data were collected through experimental longlining, targeted baiting, and opportunistic encounters, including sightings of mixed-species groups involving oceanic sharks and short-finned pilot whales *Globicephala macrorhynchus*, from 2011 to 2020 at multiple locations in the eastern Bahamas. Unfortunately, due to logistical challenges arising from the COVID-19 pandemic followed by unrelated changes to The Bahamas' scientific permitting process, all data collection paused indefinitely in 2020, providing an incentive to update and summarize the general knowledge of oceanic sharks in the region, particularly at CI. Conclusions are limited by data being drawn from disparate surveys, but, given very limited information about poorly studied open-ocean shark species in this region, this study can generate hypotheses that guide future research and inform species-specific and area-based management of highly threatened oceanic sharks.

2. Material and Methods

2.1. Study Area

Catch and sometimes effort data pertaining to oceanic sharks were collected over nine years at four sites in the eastern Bahamas: north-eastern Exuma Sound (NES; just west of Powell Point, Eleuthera, The Bahamas; 24.819° N, 76.341° W), Columbus Point, Cat Island (CI; within 20 km of 24°07′ N, 75°17′ W), San Salvador Seamount (SSSM; within 10 km of 24°13′ N, 74°29′ W), and Mayaguana (within 5 km of 22°28′ N, 73°09′ W; Figure 2). NES represented 'typical' or 'baseline' shelf-edge habitats in the region (i.e., based on local knowledge, this site was unlikely to aggregate fishes and lacked notable bathymetric features, such as seamounts). Fishing occurred at CI because fishers and divers suggested high densities of oceanic sharks [23]. It was hypothesized that the seamount at SSSM would host oceanic sharks based on its unique bathymetry; the 1.3 km^2 seamount rises from 360 m along its southern edge to a platform at 67–91 m, then drops off at its northern edge to over 800 m [43]. Mayaguana was fished opportunistically.

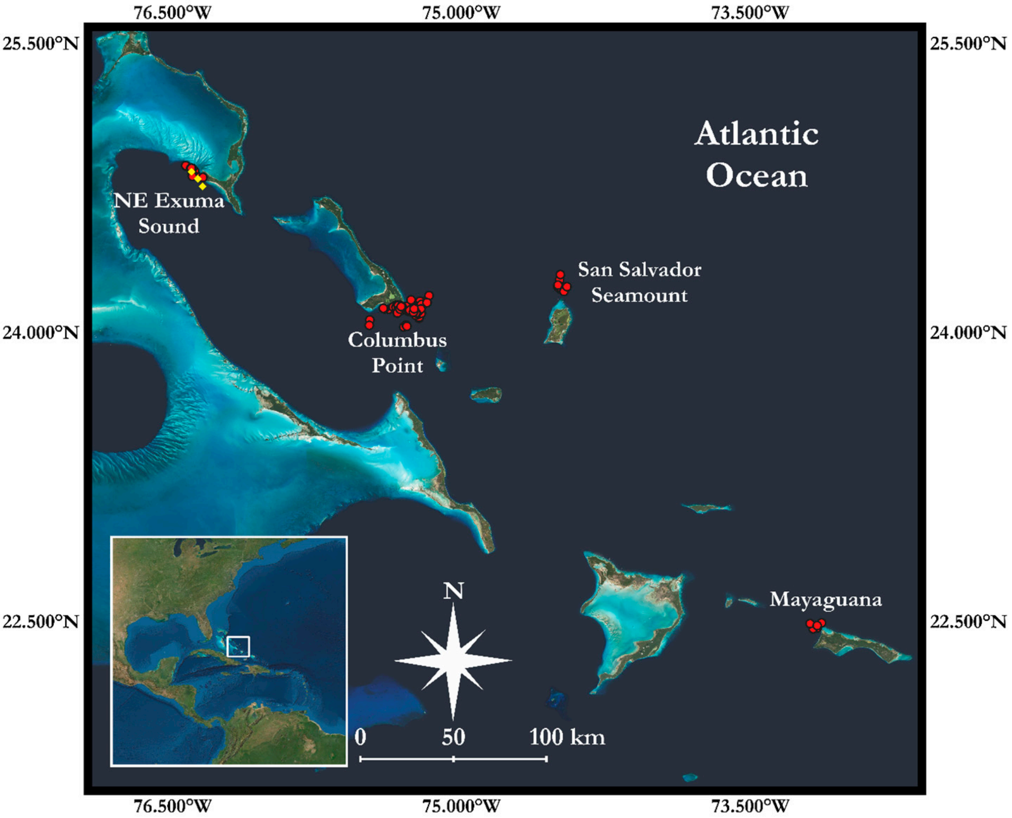

Figure 2. Map of the eastern Bahamas, including four study areas: north-eastern (NE) Exuma Sound, Columbus Point (Cat Island), San Salvador Seamount, and Mayaguana. Fishing locations of standardized pelagic longline surveys in NE Exuma Sound are marked with yellow diamonds. Shark capture or observation sites are marked with red circles. The inset displays this area within the western Atlantic Ocean. Map base layer source: Esri®.

Across sites, most data were collected through targeted baiting and opportunistic encounters while conducting fieldwork in support of other research. However, standardized pelagic longline surveys were conducted at NES to comprehensively characterize the oceanic shark assemblage for this study. Details on each method are provided below, and summaries of where and when each method was used appear in Table 1.

Table 1. Composition of shark catches and observations from all research activities in oceanic habitats at four sites in the eastern Bahamas from 2011 to 2020. STL is stretched total length.

Site	Methods and Effort	Common Name	N (% Catch and Observations)	N Female (N Mature)	N Male (N Mature)	% Female	Male STL (cm) Range	Female STL (cm) Range	Mean STL ± SD (cm)
Northeastern Exuma Sound	Pelagic longline surveys (*n* = 73 sets, September 2018–March 2020), targeted baiting (35 occasions, September 2018–March 2020), opportunistic encounters (2014–2020)	Silky shark	20 (59)	11 (1)	5 (1)	69	110–240	94–240	134 ± 39
		Dusky shark	5 (15)	2 (1)	3 (3)	40	260–300	222–310	277 ± 36
		Oceanic whitetip shark	3 (9)	2 (1)	1 (1)	67	210	92–190	164 ± 63
		Lemon shark	1 (3)	0	1 (1)	0	263	-	263
		Tiger shark	5 (15)	2 (1)	1 (0)	67	179	202–327	252 ± 63
		Total	*34 (100)*			*61*			*179 ± 74*
Columbus Point, Cat Island	Targeted baiting (62 occasions in April–May from 2011–2018, 15–16 July 2019, 16–18 and 22 June 2020, 29 July 2020), opportunistic encounters (16–18 and 22–23 June 2020)	Silky shark	15 (7)	5 (0)	8 (2)	38	114–260	99–199	167 ± 45
		Dusky shark	3 (1)	-	1 (1)	0	238	-	238
		Oceanic whitetip shark	187 (90)	167 (162) *	20 (20)	89	207–285	194–307	245 ± 23
		Blue shark	2 (1)	2 (1)	-	100	-	208–260	234 ± 37
		Tiger shark	1 (0.5)	-	1 (0)	0	232	-	232
		Total	*208 (100)*			*85*			*237 ± 34*
San Salvador Seamount	Targeted baiting (6 occasions, 22 January–5 February 2019; 1 occasion, 1 September 2020)	Silky shark	14 (61)	7 (2)	7 (0)	50	136–170	110–281	167 ± 45
		Oceanic whitetip shark	9 (39)	3 (3)	2 (1)	60	158–258	189–264	226 ± 49
		Total	*23 (100)*			*53*			*182 ± 52*
Mayaguana	Pelagic longline (*n* = 1 set, 12 July 2019), targeted baiting (2 occasions, 12–13 July 2019)	Silky shark	1 (17)	-	1 (1)	0	262	-	262
		Oceanic whitetip shark	5 (83)	3(3)	2 (1)	60	178–244	207–240	221 ± 28
		Total	*6 (100)*			*50*			*228 ± 30*

* Maturity was not assessed for five female oceanic whitetip sharks.

2.2. Pelagic Longline Surveys

From September 2018 to March 2020, 73 standardized pelagic longline surveys were fished at three sites in NES that were 5 km apart in open water deeper than 900 m. These sites were ~2.75 km from the near-vertical shelf wall, where depth rapidly increased from 30 m to >300 m across 100–300 m of horizontal space. Attempts were made to fish each site at least once per month to assess seasonal changes in the shark assemblage. Night sets occurred primarily from September 2018 to May 2019, whereas daytime sets occurred throughout the study period.

Each longline was ~1150 m long and made of 6.4 mm diameter tarred, braided nylon in two configurations: (1) a deep set, which was designed to fish from the surface to ~400 m (i.e., one basket) and (2) a shallow set, which was designed to fish from the surface to ~120 m. Large ball floats (0.9 m diameter) and high-fliers were attached to each end of both configurations. Additional ball floats (0.5 m diameter; $n = 3$) were attached between 18 hook baskets on the shallow sets. To estimate the maximum hook depths and minimum hook temperatures (recorded as the deepest and coldest points measured for a given set), an archival temperature and depth recorder (TDR; Lotek LAT-1400) that recorded depth and temperature every 4 s was attached to the midpoint of the line (deep set; $n = 2$ TDR deployments) or the midpoint of the basket (shallow set; $n = 8$ TDR deployments). Both configurations were stretched along the surface while setting and then allowed to sink to their maximum allowable depths, which took roughly 2 h 45 min for deep sets and 1 h 55 min for shallow sets.

Between 36 and 72 gangions (mean ± SD = 70.81 ± 4.63 hooks) were attached to each line at 15 m intervals. The general gangion template included a stainless-steel longline snap attached to a length of white, low-stretch, solid braid, dacron polyester cord (3.2 mm, >158 kg test) tied to a swivel, which was crimped to either stainless steel wire or clear monofilament leader. Polyester cord and wire/monofilament leaders were of equal length per gangion. Small, medium, and large gangions were used on each set to target a variety of shark species and sizes. They varied in length (0.5, 1.5, and 3 m), leader thickness (wire: 1.8, 2.0, and 2.2 mm; monofilament: 136, 249, and 318 kg test), and non-offset circle hook size (12/0, 14/0, and 16/0), and each was paired with appropriately sized bait. Wire leaders were baited with mullet *Mugil cephalus*, and monofilament leaders were baited with squid (shortfin squid *Illex illecebrosus* or opalescent squid *Loligo opalescens* depending on availability). Gangions were set as follows (hook size–leader–bait type): 12/0–wire–mullet, 14/0–wire–mullet, 16/0–wire–mullet, 12/0–monofilament–squid, 14/0–monofilament–squid, and 16/0–monofilament–squid. To minimize at-vessel mortality, particularly of dusky sharks *C. obscurus* (see [44]), longlines were soaked for 3–4 h (from the last hook in to the first hook out).

On one occasion at Mayaguana, a 1 km drifting epipelagic longline fished 94 gangions in 10 hook baskets on a 2.2 mm monofilament mainline. Each gangion consisted of a longline snap crimped to 3 m of doubled 2.2 mm monofilament leader crimped to a 16/0 circle hook baited with little tunny *Euthynnus alletteratus*.

2.3. Targeted Baiting and Opportunistic Sightings

Targeted baiting involved near-constant flaking of little tunny, great barracuda *Sphyraena barracuda*, or other fish, often while dragging a 15 L crate filled with fish scraps to create a chum slick while drifting for 4–8 h. The time of a shark's first arrival (i.e., time of first observation from the boat) was recorded during a subset of baiting days to provide a very coarse proxy for relative abundance [45]. To maximize shark encounters on windless days, the slick was extended by slowly and intermittently moving the boat. The boat engine was occasionally revved to attract sharks with auditory cues. Baiting sometimes occurred at night at NES. Occasionally, a bait crate was attached to a subsurface, moored fish aggregation device (described in [46]) at NES, and snorkelers intermittently conducted visual surveys of those sites to document sharks. A shark-dive charter company (Epic Diving; V. and D. Canabal) also baited and reported sightings of tagged sharks at CI.

Details on opportunistic shark encounters in the absence of bait were also recorded, such as when sharks were seen alongside cetaceans or tunas offshore at NES or during brief expeditions to CI in June–July 2020. Detection effort was not standardized during these chance encounters, and, because cetacean and tuna groups were often spread out over larger areas than were scanned by a snorkeler in the water, fewer sharks were probably detected than were present. A shark was considered to be associated with cetaceans or tunas in a mixed-species group whenever they overlapped in space (i.e., within tens of meters) and time (i.e., appeared within minutes of other species).

2.4. Shark Capture and Workup

Sharks were captured after targeted baiting and opportunistic sightings using a single-hook rig consisting of a circle hook crimped to a doubled monofilament leader tied to 20 m of nylon throwline terminating in two staggered ball floats. The float closest to the hook created drag, and the second float caused additional drag and marked the shark's location. The size of the hook, leader, and floats was tailored to the size of the shark.

Captured sharks were secured alongside the boat to identify species, determine sex based on external morphology, and measure length. Given the large size of many oceanic sharks and the size and design of vessels used for fieldwork, sharks remained in the water and were measured over the body's dorsal surface using a flexible tape as opposed to in a horizontal straight line alongside the body. Francis [47] recommended taking multiple measurement types whenever possible, but suggested flexed total length (TL_{flex}) as the best general index of shark size, which is measured from the "tip of the snout to the posterior tip of the tail, with the tail flexed down so that the upper lobe lies along the body midline". This is comparable to stretched total length (STL), which was measured from the tip of the snout to the precaudal notch to the tip of the caudal fin's upper lobe in its natural position. Precaudal (PCL), fork (FL), and sometimes natural total length (TL_{nat}; measured from the tip of the snout to the precaudal notch, then to a perpendicular with the posterior tip of the caudal fin's upper lobe in its natural position) were also measured. Stretched total length is presented throughout the paper unless otherwise noted.

Maturity was assessed based on the degree of clasper calcification and rotation for males [48] and the following size-at-maturity estimates for females—silky shark: >238.5 cm TL_{flex} [49]; oceanic whitetip shark: >190.6 cm STL (converted from 170 cm TL_{nat} [50] using this study's length–length relationship; Table 2); dusky shark: >235 cm FL [51]; tiger shark *Galeocerdo cuvier*: >262 cm FL [52]; and blue shark *Prionace glauca*: >185 cm FL [53]. A subset of female sharks was examined for reproductive status using ultrasonography (Ibex Pro, E.I. Medical Imaging) as described in Madigan et al. [21]. Sharks with a visible but closed umbilical scar were designated young-of-year (YOY [54,55]). Sharks were tagged with a stainless-steel dart tag (Hallprint, Victoria Harbour, Australia/United States National Marine Fisheries Service Cooperative Shark Tagging Program M-Type) in the musculature below the first dorsal fin and a rototag-style livestock tag (DuFlex, Destron Fearing, South St. Paul, MN, USA/Dalton ID Systems, Newark, Nottinghamshire, UK) in the leading edge of the first dorsal fin prior to hook removal and release. During release, shark condition was often noted following Grubbs et al. [56]. When sharks were observed, but not caught, their STL was visually estimated based on expert opinion.

Table 2. Relationships between pre-caudal (PCL), fork (FL), natural total (TL_{nat}; tip of the snout to the precaudal notch, then to a perpendicular with the posterior tip of the caudal fin's upper lobe in its natural position), and stretched total (STL; tip of the snout to the precaudal notch, then to the tip of the caudal fin's upper lobe in its natural position) length measurements (cm) for oceanic whitetip sharks *Carcharhinus longimanus* and silky sharks *Carcharhinus falciformis* caught in the eastern Bahamas. Sharks were measured in the water alongside a small vessel using a flexible tape over the body's dorsal surface.

Species	y		a		b		x	r^2	N	STL Range
Oceanic whitetip shark	PCL	=	*−6.65 (2.55)*	+	*0.93 (0.01)*	×	FL	0.97	158	92–307
	PCL		14.31 (13.73)		*0.69 (0.06)*		TL_{nat}	0.88	24	201–285
	PCL		*−16.78 (3.45)*		*0.80 (0.01)*		STL	0.96	147	92–307
	FL		*12.58 (2.56)*		*1.04 (0.01)*		PCL	0.97	158	92–307
	FL		*32.10 (13.15)*		*0.70 (0.05)*		TL_{nat}	0.89	24	201–285
	FL		*−8.65 (3.51)*		*0.85 (0.01)*		STL	0.96	147	92–307
	TL_{nat}		12.57 (18.99)		*1.28 (0.10)*		PCL	0.88	24	201–285
	TL_{nat}		−13.16 (19.76)		*1.27 (0.10)*		FL	0.89	24	201–285
	TL_{nat}		−40.97 (21.93)		*1.13 (0.09)*		STL	0.94	13	201–285
	STL		*30.56 (3.77)*		*1.19 (0.02)*		PCL	0.96	147	92–307
	STL		*19.45 (3.80)*		*1.13 (0.02)*		FL	0.96	147	92–307
	STL		*49.50 (15.62)*		*0.83 (0.06)*		TL_{nat}	0.94	13	201–285
Silky shark	PCL	=	*−2.84 (0.99)*	+	*0.93 (0.01)*	×	FL	0.99	46	94–281
	PCL		−1.12 (1.23)		*0.74 (0.01)*		STL	0.99	46	
	FL		*3.42 (1.05)*		*1.08 (0.01)*		PCL	0.99	46	
	FL		2.08 (1.42)		*0.8 (0.01)*		STL	0.99	46	
	STL		2.21 (1.64)		*1.35 (0.01)*		PCL	0.99	46	
	STL		−1.79 (1.80)		*1.25 (0.01)*		FL	0.99	46	

Linear regression coefficients for the model $y_i = a + bx_i$. Numbers in parentheses are standard errors. Italics denote $p < 0.05$.

2.5. Data Analysis

Count data per longline set at NES were analyzed using Bayesian generalized linear models in the R-INLA package with an offset of log (hook minutes) and various model families (e.g., Poisson, negative binomial) [57]. Count data were also reduced to presence/absence by set and analyzed using logistic regression. However, due to low catches, the models fit poorly, and no predictor variables (e.g., survey type (shallow or deep), fishing site (north, middle, south), time of day (day or night), sea surface temperature (SST)) had significant effects. As such, descriptive analyses of longline catch data were preferred, and catch-per-unit-effort (CPUE) in the form of catch hook^{-1} h^{-1} or catch per 1000 hooks was reported. Trends in catch relative to hook size, bait type, leader type, and gangion depth (estimated as maximum possible depth if the line were stretched vertically) were described. Differences in the number of catches of all fishes, as well as shark and teleost components, were tested between wire–mullet and monofilament–squid gangions using χ^2 tests.

Species-specific catch data were summarized at each site. Baiting practices were poorly standardized due to variable wind, current speed, and bait quantity and quality among other factors; thus, direct comparisons of baiting-derived CPUE (# sharks caught or observed per baiting day) were omitted, but large-magnitude differences in relative abundance were qualitatively considered between sites. Species-specific catches for species with $n > 30$ at a given site were tested for a departure from a 1:1 sex ratio using χ^2 tests. Catches from all sites were then grouped to examine species-specific population characteristics. Length-to-length conversion formulas were estimated for combined sexes using linear regression between all available measurement types (PCL, FL, TL_{nat}, and STL) for the oceanic whitetip shark and silky shark. Stretched total length was also compared between females and males using a Mann–Whitney *U* test.

Lastly, growth rates of oceanic whitetip sharks were examined using measurements taken after >345 days at liberty (DAL; i.e., measured during distinct annual expeditions). If an individual was measured multiple times during the same expedition, the mean of those measurements was taken to represent its length that year. Sometimes, multiple but distinct growth measurements were used from the same individual recaptured repeatedly. One growth measurement that was outside the bounds of reasonable error was omitted. Normality was confirmed using Shapiro–Wilk tests, and homogeneity of variance was confirmed by examining residual plots. The relationship between STL at first capture and annual growth rate was described using linear regression. Adult growth rate was also estimated for recaptured individuals using linear regression of STL and years at liberty (YAL [58]). Importantly, tagged individuals were sometimes prioritized for capture to collect growth data when they appeared; as such, recapture rate estimates were positively biased. All analyses were conducted in R Version 3.6.3 [59].

3. Results

3.1. North-Eastern Exuma Sound

3.1.1. Pelagic Longline Survey: Effort and Catch

Fifty-five deep longlines were fished from September 2018 to October 2019 for a total of 12,572 hook hours split between fishing sites (4190.6 ± 536.7 hook h per site; mean ± SD), months (4.6 ± 1.8 sets per month), and time of day ($n_{\text{day}} = 43$, $n_{\text{night}} = 12$). The maximum depth of fishing ranged from 397 to 419 m (408 ± 15 m), and the minimum temperature ranged from 16.8 to 17.8 °C (17.3 ± 0.7 °C). Sea surface temperature ranged from 23.4 to 32 °C (27.9 ± 2.0 °C). Fifteen individuals of nine species, comprising more sharks ($n = 9$) than teleosts ($n = 6$; Table 3), were captured. Silky sharks and tiger sharks were the most common ($n = 3$ of each species; i.e., 20% of catch, respectively). Catch-per-unit effort was very low for sharks and teleosts combined (0.001 fishes hook^{-1} h^{-1}). The one oceanic whitetip shark captured via this survey was a female with a visible, well-healed umbilical scar, suggesting it was YOY at 92 cm STL [60]. It was captured in October.

Eighteen shallow longlines were fished from October 2019 to March 2020 for a total of 4022 hook hours split between fishing sites (1340.6 ± 227.6 hook h per site) and months (3.0 ± 0.6 sets per month) during daylight hours. The maximum depth of fishing ranged from 94 to 147 m (121 ± 19 m), and the minimum temperature ranged from 21.9 to 26.0 °C (24.3 ± 1.2 °C). Sea surface temperature ranged from 24.2 to 31.1 °C (26.9 ± 1.8 °C). Five species were captured, each represented by a single individual (Table 3). Catch-per-unit effort for sharks and teleosts combined was very low (0.001 fish hook^{-1} h^{-1}).

Across shallow and deep surveys combined, there was no difference between the number of catches on wire leaders baited with mullet and monofilament leaders baited with squid for all fishes ($\chi^2 = 2.6$, df = 1, $p > 0.05$), sharks only ($\chi^2 = 2.3$, df = 1, $p > 0.05$), or teleosts only ($\chi^2 = 0.5$, df = 1, $p > 0.05$). All sharks but one were caught on 14/0 or 16/0 hooks. Teleosts were caught on all hook sizes. Most fishes with a recorded hooking location (77.8%, $n = 14$ of 18) were hooked in the corner jaw; others were hooked in the throat or gut (16.7%, $n = 3$ of 18) or head (5.6%, $n = 1$ of 18). Nearly all captures with estimated hooking depths (93.3%, $n = 14$ of 15) occurred <75 m deep, including the mesopelagic snake mackerel *Gempylus serpens* and oilfish *Ruvettus pretiosus*, which were caught at night in the top 10 m. In January and February (25.4 ± 0.8 °C SST) of each year, unicorn filefish *Aluterus monoceros* appeared in large schools and often followed the longline during haulback. The mean number of baits lost per hook per hour of fishing was 5.6 times higher during this period (0.08 ± 0.09 baits hook^{-1} h^{-1}) compared to other months (0.01 ± 0.01 baits hook^{-1} h^{-1}); it was unclear whether bait was removed during or prior to haulback. On occasion, large schools of small tunas (Scombridae: Thunnini) and schools of mahi-mahi *Coryphaena hippurus* were observed near longlines, but not caught.

Table 3. Catch composition and catch-per-unit effort (CPUE) for shallow (targeting 0 to 120 m; n = 18 sets) and deep (targeting 0 to 400 m; n = 55 sets) longline surveys at three sites in open-ocean habitats in north-eastern Exuma Sound, The Bahamas (NES) from 2018 to 2020.

Common Name	**Scientific Name**	**N Shallow**	**N Deep**	**% Total Catch**	**% Female**	**Mean STL ± SD (cm)**	**Shallow NES CPUE (n/hook/h)**	**Deep NES CPUE (n/hook/h)**	**NES CPUE 2018–2020 (n/1000 hooks)**
Silky shark	*Carcharhinus falciformis*	1	3	20	25	115.9 ± 5.9	0.000249	0.000239	0.77
Tiger shark	*Galeocerdo cuvier*	1	3	20	67	252 ± 72.5	0.000249	0.000239	0.77
Dusky shark	*C. obscurus*	1	2	15	67	274.7 ± 46.5	0.000249	0.000159	0.58
Oceanic whitetip shark	*C. longimanus*	0	1	5	100	92	0	0.000080	0.19
Sharks		*3*	*9*	*60*	*54.5*	*199 ± 89.3*	*0.000746*	*0.000716*	*2.32*
Great barracuda	*Sphyraena barracuda*	1	2	15		98.7 ± 7.8	0.000249	0.000159	0.58
Mahi-mahi	*Coryphaena hippurus*	1	1	10		108.5 ± 3.5	0.000249	0.000080	0.39
Snake mackerel	*Gempylus serpens*	0	1	5		70.2	0	0.000080	0.19
Oilfish	*Ruvettus pretiosus*	0	1	5		43.5	0	0.000080	0.19
Cottonmouth jack	*Uraspis secunda*	0	1	5		-	0	0.000080	0.19
Teleosts		*2*	*6*	*40*		*89.5 ± 24.5*	*0.000497*	*0.000477*	*1.55*
Total		*5*	*15*	*100*		*158.6 ± 89.5*	*0.001243*	*0.001193*	*3.87*

3.1.2. Baiting and Other Techniques: Effort and Catch

Eleven sharks were caught while baiting open-ocean habitats at NES on 35 occasions ($n_{\text{day}} = 30$, $n_{\text{night}} = 5$). Ten were silky sharks (90.9%), and one was a lemon shark *Negaprion brevirostris* (9.1%, $n = 1$ of 11), which was caught while baiting at night 1.5 km from the insular-shelf wall during a drift that began over shallow reef. One immature female silky shark was recaptured 5.5 km from its initial capture location after 339 days.

Eleven sharks were encountered while conducting other research offshore. These comprised silky sharks (54.5%, $n = 6$ of 11), dusky sharks (18.2%, $n = 2$ of 11), oceanic whitetip sharks (18.2%, $n = 2$ of 11), and a tiger shark (9.1%, $n = 1$ of 11). Length and demographic information for all sharks captured or observed using all survey methods combined at NES appears in Table 1.

3.1.3. Multispecies Associations

Some (14.7%, $n = 5$ of 34) of the sharks caught on longline surveys ($n = 1$ of 12) or observed opportunistically in the absence of bait ($n = 4$ of 11) at NES were within tens of meters of short-finned pilot whales (group size: 6 to 22 individuals; Table 4). No sharks that were observed while baiting were associated with short-finned pilot whales ($n = 0$ of 11). On one occasion, pilot whales and pantropical spotted dolphins *Stenella attenuata* appeared near a longline soon after it was set. It was assumed that an immature female silky shark caught on that line was associated with the cetaceans. Among oceanic shark species (silky, dusky, and oceanic whitetip sharks), 17.9% ($n = 5$ of 28) of individuals and 37.5% ($n = 3$ of 8) of mature individuals were observed or caught near pilot whales. All silky sharks alongside pilot whales were immature, whereas all dusky sharks and oceanic whitetip sharks were mature. At least one oceanic shark was observed on 37.5% ($n = 3$ of 8) of occasions when a group of pilot whales was observed. Two mature silky sharks (~240 cm STL; $n = 1$ male, 1 female) and one mature dusky shark (~260 cm STL, male) were also observed alongside tunas (Table 4). Most mature oceanic sharks at NES (75%, $n = 6$ of 8) were caught or observed alongside short-finned pilot whales or tunas. This is likely an underestimate of the true number of sharks associated with observed pods or schools.

Table 4. Opportunistic observations of multispecies groups of sharks and cetaceans or tunas in oceanic habitats in north-eastern Exuma Sound (2014–2020) and off Columbus Point, Cat Island, The Bahamas (2020). Length measurements are expressed as stretched total length (STL) and '~' denotes an in-water STL estimate.

Site	Shark Species 1	Shark Species 2	Other Species 1	Other Species 2
Northeast-ern Exuma Sound	Oceanic whitetip shark (*Carcharhinus longimanus*), $n = 2$: 1 mature male (~210 cm), 1 mature female (~190 cm)	Dusky shark $n = 1$, mature male, ~300 cm	Short-finned pilot whale (*Globicephala macrorhynchus*) $n > 15$	-
	Silky shark (*C. falciformis*) $n = 1$, immature (~110 cm)	-	Short-finned pilot whale $n = 22$	-
	Silky shark $n = 1$, immature female (124 cm)	-	Short-finned pilot whale $n = 6$	Pantropical spotted dolphin (*Stenella attenuata*) $n = 8$
	Silky shark $n = 2$: 1 mature female (~240 cm), 1 mature male (~240 cm)	-	Tunas (Thunnini) $n > 25$	-
	Dusky shark (*C. obscurus*) $n = 1$, mature male (~260 cm)	-	Tunas $n > 25$	-
Columbus Point, Cat Island	Silky shark $n = 2$: 1 immature (160 cm), 1 immature (220 cm)	Whale shark (*Rhincodon typus*) $n = 1$, mature male (>9 m)	Skipjack tuna (*Katsuwonus pelamis*) $n > 20$, Blackfin tuna (*Thunnus atlanticus*) $n > 20$, Yellowfin tuna (*Thunnus albacares*) $n > 20$	Anchovies (Engraulidae) $n > 1000$
	Silky shark $n = 1$, mature male (260 cm)	-	Tunas $n > 25$	-

3.2. Columbus Point, Cat Island

3.2.1. Baiting: Effort and Catch

Open-ocean habitats at CI were baited on 62 days, the majority of which (77.4%, n = 48 of 62) were in May. Fewer baiting days (22.6%, n = 14 of 62) occurred in April, June, or July. Effort was highest in 2011–2014 (n = 36 total baiting days) and lower in 2015–2020 (n = 26 total baiting days). Mean sea surface temperature was 25.1 ± 1.1 °C (range: 23.7 to 27.8 °C). Baiting occurred for a mean of 351 ± 132 min per day (n = 16 days measured).

On 208 occasions (n = 166 captures, 42 sightings), 138 individual sharks were documented. The at-vessel mortality rate of captured sharks was 0%, and only three individuals of those assessed for release condition (2.4%, n = 3 of 126) were given a score of 'poor'. Although only one of two female blue sharks was larger than the estimated female size at maturity, both had putative mating wounds (see [61]).

Oceanic whitetip sharks dominated captures and sightings at CI (89.9%, n = 187 of 208; Table 1). Their mean time of first arrival during targeted baiting was 98 ± 82 min (n = 17 days measured). Mean oceanic whitetip shark length (n = 117 individuals; n = 147 measurements including recaptured individuals in distinct years) was 245 ± 23 cm STL (Table 1). Most oceanic whitetip sharks (83.8%, n = 98 of 117) were female, resulting in a female-biased sample (female:male ratio = 5.2:1; χ^2 = 53.3, df = 1, $p < 0.05$). Ultrasound data collected in unique years, but sometimes for the same individuals, showed that females were often gravid (65.7%; n = 46 of 70 examined for pregnancy), and gravid females were present in all months when ultrasound data were collected (April, May, and July). Putative bullet wounds were observed on two oceanic whitetip sharks (1.3%, n = 2 of 149 captures). Both were on the head; one appeared to be from a shotgun or bang stick and the other from a single bullet. Thirteen hooks and one trolling lure were also removed from oceanic whitetip sharks (6.7%, n = 10 of 149 captures), and one hook was removed from a silky shark (6.6%, n = 1 of 15 captures).

At least 20.5% of oceanic whitetip sharks (n = 24 of 117 individuals) were recaptured at CI. However, seven individuals were also captured with clear evidence of total tag loss. If we assume that none of those individuals had already been recaptured, the recapture rate could be as high as 26.5% (n = 31 of 117 individuals). A higher percentage of total oceanic whitetip shark records (38%, n = 71 of 187), as opposed to individuals, represented recapture or resighting events. However, these estimates were positively biased due to our targeted capture of tagged sharks, and we interpret them insofar as a meaningful number of oceanic whitetip sharks exhibit site fidelity to CI.

Nearly all recaptured or resighted sharks were female (n = 30 females, 1 male), and nearly all recapture or resighting events were of females (n = 70 female, 1 male). Across the tag histories of 27 individuals, 36 recaptures and 28 resighting events were documented (Figure 3). Sharks were recaptured or resighted at the following frequencies: 12 sharks one time, 4 sharks two times, 6 sharks three times, 3 sharks four times, 1 shark six times, and 1 shark eight times. Days at liberty between the first capture and final recapture or resighting event ranged from 3 to 1823 (768 ± 623 days; mean ± SD), with four sharks recaptured after approximately five years at liberty. The number of unique years during which each individual was observed ranged from 1 to 5 (2.3 ± 1.1 years), with 7 individuals observed in only one year, 11 individuals observed in two years, 4 individuals observed in three years, 4 individuals observed in four years, and 1 individual observed in five years. Twelve sharks were observed in consecutive years, including seven in two consecutive years, two in three consecutive years, and three in four consecutive years (Figure 3).

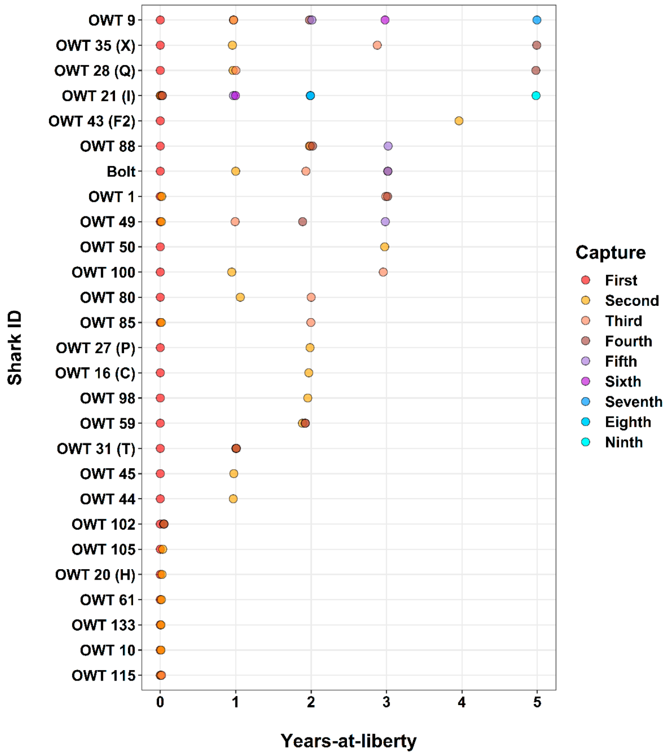

Figure 3. Recapture (n = 36) and resighting (n = 27) events of 27 oceanic whitetip sharks *Carcharhinus longimanus* at Columbus Point, Cat Island, The Bahamas from 2011 to 2018. Shark ID 'OWT 45′ was the only male; all others were female. Fishing occurred only in March, April, and/or May of each year; no fishing occurred between annual expeditions. First captures/sightings were aligned with 0 years-at-liberty. Some recapture and resighting events were overlaid due to consecutive observations days apart.

3.2.2. Multispecies Associations

Two multispecies associations involving oceanic sharks were observed at CI in 2020 (Table 4). Two silky sharks were observed at a large surface boil that included tunas, various seabirds, and a mature male whale shark *Rhincodon typus* with claspers that extended well past the pelvic fins [62] feeding on a shoal of anchovies (Engraulidae). Silky sharks did not feed during the observation. Separately, after baiting CI for multiple hours during which no sharks appeared, a large school of tunas began feeding at the surface near the boat; a mature male silky shark (260 cm TL) was then captured within minutes.

3.3. San Salvador Seamount and Mayaguana

During seven days of baiting at SSSM in 2019–2020, more silky sharks (61%, n = 14 of 23) were caught or observed than oceanic whitetip sharks (39%, n = 9 of 23; Table 1). Oceanic whitetip sharks were only caught or observed in January and February, when most mature females were gravid (67%; n = 2 of 3 examined for pregnancy); no oceanic whitetip sharks were observed during one day of baiting in September.

During two days of baiting and fishing one epipelagic longline for 3 h 28 min off Mayaguana in July 2019 (SST: 30 °C), three barracuda, one wahoo *Acanthocybium solandri*, one silky shark, and five oceanic whitetip sharks were caught (Table 1). Two of the three mature female oceanic whitetip sharks that were examined for pregnancy were gravid.

3.4. All Sites: Species-Specific Catch Characteristics

3.4.1. Silky Shark

There was no significant difference in STL between female (range: 94–281 cm STL, median = 145 cm STL) and male silky sharks (range: 110–262 cm STL, median = 154 cm STL;

Mann–Whitney *U* test, $p > 0.05$; Figure 4a). There were significant length-to-length relationships with high r^2 values (≥ 0.99) that allow for conversions between length measurements (Table 2). In immature males with clasper measurements ($n = 8$; range: 114–187 cm STL), mean inner clasper length was 8.2 cm ± 2.5 cm (range: 4.5–12 cm), and mean outer clasper length was 4.8 ± 2.1 cm (range: 2.5–9 cm). One mature male (262 cm STL) had inner and outer clasper length measurements of 29 and 19 cm, respectively. One female silky shark at NES grew 25.5 cm yr^{-1} STL (19.1 cm yr^{-1} PCL) from an estimated 2 to 3 years of age (Table S1; [49]).

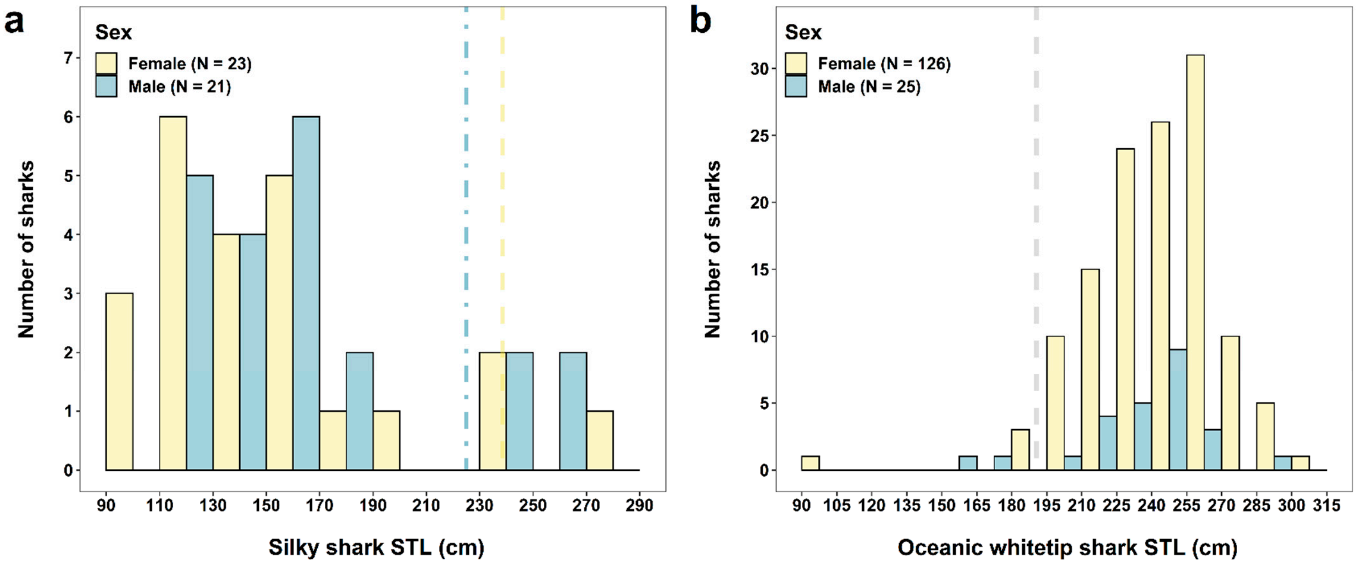

Figure 4. Stretched total length (STL) frequencies of (**a**) silky sharks *Carcharhinus falciformis* and (**b**) oceanic whitetip sharks *Carcharhinus longimanus* measured at four sites in the eastern Bahamas: north-eastern Exuma Sound, Columbus Point (Cat Island), San Salvador Seamount, and Mayaguana. Females appear in yellow, and males appear in blue. For silky shark, approximate female size at maturity (238.5 cm TL_{flex}) is shown as a yellow dashed line, and approximate male size at maturity (225 cm TL_{flex}) is shown as a blue dot-dashed line [49]. For oceanic whitetip shark, approximate size at maturity for both males and females (190.6 cm STL; converted from 170 cm TL_{nat} [50] using this study's length–length relationship) is shown as a grey dashed line.

3.4.2. Oceanic Whitetip Shark

There was no significant difference in STL between female (range: 92–307 cm STL, median = 246 cm STL) and male oceanic whitetip sharks (range: 158–285 cm STL, median = 241 cm STL; Mann–Whitney *U* test, $p > 0.05$; Figure 4b). There were significant length-to-length relationships with high r^2 values (≥ 0.88; Table 2). One immature male (158 cm STL) had inner and outer clasper length measurements of 7 and 5 cm, respectively. In mature males with clasper measurements ($n = 15$; range: 216–285 cm STL), mean inner clasper length was 24.9 cm ± 1.8 cm (range: 23–28 cm), and mean outer clasper length was 19.3 ± 1.7 cm (range: 17–23 cm).

Growth was measured after >345 DAL (mean ± SD: 793 ± 471 days, range: 346–1822 days) in 18 adult oceanic whitetip sharks ($n = 17$ females, 1 male) captured at CI on 22 occasions ($n = 21$ female, 1 male; Table S1). The maximum growth rate was 15.4 cm yr^{-1} STL (15.6 cm yr^{-1} PCL) for a female recaptured after nearly 1 year at liberty. The minimum, non-negative growth rate was 1.5 cm yr^{-1} STL (-2.5 cm yr^{-1} PCL) for a female recaptured after two years at liberty. Annual growth rate decreased as initial shark STL increased ($r^2 = 0.38$, $F_{1,18} = 12.8$, $p < 0.05$). Adult growth rate was described using the formula $\text{Growth}_{\text{STL (cm)}} = 5.39 \times \text{YAL} - 4.18$ ($r^2 = 0.21$, $F_{1,18} = 6.0$, $p < 0.05$), suggesting a growth rate of 5.4 cm yr^{-1} STL (Figure 5).

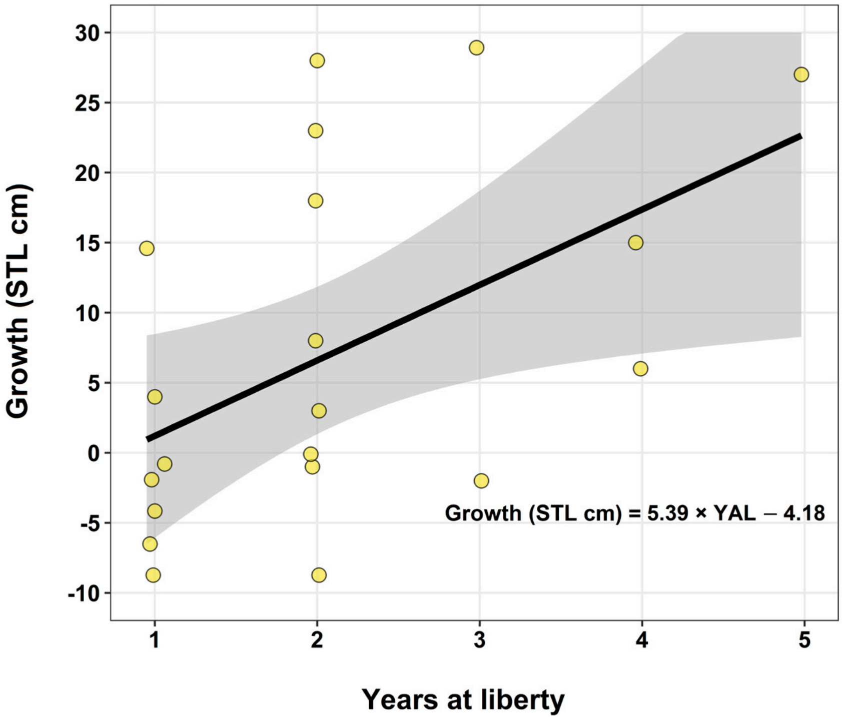

Figure 5. Linear regression between growth in stretched total length (STL cm) and years at liberty for adult oceanic whitetip sharks *Carcharhinus longimanus* (n = 19 females, 1 male) recaptured at Columbus Point, Cat Island, The Bahamas from 2011 to 2018. Yellow circles represent growth of individual sharks (where negative growth indicates measurement error), the grey ribbon indicates the confidence interval around the regression line, and the equation describing annual growth (STL cm yr^{-1}) appears at the bottom right, where YAL stands for years at liberty.

4. Discussion

4.1. Variable Species-Specific Conservation Value of Sites in the Eastern Bahamas

Comparisons between shark catches in our NES longline survey and surveys of shark bycatch in U.S. Atlantic pelagic longline fisheries [63,64] suggest NES hosts a typical shark assemblage at low relative abundance for an oligotrophic open-ocean habitat in the subtropical western North Atlantic Ocean. However, qualitative comparisons of catches from targeted baiting at our four study sites suggest the relative abundance of silky sharks and oceanic whitetip sharks varies dramatically over relatively small spatial scales in the eastern Bahamas and that CI and possibly SSSM are remarkable aggregation sites for these species.

The rarity of oceanic sharks at NES is not due to local fishing; The Bahamas reported few commercial shark catches even prior to the longline ban (1993) and Shark Sanctuary designation (2011) [65]. Some species that were caught infrequently at NES are more common in other habitat types; tiger sharks, for example, are commonly caught on shallow banks adjacent to the open-ocean sites surveyed in this study [39]. Other species, such as blue sharks and shortfin mako sharks *Isurus oxyrinchus*, were occasionally recorded in the eastern Bahamas in this study and elsewhere (e.g., [66]), but are poorly studied in the region, less common than other species, and/or less likely to be detected by baiting at the surface given their regular use of cooler, deeper, and/or temperate waters [61,64,66]. Although night shark *C. signatus* and scalloped hammerhead *Sphyrna lewini* were among the most abundant semi-oceanic sharks off eastern Florida in 1981–1983 [63], their abundances may have declined over time [63,64,67,68], and we suspect these species are very rare at NES given their absence from our longline catches. They may occur at other study sites in the eastern Bahamas at higher relative abundance than we detected through baiting alone; for example, scalloped hammerheads have been reported by divers off San Salvador (Y.

Papastamatiou pers. obs.). The dusky shark—the largest carcharhinid and among the largest sharks in this region—also appears to be rare in the eastern Bahamas, although we did occasionally catch adults. Given overfishing and the high vulnerability of dusky sharks to longline fishing elsewhere in the western North Atlantic Ocean [69–72], there is likely regional conservation value in large adults finding refuge from fishing in the eastern Bahamas.

Silky sharks appear to be far more common at SSSM (14 silky sharks in 7 days of baiting in January, February, and September) than at NES (10 silky sharks in 35 days of baiting in all seasons) or CI (15 silky sharks in 62 days of baiting in April–July). Our understanding of silky shark ecology is limited in the western Atlantic Ocean despite the silky shark being among the most common shark species caught by pelagic fisheries in the region [1,64,73]. We mostly caught juveniles (i.e., 110–170 cm STL, ~1–5 years of age; [49,74]), which also dominate pelagic longline and purse seine fishery catches elsewhere in the Caribbean Sea and Atlantic Ocean [3,29,64,73] and are common off north-western Cuba [1]. We caught no neonates (60–77 cm STL [49]) or YOY (<98 cm STL [49]) with a visible umbilical scar, although our smallest record of 94 cm STL at NES was probably less than one year old [49,74]. Neonates are rarely caught offshore, but some silky sharks as small as 60 cm STL are caught as bycatch on bottom longlines targeting reef fishes in the U.S. Gulf of Mexico [75], which supports the hypothesis that silky sharks spend their first months living a benthopelagic lifestyle on deep reefs along the outer shelf edge before transitioning to a pelagic lifestyle in oceanic habitats [74,76–78]. If silky sharks go through a benthopelagic-shelf stage in the eastern Bahamas, it is most likely to occur at SSSM or a similar submerged platform, because intermediate depths elsewhere are compressed into near-vertical walls that delineate shallow reefs (0–30 m) and the deep open ocean (>200 m). Seamounts may attract silky sharks to abundant, vulnerable, or accessible prey [28,79] and provide some refuge from predators. For example, a large school (>12 individuals) of juvenile silky sharks has been observed at Tartar Bank, a shallow seamount at the western edge of southern Cat Island (S. Williams pers. obs.). Alternatively, juveniles may recruit to the eastern Bahamas following a brief benthopelagic-shelf stage elsewhere, but then appear to be restricted to either a benthopelagic lifestyle at the only intermediate depths available (e.g., at seamounts) or a pelagic lifestyle in the open ocean, often in association with floating structure. The lack of juvenile refuge in oceanic habitats and subsequent predation risk may select for fast early growth [80,81], which we recorded for one silky shark that was recaptured at NES after growing 24 cm STL in nearly one year. This local recapture suggests some degree of site fidelity or residency. Juvenile schooling behavior may also be adaptive in these habitats [74,80]; we did observe a school of four juveniles (94–144 cm STL) at the surface in deep water (~600 m) at NES. Like elsewhere, we found that silky sharks also associate with tunas offshore [8,82]. More information on the diet, movement, and habitat associations of silky sharks through ontogeny is required to better understand the silky shark life cycle in the western Atlantic Ocean.

Oceanic whitetip sharks were nearly absent from NES, whereas they were incredibly common at CI in at least April–May, when multiple individuals were routinely attracted to bait in less than two hours. Oceanic whitetip sharks were sufficiently abundant at CI to deploy satellite tags on 11 individuals during a one-week expedition in 2011 [23], collect tissue samples for stable isotope analysis from 19 individuals during a 10-day expedition in 2014 [21], and collect tissue samples to quantify mercury concentrations from 27 individuals during a 10-day expedition in 2017 [83]. Comparisons to areas outside of The Bahamas further indicate high relative abundance of oceanic whitetip sharks at CI; for example, during just two days of baiting at CI in May 2013, we caught more oceanic whitetip sharks (n = 16) than were caught in 111 longline sets fishing more than 13,799 hooks targeting swordfish off Florida's east coast from 1981 to 1983 (n = 13 [63]). Similarly, we recorded more oceanic whitetip sharks during all short expeditions to CI than were recorded in the landings of around 400 pelagic longline sets targeting large teleosts and sharks off Cojímar, Cuba from 2011 to 2019 [1]. The true relative abundance of oceanic whitetip sharks at CI is even higher than suggested by these comparisons because sometimes we only recorded data for captured sharks as opposed to all sharks in the area.

Most of the oceanic whitetip sharks at CI were large, gravid, adult females, many of which exhibited site fidelity to CI [21,23] despite being highly migratory [23]. Very large (i.e., >250 cm STL) female oceanic whitetip sharks are rarely caught elsewhere [1,14,50,84,85], but they dominated our catches in the eastern Bahamas, confirming previous findings that oceanic whitetip sharks exhibit geographical sexual segregation [84]. These catches included one female that measured 307 cm STL, which may be the largest contemporary record worldwide [14,86]. Adult females larger than 300 cm STL could be more than 30 years old according to growth parameters estimated in the southwestern Atlantic Ocean (Figure S1 [85]). Although we did not estimate longevity, we did find a record of a uniquely identifiable female ("Bolt") in documentary footage from CI that was released in 2006 (Canabal D, Canabal V, 2022, personal communication). Based on its size, Bolt would have been, at a minimum, 6–7 years old [85]. We resighted Bolt ten years later, in 2016, suggesting it was already at or beyond the estimated longevity of oceanic whitetip sharks (11–19 years [14]). Large adults grow slowly as they approach the species' estimated asymptotic mean length at age (284.9 cm TL_{nat} [85]), suggesting our estimated growth rate of 5.4 cm STL yr^{-1} was reasonable for adults between 213 and 288 cm STL (Figure S1 [85]). Female length is positively correlated with litter size [84,87]; thus, the eastern Bahamas, particularly CI, hosts oceanic whitetip sharks with high reproductive value to the western Atlantic population [88]. Gravid females at CI may give birth north of The Bahamas [89], off northern Cuba [1], in the northern Lesser Antilles, and/or in the Windward Passage [23,90], highlighting the need for multinational management of this population.

It is unclear what mechanisms underpin the apparent spatial variability in species-specific relative abundance of oceanic sharks in the eastern Bahamas. We hypothesize that a combination of environmental factors (e.g., bathymetry, tidal flow, currents) acting over multiple temporal and spatial scales may enhance foraging opportunities that lead to the formation of predictable oceanic shark hotspots [91–93]. Indeed, oceanic predators can be attracted to foraging areas [94,95] where environmental characteristics (e.g., local bathymetry, ocean currents, on-shelf reef area [93]) enhance bottom–up processes [96,97] that attract potential prey [98,99]. For example, abundant pelagic teleost prey may attract wide-ranging oceanic whitetip sharks to CI in April–May, after which the high density of sharks may facilitate and coincide with mating in summer [21–23]. We encourage future research to clarify (1) temporal shifts in shark diversity, relative abundance, and demographic structure at apparent aggregation sites and (2) spatial variation in relative abundance between sites. A standardized, temporally and spatially balanced, pelagic baited remote underwater video survey conducted alongside an assessment of environmental characteristics would be useful in this regard [100].

4.2. Multispecies Associations

We observed oceanic whitetip sharks associating with short-finned pilot whales in The Bahamas, as they do in the Pacific [31,101–104], and extended this association to dusky sharks and silky sharks [8]. We also observed shark–tuna associations similar to those off northern Cuba and Honduras [26,105]. Most of these associations are probably best described as mixed-species groups, where the ephemeral presence and synchronized arrival and departure of multiple species is not clearly tied to a shared resource or environmental cue [32].

Mixed-species groups may provide oceanic sharks with food subsidies through facilitation (by cetaceans and tunas) and/or direct predation (of tunas, but not cetaceans [8,21,30,82,84,106,107]), thereby increasing oceanic shark foraging efficiency in oligotrophic, food-limited habitats [33]. At CI, for example, we witnessed an oceanic whitetip shark accelerate rapidly towards the surface through a school of tuna at 15 to 20 m deep in an apparent feeding attempt (S. Williams pers. obs.). It is also widely hypothesized that cetaceans, which have high metabolism and feeding rates, facilitate oceanic shark foraging on shared prey [108,109] by locating prey at depth, herding prey, or providing substantial food subsidies (e.g., regurgitated remains, food scraps, or feces), particularly at the sea surface [102,103,109]. This foraging advantage hypothesis is supported by overlapping dive profiles [26,110–112] and similar muscle stable isotope values between oceanic whitetip sharks and short-finned pilot whales [21], which suggest they may share mesopelagic prey such as squids. Additionally, juvenile silky sharks have been observed feeding on short-finned pilot whale feces in a large multispecies group (n = 10–12 silky sharks, 60 short-finned pilot whales, 12 rough-toothed dolphins *Steno bredanensis*) in the central Bahamas (Claridge D, Dunn C, 2022, personal communication). Considering few observations of large oceanic sharks at NES and that at least 75% of those observations involved short-finned pilot whales or tunas, whereas solitary, large oceanic sharks were more often observed at other sites where prey may be more abundant (e.g., Cat Island [21]), we question whether the relative importance of these associations to oceanic sharks is positively correlated with shark size and negatively correlated with prey availability.

4.3. Conclusions

Although poorly studied, highly threatened oceanic sharks [6,15,71] are protected from longline fishing and shark fishing throughout the Bahamian EEZ, their species-specific relative abundance varies across shelf-edge, open-ocean habitats within the eastern Bahamas. Whereas there are few oceanic whitetip sharks and silky sharks off a typical insular-shelf wall at NES, preliminary data suggest they are more common at SSSM and perhaps Mayaguana. Most importantly, CI is clearly a unique fixed feature that attracts an important demographic (large, often gravid females) of wide-ranging oceanic whitetip sharks year after year in at least April–May; we are unaware of other sites with such high contemporary abundance of adult oceanic whitetip sharks in the western Atlantic Ocean. This site also meets multiple life-history criteria for an ISRA designation [19], and the Cat Island community has proposed that CI be designated a multi-use marine protected area to manage current uses, including economically important shark-dive tourism [113] and recreational fishing [35,114]. Unfortunately, however, Bahamian fisheries regulations are rarely enforced [115], and marine species at CI are threatened by uncontrolled use, foreign poaching, and illegal fishing [114]. Indeed, we found evidence of harmful and sometimes illegal human–shark interactions, such as retained hooks and lures in shark mouths and putative bullet wounds on oceanic whitetip sharks, which may suggest recreational fisher retaliation to shark depredation [21]. Given that slow-growing, highly threatened species are particularly vulnerable to unsustainable fishing at aggregation sites [116], we suggest The Bahamas directs its limited fisheries management resources and surveillance capabilities [115] towards the enforcement of existing shark fishing regulations at CI and other shark aggregation sites.

Supplementary Materials: The following supporting information can be downloaded at: https://www.mdpi.com/article/10.3390/su16010200/s1, Table S1. Growth of mature oceanic whitetip sharks *Carcharhinus longimanus* (n = 22) recaptured at Columbus Point, Cat Island and one immature silky shark *Carcharhinus falciformis* recaptured at northeastern Exuma Sound, in the eastern Bahamas. Figure S1. Oceanic whitetip shark *Carcharhinus longimanus* growth (TL_{nat} cm; converted from STL using the equation from this study; Table 2) measured between capture (red circles) and recapture (orange circles) events from 2011 to 2018 at Columbus Point, Cat Island, The Bahamas, where TL_{nat} at first capture was substituted into the von Bertalanffy growth equation generated from observed length-at-age data (solid line; [85]) to estimate age at capture, and age at recapture was then calculated by adding the known years at liberty. A similar growth equation generated from back-calculated lengths (dashed line; [85]) is provided for additional context.

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Data Availability Statement: Data are available upon reasonable request to the corresponding author.

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Conflicts of Interest: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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