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REVIEWS

The biology and conservation status of the oceanic whitetip shark (*Carcharhinus longimanus*) and future directions for recovery

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Abstract The oceanic whitetip shark (*Carcharhinus longimanus*) was once considered one of the most abundant and ubiquitous pelagic shark species in tropical seas globally. However, over the last several decades, the oceanic whitetip has experienced substantial population declines throughout its range due to fishing pressure and utilization in the international fin trade. In recent years, a significant amount of research has been undertaken on this species, revealing new information on life history, movements and behavior, and threats to the species. Additionally, a recent surge of protective measures has been implemented for the oceanic whitetip shark, both internationally and nationally. These include (but are not limited to) retention prohibition measures in every major tuna Regional Fishery Management Organization (RFMO), its listing in Appendix II of the Convention on International Trade in Endangered Species of Wild Flora and Fauna (CITES), and its listing under the U.S. Endangered Species Act (ESA) as a threatened species. However, despite its global distribution and common occurrence in many commercial fisheries in tropical waters, little is still known regarding the oceanic whitetip shark's biology and population status. Therefore, we summarize what is known on the biology and conservation of the oceanic whitetip shark, identify information gaps, and discuss future directions for recovery of this imperiled species.

Keywords Fisheries · Threatened species · Endangered Species Act · Pelagic shark

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Introduction

The oceanic whitetip shark is a large, pelagic predatory shark, described historically as one of the most abundant shark species in tropical waters worldwide (Mather and Day 1954; Backus et al. 1956; Compagno 1984). During exploratory research surveys in the 1950s in the Gulf of Mexico, historical accounts of the oceanic whitetip described the species as "remarkably persistent", noting that several individuals often gathered at the surface around longlines, persistently investigated baited hooks, and occasionally attacked dead or dying tuna before they were hauled in. These sharks were so prevalent and persistent, even attempts to drive them away by using underwater explosives were largely unsuccessful (Backus et al. 1956). According to logbook data of some Japanese institutional tuna longline vessels operating in the eastern Pacific from 1967 to 1968, the oceanic whitetip comprised 21.3% of the total shark catch (Taniuchi 1990). In scientific surveys conducted in the 1950s by the National Marine Fisheries Service (NMFS), oceanic whitetip sharks were the third most abundant of the 21 species most frequently caught in the study region of the tropical Pacific (Ward and Myers 2005). However, since those historical observations were made, the oceanic whitetip shark has experienced significant declines in abundance throughout its global range (e.g. Young et al. 2017; Rigby et al. 2019). As a common bycatch species in pelagic fisheries globally, only recently has the oceanic whitetip shark received much attention in terms of regulatory and management protections, both internationally and nationally (Young et al. 2017). Therefore, as this species is likely one of the most threatened pelagic shark species, with a designation of "Threatened" under the U.S. Endangered Species Act (ESA) (83 FR 4153; January 30, 2018) and recent classification as Critically Endangered on the International Union for the Conservation of Nature (IUCN) Red List (Rigby et al. 2019), the purpose of this overview will be to provide a comprehensive summary of the biology and conservation status of the species, as well as a discussion of future directions necessary for recovery.

Taxonomy and species description

The oceanic whitetip belongs to the family Carcharhinidae and is a member of the genus *Carcharhinus*. It has a stocky build, with a short and bluntly rounded nose and small circular eyes. The oceanic whitetip has a large rounded first dorsal fin, and very long, wide paddle-like pectoral fins (Compagno 1984). The oceanic whitetip can be distinguished from other species of shark by the unique color pattern of mottled white tips on its front dorsal, caudal, and pectoral fins (hence the name whitetip); it also has black tips on its anal fin and on the ventral surfaces of its pelvic fins (Bass et al. 1973; Compagno 1984). Body color varies depending on geographic location, but is generally grayish bronze to brown, with a whitish underside and yellow tinge on some individuals (Compagno 1984) (Fig. 1).

Distribution and movements

The oceanic whitetip shark is an epipelagic species that is widely distributed in tropical and subtropical waters worldwide (Fig. 2) between 10°N and 10°S, but can also be found out to latitudes of 30°N and 35°S, with abundance decreasing with greater proximity to continental shelves (Backus et al. 1956; Strasburg 1958; Compagno 1984). Oceanic whitetip sharks are typically found offshore, along the edges of continental shelves, or around oceanic islands in deep water greater than 184 m, and from the surface to at least 152 m depth (Backus et al. 1956; Strasburg 1958; Compagno 1984; Bonfil et al. 2008). This species appears to be thermally sensitive and exhibits a strong preference for the surface mixed layer in warm waters above 20 °C (Bass et al. 1973; Bonfil et al. 2008). Musyl et al. (2011) reported that they spend $> 95\%$ of their time within 2 degrees of the warmest water.

Fig. 1 Lateral and dorsal image of oceanic whitetip shark. Photos used with permission from Andy Mann and Trevor Bacon

Fig. 2 Global distribution of oceanic whitetip shark. The distribution was adapted from the International Union for Conservation of Nature (IUCN) 2012. *Carcharhinus longimanus*. The IUCN Red List of Threatened Species. Version 2019-2 and Ebert et al. (2013). The question mark over the Mediterranean Sea represents its unconfirmed presence there (Young et al. 2017)

Several archival satellite tagging studies from various regions of the species' range indicate that oceanic whitetip sharks spend most of their time in less than 200 m of water (above the thermocline) (Musyl et al. 2011; Carlson and Gulak 2012; Howey-Jordan et al. 2013; Tolotti et al. 2017). Although the species has been observed conducting deep dives into the mesopelagic zone (> 200 m), appearing to tolerate colder waters down to 7.75° (Howey-Jordan et al. 2013; Howey et al. 2016; Tolotti et al. 2017), exposures to these cold temperatures are not sustained for long periods (Musyl et al. 2011; Tolotti et al. 2015). There have also been observations of the species emigrating from waters below 21 °C (e.g., the Gulf of Mexico in winter) (Backus et al. 1956). The reasons for these deep excursions have yet to be confirmed, but it may be that oceanic whitetip sharks commonly explore extreme environments (e.g., deep depths, low temperatures) as a potential foraging strategy (Howey-Jordan et al. 2013).

Oceanic whitetip sharks can travel great distances in the open ocean but also appear to return to certain areas regularly. Conventional mark-recapture data (n = 645 tagged and 8 recaptured) from the NMFS Cooperative Shark Tagging Program indicated a maximum distance traveled of 2270 km (Kohler et al. 1998; NMFS unpublished data). Oceanic whitetip sharks tagged with pop-up satellite archival transmitting (PSAT) tags at Cat Island, Bahamas stayed within 500 km of the tagging site for ~ 30 days before individuals moved to several different destinations across a large area (16,422 km^2) of the western North Atlantic (Howey-Jordan et al. 2013). Many sharks returned to the Bahamas after ~ 150 days and estimated residency times within the Bahamas Exclusive Economic Zone (EEZ), were generally high (mean = 68.2 percent of time; Howey-Jordan et al. 2013). Oceanic whitetip sharks showed similar movement patterns and site fidelity in a PSAT tagging study conducted in Northeast Brazil (Tolotti et al. 2015). In the central Pacific, the largest linear movement was 4285 km over a period of 95 days (Musyl et al. 2011) and in the Indian Ocean, oceanic whitetips have exhibited trans-equatorial migrations and one individual traveled approximately 6500 km over 100 days (Mejuto et al. 2005; Filmalter et al. 2012). Comparison of current genetic information with PAT tag studies also suggest oceanic whitetip sharks can be philopatric (Camargo et al. 2016). This could potentially cause localized depletions from fisheries in both abundance and genetic diversity. Overall, oceanic whitetip sharks are highly migratory with some evidence of philopatry. However, more research on the movement patterns and migration paths of this species is needed.

Life history

Oceanic whitetip sharks exhibit life-history traits and population parameters that are generally intermediary among other shark species (Table 1), with the first studies to describe life history including Backus et al. (1956) in the Northwest Atlantic and Strasburg (1958) in the eastern Pacific. The maximum size for oceanic whitetip shark is about 325 cm total length (TL; straight line measure from the tip of the snout to the caudal fin in its natural position) but the most common sizes are below 300 cm TL, with individuals larger than 270 cm TL seemingly rare (Lessa et al. 1999; D'Alberto et al. 2017).

Growth rates are variable throughout its range, with similar rates for both sexes, and generally indicate slow-moderate growth (growth coefficient (K) = 0.075 – 0.103) (Table 1). Age and size of sexual maturity also vary depending on geographic location, with sharks in the Southwest Atlantic reaching sexual maturity at approximately 6–7 years and 180–190 cm TL (both sexes) (Seki et al. 1998; Lessa et al. 1999), and sharks from the North Pacific maturing later at ages of 8.5–8.8 years for females and 6.8–8.9 years for males (Joung et al. 2016). Observed maximum ages based on vertebral ring counts range from 12 to 18 years in the North Pacific and Western and Central Pacific, respectively (Joung et al. 2016; D'Alberto et al. 2017), and from 13 to 19 in the South Atlantic (Seki et al. 1998; Lessa et al. 1999; Rodrigues et al. 2015).

Like other carcharhinid species, the oceanic whitetip shark is viviparous (i.e., the species gives birth to live young) with placental embryonic development. The reproductive cycle is thought to be biennial, giving birth on alternate years, after a 10–12 month gestation period (Backus et al. 1956; Seki et al. 1998; Tambourgi et al. 2013). However, recent unpublished data obtained via ultrasonography of pregnant females over multiple years suggests that at least for a proportion of the population, reproduction could be annual (James Gelsleichter, University of North Florida, unpublished data). The number of pups per litter ranges from 1 to 14 (average of 6), and there is a positive correlation between female size and number of pups per litter, with larger sharks producing more offspring (Backus et al. 1956; Strasburg 1958; Bass et al. 1973). The size trend is especially troubling if indeed maternal effects are evident and effective breeding sizes are declining, which might cause significant variability in reproductive success.

There is little information on the genetics and population structure of the oceanic whitetip shark. Camargo et al. (2016) compared the mitochondrial control region from the Indian Ocean and eastern and western Atlantic Ocean and found significant genetic differentiation (based on haplotype frequencies) between the eastern and western Atlantic Ocean ($\Phi ST = 0.1039$, $P < 0.001$). However, there were complex patterns within some subpopulations being significantly differentiated whereas others were not. Additionally, the sample size from the Indian Ocean was inadequate to detect statistically significant genetic structure between this and other regions. Ruck (2016) initially compared the mitochondrial control region of oceanic whitetip shark from all oceans and detected no fine-scale matrilineal structure within ocean basins. However, after comparing and reanalyzing samples from Camargo et al. (2016), results showed significant maternal population structure within the western Atlantic with evidence of matrilineal lineages in the Northwest Atlantic and western Atlantic Ocean (C. Ruck, personal communication, 2016).

Globally, Ruck (2016) found that the most common mitochondrial haplotypes were shared by individuals in the Atlantic, Indian, and Pacific Oceans, with no clear phylogeographic partitioning of haplotypes. Mitochondrial and nuclear analyses indicated weak but significant differentiation between western Atlantic and Indo-Pacific Ocean populations. Although significant inter-basin population structure was evident, Ruck (2016) also noted an association with deep phylogeographic mixing of mitochondrial haplotypes and evidence of contemporary migration between the western Atlantic and Indo-Pacific Oceans. Both available studies also used mitochondrial DNA, which does not reflect male mediated gene flow. Therefore, we agree with conclusions made by Young et al. (2017) that neither study provides unequivocal evidence for genetic

Table 1 Life history parameters of oceanic whitetip shark (m = male; f = female; PCL = Precaudal length; TL = Total Length as the distance from the tip of the snout to the caudal fin in its natural position). Adapted from Young et al. (2017)

Parameter	Estimate	References
Growth rate (von Bertanlanffy k, L_∞)	0.075–0.099 $year^{-1}$, L_∞ = 284.9 cm TL (SW Atlantic; both sexes)	Lessa et al. (1999)
	0.103 $year^{-1}$, L_∞ = 341.7 cm TL (N. Pacific; both sexes)	Seki et al. (1998)
	0.085 $year^{-1}$, L_∞ = 30.9.4 cm TL (western N. Pacific; both sexes)	Joung et al. (2016)
	0.045 $year^{-1}$, L_∞ = 342.5 cm TL (western N. Pacific; both sexes)	D'Alberto et al. (2017)
Observed maximum length	325 cm TL (SW Atlantic)	Lessa et al. (1999)
	245 cm PCL (342 cm TL; N. Pacific)	Seki et al. (1998)
	252 cm TL (f; SW Atlantic)	Coelho et al. (2009)
	253 cm TL (m; SW Atlantic)	Tambourgi et al. (2013)
	227 cm TL (f; SW Atlantic)	Rodrigues et al. (2015)
	242 cm TL (m; SW Atlantic)	
	252 cm TL (f; S. Atlantic)	
	242 cm TL (m; S. Atlantic)	
Age at maturity (years)	6–7 (SW Atlantic; both sexes)	Lessa et al. (1999)
	4–5 (N. Pacific; both sexes; 8–9, f; 7–9, m)	Seki et al. (1998);
		Joung et al. (2016)
Length at maturity (cm TL)	180–190 cm (SW Atlantic; both sexes)	Lessa et al. (1999)
	170 cm (SW Atlantic; f)	Tambourgi et al. (2013)
	170–190 cm (SW Atlantic; m)	Seki et al. (1998)
	168–196 cm (N. Pacific; f)	IOTC (2015a)
	175–189 cm (N. Pacific; m)	D'Alberto et al. (2017)
	190–240 cm (Indian Ocean; both sexes)	
	193 cm (W Pacific; m)	
	224 cm (W. Pacific, f)	
Longevity (years)	19 (SW Atlantic)	Rodrigues et al. (2015)
	17 (SW Atlantic)	Lessa et al. (1999)
	11 (N. Pacific)	Seki et al. (1998)
	18 (W. Pacific)	D'Alberto et al. (2017)
Size at birth	63–77 cm TL (N. Pacific)	Seki et al. (1998)
	50–65 cm TL (Indian Ocean)	White (2007)
Litter size (number of pups)	5–6 (SW Atlantic)	Lessa et al. (1999)
	1–14 (average = 6; N. Pacific)	Seki et al. 1998
	10–11 (W. Pacific)	Joung et al. (2016)
	12 (Indian Ocean)	IOTC (2015b)

discontinuity or marked separation between Atlantic and Indo-Pacific subpopulations.

The oceanic whitetip shark is a relatively productive species. Cortés (National Marine Fisheries Service, unpublished analysis) recently updated estimates of vital rates and productivity using five methods (see Cortés 2016 for details) for a National Marine Fisheries Service workshop to gather information and perspectives on how to recover the oceanic whitetip shark (https://www.fisheries.noaa.gov/event/oceanic-whitetip-shark-recovery-planning-workshop-november-2019). The maximum intrinsic rate of population increase (r_{max}) averaged 0.126 $year^{-1}$ in the Atlantic Ocean and 0.135 $year^{-1}$ in the Pacific

Ocean. Based on these values, the oceanic whitetip is considered a medium-growing species when compared to 65 other shark species and populations (Cortés 2016). However, estimates presented here are meant to approximate maximum values, as it is unclear to what level of exploitation the vital rates used correspond and there is a need to improve basic life history information.

Population status and trends

The oceanic whitetip shark was characterized historically as one of the most abundant oceanic sharks in tropical seas worldwide (Backus et al. 1956; Compagno 1984). In fact, in Lineaweaver and Backus's (1969) book "Natural History of Sharks" oceanic whitetip sharks were described as "extraordinarily abundant, perhaps the most abundant large animal, large being over 100 lb [45 kg] on the face of the earth." Currently, there is no global population size estimate available for the oceanic whitetip shark; however, numerous lines of evidence, including the results of a recent stock assessment and several other abundance indices (e.g., trends in occurrence and composition in fisheries catch data, standardized catch-per-unit-effort (CPUE) data, and various biological indicators) indicate that the oceanic whitetip shark has experienced significant population declines throughout a majority of its global range (Fig. 3).

Eastern Pacific Ocean

In the Eastern Pacific, oceanic whitetip sharks were historically the second most common shark species caught in the tropical tuna purse seine fishery after silky sharks (*C. falciformis*), and comprised approximately 20 percent of the total shark catch from 2000 to 2001 (Roman-Verdesoto and Orozco-Zoller 2005) and 9% of the estimated yearly average capture of sharks from 1993 to 2009 (Hall and Román 2013). However, both nominal catches and encounters with oceanic whitetip sharks in all set types declined significantly since 1994, representing an 80–95% population decline (Hall and Román 2013). Further, size trends in this fishery show that small oceanic whitetip sharks (< 90 cm), which comprised 21.4% of the oceanic whitetip sharks captured in 1993, have been virtually eliminated from the population, indicating the possibility of recruitment failure in the population (Hall and Román 2013; M. Hall, personal communication, 2016). Although it is possible other factors aside from fishing pressure may have affected catches of oceanic whitetip shark during this period, such a significant level of decline makes it unlikely (Hall and Román 2013) (Fig. 4).

Western and Central Pacific Ocean

The oceanic whitetip shark was once one of the most abundant pelagic shark species throughout the Western and Central Pacific Ocean (WCPO), comprising up to 28% of the shark catch during the 1950s (Strasburg 1958). However, recent trends in abundance from analyses of CPUE data from the Hawaii-based pelagic longline fishery showed a decline in relative abundance of 90% from 1995 to 2010 (Brodziak et al. 2013). Additionally, stock assessments have been conducted in the WCPO that also show significant declines in the oceanic whitetip population (Rice and Harley 2012; Tremblay-Boyer et al. 2019). Tremblay-Boyer et al. (2019) analyzed population trends across multiple models covering a wide range of uncertainty scenarios, including stock productivity and discard mortality. They concluded that current spawning stock biomass is predicted to be below 5% of the unfished spawning biomass and the population could go extinct on the long-term under current levels of fishing mortality (Tremblay-Boyer et al. 2019). Size trends for oceanic whitetip have also declined in the WCPO. Declining median size was observed in all regions and sexes in both longline and purse seine fisheries until samples became too rare for analysis to continue (Clarke et al. 2011). These size trends were significant for females in longline and purse seine fisheries in the equatorial region of the WCPO, which represents the species' core habitat areas and contains 98 percent of the operational-level reported purse seine sets and majority of longline fishing effort (Clarke et al. 2011; Rice et al. 2015). Interestingly, D'Alberto et al. (2017) only collected two mature females in an area where oceanic whitetip abundance should be high. The decline in median size of female oceanic whitetip sharks is particularly concerning due to the potential correlation between maternal length and litter size, which has been documented in the Atlantic and Indian Oceans (Bass et al. 1973; Lessa et al. 1999; Varghese et al. 2016).

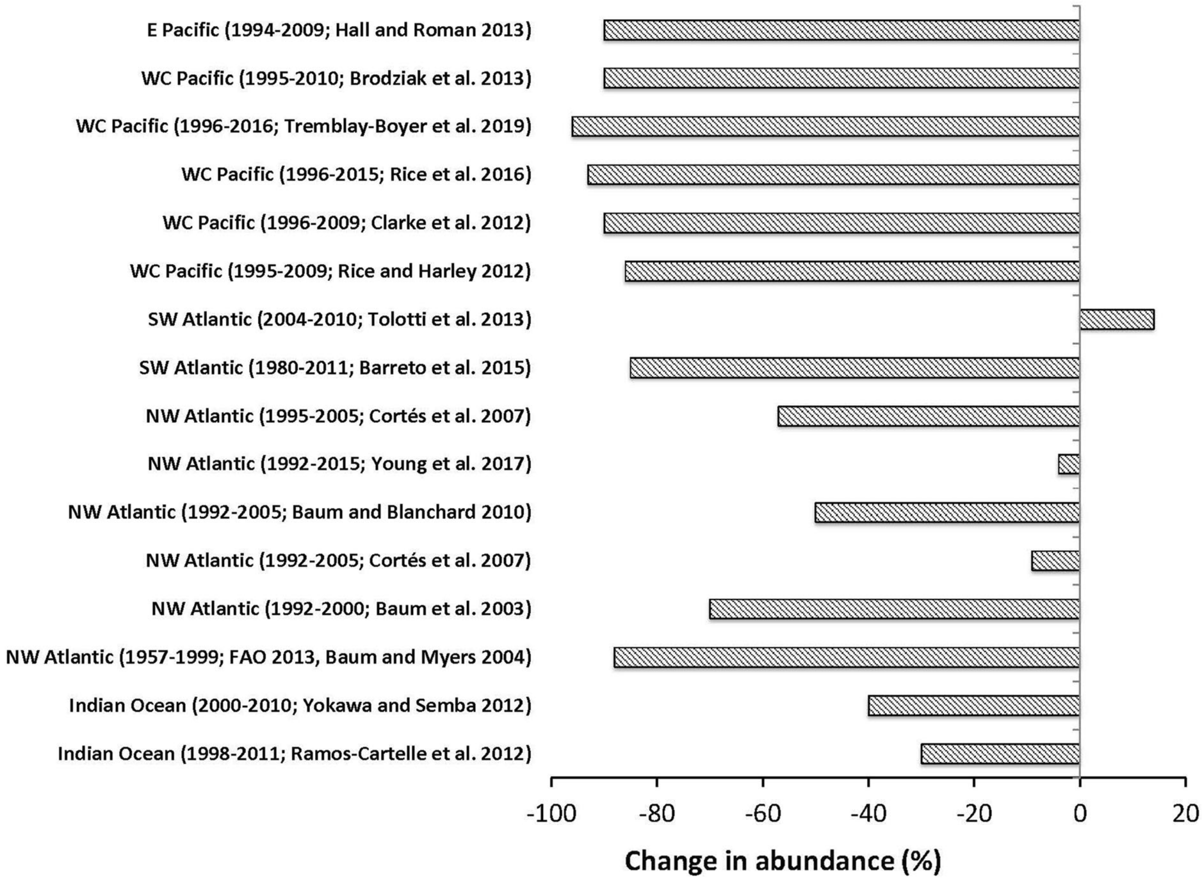

Fig. 3 Summary of the trends in abundance for oceanic whitetip shark based on stock assessments and standardized catch rates, with the exception of the E. Pacific, which is based on nominal catches

Atlantic Ocean

Population declines have been reported for oceanic whitetip sharks in the Atlantic Ocean as well, although there has been significant debate regarding the magnitude (Burgess et al. 2005a, b). Declines in abundance from the 1990s to the early 2000s have ranged from 9 to 70% depending on the data source and area (Baum et al. 2003; Cortés et al. 2007; Baum and Blanchard 2010). The most significant decline reported was a 99.9% decrease in abundance in the Gulf of Mexico since the 1950s based on a comparison of longline research surveys from 1954 to 1957 and data from fisheries observers collected on commercial pelagic longline sets from 1995 to 1999. However, the claim of such drastic declines was criticized for a lack of understanding of data, and for not taking into consideration the increase in the average depth of sets and the discontinued use of wire leaders that could have reduced catchability (Burgess et al. 2005a, b). The Food and Agriculture Organization of the United Nations (FAO) (2012) utilized data from Driggers et al. (2011) to demonstrate the catch rates of Baum and Myers (2004) for the recent period would have been 0.55 sharks per 1000 hook-hours rather than 0.02 per 1000 hook-hours when using wire leaders. Comparing the recent 0.55 value with the Baum and Myers (2004) of 4.62 for the 1950s gives an estimated extent of decline of 88 percent. An analysis of the most recent observer data from the U.S. Northwest Atlantic Pelagic Longline Fishery from 1992 to 2015 indicated that while there is high variability in the initial years of the time series, overall, the trend in abundance was relatively flat with about a 4% decline (Young et al. 2017). Thus, while it is likely that significant historical declines occurred, it appears that the population in the Northwest Atlantic may have stabilized. This may be due to management actions implemented in 1993,

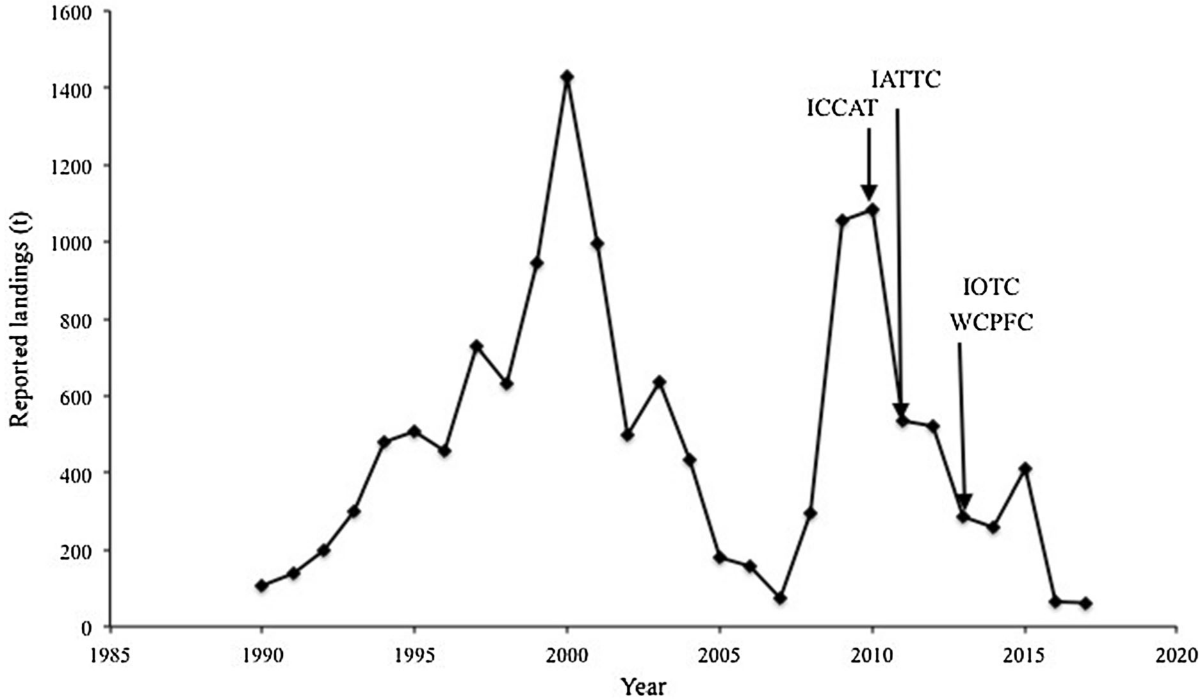

Fig. 4 Global capture production for oceanic whitetip shark from 1990 to 2017. Global capture production is production weight of the retained individuals before processing and thus may differ from landings weights. Arrows indicate the year the specific Regional Fishery Management Organization no-retention measures were implemented relative to oceanic whitetip shark. ICCAT = The International Commission for the Conservation of Atlantic Tunas, IATTC = Inter-American Tropical Tuna Commission, IOTC = Indian Ocean Tuna Commission, WCPFC = The Western and Central Pacific Fisheries Commission. *Source*: FAO Global Capture Production; accessed July 15, 2019

including the first Federal Fishery Management Plan for Sharks (NMFS 1993), and subsequent regulations that included trip limits and quotas.

Information from the South Atlantic on the abundance and population trends of ocean whitetip shark is limited, with most information coming from a few countries in South America. Analyses of fisheries data from 1980 to 2011 indicate the oceanic whitetip shark has undergone at least an 85% decline (Barreto et al. 2015). However, it was noted in Young et al. (2017) that there were issues with the methodology used in this study. The Government of Brazil, in its justification for listing the oceanic whitetip as Vulnerable on its List of Species of Brazilian Fauna Threatened with Extinction (MMA Ordinances No. 444/2014 and No. 445/2014) estimated that the oceanic whitetip population has potentially declined by up to 79% (ICMBio 2014).

Information regarding oceanic whitetip shark abundance and trends is largely unavailable from the eastern Atlantic and off the coast of western Africa. Domingo et al. (2007) recorded 0.098 sharks per 1000 hooks in the Gulf of Guinea and only 10 individuals caught in 3 years, whereas Castro and Mejuto (1995) reported 0.26 sharks per 1000 hooks in this same area 10 years prior in 1993, with 63 oceanic whitetip sharks caught in only 4 months. As such, the population status of the oceanic whitetip shark in this area is highly uncertain.

Indian Ocean

In the Indian Ocean, historical research data shows overall declines in both CPUE and mean weight of oceanic whitetip sharks, with anecdotal reports suggesting that the species has become rare throughout much of the Indian Ocean over the past 20 years (Romanov et al. 2008; IOTC 2015a). In addition, the Indian Ocean Tuna Commission (IOTC) reports that despite limited data, oceanic whitetip shark abundance has likely declined over recent decades (IOTC 2015a). Standardized CPUE data from various fisheries operating in the Indian Ocean also indicate variable population declines ranging from 25 to 40% since the late 1990s (Yokawa and Semba 2012; Ramos-Cartelle et al. 2012). Data collection on shark abundance from the Maldives from the mid-1980s to mid-2000s (Anderson and Waheed 1990; Anderson et al. 2011) indicate a potentially significant decline of oceanic whitetip abundance of up to of 90% (FAO 2012), with sightings of the species in Maldives and Reunion Island increasingly rare (IOTC 2011). Tolotti et al. (2015) also reported a marked decline in the proportion of FADs with oceanic whitetip sharks present in the French tuna purse seine fishery operating in the western Indian Ocean, from 20% in the mid 1980s–1990s, to less than 10% from 2005 to 2014. Due to the significant increase in FADs since the 1990s, this could be indicative of a significant population decline (Tolotti et al. 2015). However, the studies discussed have caveats and limitations making the abundance trend information from the Indian Ocean fairly limited. Therefore, the current population status for oceanic whitetip shark is highly uncertain in this part of its range and more robust research and data are needed.

Overall, stock assessments are only available in the Western and Central Pacific Ocean for the oceanic whitetip shark. However, in areas where oceanic whitetip shark data are available, trends from throughout the species' global range show a consistent pattern of large historical declines and low abundance. Using a Bayesian state-space tool for trend analysis of abundance indices for IUCN Red List assessments (Sherley et al. 2019), the global population change over 3 generations was 87–88% resulting in an assessment of Critically Endangered (Rigby et al. 2019). Accordingly, we conclude that despite data limitations noted above, the oceanic whitetip shark has likely undergone significant population declines throughout its global range.

Threats

Overexploitation due to incidental bycatch in commercial fisheries is the single most important threat to the oceanic whitetip shark. The oceanic whitetip is generally not a targeted species, but its tendency to remain in surface waters (< 152 m depth) and in tropical latitudes where fishing pressure is often most concentrated for target species such as tuna, results in frequent interactions in numerous fisheries throughout its global range. This species is commonly caught with pelagic longlines, purse seines, handlines, troll and occasionally pelagic and even bottom trawls (Compagno 1984); but undoubtedly, the largest source of mortality of oceanic whitetip sharks is bycatch-related mortality in commercial longline fisheries (Young et al. 2017; Tremblay-Boyer et al. 2019). Additionally, the oceanic whitetip shark is a preferred species for opportunistic retention because its large fins obtain a high price per kg in the Asian fin market (CITES 2013). This high value for oceanic whitetip fins incentivizes the opportunistic retention and subsequent finning of oceanic whitetip sharks when caught, and thus represents the main economic driver of mortality of this species in commercial fisheries throughout its global range. Below, we discuss threats from commercial fisheries by ocean basin, including the Eastern Pacific, Western and Central Pacific, Atlantic, and Indian Oceans. We also discuss the threat of the international trade in shark fins and products to the oceanic whitetip shark.

Globally, catches of oceanic whitetip sharks generally peaked between 1995 to 2000 followed by precipitous declines over the next 10 years (Hazin et al. 2007; Clarke et al. 2012; Hasarangi et al. 2012; Hall and Román 2013; Young et al. 2017; Tremblay-Boyer et al. 2019), although it should be noted that this rise in catches is in part the result of increased reporting over the same time period.

Eastern Pacific Ocean

Oceanic whitetip sharks are caught incidentally on a variety of gear, including pelagic longlines and purse seine gear targeting tunas and swordfish (IATTC 2007). In the tropical purse seine fishery, estimated catches of oceanic whitetip shark peaked in 1995, with approximately 9709 individuals caught in all sets. Within 10 years, catches dropped dramatically and continued to decline thereafter (Hall and Román 2013), with only 120 sharks caught in 2015 (Young et al. 2017). Not only are oceanic whitetip sharks encountered in purse seine fisheries in the eastern Pacific, they are sometimes a significant component of the bycatch in longline fisheries (IATTC 2007). Oceanic whitetip sharks have been reported in catches from Mexico (Sosa-Nishizaki et al. 2008), Costa Rica

(Dapp et al. 2013; Arauz 2017), Ecuador (Martinez-Ortiz et al. 2015), and Peru (Gonzalez-Pestana et al. 2014). However, detailed information from these fisheries is largely unavailable. Therefore, efforts should be made for increased data collection from these fisheries to better understand the level of utilization the oceanic whitetip shark is experiencing in this portion of its range.

Western and Central Pacific Ocean

Oceanic whitetip sharks are also caught in numerous fisheries in the Western and Central Pacific, with at least 20 member nations of the Western and Central Pacific Fisheries Commission (WCPFC) recording the species in their fisheries. In addition to being caught indirectly as bycatch, some targeting of oceanic whitetip shark occurred historically in the waters near Papua New Guinea, and due to the high value of oceanic whitetip fins (CITES 2013) and low level of observer coverage, it is likely that targeting has occurred in other areas as well (Rice and Harley 2012). Catches of oceanic whitetip shark have declined in both longline and purse seine fisheries in this region (Lawson 2011; Clarke et al. 2011; Rice and Harley 2012; Rice et al. 2015; Tremblay-Boyer et al. 2019). Based on a historical catch reconstruction conducted by Tremblay-Boyer et al. (2019), catches of oceanic whitetip shark in the WCPO longline fishery peaked around 2001 at ~ 540,000 individuals and declined to only ~ 80,000 individuals in 2016. Although some improvement in biomass was observed since 2013, likely due to conservation measures that prohibit retention of the species in WCPO fisheries, Tremblay-Boyer et al. (2019) concluded that the population chould go extinct in the long-term under current levels of fishing mortality.

Atlantic Ocean

The oceanic whitetip shark is caught incidentally as bycatch by a number of fisheries in the Atlantic, with numerous member nations of the International Convention on the Conservation of Atlantic Tunas (ICCAT) reporting oceanic whitetip sharks in their catches. According to nominal catch data reported to ICCAT, approximately 2430 mt of oceanic whitetip catches were reported from 1990 to 2014, with approximately 89% of the catch (2153 mt) caught by the Brazilian fleet (Young et al. 2017). The U.S. pelagic longline fleet also catches oceanic whitetip sharks incidentally; but catches from the 1980s through 2008 suggests they are caught infrequently relative to target species (NMFS 2009). Oceanic whitetip sharks are also caught in Cuban fisheries (Claro et al. 2001; Aguilar et al. 2014). Recently, Valdés et al. (2016) report a prevalence of small juvenile oceanic whitetip sharks in Cuba's catches, which may be indicative of a potential nursery area for the species in the region. However, because these individuals are small and less valuable, fishermen typically use them as bait, a practice that is likely undermining conservation of the species in the region (Valdés et al. 2016). Oceanic whitetips are caught as bycatch in a number of fisheries in the South Atlantic, including longline fisheries of Brazil, Uruguay, Taiwan, Japan, Venezuela, Spain and Portugal. However, the country with the greatest harvest of oceanic whitetip shark is Brazil (Young et al. 2017). Oceanic whitetip sharks were once considered common bycatch in commercial longline fisheries in Brazil, comprising nearly 30% of all shark catches in surveys from the 1990s (Lessa et al. 1999). However, despite the fact that the oceanic whitetip shark is a protected species in Brazil and is prohibited from being landed, the species continues to be landed by national and leased foreign fleets (Fiedler et al. 2017).

Overall, it appears that the oceanic whitetip shark is less abundant in this region of the Southwest Atlantic, with very low CPUE rates across the region and most captures comprised of juveniles (Domingo 2004; Domingo et al. 2007; Coelho et al. 2009; Tolotti et al. 2013; Frédou et al. 2015).

Indian Ocean

The oceanic whitetip shark is reported as bycatch in all three major fisheries operating in the Indian Ocean. The species is considered "frequent" in both pelagic longline and purse seine fisheries, and "very frequent" in the gillnet fishery (Murua et al. 2013b) and is estimated to comprise 11% of the total shark catch (Murua et al. 2013a). The species is deemed to be the 5th most vulnerable shark species caught in longline fisheries in the region (out of 16 species assessed), and the most vulnerable shark species caught in purse seines, due to its high susceptibility (defined as the potential effect of the fisheries in the stock) to capture in the fishing gear (Murua et al. 2012; IOTC 2015a). Several fleets operating in the Indian Ocean report oceanic whitetip shark in their catches, including (but not limited to) Indonesia (Dermawan et al. 2013; Novianto et al. 2014; Sembiring et al. 2015); India (Varghese et al. 2015); Sri Lanka (Hasarangi et al. 2012; Jayathilaka and Maldeniya 2015); Taiwan (Huang and Liu 2010); Japan (Yokawa and Semba 2012); and the African semi-industrial fleet, which includes Madagascar, Mauritius, Reunion, and Seychelles (Moreno and Herrera 2013). Aside from an unusual trend in 2013 and 2014, nominal catches of oceanic whitetip in the Indian Ocean substantially increased throughout the 1990s, peaking at 3050 mt in 1999, and then sharply and continuously declining in the 2000s (IOTC 2015b). Although it should be noted that inclusion of shark catches in annual reports did not officially start in the IOTC until 2005, and therefore this introduces a large amount of uncertainty regarding whether these catch trends are reflective of population trends in the Indian Ocean.

International trade

In addition to pressures from commercial fisheries and bycatch-related mortality, the oceanic whitetip shark is commonly utilized in the international shark fin trade because its fins are highly valuable, selling for USD $45 to USD $85 per kg (CITES 2013) and comprises part of the "first choice" category in the China, Hong Kong SAR fin market (Vannuccini 1999). In order to determine the species composition of the shark fin trade, Clarke et al. (2006a) analyzed 1999–2001 Hong Kong trade auction data in conjunction with species-specific fin weights and genetic information to estimate the annual number of globally traded shark fins. Using this approach, the authors discovered that oceanic whitetip sharks are sold under their own category "*Liu Qiu*" and represented approximately 1.8% of the Hong Kong shark fin market from 1999 to 2001. This equates to approximately 700,000 oceanic whitetip sharks (range: 200,000–1,200,000 individuals), with an equivalent median biomass of around 21,000 mt (range 9,000–48,000 mt), traded annually (Clarke et al. 2006b). Since initial studies of Clarke et al. (2006a, b), genetic tests of fins conducted in various fish markets in Taiwan (Liu et al. 2013), United Arab Emirates (Jabado et al. 2015), and Indonesia (Sembiring et al. 2015) confirm the ongoing utilization of oceanic whitetip shark fins in markets around the world. Although the oceanic whitetip shark has been prohibited from retention by all the relevant major tuna RFMOs (see Conservation and Management section below), oceanic whitetip fins were still commonly found in the Hong Kong fin market in a survey conducted from 2014 to 2016 (Cardeñosa et al. 2018). Therefore, trade of oceanic whitetip fins is ongoing even subsequent to implementation of RFMO no-retention measures.

In summary, the oceanic whitetip shark is caught in numerous commercial fisheries globally and has been heavily impacted by fishing pressure in all oceans and regions where the species occurs. This is likely due to the species' distribution in tropical and subtropical waters where fishing effort is often most concentrated, combined with its tendency to remain in shallow surface waters where chances of interactions with fishing gear are prevalent. Consequently, incidental bycatch and opportunistic utilization of the species' fins for international trade have resulted in large population declines globally, and these threats are ongoing. Although the oceanic whitetip may be moderately productive relative to other shark species, it is unlikely able to withstand such heavy harvest pressure.

Conservation and management

In recent years, there has been a surge of management measures implemented for the oceanic whitetip shark in efforts to improve the species' conservation status. For example, all relevant major tuna-RFMOs (ICCAT, IATTC, IOTC, and WCPFC) have taken steps towards protecting the species by implementing measures prohibiting retention of the species in certain fisheries, improving data reporting, and expanding research (Table 2).

Measures prohibiting retention of oceanic whitetip, if adequately implemented and enforced, could reduce overall bycatch mortality to some extent, because the species appears to have relatively higher at-vessel survivorship compared to some other sharks (Musyl et al. 2011); therefore, a large proportion of individuals caught and released alive may be able to survive. However, estimates of post-release survival rates are unknown for the oceanic whitetip shark, and no-retention measures do not mitigate for potential post-

Table 2 A summary of the current regulations within Regional Fishery Management Organizations (RFMO) specific to the oceanic whitetip shark

Regional fishery management organization	Date adopted	Regulation
International Commission for the Conservation of Atlantic Tunas (ICCAT)	2010	Recommendation 10-07 specifically prohibits the retention, transshipping, landing, storing, selling, or offering for sale any part or whole carcass of oceanic whitetip sharks (*C. longimanus*) in any fishery
Inter-American-Tropical-Tuna-Commission (IATTC)	2011	Resolution C-11-10 on the conservation of oceanic whitetip sharks caught in association with fisheries in the Antigua Convention Area prohibits retaining onboard, transhipping, landing, storing, selling, or offering for sale any part or whole carcass of oceanic whitetip sharks in the fisheries covered by the Antigua Convention
Western and Central Pacific Fisheries Commission (WCPFC)	2013	Conservation Management Measure (CMM) 2011-04 prohibits vessels flying their flag and vessels under charter arrangements to the CCM from retaining onboard, transshipping, storing on a fishing vessel, or landing any oceanic whitetip shark, in whole or in part, in the fisheries covered by the Convention. WCPFC also adopted a CMM 2014-05 (effective July 2015) that requires each national fleet to choose either banning wire leaders or banning the use of shark lines
Indian Ocean Tuna Commission (IOTC)	2013	Resolution 13/06 prohibits, as an interim pilot measure, all fishing vessels flying their flag and on the IOTC Record of Authorized Vessels, or authorized to fish for tuna or tuna-like species managed by the IOTC on the high seas to retain onboard, transship, land or store any part or whole carcass of oceanic whitetip sharks with the exception of scientific observers collecting biological samples. The provisions of this measure do not apply to artisanal fisheries operating exclusively in their respective Exclusive Economic Zone (EEZ) for the purpose of local consumption. This measure is also not binding on India

release mortality that may occur because of the interaction. Therefore, an increase in the number of sharks released alive may not necessarily translate into substantial increases in survival (Clarke 2013). Additionally, no-retention measures are not likely to improve mortality rates in purse seine fisheries if sharks are subjected to the brailing process (Poisson et al. 2014). Studies of shark mortalities in various purse seine fisheries have shown that ~ 60–80% of sharks are dead when they are first observed at net retrieval and approximately half of those which survive retrieval die after release (Poisson et al. 2014; Hutchinson et al. 2015). Though mortality rates of oceanic whitetip in purse seine fisheries are not available, it can be cautiously inferred that oceanic whitetip sharks experience high mortality rates similar to congener *C. falciformis* (i.e., ~ 85% in Western and Central Pacific and Indian Ocean tropical purse seine fisheries) (Poisson et al. 2014; Hutchinson et al. 2015) during and after interactions with purse seine fisheries. Additionally, implementation and enforcement of these measures are highly variable across the species' global range. As a result, these measures may only be partially effective and thus inadequate to prevent further population declines from occurring (Clarke 2013; Young et al. 2017).

In addition to management measures implemented in commercial fisheries, the oceanic whitetip shark is listed under Appendix II of Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) in 2013 due to reported population declines driven by incidental bycatch and opportunistic trade of its fins. This listing went into effect in September 2014. Because the oceanic whitetip is a pelagic species mostly occurring in waters not under the jurisdiction of any country, Introduction from the Sea (i.e., transport of captured specimens from international waters to areas under national jurisdiction) would likely occur frequently in fisheries regulated by Regional Fishery Management Organizations (RFMOs) that allow the species to be landed (FAO 2012). Under CITES, introductions from the sea require a certificate from the country to whose jurisdiction the specimens are brought. This includes a Non-detriment finding, wherein the Scientific Authority of the country of introduction advises that the introduction will not be detrimental to the survival of the species, and a legal acquisition finding. All major tuna-RFMOs prohibit the retention of the oceanic whitetip shark; as such, export of oceanic whitetip fins from most RFMO member countries (with the exception of those countries that have taken reservations to the prohibitions (e.g., India), should not be occurring and would be in contravention of RFMO regulations. However, in 2015, seven nations reported trading CITES listed sharks with Hong Kong, with oceanic whitetips comprising 5.6% of all species by weight (Cardeñosa et al. 2018). Oceanic whitetip sharks also comprised 1.0% (by weight) of the genetically identified fin trimmings from the retail market of Hong Kong in 2014–2015 (Fields et al. 2017). Moreover, illegal trade also exists for fins. Data from Hong Kong's Agriculture Fisheries Conservation Department (AFCD) from 2014 (when the listing of oceanic whitetip sharks under CITES Appendix II went into effect) to 2016, indicates approximately 1263 kg (2784 lbs) of oceanic whitetip fins have been confiscated upon entry into Hong Kong because the country of origin did not include the required CITES permits or equivalent paperwork. Confiscated oceanic whitetip fin shipments included 940.46 kg from Colombia, 10.96 kg from the Seychelles, and 272.49 kg from the United Arab Emirates (AFCD, Unpublished data reported in Young et al. 2017). Additionally, in the first two months of 2017 alone, more than a ton of shark fins from hammerhead and oceanic whitetip sharks were seized by Hong Kong customs (https://phys.org/news/2017-03-massive-hong-kong-shark-fin.html). In November 2018, fishermen from Indonesia were caught illegally smuggling oceanic whitetip fins in and out of ports in Honolulu, Hawaii (https://www.apnews.com/870efac8a5024a35b92f70b12249a569). Therefore, although laws and regulations are in place to regulate trade and utilization of the species, it may not be enough to stem ongoing illegal fishing and trade activities that are likely detrimentally affecting the conservation status of the species.

Future directions for recovery

It is clear that the oceanic whitetip shark faces a high degree of threat from commercial fishing activities and international trade of its fins despite regulations to curb these threats (e.g. no retention measures, CITES). Its management is complicated by the fact that it is globally distributed, highly migratory, and its core distribution overlaps with areas of high fishing effort for target species, such as tuna. Although implementation of no-retention measures by international RFMOs and individual countries at the national level is a positive step forward, these measures do not prevent capture nor any at-vessel or post-release mortality that may result from fisheries interactions. Additionally, no retention measures may complicate monitoring of the species' status as well as collection of samples to update their biology. Fishers may not record discarded individuals or, on longline vessels, cut the line before the individual is landed and the catch is recorded. This may result in catch rates from logbooks appearing to decline when they are in fact underreported, thereby preventing accurate tracking of any population recovery following regulations. Therefore, the priority for stabilizing and eventually recovering the oceanic whitetip population should be to reduce the overall level of fisheries interactions and improve overall survivorship when these interactions occur, while also increasing population monitoring and collection of important biological data. Along these lines, observer coverage remains very low on longline vessels across most RFMOs (Clarke 2013). As such, improving observer coverage through increasing on-board human observers or the use of electronic monitoring (e.g. cameras) in commercial fisheries to meet minimum requirements should be a priority to ensure compliance with existing regulations and improve data collection.

Factors affecting catch rates and associated mortality of oceanic whitetip sharks in pelagic longlines are not well understood. Because oceanic whitetip sharks are a highly mobile, oceanic species, assessments of population trends have relied on fishery-dependent catch-and-effort data rather than scientific surveys. As previously noted, there are multiple issues with gear configuration and fishing tactics that can affect the standardization of abundance trends. For example, oceanic whitetip sharks have higher capture and mortality rates when shark lines and wire traces are utilized in longline fisheries (Harley et al. 2015). Although some regions have implemented conservation measures to reduce this impact (e.g., WCPFC Conservation and Management Measure 2014-05, which allows the use of one or the other), Monte Carlo simulation modelling shows that mortality of oceanic whitetip sharks is reduced by 40% when both shark lines and wire traces are banned (Harley et al. 2015). Beyond issues noted in Burgess et al. (2005a, b), evidence suggests that the catchability of oceanic whitetip sharks may be sensitive to factors such as temperature and hook depth (Tolotti et al. 2013). Additionally, studies show that although oceanic whitetip sharks may experience higher capture rates in longlines when circle hooks are used (Fernandez-Carvalho et al. 2015), higher mortality has been reported when J-style hooks are used (Afonso et al. 2011). Therefore, an improved understanding of how these and other various factors (e.g., spatial and temporal fishing effort) affect bycatch and associated mortality rates for the species in key fisheries is needed (see review in Davis 2002). Additionally, investigating and implementing best methodologies for reducing stress during capture (e.g., shorter soak times), as well as safe handling and release of this species upon capture would likely increase post-release survivorship. A recent meta-analysis by Musyl and Gillman (2019) found only 1 mortality for 15 sharks tagged with archival satellite tags on pelagic longline gear and that condition at capture was a strong predictor of post-release mortality. Hutchinson and Bigelow (2019) also concluded that post-release survivorship of oceanic whitetip sharks is high to 30 days if release condition is good and trailing gear is minimized to no more than 2.5 meters. Therefore, implementation of safe handling and release guidelines, including a recommendation for minimizing trailing gear when individuals are cut from the line, could improve the efficacy of current no-retention measures (Hutchinson and Bigelow 2019; Common Oceans (ABNJ) Tuna Project 2019). Along these lines, safety of the crew should be included while developing any safe release measure. In addition, measures designed to reduce bycatch of oceanic whitetip shark should be assessed to determine whether they would affect other species negatively.

Major gaps in knowledge with regard to the species' abundance, distribution, movements, population structure and connectivity, and life history are likely inhibiting a better understanding of the species' conservation needs. In particular, information on where and when the species undertakes critical life history functions, such as breeding and pupping, is extremely important for informing future management measures. Identifying these areas through research and monitoring and implementing measures to protect the species during these critical times and within these areas would help ensure that the species is able to increase its abundance and eventually recover to sustainable levels. Recently, at a National Marine Fisheries Service workshop to gather information and perspectives on how to recover the oceanic whitetip shark (https://www.fisheries.noaa.gov/event/oceanic-whitetip-shark-recovery-planning-workshop-november-2019), Aquino (unpublished) reported on the prevalence of small juveniles captured by artisanal fishermen in waters off the coast of Haiti. This could indicate a potential and critical pupping area for the oceanic whitetip shark, where the species does not have any protections at this time. Identification and subsequent protection of these areas will be crucial for ensuring recovery of the species. While substantial uncertainty and debate remains regarding the benefit of marine protected areas for sharks (e.g. Davidson 2012), marine reserves and protected areas may benefit the oceanic whitetip shark in areas where the species shows a high level of site fidelity (e.g., Bahamas, Northeast Brazil). In the Bahamas, where oceanic whitetip sharks exhibit high resident times throughout the year (Howey-Jordan et al. 2013), both longline fishing and shark fishing (and trade) has been banned throughout the entire EEZ, effectively creating a shark sanctuary. These measures likely provide some benefit to the oceanic whitetip population in this area.

The limited genetic information available for oceanic whitetip shark also poses a challenge regarding recovery and limits our knowledge of fisheries-induced-evolution (FIE) or determination of the effective genetic population size. Genetic diversity also appears to be low when compared to eight other circumtropical elasmobranch species. The oceanic whitetip shark ranks the fourth lowest in global mtCR genetic diversity and the relatively low mtDNA genetic diversity raises potential concern for the future genetic health of this species (Ruck 2016). Low genetic variability, as exhibited by the oceanic whitetip shark, may represent a risk in terms of the species' ability to adapt, leading to a weaker ability to respond to environmental changes (Camargo et al. 2016). Therefore, standardized genetic collection protocols and the use of molecular markers with high resolving power (e.g., next generation sequencing) need to be implemented in all ocean basins to improve sampling and gain a better understanding of diversity, stock structure, and connectivity to inform future conservation needs.

International cooperation will be an important component for the recovery of the oceanic whitetip. With a global distribution in waters of at least 80 different countries, combined with the species' highly migratory nature, the level of protection and enforcement of management measures varies substantially across the species' range. While oceanic whitetip sharks may enjoy higher levels of protection in some countries' waters (e.g., United States, Bahamas), individuals will likely move across multiple jurisdictional boundaries throughout their lives and potentially be exposed to areas where protections are minimal or non-existent. For example, tagging data from the Bahamas found that over the course of the study, several individuals made transboundary movements and spent time in several different countries, including the United States, Cuba, several Caribbean Island nations, and the high seas (managed by international RFMOs) (Howey-Jordan et al. 2013). Consequently, this further underscores the importance of harmonizing management measures (such as those implemented by RFMOs) across regions where appropriate, and improving compliance and enforcement at the national and local levels.

Finally, we note that a very important consideration in the conservation and management of the oceanic whitetip shark should be outreach and education of stakeholders, in particular fishers, regarding the importance of the species to the overall ecosystem and raising awareness of best practices for ensuring its survival. In fact, recent interviews with 29 commercial fishermen in Hawaii revealed negative attitudes and perceptions of the species. Oceanic whitetip sharks were often considered as a "competitor" and "hassle" due to depredation issues and gear damage as a result of interactions (Iwane 2019). Therefore, increasing communication, facilitating knowledge exchange, and building a more collaborative environment between scientists, managers and fishers should be pursued when developing and implementing conservation and management measures for the recovery of the oceanic whitetip shark.

Conclusion

While the oceanic whitetip shark was likely one of the most abundant pelagic sharks, it is clear that the global population has experienced significant impacts due to decades of heavy fishing pressure and high demand in the international shark fin trade. Although more information has come to light about this species in recent years, significant data gaps remain that need to be addressed in order to better inform the conservation needs of the species. Specifically, more information regarding several aspects of its life history, genetics and population structure, factors affecting post-release mortality rates, and best practices to ensure increased survivorship during and after fisheries interactions in key commercial fisheries throughout the species' range, will be essential for the conservation and recovery of the species. The recent surge of regulatory mechanisms and conservation measures that have been implemented for the species in recent years provides a hopeful first step in the right direction. However, management and recovery of a globally distributed, highly migratory, pelagic shark such as the oceanic whitetip continues to be extremely challenging. Therefore, significant improvements in compliance and enforcement of regulations, coordinated efforts at the international and regional levels, and increased outreach and education will be necessary if there's any hope of reversing decades of decline for the oceanic whitetip shark and giving this enigmatic species a chance for recovery.

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