The biology and conservation status of the large hammerhead shark complex: the great, scalloped, and smooth hammerheads

Austin J. Gallagher . A. Peter Klimley

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REVIEWS

The biology and conservation status of the large hammerhead shark complex: the great, scalloped, and smooth hammerheads

Austin J. Gallagher · **A. Peter Klimley**

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Abstract Hammerhead sharks are among the most intriguing yet imperiled groups of large sharks globally. Until recently, our understanding of their biology, movements, diet, and life histories was challenged by a lack of studies. In recent years there has been a surge of published studies on this group of sharks, incorporating new information on age and growth, behavior, and the threats they face. Here we summarize and compare what is known on the biology and conservation of the three largest species of hammerhead sharks: the great hammerhead (*Sphyrna mokarran*), the scalloped hammerhead (*Sphyrna lewini*), and the smooth hammerhead (*Sphyrna zygaena*). We chose these species since they are the most well-studied of the hammerheads, and also because they are commonly captured in target and non-target fisheries worldwide. Thus, we also discuss population trends and the vulnerabilities of each species, and make recommendations for future studies on these fascinating and complex elasmobranch fishes.

Keywords Fisheries · Great · Hammerhead · Scalloped · Shark · Smooth

A. J. Gallagher (✉)
Beneath the Waves, Inc., PO Box 126, Herndon, VA 20172, USA
e-mail: austin@beneaththewaves.org

A. J. Gallagher
Marine Ecosystems and Society, Rosenstiel School of Marine and Atmospheric Science, University of Miami, Coral Gables, FL, USA

A. P. Klimley
Biotelemetry Laboratory, Department of Wildlife, Fish, and Conservation Biology, University of California, Davis, Davis, CA, USA

Introduction

Hammerhead sharks from the Family Sphyrnidae are one of the most unique groups of large sharks as they are characterized by a laterally elongated rostrum or cephalofoil. Although there are 10 species of hammerhead sharks, the largest hammerhead sharks (i.e., over 150 cm at maturity) are found worldwide, are the slowest growing, and are vulnerable to commercial, recreational, and artisanal fisheries. The large hammerhead shark complex is composed of three species: the great hammerhead (*Sphyrna mokarran*, Fig. 1a), the scalloped (*Sphyrna lewini*, Fig. 1b), and the smooth hammerhead (*Sphyrna zygaena,* Fig. 1c). Although these species are morphologically similar, the anterior margins of the three species vary and this trait is most frequently used in species differentiation (Figs. 1, 2). The great hammerhead's rostrum is straight, the scalloped hammerhead rostrum has two rounded lobes separated by a mid-line, and the smooth hammerhead has one rounded lobe with a rounded mid-line to the rostrum (Fig. 2). The great

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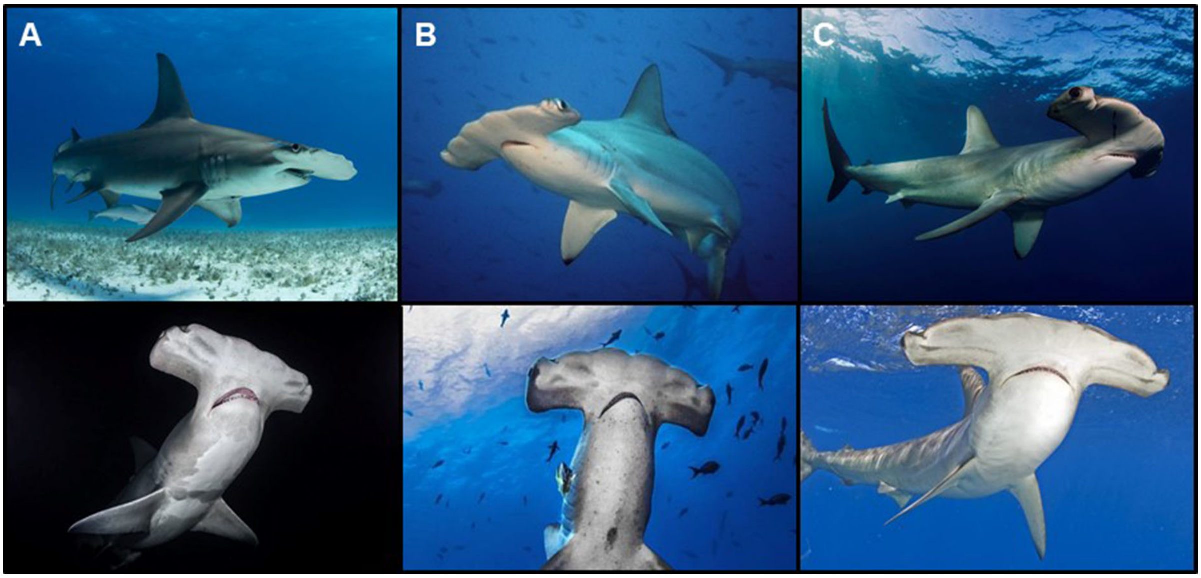

Fig. 1 Images of the three large hammerhead species: full body shots (above) and rostrum/cephalofoil (below): **a** great hammerhead [above: Austin Gallagher, below: Tanya Houppermans/Blue Elements Imaging], **b** scalloped hammerhead [above: Tom Burns; below: Christopher Gillette], and **c** smooth hammerhead [above: Kyle McBurnie; below: Chris Fallows]

hammerhead has a much larger body and disproportionately large, sickle-shaped dorsal fin than the latter two sharks, which have smaller, falcate dorsal fins (Fig. 2). The great hammerhead is a tropical and subtropical species whereby the scalloped hammerhead and smooth hammerhead sharks are found more in subtropical and even some temperate waters. Their behavior also varies within the complex, ranging from nomadic and solitary (great) to social and aggregative (scalloped hammerhead). The purpose of this overview will be to provide a comprehensive summary of the biology and conservation of these three, largest species of hammerhead sharks. We chose to focus on these three species for two primary reasons: (1) the relative volume of scientific information is highest among these species compared to other hammerhead species; and (2) these species are heavily exploited in fisheries worldwide, are prized in the shark fin industry, and are of conservation concern. We recognize that smooth hammerheads remain relatively poorly understood compared to the other two species in this complex; however, there has yet to be a synthesis of what is known on this data-deficient species in comparison to its closely-related counterparts, which could be useful for future studies. We realize the winghead shark (*Eusphyra blochii*) and the Carolina hammerhead (*Sphyrna gilberti*) are both relatively large hammerhead species; however, they were not included here as virtually no information exists on their biology. The three species we are focusing on here vary in their life history, feeding habits, habitat and range, and population status. Until very recently, there was a paucity of information on the biology and conservation of these large hammerhead sharks. It is our hope that this overview will provide a holistic understanding of the biology and conservation needs of these species, while pointing a way forward for future studies on these enigmatic, cryptic, and threatened elasmobranch fishes.

Movements and connectivity

Great hammerhead

There is a moderate but growing body of knowledge on great hammerhead movements and connectivity, however most of this information comes from North America, leaving a gap among other regions where they are found. The great hammerhead shark is a circumtropical species occurring throughout the tropics worldwide, primarily in warmer coastal waters

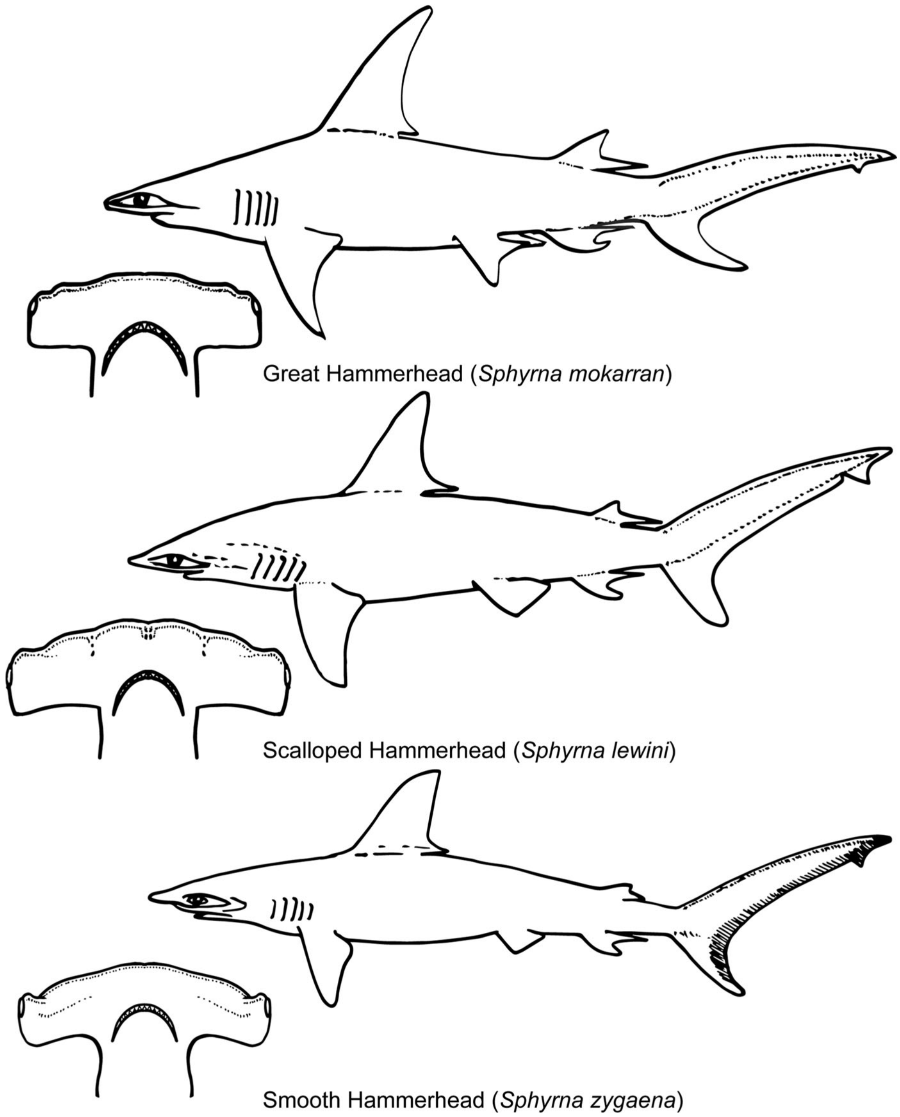

Fig. 2 Head and torso of the great, scalloped, and smooth hammerhead sharks. Modified from Compagno et al. (2005)

from 40°N to 37°S (Compagno et al. 2005, Fig. 3a). They are primarily a coastal species, although they appear to engage in off-shore migrations into pelagic regions (Hammerschlag et al. 2011a, b; Graham et al. 2016). In general, great hammerhead sharks prefer shallow coastal waters in the upper water column, although they are captured by fisheries in depths up to 60 m (Morgan and Carlson 2010; Harry et al. 2011). Due to their rarity, cryptic nature, and sensitivity to capture, few tagging studies have been conducted on the great hammerhead shark. The first published satellite tagging study of the great hammerhead was conducted by Hammerschlag et al. (2011a), whom reported a range extension for this species. The tagged shark moved in a direct line from the Florida Keys north into the continental shelf off New Jersey, 700 km north of its previous northerly range of North Carolina in the Atlantic. This northerly habitat use was corroborated by Graham et al. (2016) who reported habitat-use metrics for 18 individuals in the Northwest Atlantic tracked up to 154 days. The core habitat use areas for these sharks fell almost entirely within Florida state waters and the US Exclusive Economic Zone. The authors found a 91.57% overlap between the core habitat of the species and the US EEZ, although most of the sharks were from a single tagging region. This species was also found to make repeated movements into the Atlantic Ocean associated with

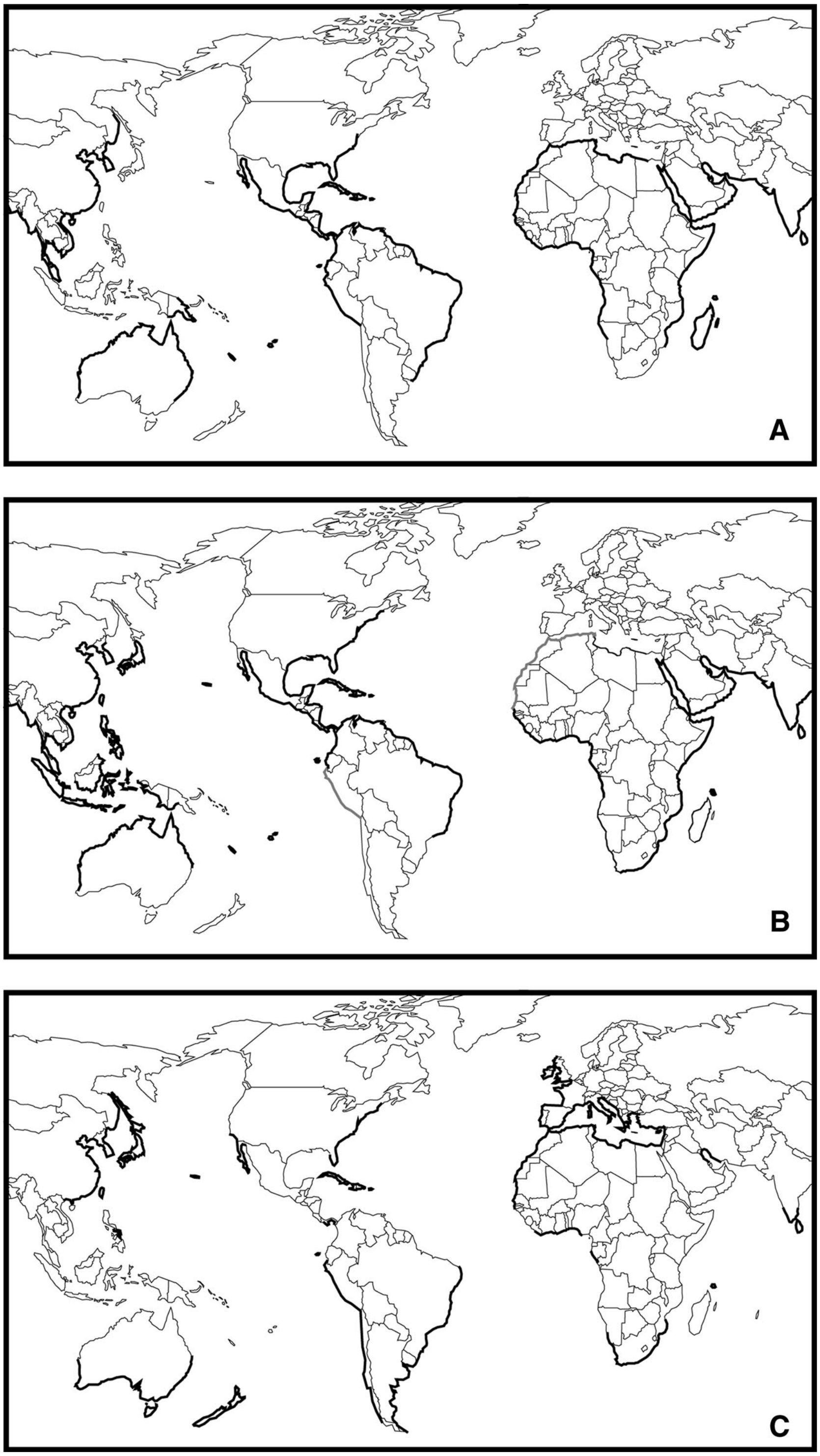

Fig. 3 Geographical distributions of the **a** great, **b** scalloped, and **c** smooth hammerhead sharks. Modified from Compagno et al. (2005)

the use of oceanographic zones where they are targeted by commercial longline fisheries exploiting continental shelf areas, although these migrations were less frequent (Queiroz et al. 2016). Through a combination of acoustic and satellite tagging as well as photo identification of a population of great hammerheads in the Bahamas, Guttridge et al. (2017) provided more evidence for large-scale migrations (up to > 3000 km away from the tagging site) and also demonstrated connectivity via seasonal residency to coastal areas and site fidelity where sharks returned to the original tagging site. Recently, some of the first ever young-of-the-year great hammerhead sharks were identified off coastal South Carolina, suggesting this area could serve as a potential pupping ground for Northwest Atlantic population (Barker et al. 2017). These limited studies suggest great hammerhead sharks are primarily found in coastal waters throughout most of their range but they will venture out into pelagic zones, and they have the ability to hone back to core habitats. Our knowledge base of this species movements and connectivity is largely restricted to the Northwest Atlantic, although Chin et al. (2017) constructed an assessment framework for evaluating connectivity of this species in the Australasian region. More research on the behavior of this species is needed in areas such as the Gulf of Mexico, Caribbean, Central America, and the Indo-Pacific.

Scalloped hammerhead

There is a relatively robust body of knowledge on scalloped hammerhead movements and connectivity—certainly the most compared to the other two species in this paper—and multiple global regions are represented. The scalloped hammerhead shark is a circumtropical species found worldwide in coastal, pelagic, and semioceanic waters off and on continental shelves of the Atlantic, Indian Oceans, and Pacific Oceans (Compagno 1984). They are also found in the Mediterranean and Red Sea (Compagno 1984). They occur in warm-temperate and tropical waters

Table 1 Qualitative summary of the current knowledge base of large hammerhead shark biology and conservation based on our overview

	Great hammerhead	Scalloped hammerhead	Smooth hammerhead
Life history	Fair	Good	Fair
Movements	Poor	Good	Poor
Foraging and diet	Fair	Good	Poor
Population status	Poor	Fair	Poor

Table 2 Life-history characteristic of the large hammerhead sharks, collated from the literature

	Growth rate (*k*)	Size at maturity (cm)	Fecundity (avg:max)	Max age (years)
Great hammerhead	0.11–0.16 (ATL), 0.079 (I)	238–285 (ATL + GOM), 145–237 (I)	15:33	42–44 (ATL + GOM), 32–39 (I)
Scalloped hammerhead	0.05–0.09 (ATL), 0.09–0.13 (GOM), 2.2–2.5 (WP), 0.076 (I)	300–303 (ATL), 180–250 (GOM), 198–210 (WP), 140–200 (I)	~ 20:40†	31–32 (ATL), 30.5 (GOM), 14 (WP)
Smooth hammerhead	0.06–0.09 (ATL)	210–240†	~ 30:49†	n/a

ATL Atlantic Ocean, *GOM* Gulf of Mexico, *I* Indian Ocean, *WP* Western Pacific Ocean

†An area where data were grouped due to a lack of regional studies

worldwide, primarily from 45°N to 30°S (Compagno et al. 2005, Fig. 3b). This species forms seasonal aggregations at oceanic seamounts, particularly in the Pacific (Klimley and Nelson 1981, 1984; Hearn et al. 2010; Bessudo et al. 2011; Ketchum et al. 2014a, b), some of which number into the hundreds (Salinas de León et al. 2016). Here females compete for males, with dominant individuals forcing subordinates to the edges of the schools (Klimley 1985). Males pair with the large females at the center of the schools. Scalloped hammerheads are most commonly encountered within the top 200 m of the water column (Compagno 1984), although they have been shown to make dives down to 964 m in the Gulf of Mexico (Hoffmayer et al. 2013), 971 m in the Red Sea (Spaet et al. 2017) and 980 m in the Pacific (Jorgensen et al. 2009). Many of these deep dives have occurred at night and are thought to be correlated to feeding events (Jorgensen et al. 2009; Hoffmayer et al. 2013; Hoyos-Padilla et al. 2014; but see Spaet et al. 2017). They have been shown to perform 'yo-yo' dives and exhibit high directionality during movement to and from seamounts, while swimming at depths greater than 200 m deep (Klimley 1993; Klimley et al. 1993; Bessudo et al. 2012; Ketchum et al. 2014a, b).

A fair number of studies have been conducted on scalloped hammerhead horizontal movements in disparate locations, over short and long time frames using acoustic and satellite-based tagging. Adult scalloped hammerhead sharks are highly selective of habitat and show high site fidelity to oceanic seamounts such as Espiritu Santo Seamount (Klimley and Butler 1988; Klimley et al. 1988) in the Gulf of California and islands such as the Galapagos, Malpelo Island, and Cocos Island (Hearn et al. 2010; Bessudo et al. 2011). Scalloped hammerhead sharks inhabit the Gulf of California from late spring to early fall (Galvan-Magaña et al. 1989; Klimley et al. 2005; Jorgensen et al. 2016) and migrate into the gulf following pelagic fishes (Klimley and Butler 1988). They also move between islands (Ketchum et al. 2014a, b). They are often found in areas of high marine biomass (White et al. 2015), which is why these areas are also targeted by fisheries operations (Hearn et al. 2010). Conventional tagging of scalloped hammerheads off Eastern Africa found the average distance traveled for this species was ~ 148 km and the maximum distance traveled was 629 km (Diemer et al. 2011), although others have documented displacement up to 1500 km (Kohler and Turner 2001). Recently, a single scalloped hammerhead moved over 3,350 km over 11 months in the Gulf of California (Hoyos-Padilla et al. 2014). Another single scalloped hammerhead tagged with a pop-off tag in the Red Sea traveled a circular distance of over 1000 km in 6 months (Spaet et al. 2017). Females may move offshore earlier to maximize growth and reach the larger size of maturity.

Scalloped hammerhead sharks were outfitted with coded acoustical beacons and their inter-island movements could be determined within the Galapagos as well as between more distant islands, where the species is abundant, such as Malpelo, offshore of Colombia and Cocos offshore of Costa Rica. There is considerable movement of scalloped hammerhead sharks between islands such as Wolf and Darwin in the Galapagos archipelago, and evidence to suggest a shark highway form these areas to distant islands such as Cocos and Malpelo in the eastern Pacific Ocean (Ketchum et al. 2014a, b). This may be partly due to the external attachment of the transmitters, which results in their loss through contact with the substrate or seizure by school mates. Single hammerhead sharks departing from Wolf and Darwin arrived at Cocos Islands almost simultaneous in time, indicating that they may join in a school and arrive together. Genetic samples indicate significant genetic connectivity between coastal sites ranging between Central Mexico and Ecuador (Nance et al. 2011). However, samples were not collected from scalloped hammerheads at the offshore islands, and it remains unknown whether there is genetic connectivity between inshore and offshore sites in these regions. Duncan et al. (2006) suggested that oceanic dispersal in this species is likely rare, although they found evidence for high coastal connectivity among nursery grounds.

Scalloped hammerheads are also the only large hammerhead for which nursery grounds have been well described. Studies have documented the occurrence of adults at in-shore nursery grounds (Branstetter 1990; Compagno 1984; Simpfendorfer and Milward 1993). It has been estimated that nearly 8000 individuals are born every year in the well-studied nursery ground off Kāne'ohe Bay, Ō'ahu, Hawaii (Holland et al. 1993; Duncan and Holland 2006). Recently, a nursery ground was discovered for this species in a river estuary in Fiji (Brown et al. 2016). Collectively, the available information suggests that this species is highly migratory, can move long distances, and shows moderate levels of connectivity within regions, although there is a general lack of comprehensive long-term horizontal data.

Smooth hammerhead

There is limited information and thus high uncertainty regarding the movements and connectivity of the smooth hammerhead, although a few studies have been conducted. The smooth hammerhead shark is a circumtropical species found worldwide in coastal, pelagic, and semioceanic waters off and on continental shelves of the Atlantic, Indian Oceans, and Pacific Oceans (Compagno 1984). They are also found in the Mediterranean and Red Sea (Compagno 1984). They occur in warm-temperate and tropical waters worldwide, primarily in warmer coastal waters from 40°N to 37°S (Casper et al. 2005; Compagno et al. 2005, Fig. 3c), although they are also tolerant of temperate waters and have been found as north as Nova Scotia and the British Isles (Southall and Sims 2008). It appears as if the juveniles of this species prefer coastal waters whereas adults are found more commonly offshore (Smale 1991). Smooth hammerheads prefer the top 20 m of the water column (Compagno 1984) although this may be a pattern common around coastal areas (Pérez-Jiménez et al. 2005), as they are encountered in pelagic longline fisheries in depths up to 68 m (Crow et al. 1996). In general, they are not frequently captured in pelagic longline fisheries although some regional fisheries may encounter them commonly and in high abundance in specific times or areas (Coelho et al. 2012; Cortés et al. 2010). Conventional tagging of smooth hammerheads off Eastern Africa found that of the 20 recaptured sharks from 1980 to 2008, the average distance traveled was ~ 141 km and the maximum distances traveled was 384 km (Diemer et al. 2011). These movements were far less wide-ranging than scalloped hammerheads, suggesting the species may not be as migratory as other large pelagic sharks. To date, there have been no published satellite tagging studies conducted on the smooth hammerhead shark, prompting future work.

Feeding and trophic dynamics

Great hammerhead

A small number of dietary studies have been performed on this species, and the literature is composed of descriptive reports and observations. Great hammerheads are apex predators and feed primarily on teleost fishes and other elasmobranchs, from small rays to large sharks. They have sharp pointed teeth on the lower jaws for seizing and holding prey, and serrated triangular teeth in the upper jaws for cutting prey (Fig. 4). The teeth of the great hammerhead appear to be more robust, and this may be because they feed on elasmobranch prey. Off northern Australia, fishes composed 87.5% of non-empty stomachs, many of which were demersal sharks and rays (Stevens and Lyle 1989). The notion that rays may be an important prey item for great hammerhead sharks is supported by observations of hunting and consumption by Strong et al. (1990, southern stingray *Dasyatis americana*) and Chapman and Gruber (2002, *Aetobatus narinari*), as well as stomach content analyses (Cliff 1995). There is evidence in the literature for great hammerheads consuming other large sharks (Mourier et al. 2013; Roemer et al. 2016), however comprehensive dietary studies corroborating this are limited (Bass et al. 1975), likely due to the difficulties of observing natural kills and the culture shift away from lethal sampling (Hammerschlag and Sulikowski 2011). Unlike their congeners (as described below), cephalopods do not appear to be an important prey item for this species (Smale and Cliff 1998).

Scalloped hammerhead

The diet and foraging of scalloped hammerheads have been relatively well-studied, and they have been described as both generalist and specialist feeders throughout their range (e.g., Kiszka et al. 2015; Flores-Martínez et al. 2017). Scalloped hammerheads feed on a mixture of fish, crustaceans, and cephalopods, with squid as a primary prey item, reflected by their smaller teeth than the great hammerhead (Fig. 4). This has been established through the examination of stomach contents in hammerhead sharks captured in the Central Pacific Ocean in Kāne’ohe Bay, Ō’ahu, Hawaii (Bush and Holland 2002; Clarke 1971; Duncan and Holland 2006), Tropical Eastern Pacific Ocean off

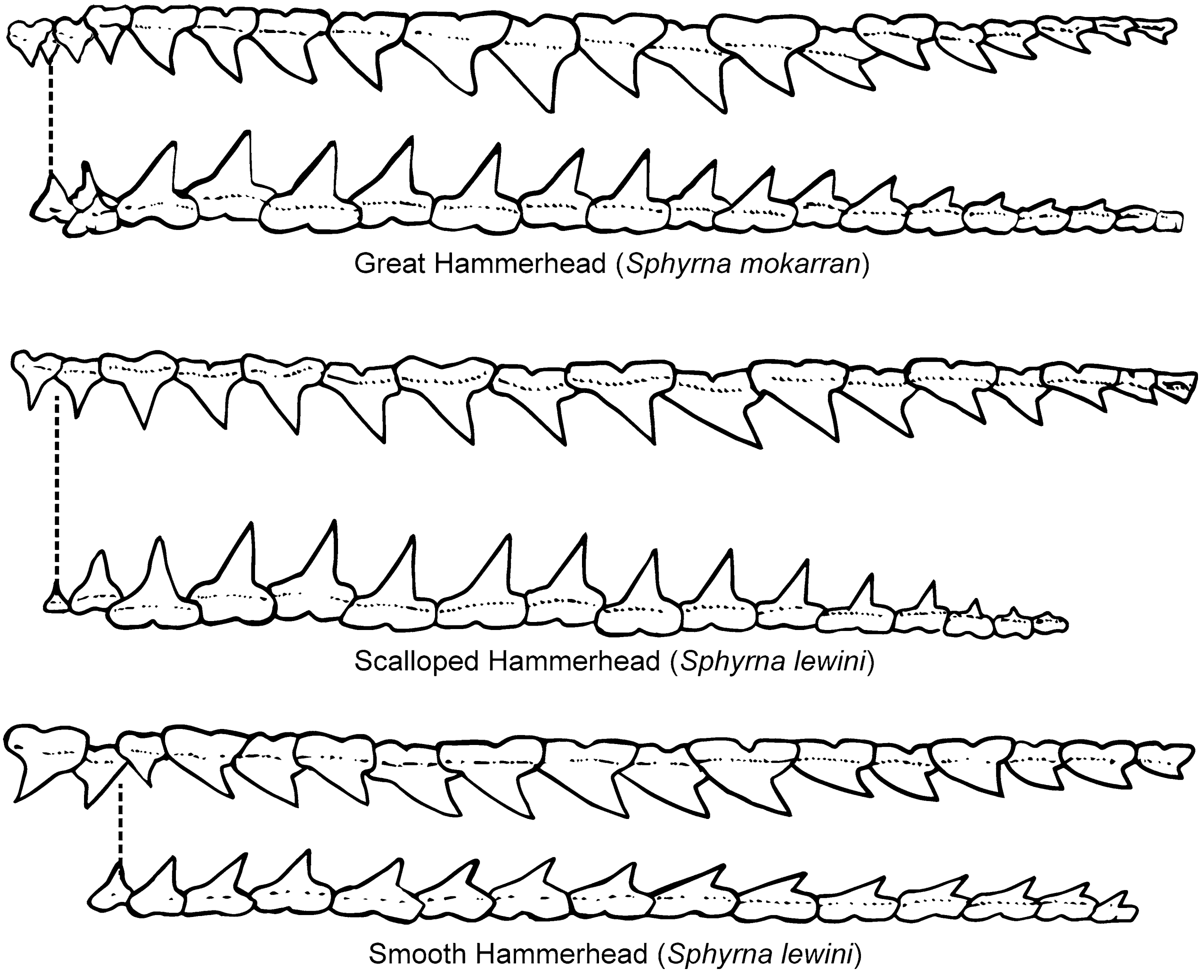

Fig. 4 Upper and lower tooth series of great, scalloped, and smooth hammerhead sharks. Modified from Bigelow and Schroeder (1948)

southwestern Mexico (Manjarrez-Acosta et al. 1983; Saucedo-Barrón et al. 1982; Torres-Rojas et al. 2010), southern Africa (Smale and Cliff 1998), and parts of Australia (Stevens and Lyle 1989), and Gulf of California (Klimley 1983, 1987). Squid appear to be less important when compared to teleost fishes for scalloped hammerheads in the south Atlantic (Brazil, Bornatowski et al. 2014). The subjects of most of these studies were juveniles, and Torres-Rojas et al. (2010) found no difference in the diets of the male and female juveniles. Based on finding a low value of the tropic-width niche, they classified the juveniles as opportunist feeders, as did Klimley (1983).

Insights into the drivers of sexual segregation may be gained by discriminating differences in stomach contents between of difference sizes and behavior (Klimley 1987). Juvenile males and females inhabit shallow inshore waters in the Gulf of California, where both feed upon benthic prey such as isopods (Isopoda), octopods (*Octopus* sp.), scorpion fish (*Scorpaena sonorae*), and neritic prey such as grunts (*Adioryx suborbitalis*) and mackerel (*Scomber japonicus*). Females move offshore at a smaller size than males, based on the higher proportion of females captured at depths exceeding 50 m in the 74–125 cm size class. Furthermore, schools of hammerhead sharks, measured using stereophotography, at offshore islands and seamounts in the Gulf of California contain many subadult females 100–140 cm, yet few males in this size range. This movement of female scalloped hammerhead sharks at an earlier age than males results in their having different diets. Females less than 160 cm fed on a higher percentage of pelagic prey than do males. Mesopelagic prey form 27.5% and epipelagic prey 5.5% of the female diet, while such prey forms only 18.1% and 3.6% of the male diet. The subadult females feed on deep water squid (*Mastigoteuthis* sp.) and pelagic crabs (*Pleuroncodes planipes*) near the surface. By moving off shore, the females maximize their feeding success as indicated by greater stomach fullness than males of the same size. Klimley (1987) hypothesized that females increase their fitness by migrating offshore earlier, feeding more successfully in the pelagic environment, and growing more rapidly than the males. The larger males and females, exceeding 160 cm feed mainly on mesopelagic squids (*Ancistocheirus leseuri*, *Mastigoteuthis* sp., and *Moroteuthis robustus*), epipelagic squid (*Dosidiscus gigas*) and mackerel (*Scomberomorus sierra*).

Smooth hammerhead

Fewer studies have been conducted on the diet and trophic dynamics of smooth hammerheads, although the available literature suggests they feed largely on squid and this is reflected in their similar dentition to scalloped hammerheads (Fig. 4). Off southern Africa, neritic and oceanic cepahlopods composed 55.81% and 21.31% wet mass of prey from non-empty stomachs (Smale and Cliff 1998). In the southern Atlantic, smooth hammerheads appear to primarily feed on cephalopods (Bornatowski et al. 2014). In the eastern Pacific Ocean, the smooth hammerhead diet is dominated by jumbo flying squid (*Dosidicus gigas*) and the Patagonian squid (Doryteuthis (*Amerigo gahi*), and there is evidence to suggest an ontogenetic shift in diet and habitat (Gonzalez-Pestana et al. 2017). Isotopic studies also suggest a similar trophic niche breadth but lack of overlap with co-occuring scalloped hammerheads (Loor-Andrade et al. 2015).

Life history

Great Hammerhead

Great hammerhead sharks are relatively slow growing and attain large sizes (Table 2). Growth rates for great hammerhead sharks in the Atlantic Ocean suggest a growth coefficient (k) of 0.13 (Cortés et al. 2015), and 0.079 in the Eastern Indian (Harry et al. 2011). In the Northwest Atlantic and Gulf of Mexico, growth rates were reported as 0.16 for males and 0.11 for females (Piercy et al. 2010). These values suggest moderate rates of biological productivity compared to other shark species (Branstetter 1990). In the Eastern and Southwestern Indian Oceans, males appear to reach sexual maturity between 155 and 217 cm total length, whereas females attain maturity between 145 and 237 cm (Cliff 1995; Stevens and Lyle 1989). Cortés (2000) reported sizes at maturity from the Eastern Indian Ocean at 225 cm for males and 210 cm for females (Harry et al. 2011 found that 50% of individuals were mature around 8 years in this region), and significantly larger sizes for the Southwestern Indian Ocean (335 for males and 309 for females). In the Northwest Atlantic and Gulf of Mexico, median length at maturity was 285 cm for females and 238 cm for males (Piercy et al. 2010) with a mean age at maturity of 20 years (Cortés et al. 2015). In the Eastern Indian Ocean sharks reach ~ 32 years for males and 39 years for females (Harry et al. 2011), and 42 years for males and 44 years for females in the Northwest Atlantic and Gulf of Mexico (Passerotti et al. 2010; Piercy et al. 2010). This species likely reproduces on a biennial cycle (at least in the Atlantic, Cortés et al. 2015). The average fecundity is 15 pups per litter in both the Atlantic and Eastern Indian, ranging up to 33 pups (Cortés 2000; Cortés et al. 2015).

Scalloped Hammerhead

There is a larger base of information on the life history of the scalloped hammerhead shark, suggesting that this species is relatively faster growing and attains moderate sizes (Table 2). The most recent growth rates for smooth hammerhead sharks in the Northwest Gulf of Mexico suggest a growth coefficient (k) of 0.09 for females and 0.13 for males (Piercy et al. 2007), 0.249 for females and 0.222 for males in the Western Pacific (Cortés 2000), 0.09 for both sexes in the North Atlantic and 0.05 for both sexes in the South Atlantic (Cortés et al. 2015), and 0.076 for both sexes in the Eastern Indian (Harry et al. 2011). These results suggest somewhat varying rates of biological productivity worldwide (Branstetter 1990). Age at maturity for this species has been estimated at 15 years for females and 9–10 for males in the Northwest Gulf of Mexico, and 4.1 for females and 3.8 for males in the Western Pacific (Cortés 2000). In the Eastern Indian, Harry et al. (2011) found that 50% of males were mature around 5.7 years in tropical waters and 8.9 years in temperate waters, whereas female age at maturity was speculated to occur > 10 years. There is also a high degree of variation in maximum size and size at maturity. Maximum sizes for scalloped hammerheads, according to region, are as follows (Cortés 2000): Northwest Gulf of Mexico = 310 cm (females), 300 cm (males); Eastern Indian = 346 cm (females), 301 (males); and Western Pacific = 324 (females), 305 (males). There is also variation in the size at maturity estimates (Cortés 2000, Cortés et al. 2015): North Atlantic = 303 cm (both); South Atlantic = 300 cm (both); Northwest Gulf of Mexico = 250 cm (females), 180 cm (males); Eastern Indian = 200 cm (females), 140–160 cm (males); and Western Pacific = 210 cm (females), 198 cm (males). In the Northwestern Gulf of Mexico, maximum age was estimated at 30.5 years for both sexes (Piercy et al. 2007), compared to 14 years in the Western Pacific (Cortés 2000). Female longevity was estimated at 31 years in the North Atlantic and 32 years in the South Atlantic (Cortés et al. 2015). Data suggest a biennial reproductive cycle in the North Atlantic and an annual cycle in the South Atlantic (Cortés et al. 2015). Fecundity also ranges from 13–23 pups (Eastern Pacific) to 12–38 pups (Western Pacific), and 30–40 pups (Northwest Gulf of Mexico; Cortés 2000). The average number of pups for the North and South Atlantic is 24 pups per litter and 18.5 pups per litter, respectively (Cortés et al. 2015).

Smooth hammerhead

There is a lack of regional information on smooth hammerhead life history (Table 2). Growth rates for smooth hammerhead sharks in the Eastern Atlantic Ocean suggest a growth coefficient (k) of 0.06 for males, 0.07 for females, and 0.06 for both sexes combined (Coelho et al. 2011). New information using updated growth models suggested a (k) of 0.09 for both males and females, with maximum sizes of 285 cm and 293 cm, respectively (Rosa et al. 2017). These values appear to be slightly lower than their relatives the great and scalloped hammerheads (Harry et al. 2011), suggesting the smooth hammerhead is the slowest-growing species of large hammerhead complex. In the southern hemisphere, it is thought males appear to reach sexual maturity between 250 and 260 cm total length, whereas females attain maturity around 260 cm (Stevens 1984). Due to a lack of regional information, Cortés (2000) estimated maturity between 210 and 240 cm total length for all stocks combined. No detailed age at maturity information exist for this species. Fecundity is relatively high, with a range of 20–49 pups per litter (Compagno 1984; Cortés 2000).

Vulnerabilities and population status

Large hammerhead sharks are prized in both commercial and recreational fisheries. Many species of hammerhead sharks are closely similar and difficult to distinguish from one another, and as such misidentification of hammerhead species is a common problem in fisheries research and management in many countries (Clarke et al. 2006a). As a result, species-specific data on hammerhead catch rates, bycatch, and fins are sometimes referred to as "*Sphyrna* spp," and not identified to the species level. In Hong Kong, the epicenter of the global shark fin trade, hammerhead shark fins are among the most valuable and popular (Abercrombie et al. 2005; Clarke et al. 2006b). Hammerhead shark fins (composed of all large hammerhead sharks from the *Sphyrna* Family) represented a significant proportion of the total shark fin trade, at 5.9% (Clarke et al. 2006b). Bycatch remains a significant threat to over a quarter of pelagic shark species (Dulvy et al. 2014), and it is well-known that large hammerhead sharks (*Sphyrna* spp.) are highly vulnerable to bycatch due to their aggregative behavior and high rates of at-vessel and post-release mortality following capture (Butcher et al. 2015; Gallagher et al. 2014b, c; Morgan and Carlson 2010).

Great hammerhead

The IUCN lists the great hammerhead as Endangered globally and identifies harvest as the major threat to this species. Great hammerhead sharks are not as commonly encountered in pelagic fisheries as their relatives the scalloped and smooth hammerhead. Great hammerhead fins were actually preferred by consumers in markets compared to other shark species including other hammerhead species (Abercrombie et al. 2005). This finding is significant because it suggests that hammerhead fins are prized and distributors and consumers can distinguish between biologically-similar hammerhead species. Non-harvest fisheries also pose a significant threat to this species. Recent data showed that great hammerhead sharks had an at-vessel mortality rate of 56%, with 3.8 h being the predicted time at the onset of mortality (Gulak et al. 2015). Working off Florida, Gallagher et al. (2014c) suggested a post-release mortality rate of ~ 50% of great hammerheads, likely due to the pronounced behavioral and physiological stress responses they mount when caught. A recent ecological risk assessment for this species in relation to pelagic longline fisheries suggested an overall moderate level of vulnerability based on low susceptibility (except for a few countries in the subtropical regions) and moderate productivity (Cortés et al. 2015). Great hammerheads are also highly prized in the recreational sector, particularly for those interested in obtaining records (Gallagher et al. 2017; Shiffman et al. 2014). Available catch rate data suggest declines in multiple regions. In the coastal waters in the Southwest Indian Ocean, catches of great hammerheads declined 89% and catch rates declined 79% (Dudley 2002; Denham et al. 2010). This decline was thought to be as a result of illegal longline operations targeting hammerheads during this time (Dudley and Simpfendorfer 2006). In the Northwest Atlantic, a 90% decline for this species was documented (Beerkircher et al. 2002).

Scalloped hammerhead

The majority of what we know about hammerhead vulnerability comes from studies on scalloped hammerhead sharks. Fisheries exploitation is the greatest threat facing the scalloped hammerhead shark, and exploitation occurs on every major continent (Baum et al. 2007). The IUCN lists the scalloped hammerhead as Endangered globally and identifies harvest as the major threat to this species. It is estimated that 1.3–2.7 million scalloped hammerhead (and smooth) sharks appear in the shark fin trade each year (Clarke et al. 2006b). It is well-known that scalloped hammerhead sharks are highly vulnerable to pelagic longline and bottom longline bycatch due to their aggregative behavior and high rates of at-vessel and post-release mortality, upwards of 90% following capture (Bromhead et al. 2012; Butcher et al. 2015; Coelho et al. 2012; Gallagher et al. 2014b; Morgan and Burgess 2007). This species is also vulnerable to bycatch in trawls, driftnets, purse-seines, and also artisanal fisheries (Baum et al. 2007). Juveniles may be caught by nets and in-shore fisheries (Baum et al. 2007). A recent ecological risk assessment was conducted for this species in relation to pelagic longline fisheries suggest an overall moderate level of vulnerability based on moderate productivity (Cortés et al. 2015); however this study did not take into account their high at-vessel and post-release mortality rates (Gallagher et al. 2012). Scalloped hammerheads are also prized in the recreational sector and are landed in significantly higher numbers than in the commercial section in some areas (Hayes et al. 2009), although these catches have significantly declined since the 1980s (Hayes et al. 2009).

Scalloped hammerhead sharks are declining at a global scale. In the Northwestern Atlantic, over 60,000 scalloped hammerheads were caught between 1986 and 2005 (Baum et al. 2003). Using fishery logbook and observer records from the pelagic longline fishery, a 89% decline in scalloped hammerhead sharks was reported from 1986 to 2000 (Baum et al. 2003), and a 76% decline from 1992 to 2005 (Baum and Blanchard 2010). The probability of catching scalloped hammerheads declined by an order or magnitude off Virginia, USA, in an analysis of a fishery-independent survey from 1975 to 2005 (Ha 2006). A 98% decline of scalloped hammerhead sharks was estimated from 1972 to 2003 in another fishery-independent survey off North Carolina, USA (Myers et al. 2007); although findings from this study have been contested (Grubbs et al. 2016). A 66% decline was estimated from 1983/1984 to 1994/1995 off South Carolina (Ulrich 1996). Scalloped hammerhead sharks are also exploited in the Caribbean and are largely absent from those reefs (Ward-Paige et al. 2010), although fishery records are unavailable. Scalloped hammerheads have declined by over 95% in the Southern Atlantic since 1979 (Barreto et al. 2016). A 64% decline was documented off the Western Indian Ocean using fishery-independent survey methods from 1978 to 2003 (Dudley and Simpfendorfer 2006). There has been a 50% decrease in the abundance of scalloped hammerhead sharks at Darwin and Wolf Islands in the Galapagos Islands in recent years (Peñaherrera-Palma et al. 2017). Over 100,000 tonnes of scalloped hammerhead sharks were landed in 2002 and 2003 in Indonesia (White et al. 2008), the largest shark fishing nation globally, and, although time-series data are unavailable, it is within reason to assume these populations are also in serious decline. Recent stock assessments of scalloped hammerhead sharks in the United States estimate a 70–83% decline in abundance since 1981 (Hayes et al. 2009; Jiao et al. 2009), with current levels estimated to be 17% of what they were in 1981 (Hayes et al. 2009). This species is declining rapidly alongside other large hammerhead sharks (Jiao et al. 2011). Scalloped hammerhead sharks are also heavily fished in the Red Sea and Eastern Pacific (Baum et al. 2007), and scalloped hammerheads have been extirpated from the Gulf of California (Pérez-Jiménez 2014). In 2014, the scalloped hammerhead became the first shark to be protected by the U.S. Endangered Species Act, citing four of the six distinct population segments as threatened (Indo-West Pacific, and Central/Southwest Atlantic) or endangered (Eastern Atlantic and Eastern Pacific).

Smooth hammerhead

While species-specific data on smooth hammerhead catch rates and incidence in fisheries may be lacking, smooth hammerheads are clearly caught in commercial longline fisheries and they sometimes naturally occur with scalloped hammerheads (Compagno et al. 2005). Therefore, they share many of the same threats as scalloped hammerheads. Bonfil (1994) reported that smooth hammerheads were caught in directed fisheries off USA, Brazil, Spain, Taiwan, and the Philippines. They were also harvested off Australia and Africa, and juveniles may be particularly vulnerable off the continental shelf of the Southwestern Atlantic Ocean (Casper et al. 2005). The IUCN lists the smooth hammerhead as Vulnerable globally and identifies harvest as the major threat to this species (Casper et al. 2005). It is estimated that 1.3–2.7 million smooth and scalloped hammerhead sharks (combined) appear in the shark fin trade each year (Clarke et al. 2006b). Smooth hammerhead fins are commonly identified in Hong Kong markets (Abercrombie et al. 2005) and they are the most common hammerhead fished off western South America for export to Asia, including in protected waters such as the Galápagos (Carr et al. 2013; Sebastian et al. 2008). Few studies have considered smooth hammerheads in evaluations on the impacts of bycatch, although they are commonly encountered as such particularly in pelagic longlines and drift gillnets operating near temperate and subtropical continental shelves (Casper et al. 2005). Smooth hammerhead sharks show low survivability to incidental capture (i.e., 70–90% mortality) like their close relatives (Reid et al. 2011; Coelho et al. 2012). A recent ecological risk assessment for this species in relation to pelagic longline fisheries suggested a low level of vulnerability (Cortés et al. 2015). It should be noted, however, that this and other studies cautioned conclusions about smooth hammerhead risk due to the lack of biological information and the fact that significant and underreported fishing mortality was likely to be occurring (Coelho et al. 2011). There is a lack of data specific to smooth hammerhead abundance worldwide, but available catch rate data suggest global declines. In the coastal waters off New South Wales, Australia, incidental catches of smooth hammerheads declined precipitously over 50 years (Reid et al. 2011). Smooth hammerheads were among the most commonly captured shark in a Mexican artisanal fishery in the Pacific in the mid 1990s, (Pérez-Jiménez et al. 2005), and were abundant in the 1960s (Pérez-Jiménez 2014), but now all hammerheads in the region have been drastically reduced in abundance (Pérez-Jiménez 2014). This species has virtually disappeared from catches off the central and southern Mediterranean Sea since 1986 (Walker et al. 2005). The number of tagged smooth hammerheads also declined significantly from the 1980s to early 2000s off Eastern Africa (Diemer et al. 2011). By summarizing catches from commercial, recreational, and artisanal catches, Jiao et al. (2011) found a decline from upwards of 12,000 fish total in the early 1980s to nearly 0 in 2005 off the Atlantic and Gulf of Mexico. Using a modeling approach applied to data-poor shark stocks, Jiao et al. (2011) illustrated consistent patterns of population decline for the smooth hammerhead over this time frame with a collapse beginning in the early 1990s and a contemporary abundance that is equal or lower than that of the scalloped hammerhead.

Conservation

The high degree of threat facing hammerhead sharks is becoming increasingly apparent to the scientific, policy, and public communities, although their conservation remains complex (Gallagher et al. 2014a). There are inherent difficulties in species identification, and the three species of large hammerheads are often grouped together in fisheries logbook database records, resulting in inaccuracies with catch records. In some cases, population trajectories have been based on this grouping. For example, a 99% decline in "hammerhead" sharks was detected from 1900 to 1995 in a coastal artisanal fishery in the Mediterranean Sea (Ferretti et al. 2008), and a 89% decline in "hammerhead" sharks was also found from 1986 to 2000 in the Northwest Atlantic using commercial longline records (Baum et al. 2003). Findings from the latter study were corroborated by a re-analysis of the same database from 1992 to 2000, showing a 76% decline (Baum and Blanchard 2010). In these above-studies, hammerhead shark declines were among the most drastic of any species assessed (Baum and Blanchard 2010), and hammerheads declined the fastest of any species in Ferretti et al. (2008).

Marine reserves could result in lower fishing mortality while affording local populations of the species the chance to recover. For great hammerheads, their alternating of coastal and pelagic zones makes their management complex, however recent data suggested that—at least for the stock in the Northwestern Atlantic—prohibiting their catch in the US waters would protect over 90% of their core habitat (Graham et al. 2016). Therefore, time-area closures of core great hammerhead habitat might be effective. Marine reserves may be more beneficial to scalloped hammerheads, and to a lesser extent smooth hammerheads (although little is known about this species), as these species tend to aggregate at offshore islands and seamounts. It has been argued that the daily extent of the movements of individual scalloped hammerheads may be limited by the availability of geomagnetic cues associated with the volcanic nature of their habitat (Klimley 1993; Klimley et al. 2015). The fact that the scalloped hammerheads are aggregated at topographic features and tend to have well-defined nurseries makes it feasible to protect them through the establishment of well-placed marine protected areas and areas where they are prized as a non-consumptive resource through shark-diving tourism (Gallagher and Hammerschlag 2011).

It is increasingly apparent that hammerhead species are in general more sensitive to capture than other shark species (Gallagher et al. 2014a; Gulak et al. 2015; Jerome et al. 2017; Drymon and Wells 2017), which has important implications for both catch and release shark fisheries as well as bycatch reduction in pelagic longline fishing. However, trying to avoid the catching of hammerheads under various operational fishery settings is undeniably challenging to implement, although there have been some advances in bycatch reduction devices with a specific focus on hammerhead sharks (e.g., O'Connell et al. 2015). While recent conservation successes such as the three species' listings on Appendix II of CITES in 2014 and the CMS in 2015 are laudable, regulating the trade of these highly prized and easily misidentified species is not likely to provide short nor long-term solutions to dealing with the issue of fisheries mortality. Clearly more science is needed to be conducted on the large hammerhead complex in order to better inform future management scenarios, however, precautionary actions for these highly threatened species are warranted in order to establish better population parameters, abundance estimates, and to allow recovery.

Conclusion

The large hammerhead shark complex provides an exciting look into the evolution of unique life histories, behaviors, and other specializations not seen in other sharks. A moderate volume of information has been collected on these species to date, however, there are clearly gaps in certain areas (Table 1). The scalloped hammerhead is by far the most well studied species in this complex, followed by the great hammerhead and the smooth hammerhead. The differential life histories among and within these three species suggests that there may be much still to learn from the Family Sphyrnidae, which in turn may help us understand more about elasmobranch fish biology, physiology, and behavior. Improved information on the movements and connectivity of great and smooth hammerheads is direly needed. We chose not to include phylogenetic studies into this review as those data may be better suited to a separate broader-scale elasmobranch review with the requisite molecular contexts, although connectivity within and among these species is clearly important for future assessments and to improve management globally (Chin et al. 2017). It is also clear that this group of sharks is highly threatened, and future work designed to fill the above research gaps could go a long way for improving our understanding of the conservation needs of these species.

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