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Evolved for Extinction: The Cost and Conservation Implications of Specialization in Hammerhead Sharks

AUSTIN J. GALLAGHER, NEIL HAMMERSCHLAG, DAVID S. SHIFFMAN, AND SEAN T. GIERY

The interactions between the evolutionary history of species and contemporary changes in their environment can result in both positive and negative outcomes for fitness and survival. Sharks are one the oldest groups of all extant vertebrates but, today, are among the most threatened globally, primarily because of destructive fishing practices. Hammerhead sharks (Sphyrnidae) exhibit extremely specialized traits and complex behaviors that have increased their vulnerability to human exploitation, which impedes conservation efforts. By bringing together published data on aspects of hammerhead shark phylogeny, morphology, biology, physiology, and ecology, we argue that the same novel adaptations that have historically contributed to evolutionary success have become maladaptive under current levels and modes of exploitation. Therefore, we suggest that future management be made in light of—rather than in spite of—the unique evolutionary and ecological traits possessed by hammerhead sharks, because similar patterns are threatening other taxa with high extinction risk.

Keywords: apex predator, specialization, vulnerability, evolution, anthropogenic disturbance

It has recently been argued that the loss of apex consumers is the most pervasive impact of humankind on the natural world (Estes et al. 2011), and these removals can initiate trophic cascades, ultimately affecting diverse ecological processes and biogeochemical cycles. Marine ecosystems have recently become a focus of such predator extinctions (Jackson 2008). Harnik and colleagues (2012) recently argued that, because of the contemporary and future challenges to the functional integrity of entire marine ecosystems caused by predator extirpation, there is an urgent need to determine which species will adapt and which will go extinct.

Overfishing is considered the largest threat facing marine fishes and ecosystems (Jackson et al. 2001), and the vulnerability of marine top predators (i.e., tuna, billfish, sharks, pinnipeds) to fisheries exploitation is largely driven by a suite of biological factors, such as slow intrinsic rates of population growth, late age at maturity, and low rates of fecundity (Musick 1999). Obtaining detailed life-history data from these species is important for generating accurate population models, but this process can be challenging because of the rarity of species, logistical constraints, and ethical issues. However, species may become disproportionately susceptible to human-driven threats, independent (but not exclusive) of their life-history characteristics, as a result of highly evolved behavioral and ecological specializations (Futuyma and Moreno 1988, Irschick et al. 2005, Gallagher et al. 2012). This additional susceptibility can be triggered when traits or behaviors that were presumably adaptive under historical selection regimes suddenly become maladaptive under recent anthropogenic change (Harcourt et al. 2002). This dynamic can drive significant population declines that can lead to a species' extinction (Rodewald et al. 2011).

The notion that species with specialized life histories or adaptations are more vulnerable than are generalized species is not a novel concept (Clavel et al. 2011); however, it has rarely been included in or applied to the conservation planning of threatened marine predators (Gallagher et al. 2012). This is especially the case with sharks, a group of marine fishes that has been evolving for roughly 450 million years (Klimley 2013).

Sharks are a diverse group of animals with a suite of behavioral, physiological, and ecological adaptations, and these species are subject to varying degrees of threat. The larger-body species tend to be the ones for which the greatest amount of scientific information exists and are species that are generally the most valued in fisheries. Hammerhead sharks are perhaps the most recognizable and intriguing shark species to both scientists and the public. The group of

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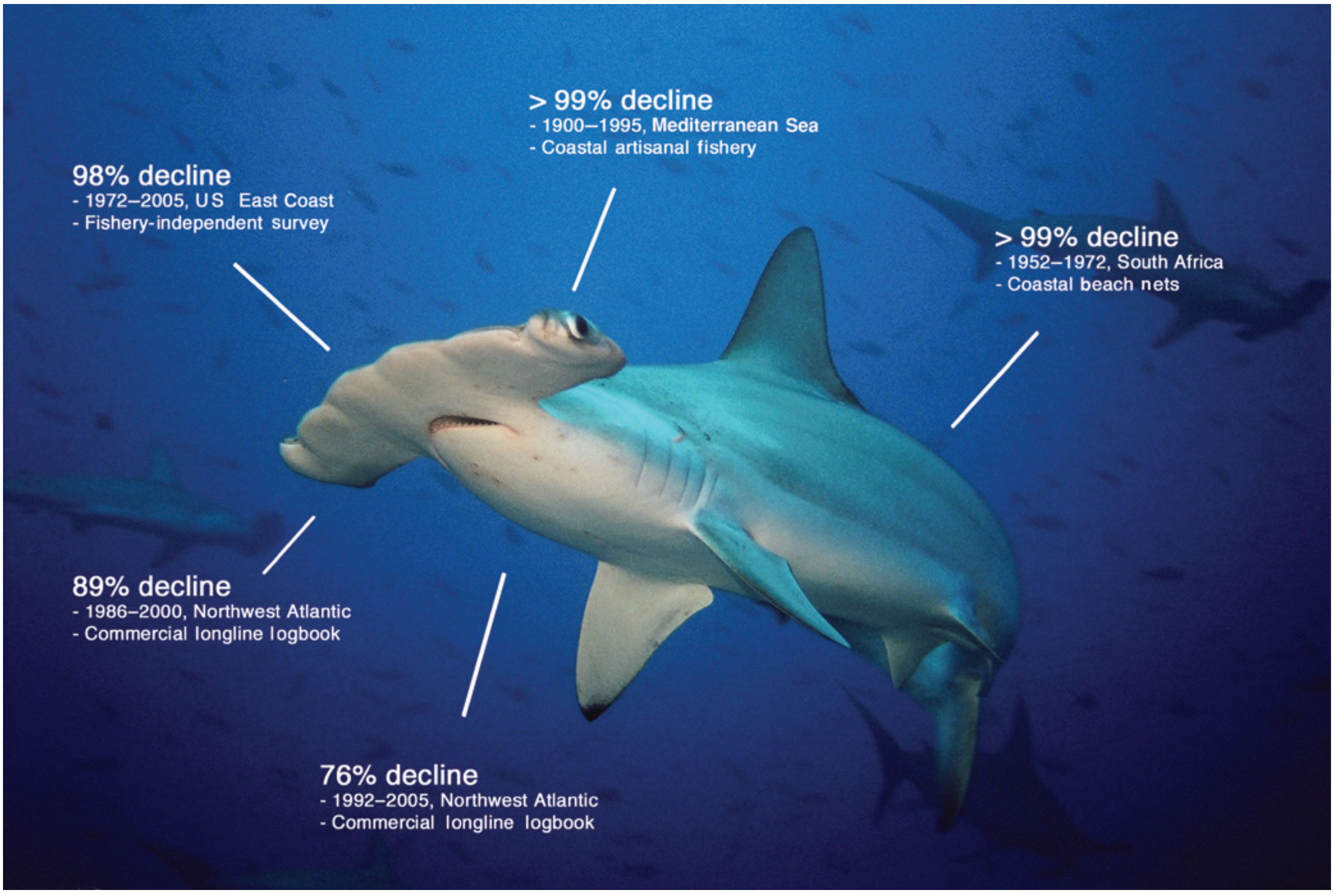

Figure 1. Published scientific estimates of hammerhead shark population declines from various ocean basins worldwide. The estimated decline, the year and area (ocean basin), and the sampling tool are noted in each example. Sources: The relative published population estimates are, starting at top right and moving counterclockwise, from Ferretti and colleagues (2010), Ferretti and colleagues (2008), Myers and colleagues (2007), Baum and colleagues (2003), and Baum and Blanchard (2010). In all cases, declines were categorized for the large hammerheads (listed as* hammerhead spp. *except in Ferretti et al. 2010 and Myers et al. 2007, who identified* Sphyrna lewini *specifically). Ferretti and colleagues (2010) showed that, at one of two studied beach sites, scalloped hammerheads experienced the most severe population declines in the analysis; Ferretti and colleagues (2008) noted that hammerhead shark populations declined the fastest of any assessed species; Myers and colleagues (2007) and Baum and colleagues (2003) affirmed that the hammerhead population declines were among the most severe of any studied species; and Baum and Blanchard (2010) most recently reaffirmed that hammerhead population declines were "precipitous" and remained the most severe of any studied species. Some of these estimates have been challenged in the literature (i.e., see Burgess et al. 2005). A scalloped hammerhead (*S. lewini*) is pictured. Photograph: Tom Burns.

nine species (family Sphyrnidae) are among the phylogenetically youngest of all extant shark species, having diverged from the rest of Carcharhiniformes around 10–20 million years ago (Lim et al. 2010, Klimley 2013) and having evolved phenotypic divergence defined by unique behavioral, physiological, and morphological adaptations not seen in their relatives. It is thought that some of these adaptations (e.g., their "hammer") afford hammerhead sharks enhanced foraging and sensory capabilities (McComb et al. 2009). In fisheries analyses, it has been reported that hammerhead sharks are experiencing drastic population declines (although some of these analyses have been challenged) in excess of 90% in several parts of their global range because of overexploitation (see figure 1 for references). In this Forum, we explore the idea that the relatively extreme specialization and drastic population declines seen in hammerhead sharks are causally related. Moreover, using hammerhead sharks as a case study, we seek to illustrate how aspects of specialization may increase the vulnerability of a marine predator to human exploitation, resulting in a de facto evolutionary trap that can significantly impede conservation efforts and subsequent recovery under current harvest regimes and management strategies. Although specialization is most generally defined by species that occupy a narrow range of habitats or environmental envelopes, we follow the definition provided by Irschick and colleagues (2005), in which specialization is considered a continuum with three components that may not be mutually exclusive: ecology, behavior, and function.

The purpose of this Forum is not to redefine *specialization*, nor to argue the merit of one approach over another. Rather, we focus our discourse on hammerheads as specialized species requiring special conservation considerations.

Ecological specialization

Ecological specialization is driven by parameters that may restrict the niche volume of species and that may affect the prevalence of other traits, such as biological productivity (Irschick et al. 2005). Although hammerhead sharks are found globally in tropical and temperate ecosystems, they (like most shark species) have evolved a life-history strategy that features slow growth, a late onset of sexual maturity, and low reproductive rates. Whereas most shark species are long lived, the great hammerhead (*Sphyrna mokarran*) can live up to 44 years, one of the oldest reported ages of any elasmobranch (Piercy et al. 2010).

A look into the neurophysiology and development of hammerhead sharks suggests that some of the unique and derived behaviors and traits may be closely correlated with specializations in brain and neural organization, termed *cerebrotypes* (Northcutt 1978, Yopak 2012). For example, variations in brain size and complexity are directly linked to phylogeny and ecology (Yopak 2012), whereby neural development can reflect adaptation and ecological specialization in vertebrates (Yopak 2012). In a recent analysis of brain organization across 84 species of cartilaginous fishes, three large hammerhead species (the great hammerhead [*S. mokarran*], the scalloped hammerhead [*Sphyrna lewini*], and the smooth hammerhead [*Sphyrna zygaena*]) exhibited extremely large brains relative to their body mass (encephalization), comparatively enlarged telencephalons and cerebellums, and the highest levels of cerebellar foliation (a measure of complexity; Yopak et al. 2007, Yopak 2012). Relative enlargement of these brain areas has been linked with higher cognitive capabilities, such as increased sociality or social intelligence (Yopak et al. 2007), complex sensorimotor integration, habitat complexity, long-distance migrations, and agile prey capture (Yopak 2012). Moreover, hammerheads have also evolved a derived form of viviparous embryonic nutrition, which includes the merging of a yolk sac with the uterus to form an early placenta-like organ that nourishes pups throughout their yearlong gestation (Stevens and Lyle 1989). Increased energy flow from the mother to the fetus is a prerequisite for the development of large brains in mammals (Martin RD 1996), which suggests an important evolutionary link between brain size and maternal investment, which may have contributed to the presently high rates of encephalization documented in hammerhead species (Mull et al. 2011). With very few natural predators, these biological adaptations permit hammerheads to invest substantial resources in the long-term development of a relatively small number of offspring, similar to mammalian species. However, under the current conditions of overfishing, these ecological and developmental specializations make them disproportionately vulnerable to even low levels of harvest (Ferretti et al. 2010).

Behavioral specialization

Behavioral specializations are defined by a small range of behaviors that are used for generalized tasks (e.g., mating, feeding, predator avoidance; Irschick et al. 2005). In general, schooling fishes are prone to higher rates of exploitation, and many shark species form aggregations. However, the scalloped hammerhead, *S. lewini*, is one of the only extant, large-body shark species that displays highly organized and complex social schooling behavior (Klimley and Nelson 1981, Klimley 1985). Large, partially sexually segregated groups (of more than 200 individuals) are highly migratory but known to school in a few predictable locations, including Cocos Island, and in the northern Galápagos Archipelago (Hearn et al. 2010, Bessudo et al. 2011). Presumably, this behavior is adaptive, because it allows males to easily locate, court, and copulate with the largest and fittest females in the school (Klimley and Nelson 1981, Klimley 1985). However, because industrialized fishing practices target these aggregations (Carr et al. 2013), this behavior has rendered the scalloped hammerhead increasingly susceptible to targeted exploitation as well as incidental nontarget bycatch (in which mortality is very high; see below).

Across their ontogeny, both scalloped and great (*S. mokarran*) hammerhead alternate between coastal and pelagic phases. Off the US East Coast, the great hammerhead also undergoes extensive migrations into international waters, where little or no protection exists, which makes them particularly prone to unregulated harvest, despite the reduced threats that would have been associated with aggregative behavior (Hammerschlag et al. 2011). However, despite the well-documented risks to large sharks from commercial fisheries and bycatch, coastal habitats can often be highly altered and, therefore, pose numerous threats to these species. Gravid great hammerhead sharks, for example, enter shallow tropical coastal bays to give birth, which subjects the pregnant females and their young to coastal fishing and a potentially higher degree of anthropogenic impacts because of pervasive and intensifying coastal development. Indeed, recent work suggests that recreational fishers disproportionately target great hammerhead sharks compared with other species (Shiffman and Hammerschlag 2014).

Functional specialization

Functional specializations arise when a species' body plan, morphology, or physiology constrains it to a subset of available resources (Irschick et al. 2005). Understanding the links between an organism's physiology and its physical environment is crucial for understanding survival and performance when the organism is exposed to natural and anthropogenic stressors (Ricklefs and Wikelski 2002), and the stress responses of individuals or species exemplify this relationship. A common stress response in fishes results from capture. A recent study by Gallagher and colleagues (2014) showed that hammerhead sharks exhibited highly disturbed physiological parameters immediately after capture (among the most relatively disturbed blood chemistry values in the literature), which were thought to be related to their strategy of prey capture, which requires burst swimming behavior (Gallagher et al. 2014). Although the prolonged excitation of these physiological states may support agile prey capture, they result in high rates of at-vessel and postrelease mortality (60%–80%) when the sharks are engaged in fisheries capture scenarios (bycatch in commercial fisheries; Morgan and Burgess 2007). Furthermore, it is plausible that the evolution of a divergent body plan (i.e., the "hammer") has resulted in a trade-off in the performance of other functional and morphological features (i.e., decreased mouth size, which may limit oxygen assimilation). These types of constraints, due to physiological or morphological adaptation, may actually be more common than was previously thought and, here, show promise for explaining the high rates of incidental fishing mortality in bycatch; however, the validation of this trade-off requires further research.

Taxonomic differences

This case study represents an attempt to frame a species' precipitous decline that is linked not only to life-history traits but to a suite of ecological, behavioral, and functional adaptations that predispose the species to overharvest. To reinforce this perspective, we briefly contrast hammerheads with the adaptations and conservation status of tiger sharks (*Galeocerdo cuvier*), a sympatric predator. The tiger shark is a large-body coastal and semipelagic shark species with a temperate and tropical distribution (Heithaus 2001). Ecological and dietary studies suggest that this species is an adaptive generalist that feeds on a wide range of prey items, including birds, reptiles, fishes, and other sharks (Heithaus 2001, Gallagher et al. 2011). Like hammerheads (and most other sharks), tiger sharks exhibit life histories that make them susceptible to overharvest; however, a different suite of ecological and behavioral adaptations appears to attenuate that risk. From a physiological perspective, tiger sharks exhibit low-stress responses when hooked on a fishing line and extremely high survival rates when captured and released (Gallagher et al. 2014). Moreover, tiger sharks do not appear to exhibit the degree of aggregation behavior that predisposes species such as the scalloped hammerhead shark to targeted (and often unregulated) overharvest. Instead, they are habitat generalists, migrating over thousands of kilometers during yearlong migrations in the many ocean basins (e.g., Hammerschlag et al. 2012). Although many species of large-body sharks are currently displaying declines, recent data show a stabilizing trend for tiger sharks (Baum and Blanchard 2010, Ferretti et al. 2010). We are unable to ascertain whether the contrasting demographic trend between hammerheads and tiger sharks is explained by their differing degrees of ecological and physiological specialization; indeed, these trends may result from the interaction of many factors (including their value in fisheries and changes in fishing effort or gear). However, this comparison strongly suggests that life-history parameters, in isolation, cannot explain overharvest.

Managing specialization in top predators

Clearly, there is a mismatch between the evolutionary history of hammerhead sharks and fisheries. By understanding how specialization and fishing interact to influence hammerhead vulnerability, fishers may be able to adjust fishing behavior and techniques to improve conservation strategies. These modifications include avoiding peak areas or periods of shark abundance, adjusting fishing depth or leader material, improving shark handling, and reducing sharks' detection of baited hooks (Gilman et al. 2008). For example, sharks are commonly encountered incidentally as bycatch; however, as was discussed earlier, the impact of this encounter can result in higher mortality for certain species, such as hammerheads. However, recent studies have shown that the hammerhead's highly specialized sensory systems detect electric fields from greater distances than do those of other shark species (Rigg et al. 2009). This extreme sensory adaptation might permit some degree of mitigation of fisheries bycatch if it can be coopted in ways that deter hammerheads (and other sharks) from fishing gear. For example, lanthanide metal hooks produce an electric field when they are placed in seawater and have been examined as a potential elasmobranch bycatch–mitigation technique (Rigg et al. 2009). Recent experiments have shown that the overall catch of scalloped hammerheads is significantly lower on experimental lanthanide hooks than on control hooks (e.g., Hutchinson et al. 2012). Additional research is needed to test the viability, validity, and feasibility of implementation of these techniques and other approaches, but we believe that this illustrates an important strategy for mitigating effects on nontarget species—that is, capitalizing on the unique adaptations of organisms for management and conservation. Future fisheries management models may benefit from a more explicit integration of parameters reflective of the ecological, physiological, and behavioral adaptations of the target species, as is occasionally done in other environmental policy and management areas (e.g., invasive species managed by ecological niches). Finally, hammerheads are popular and well known. For example, *hammerhead* was the most popular choice of favorite shark when we asked citizen scientists on our research trips (22% of 1800 responses), and hammerhead sharks were the most popular species of shark among clients hiring shark-fishing charters in Florida (Shiffman and Hammerschlag 2014). Therefore, there may be great potential to instill a conservation ethic among the public, who hold these species in high regard or can easily recognize them because of their unique appearance.

Hammerhead sharks have the reproductive potential to recover from population depletion if mortality levels are decreased (Hayes et al. 2009, Piercy et al. 2010). Three species of hammerhead (scalloped, great, and smooth) were recently added to Appendix II of the Convention on International Trade in Endangered Species (*www.cites.org/eng/app/appendices.php*), which will better regulate trade in hammerhead shark products. This achievement is laudable, because large hammerhead sharks are highly valued in certain fisheries, which is likely due to their large (and relatively more specialized) fin size and high fin-ray count (Baum et al. 2007). However, their inclusion is unlikely to wholly solve the issue of overexploitation or bycatch. Perhaps one of the best conservation strategies is to limit interactions between hammerheads and fishing gear. Recently, the US National Marine Fisheries Service announced that both the great hammerhead (document no. NOAA-NMFS-2013-0046) and the scalloped hammerhead (document no. NOAA-NMFS-2011-0261) are being considered for listing under the Endangered Species Act; if this is successful, they would be the first shark species listed. We believe that, because of the population declines and mismatches with human threats outlined above, both species are good candidates for listing. Moreover, through molecular analyses, a new species of large hammerhead was recently discovered off the US East Coast, previously thought to be the scalloped hammerhead (Quattro et al. 2013), thus increasing the risks to the latter species and adding complexity to these management issues. Furthermore, although we focused primarily on the two large hammerhead species for which the most information is available (scalloped and great), the patterns of specialization may be similar among the handful of other hammerhead species, whose maximum size is smaller (e.g., the smooth hammerhead [*S. zygaena*] and the scoophead hammerhead [*Sphyrna media*]).

Conclusions

We are just beginning to understand the complexities of how the evolutionary histories of species interact with the human-induced stressors of a changing world. Our discourse adds to the growing realization that the adaptive optimum for top predators and other large vertebrates is shrinking because of modern anthropogenic impacts. These changes may break the correlation between the phenotype and the adaptive landscape faster than the speed at which adaptive evolution can occur (Law 2007), especially in apex marine predators, which have among the slowest rates of molecular evolution of all extant vertebrates (Martin AP and Palumbi 1993). Some of the novel adaptations that have historically contributed to their evolutionary and ecological successes may now be maladaptive under current levels of exploitation. This type of dead end is supported by work in terrestrial systems showing that EDGE (evolutionarily distinct and globally endangered) vertebrate species are often at higher risk of extinction because of the unique adaptations that they exhibit (Isaac et al. 2007).

Hammerhead sharks are familiar, fascinating, and distinctive animals. They are developmentally advanced and exhibit exceptionally complex behavior and novel adaptations that make them highly vulnerable to exploitation, and, therefore, they require special and aggressive conservation considerations. However, hammerheads are also not an isolated case of a specialized group of taxa being exceptionally vulnerable to exploitation; other species display patterns of specialized parameters and a high risk of extinction, such as large tunas (*Thunnus* spp.), the kakapo (*Strigops habroptilus*), the northern right whale (*Eubalena glacialis*), and many species of leopards (subfamily Pantherinae), just to name a few. The performance of specialized behavioral, functional, and physiological adaptations in contemporary environments is central to human–ecological conflicts. These patterns extend beyond a sole species or group of species and may be applied to other threatened taxa exhibiting declines. Given the limited resources and political will, consideration of these factors will further a comprehensive understanding of a species' susceptibility to exploitation and propensity for recovery, thus allowing managers to most effectively triage at-risk species for conservation efforts.

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Austin J. Gallagher (agallagher@rsmas.miami.edu), Neil Hammerschlag, and David S. Shiffman are affiliated with the Leonard and Jayne Abess Center for Ecosystem Science and Policy, in Coral Gables, Florida, and with the R. J. Dunlap Marine Conservation Program, at the University of Miami, in Miami, Florida. NH is also affiliated with the Rosenstiel School of Marine and Atmospheric Science, at the University of Miami. Sean T. Giery is affiliated with the Department of Applied Ecology at North Carolina State University, in Raleigh.