REVIEW SUMMARY

CONSERVATION

Ecological roles and importance of sharks in the Anthropocene Ocean

Simon Dedman*†, Jerry H. Moxley†, Yannis P. Papastamatiou, Matias Braccini, Jennifer E. Caselle, Demian D. Chapman, Joshua Eli Cinner, Erin M. Dillon, Nicholas K. Dulvy, Ruth Elizabeth Dunn, Mario Espinoza, Alastair R. Harborne, Euan S. Harvey, Michelle R. Heupel, Charlie Huveneers, Nicholas A. J. Graham, James T. Ketchum, Natalie V. Klinard, Alison A. Kock, Christopher G. Lowe, M. Aaron MacNeil, Elizabeth M. P. Madin, Douglas J. McCauley, Mark G. Meekan, Amelia C. Meier, Colin A. Simpfendorfer, M. Tim Tinker, Megan Winton, Aaron J. Wirsing, Michael R. Heithaus

BACKGROUND: Pervasive losses of predators on land, in freshwater habitats, and in oceans have disrupted ecosystems, prompting interest in rebuilding their populations to ecologically functional levels. Predator restoration may also facilitate nature-based climate solutions by indirectly increasing carbon sequestration through sharks' direct predation and risk effects on herbivores and herbivores' predators and by enhancing ecosystem resilience. However, selecting target species for these efforts requires a functional understanding of their ecosystem roles.

Sharks are a diverse (more than 500 species) group of predators found within marine, estuarine, and freshwater ecosystems. Although there is considerable variation in feeding modes and body sizes, sharks are often presumed to be critical to ecosystem structure, function, and resilience through top-down forcing of ecological communities. Although often valid, this presumption oversimplifies the many roles played by sharks. It also minimizes examples of functional redundancy and small ecological effects. Precipitous population declines in many species are a cause for concern and an impetus to investigate whether reversing declines could benefit ecosystems. Yet a functional understanding of ecological roles and importance of sharks is lacking because of the inherent difficulties of studying their interactions and the mechanisms through which sharks may—or may not—affect ecosystems.

In this Review, we have evaluated historical and ongoing global depletions—and occasional recoveries—of sharks to elucidate their diverse ecological roles, and we highlight the value of understanding their past, present, and future roles. We investigated where sharks play important roles, identified where population restorations may be particularly beneficial, and evaluated policies that can support role recovery.

ADVANCES: Empirical studies of the ecological roles and importance of sharks have revealed considerable cascading effects of macropredatory sharks [such as the tiger shark (*Galeocerdo cuvier*) and white shark (*Carcharodon carcharias*)] in coastal seagrass and kelp ecosystems, which influence habitat quality and carbon sequestration. These shark-initiated indirect effects may enhance the resilience of ecosystems that are increasingly experiencing extreme climate events (such as marine heat waves). However, not all sharks exert large top-down effects on prey or wider communities, although long-term overfishing causing large-scale depletions may obscure historical roles, particularly in difficult-to-study habitats such as pelagic systems or deep waters. Previously unappreciated roles of sharks (for example, facilitating ecosystems through nutrient transp[illegible] have recently become apparent in multi[illegible] ecosystems and taxa.

Climate change and industrializing oceans (such as overfishing, resource extraction, and tourism) are creating new roles for sharks and modifying the spatiotemporal patterns and importance of their effects. Warming oceans are expanding some shark ranges to higher latitudes, suggesting broadening importance across wider geographies, and thermal asymmetries in the metabolic costs and performance of sharks and marine mammals could affect competitive and predator-prey interactions. Range shifts and the recovery of white sharks, for example, are limiting the recolonization of sea otter historic ranges, which necessitates understanding how shark ecologies and species interactions affect broader ecosystem recovery. In multiple ocean basins, killer whale (*Orcinus orca*) predation risk has shifted distributions of white sharks, disrupting shark feeding patterns and ecological roles. Other accelerating anthropogenic pressures such as aquaculture, wildlife tourism, and extractive activities such as fishing are diversifying shark-human interactions and altering the manner and magnitude of spatiotemporal impacts of sharks on ecosystems.

Sharks influence ecosystems through various mechanisms. Tiger sharks and other large species are important to the development, maintenance, and resilience of seagrass and other macrophyte communities through top-down effects on their prey. Other species transport limiting nutrients or play less understood roles. Management must preserve diverse shark roles in a rapidly developing ocean and changing climate.

OUTLOOK: Gaps remain in our understanding of the ecological importance of sharks in today's oceans, necessitating research especially on small-bodied and deepwater sharks and shark-driven nutrient transport. Concurrently, management should aim to maintain ecological function rather than just maximum sustainable yield or population persistence, especially for influential and threatened macropredatory species. Given the potential for diverse and hidden roles, managing for shark biodiversity is important. Although transitions in fisheries and recovery goals will be challenging (for example, owing to commercial value and fisheries depredation), they are necessary to ensure healthy ecosystems in a changing ocean. ■

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Ecological roles and importance of sharks in the Anthropocene Ocean

Simon Dedman[1]*†, Jerry H. Moxley[1]†, Yannis P. Papastamatiou[1], Matias Braccini[2], Jennifer E. Caselle[3], Demian D. Chapman[4], Joshua Eli Cinner[5], Erin M. Dillon[6,7], Nicholas K. Dulvy[8], Ruth Elizabeth Dunn[9,10], Mario Espinoza[11,12,13], Alastair R. Harborne[1], Euan S. Harvey[14], Michelle R. Heupel[15,16,17], Charlie Huveneers[18], Nicholas A. J. Graham[9], James T. Ketchum[13,19,20], Natalie V. Klinard[21], Alison A. Kock[22,23], Christopher G. Lowe[24], M. Aaron MacNeil[21], Elizabeth M. P. Madin[25], Douglas J. McCauley[3,6], Mark G. Meekan[26], Amelia C. Meier[25], Colin A. Simpfendorfer[15,27], M. Tim Tinker[28,29], Megan Winton[30], Aaron J. Wirsing[31], Michael R. Heithaus[1]

In ecosystems, sharks can be predators, competitors, facilitators, nutrient transporters, and food. However, overfishing and other threats have greatly reduced shark populations, altering their roles and effects on ecosystems. We review these changes and implications for ecosystem function and management. Macropredatory sharks are often disproportionately affected by humans but can influence prey and coastal ecosystems, including facilitating carbon sequestration. Like terrestrial predators, sharks may be crucial to ecosystem functioning under climate change. However, large ecosystem effects of sharks are not ubiquitous. Increasing human uses of oceans are changing shark roles, necessitating management consideration. Rebuilding key populations and incorporating shark ecological roles, including less obvious ones, into management efforts are critical for retaining sharks' functional value. Coupled social-ecological frameworks can facilitate these efforts.

Globally, predator loss across terrestrial (*1*), freshwater (*2*), and marine (*3*, *4*) ecosystems is concerning because of their roles in structuring communities and altering ecosystem processes through indirect interactions (*5*–*7*) and enhancing ecosystem resilience to multiple stressors, including climate change (*8*, *9*). This has led to an understanding that conservation policies should incorporate ecological roles to support more widespread ecosystem restoration. Indeed, there have been calls to rebuild predator populations to ecologically functional levels to restore ecosystems and communities (*7*, *10*–*12*) and as a nature-based climate solution to indirectly increase carbon sequestration (*13*). However, selecting species for management prioritization requires an understanding of their ecological roles and their overall importance: the magnitude of a predator's effect on aspects of their communities and ecosystems as a function of their presence, absence, or abundance (*5*).

Whereas progress has been made in terrestrial ecosystems (*1*, *7*), the use of predator conservation to manage marine ecosystems has lagged behind. This slower progress is driven primarily by two factors. First, there are large gaps in the understanding of ecological roles and importance of large marine predators, especially sharks, that need to be addressed before using predator restoration to achieve broader ecosystem responses. Advancing this understanding has been challenging because of the logistical difficulties of studying this diverse and often highly mobile group of marine predators, including their interactions with other species. There also has been a lack of synthesis of existing information that would enhance the ability to target conservation and management efforts. Second, differences in the drivers of declines in terrestrial predators (historical targeted removal) and sharks (ongoing commercial harvest) have shaped the nature of, and support for, conservation and management approaches.

As the extent, intensity, and accumulation of threats to marine systems continue to escalate, ecological communities and species' roles must be understood within the context of a human-dominated ocean to guide effective conservation of sharks and their ecosystems. Pervasive overfishing, "blue economy" expansion, climate change, and efforts to protect and restore ocean ecosystems all influence the roles and importance of sharks. In this Review, we summarize extensive historical and ongoing global shark declines; describe the diverse ecological roles of sharks; and highlight the value of understanding their past, present, and future roles. We investigated where roles are currently important, identified where population restorations may be particularly valuable, and evaluated policies that can support shark role recovery.

Shark population declines before and during the Anthropocene

Shark populations have declined for longer and more severely than is often appreciated. Paleontological records of sharks (accumulation rates of shark scales) on Caribbean coral reefs over the past several millennia suggest a 71% decline in abundance, presumably because of subsistence fisheries that predate industrial fishing (Fig. 1A) (*14*). In modern times, catch per unit effort has steadily declined for global shark landings since the 1950s, indicating declining abundances (Fig. 1B) (*15*, *16*). Three other lines of evidence support widespread and dramatic population declines. First, global oceanic shark abundances have declined ~71% since 1970 (*17*). Second, catch rates of large coastal sharks in the Australian beach protection program have declined by 90% since the 1960s (*18*). Third, a globally standardized baited remote underwater video station (BRUVS) survey (*19*) along a gradient of human pressure revealed a 63% mean depletion

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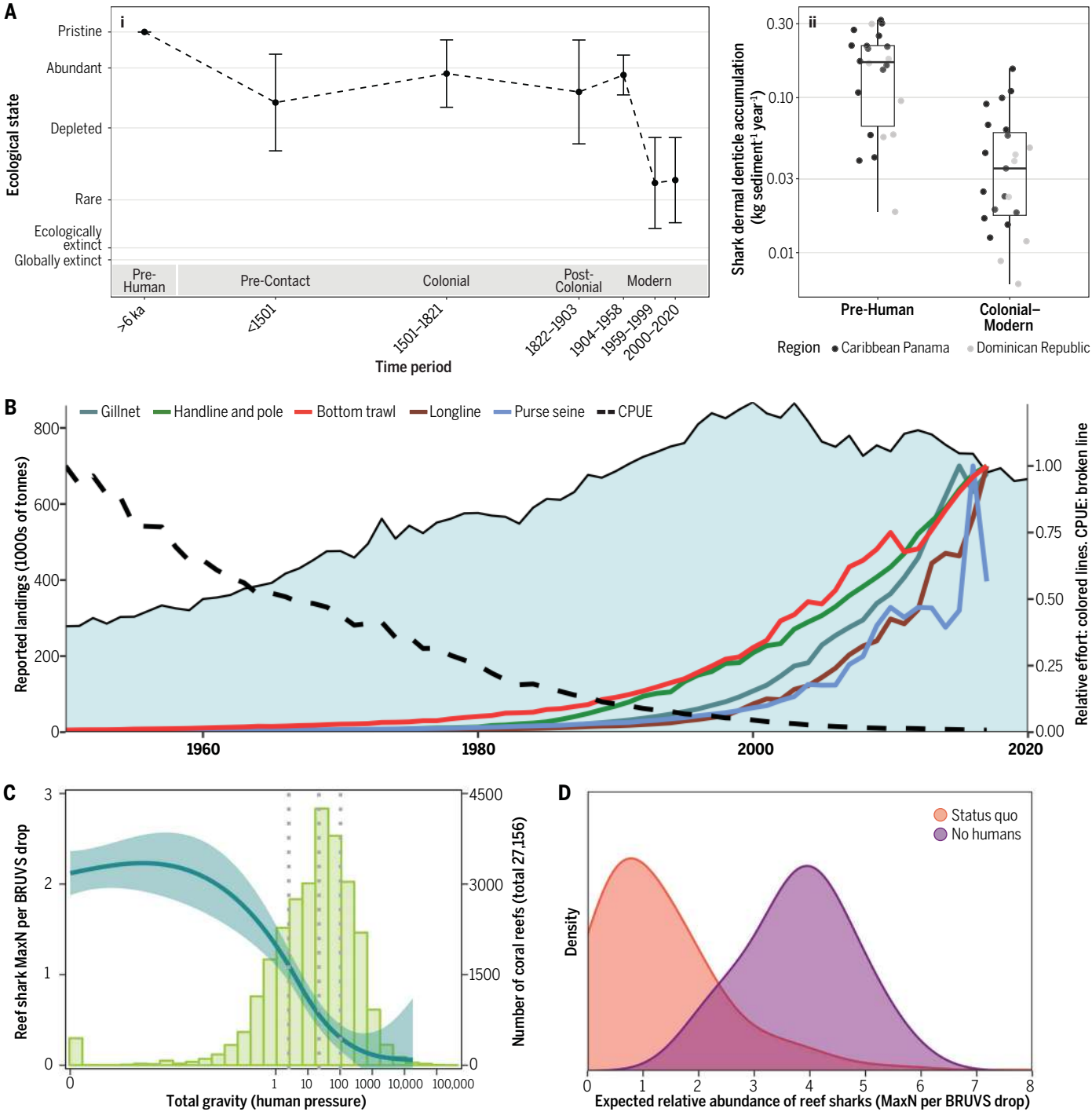

Fig. 1. Estimated abundance declines of sharks across data sources and timescales. (**A**) Millennial-scale changes in relative reef shark abundance. (i) Perceived mean and SD of abundance of sharks in Caribbean Panama inferred from archaeological, historical, ecological, and fisheries records [based on (*14*)]. ka, thousand years ago. (ii) Falling dermal denticle (shark scales) accumulation rates suggest 71% (Caribbean Panama; black circles) and 75% (Dominican Republic; gray circles) declines in reef shark abundances since the mid-Holocene [modified from (*14*)]. (**B**) Shark landings (blue area), relative effort (lines), and catch per unit effort (CPUE; dashed line) through time. (**C**) Reef shark relative abundance [blue line with 95% confidence interval (CI) (*21*)] and number of global coral reefs [green histogram; vertical dotted lines are quartiles (*140*)] along a gradient of human pressure [total gravity (*19*, *140*)]. Shark abundances are highest on remote reefs, which are rare. (**D**) Counterfactual predictions of relative abundance of reef sharks with (status quo) and without humans [models from (*140*) set human-related variables to zero]. Expected relative abundance was estimated by using MaxN measurements from 371 reefs globally (*21*).

of the five main reef shark species (*20*) relative to unfished healthy reefs. The fourth quartile of most fished reefs had a mean "maximum number of sharks per video frame" (MaxN) only 14.2% of the least fished reefs (Fig. 1C). Almost 20% of surveyed reefs recorded no sharks. Using these data and assuming no human impacts, reef shark relative abundances would be 6X (4.7X, 7.02X) [median

(95% highest posterior density)] higher without humans [based on (21)] (Fig. 1D).

Collectively, such studies show that shark populations in different global ecosystems are greatly reduced, even from populations heavily affected by humans before baseline data collection. Consequently, the International Union for the Conservation of Nature (IUCN) Red List reassessment identified ~31% of 536 shark species as threatened with extinction worldwide (3), with ~60% of coral reef–associated sharks and rays identified as threatened (22). Fishing also selectively removes the largest and highest trophic-level individuals and species (23–25) that likely play outsized roles in species interactions and ecosystem-level effects (26, 27). Therefore, the importance of sharks to ecosystems currently being measured in Anthropocene oceans is likely much less than at historical abundances in most ecosystems [for example, (21)].

Ecological roles of sharks

Modern forms of sharks arose ~150 million years ago (28), and the more than 500 extant species are found throughout virtually all marine ecosystems, from deep seas to estuaries and in some freshwater habitats (29). Sharks are generally viewed by scientists and society as archetypal macropredators: upper trophic–level predators that consume large-bodied prey. Sharks, however, span an incredible range of adult lengths, from 20 cm to more than 18 m; they also fill diverse feeding guilds, from large filter feeders, similar to whales; to parasites, small predatory species that feed on crustaceans and worms; and larger-bodied predators that feed largely on cephalopods and teleosts. Although adults of large predatory sharks may be macropredators—feeding on large teleosts, marine reptiles, other sharks, and marine mammals—most species, and even the young of macropredatory species, are mesopredators (Fig. 2). As such, they typically feed on smaller and lower trophic–level prey (27) and must trade off foraging opportunities against predation risk (26), fill different ecological roles, and likely have fewer and smaller effects on their prey and ecosystems than those from macropredatory sharks (Fig. 2) (30). Given their diverse adult body sizes and habitats, it is unsurprising that sharks fill many roles in ecosystems, including modifying prey traits and behaviors, structuring species interactions, affecting prey and predator population sizes, and influencing community structure and ecosystem functioning (Fig. 2). Most sharks shift their diets and their potential ecological roles and importance considerably through ontogeny owing to changes in body size, habitat, and movement patterns (27).

Recent field studies demonstrate that the ecological importance of sharks varies markedly within and among populations and across ecological contexts (Fig. 2) (26). Top-down effects may occur through direct predation, prey behavioral shifts, and their interaction (5). Macropredatory and large mesopredatory sharks often induce behavioral shifts in their potential prey through predation risk and possibly competitive interactions with other predators. Declines in these shark populations are sometimes linked to relaxed antipredator behavior (for example, use of wider ranges of habitat) and increased densities of mesopredators and herbivores (Fig. 3A). There is strong empirical support for direct and indirect top-down roles of macropredatory sharks (such as the white shark and tiger shark) on prey—especially marine mammals and other long-lived taxa—in primarily macrophyte-dominated systems (Fig. 3B) (30, 31). In those systems, shark predation and predation risk indirectly influence basal ecosystem dynamics, including macroalgal establishment, seagrass biomass and persistence, macrophyte biodiversity, and/or biogeochemical pathways such as carbon storage (Fig. 3A) (8, 32–34). For example, the presence of large tiger sharks in a model Western Australian seagrass ecosystem induces shifts in foraging habitats and tactics by multiple prey taxa, including large-bodied grazers [such as the green turtle (*Chelonia mydas*) and dugong (*Dugong dugon*) (32)], that promote the persistence of dense seagrass beds (6, 8, 34). These results have been observed in multiple locations and ocean basins, suggesting that macropredatory sharks have strong structuring roles in multiple macrophyte communities today and played greater roles at historic population levels. In other ecosystems, strong cascading effects of sharks are absent, evidence is mixed, or cascading effects are highly context dependent (26). For example, recent studies on coral reefs demonstrate that strong, cascading effects of sharks on reef macroalgae can arise under specific conditions (35), yet in most circumstances, sharks apparently have limited effects on coral reef fish and benthic communities (Fig. 3A) (36, 37). Strong effects, where they exist, are likely driven by a predictable occurrence of predation risk in space or time for herbivores that exert considerable effects on primary producers (26, 35). Factors that contribute to the presence of weak or inconclusive shark effects on coral reefs include the reticulate and size-structured nature of these diverse food webs, high degrees of functional redundancy, diffuse ecosystem connections (such as omnivory), bottom-up buffering, simultaneous fishing of predators and prey, historical removal of macropredatory sharks, and challenges in conducting studies of trophic cascades on reefs (36, 37).

The prevalence and importance of bottom-up effects of sharks is only beginning to be explored. Sharks can transport nutrients from pelagic environments to coral reefs (38, 39), shallow to deep mesophotic coral reefs (40) and vice versa (39), coastal oceans to estuarine waters (41), and across latitudinal gradients (42). Nutrients can be deposited through egestion and excretion or carcasses of sharks that die or are eaten in habitats distant from where foraging occurred (26). However, the effects of nutrient fluxes on ecosystem productivity remain unclear and virtually unstudied. In one dedicated study, a population of reef sharks at a small Pacific atoll transported at least 44 kg of nitrogen per day from pelagic ecosystems where they foraged to core areas of the reef where they spent time between foraging bouts. The ecological importance of this deposition is unknown (39). Other potential roles of sharks, including facilitating other species, are even less known. For example, while scavenging on large carcasses, sharks may facilitate foraging by smaller species, and sharks may facilitate cleaning opportunities for other species (Fig. 2); the importance of these interactions is poorly known. Overall, studies of shark importance are primarily restricted to inshore and shelf regions, for macropredatory and some mesopredatory sharks, and are focused almost entirely on top-down effects (Fig. 3B) despite the variety of roles they fulfill (Figs. 2 and 3).

Loss of ecological roles and function with overfishing

The overall effect that sharks exert on other species, their communities, or ecosystems is a function of abundance, but the relationship shape may vary with shark species and ecological context (Fig. 4). Measuring such response curves is difficult but is important for predicting how other species and ecosystems will respond to changes in shark populations. Regardless, overfishing has caused profound effects on shark abundances from local to global scales and on the composition of shark traits—innate biological features related to ecological roles. Human activities are threatening functional diversity within sharks and rays to a greater degree than that in other large marine predators (such as bony fish and marine mammals), and species with distinct functional traits (such as habitats, position in the water column, and diets) are particularly at risk (23, 24).

In temperate and tropical systems, serial depletion of sharks consistently affects larger individuals and large-bodied species that are (i) more valuable (in terms of ecosystem-shaping roles) than many other species per individual (43), (ii) more sensitive to fishing owing to slow intrinsic growth rates, and (iii) more susceptible to some fishing gear types. Mean caudal fin aspect ratio [correlating to average swimming speeds and scale of movements (44)] and geographic range at the guild scale decline with increasing human impact (Fig. 5B), reducing connectivity and the potential for shark-mediated nutrient flow through the

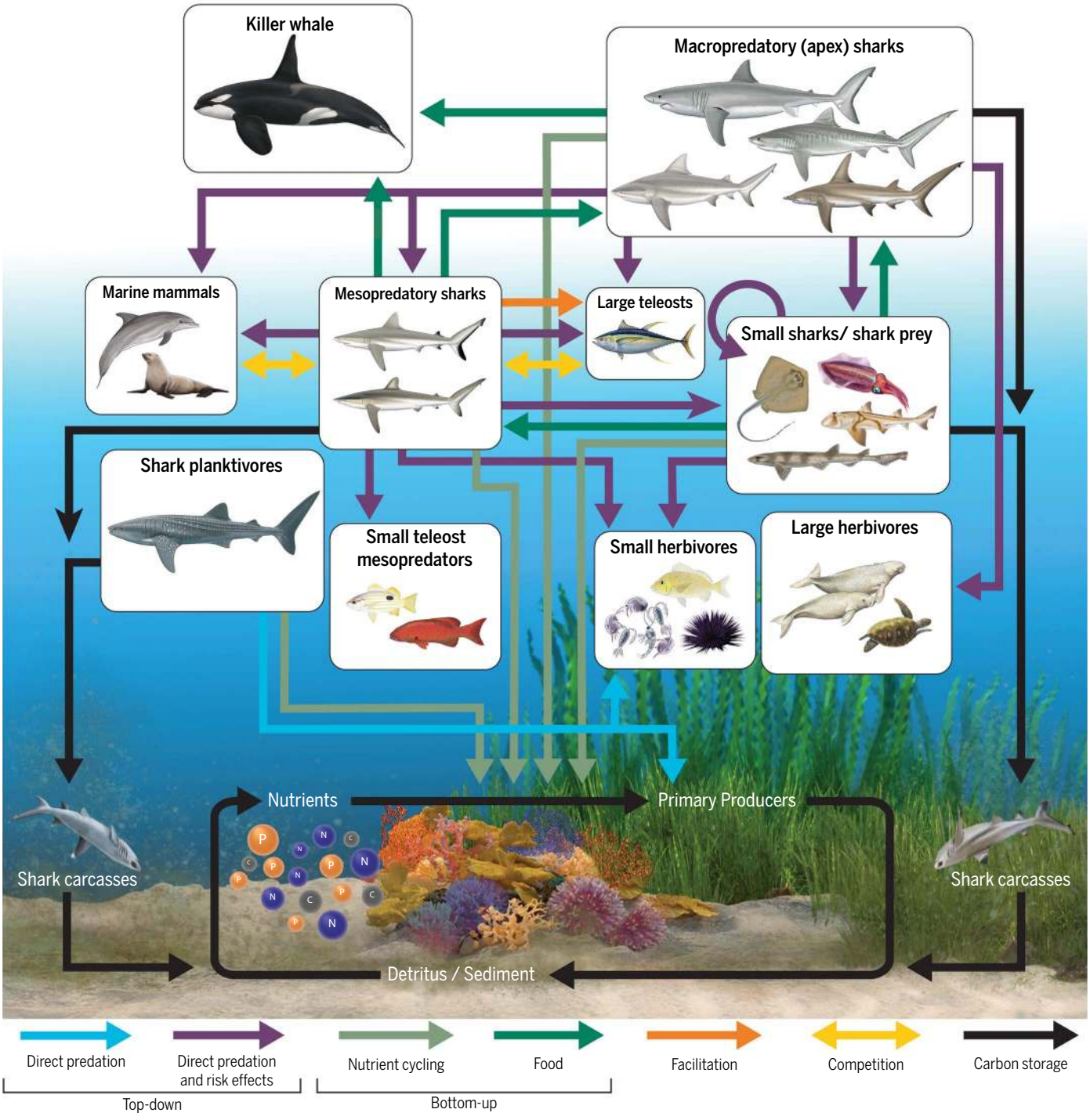

Fig. 2. Conceptual model of the current state of knowledge of the ecological roles and importance of sharks in aquatic food webs. Sharks play multiple roles in ecosystems through top-down processes (such as direct predation and risk effects), bottom-up processes (such as food provisioning and nutrient cycling), and species interactions (such as competition and facilitation). Only interactions involving sharks are displayed. [Figure design by SayoStudio; vertebrate illustrations by Marc Dando]

loss of large-bodied, wide-ranging species (*38*, *39*, *42*). Human impacts drive decreases in mean trophic levels of macro- and mesopredatory species (Fig. 5B), suggesting that studies underestimate historical importance of sharks through top-down mechanisms. Long-term studies in a relatively pristine ecosystem demonstrate that even at current population sizes, large macropredatory sharks can exert strong top-down impacts through multiple pathways, but these effects would be lost or substantially degraded with the loss of large size classes or further reductions in population sizes (*6*, *26*, *32*).

Reduced predatory and competitive influences due to removals of larger, slower-growing sharks have led to mesopredator release and profound community shifts in multiple ecosystems [Northeast Atlantic shelf (Fig. 5A) (*45*), Mediterranean Sea (*46*), South China Sea (*47*), and waters off Costa Rica (*48*) and South

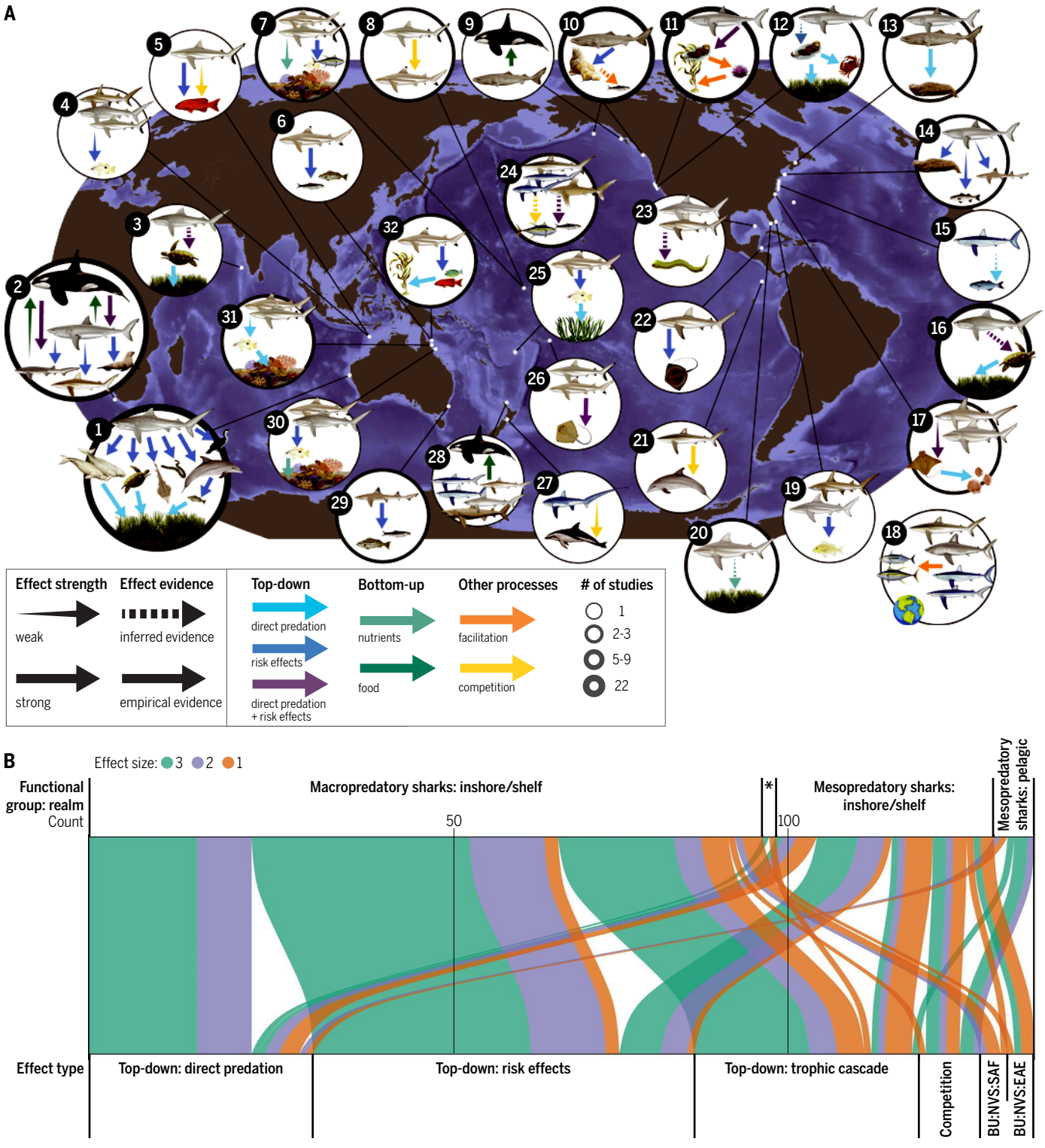

Fig. 3. Empirical studies of ecosystem effects of sharks. (**A**) Macropredatory sharks in coastal ecosystems can have large effects on prey that cascade to basal macrophyte communities. Shark effects on reefs are variable but may influence mesopredator abundance, behavior, and community composition. Effect sizes in other interactions and ecosystems are lower or unclear. Smaller sharks may be important food for other species, but their top-down effects are generally small or unresolved. Circled numbers reference studies in table S1. Arrow hue indicates effect type; arrow tails indicate effect strength; and hatched and solid indicate inferred and empirical evidence, respectively. (**B**) Alluvial plot of studied ecotypes and ecological roles of sharks and their strength of evidence from studies listed in table S1. Competition and/or bottom-up processes were not included because of small sample size. Effect size and strength of evidence were rated by 30 investigators' expert opinions, scoring source paper metrics on a low-medium-high scale. Asterisk indicates macropredatory sharks, Pelagic. BU, bottom up; NVS, nutrient vector, storage; SAF, sharks as food; EAE, excretion and egestion. [Figure design by SayoStudio; vertebrate illustrations by Marc Dando]

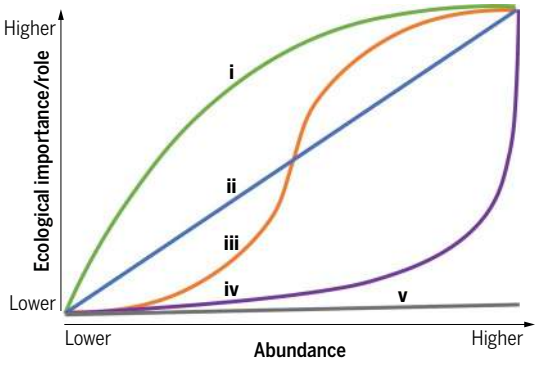

Fig. 4. Theoretical relationships of ecological importance as a function of shark population abundances. As shark population sizes increase, their effects on ecosystems may increase (i) rapidly at low abundances; (ii) linearly; [(iii) and (iv)] slowly until reaching thresholds; or (v) remain low. Empirical understanding of the shape and slope of these patterns is important for predicting effects of shark population declines or rebuilding but remains poorly known.

Africa (*49*)]. This pattern is emerging in less-monitored tropical shelf seas (*3*) such as the Bay of Bengal, which is one of the most heavily fished regions of the world (*50*). As fishing increased, the largest shark (and ray) species with the highest-value fins and slow life histories disappeared, followed by species with moderately productive life histories (Fig. 5, B and C). In their place, small, more productive species persist despite intense fishing, suggesting predatory or competitive release, presumably with large gaps in the diversity of ecological roles sharks played, because of differences in functional traits left in the assemblage (Fig. 5B) (*51*).

Herbivorous reef fish grazing patterns near coral reefs show how fishing has reduced the predatory role of sharks and other reef predators, including how these effects can cascade indirectly through herbivores to primary producers (Fig. 2) and affect nutrient fluxes and subsidies from the pelagic ocean. "Halos" are sand rings denuded of seagrass and macroalgae within a perceived safe distance around coral patch reefs (*52*). Halos are smaller on reefs with greater and longer protection from fishing, which suggests that sharks and large teleost piscivores have positive effects on the biomass of reef-adjacent primary producers (*53*) and their potential to sequester carbon in sediment (*33*). Halos are predicted to change according to the composition of the predator community present and should be narrowest, with their boundaries well-defined, when risk to foraging teleosts is highest because they cannot safely move far from reefs (Fig. 5C). Risk to teleosts that form halos, however, may be reduced on the basis of the loss of their predators or the presence of larger sharks that threaten the predators or halo-forming species.

Implementations of restrictive management regimes have led to recoveries in some shark populations, providing insights into their ecological roles in manners analogous to recovering terrestrial predator populations (*7*). The Northeast Pacific population of white sharks likely declined for more than a century (*54*). After protection from fisheries in California in 1994, the number of juvenile white sharks using coastal beach habitats has steadily increased (*55*). Continued population gains of protected pinnipeds (*56*), despite population gains in sharks, suggest that white shark predation does not regulate pinniped abundance (*57*). However, white shark predation risk affects pinniped behavior, inducing shifts in foraging/resting cycles, movement, social behavior, and at-sea group formation (*31*, *58*). White shark recoveries in the Northwest Atlantic (*59*) are inducing behavioral changes in gray seals (*Halichoerus grypus*) (*31*). The ecological implications of these risk effects on pinnipeds remain largely unknown. Broader food-web effects of shark recovery are more apparent off the coast of California: Over the past 20 years, increasing white shark–inflicted mortality has negatively affected sea otter (*Enhydra lutris*) populations and limited their distribution in exposed coastal habitats, where they are susceptible to shark mortality (*60*–*62*). By contrast, sea otter abundance has dramatically increased in an estuary where predation risk from sharks is low (*63*). The reduced sea otter abundance and distribution on the outer coast has contributed to a collapse of kelp forests in areas where sea otters would otherwise limit the grazing of urchins and enhance kelp forest resilience (*64*, *65*), whereas in protected estuarine habitats, the effects of increased sea otter foraging have positively affected seagrass abundance and salt marsh stability (*66*, *67*).

New threats and changing ecological roles for sharks in the Anthropocene

Rapid industrialization in many marine sectors (*68*) is modifying shark importance, changing the spatial distribution of roles, and yielding new ecological roles (Table 1).

Activities such as shipping, seismic surveys, offshore wind farms, and pile-driving expose sharks to low-frequency noise (*69*) and electromagnetic fields that overlap their sensitivity thresholds (*70*). Responses of sharks to noise or electromagnetic fields could lead to disrupted predator-prey interactions and/or changes in habitat use that might shift spatial patterns of shark effects. However, noise could also increase prey vulnerability (*71*) and increase shark hunting success. The direct and indirect effects of noise pollution and electromagnetic fields warrant further study.

Other aspects of the blue economy—including tourism, aquaculture, discards or depredation from fisheries, and recreational fishing—could modify shark densities and behaviors, with cascading consequences for ecosystems or interactions with humans. Wildlife tourism such as shark feeding or (cage) diving can affect sharks (*72*, *73*), including changing behaviors (*74*), elevating local densities (*75*), shifting diets (*76*), and intensifying predation rates and/or risk effects on prey. If shark tourism influences distributions rather than population sizes, areas could experience reduced shark effects away from feeding sites, creating spatial heterogeneity in effects. Although direct predation and risk effects could lead to wider ecosystem consequences, these are little studied in the context of shark food subsidies. Also unexplored is how tourism might affect sharks as vectors for nutrient translocation across ecosystem boundaries if shark movements become more restricted.

Shark depredation has become ubiquitous in various commercial, small-scale, and recreational fisheries (*77*). Food subsidies from fishing and aquaculture (such as hooked fish, discarded bait, and uneaten feed) can change shark behavior (distribution and movement matching fishing vessels), increase their abundances, shift diets and life history parameters, and potentially reduce per capita predation pressure on natural shark prey when subsidies are large (*78*). For example, high depredation of fishers' catches by sharks close to a tourism provisioning site resulted in reduced overall fishing effort and increased fish abundance and altered benthic communities (*79*). Such changes to shark roles in natural ecosystems due to food subsidies could match ecological shifts, including enhanced effects on prey and competitors, that have been observed in terrestrial predators depredating livestock or receiving other food subsidies (*80*).

Anthropogenic activities that change water clarity or productivity can modify shark roles. Reduced water clarity might enhance the importance of shark risk effects because prey that rely on vision would be able to detect and respond to predators over shorter distances and therefore need to invest more heavily in antipredator behavior (*26*, *81*). Similarly, reductions in food available to prey populations are predicted to increase the importance of shark direct predation because of condition-dependent risk-taking in energetically stressed prey (*5*). Therefore, coastal development, increased nutrient inputs to rivers and coasts, and dredging are likely to modify shark importance in ecosystems and the pathways through which their effects might manifest. Management regulations and spatial conservation planning that contribute to species recovery can also modify

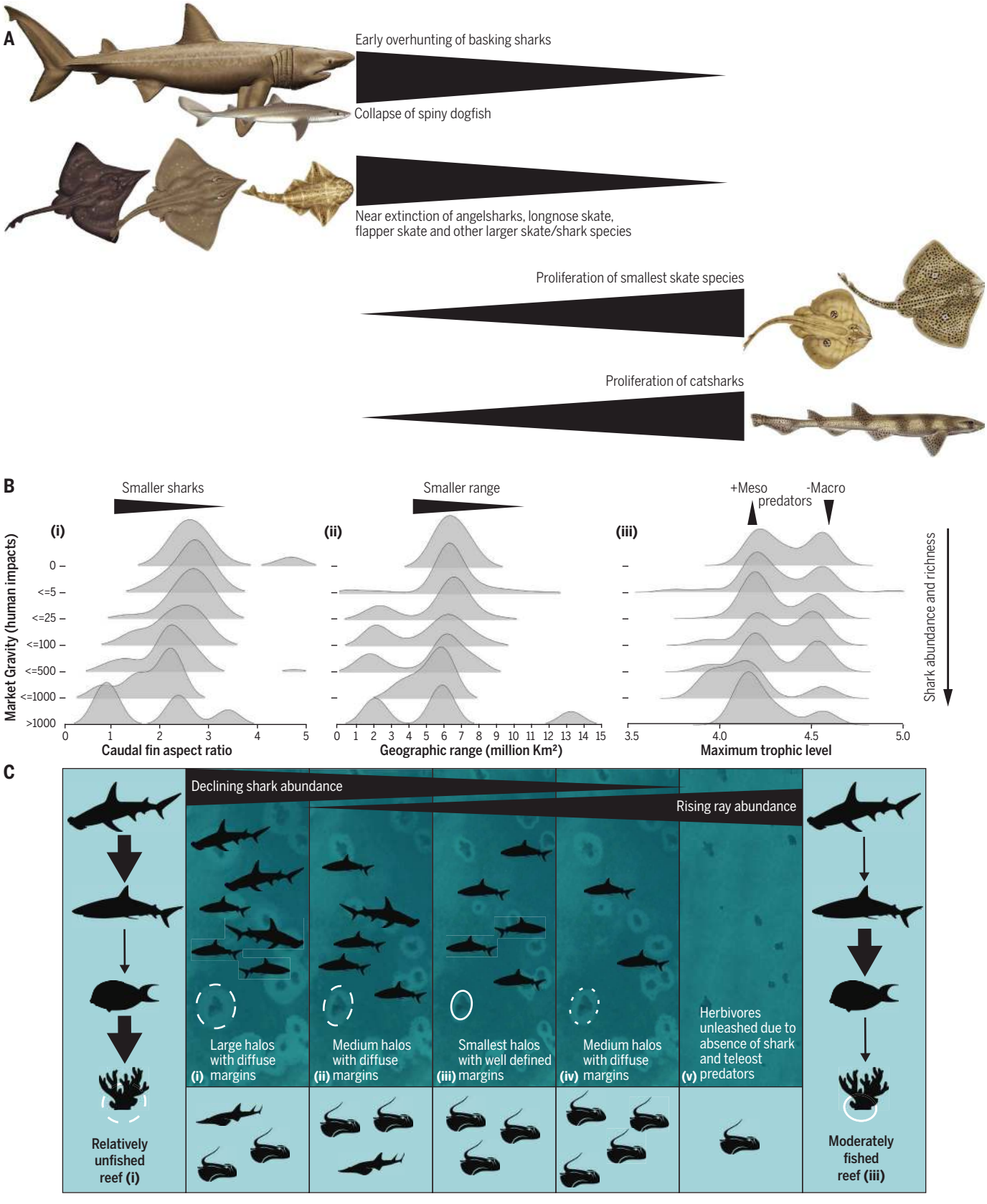

Fig. 5. Changing ecological roles of sharks in an age of overfishing. (**A**) Fishing has shifted elasmobranch communities over time, causing a ~60% drop in predatory fish abundance throughout the North Atlantic shelf since 1950 (*141*), especially of larger elasmobranchs (*45*, *120*). Similar declines occurred in the Mediterranean Sea (*46*) and Bay of Bengal (*50*). Smaller elasmobranch species abundances have risen (*16*, *45*), which suggests that larger species

suppress smaller species through predation and competition. (**B**) Species richness and abundance of sharks decrease along a gradient of market gravity (human impact) along with traits that influence shark movement and trophic interactions. Communities lose wide-ranging individuals that connect habitats, have flexible habitat adaptations that increase resilience, and feed at upper trophic levels. Data are from (*3*, *20*, *44*). (**C**) Indirect effects of predation pressure are documented in grazing patterns [halos (*52*)] adjacent to patch reefs. Reductions in predation pressure, including depletions of sharks, influence safe distances for herbivorous fish in habitats adjacent to reefs (*53*). With little risk, herbivorous fish feed further from reefs, which leads to reduced primary producer biomass (*52*) and sedimentary carbon stores (*33*). [Vertebrate illustrations by Marc Dando]

Table 1. Threats differentially affect sharks and their ecological roles. Increased blue economy activities—including maritime industrialization, energy and aquaculture development, and ecosystem management—will affect ecological processes that involve sharks in coastal and offshore environments. Processes are A, changes to distribution, movements, and/or residency of prey and predators; B, misdirected predation (such as toward electric cables or unusual prey); C, prey disorientation (such as from noise); D, health condition affecting foraging requirements, ability, and success; E, change of abundance of less abundant or vulnerable species; F, reliance on food and provisioning by humans; G, changes in food requirements (increased energy expenditure); H, introduction of new prey in ecosystems; I, reduced habitat quality affects recruitment success, prey availability, and/or prey-predator detection; and J, direct changes to prey and/or predator abundance.

Group	Sector, threat, or change	Pressure	Coastal or offshore prevalence	Processes	Evidence of impacts
Blue economy (or maritime industrialization)	Renewable energy (such as wind farms and tidal power)	Noise, infrastructure, and electric cables	Both	A, B, and C	(*69*, *142*)
	Seismic surveys	Noise	Offshore	A and C	(*69*, *143*)
	Oil and gas operations and deep sea mining	Noise and pollution	Offshore	A, C, and D	(*144*, *145*)
	Industrial shipping and marine traffic	Noise and collision	Both	A, C, and E	(*146*)
	Tourism	Food input, pollution, behavioral modification, and human-shark conflict	Coastal	A, D, F, and G	(*72*, *73*)
	Aquaculture	Eutrophication, anoxia or hypoxia, infrastructure, pollution, escapees, and predator interactions	Mostly coastal	A, B, D, and F	(*78*)
	Urban expansion (such as port development)	Habitat modification, sedimentation, noise, pollution, contaminants, and water quality	Coastal	A, D, and I	(*147*, *148*)
	Fishing, including subsistence and artisanal	Human-shark conflict and prey availability on fishing gear (depredation)	Mostly coastal	B	(*77*)
Other changes (or ecosystem management)	Invasive species (including species outbreaks)	Introduction of new prey	Coastal	B andH	(*149*)
	Ecological surprises (such as orca pressure on white shark and white shark pressure on otter)	Changes in predator-prey relationships	Coastal	B	(*60*, *86*, *150*)
	Species protection and spatial conservation planning (such as MPAs)	Protection of sharks, other predators, and/or forage populations	Mostly coastal	J	(*115*)

the roles of sharks and reveal their importance. For example, rebuilding green turtle populations in the context of greatly reduced tiger shark populations can lead to overgrazing that collapses seagrass ecosystems and eliminates critical ecosystem services for fisheries and blue carbon storage (*82*, *83*).

Ecological surprises refer to temporary or permanent changes in the natural environment that disrupt the functioning of an ecosystem in a manner inconsistent with human expectations (*84*). The disturbances that trigger ecological surprises can be natural (hurricanes, thermal anomaly, or new species interactions) or anthropogenic (overfishing and climate change) and can provide important insights into ecological dynamics (*85*). One example that provides insight into the ecological roles of sharks and how they may change in the face of anthropogenic influences is the emergent behavior of killer whales as predators and antagonistic competitors. In this case, killer whales have been documented killing white sharks in South Africa (*86*), a pattern that results in sharks temporarily abandoning the site (*87*). Their absence preceded increased abundances of broadnose sevengill (*Notorynchus cepedianus*) and bronze whaler (*Carcharhinus brachyurus*) sharks, likely through mesopredator and competitive release (*88*), before killer

whale predation on sevengill sharks led to their abandoning the site (*89*).

Shark ecological roles and importance in a changing climate

Climate change may directly affect the physiology of sharks or indirectly cause changes in distribution, abundance, behavior, and/or performance of their prey or competitors. Recent studies are elucidating how these effects will or will not modify ecological roles and how sharks might indirectly influence carbon cycles and ecosystem resilience. Changing climate affects marine animals primarily through warming waters (fig. S1, A and B), decreases in pH (ocean acidification) (fig. S1C), and reduced dissolved oxygen concentration (fig. S1D) (*90*). Sharks unable to obtain enough resources to meet increased demands of warming waters (which increase metabolic rates) may disappear from some habitats [for example, bull shark *Carcharhinus leucas* (*91*)].

The ability of sharks to catch prey is partially dependent on how swim speed and muscle physiology of predator and prey respond to temperature. Animal performance often follows a thermal performance curve (*92*), with an optimum temperature for physiological processes nested within critical thermal limits, which can vary between populations (fig. S1, A and B) (*93*). Asymmetries in the thermal response curves of predator and prey may change predator-prey interaction outcomes and food web–level effects (*94*, *95*). Thus, understanding how the role of sharks as predators may change in the future will depend on the interplay of climate effects on sharks and their prey. Similarly, the performance of sharks in the face of warming oceans relative to that of potential competitors, such as marine mammals, may shape the future of ocean ecosystems (*96*). Rising water temperatures may decrease the advantage that homeothermic mammals currently gain from their warmer muscle temperatures, which may also apply to warm-bodied lamnid sharks such as white, salmon (*Lamna ditropis*), and mako (*Isurus oxyrinchus*) sharks (*97*, *98*). Because sharks have begun—and are expected to continue—to expand their ranges poleward with warming temperatures (*93*, *99*, *100*), they may play increasingly important roles as macropredators and large mesopredators in ecosystems they colonize. The degree to which this occurs, however, will depend on the responses of species they interact with. For example, seagrasses moving poleward in response to rising temperatures become less resilient to herbivory owing to light limitation (*101*). Therefore, any roles that sharks might play in limiting herbivory may be more critical as ecosystems shift poleward in a warming climate.

Climate change and anthropogenic nutrient inputs expand "dead zones" of depleted oxygen, also raising the depth of the oxygen minimum zone in pelagic ecosystems (*102*), rendering habitats unavailable or marginal (*103*). Vertical and horizontal range reductions are expected for many sharks and their prey (*90*), although at least one species (sixgill shark; *Hexanchus griseus*) maintains high activity levels in low-oxygen waters, suggesting that consequences may vary among species (fig. S1D) (*104*) and are probably more severe for active surface-oriented species that use the epipelagic zone for foraging [for example, many pelagic sharks (*105*)]. Nonetheless, depth range compression may increase predation rates by sharks in shallow waters and change nutrient distribution—and resulting productivity—patterns if sharks act as vertical nutrient pumps (*106*, *107*). Relatedly, as increasing anthropogenic inputs of pollutants and fertilizers degrade water quality and visibility, the general predatory success of sharks may increase because prey are less able to detect and evade predators such as sharks.

Climate change–driven coral bleaching, mortality, and "flattening" (loss of architectural complexity) of reefs (*108*) will affect prey capture probabilities of sharks and the spatial extent of risk effects they induce. For example, loss of reef structure shifts the composition of fish assemblages (*109*) and reduces refuge availability. Thus, shark predation on reef fish will likely increase, at least temporarily, as reefs flatten (*110*). Because reef flattening will affect the distribution and abundance of prey refugia, and prey's ability to detect predators, shark predation risk effects on prey (such as shifts in group size, and spatial extent and duration of foraging) will change as prey navigate food-safety trade-offs (*32*, *111*, *112*). Examining changes in the direct and indirect effects of sharks on prey species as reefs lose structure, and other human impacts that change food availability to reef species, is a challenging but crucial research frontier for understanding predator-prey relationships and their potential cascading consequences on reefs.

Maintaining biodiversity, including large predators, is becoming recognized as critical to the mitigation of climate effects through protection and development of sedimentary carbon stores (*13*). Large macropredatory sharks may be particularly important in facilitating the maintenance of carbon stores in the form of primary producer biomass [for example, seagrass (*8*, *34*, *82*)] and sediment (*33*) by controlling grazing through predation and fear effects (*32*, *34*). Sharks may also help ecosystems rebound from extreme climate events. For example, tiger shark predation risk reduced grazing pressure on slower-growing foundational seagrasses damaged in a marine heat wave, promoting ecosystem resilience (*8*). An absence of tiger sharks would have facilitated a phase-shift to a lower seagrass biomass system dominated by faster-growing species owing to intense herbivory. On coral reefs, large predator presence, including sharks, is linked to higher rates of carbon deposition in sediment (*33*), which suggests that sharks promote blue carbon stores across multiple ecosystems. The overall contribution of sharks to carbon sequestration requires further investigation but may be considerable in some contexts (*33*).

Managing the shifting ecological roles and importance of sharks

Unlike terrestrial predators, sharks are mainly depleted because they are exploited for human consumption. As a result, fisheries management, where it exists, has focused on sustainable yield as opposed to rebuilding populations to restore the functional roles of sharks across large spatial scales (*113*). Although recent initiatives promote change by developing conservation metrics and assessment frameworks that are focused on function (*23*, *114*), typical fisheries management approaches may often fail to restore shark functional roles. For example, "ensuring sustainable populations" (current standing biomass > biomass at maximum sustainable yield) will not guarantee the levels of abundance required for ecological functionality and rarely protects the largest individuals that exert outsized roles (*23*, *24*, *27*). Although managing for sustainable use may avoid extinctions, fisheries management approaches that also recover functional diversity, historic high abundances, and large species and individuals are also needed. Fishing gear restrictions that promote the use of lighter leaders or smaller hooks can, for example, allow macropredatory sharks to break off and thus allow more targeted catch of smaller individuals and species. National or regional prohibition on the retention of some large macropredatory species can also be effective if the species survives or largely avoids incidental capture. Marine protected areas (MPAs)—especially no-take MPAs—can be used within national waters and potentially soon on the high seas to reduce fishing threats and promote high local shark abundance. Such use has been successful across the range of national management capacities (*21*, *115*) but is relatively recent, with only 12 shark species having >10% of their range protected (*116*), and barriers remain in enforcement and achieving representative coverage (*117*). Combining MPAs with broader national or regional fisheries management can enhance shark protections (*118*) and should be deployed widely, especially to restore the functional role of highly mobile macropredatory species that are difficult to protect within smaller MPAs.

Individual nations and regions are differentially poised to address shifting management

approaches, especially when it comes to engaging them on the very large spatial scales needed to restore functional populations of macropredatory sharks. Progress of ecosystem-based fisheries management by basin-scale regional organizations has been poor (*119*), and although some developed nations already manage some sharks sustainably and have protected key species, most lack the capacity and/or willingness to develop, implement, and enforce suitable controls throughout their jurisdiction (*22*, *117*). Even when shark populations persist, inadequate management often leads to lost ecological roles from local populations [functional extinction (*3*, *21*, *24*, *120*)]. In addition to better managing legal fishing, better strategies must be adopted to reduce the impact of illegal, unreported, and unregulated (IUU) fishing on sharks (*15*). Many new technological advances can assist combating IUU fishing and strengthen management of legal fisheries—for example, diverse satellite technologies to track vessels (*121*, *122*); onboard electronic systems to monitor intended and unintended shark catch (*123*); electronic information exchange systems to strengthen the Port State Measures Agreement, which sets standards for vessels in foreign ports (*124*); genetic screening tools to identify illicit trade of shark products and promote supply chain transparency (*125*); and shark loggers that can detect poaching and directly measure overlap between fishers and sharks (*126*). All can help nations govern at the scale required to widely restore shark ecological functions.

If successful, managers must consider the consequences of shark recovery and anticipate increased shark-human interactions, fishery depredation, and other blue economy interactions that may stall or reverse improved biological outcomes of shark conservation (*117*, *127*) and may lead to calls for shark culls. Similarly, managers must prepare for shark-human interactions as climate change shifts species ranges. New threats will continue to emerge, necessitating management solutions that enhance the resilience of shark populations and their ability to adapt to changing conditions (*128*). Emerging threats are largely nonextractive and may require approaches different from those used to address fishing impacts; a systemic horizon scan of anticipated future threats would be an asset for long-term management planning. Continued development of spatial and dynamic management measures that reduce pressure on populations of sharks and species with which they interact are likely to be important. Studies on how ecological importance varies within and among ecosystems, species, and populations, and across variable population densities of sharks, are still urgently needed. Although these massive knowledge gaps remain, a precautionary approach that aims to maintain shark diversity should be emphasized, given our emerging view of the myriad mechanisms and pathways through which sharks might influence their ecosystems.

Leveraging ecosystem services, relational and cultural value

Addressing emergent and/or increasing challenges of shark management will be facilitated by new means of garnering public and policy support. First, highlighting benefits of large predators historically engenders conservation policy support (*129*). Wolves' role in restoring plant and avian communities in the Greater Yellowstone Ecosystem (*10*) informed global perceptions of predators, led to calls for population reintroductions (*7*), and prompted reevaluation of other roles such as that of the dingo (*Canis dingo*) (*11*). Similarly, sea otters' maintenance of kelp forest and estuarine ecosystems through urchin predation (*12*) galvanized conservation, recovery, and reintroduction efforts after near extirpation by humans. Documented ecosystem effects of sharks, including the importance of tiger sharks for seagrass meadows (*8*, *34*), and other studies (Fig. 3A) could be leveraged similarly (*130*). However, sharks may perform multiple subtle roles that change across their life history and occur within reticulate marine food webs that confound simple cause-effect framing.

Second, coupled social-ecological frameworks facilitate the inclusion of more diverse human value systems and traditions relating to human-shark interactions. Narratives on top-down predatory effects capture one aspect yet can be challenging to implement effectively. Harnessing local knowledge systems and cultural diversity through adaptive governance and integrative comanagement encourages participation and facilitates stakeholder agency in ways that can reinforce shared outcomes (*131*, *132*). Embracing local relational values and cultural traditions that are consistent with sustainable use and/or conservation of shark populations may be critical to preserve the ecological roles of some sharks and facilitate human-shark coexistence (*133*). In resource conflicts between sea otters and humans in northwestern North America, a bottom-up approach empowering community-level participation in management and decision-making—respecting local values, traditional knowledge, and resource-use practices—was more likely to lead to successful coexistence (*134*). Similarly, shark conservation success is underwritten with cultural support from communities that choose to prioritize shark preservation against other uses (*56*)—for example, Hawaiian cultural rejection of tiger shark culls (*135*), collective action toward alternate uses of marine environments (*132*), and public campaigns and support for fin-sale bans (*136*).

Conclusions and future directions

Sharks can play important roles across multiple ecosystem types by removing prey and changing their behaviors and through bottom-up pathways, which are pertinent in the face of coastal development and conservation. The greatest top-down effects of sharks have been identified for the largest individuals of macropredatory species in coastal macrophyte systems, but directed studies of top-down effects of smaller taxa are needed. Although these results are consistent across diverse locations and species, further investigations on the context dependence of the strength of top-down effects are needed. Top-down impacts on coral reefs are equivocal and likely variable, and bottom-up effects of prey availability to shark populations may mean reefs are more important to sharks than sharks are to reefs in most contexts. Given the economic and societal value of these ecosystems, further studies that leverage global datasets are crucial. Empirical evidence suggests that shark impacts in pelagic ecosystems are weaker and less important than in macrophyte-dominated systems; however, incredible declines in shark abundances and size structure shifts in the Anthropocene obscure insights into whether their importance was greater in these ecosystems historically. There are virtually no data to address the importance of sharks in deep sea and polar ecosystems (*137*), for smaller-bodied species, and for smaller age classes of large species in most ecosystems. Furthermore, sharks can exhibit marked and persistent individual behavioral variation within populations (*41*, *138*), resulting in considerable differences in the ecological roles and threats that individuals face. Understanding the prevalence, magnitude, and nature of individual specialization is important for understanding the importance of sharks in ecosystems and developing adequate management strategies.

Although overfishing is the overwhelming force degrading ecological roles of sharks, climate change, habitat loss, and the blue economy (such as energy, mining, shipping, and aquaculture) will further influence sharks and their ecological roles, affecting abundance, distribution, health, and behavior of sharks and their prey, potentially creating opportunities for new roles. Furthermore, shark roles can affect ecosystems over multidecadal time scales and will spatially shift with climate change. Resolving these long-term impacts and the importance of sharks in promoting ecosystem resilience in the face of disturbance events (*8*) is important for predicting future ecosystem trajectories.

Last, management must move beyond the maximum sustainable yield target toward the

rebuilding and sustaining of ecological roles. Regional and national-scale fisheries management and large protected areas are required to conserve highly mobile macropredatory species, which is now achievable owing to technological advances that facilitate enforcement on such large spatial scales (such as drones, video monitoring systems, and satellite-based vessel tracking). Harnessing public support, including integration of local cultural values into management regimes, will increase the chances of rebuilding and maintaining the important ecological functions of sharks in the context of pervasive human presence in the oceans.

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SUPPLEMENTARY MATERIALS

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Fig. S1
Table S1
Reference (*151*)
MDAR Reproducibility Checklist

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