Ecological roles and importance of sharks in the Anthropocene Ocean

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One Sentence Summary

A review of the changing ecological roles and their importance in ecosystems, owing to overfishing, habitat loss, climate change, and other human activities, and how adaptive management can help conserve them through cultural values and emerging technologies.

Enhanced Abstract

Background

Pervasive losses of predators on land, in freshwater habitats, and in oceans have disrupted ecological communities, prompting interest in rebuilding their populations to functional levels. Predator restoration may also facilitate nature-based climate solutions by indirectly increasing carbon sequestration and enhancing ecosystem resilience. Selecting target species for these efforts, however, requires a functional understanding of their ecosystem roles.

Sharks are a diverse (> 500 species) group of predators found within marine and estuarine ecosystems, and some freshwater environments. 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. While sometimes valid, this presumption oversimplifies the many roles performed by sharks. It also discounts 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 due to the inherent difficulties of studying their interactions and the mechanisms through which sharks may – or may not – affect ecosystems.

Here, we evaluate historical and ongoing global depletions – and occasional recoveries – of sharks, elucidate their diverse ecological roles, and highlight the value of understanding their past, present, and future roles. We investigate where roles are currently important, identify where population restorations may be particularly beneficial, and evaluate 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 [tiger shark (*Galeocerdo cuvier*), white shark (*Carcharodon carcharias*)] in coastal seagrass and kelp ecosystems, which influence habitat quality and carbon sequestration through sharks’ direct predation and risk effects on herbivores

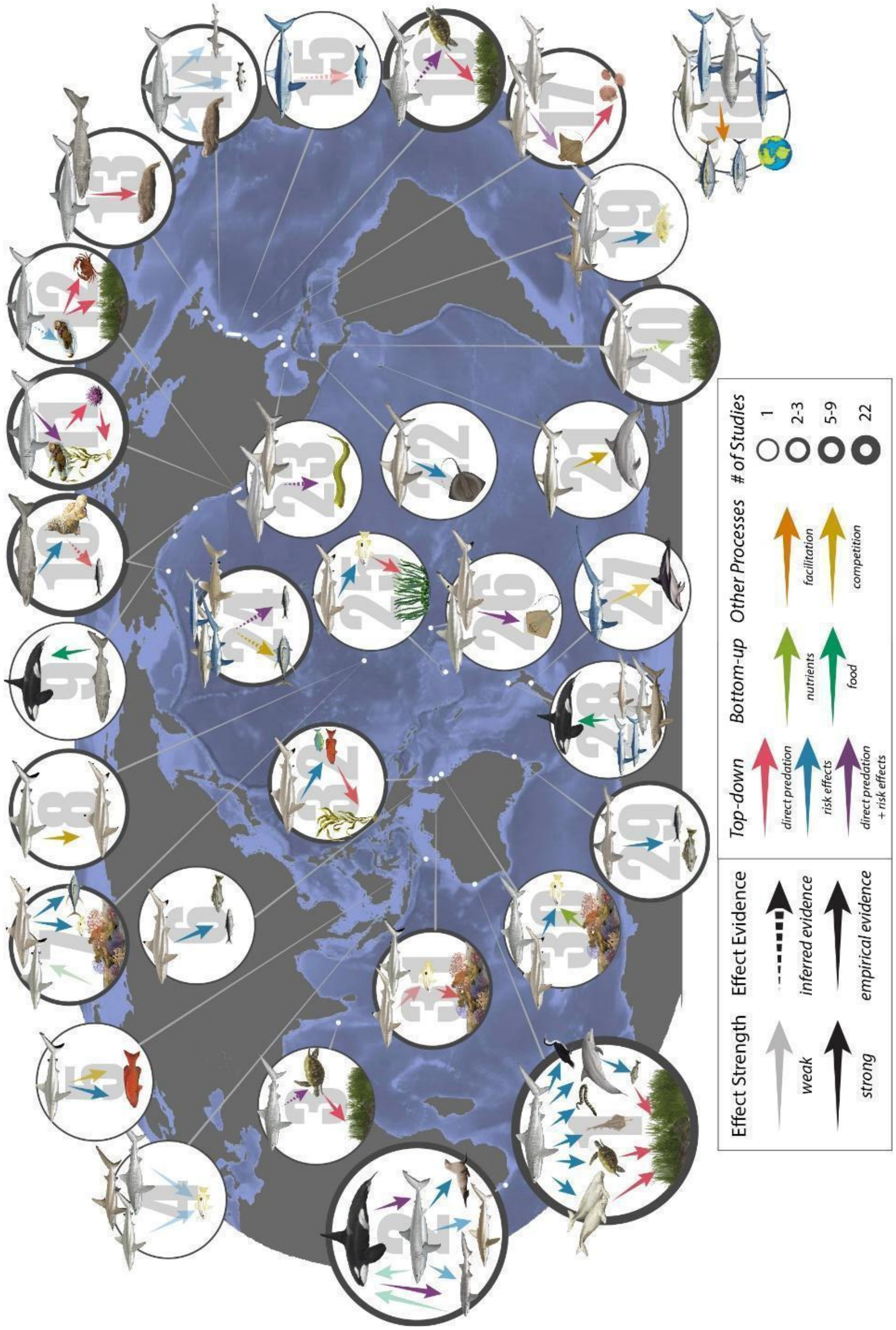
and herbivores' predators. These shark-initiated indirect effects may enhance resilience of ecosystems increasingly experiencing extreme climate events (e.g., marine heatwaves). Not all sharks, however, exert large top-down effects on prey or wider communities, although long-term overfishing causing large-scale depletions may obscure historical roles, particularly in difficult-to-study habitats like pelagic systems or deep waters. Previously unappreciated roles of sharks (e.g., facilitating ecosystems via nutrient transport) have recently become apparent in multiple ecosystems and taxa.

Climate change and industrializing oceans (e.g., overfishing, resource extraction, tourism) are creating novel 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, while 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 recolonization of sea otter historic ranges, necessitating understanding of 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 like aquaculture, wildlife tourism, and extractive activities like fishing, are diversifying shark-human interactions, and altering the manner and magnitude of spatiotemporal impacts of sharks on ecosystems.

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. While transitions in fisheries and recovery goals will be challenging (e.g. due to commercial value and fisheries depredation), they are necessary to ensure healthy ecosystems in a changing ocean.

Summary Figure



Empirical studies (n = 89) reveal that macropredatory sharks in coastal ecosystems can have large effects on prey that cascade to basal macrophytes. Shark effects on reefs are variable, but can modify mesopredator abundance, behavior and community composition. Effect sizes of sharks in other interactions and ecosystems are lower or remain unclear.

Abstract

Historically, sharks performed roles as predators, competitors, facilitators, and nutrient transporters. However, overfishing and other threats have greatly reduced shark populations globally and altered their roles and ecosystem importance. We review these changes to shark populations and ecological roles, and their implications for ecosystem function and management. Some macropredatory sharks are disproportionately impacted by humans, yet have large effects on prey and coastal ecosystems, including facilitating carbon sequestration. Like predators on land, these species may be particularly crucial to ensuring ecosystem function in a changing climate. Important roles of sharks, however, are not ubiquitous. Increasing human uses of oceans are changing shark roles, which must be considered in future planning. Rebuilding populations of key species and incorporating shark ecological importance and less obvious roles into management efforts are critical to retaining the functional importance of sharks; coupled social-ecological frameworks can assist in facilitating this shift in management goals.

Background

Globally, predator loss across terrestrial (1), freshwater (2), and marine (3, 4) ecosystems is concerning due to their potentially important 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 functional levels to restore ecosystems and communities (7, 10–12), and as a nature-based climate solution to indirectly increase carbon sequestration (13). Selecting species for management prioritization, however, requires an understanding of their ecological roles and overall *importance* (community and ecosystem consequences of changes in their abundance; (5).

Whereas progress has been made in terrestrial ecosystems (1, 7), using 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 due to 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 depletions, describe the diverse ecological roles of sharks, and highlight the value of understanding their past, present, and future roles. We investigate where roles are currently important, identify where population restorations may be particularly valuable, and evaluate 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 (i.e., 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 (14) (Fig 1A). In modern times, catch per unit effort has steadily declined for global shark landings since the 1950s, indicating declining abundances (15, 16) & Fig 1B). 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 survey (19) along a gradient of human pressure revealed a 63% mean depletion of the five main reef shark species (20) relative to unfished healthy reefs. Indeed, 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).

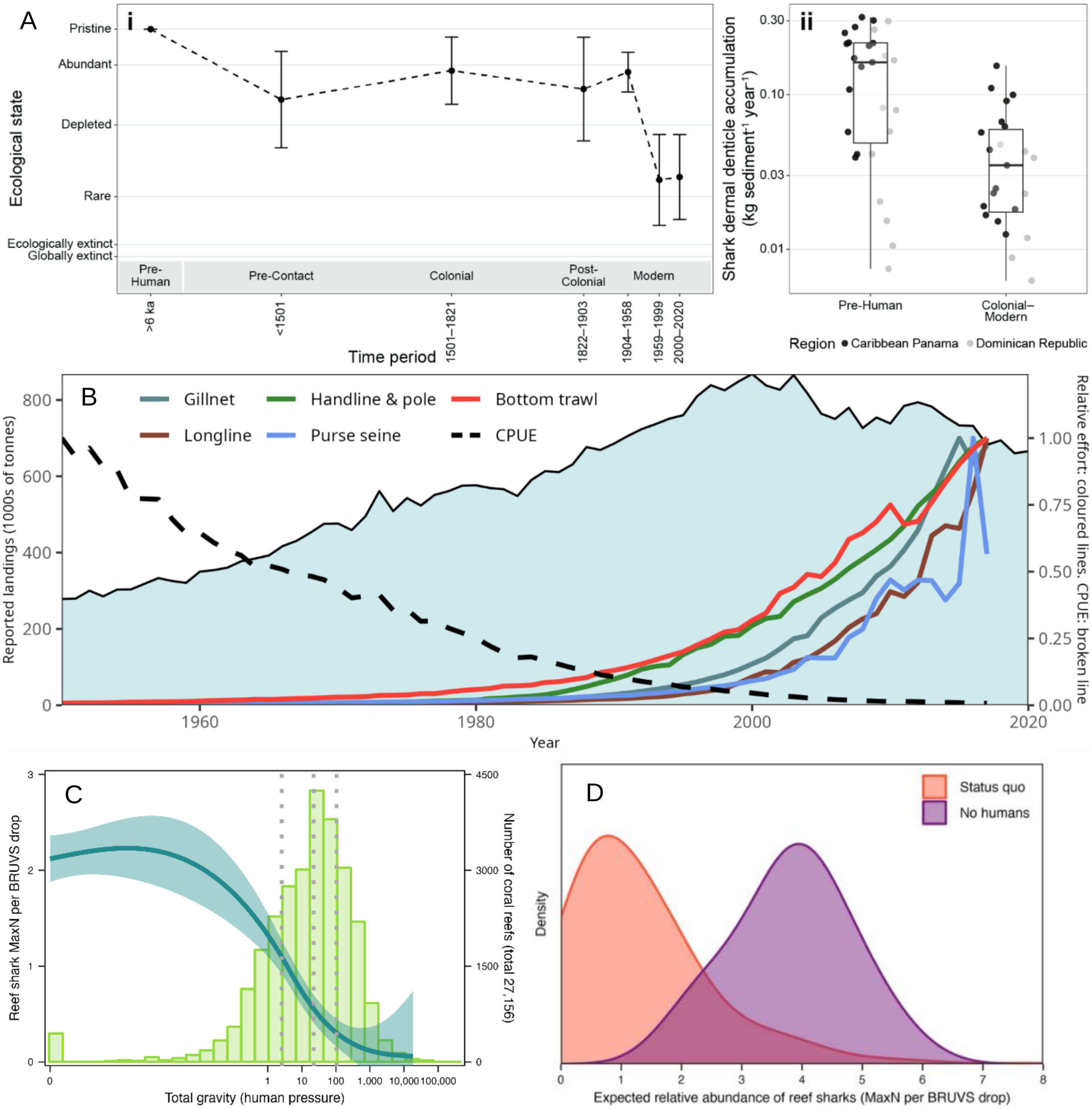


***Figure 1. Estimated abundance declines of sharks across data sources and time scales**. A) Millennial-scale changes in relative reef shark abundance. i: Perceived abundance of sharks in Caribbean Panama inferred from archaeological, historical, ecological, and fisheries records (based on* (14)*). 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% CI;* (21)*) and number of global coral reefs (green histogram; vertical dotted lines are quartiles* (22)*) along a gradient of human pressure (total gravity* (19, 22)*). 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 (*(22) *models set human-related variables to zero). Expected relative abundance was estimated using MaxN measurements from 371 reefs globally* (21).

Collectively, such studies show shark populations in different global ecosystems are greatly reduced, even from populations heavily impacted by humans before baseline data collection. Consequently, the 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 (23). Fishing also selectively removes the largest and highest trophic-level individuals and species (24–26) that likely play outsized roles in species interactions and ecosystem-level effects (27, 28). Therefore, the ecosystem importance of sharks currently being measured in Anthropocene oceans is likely much less than at historical abundances in most ecosystems (e.g. (21)).

Ecological roles of sharks

Modern forms of sharks arose ~ 150 MA ago (29), and the more than 500 extant species are found throughout virtually all marine ecosystems, from deep seas to estuaries, and in some freshwater habitats (30). Sharks are generally viewed by scientists and society as archetypal macropredators – upper trophic level predators that consume large-bodied prey – and are presumed to be critical to the structure, function, and resilience of ecosystems through top-down effects. Sharks, however, span an incredible range of adult lengths — from 20 cm to over 18 m and fill diverse feeding guilds from large filter feeders, similar to whales, to parasites, small predatory species feeding on crustaceans and worms, and larger-bodied predators feeding largely on cephalopods and teleosts. While 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 (28) and must tradeoff foraging opportunities against predation risk (27), fill different ecological roles, and likely have fewer and smaller effects on their prey and ecosystems than macropredatory sharks ((31); Fig 2). Given their diverse adult body sizes and habitats, it is unsurprising that sharks can 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 through various top-down and bottom-up pathways (Fig 2). Unlike terrestrial mammalian predators, most sharks shift their diets, and their potential ecological roles and importance, considerably through ontogeny due to changes in body size, habitat, and movement patterns (28).

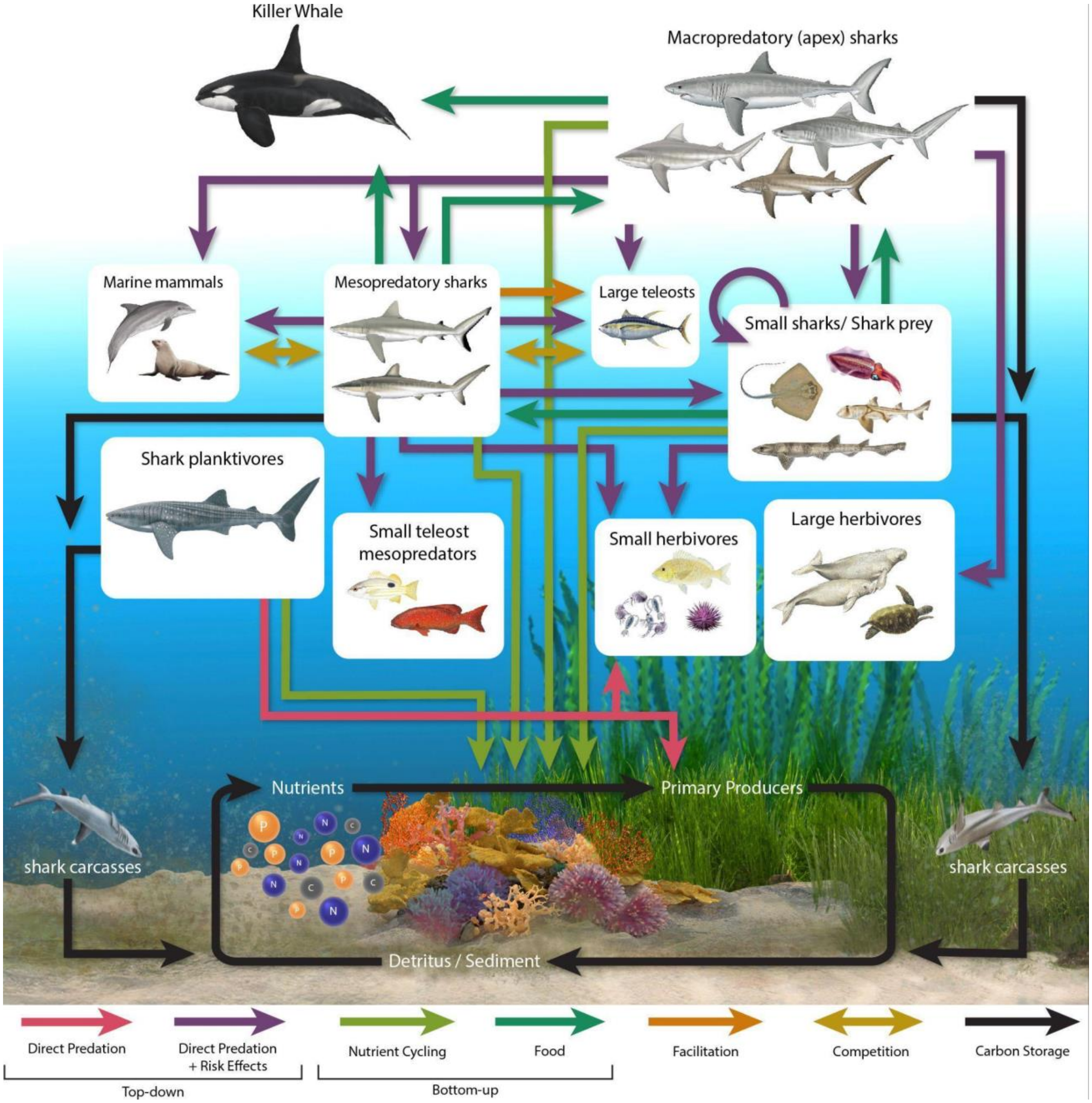


***Figure 2*. Conceptual model of the current state of knowledge of the ecological roles and importance of sharks in aquatic food webs**. *Sharks play multiple roles in ecosystems through top-down (e.g., direct predation, risk effects) and bottom-up (e.g., food provisioning, nutrient cycling) processes, and species interactions (e.g., competition and facilitation). Only interactions involving sharks are displayed.*

Recent field studies demonstrate that the ecological importance of sharks varies markedly within and among populations and across ecological contexts ((27); Fig 2). 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 anti-predator behavior (e.g., 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 (white shark, tiger shark) on prey – especially marine mammals and other long-lived taxa – in primarily macrophyte-dominated systems ((31, 32); Fig 3B). Here, shark predation and predation risk indirectly influence basal ecosystem dynamics, including macroalgal establishment, seagrass biomass and persistence, macrophyte biodiversity, and/or biogeochemical pathways including carbon storage ((8, 33–35); Fig 3A). For example, 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 (green turtle, *Chelonia mydas*; dugong *Dugong dugon*; (33)) that promotes the persistence of dense seagrass beds (6, 8, 35). These results have been observed in multiple locations and ocean basins, suggesting 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 (27). For example, recent studies on coral reefs demonstrate that strong, cascading effects of sharks on reef macroalgae can arise under specific conditions (36), yet in most circumstances it appears that sharks have limited effects on coral reef fish and benthic communities ((37, 38); Fig 3A). 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 (27, 36). 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 (e.g., 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 (37, 38).

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 (39, 40)), shallow to deep mesophotic coral reefs (41), and vice versa (40), coastal oceans to estuarine waters (42), and across latitudinal gradients (43). Nutrients can be deposited through egestion and excretion or carcasses of sharks that die or are eaten in habitats distant from where foraging occurred (see (27)). The effects of nutrient fluxes on ecosystem productivity, however, 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 significance of this deposition is unknown (40). 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/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 & 3).

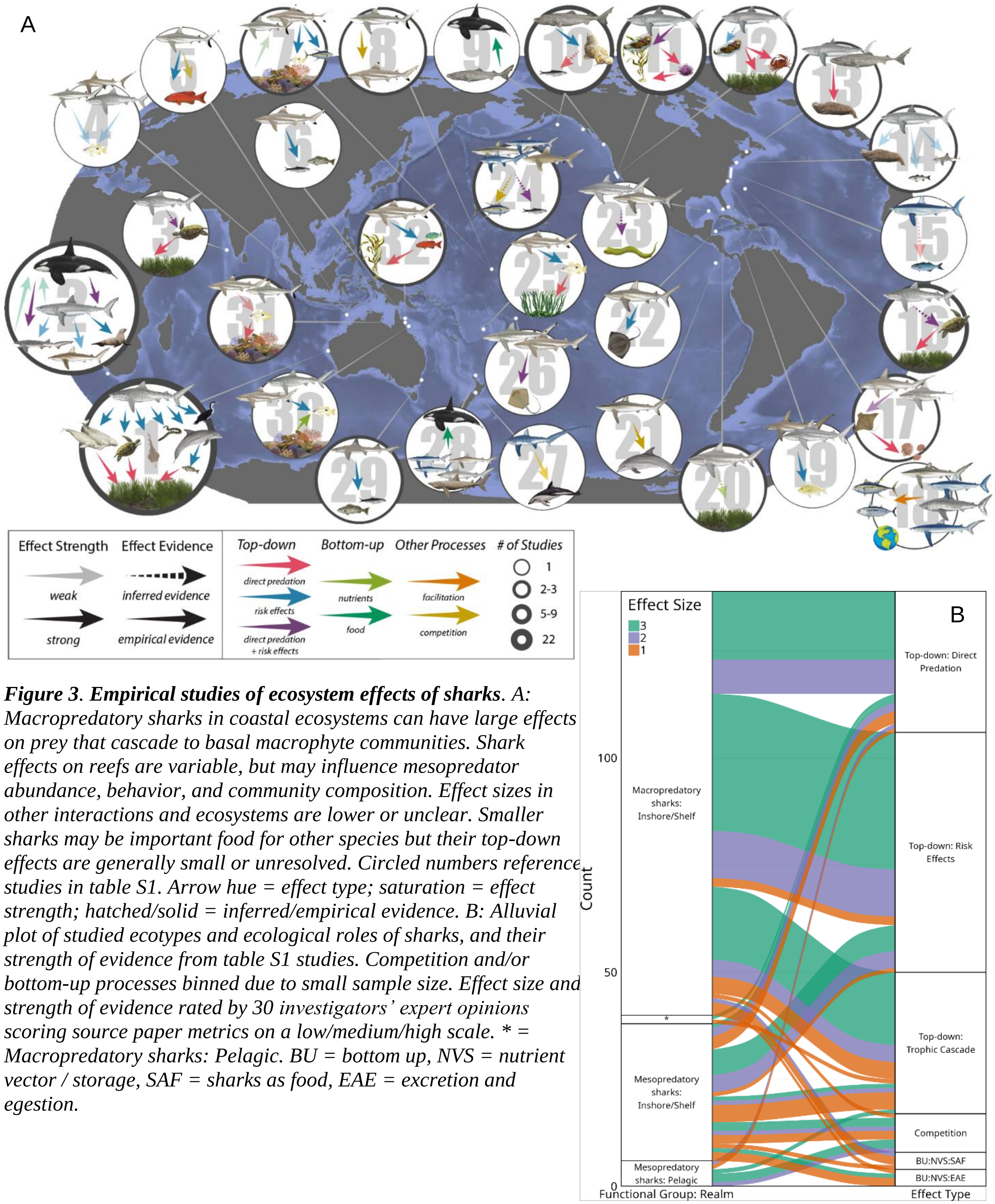


Figure 3*. *Empirical studies of ecosystem effects of sharks. *A: Macropredatory sharks in coastal ecosystems can have large effects on prey that cascade to basal macrophyte communities. Shark effects on reefs are variable, but may influence mesopredator abundance, behavior, and community composition. 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 = effect type; saturation = effect strength; hatched/solid = inferred/empirical evidence. B: Alluvial plot of studied ecotypes and ecological roles of sharks, and their strength of evidence from table S1 studies. Competition and/or bottom-up processes binned due to small sample size. Effect size and strength of evidence rated by 30 investigators' expert opinions scoring source paper metrics on a low/medium/high scale. * = Macropredatory sharks: Pelagic. BU = bottom up, NVS = nutrient vector / storage, SAF = sharks as food, EAE = excretion and egestion.*

Loss of ecological roles and function with overfishing

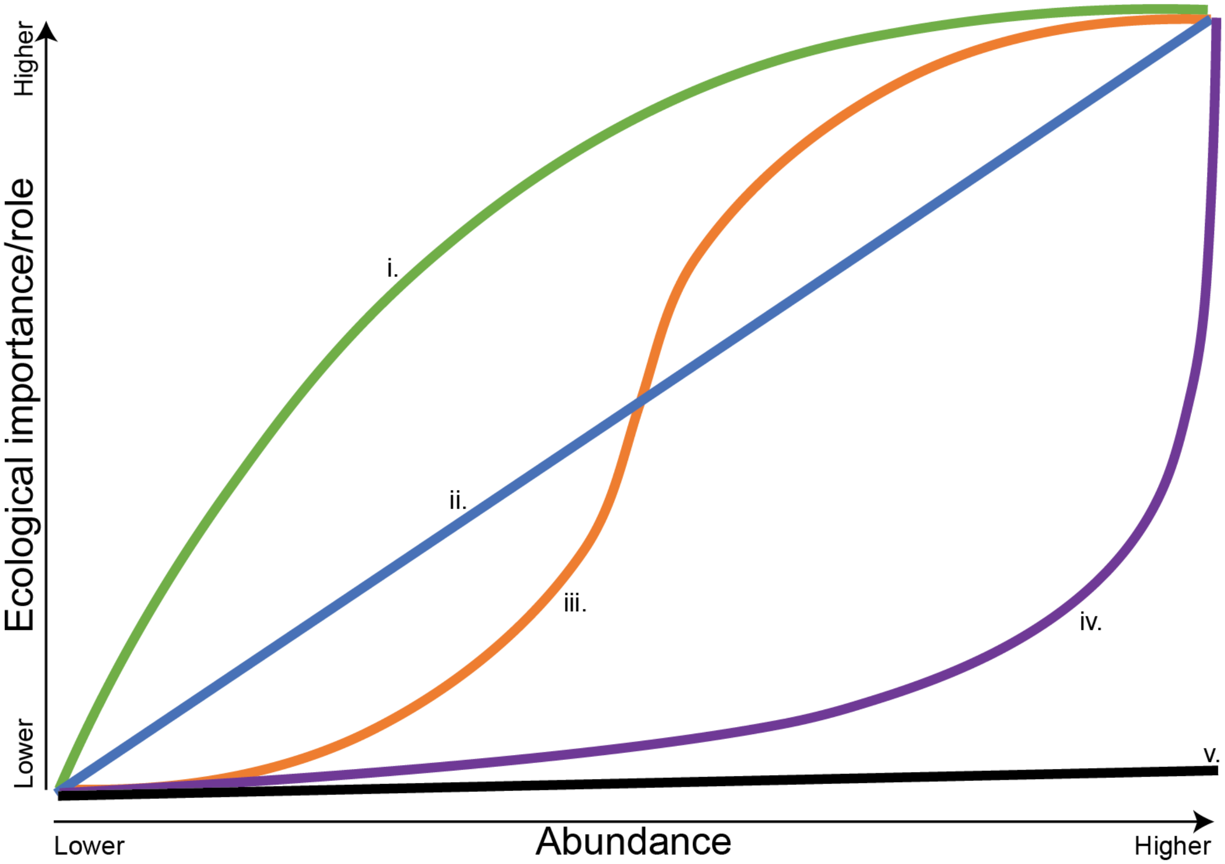


***Figure 4: Theoretical relationships of ecological importance as a function of shark population abundances**. As shark population sizes increase, their effects on ecosystems may increase (i/green) rapidly at low abundances, (ii/blue) linearly, or (iii/orange, iv/purple) slowly until reaching thresholds, or (v/black) 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.*

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. Indeed, human activities are threatening functional diversity within sharks and rays to a greater degree than other large marine predators (e.g. bony fish, marine mammals), and species with unique functional traits (e.g. habitats, position in the water column, and diets) are particularly at risk (24, 25).

In temperate and tropical systems, serial depletion of sharks consistently affects larger individuals and large-bodied species that are (A) more valuable than many other species per individual (44), (B) more sensitive to fishing due to slow intrinsic growth rates, and (C) can be more susceptible to some fishing gear types. Mean caudal fin aspect ratio (correlating to average swimming speeds and scale of movements (45)) 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 loss of large-bodied, wide-ranging species (39, 40, 43). Human impacts drive decreases in mean trophic levels of macro- and mesopredatory species (Fig 5B), suggesting 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, 27, 33).

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 ((46); Fig 5A), Mediterranean Sea (47), South China Sea (48), waters off Costa Rica (49) and South Africa (50)]. This pattern is emerging in less-monitored tropical shelf seas (3) like the Bay of Bengal – one of the most heavily fished regions of the world (51). As fishing increased, the largest shark (and ray) species with highest-value fins and slow life histories disappeared, followed by species with moderately productive life histories (Fig 5B, 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; see (52)).

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 (53). Halos are smaller on reefs with greater and longer protection from fishing suggesting sharks and large teleost piscivores have positive effects on the biomass of reef-adjacent primary producers (54) and their potential to sequester carbon in sediment (34)). Halos are predicted to change based on 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 based on the loss of their predators or the presence of larger sharks that threaten the predators or halo-forming species.

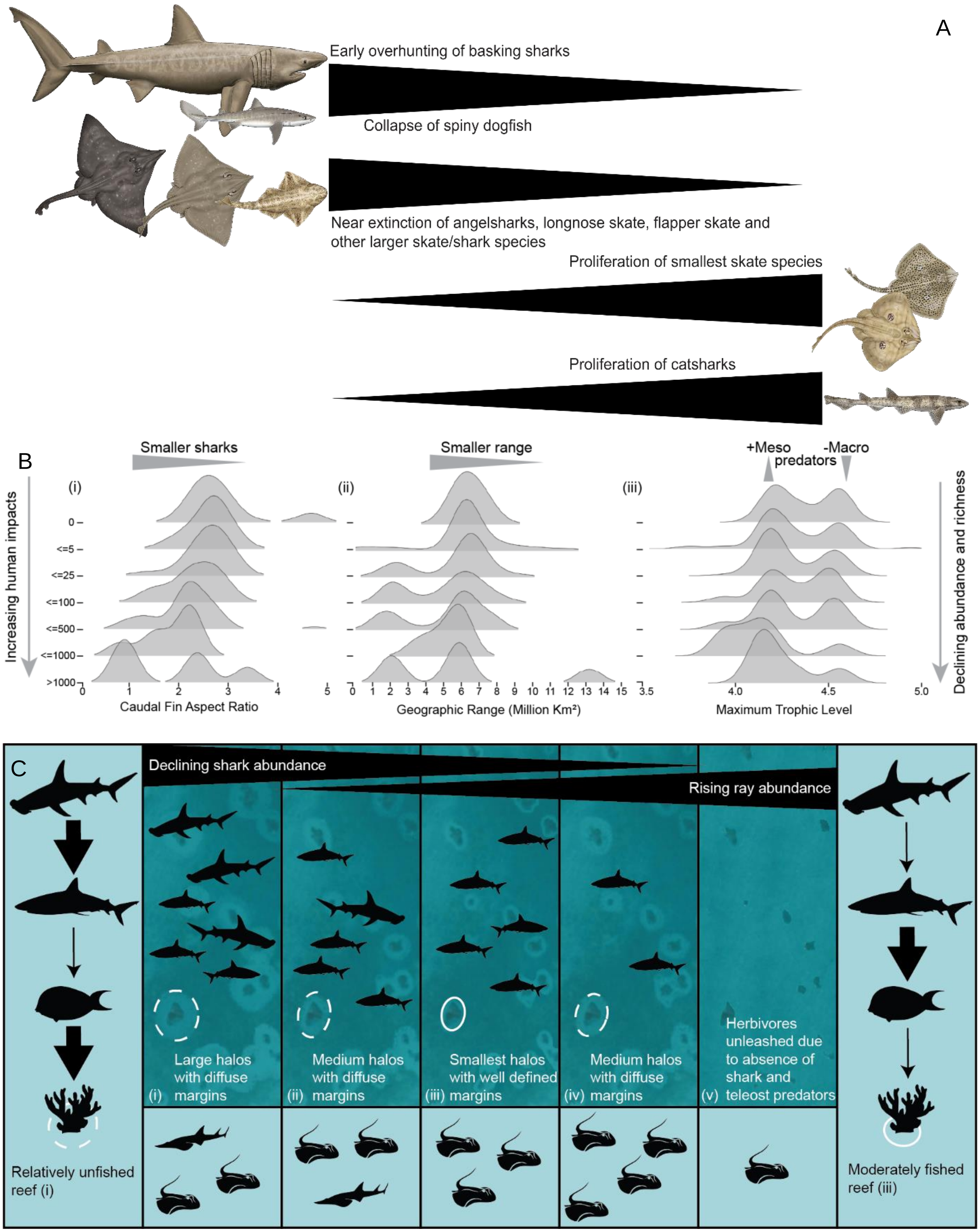


Figure 5. Changing ecological roles of sharks in an age of overfishing*. A) Fishing has shifted elasmobranch communities over time, causing a ~60% drop in predatory fish abundance throughout the North Atlantic shelf since 1950* (55), *especially larger elasmobranchs* (46, 56). *Similar declines occurred in the Mediterranean Sea* (47), *and Bay of Bengal* (51). *Smaller elasmobranch species abundances have risen* (16, 46), *suggesting larger species*

suppress smaller species through predation and competition. B) Species richness and abundance of sharks decreases along a gradient of market gravity (human impact), along with traits influencing 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 from (3, 20, 45). *C) Indirect effects of predation pressure are documented in grazing patterns ('halos'* (53)*) adjacent to patch reefs. Reductions in predation pressure, including depletions of sharks, influence safe distances for herbivorous fish in habitats adjacent to reef* (54). *With little risk herbivorous fish feed further from reefs leading to reduced primary producer biomass* (53) *and sedimentary carbon stores* (34).

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 North-Eastern Pacific population of white sharks likely declined for over a century (57). Following protection from fisheries in California in 1994, the number of juvenile white sharks using coastal beach habitats have steadily increased (58). Continued population gains of protected pinnipeds (59), despite population gains in sharks, suggest white shark predation does not regulate pinniped abundance (60). White shark predation risk, however, affects pinniped behavior, inducing shifts in foraging/resting cycles, movement, social behavior, and at-sea group formation (32, 61). Indeed, white shark recoveries in the NW Atlantic (62), are inducing behavioral changes in gray seals (*Halichoerus grypus;* (32)). 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 last 20 years, increasing white shark-inflicted mortality has negatively impacted sea otter (*Enhydra lutris*) populations and limited their distribution in exposed coastal habitats where they are susceptible to shark mortality (63–65). In contrast, sea otter abundance has dramatically increased in an estuary where predation risk from sharks is low (66). 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 (67, 68), while in protected estuarine habitats the effects of increased sea otter foraging have positively impacted seagrass abundance and salt marsh stability (69, 70).

Novel threats and changing ecological roles for sharks in the Anthropocene

Rapid industrialization in many marine sectors (71) is modifying shark importance, changing the spatial distribution of roles, and yielding novel ecological roles (Table 1).

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 involving sharks in coastal and offshore environments.*

Group	Sector/Threat/Change	Pressure	Coastal/Offshore Prevalence	Process*	Evidence of Impacts
Blue economy (or maritime industrialization)	Renewable energy (e.g., wind farms, tidal power)	Noise, infrastructure, electric cables	Both	A, B, C	(72, 73)
	Seismic surveys	Noise	Offshore	A,C,	(73, 74)
	Oil and gas operations / deep sea mining	Noise, pollution	Offshore	A,C,D	(75, 76)
	Industrial shipping, marine traffic	Noise, collision	Both	A,C,E	(77)
	Tourism	Food input, pollution, behavioral modification, human-shark conflict	Coastal	A,D,F, G	(78, 79)
	Aquaculture	Eutrophication, anoxia/hypoxia, infrastructure, pollution, escapees, predator interactions	Mostly coastal	A,B,D, F	(80)
	Urban expansion (e.g., port development)	Habitat modification, sedimentation, noise, pollution, contaminants, water quality	Coastal	A,D, I	(81, 82)
	Fishing, including subsistence and artisanal	Human-shark conflict, prey availability on fishing gear (depredation)	Mostly coastal	B	(83)
Other changes (or ecosystem management)	Invasive species (including species outbreaks)	Introduction of novel prey	Coastal	B,H	(84)
	Ecological surprises (e.g., orca pressure on white shark, white shark on otter)	Changes in predator-prey relationships	Coastal	B	(63, 85, 86)
	Species protection & spatial conservation planning (e.g., MPAs)	Protection of sharks, other predators, and/or forage populations	Mostly coastal	J	(87)

*Processes: A: changes to distribution, movements, residency of prey and predators. B: misdirected predation (e.g., towards electric cables, unusual prey). C: prey disorientation (e.g., from noise). D: health condition affecting foraging requirements, ability, and success. E: change of abundance of less abundant/vulnerable species. F: reliance on food/provisioning by humans. G: changes in food requirements (increased energy expenditure). H: introduction of novel prey in ecosystems. I: reduced habitat quality affects recruitment success, prey availability, prey/predator detection. J: direct changes to prey / predator abundance.

Activities like shipping, seismic surveys, offshore wind farms, and pile-driving expose sharks to low-frequency noise (73) and electromagnetic fields that overlap their sensitivity thresholds (88). 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 (89) 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 like shark feeding or (cage) diving can affect sharks (78, 79), including changing behaviors (90), elevating local densities (91), shifting diets (92), 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. While 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 impact 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 (83). Food subsidies from fishing and aquaculture (e.g., hooked fish, discarded bait, 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 (80). 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 (93). Such changes to shark roles in natural ecosystems due to food subsidies could match ecological shifts, including enhanced effects on prey and competitors, observed in terrestrial predators depredating livestock or receiving other food subsidies (94).

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 detect and respond to predators over shorter distances and, thereby, need to invest more heavily in anti-predator behavior (27, 95). Similarly, reductions in food available to prey populations are predicted to increase the importance of shark direct predation due to 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 the roles of sharks and reveal their importance. For example, rebuilding green turtle (*Chelonia mydas*) 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 (96, 97).

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 (98). The disturbances that trigger ecological surprises can be natural (hurricanes, thermal anomaly, novel species interactions) or anthropogenic (overfishing, climate change) and can provide important insights into ecological dynamics (99). 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, killing white sharks in South Africa (85), resulting in their temporary site abandonment (100). Their absence preceded increased abundances of broadnose sevengill (*Notorynchus cepedianus*) and bronze whaler (*Carcharhinus brachyurus*) sharks, likely through mesopredator and competitive release (101), before killer whale predation on sevengill sharks led to their site abandonment (102).

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 impacts marine animals primarily via warming waters (fig S1A,B), decreases in pH (ocean acidification; fig S1C), and reduced dissolved oxygen concentration (103); fig S1D). Sharks unable to obtain enough resources to meet increased demands of warming waters (which increase metabolic rates) may disappear from some habitats (e.g., bull shark *Carcharhinus leucas*; (104)), removing their ecological roles.

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 (105), with an optimum temperature for physiological processes nested within critical thermal limits, which can vary between populations ((106); fig S1A,B). Asymmetries in the thermal response curves of predator and prey may change predator-prey interaction outcomes and food-web-level effects (107, 108). Thus, understanding how the role of sharks as predators might 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, like marine mammals, may shape the future of ocean ecosystems (109). Rising water temperatures may decrease the advantage 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 (110, 111). Because sharks have begun – and are expected to continue – expand their ranges poleward with warming temperatures (106, 112, 113), they may play increasingly important roles as macropredators and large mesopredators in ecosystems they begin to inhabit. 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 due to light limitation (114). Therefore, any roles 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 (115), rendering habitat unavailable or marginal (116). Vertical and horizontal range reductions are expected for many sharks and their prey (103), though at least one species (sixgill shark; *Hexanchus griseus*), maintains high activity levels in low-oxygen waters, suggesting that consequences may vary among species ((117); fig S1D), and are probably more severe for active surface-oriented species that use the epipelagic zone for foraging (e.g. many pelagic sharks (118)). 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 (119, 120). Relatedly, as increasing anthropogenic inputs of pollutants and fertilizers degrade water quality and visibility, general predatory success of sharks may increase, as prey are less able to detect and evade predators like sharks.

Climate-change-driven coral bleaching, mortality, and ‘flattening’ of reefs (121) 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 (122), and reduces refuge availability. Thus, shark predation on reef fish will likely increase, at least temporarily, as reefs flatten (123). 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 (e.g. shifts in group size, spatial extent/duration of foraging) will change as prey navigate food-safety trade-offs (33, 124, 125). Examining changes in the direct and indirect effects of sharks on prey species as reefs lose structure, and other human impacts 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 mitigating 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 (e.g. seagrass; (8, 35, 96)) and sediment (34) by controlling grazing through predation and fear effects (33, 35). 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 heatwave, 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 due to intense herbivory. On coral reefs, large predator presence, including sharks, is linked to higher rates of carbon deposition in sediment (34), suggesting sharks promote blue carbon stores across multiple ecosystems. The overall contribution of sharks to carbon sequestration requires further investigation but is considerable in some contexts.

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 (126). Although recent initiatives promote this change, developing conservation metrics and assessment frameworks focused on function (24, 127), 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 (24, 25, 28). While managing for sustainable use may avoid extinctions, fisheries management approaches that also recover functional diversity, historic high abundances, and large species/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, 87), but is relatively recent with only 12 shark species having >10% of their range protected (128), and barriers remain in enforcement and achieving representative coverage (129). Combining MPAs with broader national or regional fisheries management can enhance shark protections (130), 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 (131), and while 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 (23, 129). Even when shark populations persist, inadequate management often leads to lost ecological roles from local populations (functional extinction; (3, 21, 25, 56). In addition to better managing legal fishing, better strategies must be adopted to reduce the impact of illegal and unregulated (IUU) fishing on sharks (15). Many new technological advances can assist combating IUU and strengthen management of legal fisheries e.g. diverse satellite technologies to track vessels (132, 133); onboard electronic systems to monitor intended /unintended shark catch (134); electronic information exchange systems to strengthen the Port State Measures Agreement (135); genetic screening tools to identify illicit trade of shark products and promote supply chain transparency (136); shark loggers that can detect poaching and directly measure overlap between fishers and sharks (137). 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 (129, 138), and may lead to calls for shark culls. Similarly, managers must prepare for shark-human interactions as climate change shifts species ranges. Novel threats will continue to emerge, necessitating management solutions that enhance the resilience of shark populations and their ability to adapt to changing conditions (139). Emerging threats are largely non-extractive and may require different approaches than 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. While these massive knowledge gaps remain, a precautionary approach aiming 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 (140). Wolves' role in restoring plant and avian communities in the Greater Yellowstone Ecosystem (10) informs global perceptions of predators, led to calls for population reintroductions (7), and prompted reevaluation of other roles like 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, following near extirpation by humans. Documented ecosystem effects of sharks, including the importance of tiger sharks for seagrass meadows (8, 35), and other studies (Fig 3A), could be leveraged similarly (141). However, sharks may perform multiple subtle roles that change across their life history and occur within reticulate marine food webs which confound simple cause-effect framing. Research on the ecological importance of sharks will demonstrate their conservation and ecosystem services benefits.

Second, coupled social-ecological frameworks facilitate including 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 co-management encourages participation and facilitates stakeholder agency in ways that can reinforce shared outcomes (142, 143). 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 (144). 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 (145). Similarly, shark conservation success is underwritten with cultural support from communities choosing to prioritize shark preservation against other uses (59), e.g. Hawaiian cultural rejection of tiger shark culls (146), collective action towards alternate uses of marine environments (143), and public campaigns and support for fin-sale bans (147).

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. While 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 some contexts. Given the economic and societal value of these ecosystems, further studies leveraging global datasets are crucial. Empirical evidence suggests 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 (148), 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 (42, 149) resulting in considerable differences in the ecological roles and threats individuals face (150). Understanding the prevalence, magnitude, and nature of individual specialization is important for understanding the importance of sharks in ecosystems and developing adequate management strategies.

While overfishing is the overwhelming force degrading ecological roles of sharks, climate change, habitat loss, and the blue economy (e.g., energy, mining, shipping, aquaculture), will further impact sharks and their ecological roles, affecting abundance, distribution, health, and behavior of sharks and their prey, potentially creating opportunities for novel roles. Furthermore, shark roles can impact ecosystems over multi-decadal timescales 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.

Finally, 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 due to technological advances that facilitate enforcement on such large spatial scales (e.g., drones, video monitoring systems, satellite-based vessel tracking). Harnessing public support, including integrating 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.

References

1. W. J. Ripple, J. A. Estes, R. L. Beschta, C. C. Wilmers, E. G. Ritchie, M. Hebblewhite, J. Berger, B. Elmhagen, M. Letnic, M. P. Nelson, O. J. Schmitz, D. W. Smith, A. D. Wallach, A. J. Wirsing, Status and ecological effects of the world's largest carnivores. *Science*. **343**, 1241484 (2014).

2. F. He, C. Zarfl, V. Bremerich, A. Henshaw, W. Darwall, K. Tockner, S. C. Jaehnig, Disappearing giants: a review of threats to freshwater megafauna. *Wiley Interdisciplinary Reviews: Water*. **4**, e1208 (2017).

3. N. K. Dulvy, N. Pacoureau, C. L. Rigby, R. A. Pollom, R. W. Jabado, D. A. Ebert, B. Finucci, C. M. Pollock, J. Cheok, D. H. Derrick, K. B. Herman, C. S. Sherman, W. J. VanderWright, J. M. Lawson, R. H. Walls, J. K. Carlson, P. Charvet, K. K. Bineesh, D. Fernando, G. M. Ralph, J. H. Matsushiba, C. Hilton-Taylor, S. V. Fordham, C. A. Simpfendorfer, Overfishing drives over one-third of all sharks and rays toward a global extinction crisis. *Current Biology* (2021), doi:10.1016/j.cub.2021.08.062.

4. D. J. McCauley, M. L. Pinsky, S. R. Palumbi, J. A. Estes, F. H. Joyce, R. R. Warner, Marine defaunation: Animal loss in the global ocean. *Science*. **347**, 1255641 (2015).

5. M. R. Heithaus, A. Frid, A. J. Wirsing, B. Worm, Predicting ecological consequences of marine top predator declines. *Trends in Ecology & Evolution*. **23**, 202–210 (2008).

6. J. A. Estes, M. Heithaus, D. J. McCauley, D. B. Rasher, B. Worm, Megafaunal impacts on structure and function of ocean ecosystems. *Annual Review of Environment and Resources*. **41**, 83–116 (2016).

7. W. J. Ripple, C. Wolf, M. K. Phillips, R. L. Beschta, J. A. Vucetich, J. B. Kauffman, B. E. Law, A. J. Wirsing, J. E. Lambert, E. Leslie, C. Vynne, E. Dinerstein, R. Noss, G. Wuerthner, D. A. Dellasala, J. T. Bruskotter, M. P. Nelson, E. Crist, C. Darimont, D. M. Ashe, Rewilding the American West. *BioScience* (2022), doi:10.1093/biosci/biac069.

8. R. J. Nowicki, J. A. Thomson, J. W. Fourqurean, A. J. Wirsing, M. R. Heithaus, Loss of predation risk from apex predators can exacerbate marine tropicalization caused by extreme climatic events. *Journal of Animal Ecology*. **90**, 2041–2052 (2021).

9. D. B. Rasher, R. S. Steneck, J. Halfar, K. J. Kroeker, J. B. Ries, M. T. Tinker, P. T. Chan, J. Fietzke, N. A. Kamenos, B. H. Konar, J. S. Lefcheck, C. J. Norley, B. P. Weitzman, I. T. Westfield, J. A. Estes, Keystone predators govern the pathway and pace of climate impacts in a subarctic marine ecosystem. *Science*. **369**, 1351–1354 (2020).

10. M. S. Boyce, Wolves for Yellowstone: dynamics in time and space. *Journal of Mammalogy*. **99**, 1021–1031 (2018).

11. T. M. Newsome, G.-A. Ballard, M. S. Crowther, J. A. Dellinger, P. J. Fleming, A. S. Glen, A. C. Greenville, C. N. Johnson, M. Letnic, K. E. Moseby, D. G. Nimmo, M. P. Nelson, J. L. Read, W. J. Ripple, E. G. Ritchie, C. R. Shores, A. D. Wallach, A. J. Wirsing, C. R. Dickman, Resolving the value of the dingo in ecological restoration. *Restoration Ecology*. **23**, 201–208 (2015).

12. J. A. Estes, J. F. Palmisano, Sea otters: their role in structuring nearshore communities. *Science*. **185**, 1058–1060 (1974).

13. O. J. Schmitz, M. Sylvén, T. B. Atwood, E. S. Bakker, F. Berzaghi, J. F. Brodie, J. P. Cromsigt, A. B. Davies, S. J. Leroux, F. J. Schepers, F. A. Smith, S. Stark, J.-C. Svenning, A. Tilker, H. Ylänne, Trophic rewilding can expand natural climate solutions. *Nature Climate Change*, 1–10 (2023).

14. E. M. Dillon, D. J. McCauley, J. M. Morales-Saldaña, N. D. Leonard, J. Zhao, A. O'Dea, Fossil dermal denticles reveal the preexploitation baseline of a Caribbean coral reef shark community. *Proceedings of the National Academy of Sciences*. **118**, e2017735118 (2021).

15. L. N. Davidson, M. A. Krawchuk, N. K. Dulvy, Why have global shark and ray landings declined: improved management or overfishing? *Fish and Fisheries*. **17**, 438–458 (2016).

16. F. Ferretti, R. A. Myers, F. Serena, H. K. Lotze, Loss of large predatory sharks from the Mediterranean Sea. *Conservation Biology*. **22**, 952–964 (2008).

17. N. Pacoureau, C. L. Rigby, P. M. Kyne, R. B. Sherley, H. Winker, J. K. Carlson, S. V. Fordham, R. Barreto, D. Fernando, M. P. Francis, R. W. Jabado, K. B. Herman, K.-M. Liu, A. D. Marshall, R. A. Pollom, E. V. Romanov, C. A. Simpfendorfer, J. S. Yin, H. K. Kindsvater, N. K. Dulvy, Half a century of global decline in oceanic sharks and rays. *Nature*. **589**, 567–571 (2021).

18. G. Roff, C. J. Brown, M. A. Priest, P. J. Mumby, Decline of coastal apex shark populations over the past half century. *Communications Biology*. **1**, 223 (2018).

19. J. E. Cinner, E. Maire, C. Huchery, M. A. MacNeil, N. A. Graham, C. Mora, T. R. McClanahan, M. L. Barnes, J. N. Kittinger, C. C. Hicks, S. D'Agata, A. S. Hoey, G. G. Gurney, D. A. Feary, I. D. Williams, M. Kulbicki, L. Vigliola, L. Wantiez, G. J. Edgar, R. D. Stuart-Smith, S. A. Sandin, A. Green, M. J. Hardt, M. Beger, A. M. Friedlander, S. K. Wilson, E. Brokovich, A. J. Brooksa, J. J. Cruz-Mottab, D. J. Boothc, P. Chabanetd, C. Goughe, M. Tupperf, S. C. Ferseg, U. R. Sumailah, S. Pardede, D. Mouillot, Gravity of human impacts mediates coral reef conservation gains. *Proceedings of the National Academy of Sciences*. **115**, E6116–E6125 (2018).

20. C. A. Simpfendorfer, M. R. Heithaus, M. R. Heupel, M. A. Macneil, M. Meekan, E. Harvey, C. S. Sherman, L. M. Currey-Randall, J. S. Goetze, J. J. Kiszka, M. J. Rees, C. W. Speed, V. Udyawer, M. E. Bond, K. I. Flowers, G. M. Clementi, J. Valentin-Albanese, M. S. Adam, K. Ali, J. Asher, E. Aylagas, O. Beaufort, C. Benjamin, A. T. F Bernard, M.

L. Berumen, S. Bierwagen, C. Birrell, E. Bonnema, R. M. K Bown, E. J. Brooks, J. J. Brown, D. Buddo, P. J. Burke, C. Cceres, M. Cambra, D. Cardeosa, J. C. Carrier, S. Casareto, J. E. Caselle, V. Charloo, J. E. Cinner, T. Claverie, E. E. G Clua, J. E. M Cochran, N. Cook, J. E. Cramp, B. M. Dalberto, M. D. Graaf, M. C. Dornhege, M. Espinoza, A. Estep, L. Fanovich, N. F. Farabaugh, D. Fernando, C. E. L Ferreira, C. Y. A Fields, A. L. Flam, C. Floros, V. Fourqurean, L. Gajdzik, L. G. Barcia, R. Garla, K. Gastrich, L. George, T. Giarrizzo, R. Graham, T. L. Guttridge, V. Hagan, R. S. Hardenstine, S. M. Heck, A. C. Henderson, P. Heithaus, H. Hertler, M. H. Padilla, R. E. Hueter, R. W. Jabado, J.-C. Joyeux, V. Jaiteh, M. Johnson, S. D. Jupiter, M. Kaimuddin, D. Kasana, M. Kelley, S. T. Kessel, B. Kiilu, T. Kirata, B. Kuguru, F. Kyne, T. Langlois, F. Lara, J. Lawe, E. J. I Lde, S. Lindfield, A. Luna-Acosta, J. Q. Maggs, B. M. Manjaji-Matsumoto, A. Marshall, L. Martin, D. Mateos-Molina, P. Matich, E. Mccombs, A. Mcivor, D. Mclean, L. Meggs, S. Moore, S. Mukherji, R. Murray, S. J. Newman, J. Nogus, C. Obota, D. Ochavillo, O. O'Shea, K. E. Osuka, Y. P. Papastamatiou, N. Perera, B. Peterson, C. R. Pimentel, F. Pina-Amargs, H. T. Pinheiro, A. Ponzo, A. Prasetyo, L. M. Sjamsul Quamar, J. R. Quinlan, J. A. Reis-Filho, H. Ruiz, A. Ruiz-Abierno, E. Sala, P. S. De-Len, M. A. Samoilys, W. R. Sample, M. S.- Umpierre, A. M. Schlaff, K. Schmid, S. N. Schoen, N. Simpson, A. N. H Smith, J. L. Y Spaet, L. Sparks, T. Stoffers, A. Tanna, R. Torres, M. J. Travers, M. V. Zinnicq Bergmann, L. Vigliola, J. Ward, J. D. Warren, A. M. Watts, C. K. Wen, E. R. Whitman, A. J. Wirsing, A. Wothke, E. Zarza-Gonzlez, D. D. Chapman, Widespread diversity deficits of coral reef sharks and rays. *Science*. **380**, 1155–1160 (2023).

21. M. A. MacNeil, D. D. Chapman, M. Heupel, C. A. Simpfendorfer, M. Heithaus, M. Meekan, E. Harvey, J. Goetze, J. Kiszka, M. E. Bond, L. M. Currey-Randall, C. W. Speed, C. S. Sherman, M. J. Rees, V. Udyawer, K. I. Flowers, G. Clementi, J. Valentin-Albanese, T. Gorham, M. S. Adam, K. Ali, F. Pina-Amargós, J. A. Angulo-Valdés, J. Asher, L. García Barcia, O. Beaufort, C. Benjamin, A. T. Bernard, M. L. Berumen, S. Bierwagen, E. Bonnema, R. M. Bown, D. Bradley, E. Brooks, J. J. Brown, D. Buddo, P. Burke, C. Cáceres, D. Cardeñosa, J. C. Carrier, J. E. Caselle, V. Charloo, T. Claverie, E. Clua, J. E. Cochran, N. Cook, J. Cramp, B. D'Alberto, M. de Graaf, M. Dornhege, A. Estep, L. Fanovich, N. F. Farabaugh, D. Fernando, A. L. Flam, C. Floros, V. Fourqurean, R. Garla, K. Gastrich, L. George, R. Graham, T. Guttridge, R. S. Hardenstine, S. Heck, A. C. Henderson, H. Hertler, R. Hueter, M. Johnson, S. Jupiter, D. Kasana, S. T. Kessel, B. Kiilu, T. Kirata, B. Kuguru, F. Kyne, T. Langlois, E. J. Lédée, S. Lindfield, Luna-Acosta, J. Maggs, B. M. Manjaji-Matsumoto, A. Marshall, P. Matich, E. McCombs, D. McLean, L. Meggs, S. Moore, S. Mukherji, R. Murray, M. Kaimuddin, S. J. Newman, J. Nogués, C. Obota, O. O'Shea, K. Osuka, Y. P. Papastamatiou, N. Perera, B. Peterson, A. Ponzo, A. Prasetyo, L. S. Quamar, J. Quinlan, A. Ruiz-Abierno, E. Sala, M. Samoilys, M. Schärer-Umpierre, A. Schlaff, N. Simpson, A. N. Smith, L. Sparks, A. Tanna, R. Torres, M. J. Travers, M. van Zinnicq Bergmann, L. Vigliola, J. Ward, A. M. Watts, C. Wen, E. Whitman, A. J. Wirsing, A. Wothke, E. Zarza-Gonzâlez, J. E. Cinner, Global status and conservation potential of reef sharks. *Nature*. **583**, 801–806 (2020).

22. J. E. Cinner, C. Huchery, M. A. MacNeil, N. A. Graham, T. R. McClanahan, J. Maina, E. Maire, J. N. Kittinger, C. C. Hicks, C. Mora, E. H. Allison, S. D'Agata, A. Hoey, D. A.

Feary, L. Crowder, I. D. Williams, M. Kulbicki, L. Vigliola, L. Wantiez, G. Edgar, R. D. Stuart-Smith, S. A. Sandin, A. Green, M. J. Hardt, M. Beger, A. Friedlander, S. J. Campbell, K. E. Holmes, S. K. Wilson, E. Brokovich, A. J. Brooks, J. J. Cruz-Motta, D. J. Booth, P. G. C. Chabanet, M. Tupper, S. C. Ferse, U. R. Sumaila, D. Mouillot, Bright spots among the world’s coral reefs. *Nature*. **535**, 416–419 (2016).

23. C. S. Sherman, C. A. Simpfendorfer, N. Pacoureau, J. H. Matsushiba, H. F. Yan, R. H. Walls, C. L. Rigby, W. J. VanderWright, R. W. Jabado, R. A. Pollom, J. K. Carlson, P. Charvet, A. B. Ali, Fahmi, J. Cheok, D. H. Derrick, K. B. Herman, B. Finucci, T. D. Eddy, M. L. D. Palomares, C. G. Avalos-Castillo, B. Kinattumkara, M.-D.-P. Blanco-Parra, Dharmadi, M. Espinoza, D. Fernando, A. B. Haque, P. A. Mejía-Falla, A. F. Navia, J. C. Pérez-Jiménez, J. Utzurrum, R. R. Yuneni, N. K. Dulvy, Half a century of rising extinction risk of coral reef sharks and rays. *Nature Communications*. **14**, 15 (2023).

24. C. Pimiento, C. Albouy, D. Silvestro, T. L. Mouton, L. Velez, D. Mouillot, A. B. Judah, J. N. Griffin, F. Leprieur, Functional diversity of sharks and rays is highly vulnerable and supported by unique species and locations worldwide. *Nature Communications*. **14**, 7691 (2023).

25. C. Pimiento, F. Leprieur, D. Silvestro, J. Lefcheck, C. Albouy, D. Rasher, M. Davis, J.-C. Svenning, J. Griffin, Functional diversity of marine megafauna in the Anthropocene. *Science Advances*. **6**, eaay7650 (2020).

26. T. B. Letessier, D. Mouillot, L. Mannocci, H. J. Christ, E. M. Elamin, S. M. Elamin, A. M. Friedlander, A. R. Hearn, J. B. Juhel, A. R. Kleiven, E. Moland, N. Mouquet, P. J. Nillos-Kleiven, E. Sala, C. D. Thompson, L. Velez, L. Vigliola, J. J. Meeuwig, Divergent responses of pelagic and benthic fish body-size structure to remoteness and protection from humans. *Nature* (2024), doi:10.1126/science.adi7562.

27. M. R. Heithaus, R. E. Dunn, N. F. Farabaugh, E. Lester, E. Madin, M. G. Meekan, Y. P. Papastamatiou, G. Roff, J. J. Vaudo, A. J. Wirsing, "Advances in Our Understanding of the Ecological Importance of Sharks and Their Relatives" in *Biology of Sharks and Their Relatives, Third Edition*, Carrier, Jeffrey C and Simpfendorfer, Colin C and Heithaus, Michael R and Yopak, Kara E, Ed. (CRC Press, 2022), vol. 3, pp. 487–521.

28. M. R. Heupel, D. M. Knip, C. A. Simpfendorfer, N. K. Dulvy, Sizing up the ecological role of sharks as predators. *Marine Ecology Progress Series*. **495**, 291–298 (2014).

29. L. B. Whitenack, S. L. Kim, E. C. Sibert, "Bridging the gap between chondrichthyan paleobiology and biology" in *Biology of Sharks and Their Relatives, Third Edition*, Carrier, Jeffrey C and Simpfendorfer, Colin C and Heithaus, Michael R and Yopak, Kara E, Ed. (CRC Press, 2022), vol. 3, pp. 1–29.

30. D. A. Ebert, M. Dando, S. Fowler, *Sharks of the World: A Complete Guide* (Princeton University Press, 2021), vol. 19.

31. M. R. Heithaus, A. J. Wirsing, J. A. Thomson, D. A. Burkholder, A review of lethal and non-lethal effects of predators on adult marine turtles. *Journal of Experimental Marine Biology and Ecology*. **356**, 43–51 (2008).

32. J. H. Moxley, G. Skomal, J. Chisholm, P. Halpin, D. W. Johnston, Daily and seasonal movements of Cape Cod gray seals vary with predation risk. *Marine Ecology Progress Series*. **644**, 215–228 (2020).

33. M. R. Heithaus, A. Wirsing, L. Dill, The ecological importance of intact top-predator populations: a synthesis of 15 years of research in a seagrass ecosystem. *Marine and Freshwater Research*. **63**, 1039–1050 (2012).

34. T. B. Atwood, E. M. Madin, A. R. Harborne, E. Hammill, O. J. Luiz, Q. R. Ollivier, C. M. Roelfsema, P. I. Macreadie, C. E. Lovelock, Predators shape sedimentary organic carbon storage in a coral reef ecosystem. *Frontiers in Ecology and Evolution*. **6**, 110 (2018).

35. D. A. Burkholder, M. R. Heithaus, J. W. Fourqurean, A. Wirsing, L. M. Dill, Patterns of top-down control in a seagrass ecosystem: could a roving apex predator induce a behaviour-mediated trophic cascade? *Journal of Animal Ecology*. **82**, 1192–1202 (2013).

36. D. B. Rasher, A. S. Hoey, M. E. Hay, Cascading predator effects in a Fijian coral reef ecosystem. *Scientific Reports*. **7**, 1–10 (2017).

37. A. A. Desbiens, G. Roff, W. D. Robbins, B. M. Taylor, C. Castro-Sanguino, A. Dempsey, P. J. Mumby, Revisiting the paradigm of shark-driven trophic cascades in coral reef ecosystems. *Ecology*. **102**, e03303 (2021).

38. G. Roff, C. Doropoulos, A. Rogers, Y.-M. Bozec, N. C. Krueck, E. Aurellado, M. Priest, C. Birrell, P. J. Mumby, The ecological role of sharks on coral reefs. *Trends in Ecology & Evolution*. **31**, 395–407 (2016).

39. D. J. McCauley, H. S. Young, R. B. Dunbar, J. A. Estes, B. X. Semmens, F. Micheli, Assessing the effects of large mobile predators on ecosystem connectivity. *Ecological Applications*. **22**, 1711–1717 (2012).

40. J. J. Williams, Y. P. Papastamatiou, J. E. Caselle, D. Bradley, D. M. Jacoby, Mobile marine predators: an understudied source of nutrients to coral reefs in an unfished atoll. *Proceedings of the Royal Society B: Biological Sciences*. **285**, 20172456 (2018).

41. Y. P. Papastamatiou, C. G. Meyer, R. K. Kosaki, N. J. Wallsgrove, B. N. Popp, Movements and foraging of predators associated with mesophotic coral reefs and their potential for linking ecological habitats. *Marine Ecology Progress Series*. **521**, 155–170 (2015).

42. P. Matich, M. R. Heithaus, Individual variation in ontogenetic niche shifts in habitat use and movement patterns of a large estuarine predator (*Carcharhinus leucas*). *Oecologia*.

178, 347–359 (2015).

43. C. S. Bird, A. Veríssimo, S. Magozzi, K. G. Abrantes, A. Aguilar, H. Al-Reasi, A. Barnett, D. M. Bethea, G. Biais, A. Borrell, M. Bouchoucha, M. Boyle, E. J. Brooks, J. Brunnschweiler, P. Bustamente, A. Carlisle, D. Catarino, S. Caut, Y. Cherel, T. Chouvelon, D. Chirchill, J. Ciancio, J. Claes, A. Colaço, D. L. Courtner, P. Cresson, R. Daly, L. de Necker, T. Endo, I. Figueiredo, A. J. Frisch, J. Holst Hansen, M. Heithaus, N. E. Hussey, J. Iitembu, F. Juanes, M. J. Kinney, D. J. Kiszka, S. A. Klarian, D. Kopp, R. Leaf, Y. Li, A. Lorrain, D. J. Medigan, A. Maljković, L. Malpica-Cruz, P. Matich, M. G. Meekan, F. Ménard, G. M. Menezes, S. E. Munroe, M. C. Newman, Y. P. Papastamatiou, H. Pethybridge, J. D. Plumlee, C. Polo-Silva, K. Quaeck-Davies, V. Raoult, J. T.-R. Y. E. Reum, D. S. Schiffman, O. N. Shipley, C. W. Speed, M. D. Staudinger, A. K. Teffer, A. Tilley, M. Valls, J. J. Vaudo, T.-C. Wai, R. D. Wells, A. S. Wyatt, A. Yool, C. N. Trueman, A global perspective on the trophic geography of sharks. *Nature Ecology & Evolution*, 10 (2018).

44. L. McClenachan, A. B. Cooper, N. K. Dulvy, Rethinking trade-driven extinction risk in marine and terrestrial megafauna. *Current Biology*. **26**, 1640–1646 (2016).

45. A. S. Iliou, W. Vanderwright, L. Harding, D. M. Jacoby, N. L. Payne, N. K. Dulvy, Tail shape and the swimming speed of sharks. *Royal Society Open Science*. **10**, 231127 (2023).

46. N. K. Dulvy, J. D. Metcalfe, J. Glanville, M. G. Pawson, J. D. Reynolds, Fishery stability, local extinctions, and shifts in community structure in skates. *Conservation Biology*. **14**, 283–293 (2000).

47. F. Ferretti, G. C. Osio, C. J. Jenkins, A. A. Rosenberg, H. K. Lotze, Long-term change in a meso-predator community in response to prolonged and heterogeneous human impact. *Scientific Reports*. **3**, 1057 (2013).

48. V. Y. Lam, Y. Sadovy de Mitcheson, The sharks of South East Asia-unknown, unmonitored and unmanaged. *Fish and Fisheries*. **12**, 51–74 (2011).

49. M. Espinoza, T. Araya-Arce, I. Chaves-Zamora, I. Chinchilla, M. Cambra, Monitoring elasmobranch assemblages in a data-poor country from the Eastern Tropical Pacific using baited remote underwater video stations. *Scientific Reports*. **10**, 1–18 (2020).

50. R. P. van der Elst, A proliferation of small sharks in the shore-based Natal sport fishery. *Environmental Biology of Fishes*. **4**, 349–362 (1979).

51. A. B. Haque, R. D. Cavanagh, N. Seddon, Evaluating artisanal fishing of globally threatened sharks and rays in the Bay of Bengal, Bangladesh. *PLoS ONE*. **16**, e0256146 (2021).

52. R. P. Streit, D. R. Bellwood, To harness traits for ecology, let’s abandon “functionality.” *Trends in Ecology & Evolution*. **38**, 402–411 (2022).

53. E. M. Madin, J. S. Madin, D. J. Booth, Landscape of fear visible from space. *Scientific Reports*. **1**, 1–4 (2011).

54. E. M. Madin, K. Precoda, A. R. Harborne, T. B. Atwood, C. M. Roelfsema, O. J. Luiz, Multi-trophic species interactions shape seascape-scale coral reef vegetation patterns. *Frontiers in Ecology and Evolution*. **7**, 102 (2019).

55. V. Christensen, S. Guénette, J. J. Heymans, C. J. Walters, R. Watson, D. Zeller, D. Pauly, Hundred-year decline of North Atlantic predatory fishes. *Fish and Fisheries*. **4**, 1–24 (2003).

56. J. M. Lawson, R. A. Pollom, C. A. Gordon, J. Barker, E. K. Meyers, H. Zidowitz, J. R. Ellis, Á. Bartolí, G. Morey, S. L. Fowler, D. J. Alvarado, S. V. Fordham, R. Sharp, A. R. Hood, N. K. Dulvy, Extinction risk and conservation of critically endangered angel sharks in the Eastern Atlantic and Mediterranean Sea. *ICES Journal of Marine Science*. **77**, 12–29 (2020).

57. C. G. Lowe, M. E. Blasius, E. T. Jarvis, T. J. Mason, G. D. Goodmanlowe, J. B. O’Sullivan, "Historic Fishery Interactions with White Sharks in the Southern California Bight" in *Global Perspectives on the Biology and Life History of the White Shark*, Domeier, Michael L, Ed. (CRC Press, 2012), p. 169.

58. J. M. Anderson, A. J. Clevenstine, B. S. Stirling, E. S. Burns, E. N. Meese, C. F. White, R. K. Logan, J. O’Sullivan, P. T. Rex, J. I. May, K. Lyons, C. Winkler, E. García-Rodríguez, O. Sosa-Nishizaki, C. G. Lowe, Non-random Co-occurrence of Juvenile White Sharks (*Carcharodon carcharias*) at Seasonal Aggregation Sites in Southern California. *Frontiers in Marine Science*, 1095 (2021).

59. S. Larson, D. Lowry, N. K. Dulvy, J. Wharton, F. Galván-Magaña, A. B. Sianipar, C. G. Lowe, E. Meyer, "Current and future considerations for shark conservation in the Northeast and Eastern Central Pacific Ocean" in *Advances in Marine Biology* (Elsevier, 2021), vol. 90, pp. 1–49.

60. A. C. Brown, D. E. Lee, R. W. Bradley, S. Anderson, Dynamics of white shark predation on pinnipeds in California: effects of prey abundance. *Copeia*. **2**, 232–238 (2010).

61. A. De Vos, M. Justin O’Riain, M. A. Meyer, P. G. H. Kotze, A. A. Kock, Behavior of Cape fur seals (*Arctocephalus pusillus pusillus*) in relation to temporal variation in predation risk by white sharks (*Carcharodon carcharias*) around a seal rookery in False Bay, South Africa. *Marine Mammal Science*. **31**, 1118–1131 (2015).

62. T. H. Curtis, C. T. McCandless, J. K. Carlson, G. B. Skomal, N. E. Kohler, L. J. Natanson, G. H. Burgess, J. J. Hoey, H. L. Pratt Jr, Seasonal distribution and historic

trends in abundance of white sharks, Carcharodon carcharias, in the western North Atlantic Ocean. *PloS one*. **9**, e99240 (2014).

63. J. H. Moxley, T. E. Nicholson, K. S. Van Houtan, S. J. Jorgensen, Non-trophic impacts from white sharks complicate population recovery for sea otters. *Ecology and Evolution*. **9**, 6378–6388 (2019).

64. M. T. Tinker, B. B. Hatfield, M. D. Harris, J. A. Ames, Dramatic increase in sea otter mortality from white sharks in California. *Marine Mammal Science*. **32**, 309–326 (2016).

65. T. E. Nicholson, K. A. Mayer, M. M. Staedler, J. A. Fujii, M. J. Murray, A. B. Johnson, M. T. Tinker, K. S. Van Houtan, Gaps in kelp cover may threaten the recovery of California sea otters. *Ecography*. **41**, 1751–1762 (2018).

66. K. A. Mayer, M. T. Tinker, T. E. Nicholson, M. J. Murray, A. B. Johnson, M. M. Staedler, J. A. Fujii, K. S. Van Houtan, Surrogate rearing a keystone species to enhance population and ecosystem restoration. *Oryx*. **55**, 535–545 (2021).

67. T. E. Nicholson, L. McClenachan, K. R. Tanaka, K. S. Van Houtan, Sea otter recovery buffers century-scale declines in California kelp forests. *PLOS Climate*. **3**, e0000290 (2024).

68. J. G. Smith, J. Tomoleoni, M. Staedler, S. Lyon, J. Fujii, M. T. Tinker, Behavioral responses across a mosaic of ecosystem states restructure a sea otter-urchin trophic cascade. *Proceedings of the National Academy of Sciences*. **118**, e2012493118 (2021).

69. B. B. Hughes, K. M. Beheshti, M. T. Tinker, C. Angelini, C. Endris, L. Murai, S. C. Anderson, S. Espinosa, M. Staedler, J. A. Tomoleoni, M. Sanchez, B. R. Silliman, Top-predator recovery abates geomorphic decline of a coastal ecosystem. *Nature*. **626**, 111–118 (2024).

70. B. B. Hughes, R. Eby, E. Van Dyke, M. T. Tinker, C. I. Marks, K. S. Johnson, K. Wasson, Recovery of a top predator mediates negative eutrophic effects on seagrass. *Proceedings of the National Academy of Sciences*. **110**, 15313–15318 (2013).

71. J.-B. Jouffray, R. Blasiak, A. V. Norström, H. Österblom, M. Nyström, The blue acceleration: the trajectory of human expansion into the ocean. *One Earth*. **2**, 43–54 (2020).

72. A. B. Gill, J. A. Kimber, The potential for cooperative management of elasmobranchs and offshore renewable energy development in UK waters. *Journal of the Marine Biological Association of the UK*. **85**, 1075–1081 (2005).

73. C. M. Duarte, L. Chapuis, S. P. Collin, D. P. Costa, R. P. Devassy, V. M. Eguiluz, C. Erbe, T. A. Gordon, B. S. Halpern, H. R. Harding, M. N. Havlik, M. Meekan, N. D. Merchant, J. L. Miksis-Olds, M. Parsons, M. Predragovic, A. N. Radford, C. A. Radford,

S. D. Simpson, H. Slabbekoorn, E. Staaterman, I. C. Van Opzeeland, J. Winderen, X. Zhang, F. Juanes, The soundscape of the Anthropocene ocean. *Science*. **371**, eaba4658 (2021).

74. B. Bruce, R. Bradford, S. Foster, K. Lee, M. Lansdell, S. Cooper, R. Przeslawski, Quantifying fish behaviour and commercial catch rates in relation to a marine seismic survey. *Marine Environmental Research*. **140**, 18–30 (2018).

75. J. B. Haugen, Y. Papastamatiou, Observation of a porbeagle shark *Lamna nasus* aggregation at a North Sea oil platform. *Journal of Fish Biology*. **95**, 1496–1499 (2019).

76. D. P. Robinson, M. Y. Jaidah, R. W. Jabado, K. Lee-Brooks, N. M. Nour El-Din, A. A. Al Malki, K. Elmeer, P. A. McCormick, A. C. Henderson, S. J. Pierce, R. F. G. Ormond, Whale sharks, *Rhincodon typus*, aggregate around offshore platforms in Qatari waters of the Arabian Gulf to feed on fish spawn. *PLoS ONE*. **8**, e58255 (2013).

77. F. C. Womersley, N. E. Humphries, N. Queiroz, M. Vedor, I. da Costa, M. Furtado, J. P. Tyminski, K. Abrantes, G. Araujo, S. S. Bach, A. Barnett, M. L. Berumen, S. B. Lion, C. D. Braun, E. Clingham, J. E. M Cochran, R. D. La Parra, S. Diamant, A. D. M Dove, C. L. Dudgeon, M. V. Erdmann, E. Espinoza, R. Fitzpatrick, J. G. Cano, J. R. Green, H. M. Guzman, R. Hardenstine, A. Hasan, F. H. V Hazin, A. R. Hearn, R. E. Hueter, M. Y. Jaidah, J. Labaja, F. Ladino, B. C. L Macena, J. J. Morris Jr, B. M. Norman, C. Peñaherrera-Palma, S. J. Pierce, L. M. Quintero, D. Ramírez-Macías, S. D. Reynolds, A. J. Richardson, D. P. Robinson, C. A. Rohner, D. R. L Rowat, M. Sheaves, M. S. Shivji, A. B. Sianipar, G. B. Skomal, G. Soler, I. Syakurachman, S. R. Thorrold, D. H. Webb, B. M. Wetherbee, T. D. White, T. Clavelle, D. A. Kroodsma, M. Thums, L. C. Ferreira, M. G. Meekan, L. M. Arrowsmith, E. K. Lester, M. M. Meyers, L. R. Peel, A. M. M Sequeira, V. M. Eguíluz, C. M. Duarte, D. W. Sims, Global collision-risk hotspots of marine traffic and the world’s largest fish, the whale shark. *Proceedings of the National Academy of Sciences*. **119**, e2117440119 (2022).

78. P. F. Brena, J. Mourier, S. Planes, E. Clua, Shark and ray provisioning: functional insights into behavioral, ecological and physiological responses across multiple scales. *Marine Ecology Progress Series*. **538**, 273–283 (2015).

79. A. J. Gallagher, G. M. Vianna, Y. P. Papastamatiou, C. Macdonald, T. L. Guttridge, N. Hammerschlag, Biological effects, conservation potential, and research priorities of shark diving tourism. *Biological Conservation*. **184**, 365–379 (2015).

80. Y. P. Papastamatiou, D. G. Itano, J. J. Dale, C. G. Meyer, K. N. Holland, Site fidelity and movements of sharks associated with ocean-farming cages in Hawaii. *Marine and Freshwater Research*. **61**, 1366–1375 (2010).

81. B. S. Rangel, N. Hammerschlag, L. A. Martinelli, R. G. Moreira, Effects of urbanization on the nutritional ecology of a highly active coastal shark: Preliminary insights from trophic markers and body condition. *Science of The Total Environment*. **826**, 154082

(2022).

82. D. E. Jennings, S. H. Gruber, B. R. Franks, S. T. Kessel, A. L. Robertson, Effects of large-scale anthropogenic development on juvenile lemon shark (*Negaprion brevirostris*) populations of Bimini, Bahamas. *Environmental Biology of Fishes*. **83**, 369–377 (2008).

83. J. D. Mitchell, J. Drymon, J. Vardon, P. Coulson, C. Simpfendorfer, S. Scyphers, S. Kajiura, K. Hoel, S. Williams, K. Ryan, A. Barnett, M. R. Heupel, A. Chin, M. Navarro, T. Langlois, M. J. Ajemian, E. Gilman, E. Prasky, G. Jackson, Shark depredation: future directions in research and management. *Reviews in Fish Biology and Fisheries*, 1–25 (2022).

84. P. J. Mumby, A. R. Harborne, D. R. Brumbaugh, Grouper as a natural biocontrol of invasive lionfish. *PLoS ONE*. **6**, e21510 (2011).

85. A. V. Towner, A. A. Kock, C. Stopforth, D. Hurwitz, S. H. Elwen, Direct observation of killer whales preying on white sharks and evidence of a flight response. *Ecology*, e3875 (2022).

86. S. J. Jorgensen, S. Anderson, F. Ferretti, J. R. Tietz, T. Chapple, P. Kanive, R. W. Bradley, J. H. Moxley, B. A. Block, Killer whales redistribute white shark foraging pressure on seals. *Scientific Reports*. **9**, 6153 (2019).

87. C. W. Speed, M. Cappo, M. G. Meekan, Evidence for rapid recovery of shark populations within a coral reef marine protected area. *Biological Conservation*. **220**, 308–319 (2018).

88. T. H. Bullock, J. T. Corwin, Acoustic evoked activity in the brain in sharks. *How do Brains Work? Papers of a Comparative Neurophysiologist*, 437–448 (1993).

89. L. Velasquez Jimenez, E. P. Fakan, M. I. McCormick, Vessel noise affects routine swimming and escape response of a coral reef fish. *PLoS ONE*. **15**, e0235742 (2020).

90. C. Huveneers, P. J. Rogers, C. Beckmann, J. M. Semmens, B. D. Bruce, L. Seuront, The effects of cage-diving activities on the fine-scale swimming behaviour and space use of white sharks. *Marine Biology*. **160**, 2863–2875 (2013).

91. J. M. Brunnschweiler, K. G. Abrantes, A. Barnett, Long-term changes in species composition and relative abundances of sharks at a provisioning site. *PLoS ONE*. **9**, e86682 (2014).

92. A. Maljkovic, I. M. Côté, Effects of tourism-related provisioning on the trophic signatures and movement patterns of an apex predator, the Caribbean reef shark. *Biological Conservation*. **144**, 859–865 (2011).

93. A. Maljkovic, Non-lethal human-shark interactions and their ecological consequences. Ph.D. Thesis, Simon Fraser University. Burnaby, British Columbia, Canada (2018).

94. T. M. Newsome, J. A. Dellinger, C. R. Pavey, W. J. Ripple, C. R. Shores, A. J. Wirsing, C. R. Dickman, The ecological effects of providing resource subsidies to predators. *Global Ecology and Biogeography*. **24**, 1–11 (2015).

95. A. J. Wirsing, M. R. Heithaus, J. S. Brown, B. P. Kotler, O. J. Schmitz, The context dependence of non-consumptive predator effects. *Ecology Letters*. **24**, 113–129 (2021).

96. M. R. Heithaus, T. Alcoverro, R. Arthur, D. A. Burkholder, K. A. Coates, M. J. Christianen, N. Kelkar, S. A. Manuel, A. J. Wirsing, W. J. Kenworthy, J. W. Fourqurean, Seagrasses in the age of sea turtle conservation and shark overfishing. *Frontiers in Marine Science*. **1**, 28 (2014).

97. J. W. Fourqurean, S. A. Manuel, K. A. Coates, S. C. Massey, W. J. Kenworthy, Decadal monitoring in Bermuda shows a widespread loss of seagrasses attributable to overgrazing by the green sea turtle *Chelonia mydas*. *Estuaries and Coasts*. **42**, 1524–1540 (2019).

98. D. F. Doak, J. A. Estes, B. S. Halpern, U. Jacob, D. R. Lindberg, J. Lovvorn, D. H. Monson, M. T. Tinker, T. M. Williams, J. T. Wootton, I. Carroll, M. Emmerson, F. Micheli, M. Novak, Understanding and predicting ecological dynamics: are major surprises inevitable? *Ecology*. **89**, 952–61 (2008).

99. P. J. Burton, A. Jentsch, L. R. Walker, The ecology of disturbance interactions. *BioScience*. **70**, 854–870 (2020).

100. A. V. Towner, R. Watson, A. A. Kock, Y. Papastamatiou, M. Sturup, E. Gennari, K. Baker, T. Booth, M. Dicken, W. Chivell, S. Elwen, T. Kaschke, D. Edwards, M. Smale, Fear at the top: killer whale predation drives white shark absence at South Africa's largest aggregation site. *African Journal of Marine Science*. **44**, 139–152 (2022).

101. N. Hammerschlag, L. Williams, M. Fallows, C. Fallows, Disappearance of white sharks leads to the novel emergence of an allopatric apex predator, the sevengill shark. *Scientific Reports*. **9**, 1–6 (2019).

102. T. M. Engelbrecht, A. A. Kock, M. J. O'Riain, Running scared: when predators become prey. *Ecosphere*. **10**, e02531 (2019).

103. J. L. Rummer, I. A. Bouyoucos, C. R. Wheeler, C. P. Santos, R. Rosa, "Climate Change and Sharks" in *Biology of Sharks and Their Relatives, Third Edition*, Carrier, Jeffrey C and Simpfendorfer, Colin C and Heithaus, Michael R and Yopak, Kara E, Ed. (CRC Press, 2022), vol. 3, pp. 767–793.

104. K. O. Lear, D. L. Morgan, J. M. Whitty, N. M. Whitney, E. E. Byrnes, S. J. Beatty, A. C. Gleiss, Divergent field metabolic rates highlight the challenges of increasing temperatures

and energy limitation in aquatic ectotherms. *Oecologia*. **193**, 311–323 (2020).

105. N. L. Payne, C. G. Meyer, J. A. Smith, J. D. Houghton, A. Barnett, B. J. Holmes, I. Nakamura, Y. P. Papastamatiou, M. A. Royer, D. M. Coffey, J. M. Anderson, M. R. Hutchinson, K. Sato, L. G. Halsey, Combining abundance and performance data reveals how temperature regulates coastal occurrences and activity of a roaming apex predator. *Global Change Biology*. **24**, 1884–1893 (2018).

106. C. F. White, K. Lyons, S. J. Jorgensen, J. O'Sullivan, C. Winkler, K. C. Weng, C. G. Lowe, Quantifying habitat selection and variability in habitat suitability for juvenile white sharks. *PLoS ONE*. **14**, e0214642 (2019).

107. A. I. Dell, S. Pawar, V. M. Savage, Temperature dependence of trophic interactions are driven by asymmetry of species responses and foraging strategy. *Journal of Animal Ecology*. **83**, 70–84 (2014).

108. J. P. Gibert, J. M. Grady, A. I. Dell, Food web consequences of thermal asymmetries. *Functional Ecology*. **36**, 1887–1899 (2022).

109. A. Hasenei, J. M. Donelson, T. Ravasi, J. L. Rummer, Sharks and their relatives: can their past help predict their future? *Frontiers in Marine Science* (2023), doi:10.3389/fmars.2023.1268532.

110. J. M. Grady, B. S. Maitner, A. S. Winter, K. Kaschner, D. P. Tittensor, S. Record, F. A. Smith, A. M. Wilson, A. I. Dell, P. L. Zarnetske, H. J. Wearing, B. Alfaro, J. H. Brown, Metabolic asymmetry and the global diversity of marine predators. *Science*. **363**, eaat4220 (2019).

111. Y. Y. Watanabe, K. J. Goldman, J. E. Caselle, D. D. Chapman, Y. P. Papastamatiou, Comparative analyses of animal-tracking data reveal ecological significance of endothermy in fishes. *Proceedings of the National Academy of Sciences*. **112**, 6104–6109 (2015).

112. C. W. Bangley, L. Paramore, D. S. Shiffman, R. A. Rulifson, Increased abundance and nursery habitat use of the bull shark (*Carcharhinus leucas*) in response to a changing environment in a warm-temperate estuary. *Scientific Reports*. **8**, 1–10 (2018).

113. K. R. Tanaka, K. S. Van Houtan, E. Mailander, B. S. Dias, C. Galginaitis, J. O'Sullivan, C. G. Lowe, S. J. Jorgensen, North Pacific warming shifts the juvenile range of a marine apex predator. *Scientific Reports*. **11**, 1–9 (2021).

114. J. E. Campbell, O. Kennedy Rhoades, C. J. Munson, A. H. Altieri, J. G. Douglass, K. L. Heck, V. J. Paul, A. R. Armitage, S. C. Barry, E. Bethel, L. Christ, M. J. Christianen, G. Dodillet, K. Dutton, J. W. Fourqurean, T. K. Frazer, B. M. Gaffey, R. Glazner, J. A. Goeke, R. Grana-Valdes, V. J. Jenkins, O. A. Kramer, S. T. Linhardt, C. W. Martin, I. G. Martinez Lopez, A. M. Mcdonald, V. A. Main, S. A. Manuel, C. Marco-Méndez, D. A.

O’Brien, O. R. O’Shea, C. J. Patrick, C. Peabody, L. K. Reynolds, A. Rodriguez, L. M. Rodriguez Bravo, A. Sang, Y. Sawall, K. Smith, F. O. Smulders, U. Sun, J. E. Thompson, B. V. Tussenbroek, W. L. Wied, Herbivore effects increase with latitude across the extent of a foundational seagrass. *Nature ecology \& evolution*, 1–13 (2024).

115. D. Bianchi, E. D. Galbraith, D. A. Carozza, K. Mislan, C. A. Stock, Intensification of open-ocean oxygen depletion by vertically migrating animals. *Nature Geoscience*. **6**, 545–548 (2013).

116. L. Stramma, E. D. Prince, S. Schmidtko, J. Luo, J. P. Hoolihan, M. Visbeck, D. W. Wallace, P. Brandt, A. Körtzinger, Expansion of oxygen minimum zones may reduce available habitat for tropical pelagic fishes. *Nature Climate Change*. **2**, 33 (2012).

117. D. M. Coffey, M. A. Royer, C. G. Meyer, K. N. Holland, Diel patterns in swimming behavior of a vertically migrating deepwater shark, the bluntnose sixgill (*Hexanchus griseus*). *PLoS ONE*. **15**, e0228253 (2020).

118. C. D. Braun, M. C. Arostegui, S. R. Thorrold, Y. P. Papastamatiou, P. Gaube, J. Fontes, P. Afonso, The functional and ecological significance of deep diving by large marine predators. *Annual Review of Marine Science*. **14**, 129–159 (2022).

119. Y. P. Papastamatiou, Y. Y. Watanabe, U. Demšar, V. Leos-Barajas, D. Bradley, R. Langrock, K. Weng, C. G. Lowe, A. M. Friedlander, J. E. Caselle, Activity seascapes highlight central place foraging strategies in marine predators that never stop swimming. *Movement Ecology*. **6**, 1–15 (2018).

120. G. Le Croizier, A. Lorrain, J. E. Sonke, E. M. Hoyos-Padilla, F. Galván-Magaña, O. Santana-Morales, M. Aquino-Baleytó, E. E. Becerril-García, G. Muntaner-López, J. Ketchum, B. A. Block, A. Carlisle, S. J. Jorgenson, L. Besnard, A. Jung, G. Schaal, D. Point, The twilight zone as a major foraging habitat and mercury source for the great white shark. *Environmental Science & Technology*. **54**, 15872–15882 (2020).

121. L. Alvarez-Filip, J. Gill, N. Dulvy, A. Perry, A. Watkinson, I. Côté, Drivers of region-wide declines in architectural complexity on Caribbean reefs. *Coral Reefs*. **30**, 1051–1060 (2011).

122. N. A. Graham, K. L. Nash, The importance of structural complexity in coral reef ecosystems. *Coral Reefs*. **32**, 315–326 (2013).

123. A. Rogers, J. L. Blanchard, P. J. Mumby, Fisheries productivity under progressive coral reef degradation. *Journal of Applied Ecology*. **55**, 1041–1049 (2018).

124. E. K. Lester, T. J. Langlois, S. Simpson, M. McCormick, M. G. Meekan, Reef-wide evidence that the presence of sharks modifies behaviors of teleost mesopredators. *Ecosphere*. **12**, e03301 (2021).

125. E. M. Madin, L. M. Dill, A. D. Ridlon, M. R. Heithaus, R. R. Warner, Human activities change marine ecosystems by altering predation risk. *Global Change Biology*. **22**, 44–60 (2016).

126. H. Booth, D. Squires, E. Milner-Gulland, The neglected complexities of shark fisheries, and priorities for holistic risk-based management. *Ocean & Coastal Management*. **182**, 104994 (2019).

127. M. K. Grace, H. R. Akçakaya, E. L. Bennett, T. M. Brooks, A. Heath, S. Hedges, C. Hilton-Taylor, M. Hoffmann, A. Hochkirch, R. Jenkins, D. A. Keith, B. Long, D. P. Mallon, E. Meijaard, E. Milner-Gulland, J. P. Rodriguez, P. Stephenson, S. N. Stuart, R. P. Young, P. Acebes, J. Alfaro-Shigueto, S. Alvarez-Clare, R. R. Andriantsimanarilafy, M. Arbetman, C. Azat, G. Bacchetta, R. Badola, L. M. Barcelos, J. P. Barreiros, S. Basak, D. J. Berger, S. Bhattacharyya, G. Bino, P. A. Borges, R. K. Boughton, H. J. Brockmann, H. L. Buckley, I. J. Burfield, J. Burton, T. Camacho-Badani, L. S. Cano-Alonso, R. H. Carmichael, C. Carrero, J. P. Carroll, G. Catsadorakis, D. G. Chapple, G. Chapron, G. W. Chowdhury, L. Claassens, D. Cogoni, R. Constantine, C. A. Craig, A. A. Cunningham, N. Dahal, J. C. Daltry, G. C. Das, N. Dasgupta, A. Davey, K. Davies, P. Develey, V. Elangovan, D. Fairclough, M. Di Febbraro, G. Fenu, F. M. Fernandes, E. P. Fernandez, B. Finucci, R. Földesi, C. M. Foley, M. Ford, M. R. Forstner, N. García, R. Garcia-Sandoval, P. C. Gardner, R. Garibay-Orijel, M. Gatan-Balbas, I. Gauto, M. G. U. Ghazi, S. S. Godfrey, M. Gollock, B. A. González, T. D. Grant, T. Gray, A. J. Gregory, R. H. van Grunsven, M. Gryzenhout, N. C. Guernsey, G. Gupta, C. Hagen, C. A. Hagen, M. B. Hall, E. Hallerman, K. Hare, T. Hart, R. Hartdegen, Y. Harvey-Brown, R. Hatfield, T. Hawke, C. Hermes, R. Hitchmough, P. M. Hoffmann, C. Howarth, M. A. Hudson, S. A. Hussain, C. Huveneers, H. Jacques, D. Jorgensen, S. Katdare, L. K. Katsis, R. Kaul, B. Kaunda-Arara, L. Keith-Diagne, D. T. Kraus, T. M. de Lima, K. Lindeman, J. Linsky, E. Louis Jr., A. Loy, E. Nic Lughadha, J. C. Mange, P. E. Marinari, G. M. Martin, G. Martinelli, P. J. McGowan, A. McInnes, E. T. B. Mendes, M. J. Millard, C. Mirande, D. Money, J. M. Monks, C. L. Morales, N. N. Mumu, R. Negrao, A. H. Nguyen, M. N. H. Niloy, G. L. Norbury, C. Nordmeyer, D. Norris, M. O’Brien, G. A. Oda, S. Orsenigo, M. E. Outerbridge, S. Pasachnik, J. C. Pérez-Jiménez, C. Pike, F. Pilkington, G. Plumb, R. de C. Q. Portela, A. Prohaska, M. G. Quintana, E. F. Rakotondrasoa, D. H. Ranglack, H. Rankou, A. P. Rawa, J. T. Reardon, M. L. Rheingantz, S. C. Richter, M. C. Rivers, L. R. Rogers, P. da Rosa, P. Rose, E. Royer, C. Ryan, Y. J. S. de Mitcheson, L. Salmon, C. H. Salvador, M. J. Samways, T. Sanjuan, A. S. dos Santos, H. Sasaki, E. Schutz, H. A. Scott, R. M. Scott, F. Serena, S. P. Sharma, J. A. Shuey, C. J. P. Silva, J. P. Simaika, D. R. Smith, J. L. Spaet, S. Sultana, B. K. Talukdar, V. Tatayah, P. Thomas, A. Tringali, H. Trinh-Dinh, C. Tuboi, A. A. Usmani, A. M. Vasco-Palacios, J.-C. Vié, E. Virens, A. Walker, B. Wallace, L. J. Waller, H. Wang, O. R. Wearn, M. van Weerd, S. Weigmann, D. Willcox, J. Woinarski, J. W. Yong, S. Young, Testing a global standard for quantifying species recovery and assessing conservation impact. *Conservation Biology*. **35**, 1833–1849 (2021).

128. L. N. Davidson, N. K. Dulvy, Global marine protected areas to prevent extinctions. *Nature Ecology & Evolution*. **1**, 0040 (2017).

129. C. A. Simpfendorfer, N. K. Dulvy, Bright spots of sustainable shark fishing. *Current Biology*. **27**, R97–R98 (2017).

130. J. Goetze, M. Heithaus, M. MacNeil, E. Harvey, C. Simpfendorfer, M. Heupel, M. Meekan, S. Wilson, M. Bond, C. Speed, L. Currey-Randall, R. Fisher, C. Sherman, J. Kiszka, M. Rees, V. Udyawer, K. Flowers, G. Clementi, J. Asher, O. Beaufort, A. Bernard, M. Berumen, S. Bierwagen, T. Boslogo, E. Brooks, J. Brown, D. Buddo, C. Cáceres, S. Casareto, V. Charloo, J. Cinner, E. Clua, J. Cochran, N. Cook, B. D'Alberto, M. de Graaf, M. Dornhege, L. Fanovich, N. Farabaugh, D. Fernando, C. Ferreira, C. Fields, A. Flam, C. Floros, V. Fourqurean, L. García Barcia, R. Garla, K. Gastrich, L. George, R. Graham, V. Hagan, R. Hardenstine, S. Heck, P. Heithaus, A. Henderson, H. Hertler, R. Hueter, M. Johnson, S. Jupiter, M. Kaimuddin, D. Kasana, M. Kelley, S. Kessel, B. Kiilu, F. Kyne, T. Langlois, E. Lédée, S. Lindfield, J. Maggs, B. Manjaji-Matsumoto, A. Marshall, P. Matich, E. McCombs, D. McLean, Meggs, S. Moore, S. Mukherji, R. Murray, S. Newman, O. O'Shea, K. Osuka, Y. Papastamatiou, N. Perera, B. Peterson, F. Pina-Amargós, A. Ponzo, A. Prasetyo, L. Quamar, J. Quinlan, F. Rolim, A. Ruiz-Abierno, H. Ruiz, M. Samoilys, E. Sala, W. Sample, M. Schärer-Umpierre, S. Schoen, A. Schlaff, A. Smith, L. Sparks, T. Stoffers, A. Tanna, R. Torres, M. Travers, J. Valentin-Albanese, J. Warren, A. Watts, C. Wen, E. Whitman, A. Wirsing, E. Zarza-González, D. Chapman, Directed conservation of the world's reef sharks and rays. *Nature Ecology & Evolution*. **In Press** (2024).

131. M. J. Juan-Jordá, H. Murua, H. Arrizabalaga, N. K. Dulvy, V. Restrepo, Report card on ecosystem-based fisheries management in tuna regional fisheries management organizations. *Fish and Fisheries*. **19**, 321–339 (2018).

132. D. J. McCauley, P. Woods, B. Sullivan, B. Bergman, C. Jablonicky, A. Roan, M. Hirshfield, K. Boerder, B. Worm, Ending hide and seek at sea. *Science*. **351**, 1148–1150 (2016).

133. F. Paolo, D. Kroodsma, J. Raynor, T. Hochberg, P. Davis, J. Cleary, L. Marsaglia, S. Orofino, C. Thomas, P. Halpin, Satellite mapping reveals extensive industrial activity at sea. *Nature*. **625**, 85–91 (2024).

134. A. T. van Helmond, L. O. Mortensen, K. S. Plet-Hansen, C. Ulrich, C. L. Needle, D. Oesterwind, L. Kindt-Larsen, T. Catchpole, S. Mangi, C. Zimmermann, H. J. Olesen, N. Bailey, H. Bergsson, J. Dalskov, J. Elson, M. Hosken, L. Peterson, H. Mcelderry, J. Ruiz, J. P. Pierre, C. Dykstra, J. J. Poos, Electronic monitoring in fisheries: lessons from global experiences and future opportunities. *Fish and Fisheries*. **21**, 162–189 (2020).

135. FAO, Agreement on Port State Measures to Prevent, Deter and Eliminate Illegal, Unreported and Unregulated Fishing (2017).

136. L. M. Feitosa, A. P. B. Martins, T. Giarrizzo, W. Macedo, I. L. Monteiro, R. Gemaque, J. L. S. Nunes, F. Gomes, H. Schneider, I. Sampaio, R. Souza, J. B. Sales, L. F. Rodrigues-Filho, L. Tchaicka, L. F. Carvalho-Costa, DNA-based identification reveals illegal trade of threatened shark species in a global elasmobranch conservation hotspot. *Scientific reports*. **8**, 3347 (2018).

137. D. Bradley, J. Mayorga, D. J. McCauley, R. B. Cabral, P. Douglas, S. D. Gaines, Leveraging satellite technology to create true shark sanctuaries. *Conservation Letters*. **12**, e12610 (2019).

138. C. A. Simpfendorfer, M. R. Heupel, D. Kendal, Complex human-shark conflicts confound conservation action. *Frontiers in Conservation Science*, 35 (2021).

139. A. Chin, P. M. Kyne, T. I. Walker, R. B. McAuley, An integrated risk assessment for climate change: analysing the vulnerability of sharks and rays on Australia's Great Barrier Reef. *Global Change Biology*. **16**, 1936–1953 (2010).

140. I. Giovos, A. Barash, M. Barone, C. Barría, D. Borme, C. Brigaudeau, A. Charitou, C. Brito, J. Currie, M. Dornhege, L. Endrizzil, K. Forsberg, A. Jung, P. Kleitou, A. Macdiarmid, D. K. Moutopoulos, S. Nakagun, J. Neves, F. L. D. Nunes, D. Schröder, R. H. Thurstan, M. Tull, S. Tuncer, C. Mazzoldi, Understanding the public attitude towards sharks for improving their conservation. *Marine Policy*. **134**, 104811 (2021).

141. J. Neves, T. McGinnis, J.-C. Giger, Changing trends: Beliefs and attitudes toward sharks and implications for conservation. *Ethnobiology and Conservation*. **11** (2022), doi:10.15451/ec2022-05-11.11-1-11.

142. C. Folke, T. Hahn, P. Olsson, J. Norberg, Adaptive governance of social-ecological systems. *Annual Review of Environmental Resources*. **30**, 441–473 (2005).

143. R. B. Anderson, Beyond "Success": community, governance, and the future of Cabo Pulmo National park. *Human Organization*. **78**, 147–157 (2019).

144. R. A. Skubel, M. Shriver-Rice, G. Maranto, Introducing relational values as a tool for shark conservation, science, and management. *Frontiers in Marine Science*. **6**, 53 (2019).

145. J. M. Burt, K. B. J. Wilson, T. Malchoff, W. A. Mack, S. H. A. Davidson, A. K. Salomon, Enabling coexistence: Navigating predator-induced regime shifts in human-ocean systems. *People and Nature*. **2**, 557–574 (2020).

146. B. M. Wetherbee, C. G. Lowe, G. L. Crow, A review of shark control in Hawaii with recommendations for future research (1994).

147. S. Whitcraft, A. Hofford, P. Hilton, M. O'Malley, V. Jaiteh, P. Knights, Evidence of declines in shark fin demand, China. *San Francisco: WildAid*, 21 (2014).

148. B. Finucci, N. Pacoureau, C. L. Rigby, J. H. Matsushiba, N. Faure-Beaulieu, C. S. Sherman, W. J. Vanderwright, R. W. Jabado, P. Charvet, P. A. Mejía-Falla, A. F. Navia, D. H. Derrick, P. M. Kyne, R. A. Pollom, R. H. L Walls, K. B. Herman, B. Kinattumkara, C. F. Cotton, J.-M. Cuevas, R. K. Daley, Dharmadi, D. A. Ebert, D. Fernando, S. M. C Fernando, M. P. Francis, C. Huveneers, H. Ishihara, D. W. Kulka, R. W. Leslie, F. Neat, A. M. Orlov, G. Rincon, G. J. Sant, I. V. Volvenko, T. I. Walker, C. A. Simpfendorfer, N. K. Dulvy, Fishing for oil and meat drives irreversible defaunation of deepwater sharks and rays. *Science*. **383**, 1135–1141 (2024).

149. J. Finger, T. Guttridge, A. Wilson, S. Gruber, J. Krause, Are some sharks more social than others? Short-and long-term consistencies in the social behavior of juvenile lemon sharks. *Behavioral Ecology and Sociobiology*. **72**, 1–10 (2018).

150. P. A. Biro, J. R. Post, Rapid depletion of genotypes with fast growth and bold personality traits from harvested fish populations. *Proceedings of the National Academy of Sciences*. **105**, 2919–2922 (2008).

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List of Supplementary Materials

***Figure S1. Potential effects of climate change on the ecological role of sharks**. A) Thermal performance curve relating animals' fitness in relation to water temperature. Optimal temperature for fitness is nested between critical minimum/maximum temperatures for survival. B) Thermal performance curve fitted to swimming activity of tiger sharks measured via biologgers. Larger circles represent higher density of tiger shark activity at that water temperature* (103). *C) Effects of water pH and temperature on the time taken to accept prey in Port Jackson shark* (150). *D) Swimming activity of sixgill shark as a function of depth and oxygen saturation, as determined by biologgers. Red designates high activity percentages* (113).

***Table S1: Published studies regarding ecological roles of sharks.** Published studies regarding ecological roles of sharks, with location, shark species, ecosystem, other species involved, evidence type,* *effect size and strength of evidence for nine types of top-down, guild interaction, and bottom-up effects, plus blue carbon implications, as well as unique ID for paper reference in Sharkipedia.org.*

Figures and Tables

Figure 1. Estimated abundance declines of sharks across data sources and time scales*. A) Millennial-scale changes in relative reef shark abundance. i: Perceived abundance of sharks in Caribbean Panama inferred from archaeological, historical, ecological, and fisheries records (based on* (14)*). 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% CI;* (21)*) and number of global coral reefs (green histogram; vertical dotted lines are quartiles* (22)*) along a gradient of human pressure (total gravity* (19, 22)*). 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 ((*22) *models set human-related variables to zero). Expected relative abundance was estimated using MaxN measurements from 371 reefs globally* (21).

Figure 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 (e.g., direct predation, risk effects) and bottom-up (e.g., food provisioning, nutrient cycling) processes, and species interactions (e.g., competition and facilitation). Only interactions involving sharks are displayed.*

Figure 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 = effect type; saturation = effect strength; hatched/solid = inferred/empirical evidence. B: Alluvial plot of studied ecotypes and ecological roles of sharks, and their strength of evidence from table S1 studies. Competition and/or bottom-up processes binned due to small sample size. Effect size and strength of evidence rated by 30 investigators' expert opinions scoring source paper metrics on a low/medium/high scale. * = Macropredatory sharks: Pelagic. BU = bottom up, NVS = nutrient vector / storage, SAF = sharks as food, EAE = excretion and egestion.*

Figure 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/green) rapidly at low abundances, (ii/blue) linearly, or (iii/orange, iv/purple) slowly until reaching thresholds, or (v/black) 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.*

Figure 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* (55)*, especially larger elasmobranchs* (46, 56)*. Similar declines occurred in the Mediterranean Sea* (47)*, and Bay of Bengal* (51)*. Smaller elasmobranch species abundances have risen* (16, 46)*, suggesting larger species suppress smaller species through predation and competition. B) Species richness and abundance of sharks decreases along a gradient of market gravity (human impact), along with traits influencing 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 from* (3, 20, 45)*. C) Indirect effects of predation pressure are documented in grazing patterns ('halos'* (53)*) adjacent to patch reefs. Reductions in predation pressure, including depletions of sharks, influence safe distances for herbivorous fish in habitats adjacent to reef* (54)*. With little risk herbivorous fish feed further from reefs leading to reduced primary producer biomass* (53) *and sedimentary carbon stores* (34).

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 involving sharks in coastal and offshore environments.*