

Review

Ecosystem Function and Services of Aquatic Predators in the Anthropocene

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Arguments for the need to conserve aquatic predator (AP) populations often focus on the ecological and socioeconomic roles they play. Here, we summarize the diverse ecosystem functions and services connected to APs, including regulating food webs, cycling nutrients, engineering habitats, transmitting diseases/parasites, mediating ecological invasions, affecting climate, supporting fisheries, generating tourism, and providing bioinspiration. In some cases, human-driven declines and increases in AP populations have altered these ecosystem functions and services. We present a social ecological framework for supporting adaptive management decisions involving APs in response to social and environmental change. We also identify outstanding questions to guide future research on the ecological functions and ecosystem services of APs in a changing world.

Highlights

APs contribute to various ecosystem functions and services.

AP population declines and increases can lead to alterations in these processes.

Research priorities remain, including effects of climate change.

Application of a social ecological framework can support adaptive management of APs.

The Functional Role of APs in the Anthropocene

Upper-trophic-level predators are ecologically, economically, and culturally important [1–3]. However, many marine and freshwater predators have declined across their range [4–7]. This has sparked efforts to conserve and manage aquatic species, which have resulted in some population rebounds [8,9]. Accordingly, we sought to understand the ecological, evolutionary, and socioeconomic roles played by APs and the consequences of their population declines and increases on social and ecological systems.

Most reviews describing the **ecological roles** (see [Glossary](#)) of APs have focused on food web dynamics involving marine megafauna [10,11]. Yet even smaller APs, particularly in freshwater environments, can affect food webs. Growing evidence further suggests that APs are directly and indirectly connected to several other **ecosystem functions**, including nutrient and carbon cycling [12,13], habitat modification [14,15], disease transmission [16], and invasion by exotic species [17,18]. Moreover, APs are linked to **socioecological systems** (SESs) that encompass relationships between humans and the environment [19]. Indeed, APs provide diverse **ecosystem services**, including tourism (e.g., whale watching, shark diving; [20]) and food security [21], as well as the jobs that depend on them. Less obvious is that APs can help mitigate climate change [22,23] and lead to **bioinspired materials** and products that benefit human wellbeing [24].

In the sections that follow, we review the ecological roles that APs provide for ecosystem functioning and the attendant ecosystem services they afford to humans (Figure 1). We provide examples of ecosystem consequences arising from human-driven declines and increases in AP populations (Table 1 and Box 1). We also describe how SESs can be used as a resource

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management tool to help guide adaptive decision-making involving APs in response to social and environmental change (Box 2). Finally, we identify outstanding questions to guide future research (see Outstanding Questions).

We consider APs to be animals that hunt at tertiary or greater trophic levels within aquatic systems including oceans, bays, estuaries, rivers, streams, lakes, and wetlands. We note upfront that some of the ecosystem functions and services reviewed here are not exclusive to APs, nor should they be ubiquitously attributed to all APs and/or in all contexts. Indeed, a key research priority is to understand the extent to which APs affect ecosystem functions and services. We also note that many of the direct and indirect effects of APs on ecosystem functioning also yield ecosystem services.

Controlling Food Webs

APs can influence food webs through their **consumptive effects** on prey. Associated reductions in prey populations can initiate **trophic cascades** within and across ecosystems [25]. For example, when predatory largemouth bass (*Micropterus salmoides*) are introduced to lakes within Michigan (USA), populations of zooplanktivorous prey fishes decline via predation from bass. This, in turn increases zooplankton abundance, which then reduces phytoplankton blooms, thereby improving water clarity [26]. When they feed on competitively dominant prey, APs can also promote biodiversity among prey species (i.e., by precluding competition exclusion by dominant prey) [27]. If APs leave behind parts of the prey carcass for other species to scavenge on, they also create food subsidies to other community members [28].

In addition to consumptive effects, predation risk can induce plastic and/or genetic alterations in prey traits, including changes in prey behavior [29], morphology [30], life history [31], and physiology [32]. Such **risk effects** can also initiate trophic cascades [33,34]. For example, in Fijian coral reef systems, herbivorous fish avoid areas patrolled by reef sharks, which creates a spatial refuge for seaweeds, thereby altering vegetation abundance and diversity [35]. In essence, APs can cause community-wide alterations by changing prey abundance via consumptive effects, and by altering average prey traits either via prey plasticity, evolution, or species replacements, and these trait changes can reduce per capita impacts of prey on the rest of the community.

Food web dynamics can change after human-driven AP population declines (Table 1). For example, off Northwest Australia, shark removals have altered the abundance, diversity, diet, body condition, and morphology of reef fishes (Figure 1A; [36–39]). Although evidence for top-down food web effects due to AP increases from conservation efforts exist, they are limited (Table 1).

Nutrient Cycling

APs act as nutrient sources, through rapid nutrient turnover via excretion and egestion, and as nutrient stores, by sequestering nutrients in body tissues [13,40–43]. Many APs are highly mobile, and redistribute nutrients when they feed in one location and egest in another. By foraging at night in offshore waters and then resting during the day within Palmyra Atoll in the Central Pacific, the grey reef shark (*Carcharhinus amblyrhynchos*) population egests an estimated 95 kg of nitrogen daily onto the nutrient-limited reef, supporting coral health [43]. Migrations by diadromous fishes can bring nutrient subsidies into freshwaters [44], for example, when Pacific salmon (*Oncorhynchus* spp.) release nutrient pulses into streams, lakes, and adjacent riparian habitats during spawning migrations [45,46] (Figure 1B). APs with limited mobility can also cycle nutrients by intercepting and consuming mobile species as they move between habitats, thereby shunting nutrients into local ecosystems [47]. Large-bodied APs,

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such as toothed whales, can contribute to local biogenic mixing in the ocean via the mechanical energy generated by their swimming, transporting nutrient-rich water from the bottom to the surface, increasing phytoplankton productivity [48,49]. Moreover, air-breathing ocean predators including seals, seabirds, and toothed whales can mix elements such as iron, by feeding at great depths and then releasing nutrients close to the surface or even on land [50].

APs can also indirectly modulate nutrient cycling via trophic interactions. Size-selective predation can alter stoichiometric relationships in prey nutrient content and consumer nutrient recycling [51]. APs also influence nutrient cycles via risk effects [52,53]. For example, pike cichlids (*Crenicichla alta*), an abundant predator of guppies (*Poecilia reticulata*) in many Trinidad streams, constrain guppy foraging and food intake [52,54]. Chemical cues of pike cichlids alone are sufficient to increase guppy nitrogen assimilation and retention efficiencies, ultimately reducing guppy nitrogen excretion.

The effects of AP declines on nutrient cycling have been explored for several systems [55,56] (Table 1). For example, overfishing has reduced storage and resupply of fish-derived nutrients on coral reefs by nearly 50%, resulting in diminished coral growth and primary productivity [56]. However, the recovery of migratory fish has seen the restoration of their function as nutrient vectors (Table 1). The year after removing the Elwha Dam in Washington State, salmon returned to the upper reaches of the river, restoring lost nutrient subsidies [57].

Ecosystem Engineers

Ecosystem engineering is a process by which organisms create and modify habitats through changes in their abiotic environment [58]. One of the most direct ways that APs engineer their environment is by creating habitat, including that generated by the leftover carcasses of animals they have killed [59] or the sinking carcasses of the APs themselves following death [14,15]. In particular, whale carcasses form an immediate rich habitat in energy-poor deep-sea environments [14,15,60]. Commercial whaling is believed to have indirectly led to the extinctions of some invertebrates that were whale-fall specialists [14].

Bioturbation is another way aquatic predators can alter their environment. By excavating sandflats to feed on buried infaunal invertebrates, stingrays enable oxygen and organic matter to penetrate deeper into sediments, supporting biogeochemical cycling and the associated microbial assemblages that drive these processes [61,62]. Alligators (*Alligator mississippiensis*) rearrange sediments and remove vegetation, creating small ponds (alligator holes) that sustain many aquatic and semiaquatic vertebrates and invertebrates (Figure 1C) [63,64]. APs can also engineer ecosystems via trophic interactions, whereby predators influence other organisms that create or modify habitat [65]. For example, sea otters (*Enhydra lutris*) feed on herbivorous sea urchins that would otherwise consume kelp, thereby promoting kelp forests and several kelp-associated fishes and invertebrates [66]. Given that AP population declines and increases have led to changes in the habitats they create or modify – and the species that depend on these habitats (Table 1) – some AP ecosystem engineers might serve as key mechanistic links to habitat restoration and the recovery of species that depend on them.

Disease Transmission

It has long been surmised that predators benefit prey populations by weeding out the sick and old [67]. APs might distinguish easy targets when healthy prey are difficult or dangerous to capture [68,69]. If sick animals are targeted by APs, mathematical models suggest predation can reduce host-specific infectious diseases that have **density-dependent transmission** [67]. However,

Glossary

Bioinspired materials: synthetic materials that draw inspiration from nature.

Consumptive effects: reductions in prey numbers or density resulting from predators killing and consuming prey.

Density-dependent transmission: when disease transmission success increases in direct proportion to host density.

Ecological role: the niche a species has in its environment and the role it fulfills in the ecosystem.

Ecosystem function: biological, geochemical, and physical processes that occur within an ecosystem, including collected interactions of biota and the environment, that are an integral part of biodiversity.

Ecosystem service: benefits humans freely gain from naturally functional ecosystems and the environment.

Food and Agricultural Organization of the United Nations:

Nations: an international body that deals with issues related to fisheries and aquaculture that support livelihoods and food security.

Macrophyte: plants that grow in or near water.

Nature-based tourism: portion of the global tourism industry that focuses on wildlife viewing.

Risk effects: predation risk-induced shifts in prey behavior, morphology, life history and/or physiology that have consequences for their fitness and/or population dynamics; also known as nonconsumptive predator effects.

Socioecological system (SES): system of components (resource, resource users, governance, and resource system), including their interactions leading to outcomes for social and ecological actors in the system.

Trophic cascade: indirect species interactions that originate with predators and spread downward through food webs. A classical trophic cascade usually results in sequentially alternating high and low abundance of species as one moves down trophic levels of a food chain due to predator–prey interactions.



Trends in Ecology & Evolution

Figure 1. Ecosystem Functions and Services of Aquatic Predators. (A) Controlling food webs: large bodied sharks alter the abundance, diversity, behavior, diet, and shape of coral reef fishes [36–39]. (B) Nutrient cycling: spawning migrations of Pacific salmon effectively transfer nutrients from oceans to rivers, streams and

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most evidence that predators reduce infectious diseases comes from predators reducing prey density, thereby limiting transmission of density-dependent parasites. Older prey are more likely to carry parasites because they have been exposed longer to infectious agents than younger prey have been [70]. By preferentially removing sick or old individuals already close to death, APs can reduce parasites without increasing population mortality rates of prey [67].

Although APs can limit the transmission of parasites, they can also promote disease spread. Many parasites have complex life cycles that use APs as hosts, and, therefore, APs can spread parasites, including some that infect people [71]. For instance, larval worms in predatory fishes consumed by humans can expose people to a range of pathogenic parasites [72].

Human-driven changes to AP populations can alter disease transmission (Table 1), such as in tropical rivers, where predatory prawns (*Macrobrachium* spp.) eat snails that are hosts for human schistosomiasis [16,73]. Loss of these predatory prawns from damming rivers increases snails and subsequent infection rates in humans (Figure 1D). In turn, restoring the predatory prawns back to the system can reduce human infection rates [16,73,74].

Mediating Species Invasions

Many aquatic systems have been invaded by exotic species that can affect native species [75]. In many well-known cases, damaging invaders are introduced APs [18]. The converse potential role of native APs in controlling invasions, however, is less understood [76,77]. Key to whether native APs reduce the vulnerability of a system to species invasion depends on whether APs preferentially feed on exotic species. APs that target exotic prey over native prey have both a higher potential to suppress invaders and reduce impacts on native prey. APs tend to feed on what they can catch and consume, such as prey with ineffective antipredator defenses [78]. APs should thus be more likely to control invaders that exhibit weak antipredator defenses [79], which can occur when naïve, exotic prey do not recognize or sufficiently respond to native APs. Alternatively, if exotic prey exhibit strong antipredatory responses to native APs, then risk effects may constrain invader populations. For example, in response to predation risk from native red groupers (*Epinephelus morio*), invasive lionfish (*Pterois* spp.) shift their foraging from more energy-rich fishes to energy-poor benthic invertebrates [80]. Conversely, invaders tend to be more successful if native APs do not recognize the invaders as potential prey [81,82]. Native APs may also benefit from exotics, for example, if invasive prey become additional food for native APs or exotics negatively affect competitors or predators of native APs [83].

Both theory and empirical field evidence suggest that removals of APs by humans can release invaders from potential predators and competitors (Table 1). For example, in the Black Sea, overexploitation of large predatory fishes appears to have increased non-native comb jellies [84]. In contrast, evidence for changes in invader populations following AP recoveries is lacking (Table 1).

lakes, via nutrient excretion, salmon consumption by predators, and through decomposition of carcasses post spawning [44–46]. (C) Ecosystem engineers: in wetlands, alligators bulldoze sediments and vegetation, creating water-filled alligator holes, which serve as critical habitat for fishes and turtles and sources of drinking water for birds and small mammals [63,64]. (D) Disease transmission: in tropical rivers, predatory prawns (*Macrobrachium* spp.) eat the snails that are hosts for human schistosomiasis [73,74]. (E) Species invasions: off the Pacific Northwest, sea otters and large *Pisaster* starfish selectively feed on native mussels, facilitating the invasion of an exotic bryozoan by reducing competition for space [113]. (F) Climate change mediation: in Western Australia, the presence of tiger sharks appears to cause dugongs and sea turtles to limit their consumption of seagrass, which increases primary production, CO₂ uptake, and maintains sediment carbon stocks [23]. (G) Tourism: viewing of toothed-whales creates jobs and supports local economies [92,95,96]. (H): Fisheries: humans depend on fish as a source of food, recreation (angling), and jobs. (I) Bioinspiration: novel materials engineered with shark skin-mimicking surfaces are being used to design more aerodynamic drones, planes, and wind turbines [24].

Table 1. Examples of Alterations in Ecosystem Processes Resulting from Population Declines and Increases of APs

Ecosystem function/service	AP	Location	Decline or increase	Ecosystem consequence	Refs
Controlling food webs	Sharks (<i>Galeocerdo cuvier</i> , <i>Sphyrna lewini</i> , <i>Sphyrna mokarran</i> , <i>Carcharhinus albimarginatus</i> , <i>Carcharhinus amblyrhynchos</i>)	Scott Reefs, Northwest Australia	Decline	Predation release driving increased abundances of prey fishes, but decreased diversity (possibly from release of competitive dominants). Shark declines also associated with changes to diet, body condition, and morphology of prey fishes.	[36–39]
Controlling food webs	Harbor seals (<i>Phoca vitulina</i>)	Wadden Sea & coastal areas	Increase	Increased predation on prey fish resulting in fish population declines, but increasing fish growth (possibly from reduced density-dependent competition).	[114]
Nutrient cycling	Hooded seal (<i>Cystophora cristata</i>), Short-finned pilot whale (<i>Globicephala macrorhynchus</i>), northern bottlenose whale (<i>Hyperoodon ampullatus</i>), long-finned pilot whale (<i>Globicephala melas</i>), New Zealand sea lion (<i>Phocartos hookeri</i>), northern elephant seal (<i>Mirounga angustirostris</i>), southern elephant seal (<i>Mirounga leonine</i>), sperm whale (<i>Physeter microcephalus</i>), fin whale (<i>Balaenoptera physalus</i>), Cuvier's beaked whale (<i>Ziphius cavirostris</i>), Weddell seal (<i>Leptonychotes weddellii</i>)	World oceans	Decline	Vertical movement of phosphorus by marine mammal predators estimated to be reduced to 23% of historical values due to overharvest	[12]
Nutrient cycling	Chinook salmon (<i>Oncorhynchus tshawytscha</i>), American dipper (<i>Cinclus mexicanus</i>)	Elwha River, WA, USA	Increase	Rapid return of marine-derived nitrogen subsidy by migratory salmon following Elwha Dam removal; observed increases in marine-derived nitrogen in American dipper following dam removal.	[57]
Ecosystem engineering	American alligator (<i>Alligator mississippiensis</i>)	Everglades, FL, USA	Decline	Alligator declines from reduced areas of inundation and increased salinization, resulted in decreased capacity to create critical habitat alligator holes supporting a variety of species.	[115]
Ecosystem engineering	Sea otters (<i>Enhydra lutris</i>)	North Pacific Ocean ecosystems	Decline/increase	Demise of kelp forests, a critical habitat for many species, indirect result of exploitation of sea otters by fur hunters; recovery of kelp forests following recovery of sea otter populations.	[10]
Disease transmission	Predatory prawns (<i>Macrobrachium</i> spp.)	Senegal River	Decline/increase	Loss of predatory prawns from damming rivers increases snails that transmit schistosomiasis to humans. Restoration of the prawns back to the system has reduced risk of human infection.	[16,68,73,74]
Disease transmission	Seals (<i>Phoca vitulina</i> , <i>Halichoerus grypus</i>)	Canadian Maritimes	Decline	Population declines in seals from culling has been found to reduce parasitism in cod and increase fisheries value	[116]
Mediating species invasions	Bonito (<i>Sarda sarda</i>), bluefish (<i>Pomatomus saltatrix</i>), mackerel (<i>Scomber scombrus</i>)	Black Sea	Decline	Overfishing of pelagic APs caused a regime shift including an increase in exotic comb jellies	[84]

Table 1. (continued)

Ecosystem function/service	AP	Location	Decline or increase	Ecosystem consequence	Refs
Climate mitigation	Blue crabs (<i>Callinectes sapidus</i>), predatory fish	East Coast, USA, Salt Marshes	Decline	AP declines has led to an overabundance of sesamid crabs that undertake extensive burrowing and grazing, resulting in large-scale coastal erosion, the re-suspension of century-old soil carbon stocks, and a reduction in soil carbon sequestration rates by >300%.	[23,117,118]
Climate mitigation	Sea otters (<i>Enhydra lutris</i>)	West Coast of North America	Increase	Increase predation of sea urchins from recovered sea otter populations has increased carbon storage in living kelp by 4.4 to 8.7 million tons	[22]
Tourism	Orca (<i>Orcinus orca</i>)	Pacific Northwest, North America	Decline	Losses in salmon have crippled southern resident orca whale populations and the tourism sector that relies on their presence.	[119]
Tourism	Sperm whales (<i>Physeter microcephalus</i>)	Kaikoura, New Zealand	Increase	Recovery of sperm whale populations following decades of whaling created a tourism industry that has increased tourism visitation 25 times.	[96]
Fisheries	Atlantic cod (<i>Gadus morhua</i>)	North Atlantic – especially in Canadian waters	Decline	Collapse of Atlantic cod lead to socioeconomic devastation to coastal fishing communities	[120]
Fisheries	Lake trout (<i>Salvelinus namaycush</i>)	Lake Superior in the Laurentian Great Lakes	Increase	Following dramatic population declines in the mid-1900s due to overfishing and other stressors, strict fisheries regulations lead to a lucrative and sustainable recreational fishery for lake trout.	[121]

Box 1. Lessons Learned from the Collapse of the Atlantic Cod Fishery

When fisheries selectively remove the largest individuals, they also remove adults with higher potential breeding output (and their genes) such that fisheries exploitation can induce rapid genetic changes in fish populations, yielding smaller adults with lower reproductive output [30]. The combination of decreases in AP abundance, and evolutionary change favoring individuals with lower reproductive output, has implications for trophic control of marine ecosystems, including capacity of the ocean to mitigate climate change, such as in the case of Atlantic cod (*Gadus morhua*) in the North Atlantic (Figure 1).

As dominant APs, large adult cod eat mid-sized fishes such as hake, squid, herring, and mackerel. These species eat larval cod and large zooplankton. Before over-fishing (Figure 1, left panel), large adult cod controlled mid-sized fish populations, which in turn helped ensure a strong source of larval cod to support future adult populations. These abundant larval cod and large zooplankton selectively fed on large dinoflagellate phytoplankton, leaving behind smaller diatom phytoplankton. The surviving smaller mid-sized fishes fed on small zooplankton, which also increased abundances of diatoms. These diatoms played an important role in carbon storage in the North Atlantic, by sequestering carbon in their tissues during photosynthesis and then sinking to the deep ocean, settling within the sediment and effectively stockpiling the carbon (known as the biological pump). Upwelled nutrients further helped support photosynthesis.

Over-fishing cod in the 1990s triggered changes in top-down control of the entire ecosystem, indirectly weakening the biological pump of the North Atlantic Ocean (Figure 1, right panel, [122–124]). Specifically, the cod collapse triggered an increase in mid-sized fish that in turn caused decreases in both larval cod and large zooplankton, leaving behind mostly smaller zooplankton. The increased predation on larval cod further impaired recovery of the adult population. Reductions in large zooplankton subsequently increased dinoflagellate abundance; whereas, the increased abundance of small zooplankton caused reduced diatoms. This loss of diatoms weakened the biological pump. Further hindering carbon sequestration was reduced nutrient upwelling to the phytoplankton due to increased water stratification from rising water temperature due to climate change. While climate change effects may be more difficult to reverse, recovering the adult cod population could restore the strength of the North Atlantic biological pump and its ecosystem service of lowering atmospheric CO₂.

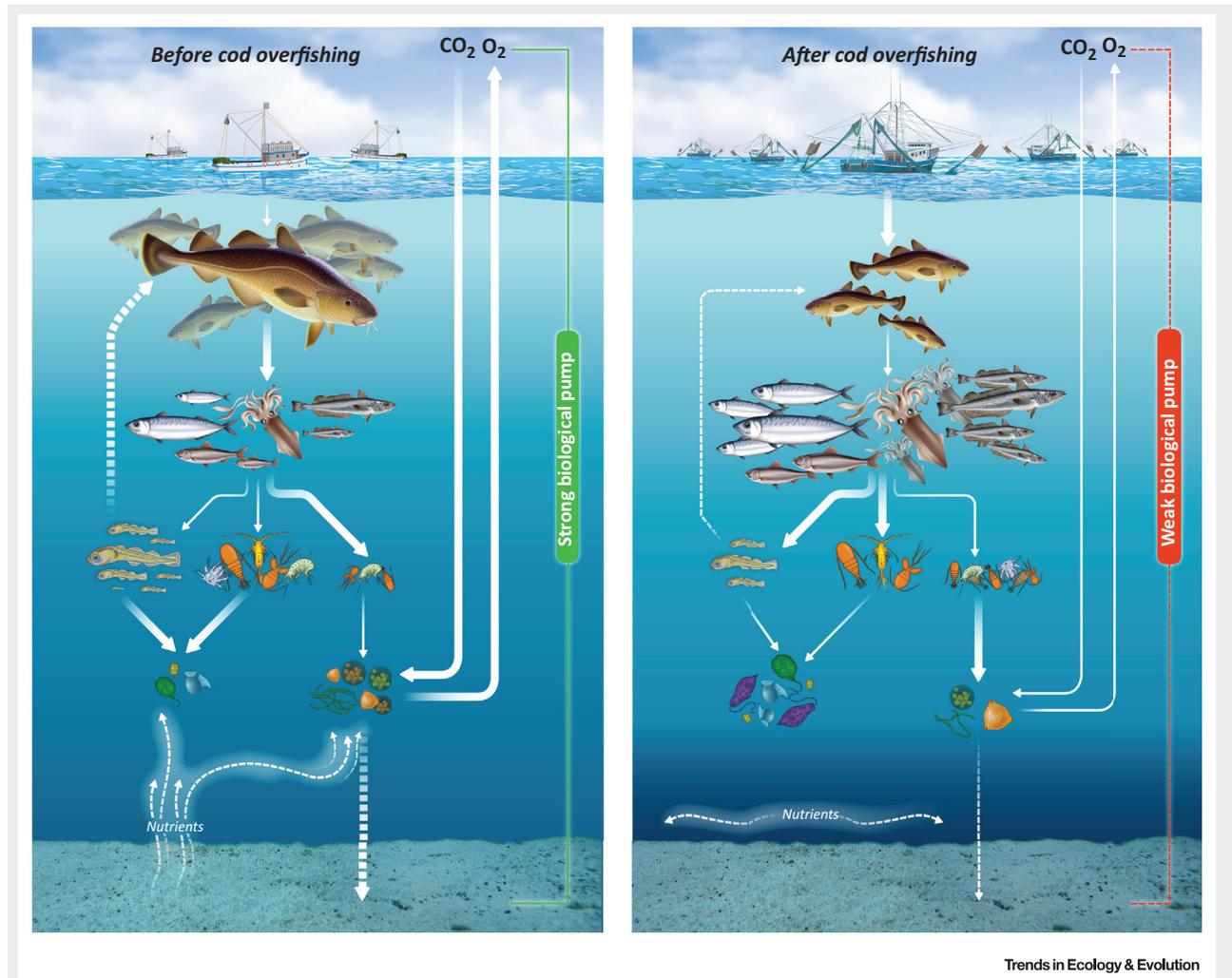


Figure 1. Offshore Shelf Ecosystem in the North Atlantic Ocean before (Left Panel) and after (Right Panel) Overfishing of Large Adult Atlantic Cod (*Gadus morhua*). Arrow thickness represents interaction strengths (thick arrow = strong interactions/thin arrows = weak interactions). Before overfishing, large cod fed on mid-sized fishes, which increased larval cod and large zooplankton that would otherwise be consumed. This helped support larval cod recruitment to the adult stock. Together with large zooplankton, larval cod ate large phytoplankton species (dinoflagellates), leaving behind smaller phytoplankton species (diatoms). The surviving smaller mid-sized fishes fed on small zooplankton, which also increased diatoms species. These diatoms released oxygen and sequestered carbon. Thereafter, these diatoms sank to deep sea sediments, effectively stockpiling photosynthesized carbon (biological pump). Furthermore, upwelling of deep ocean nutrients helped increase photosynthesis. After overfishing of adult cod, mid-sized fishes previously consumed by adult cod increased in abundance, consequently reducing large zooplankton and larval cod, leaving behind small zooplankton. Reductions of large zooplankton subsequently increased dinoflagellates, whereas the surviving small zooplankton reduced diatoms. The overall loss of diatoms weakened the biological pump. Moreover, increased water stratification associated with warming temperatures has limited nutrient upwelling and photosynthesis.

Mediating Climate Change

Aquatic systems play a fundamental role in the global carbon cycle. In addition to the 400 billion tons of inorganic carbon in the water column, marine ecosystems store substantial carbon in plant biomass and organic sediments. Conversely, inland freshwaters emit enough CO₂ and methane to offset ~80% of the global land sink. APs can increase net primary production and soil carbon sequestration by decreasing herbivore abundances via predation or reducing herbivore foraging activity via risk effects [85–87]. This is because herbivores consume plant

biomass, which can reduce the amount of carbon fixed through photosynthesis [86,88]. Herbivory can also reduce the amount of carbon sequestered into sediments [23]. Furthermore, herbivores can influence soil carbon sequestration by reducing plant canopy height and damaging **macrophyte** roots [89]. In coastal areas of Australia, sharks limit herbivore (green sea turtles *Chelonia mydas*, herbivorous fish, and dugongs *Dugong dugon*) consumption of seagrass and/or algae, thereby increasing CO₂ uptake and fostering higher sediment carbon stocks (Figure 1F) [23,90].

Growing evidence suggests that conservation of APs may help reduce natural greenhouse gas emissions or enhance carbon uptake and storage in aquatic ecosystems (Table 1). For example, by suppressing sea urchin populations, the recovery of sea otters in the Pacific Northwest has led to an estimated 4.4–8.7 megaton increase in carbon storage by kelp [22]. Yet, APs are declining in many systems [6,7,25], and the resulting increases in herbivore abundances and grazing rates could reduce the effectiveness of the marine carbon sink by several million tons of CO₂ [23]. A loss of the upper sediment layer in only 1% of vegetated coastal ecosystems could lead to the release of 460 million tons of CO₂ into the atmosphere [23]. This is equivalent to the annual CO₂ production of ~97 million cars [23]. However, the direction of predator effects on carbon processes is dependent on food chain length; in some cases, predators may decrease carbon storage or enhance greenhouse gas emissions [85].

Tourism

Large predators are among the most popular and socioeconomically valuable species for **nature-based tourism** [91]. The thrill of experiencing predatory species in the wild leads to local and national economic benefits worth several billion US dollars per year [92,93]. Subsequently, the ecosystem service of APs to ecotourism has become a leading argument for their conservation in certain contexts [91,94]. Toothed whales such as orcas (*Orcinus orca*), dolphins, and sperm whales (*Physeter microcephalus*) are iconic APs that capture a significant portion of the global whale watching industry (Figure 1G) [95]. A similar trend can be seen with shark tourism, with an estimated total value of US\$315 million/year with over 500 000 tourists,

Box 2. Considering Ecosystem Services of APs in an SES Framework

An SES has multiple interacting human and non-human components [19], such as APs and other natural resources (e.g., prey items and predators, and physical habitats) or processes (e.g., oceanography). These components interact, such that a change in one component can initiate shifts throughout the SES [19]. This framework, outlined in Figure 1, can be used as an analytical tool in ecosystem or resource management to understand *a priori* interactions among SES components and help identify meaningful indicators for system functionality across both social and ecological spheres [125]. In constructing an SES, following nomenclature of [19] and [126], the spatial area under management is the resource system, the AP is the resource unit, any humans using the resource system (fishers, tourists, and shipping vessels) are actors, and the governance system is composed of the regulators, regulations on fishing limits, and/or protected areas, and parties responsible for enforcement.

In management and policy settings, the SES framework has been used as a tool to assess performance of ongoing management regimes, rather than a starting point for management design [127]. For instance, recognizing network structure or feedbacks among actor groups, including actors' perception of rule-making processes and potential influences of external environmental shifts. By conceptualizing the SES at an early time point, managers can account for otherwise unforeseen interactions that could impact management outcomes and mobilize any additional expertise or resources needed to monitor indicators (e.g., socioeconomic or sociocultural indicators), thereby allowing a more comprehensive long-term record of the effectiveness of policy. The reflexive approach facilitates adaptive management, by demonstrating ramifications of fluctuations in SES indicators (e.g., management changes or environmental fluctuations), which may lead to revisions of the resource management strategy.

To demonstrate the SES framework and its functionality as an analytical tool, Figure 1 provides a hypothetical example of an Arctic SES. Instructions on how to operationalize an SES framework is beyond the scope of this review; however, we recommend constructing the SES following [19,126–128], and identifying indicators as outlined by [129].

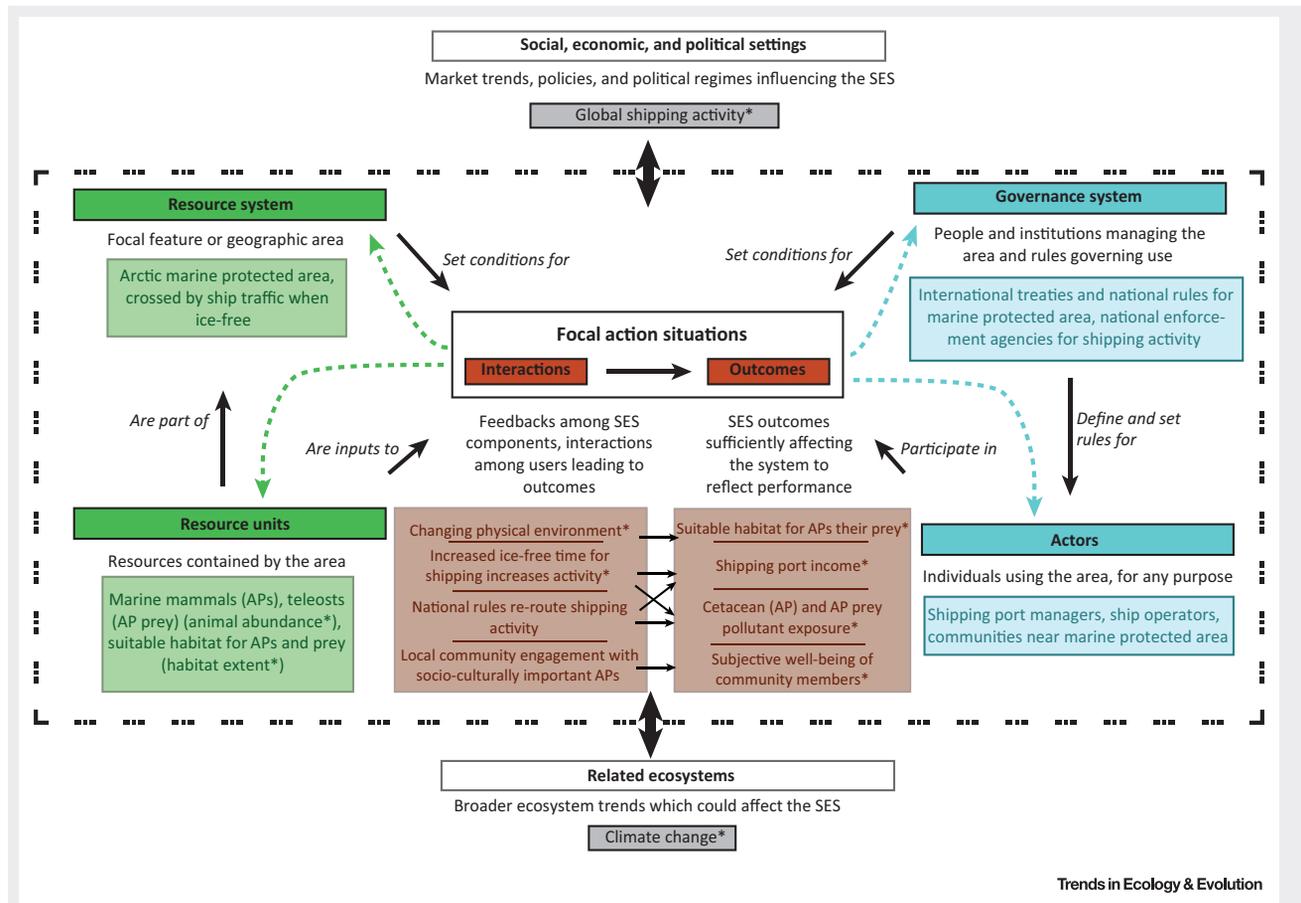


Figure 1. Hypothetical Example of an Arctic SES Involving Marine Mammals under Social and Environmental Change. The SES framework presented here is adapted from [19], which includes the resource system, resource units, actors using the resource, and governance systems which combine to yield focal action situations where interactions lead to outcomes, which then affect constituent SES components. The broader social, economic, political, and ecological contexts within which the SES operates can affect each component, and thus the SES as a whole. A hypothetical example for a complex SES is given, in light colored boxes, of an Arctic marine protected area (MPA) (resource system), which, during ice-free seasons, is crossed by shipping vessels, and visited by local community members for cultural and subsistence purposes (all of which are the actors), who interact with, and can impact, resource units [marine mammals (APs), teleosts (AP prey) via noise and chemical pollution from shipping]. Here, external shifts such as higher ocean temperature from anthropogenic climate change (related ecosystems, under the SES framing) and increased global shipping activity owing to economic trends (social, economic, and political settings) can increase both the length and spatial extent of the ice-free season, and the shipping activity within the MPA. As a result, APs and their prey have less suitable habitat, and more pollutant exposure, which can compromise accessibility of APs for local community members to whom they have sociocultural significance. The various national governments and international treaties, which govern and monitor activity in the area, comprise the governance system. Members of the governance system can use this SES framing to identify focal action situations where interactions among components lead to measurable outcome measures, and how these local indicators shift with external conditions, to both define and adapt rules for use of the MPA, and monitor performance of rules – for instance, redirecting shipping routes to minimize interaction with the MPA, to reduce AP pollutant exposure and improve potential for long-term wellbeing of the local community. Throughout the SES, asterisks note where indicators may be gathered to monitor SES functionality and performance of management rules.

directly supporting 10 000 jobs [93]. The decline and recovery of cetaceans, including toothed whales, is arguably the most striking example how changes in AP populations have impacted tourism sectors (Table 1). In Kaikoura, New Zealand, following the introduction of whale-watching tourism for sperm whales in 1987, the community transformed from an economically depressed town to a bustling tourism hub [96].

Fishing and Hunting

Fishing, and to a lesser extent, hunting, probably represents the most widespread and obvious use of APs by humans (Figure 1H). Statistics analyzed from the **The Food and Agriculture Organization of the United Nations** suggest that predatory fish are heavily targeted [97] and considered among the most valuable for fisheries on a per unit mass basis [e.g., bluefin tuna (*Thunnus thynnus*), black marlin (*Istiompax indica*), and Patagonian toothfish (*Dissostichus eleginoides*)]. Indigenous Arctic peoples depend on APs for food, with estimates of ~17 000 ringed seals (*Pusa hispida*) removed annually [21]. Clearly, APs are significant components of human diets, particularly in certain coastal communities (e.g., Japan and Scandinavia).

Population declines and increases in APs that support food production and jobs present obvious socioeconomic consequences (Table 1). The immediate effects on fisheries can be substantial if exploitation rates are suddenly restricted, or alternatively if exploited fish abundances fall to the point where fisheries are no longer economically viable—neither outcome is good for people. Overfishing of Atlantic cod (*Gadus morhua*) and associated socioeconomic devastation in coastal fishing communities provides a classic example (see Figure 1 in Box 1). In a similar manner, increases of economically important APs through effective management have led to increased socioeconomic benefits (Table 1). In contrast, the apparent overabundance of some APs, such as seals, has created conflict with fishers and led to calls for increased seal hunting to benefit fish populations [98].

Bioinspiration

APs often rely on high swimming performance to capture prey [99] and consequently have a number of specialized hydrodynamic structures. Therefore, APs tend to be a focus of bio-inspired materials for enhanced hydrodynamic performance [100–102]. Structures covered in 3D-printed shark skin have reduced energy consumption (~5.9%), and increased swimming speed (~6.6%) compared to similar structures lacking synthetic shark skin [103], and might improve aerial devices [24]. In other applications, marine mammals possess skin textures that inhibit fouling organisms, which may allow for new innovation in antifouling materials for creating fuel-efficient propellers, ship hull designs, submarines, and aquatic robots [104]. APs can also provide novel biomedical applications for human health. For example, small antibodies found in some sharks may offer new molecular tools for battling human diseases [105,106]. Even when bioinspiration is not commercialized, it can lead to rethinking of designs and approaches for innovation [107]. Accordingly, the loss of APs could reduce bioinspiration opportunities.

Concluding Remarks

Predators, aquatic and otherwise, are widely recognized for their influence on food webs via trophic cascades. However, this awareness is largely for consumptive effects; whereas, the strength and breadth of risk effects on communities is lesser known and underappreciated, although growing. Although often overlooked in both discussions and studies of their ecological roles and attendant ecosystem services, APs can impact nutrient cycling, act as ecosystem engineers, and function as both disease/parasite vectors or regulators. Moreover, APs generate cultural and provisioning services that benefit humans in diverse ways including climate change mitigation, as a source of spirituality (not reviewed here), nutritional security, livelihood support/wealth generation, leisure (e.g., recreational fishing), and a source of bioinspired materials (e.g., aviation and medicine).

Although difficult to detect in aquatic systems, both human-driven declines and increases of AP populations alter ecosystem functions and services (Table 1 and Box 1). However, investigating such processes is challenging for several reasons. In many cases where APs have been exploited, other anthropogenic effects have also occurred (e.g., pollution and habitat degradation), making it

Outstanding Questions

Controlling Food Webs

How fast do prey traits respond (via prey plasticity, evolution, or species replacements) to changes in AP population declines or recoveries?

How prevalent is food web omnivory by APs (i.e., feeding across multiple trophic levels) and does it reduce the strength of AP consumptive or risk effects on prey?

Nutrient Cycling

To what degree are nutrient demands of ecologically important habitats (e.g., mangrove, seagrass, coral reefs, and wetlands) supported by APs?

What are the mechanisms and extent to which APs influence micronutrient and trace element fluxes within ecosystems?

Disease Transmission

To what extent do APs reduce the spread of infectious diseases by selectively targeting weak, sick, or old prey?

What is the magnitude of AP transmitted parasites in the ocean? What are the primary mechanism by which this occurs?

Mediating Species Invasions

Can APs control non-native species by either learning or evolving to target invaders?

Does the removal of APs increase the vulnerability of aquatic systems to species invasions?

Mediating Climate Change

To what extent do local predator effects on carbon sequestration processes scale up to regional and global carbon budgets?

Is the conservation or recovery of APs a legitimate means of mitigating CO₂ emissions?

difficult for scientists to isolate ecosystem changes driven by AP declines alone. Moreover, in the case of ecosystem changes from AP declines, these most likely already occurred prior to monitoring. In the case of ecosystem changes associated with AP increases, their population rebounds have been relatively limited and slow, as have likely their associated ecological effects. Traditional manipulative techniques, such as removals, exclusions or additions, are often unfeasible with APs given obvious logistical, technological and ethical constraints. This means that researchers will have to rely on comparative and correlational approaches [108], such as by studying anthropogenic-driven losses of APs through targeted removals or increases in AP populations through protective measures (prohibitions and reserves) and stocking efforts. Central to this future research will be trying to understand under which scenarios declines and/or increases of APs lead to alterations in ecosystem processes or not, and how long these changes may take to occur.

Based on our synthesis of the literature, we list 16 outstanding questions as research priorities for understanding the ecosystem functions of APs under human-driven environmental change (see Outstanding Questions). A key priority will be to understand how APs affect biodiversity at local, regional, and global levels, and in turn, how AP population declines and recoveries will affect biodiversity. Moreover, it remains uncertain how imminent climate-driven changes to water temperatures, oxygen concentrations, pH levels, and frequency of extreme weather events might affect the ecosystem functions and services of APs.

New and refined technologies make it easier to study APs at relevant spatial and temporal scales. Innovations in biotelemetry [109], biochemical tracers [110,111], remote video-surveillance, and increasingly sophisticated human dimensions methods [19,112], now provide researchers with the ability to study the ecology of APs at the scale of watersheds or ocean basins, and their inextricably linked relationships to humans. Indeed, many of the research gaps identified here are at the forefront of modern ecology and will shape the research careers of many future scientists. Finally, we suggest that application of an SES Framework (see Figure 1 in Box 2) for optimizing the socioeconomic and ecosystem services generated by APs in a changing world, which will require more explicit collaboration with scientists working in fields such as social sciences and humanities.

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Tourism

Can interacting with APs for tourism sufficiently impact their behavior and/or physiology to alter their ecological functions?

Fisheries

Is aquaculture and stocking an effective approach for supporting or restoring AP populations and their ecological functions or services?

General

How do food chain length and food web omnivory influence the magnitude and direction of varying AP impacts on ecosystem function?

What is the contribution of various APs ecosystem functions to biodiversity at local, regional, and global levels, and in turn, how will changes in AP population abundances affect these processes?

How are imminent climate-change-associated changes to aquatic systems (water temperature, oxygen concentration, pH level, and frequency of extreme weather events) going to impact ecological functions and services of APs, either directly or indirectly, and if so, at what spatial and temporal scales?

Does coastal urbanization effects on adjacent aquatic systems (e.g., boat traffic or chemical, noise, and light pollution) directly or indirectly alter ecological function or services of APs?

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