

REVIEW SUMMARY

MARINE CONSERVATION

Marine defaunation: Animal loss in the global ocean

Douglas J. McCauley,* Malin L. Pinsky, Stephen R. Palumbi, James A. Estes, Francis H. Joyce, Robert R. Warner

BACKGROUND: Comparing patterns of terrestrial and marine defaunation helps to place human impacts on marine fauna in context and to navigate toward recovery. Defaunation began in earnest tens of thousands of years later in the oceans than it did on land. Although defaunation has been less severe in the oceans than on land, our effects on marine animals are increasing in pace and impact. Humans have caused few complete extinctions in the sea, but we are responsible for many ecological, commercial, and local extinctions. Despite our late start, humans have already powerfully changed virtually all major marine ecosystems.

ADVANCES: Humans have profoundly decreased the abundance of both large (e.g.,

whales) and small (e.g., anchovies) marine fauna. Such declines can generate waves of ecological change that travel both up and down marine food webs and can alter ocean ecosystem functioning. Human harvesters have also been a major force of evolutionary change in the oceans and have reshaped the genetic structure of marine animal populations. Climate change threatens to accelerate marine defaunation over the next century. The high mobility of many marine animals offers some increased, though limited, capacity for marine species to respond to climate stress, but it also exposes many species to increased risk from other stressors. Because humans are intensely reliant on ocean ecosystems for food and other ecosystem services, we are deeply affected by all of these forecasted changes.

Three lessons emerge when comparing the marine and terrestrial defaunation ex-

periences: (i) today's low rates of marine extinction may be the prelude to a major extinction pulse, similar to that observed on land during the industrial revolution, as the footprint of human ocean use widens; (ii) effectively slowing ocean defaunation requires both protected areas and careful management of the intervening ocean matrix; and (iii) the terrestrial experience and current trends in ocean use suggest that habitat destruction is likely to become an increasingly dominant threat to ocean wildlife over the next 150 years.

OUTLOOK: Wildlife populations in the oceans have been badly damaged by human activity. Nevertheless, marine fauna generally are in better condition than terrestrial fauna: Fewer marine animal extinctions have occurred; many geographic ranges have shrunk less; and numerous ocean ecosystems remain more wild than terrestrial ecosystems. Consequently, meaningful rehabilitation of affected marine animal populations remains within the reach of managers. Human dependency on marine wildlife and the linked fate of marine and terrestrial fauna necessitate that we act quickly to slow the advance of marine defaunation. ■

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Timeline (log scale) of marine and terrestrial defaunation. The marine defaunation experience is much less advanced, even though humans have been harvesting ocean wildlife for thousands of years. The recent industrialization of this harvest, however, initiated an era of intense marine wildlife declines. If left unmanaged, we predict that marine habitat alteration, along with climate change (colored bar: IPCC warming), will exacerbate marine defaunation.

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Douglas J. McCauley,^{1*} Malin L. Pinsky,² Stephen R. Palumbi,³ James A. Estes,⁴ Francis H. Joyce,¹ Robert R. Warner¹

Marine defaunation, or human-caused animal loss in the oceans, emerged forcefully only hundreds of years ago, whereas terrestrial defaunation has been occurring far longer. Though humans have caused few global marine extinctions, we have profoundly affected marine wildlife, altering the functioning and provisioning of services in every ocean. Current ocean trends, coupled with terrestrial defaunation lessons, suggest that marine defaunation rates will rapidly intensify as human use of the oceans industrializes. Though protected areas are a powerful tool to harness ocean productivity, especially when designed with future climate in mind, additional management strategies will be required. Overall, habitat degradation is likely to intensify as a major driver of marine wildlife loss. Proactive intervention can avert a marine defaunation disaster of the magnitude observed on land.

Several decades of research on defaunation in terrestrial habitats have revealed a serial loss of mammals, birds, reptiles, and invertebrates that previously played important ecological roles (1). Here, we review the major advancements that have been made in understanding the historical and contemporary processes of similar defaunation in marine environments. We highlight patterns of similarity and difference between marine and terrestrial defaunation profiles to identify better ways to understand, manage, and anticipate the effects of future defaunation in our Anthropocene oceans.

Patterns of marine defaunation

Delayed defaunation in the oceans

Defaunation on land began 10,000 to 100,000 years ago as humans were expanding their range and coming into first contact with novel faunal assemblages (2–4). By contrast, the physical properties of the marine environment limited our capacity early on to access and eliminate marine animal species. This difficulty notwithstanding, humans began harvesting marine animals at least 40,000 years ago, a development that some have suggested was a defining feature in becoming “fully modern humans” (5). Even this early harvest affected local marine fauna (6). However, global rates of marine defaunation only intensified in the last century with the advent of industrial fishing and the rapid expansion of coastal populations (7). As a result, extant global marine faunal

assemblages remain today more Pleistocene-like, at least with respect to species composition, than terrestrial fauna. The delayed onset of intensive global marine defaunation is most visible in a comparative chronology of faunal extinctions in which humans are likely to have directly or indirectly played a role (8) (Fig. 1).

Comparing rates of animal extinction

Despite the recent acceleration of marine defaunation, rates of outright marine extinction have been relatively low. The International Union for Conservation of Nature (IUCN) records only 15

global extinctions of marine animal species in the past 514 years (i.e., limit of IUCN temporal coverage) and none in the past five decades (8, 9). By contrast, the IUCN recognizes 514 extinctions of terrestrial animals during the same period (Fig. 1). While approximately six times more animal species have been cataloged on land than in the oceans (10), this imbalance does not explain the 36-fold difference between terrestrial and marine animal extinctions.

It is important to note that the status of only a small fraction of described marine animal species have been evaluated by the IUCN, and many assessed species were determined to be data deficient (11) (Fig. 2). This lack of information necessitates that officially reported numbers of extinct and endangered marine fauna be considered as minimum estimates (11). There remain, however, a number of data-independent explanations for the lower extinction rates of marine fauna. Marine species, for instance, tend to be more widespread, exhibit less endemism, and have higher dispersal (12, 13).

Complacency about the magnitude of contemporary marine extinctions is, however, ill-advised. If we disregard the >50,000-year head start of intense terrestrial defaunation (Fig. 1) and compare only contemporary rates of extinction on land and in the sea, a cautionary lesson emerges. Marine extinction rates today look similar to the moderate levels of terrestrial extinction observed before the industrial revolution (fig. S1). Rates of extinction on land increased dramatically after this period, and we may now be sitting at the precipice of a similar extinction transition in the oceans.

Three other kinds of extinction

The small number of species known to be permanently lost from the world's oceans inadequately

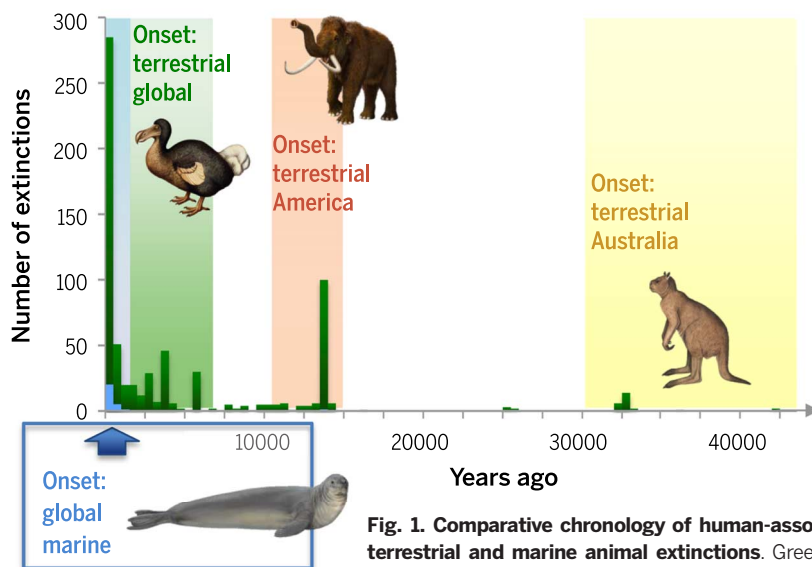


Fig. 1. Comparative chronology of human-associated terrestrial and marine animal extinctions. Green bars indicate animal extinctions that occurred on land, and blue bars indicate marine animal extinctions. Timeline measures years before 2014 CE. Only extinctions occurring less than 55,000 years ago are depicted. Defaunation has ancient origins on land but has intensified only within the last several hundred years in the oceans. See details in (8).

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reflects the full impacts of marine defauna-tion. We recognize three additional types of defauna-tion-induced extinction.

Local extinction

Defauna-tion has caused numerous geographic range constrictions in marine animal species, driving them locally extinct in many habitats. These effects have been particularly severe among large pelagic fishes, where ~90% of studied species have exhibited range contractions (8, 14) (Fig. 3). Local extinctions, however, are not unique to large pelagic predators. Close to a third of the marine fishes and invertebrates off the North American coasts that can be reliably sampled in scientific trawl surveys (often small to medium-bodied species) have also exhibited range contractions (Fig. 3). Such contractions can result from the direct elimination of vulnerable subpopulations or from region-wide declines in abundance (14). Available data suggest that the magnitude of the range contractions for this diverse set of trawl-surveyed marine species is, on average, less than the contractions observed for terrestrial animals such as mammals, birds, and butterflies. Though data deficiencies are abundant, most marine animal species also do not yet seem to exhibit some of the most extreme range contractions recorded for terrestrial animals. Asian tigers, for example, have lost ~93% of their historical range (15), whereas tiger sharks still range across the world's oceans (16).

Ecological extinction

Reductions in the abundance of marine animals have been well documented in the oceans (17). Aggregated population trend data suggest that in the last four decades, marine vertebrates (fish, seabirds, sea turtles, and marine mammals) have declined in abundance by on average 22% (18). Marine fishes have declined in aggregate by 38% (17), and certain baleen whales by 80 to 90% (19). Many of these declines have been termed ecological extinctions—although the species in question are still extant, they are no longer sufficiently abundant to perform their functional roles. Ecological extinctions are well known in terrestrial environments and have been demonstrated to be just as disruptive as species extinctions (20). On land, we know of the phenomenon of “empty forests” where ecological extinctions of forest fauna alter tree recruitment, reshape plant dispersal, and cause population explosions of small mammals (1, 20, 21). We are now observing the proliferation of “empty reefs,” “empty estuaries,” and “empty bays” (7, 14, 22).

Commercial extinction

Species that drop below an abundance level at which they can be economically harvested are extinct from a commercial standpoint. On land, commercial extinctions affected species ranging from chinchilla to bison (23). Cases of commercial extinction are also common in the oceans. Gray whales were commercially hunted starting in the 1840s. By 1900, their numbers were so depleted that targeted harvest of this species was no longer re-

gionally tenable (24). Likewise, the great whales in Antarctica were serially hunted to commercial extinction (25).

Not all species, however, are so “lucky” as to have human harvesters desist when they become extremely rare. Demand and prices for certain highly prized marine wildlife can continue to increase as these animals become less abundant—a phenomenon termed the anthropogenic Allee effect (26). Individual bluefin tuna can sell for >US\$100,000, rare sea cucumbers >US\$400/kg, and high-quality shark fins for >US\$100/kg. Such species are the rhinos of the ocean—they may never be too rare to be hunted.

Differential vulnerability to defauna-tion

Are certain marine animals more at risk than others to defauna-tion? There has been considerable attention given to harvester effects on large marine animals (27). Selective declines of large-bodied animals appear to be evident in certain contexts (28, 29). As a result of such pressures, turtles, whales, sharks, and many large fishes are now ecologically extinct in many ecosystems, and the size spectra (abundance–body mass relationships) of many communities have changed considerably (7, 30, 31). Marine defauna-tion, however, has not caused many global extinctions of large-bodied species. Most large-bodied marine animal species still exist somewhere in the ocean. By contrast, on land, we have observed the extinction of numerous large terrestrial species and a profound restructuring of the size distribution of land-animal species assemblages. The mean body mass for the list of surviving terrestrial mammal

species, for example, is significantly smaller than the body mass of terrestrial mammal species that lived during the Pleistocene (1, 32). Such effects, however, are not evident for marine mammals (8) (fig. S2). Recent reviews have drawn attention to the fact that humans can also intensely and effectively deplete populations of smaller marine animals (29, 33). These observations have inspired a belated surge in interest in protecting small forage fishes in the oceans.

A review of modern marine extinctions and listings of species on the brink of extinction reveals further insight into aggregate patterns of differential defauna-tion risk in the oceans (Fig. 2). Sea turtles have the highest proportion of endangered species among commonly recognized groupings of marine fauna. No modern sea turtle species, however, have yet gone extinct. Pinnipeds and marine mustelids, followed very closely by seabirds and shorebirds, have experienced the highest proportion of species extinctions. Many of the most threatened groups of marine animals are those that directly interact with land (and land-based humans) during some portion of their life history (Fig. 2). Terrestrial contact may also explain why diadromous/brackish water fishes are more threatened than exclusively marine fishes (Fig. 2).

Although many marine animal species are clearly affected negatively by marine defauna-tion, there also appears to be a suite of defauna-tion “winners,” or species that are profiting in Anthropocene oceans. Many of these winners are smaller and “weedier” (e.g., better colonizing and faster reproducing) species. Marine invertebrates, in particular, have often been cited as examples of

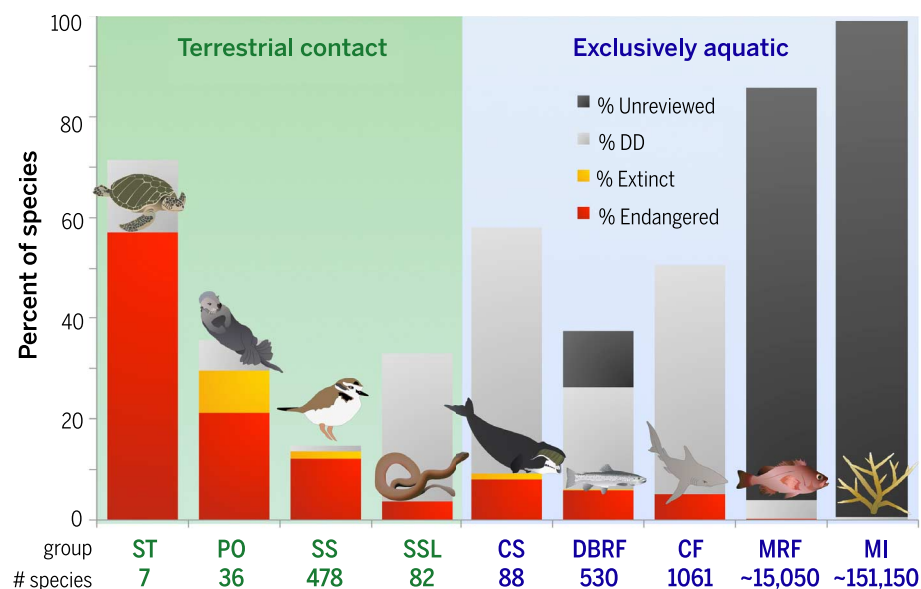


Fig. 2. Marine defauna-tion threat. Threat from defauna-tion is portrayed for different groups of marine fauna as chronicled by the IUCN Red List (113). Threat categories include “extinct” (orange), “endangered” (red; IUCN categories “critically endangered” + “endangered”), “data deficient” (light gray), and “unreviewed” (dark gray). Groups that contact land during some portion of their life history (green) are distinguished from species that do not (light blue). The total number of species estimated in each group is listed below the graph. Species groupings are coded as follows: ST, sea turtles; PO, pinnipeds and marine mustelids; SS, seabirds and shorebirds; SSL, sea snakes and marine lizard; CS, cetaceans and sirenians; DBRF, diadromous/brackish ray-finned fishes; CF, cartilaginous fishes; MRF, exclusively marine ray-finned fishes; MI, marine invertebrates. See further details in (8).

species that are succeeding in the face of intense marine defaunation: lobster proliferated as predatory groundfish declined (34), prawns increased and replaced the dominance of finfish in landings (35), and urchin populations exploded in the absence of their predators and competitors (36). Numerous mid-level predators also appear to benefit from the loss of top predators [e.g., small sharks and rays; (37)]—a phenomenon analogous to mesopredator release observed in terrestrial spheres (38). The status held by some of these defaunation winners in the oceans may, however, be ephemeral. Many of the marine species that have initially flourished as a result of defaunation have themselves become targets for harvest by prey-switching humans as is evidenced by the recent global expansion of marine invertebrate fisheries (39).

Spatial patterns of vulnerability

Patterns of marine defaunation risk track differences in the physical environment. Global assessments of human impact on marine ecosystems suggest that coastal wildlife habitats have been more influenced than deep-water or pelagic ecosystems (40). The vulnerability of coastal areas presumably results from ease of access to coastal zones. This relationship between access and defaunation risk manifests itself also at smaller spatial scales, with populations of marine wildlife closest to trade networks and human settlements appearing often to be more heavily defaunated (41, 42). The relative insulation that animal populations in regions like the deep oceans presently experience, however, may be short-lived because depletions of shallow-water marine resources and the development of new technologies have created both the capacity and incentive to fish, mine, and drill oil in some of the deepest parts of the sea (28, 43).

Coral reefs, in particular, have consistently been highlighted as marine ecosystems of special

concern to defaunation. Coral reefs have been exposed to a wide range of impacts and disturbances, including sedimentation and pollution, thermal stress, disease, destructive fishing, and coastal development (44, 45). Such stressors negatively influence both corals and the millions of species that live within and depend upon reefs (46). Risk, however, is not uniform, even across a reefscape. Shallow backreef pools, for example, routinely overheat, and consequently, corals in these parts of the reef are more resistant to ocean warming (47). Environmentally heterogeneous areas may in fact act as important natural factories of adaptation that will buffer against some types of marine defaunation.

Effects of marine defaunation

Extended consequences of marine defaunation

Marine defaunation has had far-reaching effects on ocean ecosystems. Depletions of a wide range of ecologically important marine fauna such as cod, sea otters, great whales, and sharks have triggered cascading effects that propagate across marine systems (37, 48–51). Operating in the opposite direction from trophic cascades are changes that travel from the bottom to the top of food chains as a result of the declining abundance of lower-trophic level organisms (52). Depletions of fauna such as anchovies, sardines, and krill cause reductions in food for higher-trophic level animals such as seabirds and marine mammals, potentially resulting in losses in reproduction or reductions in their population size (33, 53).

The extended effects of defaunation on marine ecosystems also occur beyond the bounds of these top-down or bottom-up effects. Defaunation can reduce cross-system connectivity (54, 55), decrease ecosystem stability (56), and alter patterns of biogeochemical cycling (57). The ill effects of food

web disarticulation can be further amplified when they occur in association with other marine disturbances. For example, mass releases of discarded plant fertilizers into marine ecosystems from which defaunation has eliminated important consumers can create “productivity explosions” by fueling overgrowth of microbes and algae that fail to be routed into food webs (58, 59).

The selective force of human predation has also been sufficiently strong and protracted so as to have altered the evolutionary trajectory of numerous species of harvested marine fauna (60). Harvest has driven many marine animal species to become smaller and thinner, to grow more slowly, to be less fecund, and to reproduce at smaller sizes (61). There is also evidence that harvest can reduce the genetic diversity of many marine animal populations (62). The genetic effects of defaunation represent a loss of adaptive potential that may impair the resilient capacity of ocean wildlife (63).

Importance of marine defaunation to humans

Marine defaunation is already affecting human well-being in numerous ways by imperiling food sustainability, increasing social conflict, impairing storm protection, and reducing flows of other ecosystem services (64, 65). The most conspicuous service that marine fauna make to society is the contribution of their own bodies to global diets. Marine animals, primarily fishes, make up a large proportion of global protein intake, and this contribution is especially strong for impoverished coastal nations (66). According to the U.N. Food and Agriculture Organization (FAO), 40 times more wild animal biomass is harvested from the oceans than from land (67). Declines in this source of free-range marine food represent a major source of concern (65).

A diverse array of nonconsumptive services are also conferred to humanity from ocean animals, ranging from carbon storage that is facilitated by whales and sea otters to regional cloud formation that appears to be stimulated by coral emissions of dimethylsulphoniopropionate (DMSP) (57, 68, 69). Another key service, given forecasts of increasingly intense weather events and sea-level rise, is coastal protection. Coral, oyster, and other living reefs can dissipate up to 97% of the wave energy reaching them, thus protecting built structures and human lives (70). In some cases, corals are more than just perimeter buffers; they also serve as the living platform upon which entire countries (e.g., the Maldives, Kiribati, the Marshall Islands) and entire cultures have been founded. Atoll-living human populations in these areas depend on the long-term health of these animate pedestals to literally hold their lives together.

Outlook and ways forward

Will climate change exacerbate marine defaunation?

The implications of climate change upon marine defaunation are shaped by ocean physics. Marine species live in a vast, globally connected fluid

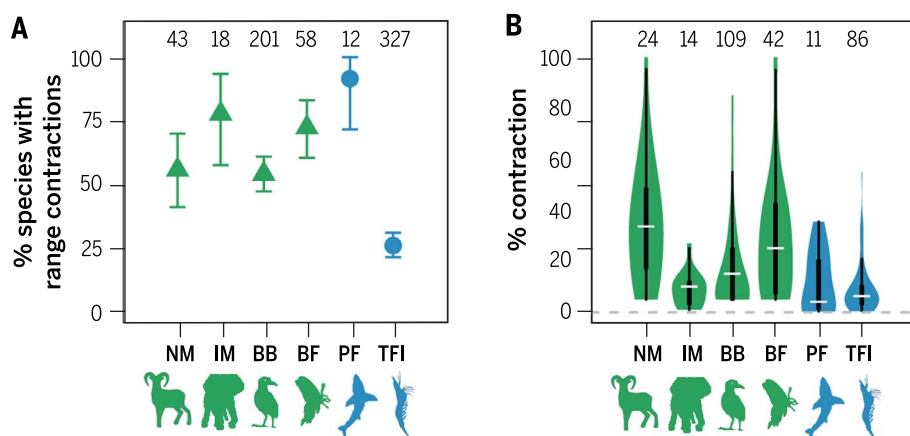


Fig. 3. Comparisons of range contractions for select marine and terrestrial fauna. Terrestrial (green) and marine cases (blue) include evaluations of geographical range change for: 43 North American mammals over the last ~200 years (NM) (114), 18 Indian mammals over the last 30 years (IM) (115), 201 British birds from ~1970 to 1997 (BB) and 58 British butterflies from ~1976 to 1997 (BF) (116), 12 global large pelagic fishes from the 1960s to 2000s (PF) (14), and 327 trawl-surveyed North American marine fish and invertebrates from the 1970s to 2000s (TFI). (A) Percent of species whose ranges have contracted with binomial confidence intervals and (B) distribution of percent contraction for those species that have contracted (violin plot). Sample sizes are shown above each data point, white horizontal lines (B) show the medians, and thick vertical black lines display the interquartile range. See details in (8).

medium that has immense heat-storage capacity and has exhibited a historically robust capability to buffer temperature change over daily, annual, and even decadal time scales (71). While this buffering capacity at first seems to confer an advantage to marine fauna, the thermal stability of the oceans may have left many subtidal marine animals poorly prepared, relative to terrestrial counterparts, for the temperature increases associated with global warming. The same logic supports related predictions that terrestrial fauna living in more thermally stable environments will be more vulnerable to warming than those found in areas of greater temperature variability (72).

Ocean warming presents obvious challenges to polar marine fauna trapped in thermal dead ends (73). Tropical marine species are, however, also highly sensitive to small increases in temperature. For example, coastal crabs on tropical shores live closer to their upper thermal maxima than do similar temperate species (74). Likewise, the symbiosis of corals and dinoflagellates is famously sensitive to rapid increases of only 1° to 2°C (75). Even though corals exhibit the capacity for adaptation (47), coral bleaching events are expected to be more common and consequently more stressful by the end of the century (76). The effects of rising ocean temperature extend well beyond coral reefs and are predicted to affect both the adult and juvenile stages of a diverse set of marine species (77), to reshuffle marine community composition (78), and to potentially alter the overall structure and dynamics of entire marine faunal communities (79).

The wide range of other climate change-associated alterations in seawater chemistry and physics—including ocean acidification, anoxia, ocean circulation shifts, changes in stratification, and changes in primary productivity—will fundamentally influence marine fauna. Ocean acidification, for example, makes marine animal shell building more physiologically costly, can

diminish animal sensory abilities, and can alter growth trajectories (80, 81). Climate change impacts on phytoplankton can further accentuate defaunation risk (82). At the same time that humans are reducing the abundance of marine forage fish through direct harvest, we also may be indirectly reducing the planktonic food for forage fish and related consumers in many regions.

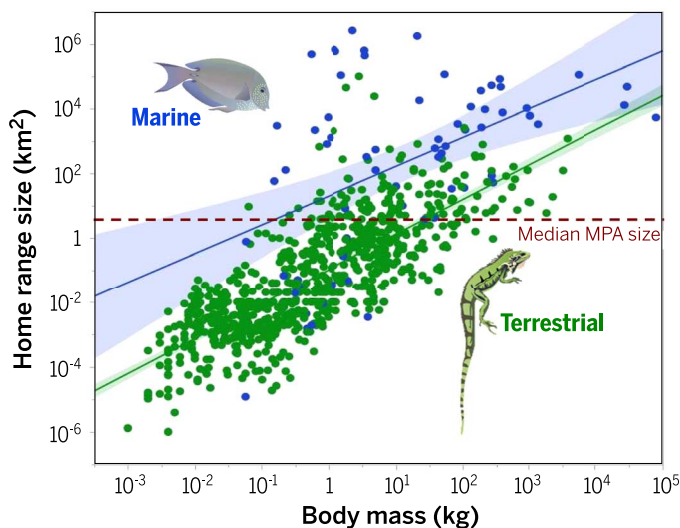
Mobility and managing defaunation

Many marine animals, on average, have significantly larger home ranges as adults [Fig. 4 and figs. S3 and S4; (8)] and disperse greater distances as juveniles than their terrestrial counterparts (13). This wide-ranging behavior of many marine species complicates the management of ocean wildlife as species often traverse multiple management jurisdictions (83–85). On the other hand, the greater mobility of many marine animal species may help them to better follow the velocity of climate change and to colonize and recolonize habitats, so long as source population refuges are kept available (71, 73, 78, 86, 87).

Marine protected areas can offer this sort of refuge for animal populations (88). The establishment of protected areas in the oceans lags far behind advancements made on land, with an upper-bound estimate of only about 3.6% of the world's oceans now protected (8) (fig. S5). One source of optimism for slowing marine defaunation, particularly for mobile species, is that the mean size of marine protected areas has increased greatly in recent years (fig. S5). However, most marine protected areas remain smaller (median 4.5 km²) than the home range size of many marine animals (Fig. 4). Though much is lost in this type of crude comparison, this observation highlights what may be an important disconnect between the scales at which wildlife use the oceans and the scale at which we typically manage the oceans.

Fig. 4. Mobility of terrestrial and marine fauna. Because mobility shapes defaunation risk, we compare the size-standardized home range size of a representative selection of marine (blue)

and terrestrial (green) vertebrates. Data are presented for adults over a full range of animal body sizes, plotted on a logarithmic scale. Species include seabirds, marine reptiles, marine fishes, marine mammals, terrestrial birds, terrestrial reptiles, and terrestrial mammals (see details in (8); table S2 and fig. S3). Regression lines enclosed by shaded confidence intervals are plotted for all marine and all terrestrial species. The dotted red line demarcates the current median size of all marine protected areas (MPAs).



This spatial mismatch is just one of many reasons why protected areas cannot be the full solution for managing defaunation (83). We learned this lesson arguably too late on land. Protected areas can legitimately be viewed as some of our proudest conservation achievements on land (e.g., Yosemite, Serengeti, Chitwan National Parks), and yet with four times more terrestrial area protected than marine protected area, we have still failed to satisfactorily rein in terrestrial defaunation (1) (fig. S5). The realization that more was needed to curb terrestrial defaunation inspired a wave of effort to do conservation out of the bounds of terrestrial protected areas (e.g., conservation easements and corridor projects). The delayed implementation of these strategies has, however, often relegated terrestrial conservation to operating more as a retroactive enterprise aimed at restoring damaged habitats and triaging wildlife losses already underway. In the oceans, we are uniquely positioned to preemptively manage defaunation. We can learn from the terrestrial defaunation experience that protected areas are valuable tools, but that we must proactively introduce measures to manage our impacts on marine fauna in the vast majority of the global oceans that is unprotected.

Strategies to meet these goals include incentive-based fisheries management policies (89), spatially ambitious ecosystem-based management plans (83), and emerging efforts to preemptively zone human activities that affect marine wildlife (90, 91). There have been mixed responses among marine managers as to whether and how to embrace these tools, but more complete implementation of these strategies will help chart a sustainable future for marine wildlife (43, 90, 91). A second, complementary set of goals is to incorporate climate change into marine protected area schemes to build networks that will provide protection for ocean wildlife into the next century (92). Such built-in climate plans were unavailable, and even unthinkable, when many major terrestrial parks were laid out, but data, tools, and opportunity exist to do this thoughtfully now in the oceans.

Habitat degradation: The coming threat to marine fauna

Many early extinctions of terrestrial fauna are believed to have been heavily influenced by human hunting (2, 93), whereas habitat loss appears to be the primary driver of contemporary defaunation on land (1, 11, 86, 94). By contrast, marine defaunation today remains mainly driven by human harvest (95, 96). If the trajectory of terrestrial defaunation is any indicator, we should anticipate that habitat alteration will ascend in importance as a future driver of marine defaunation.

Signs that the pace of marine habitat modification is accelerating and may be posing a growing threat to marine fauna are already apparent (Fig. 5). Great whale species, no longer extensively hunted, are now threatened by noise disruption, oil exploration, vessel traffic, and entanglement with moored marine gear (fig. S6) (97). Habitat-modifying fishing practices (e.g., bottom trawling)

have affected ~50 million km² of seafloor (40). Trawling may represent just the beginning of our capacity to alter marine habitats. Development of coastal cities, where ~40% of the human population lives (98), has an insatiable demand for coastal land. Countries like the United Arab Emirates and China have elected to meet this demand by “seasteading”—constructing ambitious new artificial lands in the ocean (99). Technological advancement in seafloor mining, dredging, oil and gas extraction, tidal/wave energy generation, and marine transport is fueling rapid expansion of these marine industries (43, 100). Even farming is increasing in the sea. Projections now suggest that in less than 20 years, aquaculture will provide more fish for human consumption than wild capture fisheries (101). Fish farming, like crop farming, can consume or drastically alter natural habitats when carried out carelessly (102). Many of these emerging marine development activities are reminiscent of the types of rapid environmental change observed on land during the industrial revolution that were associated

with pronounced increases in rates of terrestrial defaunation. Marine habitats may eventually join the ranks of terrestrial frontier areas, such as the American West, the Brazilian Amazon, and Alaska, which were once believed to be impervious to development, pollution, and degradation.

Land to sea defaunation connections

The ecologies of marine and terrestrial systems are dynamically linked. Impacts on terrestrial fauna can perturb the ecology of marine fauna (54) and vice versa (103). Furthermore, the health of marine animal populations is interactively connected to the health of terrestrial wildlife populations—and to the health of society. People in West Africa, for example, exploit wild terrestrial fauna more heavily in years when marine fauna are in short supply (104). It is not yet clear how these linkages between marine and terrestrial defaunation will play out at the global level. Will decreasing yields from marine fisheries, for example, require that more terrestrial wildlands be brought into human service as fields and

pastures to meet shortfalls of ocean-derived foods? Marine ecosystem managers would do well to better incorporate considerations of land-to-sea defaunation connections in decision making.

Not all bad news

It is easy to focus on the negative course that defaunation has taken in the oceans. Humans have, however, demonstrated a powerful capacity to reverse some of the most severe impacts that we have had on ocean fauna, and many marine wildlife populations demonstrate immense potential for resilience (47, 105–107). The sea otter, the ecological czar of many coastal ecosystems, was thought to be extinct in the early 1900s but was rediscovered in 1938, protected, and has resumed its key ecological role in large parts of the coastal North Pacific and Bering Sea (108). The reef ecosystems of Enewetak and Bikini Atolls present another potent example. The United States detonated 66 nuclear explosions above and below the water of these coral reefs in the 1940s and 1950s. Less than 50 years later, the coral and reef fish fauna on these reefs recovered to the point where they were being described as remarkably healthy (109).

There is great reason to worry, however, that we are beginning to erode some of the systemic resilience of marine animal communities (110). Atomic attacks on local marine fauna are one thing, but an unimpeded transition toward an era of global chemical warfare on marine ecosystems (e.g., ocean acidification, anoxia) may retard or arrest the intrinsic capacity of marine fauna to bounce back from defaunation (75, 111).

Conclusions

On many levels, defaunation in the oceans has, to date, been less severe than defaunation on land. Developing this contrast is useful because our more advanced terrestrial defaunation experience can serve as a harbinger for the possible future of marine defaunation (3). Humans have had profoundly deleterious impacts on marine animal populations, but there is still time and there exist mechanisms to avert the kinds of defaunation disasters observed on land. Few marine extinctions have occurred; many subtidal marine habitats are today less developed, less polluted, and more wild than their terrestrial counterparts; global body size distributions of extant marine animal species have been mostly unchanged in the oceans; and many marine fauna have not yet experienced range contractions as severe as those observed on land.

We are not necessarily doomed to helplessly recapitulate the defaunation processes observed on land in the oceans: intensifying marine hunting until it becomes untenable and then embarking on an era of large-scale marine habitat modification. However, if these actions move forward in tandem, we may finally trigger a wave of marine extinctions of the same intensity as that observed on land. Efforts to slow climate change, rebuild affected animal populations, and intelligently engage the coming wave of new marine development activities will all help to change the

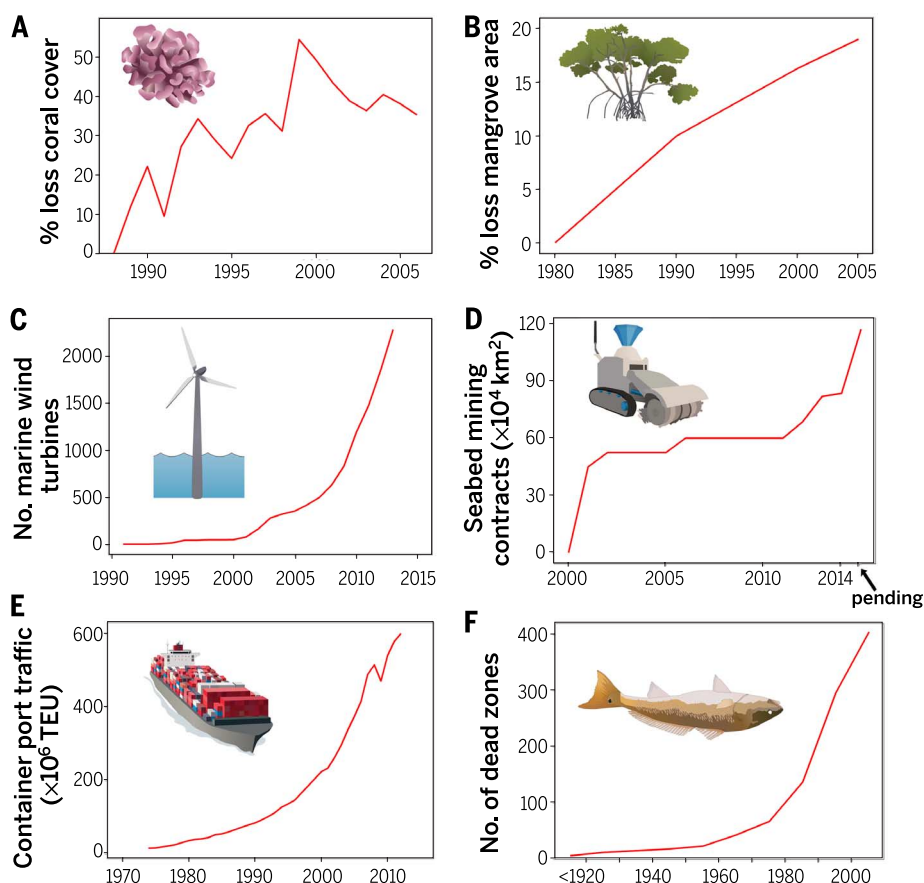


Fig. 5. Habitat change in the global oceans. Trends in six indicators of marine habitat modification suggest that habitat change may become an increasingly important threat to marine wildlife: (A) change in global percent cover of coral reef outside of marine protected areas [percent change at each time point measured relative to percent coral cover in 1988 (44)]; (B) global change in mangrove area (percent change each year measured relative to mangrove area in 1980) (117); (C) change in the cumulative number of marine wind turbines installed worldwide (118); (D) change in the cumulative area of seabed under contract for mineral extraction in international waters (119); (E) trends in the volume of global container port traffic (120); and (F) change in the cumulative number of oxygen depleted marine “dead zones.” See details and data sources in (8).

present course of marine defaunation. We must play catch-up in the realm of marine protected area establishment, tailoring them to be operational in our changing oceans. We must also carefully construct marine spatial management plans for the vast regions in between these areas to help ensure that marine mining, energy development, and intensive aquaculture take important marine wildlife habitats into consideration, not vice versa. All of this is a tall order, but the oceans remain relatively full of the raw faunal ingredients and still contain a sufficient degree of resilient capacity so that the goal of reversing the current crisis of marine defaunation remains within reach. The next several decades will be those in which we choose the fate of the future of marine wildlife.

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SUPPLEMENTARY MATERIALS

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Materials and Methods

Figs. S1 to S7

Tables S1 and S2

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