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# Megafaunal Impacts on Structure and Function of Ocean Ecosystems

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## Keywords

consumer, prey, trait-mediated effects, trophic cascades

## Abstract

Here, we identify the extant species of marine megafauna (>45 kg maximum reported mass), provide a conceptual template for the ways in which these species influence the structure and function of ocean ecosystems, and review the published evidence for such influences. Ecological influences of more than 90% of the 338 known species of extant ocean megafauna are unstudied and thus unknown. The most widely known effect of those few species that have been studied is direct prey limitation, which occurs through consumption and risk avoidance behavior. Consumer-prey interactions result in indirect effects that extend through marine ecosystems to other species and ecological processes. Marine megafauna transport energy, nutrients, and other materials vertically and horizontally through the oceans, often over long distances. The functional relationships between these various ecological impacts and megafauna population densities, in the few well-studied cases, are characterized by phase shifts and hysteresis.

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## INTRODUCTION

Large bodied animals (megafauna) have existed on Earth since soon after the rise of metazoans, some half billion years ago. Although numerous lineages arose during the Cambrian explosion, it was the chordates that led to the largest and most well-known megafaunal species. Large vertebrates radiated into virtually all global ecosystems for which production was high enough to support viable populations (1), and these radiations occurred repeatedly following mass extinction events and as particular species and lineages inevitably dwindled to extinction over the immense sweep of time. Our purpose in this review is to describe the diversity of megafaunal species in modern oceans, provide a conceptual framework for potential functional roles of these species,

and explore in more detail the known or suspected ecological consequences of this important class of life.

Any discussion of megafauna begs the question of precisely how to distinguish them from other animal species. The obvious metric for doing this is body mass, and although any point of distinction is necessarily arbitrary because of the continuous distribution of mean or maximum body mass across species, we follow maximum body size patterns reported by Lyons et al. (2) for elevated rates of Pleistocene extinction in terrestrial mammals of approximately 45 kg (100 lb) or larger. We exclude from consideration here cnidarian megafauna (e.g., colonial reef-forming scleractinian corals).

Why megafauna? We recognize four general attributes of megafauna that make them deserving of a dedicated review. First, these organisms typically consume large amounts of biomass, thereby potentially impacting trophic dynamics as a result of this uptake. And what is absorbed by megafauna must be excreted—consequently, this class of species is also responsible for profoundly shaping patterns of spatial redistribution of nutrients and energy in a fashion that can have important consequences on ecosystem ecology (3, 4). Second, given established positive relationships between body size and space use (5), individual megafauna often range widely, thereby connecting ocean ecosystems over large spatial scales and potentially stabilizing meta-ecosystem dynamics (6). Third, by virtue of their large size, megafauna often interact in mechanically powerful ways with ecosystems and physically reengineer and structurally modify these affected systems as a result of locomotion and foraging (3, 7). Lastly, and perhaps most obviously, megafauna are charismatic, which translates into enhanced social, historic, and economic values. These values can work both to the advantage (e.g., motivating conservation) and disadvantage (e.g., accelerating demand for rare, high-value species) of marine megafauna. Increasing our knowledge of the ecological influence of megafauna better positions us to assess and manage these types of values.

Megafauna profoundly influence the ecology of terrestrial, marine, and freshwater ecosystems. In this review, we focus specifically on megafauna in marine ecosystems because they differ from their freshwater and terrestrial counterparts in at least four interesting ways. First, megafauna have a longer evolutionary history in the oceans than they do in either freshwater or terrestrial ecosystems. Although some early marine forms may have radiated soon thereafter into freshwater environments, the ephemeral nature of even large lakes and rivers through geological time, and the inability of smaller bodies of water to support larger-bodied species of higher trophic status (8) is a clear dichotomy between marine and freshwater ecosystems. The appearance of the first megafauna on land occurred with the rise of large Permian terrestrial tetrapods, nearly 300 Mya (9).

Second, the evolution of marine megafauna was characterized by a cumulative progression of the major vertebrate taxa, from cartilaginous and bony fishes to reptiles to birds and mammals, all of which occur in the extant marine megafauna, whereas terrestrial megafauna were comprised exclusively of reptiles during the early period (from about 250 to 60 Mya) and birds, reptiles, and mammals thereafter. The extant terrestrial megafauna are mostly mammals, although these fauna are taxonomically and functionally diverse, whereas the modern marine avian and reptilian megafauna are impoverished.

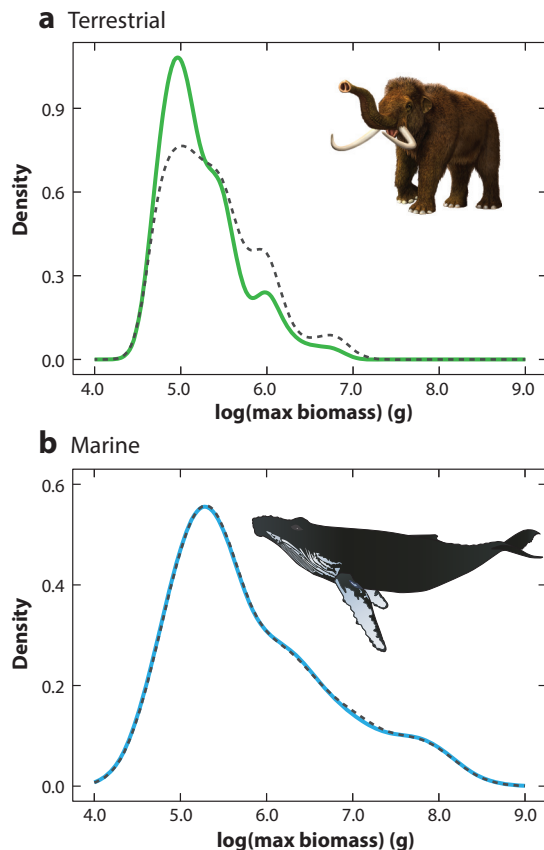
Third, from the late Pleistocene onward, approximately half of the world's terrestrial megafauna were lost to extinction, whereas the Pleistocene marine megafauna remain much less affected, at least at the level of species. This comparatively intact nature of marine megafauna is evident when the body size distribution of Pleistocene megamammals is compared to the distribution of extant megamammals in both terrestrial and marine systems (**Figure 1**). Extant terrestrial megamammals are significantly smaller than their Pleistocene counterparts ( $D = 0.15, p < 0.01$ ), but there is no such difference apparent in the oceans ( $D = 0.01, p = 1$ ). Only three known marine megafaunal

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**Cnidarian:** a member of a phylum (Cnidaria) of predominately marine species whose most distinguishing feature is modified cells for capturing prey

**Scleractinian:** refers to hard or stony corals

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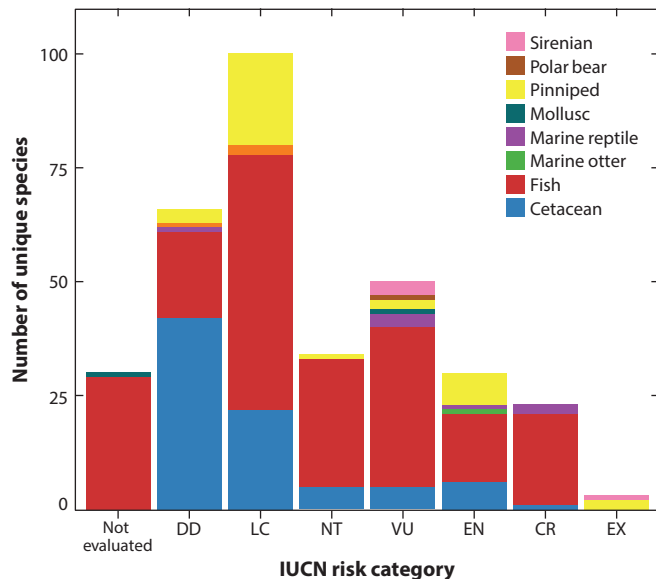


**Figure 1**

(a) Terrestrial and (b) marine mammal megafaunal ( $\geq 45$  kg) mammal body size distributions during the late Pleistocene (gray dashed line) and present day (green, terrestrial; blue, marine). The loss of many terrestrial Pleistocene megafaunal species significantly altered terrestrial body size distributions between the Pleistocene and the present ( $D = 0.15$ ,  $p < 0.01$ ). No such differences are observable in the ocean, suggesting that modern marine megamammals are effectively as large as they were during the Pleistocene ( $D = 0.01$ ,  $p = 1$ ). Humpback whale image from T. Saxby, IAN Image and Video Library, Integration and Application Network (IAN), University of Maryland Center for Environmental Science (<http://ian.umces.edu/imagelibrary/>); mammoth image from Ozja/Shutterstock.com.

extinctions occurred during this period, all quite recently: the Caribbean monk seal (*Neomonachus tropicalis*) was last seen in 1952, the Japanese sea lion (*Zalophus japonicus*) disappeared in the 1970s, and Steller's sea cow (*Hydrodamalis gigas*) survived until at least 1768 (Figure 2). These relatively low rates of global marine megafaunal extinction obscure the risk of extinction faced by many such species. The International Union for Conservation of Nature (IUCN) has designated numerous species of marine megafauna, across most major taxonomic classes, as being at risk of extinction (10) (Figure 2). The observation that most modern marine megafauna have not been driven extinct by human activity and yet their future may be tenuous is a strong motivator to better describe their ecological role in the oceans.

Finally, although megafauna have suffered across the globe from exploitation and habitat destruction (11–14), range reductions and population declines are often more extensive on land than



**Figure 2**

Distribution of extinction risk for marine megafauna. Risk data are drawn from the International Union for Conservation of Nature (IUCN) (10). Only three species of marine megafauna are recognized as having been driven extinct in the last 515 years, but numerous megafaunal species are categorized as being at risk of extinction. The group with the largest absolute number of at-risk species is marine fishes, but this is also the most species-rich group of ocean megafauna. IUCN risk categorizations are as follows (in order of increasing severity): LC, least concern; NT, near threatened; VU, vulnerable; EN, endangered; CR, critically endangered; and EX, extinct. DD indicates species for which data are deficient.

in the sea (5). Large predators and megaherbivores, in particular, are now absent from most terrestrial environments (13, 14). In contrast, the ocean’s megafauna—cetaceans, pinnipeds, reptiles, and fishes—can still be found throughout much of their natural ranges, albeit often in depressed numbers.

Despite the charismatic nature of marine megafauna, much remains to be learned about these animals. Close to 10 new species of cetaceans have been described in the last several decades, and the giant squid (*Architeuthis dux*, >15 m in length) was only first filmed alive in its natural habitat in 2013 (15). The proposition of newly discovering and viewing 15-m-long megafauna on land is nearly inconceivable and highlights the paucity of information on marine megafauna. Here, we review what information is now available about the ecological influence of megafauna in the global oceans and highlight important gaps in our understanding of this critically important group of organisms.


## MARINE MEGAFUNA

In contrast with the terrestrial realm, where habitats have been divided into biomes based largely on patterns of variation in temperature, precipitation, and dominant plant communities, marine habitats have been categorized relative to their oceanography and bottom types (e.g., water column versus benthic, seasonally or permanently frozen versus unfrozen, continental shelf versus oceanic, reef versus soft sediment, and shallow water versus deep sea). Regardless of how marine ecosystems are categorized, marine megafauna occupy and move between all ecosystem types.

**Biome:** a vegetation type (e.g., tropical rain forests) determined largely by temperature and precipitation

**Benthic:** refers to the bottom of a body of water

**Forage fish:** typically small schooling fishes that are fed on by larger organisms

 **Supplemental Material**

## Cetaceans

There are currently more than 80 recognized species of cetaceans (whales, dolphins, and porpoises), which occur throughout the world's oceans (**Supplemental Table 1**; follow the **Supplemental Material link** in the online version of this article or at <http://www.annualreviews.org/>). The mysticetes (large baleen whales) are migratory, typically foraging in shallow waters at higher latitudes and returning to lower latitudes to calve. Most mysticetes feed on schooling crustaceans (e.g., krill, mysids, amphipods) or forage fish (e.g., herring, capelin, sardines, anchovies). A few, like the gray whale (*Eschrichtius robustus*), are primarily shallow benthic foragers. Mysticetes include the largest of the extant marine megafauna. The blue whale (*Balaenoptera musculus*, up to 180,000 kg) is thought to be the largest animal ever to have lived on earth, outweighing even the largest known sauropod dinosaurs (up to 65,000 kg). The odontocetes (toothed whales) are more diverse in body size and foraging ecology. Some, like sperm and beaked whales, dive to depths in excess of 2,000 m and remain submerged for more than 1 hour during foraging dives. The sperm whale (*Physeter microcephalus*) is the largest predatory species ever known. Other species, like killer whales (*Orcinus orca*) and the schooling tropical dolphins, are shallow divers, seldom exceeding depths of 300 m or dive durations of 10 min. Odontocetes are diverse foragers, which depending on species and individual preferences, may consume prey from as small as krill and forage fish to as large as blue whales. Small odontocetes occur throughout the world's oceans and even in large rivers. Despite enormous public interest in this group of megafauna, there remains a deficiency of data on the conservation status of many cetaceans (**Figure 2**).

## Pinnipeds

The Pinnipedia contains more than 30 extant species in three families (Phocidae, true seals; Otariidae, eared seals; and Odobenidae, walruses) (**Supplemental Table 1**). Except for two extant species of tropical monk seals, most pinnipeds live in temperate to polar environments. Depending on species, pinnipeds tend to feed on schooling fishes, benthic invertebrates, and squid. Some occasionally consume larger fishes, such as Pacific halibut (*Hippoglossus stenolepis*) and Antarctic toothfish (*Dissostichus mawsoni*). One species, the leopard seal (*Hydrurga leptonyx*), feeds on seabirds and large marine mammals but also has the capacity to filter feed on small krill (16).

## Sirenians

The Sirenia includes four extant species, dugongs (*Dugong dugong*) and three species of manatees (*Trichechus* spp.). All are tropical/subtropical in distribution. Dugongs feed mainly on seagrasses in shallow waters of the Indo-Pacific region. Although manatees occasionally enter the open sea, they occur more commonly in rivers and estuaries.

## Marine Otters

Although various otter species range into coastal marine environments at higher latitudes around all continents except Australia, the sea otter (*Enhydra lutris*) is the only one of these to qualify as marine megafauna (maximum recorded body mass of 53 kg). Sea otters occur in shallow coastal waters across the temperate to boreal North Pacific Ocean, where they feed on a diverse array of benthic invertebrates and occasionally fish (17).

## Polar Bears

Polar bears (*Ursus maritimus*) occur across the permanently to seasonally frozen Arctic marine realm, denning on land or shore-fast ice and foraging across the shore-fast and seasonal pack ice. Although polar bears are known to consume a wide array of marine and terrestrial plants and animals, they feed mostly on ice-inhabiting pinnipeds, especially ringed seals (*Pusa hispida*).

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**Trophic level:** the position of a species in a food web based on diet and relative to autotrophs (plants)

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## Primates


Although *Homo sapiens* is of course a predominantly terrestrial species, like the polar bear it has expanded into marine habitats and evolved very efficient hunting techniques there. In fact, the exploitation rate of humans on their marine prey is on average more than 14-fold higher than that of the average nonhuman marine predator (18). Due to these intense aggregate effects, we believe it is fair to include humans as marine megafauna.

## Seabirds

Whereas a diversity of seabird species occur in abundance across the world's oceans, only one of these (the Emperor penguin, *Aptenodytes forsteri*), with a maximum reported body mass of approximately 45 kg, qualifies as megafauna by our definition. We note the occurrence of quite large extinct seabird species (e.g., *Palaeudyptes klekowskii*, a 115-kg penguin, Eocene; *Pelagornis sandersi*, an albatross with a 7-m wingspan, Oligocene). Given the impoverished state of extant avian megafauna, we do not include seabirds in this review.

## Marine Reptiles

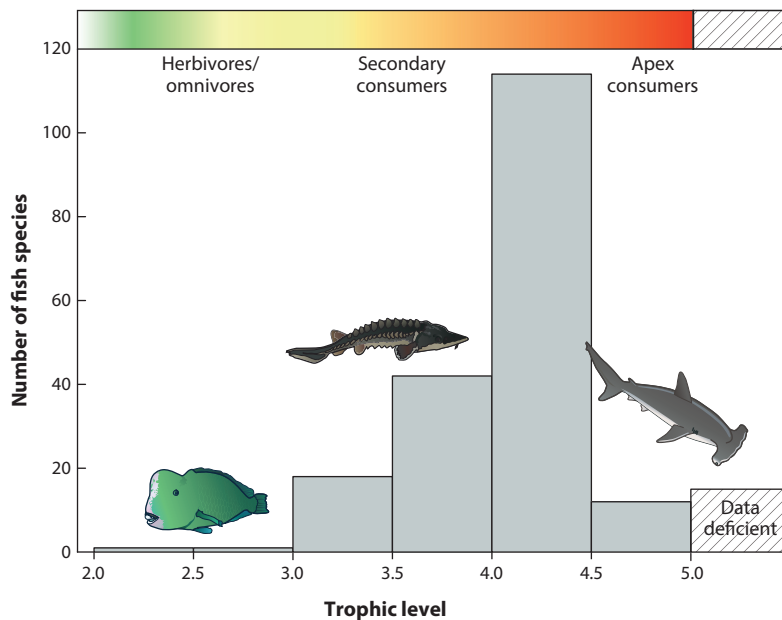
Late Paleozoic and Mesozoic oceans contained a diversity of reptilian megafauna, most notably ichthyosaurs, plesiosaurs, marine turtles (superfamily Cheloniodea), and crocodylomorphs (marine crocodiles and alligators). Many of these species were predators. Marine turtles and crocodylians are the only surviving marine reptilian megafauna. There are seven extant species of marine turtles (**Supplemental Table 1**), most of which are omnivores that consume a wide variety of algae and invertebrates. Except for leatherbacks, which range into higher-latitude oceans as adults, all extant marine reptiles are largely confined to tropical/subtropical oceans.

 **Supplemental Material**

## Fishes

Piscine megafauna occur in the Chondrichthyes (sharks, skates, and rays) and Osteichthyes (bony fishes), both of which have distinct evolutionary histories from the early to mid-Paleozoic, some 450 Mya. Seventy-two extant species of cartilaginous fishes and 129 species of bony fishes qualify as megafauna by our criterion (**Supplemental Table 1**). Members of both classes occur throughout the world's oceans, from surface waters to the deep seas. These megafaunal fishes span several trophic levels (**Figure 3**). Some species of piscine megafauna, similar to some of the cetaceans, may consume prey as small as plankton, whereas others take prey as large as pinnipeds and odontocetes. The majority of piscine marine megafaunal species are top predators. Marine fish make up the largest proportion of ocean megafauna that are classified by the IUCN as either endangered or critically endangered, but they are also the most speciose group of marine megafauna (**Figure 2**).





**Figure 3**

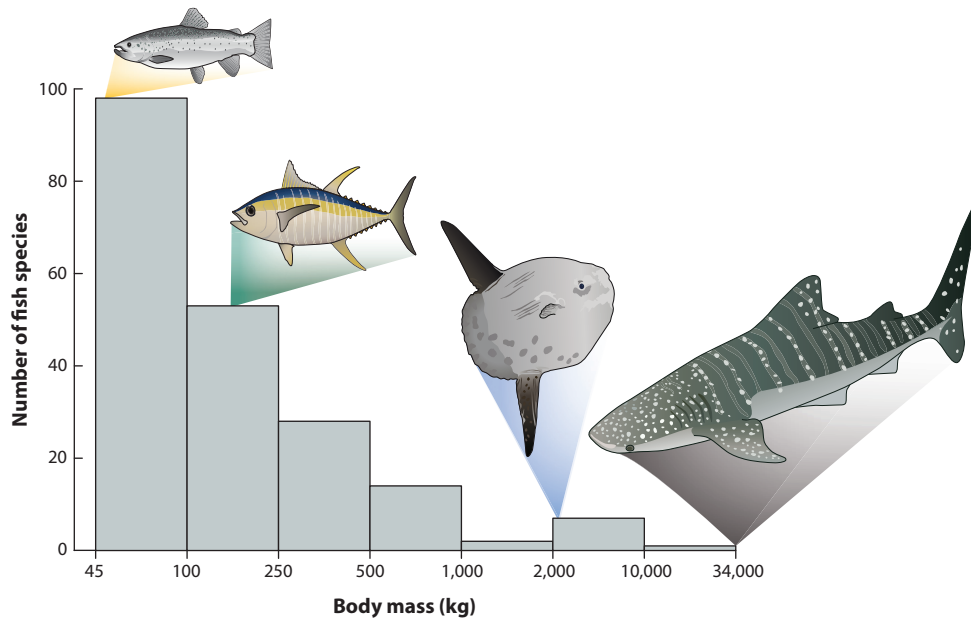
Histogram of the trophic level of marine megafaunal fishes. Most megafauna marine fishes are high-level predators, but a diverse array of feeding modes (e.g., herbivores, filter-feeding planktivores, and omnivores) are present. Trophic-level data were obtained from FishBase (152) for all marine and brackish water fishes  $\geq 45$  kg. Parrotfish, hammerhead, and sturgeon images from T. Saxby, IAN Image and Video Library, Integration and Application Network (IAN), University of Maryland Center for Environmental Science (<http://ian.umces.edu/imagelibrary/>).

The largest-bodied marine fish species are now extinct. *C. megalodon* (a mid-Miocene to late Pliocene lamnid shark) and *Leedsichthys problematicus* (a mid-Jurassic bony fish from the extinct Pachycormidae) represent the largest known cartilaginous and bony fish species, respectively, with estimated body lengths in excess of 15 m. Although approximately half of the extant piscine megafaunal species do not exceed a maximum size of 100 kg, this modern assemblage does include an impressive representation of extremely large fishes; the whale shark (*Rhincodon typus*) grows to 16 m in length and 34 tonnes in weight (**Figure 4**).

## Molluscs

The only invertebrates that qualify as megafauna by our classification are a small number of molluscan species—teuthid (squid) and octopod (octopi) cephalopods, and a single bivalve. The largest molluscan species (*Architeuthis* spp., giant squids; *Mesonychoteuthis hamiltoni*, colossal squid, reported maximum mass approximately 500 kg) reside primarily in the deep sea and are thus poorly known. Humboldt squid (*Dosidicus gigas*), a highly predatory species in the eastern North and South Pacific oceans, attain a maximum size of approximately 50 kg. The largest octopods (*Octopus dofleini*) can reach a body mass of 70 kg. Giant clams (*Tridacna gigas*), which occur in shallow waters of the tropical western Pacific and Indian oceans, reportedly attain a mass of  $>200$  kg, although most of this mass is calcified exoskeleton.

**Lamnid:** refers to sharks of the family Lamnidae



**Figure 4**

Histogram of the maximum body mass of marine megafaunal fishes. Body mass data were drawn from FishBase (152) for fishes  $\geq 45$  kg that were present in either marine or brackish water habitats. In instances where maximum body mass data were not reported, mass was estimated using reported maximum-length values and length-weight relationships. The highest number of megafaunal fishes reach maximum weights of  $< 100$  kg, but marine fishes weighing up to 34,000 kg remain extant. Salmon image from J. Hawkey, IAN Image and Video Library; tuna, ocean sunfish, and whale shark from T. Saxby, IAN Image and Video Library, Integration and Application Network (IAN), University of Maryland Center for Environmental Science (<http://ian.umces.edu/imagelibrary/>).

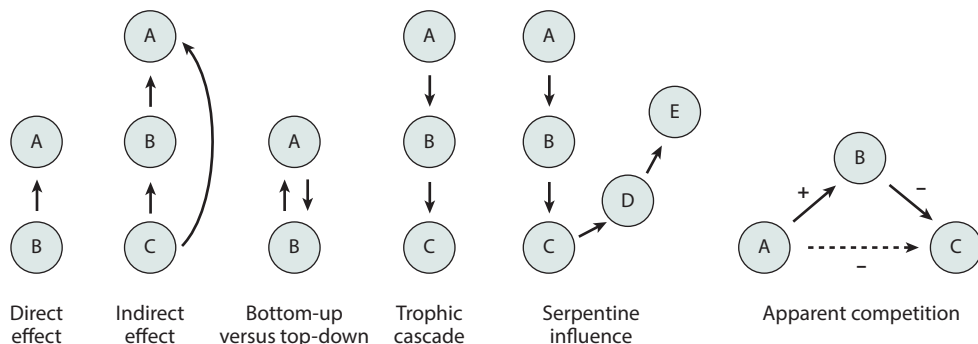
## A TAXONOMY OF FUNCTION

Our central purpose in this review is to characterize the ecological roles of ocean megafauna. To do this, we first provide an overview of potential ecological functions—descriptions of the way in which species (megafauna in this particular case) can influence associated species, communities, and ecosystems. The three fundamental elements in this view of nature are the physical environment, species, and species interactions. A general model of ecological function is thus well served by the idea of an interaction web (19), which defines linkages (interactions) among species and between these species and their physical environment. The more widely recognized idea of a food web, a road map of who is eaten by whom (20), is embedded in this more encompassing notion of an interaction web. We have chosen to frame our discussion of the ecological influences of megafauna in the context of interaction webs rather than food webs because important interactions among species are not necessarily trophic (although most are), and species interactions can feed back to influence the abiotic environment. In the remainder of this section, we define what we believe to be the more important structural and functional properties of interaction webs.

### Direct Versus Indirect Interactions

Linkages between species can be direct (no intervening species) or indirect (one or more intervening species) (Figure 5). The number of potential indirect interactions is vastly greater than

**Interaction web:**  
the network of interactions among species and their physical environment



**Figure 5**

Schematic of some of the ways in which species (or functional groups) can interact with one another. By our definition, serpentine influences involve both relatively long interaction chains and changes of direction (i.e., from bottom-up to top-down, or vice versa) or changes in the nature of species interactions (e.g., from predator-prey to competitive).

the number of potential direct interactions in all but the most simple interaction webs (21). Indirect interactions can potentially link up across numerous species, creating what we refer to as serpentine pathways.

### Drivers Versus Recipients

Many interactions among species and between species and the elements of their abiotic environments are asymmetrical, which means that one member of the interacting pair is a driver and the other a recipient. The loss or reestablishment of drivers should have stronger effects on ecosystem structure and function than loss or reestablishment of recipients.

### Interaction Strength

The functional importance of species usually covaries positively with interaction strength (22), defined most simply as the difference in abundance of a recipient species ( $R$ ) when the driver is present ( $R_{dp}$ ) versus when the driver is absent ( $R_{da}$ ). Interaction strength is also defined on a per capita basis as  $(R_{dp} - R_{da})/D$ , where  $D$  is driver abundance. When  $(R_{dp} - R_{da})$  and  $D$  are both large, the driver is referred to as a dominant species; when  $(R_{dp} - R_{da})$  is large and  $D$  is small, the driver is referred to as a keystone species (23).

### Bottom-Up Versus Top-Down

Trophic interactions, which necessarily define much of an interaction web's structure and function, vary fundamentally depending on which member of the consumer-prey pair is the driver and which is the recipient. When prey are drivers of the distribution and abundance of their consumers (through maintenance, growth, and reproduction), the interaction web is said to operate through bottom-up control, thus implying that net primary production (NPP) and the efficiency of energy and material transport upward across trophic levels primarily control the distribution and abundance of species. Conversely, when consumers are drivers, the interaction web is said to operate through top-down control, meaning that either mortality or behavioral effects imposed by consumers on prey are the important controlling processes. All interaction webs operate to a

**Driver:** a species with a strong influence on the distribution and abundance of other species

**Keystone species:** a comparatively rare species with large effects on the distribution and abundance of other species

greater or lesser degree through both bottom-up and top-down control. Marine megafauna can influence both processes.

## Emergent Properties

Strong bottom-up control results in ecosystems (interaction webs) in which the distribution and abundance of species are largely predictable from two processes, primary production and transfer efficiency across trophic levels. Under this condition, the qualitative relationship between consumers and prey is always the same, regardless of trophic status or food chain length. That is, prey are always the drivers and consumers the recipients, so that the nature of interactions upward across trophic levels is neutral for prey and positive for consumers. Variation in primary production has a uniform enhancing or reducing effect on all species, irrespective of trophic status or position in the interaction web.

Strong top-down control, or the mixing of bottom-up and top-down control, often creates qualitative variation in the nature of species interactions (**Figure 5**). For example, increasing food chain length by one trophic level by adding a new apex predator alters the strength of direct consumer-prey interactions throughout the food web, thus shifting the strength (from weak to strong, or vice versa) of all direct trophic interactions and the sign (from negative to positive, or vice versa) of all indirect trophic interactions. Top-down influences by a species of high trophic status downward through a food web is known as a trophic cascade (24). Bottom-up forcing can also modulate the relative abundance of multiple prey species for a common predator through apparent competition (25) (**Figure 5**), whereby one prey species may be eliminated (or its abundance greatly reduced) in a habitat by a predator that is attracted to an alternative prey species that is able to persist in the presence of the shared predator. Additional variation in food web structure based on indirect effects and directionality of forcing is discussed in greater detail by Schoener (26) and Estes et al. (21).

## Scale

To observe and document the ecological influences of marine megafauna, one must understand the spatial and temporal scales over which controlling processes operate. Most marine megafauna are highly mobile (27), and even weakly motile or sedentary species of marine autotrophs and invertebrates (e.g., phytoplankton, kelp, corals), which are key elements of the ecosystems within which marine megafauna live and interact, have dispersive life stages that sometimes move great distances across oceans via currents and internal waves (28). Generation times for marine megafauna are typically long (this is especially true for marine turtles and marine mammals), thus limiting the rates at which populations can recover from depletions. The capacity to interact with widely separated systems can act to space out the interactions of megafauna in time as well. Transient populations of killer whales visit islands or atolls at intervals of years or longer; tiger sharks may arrive annually to reefs. These brief interactions, though hard to observe and study, may still be ecologically consequential. As a general rule of thumb, the spatial and temporal scales over which the ecological influences of marine megafauna occur (and thus can be observed and documented) are large (e.g., 1–10,000 km, weeks to decades).

## Modularity

As with any network, interaction web structure and function are often influenced by modularity, the tendency of nodal elements (species and abiotic elements) to aggregate such that the resulting groupings are strongly interconnected within groups but more weakly connected among groups.

---

**Trophic cascade:** the propagation of indirect effects of higher trophic-level consumers downward through a food web

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**Phase shift:** a rapid shift between states of an ecosystem

**Hysteresis:** the condition in which a functional relationship follows different specific pathways depending on directionality

## Direct Predation Versus Risk Effects

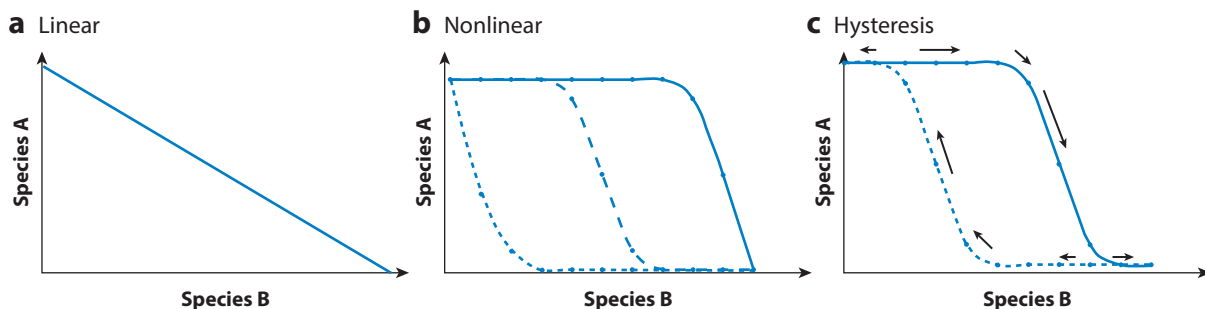
Consumers can influence their prey through two distinct but often interacting processes: direct predation (also called consumptive effects) and risk effects (also called trait-mediated, or nonconsumptive, effects) (see 26–28). Consumer effects can be manifested through demographic consequences to their prey from being eaten (or injured), but the risk of predation can also influence prey population sizes by inducing costly physiological or behavioral changes that affect access to food resources. These predator impacts on prey often interact, and the relative strength of risk effects and those of direct predation may be mediated by the degree of resource availability and body condition of prey (29). For trait-mediated effects, the influences of consumers on their prey behavior and the knock-on influences to the interaction web have together become known as the ecology of fear (30–32). Importantly, risk effects may be strong even for prey species that are rarely successfully captured by a predator. Therefore, a particular predator does not have to be a primary mortality source for a given prey species and that prey species does not have to be common in the diet of the predator for there to be strong top-down effects (33, 34).

## Functional Relationships

As ecological drivers, megafauna exert influences on their ecosystems that might vary linearly or nonlinearly with population size or density. Nonlinear relationships between megafaunal density and ecological function can in turn cause abrupt phase shifts and result in hysteresis (Figure 6) and alternative stable states in the composition of communities (35).

## Biodiversity

The aforementioned processes interact to influence ecosystems and biodiversity in various ways. One of these is through the creation of biogenic habitat for other species. Another is through the selective consumption of competitive dominants, thus enhancing biodiversity through the prevention of competitive exclusion. Abundant marine megafauna may also provide food and detritus for other species. Additionally, these megafauna can transfer energy and materials (e.g., carbon or key limiting nutrients) horizontally (following migrations and other long-distance movements) and vertically (from the deep sea to surface waters via diving/foraging, or vice versa via whale falls), thereby influencing ecosystem processes and biodiversity.



**Figure 6**

Hypothetical functional relationships between the abundance of ecological drivers (species B) and recipients (species A): (a) linear, (b) nonlinear, (c) hysteresis. Line styles simply indicate differing trajectories in state space. Arrows represent directionality.

## APPROACHES TO UNDERSTANDING ECOLOGICAL FUNCTION

Understanding the ecological function of any species in nature is a two-step process. The first step is to describe the interaction web and, in particular, how the species of interest is linked to the interaction web's various nodes. Normally, this is done by chronicling trophic relationships through, for example, foraging observations, visual or genetic analyses of gut content, fecal analyses, isotope and fatty acid analyses for food web structure, and a general knowledge of the species' physiology, behavior, and natural history. The second step is to characterize the dynamic nature of these linkages. Dynamic process (i.e., direct and indirect responses of recipients to drivers) usually cannot be inferred from static systems with any degree of confidence. Understanding interaction web dynamics thus requires that drivers be perturbed and the various recipients' responses observed and measured in such a manner that those responses can be ascribed to the driver with reasonable confidence. The most powerful way of doing this is through purposeful experimental manipulations wherein the purported driver is varied in a replicated and well-controlled way. Such experimental manipulations of marine megafauna have been attempted (36–39) and yielded some important insight, especially when combined with observational approaches and meta-analysis (39). However, these experiments are also logistically challenging, especially when attempting to determine impacts on mobile prey (40). Therefore, most of what is known about the ecological functions of these animals, and what is likely to be known about them in the future, must be founded on some other approach.

Two general approaches have been employed in the large majority of studies on the ecological roles of marine megafauna. One of these is through what are often referred to as natural or quasi-experiments, wherein changes to the interaction web's structure are noted following the nonpurposeful or fortuitous addition or removal of the hypothesized megafaunal driver. This has been done in two primary ways: by analyses of data from systems in which the megafaunal species of interest varies through time and as spatial contrasts of otherwise similar ecosystems in which the megafaunal species of interest is present or absent. The time series approach has been applied at three scales: (a) short term (behavioral), wherein dynamic processes are inferred from seasonal changes in the distribution and abundance of megafauna; (b) midterm (demographic), wherein processes are inferred with the population growth or decline of megafauna; and (c) long term (historical), wherein information from biological, archaeological, and geological archives is used to infer the presence, absence, or relative abundance of megafauna and their associated influences on interaction web dynamics. Such inferences are potentially confounded by extraneous temporal and spatial variation that is not attributable to the ecological influences of megafauna. One solution to this difficulty is replication, whereby multiple independent time series or spatial contrasts are combined in a meta-analysis of species interactions (41, 42) or where seasonal variation in the presence of megafauna may vary across years (43, 44). The spatial contrast approach has often been used along gradients of varying fishing pressure (e.g., archipelagos with different human settlement histories and population sizes) or inside and outside of protected areas (44, 45). Spatial comparisons of this type, though often informative, can be problematic if the units of comparison are not sufficiently separated to prevent the intermixing of vagile megafauna. As explained further below, this is one of the key reasons why the ecological impacts of sea otters (a comparatively sedentary species) have been relatively easy to discern whereas those of killer whales (a highly mobile species) have been more difficult.

The second general approach that has been used in an attempt to understand the ecological roles of marine megafauna is ecosystem modeling. In this case, dynamic influences of drivers on recipients are imagined as functional relationships and then estimated from quantitative or qualitative algorithms based on demographic processes (e.g., the mortality effects of a consumer on

its prey, or the growth and reproductive effects of a prey on its consumer) and/or the flux and balance of materials (e.g., carbon or various nutrients) and energy. The Ecopath/Ecosim family of models is a well-known example of this approach, although there are others, some of which operate in different ways (46, 47). Generally, it is considered best practice to compare results from different models, again providing a form of independent replication to hedge against weaknesses and assumptions of any particular model structure (48). A major shortcoming in contemporary marine megafaunal science has been the inability to compare patterns derived from purely theoretical models with empirical data. Given this frequent disconnect, our review here forward will consider only published examples for which there are data from natural or quasi-experiments.

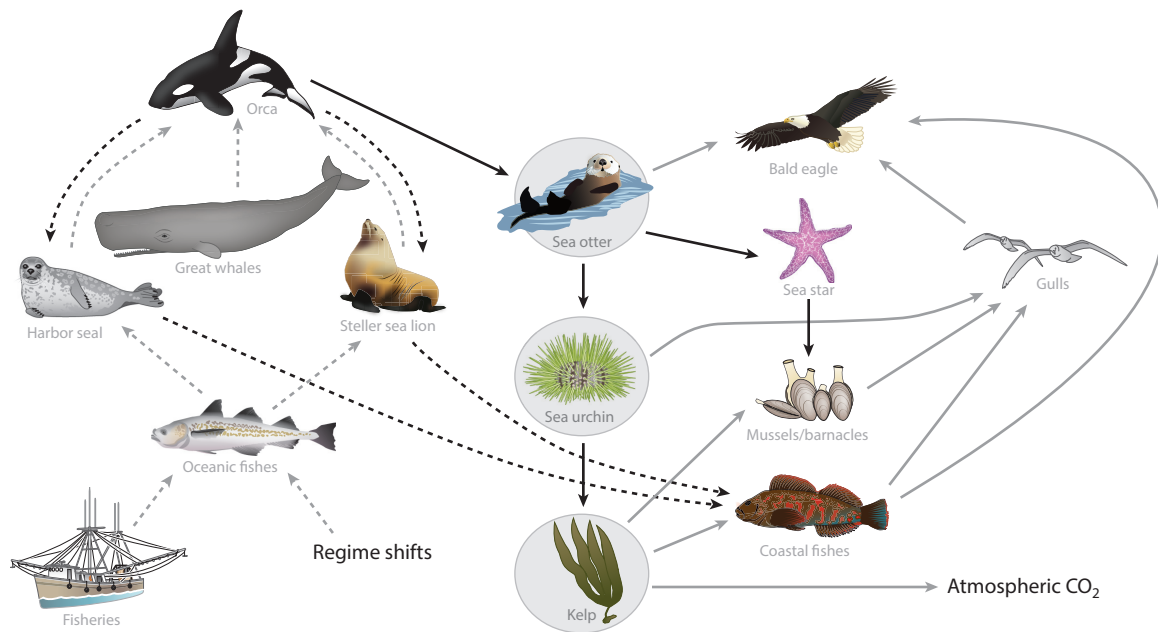
## CASE STUDIES

### Marine Mammals

Extant marine mammals are represented by five independently evolved species or groups of species. Their ecological influences are discussed below.

**Marine otters.** Sea otters (*Enhydra lutris*) provide what is arguably the most extensively studied and best-known example of ecological influences by a marine megafaunal species. This is due in large measure to five particular attributes of sea otters and their associated ecosystems. One attribute is history. Sea otters were exploited to near extinction during the Pacific maritime fur trade, after which populations recovered in areas with surviving remnant colonies but remained absent in nearby areas in which the species had been driven to complete extinction. Half a century later, after many of the surviving remnant colonies had grown to large sizes, translocations were used to establish additional colonies. The ecological influences of sea otters were identified by comparing nearby areas in which the species was present or absent, and by observing change at particular locations as otter populations waxed or waned through time. A second attribute is replication. The aforementioned historical patterns played out repeatedly across the sea otter's natural range, from the northern Japanese archipelago, across the Pacific Rim, to the central Pacific coast of Baja California, Mexico. A third, key attribute is the tendency of individual otters to live their entire lives within relatively small home ranges. This particular feature of the species' natural history, which is unusual for marine megafauna, prevents large-scale diffusion and mixing with population recovery, thereby maintaining high levels of spatial granularity in nearshore ecosystems with and without sea otters. Two final attributes of the system are the ease with which other key elements of the sea otter's interaction web (e.g., macroalgae, benthic macroinvertebrates, reef fish, etc.) can be observed and measured and the capabilities of these species to recover quickly following pulse perturbations or relaxation from press perturbations.

The sea otter's ecological influence has been studied and chronicled in all three major ecosystem types in which it occurs, rocky reefs, soft-sediments, and estuaries (**Figure 7**). In all cases, the principal driver of ecosystem change is a strong reduction of macroinvertebrate size and density by sea otter predation. In kelp forest systems, this direct predator-prey interaction spreads through the interaction web via two currently known pathways (**Figure 7**): from herbivorous macroinvertebrates (commonly sea urchins but also molluscs) to kelp and other macroalgae, and from predatory asteroids to their various invertebrate prey. The otter-macroherbivore-kelp pathway (a trophic cascade), which transitions as an abrupt phase shift between lush algal forests and deforested barrens with varying sea otter density (49–51), in turn influences numerous other species and ecological processes in coastal ecosystems (**Figure 8**). NPP is greater where sea otters are sufficiently abundant to force the kelp-dominated phase state, thus fueling elevated secondary production



**Figure 7**

Depictions of some of the sea otter's serpentine linkages and influences in North Pacific Ocean ecosystems. Both top-down (*black arrows*) and bottom-up (*gray arrows*) forcing are depicted, with a distinction made between known or reasonably well-documented effects (*solid arrows*) and those that are more speculative (*dashed arrows*). Elements to the left of the otter–sea urchin–kelp trophic cascade represent the oceanic realm, whereas elements to the right are for the coastal ocean.

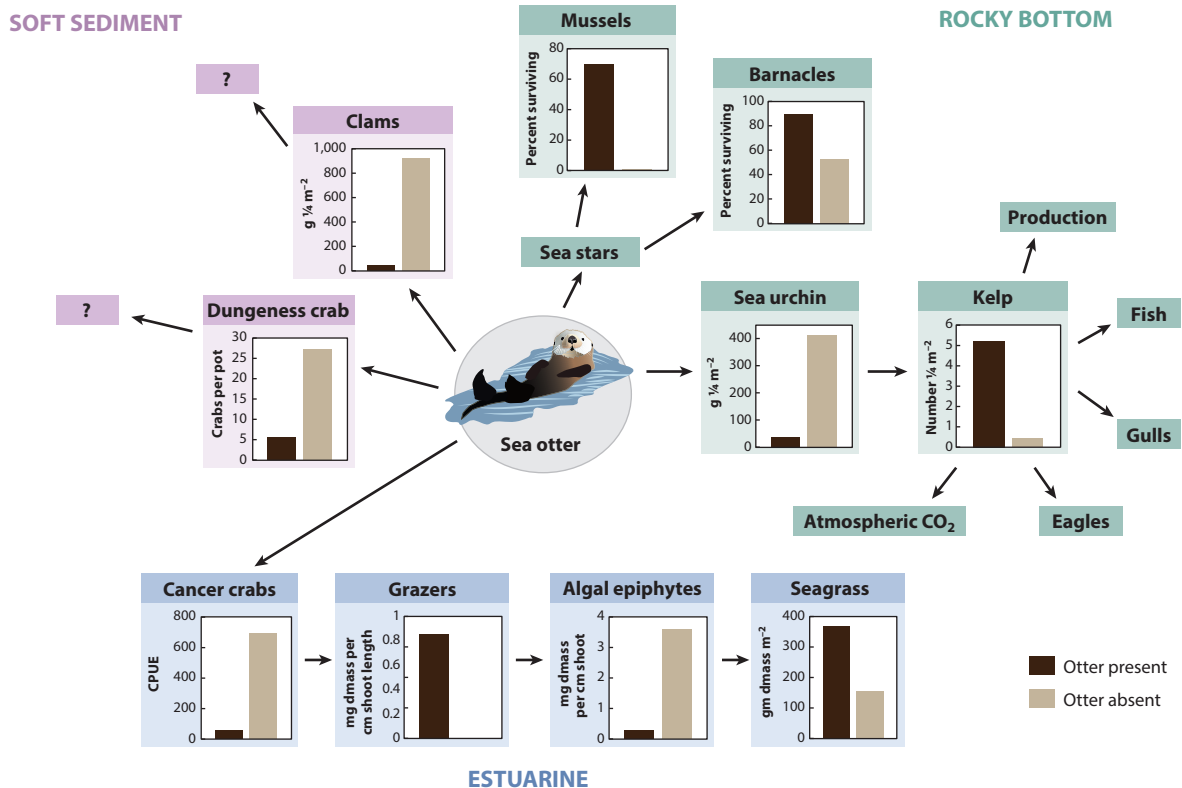
through kelp and a detritus-based food web. Growth rates of suspension-feeding invertebrates are two- to threefold greater in forested compared with deforested systems (52); fish population densities are significantly enhanced where systems are in the forested state (53, 54); and the diets and foraging behaviors of other high trophic-level consumers are strongly influenced by the sea otter–sea urchin–kelp trophic cascade. For example, glaucous-winged gulls (*Larus glaucescens*) switch from piscivory to invertebrivory where sea otters are lost from coastal ecosystems (55); bald eagle (*Haliaeetus leucocephalus*) diets shift from a roughly even mix of marine mammals, fish, and seabirds where otters are abundant to one that is more strongly comprised of seabirds where otters are absent (56). Dense kelp forests in systems with sea otters also draw down CO<sub>2</sub> from the overlying atmosphere, thus potentially influencing carbon sequestration (depending on the rate of organic carbon remineralization from kelp detritus and the extent to which kelp detritus is transported into the deep sea) and the carbon dioxide–bicarbonate balance and pH in the surrounding sea water (57). By preying on predatory asteroids, sea otters reduce asteroid-induced mortality rates in filter-feeding mussels and barnacles (58).

Sea otters have comparably strong limiting influences on bivalve molluscs (59) and decapod crustaceans (60) in soft-sediment ecosystems (**Figure 8**). Indirect knock-on effects to other species and processes in these soft-sediment systems, though probably important, are largely unknown.

Seagrass-dominated estuarine systems are also influenced by sea otters that consume predatory decapods, which in turn feed on algivorous isopods and opisthobranch molluscs (sea hares) (61). Increased anthropogenic nitrification from local agriculture has enhanced the spread of epiphytic algae, thus overgrowing and reducing estuarine seagrass beds. Reestablishment of sea otters into

**Asteroids:**  
echinoderms  
belonging to the class  
Asterozoa containing  
starfish or sea stars





**Figure 8**

Known direct and indirect effects of sea otters in kelp forest, estuarine, and soft sediment systems. Data are from the following sources: sea urchins and kelp (153); production (52); fish (53); gulls (55); eagles (56); carbon (57); sea stars, mussels, and barnacles (58); estuarine crabs, epiphytic grazers, epiphytes, and seagrasses (61); soft-sediment crabs (154); and clams (155). Abbreviations: CPUE, catch per unit effort; dmass, dry mass.

Elkhorn Slough (central California) has substantially reduced the size and density of Dungeness crabs (*Cancer magister*), thereby releasing isopods and sea hares from limitation by crab predation, thereby further increasing rates of removal of epiphytic algal overgrowth from seagrass blades, and ultimately facilitating seagrass bed recovery (61).

**Cetaceans.** Relatively little is known about the ecological influences of small cetaceans (62). Their high metabolic rates and locally high population densities have the potential to exert considerable top-down control on populations of some prey species (e.g., 63, 64), but few studies have chronicled any such influences. Recent evidence suggests not only that bottlenose dolphins (*Tursiops aduncus*) kill porpoises (*Phocoena phocena*) (64) but that risk effects induced by dolphins increase porpoise starvation mortality (65). Together, these effects may influence population dynamics of porpoises. Killer whales induce numerous behavioral modifications in their potential prey (66), which could play an important role in population processes. Small cetaceans, along with other pelagic megafauna including sharks, tunas, and billfish, may play an important role in facilitating foraging of pelagic seabirds. Indeed, without these megafauna pushing prey toward the surface, pelagic birds likely would not have access to these resources (32, 67).

Large-bodied cetaceans (great whales) are known or suspected to influence ocean ecosystems via four general processes: as consumers, as prey, as detritus, and through material storage and vectoring (3, 68).

Due in large measure to the effects of large body size, great abundance, and high mass-specific metabolic rate resulting from endothermy, the great whales are important to mass balance and energy flow, or were prior to industrial whaling. Combining estimates of these parameters with assimilation efficiencies, Croll et al. (69) calculated that the great whales (sperm whales and large mysticetes) would have consumed 53–86% of the North Pacific Ocean's NPP prior to industrial whaling. Similarly high consumption rates by great whales probably occurred throughout the world's oceans during this period. The consequences of such high consumption rates are best known for the Southern Ocean where krill (*Euphausia* spp.) is a key shared prey resource among baleen whales, penguins, pinnipeds, and fish, and where whaling thus may have led to population increases by these other groups of species (70, 71). In support of that idea, Emslie & Patterson (72) demonstrated a dietary shift by Adélie penguins (*Pygoscelis adeliae*) from forage fish to krill following depletion of great whales in Antarctica. In addition to prey regulation, the mere movement of large animals through water influences their physical environment. For example, drag and turbulence created by foraging whales can help mix otherwise depth-stratified sea water (73); humpback whales (*Megaptera novaeangliae*) exhale air at depth, thereby creating bubble nets that disrupt prey behavior (74); and gray whales (*Eschrichtius robustus*) mix and restructure enormous amounts of seafloor sediments in the Bering Sea and Arctic Ocean while feeding on benthic invertebrates (75).

The great whales are important prey resources for killer whales (76, 77) and possibly sharks. A combined analysis of marine mammal demography and energetics indicated that transient killer whale populations (those that consume marine mammals) would have been unsustainable on a diet that did not include great whales (78). Earlier suspicion of this nutritional dependency led Springer et al. (79) to the megafaunal collapse hypothesis, a proposal that industrial whaling caused transient killer whales in the North Pacific Ocean and southern Bering Sea to expand their diets to include harbor seals (*Phoca vitulina*), Steller sea lions (*Eumetopias jubata*), and sea otters, thus driving populations of these species sharply downward. Ecological consequences of the pinniped declines are uncertain but may have led to increases in finfish populations and declines of the finfishes' crustacean (shrimp and crab) prey (80). The sea otter decline clearly resulted in a cascade of influence on coastal ecosystems, including collapse of the region's kelp forests (81) and associated changes in ecological processes that are linked to kelp (Figure 7; above section, Marine Otters). The great whales may also have been important prey for extinct megapredators (e.g., *C. megalodon* and *Leviathan melvillei*) with comparably important linkages to ancient marine ecosystems.

After death, whale carcasses often sink to the seafloor where, because of their large size and high nutrient content, they provide food and habitat for deep-sea organisms (82, 83). Successional changes associated with carcass decomposition can proceed for decades, during which time hundreds of associated species are supported by this nutritionally rich and highly pulsed resource. More than 60 species of deep-sea macrofauna are known only from whale falls (82), and numerous species associated with cold seeps and hydrothermal vents have also been found to occur on whale falls (84). Moreover, approximately 25% of the seep- and vent-associated fauna first appeared with early whales in the Eocene (85). Because of these various associations and the intrinsically short-lived nature of vent communities, whale falls may be important stepping stones in a temporally dynamic spatial ecology of the deep sea. Whale carcasses are scavenged at sea by sharks, whereas stranded carcasses are also consumed by coastal scavengers, such as condors, bears, and perhaps other now extinct species (3, 86). The present depressed state of this stranded carcass resource has caused California condors (*Gymnogyps californianus*) to depend more heavily on terrestrial wildlife, from which dependence they suffer increased lead toxicity (87).

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**Endothermy:**

process of core body temperature regulation by endotherms, which are animals that maintain a favorable body temperature through variation in metabolic rate

**Hydrothermal vent:**

a fissure in the seafloor from which geothermally heated water emerges

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Because of their great abundance, large size, and extensive movements vertically (in feeding) and horizontally (during routine movements and especially migrations), cetaceans are important vectors of material transport in ocean ecosystems. Roman & McCarthy (4) have argued for an increase in the primary production attributed to humpback whales in the Gulf of Maine due to their feeding at or near the thermocline and excreting the remains of these consumed nutrients at or near the sea surface. Similar processes involving other whale species surely occur elsewhere in the world's oceans. Because of their large body size and the resulting low mass-specific metabolic rate compared with smaller endotherms, whales have the capacity both to store carbon and to transport via whale falls significant amounts of carbon from the atmosphere to the deep sea (88). A final example of nutrient vectoring by whales involves iron in the Southern Ocean. Iron is both a key limiting micronutrient in ocean production and intrinsically rare in southern hemisphere oceans because of limited aeolian input from a reduced continental landmass (89). Great whales apparently played a central role in elemental iron availability through the consumption of krill and the excretion of iron-rich fecal matter in the euphotic zone. After the reduction of great whales by industrial whaling, the limiting supply of iron is believed to have become bound in the greatly increased krill biomass, thus reducing iron availability for NPP and overall production of the Southern Ocean (90, 91).

**Pinnipeds.** Relatively little is known about the roles of pinnipeds in ecosystem dynamics (62, 92). As with small cetaceans, the absence of empirical evidence is due in part to perspective and in part to tractability. Most research on pinniped ecology has been conducted with a mind-set to bottom-up forcing, thus inevitably leading to questions concerning environmental influences on these animals rather than their influences on the environment. Moreover, pinnipeds commonly forage in environments that are difficult for humans to access and on species that are difficult to observe and measure.

We have identified just five published studies of the ecological influences of pinnipeds. One of these involves harbor seals trapped in eastern Canadian lakes following retreat of the Pleistocene ice sheet. Contrasts of lakes with and without seals suggest strong impacts of seal predation on the abundance, size, species composition, and life history of salmonids (93). Walrus (*Odobenus rosmarus*) foraging over the shallow Bering Sea shelf consume bivalve molluscs and other infauna, substantially influencing the benthos by prey depletion and sediment excavation. Both prey and nonprey differ in size, abundance, and species composition between foraging pits and nearby undisturbed areas (94). Leopard seals (*Hydrurga leptonyx*) prey on the pups of Antarctic fur seals (*Arctocephalus gazella*) in the South Shetland Islands, thereby limiting fur seal population growth and rate of recovery from overharvest during the era of commercial sealing (95). Predation by recovering populations of Australian and New Zealand fur seals (*A. pusillus* and *A. forsteri*) appears to significantly limit benthic-feeding fishes on shallow reefs in southeast Australia, thus potentially detrimentally influencing kelp forests by disrupting the limiting influence of fishes on their herbivorous invertebrate prey (96). Finally, an increase in gadoid fish abundance and decline in shrimp abundance following the collapse of Steller sea lions and harbor seals in the western Gulf of Alaska, in conjunction with findings by Worm & Myers (41) from the North Atlantic Ocean, led Estes et al. (80) to suggest a trophic cascade from killer whales to pinnipeds to fish to shrimp (see above discussion, as this example links pinnipeds with cetaceans).

Studies of risk effects of pinnipeds on their prey suggest that they likely play an important role in marine communities, but the literature remains in its infancy. Fish reduce their rates of grazing on algae in the presence of New Zealand fur seals, which has the potential to influence primary producer biomass (97), and risk from leopard seals appears to influence the location of penguin foraging grounds and their movements while foraging (98).

**Sirenians.** Empirical evidence for the ecological influences of sirenians in ocean systems is restricted to a single species, the dugong (*Dugong dugong*). Dugongs feed in shallow seagrass meadows, reducing seagrass biomass aboveground by cropping and belowground by uprooting plants, generating organic detritus, and suspending sediments, thereby creating habitat heterogeneity across the seafloor, resetting seagrass succession, and influencing the distribution and abundance of various associated species of plants, invertebrates, and fishes (99, 100). In a behavioral analog of apparent competition, dugongs in Western Australia appear to have a serpentine impact on dolphins and other shark prey by attracting their shared predator, tiger sharks (*Galeocerdo cuvier*) (43).

**Polar bears.** Arctic pinnipeds seek refuge from danger by entering water, whereas Antarctic pinnipeds do so by hauling out on ice (101). This behavioral difference is thought to be an evolutionary response to differences between the poles in predation risk: from the ice in the Arctic by polar bears and humans, and from the water in Antarctica by killer whales and leopard seals. Although that explanation seems reasonable given both the current and historical distributions of these various predators, the relative importance of polar bear predation is uncertain because of the confounding influence of aboriginal peoples in the Arctic. It appears, however, that the distribution of ringed seal lairs is driven at least partially by the risk of predation from polar bears (102).

## Marine Reptiles

Although saltwater crocodiles are fearsome predators, their ecological influences are unknown aside from a few dietary studies and risks to human safety. Ecological impacts are known or suspected for three (green, *Chelonia mydas*; hawksbill, *Eretmochelys imbricata*; and leatherback, *Dermodochelys coriacea*) of the seven extant species of marine turtles (103). Hawksbill turtles may promote biodiversity on reefs by preferentially consuming sponges that are strong space competitors (104) and facilitating foraging of other species; the loss of hawksbills on Caribbean reefs may have thus contributed to recent phase shifts in reef communities (105). Green turtles consume seagrasses and macroalgae in shallow tropical oceans and can have large influences on primary producer community structure, biomass, and dynamics (103, 106). Green turtles can limit macroalgae on reefs (107) and have strong limiting influences on seagrass meadows in places where the turtles are sufficiently abundant (108, 109). Beyond these simple limiting influences, green turtle grazing is thought to stimulate production and inhibit detrital and epiphytic smothering (110). They also short-circuit detrital cycles in seagrass ecosystems and can influence sediment carbon stores (111). These various interactions together with a history of green turtle overexploitation and recovery have led to a conundrum over the current and historical ecological influences of this species. Growing turtle populations in some areas (e.g., marine protected areas in the western tropical Pacific, Bermuda) have created a perception of ecosystem collapse from overgrazing (112), whereas elsewhere (e.g., the Caribbean) historical turtle numbers are believed to have been vastly greater than they presently are anywhere in the modern world (113). These seemingly conflicting observations lead to questions of how seagrass ecosystems functioned before sea turtle declines and whether turtles might have been limited by other now missing interactions, such as predation by sharks, which is discussed in the next section (see 114).

Leatherback turtles, obligate consumers of gelatinous zooplankton (106), are critically endangered, especially in the Pacific Ocean. The depletion of leatherbacks and other consumers of gelatinous zooplankton, such as some fish species, is thought by some to have contributed to recent outbreaks of jellyfish (115, 116), although this link is largely hypothetical.

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**Gelatinous zooplankton:** animals with soft and easily damaged body structures that live in the water column

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Sea turtles can play important roles in the dynamics of beach ecosystems in places where they nest (117, 118). Estimates from a loggerhead turtle nesting beach suggest that less than a third of energy and nutrients deposited in the form of eggs reenters marine habitats as hatchlings. These marine resources can facilitate terrestrial plant growth and populations of egg and hatchling predators.

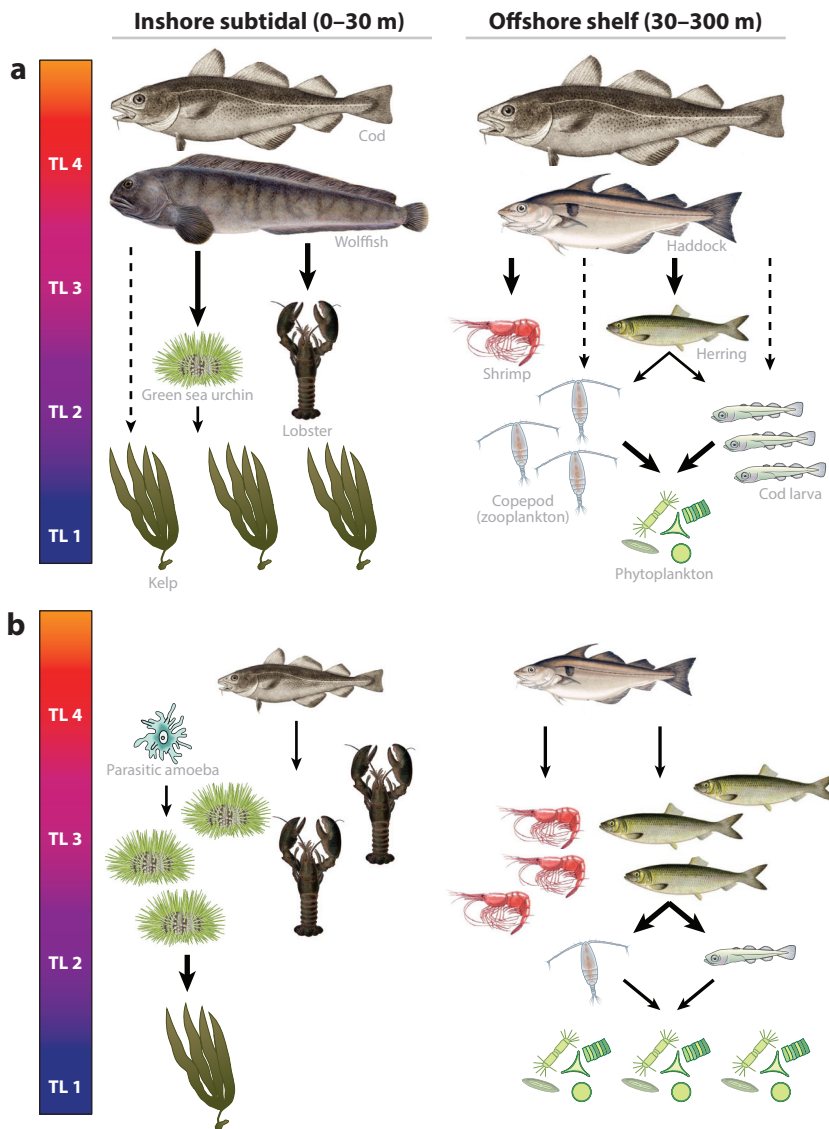
## Fishes

Although 129 species of marine bony fishes qualify as megafauna by our criterion, the ecological impacts for most of these are poorly known. This is probably due in part to historical depletion of the largest individuals of large-bodied species from coastal ecosystems, where species interactions are more easily studied (119). Large bony fishes do remain in the more isolated parts of the world's oceans, for example, Pacific halibut in the North Pacific Ocean and Bering Sea, toothfish in the Southern Ocean, and numerous scombroid fishes (especially tunas and billfishes) across the tropics and subtropics, although quite a few of these stocks have also exhibited pronounced declines (120, 121).

Atlantic cod (*Gadus morhua*) provide a notable exception to this dearth of information on the ecological influences of large bony fishes. Atlantic cod can be legitimately classified as megafauna because, though individuals >45 kg are now rare, individuals approaching 100 kg occurred before the species was depleted by overfishing (110). This observation also raises the question of how many other marine fishes may not be classified or studied as megafauna because of historical reductions in size (122). Cod influence both inshore subtidal and offshore shelf ecosystems of the Northwest Atlantic Ocean (**Figure 9**). In the coastal zones, they feed on smaller fishes and large benthic invertebrates, possibly limiting the size and abundance of these species. Depletion of large cod, along with other coastal predators such as wolffish (*Anarhichas* spp.), had two notable consequences in coastal reef ecosystems: a trophic cascade wherein sea urchins increased and kelp forests collapsed (49) and increased abundance of American lobsters (*Homarus americanus*) (123, 124).

The trophic cascade seemingly led the system to an alternate stable state dominated by urchin barrens (125). The cod collapse, again in conjunction with reductions of other large groundfish, has also caused significant reorganization of offshore food webs, which has been well documented by scientific trawl surveys in multiple regions. Concomitant with the decline and collapse of cod, shrimp stocks increased dramatically (41), along with forage fishes such as herring and capelin (126). This resulted in a trophic cascade from forage fish to zooplankton and phytoplankton on both sides of the Atlantic Ocean (127, 128). As with coastal kelp forests, altered species interactions resulting from the collapse of groundfish appear to have driven parts of the North Atlantic oceanic ecosystem to an alternative stable state in which cod recovery is inhibited (126, 129–131). Only recently, a crash in forage fish abundance, possibly driven by overgrazing of their food sources, has led to the beginning of recovery in large groundfish (126). In nearshore ecosystems, a warm-water pathogen (*Paramoeba invadens*) now occasionally exerts high mortality on sea urchins, leading to the recovery of kelp forests. Notwithstanding, present kelp cover along the shore of Nova Scotia is 85–99% reduced when compared with the period prior to the cod collapse (132–134) (**Figure 9**).

This well-documented example, which played out across large parts of the Atlantic, beckons the question of how general such strong effects of large fish are or were on their respective ecosystems. If such effects are more general, and there is little a priori reason to doubt this, the implications for fisheries management will be profound. In support of this notion, a recent global meta-analysis of northern hemisphere marine food webs revealed strong evidence of top-down control in



**Figure 9**

Ecological role of cod and other large fishes in the Northwest Atlantic food web (*a*) before and (*b*) after groundfish stock collapsed in the early 1990s. High predator diversity, biomass, and body size (shown are large cod, *Gadus morhua*; wolffish, *Anarhichas lupus*; and haddock, *Melanogrammus aeglefinus*) historically exerted powerful top-down control (*thick solid arrows*) on benthic invertebrates and forage fish (shown are sea urchins, *Strongylocentrotus droebachiensis*; lobster, *Homarus americanus*; shrimp, *Pandalus borealis*; and herring, *Clupea harengus*). Indirect positive effects (*dashed arrows*) maintained kelp forests inshore and large zooplankton and cod larval populations offshore. After predator populations collapsed, invertebrates and forage fish multiplied, due to weakened top-down control (*thin solid arrows*), with documented trophic cascades to kelp (which decreased) and phytoplankton (which increased). In the new configuration, a warm-water, parasitic amoeba (*Paramoeba invadens*) periodically invades, eliminates urchins, and releases kelp. Cod larval survival is reduced by forage fish predation, leading to an alternative stable state. Cod, haddock, wolffish, shrimp, herring, and lobster images are public domain (Wikipedia/Wikimedia commons) Abbreviation: TL, trophic level.

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**Table corals:**

corals that form broad horizontal surfaces

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cold-water systems and possibly in the tropics, but less so in warm-temperate waters (133). Weakly exploited stocks and those feeding at a high trophic level were also found to be more likely to exhibit strong top-down control on their respective ecosystems (133).

Another notable example comes from tropical coral reef ecosystems of the Indo-Pacific region, where there is a growing understanding of the ecological effects of the bumphead parrotfish (*Bombometopon muricatum*, maximum mass 46 kg), a large teleost megaherbivore/corallivore. Classified functionally as an excavator, this species consumes both its benthic algal prey and the underlying reef matrix. It also directly consumes certain species of live stony coral in roughly equal proportion to algal prey (7, 134). The capacity of the bumphead parrotfish to prey so heavily on structurally well-defended stony corals derives in large part from its great size and the associated forces it is able to generate while feeding. Studies of the fish in remote, near-pristine ecosystems have revealed that each individual removes approximately 4 to 5 tonnes of benthic material from the reef annually, a level of intake that some believe may approximate or exceed rates of carbonate accretion in these reefs (7, 134). The consequences of this behavior to the mass transport and redistribution of carbonate sediments are obvious but not well quantified. Grazing by *B. muricatum* is beneficial to the resilience of coral reefs in that it routinely creates cleared space on the reef for larval coral settlement (134). And, whereas *B. muricatum* is likely to incidentally consume coral recruits while grazing, the parrotfish's removal of competitively superior seaweeds from the benthos may balance or outweigh this negative effect (37). The fish's discriminant predation on adult coral appears to promote reef resilience as well, in that in some areas it reduces the relative abundance of structurally weak table corals that would otherwise come to undermine the stability of the reef matrix. Because no other species performs the same ecological role in the region, *B. muricatum* seems to control a diverse suite of ecosystem processes on the Indo-Pacific reefs where it remains (135).

Strong evidence for ecological effects of large sharks has also emerged more recently (136). Multiple datasets from the Atlantic Ocean, Gulf of Mexico, and Indian Ocean show that declines in the abundance of large sharks are associated with increases in smaller-bodied predators (mesopredator release) including small sharks and rays. Some of these taxa may have powerful influences on benthic communities, suggesting that loss of large sharks has triggered trophic cascades (39). White shark attack rate on sea otters in central California has increased markedly over the past three decades from just several carcasses recovered per year in the mid-1980s to almost 100 per year at present (137). This sharp increase in shark-inflicted mortality on sea otters may have resulted from the attraction of sharks to increased numbers of pinnipeds in the area over this same period. Regardless of the reason, increased shark mortality is almost certainly limiting recovery of the threatened California sea otter. Increasing shark predation was also identified as driving a population decline of harbor seals on Sable Island in the Atlantic Ocean (138). The relaxation of predation and risk from tiger shark depletion may help to explain increases in green turtle populations to levels that have resulted in degradation of seagrass beds in several ocean basins (114).

Large sharks also influence various other species and ecosystems through risk effects. For example, the distribution and foraging behavior of dugongs in Shark Bay, Western Australia (139), and distributions of green turtles in this region and elsewhere (140) are driven by predation risk from tiger sharks (**Figure 10**). Experimental studies show that this results in megagrazers being largely excluded from risky habitats, where dense seagrass beds then form, and being concentrated in lower-risk habitats, where their grazing keeps seagrass communities in an early successional state with pioneer species and at low biomass (36, 139). These indirect effects will cascade through ecosystems because fish and invertebrate communities are linked to the abundance and species composition of seagrasses. In addition, high-risk habitats feature higher carbon stores than low-risk

habitats, suggesting that marine megafauna could play an important role in blue carbon dynamics (111). Tiger sharks also induce foraging habitat shifts in dolphins, sea snakes, and seabirds, but the ecological consequences of these shifts have yet to be explored (43).

## Invertebrates

Humboldt squid invaded temperate waters of the eastern North Pacific during the mid- to late 1990s, purportedly in response to changing oceanographic conditions but possibly also from the relaxation of competition with or predation by tunas and other large predatory fishes (from depletion of the large fishes by fisheries) in the eastern tropical Pacific Ocean (141). Squid were observed feeding on hake (*Merluccius productus*), and the squid invasion coincided with a decline in hake abundance. Giant clams may be similarly influential in coral reef ecosystems as they can build and shape reef topography, affect carbonate budgets, and potentially influence water quality by filtering tens of liters of water per hour (142).

## EVOLUTIONARY EFFECTS

Strong interactions among species or on species by their abiotic environments, if sustained, inevitably result in selection and evolution (143). Moreover, ecology and evolution are now recognized as often occurring in lockstep (144), with evolutionary change in response to ecological processes proceeding rapidly (145). These observations raise the question, If and where marine megafauna have strong direct or indirect effects on other species, what are the evolutionary consequences?

Being attacked by a consumer has considerable negative effects on prey fitness, often ending any possibility for future reproduction. This simple logic underlies the ecology of fear and the many neurological, physiological, and behavioral manifestations expected of any and all species that live with a significant risk of being eaten. Although experiential learning is undoubtedly important in setting the behavior of any particular individual, the capacity to learn joins hardwired behavioral, physiological, and morphological adaptations and life history evolution as the suite of overall categories within which evolutionary responses to consumers might occur. For instance, diel vertical migrations of squid, forage fish, and zooplankton may very well have been selected for by visually oriented, air-breathing megafauna. Even the migrations of great whales to low-latitude calving areas have been proposed as a means of lessening the risk of predation on newborn calves (146). Although numerous other evolutionary influences might easily be imagined, such selection and evolution are rarely evoked in the oceans, probably in large measure because of the strong general mind-set on bottom-up forcing and the fact that they are difficult to demonstrate.

More complex evolutionary responses to selection by marine megafauna have been proposed for coastal species in the North Pacific and Atlantic oceans. Kelps (Order Laminariales) diversified in the North Pacific following the onset of late Cenozoic polar cooling, and thus sea otters and their recent ancestors probably created an environment for the evolution of kelps in which the intensity of herbivory from sea urchins and other macroinvertebrate grazers was low (147). This scenario has been used to explain why northern hemisphere kelps are poorly defended by secondary metabolites (phlorotannins) whereas southern hemisphere kelps and their analogues are comparatively well defended, and why southern hemisphere herbivores are more resistant to phlorotannins than their northern hemisphere counterparts (148). The chemically poorly defended (and thus nutritionally more valuable) northern hemisphere flora might further explain why the world's largest abalones (149) and only known kelp-eating sirenian (150) arose and lived in the North Pacific Ocean. The absence of sea otters and otariid pinnipeds from the North Atlantic have been evoked to further

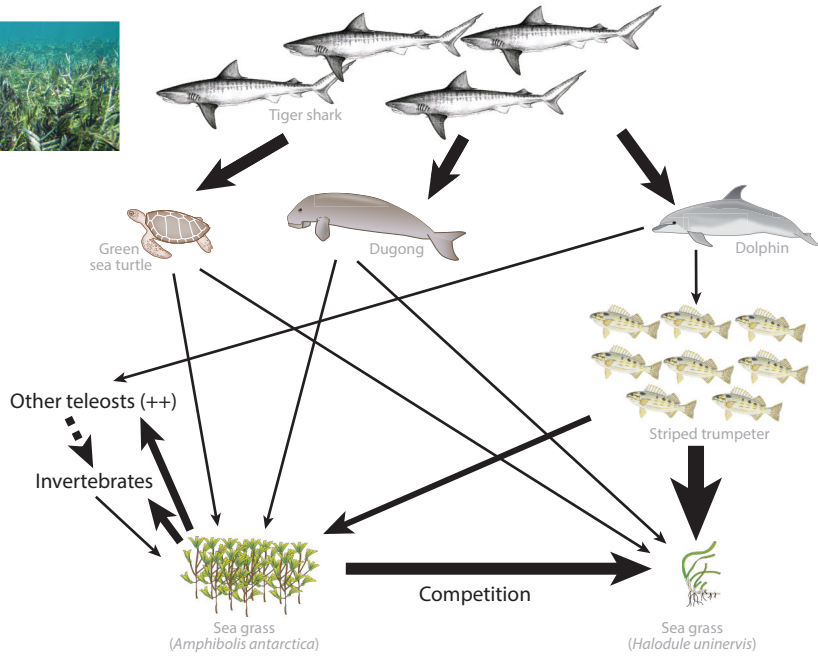
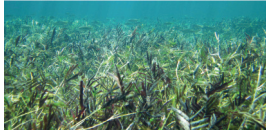
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**Phlorotannin:** a type of tannin that occurs in brown algae and is formed as an oligomer of phloroglucinol

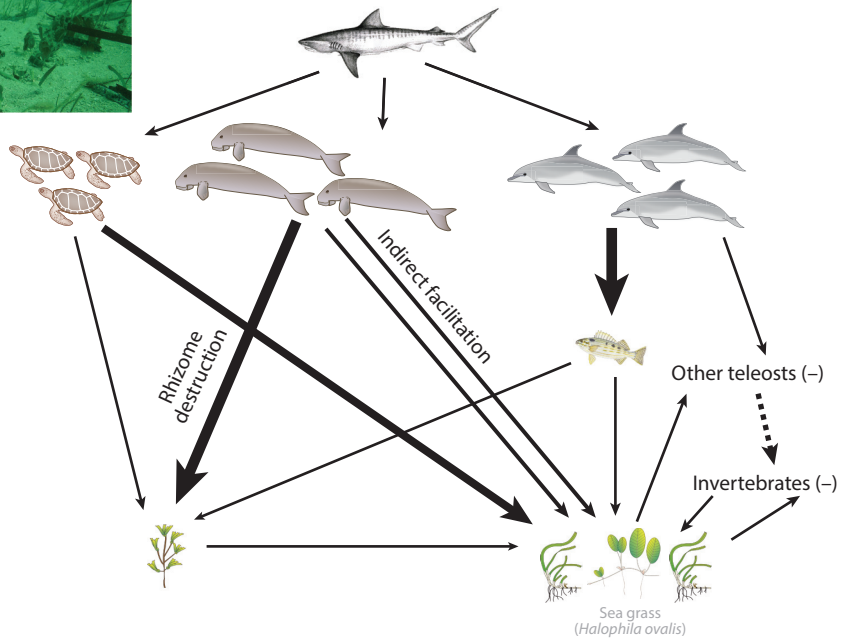
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### High risk




### Low risk



explain why Atlantic cod became such a large, ecologically dominant predator in North Atlantic kelp forest and shelf ecosystems (80).

## SYNTHESIS

Our main purpose in this article has been to identify the ways in which marine megafauna might influence their associated ecosystems and to review the published evidence for any such influences. A general topology of the ways in which any species (but marine megafauna in this case) might influence their associated ecosystem is shown in **Figure 5**. For the great majority of marine megafauna (at least 287 of the 338 species listed in **Supplemental Table 1**), no interactive influences of any kind have been reported. Part of this dearth of information is a consequence of the large number of megafaunal species that occur in the ocean and the limited time and resources that have been available to study them. But even when we aggregate marine megafauna into 10 major taxonomic groups and limit the breadth of influence to simple, direct effects (e.g., positive or negative influences on a predator, prey, competitor, or mutualist), direct ecological influences from marine megafauna are unreported for three of these groups (**Supplemental Table 1**). Effects of direct predation (consumptive) of marine megafauna on their prey are unreported for three groups and risk effects (behavioral) are unreported for four groups. Indirect effects have been reported for species in six groups. These indirect effects have been identified as trophic cascades in just three of the groups (**Figures 7–10**). Serpentine influences of marine megafauna through their interaction webs have been reported or can be inferred for four groups (sea otters, sirenians, turtles, and cartilaginous fishes), although by association this effect extends to large and small cetaceans by way of the influences of great whales on killer whales and of killer whales on sea otters. Clear functional relationships between population density and ecological effect have been reported for a single species, the sea otter. Abrupt phase shifts resulting from the influences of marine megafauna are known or can be reasonably inferred from the published literature on three groups, sea otters, bony fishes, and marine turtles. Hysteresis in the functional relationship between population density of a marine megafaunal species and that species' ecological influence is known or can be inferred for species in just two groups, sea otters and bony fishes. Ecological influences involving larger spatial linkages across ecosystems are known from the published literature on four of the nine groups.

 Supplemental Material

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### Figure 10

Risk effects, trophic cascades, and possible serpentine effects initiated by marine megafauna in Shark Bay, Western Australia, revealed by a combination of long-term observational data and experimental studies. The relative differences in species abundance between high-risk (*top*) and low-risk (*bottom*) scenarios are indicated by the number of images. Arrow direction represents the direction of effect rather than the flow of energy. Arrow width suggests relative interaction strength, and dashed arrows indicate places where relative interaction strength is unknown. Most dugongs and sea turtles avoid habitats where risk from tiger sharks is high (*top*). Those dugongs that do remain forage by cropping leaves of seagrasses, leaving rhizomes intact. This allows dense beds of a competitive, dominant seagrass (*Amphibolis antarctica*) to become established. Pioneer seagrass species are quickly removed by large schools of omnivorous teleosts (i.e., striped trumpeters; *Pelates octolineatus*) that can forage largely free from risk of predation by dolphins (*Tursiops aduncus*), which avoid these high-risk habitats. The dense beds of seagrass provide abundant habitat for invertebrates, support a diverse and high-biomass teleost community, and sequester considerable carbon. In low-risk habitats (*bottom*), densities of dugongs, sea turtles, and dolphins are high. In addition, dugongs are able to excavate rhizomes of seagrass, which facilitates pioneer species. These species are heavily cropped but are maintained by excavation foraging of dugongs that prevents the establishment of *A. antarctica*. The result is a low-biomass seagrass habitat with lower carbon storage and less diverse teleost communities that are characterized by lower biomass. Tiger shark courtesy of Lindsay Marshall (<http://stickfigurefish.com.au>); seagrass courtesy of Tracey Saxby (*Amphibolis antarctica*) and Catherine Collier (*Halodule uninervis*, *Halophila ovalis*), Integration and Application Network, University of Maryland Center for Environmental Science (<http://ian.umces.edu/imagegallery/>); striped trumpeter available at <http://efishalbum.com>; photos courtesy of the Shark Bay Ecosystem Research Project (<http://www2.fiu.edu/~heithaus/SBERP/>).

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**Passenger:** a species with little or no influence on the distribution and abundance of other species

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When examined across the 10 major taxonomic groupings of marine megafauna, ecological impacts have been carefully studied and are reasonably well known for just five of these—sea otters, sirenians, turtles, bony fishes, and cartilaginous fishes—and for very few species in the latter four groups. For bony fishes, the published evidence is decent for only 2 of 16,000 known marine species, the Atlantic cod and bumphead parrotfish; for sharks, the effects of individual species have rarely been investigated.

Why is there such a disparity of understanding among these taxonomic groups? Part of the reason could be a lack of effect by most species, an explanation reinforced by the tendency for negative evidence to go unpublished. Although possible, we think this explanation is unlikely given the rapidly growing evidence for strong species-level influences by large-bodied animals elsewhere on the planet (5, 11, 12). Three other factors more likely explain the lack of evidence for ecological effects by marine megafauna: (a) logistical and methodological difficulties in the study of ecological process throughout most of the world's oceans (both because of difficulty of access and the mobility of species); (b) a shifting baseline where megafauna depletion preceded scientific inquiry (110, 119); and (c) the historical tendency by the ocean science community to focus attention on bottom-up forcing processes, a view that de facto relegates marine megafauna to the role of passengers rather than drivers of their ecosystems.

## CONCLUDING REMARKS

Except for their intrinsic existence value and concerns about extinction as part of the global biodiversity crisis, marine megafauna are not sufficiently well recognized by many scientists, managers, and politicians as pressing important to marine conservation and management. A cursory examination of what is known of the ecological function of most extant species might be taken to support that view because there is limited evidence that most of these species are functionally significant players in ocean ecosystems. However, that view would be based on a lack of positive evidence rather than a weight of negative evidence. In those few cases where scientists have looked carefully and sufficient data could be obtained, there is indeed evidence for strong and in some cases far-reaching ecological and evolutionary influences of marine megafauna. If these few examples are in any way representative of the many species and systems for which studies and data are lacking, then one is left with a rather different view of marine megafauna, one in which they matter considerably to the structure and function of the world's oceans. By this latter view, maintenance or restoration of marine megafauna at ecologically effective densities (151) should be a high priority for marine conservation and management.

To what degree is further empirical evidence needed for explaining the ecological roles of marine megafauna, and if the need for detailed further understanding is truly pressing, how might the next generation of marine scientists go forward in obtaining the necessary data? At the most fundamental level, science is always the quest for further understanding. We strive to learn because that is what humans have always done. Learning and understanding are a central essence of humanity. We should endeavor to understand the ecological roles of marine megafauna because they are part of nature, because all current hints point to their effects as being important to human welfare, and because we presently know so little. But several new developments will be needed if science is to proceed along such a path. One is that marine scientists must focus on biological processes, especially those that are linked to species interactions, often underrepresented in pattern-oriented fields such as macroecology and biological oceanography. The other is the need to gather primary data in replicate areas that show depletion or recovery of marine megafauna so as to provide further insight into the dynamics caused by the ecological roles of megafauna. Advancing along these pathways will help fill out our understanding of this important class of

species and in so doing will almost certainly improve our broader understanding of how our own effects compare to those of other species in our size class (18).

### SUMMARY POINTS

1. Megafauna (animals with body mass >45 kg) are components of all ocean ecosystems and have been present since soon after the Cambrian explosion.
2. The known extant marine megafauna include at least 338 species of invertebrates, fish, reptiles, birds, and mammals.
3. In contrast with the terrestrial realm, there have been few extinctions of ocean megafauna since the Pleistocene/Holocene border.
4. The ecological roles of marine megafauna are unstudied or unknown for most species in most oceans.
5. The dearth of information on the ecological roles of marine megafauna is largely the consequence of logistical difficulties in putting specific hypotheses to experimental test and a lack of dedicated empirical studies of megafauna and ecosystem responses to their presence or absence by ocean scientists.
6. Powerful and often wide-ranging ecological impacts have been demonstrated or strongly suggested for the few well-studied species of large-bodied sharks, bony fish, marine turtles, sea otters, and great whales.
7. These species variously influence their associated ecosystems as consumers, prey, sources of detritus, and nutrient vectors. Their impacts spread across species through direct and indirect interactions and over large scales of space and time.
8. Nonconsumptive effects of large megafauna on the behavior of other species can be as important as or even more powerful than the direct effects of predation.
9. Sea otters and their recent ancestors likely acted to block the coevolution of defense and resistance between marine macroalgae and their most important potential herbivores in the North Pacific Ocean. Otherwise, the direct and indirect evolutionary consequences of marine megafauna are unknown.
10. The great importance of marine megafauna in coastal and oceanic food webs coupled with their inherent vulnerability to exploitation necessitate appropriate conservation measures.

### FUTURE ISSUES

1. Additional research will be needed to determine the degree to which findings from the few currently available studies of the ecological influences of marine megafauna are generalizable across the world's oceans.
2. Further study of the ecological roles of marine megafauna should focus on spatial contrasts of interaction webs between otherwise similar areas with and without the species of interest, that is, time series over which the abundance and distribution of species of interest wax or wane, and should be undertaken with the assistance of well-conceived and properly parameterized modeling efforts.

3. Investigation of the evolutionary consequences of megafaunal-induced species interactions offers great potential for future understanding of how and why the oceans function as they do.
4. In considering both the conservation of marine biodiversity and the sustainable human use of renewable marine resources, recognition of the important ecological roles played by megafauna and a better understanding of the details of these processes will be imperative.

## DISCLOSURE STATEMENT

The authors are not aware of any affiliations, memberships, funding, or financial holdings that might be perceived as affecting the objectivity of this review.

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## Errata

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