

Historical Perspectives

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(Born 2 October 1945)

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The History and Future of Marine Mammal Ecology

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In autumn of 1976, less than two years after completing my doctorate, I spoke to a class taught by Roger Gentry at the University of Washington entitled “The Marine Mammal Phenomenon.” The U.S. Marine Mammal Protection Act had been signed into law a few years earlier, and Roger’s purpose was to explore rapidly growing societal interests in marine mammal science and policy. While my interests and background occurred within the realm of what might have been viewed as marine mammal science, the species (sea otter), system (shallow coastal ocean), and process (predation) I had studied and knew best seemed only marginally relevant to and perhaps even idiosyncratic with the larger questions of marine mammal science and policy.

I see it differently now. Sea otters have taught us much that is germane to other species of marine mammals; the coastal ocean has been a productive arena for understanding ecological processes that are difficult to study and understand in other ocean ecosystems; and the effects of sundry predators are known to influence the structure and functioning of diverse ecosystems. The former assertions all occur within the prefecture of ecology, defined broadly as a search to understand the distribution and abundance of species.

I think of myself first and foremost as an ecologist. For these reasons and because aquatic mammals are the unifying subject of this journal, my aim in writing this Historical Perspectives essay is to explore the intersection between aquatic mammals and ecology. I’ll begin with a discussion of science and aquatic mammals, the purposes of which are to juxtapose the intersection of aquatic mammals and ecology with similar intersections of aquatic mammals and other scientific disciplines, and to remind readers of the diversity of aquatic mammal species and the environments in which they live.

Science and Aquatic Mammals

Most aquatic mammals are marine-living. My focus from here forward will thus be on marine mammals. Mammals arose and initially diversified on land from which several lineages radiated into aquatic habitats. All extant freshwater-living mammals are either semi-aquatic (i.e., they have an obligate association with land; e.g., otters,

mink, and beaver) or are expatriates from lineages that arose in the sea (e.g., river dolphins and sire-nians). All extant marine mammals arose on land and radiated into the sea via fresh water or across the land–sea interface. The remarkable taxonomic and functional diversity of marine mammals has been molded largely by life in the sea.

Much of the strong human interest in marine mammals is the product of this evolution and adaptation. Large body size engenders an intrinsic sense of excitement and awe, which is why we keep records of the biggest but almost never the smallest. Our own modest abilities to swim and dive make us marvel over the ability of air-breathing homeotherms to live in stormy, frigid waters while at the same time diving for long durations to great depths, all with apparent normalcy and disregard for conditions that to humans would be instantly fatal. We are intrigued by marine mammal intelligence, social interactions, modes of communication, and any number of features of form and function that bear on their enthralling natural histories. These and other features of marine mammals motivate human interest in these creatures, and human interest, in turn, motivates science.

Research on marine mammals has left a distinct mark on many divisions of organismal biology. The study of morphology has been enriched by the immense size of marine mammals and their structural adaptations for swimming and feeding (Goldbogen, 2010); physiology and biochemistry have benefitted from the study of marine mammal diving (Kooyman et al., 1980); the understanding of mating systems and social behavior has been informed by work on pinnipeds (Le Boeuf & Peterson, 1969; Bartholomew, 1970); studies of bottlenose dolphins (*Tursiops truncatus*) and sea otters (*Enhydra lutris*) have added data-rich analyses and novel perspectives to the understanding of prey selection and foraging behavior (Smolker et al., 1997; Tinker et al., 2008); and the intersection of biogeography, the fossil record, and genetics of marine mammals has led to significant advances in the study of systematics and evolution (Hoelzel, 2002).

In contrast, marine mammals have played a minor role in the growth of ecology. Although substantial

effort has gone into monitoring, obtaining reliable information on the distribution and abundance of marine mammals is difficult. This is because most species range over vast areas that change seasonally, are difficult to see or detect on the ocean's surface, are undetectable when they are submerged in a dive, aggregate in ways that create high sampling variance, and are difficult and costly to mark or tag. Population estimates for marine mammals are notoriously imprecise (Estes & Gilbert, 1978; Taylor et al., 2007), the upshot being that any question whose answer requires a measure of distribution and abundance is beset by challenges from the outset.

Marine mammals also have upsides that expedite thinking about their distribution and abundance. In contrast with air, water is buffered against rapid temperature change by the capacity to store heat, creating an ocean environment in which neither temperature nor the availability of water (the two most important physically limiting factors for many terrestrial organisms) vary rapidly or extensively in space or time. By virtue of their large body size, endothermic metabolism, and the high thermal conductivity of water (the medium in which all marine mammals live), the distribution and abundance of marine mammals thus may be influenced more strongly by their biological surroundings than by direct influences of their physical-chemical environment.

It therefore strikes me that two simple questions define the backbone of marine mammal ecology: (1) How do other species influence the distribution and abundance of marine mammals? and (2) How do marine mammals influence the distribution and abundance of other species? Answers to these questions depend on the ways in which species interact with one another, which, in turn, are limited to just a few possibilities. The influence of a species on some other species can be positive, negative, or neutral. When the influences of two interacting species on one another are both negative, we call this *competition*; when the influences are both positive, we call this *mutualism*; and when the influence of species 1 on species 2 (or 2 on 1) is positive and the influence of species 2 on 1 (or 1 on 2) is negative, we call these *agonistic* interactions. Agonistic interactions most commonly occur when one of the two species is a predator and the other is its prey. All species have predators, all species have prey, and the network of these predator-prey interactions define what is known as a *food web*. Food web dynamics do not encompass all of ecology, but most of ecology intersects in one way or another with food web dynamics.

The preceding paragraph provides an underpinning for thinking about marine mammal ecology. In the remainder of this essay, I will briefly recount the history of ecology as a scientific discipline,

summarize what I see as the highpoints of marine mammal ecology, discuss how these highpoints map onto the foundations of modern ecology, and look forward to the needs and opportunities for advance in marine mammal ecology.

A Brief History of Ecology

The formal study of ecology began in the late 19th century in an effort to better understand the distribution and abundance of plants. Attention to animals and their roles in the dynamics of nature gained force with people like Sir Arthur George Tansley (1871-1955; Figure 1), who developed the ecosystem concept, and Charles Sutherland Elton (1900-1991; Figure 2), who conceived of what has come to be known as the Eltonian Pyramid—a characterization of ecosystems as having reduced biomass and production across successively higher trophic levels and the associated ideas of food chains (consumer-prey linkages across multiple trophic levels) and food webs (consumer-prey networks). Elton's Pyramid was especially influential because it implied that the distribution and abundance of species is controlled by just two key processes: (1) net primary production (NPP) and (2) the efficiency of energy and material transfer from prey to consumer. George Evelyn Hutchinson's (1903-1991; Figure 3) concurrent interest in diversity led to such groundbreaking advances as the species/area function (Connor & McCoy, 1997), the theory of island biogeography (MacArthur & Wilson, 1967), latitudinal patterns of species diversity (Pianka, 1966), and the local control of species diversity (Paine, 1966; Connell, 1978).

Three of Hutchinson's protégées, Robert Helmer MacArthur (his graduate student; 1930-1972; Figure 4), Frederick Edward Smith (another of his graduate students; 1920-2012; Figure 5), and Raymond Laurel Lindeman (a post doc with Hutchinson; 1915-1942; Figure 6) set the course for much of what followed.

Much of ecology's trajectory from the early 1960s to the mid-1980s grew from MacArthur's belief that competition ruled the world (MacArthur, 1972; Salt, 1983).

Lindeman's (1942) 10% rule, the proposal that only about 10% of the energy from one trophic level is captured by the next higher trophic level (the remainder being lost to the inefficiency of trophic transfer, respiration, and excretion) explained the Eltonian Pyramid. This revelation spawned modern ecosystem ecology which endeavors (in a nutshell) to explain the distribution and abundance of species through *bottom-up forcing*—the idea that food web dynamics operate largely via the nutritional influences of prey on survival, growth, and reproduction



Figure 1. Arthur George Tansley



Figure 3. George Evelyn Hutchinson

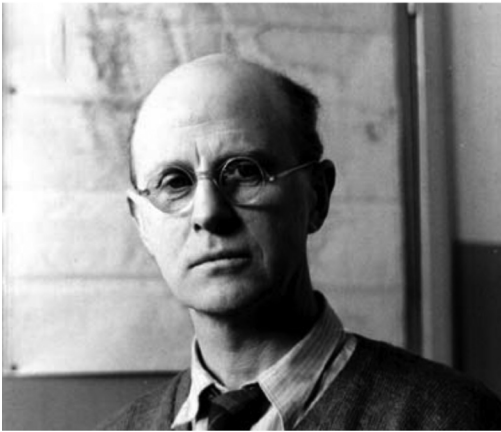


Figure 2. Charles Sutherland Elton

of their consumers. Bottom-up forcing implies resource limitation, which, in turn, implies competition. Lindeman's and MacArthur's views, therefore, were mutually reinforcing.

Hutchinson's legacy through Fred Smith took a different path. Smith, who taught at the University of Michigan, joined forces with Nelson Hairston Sr. and Lawrence Slobodkin to formulate the *Green World Hypothesis* (Hairston et al., 1960), a proposal that the great abundance of plants and green biomass in terrestrial ecosystems (and, hence, a green world) is an epiphenomenon of herbivore limitation by their predators. The Green

World Hypothesis was founded on *top-down forcing*, the idea that food web dynamics are regulated largely by the influences of consumers on their prey.

Robert Treat Paine (1933-2016; Figure 7), a Smith student, altered the course of modern ecology through his now famous *Pisaster* (a predatory starfish) removal experiment, which established an influence of predation on species diversity. Paine's work and thinking led to the ideas of *keystone species* and *trophic cascades*, both of which have become foundational ecological concepts. Just as architectural keystones prevent an arch from collapsing, Paine (1969) imagined that ecosystems are held together by one or several keystone species. Mary Power and colleagues (1996) pointed out that such disproportionately important species could vary from abundant (as with certain plants) to rare (as with Paine's sea stars) and proposed that the common ones be referred to as numerical dominants or foundation species whereas the moniker of *keystone* be applied only to those that are rare. For this reason, many currently recognized keystone species are predators whose influence on the distribution and abundance of other species occurs through top-down forcing.

The effect of a keystone species often occurs via what Paine (1980) referred to in his Tansley Lecture to the British Ecological Society as a trophic cascade. William Ripple and colleagues

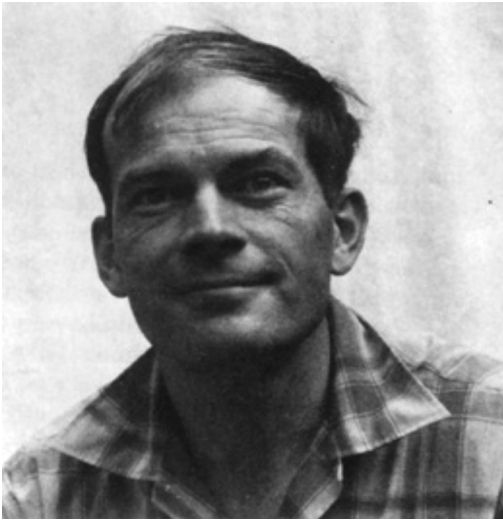


Figure 4. Robert Helmer MacArthur



Figure 6. Raymond Laurel Lindeman

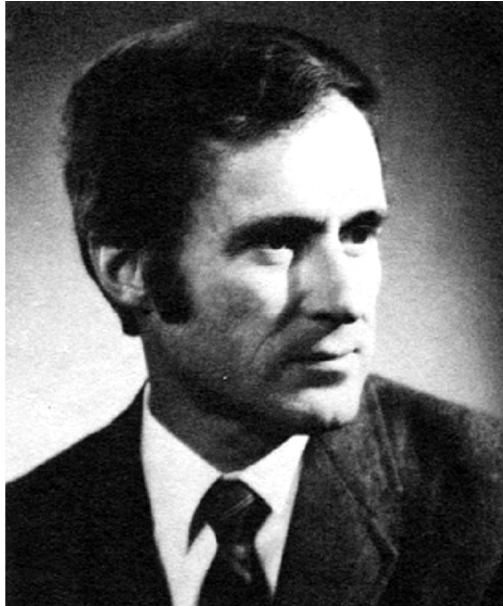


Figure 5. Frederick Edward Smith



Figure 7. Robert Treat Paine

(2016) further proposed that the term *trophic cascade* be limited to indirect interactions that are exclusively top down in nature, in which case neither strong direct effects of consumers on their prey nor indirect effects of prey on species of higher trophic status (see Figure 8) are trophic cascades. The notion of trophic cascades led to Stephen Fretwell's (1987) recognition that the limitation of autotrophs by their herbivores via trophic cascades (as in the Green World Hypothesis) should only occur in

food chains with an even number of trophic levels, whereas trophic cascades in odd-numbered food chains should lead to weak plant–herbivore interactions (Figure 8). Lauri Oksanen and colleagues' (1981) Exploitation Ecosystem Hypothesis, which envisioned food chain length as a function of NPP,

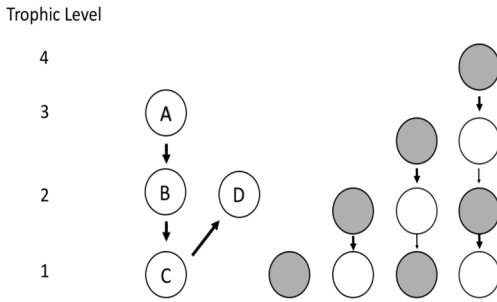


Figure 8. Food web cartoons. Circles represent species and arrows represent consumer–prey interactions. Trophic level is on the left. In the middle module, the indirect interaction of $A \rightarrow B \rightarrow C$ is a trophic cascade. The direct interaction $A \rightarrow B$ is not a trophic cascade, nor is the indirect interaction of $A \rightarrow B \rightarrow C \rightarrow D$ because $C \rightarrow D$ is bottom-up in nature. In the right module (after Fretwell, 1986), shaded circles represent trophic levels at which species are limited by competition, whereas open circles represent trophic levels at which species are limited by their consumers. Strong consumer–prey interactions are depicted by heavy arrows; weak consumer–prey interactions are depicted by light arrows.

is a variation on this theme—important in the history of ecology as an early effort to develop a theory of food web dynamics based on both top-down and bottom-up forcing.

This primer of ecology’s conceptual legacy has two further elements. One of these is evolutionary in nature in that strong top-down interactions between any two adjacent trophic levels (as, for example, between plants and herbivores in odd-numbered food chains) will lead to the co-evolution of defense (by the prey) and resistance to that defense (by the consumer) as in Van Valen’s (1973) Red Queen Hypothesis. The other is ecological in nature and occurs when the *knock on effects* of trophic cascades resonate through ecosystems via diverse pathways to influence other species and ecological processes (Ripple et al., 2016).

Consumer–prey interactions are nature’s most vital interactive processes because without them the living world would contain only autotrophs. The connection of consumer–prey interactions into food chains and the merger of food chains into food webs thus establishes an entity that includes much of what is important in ecology. Just as photosynthesis fuels growth and reproduction of most autotrophs, the flow of energy and materials upward across trophic levels through food webs fuels the life of heterotrophs. Although this process sets upper limits to the distribution and abundance of all species, it does not necessarily explain the distribution and abundance of species in nature. Similarly, while

top-down control may intercede to limit the distribution and abundance of some species, there is no logical reason why the distribution and abundance of any species must be limited by top-down control. Any reasonable effort to understand the distribution and abundance of species, therefore, must consider the relative importance of bottom-up and top-down forcing, how these processes interact, and how those interactions vary in space and time.

Marine Mammal Ecology

I have argued that consumer–prey interactions and food web dynamics involving the interplay between bottom-up and top-down forcing defines much of what is important to ecology. To what degree has marine mammal ecology embraced this interplay? Weakly, in my view. Marine mammal ecology has mostly followed the prevailing mindset of ocean science in attributing the distribution and abundance of species to temperature, nutrients, NPP, and bottom-up forcing. Explanations for the distribution and abundance of marine mammals commonly default to production and food. There is plenty of evidence that production and bottom-up forcing matters a great deal. For instance, many species of marine mammals are most abundant in higher latitude oceans where NPP is greater than it is in the tropics and subtropics. This is clearly the case for mysticetes, pinnipeds, and marine-living otters, although it may be less true for odontocetes, which can occur at high densities in tropical oceans, and extant sirenians, which are exclusively tropical. Reduced body condition and starvation-induced mortality in various pinnipeds during El Niño Southern Oscillation (ENSO) events (Trillmich et al., 1991) are also strong evidence for bottom-up forcing.

Ocean ecosystems conceivably are regulated principally through bottom-up control. However, predation and top-down forcing have been shown to be important in diverse ecosystems (Pace et al., 1999; Shurin et al., 2002; Terborgh & Estes, 2010)—on land and in the water, and from the tropics to near the poles. Of particular note is evidence from lakes which, like oceans, are made up of phytoplankton, zooplankton, planktivorous fishes, and higher trophic-level piscivores but, unlike open ocean systems, have been shown experimentally to be under both bottom-up and top-down control (Carpenter et al., 2001), thus raising the questions of whether lake and ocean food webs operate in fundamentally different ways and, if so, why. A growing body of research is beginning to show important top-down influences by several groups or species of marine mammals on the structure and function of their associated ecosystems.

Highpoints from this work are summarized in the following sections, recounted in part from Estes et al. (2016).

Cetaceans

The earliest credible proposal for an influence by marine mammals on ocean ecosystems was from Richard Maitland Laws' (1926-2014; Figure 9) pioneering work in the Southern Ocean. Laws (1977) proposed that krill, the principal prey of Southern Ocean mysticetes, became more numerous in response to the depletion of great whales by industrial whaling, in turn fueling or otherwise impacting other groups of species, including pinnipeds, penguins, and fish. Although this proposal is well known, it has been overshadowed by subsequent work on the effects of sea ice on krill (e.g., Loeb et al., 1997). Nonetheless, several lines of evidence and thinking continue to support Laws' whale/krill hypothesis. For example, Emslie & Patterson (2007) demonstrated through carbon and nitrogen isotope analyses of ancient Adelie penguin (*Pygoscelis adeliae*) egg shells that penguins consumed mostly fish from > 8,000 years ago through the 19th century, at which point their diet transitioned sharply to krill. The dietary transition by Adelie penguins from fish to krill corresponds closely in time with industrial whaling. Krill sequester elemental iron in their body tissues; iron is an essential micronutrient for the growth and reproduction of phytoplankton; whales recycle iron between krill and sea water through their fecal plumes; and, thus, the reduction of whales by industrial whaling purportedly caused a reduction of elemental iron in sea water and an associated reduction in NPP of the Southern Ocean (Nicol et al., 2010; Smetacek et al., 2012). Roman & McCarthy (2010) invoke a similar process in what they refer to as *the whale pump*—nitrogen concentration (in the nutritionally useful form of nitrate) near the sea surface from fecal plumes of foraging whales from which they envision historically higher ocean NPP in areas of the world oceans where whales once occurred in greater abundance than they do today.

Vectoring and recycling of nutrients via the whale pump is one of four general pathways by which Roman et al. (2014) envisaged the great whales (and possibly other large marine vertebrates) impacting the structure and dynamics of marine ecosystems. A second pathway is top-down forcing. Laws' (1977) above-mentioned scenario for mysticetes and Southern Ocean krill operates by this pathway. If such top-down influences extend downward through the food web one or more trophic levels, the interaction becomes a trophic cascade (*sensu* Ripple et al., 2016). Empirical evidence remains lacking for great whale-induced trophic cascades, although that

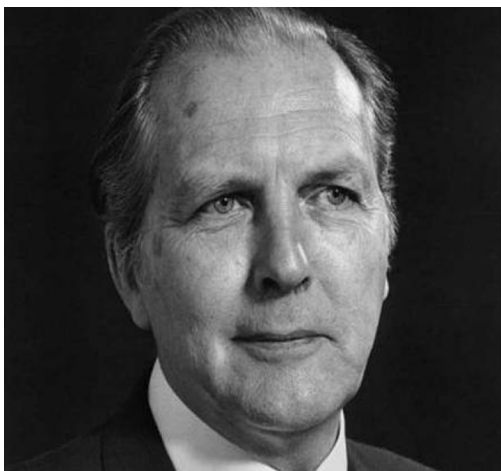


Figure 9. Richard Maitland Laws

may be due to difficulty in documenting such processes or a lack of looking. Foraging by great whales can also alter the physical environment as Oliver & Slattery (1985) have demonstrated for bioturbation and resuspension of sediments by benthic-foraging grey whales (*Eschrichtius robustus*) over the continental shelves of the Bering and Chukchi Seas.

A third pathway by which whales can influence ocean ecosystems is as prey for such megapredators as killer whales (*Orcinus orca*) and sharks. Springer et al. (2003) invoked this process in their *Megafauna Collapse Hypotheses*, which proposed that the reduction of great whales in the North Pacific Ocean by post-World War II industrial whaling caused transient (marine mammal eating) killer whales to broaden their diets so as to feed more intensively on harbor seals (*Phoca vitulina*), Steller sea lions (*Eumetopias jubatus*), and sea otters, thus driving populations of these smaller, rarer, and less well-defended species sequentially downward from the 1960s to the early 1990s. *Carcharocles megalodon*, a 20-m-long shark with massive serrated teeth that roamed the world's oceans in apparently great abundance from the early Miocene through the Pliocene (23 to 2.6 mya) is believed to have preyed on whales and other large vertebrates. *Livyatan melvelli*, an equally large raptorial sperm whale with even larger teeth than those of *C. megalodon* that occurred from the late Miocene into the Pliocene, may also have preyed on large whales.

A fourth pathway by which great whales influence the distribution and abundance of other species is as food for detritivores and scavengers. Stranded whales are fed on by bears, foxes, eagles, and various other carnivorous vertebrates, some of whom may have depended on the lipid- and energy-rich carcasses of dead whales. For example, California condors (*Gymnogyps californianus*) derived much

of their nutritional sustenance from stranded whales and possibly other marine species (Chamberlain et al., 2005) prior to the era of industrial sealing, whaling, and fishing; the California grizzly bear (*Ursus arctos californicus*) probably owed its large size to marine subsidies (Hittell, 1860) from salmon, stranded marine mammals, and perhaps other marine species; scavenging on stranded whale carcasses may have allowed polar bears (*Ursus maritimus*) to survive ice-free interglacial periods of the Pleistocene (Laidre et al., in press); and whale falls (carcasses that sink into the deep sea) are an important source of nutrition for various deep ocean species, including the denizens of chemosynthetically nourished deep sea vent communities as they disperse among vents that disappear and reform over typically short time periods (Smith, 2006).

Pinnipeds

Although pinnipeds are large and abundant in many areas, little is known of their influence on ocean ecosystems. I suspect this is not because they are unimportant but, instead, because of logistical challenges to putting the questions and hypotheses to reasonable tests and the aforementioned lack of interest in and attention to top-down forcing by many ocean scientists. While the above-described pathways of influence by cetaceans (Roman et al., 2014) on ocean ecosystems might apply equally to pinnipeds, the only available evidence from pinnipeds is for their influences as predators and as prey.

Evidence for the impacts of pinnipeds as predators is spotty. The comparatively slow recovery rate of Antarctic fur seals from industrial sealing at South Shetland Island was probably influenced by leopard seal (*Hydrurga leptonyx*) predation (Boveng et al., 1998). Pits created by foraging walrus (*Odobenus rosmarus*) in the shallow benthos of the Bering and Chukchi Seas affect the structure and organization of this ecosystem (Oliver, 1983).

Whereas most pinnipeds are piscivores, much of the evidence for an influence of pinniped predation on fish populations is based on modelling or computational analyses. I'm aware of two anecdotal cases that suggest an influence of pinniped predation on fish in ocean ecosystems.

Fish were comparatively rare, and the larger-bodied species (rock greenling [*Hexagrammos lagocephalus*], red Irish Lord [*Hemilepidotus hemilepidotus*], and great sculpin [*Myoxocephalus polyacanthocephalus*]) fled from divers when I first began diving in Aleutian kelp forests in the mid-1970s. Piscivorous pinnipeds (harbor seals and Steller sea lions) abounded in the Aleutians at the time. This great abundance coupled with large body size and the high mass specific energy requirement of endothermy created the potential

for a very high consumption rate of fish by pinnipeds. Furthermore, fish eyes adjust slowly (i.e., between photopic and scotopic vision; McFarland & Munz, 1975) to the rapidly changing quality and intensity of light at dawn and dusk, whereas the dialatory pupil of the mammalian eye accommodates more quickly to changing light levels. For years, I wondered if these various features of pinnipeds caused or contributed to the elusive behavior and overall rarity of kelp forest fishes in the Aleutians. I could not think of any way to test those hypotheses. But then the once-abundant pinniped populations collapsed across the Aleutian archipelago during the 1970s and 1980s (Springer et al., 2003). Soon thereafter (mid-1980s to early 1990s), I began seeing dusky rockfish (*Sebastes ciliatus*)—sometimes dozens on a single dive—a species I had not previously observed in the central and western Aleutians. Rock greenling, the most common large-bodied kelp forest fish in the Aleutians, remained skittish and unapproachable, whereas dusky rockfish were less obviously responsive to divers. I then began catching the occasional Atka mackerel (*Pleurogrammus monopterygius*) in the late 1980s, also a species I had not seen before in coastal waters of the Aleutians. By the early to mid-1990s, Atka mackerel occurred in immense schools, thousands of square meters in area and extending from the water's surface to the sea floor. Physical oceanographic change (the default explanation by many for such change; e.g., Anderson & Piatt, 1999) may have been responsible for what we saw in the Aleutian Islands. However, that explanation neither lines up very well with the patterns of change through time nor offers a causal mechanism. The pinniped predation hypothesis makes more sense to me (Estes et al., 2013).

Another empirical example of pinniped predation on fish comes from Kelaher et al.'s (2015) work on marine reserves in southeast Australia. With a relaxation of human fishing pressure, the size and density of various reef fishes has increased in marine reserves worldwide (Halpern, 2003; Lester et al., 2009), including several in New Zealand and southeastern Australia (Babcock et al., 1999). Until recently, these latter reserves lacked Australian and New Zealand fur seals (*Arctocephalus pusillus* and *A. forsteri*) because the once-abundant pinnipeds were hunted to low levels and have only just begun to recover. Kelaher et al. (2015) reported a significant negative correlation between fish abundance and pinniped sightings in the reserves.

While pinnipeds are preyed on by sharks (Klimley, 1994; Hammerschlag, 2006), killer whales, polar bears, and other pinnipeds in some parts of the world, their nutritional importance to most of these predators is poorly understood. To

date, there is no evidence that pinnipeds vector significant quantities of materials or nutrients through ocean systems or that their carcasses provide significant nutrition to detritivores and scavengers in the deep sea or along shorelines, although that absence of evidence might be for the above-mentioned lack of looking.

Marine Otters

The ecological influences of sea otter predation are the most well known of any marine mammal. Ironically, all other marine mammal species are larger, and many are more abundant than sea otters—features that ought to enhance their impacts on ecosystems. Are sea otters really so disproportionately influential or are similarly important ecological roles by other marine mammal species undiscovered? I don't know, although I can understand how various features of sea otters and their associated ecosystems make them easier to understand than other marine mammal species and their associated ecosystems.

One such feature is *historical* in nature. Sea otters were exploited to near extinction during the Pacific maritime fur trade, after which they were protected and recovered in areas with surviving remnant colonies but remained absent elsewhere. Sea otters were also reintroduced to southeast Alaska, British Columbia, Washington, and southern California. The ecological influences of sea otters were thus easily identified by comparing nearby locations with and without sea otters and by chronicling patterns of change at particular locations as populations waxed and waned through time. Associated patterns of coastal ecosystem structure with and without sea otters have been documented repeatedly across the species' natural range, thus fortifying the inference that these patterns were indeed caused by sea otter predation.

Another important feature is *behavioral* in nature. Although the aforementioned vagaries of history provided a window for inferring the ecological influences of sea otter predation, that window only existed because of the penchant of individual sea otters to move short distances within small home ranges. This behavior, unusual among marine mammals, acted against dispersion and larger scale spreading as sea otter populations recovered from the fur trade. As a result, high population densities developed in some areas, while nearby areas remained sea otter-free.

Yet another revealing feature of coastal ecosystems is the ease with which the important ecological players (e.g., macroalgae, the sea otter's macroinvertebrate prey, and sea otters themselves) can be observed, measured, and counted in the field. The principal autotrophs (phytoplankton), herbivores (zooplankton), and prey (fish) in the water column ecosystems inhabited by marine mammals are far more difficult to observe and sample.

A final useful feature of the sea otter system is the speed with which kelp and other macroalgae settle and grow following a reduction in herbivory with the repatriation of sea otters on the one hand and disappear following an increase in herbivory with the loss of sea otters on the other. Water column systems also change quickly for the same reasons, but most terrestrial systems do not, owing largely to the much longer generation times of trees and other woody plants.

These features of sea otters and their associated ecosystems have combined to reveal the sea otter's ecological influences in rocky reef, soft-sediment, and estuarine systems. The driving force in all cases was a reduction in density and size of benthic or infaunal macroinvertebrates by sea otter predation. This direct effect spreads through rocky reef systems via two indirect pathways (Estes et al., 2016): (1) from herbivorous sea urchins (the sea otter's prey) to kelp and other macroalgae (the sea urchin's prey), and (2) from predatory sea stars (the sea otter's prey) to mussels and barnacles (the sea star's prey). The sea otter–sea urchin–kelp pathway (a trophic cascade), in turn, influences numerous other species and ecological processes in coastal ecosystems. For example, NPP is greater where sea otters have transformed rocky reef communities from urchin barrens to kelp forests, thereby fueling elevated secondary production through kelp growth and a detritus-based food web. Growth rates of suspension-feeding invertebrates are two- to three-fold greater on forested compared with deforested reefs (Duggins et al., 1989); reef fish populations are enhanced by denser and more extensive kelp forests (Reisewitz et al., 2006; Markel & Shurin, 2015); and the diets and foraging behaviors of other high trophic-level consumers are affected by the sea otter–sea urchin–kelp trophic cascade. For example, glaucous-winged gulls (*Larus glaucescens*) switch from eating fish to macroinvertebrates when sea otters are lost from coastal ecosystems (Irons et al., 1986); bald eagles (*Haliaeetus leucocephalus*) shift from feeding on a mix of marine mammals (mostly sea otter pups), fish, and seabirds where sea otters are abundant to mostly seabirds where sea otters are absent (Anthony et al., 2008). Kelp forest enhancement via the sea otter–urchin–kelp trophic cascade draws down CO₂ from the overlying atmosphere, thereby influencing carbon dioxide–bicarbonate balance and reducing acidification in the surrounding sea water (Wilmers et al., 2012). By preying on predatory sea stars, sea otters reduce mortality from sea star predation on filter-feeding mussels and barnacles (Vicknair & Estes, 2012).

Seagrass-dominated estuarine systems are affected by sea otter predation on crabs that consume algivorous isopods and sea hares. Anthropogenic eutrophication of estuaries from fertilizers in

agricultural runoff enhances epiphytic algae, which, in turn, overgrows seagrasses and reduces estuarine seagrass beds. The reestablishment of sea otters in central California's Elkhorn Slough reduced the size and density of Dungeness crabs (*Cancer magister*), thus releasing algivorous isopods and sea hares from limitation by crab predation, thus increasing rates of removal of epiphytic algal overgrowth on seagrass, thus promoting seagrass recovery (Hughes et al., 2013).

While sea otter predation has been shown to limit bivalve molluscs (Kvitek et al., 1992) and decapod crustaceans (Garshelis et al., 1986) in soft-sediment ecosystems, indirect effects of these predator-prey interactions on other species and ecological processes are unstudied and, hence, unknown.

Sirenians

Although manatees occasionally venture from rivers into estuaries and coastal oceans, dugongs (*Dugong dugong*) are exclusively marine living. Dugongs feed in shallow seagrass meadows of the tropical Pacific and Indian Oceans, reducing seagrass biomass aboveground by cropping and belowground by uprooting plants. These foraging activities generate organic detritus, suspend sediments in the overlying water column, and create habitat heterogeneity across the sea floor. Foraging by dugongs resets succession in seagrass meadows, thereby influencing the distribution and abundance of associated species of plants, invertebrates, and fishes (Preen, 1995; Nakaoka, 2005). By attracting predatory tiger sharks (*Galeocerdo cuvier*), dugongs have a negative impact on dolphins and other shark prey species (Heithaus et al., 2012).

Seagrass declines are detrimental to dugongs. For example, Preen & Marsh (1995) demonstrated an increase in starvation-induced mortality, the near-cessation of reproduction, and long distance emigration following a typhoon-induced decline in seagrass in southern Queensland. My colleagues and I have argued that kelp losses following the collapse of sea otters across the Pacific rim during the 18th and 19th centuries must have had similar negative influences on the kelp-eating Steller sea cow (*Hydrodamalis gigas*), thus causing or contributing to the sea cow's demise and extinction in the North Pacific Ocean (Estes et al., 2015).

Polar Bears

Polar bears obtain most of their nutrition through predation on and scavenging other marine mammals. As predators, they feed mainly on pagophilic (ice-inhabiting) pinnipeds. A negative influence of polar bear predation on pinnipeds is suggested by the striking behavioral differences between Arctic pinnipeds, which seek refuge from danger by entering water, and Antarctic pinnipeds, which

seek refuge from danger by hauling out on ice (Stirling, 1977). 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. Indirect effects of these predator-prey interactions are unstudied and thus unknown.

Retrospection and a View to the Future

At the beginning of this essay, I defined *ecology* as the science of understanding the distribution and abundance of species. Most ecologists probably would not quibble too much with that definition despite their often-differing views on how to practice ecology and the importance of different processes. There should be no debate over the role of history in this endeavor as all species are the products of 300+ million years of evolution since the Cambrian Explosion, and all extant species also owe their geographic distributions to continental drift, sea level change, biotic interchanges, and a host of other factors that occur within the province of historical biogeography.

The distribution and abundance of species is also limited or influenced by features of the contemporary physical and chemical environment—temperature, precipitation, nutrient availability, and the like. But such factors in and of themselves are insufficient predictors of distribution and abundance because they fail to account for species interactions. Species interactions influence the distribution and abundance of species in various ways. I have argued that consumer-prey interactions are of paramount importance because all consumers must eat to survive and reproduce, and most prey (plants and animal hosts to pathogens and parasites being the two exceptions) immediately die upon being eaten. From this logic, I have argued that food webs connect species in a universally important manner and that food web dynamics, therefore, is ecology's most important province of inquiry and understanding.

Although food web dynamics is a subject of immense complexity, I have further argued that much of what ecologists should be striving to learn boils down to four simple questions (by simple, I mean that the questions are easy to ask, not that they will be easy to answer):

1. What are the effects of both bottom-up and top-down forcing to the pattern of living nature? We cannot hope to understand the distribution and abundance of species without considering both.
2. How important are indirect effects? Indirect effects are ubiquitous in nature, sometimes

linking species together in food webs through long and often meandering chains of consumer–prey interactions. Ecologists cannot expect to understand the distribution and abundance of species without considering indirect effects.

3. Over what spatial and temporal scales do species interact? Only by looking at nature through a proper lens of scale can ecologists hope to see pattern and process, even when it is otherwise right before their eyes.
4. To what degree do different species and ecosystems function in similar ways?

Whereas the points and arguments from the preceding two paragraphs apply to all species and ecosystems, my focus in this essay has been on marine mammals. I will thus conclude with an assessment of how well marine mammal ecology has followed ecology writ large in both considering and answering the preceding four questions. These are opinions, not facts. Others may see it differently.

Although the past two decades have provided growing evidence for top-down forcing and trophic cascades in diverse ecosystems (Pace et al., 1999; Shurin et al., 2002; Terborgh & Estes, 2010; Estes et al., 2011), belief and interest across most of ecology continue to favor bottom-up forcing as the conceptual template for understanding nature. I do not believe attention to bottom-up forcing is wrong, except when top-down forcing falls to the wayside as a viable alternative or complementary hypothesis. In a perfect world, one should try to understand the relative importance of both forcing processes in setting the distribution and abundance of species. This will be a tall order. A more realistic goal might be to fairly consider the evidence for both bottom-up and top-down forcing processes as potential explanations for pattern through the formulation and testing of multiple alternative hypotheses (Platt, 1964). Such an endeavor is not so difficult as it may seem. For any observed pattern, a list of reasonable potential explanations (hypotheses) can be assembled and evaluated for consistency with a weight of *available evidence*. The available evidence is often considerable. Consistencies between a particular hypothesis and the weight of evidence, while interesting, do not lead to strong inference. Inconsistencies, however, often do lead to strong inference because hypotheses by their very nature are difficult to accept based on consistencies with expectation but easy to reject when there is an inconsistency.

Good science always takes this approach to drawing inference. Marine mammal ecology has

not always endeavored to test multiple alternative hypotheses. For that reason, there is strong evidence for the importance of both bottom-up and top-down forcing processes for just two species: (1) sea otters and (2) dugongs. The formulation and testing of multiple alternative hypotheses is especially lacking for ecological studies of cetaceans and pinnipeds in oceanic and water column ecosystems. If there is to be any hope for marine mammal ecology, the exclusive focus by many marine mammalogists and oceanographers on bottom-up forcing must be broadened. On a more hopeful note, ocean scientists have begun to amass reasonably strong evidence for top-down forcing and trophic cascades in several oceanic ecosystems (Shiomoto et al., 1997; Worm & Myers, 2003; Frank et al., 2005; Casini et al., 2009; Springer & van Vliet, 2014).

I am aware of two arguments against and three arguments in favor of the need for marine mammal ecologists to pay more attention to indirect effects. The arguments against are that (1) the strength of any direct effect ought to diffuse or attenuate over increasingly long chains of indirect effects and (2) indirect effects are more difficult to see and demonstrate than are direct effects. Both may be correct. On the other hand, strong indirect effects are well known, some of which have been shown to occur across long chains of species interactions. Using the basic measures of interaction strength from Berlow et al. (1999), the indirect effect of sea otters on kelp is at least as strong as the direct effect of sea otters on sea urchins. We have also seen striking outcomes from long and complex chains of species interactions. The direct effect of killer whales on sea otters has led to an explosion of sea urchins, a resulting collapse of kelp, a resulting reduction in kelp forest fish abundance, and a resulting shift in the diet of bald eagles (Anthony et al., 2008). The near extinction of sea otters in the maritime fur trade led to the introduction of Arctic foxes on hundreds of Alaskan islands as an alternate source of fur and revenue. The foxes decimated ground nesting and roosting seabirds, in turn reducing the transport of marine-derived nutrients by foraging seabirds from sea to land, in turn transforming terrestrial plant communities from marine grasslands to maritime tundra, in turn influencing associated animal species (Croll et al., 2005). McCauley et al. (2012) demonstrated an even more complex linkage from introduced coco palms, to seabirds, to nutrient deposition on land, to nutrient runoff into the adjoining coastal ocean, to phytoplankton production, to the secondary production of zooplankton, to the distribution and abundance of planktivorous manta rays (*Manta alfredi*). Such strong and complex linkages among species and across ecosystems may be more commonplace and important in nature than most ecologists believe.

A second argument for the need to pay more attention to indirect effects is that within any assemblage of species, the potential number of indirect pathways far exceeds the potential number of direct pathways. Consider, for example, a food web with just five species, all of which are capable of eating one another. Within this five species assemblage, there are 25 possible direct pathways and 3,875 possible indirect pathways from consumer to prey.

In his MacArthur Lecture to the Ecological Society of America, Simon Levin (1992) discussed the problem of pattern and scale in ecology. Scale, he noted, has two dimensions: (1) space and (2) time. From the spatial dimension, one must consider both the scale at which a process occurs and the scale at which it can be seen and, thus, should be looked for. Consider the futility of trying to demonstrate the influence of sea otters on kelp forests via an experiment in which the treatments (presence or absence of sea otters) are applied to small plots on the sea floor. The spatial scale of such an experiment is too small to capture the process. The scale of observation can also be too large. Consider the same example of sea otters and kelp forests and trying to observe this trophic cascade by comparing the entire North Pacific Ocean (where sea otters occur) with the entire North Atlantic Ocean (where they do not occur). Such a comparison would reveal nothing of value in answering the question at hand, even if the respective ocean basins were thoroughly and properly sampled. The same general issue pertains to time in that sufficient time must follow a perturbation (e.g., the addition to or loss of sea otters from some place) for a response to occur. Although the overall effects are usually predictable, in some places or times they occur quickly (weeks to months) whereas at other places or times they occur more slowly (years to decades).

Whereas food web dynamics might be imagined as always arising from the influences of prey on their predators (bottom-up forcing) on the one hand and the influences of predators on their prey (top-down forcing) on the other, we have seen that process can be more subtle and complex than that. The influences of prey consumption by great whales not only reduce prey but vector nutrients through the ecosystem. The influence of production may act progressively upward through diverse food webs via traditional bottom-up forcing processes, while the influence of predators may act progressively downward through diverse food webs via traditional trophic cascades. But these are not the only ways by which consumers and prey link together in nature.

The history of marine mammal ecology in my view is monolithic and unnecessarily boring, punctuated here and there by moments of insight and excitement. If I were asked for guidance or words of

wisdom by a future marine mammal ecologist, they would be just this: First, remain open to process. Be imaginative in thinking about how a species might be influenced by its physical environment and the ways in which a species can interact with other species. Second, look for perturbations as windows into ecological processes. On occasion, these may be purposeful experiments; more often, you will learn from what nature offers. Pay particular attention to history, as change through time is the most common way in which nature is perturbed. Third, be cognizant of scale. Think about how large or small an area to consider to see the possible consequences of a perturbation and how long it might take nature to change in response. Finally, although you inevitably will develop favored opinions on how nature works, remain open to all reasonable alternatives, and practice science by trying to figure out why you might be wrong, not through the continued gathering of evidence in support of your favored view. Re-read Platt (1964) at least once each decade. Armed with these few guidelines, you stand to learn vastly more than those who came before.

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