Predator–Prey Relationships

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Most marine mammals are predators, but some are also preyed upon by other species. Theoretically, the interaction between marine mammals and their prey influences the structure and dynamics of marine ecosystems. Similarly, predators and prey have shaped each other's behaviors, physiologies, morphologies, and life-history strategies. However, there is little empirical evidence of these influences due to the relative scale and complexity of marine ecosystems and the inherent difficulties of observing and documenting marine mammal predator–prey interactions.

I. Evolutionary Time Scales

Predator–prey relationships have been likened to an evolutionary arms race—the prey become more difficult to capture and eat, while the predators perfect their abilities to catch and kill their prey. Just how strong these selective forces are probably depends on the strength of the interactions between the predators and their prey (Taylor, 1984).

As predators, marine mammals feed primarily upon fish, invertebrates, or zooplankton, which in turn feed primarily upon other species of fish, invertebrates, zooplankton, and phytoplankton (Fig. 1). To capture their prey, marine mammals have evolved special sensory abilities (e.g., vision and hearing), morphologies (e.g., dentition), and physiologies (e.g., diving and breath-holding abilities) (Trites *et al*., 2006). They have also evolved specialized strategies to capture prey, such as cooperation to corral fish, or the production of curtains of air bubbles used by humpback whales (*Megaptera novaeangliae*) to capture herring. Marine mammals have also evolved specialized

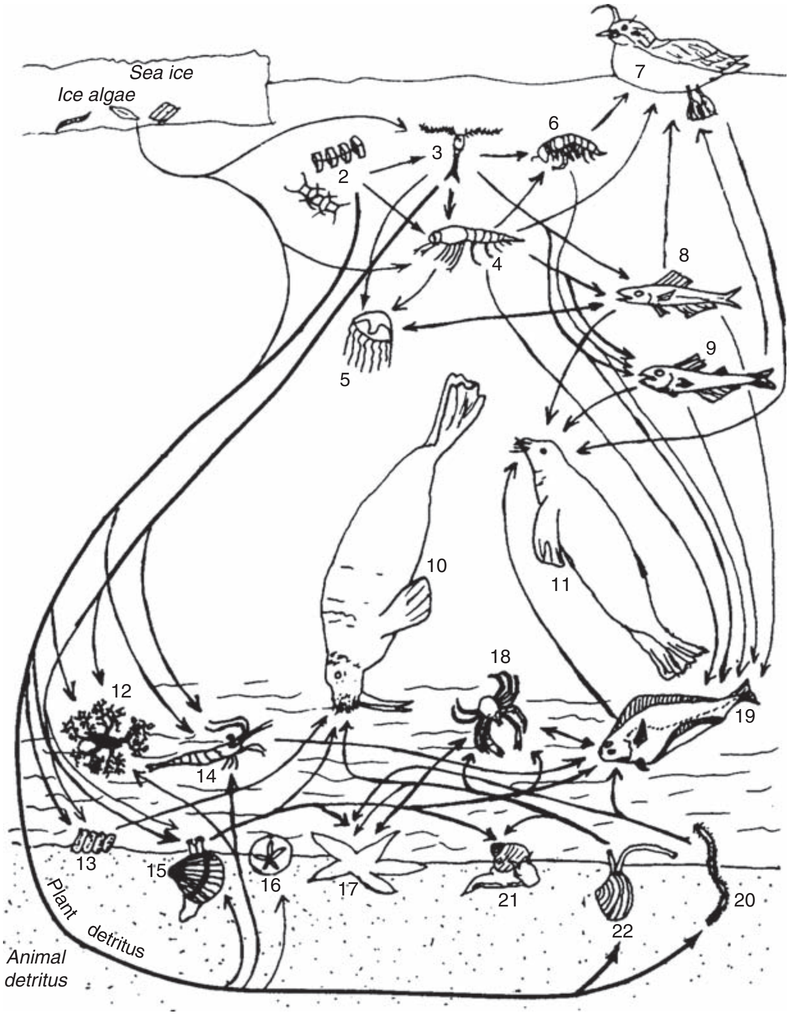

Figure 1 *A simplified depiction of the Bering Sea food web; (1) ice algae; (2) phytoplankton; (3) copepods; (4) mysids and euphausiids; (5) medusae; (6) hyperid amphipods; (7) seabirds; (8, 9) pelagic fishes; (10) walrus; (11) seals; (12) basket stars; (13) ascideans; (14) shrimps; (15) filter-feeding bivalves; (16) sand dollars; (17) sea stars; (18) crabs; (19) bottom feeding fishes; (20) polychaetes; (21) predatory gastropods; and (22) deposit feeding bivalves. From McConnaughey and McRoy (1976).*

feeding behaviors to capture prey that move diurnally up and down the water column or to capture prey that move seasonally across broad geographic ranges. This in turn has likely influenced the life-history strategies of marine mammals and their prey. For example, baleen whales feed for about 6 months when plankton are abundant and concentrated in shallow water, and then fast for the remainder of the year when the plankton are too dispersed to make them worth finding.

As prey, marine mammals have had to escape aquatic and terrestrial predators (Taylor, 1984; Morisaka and Connor, 2007). Porpoise (phocoenidae) for example are preyed upon by killer whales (*Orcinus orca*) and may have evolved an echolocation and communication system through the selective pressures of predation that falls within a range of sounds that killer whales hear poorly or not at all (<2 and >100 kHz). Other species such as pinnipeds can reduce their risk of being eaten by aquatic predators (sharks and killer whales) by hauling out and resting onshore; while species such as Steller sea lions (*Eumetopias jubatus*) and northern fur seals (*Callorhinus ursinus*) reduce their risk of being eaten by terrestrial predators [wolves (*Canis lupus*) and bears] by breeding and hauling out on offshore rocks and islands where terrestrial predators are absent. Other species, such as ringed seals (*Pusa hispida*), give birth in caverns formed between ice and snow to avoid predation by polar bears (*Ursus maritimus*).

Fish and other cold-blooded species of prey have also evolved a number of strategies to increase their chances of survival (Trites *et al*., 2006). One is cryptic countershading that enables fish to blend in with the bottom when viewed from above, and avoid detection when seen from below against a bright sea surface. Many species of fish, invertebrates, and zooplankton take refuge from predators in the deep, dark waters during the day and move toward the surface to feed under the cover of night. Another strategy evoked by the prey of marine mammals is predator swamping, such as large aggregations of spawning salmon and herring (*Clupea* spp.) that reduce the numerical effect of predators on their prey populations. Schooling is another antipredator behavior that creates confusion through the sheer volume of stimuli from a fleeing school, making it difficult for a marine mammal to actively select and maintain pursuit of single individuals. Scattering and fleeing is yet another option to reduce predation and is used by some prey when attacked by bulk feeders such as baleen whales [e.g., humpback whales and capelin (*Mallotus villosus*)]. The line between feeding and fleeing is undoubtedly fine for species of prey and must be continually evaluated by prey to minimize vulnerability to predation.

Marine mammals may also have indirectly influenced the evolution of nontargeted species in their ecosystems by consuming the predators of these species (Estes, 1996). The best example of this is the apparent influence of sea otters (*Enhydra lutris*) on kelp and other marine algae. Most species of marine algae use secondary metabolites to defend against herbivores. However, marine algae in the North Pacific Ocean have lower levels of chemical defenses where sea otters occur compared to algae species inhabiting the southern oceans where sea otters are not present. Sea otter predation on sea urchins and other herbivores may have removed selective pressure for species of marine algae to defend themselves against herbivores. Because secondary metabolites are expensive to produce, this may have allowed algae, like kelp, to radiate and diversify without the added cost of evolving and producing antigrazer compounds.

II. Ecological Time Scales

On a shorter time scale than the evolutionary time scale, predators and prey can directly affect the relative abundance of each other, or they can indirectly affect the abundance of other species. Their interaction may also affect the physical complexity of the marine environment (Katona and Whitehead, 1988; Bowen, 1997; Trites, 1997).

Predation by sea otters on sea urchins is probably the best example of how marine mammals can alter ecosystem structure and dynamics (Estes, 1996). Sea otters were hunted to near extinction in the late 1800s throughout their North Pacific range. Without predation, urchin populations grew unchecked and overgrazed the fleshy algae. Kelp did not replace the underwater barrens until reintroduced sea otters once again began preying upon sea urchins.

Primary production has been estimated to be three times higher in areas where sea otters are present compared to those areas where sea otters are absent, allowing those organisms that feed upon primary production to grow faster and attain larger sizes (e.g., mussels and barnacles). The increase in primary production may even alter settlement patterns of invertebrates. The kelp also provides habitat for fish and suspension feeding invertebrates to spawn, grow, and flourish. It can also change water motion and reduce onshore erosion and may even block the shoreward movement of barnacle larvae. Thus a top predator such as the sea otter can change the structure and dynamics of marine ecosystems.

Gray whales (*Eschrichtius rohustus*) and walruses (*Odobenus rosmarus*) are other species of marine mammals whose foraging behavior can also affect community structure. For example, gray whales turn over an estimated 9–27% of the bottom substrate each year in the Bering Sea. The feeding pits created by gray whales draw 2–30 times more scavengers and other invertebrates compared to adjacent sediments. The disturbed sediments may also help maintain the high abundance of gray whale prey and other early colonizing species. Similarly, walruses turn over bottom substrate in their search for clams and other bivalves. There is some evidence that they may feed selectively on certain size classes and certain species and that their defecation may result in the redistribution of sediment. Thus, the interaction of benthic feeding marine mammals with their prey can result in food for scavengers and habitat for other species.

Interactions between predators and prey also influence the shapes of their respective life tables (i.e., age-specific survival and pregnancy rates). In Quebec, Canada, for example, there are a number of freshwater lakes that are home to landlocked harbor seals (*Phoca vitulina*). Studies have found that the trout in these lakes are younger, grow faster, attain smaller sizes, and spawn at younger ages compared to adjacent lakes without seals. As for marine mammals, they typically have elevated mortality rates during their first few years of life. This is likely due to a number of factors, including their relative vulnerability to predators and their inexperience at capturing prey and securing optimum nutrition.

In the Gulf of Alaska and Bering Sea, killer whales have been implicated as a contributing factor, but not the main one, in the decline of Steller sea lions and harbor seals through the 1980s (Williams *et al*., 2004). Field observations along the Aleutian Islands indicate that these population declines were followed by a decline of sea otters in the 1990s and that this decline was caused by killer whale predation. Some killer whales may have begun supplementing their diet with sea otters because they could not sustain themselves on the low numbers of remaining seals and sea lions. What ultimately caused the decline of Steller sea lions and began this spiraling change of events is a matter of considerable scientific debate. However, it is apparent from mathematical calculations of population sizes and energetic requirements that there are sufficient numbers of killer whales in Alaska to prevent the recovery of pinniped populations. Thus, it is conceivable that populations of pinnipeds and otters may not recover to former levels of abundance until the predation by killer whales is reduced by a reduction in killer whale numbers or by a shift in killer whale diet to other species of mammals such as dolphins and porpoises.

In addition to directly affecting the abundance of their prey, marine mammals can indirectly affect the abundance of other species by outcompeting them or by consuming species the prey upon them (Trites, 1997). A case in point is harbor seals in British Columbia whose diet was about 4% salmon and 43% hake in the 1980s. Contrary to popular opinion, the harbor seals were likely benefiting salmon because they affected the abundance of hake, a species of fish that is one of the largest predators of salmon smolts. Further north in Alaska's Copper River Delta, harbor seals were culled in the 1960s to reduce the predation on salmon. However, the immediate result of the cull was not an increased number of salmon caught, but a decrease and failure of the razor clam (*Siliqua patula*) fishery. It turned out that the seals were primarily eating starry flounder (*Platichthys stellatus*), which fed on the razor clams. Without the seals, the predatory flounder population grew unchecked.

In the Antarctic, commercial whaling systematically removed over 84% of the baleen whales and freed an estimated 150 million tons of krill for other predators to consume each year (Knox, 1994). Species such as crabeater seals (*Lobodon carcinophaga*), Antarctic fur seals (*Arctocephalus gazella*), leopard seals (*Hydrurga leptonyx*), and penguins [chinstrap (*Pygoscelis antarcticus*), Adelie (*P. adeliae*), and macaroni (*Eudyptes chrysolophus*)] increased and moved the Antarctic marine ecosystem to new equilibrium levels. Increases were also observed in Antarctic minke whales (*Balaenoptera bonaerensis*) and squid-eating king penguins (*Aptenodytes patagonicus*) due perhaps to reductions in the respective abundance of blue whales (*Balaenoptera musculus*) and sperm whales (*Physeter macrocephalus*). All of these species appear to have directly benefited from an increase in prey, which was caused by the removal of whales. Penguins and seals may now be hindering the recovery of baleen whale stocks in the Antarctic.

Marine mammals are generally considered to be opportunistic foragers who select from a number of alternative prey according to availability. This is based on the relatively large number of different species that have been reported in the stomachs and feces of marine mammals. Steller sea lions, for example, are known to eat over 50 different species of fish, and even the occasional seabird. However, their diets are typically dominated by five or fewer species, suggesting that they may not be truly opportunistic feeders. Little is yet known about the choices that marine mammals make when foraging. Presumably what marine mammals eat is a function of nutritional value, ease of capture, and digestibility, all of which are invariably linked to the abundance of both predators and prey. These are complex biological interactions about which little is known.

Functional response curves represent rates of predation in relation to the density of prey (Mackinson *et al*., 2003; Middlemas *et al*., 2006). In most species, the rate of capture rises with the density of prey to some maximum level. These relationships between prey density and predation rates tend to be sigmoidal (nonlinear and asymptotic), indicating that there are maximum limits to the rate that predators can capture and process prey, which are independent of prey population size. Establishing these functional relationships for different species of prey is fundamental to fully understanding the foraging ecology of marine mammals. Establishing these relationships is beginning to been done for marine mammals and will require further experimentation in captivity or observational studies in the wild.

Ecosystem models are another technique for gaining insight into the effects of predator–prey relationships on ecosystem dynamics and structure (Trites *et al*., 1999; Morissette *et al*., 2006). Using a series of mathematical equations to account for the flow of energy from one group of species to another, the models can estimate the extent of competition between species and the effect that changes in abundance of one species will have on other species in the ecosystem. One such ecosystem model describing the Gulf of St. Lawrence revealed that harp seals (*Pagophilus groenlandicus*), gray seals (*Halichoerus grypus*), and hooded seals (*Cystophora cristata*) negatively affect the abundance of the higher trophic level fish they target, which in turn reduces predation pressure on the prey of the species these seals eat. Another ecosystem model constructed for the eastern Bering Sea examined trophic relationships to determine whether the declines of Steller sea lions and forage fishes (such as herring) and the increases in pollock (*Pollachius* spp.) and flatfish between the 1970s and the 1980s were related to the commercial removal of whales.

Removing historic numbers of whales from the simulated Bering Sea ecosystem resulted in an increase in numbers of pollock. However, the increase was only in the order of 10–20%, not the 400% increase believed to have actually occurred. The ecosystem model suggested that the Bering Sea may exist in two alternative states (consisting of two different complexes of species) and that environmental shifts (from periods of cold to warm water years) may ultimately determine when and for how long these shifts occur. The model also suggested that curtailing fishing on pollock (a major prey of Steller sea lions) may affect the Steller sea lion negatively. The explanation for this counterintuitive prediction was that commercial fisheries primarily removed larger pollock than Steller sea lions consumed. Given that pollock are cannibalistic, increasing the size of the adult stock resulted in the increased predation of younger pollock, leaving fewer fish for Steller sea lions to consume. Thus, ecosystem models are useful tools for exploring the influence of predator–prey interactions on one another and on other components of their ecosystems.

III. Synthesis

Marine mammal predator–prey interactions occur over different spatial and temporal scales, making it difficult to empirically decipher the influences they have on one another and on their ecosystems. However, their coexistence suggests that marine mammal predators and their prey have had profound influences on each other's behaviors, physiologies, morphologies, and life-history strategies. The diversity of niches filled by marine mammals makes it difficult to generalize about the evolutionary consequences of their interactions with prey, beyond stating the obvious: marine mammals have adapted to catch food, while their prey have adapted to avoid being caught.

On the shorter ecological time scale, marine mammals can affect the abundance of other species by consuming or outcompeting them. They can also indirectly affect the abundance of nontargeted species by consuming one of their predators, and can have strong impacts on the overall dynamics and structure of their ecosystems. One of the best tools for understanding marine mammal predator–prey interactions is the ecosystem model. However, more work is required through experimental manipulations and observational studies to evaluate the choices made by marine mammals and the costs of obtaining different species of prey.

See Also the Following Articles

Feeding Strategies and Tactics ■ Hearing ■ Predation on Marine Mammals ■ Vision

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Pygmy and Dwarf Sperm Whales

Kogia breviceps and *K. sima*

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I. Characteristics and Taxonomy

In form, *Kogia* spp. are porpoise-like and robust with a distinctive underslung lower jaw. This latter feature has been described as giving these whales a shark-like appearance (Fig. 1). Although height and position of the dorsal fin have been reported as distinguishing the two currently recognized species, they are probably not separable at sea except under exceptional circumstances. Pygmy sperm whales reach a maximum size of about 3.8 m and a weight of 450 kg. Dwarf sperm whales are smaller at 2.7 m and 272 kg. Adults of both species are dark bluish-gray to blackish-brown dorsally and light below. On the side of the head between the eye and the flipper there is often a crescent-shaped, light colored mark referred to as a "false gill." These whales have the shortest rostrum among living cetaceans, and the skull is markedly asymmetrical. The mandibles are delicate, and the teeth are very sharp, thin, and lack enamel. *K. breviceps* lacks teeth in the upper jaw, but *K. sima* may have up to three pairs of vestigial teeth in this position. Although now recognized as the sole genus within the family Kogiidae, originally these whales were placed within the Physeteridae, with the sperm whale, *Physeter macrocephalus*. Fossil forms of Kogiidae have been described rarely from fragments of teeth, cranium, and lower jaws of late Miocene to early Pliocene age. Most of these may be only distantly related to extant *Kogia* spp. However, *Praekogia cedrosensis*, described from the early Pliocene in the Almejas Formation on Isla Cedros Baja California, Mexico, is reported to clearly be ancestral to living *Kogia*. It is only since 1966 that two species of *Kogia* have been recognized, and no subspecies have been described. On the basis of recent evidence from the mitochondrial cytochrome *b* gene it has been suggested that *K. sima* may consist of two apparently parapatric species occupying the Atlantic and Indo-Pacific Oceans (Chivers *et al.*, 2005). Full recognition of this putative third *Kogia* sp. awaits further supporting evidence.

II. Distribution and Abundance

Dwarf and pygmy sperm whales occur worldwide in temperate and tropical waters of the Atlantic, Pacific, and Indian Oceans. Although rarely sighted at sea, these whales commonly strand in some regions, and much of the relatively little that is known of their ecology has been gleaned from such stranded animals. In the NE Atlantic most strandings occur in autumn and winter, but more broadly there is little indication for seasonality in the distribution or the migration of these whales. Evidence shows that *K. sima* may prefer warmer seas than *K. breviceps*. The precise at-sea DISTRIBUTION of *Kogia* spp. is unknown, as most records are based on stranded animals, but some evidence suggests *K. sima* may have a more pelagic distribution and feed in deeper water. Analysis of prey in stranded animals suggests that both species of *Kogia* generally inhabit waters along the continental shelf and slope in the epi- and mesopelagic zones.

Although many writers have stated that dwarf and pygmy sperm whales are rare, there is insufficient information to classify the world status of *Kogia* species; neither their population sizes nor trends are known (Baird *et al.*, 1996; Willis and Baird, 1998). The frequency with which *Kogia* strand on certain coasts, especially in southeastern United States and South Africa, suggests that in some regions they may be uncommon rather than rare.

III. Ecology

Kogia spp. feed mostly on mid and deepwater cephalopods but also consume fish and occasionally crustaceans, such as shrimp and crabs (McAlpine *et al.*, 1997; Santos *et al.*, 2006). Stomach contents that have been analyzed have contained cephalopod beaks from at least 55 species representing 15 families, although in NE Atlantic *K. breviceps* squids of the genus *Histioteuthis* predominate. It has been suggested that there may be some competition for prey between adult pygmy sperm whales and juvenile sperm whales. Most feeding seems to takes place on or near the bottom, probably using ECHOLOCATION to find prey. Kogiid hyoid anatomy suggests powerful suction feeding.