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MARINE MAMMAL TROPHIC LEVELS AND INTERACTIONS

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Introduction

Trophic levels are a hierarchical way of classifying organisms according to their feeding relationships within an ecosystem. By convention, detritus and producers (such as phytoplankton and algae) are assigned a trophic level of 1. The herbivores and detritivores that feed on the plants and detritus make up trophic level 2. Higher order carnivores, such as most marine mammals, are assigned trophic levels ranging from 3 to 5. Knowing what an animal eats is all that is needed to calculate its trophic level.

Marine mammals are commonly thought to be the top predator in marine ecosystems. However, many species of fish occupy trophic levels that are on par or are above those of marine mammals. Some species such as killer whales and polar bears (that feed on other marine mammals) are indeed top carnivores, but others such as manatees and dugongs feed on plants at the bottom of the food web. Thus, marine mammals span four of the five trophic levels.

Marine mammals are a diverse group of species whose behaviors, physiologies, morphologies, and life history characteristics have been evolutionarily shaped by interactions with their predators and prey. It is therefore difficult to generalize about how marine mammals affect the dynamics and structure of their ecosystems. Similarly, it is difficult to generalize about how the interactions between marine mammals and their prey (or between marine mammals and their predators) affect one another, as well as how they affect the dynamics of unrelated species. Nevertheless, some insights into marine mammal trophic interactions can be gleaned from mathematical models and from field observations following the overharvesting of marine mammal populations in the nineteenth and twentieth centuries.

Trophic Levels (Diet Composition)

Trophic levels depend on what a species eats. As an example, a fish consuming 50% herbivorous-zooplankton (trophic level 2) and 50% zooplankton-eating fish (trophic level 3) would have a trophic level of 3.5. Trophic levels (TL) can be calculated from

$$TL = 1 + \frac{\sum_{i=1}^{n} (TL_i \cdot DC_i)}{\sum_{i=1}^{n} DC_i} \qquad [1]$$

where n is the number of species or groups of species in the diet, DC_i is the proportion of the diet consisting of species i, and TL_i is the trophic level of species i. Thus, the trophic level of the predator is determined by adding 1.0 to the average trophic level of all the organisms that it eats.

Applying eqn [1] to marine mammals shows that sirenians (dugong and manatees) have a trophic level of 2.0, whereas blue whales (which feed on large zooplankton, trophic level 2.2) are at trophic level 3.2 ($= 1.0 + 2.2$). Moving higher up the food chain, Galapagos fur seals have a trophic level of 4.1. Their diet consists of approximately 40% small squids, 20% small pelagic fishes (such as clupeoids and small scombroids), 30% mesopelagic fishes (myctophids and other groups of the deep scattering layer) and 10% miscellaneous fishes (from a diverse group consisting mainly of demersal fish). Substituting these proportions into eqn [1], along with the respective mean trophic levels (TL_i) of these four types of prey (3.2, 2.7, 3.2, and 3.3, respectively), yields a trophic level of 4.11 for Galapagos fur seals. A polar bear that feeds exclusively on ringed seals (3.8) would have a trophic level of 4.8.

Dugongs and manatees occupy the lowest trophic level (2.0) of all marine mammals. They are followed (see **Figure 1**) by baleen whales (3.35: range 3.2–3.7), sea otters (3.45: range 3.4–3.5), pinnipeds (3.97: range 3.3–4.2), and toothed whales (4.23: range 3.8–4.5), with the highest trophic level belonging to the polar bear (4.80).

Trophic interactions between marine mammals and other species can be depicted by flowcharts showing the flow of energy between species in an ecosystem. An example is shown in **Figure 2** for the

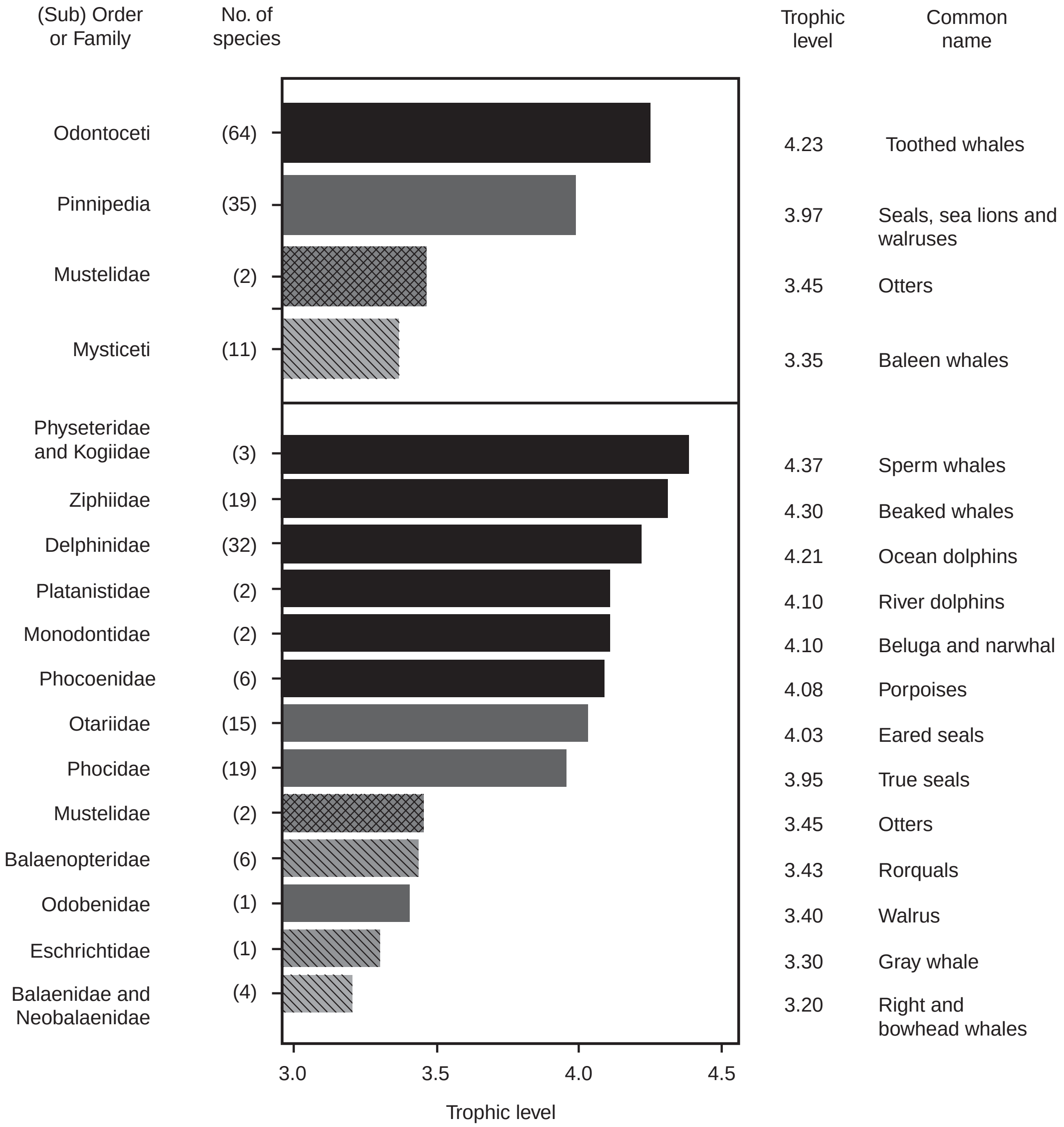

Figure 1 Mean trophic levels for 112 species of marine mammals grouped by families, orders and suborders. Numbers of species averaged within each grouping is shown in brackets. Species not shown are dugong and manatees (Sirenia: trophic level 2.0) and polar bears (Ursidae: trophic level 4.8).

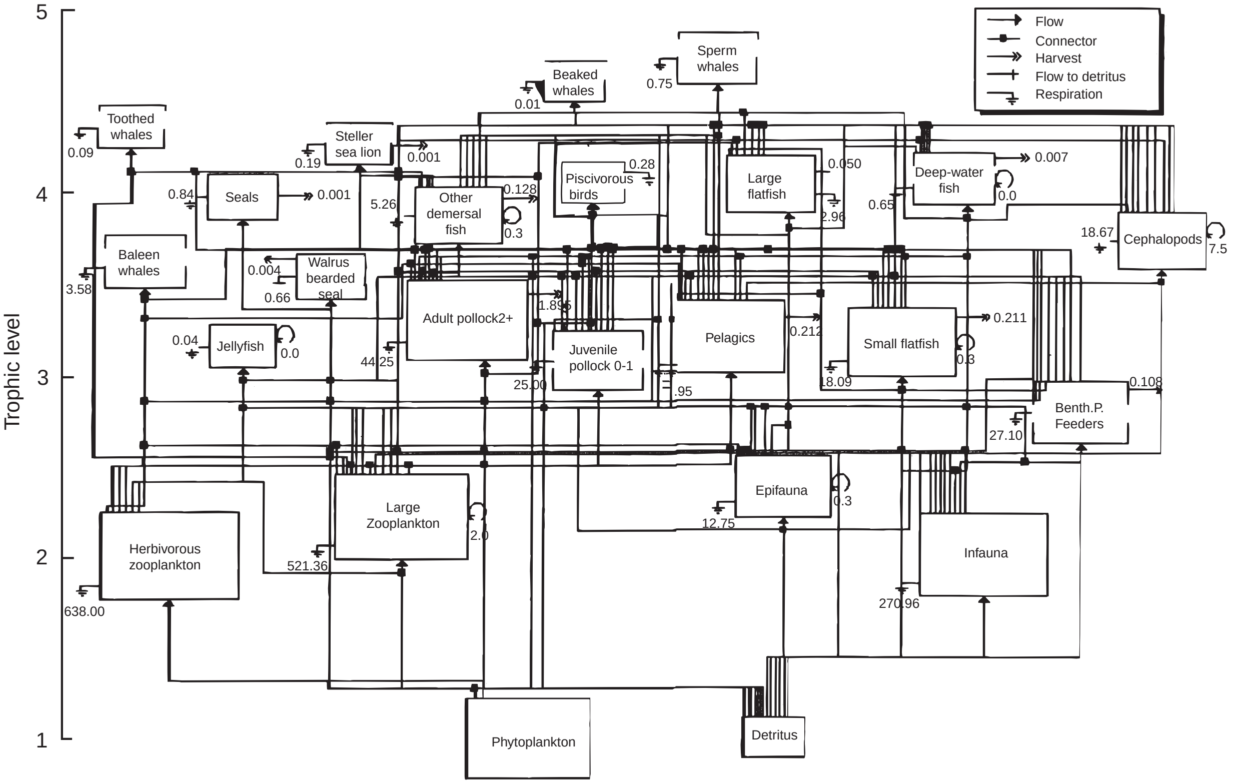

Figure 2 Flowchart of trophic interactions in the eastern Bering Sea during the 1980s. All flows are in t km^{-2}y^{-1}. Minor flows are omitted as are all backflows to the detritus. Note that size of each box is roughly proportional to the biomass therein, and that each box is placed according to its trophic level in the ecosystem.

eastern Bering Sea. Each of the boxes in this flowchart represents a major species or group of species within this system during the 1980s. The boxes are arranged by trophic levels and are proportional in size to their biomass. Lines connecting the boxes show the relative amounts of energy flowing between the groups of species.

Figure 2 shows a large number of flows in the Bering Sea emanating from three species at trophic level 3 – pollock, small flatfish and pelagic fishes. Major level 4 consumers include large flatfish, deep-water fish, other demersal fishes, marine mammals and birds. Thus, large flatfish and other species of fish share the pedestal with marine mammals as top predators of marine ecosystems. These fish are also major competitors of marine mammals.

Trophic levels depicted in **Figures 1** and **2** are approximate, and are based on generalized diets and the mean trophic levels of prey types. In actual fact, trophic levels of most marine mammals probably vary from season to season, or from year to year, because diet is unlikely to remain constant. How much they might vary is not known, but is probably within ± 0.2 trophic levels.

Trophic Levels (Stable Isotopes)

Diets have traditionally been described from stomach contents of shot or stranded animals. This has been augmented by the identification of prey from the bony remains found in feces (primarily from pinnipeds), and from fatty acid signatures of prey species that have been laid down in the blubber of marine mammals. Unfortunately, the diets of most species of marine mammals are poorly understood due to incomplete sampling across time and space.

There is another way to estimate trophic levels without stomach contents or other dietary information. It is referred to as stable isotope analysis and relies on the relative concentration of two isotopes (nitrogen-14 and nitrogen-15). Marine mammals and other organisms tend to accumulate the heavier isotope (nitrogen-15) in their tissues. Thus, as matter moves from one trophic level to the next, the ratio of the two isotopes shifts by a roughly constant amount. Trophic levels can be calculated by dividing the difference between the isotopic ratio in the marine mammal tissue and the isotopic ratio of the organism at the bottom of the local food chain, by this constant difference between trophic levels.

A comparison of the isotopic estimates of trophic levels for species in Prince William Sound, Alaska with estimates derived from dietary analysis (eqn [1]) suggests that the two techniques produce comparable results. One of the strengths of the isotopic analysis is that it can be conducted from biopsy samples and does not require killing the animal to examine stomach contents. This is particularly useful for assessing the trophic levels of cetaceans. Stable isotope analysis can also be used to probe the past to learn about the trophic levels that marine mammal populations once occupied. As predators, marine mammals are better samplers of the marine environment than biologists. Thus, analyzing seasonal and annual changes in the nitrogen concentrations contained along growing whiskers and baleen can provide a time series of dietary information. Similarly, trophic levels can be calculated from nitrogen concentrations in bones and teeth archived in museums or recovered from archaeological digs.

Another useful stable isotope ratio is the relative concentration of carbon-13 and carbon-12. Studies have shown that there is a very slight enrichment of carbon from one trophic level to another (0.1–0.2%). In the marine environment, slight enrichment occurs at low trophic levels, but not among vertebrate consumers. Thus, isotopic carbon ratios are not useful for assessing trophic level, but they are useful for tracking carbon sources through a food chain and for assessing long-term changes in ocean productivity.

Isotopic analyses of marine mammal tissues have shown that species inhabiting the northern oceans have higher nitrogen-isotope ratios than those from southern oceans. This indicates that southern species feed at lower trophic levels, and presumably consume larger amounts of invertebrates. Measuring the isotopic carbon ratio of baleen plates from bowhead whales further shows that primary productivity declined in the Bering Sea through the 1970s–1990s. This drop in primary productivity may reflect an overall lowering of carrying capacity and may have a bearing on the observed decline of Steller sea lions, harbor seals, and northern fur seals during this period. Thus, isotopic analysis is a useful tool for estimating trophic levels of marine mammals, and for detecting shifts in ocean productivity and diets of marine mammals.

Trophic Interactions

Changes at one level of a food web can have cascading effects on others. One of the best ways to explore the direct and indirect impacts of competition and predation by marine mammals on other species is with mathematical descriptions of ecosystems (i.e., ecosystem models). Ecosystem models, such as the one developed for the Bering Sea (**Figure 2**), allow changes in abundance to be tracked over time, and predictions to be made about the strength and significance of predator–prey interactions on each other, and on other components of their ecosystem.

Major changes have occurred in the abundance of a number of species in the Bering Sea since the mid-1970s. Most notable has been the decline of Steller sea lions, harbor seals, crabs, shrimp and forage fishes (such as herring and capelin). In contrast, populations of walleye pollock and large flatfish (mostly arrowtooth flounder) increased through the 1970s and 1980s. Some have felt that commercial whaling prompted these changes by removing a major competitor of pollock – the baleen whales. Mathematically, removing whales can be shown to positively affect pollock by reducing competition for food. However, whaling alone is insufficient to explain the 400% increase in pollock that is believed to have occurred. Overall, the models developed to date suggest that changes in the biomass of marine mammals have little or no effect on changes in the biomass of other groups in the Bering Sea. Most impacts on this northern marine ecosystem appear to be associated with changing the biomass of lower trophic levels (such as primary production).

The conclusions drawn from the eastern Bering Sea model may be indicative of marine mammals in long-chained food webs, and may not reflect the role of marine mammals in shorter-chained food webs such as in the Antarctic. A case in point is the increase in abundance of krill-eating Antarctic fur seals, crabeater seals, leopard seals, and penguins that followed the cessation of commercial whaling. Commercial whaling removed over 84% of the baleen whales from the Antarctic and 'freed up' millions of tons of krill for other species to consume. Some believe that the increase in these other krill-eating species is now impeding the recovery of Antarctic whales.

Sea otters and sea urchins form another short-chained food web with strong trophic interactions. By the turn of the twentieth century, sea otters had been hunted to near extinction. Without predation by otters, sea urchin populations grew unchecked and overgrazed the fleshy algae along the Pacific coast of North America. The once productive kelp forests became underwater barrens. With the reintroduction of sea otters however, productivity increased three-fold as urchins were removed and kelp and other fleshy algae began to regenerate. Kelp provides habitat for fish and invertebrates, changes water motion, and can affect onshore erosion and the recruitment of fish and invertebrates. Thus, sea otters can change the state of near-shore ecosystems and the way they function.

Other examples of marine mammals affecting their prey include harbor seals in freshwater lakes, and killer whales preying on sea otters in Alaska. A number of lakes in Quebec, Canada, are home to land-locked harbor seals that feed on trout. Studies have shown that the trout in these lakes are younger and spawn at younger ages than adjacent lakes without harbor seals. The trout also grow faster and attain smaller sizes in the lakes inhabited by harbor seals.

Marine mammals may also significantly affect prey abundance, as in the case of killer whales eating sea otters, Steller sea lions, and other warm-blooded species. Killer whales were observed eating sea otters along the Aleutian Islands in the 1990s and may be responsible for reported declines in sea otter population abundance. Killer whales have also been implicated as a contributing factor in the decline of Steller sea lions and may be impeding their recovery.

Despite the apparent effects of some species of marine mammals on their prey, there are a number of cases where mass removals of marine mammals did not appear to have a major effect on other components of their ecosystems. Examples are the overhunting of elephant seals and California sea lions along the coast of California, the overhunting of northern fur seals in the Bering Sea, and the culling of harbor seals in British Columbia. One explanation for the lack of tractable impacts in these cases is that their food webs are more complex relative to other systems (i.e., predators consuming many different species of prey, may have no noticeable impact on any single prey type). Another reason might be related to the type of marine ecosystems that these species inhabit (i.e., whether they inhabit shelf or deep-water systems, or whether they are primarily benthic or mid-water feeders). Further insights might be gained by developing ecosystem models for these systems.

Quantifying the feeding relationships between marine mammals and other species provides a means for assessing competition between species at similar trophic levels. Some species may significantly compete with more than one species. In the Bering Sea, for example (**Figure 2**), baleen whales and pollock have high overlaps in their diets (73–86%). There is also a significant amount of competition between seals and adult pollock for prey. Toothed whales, for example, compete primarily with beaked whales and seals, whereas the largest competitors of sea lions appear to be seals, toothed whales, and large flatfish. Fish, it turns out, can be major competitors of marine mammals.

Competition can affect body growth, reproduction and survival of marine mammals. In the Bering Sea and Gulf of Alaska, for example, the growth of Steller sea lions and northern fur seals (as measured by length) appears to have been stunted during the 1980s compared to the 1970s. Eastern Pacific populations of gray whales also appear to be in poorer condition (as measured by the ratio of girth to body length) in the 1990s compared to earlier decades. These changes in body size may be density-dependent responses to reduced prey availability or may be indicative of populations that have approached or attained their carrying capacities.

Reductions in prey abundance have been recorded in the Antarctic (i.e., krill), and along the coasts of California and South America during El Niño events. Pinniped pups born during these periods of reduced prey abundance incur high rates of mortality (typically 2–3 times normal levels) and are weaned at lower weights than normal (typically 15–20% lighter). Lactating females must also spend longer periods of time away from their pups to search for prey. Such temporal changes in prey abundance may result in the loss of an entire year class, and may be one of the evolutionary forces that shaped the life history of marine mammals (i.e., they are long-lived, have low reproductive rates and can endure short-term reductions in prey abundance).

Although it has not yet been demonstrated for marine mammals, reductions in prey availability can theoretically delay the onset of sexual maturity, and reduce fertility (by causing a female to not ovulate, or by causing a fetus to be reabsorbed or aborted). Reduced nutrition may also compromise an organism's resistance to disease, and may increase vulnerability to predation. Food deprivation may mean, for example, that a seal must spend increased amounts of time searching for prey and less time hauled out on shore away from predators such as killer whales and sharks.

Conclusions

Calculating trophic levels is a necessary first step to quantifying and understanding trophic interactions between marine mammals and other species in marine ecosystems. This can be achieved using dietary information collected from stomachs and scats, or by measuring isotopic ratios contained in marine mammal tissues. These data indicate that marine mammals occupy a wide range of trophic levels beginning with dugong and manatees (trophic level 2.0), and followed by baleen whales (3.35), sea otters (3.45), seals (3.95), sea lions and fur seals (4.03), toothed whales (4.23), and polar bears (4.80).

With the aid of ecosystem models and other quantitative analyses, the degree of competition can be quantified, and the consequences of changing predator–prey numbers can be predicted. These analyses show that many species of fish are major competitors of marine mammals. A number of field studies have also shown negative effects of reduced prey abundance on body size and survival of marine mammals. However, there are fewer examples of marine mammal populations affecting their prey due perhaps to the difficulty of monitoring such interactions, or to the complexity of most marine mammal food webs.

See also

Baleen Whales. Bioacoustics. Fishery Management. Large Marine Ecosystems. Marine Mammal Diving Physiology. Marine Mammal Evolution and Taxonomy. Marine Mammals, History of Exploitation. Marine Mammal Migrations and Movement Patterns. Marine Mammal Overview. Marine Mammal Socal Organization and Communication. Network Analysis of Food Webs. Seals. Sea Otters. Sirenians. Sperm Whales and Beaked Whales.

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MARINE MAMMALS, HISTORY OF EXPLOITATION

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Introduction

Products obtained from marine mammals – defined to include the cetaceans (whales, dolphins, and porpoises), pinnipeds (seals, sea lions, and walrus), sirenians (manatees, dugong, and sea cow), sea otter, and polar bear – have contributed in many ways to human survival and development. Maritime communities, from the tropics to the poles, have depended on these animals for food, oil, leather, ivory, bone, baleen, and other materials. Some marine mammal products have had strategic value to nations. For example, for several centuries, streets and homes in much of the western world were illuminated with sperm oil candles and whale oil lanterns. Delicate machinery and precision instruments were lubricated with the head oil of toothed whales. Whale oil was an important source of glycerine during World War I and a key ingredient in margarine during and after World War II.

Other uses of marine mammal products have been more frivolous. Seal penises are sold as aphrodisiacs; narwhal (*Monodon monoceros*) and walrus (*Odobenus rosmarus*) tusks and polar bear (*Ursus maritimus*) hides are displayed as ‘trophies’ in homes and offices (**Figure 1**). Spermaceti and ambergris, both obtained from sperm whales (*Physeter macrocephalus*), were highly valued by the perfume and cosmetics industries. Baleen used to be a stiffener for ladies’ hoop skirts and undergarments.