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MARINE MAMMAL SOCIAL ORGANIZATION AND COMMUNICATION

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Introduction

All animals face the same basic behavioral problems – obtaining food, avoiding predators and parasites, orienting in the environment, finding and selecting a mate, maintaining contact with relatives and group members. When the ungulates and carnivores that ultimately evolved into today's marine mammals entered the sea, the basic problems did not change, but the context in which the animals had to solve them changed radically. Different marine mammal groups have a different balance in the extent to which they use the underwater versus the in-air environments. All sirenians and cetaceans live their entire lives in the sea, and cetaceans show the most elaborate and extreme specializations for life in the sea. All marine mammals other than sirenians, the sea otter, and cetaceans spend critical parts of their lives on land or ice. These other species, including the pinnipeds and polar bear (*Ursus maritimus*), rely upon land refuges for giving birth, and for taking care of the young.

The ocean is a hostile environment for air-breathing mammals. There is little room for error – if an animal misjudges a dive or becomes incapacitated, it may have only minutes to correct the error or there is a risk of drowning. In the days of sail, humans responded to the notion that 'the sea is a harsh mistress' with an apprenticeship system, whereby a young cabin boy spent years learning the ropes before being entrusted to make the decisions required of a captain. Some cetaceans have similarly long periods of dependency when the young can learn how to feed, avoid predators, dive, and orient within their natal group. Pilot whales and sperm whales may even continue to suckle up to 13–15 years of age, and pilot whale females have a post-reproductive period when they switch their reproductive effort fully to parental care. By contrast, some seals that suckle on land have drastically curtailed the period of lactation, so that their young can leave the land-based refuge early. The hooded seal suckles her young twice an hour for an average of just four days before the pup is weaned. Even seals that lactate longer may still leave the young to an early independence. Elephant seals are deep divers on a par with the sperm whale, yet they must learn to navigate the sea alone. When an elephant seal pup is weaned, the mother leaves the pup on the beach. Pups spend about 2.5 months on the rookery, learning to swim and dive. They must fend for themselves as they make their first pelagic trip, lasting about four months. This solo entry into the sea exerts a heavy cost; fewer than half of the pups survive this trip.

Feeding Behavior

Behavioral ecologists divide feeding behavior into a sequence of steps: searching for prey, pursuit, capture, and handling prey. Marine mammals use many different senses to detect their prey. Walruses, sea otters, and gray whales feed on benthic prey. The walrus uses vibrissae in its mustache to sense shells in the mud; experiments with captive walrus show that they can use vibrissae to determine the shape of objects. Most seals are thought to use vision to find their prey – seals that feed at depth have eyes adapted to low light levels. Most toothed whales produce click sounds, and those species tested in captivity have sophisticated systems of echolocation. When a dolphin detects a target and closes in, it usually increases the repetition rate of its clicks into a buzz sound. If other animals intercept this sound, they may learn about prey distribution whether or not the echolocating animal wants to broadcast this information. Captive experiments show that one dolphin can detect an object by listening to echoes from the clicks of another dolphin. Both of these features of echolocation may favor coordinated social feeding. Many questions remain about how some marine mammals search for prey; we have no idea how baleen whales find patches of prey in the water column.

Most marine mammals catch and process prey using their teeth, as most mammals do (**Figure 1A–C**), but the mysticete whales have baleen, a sievelike set of plates that descend from the lower jaw (**Figure 1D**), instead of teeth. Baleen whales are able to engulf many prey items in one gulp and then use this baleen to strain out the sea water. Baleen whales feed on patches of prey, and will often aggregate when they are feeding on large patches; the larger the patch, the more whales in the group. Whales feeding on slow-moving prey, such as copepods, may feed in loose aggregations; those feeding on more mobile prey, such as schooling fish, may feed in a more coordinated fashion. Humpback whales may feed in stable groups in which each individual plays a distinct role.

Toothed whales tend to feed on mobile prey such as fish and squid, and they must catch one prey item at a time in their mouths. When dolphins feed on schooling fish, they usually feed socially in a coordinated group. Some dolphins appear to corral the school near the surface, while others swim through capturing a few fish. Marine mammalogists have often described these groups as cooperative, but little is known about the costs and benefits of social feeding, so one must be careful to distinguish between coordinated feeding behavior and behavior following more complex models of cooperation. The normal usage of 'cooperation' in English is just to work together toward a common goal; in ecology, studying cooperation demands measuring the costs and benefits of different behaviors. Different evolutionary models of cooperation involve different kinds of exchanges. One simple model covers the situation in which animals feeding together on a patch may each feed more efficiently than if they were feeding alone – this may apply to some coordinated feeding in whales. One-sided cooperation may be favored when one animal provides benefits to related animals; kin selection of this sort favors parental care and even cooperation with more distant relatives under some circumstances. More complex models of cooperation between unrelated

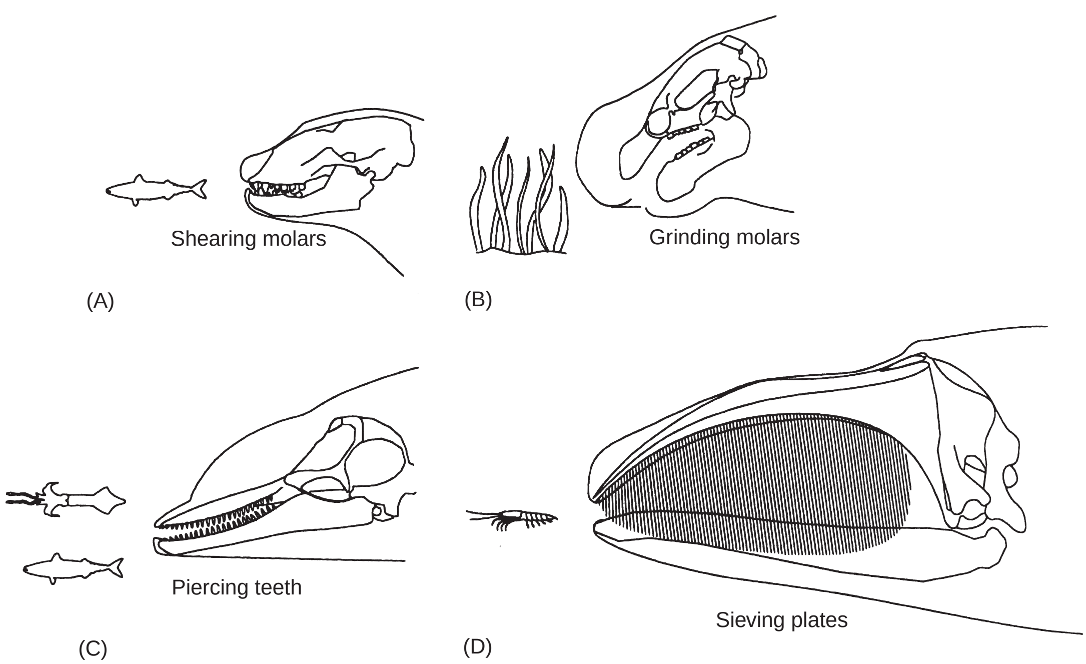

Figure 1 Feeding mechanisms of baleen whales and toothed marine mammals. (A) Polar bears, otters, and most seals have shearing teeth similar to those of terrestrial carnivores. (B) Sirenians have grinding molars that are replaced throughout life. (C) Toothed whales are homodonts; some beaked whales have only one tooth per row, most dolphins have dozens per row. (D) Baleen of a balaenid whale. (Adapted from Figures 2–17 of Reynolds and Rommel (1999).)

animals involve separated interactions of reciprocation, in which one animal may provide a benefit to a partner, expecting the partner to reciprocate at some later date. When a lone dolphin discovers a patch, it may direct a feeding call to other animals, which approach to join in. Feeding calls of this sort may evolve through reciprocation. If search costs are high and if a dolphin discovers a patch too large for it to consume, it may benefit from calling to partners in the expectation that the partners may reciprocate.

Sea otters use tools to process food; they dive to catch animals with hard shells, and then bring the prey to the surface, where they break it open on a stone that they carry while foraging. Some marine mammals may also have social mechanisms for processing prey. Some toothed whales catch large oceanic fish such as mahi-mahi (*Coryphaena* spp.), which are almost as big as they are. It may take one animal to hold the prey and another to rip off pieces in order to consume the flesh efficiently.

Defense from Predators

Marine mammals have different strategies for defending themselves from predators. Many of the toothed whales are thought to use their social groups to increase their probability of detecting predators and to protect vulnerable members of the group. Behavioral ecologists studying many animals have found that animals feeding in a group spend less time than lone animals breaking off from feeding to look for predators, and that they also detect the predators at larger ranges, enabling more successful escape strategies. K. Norris has urged that schools of dolphins function in this way to integrate sensory information from each member of the group using social communication to bolster the sensory abilities of each individual.

Some of the large toothed whales use a social defense from predators once the predators are detected. The best observations come from sperm whales. The most dangerous predators of sperm whales are killer whales and human whalers. When killer whales attack a sperm whale group, the adult sperm whales circle around the young with their flukes facing out, and they will attack approaching killer whales with their flukes. If an adult is injured, the sperm whales will circle around that animal to protect it as well. Human whalers knew about this, and they would often harpoon a whale in the group to wound it and then kill each adult in turn as the whales remained nearby to protect the wounded whale.

Other marine mammals appear to have a strategy opposite to grouping for protection from predators. When humpback whale females have a young calf, they do not join with other females but seem to space themselves out in protected clear waters. You might think that these whales are so big they do not need help to defend themselves from predators, but sperm whales are almost as big, yet rely upon social defense. Smaller animals such as seals may also spread out rather than group in response to predator pressure and some seals appear to dive in response to predators, adding a third dimension to this response. The ocean does not have many hiding places, but is so vast that these responses may represent a strategy to spread out to avoid detection.

Finding and Selecting a Mate

Evolutionary biologists assume that selection acts to maximize lifetime reproductive success, including both an animal's own offspring and those of relatives, weighted according to the degree of genetic relationship. Mating behavior is closely related to this goal. The mating behavior of male and female mammals differs in part because of the physiology of mammalian reproduction. Female mammals gestate their young internally and provide nutrition after birth through lactation. Once a female has become pregnant, she must usually wait until her young is born and often even weaned before becoming receptive again. This means that reproduction in females is limited primarily by their ability to gather energy to produce young. While male mammals can provide parental care, it is more common for them not to do so, and paternal care is not known among marine mammals. A male is capable of inseminating another female soon after a previous mating. Males often compete for the opportunity to mate with females, and reproductive success in males is often limited by the number of females they can inseminate. The ratio between the number of receptive males to the number of receptive females is called the operational sex ratio. The more receptive males per female, the higher the selection pressure for competition between males for access to females.

Females have a variety of mating strategies, where 'strategy' is used in an evolutionary rather than purely cognitive sense. A female may have one or more estrous cycles per year, and these may be spontaneous or induced by copulation. A receptive female may search for and select a male either on the basis of specific resources the male may provide, or of judgments of male quality as a mate. A female who is not relying upon resources provided by a male may either elicit competition between the sperm of several males with which she has mated, or incite behavioral competition between males and select the winner.

There are also a variety of mating strategies available to males. A male may defend, from other males, resources used by females. An example of this occurs with fur seals, where males will defend areas on the beach that females use to give birth and for thermoregulation. The goal of the male strategy is to exclude other males from their territory, in hopes that females coming to their territory for the resources will become receptive there. Alternatively, males may defend females directly. Elephant seal females may cluster on a beach. Males establish a dominance hierarchy before the breeding season, and the dominant few males defend receptive females from other males. In bottlenose dolphins, coalitions of 2 or 3 males also have been observed to defend females to prevent them from choosing another mate. Males within a coalition have a strong bond, and are typically sighted together most of the time for many years. The males may chase and herd a female away from the group in which they initially find her, and may escort her for days. Why does this involve coalitions of males? It may be impossible for a lone male to preempt female choice with such maneuverable animals in a three-dimensional medium.

Male strategies often depend upon the distribution of females. In the bottlenose dolphin case, females live in small fluid groups and males search for one receptive female, often guarding her when found. By contrast, sperm whale females live in stable groups of several females with their young. Adult male sperm whales join with these groups for varying amounts of time during the breeding season. Computer models suggest that males should rove between female groups if the duration of estrous is greater than the time it takes to swim between groups. This illustrates a general pattern that the distribution of females is often driven by the distribution of resources, while the distribution of males during the breeding season is often driven by the distribution of receptive females.

Most of the strategies listed above can be viewed as strategies used by males to limit or preempt the ability of a female to select a mate. In situations where males have a limited ability to preempt this choice, males may evolve signals to attract mates and may display to influence female choice. If females select mates on the basis of the display, then the male displays may be under a strong selection pressure to develop whatever features are used by females to select a mate. Darwin distinguished this kind of sexual selection from natural selection. Sexual selection stems from competition between members of the sex with the least parental investment (typically males) for access to mating with the sex that provides the largest parental investment (typically females). Earlier paragraphs described selection arising from competition between males; this is called intrasexual selection, and often leads to the development of weapons and large body size. Selection arising from competition between males to influence female choice is called intersexual selection.

Intersexual selection often leads to the evolution of elaborate displays, called reproductive advertisement displays. Examples of reproductive advertisement displays include the songs of birds and whales. Songs are usually defined as acoustic displays in which sequences of discrete sounds are repeated in a predictable pattern. Songs are known from a variety of marine mammals. The songs of the humpback whale are well known and sound so musical to our ears that they have been commercial bestsellers. Male humpback whales sing for hours, usually when they are alone during the breeding season. Bowhead whales, *Balaena mysticetus*, produce songs that are simpler than those of humpbacks, consisting of a few sounds that repeat in the same order for many song repetitions (**Figure 2**). As with humpback song, bowhead songs appear to change year after year. Bowhead whales winter in the Bering Sea, and humans have seldom studied them during their winter breeding season, but their songs have been recorded during their spring migrations past Point Barrow, Alaska. The long series of 20 Hz pulses produced by finback whales may also be a reproductive advertisement display. The seasonal distribution of these 20 Hz series has been measured near Bermuda, and it matches the breeding season quite closely.

Some pinnipeds also repeat acoustically complex songs during the breeding season. The bearded seal, *Erignatus barbatus*, produces a sirenlike warbling song that includes rapid frequency modulation superimposed upon slower modulation of the carrier frequency (**Figure 3**). The songs of bearded seals are produced by sexually mature adult males during the breeding season. Male walruses, *Odobenus rosmarus*, also perform visual and acoustic advertisement displays near herds of females during the breeding season. Males inflate modified pharyngeal pouches that can produce a metallic bell-like sound. When walruses surface during these displays, they may make loud sounds in air, including knocks, whistles, and loud breaths. They then dive, producing distinctive sounds under water, usually a series of sharp knocks followed by the gonglike or bell-like sounds. Antarctic Weddell seals also

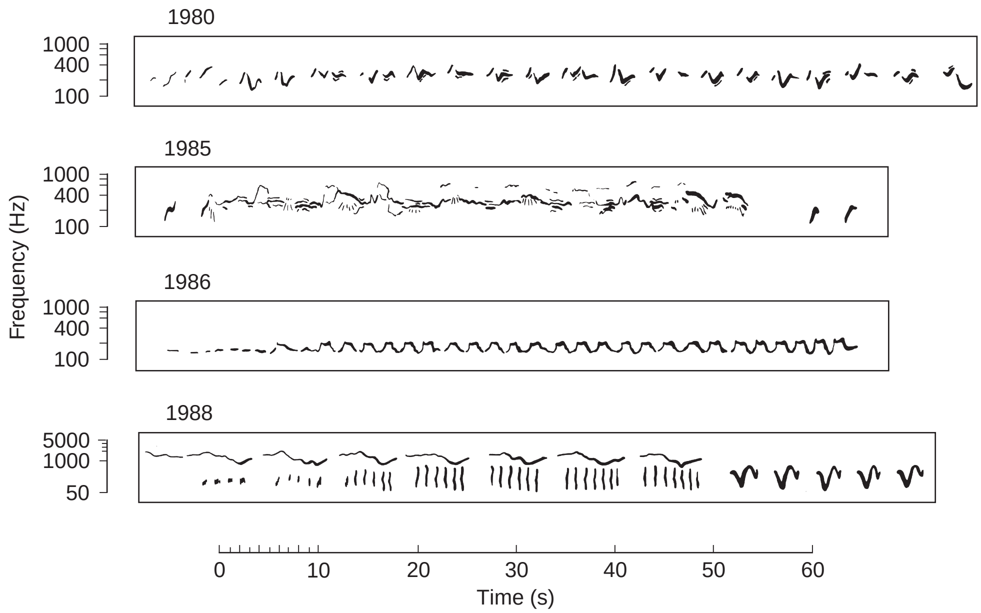

Figure 2 Spectrogram of the song of bowhead whales, *Balaena mysticetus*, recorded over 4 years during their spring migration. (From Figure 4.10 of Tyack and Clark (2000).)

have extensive vocal repertoires and males repeat underwater trills during the breeding seasons. Males defend territories on traditional breeding colonies. These trills have been interpreted as territorial advertisement and defense calls.

There is evidence that marine mammal songs play a role both in male–male competition and in female choice. Evidence for intrasexual selection includes observations that aggressive interactions between singers and other males are much more commonly observed than sexual interactions between singers and females and song appears to maintain distance between singers. However, just because the responses of males to song may be seen more frequently than those of females does not mean that the subtler responses of females to singers are not biologically significant. In many species, females will approach and join with a singer, and many acoustic features of these songs are consistent with a role in female choice.

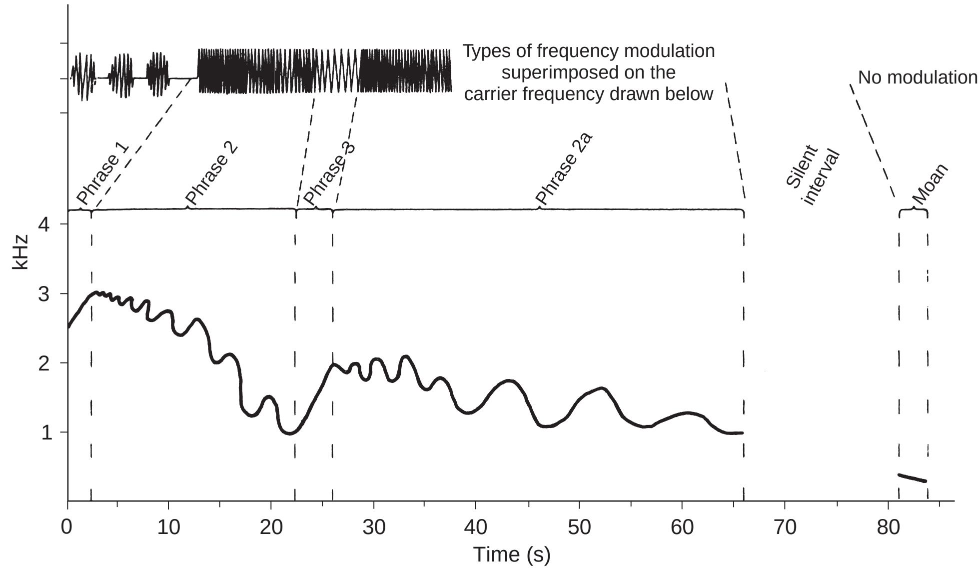

Figure 3 Lower panel: spectrographic portrayal of songs of the bearded seal, *Erignatus barbatus*. Additional frequency modulation is added to this carrier frequency; this warbling modulation is indicated in the upper panel. (From Figure 1 of Ray *et al.* (1969).)

Maintaining Contact with Recognition Calls

Mother–Infant Recognition

When mammalian young are born, they need to suckle for nutrition, and many species depend upon the mother for thermoregulation and protection from parasites and predators. This dependency has created a selection pressure for a vocal recognition system to regain contact when mother and offspring are separated. These problems of recognition between mother and young are acute in colonially breeding otariid seals. A female otariid may leave her young pup on land in a colony of hundreds to thousands of animals, feed at sea for a day or more and, when she returns, must find her pup to feed it. In the Galapagos fur seal, *Arctocephalus galapagoensis*, both mother and pup produce and recognize distinctive contact calls, and the mother often makes a final olfactory check before allowing a pup to suckle.

The young of many dolphin and other odontocete species are born into groups comprising many adult females with their young, and they rely upon a mother–young bond that is more prolonged than that of otariids. As was described in the introduction, many of these species have unusually extended parental care. Bottlenose dolphin calves typically remain with their mothers for 3–6 years. These dolphin calves are precocious in locomotory skills, and swim out of sight of the mother within the first few weeks of life. Young calves often swim with animals other than the mother during these separations. The combination of early calf mobility and prolonged dependence selects for a mother–offspring recognition system in bottlenose dolphins. Dolphin mothers and their young calves use tonal whistles as signals for individual recognition. Observations of captive dolphins suggest that whistles function to maintain contact between mothers and young. When a dolphin mother and her young calf are separated involuntarily in the wild, they whistle at higher rates; during voluntary separations in the wild, the calf often whistles as it returns to the mother. Experimental playbacks to wild dolphins show that mothers and their calves respond preferentially to each others' signature whistles, even after the calves become independent from their mothers.

Individual Recognition in Dolphins and Signature Whistles

Dolphins use whistles not just for mother–infant recognition but also for individual recognition throughout their lives. Calves show no reduction in whistling as they wean and separate from their mother. Adult males are not thought to provide any parental care, but they whistle just as much as adult females. Bottlenose dolphins may take up to two years to develop an individually distinctive signature whistle, but once a signature whistle is developed, it can be stable for decades (**Figure 4**). The signature whistles of dolphins are much more distinctive than similar recognition signals produced by other mammals. These results suggest that signature whistles continue to function for individual recognition in older animals.

Group Recognition in Killer Whales

Many marine mammals live in kin groups, and social interactions within these groups may have a powerful effect on fitness. The different structures

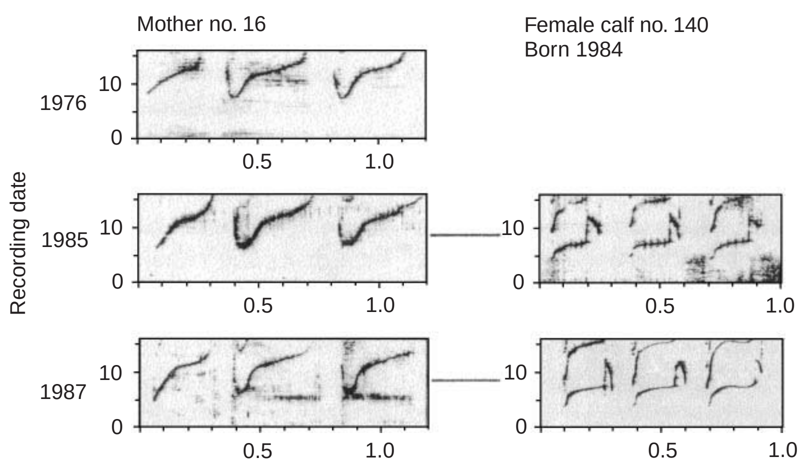

Figure 4 Spectrograms of signature whistles from one wild adult female bottlenose dolphin, *Tursiops truncatus*, recorded over a period of 11 years and of one of her calves at 1 and 3 years of age. Note the stability of both signature whistles. (From Figure 11.11 of Mann *et al.* (2000).)

of these cetacean societies create different kinds of problems of social living, and there appears to be a close connection between the structure of a cetacean society and the kinds of social communication that predominate in it. For example, stable groups are found in fish-eating or Resident killer whales, *Orcinus orca*, in the coastal waters of the Pacific Northwest of the United States, and these whales also have stable group-specific vocal repertoires. The only way a group of these killer whales, called a pod, changes composition is by birth, death, or rare fissions of very large groups. The vocal repertoire of killer whales includes discrete calls, which are stereotyped with acoustic features that change slowly and gradually over decades. Each pod of Resident killer whales has a group-specific repertoire of discrete calls. Each whale within a pod is thought to produce the entire call repertoire typical of that pod. Different pods may share some discrete calls, but none share the entire call repertoire. Since discrete calls change gradually, pods that diverged more recently produce more similar versions of some calls (**Figure 5**). The entire repertoire of a pod's discrete calls can thus be thought of as a group-specific vocal repertoire. Different pods may have ranges that overlap and pods may associate together for hours or days before diverging. These group-specific call repertoires in killer whales are thought to indicate pod affiliation, to maintain pod cohesion, and to coordinate activities of pod members.

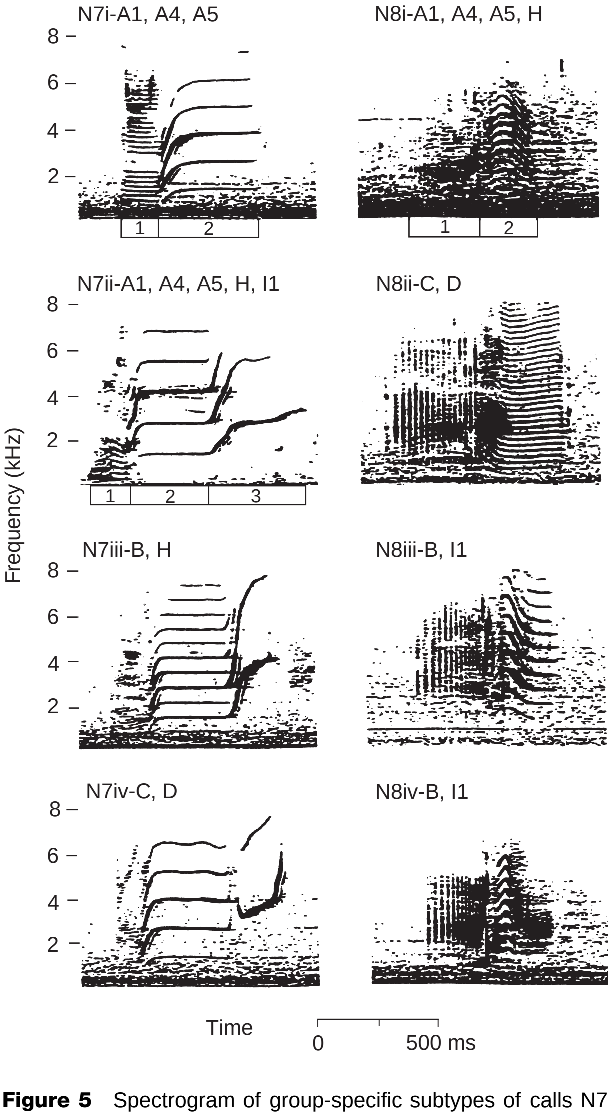

Figure 5 Spectrogram of group-specific subtypes of calls N7 and N8 of resident killer whales, *Orcinus orca.* Not only does each group have a group specific call repertoire, but there are different subtypes for many calls, and different sets of groups produce each subtype. On the upper left of each spectrogram is the subtype of the call and following the dash is a listing of the groups that make this particular call. (From Figure 1.11 of Au *et al.* (2000).)

Correlation of Acoustic Recognition Signals and Social Organization

Most communication signals evolve for the solution of specific problems of social life. In fact, communication and social behavior can be viewed as two different ways of looking at the same thing. There is a clear correlation between the types of social bonds and recognition signals seen in different cetacean groups. Individual-specific signals have been reported for species such as bottlenose dolphins with strong individual social bonds; group-specific vocal repertoires have been reported for species such as killer whales with stable groups, and population-specific advertisement displays have been reported among species such as humpback whales and some seals where adults appear to have neither stable bonds nor stable groups.

See also

Baleen Whales. Bioacoustics. Marine Mammal Migrations and Movement Patterns. Marine Mammal Overview. Marine Mammal Trophic Levels and Interactions. Sea Otters. Seals. Sirenians. Sperm Whales and Beaked Whales.

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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