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Feeding Strategies and Tactics

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I. Introduction

Marine mammals are found in a wide range of habitats including the open ocean, coastal waters, rivers, lakes, and even on ice floes and land. They feed on a variety of prey species from aquatic plants to microscopic zooplankton to the largest marine mammals, and a diverse array of strategies and tactics is used to locate and capture these prey. Some marine mammals consume huge numbers of prey items at a time (batch feeding) while others attack and consume prey items singly (raptorial feeding). Many marine mammals forage in large groups while others feed alone. In this chapter, we will consider the wide range of marine mammal foraging behaviors and the circumstances and habitats that led to the adoption of particular feeding strategies and tactics.

Before embarking upon a review of marine mammal foraging, it is important to make a distinction between a strategy and a tactic, terms which have specific meanings in the field of Behavioral Ecology. To put simply, a strategy is a genetically based decision rule (or set of rules) that results in the use of particular tactics. Tactics are used to pursue a strategy and include behaviors (Gross, 1996). Tactics may be fixed or flexible, in the latter case they depend on the condition of the individual or characteristics of the prey or environment. For example, a humpback whale's (*Megaptera novaeangliae*) strategy may be to use that tactic which will maximize energy intake at any particular time. The whale may pursue this strategy by switching between the tactics used to capture fish and those used to catch krill, depending upon the relative abundance of these two prey types.

Our understanding of marine mammal foraging is hampered by the difficulty of studying these animals. They live in an environment where observations are difficult (often beneath the surface), our presence can disturb their foraging behavior, and feeding events often occur quickly and are easy to miss. Despite this, and thanks to many emerging technologies, much is known. We will begin our review by considering ways that marine mammals find and capture their prey, continue with a discussion of group foraging, then conclude with a discussion of the causes of variation in feeding strategies and tactics.

II. Finding Prey

The first step in foraging is locating prey. This may be done over many temporal and spatial scales and can involve migrations of thousands of kilometers or switching between habitats separated by only a few meters to forage in prey-rich locations. Then, once a marine mammal is in a prey-rich area it still must locate prey.

A. Habitat Use

One way that marine mammals can increase their chances of encountering prey is to spend time foraging in those habitats with high prey abundance. There is evidence that a variety of marine mammals

tend to aggregate in areas with high food concentrations. For example, the highest densities of polar bears (*Ursus maritimus*) are found along floe-edges and on moving ice, habitats that contain the highest density of seals; resident killer whales (*Orcinus orca*) are most abundant in Johnston Strait, British Columbia when salmon migrate through the strait. Also, the distribution of humpback whales in the Gulf of Maine appears to reflect the availability of fish prey, and humpback whale distribution in southeast Alaska may partially be determined by krill abundance. When there are a variety of habitats available to marine mammals in a restricted area (such as nearshore environments), a theoretical model predicts that, if the main concern of the animals is to maximize energy intake, they should be distributed proportional to the amount of food available in each habitat (Tregenza, 1995). Testing this hypothesis is difficult since marine mammal prey availability is often hard to quantify. However, the distribution of bottlenose dolphins (*Tursiops* spp.) in Shark Bay, Western Australia, conforms to this hypothesis and matches that of their fish prey in winter months at scales of 100s of meters to kilometers. Similarly, Hawaiian spinner dolphins (*Stenella longirostris*) appear to match the availability of their vertically migrating prey at scales of 20 m to kilometers. Humpback and minke (*Balaenoptera acutostrata*) whales do not appear to conform to this hypothesis. Instead, they appear to show a threshold response to prey availability, only using a habitat once prey density has reached a particular level, but above this threshold there is a tight relationship between zooplankton abundance and whale abundance. Of course, prey availability is not the only factor that might influence habitat use of marine mammals, and this will be considered in detail later.

Many marine mammals forage over great distances, and they may have limited knowledge of the distribution of prey patches, especially in pelagic habitats. In these situations, marine mammals, including pinnipeds and cetaceans, may adopt movement tactics that should maximize the probability of encountering prey. Displacement rates are relatively high, and movements relatively linear, in areas of low prey abundance, but animals exhibit low displacement rates and high turning rates ("area restricted searches") when they encounter rich patches.

B. Migration

When suitable habitats for a marine mammal are widely spaced, movements between them are considered migrations. There is thus a continuum between habitat use decisions and migrations. Some migrations appear to be driven primarily by variation in food availability. Unlike baleen whales, sperm whales (*Physeter macrocephalus*) cannot fast for long periods of time, and female groups use migrations up to 1100 km as part of a strategy for surviving in a variable habitat with low local food abundance and poor foraging success. In fact, this tactic may be the reason that female sperm whales are found in permanent social groups as they may benefit from the experience of old females during migrations.

Migration frequently involves trade-offs between feeding and another factor, like reproduction. Baleen whales and some pinnipeds feed only for a relatively short period of time in high productivity high latitude waters, then fast during the rest of the year while moving to, and spending time at, low latitude breeding grounds. For example, northern elephant seals (*Mirounga angustirostris*) forage along the entire North Pacific, then migrate to a few beaches on the California coast to breed and molt. Also, some humpback whales in the Pacific Ocean reproduce in warm, low productivity, Hawaiian waters, then move to the more productive waters of the north Pacific to feed during the summer months. However, some humpback whales remain in the southeast Alaska feeding grounds yearround, and individuals that

do not consume enough prey during the feeding season may forego migration to continue feeding.

C. Searching and Diving

The way in which an animal moves through its environment can influence its encounter rate with prey, and many animals exhibit stereotyped search patterns. Marine mammals that forage on concentrated prey may continually patrol through areas where they expect to encounter concentrations. For example, leopard seals (*Hydrurga leptomix*) will patrol along ice edges where departing and returning penguins congregate and killer whales patrol nearshore areas in search of seals. When groups of marine mammals forage, they often spread out into widely spaced subgroups and/or move forward in a line abreast formation (e.g., dusky dolphins [*Lagenorhynchus obscurus*], pilot whales [*Globicephala* spp.], Risso's dolphins [*Grampus griseus*], bottlenose dolphins, killer whales). Spreading out in such fronts may either reduce foraging competition among individuals or increase the probability that prey is detected so the subgroups can converge to feed.

Once a marine mammal has selected a habitat for foraging, it must execute a strategy that will optimize its net energy intake rate, often with respect to trade-offs and constraints. For a diving animal this means that it must balance the energetic costs of diving with the energetic gains of foraging. The costs of diving vary greatly among marine mammals. Polar bears, sea otters (*Enhydra lutris*), and most pinnipeds are divers—they spend most of their time above water or have long surface intervals between food gathering dives. In contrast, most cetaceans and sirenians can best be thought of as surfacers—they spend the majority of their time submerged, and make trips to the surface only to breathe (see Boyd, 1997).

Theoretical studies of optimal diving suggest that as the depth at which prey are located increases, both dive times and surface times should increase (Kramer, 1988), and the type of dive a marine mammal executes will depend on the depth and the distribution of prey. Some predictions of optimal diving theory are supported by several studies of marine mammals, and both dive times and surface times increase with dive depth in pinnipeds, cetaceans, and sirenians. Because a diving individual should behave in a manner that optimizes its net energy intake, marine mammals may exceed aerobic limits when the energetic pay-off is sufficient. In addition to energetic considerations, predation risk may influence the diving behavior of marine mammals, and therefore result in deviations from optimal diving predictions, based on energetic currencies alone (Frid et al., 2006).

There is a great deal of variation in the depths to which marine mammals dive. Some, like sea otters, nearshore odontocetes, and otariids, tend to be shallow divers. Others, including sperm whales, elephant seals (*Mirovinga* spp.), and beaked whales are extremely deep-divers, sometimes foraging over 1000 m from the surface. Some species minimize the depths to which they must dive, and thus the costs, by modifying their diel pattern of foraging. For example, some dolphins and pinnipeds are nocturnal foragers on prey whose daily movements bring them closer to the surface at night (e.g., spinner dolphins, northern fur seals [*Callorhinus ursinus*], Antarctic fur seal [*Arctocephalus gazella*]). The diving tactics of beluga whales (*Delphinapterus leucas*) may be influenced by competition with pinnipeds, which are superior divers. The belugas generally forage over the deepest waters and, because of their body size, are able to gain access to benthic areas that the smaller pinnipeds cannot. Although the time spent at the bottom decreases with increasing depth, belugas compensate by increasing their ascent and descent rates as dive depth increases, a result also found in narwhals (*Monodon monoceros*).

D. Prey Detection

Marine mammals have many ways to detect their prey including vision, various types of mechanoreception, echolocation, and hearing. Most marine mammals appear to rely on vision to at least some extent. The large, forward pointing eyes of pinnipeds suggest that vision is an important method for detecting prey. Even species that dive to extreme depths, like the elephant seal, are capable of using vision to find prey in dark waters at their foraging depth. Vision may be less important in other taxa. For example, river dolphins (*Platanista gangetica*) of the Indian subcontinent have eyes that are greatly reduced and may be mostly blind. Sea otters can use their forepaws to find food and discriminate prey items without the aid of vision, and many pinnipeds are found in turbid waters, making vision a poor method of prey detection. However, they are able to use their vibrissae (whiskers) to detect prey through active touch or through minute water movements caused by their prey.

Odontocete cetaceans have a method of prey detection not available to other marine mammals—echolocation. In controlled situations, odontocetes can detect relatively small objects at a considerable distance. For example, a bottlenose dolphin can detect a 7.62-cm diameter sphere from over 100 m. However, it is still unclear how efficient echolocation is under natural conditions. It is likely to be less efficient than suggested by laboratory and controlled experiments (as has been shown for bats), and may vary greatly depending on environmental conditions such as noise.

Echolocation is not always an effective way to detect prey. While most fish cannot hear echolocation calls, clupeid fish and other marine mammals can. Therefore, odontocetes foraging on prey that can detect their echolocation may have to use tactics other than echolocation for detecting prey. This difference in the ability of potential prey to detect echolocation is reflected in the foraging behavior of fish-eating (“resident”) and mammal-eating (“transient”) killer whales off British Columbia. While resident whales commonly use echolocation during foraging, transients do not. Also, when transients echolocate, their pulses are of low intensity and are irregular in timing, frequency, and structure; a pattern that may be difficult for prey to detect. Instead of echolocation, mammal-eating killer whales appear to use passive listening to detect their prey. Other marine mammals probably use passive listening opportunistically, especially bottlenose dolphins that feed on a variety of noisy fish species. Elephant seals and other pinnipeds also have good hearing abilities in water and may use passive listening to find prey.

III. Capturing and Consuming Prey

A diverse array of tactics is used by marine mammals to capture and consume their prey once they have located it (Fig. 1). The most widespread tactic of raptorial predators is to simply chase down individual prey items that they have encountered. However, there are many other, more unique tactics employed by marine mammals.

A. Stalking and Ambushing

Marine mammals often hunt prey that are non-sessile, fast-moving, and have good sensory abilities and, thus, could avoid predators if their approach were too obvious. For example, seals can avoid polar bears by diving back through the ice, and penguins can avoid leopard seals by hauling out, as can pinnipeds approached by killer whales near land. When hunting elusive prey, a predator must rely on either stalking or ambushing. A stalking predator attempts to conceal its identity or presence until it approaches its prey close enough

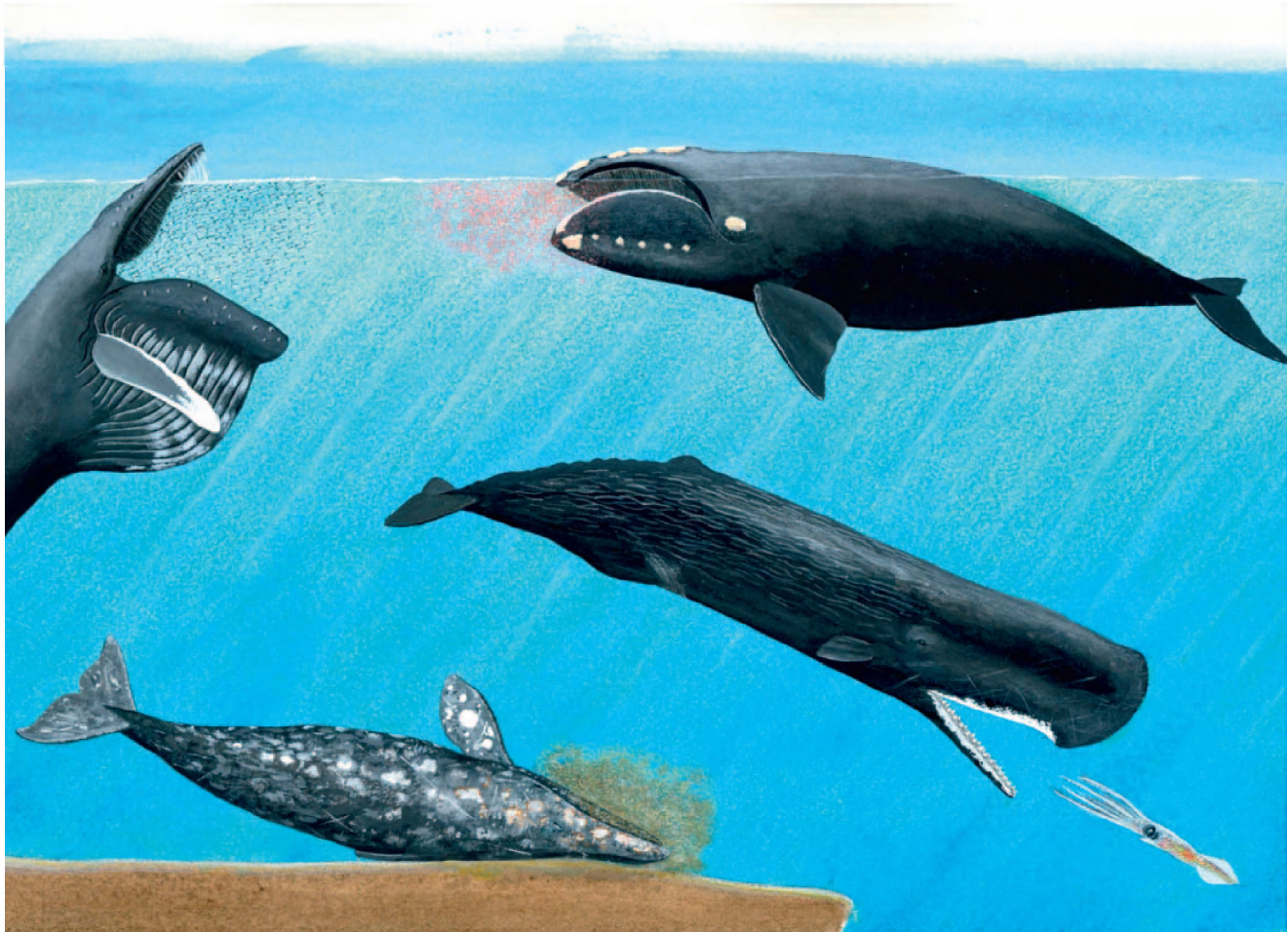


Figure 1 Whales employ a diverse array of foraging tactics. Art by Pieter A. Folkens/Higher Porpoise DG.

for a sudden, successful attack. In contrast, an ambush predator conceals itself and lies in wait, leaving the approach to the prey.

Polar bears use both stalking and ambush methods when hunting seals hauled out on the ice near breathing holes. In terrestrial stalking, bears creep forward and use ice for cover to closely approach their intended prey. Bears also stalk seals by swimming circuitously through interconnected channels or even under the ice, occasionally surfacing through holes to breathe and monitor their prey. However, an ambushing tactic, where a bear lies, sits, or stands next to a breathing hole waiting for a seal to surface, is the most energy-efficient and most commonly used foraging tactic.

Leopard seals also use both stalking and ambush tactics when foraging. Stalking leopard seals may swim under the ice below a penguin, then break through to capture the bird, or they may swim submerged near a fur seal beach and lunge at pups when they get close enough. Alternatively, leopard seals may ambush their prey by hiding between ice flows near a penguin landing beach. Sea otters will stalk birds by swimming underwater and grabbing them from below, a tactic similar to that used by Steller sea lions (*Eumetopias jubatus*) hunting northern fur seal pups and leopard seals stalking Adelie penguins (*Pygoscelis adeliae*).

Another behavior that could be considered stalking is wave riding and intentional beaching used to capture young pinnipeds and

penguins near the water's edge. This tactic is commonly used by killer whales and occasionally by Steller sea lions and leopard seals. This may be a particularly dangerous foraging tactic, especially for young killer whales that may not be able to return to the water if they strand too high on the beach.

Some stalking predators make detours that involve moving away from the prey and potentially losing visual contact temporarily before making another approach. Polar bears will make detours from their prey while stalking aquatically, and dolphin subgroups may detour away from a school of fish to attack it from opposing sides. Weddell seals (*Leptonychotes weddellii*) have also been observed making detours when stalking cod under fast ice. These detours allow the seal to remain out of the fish's view and to attack from very close range below the fish.

B. Prey Herding and Manipulation

To capture them more efficiently, marine mammals may actively manipulate the behavior of their prey. In other words, marine mammals take advantage of normal prey behaviors to enhance their ability to capture them. These manipulations may help a marine mammal flush prey from hiding, capture an individual prey item, or increase the density of prey aggregations so as to increase the forager's

energetic intake rate. Prey herding is a common tactic used by dolphins, porpoises, whales, and pinnipeds and may be considered prey manipulation when they take advantage of natural schooling and flight behavior of their prey. Dolphin and porpoise groups and individuals have been observed herding prey against shorelines or other barriers, reducing the number of escape routes. Dolphins use shorelines for more than herding fish. Bottlenose dolphins inhabiting salt marshes sometimes form small groups that rush at fish trapped against a mudbank. The wave created by the rapid swim causes fish to strand on the mudbank, and the dolphins slide up the bank and pick fish off the mud before sliding back into the water. A similar behavior is performed by both individuals and groups of humpback dolphins (*Sousa* spp.) foraging around sandbanks off Mozambique.

Marine mammals also herd fish in open waters. When schools are at the surface, dolphins may split into groups to attack from different directions, herding the fish into a ball between subgroups. Other times, fish may be herded up from deeper waters, and trapped between circling individuals and the surface. During a herding event, individuals swim around the fish school, and below it, preventing its escape. Fish herding in open waters has been reported in many dolphin species, porpoises, and sea lions. Sea lions are also found feeding on schools of fish that are herded to the surface by dusky dolphins, but it is unclear if the sea lions aid in fish herding. The tactic of herding fish is found in a variety of marine predators. Although there are no reports of prey herding for many species of pelagic dolphins, it is probably a wide-spread tactic employed by marine mammals feeding on schooling fish.

During a prey-herding event, many different tactics may be used to cause the fish to move into a tight ball and to capture fish in these balls. Splashing at the surface causes fish schools to compact. Dusky dolphins perform leaps at the edge of fish schools that they are herding, and spotted dolphins (*Stenella* spp.) have been observed tail-slapping and splashing at the edge of a fish school when it started to break apart or move in a different direction, but the function of these behaviors is still unclear. Killer whales in Norway and humpback whales in the northwest Atlantic also use tail-slaps when they near schools of prey. Tail-flicks by humpbacks may also be used to concentrate schooling euphausiid prey in southeast Alaska, though this may simply be a hydro-mechanical effect.

Another tactic that marine mammals can use to herd prey is flashing light-pigmented areas of their body toward a fish school. Killer whales herding herring swim under the school and flash their white undersides to keep the school from diving, and a similar behavior has been noted in spotted dolphins. Humpback whales in southeast Alaska may also use flashes to help concentrate prey by rotating their elongated pectoral flippers while they herd herring, thereby showing the highly visible white undersides.

Fish show strong avoidance responses to bubbles and are reluctant to cross barriers composed of them. Not surprisingly, marine mammals take advantage of this response. The use of bubbles during foraging has been observed in many odontocetes, mysticetes, and pinnipeds. Spotted dolphins use bubbles to isolate individual fish, pulling them away from the school with the water disturbance created by the passing bubble, so they can be consumed, and Weddell seals blow bubbles into ice crevices where fish are hiding to flush them out. Killer whales also use bubbles to flush prey, and blow large bubbles toward rays buried in the sediment, causing them to move. However, bubbles are primarily used to concentrate and contain schools of fish. For example, killer whales blow large bubbles near the surface to keep fish in a tight ball. Humpback whales are the best-known bubble users and bubble feeding may be conducted by individual whales

or in large groups. Whales deploy bubbles in a variety of formations including columns, curtains, nets, and clouds, with the tactic used dependent on the characteristics of the prey aggregations.

Sound and pressure waves may also be used to manipulate prey behavior. For example, bubble-netting humpback whales in southeast Alaska produce loud “feeding calls” as they rise to the surface, presumably herding prey up into bubble nets which are meters above the herding schools. Similarly, Icelandic killer whales may use low-frequency calls to herd herring schools into tighter groups. Bottlenose dolphins off Australia and Florida use tail-slaps known as “kerplunks” while foraging in shallow seagrass habitats. The kerplunk displaces a significant amount of water, creates a plume of bubbles, and causes a low-frequency sound. Kerplunks may cause startle responses in fish and help the dolphin locate and flush their prey, while the bubbles may provide a barrier to contain the fish. Humpback whales in the western Atlantic may flush burrowing fish (sand lance) from the bottom by scraping the substrate with their head, then feed on the fish once they have entered the water column.

C. Prey Debilitation

Marine mammals sometimes debilitate their prey before they consume it. Killer whales attacking mysticetes often swim onto their backs when the prey tries to surface, and in some cases the victim may drown instead of dying from its wounds. While killer whales are herding herring, individuals thrash their tail through the school, stunning fish with the physical impact of their flukes; they then feed on the stunned and injured fish. The whales probably use this tactic because it is energetically more efficient than whole body attacks. Bottlenose dolphins strike fish with their tails (“fish whacking”) when foraging alone or in groups, sometimes knocking the fish through the air. Also, there is evidence that walrus (*Odobenus rosmarus*) may use their tusks to kill or stun intended seal prey. Recent studies suggest that the hypothesis that odontocetes use sound to debilitate prey cannot be supported at this time.

D. Tool Use

“Tool use is the external employment of an unattached environmental object to alter more efficiently the form, position or condition of another object, another organism, or the user itself when the user holds or carries the tool during or just prior to use and is responsible for the proper and effective orientation of the tool” (Beck, 1980). Tool use by marine mammals is reviewed in detail elsewhere in this volume, but more marine mammals use tools during foraging than is generally appreciated, so this behavior deserves brief mention here.

Sea otters are the best-known marine mammal tool users and will pick up rocks from the bottom and place them on their chest to use as an anvil for crushing mussels, crabs, or urchins, or use them to smash or dislodge abalone (*Haliotis* spp.) off rocks. In some cases, the rocks are retained between foraging dives to be reused. Certain bottlenose dolphins carry sponges on their rostra, apparently as a tool to aid foraging (Fig. 2). Also, there are popular accounts of polar bears throwing blocks of ice at basking seals to injure or trap them, and polar bears in captivity are often observed throwing large objects, raising the possibility of tool use in the wild. Another behavior that might be considered tool use involves killer whales creating waves to wash hauled out seals into the water. Finally, the use of bubbles to concentrate schooling fish or aid in flushing fish from hiding or a school (discussed earlier) fits Beck’s definition of tool use.



Figure 2 Bottlenose dolphins (*Tursiops aduncus*) use sponges as tools to aid in foraging. Photograph by Michael R. Heithaus.

E. Benthic Foraging

While most marine mammals pursue their prey in the water column, several species forage on benthic organisms. There are three basic methods that marine mammals use to obtain prey from the bottom: collecting, extracting, and engulfing. Epibenthic prey is simply collected by foraging marine mammals. Sea otters collect echinoderms (mostly sea urchins), crabs, and other benthic organisms with their forepaws.

Infaunal prey items must be extracted from the substrate and require the predator to excavate in some manner. Sea otters use their forepaws to dig for clams in soft-sediment areas and may produce large pits over the course of several dives, occasionally surfacing with a clam. Harbor seals (*Phoca vitulina*) dig for prey in sandy habitats with their foreflippers or snouts while narwhals and belugas use water jets to dislodge mollusks buried in the sea floor. Walrus use a combination of tactics to obtain buried bivalves including digging with their snouts (not tusks) and hydraulic jetting. Walrus make multiple excavations on each dive and have been recorded consuming at least 34 clams on a single dive. Killer whales, in New Zealand, engage in benthic foraging on rays and have been observed pinning them to the bottom and may also be digging for them. Bottlenose dolphins in the Bahamas also dig for infaunal prey ("crater feeding"), and once a burrowing fish has been located, the dolphin will dive into the soft sand and use its flukes to drive deeper, almost up to the flippers, to catch the fish.

If many small infaunal prey items are consumed in a single feeding event, they may be engulfed while still in the sediment. Gray whales (*Eschrichtius robustus*) feeding near the bottom use suction to pull sediment and prey into their mouths, then filter the sediment and water out through their baleen.

F. Batch Feeding

Batch feeding is a tactic employed to consume a large number of prey items in a single feeding event. While mysticetes are obligate batch feeders, some pinnipeds facultatively use this tactic. There are two basic types of batch feeding: skimming and engulfing. Skimmers, most notably the right whales (*Eubalaena* spp.) and bowhead whale (*Balaena mysticetus*), swim through concentrations of zooplankton, either at the surface or in the water column, with their mouths open, filtering water through their fine baleen plates which traps prey.

Engulfers include the rorqual whales and several pinnipeds. These species engulf large amounts of water and prey, then filter the water back through their baleen plates or teeth. Rorquals have a suite of adaptations, including expandable gular pleats and a lower

jaw that can disarticulate from the upper jaw, that allow them to engulf huge volumes of water, and fish or crustacean prey, in each feeding attempt. "Lunge feeding" is one of the most common tactics of rorqual whales feeding near the surface and may take several forms. During a typical lunge, a whale surfaces with its mouth open to capture prey near the surface. Lunge feeding may be done singly or in groups, and in combination with many of the prey concentration tactics.

All Antarctic seals (crabeater [*Lobodon carcinophaga*], Weddell, Ross [*Ommatophoca rossii*], leopard seals) include zooplankton in their diet, as do some Arctic seals (ringed [*Pusa hispida*], ribbon [*Histiophoca fasciata*], harp [*Pagophilus groenlandicus*], largha [*Phoca largha*], and harbor seals). Of these, the crabeater seal is the most specialized batch feeder and zooplankton may comprise up to 94% of its diet. The cheek teeth of crabeater and some other seals are modified for straining krill, which are probably sucked into the mouth when the seal depresses its tongue, then trapped against the cheek teeth as the water is expelled.

G. Ectoparasitism, Kleptoparasitism, and Scavenging

Predators kill their prey in the course of consuming it (Ricklefs, 1990). While most marine mammal foraging is predatory, there are several ways that animals may forage which do not involve killing their own prey. For example, an animal may gouge mouthfuls of flesh from a "host" without killing it (sometimes referred to as ectoparasitism). Although marine mammals fall victim to such ectoparasites (small sharks), there are no concrete examples of marine mammals using this tactic. However, killer whales may effectively ectoparasitize large whales as some attacks do not kill the victim. Kleptoparasitism (food stealing) has been observed only in otters and polar bears but may occur in other species. For example, pilot whales were observed harassing sperm whales until they regurgitated and the pilot whales consumed the regurgitated food. Scavenging is a common foraging tactic, but it does not appear to be widespread among marine mammals. However, it may be an important tactic for polar bears and some pinnipeds. Also, several odontocete species that feed on trawler discards or longline catches could be considered facultative scavengers.

H. Herbivory

Sirenians (manatees [*Trichechus* spp.] and dugongs [*Dugong dugon*]) are the only marine mammals that routinely feed on plants, and both manatees and dugongs may be found foraging individually or in large groups. Manatee feeding appears to be more flexible than that of dugongs as the former will consume either floating or rooted vegetation and sometimes leaves from overhanging branches or vegetation along banks. Dugongs feed almost exclusively on seagrasses but may also intentionally consume benthic invertebrates. While manatees tend to crop vegetation, dugongs often dig up rhizomes and leave large feeding trails through seagrass beds, which can have a large impact on seagrass biomass, both above and in the sediment (Fig. 3), and even on invertebrate communities of the seagrass.

I. Prey Preparation and Consumption

While some marine mammal prey can be consumed immediately after capture, others require extensive handling before they are eaten, and some are only partially consumed. Sea otters remove the heads of birds that they capture and strip the muscle from the breast,



Figure 3 Dugongs (*Dugong dugon*) preferentially forage on below-ground portions of many seagrass species, creating a cloud of sediment during foraging activity. Photograph by Michael R. Heithaus.

neck, and legs. Many dolphins and sea lions remove the heads from large fish before consuming them, and bottlenose dolphins will strip flesh from spiny fish. Head and spine removal may reduce the probability that a predator is injured while consuming prey, but it may also be a mechanism to reduce the intake of bony material that provides no nutritional value. Dolphins do not always consume their prey correctly, and sharp spines have been implicated in deaths of bottlenose dolphins stranded in Texas and Florida.

Odontocetes cannot chew prey and must spend considerable time handling large prey items. For example, bottlenose dolphins will drag large fish along sandy bottoms until pieces that are small enough to swallow are broken off. Killer whales are well known for their extensive handling of prey, especially pinnipeds, after capture. Killer whales often breach upon sea lion and seal prey as well as slap them with their tails. The function of these behaviors is unclear, but they may tenderize the prey, aid in training calves in hunting techniques, or even debilitate dangerous prey. Selective feeding on energy-rich portions of prey is common in both killer whales and polar bears. Killer whales will selectively eat the blubber and tongue of whales that they kill and polar bears prefer the blubber and muscle of seals and narwhals over the internal organs. Finally, harbor seals will regurgitate after feeding on sand lance to remove sand from their stomachs. The regurgitated fish are re-swallowed before they sink to the bottom.

IV. Group Foraging

Many foraging tactics are executed by groups of marine mammals. Sometimes these groups are merely aggregations of animals attracted to the same resource, and there appears to be little interaction among individuals as they pursue prey individually. Other group foraging behaviors, like herding of prey, appear to be highly coordinated efforts and may involve animals cooperating with each other to increase their net energy intake rate. It is not always easy to determine whether group foraging marine mammals are cooperative or not. For example, the echolocation rate of an individual resident killer whale decreases as group size increases, suggesting that there may be information transfer. While this could represent cooperative information sharing, it is also possible that individual whales are parasitizing the information of others, as shown in bats. In many cases it is difficult to assess whether marine mammals are foraging cooperatively because group-living may be selected for by factors other than food, and group-foraging, whether cooperative or non-cooperative, is therefore simply a necessary epiphenomenon. One important consideration in studies of cooperation is whether groups are kin based as individuals in kin groups are more likely to engage in cooperative behavior to increase their inclusive fitness.

A. Cooperative Foraging, Food Sharing, and Cultivation

Cooperation can be defined as “an outcome that—despite individual costs—is “good” in some appropriate sense for the members of the group ... and whose achievement requires collective action” (Mesterson-Gibbons and Dugatkin, 1992). Most cooperation is achieved through a mechanism of by-product mutualism, in which an individual acts selfishly to benefit itself, and its actions incidentally benefit other individuals, but not all by-product mutualisms are cooperative. A possible example of by-product mutualism involves bowhead whales skim-feeding in groups with whales staggered in an inverse “V” formation. This formation may aid a whale in prey capture by using adjacent whales as a wall to trap prey or to catch prey that have escaped from the whale in front. These groups sometimes appear to be coordinated, with whales changing direction and leadership. All individuals probably act selfishly, but their presence may benefit other whales.

The above definition of cooperation requires three things be shown to support the hypothesis that a group is cooperative. First, individuals acting cooperatively must realize a short-term cost. This cost may include having to share food with other individuals or an opportunity cost by not attacking prey immediately while herding. Next, energy intake rate of individuals benefiting from cooperation must be higher than what they would have gained without cooperation. Finally, collective action must be required for the hunt to be successful. It is worth noting that in cooperative groups not all group members are required to receive equal benefits, and in groups that appear to be cooperative, a number of individuals may be non-cooperative (Packer and Rutten, 1988).

There are many possible examples of cooperative foraging in the marine mammal literature involving mysticetes, odontocetes, pinnipeds, and sirenians. However, most anecdotal accounts of possible cooperative foraging behavior do not provide enough detail to determine whether these groups were truly cooperative. For example, many dolphin species are known to break into subgroups that spread out across a large front when foraging or to travel in line abreast formation. Generally, when one subgroup finds fish, other subgroups join to feed. This behavior has often been considered

cooperative foraging. However, none of the three criteria for cooperation outlined previously have been shown to apply to these cases. Furthermore, although some authors have assumed that joining subgroups were recruited, they may simply be converging once they determine that another group located food. Fish herdings by dolphins, porpoises, whales, and sea lions have all been cited as examples of cooperative foraging. In these cases, there does appear to be a cost involved as individuals do not start foraging immediately but wait until the school has been herded to the surface (“temporary restraint”). Larger groups of dusky dolphins forage on a single fish school for longer periods of time than do small groups. Some authors have suggested that this indicates an increase in individual intake and that herding requires collective action. However, it is important to measure individual intake rates because longer foraging durations of large groups may simply be the result of larger schools being herded (and increased time until school depletion) or of increased foraging interference in large groups. More studies are required to support the hypothesis that such groups are cooperative.

Deliberate prey sharing provides strong evidence for cooperative hunting but must be viewed with caution as some apparent food sharing may represent intense competition for large prey items or kleptoparasitism (Packer and Rutan, 1988). Prey-sharing has been observed in few marine mammal species but has been documented in both mammal-eating and fish-eating killer whale populations. Also, an apparent case of prey-sharing has been documented in leopard seals when two seals killed penguins, but one individual released its penguin to be consumed by the other. Prey sharing also has been documented in false killer whales (*Pseudorca crassidens*).

There are a few other examples of marine mammal foraging which appear to represent cooperative foraging. Leopard seals have been observed hunting in a coordinated fashion, with one seal driving penguins toward a second seal hiding behind an ice flow. The process was repeated several times, and both seals caught penguins each time, sharing prey in one instance. Collective action is required if killer whales are to capture large or swift prey and, in general, larger groups are seen when transient killer whales attack such prey.

There may even be a division of labor during their hunts. Also, there is a cost as prey are divided among group members. Bubble-netting humpback whales feeding on herring in southeast Alaska represent another potential example of cooperative foraging. In these groups, one whale deploys a bubble net, starting at a depth shallower than the herring schools. The whales then apparently drive the prey up into the bubble net and simultaneously lunge through the herring trapped against the surface (Fig. 4). Although there are apparently costs to this behavior and coordination is probably required, no data exists on intake rates in these groups. Finally, it is possible that large groups of synchronously diving crabeater seals cooperatively herd krill, but future studies are needed to verify this possibility.

One study has suggested that dugongs cultivate seagrass as they forage in large groups moving among seagrass banks. Although dugong grazing changes seagrass communities to stands of more profitable species, for deliberate cultivation to occur, cooperation among dugongs would be required. In general, true cultivation (gardening) is favored to evolve only when the individual that cultivates an area realizes the benefits of that action (Branch *et al.*, 1992). This implies both a fixed and a defendable feeding site (Branch *et al.*, 1992). Cooperative cultivation by dugongs is unlikely since individual dugongs that moved to a previously cultivated area, before the cultivating individuals, would benefit from reduced foraging competition. Also, there do not appear to be any mechanisms to prevent such cheating. A more likely explanation for the observed pattern of dugong foraging is “traplining” where dugong groups rotate among the most profitable seagrass meadows, and the changes in seagrass communities are an incidental by-product of dugong foraging on rhizomes.

B. Optimal Group Size

The question of why particular group sizes are observed has been raised several times. For some species, group size has been suggested to be that which maximizes the intake rate of individuals in the group (optimal group size). However, this may not generally be the case. When it is difficult for a group to exclude joiners (e.g., when foraging



Figure 4 Humpback whales (*Megaptera novaeangliae*) in southeast Alaska cooperate to catch herring. They use a variety of tactics to manipulate the behaviour of herring, including the use of bubbles as tools. Photograph by Michael R. Heithaus.

on a large fish school), the observed group size will often be greater than that which maximizes intake of each group member, since individuals will continue to join a foraging group until the average energy intake in the group approaches that of a solitary forager (stable group size; Giraldeau, 1988). Also, the benefits of defending resources may be low in large groups since individuals that do not defend the resource will realize higher intake rates than those individuals that try to defend against joining individuals. Finally, group size is likely to be larger than that which is optimal for foraging considerations if there are other benefits of being in a group (e.g., mating opportunities, protection from predators). Therefore, it is likely that most dolphins feeding on large schools of fish are in groups larger than those that would maximize energy intake of each group member. However, some marine mammals may be found in groups that are of optimal size for maximizing energy intake. For example, killer whales feeding on marine mammals may be able to regulate group size as individual prey items are easily defended, and groups (which are kin based) may be able to exclude other individuals before foraging commences. This may explain why the modal group size of three individuals observed in foraging transient killer whales is the group size that maximizes its members' energy intake.

V. Variation in Feeding Strategies and Tactics

Marine mammals show a high degree of variability and flexibility in their foraging tactics. Individuals may be flexible in their foraging tactics depending on their state or circumstances, and this flexibility may lead to variation in foraging tactics among populations, individuals, and age/sex classes. Variation in feeding tactics may also arise from differences in the ways individuals solve cost-benefit trade-offs. Some of these differences among individuals may be genetically based and thus considered strategic variation.

A. Trade-offs

Evolution favors strategies that maximize fitness (usually by maximizing lifetime reproductive success). For example, animals may pursue a strategy that maximizes their expected lifetime energy intake, which may involve a trade-off between maximizing short-term energy intake and minimizing predation risk because habitats that are prey rich are often the most dangerous (Lima and Dill, 1990, Fig. 5). Therefore, marine mammals may sometimes accept lower energetic returns to forage in safe habitats (see Wirsing *et al.*, 2008). For example, bottlenose dolphins in Shark Bay, Western Australia, match the distribution of their prey when their primary predator, the tiger shark (*Galeocerdo cuvier*), is absent but shift to forage mostly in low-risk, low-food areas when sharks are abundant. Dugongs in Shark Bay also reduce their use of food-rich but dangerous shallow habitats as tiger shark abundance increases. In addition, dugongs primarily excavate seagrass rhizomes when tiger sharks are scarce but switch almost exclusively to cropping seagrass leaves, which allows greater vigilance, when sharks are abundant. Finally, female polar bears with cubs often select habitats with lower food abundance to avoid potentially infanticidal adult males, and trade-offs between predation risk to calves and food availability at high latitudes may have led to the evolution of seasonal migrations in baleen whales.

Trade-offs between feeding and predation may also result in habitat use patterns that vary with behavior. For example, spinner dolphins rest in shallow nearshore coves with sandy bottoms during the day, possibly to reduce the probability of shark attack, then

move offshore to feed on deep scattering layer organisms at night. Similarly, bottlenose dolphins in Shark Bay rest almost exclusively in safer, relatively deep waters, but will sometimes move into higher risk but more productive shallow habitats to feed.

Trade-offs between feeding and reproduction also may influence foraging patterns. For example, most phocid females fast during lactation and must consume sufficient food before the breeding season while female otariids make foraging trips of variable duration throughout lactation (see Wells *et al.*, 1999 for a review).

Prey selection can be viewed as the result of another type of trade-off. Each potential prey item differs in the energy required to capture it and the amount of energy the predator will gain from eating it. This trade-off sometimes results in selective foraging where one prey type is favored over others irrespective of its relative abundance. For example, harp seals always preferentially feed on capelin (*Mallotus villosus*) and select Arctic cod (*Arctogadus glacialis*) only in nearshore waters. Prey preferences have also been shown in resident killer whales. Off Alaska, resident killer whales prefer coho salmon (*Oncorhynchus kisutch*), while those off British Columbia prefer chinook salmon (*O. tshawytscha*) that are energy rich but relatively scarce. Prey-selection may also take the form of capturing a particular size of prey. For example, harbor seals in Scotland feed primarily on the most abundant fish species but prefer fish of 10–16 cm in length. Changes in the relative costs and benefits of particular prey items may lead to prey switching, which has been observed in some marine mammals.

B. Ontogenetic Variation

There are often distinct differences in the foraging behaviors of marine mammals of different ages. Such differences may be the result of changing physiological or foraging abilities, the relative importance of energy intake and survival at different life history stages, or differences in experience if a learning period is required for the successful use of a particular foraging tactic. Diving by young seals and sea lions is constrained by physiological development, and they typically make shorter and shallower dives than do adults (e.g., Steller and Australian [*Neophoca cinerea*] sea lions, Weddell and elephant seals). During their first trip to sea, elephant seal pups make a transition from short, shallow dives to a pattern similar to adult seals, with longer deeper



Figure 5 Foraging decisions made by individuals can be influenced by the presence of predators. Some individuals may forage in areas where they are more likely to be attacked by predators if the energy gain in these habitats is sufficient. Photograph by Michael R. Heithaus.

dives that show diel fluctuations. This transition appears to be related to both changes in the physiology of young seals and possibly prey distribution. Young seals of different sizes may adopt different diving tactics. For example, larger yearling Weddell seals engage in relatively shallower dives to forage on benthic prey compared to small yearlings which make deeper dives to forage on energy rich prey. However, the cause of this variation is unclear.

Learning and cultural transmission of foraging tactics play important roles in the acquisition of foraging tactics in cetaceans. For example, there is a long period of practice required for young killer whales to become adept at using the intentional stranding tactic to capture pinnipeds. This period of learning may involve calves preferentially associating with the female pod-members (not necessarily their mother) that engage in this tactic most frequently. Similarly, it appears that sponge-carrying by bottlenose dolphins is socially passed within matrilineal groups, especially to female offspring. Finally, sea otters tend to display the diet preferences of their mothers.

C. Inter-Individual Variation

Within many marine mammal populations substantial differences exist among individuals in the foraging tactics that they employ. Northern fur seal females perform two distinct types of foraging dives: shallow dives, which seem to be directed towards vertically migrating prey, and deep dives to feed near the bottom. Shallow dives are made only between dusk and dawn while deep dives occur both at night and during daylight hours. Some individual seals specialize in one dive type or the other while other individuals use a mix of tactics. Southern sea lion (*Otaria flavescens*) individuals differ in their propensity to hunt fur seal pups. In Alaska, only juvenile male Steller sea lions prey upon fur seal pups while in Peru, most hunting is done by just a few adult males, and there are large differences in the success rates of different individuals. Similarly, sea otter predation on birds appears to be largely restricted to a few individuals, and a few individual sea lions have learned to wait at fish ladders and at the mouths of freshwater streams to take advantage of spawning steelhead. Leopard seals also vary in their hunting tactics. For example, a single individual was responsible for all ambushing attacks on Adelie penguins observed in Prydz Bay, Antarctica. In gray seals (*Halichoerus grypus*), there are distinct differences between sexes in diet and foraging behavior (Beck *et al.*, 2007). Finally, individual variation in the prey species consumed by sea otters may be a result of differences in diving tactics as juvenile males forage further offshore and make longer dives than other age/sex classes.

Cetaceans also show individual variation in feeding tactics. In Shark Bay, many unique tactics including kerplunking, sponge-carrying, and extreme shallow water foraging are restricted to a small number of individual bottlenose dolphins. Adult female killer whales perform most of the intentional strandings to catch elephant seals, and within a pod individual females differ in their use of this tactic. Most individual minke whales around the San Juan Islands specialize in either lunge feeding or feeding in association with birds. These two tactics are usually observed in different regions with individual whales showing inter- and intra-seasonal site fidelity. Individual humpback whales differ in their use of various types of lunge-feeding and bubble-netting tactics that may relate to dietary specializations on either krill or herring (*Clupea* spp.) and to the distribution of these prey items. Finally, reproductive state may influence the foraging tactics of cetaceans as lactating female bottlenose, common (*Delphinus* spp.), and pantropical spotted dolphins (*S. attenuata*) consume different prey items than do other dolphins.

D. Intra-Individual Variation

Individual marine mammals can switch among foraging locations and tactics depending on their age, body condition, group size, and prey distribution and abundance. For example, pinnipeds can change their diving behavior in response to increased foraging costs as seals make shallower dives and dive at a steeper angle to maximize their time at a foraging depth. Individuals that encounter different habitats often switch among tactics depending on their location. For example, humpback whales may switch between foraging in large bubble-netting groups and engaging in individual lunges to capture krill. Sperm whale foraging behavior is linked to foraging success, and foraging is more common when prey availability is high or the energetic cost of capturing prey is relatively low. Also, sea otters change the number of prey items they collect on each foraging dive depending on the average prey size available. Offshore of Sable Island, Nova Scotia, harbor seals switch between pursuit and benthic foraging tactics depending on prey type, and Baikal seals (*Pusa sibirica*) shift their foraging tactics between day and night. They use visual cues to feed on pelagic fishes during the day but move to shallow waters, likely to feed on crustaceans using tactile cues, at night.

The flexibility of marine mammals is highlighted by their ability to take advantage of human activities. Many odontocetes, pinnipeds, and sea otters have learned to steal fish from nets. Seal lions will even jump into encircling nets to feed or will follow fishing vessels for days to take advantage of the abundant food resources offered by fishing operations. Bottlenose dolphins are well known for foraging behind trawlers and feeding on discarded fish or fish in nets. Some individual bottlenose dolphins also have learned to take advantage of direct handouts of fish offered by people, and many species of odontocetes remove either bait or fish from fishing lines. In the Bering Sea and off Southern Brazil, killer whales may damage over 20% of the fish captured by longline fisheries.

Both the diversity of habitats in which marine mammals live and the flexibility of individuals has led to the wide variety of foraging tactics exhibited by the group. However, further studies of these tactics are still of great interest, especially systematic investigations of the function and use of particular tactics and the circumstances in which they are employed. For example, current studies are beginning to use a multivariate approach to teasing apart the roles of cultural transmission, genetics, and environmental factors on inter-individual variation in the use of foraging tactics within a population. Such detailed studies will improve the ability to predict influences of anthropogenic changes to marine habitats and prey availability on marine mammals and aid in efforts to conserve them.

See Also the Following Articles

Behavior, Overview ■ Feeding Morphology ■ Filter Feeding ■ Tool Use

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mesovarium, which attaches to the dorsal side of the broad ligament. Dugong (*Dugong dugon*) ovaries are also attached to the diaphragm by peritoneal folds that form pouches in the dorsal abdominal wall.

The ovaries are surrounded by the ovarian bursa, a fold of mesosalpinx which forms a peritoneal capsule. There is considerable variation in development and in the extent to which the bursa communicates with the celomic cavity. The ovarian bursa of odontocetes develops *in utero* whereas in mysticetes it develops after birth. In polar bears (*Ursus maritimus*) and other carnivores, the periovarian space between the ovary and peritoneal lining of the bursa communicates with the peritoneal cavity by a narrow passage which may become distended at estrus with fluid of unknown origins. In all marine mammals, and mammals in general, the function of the bursa is to ensure that the ova pass into the oviduct where fertilization occurs.

Marine mammal ovaries vary in size and shape. Quiescent dugong ovaries are small, flattened ovoids or spheres. Ovaries in the Amazonian manatee (*Trichechus inunguis*) are broad and flattened against a short mesovarium. Sea otters (*Enhydra lutris*) have lenticulate, compressed oval ovaries. The odontocete ovary is more or less spherical to ovoid in shape, with a smooth surface in the resting condition whereas in mysticetes ovaries are flat and elongated. Phocid ovaries are ovoid and smooth in the resting state. In some species of phocids, (e.g., gray seals, *Halichoerus grypus*), fetal hypertrophy of the ovaries exists through hormonal influence of the pregnant female. This condition may be less pronounced in otariids.

Typically, eggs ripen and ovulate alternately between the ovaries in successive reproductive cycles and the ovaries are of similar size. However, in some odontocetes there is a prevalence of activity in the left ovary (e.g., 70% in pilot whales, *Globicephala*) and the left ovary is larger than the right (Slipper, 1966). The right ovary may become active later in life.

The mammalian ovary is covered by germinal epithelium (Fig. 1) below which lies connective tissue (*tunica albuginea*) of varying thickness. Germinal epithelium is often invaginated into the *tunica albuginea*, forming small folds, pits, or subsurface crypts. These invaginations are particularly well developed in pinnipeds and form surface fissures in sea otter ovaries. Below the *tunica albuginea* is a layer of follicles and corpora that are derived from them. The ovary also contains stromal and connective tissue, interstitial tissue, vascular, nervous and lymphatic tissues, and embryological remnants. The interstitial cells of cetaceans are less numerous and less prominent than those in some other mammalian orders, such as rodents. Understanding the maturation process of the follicles, and development and subsequent regression of the luteal bodies for each species allows researchers to assess the reproductive status of females (immature, ovulating, etc.).

Follicular maturation (Fig. 1) proceeds through a series of changes characterized by two phases. In the first phase, there is a rapid increase in the size of the oocyte and a slow increase in the size of the follicle. Second, there is slow growth of the oocyte and a rapid increase in the size of the follicle which can be seen macroscopically. In dugongs, mature follicles may be just visible as translucent bodies or they may protrude from the ovarian surface. In West Indian manatees (*Trichechus manatus*) the mature follicles appear as large masses of bead-like spherules in the ovary. Similarly, mysticete ovaries may appear grape-like with protruding follicles. Maturing follicles of odontocetes and pinnipeds tend to be more widely dispersed in the ovary.

Oocytes develop within the ovary during fetal development but are dormant until puberty is reached. After puberty, and partly in

Female Reproductive Systems

R.E.A. STEWART AND B.E. STEWART

I. Introduction

The female reproductive system in marine mammals is composed of the basic mammalian reproductive organs: ovary, oviduct, uterus, cervix, vagina, clitoris, and vaginal vestibule. Under the control of endocrine system, these organs are engaged in the reproductive cycle of ovulation, fertilization, implantation, fetal growth, and parturition. Ancillary to reproduction are the mammary glands and lactation. Some variation in anatomy, morphology, and physiology of the reproductive organs, and in reproductive cycles, exists among orders of marine mammals. Species-specific differences within orders also exist, reflecting both phylogeny and the variety of environments inhabited by marine mammals. Variation also exists in how marine mammals use their basic mammalian anatomy in different marine habitats. This is discussed in other articles such as those on reproductive strategies, life history, lactation, and behavior. Here the gross anatomical and morphological characteristics of female reproductive systems are described and the functional adaptations are noted.

II. Anatomy and Morphology

The ovary is the organ where eggs or ova mature and are released during ovulation. Usually, there are two functional ovaries suspended from the abdominal or pelvic cavity by a short mesentery, the