

Habitat Use

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I. Introduction

A. Temporal and Spatial Scales in Ecology

Ecology is the study of interactions between organisms and their environment, and the distribution and abundance of organisms resulting from these interactions. The environment of any organism includes abiotic factors—non-living chemical and physical factors such as temperature and light—and biotic factors—living organisms with which any individual interacts. For instance, other organisms may compete with an individual for food and resources, prey upon it, or change its physical and chemical environment. At the core of both ecology and conservation biology are questions that examine the relative importance of various environmental components in determining the distribution and abundance of organisms.

Habitat use studies attempt to describe, explain, and predict the distribution and abundance of organisms. In these studies, identifying the factors that influence distribution and abundance at different spatial and temporal scales is fundamental. This concept can be illustrated by examining the distribution and abundance of blue whales (*Balaenoptera musculus*) from the California/Mexico populations and fin whales (*B. physalus*) from the Gulf of California population. Blue whales and to a lesser extent fin whales depend on krill (Euphausiacea) as a prey item. Krill form large, dense swarms during the day and have their largest concentrations below 100 m in depth. At night, krill come near the surface but are scattered over large areas. During winter in Bahía de Loreto, Gulf of California, México, blue and fin whales engage in deep foraging dives during the day while at night they perform shallow dives, very few of which appear to be foraging dives. During the day, krill swarms are found around underwater edges, where depth diminishes rapidly, and blue and fin whales concentrate their movements and feeding in those areas. Both blue and fin whales move out of Loreto around early spring. Bahía de Loreto is thus a short-term feeding site for both whales, which behavior and movements closely match those of krill.

By combining the information from Loreto to that from other studies, the following general picture of the California/Mexico population of blue whales emerges: In late spring, blue whales move north to feed during summer and early fall along the California coast in the Farallones Islands, Cordell Banks, and Monterey Bay, on large swarms of krill. The whales move back south in fall, feeding around the Channel Islands and perhaps off Bahía Magdalena, Mexico. During winter, whales are back in the Gulf of California, including Bahía de Loreto. However, there is a large degree of variation, and many whales may winter in the Costa Rica Dome, an oceanographic feature in the Pacific Ocean. Although the picture of the Gulf of California population of fin whales is less complete, we know that they feed during the spring in the southern region of the Gulf of California, including Loreto. During the summer, a time of year in which krill are less abundant in the gulf, they move further north into the gulf to prey on schooling fish.

This example illustrates the importance of defining temporal and spatial scales in an ecological study, and documents how the distribution of marine mammals is influenced by the environment at different spatial and temporal scales. At scales of days and tens of kilometers, blue whales are found during the day along canyon edges, feeding on

krill swarms. At scales of months and hundreds to thousands of kilometers, blue whales move to different coastal areas to exploit krill swarms. In the case of fin whales, at scales of days and tens of kilometers, they are also found during the day along canyon edges feeding on krill swarms. However, at scales of months and hundreds to thousands of kilometers, they move within the same oceanographic area (the Gulf of California) and switch prey items, from krill to schooling fish. Even closely related species of marine mammals can make different decisions regarding their distribution: blue whales move out of the Gulf of California and look for the same prey item; fin whales remain in the Gulf of California and switch prey items. Given that marine mammals are generally long lived and that their cost of locomotion in the water is relatively low, understanding their distribution and abundance at multiple temporal and spatial scales is even more crucial than for shorter-lived or less mobile organisms.

B. Research on Marine Mammal Habitat Use

Marine mammals are highly mobile, tend to cover large areas, move in three spatial dimensions, and spend the vast majority of their lives under water. Hence, controlled experiments are next to impossible to conduct, and describing, explaining, and predicting distribution and abundance present unusual challenges to researchers. In general, studies are unable to show a causal explanation between a factor or factors and the observed distribution and abundance of a marine mammal population; rather, scientists rely on quantitative correlations that are indicative of potential causal factors. For instance, several studies document that during the summer belugas (*Delphinapterus leucas*) in Alaska are distributed near coastal mud flats and river mouths; however, it is unclear whether the observed distribution is caused by prey availability, breeding, calving, molting, or shelter from predators (Goetz *et al.*, 2007).

Our understanding of marine mammal habitat use has been improved by employing remote-sensing techniques and sophisticated statistical analyses. Remote-sensing techniques allow scientists to correlate marine mammal distribution with dynamic environmental variables that take into account spatial or temporal scales. For example, in the Gulf of St. Lawrence, the distribution of blue whales, fin whales, minke whales (*Balaenoptera acutorostrata*), and humpback whales (*Megaptera novaeangliae*) is highly correlated with thermal fronts, which were described from sea-surface-temperature satellite images (Doniol-Valcroze *et al.*, 2007). Remote-sensing techniques also allow scientists to describe the three-dimensional space distribution of marine mammals and correlate it with environmental factors. For instance, the amount of time that Weddell seals (*Leptonychotes weddellii*) in Antarctica spend at the bottom phase of a dive correlates with an index of prey abundance (Mitani *et al.*, 2003; Watanabe *et al.*, 2003; Mitani *et al.*, 2004). These results were obtained by attaching recorders to individual seals, which recorded dive behavior, acceleration, geomagnetic intensity, and digital still pictures. This methodology allows scientists to describe three-dimensional spatial use of seals, which spent their time under water on a small region with a steep bottom contour, apparently searching for benthic-pelagic prey throughout the water column (Mitani *et al.*, 2004).

Sophisticated statistical analyses allow scientists to simultaneously correlate the distribution and abundance of marine mammals with many different environmental factors. In the Bahamas, the occurrence of Blainville's beaked whales (*Mesoplodon densirostris*) is correlated in decreasing order of importance with seabed aspect (facing direction), seabed gradient (slope), and water depth, an analysis conducted with generalized additive modeling (GAM). Blainville's

whales occur in areas with a northeast aspect, intermediate gradients, and depths between 200 and 1000m where bottom topography forces the Deep Western Boundary Current toward the surface (MacLeod and Zuur, 2005). The authors hypothesize that prey are concentrated in these same areas. In the Faroe-Shetland Channel north of the United Kingdom, a GAM analysis of dolphin sounds indicates that dolphin distribution is best predicted by a combination of water noise level, time of day, month, and water depth (Hastie *et al.*, 2005).

Despite our inability to determine causality and hence fully explain the relationship between marine mammal distribution and abundance, and several biotic and abiotic factors, several tools such as remote-sensing techniques and GAM analysis allow scientists to describe, predict, and partially explain the determinants of such relationships.

C. Habitat Use and Evolution

Understanding the distribution and abundance of marine mammals is important not only to ecologists, conservation biologists, environmentalists, managers, and tour operators, but also to evolutionary biologists. This is because the interactions of organisms with their environment that occur over a long period of time are important causes of evolutionary change. Lake Apoyo, a volcanic crater lake in Nicaragua, was seeded only once by the ancestral benthic species *Amphilophus citrinellus* from which the new limnetic species *A. zalius* evolved within less than 10,000 years by exploiting a different habitat (Barluenga *et al.*, 2006). These two species are both reproductively isolated and eco-morphologically distinct; thus providing a convincing example of habitat use as an agent of evolutionary change via sympatric speciation. Sympatric speciation is a contentious concept in evolutionary biology, for which few convincing examples exist worldwide. Hence, documenting evolutionary change in marine mammals due to habitat use has been extremely difficult. The apparent incipient speciation of sympatric resident and transient killer whales (*Orcinus orca*) off the west coast of Washington State and Canada may be such an example (Baird *et al.*, 1992). However, it has been suggested that the division was originally cultural (Whitehead *et al.*, 2004).

II. Intrinsic Factors in Habitat Use

Most explanations on habitat use by marine mammals refer to environmental factors, such as prey availability, predation, or temperature, which are extrinsic to the organisms. However, traits intrinsic to the organisms themselves may affect their ability to exploit certain habitats and hence determine their distribution and abundance.

A. Body Size

Body size affects many important traits in organisms, including morphology, metabolic rate, and reproductive costs. Species with large body size and large amounts of fat stored in blubber are able to travel far or to exploit very patchy resources. An example of the relationship between habitat use and large body size is the northern elephant seal (*Mirounga angustirostris*). This species makes a double migration each year: one after molting and one after breeding, with individual annual movements of 18,000–21,000km (Stewart and DeLong, 1993, 1995). Adults stay at sea for 8–9 months of the year to forage, using the California Current as a corridor to foraging areas further north that are related to water masses and the distribution of squid. While at sea, both sexes dive almost continuously, remaining submerged for about

90% of the total time. Large body size has also predisposed marine mammals to long dives, because body size augments oxygen stores and diminishes specific metabolic rate (use of oxygen per unit of mass) (Hoelzel, 2002). Because deep dives require longer dives than shallow dives, large marine mammals such as the sperm whale (*Physeter macrocephalus*) are able to exploit deep-water habitats. However, given the many different physiological adaptations for diving found in marine mammals, body size alone cannot predict the vertical distribution of marine mammals.

B. Age

Given that marine mammals are long-lived predators, the habitat that they are able to exploit may change over time to reflect increased physiological capabilities as body size increases and by increased learning. Dive and depth duration in Australian sea lions (*Neophoca cinerea*) increase with age; however, such development is slow (Fowler *et al.*, 2006). Pups at 6 months of age show minimal diving activity, they are weaned at about 17 months of age, and as 23-month-old juveniles they tend to dive to 40–50m depths (62% the depth of adults). Pup and juveniles do not reach adult depth or durations and hence occupy shallower habitats than those exploited by adults. Adult New Zealand fur seals (*Arctocephalus forsteri*) utilize continental shelf waters and deep waters over the shelf break, where presumably high densities of fishes and cephalopods are found, while juveniles use pelagic waters up to 1000km from the habitats used by adults (Page *et al.*, 2006). It is hypothesized that due to their small body size, juveniles cannot efficiently utilize prey in the same habitats as adults because they do not have the capacity to spend enough time under water at the greater depths. Hence, adult male and female New Zealand fur seals are large enough to engage in benthic feeding in shelf breaks, whereas the smaller-sized juveniles are constrained to epipelagic feeding at night.

C. Sex

Many marine mammal species segregate by sex. The harbor seal (*Phoca vitulina*) provides a good example of such segregation (Boness *et al.*, 1994; Coltman *et al.*, 1997). Females and males have similar body sizes (females weigh about 85kg; males about 110kg) and mate at sea. Females nurse their pups for about 24 days, fasting for about 1 week and then having to take regular foraging trips while lactating. Most males forage early in the season and in doing so most individuals maintain or increase body mass during this period. During the latter part of the breeding season, males rarely forage and spend time reproducing when females are receptive. Hence, the habitat occupied by both sexes is different: during the first 10 days after birth, females are on land while males are at sea diving to depths exceeding 60m; between 10 and 20 days after birth, females make trips at sea and dive to 50–60m while males are also at sea in areas where females move but diving to only 20m. It appears that the different habitat use in which females and males engage represents a balance between foraging and reproduction to maximize reproductive success.

The relationship between habitat use and sex is also related to body size in sexually dimorphic marine mammal species. Such body size differences may require the sexes to use different habitats. For instance, gray seals (*Halichoerus grypus*) are sexually dimorphic in size (Breed *et al.*, 2006). At Sable Island, Nova Scotia, males and females utilized different habitats, differences that were most pronounced just before and immediately after breeding. Females mainly used mid-shelf regions whereas males primarily used areas along the continental shelf break. It is hypothesized that these differences maximize fitness

by reducing intersexual foraging competition. Southern elephant seals (*Mirounga leonina*) from Kerguelen Island travel to the Antarctic shelf (Bailleul *et al.*, 2007). As the ice expands during winter, females appear to shift from benthic to pelagic foraging, while males continue to forage almost exclusively benthically over the continental shelf. It is hypothesized that this difference in habitat use is related to the different energetic requirements between the two sexes, or to the need for females to return to Kerguelen in the spring to give birth, whereas males can remain in the ice.

D. Individual Variability

Differences in habitat use may also be related to individual variability. For instance, there is significant variation between individual female Antarctic fur seals (*Arctocephalus gazella*) in trip durations and the maximum distance reached from the breeding beach (Staniland *et al.*, 2004). Apparently, there is a strong individual component to where a seal forages, especially in terms of the distance traveled. The authors suggest that once the foraging area is selected by an individual seal, the dive behavior within that area is determined by the area itself, perhaps related to the spatial and temporal distribution of the prey within it, and not by the individual seal.

E. Life History

Life history refers to the patterns of resource allocation to maintenance (survival), growth, and reproduction. Life history traits appear also to influence habitat use in marine mammals. As described earlier, blue whales migrate from the Gulf of California to the California coast searching for krill aggregations, while fin whales remain in the Gulf of California and switch prey items. In this case, the blue whale pattern is to move to another body of water and feed on the same prey; the fin whale pattern is to remain in the same body of water and feed on different prey. Along the Scandinavian coast, harbor porpoises (*Phocoena phocoena*) experience different ecological regimes during the year and shift from pelagic prey species in deep waters to more coastal and/or demersal prey in relatively shallow waters (Fontaine *et al.*, 2007). In this case, the harbor porpoise pattern is similar to that of fin whales: they both adapt their foraging to local oceanographic conditions rather than perform an extensive migration.

Larger body size implies a longer dive time. However, whales of the family Balaenopteridae (rorquals) dive less than expected based on body size because their foraging strategy of lunging is costly (Acevedo-Gutiérrez *et al.*, 2002). Apparently, the effort needed to accelerate a large mass increases the costs of feeding and reduces time under water. Despite engaging in behaviors to reduce such costs—such as gliding gaits during dive descent, accelerating at the beginning of a lunge and gliding throughout the rest of the lunge—rorquals do not exploit the deep waters that smaller species use. In this case, the rorqual pattern is to exploit relatively shallow habitats due to the constraints imposed by their foraging behavior.

III. Extrinsic Factors in Habitat Use

Most habitat use studies attempt to explain the distribution and abundance of marine mammals in relationship to external biotic and abiotic factors. Two important extrinsic factors influencing the distribution of a species are food availability and predation risk. In general, marine mammals should exploit areas of high prey density and avoid areas of high predator density. However, it is also important to understand the temporal and spatial scales, given that the predictability of prey distribution tends to decrease with the spatial scale.

A. Prey Availability

Prey availability is the most frequently factor invoked to explain the distribution and abundance of marine mammals, regardless of the spatial and temporal scale of the study. However, understanding the mechanism influencing prey availability itself has proved as challenging as determining the causality of marine mammal distributions. Croll *et al.* (2005) took advantage of a relatively straightforward system: blue whales feed exclusively upon dense but patchy schools of pelagic krill; hence, understanding krill distribution will assist in understanding blue whale distribution. By employing remote-sensing techniques and concurrent measurements, they examined the temporal and spatial linkages between intensity of upwelling, primary production, distribution of krill, and distribution and abundance of blue whales in Monterey Bay, California. The study indicated that seasonally high primary production supported by coastal upwelling combined with topographic breaks off California maintained high densities to allow exploitation by blue whales. Blue whales appeared in the area in late summer and early fall and fed exclusively upon adult krill *Thysanoessa spinifera* and *Euphausia pacifica* aggregations, diving to depths between 150 and 200 m on the edge of the Monterey Bay Submarine Canyon. High krill densities were supported by high primary production between April and August and a submarine canyon that provided deep water down-current from an upwelling region. Peak krill densities occurred in late summer and early fall, lagging the seasonal increase in primary production by 3–4 months, due to the growth to adulthood of krill spawned around the spring-increase in primary production, and to decreased upwelling in late summer. It is predicted that the annual migratory movements of the California blue whale population reflect seasonal patterns in productivity in other foraging areas in the Northeast Pacific. The annual increase in the abundance of blue whales was linked to wind-driven upwelling, but these linkages occurred through a sequence of bottom-up biological processes that lagged in time. Consequently, models that attempt to predict the distribution and abundance of marine mammals need to include bottom-up processes and temporal scales.

Another example of the importance of understanding the spatial and temporal distribution of prey to describe, explain, and predict marine mammal distribution is found in dugongs (*Dugong dugon*). Like other herbivores, dugongs must select quality food plants to optimize their nutrient intake. Across multiple spatial scales, they appear to prefer some seagrass pastures and avoid others. At medium spatial scale remote sensing, it was confirmed that a 24 km² seagrass meadow in Hervey Bay, Australia, is an important dugong habitat due to the presence of five species of seagrasses, which covered 91% of the total habitat area (Sheppard *et al.*, 2007). However, at a small spatial scale, dugong use within the meadow is still not well understood because the influence of seagrass food quality on dugong grazing patterns and nutritional ecology is poorly understood. Consequently, understanding the dynamics of seagrass communities is essential for predicting patterns of habitat use by dugongs.

B. Predation Risk

Predation risk is an important factor explaining the distribution and abundance of marine mammals regardless of the spatial and temporal scale of the study. For instance, tiger shark (*Galeocerdo cuvier*) predation risk correlates well with the habitat use of Indo-Pacific bottlenose dolphins (*Tursiops aduncus*) in Shark Bay, Western Australia (Heithaus and Dill, 2002, 2006). The biomass of dolphin prey is greater in shallow habitats than in deeper ones; however, when tiger sharks are present in the area, their density is highest in shallow

habitats. It is believed that shallow habitats are also inherently risky because shark detection apparently decreases as dolphin echolocation efficiency and visual detection of sharks camouflaged over seagrass diminish in shallow habitats. Hence, shallow habitats are the best places to forage for dolphins, but are also the most risky. As a result, in seasons of high shark abundance, dolphins foraged much less in the productive but risky shallow habitats than expected if food was the only relevant factor. These results suggest that dolphin habitat use reflects a trade-off between predation risk and prey availability. Besides showcasing the importance of predation risk in explaining habitat use, this study also indicates that the distribution and abundance of marine mammals is simultaneously affected by more than one factor. Further, because the distribution and abundance of tiger sharks are influenced by species other than dolphins, the distribution of the primary prey of the sharks may indirectly influence dolphin habitat use. Hence, as also exemplified by the studies described in the section on prey availability, it is important to consider the community context in studies of habitat use.

C. Intraspecific Competition

In many species, differences in habitat use between sexes are apparently a consequence of social interactions. A recent study of the Galápagos sea lion (*Zalophus wollebaeki*) indicates that sexual segregation on land was high both during the reproductive and non-reproductive periods (Wolf *et al.*, 2005). A generalized linear model of habitat use showed that adult males frequented habitat types that adult females used much less, with males being most abundant in suboptimal inland habitats. It is hypothesized that this habitat segregation resulted as a by-product of social processes, primarily intra-sexual competition and female avoidance of male harassment.

D. Human Influence

Human activities, also termed anthropogenic influences, are an important extrinsic factor affecting the distribution and abundance of marine mammals. Boat traffic is an activity with many documented cases of impact on marine mammal habitat use. In the short term, this activity may cause marine mammals to temporarily abandon or avoid a particular site. For instance, the number of harbor seals hauled out in a particular site may diminish dramatically in relation to boat traffic (Suryan and Harvey, 1999; Johnson and Acevedo-Gutiérrez, 2007). In New Zealand, the frequency of bottlenose dolphin (*Tursiops truncatus*) visits to Milford Sound has diminished as a result of boat traffic; additionally, when dolphins visit the fjord they remain at the entrance, away from tour boats (Lusseau, 2005). In the long term, boat traffic may create a permanent abandonment of areas visited by marine mammals and hence creating a permanent shift in distribution. For example, boat traffic may cause harbor seals to abandon haulout sites where alternative haulout locations are limited (Suryan and Harvey, 1999). In Shark Bay, Australia, the abundance of Indo-Pacific bottlenose dolphins has declined in areas operated by two or more dolphin-watching boats compared to areas with no boats or with only one boat (Bejder *et al.*, 2006).

Human activities may also cause marine mammals to visit rather than leave a particular area. For instance, two sympatric communities of Indo-Pacific bottlenose dolphins are found in Moreton Bay, Australia (Chilvers *et al.*, 2007). The non-trawler community does not associate with trawler vessels, whereas the trawler community associates with trawlers to feed on flushed prey. While the distribution of the non-trawler community is explained by season and tide,

the distribution of the trawler community is explained by the distribution of trawler boats.

IV. Conclusion

The habitat use of marine mammals is affected by abiotic and biotic factors, including intrinsic and extrinsic factors. The scientists' goal is to describe, explain, and understand the relative importance of each factor in the distribution and abundance of marine mammals. To reach this goal, the temporal and spatial scales of the study system need to be clearly defined. Given the challenges inherent in studying marine mammals, the use of sophisticated remote-sensing technologies and statistical models has been very successful in gathering and integrating data on habitat use. Long-term studies and studies in new regions are fundamental to answering questions on habitat use. However, the most promising line of work is to conduct integrative studies that consider community and ecosystem structure at different spatial and temporal scales, such as the study on the California/Mexico population of blue whales described throughout this chapter.

See Also the Following Articles

Cetacean Ecology ■ Distribution ■ Pinniped Ecology.

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