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FIGURE 1 A large male (front) with very vibrant reproductive colors for mating (grey-green-reddish) and a smaller female marine iguana (back), basking in the sun. Photograph by Luis R. Vinueza.

IGUANAS, MARINE

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The endemic Galápagos marine iguana, *Amblyrhynchus cristatus*, is the world's only seagoing iguanid lizard that feeds on seaweeds along the rocky shores, tidepools, and shallow subtidal rocky reefs of the Galápagos Archipelago. Marine iguanas have behavioral, morphological, and physiological adaptations to cope with their unique feeding habits, including a rounded snout, serrated teeth to mow algae, and special glands to excrete salt. Females are normally half the size of the males, which can reach up to 1.5 meters in length and weigh as much as 12 kilograms (Fig. 1). The iguanas' body size has evolved in response to sexual selection, food availability and temperature. While bigger males have access to more females, they are negatively selected (suffer higher mortalities) during periods of food shortage such as El Niño/Southern Oscillation (ENSO). The marine iguana population around the islands is estimated as 700,000 individuals, but they are considered vulnerable by the red list of the World Conservation Union (IUCN 2004) because of their endemic status, susceptibility to anthropogenic (pollution, fisheries, introduced species, global warming) and environmental (ENSO) perturbations.

FROM LAND TO SEA

Evolution

Three species of iguanas coexist in the Galápagos Islands: the two land iguanas *Conolophus subcristatus* and *C. pallidus* and the marine iguana *Amblyrhynchus cristatus*, all endemic species of this unique archipelago. It is believed that these iguanas evolved from a common ancestor of the genus *Iguana*, now widely distributed in mainland South America. For many years it was assumed that the iguanas (and much of the other extant biota) arrived at the Galápagos Islands from mainland South America in floating rafts transported by winds and currents. However, genetic studies have shown that the two sister taxa *Amblyrhynchus* and *Conolophus* differentiated between 10 and 20 million years ago. This has puzzled scientists, because the present islands emerged from the bottom of the ocean less than 5 million years ago. Nevertheless, the accepted current hypothesis for the origin of these much older lizards is that they originally inhabited the former, now sunken, Pacific–Caribbean island arcs from the early Tertiary period (~40 million years ago) off the coast of South America.

Reproductive Traits

The breeding season of marine iguanas appears to be synchronized with peaks of food availability and quality in a strategy to cope with the costs involved in egg production and to maximize their breeding success. Breeding begins in December and extends through March. Marine iguanas have a lekking mating system, in which males cluster during the mating season and defend small territories to attract

females. These leks (clusters of territorial males) occur high in the rocky coastline, where females also aggregate. The much larger males defend their mating leks by continually signaling their aggression by head-nodding to intimidate potential transgressors. Males are visited by females who select them as mates based on their size, the level of activity toward females, and lek attendance. Meanwhile, smaller males in the periphery of the leks will attempt to copulate forcibly with females. Following copulation, and approximately four weeks after mating, females will leave the colony to find a spot in the soft sand high up the shore to dig a nest. There, they will bury a clutch of between one to six eggs, whose incubation will take between 89 and 120 days.

Hybridization

Hybrids between the marine iguana *(Amblyrhynchus)* and the land iguana *(Conolophus)* have been recognized by their unusual morphology and genetic analyses. These hybrid iguanas typically behave like the land iguanas, but they have darker colors and exhibit a dorsal striping, both characteristic of juvenile marine iguanas. The fact that there is cross-breeding between the two genera of iguanas raises interesting questions about the evolutionary relationship between the two species. It is not known whether the hybrids are fertile.

Physiological Adaptations

Because marine iguanas lack temperature regulation (ectotherms), they must warm up their bodies with the equatorial sun before and after feeding in the cold sea. Most iguanas feed on rocky shores around low tide. Thus, foraging time is constrained by cold water, the duration and height of the low tide, and the height of the swell. Iguanas stop feeding when full or when cold, whichever happens first. The iguana's body temperature falls steeply in the cool season and more slowly in the hot season. When algal biomass is high, the iguana suffices with a single feeding excursion, but if algal biomass in the warm season is low, the iguana may require two or more feeding excursions during a low tide.

ECOLOGICAL ROLE

Grazing Up and Down

Typically, the marine iguanas feed during diurnal low tides (Fig. 2A). Yearlings (recently born iguanas) feed on tidepools and higher on the rocky shores to avoid wave action. As marine iguanas get older and bigger, they will venture lower on the shore, synchronizing their feeding bouts with the spring low tides. Only large individuals, mostly males, will feed subtidally on the shallow reefs of the islands down to 1.5–5 meters depth, where food is more predictable and abundant (Fig. 2B). Dive times are only a few minutes long, but it is known that marine iguanas can be submerged for more than half an hour. The preferred food for the marine iguanas includes several species of ephemeral algae, such as *Ulva* sp. (green sea lettuce) and a combination of different species of filamentous red algae that includes species of the genera *Gelidium*, *Ceramium*, *Centroceras*, *Hypnea*, and *Spermothamnion*, among others, which normally form lawns of patches or algal turfs.

FIGURE 2 (A) Juvenile marine iguana feeding among tidepools. Photograph by Luis R. Vinueza. (B) Male adult grazing underwater on the abundant algal communities. Photograph by Angel I. Chiriboga.

Mowing the Algal Lawns

Marine iguanas share their food with other grazing herbivores, including crabs, fish, and molluscs (Fig. 2A). The effect on the algal communities of this diverse group of grazing herbivores varies according to wave action, levels of nutrients, and temperature. At wave-protected sites, the iguanas and other grazers normally decrease the diversity to a few or even single dominant species (mostly green or red algae) or to grazing resistant, crust-forming species. At other locations, particularly in the western islands, the effects of these herbivores give way to more diverse communities because rocky shores are exposed to stronger wave action or higher productivity as a result of the upwelling of cold and nutrient-rich waters.

COPING WITH CLIMATE VARIATION AND EL NIÑO

Boom-and-Bust Life Histories

The climate and oceanographic conditions of the Galápagos Islands are all about change and dynamics. The unique mix of tropical and temperate seas makes finding tropical penguins and diving lizards possible. The southwestern islands harbor cold water and subtropical biota, whereas the northeastern islands have truly warm, tropical ecosystems. In addition, the El Niño/Southern Oscillation (ENSO), a large-scale oceanographic/atmospheric disruption in the tropical Pacific, has dramatic impacts on the marine iguanas and the ecosystem as whole. The variability of the sea and the alternating cycles between El Niño (wet and warm) and La Niña (dry and cold) conditions have shaped the evolutionary traits of the marine iguana. Thus, differences in food quality, availability, abundance, composition, and temperature between biogeographic regions seem to underlie the almost tenfold difference in body size and mass between the iguanas of the northern (up to 0.41 kg) and western islands (up to 12 kg). The consequences of El Niño on the intertidal and reef ecosystems of the Galápagos are dramatic. The warmth and low productivity of the otherwise rich seas starve most of the marine biota to death, including the marine iguanas. The abundance of *Ulva* sp. and filamentous red and brown algae (the most frequent species in marine iguana diet, Fig. 3A) is drastically reduced and the normally lush algae lawns and turfs are then replaced by the opportunistic *Giffordia mitchelliae*, a brown slimy filamentous alga that has been observed only during El Niño years to cover all the rocky shore habitats. *Giffordia* has a high content of tannins and a very low energetic value for the grazers, and it appears also to be difficult to digest by the now-starving iguanas (Fig. 3B). The signs of famine are evident and cause an elevated mortality among marine iguanas (up to 90% on some islands), especially among small and large individuals (Figs. 3C, 3D). After El Niño passage, marine iguanas recover rapidly because of resumed high algal production, reduced competition, and increased fecundity.

Shrinking to Survive

To cope with these stressful conditions, marine iguanas will change their diet to alternative sources of food, including coastal shrubs and carrion, or could even reduce their body size. This is in repose to the fact that smaller iguanas outcompete larger ones when food availability declines. During particularly lean (El Niño) years, some animals shrink—a net reduction in body length as well as in body mass—and those that shrink have better chances of surviving (Fig. 3C). The survival and recovery of marine iguana populations might be hindered by the presence of introduced predators, particularly dogs and cats, and by pollution, such as a recent oil spill that indirectly killed 65% of the population of marine iguanas on Santa Fe Island, where scientists had been studying them for the last 25 years. Therefore, the frequency and strength of environmental perturbations such as ENSO and climate change, together with the intensity of anthropogenic perturbations, will dictate the fate of this unique species.

FIGURE 3 Starving during El Niño. (A) In non-ENSO years, a lush and abundant algal growth of green, brown, and red algae occurs in the low and exposed rocky shore platforms of the western islands of the Galápagos archipelago. Photograph by Luis R. Vinueza. (B) A weakened marine iguana grazing on the invasive filamentous brown alga *Giffordia mitchelliae*. Photograph by Luis R. Vinueza. (C) An emaciated female marine iguana during El Niño 1997–1998. Photograph by Linda J. Cayot. (D) Dried carcass of a marine iguana that died of starvation during El Niño 1997–1998. Photograph by Luis R. Vinueza.

SEE ALSO THE FOLLOWING ARTICLES

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INTERNAL WAVES

SEE WAVES, INTERNAL

INTRODUCED SPECIES

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Introduced species are important members of many open-coast rocky-intertidal communities around the world. Also known as nonnative, nonindigenous, exotic, alien, or invasive species, introduced species are those organisms that have been transported by human action to a region in which they did not previously occur in historical time. For most regions and species, scientific records of the movement of marine organisms by humans typically date back less than 200 years, although introductions may have occurred over the past 1000 or more years. This lack of deep history may influence our understanding of the evolutionary and ecological history of many rocky shores.

VECTORS

Multiple human-mediated transport vectors have been available to move rocky-shore species across and between oceans. An early vector was the movement of intertidal rocks for ships' ballast. A wide variety of animals and plants (such as seaweeds, snails, mussels, barnacles, other crustaceans, mites, and insects) were transported for centuries in the damp holds of sailing vessels on and among ballast rocks. Open-coast rocky-shore organisms also colonize the buoys, floats, pilings, seawalls, and jetties of marine ports and harbors, and thus find themselves adjacent to ocean-going vessels, whose hulls they may colonize as fouling organisms or into whose ballast water systems they may be entrained. Edible rocky-shore animals and plants (such as snails, mussels, and seaweeds) have also been moved intentionally by people. These mechanisms, and others, have provided ample opportunity for the larvae, juveniles, and adults of many taxa to be successfully translocated around the world.

ECOLOGY OF INVADED SHORES

Studies in the Northeast Atlantic, South Africa, South America, and the Northwest Pacific provide experimental evidence for the role of invasions in rocky-shore communities. Additional observations elsewhere in the world further suggest the global nature of the impact of invasions on rocky coastlines.

Northeast Atlantic: The Canadian Maritimes and New England

The region from Nova Scotia to Long Island Sound represents one of the best-studied shores in terms of introduced species. Here scientific records of the larger and more conspicuous species date back to the early 1800s; the efforts of seashell collectors contributed importantly to our early knowledge of this coastline as well. These shores were only deglaciated in the past 10,000 years: Natural recolonization in this rigorous continental climate resulted in a low-diversity biota that greeted the species that began to arrive on and in ships.

The periwinkle snail *Littorina littorea*, well known on European shores, was first found at Halifax, Nova Scotia, in 1854, and from there (in one of the best documented invasion scenarios in the sea) spread south to New Jersey in just 30 years; its earlier history in the Gulf of St. Lawrence remains uncertain. *L. littorea* is one of the largest, most abundant, and most important consumers on all but the most exposed rocky shores of eastern Canada and New England. In the winter, *L. littorea* moves down shore, partially relieving the intertidal of predation pressure and permitting the development of extensive mats of ephemeral filamentous and leafy green and red algae on boulder tops. In the spring, vast numbers of *L. littorea* return to the middle and upper shore and reduce these winter algal populations to nearly zero percent cover. At times, algal patches a meter or more in diameter may be surrounded by hundreds of nibbling

FIGURE 2 Photograph of uplifted marine terraces cut by wave action during sea level standstills near San Onofre in southern California. Copyright © 2002–2006 Kenneth and Gabrielle Adelman, California Coastal Records Project, http://www.Californiacoastline.org.

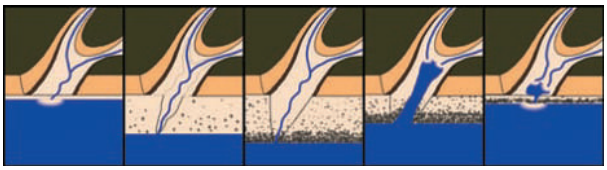

FIGURE 3 Schematic of geological transition between rocky and sandy dominated shorelines, driven by variability in sea level. Panels from left to right: (A) high-sea-level standstill; (B) regressing sea; (C) low-sea-level standstill; (D) transgressing sea; (E) beginning of high-sea-level standstill. Dark stippling represents the distribution of cobble boulders; light shading represents the distribution of sand. Reprinted with permission from Graham *et al.* (2003).

the coastline, increasing the velocity of runoff waters. The result is an increase in grain size and quantity of sediment that can be entrained in the runoff and deposited downstream. As streams travel from catchments to the sea, such erosion processes work to carve out deep coastal valleys, with coarse sediments (predominantly cobbles and boulders) transported out of the valleys and deposited along the coastline. Given a low-sea-level standstill, the cobbles begin to be distributed laterally via wave action, and the coastline takes on the general appearance of a cobbled, rocky shore. During marine transgressions, rapidly rising sea level decreases the distance between the shoreline and catchments, decreasing terrestrial runoff velocities, entraining finer sediments, and depositing them at the heads of the flooding valleys. Over time, lateral movement redistributes the sand, eventually closing off the bays, which begin to fill in with sediment and form coastal lagoons and marshes. Given an extended high-sea-level standstill, deposition of fine sediments can occur directly on the shoreline and facilitate the formation of extensive beaches. Such geomorphic processes are known to occur in temperate and subtropical regions worldwide (e.g., California, Chile, South Australia, South Africa, and the Mediterranean), suggesting continuous cycling between the extent of sandy and rocky tidal shores at local to global scales, driven by Quaternary sea level changes.

SEE ALSO THE FOLLOWING ARTICLES

Beach Morphology / Coastal Geology / Tides

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SEALS AND SEA LIONS

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Sea lions and seals are common inhabitants of the intertidal. Although they feed at sea, they return to shore to breed, give birth, mate, rest, and molt. As mammals they belong to the order Carnivora, which is divided into two suborders, Fissipedia and Pinnipedia. The suborder Fissipedia refers to members of the order Carnivora with normal feet, such as dogs, cats, weasels, raccoons, and bears. The suborder Pinnipedia (Latin for "fin-footed") refers to the seals, sea lions, fur seals, and walrus, all with finlike feet (Fig. 1). The Pinnipedia are further separated into three families. The sea lions and fur seals, also known as the eared seals, are in the family Otariidae, the true or

FIGURE 1 Male (left) and female (right) sea lions, seals, and fur seals. Along the left are (A) male California sea lion, (B) male northern elephant seal, and (C) a male Galápagos fur seal. All males in these pictures are on territories (A, C) or defending a harem (B). Along the right are (A) Australian sea lion mother and pup, (B) a northern elephant seal female and pup, and (C) Galápagos fur seal mother and pup. Photographs by the author.

earless seals are in the family Phocidae, and the walruses are in the family Odobenidae.

SEA LIONS AND FUR SEALS

Otariids are called eared seals because of the presence of external ear flaps (pinnae) (Figs. 1, 2). Sea lions and fur seals swim with their front or pectoral flippers. They can rotate their rear flippers forward and scratch like a dog, and they can walk well on land using all four flippers and are often seen considerable distance away from the water (Fig. 2). They can also climb on top of small islands. The primary difference between fur seals and sea lions is that fur seals rely almost entirely on their fur for insulation against the cold, whereas true seals and sea lions rely on blubber. Blubber serves both as insulation and as an energy store. Fur seals have a relatively pointed snout, whereas sea lions have a broader, blunter nose (Fig. 1). Sea lions are larger than fur seals. Sea lions and fur seals do not naturally occur along the east coast of the United States or in the North Atlantic Ocean, but they are quite common along the west coast of the United States and through much of the Pacific Ocean and oceans of the Southern Hemisphere. Sea lions are the most common pinnipeds seen in oceanariums and marine parks, because they are very food-motivated and therefore easy to train. The circus "seal" is usually a sea lion, because sea lions and fur seals are more acrobatic and agile on land than true seals are. They also make a barking sound. There are 17 species of Otariidae, including six extant sea lion species, one extinct sea lion species, and 10 fur seal species. The largest eared seal is the Steller sea lion, in which males can be up to 3.25 meters long and weigh 1120 kilograms. The smallest eared seal is the Galápagos fur seal (Fig. 1), of which males typically are 1.5 meters long and weigh 64 kilograms, while females are 1.2 meters long and weigh 27 kilograms.

FIGURE 2 A juvenile California sea lion shown scratching with its hind flipper, a behavior that only fur seals and sea lions can accomplish. Also notice the prominent external ears, a trait also unique to fur seals and sea lions. Photograph by the author.

TRUE OR EARLESS SEALS

Phocidae, also known as the true or earless seals, lack external ears and cannot rotate their hindlimbs forward, resulting in a clumsy undulating movement on land (Fig. 1). They can scratch only with their front flippers and are not able to move as well on land as sea lions or fur seals are. True seals use their hind flippers to swim, using a side-to-side motion, and are better divers than sea lions or fur seals. Phocid or true seals include 19 extant species and one extinct species. The largest seal is the southern elephant seal, which lives

in waters of the Southern Ocean between Antarctica and South America, South Africa and Australia. The male may grow to be 5 meters long and may weigh up to 3600 kilograms. This seal ranks second in size only to whales among all sea mammals. The smallest seal is the ringed seal of the Arctic. It is approximately 1.4 meters long and weighs up to 91 kilograms.

ROOKERIES

Rookeries are the areas where seals and sea lions congregate to breed, molt, give birth, and haul out to rest (Fig 3). Sea lion and fur seal rookeries are only located on land, but the rookeries of true seals can be on land, on islets (rocky outcrops), or on ice. Rookeries can vary in size from a single harbor seal on a rock to the extensive beach or cobble areas of the Pribilof Islands, where over 150,000 Northern fur seals may be seen. The densest rookeries are located at higher latitudes, where it is colder. At lower latitudes, where it is warmer, seals and sea lions remain in or near the intertidal so that they can cool off in the water.

FIGURE 3 A rookery of California sea lion females on San Nicolas Island, California. Photograph by the author

BREEDING BEHAVIOR

Seals and sea lions give birth to a single highly developed, or precocial, pup. They are born with their eyes open and can vocalize and walk within minutes of birth. Incredibly, harbor seal pups can swim within 20 minutes of birth. Males do not provide any care to the pup, and twins are exceptionally rare. Phocid mothers typically remain on or near the rookery continuously from the birth of their pup until it is weaned. Body reserves stored prior to parturition fuel the female's metabolic needs and are utilized for milk production. Although some phocids—most notably harbor, ringed *(Phoca hispida)*, and Weddell seals—feed during lactation, most of the maternal investment is derived from body stores. Weaning is abrupt and occurs after a minimum of 4 days of nursing (hooded seal, *Cystophora cristata*) to a maximum of 7 weeks in Weddell seals and Hawaiian monk seals. In some species such as northern elephant seals, the pup remains on or near the rookery, not drinking or eating for months after weaning. In other species such as harp or hooded seals, the pups undergo a prolonged migration lasting weeks to months.

In contrast, otariid mothers stay with their pups only the first week or so after parturition and then periodically go to sea to feed, returning to suckle their pup on the rookery. Feeding trips vary from 1 to 14 days, depending on the species, and shore visits to the pup, which has been fasting, last 1 to 3 days. The mother finds her pup out of the hundreds on the crowded rookery by calling for her pup. When the pup hears its mother call, it begins to call back. Each mother-and-pup pair have a unique call, and the mother responds only to her pup's call. Once together, the mother smells the pup to ensure that it is hers. The pups are weaned from a minimum of 4 months in the subpolar fur seals (Antarctic, *Arctocephalus gazella*, and northern, *Callorhinus ursinus*) to up to 3 years in the equatorial Galápagos fur seal *(A. galapagoensis)*. The remaining otariids are temperate. In these species, pups are usually weaned within a year of birth, although weaning age can vary both within and between species as a function of seasonal and site-specific variations in environmental conditions. Walruses can feed their offspring for up to 3 years, both while on shore and in the water.

LAND BREEDING

Extreme polygyny (one male breeds with many females) is characteristic of most land-breeding pinnipeds. Of the 21 species of land-breeding pinnipeds, 18 are highly polygynous and sexually dimorphic (Fig. 1). This includes all of the sea lions and fur seals; both species of elephant seal, *Mirounga*; and the gray seal, *Halichoerus grypus*. The remaining three species of land-breeding seals, two species of monk seals, *Monachus*, and harbor seals, *Phoca vitulina*, mate in the water near land and exhibit lesser degrees of polygyny. In general, land-breeding pinnipeds aggregate on beaches, rocks, or flat areas on islands. These island aggregations provide several potential advantages, including parturition sites for rearing pups, lack of terrestrial predators, and, for the lactating otariids, proximity to food resources. When females aggregate, males have an easier time controlling access to them, and therefore a single male can mate with many females. It is easier for males to control access to females on land, and in this situation large body size is favored. Large body size confers advantage in fighting as well as a greater fasting ability that allows males to hold onto

their territories longer. Typically the largest, most experienced males find a mate, and in some species, such as elephant seals, the competition for mates is so fierce that only one in ten males successfully breeds. The rank of males is established early in the breeding season, when males fight to establish dominance or establish at territory. Males use their long canine teeth in these battles; although the battles are often bloody, the damage is usually minimal. In elephant seals, the male's nose signifies his age and experience, where a large nose indicates an older, more experienced male. The long nose of the elephant seal serves as both a visual and acoustic indicator of the male's status, just as the number of points on the antler of a male deer indicates his age and status. The large nose also acts as a reverberation chamber and gives their vocalizations a deep bass quality that carries well in the high background noise and crashing waves of a seal rookery.

In species that compete for females in the water, males are comparatively smaller than in those species that breed on land. This is because agility is more important than size in competing for mates underwater. It is also possible for the male to leave on short foraging trips and then return to the breeding area.

ICE BREEDING

Of the 13 species of pinnipeds that breed on ice, 11 exhibit slight polygyny or serial monogamy. Females that breed on pack ice have access to vast areas of breeding substrate, but some species clump loosely. Females tend to give birth during the short period of time when the ice is most stable and come into estrus synchronously upon weaning. This synchrony, together with the degree of spatial separation, limits the ability of males to mate with many females. The rapid growth rate of seal pups and the short period that the mother needs to stay with them until they are weaned enable them to rear their young on ice.

MOLTING

All seals and sea lions undergo an annual molt, in which they shed their hair over a period of several weeks. During the molt, seals and sea lions spend more time on shore, allowing greater blood flow to their skin. Some species, such as elephant seals, remain on shore until the molt is completed. Elephant seals undergo an "explosive" molt in which they shed the skin and hair together in large pieces (Fig. 4). In contrast, fur seals do not need to haul out to molt, because they shed a few hairs at a time, so that they maintain the insulating quality of their fur.

FIGURE 4 A molting male northern elephant seal. Notice how the skin comes off in large sheets. Also notice the lack of external ears. Photograph by the author.

SENSES

Seals have very large eyes, which enable them to feed at night or in deep water where there is little light. Large eyes function just like a camera lens; the larger the lens aperture, the greater its light-gathering ability. Most seals can see well underwater, but on land they are nearsighted. True seals have better hearing underwater than sea lions and fur seals do. The whiskers on their head are very sensitive and are probably important in finding and catching prey.

DIVING OR FORAGING BEHAVIOR

Seals and sea lions have specialized sharp-pointed teeth that allow them to grasp their slippery prey. However, they cannot chew their food, because their teeth lack flat surfaces, so they either grasp and tear their prey or swallow it whole. True or earless seals are exceptional divers and are capable of deeper, longer dives than sea lions and fur seals are. These differences reflect use of different habitats. Sea lions and fur seals feed on prey nearer the surface, while seals feed on more sedentary bottom or deeper prey. The ability of true seals to dive deeper than sea lions and fur seals is related to their ability to stay submerged longer, since the deeper an animal dives, the farther it must travel. True seals can dive longer because they can store more oxygen in their muscle and blood than sea lions or fur seals can. Seals can store three times as much oxygen in their body as can humans, whereas sea lions and fur seals can store only twice as much oxygen as humans. Northern and southern elephant seals are not only the deepest-diving pinnipeds; they are among the deepest-diving mammals. Only sperm and beaked whales can dive deeper or longer. Northern elephant seals dive continuously, day and night, for periods at sea lasting

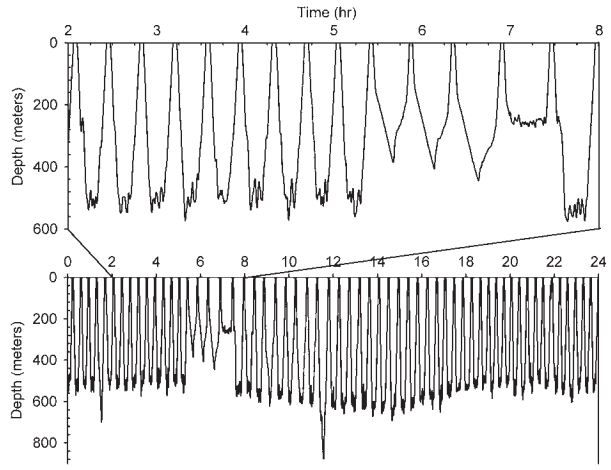

FIGURE 5 A dive record from a northern elephant seal female foraging across the North Pacific Ocean. The bottom record is a 24-hour period, with the image above a 4-hour segment of the same record. Notice the continuous diving pattern and the considerable depth to which this animal dove.

2 to 8 months (Fig. 5). They spend 90% of the time at sea submerged, average 20 minutes per dive (with maximum dive durations of over 1.5 hours) followed by less than 3 minutes at the surface between dives, and routinely diving to depths of 300 to 600 meters, with dives occasionally exceeding 1600 meters! Males travel from California to foraging areas along the continental slope from the state of Washington north to the upper reaches of the Gulf of Alaska to the eastern Aleutian Islands (Fig. 6). Female elephant seals, on the other hand, disperse widely across the northeastern Pacific, some even going as far as the international date line (180°W), in the range 44–52°N.

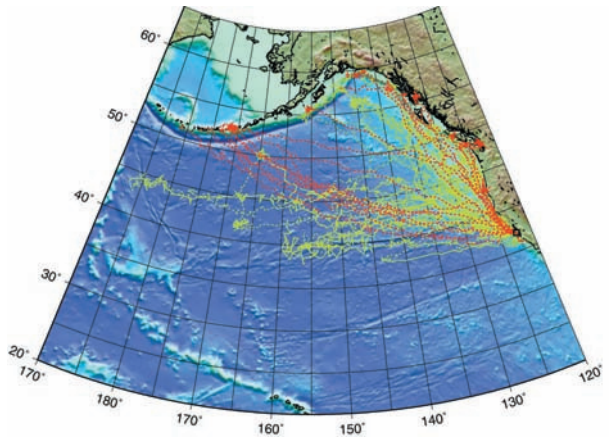

FIGURE 6 Foraging range of northern elephant seals across the North Pacific Ocean. The tracks in yellow represent female elephant seals, while the red tracks represent males. Animals were tagged at the Año Nuevo Rookery near Monterey Bay, California.

INTERACTIONS WITH HUMANS

Midden sites in coastal regions attest to a long tradition of humans hunting marine mammals for food and clothing. The commercial harvest of fur seals for their skins and seals for their oil was carried out from the late eighteenth century into the twentieth century and caused the depletion of many species. Many populations, such as elephant seals and fur seals, were harvested to the point of extinction. While not commercially harvested, the Caribbean monk seal is now extinct, and the Mediterranean and Hawaiian monk seals are highly endangered, with numbers well below 1000 individuals. The Hawaiian monk seal is listed as endangered under the Endangered Species Act, and both are protected by international agreements such as CITES (Convention in Trade of Endangered Species). In the United States, all marine mammals are protected by federal law under the Marine Mammal Protection Act, which makes it a federal crime to kill or harass (disturb) any marine mammal.

Seals, sea lions, and fishermen can compete for the same fish. Seals are often blamed for reductions in fish harvests that may in fact be due to overfishing by fishermen. It is also possible that fishermen are adversely affecting seal and sea lion populations by reducing the amount of fish available to them. For example, the Steller sea lion population in the North Pacific has been steadily declining. In 1985, 67,000 sea lions were counted in the Gulf of Alaska to the Aleutian Islands; twenty years later there were less than 25,000 sea lions in this same area. Sea lions can also have a negative effect on fish populations. For example, in the Ballard locks near Seattle, Washington, male California sea lions have learned that salmon are easy to catch when the fish get ready to go through fish ladders to go past the locks. The sea lions eat a significant proportion of the salmon, and the salmon population is in serious decline. Seals and sea lions are often accidentally caught in fishing nets used by fishermen. In most cases this does not cause significant harm to the seal or sea lion population. Sea lions and seals are also known to steal fish from fishing lines. This is especially common with salmon fishermen.

Continued increases in human population and development of coastal resources are further concerns for seal, sea lion, and fur seal populations. Pesticide residues from agricultural regions of the world and heavy metals from industrial waste have been found to build up in the tissues of many seals. In the 1970s high levels of DDT in the tissues of California sea lions caused massive premature pupping and death of these pups. Since the 1970s, when DDT production was stopped in California, the levels of

DDT in the environment have declined, as have the levels in the tissues of California sea lions. Few premature pups are seen on the rookeries today. Further concern comes from general habitat loss and degradation, as there is increasing use of the ocean for recreation, oil and gas development, and transportation. As human populations increase, there will be increased disturbance of seal and sea lion rookeries.

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SEA OTTERS

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Sea otters are coastal living marine mammals that typically forage on a wide range of invertebrates in lower intertidal and shallow subtidal systems. They are members of the family Mustelidae and are one of several otter species that have recently radiated from freshwater into the higher-latitude coastal oceans. Sea otters occupy rocky and sand/mud habitats across the Pacific Rim from Japan to Mexico. As keystone predators, they have important direct and indirect effects on the structure and function of coastal ecosystems.

ORGANISMAL BIOLOGY

Mammals arose on the land but have invaded the sea on various occasions over the course of their evolutionary history. Most extant marine mammals have been so greatly modified for life in the sea that they bear little superficial resemblance to their terrestrial ancestors. As the most recent of these terrestrial expatriates, sea otters (Fig. 1) provide a unique view of the modifications associated with marine living in mammals. These modifications are apparent in various aspects of the sea otter's morphology, physiology, life history, and behavior.

FIGURE 1 Sea otter. Note the dense, water-repellent fur. Photograph by Bryant Austin.

Because mammals must maintain high core body temperatures and the thermal conductivity of water is roughly 25 times greater than that of air, elevated heat loss is among the greatest challenges faced by aquatic mammals. Increased body size is one of the most evident responses to this challenge, because heat production and heat loss increase respectively with body mass and surface area, whereas surface-to-volume ratio declines exponentially with increasing body mass. Sea otters are the largest living members of the mustelid family and the smallest fully marine living mammal, very likely thus representing the minimum possible body size for long-term existence of endothermic mammals in cold oceans. Thermoregulation in sea otters is facilitated by efficient insulation (sea otters lack blubber but have the densest fur of any extant mammal), elevated metabolic rate, and careful management of behavioral time budgets for activities that differ in the relative extent of heat loss and heat gain.

Other features of the sea otter's physiology and morphology also reflect strong selection imposed by life in the sea. For example, sea otters typically have single-young pregnancies, more closely resembling the other marine mammals (with whom they share a common environment) than the mustelids and other terrestrial mammalian carnivores (their closest living relatives). Sea otters are unique among the mustelids in having highly modified flipper-like hind limbs, an apparent adaptation for aquatic locomotion. Sea otters have an enlarged lung, modified for deep diving by cartilaginous support structures in the bronchioles that prevent compression collapse at depth. Other features of the sea otter's