and needed. A healthy and diverse avifauna supported by a natural diverse prey base is indicative of a well functioning and healthy marine environment. Decreases in avian diversity are evident in regions with increased pollution levels. Nature abhors vacuum and life proliferates, but biodiversity creates the fabric of life that sustains the natural functioning of large-scale ecosystem processes. For the sake of the oceans and for our own benefit, it is essential to do everything possible to understand human-induced threats to the world's oceans and with or without that understanding to protect and preserve them.

See also

Anti-fouling Materials. Atmospheric Input of Pollutants. Chlorinated Hydrocarbons. Metal Pollution. Oil Pollution. Pollution Control. Pollution: Effects on Marine Communities. Pollution, Solids. Radioactive Wastes.

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SEALS

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Taxonomy

The seals, or Pinnipedia, are the suborder of the Carnivora that includes the Phocidae (earless or 'true' seals), Otariidae (eared seals, including fur seals and sea lions) and the Odobenidae (walrus). They are related to the bears, based on a common ancestry with terrestrial arctoid carnivores (**Figure 1**). The otariids retain more of the ancestral characteristics than the other two groups but all have a more or less aquatic lifestyle and display highly developed morphological and physiological adaptations to an aquatic existence.

The Pinnipedia are made up of 34 species and 48 species/subspecies groupings (**Table 1**). However, with the advent of new methods based on DNA analysis for examining phylogeny and also because of new methods used to track animals at sea many of these groupings are questionable. Several groups that were thought to have been different species have overlapping ranges and are likely to interbreed. It seems most probable that the southern fur seals (*Arctocephalus* sp., Table 1) are not distinct species. Conversely, some of the North Atlantic phocid pinnipeds that are classified as single species are likely to be better represented as a group of subspecies. The gray seal is a particular example in which three genetically distinct populations (NW Atlantic, NE Atlantic and Baltic) are recognized.

Distribution and Abundance

The greatest diversity and absolute abundances of pinnipeds occurs at temperate and polar latitudes (Table 1). Only three phocid seal species, the monk seals, are truly tropical species and all of these are either highly endangered or, in one case, may be extinct. Among the otariids, fur seals and sea lions extend their distributions into the tropics but their absolute abundance in these locations is low compared with the populations at higher latitudes.

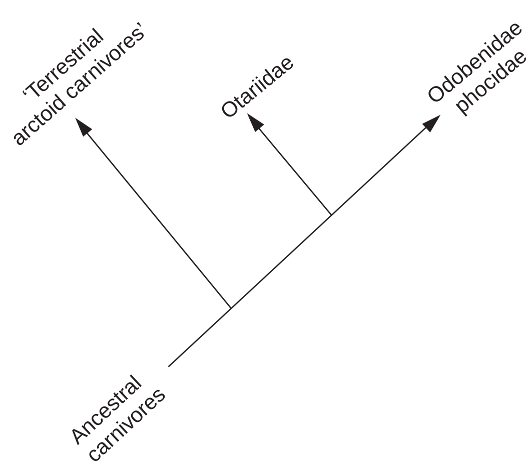

Figure 1 Pinniped phylogeny from a cladogram based on postcranial morphology. (Reproduced from Berta *et al*., 1989.)

Probably > 50% of the biomass of pinnipeds in the world is derived from one species, the crabeater seal. Some estimates of the abundance of this species have undoubtedly been exaggerated but it is nevertheless the dominant species. This is partly because its main habitat is the vast Antarctic pack ice. The ringed seal has a comparable distribution in the Arctic and it also has abundances numbered in the millions. The relative numbers of the different species are shown in Table 1.

Although the status of the populations of some species/subspecies groups is unknown, only seven (22%) groupings are in decline whereas seventeen (55%) of these groups are increasing in abundance. However, twenty-three groups (48%) are classified as being in need of some form of active conservation management. Threats to pinnipeds can be represented as: (1) *direct threats* from harvesting and international trade, incidental catch by commercial fisheries and direct killing by fishermen; (2) *intermediate threats* from episodic mass mortalities, habitat degeneration (including environmental pollution, competition for food with humans, disturbance and changes to the physical environment); (3) *longer-term threats* from climate change and reduction of genetical diversity.

Morphological and Physiological Adaptations to Aquatic Life

Morphological adaptations include the modification of limbs to form flippers for swimming, the development of a streamlined fusiform shape, the presence of insulation in the form of fur and/or a subcutaneous layer of blubber and increased visual acuity for foraging at extremely low light levels. Unlike cetaceans, an ability to echolocate has not been confirmed in pinnipeds, although some studies have purported to show that seals are capable of behavior that is consistent with echolocation abilities.

Physiological adaptations include a highly developed dive response. On submergence this involves the rapid reduction of heart rate, reduced peripheral circulation and the sequestration of large amounts of oxygen bound to myoglobin in the muscles. Pinnipeds also have high concentrations of red blood cells in the blood and changed morphology of the red blood cells themselves, which take on a 'cocked-hat' shape. The architecture of the venous system is also modified, especially amongst phocids, to allow a larger volume of blood to be stored. Included within the dive response is the ability, when at the surface between dives, to increase heart rate rapidly to clear and reprocess metabolic waste products and to re-oxygenate the tissue in preparation for the next dive.

Thermal Constraints

Perhaps the greatest single constraint on the evolution of pinnipeds as aquatic animals is the problem associated with thermoregulating in cold water that is 25 times more conductive to heat than air. Since pinnipeds are endothermic homeotherms that normally maintain a body temperature of 36–38°C, they are presented with a significant thermal challenge when they are immersed in water at or close to freezing. The observation that the greatest number and species diversity of pinnipeds is found in temperate and polar regions suggests that they have adapted well to this challenge. However, the cost associated with this seems to be that pinnipeds have retained a non-aquatic phase in their life histories. By virtue of their relatively small body size, newborn pinnipeds cannot survive for long in cold water and so they are born on land or ice and remain there until they have built up sufficient insulation to allow them to go to sea. Unlike cetaceans, pinnipeds do not appear to have solved the problem of giving birth to young with insulation already developed but many cetaceans have a much larger body size than pinnipeds (thus reducing the thermal challenge to the newborn) and many species also migrate to warmer waters to give birth. Cetaceans appear to have developed a different strategy to deal with the cold.

Pinniped Life Histories: The Constraints of Aquatic Life

An important consequence of the necessity for nonaquatic births in pinnipeds is that mothers are more or less separated from their foraging grounds by the need to occupy land or ice during the period of offspring dependency. Food abundance in the marine environment is not evenly distributed and has a degree of unpredictability in space and time. Therefore, pinniped mothers have had to trade-off the necessity to find a location to give birth which is safe from predation, since pinnipeds are vulnerable when on land, with the need to feed herself and her pup throughout the period of offspring dependency. This has apparently led to two different types of maternal behavior.

In small pinnipeds including all the fur seals, most of the sea lions and small phocids, it is not possible, by virtue of body size alone, for mothers to carry sufficient energy reserves at birth to support both her and her offspring until the offspring is able to be independent. This means that mothers must

Table 1 Species and common names, abundances, trends in abundance and conservation status for the Pinnipedia

Taxonomic classification			*Distribution*	*Abundance*[a] (*log*$_{10}$ *scale*)	*Trend in abundance*	*Conservation status*
Family Otariidae						
Subfamily Otariinae						
Eumetopias jubatus		Steller sea lion	North Pacific	***	Declining	Threatened
Zalophus californianus subspecies:	*californianus*	California sea lion	Western USA	****	Increasing	No threat
	wollebaeki	Galapagos sea lion	Galapagos Is.	***	Stable (?)	Rare
	japonicus	Japanese sea lion	Japan	*	Unknown	Possibly extinct
Ontaria byronia		Southern sea lion	South America	***	Declining	Threatened
Neophoca cinerea		Australian sea lion	Southern Australia	**	Stable	Rare
Phocarctos hookeri		Hooker's sea lion	Southern New Zealand	**	Declining	Endangered
Subfamily Arctocephalinae						
Arctocephalus townsendi		Guadalupe fur seal	Guadalupe Is.	**	Increasing	Rare
Arctocephalus galapagoensis		Galapagos fur seal	Galapagos Is.	***	Stable (?)	Rare
Arctocephalus philipii		Juan Fernandez fur seal	Juan Fernandez Is.	**	Increasing	Rare
Arctocephalus australis subspecies:	*australis*	Falkland fur seal	Falkland Is.	***	Increasing (?)	Locally vulnerable
	gracilis	South American fur seal	South America	****	Increasing	No threat
Arctocephalus tropicalis		Sub-Antarctic fur seal	Sub-Antarctic	****	Increasing	No threat
Arctocephalus gazella		Antarctic fur seal	Antarctic	*****	Increasing	No threat
Arctocephalus pusillus subspecies:	*pusillus*	South African fur seal	Southern Africa	*****	Increasing	No threat
	doriferus	Australian fur seal	Southern Australia	***	Increasing	No threat
Arctocephalus forsteri		New Zealand fur seal	Australia and New Zealand	***	Increasing	No threat
Callorhinus ursinus		Northern fur seal	North Pacific	*****	Declining (?)	No threat
Family Odobenidae						
Subfamily Odobenidae						
Odobenus rosmarus subspecies:	*rosmarus*	Atlantic walrus	Arctic	****	Unknown	Commercially threatened
	divergens	Pacific walrus	Arctic	**	Unknown	Commercially threatened
Family Phocidae						
Subfamily Phocinae						
Halichoerus grypus		Grey seal	North Atlantic	****	Increasing	No threat
Phoca vitulina subspecies:	*vitulina*	Eastern Atlantic harbor seal	NE Atlantic	***	Increasing	No threat
	concolor	Western Atlantic harbor seal	NW Atlantic	***	Increasing	No threat
	stejnegeri	Western Pacific harbor seal	NW Pacific	**	Unknown	Rare
	richardsi	Eastern Pacific harbor seal	NE Pacific	****	Increasing	No threat
	mellonae	Ungava seal	Quebec, Canada	*	Unknown	Rare

Table 1 *Continued*

Taxonomic classification			*Distribution*	*Abundance*[a] (*log_{10} scale*)	*Trend in abundance*	*Conservation status*
Phoca largha		Spotted seal	Bering Sea	****	Unknown	No threat
Phoca hispida subspecies:	*hispida*	Arctic ringed seal	Arctic	*****	Unknown	No threat
	ochotensis	Okhotsk sea ringed seal	Sea of Okhtosk	****	Unknown	No threat
	botnica	Baltic ringed seal	Baltic Sea	**	Increasing (?)	Threatened
	Saimensis	Saimaa seal	Lake Saimaa, Finland	*	Unknown	Endangered
	ladogensis	Ladoga seal	Lake Ladoga, Russia	***	Stable – increasing	Vulnerable
Phoca caspica		Caspian seal	Caspian Sea	****	Stable	Vulnerable
Phoca sibirica		Baikal seal	Lake Baikal	***	Unknown	Vulnerable
Phoca groenlandica		Harp seal	NW Atlantic & Arctic	*****	Increasing	No threat
Phoca fasciata		Ribbon seal	Bering Sea & Arctic	****	Unknown	No threat
Cystophora cristata		Hooded seal	N Atlantic & Arctic	****	Unknown	No threat
Erignathus barbatus subspecies:	*barbatus*	Atlantic bearded seal	Arctic	****	Unknown	No threat
	nauticus	Pacific bearded seal	Arctic	****	Unknown	No threat
Subfamily Monachinae						
Monachus monachus		Mediterranean monk seal	Mediterranean	*	Declining	Endangered
Monachus tropicalis		West Indian monk seal	Caribbean Sea	*	Unknown	Possibly extinct
Monachus schauinslandi		Hawaiian monk seal	Hawaiian Islands	*	Declining	Endangered
Leptonychotes weddellii		Weddell seal	Artarctica	****	Stable	No threat
Ommatophoca rossii		Ross seal	Antarctica	***	Unknown	No threat
Lobodon carcinophagus		Crabeater seal	Antarctica	******	Stable	No threat
Hydrurga leptonyx		Leopard seal	Antarctica	***	Stable	No threat
Mirounga leonina		Southern elephant seal	Sub-Antarctic	****	Declining (?)	No threat
Mirounga angustirostris		Northern elephant seal	Sub-Antarctic	****	Increasing	No threat

[a]The number of asterisks denote the range in the size of the world populations: *, 0–1000; **, 1000–10 000; ***, 10 000–100 000; ****, 100 000–1 000 000; *****, 1 000 000–10 000 000; ******, 10 000 000–100 000 000.

supplement their energy reserves by feeding during lactation. In the case of the smallest pinnipeds, the fur seals, mothers rely almost entirely on the energy from foraging and have very few reserves. Therefore, these small pinnipeds are restricted to breeding at sites which are close enough to food for the mothers to be able to make foraging trips on time scales that are less than the time it would take their pup to starve. Consequently, lactation in these small pinnipeds tends to be extended over several months and, in a few cases, can last over a year.

In contrast, pinnipeds of large body size (the transition in this case between large and small appears to occur at a maternal body mass of about 100 kg) are able to carry sufficient energy reserves to allow mothers to feed both themselves and their offspring while they are ashore. In these species, the tendency is for mothers to make only a single visit ashore and for her not to feed during lactation. As a result, these mothers have a short lactation and, in the case of the hooded seals, this is reduced to only four days, but 15–30 days is more normal.

These types of behaviors, which stem directly from the combined physical restrictions of thermoregulation in newborn pups and maternal body size, have had two further important consequences. The first of these is that larger pinnipeds are better able to exploit food resources at greater distance from the birth site and they have been shown to range over whole ocean basins in search of food. This is a necessary consequence of their larger size because, in contrast to small pinnipeds, they must exploit richer food sources because of their greater absolute food requirement. Since richer food sources are also rarer food sources, the large pinnipeds have fewer options as to where they can forage profitably. Thus, with some exceptions the large pinnipeds occupy much larger ranges than the small pinnipeds.

By mammalian standards all pinnipeds are of large body size. Even though pups are well developed at birth, this means that it takes several years for most pinnipeds to grow to a body size large enough for them to become sexually mature. The minimum duration to reach sexual maturity is about 3 years and the maximum, in species such as the grey seal, is 5–6 years. Thereafter, they only produce a single pup each year and the individuals of most species will fail to produce a pup about one year in four. However, since females may live for 20 to >40 years, they are relatively long-lived animals.

Mating Systems

The second consequence of the physical restriction that thermoregulation in newborn pups places on pinnipeds is the mating system. This feature of pinniped biology has been the subject of intensive investigations, largely because it is much the most dramatic and obvious part of pinniped life-histories. There has been much speculation as to why pinnipeds should mostly have developed mating behavior involving dense aggregations and apparent extreme polygyny but it is likely to be a consequence of the necessity for mothers to give birth out of the water. Restrictions in the availability of appropriate breeding habitat (defined in terms of both its proximity to food and its protection from predation), together with reduced risk of predation that individuals have when they are in groups, probably combined to increase the fitness of those mothers that had a tendency to give birth in groups. It is also considerably more efficient, in energetic terms, to have to return to land only once during each reproductive cycle. Females have made use of an ancestral characteristic involving the existence of a postpartum estrus at which most females are mated and become pregnant. Without this, females would have been required to seek a mate at a time when, for many species, the population would be highly dispersed over a wide area while foraging. This means that appropriate mates would have been more difficult to find than at a time of year when the population is highly aggregated.

Males that are present when there is the greatest chance of mating will be most likely to gain greatest genetical fitness. Thus, in almost all pinnipeds, a competitive mating system has developed around the rookeries of females with their pups. Moreover, this has led to selection for male morphological and behavioral characteristics that confer greater ability to dominate matings. The male hooded seal has developed a deep red septum between his nostrils that can be blown out like a balloon as a display organ; male elephant seals have developed loud vocalizations which, together with their enlarged rostrum, make a formidable display; male harbor and Weddell seals have complex and loud underwater vocalizations that are almost certainly part of a competitive mating system; and in most species there is a marked sexual dimorphism of body size in which males can be six to eight times the mass of females. This sexual dimorphism in mass may serve a double function: increased mass leads to increased muscle power and the ability to fight off rivals for matings and increased mass also confers increased staying power allowing individual males to fast while they are on the breeding grounds and maintaining their presence amongst receptive females for as long as possible. However, this larger body mass also has a cost in that, because of their greater absolute energy expenditure, the larger males must find richer food sources to be able to feed profitably and recover their condition between breeding seasons. A consequence of this is that males have lower survival rates than the smaller females.

An exception to much of this is found in many of the seals that breed on ice. In these cases, mothers often have the option to give birth in close proximity to food and, at least in the Antarctic where there are no polar bears, they are relatively safe from predation. There is no sexual dimorphism in the crabeater seal, a species which gives birth in the Antarctic pack ice without any detectable aggregation of mothers. In the Arctic, the harp seal is the rough ecological equivalent of the crabeater seal and in this species there are large aggregations, known in Canada as whelping patches. It would appear that one of the main contrasts between these species is that harp seals are exposed to polar bear predation whereas crabeater seals are not. In neither case is there marked sexual dimorphism of body size despite evidence for competitive mating. As in the case of the Weddell and harbor seals, which have only small sexual dimorphism of body size, these species mainly mate in the water rather than on land. Therefore, it may be that large body size in male pinnipeds is mainly a characteristic that is an advantage to those that have terrestrial mating.

Diet

Seals are mostly fish-eating although the majority of species have a broad diet that also includes squid, molluscs, crustaceans, polychaete worms and, in certain cases other vertebrates including seabirds and other seals. Even those that prey mainly on fish take a broad range of species although there is a tendency for specialization on oil-bearing species such as herring, capelin, sand eels/lance, sardines and anchovies. This is because these species have a high energy content and they are often in shoals so that they may be an energetically more profitable form of prey than many other species.

Perhaps the most specialized pinniped in terms of diet is the walrus which forages mainly on benthic molluscs, crustaceans and polychaetes. Its dentition is adapted to crushing the shells of molluscs and their tusks are used to stir up the sediment on the sea bed to disturb the prey within. In the Arctic, bearded seals have a similar feeding habit and several other species feed regularly on benthic invertebrates. Among gray seals there is evidence that some individuals specialize in different types of prey. For most species, feeding occurs mainly within the water column and may be associated with particular oceanic features, such as fronts or upwellings of deep water that are likely to contain higher concentrations of prey. Seals may migrate distances of up to several thousand kilometers to find these relatively rich veins of food.

The crabeater seal feeds almost entirely on Antarctic krill (a small shrimp-like crustacean) that it gathers mainly from the underside of ice floes where the krill themselves feed on the single-celled algae that grow within the brine channels within the ice. Antarctic fur seals also feed on krill to the north of the Antarctic pack ice edge and many of the Antarctic seals rely to varying degrees on krill as a source of food. In fact Antarctic krill probably sustain more than half of the world's biomass of seals and also sustain a substantial proportion of the biomass of the world's sea birds and whales. The dentition of crabeater seals is modified to help strain these small shrimps from the water.

Many species of seals will, on occasions, eat sea birds. Male sea lions of several species have been recorded as snacking on sea birds and male Antarctic fur seals regularly feed on penguins. However, the most specialized predator of sea birds and other seals is the leopard seal. This powerful predator is found mainly in the Antarctic pack ice and is credited with being the most significant cause of death amongst juvenile crabeater seals even though few cases of direct predation have been observed. Individual leopard seals may specialize on specific types of prey because the same individuals have been observed preying on Antarctic fur seals at one location in successive years and one of these has been seen at two locations over 1000 km apart where young Antarctic fur seals can be found.

Diving for Food

The development over the past decade of microelectronic instruments for measuring the behavior of pinnipeds has put the adaptations for aquatic life in these animals into a new perspective. Some pinnipeds are capable of very long and very deep dives in search of their prey. The result of this diving ability is that pinnipeds are able to exploit on a regular basis any food that is in the upper 500 m of the water column. In general, larger body size confers greater diving ability mainly because the rate at which animals of large body size use their oxygen store is less than that for small individuals. Ultimately, it is the amount of oxygen carried in the tissues that determines how long a pinniped can stay submerged and time submerged limits the depth to which pinnipeds can dive. Consequently the largest pinnipeds, elephant seals, dive longer and deeper than any others.

On average adult elephant seals dive to what seems to us as a punishing schedule. Average dive durations can exceed 30 minutes with about 2 minutes between dives and elephant seals maintain this pattern of diving for months on end, only stopping every few days to 'rest' at the surface for a slightly longer interval than normal but usually much less than an hour. Technically, elephant seals are more correctly seen as surfacers rather than divers.

Occasionally elephant seals dive to depths of 1500 m and dives can last up to 2 hours with no apparent effect on the time spent at the surface between dives. It is still a mystery to physiologists how elephant seals, and many other species including hooded seals and Weddell seals, manage to have such extended dives. Many physiologists believe that free-ranging seals like elephant seals are able to reduce their metabolic rate while submerged to such an extent that they can conserve precious oxygen stores and they can then rely on aerobic metabolism throughout the dives. This strategy may allow these animals to access food resources that the majority of air-breathing animals cannot reach. As described above, this is likely to be of critical importance to these large-bodied animals because of their need to find rich food sources.

See also

Krill. Marine Mammal Evolution and Taxonomy. Polar Ecosystems.

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SEAMOUNTS AND OFF-RIDGE VOLCANISM

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Summary

There are three major types of off-axis volcanism forming the abundant seamounts, islands, ridges, plateaus, and other volcanic landforms in the world's oceans. (1) The generally small seamounts that form near the axes of medium and fast-spreading ridges but less so at slow-spreading ones. These are most likely a result of mantle upwelling and melting in a wide zone below mid-ocean ridges, although off-axis 'mini plumes' cannot be ruled out. (2) The huge oceanic plateaus and linear volcanic chains that form from starting plumes and trailing plume conduits respectively. It is widely believed that mantle plumes originate in the lower mantle, perhaps near the core–mantle boundary. (3) Off-ridge volcanism that is not due to plumes, but which chemically and isotopically resembles plume volcanism. Emerging data indicate that much off-axis volcanism previously ascribed to mantle plumes is not plume-related. Several distinct types of activity seem to be the result of various forms of intraplate mantle upwelling, or pervasively available asthenosphere melt rising in conduits opened by intraplate stresses, or both. Seamounts, ridges, and plateaus produced by off-axis volcanism play important roles in ocean circulation, as biological habitats, and in biogeochemical cycles involving the ocean crust.

Introduction

The seafloor that is produced at mid-ocean ridges is ideally quite uniform, and except for the regular abyssal hills and the rugged linear traces of ridge offsets, it is essentially featureless. In strong contrast, real ocean crust in the main ocean basins and the marginal basins and seas is decorated with volcanic islands, seamounts, ridges, and platforms that range in size from tiny lava piles only tens of meters high to vast volcanic outpourings covering huge areas of seafloor. Volcanoes that are active close to mid-ocean ridges are related to the ridge processes that build the ocean crust, whereas those erupting farther away, so-called off-axis, off-ridge, or intraplate volcanic features, are the result of processes that are unrelated to mid-ocean ridges. The largest oceanic volcanic features, oceanic plateaus and linear chains of islands and seamounts (known