

mammal tissues. These data indicate that marine mammals occupy a wide range of trophic levels beginning with dugong and manatees (trophic level 2.0), and followed by baleen whales (3.35), sea otters (3.45), seals (3.95), sea lions and fur seals (4.03), toothed whales (4.23), and polar bears (4.80).

With the aid of ecosystem models and other quantitative analyses, the degree of competition can be quantified, and the consequences of changing predator–prey numbers can be predicted. These analyses show that many species of fish are major competitors of marine mammals. A number of field studies have also shown negative effects of reduced prey abundance on body size and survival of marine mammals. However, there are fewer examples of marine mammal populations affecting their prey due perhaps to the difficulty of monitoring such interactions, or to the complexity of most marine mammal food webs.

See also

Baleen Whales. Bioacoustics. Fishery Management. Large Marine Ecosystems. Marine Mammal Diving Physiology. Marine Mammal Evolution and Taxonomy. Marine Mammals, History of Exploitation. Marine Mammal Migrations and Movement Patterns. Marine Mammal Overview. Marine Mammal Social Organization and Communication. Network Analysis of Food Webs. Seals. Sea Otters. Sirenians. Sperm Whales and Beaked Whales.

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MARINE MAMMALS, HISTORY OF EXPLOITATION

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Introduction

Products obtained from marine mammals – defined to include the cetaceans (whales, dolphins, and porpoises), pinnipeds (seals, sea lions, and walrus), sirenians (manatees, dugong, and sea cow), sea otter, and polar bear – have contributed in many ways to human survival and development. Maritime communities, from the tropics to the poles, have depended on these animals for food, oil, leather, ivory, bone, baleen, and other materials. Some marine mammal products have had strategic value to

nations. For example, for several centuries, streets and homes in much of the western world were illuminated with sperm oil candles and whale oil lanterns. Delicate machinery and precision instruments were lubricated with the head oil of toothed whales. Whale oil was an important source of glycerine during World War I and a key ingredient in margarine during and after World War II.

Other uses of marine mammal products have been more frivolous. Seal penises are sold as aphrodisiacs; narwhal (*Monodon monoceros*) and walrus (*Odobenus rosmarus*) tusks and polar bear (*Ursus maritimus*) hides are displayed as ‘trophies’ in homes and offices (Figure 1). Spermaceti and ambergris, both obtained from sperm whales (*Physeter macrocephalus*), were highly valued by the perfume and cosmetics industries. Baleen used to be a stiffener for ladies’ hoop skirts and undergarments.



Figure 1 A male narwhal with a 2 m tusk killed in the eastern Canadian Arctic, 1975. The tusk ivory of narwhals and walrus continues to provide an important incentive for hunting them, although both species are also valued as food by native people. Most narwhal tusks are sold and exported, intact, as novelties or trophies. Photo by RR Reeves.

And, of course, the pelts of fur seals and sea otters have always been in great demand in luxury fur markets.

In general, the history of marine mammal exploitation is marked by overuse and abuse, with most wild populations having been severely overhunted. Some species and populations were extirpated or brought to the brink of extinction. Many others have been reduced and fragmented as a result of too much exploitation. It was not until well into the twentieth century that any serious restrictions were imposed on the sealing and whaling industries for the sake of conservation.

Cetaceans

Small Cetaceans (Dolphins, Porpoises, and the Smaller Toothed Whales)

Harpoon hunting of small cetaceans has occurred virtually all around the world, but mainly in coastal and shelf waters (Figure 2). It continues most notably in Japan, where 15 000–20 000 Dall's porpoises (*Phocoenoides dalli*) and at least several hundred dolphins, short-finned pilot whales (*Globicephala macrorhynchus*), and false killer whales (*Pseudorca crassidens*) are taken annually with hand harpoons, and about 150 additional pilot whales and Baird's beaked whales (*Berardius bairdii*) are taken each year with mounted harpoon guns. The meat of small cetaceans is highly valued in Japan. Eskimos in Greenland, Canada, and Alaska (USA) continue their long tradition of hunting white whales (*Delphinapterus leucas*) and narwhals. Although they formerly used kayaks, hand



Figure 2 Whale hunters from Barrouallie, St Vincent, Lesser Antilles, at sea in pursuit of short-finned pilot whales (foreground) in the 1960s. The harpoon mounted on the bow of the sailboat was fired with a shotgun. Killed whales were cut into manageable pieces alongside the boat, and these pieces were brought on board to be taken ashore. On the beach, the pieces were cut in strips, hung on bamboo racks to dry, and sold to buyers from Kingstown. In 1968, the average pilot whale was worth about \$40 US. Photo by David K Caldwell.

harpoons, and lances, today most of the hunting involves outboard-powered boats and high-powered rifles. Only in north-western Greenland are the traditional hunting techniques still used to any extent. Altogether, several thousand white whales and narwhals are taken each year. In addition, Greenlanders kill close to 2000 harbor porpoises (*Phocoena phocoena*) with rifles (Figure 3). The skin of small cetaceans is a delicacy in the Arctic. When saved, the meat and viscera are either eaten by people or fed to dogs.

A large commercial hunt for short-beaked common dolphins (*Delphinus delphis*), bottlenose dolphins (*Tursiops truncatus*), and harbor porpoises was conducted in the Black Sea, using rifles and purse seine nets, from the nineteenth century into the late twentieth century. In the 1930s, nearly 150 000 dolphins and porpoises were taken in a single year. Although dolphin hunting was banned in the Soviet Union in 1966 and in Turkey in 1983, large kills were still being made in the Turkish sector of the Black Sea as recently as 1991. Oil and

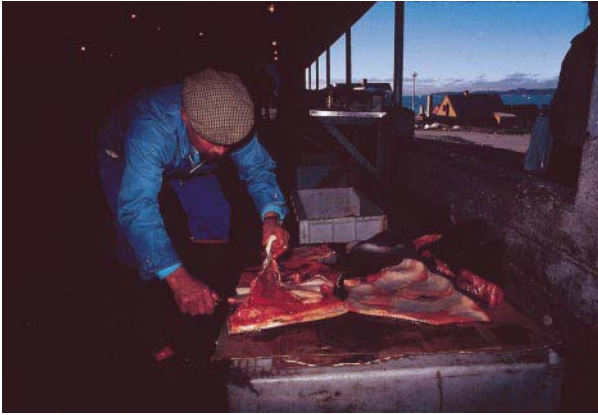


Figure 3 Meat from harbor porpoises shot in West Greenland is sold at an open-air market in Nuuk. Harbor porpoises contribute to a diverse array of wild foods consumed by the Greenlandic people, including fish, reindeer, seal, and whale. Photo by Steve Leatherwood, September 1987.

animal feed ('fish meal') were the main products, but the hunting was also prosecuted as a means of predator control. Fishermen viewed the cetaceans as serious competitors.

Some small cetaceans, particularly the pilot whales (*Globicephala* spp.), false killer whale, and melon-headed whale (*Peponocephala electra*), strand (i.e., come ashore) *en masse* in numbers ranging from tens to hundreds. This phenomenon remains unexplained but is known to occur naturally. Early coastal people would have welcomed mass strandings, as they represented windfalls of food and other useful products. It is not difficult to imagine their making the leap to a drive fishery, in which groups of animals were 'herded' toward shore, forced into shallow waters, and killed with lances or long knives. The first pilot whale drives in the Faroe Islands apparently took place at least four centuries ago, and similar drive fisheries existed elsewhere in the North Atlantic. In the Faroes, the whales have been used principally as food for humans, but in the other areas oil was a major incentive. In the post-World War II Newfoundland drive fishery, most of the catch (which reached nearly 10 000 pilot whales in 1956) was used to feed ranch mink. Drive hunting of cetaceans in the North Atlantic continues only in the Faroes, where hundreds, and in some years well over a thousand, long-finned pilot whales (*Globicephala melas*) and Atlantic white-sided dolphins (*Lagenorhynchus acutus*) are taken, and in West Greenland, where white whales and occasionally pilot whales are driven.

Drive fisheries for small cetaceans have also developed in the Solomon Islands and Japan. The Solomons example represents one of the more bizarre forms of exploitation of marine mammals.

There, fishermen in dugout canoes fan out across a wide expanse of ocean to search for schools of dolphins and small whales. Large stones are struck together underwater to produce aversive sounds and scare the animals in the desired direction. Eventually, the school is guided into an enclosed harbor where the animals are quickly dispatched. Although some of the meat is cooked and eaten, the primary purpose of the hunt is to obtain 'porpoise teeth.' Porpoise-tooth necklaces must be given to a woman's parents as 'bride price,' an essential item in marriage transactions.

Dolphin drive fisheries have existed in Japan since the late fourteenth century. Initially, sail-assisted rowing boats were used, but motor vessels were introduced in the 1920s, allowing the hunters to cover much larger areas in their search for schools of small cetaceans. In recent years, high-speed motor boats have been used to find and drive ashore striped dolphins (*Stenella coeruleoalba*), pantropical spotted dolphins (*Stenella attenuata*), bottlenose dolphins, Risso's dolphins (*Grampus griseus*), pilot whales, and a number of other species.

Long seine nets were used to catch bottlenose dolphins along the Atlantic coast of the United States starting in the late eighteenth century and continuing at Cape Hatteras, North Carolina, until the late 1920s. A line of nets was set parallel to the shore, and when a school of dolphins moved into the area between the net line and the shore, the fishermen used nets to shut off escape, then swept the dolphins onto shore. Oil was the main prize, but a supple, durable shoe leather was also made from the hides. Commercial whalers and traders in the Arctic used large seine nets to trap schools of white whales, beginning as early as the 1750s in Hudson Bay and continuing in some areas (e.g., Svalbard) until as recently as 1960. Hides, oil, and dog food were the main products of these commercial netting operations.

Large Cetaceans (Baleen Whales and the Sperm Whale)

People in the Arctic were hunting bowhead whales (*Balaena mysticetus*) as long ago as the middle of the first millennium AD, and western Europeans were taking right whales (*Eubalaena glacialis*) by the beginning of the second. The technology and culture of subsistence whaling spread eastward within the Arctic and Subarctic from the Bering Strait region. Commercial whaling originated with the Basques, who had begun hunting right whales in the Bay of Biscay by the eleventh century. Initially, small open boats were launched from shore when a whale was sighted. However, the spread of

whaling was relentless as Dutch, German, Danish, and British entrepreneurs vied to dominate the rich whaling grounds in the cold latitudes of the North Atlantic. In the 1760s, with the invention of a means to boil blubber on board the ship, it became possible to make extended offshore voyages, often lasting several years. The whaling fleets from New England, Great Britain, and France grew to dominate the industry. From the late eighteenth century to the early 1900s, commercial whaling ships penetrated all of the world's oceans except the Antarctic. The sperm whale bore the brunt of this activity (Figure 4). More than 225 000 were killed by American whalers alone from 1804 to 1876. During the peak years from the early 1830s to mid-century, over 100 000 barrels of sperm oil were delivered annually by more than 700 vessels working out of American ports. The nineteenth-century whalers often hunted blackfish (their name for pilot whales) while searching for sperm whales. They also made special voyages in pursuit of right, humpback (*Megaptera novaeangliae*), gray (*Eschrichtius robustus*), and bowhead whales. Only the fast-swimming finner whales – the blue, fin, sei, Bryde's, and minke (*Balaenoptera musculus*, *B. physalus*, *B. borealis*, *B. edeni/brydei*, and *B. acutorostrata/bonaearensis*, respectively) – were beyond their capabilities to capture.

Modern whaling, characterized by engine-driven catcher vessels and deck-mounted harpoon cannons firing explosive grenades, began in Norway in the 1860s. These inventions made possible the routine capture of any species, including the elusive finners. They also led to exploitation of the richest whaling ground on the planet, the Antarctic. In the first three-quarters of the twentieth century, factory ships from several nations, including Norway, Great

Britain, Germany, Japan, the United States, and the Soviet Union, operated in the Antarctic. At its pre-War peak in 1937–38, the modern industry's 356 catcher boats, associated with 35 shore stations and as many floating factories, killed nearly 55 000 whales, 84% of them in the Antarctic. Having exhausted the stocks of right, bowhead, gray, and humpback whales in other areas, the industry rapidly proceeded along the same path in the Antarctic, reducing the largest species first and then turning its attention to the next largest.

Commercial whaling declined in the 1970s as a result of conservationist pressure and depletion of the whale stocks. The last whaling stations in the United States and Canada were closed in 1972, and the last station in Australia ceased operations following the 1978 season. By the end of the 1970s, only Japan, the Soviet Union, Norway, and Iceland were still engaged in commercial whaling. With the decision by the International Whaling Commission (IWC) in 1982 to implement a global moratorium on commercial whaling, Japan and the Soviet Union made their final large-scale factory-ship expeditions to the Antarctic in 1986/87, and Japan stopped its coastal hunt for sperm whales and Bryde's whales in 1988. Iceland closed its whaling station in 1990, and shortly thereafter withdrew its membership in the IWC. Contrary to the widespread belief that commercial whaling had ended, however, Norway and Japan continued their hunting of minke whales through the 1990s and into the 2000s. By formally objecting to the IWC moratorium, Norway reserved its right to carry on whaling. Thus, Norwegian whalers have continued to kill more than 500 minke whales each year in the North Atlantic. Using a provision in the whaling treaty that allows member states to issue permits to hunt protected species for scientific research, Japan has continued taking more than 400 Antarctic minke whales and 100 North Pacific minke whales annually. The main incentive for continued commercial whaling is the demand for whale meat and blubber, particularly in Japan. Norway is eager to re-open the international trade in whale products so that stockpiles of blubber can be exported to Japan.

Aboriginal hunters in Russia, the United States (Alaska), and Canada kill several tens of bowheads and 100–200 gray whales every year. This hunting is primarily for human food. However, from the 1960s to early 1990s, gray whales taken by a modern catcher boat and delivered to native settlements in north-eastern Russia were used partly to feed foxes on fur farms. In recent years, native people in Washington State (USA), British Columbia (Canada), and Tonga (a South Pacific island nation) have



Figure 4 A small sperm whale killed by artisanal whalers at St Vincent, Lesser Antilles, during the 1960s. These whalers hunt for a variety of small and medium-sized cetaceans; sperm whales are taken only occasionally. The meat and oil are used locally. Photo by David K. Caldwell.

expressed interest in re-establishing their own hunts for large cetaceans in order to reinvigorate their cultures. In the spring of 1999, the Makah Indian tribe in Washington took their first gray whale in more than 50 years.

Pinnipeds

Sealing began in the Stone Age, when people attacked hauled-out animals with clubs. Later methods included the use of traps, nets, harpoons thrown from skin boats, and gaff-like instruments for killing pups on ice or beaches. The introduction of firearms transformed the hunting of pinnipeds and caused an alarming increase in the proportion of animals that were killed but not retrieved, especially in those hunts where the animals were shot in deep water before first being harpooned. This problem of sinking loss also applies to many of the cetacean hunts mentioned above.

In addition to their meat and fat, the pelts of some seals, especially the fur seals and phocids, are of value in the garment industry. Markets for oil and sealskins fueled commercial hunting on a massive scale from the late eighteenth century through the middle of the twentieth. The ivory tusks and tough, flexible hides of walrus made these animals exceptionally valuable to both subsistence and commercial hunters. Thousands of walrus are still killed every year by the native people of north-eastern Russia, Alaska, north-eastern Canada, and Greenland. The killing is accomplished with high-powered rifles, and in some areas harpoons are still used to secure the animal. Walrus meat and blubber are eaten by people or fed to dogs, and the tusks are either used for carving or sold as curios.

Native hunters in the circumpolar north also kill more than a hundred thousand seals each year, mainly ringed seals (*Pusa hispida*) but also bearded (*Erignathus barbatus*), ribbon (*Histiophoca fasciata*), harp (*Pagophilus groenlandicus*), hooded (*Cystophora cristata*), and spotted seals (*Phoca largha*) (Figure 5). Seal meat and fat remain important in the diet of many northern communities, and the skins are still used locally to make clothing, dog traces, and hunting lines. There is also a limited commercial export market for high-quality sealskins and a strong demand in Oriental communities for pinniped penises and bacula. The sale of these items, along with walrus and narwhal ivory, white whale and narwhal skin (maktak), and polar bear hides and gall bladders, has helped offset the economic losses in some native hunting communities caused by the decline in international sealskin markets (Figure 6).



(A)



(B)

Figure 5 Ringed seal killed by a Greenlander off Northwest Greenland, June 1988. Photo by Steve Leatherwood.

The scale of commercial sealing, like that of commercial whaling, has declined considerably since the 1960s. It continues, however, in several parts of the North and South Atlantic. After a period of drastically reduced killing in the 1980s, the Canadian commercial hunt for harp and hooded seals has been expanded, at least in part as a result of governmental support. An estimated 350 000 harp seals were taken by hunters in eastern Canada and West Greenland in 1998. A few tens of thousands of molting pups are clubbed to death on the sea ice, but the vast majority of the killing is accomplished by shooting. Norwegian and Russian ships continue to visit the harp and hooded seal grounds in the Greenland Sea ('West Ice') and Barents Sea ('East

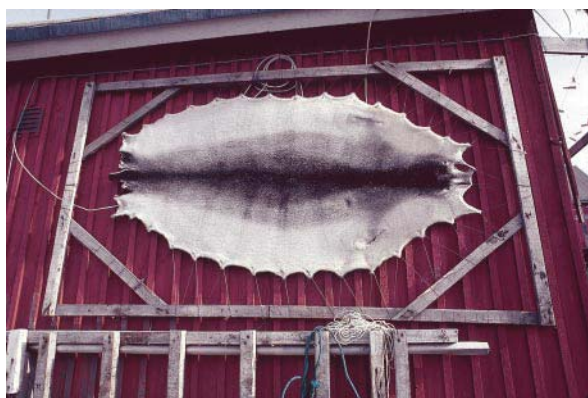


Figure 6 Pelt of a hooded seal stretched to dry on the side of a house in Upernavik, Northwest Greenland, June 1987. Photo by Steve Leatherwood.

Ice'), taking several tens of thousands of seals annually. Also in recent years, thousands of South African and South American fur seals (*Arctocephalus pusillus* and *A. australis*, respectively) have been taken in south-western Africa and Uruguay, respectively. These hunts are centuries old, having been driven initially by markets for skins and oil, and more recently by the Oriental demand for reproductive parts. Much of the hunting for pinnipeds is motivated by the desire of fishermen to see their populations reduced. Seals and sea lions are often held responsible for damaged fishing gear, the removal of fish from nets and lines, and the spread of parasitic worms which infect groundfish.

Sirenians

Sirenians have been hunted mainly for meat and blubber, which are highly prized as food. Steller's sea cow (*Hydrodamalis gigas*), a North Pacific endemic and the only modern cold-water sirenian, was hunted to extinction within about 25 years after its discovery by commercial sea otter and fur seal hunters in 1741. Sea cows were easy to catch and provided the ship crews with sustenance as they carried on the hunt for furs and oil from other marine mammals.

Manatee hides were traditionally used by people in South and Central America and in West Africa to make shields, whips, and plasters for dressing wounds. For a time, these hides were also in great demand for making glue and heavy-duty leather products (e.g., machinery belts, hoses, and gaskets). The hides of more than 19 000 manatees were exported for this purpose from Manaus, Brazil, between 1938 and 1942. For a much longer time, from the 1780s to the late 1950s, the commercial

exploitation of manatees in South America was driven by the market for mixira, fried manatee meat preserved in its own fat. Although no large-scale commercial hunt takes place today, local people continue to kill manatees for food. It is impossible to make a reasonable guess at how many manatees are killed by villagers in West Africa and South and Central America, but the total in recent years has probably been in the thousands (all three species, *Trichechus manatus*, *T. inunguis*, and *T. senegalensis*, combined). Manatees are captured in many different ways, apart from simply stalking them in quiet dugout canoes and striking them with a lance or harpoon. These involve such things as stationary hunting blinds; drop traps armed with heavy, pointed wooden posts; and fence traps or nets placed strategically in the intertidal zone or in constricted channels.

Dugongs (*Dugong dugon*), like manatees, have long been a prized food source for seafaring people. Hunting continues throughout much of their extensive Indo-Pacific range, even in areas where the species is almost extinct. Dugong hunters in some areas have used underwater explosives to kill their prey. In Torres Strait between Australia and New Guinea, portable platforms are set up on seagrass beds, and the hunter waits there overnight for opportunities to spear unsuspecting dugongs as they graze.

Sea Otter

The sea otter (*Enhydra lutris*) has one of the most luxuriant and thus desirable pelts of any mammal species. As a result, it was eagerly hunted by aboriginal people all round the rim of the North Pacific Ocean. Also, beginning soon after Vitus Bering discovered the Commander Islands in 1741, Russian, and later American and Japanese, expeditions were mounted for the explicit purpose of obtaining sea otter furs, which commanded high prices in the Oriental market. No statistics were kept, but at least half a million sea otters were taken (or received in trade) by commercial hunters between 1740 and 1911, when the species was given legal protection. The hunters sometimes used anchored nets to catch the otters, but more often they lanced them from small boats. Once rifles became available, these were used in preference to lances. In California, sea otters were sometimes shot by men standing on shore, and in Washington, shooting towers were erected at the surfline and Indians were employed to swim out and retrieve the carcasses. Alaskan natives are still allowed to hunt sea otters as long as the furs are used locally to make clothing or authentic

handicraft items. The reported annual kill during the mid to late 1990s ranged from 600 to 1200.

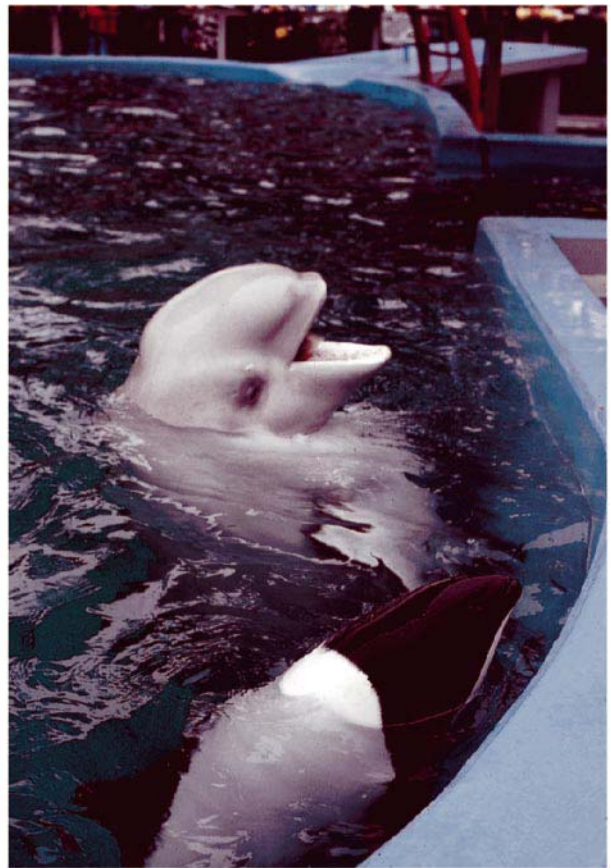
Polar Bear

Eskimos traditionally hunted polar bears with dog teams and hand lances. The meat was eaten and the hides used for clothing and bedding. White explorers, whalers, sealers, and traders in the Arctic often killed polar bears with high-powered rifles. They also provided a commercial outlet for hides obtained by the Eskimos. In modern times, the Es-

kimos hunt polar bears with rifles and search the ice in snowmobiles rather than dogsleds. Norwegian trappers and weather station crews on Svalbard formerly used poison, foot snares, and set guns to kill polar bears. The set gun consisted of a wooden box resting on poles about 75 cm above ground level, with a rifle or shotgun mounted inside. A string connected the gun's trigger to bait placed in front of the box. When the bear took the bait, the trigger was pulled and the gun fired. Sport hunters have taken thousands of polar bears as trophies, particularly in Alaska where guided hunting with aircraft



(A)



(B)

Figure 7 Commerson's dolphins are endemic to the coastal waters of southern South America and certain subantarctic islands. There is some demand for them in North American, European, and Japanese oceanaria. (A) Here, a hoop net at the end of a pole is used in an attempt to capture a dolphin from a bow-riding group off the coast of Chile, February 1984. (B) A Commerson's dolphin (foreground) shares an oceanarium tank with a white whale (beluga) at a zoo in Duisberg, Germany. Photos by Steve Leatherwood.

began in the late 1940s and continued until 1972. At least several hundred polar bears are still killed each year, most of them by Eskimos for meat and the cash value of their hides and gall bladders. Hunting permits issued to native communities in Canada are often sold to sport hunters, on the understanding that a local guide will be hired to accompany the hunter and that only the head and hide will be exported.

Live-Capture and other Forms of Exploitation

Although the numbers of marine mammals removed from the wild for captive display and research have been small in comparison to the numbers killed for meat, oil, skins, etc., the high commercial value of some species establishes this as an important form of exploitation (Figure 7). More than 1500 bottlenose dolphins were live-captured in the United States, Mexico, and the Bahamas between 1938 and 1980. Close to 70 killer whales (*Orcinus orca*) were removed from inshore waters of Washington State (USA) and British Columbia (Canada) and transported to oceanaria between 1962 and 1977, and about 50 were exported from Iceland in the 1970s and 1980s (Figure 8). Live killer whales and bottlenose dolphins are presently worth about \$1 million and \$50 000, respectively. Captive-bred animals and ‘strandlings’ (animals that come ashore and require rehabilitation) have increasingly been used to stock oceanaria, but this trend applies mainly to North America and involves primarily bottlenose dolphins, killer whales, California sea lions (*Zalophus californi-*



Figure 9 Irrawaddy dolphins have a limited coastal and fresh-water distribution in southeast Asia and northern Australia. They are fairly popular in Asian oceanaria, and live captures add to the stress on populations caused by incidental mortality in gillnets. This animal was recently on display at a facility in Thailand. Photo by Steve Leatherwood.

nianus), and harbor seals (*Phoca vitulina*). Dolphin, whale, and sea lion displays are becoming more popular in Asia and South America, and new facilities on those continents create a continuing demand for wild-caught animals, especially dolphins (Figure 9). Most polar bears and walrus brought into captivity have been young ones, orphaned when their mothers were killed by hunters. In Florida, manatees are often brought into captivity after being injured or orphaned as a result of boat strikes. Nearly 100 sea otters were taken from Alaskan waters for public display between 1976 and 1988.

It should be mentioned that marine mammals are also ‘exploited’ as the objects of tourism. Whale-



Figure 8 Killer whales are the most valuable marine mammals in the oceanarium trade. Recent success at captive breeding and rearing has relieved some of the pressure on wild populations to stock display facilities. The movie “Free Willy” inspired a campaign to return the whale “Keiko” back to its natal waters near Iceland. Photo by Steve Leatherwood.



Figure 10 Gray whales attract many tourists each year to the nearly pristine waters of Laguna San Ignacio, Baja California, Mexico. Whale-watching in the lagoon is closely regulated by Mexican authorities. The recognized economic value of nature tourism was partly responsible for the government’s decision in 2000 to reject a proposal for a large evaporative salt factory on the shores of San Ignacio. Photo by Steve Leatherwood.

dolphin-, seal-, and sea otter-watching supports an extensive network of tour operations around the world (Figure 10). Commercial fishermen 'exploit' pelagic dolphins in the tropical Pacific Ocean by using them to locate schools of tuna, and this can result in large numbers of dolphins being killed by accident.

See also

Baleen Whales. Marine Mammal Overview. Sea Otters. Seals. Sirenians. Sperm Whales and Beaked Whales.

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MARINE MATS

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The production of organic carbon in ocean surface waters and its subsequent transport to the seafloor is often referred to as the 'biological pump'. This biological pump is an important link in the global carbon cycle because phytoplankton use dissolved carbon dioxide (CO₂) gas to produce their organic matter. The concentration of dissolved CO₂ in surface waters is regulated by gas exchange with the atmosphere, so if carbon is utilized by phytoplankton which then sink, more CO₂ is drawn down from the atmosphere to compensate. One of the key steps in the biological pump is, therefore, the sinking of organic material from the surface waters – the faster organic material settles, the more efficiently the biological pump operates. Recent water column observations and complementary studies of deep-sea sediments have demonstrated that diatom mats and

large diatoms are important, and in some cases, dominant contributors to the flux of biogenic material to the seafloor. Research on deep-sea sediment cores, in particular, has shown that such diatoms are locally abundant and may form thick, extensive deposits that have accumulated at rates exceeding 30 cm per 1000 years. These are exceptionally high for the pelagic realm and would normally occur only in areas of high sediment supply near continental margins or beneath coastal upwelling zones. A synergy between biological oceanography and paleoceanography has shown that these diatoms are key players in the biogeochemical cycles of carbon and silica and may be important regulators of global change.

Ecological Significance of Diatom Mats and Large Diatoms

In contrast to the relatively well studied, small, and rapidly reproducing diatoms that dominate primary production in coastal settings, the ecology of oceanic mat-forming and large (> 50 µm) diatoms is