REVIEW OF THE
CLASS MAMMALIA
ORDER CETACEA
SUBORDER MYSTICETI

Family ESCHRICHTIIDAE (GRAY WHALE)

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Coastal North Pacific, Bering Sea, Sea of Okhotsk, Chukchi Sea, and Arctic.
Gray Whale *Eschrichtius robustus*
French: Baleine grise / **German**: Grauwal / **Spanish**: Ballena gris
Other common names: California Gray Whale, Devilfish, Hard-head, Mussel Digger, Rip Sack, Scrag Whale
1 genus, 1 species, 1 taxon.
No species threatened; none Extinct since 1600.

Taxonomy. *Balaenoptera robusta* Lilljeborg, 1861, "på Gräsön i Roslagan," Graso Island, Uppland, Sweden.
This species is monotypic.
Distribution. North Pacific, from the Arctic Ocean and Bering Sea to Baja California, the Gulf of California, and portions of the mainland coast of Mexico in the east, and to the coasts of Russia, Japan, Korea, and south-eastern China in the west. Extinct in the North Atlantic Ocean.
Medium-sized baleen whale, mottled gray color with prominent external parasites (barnacles and whale lice), lacking dorsal fin but with distinct knobs on dorsal ridge and anterior tailstock; blow is low and heart-shaped.
Migrates and feeds along coastal continental shelf areas; breeds in mid-latitude temperate and subtropical coastal bays, lagoons, and coastal areas.

Systematics

The Eschrichtiidae is represented by a single living species, the Gray Whale (*Eschrichtius robustus*), which for many years was thought to be the sole member of the clade. Very recently, three to five extinct genera have been discovered and added to the lineage. Once, eschrichtiids occurred throughout all northern ocean basins, but the present-day Gray Whale is restricted to the North Pacific Ocean and contiguous Arctic Ocean (except amazingly two vagrants are known to travel into the Atlantic; one into the Mediterranean Sea in 2010, and another was sighted south of the equator off the coast of Namibia in 2013). Extant Gray Whales are highly migratory and range primarily in the sublittoral zone (coastal waters from the high tide mark out to the edge of the continental shelf) within subtropical to polar latitudes and rarely venture into open oceanic or pelagic habitats. It is hypothesized that ancestral eschrichtiids were coastal, occupying a unique ecological position as the only benthic, suction-feeding mysticetes. Two living populations of the Gray Whale are recognized: the remnant, western North Pacific population off Asia and the far larger, eastern North Pacific

population off North America. Historical accounts indicate that Gray Whales formerly inhabited coastal waters of the North Atlantic Ocean until the 1700s. Exactly why the Gray Whale died out in the Atlantic is unknown, but it was likely extirpated by shore-based whaling activities.

The modern Gray Whale is structurally quite different from other Mysticeti. Some diagnostic characters of the skull include: a narrow attenuated rostrum with short cranium; moderately arched rostrum (lateral aspect); moderate interdigitation of the rostral and cranial bones with parietal and frontal exposed on vertex (indicating moderate telescoping); relatively small and steeply sloping supraoccipital shield with prominent paired tuberosities (where neck muscles attach); paroccipital processes robust and pointed posteriorly; lateral border of supraoccipital straight; large well-defined premaxillary; steeply sloping maxillary bones; gracile ascending process of the maxilla, large nasal bones, and large narial opening; relatively straight mandible (dorsal aspect) with large angular process and large mandibular condyle oriented posterodorsally; short mandibular symphysis with large boss dorsal to groove; and relatively thick baleen laminae, few in number (160–170 per side), with coarse bristles. Additional study is needed before the morphological differences regarded at the family, generic, or specific level are better recognized.

A plethora of taxonomic names has been assigned to the living Gray Whale, resulting in the nomenclatural confusion that persists today. Surprisingly, the holotype of *Eschrichtius robustus* was first described by W. Lilljeborg in 1861 under the name *Balaenoptera robusta*, from Holocene subfossils (4000–6000 years old) from Sweden where the Gray Whale was extinct and well before the living Gray Whale in the Pacific Ocean became known to the scientific community. Lilljeborg believed it was a new fin whale (rorqual). In 1864, J. E. Gray created the subgenus *Eschrichtius* for *Balaenoptera robusta* and referred it to the genus *Megaptera* within Balaenopteridae (rorquals and the Humpback Whale, *Megaptera novaeangliae*). In 1865, Gray raised *Eschrichtius* to generic status, but he still allied it with *Megaptera*. Meanwhile, the living Gray Whale in the Pacific Ocean was called *Rhachianectes glaucus* until A. B. Van Deinse and G. C. A. Junge finally concluded in 1937 that it was the same as the Swedish subfossil whale that had been described earlier by Lilljeborg. Thus, the odd situation exists where subfossils from the extirpated Atlantic population of the Gray Whale serve as the holotype of the live populations. The common name refers to the color of the whale.

Fossil remains of eschrichtiid whales are scarce, which limits the understanding of the evolutionary relationships of Gray Whales. The paleontological record of the Gray Whale was previously limited to finds from the North Atlantic region, which consist of Holocene and Pleistocene remains ranging from 303 years old to 30,000 years old that were unearthed in Sweden, Belgium, The Netherlands, England, and the USA (New York, New Jersey, Virginia, Delaware, North Carolina, South Carolina, Georgia, and Florida). Pleistocene (about 200,000–500,000 years old) fossils of *Eschrichtius* have also been discovered in southern California, USA, but it is unclear if these represent Gray Whales or some very closely related extinct species. The earliest known fossil referable to *Eschrichtius* is about 2·5 million years old from the late Pliocene of Hokkaido, Japan.

During the last few years, several new fossils have been discovered and described as extinct eschrichtiid genera, suggesting that Gray Whales were formerly more diverse. Only one is from the North Pacific Ocean, an unnamed genus (and species) based on several partial skeletons (including specimen SDSNH 90517 in the San Diego Natural History Museum) from southern California, dated at 2·5–4·5 million years of age (middle to late Pliocene). Two to possibly four earlier fossil genera have been described from the North Atlantic region. *Gricetoides aurorae* is based on a partial skull about 4·5 million years old from the mid-Pliocene of North CarolinaA fossil mandible (IRSNB 810 in the Institut Royal des Sciences Naturelles de Belgique) that is 4·5–7·2 million years old from the early Pliocene or late Miocene of Belgium was originally classified as *Megapteropsis robusta* and assigned to Balaenopteridae (rorquals), but it may represent another fossil species of the Gray Whale from the North Atlantic Ocean; however, this is open to debate. The earliest Gray Whale identified with certainty is *Eschrichtioides gastaldii* from the early Pliocene (3·5–5 million years ago) of northern Italy, near the shores of the ancient Tethys Sea. When first described in the 19th century, this species was attributed to the genus *Balaenoptera*, but instead it is a basal eschrichtiid. *Archaeschrichtius ruggieroi* is a putative Gray Whale from the late Miocene (7·5–11 million years ago) of southern Italy that is controversial. The holotype consists of a fragmentary dentary lacking clearly recognizable synapomorphies; thus, confirmation is needed to substantiate the validity of this taxon. Although molecular-clock methods have predicted an early Miocene divergence time for the eschrichtiid clade ranging from 14·5 million years ago to 19·3 million years ago, no fossil eschrichtiids of that age have been discovered. This suggests that the molecular evidence is incorrect or that there is a substantial gap, or ghost lineage, in the fossil record.

Evolutionary biogeographic analyses of the eschrichtiid fossil record suggest the lineage first evolved in the North Atlantic Ocean, or in a basin subsequently incorporated within the present-day Mediterranean, during the earliest Pliocene or possibly the late Miocene. Dispersal of stem eschrichtiids into the Pacific Ocean possibly occurred through the open (ice-free) Arctic Ocean or via the North Equatorial Current through the Central American Seaway prior to the emergence of the Isthmus of Panama. This gateway between the equatorial Atlantic and Pacific oceans closed about 3·5 million years ago, altering ocean circulation patterns in each ocean basin and forming the modern Gulf Stream. Evidence also suggests that the closure of this major seaway, and the subsequent, warm–wet weather over northern Europe resulted in the formation of a large Arctic ice cap and contributed to the subsequent ice age. Allopatric speciation in the North Pacific Ocean during the middle-to-late Pliocene resulted in the evolution of at least two eschrichtiid lineages, including the modern genus *Eschrichtius*. It is hypothesized that the living species, the Gray Whale, evolved in the Pacific Ocean and then dispersed back into the North Atlantic Ocean during the Pleistocene when warm interglacial periods would have melted the polar ice cap enough to form an ice-free connection throughout the Arctic Ocean. Although eschrichtiids lived in the North Atlantic until the 17th century, whether their presence was continuous or was punctuated by local extinctions and subsequent recolonization events is unknown. There is no evidence that Gray Whales ever lived in the Southern Hemisphere.

Despite extensive research, the phylogenetic position of Eschrichtiidae among the family-level clades of extant and extinct Mysticeti remains unresolved. Several contradictory scenarios have been proposed. Cladistic analyses by Steeman in 2007 using morphological data from modern and fossil mysticetes show Eschrichtiidae as the closest sister taxon to the Cetotheriidae (sensu stricto), edentulous baleen whales that lived from the late Miocene to late Pliocene, 3–12 million years ago. These studies propose Gray Whales and Cetotheriidae together constitute the Cetotherioidae clade within the Mysticeti. Analysis of morphological data by Deméré et al. in 2005 traditionally favored a close relationship between *Eschrichtius* and Balaenidae (right whales and the Bowhead Whale, *Balaena mysticetus*). Nevertheless, the proposed synapomorphies have recently proven to be unreliable, likely based on analogous rather than homologous features. The dominant hypothesis has eschrichtiids as most closely related to balaenopterids (rorquals and the Humpback Whale) in a more inclusive clade, Balaenopteroidea. Most morphological and some molecular studies (e.g. Rychel 2004) place eschrichtiids as sister to a monophyletic Balaenopteridae. Other molecular studies go so far as to propose that eschrichtiids are nested within a paraphyletic Balaenopteridae, suggesting a significant divergence of the Gray Whale from the common balaenopterid ancestor. Support for this proposal is weak or mixed. These and various other contradictory hypotheses of the evolution of Eschrichtiidae await resolution.

Morphological Aspects

Among living Mysticeti, the Gray Whale is anatomically an intermediate between the slow-moving, skim-feeding balaenids (right whales and the Bowhead Whale) and the fast-swimming, engulfment-feeding balaenopterids (rorquals and the Humpback Whale). Morphology of the Gray Whale reflects a natural history adapted to seasonal migrations along relatively shallow continental shelf areas between breeding and feeding ranges and a specialization for finding and exploiting benthic prey resources while retaining flexibility to exploit alternative planktonic and nektonic resources when they become available.
Slimmer than right whales and stockier than most rorquals, adult Gray Whales weigh 16,000–45,000 kg. Physical maturity is reached at about 40 years, at an average length of 1410 cm for females and 1300 cm for males. Female Gray Whales are slightly larger than males at all ages, with the largest female recorded at 1530 cm long and the largest male at 1460 cm long. There is no significant sexual dimorphism in their appearance, but the distance from the genital slit to the anus is wider in males. Age is estimated from growth layers in the waxy earplugs that fill the auditory canal, which suggests that longevity for males and females ranges from 40 years or 50 years to as long as 80 years for one female killed in the 1960s. The skin is mottled pale to dark gray, with whitish blotches heavily infested with species-specific epizooic barnacles (*Cryptolepas rachianecti*) and three species of ectocommensal cyamids, or "whale lice," (*Cyamus scammoni*, *C. kessleri*, and *C. ceti*) that feed on skin around barnacles, blowholes, and skin folds and swarm into wounds. Internal parasites are few and include trematodes (liver), nematodes (stomach), and cestodes and acanthocephalans (small intestine).

The head of the Gray Whale is elongate and triangular (viewed dorsally) and moderately arched compared with Balaenidae (right whales). The overall skull structure of the Gray Whale is less telescoped than in other extant mysticetes, and relatively small at about 20% of

skeletal length. Gray Whales share several morphological characteristics with balaenids that are associated with feeding, including a narrow rostrum and arched palate, a subrostral gap between anterior terminations of the baleen racks (providing a central opening into the oral cavity), a small coronoid process on the dentary, and a more dorsally oriented mandibular condyle. Other characteristics they share with balaenopterids, also related to feeding, include a relatively deep interdigitation of cranial and rostral bones, a nonsynovial fibrocartilaginous temporomandibular joint, and short coarse baleen. The fibrocartilaginous jaw articulation of Gray Whales is hypothesized to be homologous with the balaenopterid condition and represents a shared derived feature that evolved in their common ancestor.

As with all mysticetes, the Gray Whale has a double blowhole (nares) located dorsally and posteriorly on the head. Gray Whales possess coarse, cream-colored to pale yellow baleen. There are 130–180 individual baleen plates suspended from each side of the palate; they are 5–40 cm long. Baleen grows continuously from its base throughout the life of a Gray Whale to replace wear at its lingual margin. Individual vibrissae emerge from follicles on the rostrum and chin areas and represent remnant mammalian hair. There are typically 2–7 short, deep, longitudinal creases on the throat rather than the numerous long ventral pleats of Balaenopteridae (rorquals).

The Gray Whale lacks a dorsal fin; instead, a hump of variable size and shape is located on the back anterior to the base of the tail, followed by a series of fleshy knobs, or "knuckles," along the dorsal ridge of the tailstock. The flippers are relatively short and paddle shaped, with rounded margins and pointed tips that become rounded from abrasion in older individuals. The flukes of adults are broad, 300–360 cm across, and are frequently lifted before a deep dive. Unique to Gray Whales is a 10–25-cm wide "tailstock cyst" on the ventral surface of the caudal peduncle of unknown function. The blow of a Gray Whale is 300–400 cm high, heart-shaped, and "bushy" to columnar.

Habitat

Extant Gray Whales are highly migratory, and range within subtropical to polar latitudes. They primarily frequent the relatively shallow waters along the edge of the continental shelf, and only occasionally venture into open oceanic or pelagic habitats. As with all mysticetes, Gray Whales migrate seasonally from their feeding areas in the higher latitudes where during summer months long daylight hours power extensive primary production that supports the development of extensive benthic communities of macro invertebrates which constitute a primary food source. In fall the shortening days and cooling temperatures trigger the Gray Whales' southward migration along the continental shelf to their winter breeding and aggregation areas. It is believe that the warmer waters and shallow bays and lagoons offer a selective advantage for the birthing of calves and their growth during their first months of life. Following the mating and birthing season in spring, Gray Whales undertake a return migration to their high latitude feeding areas to complete their annual migratory cycle. Known predators include Killer Whales (*Orcinus orca*) and cookiecutter sharks (*Isistius*). Remains of Gray Whales have been found in the stomachs of some other species of sharks; however, because sharks are scavengers as well as predators, it is not known if ingestion was pre- or post-mortem.

General Habits

Gray Whales are unique among mysticete whales because of their habit of frequenting relatively shallow, continental shelf waters and coastal areas for feeding, migrating, and breeding. Also unique to the family is their ability to use suction as a primary mode of prey capture when feeding on benthic invertebrates, while also maintaining a limited ability to skim and engulf swimming prey. These morphological and behavioral characteristics of Gray Whales are believed to reflect adaptations in response to changing sea level and prey availability during their late Pliocene and Pleistocene evolution, and they allow the modern Gray Whale to search for, discover, and exploit a variety of resources throughout their distribution. Although Gray Whales are capable of navigating deep ocean areas, they migrate to and from their summer feeding and winter breeding areas along distinct corridors within a few kilometers of the North American coast (for the eastern population of Gray Whales) and the eastern Asian coast (for parts of the western population of Gray Whales). They disperse widely across the Arctic Ocean and polar seas during summer feeding and remain generally solitary. During migration, however, they form loose aggregations and groups, often engaging in sexual activity while they swim. Unlike other baleen whales, Gray Whales aggregate in shallow coastal areas, embayments, and lagoons in subtropical latitudes for breeding and to give birth to their offspring.

Communication

Underwater sound is the Gray Whale's primary sensory modality. They create a variety of sounds ranging from rapid, rhythmic pulses to frequency modulation (FM) signals that range from 100 Hz to 1600 Hz, with pulse durations up to 1·8 seconds. These sounds are probably used for communication among individuals, particularly between females and their offspring. Their vocalizations occupy frequency ranges above and below natural ambient noise created by invertebrates, fish, and movements of ocean water (for example waves, currents, and ice movement), thereby allowing optimization of signal strength and transmission underwater. Unfortunately, low-frequency, manmade noise (for example seismic exploration, sonar systems, and ship noise) can interfere with communication of Gray Whales (and other whale species), reducing their ability to hear natural sounds for foraging and navigation, compromising predator avoidance, and, at high sound pressures, damaging whales' hearing. When threatened, as when confronted with the sounds of predators (e.g. Killer Whales) or unknown sounds, Gray Whales respond by ceasing all sound production, blending in with the ambient noise. Outside of breeding aggregation areas, female Gray Whales with young often swim close to or within coastal kelp beds, which are believed to provide acoustic cover from detection by predators.

Food and Feeding

Gray Whales have a continuous feeding distribution that extends from the Pacific coast of Mexico, north through the Gulf of Alaska, the Bering Sea, Sea of Okhotsk, the Chukchi Sea, and the Siberian Shelf in the Arctic Ocean. Prey resources are not evenly distributed but occur in dense patches along coastal and continental shelf waters, particularly in areas of high marine productivity. Distribution of Gray Whales on their feeding grounds is not uniform; rather, it corresponds with areas of high prey densities. Low densities of Gray Whales occur

in areas with lower prey concentrations. Foraging occurs in relatively shallow water of 50 m or less. An adult Gray Whale may consume about 220,800 kg of food at a rate of 1200 kg/day for about 180 feeding days. During winter, Gray Whales do not eat very much. They rely on stored lipids in their body fat and blubber as their primary energy and water sources and may lose up to 30% of their body weight, which must be replenished during summer. Lactation represents the greatest cost of reproduction: pregnant females increase their weight 25–30% during summer feeding. Water is obtained from their food and from the metabolism of body fat.

Modern Gray Whales perfected suction feeding to exploit benthic prey while maintaining the ability to skim the surface and gulp. This allows feeding on a variety of organisms and possibly some plants. When exploiting benthic resources, Gray Whales forage primarily on or near the ocean floor and feed continuously, 24 hours a day. When foraging on infaunal (living in the soft sea bottom) prey, the Gray Whale rolls on its side and swims slowly just above the bottom, using its enlarged hyoids and muscular tongue in a piston-like action to generate pulses of intraoral suction. It takes in mouthfuls of food, water, and sediment, and then expels the water and sediment, trapping prey on the inside of its coarse baleen plates.

Primary benthic prey includes tube-dwelling ampeliscid amphipods, polychaete worms, and bivalves. When suction feeding, Gray Whales leave behind characteristic “feeding pits” approximately three meters long, one meter wide, and one-half meter deep on the seafloor, where mouthfuls of sediment containing prey were removed. Bottom-feeding Gray Whales trail clouds of sediment, or “mud plumes,” in their wake as they surface to breathe; these trail clouds attract seabirds that feed on prey brought to the surface. This surfacing suspends large amounts of sediment and opens areas of the sea floor for recolonization, thus stimulating the growth of prey communities. In doing so, some have suggested that Gray Whales may be “farming” the ocean floor by suction feeding in these areas. Indications that Gray Whales are feeding include repeatedly diving in an area, defecation, fecal slicks, and seabirds following surfacing whales.

Bottom feeding is more like grazing than hunting for prey, and it affords Gray Whales a niche with little competition for benthic food items from other cetaceans or marine mammals. Nevertheless, Gray Whales are flexible foragers, exploiting a variety of feeding opportunities throughout their coastal distribution. In addition to bottom feeding, they are capable of using engulfing and skim-feeding methods for capturing swimming crustaceans and small schooling fish that are faster, more mobile, and evasive. Mobile prey include swarming cumaceans, mysids, euphausiids, shrimps, krill, mobile amphipods, and schools of small clupeoid fish such as sardines and anchovies, and sand lances (Ammodytidae). Some plants are ingested (for example, algae, kelp, and sea grass), rendering the Gray Whale a partial herbivore. This dietary flexibility may help Gray Whales survive through periods of disruption and fluctuations in prey availabilities resulting from changes in oceanic conditions caused by climate change. It creates opportunities for the use of additional resources, but it also might result in competition with other species that feed on pelagic or nektonic prey.

Breeding

The main mating group of the Gray Whale was long believed to be a "mating trio" composed of a mating pair and a third individual thought to be a helper. Research during the breeding season has confirmed that mating groups include 20 or more individuals of mixed sexes, and bouts of sexual activity last from a few minutes to hours at a time. Pairs or trios may court and mate quite gently, but larger groups of consorting adults may be very active—rolling, pushing, splashing, and cavorting at the surface. These groups are fluid, with individuals joining and leaving; sometimes high-speed chases are involved. Male Gray Whales do not exhibit any territorial defense or conspecific aggression, and they rove throughout winter aggregating areas seeking opportunities to mate with estrous females. They may attempt to separate newborn young from their mothers and mate with the females, who usually violently reject the advances of males. The mechanism for female selection of mates is unknown. Gray Whales are thought to be promiscuous breeders, copulating with multiple partners, which, along with large testes-to-body weight ratios, suggest that sperm competition operates in this species.

Reproduction of Gray Whales is strongly seasonal and synchronized with the migratory cycle. Mating occurs during southward migration in fall and continues in the breeding areas in winter. Sexual maturity in both sexes is reached at a mean age of eight years (range 6–12 years). Males can mate annually. On average, females produce one offspring every two years. Females have one estrous cycle every two years; thus, only one-half of the females of reproductive age are available for mating each year. Ovulation occurs in late November and December, and most females conceive during migration or in one of the winter aggregation areas. If a female fails to conceive, she may undergo another estrous cycle about 40 days later. It is not known if females ovulate spontaneously.

Single young are born following gestation of 11–13 months. The sex ratio is 1:1. For the eastern population in the North Pacific Ocean, births occur from late December to early March. The median birth date is January 27 when near-term females are in or near the breeding grounds or migrating southward. Neonates are 450–500 cm long and weigh about 800 kg. Females establish a close, affectionate, and protective bond with their offspring, and they will fight fiercely to defend them. To nurse, the female swims slowly or rests motionless at the surface while her offspring approaches from below, nudging her abdominal area, whereupon the female's teat is extruded and milk is squirted into the young's mouth. Young Gray Whales consume about 200 l of milk per day; the milk is 53% fat and 6% protein. They imprint on their mothers, mimic adult behaviors, and socialize with other young and adults when they are 1–2 months of age. Weaning occurs at 7–8 months when young are 750–950 cm long. Females then have a 3–4-month resting period until November or December when a new estrous cycle begins.

Movements, Home range and Social organization

Gray Whales once had a circumpolar range in the Northern Hemisphere, but they are now extinct in the North Atlantic Ocean. The two extant populations are found only in the North Pacific Ocean: the eastern North Pacific population with about 21,000 individuals and the western North Pacific population with only about 200 individuals. They inhabit polar, subpolar, temperate, and subtropical marine climate zones. Movements of the western North

Pacific population of Gray Whales are little known. Unless otherwise noted, most of the following information is the result of research on the larger eastern North Pacific population. Gray Whales are latitudinal migrants, participating in an annual polar-to-subtropical migration in fall and a return migration in spring to polar seas—a round trip of 15,000–20,000 km. Spanning 55° of latitude, it is the longest migration of any mysticete. It is believed that the predictable seasonal production of prey shaped the evolution of the life history of the Gray Whale and other baleen whales into two periods: summers when whales feed in higher latitudes where food is abundant and weather favorable for an aquatic mammal and winters when whales migrate to lower latitudes to escape inclement weather and reproduce in warmer waters that are more conducive to mating and rearing young.

Gray Whales migrate continuously day and night at 6–7 km/h, pausing only to catnap, forage, or mate. They are adaptable and predisposed to disperse throughout their distribution in search of prey, suitable migratory routes, and breeding areas. Gray Whales in the eastern part of their distribution exit the Arctic and Bering seas from mid-November to late December, following the North American coast southward to Mexico, arriving there from January to February. An overlap of southward and northward migrating Gray Whales occurs in midwinter as the last of the southward migrants reach the coastal waters of Baja California and meet the first of the northward migrants. Only part of the population occupies the coastal waters of Mexico at any given time in winter.

Pregnant females and those with newborn young arrive off the coast of Baja California from late December to early January, with the bulk of the population arriving by mid-February to early March. The principal winter gathering areas include Laguna Ojo de Liebre (Scammon's Lagoon), Bahía de Sebastián Vizcaino, Laguna San Ignacio, Bahía de Ballenas, and Bahía Magdalena and adjacent waters. Variability in sea temperature influences distribution of Gray Whales: the southward migration diminishes during warm El Niño periods, and it increases during colder La Niña conditions.

The spring northward migration of eastern Gray Whales occurs as two phases. The first phase, from late January through March, consists of newly pregnant females, maximizing their feeding time in the Arctic Ocean. Non-pregnant adult females and males, and then juveniles, follow the newly pregnant females. The second phase, from March through May, consists of mothers with young. They remained in the breeding range for 1–3 months, allowing young to grow and strengthen before migrating. Thus, females with newborn young spend more time in the winter range and spend less time on the summer feeding grounds. They migrate alone or in pairs and stay very close to shore. Young are weaned and separate from their mothers during the summer following their birth.

The western population of Gray Whales occurs off the coasts of Russia, Japan, Korea, and China. Today this small population feeds in the northern shores of the Sea of Okhotsk, off Sakhalin Island, and the eastern coast of Kamchatka Peninsula, Russia. This population's breeding areas are not known with certainty, but historical evidence suggests these whales may winter off south-eastern China as far south as Hainan. The eastern population's distribution extends from its feeding grounds in the Arctic Ocean and Bering Sea south along

the western coast of North America to their winter aggregation areas along the Pacific coast of Baja California, the Gulf of California, and the mainland coast of Mexico south to Bahía de Banderas, Jalisco. Up to a few hundred individuals known as the "Pacific Coast Feeding Group" forage during the summer along the coasts of northern California, Oregon, Washington, and British Columbia.

Previous distributional surveys and genetic analyses suggested that the western and eastern populations of Gray Whales were separate and distinct groups. Recent photographic identification research and genetic analyses now show that these populations of Gray Whales share a feeding ground along the eastern coast of Kamchatka; that some western Gray Whales migrate in fall across the Bering Sea and North Pacific to join the southward migration of the larger eastern population along the west coast of North America; and that some Gray Whales from the western population visit the coastal breeding lagoons and winter aggregation areas in Baja California, Mexico. The presence of some Gray Whales from the western population in the migratory route and breeding grounds of the eastern population suggest that some interbreeding of these two populations occurs. Occasional incidental catches and strandings of Gray Whales off Japan and China support the contention that some individuals from the western population continue to migrate along the Asian coast, presumably to winter off the coast of China. Future genetic research will determine to what extent, if any, these two populations interbreed.

It is believed from the fossil record that eschrichtiids evolved in the Mediterranean or North Atlantic during the Miocene or earliest part of the Pliocene, dispersed westward into the Pacific Ocean through the then-open Central American Seaway, and then dispersed back into the North Atlantic Ocean during Pleistocene interglacial periods via the Arctic Ocean. Subfossil remains of Gray Whales found along the North Atlantic coasts of North America and northern Europe are evidence of their previous occupation of this region. There was support for this hypothesis, and a clear indication of the Gray Whale's propensity to wander and roam in May 2010 when a single Gray Whale was observed off the Mediterranean coast of Herzliya Marina, Israel, and the same individual resighted 22 days later off the coast of Barcelona, Spain. A second individual Gray Whale was sighted several times and photographed off the Namibian coast in May of 2013, representing the first sighting of a gray whale in the Southern Hemisphere in historical times. These individual Gray Whales were some 22,000–23,500 km from the Pacific winter breeding distribution of the eastern North Pacific population. It is believed they migrated from the North Pacific Ocean into the Arctic Ocean and followed the northern Eurasian coast, which is becoming more frequently open and ice free during summer months in recent years. They probably entered the North Atlantic through the Davis Straight between Greenland and North America, and then continued along the European coast, with the 2010 individual entering the Mediterranean and the 2013 individual continuing south to the coast of Africa.

Present-day ocean warming and reduction of Arctic sea ice, no doubt, allowed these Gray Whales to enter the North Atlantic Ocean and demonstrated that such exchanges between oceans are possible for marine species during periods of interglacial minimum ice conditions. With the shrinking of Arctic sea ice due to climate change, Gray Whales could recolonize the

North Atlantic Ocean. Only time will tell if ongoing warming of oceans and seas and reduction in polar ice as the result of climate change will continue, and whether such exchanges of various marine mammals will occur.

The Gray Whale is not known to be a social species, and information on its behavior is generalized from observations of groups. Although they form aggregations on feeding grounds and to migrate, there is no evidence of social bonding other than during copulation and between mothers–offspring pairs until the young are weaned during their first year of life. Gray Whales disperse widely across their principal feeding areas in the Bering Sea, Chukchi Sea, and Arctic Ocean to forage for prey. Feeding aggregations are associated with areas of high prey density and do not appear to have any behavioral context other than foraging. Gray Whales occasionally enter brackish estuaries, freshwater lagoons, and river mouths, where they have been observed rubbing their bodies on the bottom, perhaps to remove external parasites.

Breeding male Gray Whales do not defend territories, demonstrate aggression among conspecifics, or defend "harems" of females for breeding. Males provide no parental care or assistance with rearing young. Female Gray Whales with young remain solitary when their offspring are less than about one month of age, and they provide all care, protection, and feeding of their offspring. Mother–offspring pairs form aggregations in breeding lagoons when young are 2–4 months old. In these aggregations, females and their offspring will cavort with other mother–offspring pairs, mixing and milling and perhaps socializing with each other. Young are continuously active, are curious about all manner of objects in the water, and will frequently "play" with floating balls of kelp or sticks drifting with the tides. When migrating, mother–offspring pairs travel alone rather than in groups, perhaps to minimize detection by predators.

Aberrant sexual activity outside of the breeding season is observed on the feeding grounds and during migration, but its function, if any, remains unknown. Rare instances of apparent altruistic behavior have been observed when presumed unrelated adults appear to protect young, but any social benefit of these interactions is uncertain. When threatened by predators or humans, Gray Whales will defend themselves by swinging their tail flukes like clubs, using their heads to ram aggressors, and attempting to flee.

Relationship with Humans

Whalers referred to the Gray Whale as the "Devilfish" or "Hard-head" because if not killed quickly, its response to being harpooned was to attack and overturn whaling boats, often injuring and killing the whalers. Gray Whales were hunted throughout their distribution from prehistoric to historic times, first by indigenous people using primitive harpoons and lances and later by European and Yankee (north-east coast of the USA) whalers who established shore-based stations and pursued whales with sailing ships equipped with steel harpoons and hand lances. In the 20th century, industrial whalers used motorized vessels with deck-mounted, canon-fired explosive harpoons to kill whales. Historical accounts suggest that Basque, Icelandic, and Yankee whalers killed the last Gray Whales in the North Atlantic Ocean in the late 17th or early 18th century. Whether coastal whaling was solely responsible

for or only hastened the extinction of Gray Whales in the North Atlantic is unknown.

Gray Whales in the western North Pacific Ocean were hunted off Russia, Japan, and Korea from 1600 into the 19th century until the population was extirpated. From 1600 to 1860, European and American whalers pursued Gray Whales in the Sea of Okhotsk, and whales migrating near the shore along Japan were caught in nets and killed with harpoons and lances. During the "modern" period from 1860 to 1900, Russian, European, and American catcher boats pursued western Gray Whales, which were killed and brought to the shore-based stations for processing. From 1890 to 1966, Gray Whales were taken off the Korea Peninsula and Japan and in the Yellow Sea. Occasional catches were recorded off China from 1916 to 1958.

Commercial whaling on the eastern population of Gray Whales began in 1845–1846 when whalers entered Magdalena Bay in the southern Baja California to pursue the Gray Whale during the winter as an alternative to hunting Sperm Whales (*Physeter macrocephalus*) in the Pacific Ocean during the summer. Word spread of the wintertime concentrations of Gray Whales in the bays and lagoons of Baja California, and lagoon whaling reached its peak in the mid-1800s. From 1854 to 1901, Gray Whales also were hunted from at least 15 shore-based whaling stations located from northern California to Baja California. By the 1870s, the hunt of the Gray Whale in the eastern population was no longer economically viable, and the fishery was largely abandoned.

A period of "modern commercial whaling" involving whaling ships from the USA, Japan, Norway, and the former Soviet Union operated from 1914 to 1946 and targeted several species of Pacific whales, including Gray Whales. During this period, Gray Whales declined to critically low numbers, and they finally received international protection from commercial whaling by the International Whaling Commission in 1946. A subsistence hunt by native Arctic communities of up to 140 Gray Whales per year continues and is regulated by the International Whaling Commission and its Scientific Committee.

Today, Gray Whales in the eastern North Pacific Ocean support an ecotourism-based whale watching industry centered off the west coast of North America and in the breeding lagoons in Baja California, Mexico. One unexpected feature of whale watching in the breeding lagoons is the appearance of curious or "friendly" Gray Whales, first reported by R. M. Gilmore in 1975 from Laguna San Ignacio. He reported that Gray Whales solicited human attention by deliberately approaching whale-watching skiffs, apparently curious about the engine sound, and allowed passengers to pat them. This phenomenon continues, suggesting that if not threatened, Gray Whales are curious and will investigate boats emitting low-frequency sounds—apparently not all human interactions are disturbing to Gray Whales. The educational, recreational, and economic importance of controlled and responsible whale watching for the conservation of protected species is evident; however, Gray Whales are wild animals, and as with any wildlife, it is imperative that the whales be treated with caution and respect.

Status and Conservation

Absent formal scientific surveys, pre-whaling abundance estimates for populations of Gray Whales were extrapolated from the number of barrels of whale oil landed and ranged from 15,000 to 40,000 individuals. In more recent times, abundance of Gray Whales has been estimated from mark-recapture statistical analysis of the photographic identification of individual whales, shore-based visual surveys, and analyses of mitochondrial and nuclear genetic variation among populations.

An analysis of photographic identification of individuals revealed that approximately 120–130 Gray Whales comprised the western population in 2006, and only 26–35 of these were reproductive females. This population is projected to increase at 2–4% annually, unless additional mortality of females causes the population to decline. Genetic analyses suggest that the western population is distinct from the larger eastern population; however, in recent years, photographic identification studies confirm that the two populations share feeding grounds off the eastern coast of Kamchatka. Some photographs of individual western Gray Whales also matched photographs of individuals in the Pacific Northwest migratory range of the eastern population and the breeding lagoons of Baja California. It is presently not known to what extent, if any, these presumed western Gray Whales interbreed with eastern Gray Whales. The near-shore migration of eastern Gray Whales has allowed shore-based visual abundance censuses to be conducted periodically from Granite Canyon, California. These began in 1967 and continued to 2007. Population estimates based on these censuses have been repeatedly revised and updated as statistical analyses and modeling methods have evolved. A 2009 reanalysis of these population estimates indicated that following its protection from commercial whaling in 1946, the eastern population of Gray Whales recovered to approximately 26,000 individuals by 1988. It was believed that the eastern population reached or even exceeded carrying capacity. By 1998, the population declined to 21,135 whales, and then to 16,000 whales following a ten-fold increase in average annual mortality between 1998 and 2000. Food shortage was believed to be the likely cause of the decline.

Arctic oceanographers documented a decrease in benthic amphipod biomass during the 1990s in the primary feeding areas of Gray Whales, resulting from climate-driven ecosystem changes in the northern Bering Sea, or overgrazing of the prey base, or both. A 2007 census indicated that the eastern population increased to 19,126 whales, suggesting it was recovering and adjusting to the ongoing ecological transitions associated with global climate change. The estimated size of the eastern population was 21,000 whales in 2009.

Gray Whales received protection from commercial whaling under the 1937 International Agreement for the Regulation of Whaling and comprehensive protection under the 1946 International Convention for the Regulation of Whaling (IWC). Two US statutes provide legal protection: the Marine Mammal Protection Act (MMPA), passed in 1972, and the 1973 Endangered Species Act (ESA). In 1994, the US Department of the Interior removed the Eastern North Pacific population from the ESA's List of Endangered and Threatened Wildlife and Plants. In 2008, the International Union for Conservation of Nature (IUCN) reclassified this population from Endangered to Least Concern on *The IUCN Red List*. The western North Pacific population of Gray Whales remained listed as Endangered throughout its distribution and was reclassified by IUCN from Endangered to Critically Endangered in 2000. The Gray

Whale is also listed in Appendix I of the Convention on International Trade in Endangered Species of Wild Flora and Fauna (CITES) and Appendix II of the Convention on the Conservation of Migratory Species of Wild Animals (CMS).

In 1972, Mexico established Laguna Ojo de Liebre (also known as Scammon's Lagoon) as the world's first whale refuge in recognition of the importance of the breeding lagoons of the Gray Whale. In 1979, Laguna San Ignacio became a Whale Refuge and Maritime Attraction Zone. In 1980, Mexico extended reserve status to Laguna Manuela and Laguna Guerrero Negro. All of these lagoons lie within El Vizcaíno Biosphere Reserve, created in 1988. In 1993, the United Nations Educational, Scientific, and Cultural Organization (UNESCO) designated Ojo de Liebre and San Ignacio lagoons as World Heritage Sites, and they are also designated Ramsar-protected wetlands under The Convention on Wetlands of International Importance. In 2002, all Mexican territorial seas and Economic Exclusion Zones were declared a refuge to protect large whales. The Gray Whale also receives varying degrees of protection in the territorial waters of Canada, Russia, Japan, Korea, and China.

Assessing the cumulative effects of human and environmental risk factors to Gray Whales is critical to determining their resilience to anthropogenic disturbance and effects of climate change. Major threats to Gray Whales involve conflicts with humans and habitat disturbances throughout their geographic distribution. These include ship collisions, coastal development, oil and gas exploration and development, entanglement in fishing gear, exposure to pollution, low-frequency noise pollution from military and civilian sources, and illegal whaling.
The warming of the Arctic Ocean could have profound effects on Gray Whales—and other marine life—by disrupting feeding areas and prey populations. The continuing loss of Arctic sea ice is affecting prey types and productivity in the traditional feeding areas of Gray Whales, but changing conditions could result in the establishment of new feeding areas.

Although similar changes have occurred in geologic times, the rate of warming has accelerated in recent decades, intensified by anthropogenic inputs of carbon dioxide and other greenhouse gases into the atmosphere. In response to the changing availabilities of prey, Gray Whales are shifting their foraging distributions to more northerly and westerly areas within the Arctic Ocean. They are also now observed foraging around islands and shallow coastal areas throughout their migratory routes in numbers greater than previously recorded.

In addition to allowing access to additional resources, these transitions to new feeding areas may expose Gray Whales to competition with other marine species with which they share common prey. Fortunately, prey selection and feeding modes of Gray Whales are flexible enough that they can exploit a variety of alternative prey. This has allowed them to persist during many Pleistocene glacial and interglacial periods that resulted in rising and falling of sea levels and affected availabilities and distributions of their prey populations.

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