Marine Mammal Encyclopedia 3rd Edition
Published by Academic Press, Inc.
MAY 2016

Gray Whale

Eschrichtius robustus

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Keywords: **morphology, taxonomy, distribution, abundance, ecology, behavior, physiology, life history, bycatch, whaling, entanglement, conservation status**

I. Characteristics and Taxonomy

The gray whale (*Eschrichtius robustus*, Lilljeborg 1861) is the only living species in the family Eschrichtiidae (Ellerman and Morrison-Scott, 1951) (= Rhachianectidae; Weber, 1904). The genus name honors Danish zoologist Daniel Eschricht; *robustus* means strong or oaken in Latin.
The behavioral ecology of the gray whale is unique among mysticetes: it is the most coastal; makes the longest migration; calves near and in warm bays, lagoons, and coastal areas; and is an intermittent suction feeder (unique in cetaceans) that regularly forages on benthos (organisms living within, at, or near to the sea floor), but may also feed opportunistically on plankton and nekton by gulping and skimming.

Molecular and morphological evidence suggests a close phylogenetic relationship with rorquals (Family Balaenopteridae), and the gray whale is included in the Super Family Balaenopteroidea (Balaenopteridae + Eschrichtiidae; Demere *et al.* 2005). Although currently restricted to the North Pacific, gray whale subfossils are found on both sides of the North Atlantic where they inhabited coastal waters in historical times until their expiration in the 17th Century (Mead and Mitchell 1984). Fossil remains of *Eschrichtius* are known from the late Pleistocene off Georgia, USA (~42-30 ka; Noakes *et al.* 2013), the middle Pleistocene of southern California, USA (~300-200 ka; Barnes and

McLeod 1984), and from the late Pliocene or early Pleistocene of Hokkaido, Japan (*Eschrichtius* sp., ~3.9-2.6 Ma; Ichishima *et al.* 2006). Fossil eschrichtiids assignable to genera other than *Eschrichtius* are now known from the middle to late Pliocene of southern California, USA (possible Eschrichtius sp. cf. E. robustus; ~4.5-2.5 Ma, SDSNH 90517 & SDSNH 131162; *Deméré 2012?)*, the mid-Pliocene off North Carolina, USA (*Gricetoides aurorae*, ~4.5 Ma; Whitmore and Kaltenbach 2008), and the early Pliocene of northern Italy (*Eschrichtioides gastaldi*, ~5.3-3.5 Ma; Bisconti 2008).

Biogeographic analysis of the eschrichtiid fossil record suggests that the family evolved in the Mediterranean or North Atlantic during the latest Miocene or earliest Pliocene (Bisconti and Varola 2006). Presumably stem eschrichtiids dispersed westward (possibly via the North Equatorial Current) into the Pacific through the open Central American Seaway. Speciation in the North Pacific produced at least two lineages, one of which is represented by the modern genus. It is hypothesized the *E. robustus* evolved in the North Pacific and dispersed back into the North Atlantic during the Pleistocene via the Arctic Ocean. Glacial-interglacial oscillations and related changes in global sea level during the Pliocene and Pleistocene could have allowed multiple eschrichtiid dispersions from the Pacific into the Atlantic (Pyneson and Lindburg 2011).

The gray whale is a slow-swimming sturdy mysticete, slimmer than right whales and stockier than most rorquals. It attains a maximum length of 15.3 m (50 ft). The skin is a mottled light to dark gray with whitish blotches and heavily infested with barnacles and cyamids, or "whale lice," especially on the head. Instead of a dorsal fin, the back has a hump followed by a series of fleshy knobs, or "knuckles," along the tailstock. The baleen is cream to pale yellow, the shortest (5-40 cm), coarsest, and with fewest plates (130-180 per side) of any whale. There are typically 2-7 short, deep, longitudinal creases on the throat rather than the numerous long ventral pleats of balaenopterids. The narrow triangular head (seen from above) is moderately arched downward (seen from the side) and relatively small (~20% of skeletal length). The overall skull structure is less telescoped than in other extant mysticetes. Unique to grays is a bulging "tailstock cyst" (10-25 cm wide) of unknown function on the ventral surface of the caudal peduncle. The flukes are 3-3.6 m across and frequently lifted before a deep dive. The blow is 3-4 m high, and may be heart-shaped, bushy, or columnar.

II. Distribution and Abundance

Once found throughout the Northern Hemisphere, the gray whale became extinct in the Atlantic and now is confined to the productive neritic and estuarine waters of the North Pacific Ocean and adjacent waters of the Arctic Ocean. Mixing between Atlantic and Pacific populations was possible during warm interglacial periods (such as 1-12 Ka). Whales could have moved between the Beaufort Sea and Hudson Bay until the Little Ice Age when temperatures cooled enough for ice to form across most of the Northwest Passage of the Arctic (1400-1850) isolating the populations. Two extant Pacific populations of gray whales are currently recognized. The eastern North Pacific (ENP) population (also called the *American, California,* or *Chukchi* stock) numbers approximately 20,000 individuals (Laake *et al.*2012), and occurs in the eastern North Pacific and Amerasian Arctic Oceans (between North America and Asia). The western North Pacific (WNP) population (also called the *Asian, Korean,* or *Okhotsk stock*) occurs in the western North Pacific (off Asia), numbers less than 250 individuals, and is critically endangered.

While genetic studies using mitochondrial DNA and nuclear DNA show the western and eastern North Pacific gray whales are differentiated at the population level (Lang *et al.* 2011, LeDuc *et al.* 2002), satellite-radio tagging (Mate *et al*. 2015) and photographic-identification studies (Weller et al. 2012) indicate that these two populations mix to an undetermined degree on the feeding and on the breeding grounds of the eastern North Pacific population. A third group, the Pacific Coast Feeding Group (PCFG), numbering approximately 200 individuals (Calambokidis, *et al.* 2002) has been proposed within the eastern North Pacific population, however, current information is insufficient to determine whether this feeding group constitutes a distinctive population within the larger eastern North Pacific population (Weller *et al.* 2013).

A. North Atlantic Population(s) (Extinct)

The modern gray whale once existed in the North Atlantic in the coastal waters of Europe, Iceland, and North America. Subfossils from Europe have been found off the Baltic coast of Sweden, Belgium, the Netherlands, and England (the most recent dated 1650), and along the coast of the United States from New Jersey to Florida (the most recent from colonial times about 1675). The exchange of gray whales between the Pacific and the Atlantic would have been climate dependent

and movements across the Arctic could have occurred during the Pleistocene and early Holocene during periods when the Bering Strait was ice free (Alter *et al.* 2015).

Based on written accounts, the last few gray whales in the North Atlantic were killed in the late 17th or early 18th century by early Basque, Icelandic, and Yankee whalers. Whether coastal whaling was solely responsible for or only hastened the extinction of an already generally depleted North Atlantic population is uncertain. Genetic diversity in Atlantic gray whales suggests their population(s) declined over an extended interval that predates the period of intensive commercial whaling, indicating their decline may have been precipitated by Holocene or other ecological causes in addition to whaling (Alter *et al.* 2015).

Additional support for the exchange of gray whales between the Pacific and Atlantic comes from the sighting of a gray whale off of Israel and Spain in the Mediterranean in 2010 (Scheinin *et al.* 2011), and another sighting off of the Namibian coast of southeast Africa in 2013 (Elwen and Gridley 2013), the first confirmed sighting of a gray whale in the Southern Hemisphere in historical times. These gray whales were 22,000–23,500 km from the Pacific winter breeding grounds of the eastern North Pacific population, demonstrating the gray whales' preponderance for undertaking long migrations. Present-day climate changes, ocean warming and reduction of Arctic sea ice no doubt allowed these gray whales to enter the North Atlantic Ocean via the Arctic Sea, and demonstrate that such exchanges between oceans are possible for marine species during periods of interglacial minimum ice conditions.

B. Western North Pacific Population (Critically Endangered)

The western North Pacific gray whale is believed to be a remnant population close to extinction that occurs off Russia, Japan, Korea, and China. Although it once utilized coastal feeding sites throughout the northern Sea of Okhotsk, today the core of the population feeds primarily from June to November off the northeastern coast of Sakhalin Island, Russia. Some individuals also feed off Bering Island in the western Bering Sea, the northern Kuril Islands in the eastern Okhotsk Sea, the coastal waters of the northern Okhotsk Sea, and off eastern Kamchatka which is also utilized by the eastern North Pacific population (Weller *et al.* 2013). The Sakhalin Island foraging habitat, which is

vital especially for pregnant and lactating females, lies within a region that is undergoing massive oil and gas development (Reeves *et al*., 2005).

Knowledge of the migration routes and winter breeding grounds for the western North Pacific gray whale is fragmentary at best. Historical and contemporary capture, sighting, and stranding records suggest the population's current north-to-south migratory route includes eastern Kamchatka, the eastern shores of Sakhalin Island and mainland Russia, the Korean Peninsula, the east and west coast of Japan, the East China Sea, and the South China Sea as far south as Hainan Island in winter.

Evidence for spatial and temporal overlap between the western North Pacific and eastern North Pacific gray whales includes results of satellite-radio tagging, photographic identification studies, and genetics. Three satellite-radio tagged individuals that, rather than migrating south to presumed wintering grounds along China's coast, migrated from Sakhalin Island to the west coast of North America during the winter breeding season where one individual (a female) visited all three of the principal breeding lagoons of the eastern North Pacific population (Mate *et al.* 2015). Photographic identification matches of 23 western gray whales were made between Sakhalin Island and British Columbia, and between Sakhalin Island and the winter breeding lagoons of the eastern North Pacific population in Baja California, Mexico (Weller *et al.* 2012). Genetic matches with western gray whales were made with genetic samples collected off Santa Barbara, California, USA and Vancouver Island, British Columbia, Canada (Lang *et al.* 2011). Some western gray whales apparently migrate to the west coast of North American during the winter breeding season where they interact (and perhaps breed) with the eastern North Pacific population, while past and present observations of western gray whales off of Japan, Korea, and China demonstrate that not all western gray whales share a common wintering ground.

The western population was reduced to such low numbers by heavy international exploitation off Russia, Korea, and Japan from the 1840s to mid-1960s that it was believed to be extinct. Estimates of prior abundance are highly speculative: from 1,500 to 10,000 whales. In 2015, the population size was estimated to be only 218 whales (90% CI =196-240) (Cooke *et al*., 2015). Constraints affecting population recovery include the low estimated number of reproductive females (44; 90% CI = 38-49),

low juvenile survival, a male-biased sex ratio, and genetic mixing resulting from breeding with the eastern North Pacific gray whale population. Surviving whales continue to be threatened by occasional exploitation by Japanese and Chinese fishermen, entanglement in fishing gear, collisions with ships, oil and gas exploration/development, and predation by killer whales, especially on calves. The winter mixing of the western gray whales with the larger eastern population, suggests that the number of "true" western gray whales may be much smaller than previously believed, and be of greater conservation concern as one of the most Critically Endangered populations of whales (Weller *et al.* 2013, http://www.iucnredlist.org).

C. Eastern North Pacific Population

From late-May to early-October, the core of the eastern North Pacific population is on its feeding range in the shallow coastal and shelf waters between Alaska and Russia and along their northern coastlines. Until the late 1990s, the northern Bering Sea, especially the Chirikov Basin, as well as the southern Chukchi Sea were the primary feeding grounds and supported high biomass of benthic amphipod prey and large numbers of feeding gray whales. However, in recent years a major ecosystem shift in the northern Bering Sea has resulted in a decline in the benthic productivity of this region affecting the distribution of gray whale prey species, and the summer distribution of the whales (Grebmeier *et al*., 2006, Moore 2008). A warming trend from arctic to subarctic conditions has resulted in higher air temperatures, lower winter ice cover, increases in seawater temperature, and a decline in benthic productivity reducing food supply to benthic communities in the Chirikov Basin and no longer favoring benthic predators. Gray whales have responded by shifting their foraging distribution to areas with presumably reliable prey sources including: the Gulf of Alaska including Kodiak Island, the southeastern Bering Sea (primarily along the eastern Alaska Peninsula and mainland coast), the southern Chukchi Sea, the western Beaufort Sea (east to 130ºW off northern Canada). Additional feeding sites are located in the western Bering Sea (off the Koryak coast), along the southeastern Kamchatka Peninsula (from 51º-55ºN) where their range overlaps with western North Pacific gray whales.

This population makes the longest annual migration of any mysticete, 15,000-25,000 km (roundtrip). Spanning up to 55º of latitude, the migration connects Arctic feeding grounds with southern mating

regions, calving, and assembling grounds in temperate and subtropical coastal waters in winter, which are presumably safer from killer whale predation (Corkeron and Connor 1999). In the fall, whales start the southward migration with females in late pregnancy going first, followed by adults and immature females, then immature males. They exit the Bering Sea via Unimak Pass, Alaska, with ~90% filing through from mid-November to late December, and mainly follow the coast to Mexico (Rice and Wolman 1971). The trip averages 2-months. Mating occurs mainly during the middle of the migration, but courtship and mating also occur in the winter assembly area (Jones *et al.* 1984, Swartz 1986).

Winter grounds extend from central California south along Baja California, the Gulf of California, and mainland coast of Mexico south to Bahía de Banderas, Jalisco (20º45'N, 105º34'W). Pregnant females carrying near-term fetuses begin to arrive by late December to early January. By mid-February, the bulk of the population has arrived. Calving areas along coastal California and the west coast of the Baja California Peninsula include: San Diego Bay (possibly occupied historically, but no longer used); Laguna Ojo de Liebre (Scammon's Lagoon); Laguna Guerrero Negro (when its entrance is open); Laguna San Ignacio; and Bahía Magdalena and adjacent waters (from Estero Las Animas to Bahía Almejas); and eastern shore of the Gulf of California along the open coast of Yavaros (Sonora) and Bahía Reforma (Sinaloa) (Rice and Wolman, 1971).

While some calves are born during the latter portion of the southward migration, most calves are born near to or within the coastal lagoons and the Bahía Magdalena region. Once in their winter range, gray whales behave as two separate groups, females with calves of the year and breeding adult males and females, that segregate spatially and temporally to some degree. The majority of whales, except most mothers with newborn calves, occur outside the lagoons and in the bays in front of the lagoons, including Bahía Sebastián Vizcaíno, Bahía de Ballenas, and elsewhere along the coastline. While they move about within the winter range and the lagoons, female-calf pairs prefer the interiors of the lagoons where they aggregate in groups to nurse and care from their young, and minimize aggressive interactions with breeding adults (Swartz 1986). Photographs of gray whales indicate that some individuals return each year to specific lagoons, while others move between the major lagoons and aggregation areas. The average duration of stay in a breeding lagoon for breeding adults is 10 days,

while females with calves may stay a month or longer in one area (Urban *et al*. 2003).

El Niño (warm) and La Niña (cold) events cause variability in the temperature of the Mexican Pacific, which influences gray whale distribution and movements. During El Niño, the migration of whales, particularly females with calves, to Bahía Magdalena and Laguna San Ignacio diminishes, while it increases during periods of La Niña with some gray whales migrating into the Gulf of California presumably to find warmer water (Urban *et al.* 2003, Salvadeo *et al.* 2015).

The north migration to the summer feeding grounds occurs as two phases. The first phase (late January through March) consists of females that recently conceived and are now pregnant and migrate north first to maximize feeding time in the Arctic, followed by adult males, then juveniles. The second phase (April through May) consists primarily of females with young calves. They remain in the breeding areas longer allowing calves to strengthen and rapidly increase in size before the north migration (Swartz 1986). Mothers and calves travel very close to shore (90% are within 200 m) mostly alone or in pairs.

The north migration culminates in the dispersal of the population throughout the northern feeding grounds. Exceptions are pockets of whales that feed opportunistically south of the Bering Sea during summer, or perhaps much of the year. In some years a few whales are observed year round in Bahía San Quintin and Cabo San Lorenzo, on the Pacific coast of Baja California, and Bahía de Los Angeles in the Gulf of California.

Commercial whaling of eastern North Pacific gray whales began in 1846. Estimates of historic pre-whaling abundance differ widely. Those derived from whaling statistics range from 15,000-20,000 whales (Henderson, 1972) to 30,000-40,000 (Scammon, 1874), while a population estimate of prior abundance based on analysis of DNA diversity and stable isotopes suggests a much larger pre-whaling population (eastern and western populations combined) averaging ~96,000 individuals (range 76,000-118,000), that presumably declined as the result of changes in the ecosystem and creating in a genetic "bottleneck" concurrent with the onset of commercial whaling (Alter *et al*., 2007 and 2012). The population was hunted to very low numbers by 1939 (models suggest possibly a few

thousand). The stock finally received limited protection from commercial whaling in 1937 and full protection in 1946 under international treaty, except for a small aboriginal hunt. It is not known how many whales remained at that time. The population made a dramatic comeback to 21,000 whales, and was removed from the U.S. government's endangered species list in 1994. Growth continued through 1997/98, when abundance reached a high of 29,758 whales, and there were indications the population might be approaching carrying capacity (Rugh *et al*., 2005).

In 2000/01 the abundance estimate for the eastern population dropped alarmingly by 35% to 19,448, and in 2001/02 it was 39% less at 18,178 whales, indicating there had been a large die-off of about 11,500 whales over a four-year period (Rugh *et al.*, 2005). In addition, the number of calves produced (based on counts of calves observed in the winter breeding lagoons) annually during period from 1999 to 2001 was about 70% lower than during the previous 5-year period (Swartz *et al.* 2014). The population die-off was coincident with a spike in the number of stranded dead whales in 1999 (274 whales) and 2000 (368 whales), about ten times greater than the annual average during the previous decade (Gulland *et al.* 2005). The emaciated condition of many indicated they had starved (LeBoeuf *et al.* 2000). During this time, many living gray whales were observed to be thin or emaciated. Likely causes of these events include food shortages resulting from the downturn in benthic biomass in the gray whale's primary feeding areas during the 1990's, overgrazing of the prey base that could no longer sustain the growing population, disease, or some combination of these cannot be ruled out (Moore 2008).

The 2006/07 census suggests that the eastern North Pacific population recovered to approximately 20,000 (Laake *et al.* 2012) and likely increased to 22,000 by 2009 (Punt and Wade 2012). Winter calf abundance in the breeding lagoons of Mexico remained low between 2007 and 2010, but counts of these whales increased between 2011 and 2015 (Swartz *et al*. 2014, Urban *et al.* 2015). It is believed that recovery from the mortality event of 1999-2000 included new generations of breeding females reaching sexual maturity, and they began to contribute to the increasing number of calves observed in the breeding lagoons during the winter (Swartz *et al.* 2013 and 2014). There is also evidence that some species, like gray whales, may benefit from ecological changes in the Arctic that result in new and/or enhanced foraging opportunities such as ice-free coastal habitats and extended foraging

periods in formerly ice-covered seas (Moore and Huntington 2008). In total, these observations suggest that gray whales clearly respond to ecosystem alterations and may be indicators or "sentinels" to ecological changes that span decades and thousands of kilometers (Moore 2008).

III. Ecology

A. Diet and Feeding

The feeding ecology of gray whales is unique and complex. The diet consists of a wide variety of benthic organisms (infaunal, epibenthic, and hyperbenthic) but also includes planktonic and nektonic organisms (midwater and sea surface) and perhaps some plants. Gray whales use three foraging methods: they typically rely on intermittent suction as their primary mode but also opportunistically employ gulping and skimming to capture midwater and sea surface species. They are able to switch techniques to exploit the most optimum prey species, or assemblage of species at any one location within their summer-fall feeding range and elsewhere in the migratory and wintering areas. Foraging activity occurs at water depths of 4-120 m, but mostly at 50 m or less. Water is obtained from their food (most fish and invertebrate prey consist of 60-80% water) and metabolically derived water from the consumption of body fat when not feeding.

Most gray whales concentrate their feeding during five-months**,** from about May through October (eastern population) and June-November (western population) when they are in high-latitude high-productivity waters where food resources are patchy but dense. They forage primarily on or near the ocean floor and appear to feed continuously, 24-hours a day. Gray whales preferentially forage on aggregations of crustaceans and invertebrates. At least 60 benthic amphipod species, 80-90 other benthic invertebrate species, and small fish occur in the northern diet. Principal prey in soft-bottom habitats include infaunal amphipods (tube-dwelling ampeliscid amphipods and burrowing pontoporeid amphipods dominate), polychaete worms, and bivalves. In some areas gray whales also feed on locally abundant swarming species such as cumaceans, mysids, shrimp, krill, mobile amphipods, and shoals of sardines and anchovy. Energy might also be obtained from plant material (*e.g.*, algae, kelp, sea grass) which is deliberately ingested in some cases, probably more than has usually been assumed, rendering the gray whale a partial herbivore, but almost nothing is known about the role of plants in their feeding ecology (Nerini, 1984). During the feeding season an adult

eastern gray whale might consume ~220,800 kg of food (using 1,200 kg/day and 184 feeding days) (Zimushko and Lenskaya, 1970).

During most or all of the 6-7 months when gray whales are migrating and on the winter breeding grounds, they primarily fast and rely on stored lipid in body fat and blubber as the prime energy source. When whales return to northern feeding grounds, they will have lost 16-30% of body weight and must single-mindedly forage to replenish fat reserves (Rice and Wolman 1971). Lactation represents the greatest cost of reproduction, and pregnant females put on 25-30% more weight than other whales (exclusive of fetus). The metabolic digestion of lipids is also a critical source of water essential to maintaining water balance during fasting or greatly reduced food intake. Exceptions are small lactating females, which probably resume feeding on the north migration, and juvenile animals that tend to feed opportunistically throughout the year.

Some eastern North Pacific gray whales (~1,000 or 5% of the population) do not complete the annual migration to the feeding grounds and remain south of the Aleutian Islands during summer to forage opportunistically and sporadically in localized areas on infauna, swarming benthic invertebrates, and planktonic preys (e.g., amphipods, isopods, mollusks, cumaceans, shoaling mysids, shrimp, crabs, herring, eggs and larvae). Summer foraging gray whales are observed along Kodiak Island, southeast Alaska, British Columbia, the Pacific Northwest (i.e., the proposed Pacific Coast Feeding Group), and areas southward to Baja California (Darling, *et al.*, 1998; Moore *et al*., 2007, Calambokidis *et al.* 2002).

To suction feed, the gray whale uses gular muscles and the tongue in a piston-like action to suck prey into the mouth. When foraging on infauna (prey living within sediments), whales roll on their side with the head just above the bottom and swim slowly while suctioning prey and sediment into the side of the mouth in pulses and filtering the prey with their baleen. This creates a series of large excavations, or "feeding pits," in a single dive (pits are ~3m long, 1 m wide, and 1/2 m deep), and whales often trail clouds of sediment, or "mud plumes," in their wake (Fig. 5). This foraging on infauna significantly affects the habitat through sediment disruption and resuspension, and removal of the benthic prey assemblages. When viewed from above the sea surface, indications of suction

feeding in the water column include defecating whales, fecal slicks, whales trailed by seabirds, and animals "working" (diving repeatedly) in an area. Gray whales also commonly use intermittent suction to feed on swarming organisms in near-bottom water and shoaling prey in the water column.

As a feeding generalist and flexible forager, the gray whale is responsive to feeding opportunities along their entire range and varies its foraging method accordingly. This provides insights into gray whale survival over the millennia. During Pleistocene glacial advances, the most recent of which ended 10-12 Ka , sea level was ~75 m lower than now. Consequently, areas that are currently major feeding grounds were above sea level, and marine access to the Arctic was blocked by the Bering land bridge. The ability to use alternative prey, feeding modes, and locations may have been critical to the species during periods of glacial maxima when continental shelf areas were above sea level (Highsmith *et al*., 2006).

B. Predators and Parasites

The killer whale (*Orcinus orca*) is the only predator of gray whales. Tooth rakes often occur on living whales, thus many attacks are not fatal. Annual calf mortality from killer whale attacks may be as high as 35% of the annual production (Sumich 2014). A reduced risk of calf mortality by killer whales (more abundant at high latitudes in colder coastal seas) is proposed as the primary benefit to females migrating to give birth in the subtropics (Corkeron and Connor 1999). Even so, calves remain prime targets during the north migration. Gray whales attempt to escape from killer whales by swimming into shallow water, often inside the surf zone.

There are some reports of sharks, particularly great white sharks, attacking gray whales, and sharks are known to feed on dead whales. Because sharks are scavengers as well as predators, it is not known if ingestion was pre- or post-mortem.

Gray whales have heavy infestations of external parasites and commensals, more than any other cetacean. A host-specific barnacle, *Cryptolepas rhachianecti,* forms large colonies deeply embedded in the skin. Three species of cyamids (whale lice), *Cyamis scammoni*, *Cyamus kessleri,* and *Cyamus ceti* feed on skin around barnacles, blowholes, skin folds, and swarm into wounds. These are not

known to be harmful, and may be more accurately regarded as mutualists or commensals rather than parasites, although whales in poorer nutritional condition tend to have heavier infestations. Apparently, gray whales are less prone to internal parasites than other cetaceans. These include trematodes (liver), nematodes (stomach), and cestodes and acanthocephalans (small intestine). Some require fishes as intermediate hosts (Rice and Wolman, 1971).

IV. Behavior and Physiology

A. Social Organization

Gray whales form no long-lasting associations and apparently have little social cohesion. The bond between mother and calf stops after weaning. They migrate solo or in transitory pairs and small groups. On the feeding grounds, whales are usually single or in small groups and widely dispersed, not surprising given the large benthic area needed to supply the energy requirement of each whale. Large aggregations can occur on feeding grounds and breeding grounds but are in constant flux. There is no territoriality or aggression toward conspecifics, except that males will attempt to mate with females that have recently given birth to calves. Care-giving behavior to aid young in the calving areas and joint defense against killer whale attacks occur but are rare. Whalers report "standing-by" behavior in which whales support or refuse to leave an injured companion, making them easy targets.

B. Sensory Perception

Underwater sound rather than vision is the gray whale's primary sensory modality. They create a variety of phonations or calls, which are mostly low frequency broadband signals that range from about 100 Hz to 4 kHz but may go up to 12 kHz. Use of mostly low frequency sounds might be an adaptive strategy for grays to circumvent the high levels of natural background noise prevalent in the coastal environment (*e.g.*, waves, bubbles, currents, ice movement) by producing sounds that are generally at frequencies below it. Unfortunately, manmade noise is a rapidly increasing pollutant in the ocean. Much of it occurs in the lower frequency range and has a high level of output (*e.g.*, high-intensity air guns for seismic exploration, military and civilian sonar systems, ship-shock trials, offshore drilling and construction, industrial activities, supertankers, icebreakers). Anthropogenic noise can interfere with whale communication, reduce ability to hear natural sounds that aid in

foraging and navigation, and may damage hearing. Grays may circumvent this noise by increasing call types, rates, and loudness to enhance signal transmission and reception.

Gray whales see moderately well both in air and water, but the visual system likely is of inferior importance to that of the auditory system because of functional restrictions in turbid water and darkness. The position of the eyes suggests that they have stereoscopic vision forward and downward permitting efficient estimation of distance. The eyes are adapted for heightened sensitivity to dim light and for improving contrast and resolution underwater. Grays possess a tiny presumably functional olfactory system, but are microsmatic at best. The sense of touch is very well developed, particularly along the head, rostrum and lower jaw where highly innervated bristles or vibrissae occur, particularly on calves, but become obliterated by barnacles and cyamids in adults (Sumich 20914). Taste buds occur at the back of the tongue.

C. Swimming, Breathing and Diving

On migration, eastern gray whales mostly progress in one direction and travel at the same speed day and night. The southward trip to the winter grounds averages 55-days, at ~7-9 km/hr (144-185 km/day). Northbound grays average ~4.5 km/hr (88-127 km/day). Mothers and calves travel ~96 km/day; speed is about the same as other whales, but they pause to rest and nurse. Calves position themselves in a "drafting" or "slip-stream" position alongside their mothers, and the hydrodynamic effect is that the calf can gain thrust to swim while saving energy at traveling speed. If pursued, grays reach 13 km/hr but can only maintain that speed for a few hours. In extreme duress, speed can surge to 16 km/hr for short bursts. Breaching, spyhopping, and lobtailing are common during migration and on the breeding grounds. Maximum dive depth is ~170 m. Maximum duration of breath holding is ~26 min., associated with resting and hiding. Blow pattern varies depending on age (calf *vs.* adult) and behavior, but is generally "columnar" or "heart-shaped" when viewed from behind the animal.

V. Life History

Gray whales appear to have a promiscuous mating system, where both sexes may copulate with several partners during the breeding season. Multiple inseminations likely occur, suggesting that sperm competition is a feature in reproduction (Swartz 1986). Sexual maturity is attained at from 6

to12 years (average is 8 for both sexes), at a mean length of 11.7 m in females and 11.1 m in males. Mating and calving are strongly seasonal and synchronized with the migratory cycle. Males have a peak of spermatogenesis in late autumn or early winter correlated with the time females come into estrus (Rice and Wolman 1971). Thus, mating occurs mainly during the middle of the south migration, but courtship and mating activity also continues during January and February as whales travel into and socialize throughout the winter assembly range where most females calve (eastern North Pacific population).

Males can mate annually. Females usually have one estrous cycle per two years (rarely they may ovulate twice), thus, at most only half the reproductive females are available annually for mating. Ovulation usually occurs in late November and December within a 3-week period during the south migration (while the eastern population is still north of central California). Females usually conceive following their first ovulation but may undergo another estrous cycle about 40 days later if they fail to conceive (Rice and Wolman, 1971).

Copulation is belly to belly. Pairs or trios of whales sometimes court and mate quite gently. However, in larger groups of up to 20 consorting adults, there is a high level of activity marked by rolling, splashing, and energetic cavorting (Fig. 7). Estimates of the gestation period vary from 11 to 13 months. Females bear one calf at intervals of two years, but longer intervals of three or more years occur. Birth season for the eastern population lasts from late December to early March (median birth date is January 27) when near-term females are in or near the Mexican calving grounds and lagoons, although some are born during the southward migration off California.

A mother's bond with her calf is very close; they are unusually affectionate, protective, and will fight fiercely, even to the death, to defend young from danger. Calves consume about 189 liters of rich milk per day (53% fat, greater than any other cetacean, 6% protein). Weaning occurs at 7-8 months around August when calves are 7.6-9.5 m long. Females then have a 3-4 month resting period until November-December when estrus begins anew.

Most neonates are 4.6-4.9 m long and weigh about 680 to 920 kg. Adults weigh 16,000 to 45,000 kg

and stop growing at about 40 years, when the average female is 14.1 m long and the average male is 13.0 m. The largest female recorded was 15.3 m and the largest male 14.6 m long (Rice and Wolman 1971). After birth, females are slightly bigger than males at all ages, but there is no significant difference in their appearance (the distance from the genital slit to the anus is longer in males). While actual longevity is unknown, the age of harvested gray whales is estimated from growth layers in the waxy earplugs that fill the auditory canal , and the number of corpora albicantia in the ovaries of females (a single corpora = 2 yrs). Rice and Wolman (1971) estimated the age of a harvested female that had 34 corpora albicantia to be 76-77 years old (34 corpora x 2 = 68 years + 8-9 years to sexual maturity = 76-77 years). Long-term photographic identification research of living gray whales in Laguna San Ignacio has documented minimum ages for breeding females from 26 to 46 years (Martinez *et al. In Press* - 2016).

IV. Interactions with Humans

A. Whaling

Although the International Whaling Commission (IWC) banned commercial whaling of gray whales in 1946, it allows aboriginal whaling of the eastern population for cultural and subsistence purposes. The quota for aboriginal kills off the Chukotka Peninsula (Russian Federation) is set at 620 whales, with a maximum of 140 in any year. Whale oil, meat, bones, hide, and baleen are used.

There has been illegal hunting of gray whales in violation of the IWC moratorium on whaling, by its member nations, as well as pirate whaling by fleets acting beyond national jurisdiction. In 2000 it was revealed that this prohibited species was killed "at every sighting" by the former Soviet Union from 1961-1979. Occasionally a western North pacific gray is taken incidentally by Japanese fishermen (*e.g.*, in 2005, 3 females were killed in fishing nets). The IWC prohibits killing them deliberately, but sale as "bycatch" occurs in markets in Korea, Japan, and elsewhere. DNA profiling of whale meat suggests the true magnitude of intentional "net whaling" (deliberate entanglement in fishing nets and gear) of western gray whales sold as bycatch in Asia is larger than reported. If this mortality continues in such a small population, the western North Pacific population is projected to decline towards extirpation.

B. Whale Watching Industry and Friendly Whales

The eastern North Pacific population of gray whales supports a major whale-watching industry. Whalers dubbed the gray whale the "devil fish" for their ferocity when harpooned, yet it is gentle species if unmolested. Known today for approaching boats curiously and letting whale watchers pet them, the gray whales in Laguna San Ignacio, Mexico are popularly called the "friendly whales" or "Ballenas Misteriosas". From a conservation perspective, whale-watching eco-tourism poses both risks and benefits to gray whales. Risks arise from the potential for vital behavior patterns and essential habitat to be degraded by too much attention. Benefits come from a better-educated public more likely to highly value gray whales and to provide support for their protection and conservation of their habitats (Gómez-Gallardo *et al.* 2014).

C. Oil and Gas Development and Exploration

Ongoing oil and gas exploration, development, and production activities throughout the gray whale's coastal range and habitats constitute a continuing potential for disturbance from powerful low-frequency seismic-surveys, construction noise, and exposure to pollution. Bioenergetic models suggest that prolonged disturbance could result in energy losses with significant consequences for gray whale reproduction (Villegas-Amtmann *et al.* 2015).

Discovery of extensive oil and gas resources on the Sakhalin Shelf has placed the Critically Endangered western North Pacific gray whales in peril. Recent findings that some western gray whales overwinter with the eastern North Pacific population along the west coast of North America suggests that the number of "true" western gray whales may be much smaller than previously believed, and of greater conservation concern. The feeding ground off Sakhalin Island lies within the region which is now the site of ongoing large-scale oil and gas development by several consortia of Russian and multinational companies. Although some measures are being taken to mitigate deleterious effects, the oil and gas production, plus associated extensive shipping and aircraft traffic, may damage the habitat, stress or disturb the whales, or displace the population, which is dependent on the Sakhalin Shelf for its primary feeding ground.

D. Ship Strikes and Entanglements

Gray whales cross many commercial shipping lanes along their coastal migratory routes, and ship strikes to these slow swimming whales are inevitable. Scars from non-lethal collisions, propellers, and fishing lines are frequently seen on gray whales photographed in the breeding lagoons of Baja California. Incidental takes and entanglement in coastal fishing gear, lines and floats pose threats to individual whales, particularly calves, and can result in injury and death.

E. Pollution

Gray whales are not known to accumulate persistent organochlorine compounds or other environmental contaminants presumably because they feed low on biological food chains, and in areas with low human habitation and industrial development. However, as the ocean environment becomes increasingly contaminated with toxic fat-soluble substances, and as these substances accumulate in a gray whale's body fat and blubber during its life, they may become mobilized during annual periods of winter fasting between periods of summer feeding, and be transferred to calves in mother's milk during the first few months of life when the calves are rapidly growing.

F. International and National Protection

Gray whales received protection from commercial whaling under the 1937 *International Agreement for the Regulation of Whaling*, to which most whaling nations concurred, and more comprehensive protection under the 1946 *International Convention for the Regulation of Whaling*, to which the Soviet Union and Japan also adhered. In the United States, two statutes provide legal protection: the *Marine Mammal Protection Act*, passed in 1972; and the *Endangered Species Act*, which became law in 1973. The eastern North Pacific population recovered and in 1994 the U.S. Department of Interior removed it from the *List of Endangered and Threatened Wildlife and Plants* (under the U.S. Endangered Species Act). The World Conservation Union (IUCN) reclassified it from *Endangered* to *Lower Risk*: *conservation dependent* in the *1996 IUCN Red List of Threatened Animals.* However, these actions had no bearing on the status of the western North Pacific gray whale population, which remained *Endangered* throughout its range. It was reclassified in the IUCN (2012) Red List from *Endangered* to *Critically Endangered* (under 1996 categories and criteria) (http://www.iucnredlist.org). The gray whale is listed in Appendix 1 of CITES.

Mexico recognized the importance of the breeding lagoons along the Baja California coast to the recovery of the gray whale, and it is the only nation to provide important habitat protection for the eastern North Pacific population. In 1972, it established Ojo de Liebre Lagoon (the principle calving and nursery area) as the world's first whale refuge. In 1979, San Ignacio Lagoon became a *Whale Refuge and Maritime Attraction Zone*. In 1980, reserve status extended to Laguna Manuela and Laguna Guerrero Negro. All lie within the *El Vizcaíno Biosphere Reserve*, created in 1988, in which all whale-watching eco-tourism is regulated under sustainable management plans established in the 1990's. In 1993, the United Nations Educational, Scientific, and Cultural Organization (UNESCO) made Ojo de Liebre and San Ignacio Lagoons World Heritage Sites. Lastly, in 2002, all Mexican territorial seas and EEZ were declared a refuge to protect large whales (Dedina 2000).

References KEY REFERENCES

Andrews, R.C. (1914). Monographs of the Pacific Cetacea. I. The California gray whale (*Rhachianectes glaucus* Cope). *Mem. Am. Mus. Nat. Hist.*. **1**(5), 227-287.

Alter, S.E., Rynes, E., and Palumbi, S.R. (2007). DNA evidence for historic population size and past ecosystem impacts of gray whales. *Proceedings of the National Academy of Sciences.* **104**(38):15162-15167.

Alter, S.E., Newsome, S.D., and Plumbi, S.R. (2012). Pre-whaling genetic diversity and population ecology in eastern Pacific gray whales: Insights from ncient DNA and Stable Isotopes. PLoS ONE 7(5): e35039. doi:10.1371/journal.pone.0035039.

Bisconti, M., and Varola, A. (2006). The oldest eschrichtiid mysticete and a new morphological diagnosis of Eschrichtiidae (gray whales). *Riv. Ital. Paleo. Strat.*. **112**(3),1-11.

Bisconti, M. (2008). Morphology and phylogenetic relationships of a new eschrichtiid genus (Cetacea: Mysticeti) from the early Pliocene of northern Italy. Zoological Journal of the Linnean Society 153:161–186

Bisconti, M. (2010). New description of "*Megaptera*" *hubachi* Dathe, 1993 based on the holotype skeleton held in the Museum für Naturkunde, Berlin. Quad. Mus. St. Nat. Livorno 23:37-68.

Calambokidis, J., Darling, J.D., Deeke, V., Gearin, M., Megill, W., Tombach, C.M., Goley, D., Toropova, C., and Gisborne, B. (2002). Abundance, range, and movements of a feeding aggregation of gray whales (*Eschrichtius robustus*) from California and southeastern Alaska in 1998. Journal of Cetacean Research and management 4(3): 267-276.

Cooke, J.G., Weller, D.W., Bradford, A.L., Burdin, A.M., and Brownell, Jr. R.L. (2007). Population assessment of western gray whales in 2007. Rep. Intl. Whal. Comn. SC/59/BRG41.

Corkeron, P.J. and Connor, R.C. (1999). Why do baleen whales migrate? Marine Mammal science 15: 1228-1245.

Darling, J.D., Keogh, K.E., and Steeves, T.E. (1998). Gray whale (*Eschrichtius robustus*) habitat utilization and prey species off Vancouver Island, B.C. *Mar. Mamm. Sci.* **14**(4), 692-720.

Dedina, S. (2000). "Saving the Gray Whale: People, Politics, and Conservation in Baja California." University of Arizona Press, Tucson.

Deméré, T.A., Berta, A., and McGowen, M.R. (2005). The taxonomic and evolutionary history of fossil and modern balaenopteroid mysticetes. *J. Mamm. Evo*l. **12,** 99-143.

Deméré, T.A. (2012 - In Press). A new extinct eschrichtiid from the Pliocene San Diego Formation. SDSNH No. 90517 & 90489

Elwen, S.H. and Gridley, T. (2013). Gray whale (*Eschrichtius robustus*) sighiting in Namibia (SE Atlantic) – first record for Southern Hemisphere. Rep. Intl. Whal. Comn. SC65a/BRG30.

Geisler, J.H., and Sanders, A.E. (2003). Morphological evidence for the phylogeny of Cetacea. *J.*

Mamm. Evol. **10,** 23-129.

Gómez-Gallardo-U., A., del Monte-M, L., and Urbán-R, J. (2014). La observatión turística de ballenas en laguna San Ignacio: de México para el mundo. La Jornada Ecololgica. www.jornada.unam.mx/2014/03/31/eco-h.html.

Gulland, F.M.D., Pérez-Cortés, H., Urbán-R., J., Rojas-Bracho, L., Ylitaio, G., Weir, J., Norman, S.A., Muto, M.M., Righ, D.J., Kreuder, C., and Rowles, T. (2005). Easytern North Pacific gray whale Eschrichtius robustus) unusual mortality event, 1999-2000. U.S. Dep. Commer., NOAA Tech. Memo. NMFS-AFSC-150, 33p.

Henderson, D.A. (1972). "Men and Whales at Scammon's Lagoon." Dawson's Book Shop, Los Angeles.

Highsmith, R.C., Coyle, K.O., Bluhm, B.A., and Kona, B. (2006). Gray whales in the Bering and Chukchi Seas. *In* "Whales, Whaling, and Ocean Ecosystems" (J.A. Estes, D.P. DeMaster, D.F. Doak, T.M. Williams, and R.L Brownell, Jr., Eds.). Univ. of California Press.

Ichishima, H., Sato, E., Sagayama,T., and Kimura, M.(2006). The oldest record of Eschrichtiidae (Cetacea: Mysticeti) from the Late Pliocene, Hokkaido, *Japan. J. Paleontol.* **80**, 367-379.

Jones, M.L., Swartz, S.L. and Leatherwood, S. (Eds.). (1984). "The Gray Whale *Eschrichtius robustus*." Academic Press, Orlando, Florida, USA.

Laake, J.L., Punt, A.E., Hobbs, R., Ferguson, M., Rugh, D., and Breiwick, J. (2012). Gray whale southbound migration surveys 1967-2006: An integrated re-analysis. Journal of Cetacean Research and management 12(3):287-306.

Lang, A.R., Weller, D.W., LeDuc, R.G., Burdin, A.M., Pease, V.L., Litovka, D., Burkanov, V., Brownell, R.L. Jr. (2011). Genetic analysis of stock structure and movements of gray whales

in the eastern and western North Pacific. Rep. Intl. Whal. Commn. SC/63/BRG10.

LeBeouf, B., Perez-Cortéz, M., Urbán-R, J., Mate, B.R., and Ollervides, U. (2000). High gray whale mortality and low recruitment in 1999: potential causes and implications. Journal of Cetacean Research and management 2:85-99.

LeDuc, R.G., Weller, D.W., Hyde, J., Burdin, A.M., Rosel, P.E., Brownell, R.L. Jr., Wursig, B., and Dizon, A.E. (2002). Genetic differences between western and eastern gray whales (*Eschrichtius robustus*). Journal of Cetacean Research and Management 4(1):1-6.

Martínez-A., S., Rosales-Nanduca, H., Swartz, S., Urban-R., J., and Jones, M.L. (*In Press - 2016).* The age of living gray whales (*Eschrichtius robustus*) estimated from photographic identification data. Journal of Cetacean Research and Management - SC/67a/BRG. 7pp.

Mate, B.R., Ilyashenko, V.Y. Bradford, A.L., Vertyankin, V.V., Tsidulko, G.A., Rozhnov, V.V., and Irving, L.M. (2015). Critically endangered western gray whales migrate to the eastern North Pacific. Biology Letters. 11:20150071. http:/dx.doi.org/10.1098/rsbl.2015.0071.

Moore, S.E., Wynne, K.M., Kinney, J.C., and J.M. Grebmeier. (2007). Gray whale occurrence and forage southeast of Kodiak Island, Alaska. *Mar. Mamm. Sci.* **23**(2), 419-42

Moore, S.E. (2008). Marine mammals as ecosystem sentinels. Journal of Mammalogy, 89(3) 534-540.

Moore, S.E., Huntington, H.P. (2008). Arctic marine mammals and climate change: impacts and resilience. Ecological Applications 18(2) Supplement 2008, pp. S157-S165.

Nerini, M. (1984). A review of gray whale feeding ecology. *In* "The Gray Whale *Eschrichtius robustus*" (M.L. Jones, S.L.Swartz, and S. Leatherwood, Eds.). Academic Press, Orlando, Florida, USA.

Omura, H. (1984). History of gray whales in Japan. *In* "The Gray Whale *Eschrichtius robustus*" (M.L. Jones, S.L.Swartz, and S. Leatherwood, Eds.). Academic Press, Orlando, Florida, USA.

Pyenson, M.D., Lindberg, D.R. (2011). What happened to gray whales during the Pleistocene? The ecological impact of sea-level change on benthic feeding areas in the North Pacific Ocean. PLoS ONE 6(7): e21295. doi:10.1371/journal.pone.0021295.

Reeves, R.R. *et al.* (14 authors). (2005). "Report of the Independent Scientific Review Panel on the Impacts of Sakhalin II Phase 2 on Western North Pacific Gray Whales and Related Biodiversity." IUCN, Gland, Switzerland. [Available from http://www.iucn.org].

Rice, D.W. and Wolman, A.A. (1971). "Life History and Ecology of the Gray Whale (*Eschrichtius robustus*)." American Society of Mammalogy, Special Publication No. 3.

Rugh, D.J., Roderick, C.H., Lerczak, J.A., and J.M. Breiwick. (2005). Estimates of abundance of the eastern North Pacific stock of gray whales (*Eschrichtius robustus*) 1997-2002. *J. Cetacean Res. Manage*. **7**(1), 1-12.

Rychel, A., Reeder, T., and Berta, A. (2004). Phylogeny of mysticete whales based on mitochondrial and nuclear data. *Mol. Phylogenet. Evol*. **32,** 892-901.

Salvadeo, C.J., Gómez-Gallardo-U., A., Nájera-Caballero, M., Urbán-Ramirez, J., and Lluch-Belda, D. (2015). The effect of climate variability on gray whales (*Eschrichtius robustus*) within their wintering areas. PLoS ONE 10(8); e0134655. doi:10.1371/journal.pone.0134655.

Scammon, C.M. (1874). "The Marine Mammals of the Northwestern Coast of North America Together with an Account of the American Whale-Fishery." John H. Carmany and Co., San Francisco.

Scheinin, A.P., Kerem, D., Macleod, C.D., Gazo, M., Chicote, C.A., and Castellote, M. (2011). Gray whale (*Eschrichtius robustus*) in the Mediterranean Sea: anomalous event or early sign of climate driven distribution change? Marine Biodiversity Records, Marine Biological Associate of the United Kingdom. Vol. 4(1-5), published online www.journals.cambridge.org/abstract_S1755267211000042.

Sumich, J. (2015). "E. robustus; the biology and human history of gray whales." Whale Cove Marine Education, Corvallis, Oregon. 199 pp.

Swartz, S.L. (1986). Gray whale migratory, social and breeding behavior, Report to the International Whaling Commission, Special Issue 8: 207-229.

Swartz, S.L., Rosales-N, H., Urban-R, J., Martinez, S. (2013). Wintertime aggregations of gray whales in Laguna San Igancio. Whalewatcher 42(1): 42-46.

Swartz, S.L., Urbán-R., J., Gómez-Gallardo-U, A., Martínez-A., S., Robles-M., J.I., Gonzáles-L., I., and Rojas-Bracho, L. (2014). Numbers of gray whales (*Eschrichtius robustus*) utilizing Laguna San Ignacio and Laguna Ojo de Liebre, Baja California Sur, Mexico during the winter breeding season: 2007-22013. Rep. Intl. Whal. Comm. SC/65a/BRG06.

Tomilin, A.G. (1957). "Mammals of the U.S.S.R. and adjacent countries. Vol. IX. Cetacea." Akad. Nauk, SSSR, Moscow (transl. by Israel Program for Sci. Transl., Jerusalem, 1967).

Urbán-R., J., Rojas-Bracho, L., Pérez-Cortés, H., Gómez-Gollardo, A., Swartz, S., Ludwig, S., and Brownell, R.L., Jr. (2003). A review of gray whales (*Eschrichtius robustus*) on their wintering grounds in Mexican waters. *J. Cetacean Res. Manage*. **5**(3), 281-295.

Urbán-R., J., Swartz, S., Gómez-Gallardo-U, A., Martínez-A., S., Rosales-N., H. (2015). Report of the 2015 gray whales research in Laguna San Ignacio and Báhia Magdalena, México. Rep. Intl. Whal. Comm. SC/66a/BRG21.

Villegas-Amtmann, S., Schwartz, L.K., Sumich, J.L., and Costa, D.P. (2015). A biogenetics model to evaluate demographic consequences of disturbance in marine mammals applied to gray whales. Ecosphere 6 (10) Article 193. www.esajournals.org.

Weller, D.W., Klimek, A., Bradford, A.L., Calambokidis, J., Lang, A.R., Gisborne, B., Burdin, A.M., Szaniszlo,W. Urbán-R., J., Gómez-Gallardo-U., A., Swartz, S. and Brownwll, R.L. (2012). Movements of gray whales between the western and eastern North Pacific. Endangered Species Research 18:193-199. doi: 10.3354/esr00447.

Weller, D. W., Bettridge, S., Brownell, R.L., Laake, J.L., Moore, J.E., Rosel, P.E., Taylor, B.L., and Wade, P.R. (2013). Report of the National Marine Fisheries Service gray whale stock identification workshop. U.S. Dep. Commer. NOAA Tech. Memo. NMFS-SWFSC-507.