The Gray Whale, *Eschrichtius robustus*

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Introduction

The gray whale, *Eschrichtius robustus* (Lilljeborg, 1861), is readily recognized by its mottled gray color and lack of a dorsal fin. Instead of this fin, it has a low hump, followed by a series of 10 or 12 knobs along the dorsal ridge of the tail stock; these are easily seen when the animal arches to dive. The adult gray whale is 36-50 feet long and weighs between 16 and 45 tons.

The gray whale is currently confined to the North Pacific Ocean (Fig. 1). Because it uses coastal habitats extensively, the gray whale was especially vulnerable to shore-based whaling operations. Two stocks occur in the North Pacific: The "California" or eastern stock which breeds along the west coast of North America, and the "Korean" or western stock which apparently breeds off the coast of eastern Asia (Rice and Wolman, 1971). Both stocks were severely depleted by the early 1900's. Under legal protection, the eastern stock has recovered substantially—one of the few stocks of great whales to do so. The western stock has not recovered. The gray whale formerly occurred in the North Atlantic (van Deinse and Junge, 1937; Cederlund, 1939; Fraser, 1970; Mitchell and Mead[1]), but has been extinct there for several centuries.

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Distribution and Migration

Eastern North Pacific

Most of the California stock spends the summer feeding, mostly in the northern Bering and southern Chukchi Seas (Pike, 1962; Rice and Wolman,

[1]Mitchell, E. D., and J. G. Mead. 1977. History of the gray whale in the Atlantic Ocean. (Abstr.) *In* Proceedings of the 2nd Conference on the Biology of Marine Mammals, San Diego, California, 12-15 December 1977, p. 11. (Available from first author, Arctic Biological Station, Department of Fisheries and Oceans, 555 St. Pierre Blvd., Ste. Anne de Bellevue, Quebec, H9X 3R4, Canada).

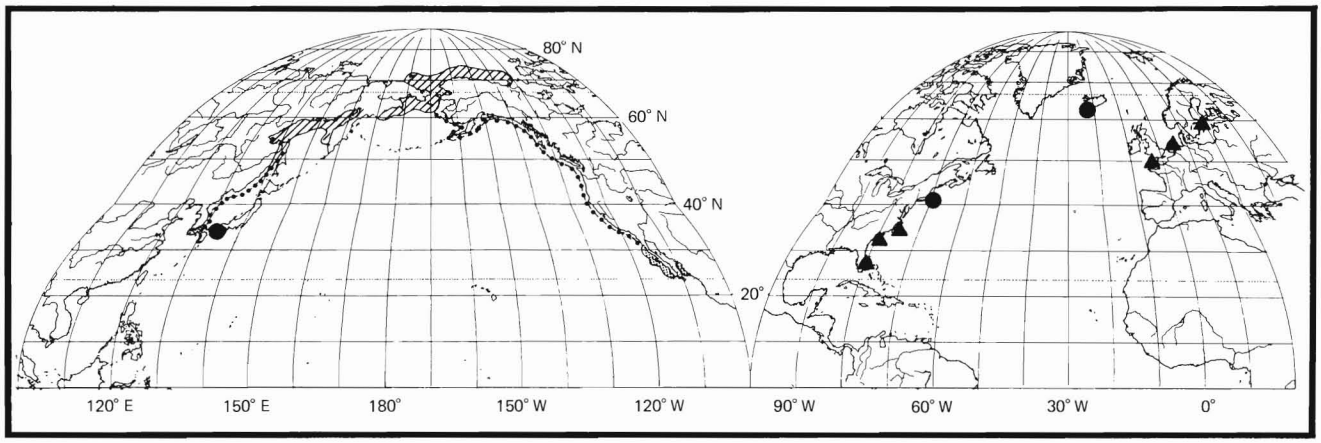


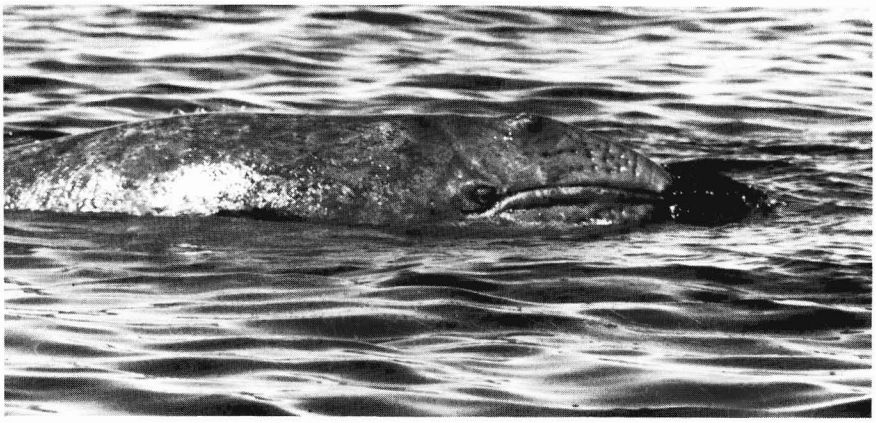
Figure 1.—Geographic distribution of the gray whale. Simple hatching indicates the summer feeding grounds. Small dots indicate the migration routes. Stippling indicates the winter grounds. In the Atlantic, the gray whale has been extinct for at least several hundred years; early historical records are indicated by large dots, subfossil finds by triangles. Perhaps extinct is the population that formerly spent the winter in southern Japan (large dot).

1971; Bogoslovskaya et al., 1981). An unknown number of individuals summer along the west coast of North America in apparently isolated locations south of Alaska from Vancouver Island, Canada, as far south as Baja California, Mexico (Patten and Samaras, 1977; Sprague et al., 1978). In the Beaufort Sea, sightings have been made of small groups as far east as long. 130°W during August (Rugh and Fraker, 1981); in the East Siberian Sea, gray whales were found along the Siberian coast as far west as 174°08'E in late September (Marquette et. al., 1982).

In October and November, the stock begins leaving the Chukchi Sea, exiting the Bering Sea through Unimak Pass, Alaska, mainly in November and December (Rugh and Braham, 1979; Braham, 1984; Rugh, 1984). The whales migrate near shore along the coast of North America from Alaska all the way to central California (92 percent pass within 1.4 km of Cape Sarichef, Unimak Pass, and 94 percent pass within 1.6 km of the Monterey-Point Sur area of central California). After passing Point Conception, Calif., the majority take a more direct offshore route across the southern California Bight to northern Baja California. Southbound migrating gray whales swim at about 7.7 km/hour, and thus travel about 185 km per day (Pike, 1962).

Migrating gray whales are temporally segregated according to sex, age, and reproductive status (Rice and Wolman, 1971). During the southward migration, the sequence of passage off California is as follows: Females in late pregnancy, followed by females that have recently ovulated, adult males, immature females, and then immature males. The earliest southbound migrants (mostly late-pregnant females) usually travel singly, whereas later migrants usually are in pods of two or more. The mean pod size through Unimak Pass is about two.

This stock winters mainly along the west coast of Baja California. The pregnant females assemble in certain shallow, nearly landlocked lagoons and bays where the calves are born from early January to mid-February.



A newborn gray whale calf in Laguna Ojo de Liebre, Baja California, Mexico. Each dimple on the snout and lower lip marks the site of a hair. Photo by D. W. Rice.

The major calving areas are Laguna Guerrero Negro (with 9 percent of the calves), Laguna Ojo de Liebre (53 percent), Laguna San Ignacio (11 percent), and Estero Soledad (12 percent). Minor calving areas (each with <6 percent) are San Juanico Bight, Bahia Magdalena, Bahia Almejas, and Bahia Santa Marina (Rice et al., 1981). Calving rarely occurs during the southbound migration north of Baja California (Rice and Wolman, 1971; Sund, 1975). A few calves are also born on the eastern side of the Gulf of California at Yavaros, Sonora, and Bahia Reforma, Sinaloa, Mexico (Gilmore, 1960). Contrary to many published statements, there is no evidence that San Diego Bay, Calif., was ever a calving area (Henderson, 1972). Recent studies have revealed that the vast majority of gray whales in Baja California (other than cows with calves) spend the winter outside the lagoons in Bahia Sebastian Viscaino and Bahia de Ballenas (Rice et al.[2]).

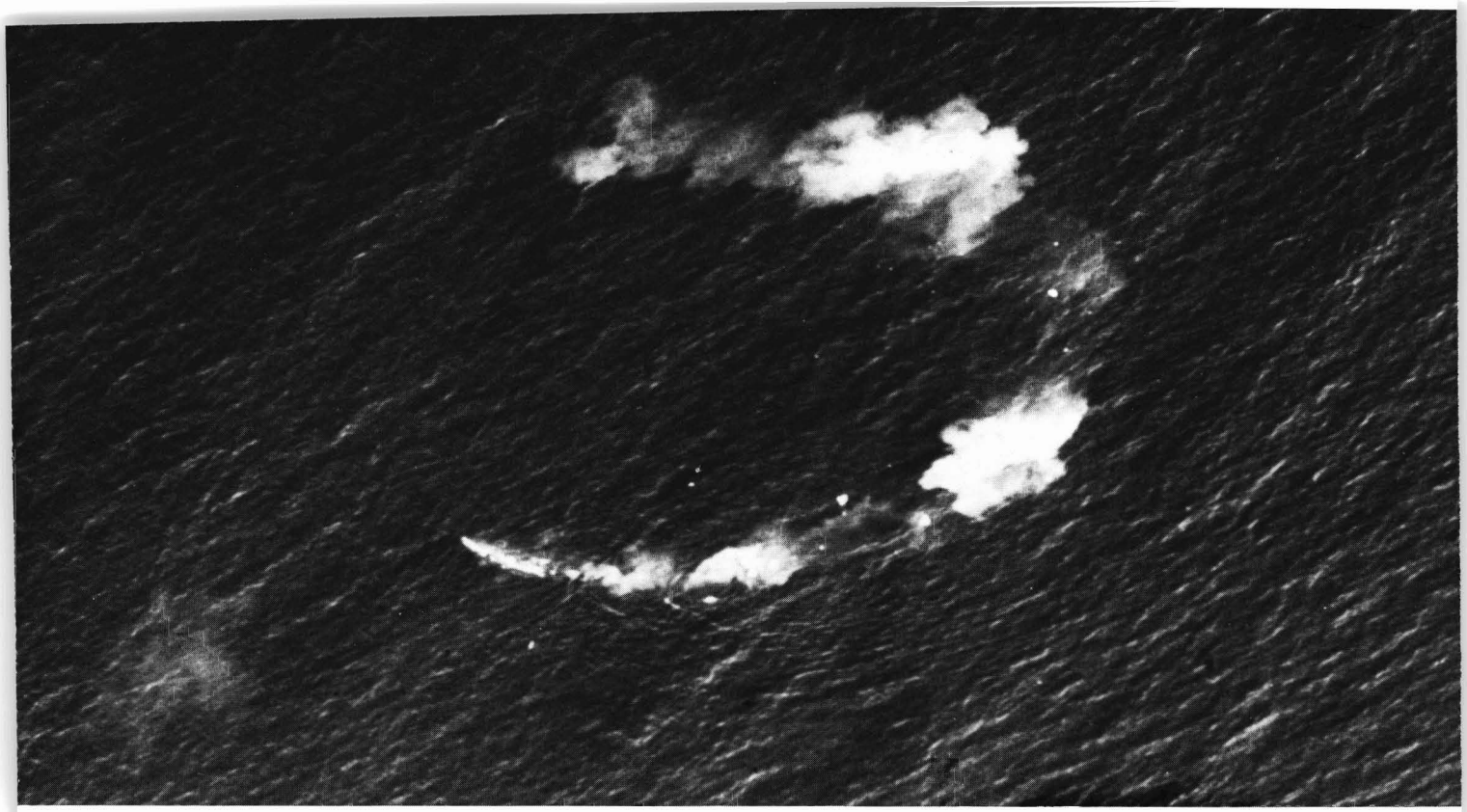
The northbound migration begins in mid-February, and by April whales begin showing up in the southern Bering Sea, which they enter through Unimak Pass (Braham et al., 1977; Braham, 1984). This migration is completely coastal, at least to the east central Bering Sea (Nunivak Island). Most animals in Alaska travel within 1 km of the coast, especially in the southeastern Bering Sea, and at least some apparently feed during migration (Braham, 1984). During the northward migration, the sequence is as follows: Newly pregnant females, followed by anestrous females, adult males, and immature males and females; cows with calves are the last animals to leave the lagoons, and most migrate after the other whales. The peak of the migration passes Point Piedras Blancas, Calif., about 1 May (Poole[3]).

Western North Pacific

The Korean stock formerly occupied the northern Sea of Okhotsk in the summer, as far north as Penzhinskaya Bay, and south to Akademii and Sakhalinskiy Gulfs on the west and the Kikhchik River on the east. Southbound whales migrated along the coast of eastern Asia to winter

[2]Rice, D. W., A. A. Wolman, and D. E. Withrow. 1984. Distribution and numbers of gray whales on their Baja California winter grounds. Unpubl. manuscr. Natl. Mar. Mammal Lab., Natl. Mar. Fish. Serv., NOAA, 7600 Sand Point Way N.E., Bin C15700, Seattle, WA 98115.

[3]Poole, M. M. 1981. The northward migration of the California gray whale, *Eschrichtius robustus*, off the central California coast. (Abstr.) *In* Proceedings of the 4th Biennial Conference on the Biology of Marine Mammals, December 14-18, 1981, San Franc., Calif., p. 96. (Available from author, Biology Department, Sonoma State University, Rohnert Park, CA 94928.



Circular mud plume pattern produced by a feeding gray whale in the northern Bering Sea. This behavior is believed to be associated with the whale returning to the location it was just at to resume feeding. Photo by H. W. Braham.

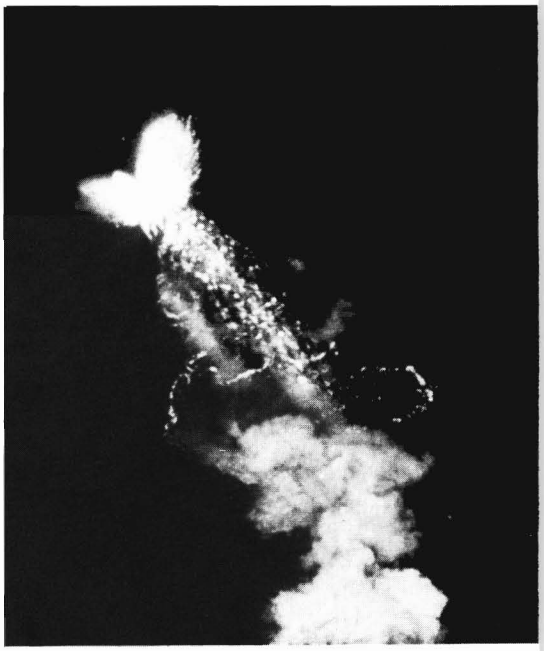
calving grounds off the south coast of Korea, passing Ulsan from late November to late January. Until the turn of this century, another migration route led down the eastern side of Japan to winter grounds in the Seto Inland Sea, Japan (Omura, 1974). Nishiwaki and Kasuya (1970) and Bowen (1974) hypothesized that three recent records of gray whales in Japan involved vagrants of the California stock rather than being Korean stock survivors. It is likely that any remnants of the Korean stock are in such low numbers (Brownell, 1977) as to be below a critical population size sufficient for recovery. This stock therefore may be almost extinct.

Life History and Ecology

Feeding

Gray whales are predominantly bottom feeders that apparently ingest their food by suction (Ray and Schevill, 1974); only rarely do they feed in midwater or at the surface. On their summer grounds in the shallow waters of the Chukchi and Bering Seas, they feed primarily on benthic gammaridean amphipods. Forty-three species have been identified from stomachs, but, depending on area, one of seven species is usually dominant (*Pontoporeia femorata*, *P. affinis*, *Anonyx nugax*, *Ampelisca macrocephala*, *A. eschrichti*, *Nototropis brueggeni*, or *N. ekmani*). In some areas polychaete worms are their main food. Incidentally ingested benthos include gastropods, ascidians, bivalves, priapulids, decapod crustaceans, isopods, sipunculids, hydrozoans, anthozoans, cumaceans, holothurians, sponges, and fish (*Ammodytes* sp.) (Zimushko and Lenskaya, 1970; Bogoslovskaya et al., 1981). Gray whales may play an important role in the rate of turnover of the epibenthos on their summer feeding grounds (Nerini and Oliver, 1983; Nerini, 1984).

Little if any food is consumed during the southbound migration off the U.S. continental coast, although rarely small quantities of decapod nauplii



Aerial view of a feeding gray whale surfacing in the northern Bering Sea, near St. Lawrence Island, Alaska. Note the heart-shaped blow and the trailing mud plume caused when the whale expells water and debris out the side of its mouth when surfacing after feeding on organisms along the bottom of the sea. Photo by H. W. Braham.

(*Pachycheles rudis* and ?*Fabia* sp.) are eaten (Rice and Wolman, 1971). There are reports that they do feed to some extent just before (Sund, 1975) and while on their winter grounds off Baja California (Swartz and Jones, 1982) although the frequency of this behavior is unknown. In the interval between their southward and northward migration past San Francisco, the whales without calves lose from 0.21 percent to 0.37 percent of their body weight per day. This weight reduction is sufficient to account for the estimated energy expenditure during the winter. Blubber thickness and oil yield also decrease during winter. Apparent feeding has been observed during the northbound migration beginning in southeastern Alaska (Braham, 1984), but again the frequency and quantitative evidence associated with energy expenditure for this is unknown.

Reproduction

Females attain puberty at an estimated mean age of 8 years (range, 5-11 years) and a mean body length of about 11.7 m (see Rice and Wolman (1971) for additional details on reproduction).

Female gray whales normally come into estrus biennially in late November and early December. Most individuals ovulate only once each season, although whales failing to conceive after their first ovulation may experience a second estrous cycle the same season. Multiple ovulations are extremely rare. Mean ovulation rates are 1.20 per breeding season for nulliparous females and 0.96 per breeding season (0.52 per year) for parous females. There is little evidence of postpartum ovulation or of ovulation at any other time of the year. However, increase in follicle size following stillbirth or early loss of the calf suggests that females might ovulate following such an event.

Most conceptions occur within a 3-week period during southward migration, with a peak about 5 December; a few occur as late as January on the winter grounds. The pregnancy rate is 0.86 per breeding season or 0.46 per year. The period of gestation is about 13.5 months; fetal growth accelerates during the last half of pregnancy and decelerates just before birth (Rice, 1983). During southward migration, late pregnant females (exclusive of their conceptus) average 25-30 percent heavier than other adult females. Most births occur within a period of 5-6 weeks, with a peak occurring about 27 January; extreme recorded dates are 26 December to 1 March (Swartz and Jones, 1983).

Lactation lasts an average of about 7 months, ending in August. Females are usually in anestrus from August to November or December. However, females that fail to ovulate or conceive during the winter are probably in anestrus for the following 12 months.

Males attain puberty at an estimated mean age of 8 years (range, 5-11 years) and a mean body length of about 11.1 m. The average weight of the testes of adult males during southward migration in December and January is 38 kg, and the mean diameter of the seminiferous tubules is 177μm. During northward migration in February and March, mean testes weight and tubule diameter are 22 kg and 148 μm, respectively. From July through October, the testes average 23 kg. These differences suggest a marked seasonal sexual cycle in the male, with a peak of spermatogenetic activity in late autumn or early winter.

Natural Mortality

No infectious diseases have been reported in gray whales. Epizoites of gray whales include the following (percentage of occurrence in parentheses) (Rice and Wolman, 1971): The barnacle *Cryptolepas rhachianecti* (100) and the cyamids *Cyamus scammoni* (99.7), *C. ceti* (99.4), and *C. kessleri* (98.1). Endoparasites include the trematodes *Lecithodesmus goliath* (0.6), *Ogmogaster pentalineatus* (>22), and *O. antarcticus* (33); two apparently undescribed species of the cestode *Priapocephalus*, one in the small intestine (30) and the other in the large intestine (0.3); the nematode *Anisakis simplex* (0.3); and two acanthocephalans, *Corynosoma* sp. (5.7) and *Bolbosoma* sp. (0.3). Obvious pathogenic effects are produced only by the liver fluke *Lecithodesmus goliath*, but it is not known whether this ever causes mortality.

The killer whale, *Orcinus orca*, appears to be the only predator on gray whales. Evidence from necropsy of 39 gray whales that stranded on St. Lawrence Island indicated that 16 had been killed by killer whales (Fay et al., 1978). The mortality rate from killer whale attacks is unknown. However, the frequency of tooth scars on gray whale carcasses indicates that killer whale attacks are often unsuccessful.

Moderate numbers of gray whale calves strand in and near the nursery lagoons (Swartz and Jones, 1983). A few adults strand every year throughout the range, but the number seems low compared with the size of the population. Rates of mortality due to stranding cannot be calculated.

Total annual mortality estimates for animals older than 8 years, calculated from the age composition as determined by ear-plug readings, were 0.095 for females and 0.081 for males; a similar estimate for sexually mature females, based on ovarian corpora counts, was 0.082 (Rice and Wolman, 1971). These estimates are probably biased upwards because the population was increasing during the 1950's and 1960's when the data were collected. Reilly (1981) estimated the adult natural mortality rate at 0.056 and the juvenile mortality rate at 0.132 during that period. The sex ratio is essentially equal throughout life.

Exploitation and Population Size

History of Exploitation

Eskimos living on the shores of the northern Bering Sea and the Chukchi Sea have hunted whales for perhaps several thousand years. In Alaska, the catch is mostly of bowhead whales, *Balaena mysticetus,* with very few gray whales taken, usually less than one per year (Marquette and Braham, 1982). However, on the Chukotka

coast of the U.S.S.R. the catch has been almost entirely gray whales. Since 1969 gray whales have been taken by the Soviet Government for the Chukchi Eskimos using one modern-style catcher boat (Ivashin and Mineev, 1981). The total aboriginal catch since 1967 has averaged about 165 gray whales per year (Table 1). The current catch limit set by the International Whaling Commission (IWC) is 179 per year.

Several Indian tribes on Vancouver Island and in the State of Washington traditionally hunted gray whales, but have not done so since 1928. Indians farther north along the coast of North America also may have taken a few gray whales (Mitchell, 1979).

From 1846 until about 1900, American whalers exploited gray whales mostly on their wintering grounds, but also took a few in northern waters during the summer. On the basis of available historical records, Henderson (1972) estimated that the total catch from 1846 to 1874 was about 8,100. During the peak of this fishery from 1855 to 1865, the annual catch averaged 474 whales. Catches during the three winter seasons from 1883-84 to 1885-86 were 58, 68, and 41, respectively (Townsend, 1887).

Modern-style whaling began on the west coast of North America in 1905. A few gray whales were taken in the winter off Baja California and California, mostly between 1925 and 1929. Factory ships took an average of 48 gray whales per year in the Bering Sea from 1933 to 1946 (Table 2), after which commercial whaling for gray whales was banned by the International Convention for the Regulation of Whaling.

Between 1959 and 1969, 316 gray whales were killed under Special Scientific Permits off California. From 1966 to 1969 the combined scientific and U.S.S.R. catches averaged 221 per year.

Current and Initial Stock Sizes

Scammon (1874) estimated that the California gray whale population was probably not over 30,000 in 1853-1856, and that by 1874 the number did not exceed 8,000 or 10,000. After a careful analysis of the historical data, however, Henderson (1972) concluded that the population did not exceed 15,000-20,000 prior to the initiation of commercial exploitation in 1846.

In 1885-86, Townsend (1887) estimated that only 160 gray whales migrated south past San Simeon, Calif. Andrews (1914) wrote that "For over 20 years [preceding 1910] the species had been lost to science and naturalists believe it to be extinct." Howell and Huey (1930) said it was

Table 1.—Catches of California gray whales by aboriginal whaling, 1948-82.

Year	U.S.S.R.[1]	Alaska[2]	Total
1948	19		19
1949	26		26
1950	10	1	11
1951	12	1	13
1952	42	2	44
1953	37	1	38
1954	36	3	39
1955	59		59
1956	121	1	122
1957	95	1	96
1958	145	3	148
1959	187	6	193
1960	156		156
1961	207	1	208
1962	147		147
1963	178	1	179
1964	188	2	190
1965	175	1	176
1966	194		194
1967	125		125
1968	135		135
1969	139	1	140
1970	146	5	151
1971	150	3	153
1972	181	1	182
1973	173		173
1974	181	3	184
1975	171		171
1976	163		163
1977	186	1	187
1978	182	2	184
1979	178	4	182
1980	179	3	182
1981	135	0	135
1982	160	4	164

[1]Data from Ivashin and Mineev (1978) and with addition of figures for 1978-82 from unpublished data of the All-Union Research Institute of Marine Fisheries and Oceanography (VNIRO), Moscow.
[2]Data from Marquette and Braham (1982): and unpublished data of the National Marine Mammal Laboratory. Actual values may be low because the taking of gray whales is often not reported.

Table 2.—Catches of California gray whales by modern-style whaling, 1913-47[1]

Year	Baja California	California	Washington	Alaska[2]	Bering and Chukchi Seas[3]	Total
1913				1		1
1914	19					19
1920		2				2
1921		1				1
1922		5				5
1924			1			1
1925	100				33	133
1926	41	1				42
1927	29	3				32
1928	9	1		2		12
1929	2					2
1933				2	2	4
1934					54	54
1935					34	34
1936					102	102
1937					14	14
1938					54	54
1939					29	29
1940					105	105
1941					57	57
1942					101	101
1943					99	99
1945					30	30
1947					1	1

[1]Data summarized from Rice and Wolman (1971), except that the figures for 1943, 1946, and 1947 have been changed to agree with those in Kleinenberg and Makarova (1955).
[2]Gulf of Alaska (shore stations at Port Armstrong and Port Hobron).
[3]Pelagic whaling.

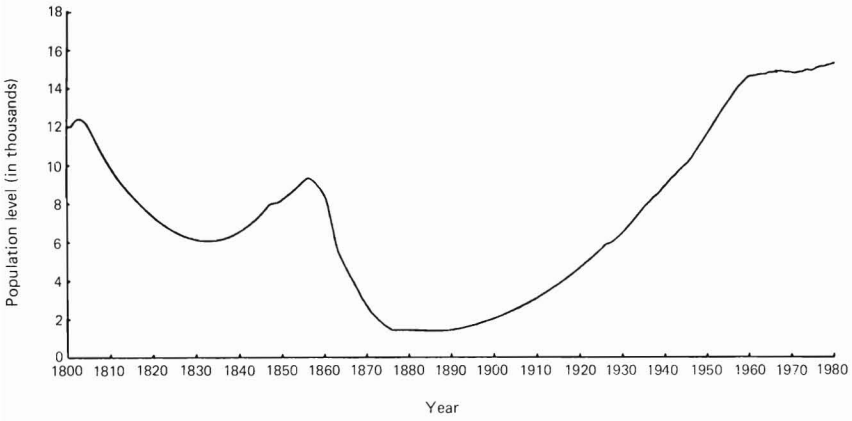


Figure 2.—Gray whale population trajectory based on an estimated maximum population size of 24,000 prior to 1800 and an aboriginal take through that time of 600 whales per year. Peaks and valleys relate to periods of heavy exploitation and recovery from commercial whaling. This modeling best fits the current population census of about 16,000 ± 3,000 (from Reilly, 1981).

" . . . doubtful whether more than a few dozen individuals survive." However, K. W. Kenyon[4] says that he commonly observed gray whales migrating past La Jolla, Calif., during the 1930's.

Systematic shore counts of the southward migration were initiated at San Diego, Calif., in 1952-53, and continued intermittently until 1976-77 (Gilmore, 1960; Rice, 1961). These counts indicated a steadily increasing population until 1959-60.

From 1967-68 to 1973-74, a shore count was made every winter at Yankee Point near Monterey, Calif. where 90 percent of the whales pass within 2 miles of shore and boat traffic is at a minimum. From 1974-75 to 1979-80 the count was made at Granite Canyon, 4 miles south of Yankee Point. A census of the population leaving the summer feeding grounds was made from 1977 to 1979 at Unimak Pass.

The 1977 estimate of the population leaving the Bering Sea was 15,099 ± 2,341 (Rugh and Braham, 1979), and for the 3 years 1977-79 Rugh (1984) estimates 17,000. The population size in 1979-80 off California was estimated at 15,647 (95 percent confidence interval of 13,450-19,201); the rate of annual net increase (less the 1.2 percent harvest mortality) during the preceding 13 years was 2.5 percent, with a standard error of 0.96 (Reilly et al., 1980; Reilly, 1981; Reilly et al., 1983). This indicates that the eastern North Pacific population has recovered to, or now exceeds, its size prior to commercial whaling.

Computer simulation models of the gray whale population size from 1800 through 1980 were run by Reilly (1981). Various forms of dynamic response of vital parameters to population density were used, as well as various carrying capacity levels, and various levels of prehistoric aboriginal removal rate. The model that produced a population trajectory in best agreement with the census data and historical evidence indicated that the carrying capacity (or maximum population size historically) may have been 24,000, and that the population had been reduced to below 12,000 by the year 1800 as a result of aboriginal takes which may have averaged 600 whales per year (Reilly, 1981). The population trajectory generated by this model for the period 1800 to the present is shown in Figure 2. Results of these assessments suggest that the population has not increased to the level that it would reach if there were no current exploitation. The population has recovered, however, to the level (which was presumably stable) that it was at before commercial whaling began in the mid-19th century.

Reilly (1981) estimated the maximum sustainable yield (MSY) as 480 gray whales per year; however, in a recent revision, he gave a new estimate of 320 per year, which would occur at a population size of 11,380 whales[5]. His revised model also predicted that, under an annual take of 180 whales per year, the population would reach 19,000 by the year 2150 and continue rising slowly thereafter, achieving stability at a level of 19,620.

Management

One potential threat to the California gray whale population may be increasing industrial development and vessel traffic in the calving lagoons and in other vital habitats along the migration route and on the feeding grounds. In the recent past, considerable harassment has been caused by commercial cruise boats which take people into the calving lagoons to see the whales and by small pleasure craft brought overland down the new Baja California highway. Harassment now may be under better control than in the past. Under existing U.S. laws, regulation and enforcement are being defined and steps taken to control vessels that interfere with gray whales on their migration path. Between 1972 and 1979, the Mexican Government designated three of the five major calving lagoons in Baja California as gray whale refuges (Reeves, 1977; Swartz and Jones, 1982). These are the lagoons visited by most of the U.S. tour boats and private tourists. The number of vessels allowed in the lagoons at any one time is limited,

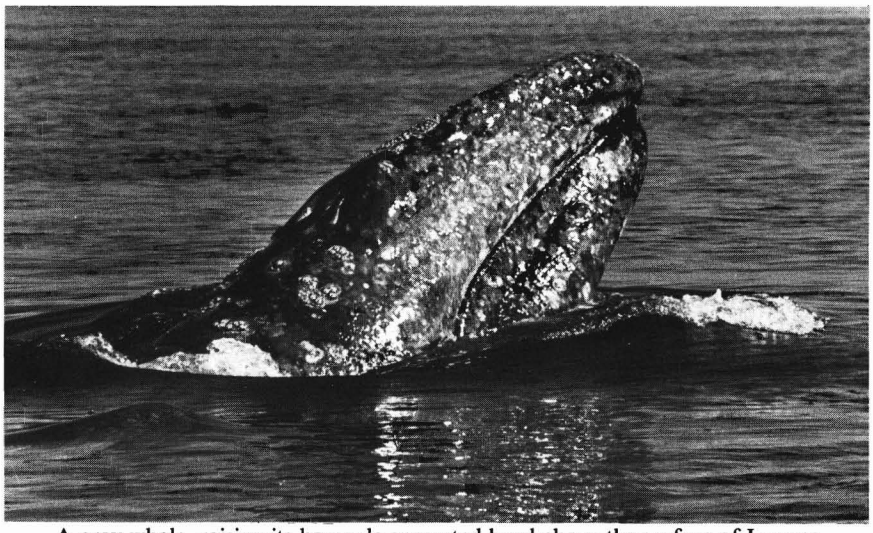
[4]K. W. Kenyon, 11990 Lakeside Place N.E., Seattle, WA 98125. Pers. commun.

[5]Reilly, S. B. 1984. Future trends in gray whale population size. Unpubl. manuscr. Southwest Fisheries Center, Natl. Mar. Fish. Serv., NOAA, P.O. Box 271, La Jolla, CA 92038.

and entry into certain areas is forbidden. Thousands of tourists and a multimillion-dollar industry result from these activities.

Oil and gas exploration is contemplated or under way on the continental shelf from California to the Beaufort Sea, throughout the migration range of this species. Annually, the gray whale population migrates by or through at least eight oil lease areas in U.S. waters alone. On the winter calving grounds, exploratory areas include sites within and adjacent to present calving and rearing areas, such as the offshore waters of Vizcaino Bay, where seismic exploration for gas deposits took place during spring 1981. The effects of oil pollution on the benthic organisms on which these whales feed are unknown. Little is known about what effects, if any, other activities associated with coastal development might have; certain man-made sounds cause migrating whales to deviate from their course (Tyack et al. [6]).

Past industrial activities have shown some impacts. For example, in the calving lagoon of Guerrero Negro, daily dredging and vessel traffic caused the whales to abandon the area from 1957 to 1967. The whales did not return until 6 years after such operations had ceased (Gard, 1974; Bryant and Lafferty, 1980). Current exploitation of phosphorus near the calving lagoon of Magdalena Bay in southern Baja California may be cause for concern (Cordoba, 1981). Because of the scarcity of suitable isolated calving and nursery areas for gray whales, and the whales' specialized feeding habits, future coastal or shallow-water development must be well monitored to determine any effects on any critical stages of this whales' life cycle. For these reasons, habitat protection of the coastal environs remains an important conservation measure.



A gray whale, raising its barnacle encrusted head above the surface of Laguna Ojo de Liebre in Baja California, reveals its paired blowholes. Photo by D. W. Rice.

[6]Tyack, P., C. Clark, and C. Malme. 1983. Migrating gray whales alter their motion in response to sounds associated with oil development. (Abstr.) *In* Proceedings of the 5th Biennial Conference on the Biology of Marine Mammals, November 27-December 1, 1983, Boston, Mass., p. 104. (Available from first author, Woods Hole Oceanogr. Inst., Woods Hole, MA 02543.)

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