

## Gray whale *Eschrichtius robustus* population and stock identity

STEVEN L. SWARTZ\*, BARBARA L. TAYLOR† and DAVID J. RUGH‡

\*NOAA Fisheries Service, Office of Science and Technology, 1315 Eastwest Highway, SSMC 3, Rm 12552, Silver Spring, Maryland 20910, USA, †Southwest Fisheries Science Center, NOAA Fisheries Service, PO Box 271, La Jolla, California 92038, USA, ‡National Marine Mammal Laboratory, Alaska Fisheries Science Center, NOAA Fisheries Service, 7600 Sand Point Way, NE, Seattle, Washington 98115, USA

---

### ABSTRACT

1. In response to conservation and management concerns about gray whale *Eschrichtius robustus* population and stock structure, we provide an overview of the life history and ecology of gray whales as a context for discussion of population and stock structure within the species. Historically eastern and western North Pacific gray whales were managed separately because: (i) their ranges do not overlap; (ii) genetic analyses indicate that the two populations are significantly different; and (iii) eastern gray whales have increased in abundance over the past century while western gray whales have not.

2. Here, we review gray whale migration timing and segregation, feeding and prey species, and reproduction and reproductive behaviour. For the eastern and western gray whale, we review their distribution, history of exploitation, abundance and current status, although most of what is known is founded on the better studied eastern gray whale and only implied for the lesser known western gray whale. Methods to investigate population and stock identity are reviewed including genetics, morphology, chemical signatures, carbon isotopes, parasites, photographic identification and trends in abundance.

3. While the evidence indicates that there is at least some degree of mixing within each of the gray whale populations, no stocks or sub-stocks can be defined. Population structure is not evident in nuclear data, and because selection occurs primarily on the nuclear genome, it is unlikely that there is structuring within each population that could result in evolutionary differences. For western gray whales, there are insufficient data to assess the plausibility of stock structure within the population, owing to its extremely depleted state. Research on eastern gray whales has focused mostly on documenting changes in abundance, feeding biology and behaviour, and suggests separate breeding groups to be unlikely. Both males and females are promiscuous breeders lending little opportunity for the nuclear genome to be anything other than well mixed as is suggested by the high haplotypic diversity of the eastern population.

4. The available data strongly indicate that western gray whales represent a population geographically isolated from eastern gray whales and therefore that the western and eastern populations should be treated as separate management units.

*Keywords:* cetaceans, marine mammals, North Pacific Ocean, population structure, stock identity, wildlife management

## INTRODUCTION

Conservation of large whales has been an international concern ever since widespread commercial hunts severely depleted whale stocks, in many cases continuing to take whales until many species were too scarce to be an economic resource (see review in Reeves, 2002). The International Whaling Commission (IWC) was formed to assess the viability of whaling practices and the size of remaining whale stocks. To develop a systematic process for defining stocks of large whales within the management regime of the IWC, the Stock Identity Working Group of the Scientific Committee examined case studies for individual whale species. The objective of these case studies was to reveal how the different life history strategies of species affect population structure, as well as how the studies reveal the utility of various types of data for evaluating stock identity and structure within populations. In response to concerns about the conservation and management of gray whale *Eschrichtius robustus* population and stock structure, the current review provides an overview of their life history and ecology.

In this review, we use 'population' to refer to units where virtually no gene flow (less than one disperser) would be expected within a generation (approximately 20 years). Such a unit is sometimes called an evolutionarily significant unit (ESU) because gene flow is sufficiently low to allow meaningful differences to develop. 'Stock' refers to a unit with a level of gene flow greater than an ESU but still small enough to be demographically important for management (Taylor, 2005). For purposes of clarity, we suppose this level to be less than 1% dispersal between units per year. Each 'population' can be composed of one or multiple 'stocks'. See the introduction of the review of bowhead *Balaena mysticetus* stock identification paper (Rugh *et al.*, 2003) for further discussion of this terminology.

## BACKGROUND

Gray whales are sufficiently distinctive relative to other cetaceans to be placed in their own family: Eschrichtiidae (Rice, 1998); however, recent molecular analysis has provided conflicting views regarding this taxonomy (Sasaki *et al.*, 2005). Although skeletal remains and sightings of live animals indicate that this species occurred historically in both the North Pacific and North Atlantic (Fig. 1), gray whales are believed to have been extinct in the North Atlantic since the early 18th century (Mead & Mitchell, 1984). It is possible that during interglacial periods in the distant past, e.g. massive glacial advances and retreats in the Quaternary (Pleistocene and Holocene), corridors were available across the Arctic, allowing for exchange of whales between the Pacific and Atlantic (Gilmore, 1978). During glaciations, sea levels dropped in the North Pacific exposing some or most continental shelf areas, which would have severely reduced gray whale habitat (as we currently know it) and eliminated their options to enter the Arctic basin, which was blocked at the time by the Bering Isthmus (Berta & Sumich, 1999). The more recent 'little ice age' investigated by Overpeck *et al.* (1997) suggests that Arctic-wide cooling and widespread glaciation within the last 400 years may have affected the distribution of the species in the North Pacific. Such an ice-driven southerly shift in their distribution could have facilitated the mixing of gray whales from the east and west sides of the North Pacific during these ice ages as has been suggested for bowhead whales (Dyke, Hooper & Savelle, 1996).

Of the two extant North Pacific populations, the western (also known as the Western North Pacific population or the Korean-Okhotsk population) remains critically depleted (Weller *et al.*, 2002) while the eastern (also known as the Eastern North Pacific population or the California-Chukchi population) has recovered from exploitation (Rugh *et al.*, 1999, 2005). The species began to receive protection from commercial whaling in the 1930s (see review in

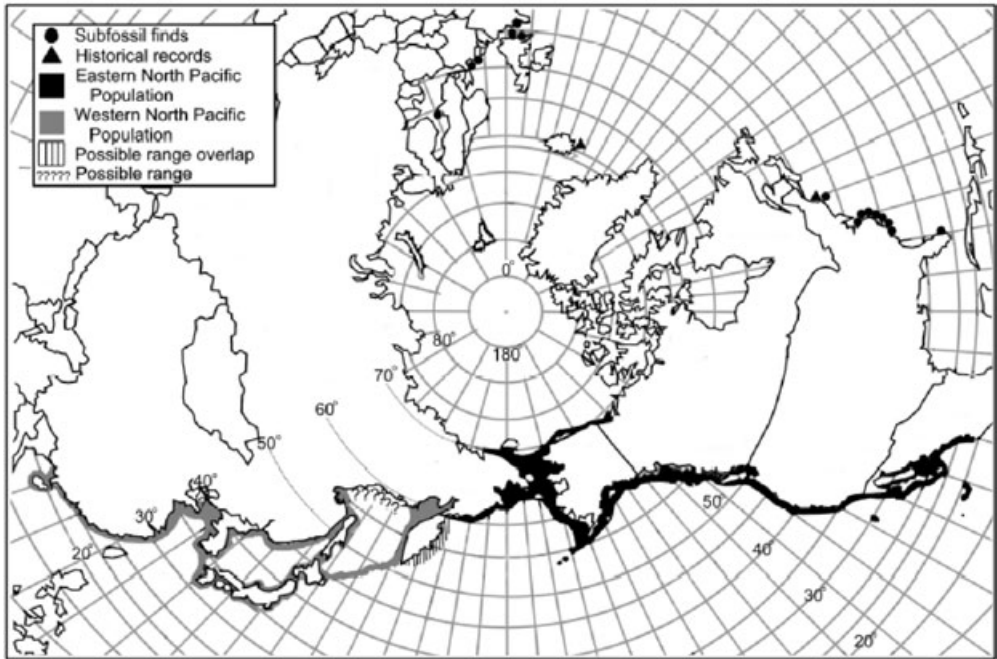


Fig. 1. The range of the gray whale, *Eschrichtius robustus*.

Reeves, 1984). However, hunting continued in the western population for many more years (Brownell & Chun, 1977). Currently, the IWC sets a quota allowing 169 gray whales to be caught annually from the eastern population for aboriginal subsistence use (IWC, 1998). In spite of the persistent subsistence hunt, the eastern population has recovered at a rate of 1.9% to a recent abundance estimate of nearly 20 000 animals (Rugh *et al.*, 2005). In contrast, the western population has shown no sign of recovery and may consist of only 100 whales (Weller *et al.*, 2002).

Management authorities, such as the US National Marine Fisheries Service and the IWC, regard both the eastern and western populations as separate management units (Rugh *et al.*, 1999; LeDuc *et al.*, 2002), and this division is supported by material presented in the current review. Under the US Endangered Species Act, these populations have separate listings as Distinct Population Segments, which are considered to be of evolutionary importance, and the populations are listed separately under the International Convention for the Conservation of Nature and Natural Resources, i.e. the IUCN (Baillie, Hilton-Taylor & Stuart, 2004). The objective of this document is to collate components of gray whale life history information (migration, feeding and reproduction), describe the two populations (relative to exploitation history, distribution and abundance), and note what tools are available for analysing population and stock differentiation (e.g. genetics, morphology and chemical signatures). Accordingly, this review will draw together a summary of what is known about population and stock structure of gray whales and provide a framework for management applications.

## GENERAL BIOLOGY

Eastern North Pacific gray whales have been studied throughout their range for many years, which is not the case for the western gray whales. While many specific details of western gray

whale life history are unknown, it can be expected that the general life history patterns are similar. Information on the general biology and life history, such as migratory routes, range and seasonal timing, provides a context for discussing possible population and stock differentiations or the lack thereof.

### Migration timing and segregation

The migrations of most mysticete whales are thought to have arisen as an evolutionary response to the seasonal production of prey in polar regions (Lipps & Mitchell, 1976). Seasonally predictable sources of food shaped the life history of baleen whales into two periods: summers when whales feed in higher latitudes with abundant food and minimal sea ice; and winters when whales migrate to lower latitudes to escape inclement weather and to calve in warmer waters. Reduced predation by killer whales *Orcinus orca* in lower latitudes also may or may not have played a significant role in the evolution of migration of some mysticete whales (Corkerton & Connor, 1999; Clapham, 2001), but in gray whales it is unclear how this evolution is influenced by the predation that is known to occur during their north-bound migration.

Gray whale migration has evolved into fall southward and spring northward migrations along the western North American coast for the eastern gray whale, and a similar seasonal migration along the eastern coast of Asia for the western gray whale. Comparatively little is known about the details of migration in the western population.

By late November, most eastern gray whales have started migrating south out of their Arctic summer feeding grounds (Rugh, 1984). The start of the migration coincides with the period of conception, which for most (but not all) gray whales occurs during a 3-week period centred in early December (Rice & Wolman, 1971). During this time, gray whales are concentrating in nearshore areas, improving opportunities for finding mates and for genetic mixing. Southward migrating gray whales are observed moving through coastal waters of the North Pacific from November to February (Rugh, Shelden & Schulman-Janiger, 2001). They begin arriving in their winter grounds as early as mid-December with peak numbers of whales passing the California coast in mid-January. The southward migration for better-known eastern gray whale population generally ends in mid-February just as the northward migration begins, with the last of the southbound animals overlapping with the first northward migrants (Rugh *et al.*, 2001). This overlap suggests that only a portion of this population is in the waters of Mexico during the winter, while the remainder are distributed in coastal waters of southern and central California (Swartz, 1986).

The southward migration of eastern gray whales is segregated by age, sex and reproductive status (Rice & Wolman, 1971); the first pulse is led by near-term pregnant females, followed by oestrous females and mature males, and the last phase includes immature animals of both sexes. Eastern gray whales reach maximum densities on their wintering grounds by mid-February (Jones & Swartz, 1984). While the majority of eastern gray whale calves are believed to be born within or near the coastal lagoons of Baja California, Mexico. Sightings of newborn calves migrating south past central and southern California in January and February have increased in recent years (Shelden, Rugh & Schulman-Janiger, 2004). Southward migration timing may be affected by how widely the population is distributed for foraging, and this is affected in part by the onset of winter and the extent of ice coverage in the Arctic.

As eastern gray whales arrive at the lagoons of Baja California, mainly in January, they segregated spatially and temporally such that their distribution, gross movements and timetable of lagoon occupation differ for each age–sex group (Jones & Swartz, 1984; Urban *et al.*,

2003). Single whales (i.e. oestrous females and mature males) are found at highest densities near lagoon inlets and in adjacent coastal waters. By contrast, females with calves concentrate within the interiors of lagoons (Jones & Swartz, 1984). With the departure of adult whales without calves in late February, females with calves shift their distribution to lagoon inlets and adjacent coastal areas, essentially abandoning the inner lagoon nurseries (Jones & Swartz, 1984). This segregation of adult whales without calves from females with calves is an extension of the age and sex segregation seen during the spring and fall migrations (Rice & Wolman, 1971).

The spring northward migration of eastern gray whales occurs in two distinct phases segregated according to age, sex and reproductive condition (Poole, 1984; Swartz, 1986). The first phase centred in February includes newly pregnant females followed 2 weeks later by adult males and anoestrous females and another week later by immature whales of both sexes. The second phase consists of mothers with calves that begin to leave the lagoons after the first phase and are observed along the migration route from March to May, generally arriving on their summer Arctic feeding grounds from May to June

### **Feeding and prey species**

Unlike more pelagic mysticete species that migrate and feed across deep ocean basins, eastern gray whales migrate along the western coast of North America where upwellings of nutrient-rich waters produce some of the world's most productive marine ecosystems and afford gray whales with a variety of potential prey species. Gray whales are primarily, although not exclusively, bottom-feeders. Their prey includes a wide range of benthic and epibenthic invertebrates such as gammaridean amphipods; these occur during the summer months in dense colonies on the continental shelf sea floor of regions like the Bering and Chukchi seas (Nerini, 1984). Limited feeding also occurs outside the primary feeding grounds, along their migration route and in some portions of their winter range (Oliver *et al.*, 1983; Nerini, 1984; Sanchez, Vasquez-Hanckin & DeSilva-Davila, 2001).

### **Reproduction and breeding behaviour**

Gray whale females normally reproduce on a 2-year cycle, producing a single calf every other year, a cycle which is intimately tied to the whales' annual migrations and environmental conditions favourable for the early development of calves (Rice & Wolman, 1971; Swartz, 1986). Rice & Wolman (1971) examined 150 female gray whales during their migration near central California 1959–69, while the population was recovering from commercial exploitation. Their data showed that gray whale breeding is highly synchronous, with females coming into oestrus in a 3-week period from late November to early December; this coincides with the initiation of the southward migration out of the summering areas. If there is no conception, a second oestrus may occur 40 days later (Rice & Wolman, 1971) when the whales are in or near their winter grounds (Jones & Swartz, 1984; Swartz & Jones, 1984). Mating behaviour is observed during most seasons (Gilmore, 1960; Rice & Wolman, 1971; Jones & Swartz, 1984; Swartz, 1986; Berta & Sumich, 1999), but conception appears to be restricted to a fairly short period between late November and early January. Both female and male gray whales are promiscuous and copulate repeatedly with more than one mate (Jones & Swartz, 1984). With a gestation period of 13 months and a mean calving date around 10 January (Rice & Wolman, 1971), some calves are born during the southward migration (Shelden *et al.*, 2004). Calves stay with their mothers for 6–7 months and are weaned and independent while on the summer feeding grounds. Following weaning, adult females remain anoestrous for several months until they enter into a new oestrus cycle and are receptive to a new pregnancy



in late autumn (Rice & Wolman, 1971). Mature male gray whales also have a marked seasonal cycle with a seasonal increase in testes weight and a peak period of spermatogenic activity that correlates closely with the time females come into oestrus (Rice & Wolman, 1971).

## EASTERN POPULATION

### Distribution

Although most of the eastern gray whale population summers on feeding grounds in the northern Bering and southern Chukchi Seas (Moore & Ljungblad, 1984), some whales in this population are distributed far to the east and west in the Arctic and along the coast as far south as California. In the Beaufort Sea, gray whales have been seen in arctic Canada (to 130°W) in August (Rugh & Fraker, 1981). In the East Siberian Sea, gray whales occur even west of Wrangel Island (to 174°E) in late September (Berzin, 1984; Reilly, 1984).

Observations of gray whales in summer months well south of Alaska are not recent occurrences and have been documented during periods of both low and high population abundance (Gilmore, 1960; Pike, 1962; Rice, 1963; Hatler & Darling, 1974; Patten & Samaras, 1977; Darling, 1984; Nerini, 1984; Mallonée, 1991; Avery & Hawkinson, 1992; Gosho *et al.*, 2001; Sanchez *et al.*, 2001; Calambokidis *et al.*, 2002). A number of identifiable individual gray whales, termed 'summer residents' or members of the 'Pacific Coast Feeding Aggregation', have returned to the same areas over the course of many summers in various locations from South-east Alaska to Vancouver Island, Canada, and off the states of Washington, Oregon and California (Hatler & Darling, 1974; Dahlheim, Fisher, & Schempp, 1984; Darling, Keogh, & Steeves, 1998; Gosho *et al.*, 2001; Calambokidis *et al.*, 2002). Photographic re-identifications suggest that these whales also range widely within other coastal areas as far south as northern California and north to Alaska, and these diverse movements could account for inconsistencies in year-to-year re-sightings of individuals at specific locations (Calambokidis *et al.*, 2002).

In the late fall/early winter, eastern gray whales migrate south along the eastern Pacific coast to their primary winter range along the west coast of Peninsula de Baja California (Fig. 1) (Gilmore, 1960; Swartz, 1986; Urban *et al.*, 2003) and along the Gulf of California (Findley & Vidal, 2002). Although there is repeated use of some lagoons, eastern gray whales do move between lagoons and spend some amount of the winter in waters outside of the lagoons (Urban *et al.*, 2003) and along the Baja California and southern California coasts.

### History of exploitation

Eskimos have hunted eastern gray whales near the shores of the northern Bering and Chukchi Seas for thousands of years. Historically, Chukotka natives killed young gray whales (Krupnik, 1984), and until 1928, several Indian tribes between the Aleutian Islands and California hunted gray whales as a part of their cultural and religious traditions (O'Leary, 1984). Aboriginal whaling diminished in the mid-19th century caused in part by declines in gray whale abundance resulting from commercial hunting and native hunting and by changes in cultural traditions following contact with westerners (Krupnik, 1984). Commercial shore whaling took gray whales along the coast of California and Mexico from the mid-1850s to the early 1900s (Sayers, 1984). The first shore whaling station was established on Monterey Bay in 1854, and over the next 45 years, 15 stations were operated at various times from Crescent City (northernmost tip of California) to Punta Eugenia (Baja California); however, by the turn of the century, whales had become scarce along the coast, and shore whaling became economically unviable (Sayers, 1984).

From 1845 to about 1900, American ‘Yankee’ whalers utilized sailing ships that launched small oar-powered skiffs (i.e. longboats) to hunt gray whales on their winter grounds in Baja California as well as along their coastal migration routes and on their summer grounds in the sub-Arctic (Scammon, 1874; Henderson, 1984). Hunts in and near the lagoons greatly reduced the reproductive capacity of the population by killing the females with calves congregating there. By the turn of the century, whaling for gray whales was no longer commercially viable. Henderson (1984) estimates that between 1845 and 1874, approximately 11 300 gray whales were killed throughout the entire eastern Pacific.

Modern ‘industrial’ whaling (that utilized steam-powered catchers and explosive harpoons) for eastern gray whales around 1914 was pursued by the United States, Japan, Norway and the Soviet Union (Reeves, 1984). From 1914 to 1946, an estimated 940 gray whales were taken by factory ships and/or fleet whalers working in the North Pacific in all seasons (Reeves, 1984). With the signing of the International Agreement for the Regulation of Whaling in 1937, gray whales were protected from commercial whaling, at least by some countries (Reeves, 1984). That agreement included a provision for natives of Chukotka and Koryak to kill gray whales for subsistence use. Catches by Russians have averaged between 100 and 200 animals annually since 1948 (Zimushko & Ivashin, 1980; IWC, 1998). From 1959 to 1969, 316 gray whales were killed off central California under IWC special research permits to establish the status of the population (Rice & Wolman, 1971).

#### **Abundance and current status**

Scammon (1874) speculated that the eastern gray whale population numbered 30 000 in 1853–56, but by 1874, following commercial exploitation, the number did not exceed 8000–10 000 whales (Henderson, 1984). Henderson (1984) examined whaling records and made a qualitative conclusion that the population did not exceed 15 000–20 000 whales before the initiation of commercial exploitation in 1846. The most recent estimates of minimum population sizes following commercial exploitation are based on back-calculation analyses that utilize records of catch histories and a range of estimates of maximum sustainable yield rates. Reilly (1981) concluded that the most likely pre-exploitation size of the population was 24 000, which had been reduced to below 12 000 by the year 1900 as the result of commercial whaling. Minimum population size estimates range from 12 000 to 15 000 animals in 1846 at the beginning of commercial exploitation (Reilly, 1992) to only 4000–5000 or perhaps as low as 1500–1900 by 1900 (Butterworth, Korrübel & Punt, 2002).

Direct estimates of current population size come from the analyses of systematic shore counts of southward migrating gray whales. These counts were initiated in 1967/68 near Monterey, California, where the majority of the population passes within 4 km of shore (Shelden & Laake, 2002). Abundance estimates from 1967/68 to 1997/98 showed a population increasing at an annual rate of 2.6% (S.E. = 0.28%), peaking at 30 000; however, in 2000/01 and 2001/02, the estimates dropped to about 18 000 (Rugh *et al.*, 2005). The drop in abundance appears to indicate that this population is reaching carrying capacity (Wade, 2002).

#### **Stock structure**

Donovan (1991) noted that a management unit is defined such that specific management goals are met (e.g. commercial or aboriginal subsistence hunts do not lead to local depletions or extirpation). It would be useful to know if hunts of gray whales occurred at specific times or seasons and at locations containing genetically distinct stocks of the eastern population of gray whales. Preferential catches from such stocks could have the potential to extirpate or deplete those stocks and/or result in abandonment of portions of the popula-

tions' range as proposed for some species of whales (Clapham & Palsbøll, 1999; Clapham & Hatch, 2000).

When most receptive for mating, females are not concentrated in a specific breeding 'area'; rather, they are distributed along the migratory route, mostly in Alaska (Rugh *et al.*, 2001). This concentration of whales along the narrow migratory corridor may play a key role in helping these animals find mates at a critical time, and provide opportunity for genetic mixing throughout the population. There is no current information available to suggest that distinct sub-components of the eastern population segregate in any specific breeding areas.

There is evidence that gray whales segregate by age and sex on their northern feeding grounds, as reflected in the Russian aboriginal subsistence catches (Yablokov & Bogoslovskaya, 1984), but no genetic data are available to gain further insight into stock structure. In general, data on the habits and genetic identity of individual gray whales in the more northern feeding areas are lacking. Historical samples are unavailable to assess whether stock structure within the lagoons existed in the past.

In recent years, about 200 identifiable individual gray whales have returned one or more summers to the same areas at various locations along the Pacific North-west coast, perhaps as a function of seasonal abundance of prey (Darling *et al.*, 1998; Goshō *et al.*, 2001; Calambokidis *et al.*, 2002). These individual whales are believed to constitute the 'Pacific Coast Feeding Aggregation' which may or may not represent a genetically distinct stock of eastern gray whales, or just a recurring temporal aggregation of individuals that frequent this portion of the migration corridor during the summer. No definitive evidence is available to suggest that this 'Aggregation' represents a genetically distinct stock of eastern gray whales.

Examination of eastern gray whale hunting records (especially locations of takes), genetic analyses of animals killed and photographic identification research could be used to address the issue of population structure and fidelity throughout this population's range.

## WESTERN POPULATION

### Distribution

Historical sighting data and whaling records indicate that summer feeding grounds of western gray whales were in coastal waters of much of the northern Sea of Okhotsk (Yablokov & Bogoslovskaya, 1984; Henderson, 1990). However, gray whale sightings are now limited to the shallow-water shelf on north-eastern Sakhalin Island, Russia (Weller *et al.*, 1999). Recent research in the region results from a US–Russian environmental agreement initiated in 1995 to determine the status of the western population and to identify a means to mitigate ongoing threats to its survival (Weller *et al.*, 1999). The seasonal site fidelity and annual return of previously identified whales to this area, including mothers with calves, make the habitat off north-eastern Sakhalin Island of considerable concern relative to the conservation of these animals (Weller *et al.*, 1999). To date, no other feeding ground has been identified for western gray whales, underscoring the importance and potential fragility of the Sakhalin habitat.

In autumn, western gray whales migrate south along several possible routes, including down the coast of eastern Asia along the Korean Peninsula or along coastal waters of Japan (e.g. Kato & Tokuhiro, 1997). Migratory routes potentially include the waters off the coast of eastern Asia from Tatarskiy Strait to south of Korea or through coastal waters of Japan (e.g. Kato & Tokuhiro, 1997).

Wintering areas are unknown, but sightings, strandings and catches from 1933 to 1996 suggest the whales may be along the coast of Guangxi and Guangdong Provinces and around the nearby Hainan Island in southern China (Wang, 1984; Henderson, 1990; Zhu, 1998). The



southernmost record of a western gray whale was from the east coast of Hainan Island (Rice, 1998). The long-held belief that western gray whales spend the winter along the south coast of Korea was based on unsupported conjecture (Rice, 1998).

The western North Pacific gray whale population is believed to be geographically independent from the eastern population because there is an apparent gap in distribution along the eastern shore of the Kamchatka Peninsula, between the Okhotsk and Bering Seas, at least as far east as the Commander Islands (IWC, 1993; Fig. 1).

### **History of exploitation**

Although pre-exploitation numbers are unknown, the western gray whale population was probably never as numerous as the eastern population. It was intensively hunted during the past three centuries, and commercial whaling for the western population ceased in the 1960s. This period of exploitation reduced the population to only a fraction of its original size, and it was thought by some to be extinct (Bowen, 1974).

Japanese harpooners may have taken gray whales as early as the 16th century, and Japanese net whalers continued to take western gray whales during the 17th to 19th centuries (Omura, 1984). Groups of Koryak natives lived in the north-eastern Okhotsk Sea and may have hunted gray whales, perhaps even into the early 1900s (Krupnik, 1984). European and American 'preindustrial' whalers operating in the western North Pacific and Okhotsk Sea took gray whales from sailing ships and oar-powered 'longboats' between the late 1840s and early 1900s. With the advent of 'industrial' whaling with steam-powered catch vessels, Russian whalers took gray whales in the coastal waters of the Far East at the end of the 1800s (Henderson, 1984; Weller *et al.*, 2002). Mizue (1951) shows a dramatic decline in gray whale catches after 1910, with much of the effort attributed to the adoption of modern 'industrial-type' whaling in 1903.

Kato & Kasuya (2002) reviewed the catch history of western gray whales by Japanese and Korean modern whaling during the 1900s and revealed a period of peak annual catches of 100–200 whales occurred in the 1910s. This was followed by a rapid decline of the catch in the 1920s and 1930s, dropping to 10–20 whales per year for over 40 years until the hunt ended in the 1960s. Japanese and Korean whalers continued to hunt gray whales until as recently as 1966 (Brownell & Chun, 1977). It is estimated that a minimum of between 1800 and 2000 gray whales were taken during the whaling period between 1891 and 1966; Kato & Kasuya (2002) concluded that this last phase of continuing small-scale exploitation could have been a major factor in suppressing the recovery of this population.

Since the signing of the International Agreement for the Regulation of Whaling in 1937, western gray whales have been protected from commercial whaling, and no catch quotas have been established (IWC, 1998).

### **Abundance and current status**

Only very rough approximations can be made of the original abundance of western gray whales. While not specifying a period of time, Yablokov & Bogoslovskaya (1984) reviewed records that suggested grey and humpback whales *Megaptera novaeangliae* were common and even abundant in the coastal waters of the northern Okhotsk Sea. They estimated that there were 1500–10 000 prior to the impact of commercial whaling. Bradford (2003) quantitatively back-calculated abundance estimates of 1000–1200 whales in 1900, which coincides with the qualitative estimate by Berzin & Vladimirov (1981) of 1000–1500 whales in 1910. Both of these estimates applied to a period prior to intensive modern whaling but after the population had already been substantially reduced by centuries of pre-modern catches.

Western gray whales were considered to be extinct or nearly so (Bowen, 1974) until records of catches and post-whaling sightings indicated the continuing existence of this population (Brownell & Chun, 1977). The population was listed as *Critically Endangered* by the IUCN in 2000 (Hilton-Taylor, 2000; Baillie *et al.*, 2004) and is considered one of the most endangered populations of large whales in the world. Current population size estimates indicate that the western population contains approximately 100 individuals (Wade *et al.*, 2003; IUCN, 2005; Weller *et al.*, 2005), and its continued ability to survive is of considerable concern (Weller *et al.*, 1999).

### **Stock structure**

It is not known if stock structure exists or existed within the western gray whale population. While the western population was previously thought to have multiple migration routes between its summer and winter grounds, insufficient information is available to determine what, if any, implications multiple migration routes may have had for stock structure. Given this population's current small size, knowledge of stock structure would not likely influence conservation and management strategies for its protection and continued recovery.

## **METHODS USED TO INVESTIGATE POPULATION AND STOCK IDENTITY**

### **Background**

The IWC defines a management unit as a grouping of whales that, if subject to regulated hunts, would be sustained and not depleted or extirpated; both a population and a stock can be considered a management unit (Donovan, 1991). Historically, the data used to define such management units included: (i) demographic information on catch and sighting distributions; (ii) discontinuities in the distribution of animals on their feeding and breeding grounds; (iii) differences in biological parameters; (iv) length distributions; and (v) mark and recapture data. The advent of genetic data allows the information about the degree of connectivity between stocks to be considered. Information on rates of exchange among presumed management units allows estimation of the amount of time required for an extirpated management unit to recover and 'recolonise' its former range. Taylor (1997) illustrated cases of metapopulation dynamics important to management. For example, if a defined management unit was incorrectly assumed to be part of a larger population, its exploitation could result in its depletion and extirpation, with time to recovery difficult to estimate without some measure of dispersal of new individuals from some other source. Alternatively, if the proposed management unit was linked to a larger population, the management unit and its removals could be sustained owing to emigration and genetic exchange from the parent population, provided that dispersal rates were adequate to compensate for removals. Thus, management units must be defined by evaluating similarities and/or differences in demographic aspects of a population; the evaluation should include rates and degree of mixing and genetic exchange within and among adjacent populations (Taylor & Dizon, 1999). There are several tools that can be used to help delineate management units. The most powerful tool is genetics because of its ability to quantify similarities or differences between whales and provide a timescale for potential divergence. Other tools include morphology, chemical signatures, carbon isotope ratios, parasites, contaminants, photographic identification and trends in abundance, as described below.

### **Genetics**

Molecular genetic methods have proven useful in clarifying the relationships between members of controversial taxa (e.g. Hillis & Moritz, 1990). Although the application of genetic

techniques to the study of gray whale populations is ongoing, differentiation between eastern and western gray whales has been found (LeDuc *et al.*, 2002; Lang *et al.*, 2005; detailed below). Genetic analysis of structure within the eastern population has also been conducted (Ramakrsihman & Taylor, 2000; Steeves *et al.*, 2001; Goerlitz *et al.*, 2003).

LeDuc *et al.* (2002) used samples from eastern ( $n = 120$ ) and western ( $n = 45$ ) gray whales to document genetic differentiation on the basis of *mtDNA* haplotype diversities. Recent analyses used both *mtDNA* sequences and alleles from six microsatellite loci amplified from eastern ( $n = 126$ ) and western ( $n = 108$ ) populations of gray whales; the results supported previous studies and indicated that the populations are significantly different from each other ( $F_{st} = 0.062$ ,  $P \leq 0.001$ , *mtDNA* data;  $F_{st} = 0.005$ ,  $P = 0.009$ , microsatellite data) (Lang *et al.*, 2005). Differentiation in *mtDNA* sequences was due to differences in haplotypic diversity (0.95 in the east and 0.77 in the west) and in differences in the relative frequencies of haplotypes within each population. Of the 33 haplotypes present in the eastern sample set, the two most common were found in 10.3% and 9.5% of sampled individuals, illustrating the fairly even distribution of haplotypes. On the other hand, the two most common haplotypes (out of 20) in the western sample set were found in 36% and 33% of sampled animals, while 15 haplotypes were found in only one or two individuals. The high haplotypic diversity found in the eastern population indicates that there was a minimal loss of genetic diversity resulting from the historical reduction in population numbers. In contrast, the relatively low haplotypic diversity of the western population may be the result of a recent population bottleneck or of a small population size being maintained over long timescales. The high number ( $n = 20$ ) of haplotypes found in the western population is surprising given what is known of the population's size and history. For comparison, the critically endangered North Atlantic right whale population contains only five extant haplotypes (Malik *et al.*, 2000) among an estimated 300 animals (Knowlton, Kraus, & Kenney, 1994).

Genetic analysis using nuclear DNA illustrated a relatively high level of microsatellite diversity ( $H_e = 0.724$ ) in the western population; this diversity was lower but comparable to that found in the eastern population ( $H_e = 0.759$ ) (Lang *et al.*, 2005). Although the results from the study by Lang *et al.* (2005) supported genetic isolation between the two populations, higher levels of differentiation were documented when only the females of each population were compared ( $F_{st} = 0.016$ ,  $P \leq 0.001$ ), and estimates of microsatellite differentiation were not significant when only the males were compared ( $F_{st} \leq 0.001$ ,  $P = 0.423$ ).

Structure within the eastern population's southern feeding grounds has been examined using *mtDNA*. These studies found no evidence of matrilineal fidelity to the Clayoquot Sound, British Columbia southern feeding area among animals believed to constitute the 'Pacific Coast Feeding Aggregation'. Photo-identification records indicate long-term fidelity of whale to the area (Hatler & Darling, 1974; Darling, 1984), raising the possibility that the southern feeding group represents a learned cultural behaviour, similar to that seen for the feeding grounds of North Atlantic humpbacks, where knowledge of preferred feeding grounds is believed to be passed down from mother to offspring as evidenced in differences in their *mtDNA* (Smith *et al.*, 1999). However, significant differences in mitochondrial haplotypes between whales in the Pacific Coast Feeding Aggregation and the general population were not found (Steeves *et al.*, 2001), indicating that either the southern feeding group has not been extant long enough to differentiate genetically, or that the gray whales are more flexible than humpbacks with regard to their learned behaviour (i.e. matrilineal fidelity is less strict).

Future studies may be able to better characterize the genetic composition of the whales in the southern feeding area by increasing sampling across the range. Recaptures in the photo-

graphic identification studies have shown a mixing across a large area. Simulation studies have suggested that even a recent colonization of the southern feeding areas along the Pacific North-west coast and elsewhere could be detected by genetic testing given sufficient sample sizes (Ramakrsihman & Taylor, 2000).

Analysis of *mtDNA* has also been used to explore matrilineal fidelity of eastern gray whales to wintering lagoons in Baja California (Goerlitz *et al.*, 2003). Weak but non-significant genetic differences were found between calving females in Laguna San Ignacio and in Laguna Ojo de Liebre, suggesting some level of natal philopatry to wintering lagoons. Differences in haplotype frequencies between calving females within and outside lagoons, as well as between single females and females with calves within each respective lagoon, were used to suggest that fidelity to lagoons might also be influenced by reproductive status (Goerlitz *et al.*, 2003). While natal fidelity of calving females to lagoons indicates that some substructuring of the eastern population occurs on the wintering grounds, this substructure may not be affecting gene flow, given that the majority of females are thought to conceive early in the migration (Rice & Wolman, 1971).

### **Morphology**

There have been few comparative studies of the morphology and/or morphometrics of gray whales. Rice (1998) summarized several studies that found no clear differences in skeletons of gray whales from the Atlantic Ocean and from the western and eastern Pacific populations. Rice & Wolman (1971) examined 316 gray whales collected from the eastern population during migration past central California. Zimushko (1972 in Yablokov & Bogoslovskaya, 1984) compared data collected by Andrews (1914) on the external morphology of western and eastern gray whale populations and suggested that differences were sufficient to indicate the populations were distinct. Andrews (1914) examined 145 western gray whales caught at a whaling station in Ulsan, South Korea. He made detailed descriptions of gray whale morphology and collected two complete skeletons. Zimushko (1972) reported that the distance from the tip of the rostrum to the base of the pectoral flippers, from the tip of the rostrum to the eye, the maximum width of the pectoral flipper, and the length of the baleen plates were statistically greater in the western gray whales, and that western gray whales had fewer baleen plates and fewer throat grooves. Unfortunately, the details of these analyses were never published. There have been no additional published comparisons on the morphology of gray whales relevant to an analysis of population and stock structure.

### **Chemical signatures**

Analysis of chemical signatures (e.g. heavy metals and organochlorines) as ecological tracers could also distinguish differences between populations or stocks of gray whales. Other animals that use inland Asian waters (e.g. North Pacific minke whales) have highly distinctive chemical signatures, characteristics which have been used to distinguish stocks within the same species (Fujise *et al.*, 2000; Nakata *et al.*, 2000). Tilbury *et al.* (2002) examined chemical contaminants from samples of gray whales killed by subsistence hunters in Russia and samples from gray whales stranded along the west coast of the USA during the northbound migration. These authors found that polychlorinated biphenyl (PCB) concentrations in whales killed in Russia were significantly lower than in stranded whales. This type of analysis of contaminant signatures could be used to discriminate small aggregations of whales that feed in a limited area with a persistent pollution feature. If there was no mixing of gray whales in the general population, then a chemical signature could theoretically identify a group of whales.

### **Carbon isotope ratios**

Reliance on prey species unique to specific geographical locations could be detected by examination of carbon isotope ratio signatures found in hard tissues (e.g. baleen) compared with those found in prey species and, by proxy, the phytoplankton supporting the prey species found in specific locations over many years. Schell & Saupe (1993) and Schell (1998) examined the isotopic record in baleen plates from Western Arctic bowhead whales and constructed a prey-location specific feeding record that extends from 1947 to 1995. A similar study conducted on gray whale samples from catches and stranded animals throughout their range could provide indications of the prevalent use of prey from certain areas and the significance of annual feeding at those areas and, by inference, the potential for a subunit of the population representing a genetically distinct stock.

### **Parasites**

Gray whales are heavily infested with ectoparasites and epizoots including a host specific barnacle *Cryptolepas rhachianecti* and three species of whale louse *Cyamus scammoni*, *C. ceti* and *C. kessler*, but gray whales have few endoparasites (Rice & Wolman, 1971). It seems that ectoparasites take advantage of the gray whales' habit of swimming slowly through shallow coastal waters rich in nutrients, but endoparasite concentrations are low because of the whales' long period of fasting each year. Although parasites can be used theoretically to recognize groups of whales that do not interact with the general population, there have been no comparative studies of gray whale parasites that could have bearing on stock structure.

### **Photographic identification**

Photographic identification data indicate high levels of annual return and pronounced seasonal site fidelity for most whales identified on the western feeding ground (Weller *et al.*, 1999, 2002). Photographic identification has also been used to evaluate abundance, range and movements of gray whales in the Pacific North-west (Darling, 1984; Calambokidis *et al.*, 2002) and in the lagoons of Baja California (Jones & Swartz, 1984; Urban *et al.*, 2003). A recent effort to locate and combine historical photographic data sets with more recent photographs of eastern gray whales has resulted in the creation of a database that includes over 5000 images of individually recognizable whales photographed in the lagoons from 1960s to 2005 (S. Swartz, unpublished data). Analyses of these photographs along with future contributions to the database may yield additional information on the fidelity of individual whales to specific lagoons and possibly provide insight concerning the potential for stock structure within the eastern gray whale population.

### **Trends in abundance**

The strongest evidence that the eastern and western gray whale populations are segregated is the lack of growth in the western population through a period in which the eastern population has made an excellent recovery. If there was a dispersal of individuals from east to west, the western population would likely have been repopulated by now, unless any immigration was offset by a currently unknown source of mortality. Mizue (1951, p. 72) points out that the take and subsequent decline of gray whales in the east sea area of Korea 'indicate[s] that the stock of gray whales in our adjacent waters was but a small one existing, as it were, independently, having no intercourse with the stocks of other waters'.



## DISCUSSION

Gray whales have experienced major changes in their distribution with the periodic closure of the Bering Sea during the Pleistocene ice ages, and ice-driven contact between eastern and western populations could have occurred as recently as 400 years ago (Overpeck *et al.*, 1997). These Arctic cold periods are relatively recent events in the evolution of cetaceans, and we should expect to see the evidence of such history in the genetic composition of North Pacific gray whales today. The dramatic declines in abundance of gray whales brought about by commercial whaling occurred on such a recent timescale that fixed or nearly fixed genetic differences – criteria often used to signify evolutionary significance – would not be expected. However, differences in gene frequencies – i.e. criteria used as evidence for population structure meaningful to management – are likely to have developed on these timescales (LeDuc *et al.*, 2002). Such differences were observed in a preliminary analysis of mtDNA and microsatellites from two bowhead whale populations (i.e. Bering-Chukchi-Beaufort and Okhotsk) that were greatly reduced in numbers by whaling. There were small but significant differences in their respective gene pools, suggesting that postglaciation separation has been sufficiently long for genetic differentiation to develop between these two allopatric populations (LeDuc *et al.*, 1998). Analyses of genetic samples from both Pacific gray whale populations did indicate that the populations are significantly different from each other (LeDuc *et al.*, 2002; Lang *et al.*, 2005). The apparent genetic differences, different coastal migratory corridors, feeding and breeding areas, and the recovery of the eastern but not the western population are evidence of allopatry and cause for concern. The available data strongly indicate that western gray whales represent a population geographically isolated from eastern gray whales and that the two populations should continue to be managed separately.

For western gray whales, there are not sufficient data to assess the plausibility of stock structure within the population, owing to its extremely depleted state. Despite there having been a great deal of research on eastern gray whales, most of that effort has gone to documenting changes in abundance, feeding biology and behaviour. Nevertheless, enough is known about breeding behaviour and biology for separate breeding groups to be unlikely. If, as it appears, both males and females are promiscuous breeders (Swartz, 1986), then there is little opportunity for the nuclear genome to be anything other than well mixed, as is indirectly suggested by the high haplotypic diversity of the eastern population (LeDuc *et al.*, 2002).

Relatively little is known about how individuals choose feeding grounds throughout their lives. Photographic data from the Pacific Coast Feeding Aggregation indicate that some individuals show site fidelity over periods of at least years while others at least appear regularly in the same areas at particular times (Calambokidis *et al.*, 2002). Data from Russian hunts show segregation by age and sex on the high-latitude northern feeding grounds (Reeves, 1984), which is also seen during migration (Rice & Wolman, 1971) and within the wintering areas (Jones & Swartz, 1984). However, the available data are from only the small portion of the whales' range where the catches occur, relative to the entire known summer feeding grounds utilized by gray whales. A better understanding of site fidelity and potential stock structure will be gained through continuation and expansion of photographic identification and satellite tagging research on the feeding grounds coupled with comparisons of genetic and pollutant/chemical samples from animals in these areas.

In conclusion, it is unequivocal that the western and eastern populations of gray whales should be treated as separate management units, and there is a strong case for treating all gray whales within each of these populations as belonging to a single unit. Although there are repeated concentrations of whales in some areas, as described for the Pacific Coast

Feeding Aggregation and the tendency of some whales to reuse certain lagoons in Baja California, there is also evidence that there is mixing within each of the respective general populations. However, it would be prudent to closely monitor small, localized feeding groups, and management should be adapted to detect and avoid adverse population changes that would result from excess mortalities in any specific habitat.

## ACKNOWLEDGEMENTS

The authors express thanks to all those researchers and wildlife managers who continue to find gray whales an interesting and informative species to investigate, both from the point of view of learning more about gray whales themselves and for the insights to other species revealed through studies of gray whale biology and natural history. Aimee Lang provided substantial material supporting the genetics section, bringing the review current with the latest information on gray whale genetic analysis. This manuscript was greatly improved by generous critiques and comments received from reviewers including: Jeff Breiwick, Robert Brownell, Jr, James Darling, Doug DeMaster, John Calambokidis, Phil Clapham, Mary Lou Jones, Tammy Steeves and an anonymous reviewer.

## REFERENCES

- Andrews, R.C. (1914) Monographs of the Pacific Cetacea. I. The California gray whale (*Rhachianectes glaucus* Cope). Its history, habits, external anatomy, osteology and relationships. *Memoirs of the American Museum of Natural History*, **1**, 227–287.
- Avery, W.E. & Hawkinson, C. (1992) Gray whale feeding in a northern California estuary. *Northwest Science*, **66**, 199–203.
- Baillie, J.E.M., Hilton-Taylor, C. & Stuart, S.N., eds. (2004) *2004 IUCN Red List of Threatened Species*. A Global Species Assessment, IUCN, Gland, Switzerland and Cambridge, UK.
- Berta, A. & Sumich, J.L. (1999) *Marine Mammals: Evolutionary Biology*. Academic Press, San Diego, CA.
- Berzin, A.A. (1984) Soviet studies on the distribution and numbers of the gray whale in the Bering and Chukchi Seas from 1968 to 1982. In: *The Gray Whale, Eschrichtius Robustus* (Ed. by M.L. Jones, S.L. Swartz & S. Leatherwood), pp. 409–419. Academic Press Inc., Orlando, FL.
- Berzin, A.A. & Vladimirov, V.L. (1981) Changes in the abundance of whalebone whales in the Pacific and the Antarctic since the cessation of their exploitation. *Report of the International Whaling Commission*, **31**, 495–499.
- Bowen, S.L. (1974) Probable extinction of the Korean stock of the gray whale (*Eschrichtius robustus*). *Journal of Mammology*, **55**, 208–209.
- Bradford, A.L. (2003) *Population assessment of western North Pacific gray whales* (*Eschrichtius robustus*). MSc Thesis. University of Washington, Seattle, WA.
- Brownell, R.L. Jr & Chun, C. (1977) Probable existence of the Korean stock of gray whales (*Eschrichtius robustus*). *Journal of Mammology*, **58**, 237–239.
- Butterworth, D.S., Korrrübel, J.L. & Punt, A.E. (2002) What is needed to make a simple density-dependent response population model consistent with data for the eastern gray whales? *Journal of Cetacean Research and Management*, **4**, 63–76.
- Calambokidis, J., Darling, J.D., Deecke, V., Gearin, P., Gosho, M., Megill, W., Tombach, C.M., Goley, D., Toropova, C. & Gisborne, B. (2002) Abundance, range and movements of a feeding aggregation of gray whales (*Eschrichtius robustus*) from California to southeastern Alaska in 1998. *Journal of Cetacean Research and Management*, **4**, 267–276.
- Clapham, P.J. (2001) Why do baleen whales migrate? A response to Corkeron and Connor. *Marine Mammal Science*, **17**, 432–436.
- Clapham, P.J. & Hatch, L.T. (2000) Determining spatial and temporal scales for population management units: lessons from whaling. Paper SC/52/SD2 presented to the International Whaling Commission Scientific Committee, June 2000, Adelaide, Australia (unpublished). [Paper available from the Office of the Journal of Cetacean Research and Management, The Red House, 135 Station Road, Impington, Cambridge, Cambridgeshire CB4 9NP, UK.]
- Clapham, P. & Palsbøll, P. (1999) Review of studies on the stock identification of humpback whales in the North Atlantic. Paper SC/51/RMP22 presented to the International Whaling Commission Scientific Committee, May 1999, Grenada, WI (unpublished). 7 pp. [Paper available from the Office of the Journal of

- Cetacean Research and Management, The Red House, 135 Station Road, Impington, Cambridge, Cambridgeshire CB4 9NP, UK.]
- Corkerton, P.J. & Connor, R.C. (1999) Why do baleen whales migrate? *Marine Mammal Science*, **15**, 1228–1245.
- Dahlheim, M.E., Fisher, H.D. & Schempp, J.D. (1984) Sound production by the gray whale and ambient noise levels in Laguna San Ignacio, Baja California Sur, Mexico. In: *The Gray Whale, Eschrichtius Robustus* (Ed. by M.L. Jones, S.L. Swartz & S. Leatherwood), pp. 511–541. Academic Press, Inc., Orlando, FL.
- Darling, J.D. (1984) Gray whales off Vancouver Island, British Columbia. In: *The Gray Whale, Eschrichtius Robustus* (Ed. by M.L. Jones, S.L. Swartz & S. Leatherwood), pp. 267–287. Academic Press, Orlando, FL.
- Darling, J.D., Keogh, K.E. & Steeves, T.E. (1998) Gray whale (*Eschrichtius robustus*) habitat utilization and prey species off Vancouver Island, B.C. *Marine Mammal Science*, **14**, 692–720.
- Donovan, G.P. (1991) A review of IWC stock boundaries. *Report of the International Whaling Commission* (special issue) **13**, 39–68.
- Dyke, A.S., Hooper, J. & Savelle, J.M. (1996) A history of sea ice in the Canadian Arctic Archipelago based on postglacial remains of the bowhead whale (*Balaena mysticetus*). *Arctic*, **49**, 235–255.
- Findley, L.T. & Vidal, O. (2002) Gray whale (*Eschrichtius robustus*) at calving sites in the Gulf of California, Mexico. *Journal of Cetacean Research and Management*, **4**, 27–40.
- Fujise, Y., Aoki, M., Niimi, S., Hakamada, T., Nakata, H., Honda, K. & Tanabe, S. (2000) An attempt to identify stocks in the western North Pacific minke whale (*Balaenoptera acutorostrata*) using the accumulation levels of heavy metals and organochlorines as ecological tracers. Paper SC/F2K/J18 presented at the JARPN Review Meeting, Tokyo, Japan, 7–10 February 2000 (unpublished). 18pp. [Paper available from the Office of the Journal of Cetacean Research and Management, The Red House, 135 Station Road, Impington, Cambridge, Cambridgeshire CB4 9NP, UK.]
- Gilmore, R.M. (1960) A census of the California gray whale. US Fish and Wildlife Service Special Scientific Report. *Fisheries*, **342**, 1–30.
- Gilmore, R.M. (1978) Some news and views of the gray whale, 1977 – migration south and north along and between the islands of southern California. *Whalewatcher*, **12**, 9–13.
- Goerlitz, D.S., Urban, J., Rojas-Bracho, L., Belson, M. & Schaeff, C.M. (2003) Mitochondrial DNA variation among Eastern gray whales (*Eschrichtius robustus*) on winter breeding grounds in Baja California. *Canadian Journal of Zoology*, **81**, 1965–1972.
- Gosho, M.E., Gearin, P.J., Calambokidis, J., Hughes, K.M., Cooke, L. & Cooke, V.E. (2001) Regional movements of gray whales off the coasts on northern Washington and southern Vancouver Island, 1996–2000. In: *Marine Mammal Protection Act and Endangered Species Act Implementation Program 2000* (Ed. by A.L. Lopez & R.P. Angliss), pp. 45–68. U.S. Department of Commerce, Seattle, WA. (AFSC Processed Report 2001–06).
- Hatler, D.F. & Darling, J.D. (1974) Recent observations of the gray whale in British Columbia. *Canadian Field-Naturalist*, **88**, 449–459.
- Henderson, D.A. (1984) Nineteenth century gray whaling: grounds, catches and kills, practices and depletion of the whale population. In: *The Gray Whale, Eschrichtius Robustus* (Ed. by M.L. Jones, S.L. Swartz & S. Leatherwood), pp. 159–186. Academic Press, Inc., Orlando, FL.
- Henderson, D. (1990) Gray whales and walers on the China coast in 1869. *Whalewatcher*, **24**, 14–16.
- Hillis, D.M. & Moritz, C. (1990) *Molecular Systematics*. Sinauer Associates, Inc., Publishers, Sunderland, MA.
- Hilton-Taylor, C. (2000) *2000 IUCN Red List of Threatened Species*. IUCN/SSC, Gland Switzerland and Cambridge.
- International Whaling Commission (1993) Report of the special meeting of the scientific committee on the assessment of gray whales, Seattle, 23–27 April 1990. *Report of the International Whaling Commission*, **43**, 241–259.
- International Whaling Commission (1998) Chairman's report of the forty-ninth annual meeting. *Report of the International Whaling Commission*, **48**, 17–52.
- IUCN (2005) *Impacts of Sakhalin II Phase 2 on Western North Pacific Gray Whales and Related Biodiversity*. Report of the Independent Scientific Review Panel. IUCN, Gland, Switzerland and Cambridge, UK. 130 pp. Available at: <http://www.iucn.org>.
- Jones, M.L. & Swartz, S.L. (1984) Demography and phenology of gray whales and evaluation of whale-watching activities in Laguna San Ignacio, Baja California Sur, Mexico. In: *The Gray Whale, Eschrichtius Robustus* (Ed. by M.L. Jones, S.L. Swartz & S. Leatherwood), pp. 309–374. Academic Press, Inc., Orlando, FL.
- Kato, H. & Kasuya, T. (2002) Some analyses on the modern whaling catch history of the western North Pacific stock of gray whales (*Eschrichtius robustus*). *Journal of Cetacean Research and Management*, **4**, 277–282.

- Kato, H. & Tokuhiro, Y. (1997) A sighting of gray whale off Kochi, southwest Japan in 1997, with some notes on its possible migration in adjacent waters of Japan. Paper SC/49/AS17 presented to the International Whaling Commission (unpublished).
- Knowlton, A.R., Kraus, S.D. & Kenney, R.D. (1994) Reproduction in North Atlantic right whales (*Eubalaena glacialis*). *Canadian Journal of Zoology*, **72**, 1297–1305.
- Krupnik, I. (1984) Gray whales and the aborigines of the Pacific Northwest: the history of aboriginal whaling. In: *The Gray Whale, Eschrichtius Robustus* (Ed. by M.L. Jones, S.L. Swartz & S. Leatherwood), pp. 103–120. Academic Press Inc., Orlando, FL.
- Lang, A.R., Weller, D.W., LeDuc, R.L., Burdin, A.M. & Brownell, R.L. Jr (2005) Genetic assessment of the western gray whale population: current research and future directions. Paper SC/57/BRG14 presented to the International Whaling Commission Scientific Committee (unpublished). 11 pp. [Paper available through the office of the Journal of Cetacean Research and Management, The Red House, 135 Station Road, Impington, Cambridge, Cambridgeshire CB4 9NP, UK.]
- LeDuc, R.G., Rosenberg, A.E., Burdin, A.M., Blokhin, S.A. & Brownell, R.L. (1998) A preliminary genetic analysis (mtDNA and microsatellites) of two populations of bowhead whales. Paper SC/50/AS11 Presented to the International Whaling Commission Scientific Committee, April 1998 (unpublished) [Paper available through the office of the Journal of Cetacean Research and Management, The Red House, 135 Station Road, Impington, Cambridge, Cambridgeshire CB4 9NP, UK.]
- LeDuc, R.G., Weller, D.W., Hyde, J., Burdin, A.M., Rosel, P.E., Brownell, R.L. Jr, Würsig, B. & Dizon, A.E. (2002) Genetic differences between western and eastern North Pacific gray whales (*Eschrichtius robustus*). *Journal of Cetacean Research and Management*, **4**, 1–5.
- Lipps, J.H. & Mitchell, E. (1976) Trophic model for the adaptive radiations and extinctions of pelagic marine mammals. *Paleobiology*, **2**, 147–155.
- Malik, S., Brown, M.W., Kraus, S.D. & White, B.N. (2000) Analysis of mitochondrial DNA diversity within and between North and South Atlantic right whales. *Marine Mammal Science*, **16**, 545–558.
- Mallonée, J.S. (1991) Behavior of gray whales (*Eschrichtius robustus*) summering off the northern California coast, from Patrick's Point to Crescent City. *Canadian Journal of Zoology*, **69**, 681–690.
- Mead, J.G. & Mitchell, E.D. (1984) Atlantic gray whales. In: *The Gray Whale Eschrichtius Robustus* (Ed. by M.L. Jones, S.L. Swartz & S. Leatherwood), pp. 33–53. Academic Press, Orlando, FL.
- Mizue, K. (1951) gray whales in the East Sea area of Korea. *Scientific Reports of the Whale Research Institute*, **5**, 71–79.
- Moore, S.E. & Ljungblad, D.K. (1984) Gray whales in the Beaufort, Chukchi, and Bering Seas: distribution and sound production. In: *The Gray Whale, Eschrichtius Robustus* (Ed. by M.L. Jones, S. Swartz & S. Leatherwood), pp. 543–559. Academic Press Inc., New York.
- Nakata, H., Tanabe, S., Niimi, S., Minh, T.B., Sakakibara, A., Fujita, K. & Fujise, Y. (2000) Population structure in minke whale from the North Pacific examined by the persistent organic pollutants as chemical tracers. Paper SC/F2K/J17 presented at the JARPN Review Meeting, Tokyo, Japan, 7–10 February, 2000 (unpublished). 9pp. [Paper available through the office of the Journal of Cetacean Research and Management, The Red House, 135 Station Road, Impington, Cambridge, Cambridgeshire CB4 9NP, UK.]
- Nerini, M. (1984) A review of gray whale feeding ecology. In: *The Gray Whale, Eschrichtius Robustus* (Ed. by M.L. Jones, S.L. Swartz & S. Leatherwood), pp. 423–450. Academic Press, Inc., Orlando, FL.
- O'Leary, B.L. (1984) Aboriginal whaling from the Aleutian Islands to Washington State. In: *The Gray Whale Eschrichtius Robustus* (Ed. by M.L. Jones, S.L. Swartz & S. Leatherwood), pp. 79–102. Academic Press Inc., Orlando, FL.
- Oliver, J.S., Slattery, P.N., Silberstein, M.A. & O'Connor, E.F. (1983) A comparison of gray whale, *Eschrichtius robustus*, feeding in the Bering Sea and Baja California. *Fishery Bulletin, U.S.*, **81**, 513–522.
- Omura, H. (1984) History of gray whales in Japan. In: *The Gray Whale Eschrichtius Robustus* (Ed. by M.L. Jones, S.L. Swartz & S. Leatherwood), pp. 57–77. Academic Press Inc., Orlando FL.
- Overpeck, J., Hughs, K., Hardy, D., Bradley, R., Case, R., Douglas, M., Finney, B., Gajewski, K., Jacoby, G., Jennings, A., Lamoureux, S., Lasca, A., MacDonald, G., Moore, J., Retelle, M., Smith, S., Wolfe, A. & Zielinski, G. (1997) Arctic environmental change of the last four centuries. *Science*, **278**, 1251–1256.
- Patten, D.R. & Samaras, W.F. (1977) Unseasonable occurrences of gray whales. *Bulletin of the of the Southern California Academy of Science*, **76**, 205–208.
- Pike, G.C. (1962) Migration and feeding of the gray whale (*Eschrichtius gibbosus*). *Journal of the Fisheries Research Board of Canada*, **19**, 815–838.
- Poole, M.M. (1984) Migration corridors of gray whales along the central California coast, 1980–82. In: *The Gray Whale, Eschrichtius Robustus* (Ed. by M.L. Jones, S.L. Swartz & S. Leatherwood), pp. 389–407. Academic Press, Inc., Orlando, FL.
- Ramakrsihman, U. & Taylor, B.L. (2000) Can gray whale management units be assessed using mitochondrial DNA? Paper SC/52/SD12 presented to the International Whaling Commission Scientific Committee, June

- 2000, Adelaide, Australia (unpublished). [Paper available through the office of the Journal of Cetacean Research and Management, The Red House, 135 Station Road, Impington, Cambridge, Cambridgeshire CB4 9NP, UK.]
- Reeves, R.R. (1984) Modern commercial pelagic whaling for gray whales. In: *The Gray Whale Eschrichtius Robustus* (Ed. by M.L. Jones, S.L. Swartz & S. Leatherwood), pp. 187–200. Academic Press Inc., Orlando, FL.
- Reeves, R.R. (2002) Conservation efforts. In: *Encyclopedia of Marine Mammals* (Ed. by W.F. Perrin, B. Wursig & J.G.M. Thewissen), pp. 276–297. Academic Press Inc., New York.
- Reilly, S.B. (1981) *Population assessment and population dynamics of the California gray whale (Eschrichtius robustus)*. PhD Thesis, University of Washington, Washington.
- Reilly, S.B. (1984) Assessing gray whale abundance: a review. In: *The Gray Whale, Eschrichtius Robustus* (Ed. by M.L. Jones, S.L. Swartz & S. Leatherwood), pp. 203–223. Academic Press, Inc., Orlando, FL.
- Reilly, S.B. (1992) Population biology and status of eastern Pacific gray whales: recent developments. In: *Wildlife 2001: Populations* (Ed. by D.R. McCullough & R.H. Barrett), pp. 1062–1074. Elsevier Applied Science Publishers, London.
- Rice, D.W. (1963) Progress report on biological studies of the larger Cetacea in the waters off California. *Norsk Hvalfangsttid*, **52**, 181–187.
- Rice, D.W. (1998) *Marine Mammals of the World Systematics and Distribution*. Special Publication No. 4. The Society for Marine Mammalogy, Allen Press Inc, Lawrence, KS.
- Rice, D.W. & Wolman, A.A. (1971) *The Life History and Ecology of the Gray Whale (Eschrichtius Robustus)*. American Society of Mammalogists, Special Publication No. 3, Stillwater, OK.
- Rugh, D.J. (1984) Census of gray whales at Unimak Pass, Alaska, November–December 1977–1979. In: *The Gray Whale, Eschrichtius Robustus* (Ed. by M.L. Jones, S.L. Swartz & S. Leatherwood), pp. 225–248. Academic Press, Inc., Orlando, FL.
- Rugh, D.J. & Fraker, M.A. (1981) Gray whale, *Eschrichtius robustus*, sightings in Eastern Beaufort Sea. *Arctic*, **34**, 186–187.
- Rugh, D.J., Muto, M.M., Moore, S.E. & DeMaster, D.P. (1999) Status review of the Eastern North Pacific stock of gray whales. *NOAA Technical Memorandum NMFS-AFSC*, **103**, 96.
- Rugh, D.J., Shelden, K.E.W. & Schulman-Janiger, A. (2001) Timing of the southbound migration of gray whales in 1998/99. *Journal of Cetacean Research and Management*, **3**, 31–39.
- Rugh, D., DeMaster, D., Rooney, A., Breiwick, J., Shelden, K. & Moore, S. (2003) A review of bowhead whale (*Balaena mysticetus*) stock identity. *Journal of Cetacean Research and Management*, **5**, 267–279.
- Rugh, D.J., Hobbs, R.C., Lerczak, J.A. & Breiwick, J.M. (2005) Estimates of abundance of the eastern North Pacific stock of gray whales (*Eschrichtius robustus*) 1997–2002. *Journal of Cetacean Research and Management*, **7**, 1–12.
- Sanchez, P.J.A., Vasquez-Hanckin, A. & DeSilva-Davila, R. (2001) Gray whales mid-spring feeding at Bahaia de los Angeles, Gulf of California, Mexico. *Marine Mammal Science*, **17**, 186–191.
- Sasaki, T. *et al.* (2005) Mitochondrial phylogenies and evolution of mysticete whales. *Systematic Biology*, **54**, 77–90.
- Sayers, H. (1984) Shore whaling for gray whales along the coast of the Californias. In: *The Gray Whale, Eschrichtius Robustus* (Ed. by M.L. Jones, S.L. Swartz & S. Leatherwood), pp. 121–157. Academic Press, Orlando, FL.
- Scammon, C.M., ed. (1874) *The Marine Mammals of the North-western Coast of North America, Described and Illustrated: Together with an Account of the American Whale-Fishery*. John H. Carmany, San Francisco, CA.
- Schell, D.M. (1998) Declining primary productivity in the Bering Sea: implications for marine mammal populations. Society for Marine Mammalogy, World Marine Mammal Science Conference, 20–24 January 1998, Monaco. pp. 120–121 [Abstract].
- Schell, D.M. & Sauppe, S.M. (1993) Feeding and growth as indicated by stable isotopes. In: *Special Publication No. 2. The Bowhead Whale*, 1st edn (Ed. by J.J. Burns, J.J. Montague & C.J. Cowles), pp. 491–509. Society of Marine Mammalogy, Lawrence, KS.
- Shelden, K.E.W. & Laake, J.L. (2002) Comparison of the offshore distribution of southbound migrating gray whales from aerial survey data collected off Granite Canyon, California, 1979–96. *Journal of Cetacean Research and Management*, **4**, 53–56.
- Shelden, K.E.W., Rugh, D.J. & Schulman-Janiger, A. (2004) Gray whales born north of Mexico: indicator of recovery or consequence of regime shift? *Ecological Applications*, **14**, 1789–1805.
- Smith, T.D., Allen, J., Clapham, P.J., Hammond, P.S., Katona, S., Larsen, F., Lien, J., Mattila, D. & Palsboll, P.J. (1999) An ocean-basin-wide mark-recapture study of the North Atlantic humpback whale (*Megaptera novaeangliae*) *Marine Mammal Science*, **15**, 1–32.



- Steeves, T.E., Darling, J.D., Rosel, P.E., Schaeff, C.M. & Fleischer, R.C. (2001) Preliminary analysis of mitochondrial DNA variation in a southern feeding group of eastern North Pacific gray whales. *Conservation Genetics*, **2**, 379–384.
- Swartz, S.L. (1986) Gray whale migratory, social and breeding behavior. *Report of the International Whaling Commission* (special issue), **8**, 207–229.
- Swartz, S.L. & Jones, M.L. (1984) Mothers and calves, from winters spent among the gray whales of San Ignacio Lagoon. *Oceans*, **17**, 11–19.
- Taylor, B.L. (1997) Defining 'population' to meet management objectives for marine mammals. In: *Molecular Genetics of Marine Mammals* (Ed. by A.E. Dizon, S.J. Chivers & W.F. Perrin), pp. 49–65. The Society for Marine Mammalogy, Lawrence, KS.
- Taylor, B.L. (2005) Identifying units to conserve. In: *Marine Mammal Research: Conservation beyond Crisis* (Ed. by J.E. Reynolds et al.). The Johns Hopkins University Press, Baltimore, MD.
- Taylor, B.L. & Dizon, A.E. (1999) First policy then science: why a management unit based solely on genetic criteria cannot work. *Molecular Ecology*, **8**, S11–S16.
- Tilbury, K.L., Stein, J.E., Krone, C.A., Brownell, R.L., Blokhin, S.A. Jr, Bolton, J.L. & Ernest, D.W. (2002) Chemical contaminants in juvenile gray whales (*Eschrichtius robustus*) from a subsistence harvest in Arctic feeding grounds. *Chemosphere*, **47**, 555–564.
- Urban, J.R., Rojas-Bracho, L., Perez-Cortez, H., Gomez-Gallardo, A., Swartz, S., Ludwig, S. & Brownell, R.L. Jr (2003) A review of gray whales on their wintering grounds in Mexican waters. *Journal of Cetacean Research and Management*, **5**, 281–295.
- Wade, P.R. (2002) A Bayesian stock assessment of the eastern Pacific gray whale using abundance and harvest data from 1967 to 1996. *Journal of Cetacean Research and Management*, **4**, 85–98.
- Wade, P.R., Burdin, A.M., Bradford, A.L., Brownell, R.L. Jr & Weller, D.W. (2003) Abundance estimates of western gray whales (*Eschrichtius robustus*) off northeastern Sakhalin Island, Russia. Paper SC/55/BRG18, International Whaling Commission Scientific Committee. (unpublished) [Paper available through the office of the Journal of Cetacean Research and Management, The Red House, 135 Station Road, Impington, Cambridge, Cambridgeshire CB4 9NP, UK.]
- Wang, P. (1984) Distribution of the gray whale (*Eschrichtius robustus*) off the coast of China. *Acta Theriologica Sinica*, **4**, 21–26. [in Chinese.]
- Weller, D.W., Würsig, B., Bradford, A.L., Burdin, A.M., Blokhin, S.A., Minakuchi, H. & Brownell, R.L. Jr. (1999) Gray whales (*Eschrichtius robustus*) off Sakhalin Island, Russia: seasonal and annual patterns of occurrence. *Marine Mammal Science*, **15**, 1208–1227.
- Weller, D.W., Burdin, A.M., Würsig, B., Taylor, B.L. & Brownell, R.L. Jr. (2002) The western gray whale: a review of past exploitation, current status and potential threats. *Journal of Cetacean Research and Management*, **4**, 7–12.
- Weller, D.W., Burdin, A.M., Bradford, A.L., Ivashchenko, Y.I., Tsidulko, G.A., Lang, A.R. & Brownell, R.L. Jr (2005) Status of western gray whales off northeastern Sakhalin Island, Russia, in 2004. Paper SC/57/BRG1 presented to the International Whaling Commission Scientific Committee (unpublished). 10pp. [Paper available through the office of the Journal of Cetacean Research and Management, The Red House, 135 Station Road, Impington, Cambridge, Cambridgeshire CB4 9NP, UK.]
- Yablokov, A.V. & Bogoslovskaya, L.S. (1984) A review of Russian research on the biology and commercial whaling of the gray whale. In: *The Gray Whale, Eschrichtius Robustus* (Ed. by M.L. Jones, S.L. Swartz & S. Leatherwood), pp. 465–485. Academic Press Inc., Orlando, FL.
- Zhu, Q. (1998) Strandings and sightings of the western Pacific stock of the gray whale *Eschrichtius robustus* in Chinese coastal waters. Paper SC/50/AS5 presented to the International Whaling Commission Scientific Committee, April 1998 (unpublished) [Paper available through the office of the Journal of Cetacean Research and Management, The Red House, 135 Station Road, Impington, Cambridge, Cambridgeshire CB4 9NP, UK.]
- Zimushko, V.V. (1972) *On the Morphology of the Gray California Whale*. Tezisy Vses Soveshch Izucheniuyu Morskikh Mlekopitayushchikh, 5th, Part, 1, 172–177.
- Zimushko, V.V. & Ivashin, M.V. (1980) Some results of Soviet investigations and whaling of Gray whales (*Eschrichtius robustus*, Lilljeborg, 1961). *Report of the International Whaling Commission*, **30**, 237–246.

Submitted 4 May 2005; returned for revision 20 July 2005 & 12 January 2006; revision accepted 7 April 2006  
 Editor: PC