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Megaptera novaeangliae.

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Megaptera Gray, 1846*a*

Megaptera Gray, 1846*a*:83. Type species is *Megaptera longipinna* (= *Balaena longimana* Rudolphi 1832 = *Balaena novaeangliae* Borowski 1781) by monotypy.

Perqualus Gray, 1846*b*:pl. 32. Subgenus of *Balaenoptera*, type species is *Balaenoptera boops* Fabricius (not Linnaeus) 1780: 36 = *Balaena novaeangliae* Borowski 1781.

Kyphobalaena Eschricht, 1849:108. Type species is *Balaenoptera boops* Fabricius (not Linnaeus) 1780:36 = *Balaena novaeangliae* Borowski 1781.

Poescopia Gray, 1864*a*:207. Subgenus of *Megaptera* Gray 1846*a*. Included species *Balaena lalandii* Fischer 1829 (= *Balaena novaeangliae* Borowski, 1781), *Megaptera novae-zelandiae* Gray, 1864*b*:207 (= *Balaena novaeangliae* Borowski, 1781).

CONTEXT AND CONTENT. Order Cetacea, Suborder Mysticeti, Family Balaenopteridae. The genus *Megaptera* is monotypic.

Megaptera novaeangliae (Borowski, 1781)

Humpback Whale

Balaena boops Fabricius, 1780:36. Type locality unknown.

Balaena novaeangliae Borowski 1781:21. Type locality unknown.

Balaena nodosa Bonnaterre, 1789:5. Type locality "New England coast."

Balaenoptera australis Lesson, 1828:372. Type locality "Cape of Good Hope."

Balaena lalandii Fischer, 1829:525. Type locality "Cape of Good Hope."

Balaena longimana Rudolphi, 1832:133. Type locality "mouth of Elbe river."

Balaenoptera capensis Smith, 1835:130. Type locality "Cape of Good Hope."

Rorqualus antarcticus Cuvier, 1836:347. Type locality unknown.

Balaenoptera leucopteron Lesson, 1842:202. Type locality unknown.

Balaena gibbosa? Gray, 1843. Type locality unknown.

Megaptera longipinna Gray, 1846*a*:83. Type locality unknown.

Megaptera poeskop Gray, 1846*b*:17. Type locality "Cape of Good Hope."

Megaptera americana Gray, 1846*b*:17. Type locality unknown.

Balaena allamack Gray, 1846*b*:17. Type locality unknown.

Megaptera kuzira Gray, 1850:30. Type locality "Southern coast of Japan."

Balaenoptera astrolabae Pucheran *in*: Jacquinot and Pucheran, 1853:42. Type locality "Southern Oceans."

Balaenoptera syncondylus Muller, 1863:38. Type locality "Ostsee und die Kurische Nehrung".

Megaptera novae-zelandiae Gray, 1864*a*:207. Type locality unknown.

Megaptera gigas Cope, 1865:179. Type locality unknown.

Megaptera osphyia Cope, 1865:180. Type locality "40 miles off Petit Manan lighthouse."

Megaptera longimanna moorei Gray, 1866:122. Type locality "Estuary of Dee River."

Megaptera? burmeisteri Gray, 1866:129. Type locality "Island between Parana Guazu and Parana de las Palmas, mouth of the Parana River."

Megaptera braziliensis Cope, 1867:32. Type locality "Near Bahia" [Brazil].

Kyphobalaena keporkak Van beneden, 1868:109. Type locality "Davis Strait."

Megaptera versabilis Cope, 1869:15. Type locality unknown.

Megaptera bellicosa Cope, 1871:103. Type locality "Santo Domingo" [Haiti].

Megaptera indica Gervais, 1883:1566. Type locality "Persian Gulf."

Balaena atlanticus Hurdis, 1897:330. Type locality unknown.

CONTEXT AND CONTENT. Context as for the genus. Tomilin (1946) recognized the southern ocean population as *M. n. lalandii* (Fischer, 1829) based on differences in total body length from *M. novaeangliae* (Borowski, 1781). Tomilin was apparently unaware of the existence of *Balaenoptera australis* Lesson, 1828, which has priority over *Balaena lalandii* Fischer, 1829. Ivashin (1958) further recognized *M. n. novae-zelandiae* (Gray, 1864*a*) as differing from *M. n. lalandii* in body length and pigmentation. The North Pacific population, if it were deemed a separate subspecies would be *M. n. kuzira* (Gray, 1850).

Humpback whales from different populations vary somewhat in size and pigmentation, but we feel that the variation does not warrant subspecific differentiation.

DIAGNOSIS. *Megaptera novaeangliae* (Fig. 1) may be most readily distinguished externally from other balaenopterids (and any other whale) by the huge pectoral fins, whose length is equivalent to approximately one third that of the body (True, 1904). The anterior (or radial) surface of the flipper has a number of large protruberances (tubercles), unlike the anterior edge of the pectoral fin of any other cetacean. Rounded tubercles are present on both upper and lower jaws as well as on the rostrum, where a line of tubercles takes the place of the medial ridge found in other members of the family. Unlike in other balaenopterids, the posterior margin of the tail is prominently serrated.

The skull of the humpback (Fig. 2) can be differentiated from the other balaenopterid whales by the narrowness of its rostrum compared to its zygomatic width. In the humpback, this ratio is 0.47–0.56 ($n = 4$). This compares to 0.60–0.72 for the minke whale (*Balaenoptera acutorostrata*, $n = 4$), 0.60–0.63 for the fin whale (*B. physalus*, $n = 4$), 0.61 for the blue whale (*B. musculus*, $n = 1$), 0.60 for Bryde's whale (*B. edeni*, $n = 1$) and 0.59–0.63 for the sei whale (*B. borealis*, $n = 3$). However, the relative width of the rostrum compared with the condylobasal width is not significantly different from that of other balaenopterids. (The condylobasal length and zygomatic width are standard mammalian skull measurements [Perrin, 1975]; to obtain the ratios given above, we have used the rostral width at the lateral confluence of the ascending process of the maxilla with the lateral margin of the skull).

There are 270–400 baleen plates on each side of the mouth. These are black, although the anteriormost plates are sometimes dull white or partly white (True, 1904).

GENERAL CHARACTERS. Female *M. novaeangliae* are

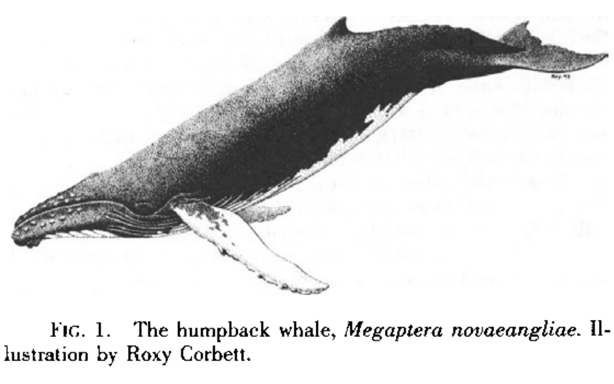

FIG. 1. The humpback whale, *Megaptera novaeangliae*. Illustration by Roxy Corbett.

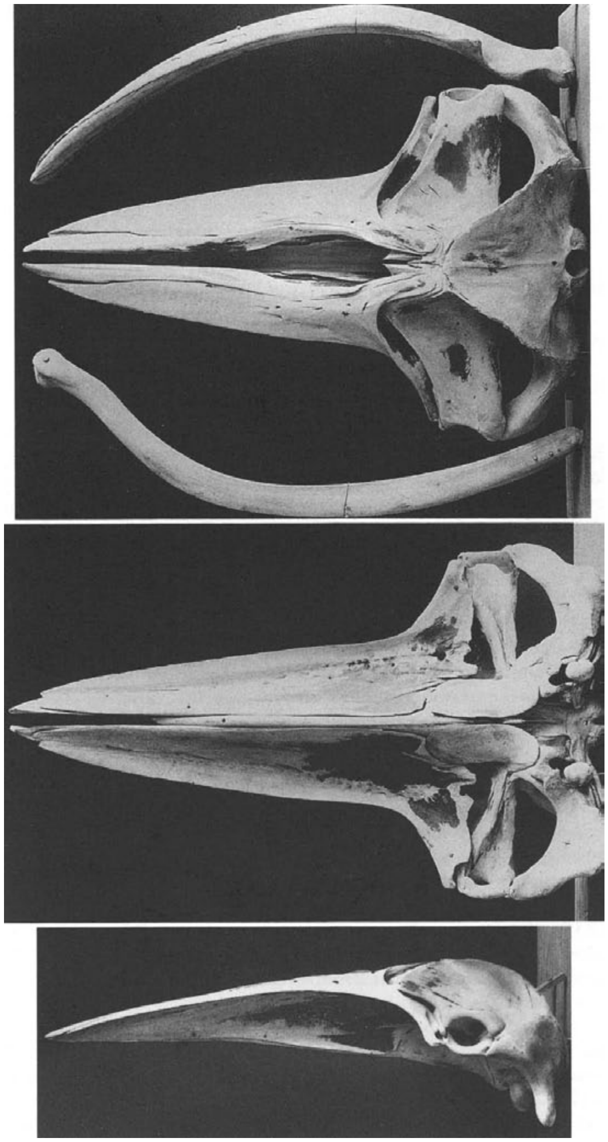

FIG. 2. Dorsal view of cranium and mandibles and ventral and lateral views of cranium of *Megaptera novaeangliae* (USNM 16252, immature female killed April 1879 off Provincetown, Massachusetts). Greatest length of skull is 231 cm. Photographs courtesy of National Museum of Natural History.

ca. 1–1.5 m longer than males (Chittleborough, 1965). By far the largest reliable data set on lengths of this species is that reported by Chittleborough (1965) for Antarctic and Australian catches made between 1949 and 1962. The largest animals among several thousand measured by Chittleborough himself were a 14.3-m male and a 15.5-m female. Chittleborough (1965) also cites numerous (presumably reliable) unpublished measurements from other southern hemisphere catches, including Australia, New Zealand and Norfolk Island; the largest individuals in these data sets were a 17.4-m male and a 16.2-m female, both taken in the Antarctic in 1934/1935. Other reliably recorded maximum lengths for this species are 14.9 m (females) and 14.75 m (males) from the Antarctic in 1926 (Matthews, 1937), and 14.2 m (females) and 14.3 m (males) from Newfoundland in 1899/1900 (True, 1904).

True (1904) also cites maximum lengths of 16.2 m (males) and 15.7 m (females) from data gathered by A. Ruud in Finnmark in 1885/1886, but it is not clear whether these figures represent total length or the now-standard measurement of tip of rostrum to notch of flukes. A similar uncertainty pertains to data reported by whaling stations at Moss Landing and Trinidad, California, between 1919 and 1926, where the largest individuals are given as 17.4 m (males) and 18.6 m (females—Clapham et al., 1997). Although these extreme values appear questionable in light of current knowledge, it must be remembered that many subsequent measurements were recorded from heavily exploited populations from which the largest individuals had been removed. While animals 17 or 18 m long seem unlikely, it is conceivable that pristine populations could contain a few individuals of this size.

The mean lengths of physically mature males and females in Chittleborough's (1965) data set were 13.0 m and 13.9 m, respectively. From the same data, mean lengths at independence (one year of age) were 9.9 m (males) and 9.7 m (females). Mean lengths at the average age at attainment of sexual maturity (five years) were 11.8 m (males) and 11.9 m (females).

The dorsal coloration of *M. novaeangliae* is black in all animals. Coloration of the ventral surface varies widely, from all black to all white through various degrees of marbling (Matthews, 1937; Mikhalev, 1997; Pike 1953; True, 1904). In some populations, many animals are characterized by extension of a white ventral surface up the flanks (Kaufman et al., 1987; Rosenbaum et al., 1995). The pattern on the ventral flukes also ranges from black to white through various combinations of the two; this pattern, together with the serration on the posterior margin of the tail, is individually distinctive (Katona and Whitehead, 1981) and has been the basis for many long-term studies of identified individuals. The ventral surface of the pectoral fins is generally white, whereas coloration of the dorsal surface varies from all white to all black (Herman and Antinoja, 1977; True, 1904). Several observers have noted clines or other interpopulation differences in pigmentation types for the ventral surface, ventral fluke pattern and dorsal surface of the pectoral fins (Chittleborough, 1965; Lillie, 1915; Omura, 1953; Pike, 1953; Rosenbaum et al., 1995). The dorsal fin is highly variable in shape and size, ranging from low and rounded to high and falcate (Clapham and Mayo, 1990; Katona and Whitehead, 1981).

The sole difference that is externally observable between male and female humpback whales is found in the urogenital area. Females possess a hemispherical lobe at the posterior terminus of the genital slit; this lobe is absent in males (Glockner, 1983). In addition, the separation between the genital slit and the anus is considerably wider in males than in females (True, 1904).

DISTRIBUTION. *Megaptera novaeangliae* is a cosmopolitan species and is found in all oceans (Fig. 3). It has been observed in the Mediterranean Sea, but its occurrence there is considered rare or aberrant (Aguilar, 1989). The species is commonly found in coastal or shelf waters throughout its range, although it frequently travels across deep water during migration (Clapham and Mattila, 1990; Dawbin, 1966).

Megaptera novaeangliae is highly migratory, thus its distribution changes with the seasons. This whale spends spring, summer, and autumn on feeding grounds in temperate or high-latitude waters (Dawbin, 1966; Mackintosh, 1942), and there are records of the species above latitude 75° in the northern hemisphere (Christensen et al., 1992). In winter, animals migrate to mating and calving grounds in tropical or subtropical waters, where they are generally found associated with islands or offshore reef systems (Baker et al., 1986; Dawbin, 1966; Mackintosh, 1942; Whitehead and Moore, 1982). Many of the major breeding concentrations occur close to latitude 20° in both hemispheres, but the winter range of some whales extends to equatorial waters (Flórez-González, 1991). The sole known exception to the typical seasonal migratory pattern is a population in the Arabian Sea, which is unique in that it appears to both feed and breed in tropical waters (Mikhalev, 1997).

In the western North Atlantic, humpback whales feed from the eastern coast of the United States to western Greenland (Katona and Beard, 1990). Other feeding grounds occur off Iceland and northern Norway, including off Bear Island and Jan Mayen (Christensen et al., 1992; Palsbøll et al., 1997). Whales from all of these areas breed primarily in the West Indies in winter (Clapham et al., 1993*a*; Katona and Beard, 1990; Palsbøll et al., 1997). A few whales of unknown northern origin migrate to the Cape Verde Islands (Reiner et al., 1996).

In the North Pacific, feeding humpbacks summer in a wide arc from California to Alaska, and along the Aleutian chain into the western North Pacific (Perry et al., 1990). Major breeding grounds are located off Mexico, Hawaii, and Japan (Darling and Mori, 1993; Nishiwaki, 1959; Perry et al., 1990).

The absence of reports of this species from 19th century whalers wintering at Hawaii, together with the lack of a word in the

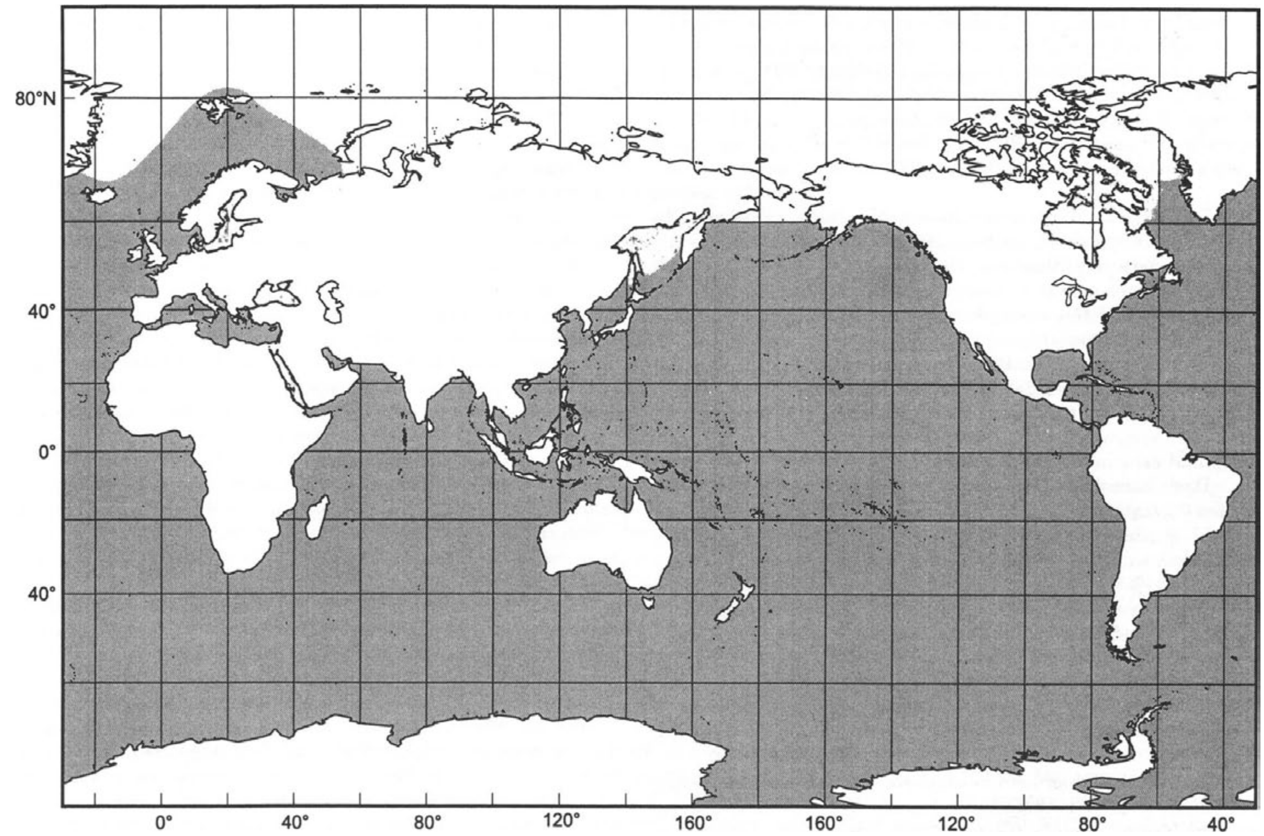

FIG. 3. Geographic distribution of *Megaptera novaeangliae.*

Hawaiian language for "humpback whale," has led to a suggestion that *M. novaeangliae* has only recently colonized this region (Herman, 1979). A similar argument has been made, on sparser data, for the area of the West Indies that includes Silver Bank, Navidad Bank and Samana Bay, which today represents the largest breeding ground in the world for this species (Mattila et al., 1994).

FOSSIL RECORD. The 19th century produced descriptions of numerous fossil forms that were supposedly related to *Megaptera* (Gray, 1866; Van Beneden, 1882). The concept of *Megaptera* differed from our current concept. In fact Gray (1864*b*) named the genus *Eschrichtius* (currently restricted to the modern gray whale) as a subgenus of *Megaptera.* Kellogg (1922) seemed to have settled on the currently recognized concept when he described *Megaptera miocaena,* the oldest known humpback (Late Miocene—ca. 6 × 10^6 years ago). The genus is also known from the Late Pliocene and Pleistocene in North America and from the Upper Pliocene in Europe (Romer, 1966). Given the confusion in the past and the lack of a current review, we consider that the paleontology of the genus *Megaptera* is extremely tentative.

FORM AND FUNCTION. The vertebral count for ten specimens examined or reviewed by True (1904) was 7 C, 14 T, 10–11 L, and 21 Ca, total 52–53. The skeleton of the humpback was described by Struthers (1889) and True (1904). Turner (1912), who writes much on the anatomy of other baleen whales, had only three pages on the humpback. One thing that is clearly evident is the enormous size of the humpback flipper. True (1904:223) found the flipper length (head of humerus to tip) in eight specimens to be 28.3–34.1% of the total length of the animal. That is compared with 11.2–13.1% for *Balaenoptera physalus* (True, 1904:117, n = 14), 13.9–16.1% for *B. musculus* (True, 1904:158, n = 20), 14–23% for *B. acutorostrata* (True, 1904:194; converted from axilla to tip; n = 11), 12.6–14.3 for *B. borealis* (Andrews, 1916:table ix, n = 14), 14.0–16.3% for *Eubalaena glacialis* (True, 1904:247; "length of pectoral"; n = 5), and 17.5–20.9% for *Eschrichtius robustus* (Andrews, 1914:245, n = 11).

The scapula of the humpback is extremely diagnostic, lacking the acromion and having a very vestigial coracoid process. In all other cetaceans, both of the processes are strikingly large and well developed, especially the acromion. Felts (1966), in his paper on the cetacean flipper, does not mention the humpback. Clearly more work needs to be conducted on the gross anatomy of the humpback flipper to demonstrate its peculiarities.

The throat grooves are wide and relatively few. Leatherwood et al. (1976:9—figures compiled from a variety of uncredited but reliable sources) gives 14–22 throat grooves for this species as opposed to 38–100 for all other North Atlantic baleen whales. As in all balaenopterids, the ventral grooves expand during feeding, allowing considerable enlargement of the buccal cavity.

ONTOGENY AND REPRODUCTION. As in most mysticetes, reproduction in *M. novaeangliae* is strongly seasonal. Females come into estrus during winter, and males exhibit a marked increase in spermatogenesis at this time (Chittleborough, 1958, 1965). In the southern hemisphere, ovulation occurs from June to November, with a peak in late July (Chittleborough, 1958, 1965). Because of the seasonal opposition of the hemispheres, estrus occurs six months later in boreal populations. The gestation period is ca. 11–12 months (Chittleborough, 1958). The fetal growth rate is among the highest of any mammal, exceeded only by that of blue (*Balaenoptera musculus*) and fin (*B. physalus*) whales (Frazer and Huggett, 1973). Although there are records of twin fetuses, there are no reliable records of a mature female nursing more than one calf (Chittleborough, 1965; Clapham and Mayo, 1990).

The peak birth months in southern and northern hemisphere populations are early August and early February, respectively (Chittleborough 1958, 1965; Herman and Antinoja, 1977). Mean length at birth is 4.5 m (Chittleborough, 1958). Calves are precocious and nurse for up to a year, although they may begin to feed independently at ca. six months (Chittleborough, 1958; Clapham and Mayo, 1987; Van Lennep and Van Utrecht, 1953). Although the great majority of calves leave their mothers during, or shortly before, their second winter, a few remain associated for two years (Baraff and Weinrich, 1993; Clapham and Mayo, 1990).

Sexual maturity is attained in both sexes at an average age of five years (Chittleborough, 1965; Clapham, 1992). Physical maturity is not reached until 8–12 years after sexual maturity (Chittleborough, 1965). In mature females, the modal and mean interbirth intervals are 2 and ca. 2.4 years, respectively (Barlow and Clapham, 1997). Annual calving has been documented in some individually identified females (Clapham and Mayo, 1990; Glockner-Ferrari and Ferrari, 1990; Weinrich et al., 1993). Whaling data indicate that most females ovulate once in a winter, but that a minority (estimated at 16–28%) ovulate twice, and a few (up to 8%) three times (Chittleborough, 1954, 1965).

ECOLOGY. *Megaptera novaeangliae* has a varied diet. In the southern hemisphere, euphausiids (notably *Euphausia superba*) are the primary prey (Matthews, 1937). Elsewhere the species feeds upon other euphausiids of several genera (including *Euphausia, Thysanoëssa* and *Meganyctiphanes*), as well as various species of schooling fish (Baker et al., 1985; Clapham et al., 1997; Geraci et al., 1989; Mikhalev, 1997; Payne et al., 1986; Rice, 1963; Watkins and Schevill, 1979; Whitehead, 1981). The latter include herring *(Clupea)*, mackerel *(Scomber scombrus)*, sand lance *(Ammodytes)*, sardines (*Sardinops* or *Sardinella*), anchovies *(Engraulis mordax)*, and capelin *(Mallotus villosus)*.

There have been infrequent observations of attacks by killer whales *(Orcinus orca)* on *M. novaeangliae* (Chittleborough, 1953; Flórez-González et al., 1994; Whitehead and Glass, 1985), and rake marks from teeth are commonly observed on the body and tail (Katona et al., 1980). However, while some mortality (notably of young calves) from this source and perhaps tropical sharks seems likely, there is no good evidence that the humpback whale exists under continual threat from predators (Clapham, 1996; Dolphin, 1987*a*). *M. novaeangliae* carries various external parasites and commensals, including the whale louse *Cyamus boopis*, and barnacles of the genera *Coronula* and *Conchoderma* (Rowntree, 1996; Scarff, 1986).

In at least the northern hemisphere, the population structure of *M. novaeangliae* is characterized by fidelity to relatively discrete summer feeding grounds (Clapham and Mayo, 1987; Clapham et al., 1993*b*; Katona and Beard, 1990; Palsbøll et al., 1997; Perry et al., 1990). However, whales from different summer areas share common breeding grounds in the tropics. In the North Atlantic, whales from virtually all areas breed in the West Indies (Clapham et al., 1993*a*; Katona and Beard, 1990). In the North Pacific, the situation is rather more complex. Existing data suggest that humpbacks which feed off Alaska migrate primarily to Hawaii, while those summering from California to Washington breed in inshore Mexican waters (Calambokidis et al., 1996; Perry et al., 1990). However, a few individually identified Alaskan whales have been sighted again in the Revillagigedos Islands (Mexico), and there is a (probably low) degree of exchange between this latter area and Hawaii (Calambokidis et al., 1997). Overall, it is noteworthy that very few whales from the Revillagigedos have been resighted in any known high-latitude habitat, implying the existence of a major undiscovered feeding area in the central or eastern North Pacific (Calambokidis et al., 1997; Úrban et al., in litt.).

An additional breeding area in Japanese waters is probably host primarily to whales from the western North Pacific (Darling and Mori, 1993), but trans-Pacific movements from Hawaii and Canada to Japan have been documented (Darling and Cerchio, 1993; Darling et al., 1996). The population status and migratory destinations of humpback whales which feed in the central Aleutian Islands have yet to be determined. However, marking studies have demonstrated a connection between the eastern Bering Sea and Japanese waters (Nishiwaki, 1966). Furthermore, a humpback whale tracked by satellite transmitter migrated from Hawaii to the central Aleutians and then west to the southern tip of Kamchatka (B. Mate, in litt.).

In circumpolar Antarctic waters, five (sometimes six) feeding areas are recognized for management purposes (Mackintosh, 1942), although marking experiments have shown a degree of exchange among them (Chittleborough, 1965). Humpback whales from these populations migrate to separate breeding grounds off Australia, Africa, Oceania, and South America in winter (Chittleborough, 1965; Flórez-González, 1991; Mackintosh, 1942).

The overall sex ratio of several studied populations does not deviate from parity (Chittleborough, 1965; Clapham et al., 1995*b*; Matthews, 1937; Palsbøll et al., 1997). However, there is evidence, from both whaling and more recent studies, suggesting that the operational sex ratio in the breeding range is biased towards males, either because of longer male residence time or non-migration of some females (Brown et al., 1995; Chittleborough, 1965; Palsbøll et al., 1997).

Migrations are among the longest of any mammal, and are known to reach almost 8,000 km (Palsbøll et al., 1997; Stone et al., 1990). Whaling catch data show that migrations to and from the tropics are loosely staggered by sex and maturational class (Chittleborough, 1965; Dawbin, 1966, 1997; Nishiwaki, 1959). Lactating females are among the first to leave the feeding grounds in late autumn, followed by immature animals, mature males, "resting" females, and lastly pregnant females. In late winter, this order is broadly reversed during the migration back to high latitudes. However, recent work off eastern Australia has suggested that not all animals undertake the migration every year; in particular, some females may remain on the feeding grounds through the winter (Brown et al., 1995). As with all mysticetes, the function of the humpback's migration is unclear; it may have evolved as a means of exploiting seasonal pulses of productivity in high latitudes while conserving energy in warm water during winter (Brodie, 1975).

Little is known about disease in this species. Infection by the giant nematode *Crassicauda boopis* appears to be endemic in many cetaceans, including *M. novaeangliae* (Baylis, 1920). Lambertsen (1992) reviewed the life cycle and associated pathology of this parasite, infection with which can result in a chronic inflammatory reaction of blood vessels and eventual renal failure.

The most precise estimates to date for calf and noncalf survival rates are 0.875 (SE = 0.047) and 0.96 (SE = 0.008), respectively, for the summer feeding population in the Gulf of Maine (Barlow and Clapham, 1997). Average and maximum life expectancies in this species are unclear, partly because whaling probably removed most of the oldest animals from the populations in which this question has been studied. Chittleborough (1965) reported that the oldest whale observed by him (out of many thousands examined in the Australian catch) was one 48 years old. This estimate is dependent upon acceptance of the age determination technique employed, which assumes that four layers (two Growth Layer Groups) per year are laid down in the laminar plug found in the auditory meatus (Clapham, 1992).

Most populations were drastically reduced by commerical whaling, primarily during this century. This whale's frequently coastal habits often resulted in it being the first species to be exploited in an area, with whalers moving to other species as the population of humpbacks declined (Clapham et al., 1997; Mitchell and Reeves, 1983). In the southern hemisphere, more than 200,000 humpback whales were killed this century (International Whaling Commission, 1995; Zemsky et al., 1995). Of this total, 48,477 whales were taken by the Soviet Union, with most caught illegally: only 2,710 were reported to the International Whaling Commission (Yablokov, 1994; Zemsky et al., 1995). Humpback whales were hunted under quota for many years and were accorded protection worldwide in 1966, but the Soviets are now known to have violated this agreement. Today, exploitation is minimal and is confined to aboriginal fisheries, including a take by the inhabitants of Bequia (southeastern Caribbean), and a probable hunt off the equatorial West African island of Pagulu (Aguilar, 1985).

Since the cessation of commercial whaling on *M. novaeangliae*, research on this species has employed various methods. The introduction of a technique with which to identify individual humpbacks from photographs of their ventral flukes patterns (Katona and Whitehead, 1981) has yielded considerable information about the biology and behavior of this whale, and several longitudinal studies are ongoing. Recently, application of molecular genetic techniques has provided a wealth of additional information (Baker et al., 1993; Larsen et al., 1996; Palsbøll et al., 1995, 1997; Palumbi and Baker, 1994; Valsecchi et al., 1997). Radio tagging (either VHF- or satellite-monitored) has had limited success to date, largely because of the difficulty of achieving prolonged tag attachment (Mate et al., 1997).

BEHAVIOR. The social organization of *M. novaeangliae* is extremely fluid at both ends of the migratory cycle. With the exception of mother/calf pairs, *M. novaeangliae* groups are typically small and unstable, and individuals frequently change associates (Clapham 1993, 1996; Mobley and Herman, 1985; Weinrich and Kuhlberg, 1991). In summer, individuals may feed alone or together, and the fluidity of associations at this time is probably a response to constantly varying prey-patch size (Clapham, 1993; Whitehead, 1983). Stable groups which remain together over weeks or even for several feeding seasons have been recorded in the Gulf of Maine (Clapham, 1993; Weinrich, 1991) and Alaska (Perry et al., 1990), but these represent a clear exception to the general pattern of social behavior during summer, and their basis is not clear. Such groups do not appear to consist of related animals, and indeed kinship seems to be of little importance among humpback whale associations (Clapham, 1993). Perry et al. (1990) suggested that the few remarkably cohesive stable groups observed in Alaskan waters consist of animals who maximize energetic intake by cooperatively using a common feeding technique. No stable groups have been documented on the breeding grounds.

Social development in humpback whales is similar to that of many other mammals. Juvenile whales of both sexes spend more time alone than do adults, and tend to associate with other immature animals. Associations with adults increase in frequency with age, and by attainment of sexual maturity the association patterns of most humpbacks are indistinguishable from those of adult conspecifics (Clapham, 1994).

During the winter breeding season, males sing, probably primarily to attract females (Payne and McVay, 1971; Tyack, 1981). They also engage in aggressive competition for access to potential mates (Baker and Herman, 1984; Clapham et al., 1992; Tyack and Whitehead, 1982). In many ways, the mating system resembles a lek (Mobley and Herman, 1985), although the territoriality that is a feature of classical leks is absent in this species, and a novel classification appears to be warranted (Clapham, 1996). Recent molecular studies have shown that calves born to individually identified females have different fathers, indicating promiscuous mating (Clapham and Palsbøll, 1997). There is some evidence that males may temporarily form coalitions to displace other males in competitive groups (Brown and Corkeron, 1995; Clapham et al., 1992), but this question requires further study.

The song of the humpback whale has received considerable attention because of its length and complexity. Songs consist of several themes which are sung in a generally invariant order, the entire song lasting from a few minutes to half an hour (Payne and McVay, 1971; Tyack, 1981). Singers, who are always male and are usually alone (Tyack 1981), will sometimes sing continuously for hours or even days. All of the whales in a given population sing the same song, and differences or similarities among areas have been used as an indicator of population discreteness or mixing (Payne and Guinee, 1983). The song changes progressively, yet all singers somehow keep up with the changes. What drives the change is unknown, but most observers assume that sexual selection plays a key role. Singing is virtually ubiquitous in the species' breeding range in winter, but it has occasionally been recorded on the feeding grounds in summer and fall, as well as on migration (Clapham and Mattila, 1990; Mattila et al., 1987; McSweeney et al., 1989).

Relative to other balaenopterids, humpback whales are not fast swimmers. Reported or inferred swimming speeds of animals traveling or migrating range from 2.2 to 8.2 knots (7.9–15.1 km/h—Chittleborough, 1953; Dawbin, 1966; Tomilin, 1957). A maximum burst speed of 14.7 knots (27 km/h) was reported for a wounded whale being chased by a whaling catcher boat (Tomilin 1957).

Foraging humpback whales are unique among balaenopterids in that they frequently employ bubbles to trap or corral prey (Jurasz and Jurasz, 1979; Hain et al., 1982). Bubble structures in the form of nets, clouds or curtains are commonly observed in all studied populations, notably when whales are feeding on schooling fish. Such behaviors are often individually specific, and may be associated with other individual foraging specializations such as "lobtail feeding" (Weinrich et al., 1992). Bubble feeding is practised by lone whales and also cooperatively by animals in groups of different sizes; in the latter, acoustic coordination of behavior by a lead whale has been suggested but not conclusively demonstrated (D'Vincent et al., 1985). Fish and Battle (1995) have hypothesized that the tubercles found on the humpback whale's flippers function to increase hydrodynamic lift at high angles of attack, and increase maneuverability during bubble-feeding behavior. There is evidence that humpback whales sometimes feed along the sea floor (Hain et al., 1995); this and other behaviors show evidence of lateralization (i.e. a tendency for the behavior to involve a consistent preference for one side, or for movement in a consistent direction—Clapham et al., 1995*a*).

Diving behavior in *M. novaeangliae* varies by time of year. In summer, most dives last <5 min, and dives exceeding 10 min are unusual (Dolphin, 1987*b*). In winter, dives average 10–15 min, and dives of >30 min have been recorded (Chu, 1988; D. Mattila, unpublished data). In this season, many long-diving whales appear to be submerging to rest, an activity which commonly takes place at the surface on the feeding grounds (Dolphin, 1987*b*). Nothing is known for certain about sleep in mysticetes, although it is often assumed that, like some delphinids, they rest one hemisphere of the brain at a time (presumably essential to a voluntary breather; Klinowska, 1986).

Megaptera novaeangliae is well known for its aerial behavior, which includes breaching (leaping out of the water), flippering (slapping one or both pectoral fins on the water surface), and lobtailing (slamming the tail down on the water). The purpose of these behaviors is not well understood. However, it is clear that they perform different functions in different contexts, since they are performed at all times of year and by both lone whales and animals in groups. For example, it has been suggested that breaching serves multiple purposes ranging from signalling position to excitement or (in calves) play (Whitehead, 1985).

GENETICS. As for most cetaceans, the chromosome count for *M. novaeangliae* is $2n = 44$ (Lambertsen et al., 1988), although Duffield et al. (1987) found an extra small chromosome in one individual. Studies of the population genetics of the species have employed mitochondrial DNA (mtDNA) and nuclear markers, notably microsatellites. The maternally directed fidelity to specific feeding grounds observed in the North Atlantic (Clapham and Mayo, 1987; Clapham et al., 1993*b*; Katona and Beard, 1990) appears to be have persisted over sufficient generations to be reflected in the genetic structure of this population. This finding is somewhat surprising given the wide-ranging nature of this species and the lack of obvious barriers to movement in the marine environment (Larsen et al., 1996; Palsbøll et al., 1995). However, analysis of nuclear DNA supports findings from behavioral studies that this population is panmictic (Palsbøll et al., 1997). MtDNA analysis also shows evidence of historic gene flow between this ocean and the southern hemisphere (Palsbøll et al., 1995; Valsecchi et al., 1997).

A similar pattern is evident from analyses in the North Pacific, with significant differences in mtDNA haplotypic frequency among feeding areas but some evidence for male-mediated nuclear gene flow (Baker et al., 1993; Palumbi and Baker, 1994). However, since (unlike in the North Atlantic) the whales sampled in different feeding areas generally migrate to separate breeding grounds, the observed differences in mtDNA may reflect these distinct breeding-ground origins. A study that used microsatellite DNA from several oceanic populations found allelic diversity to be greatest in the Antarctic, probably reflecting historically larger population sizes (Valsecchi et al., 1997); a similar finding is evident from mtDNA analysis (Baker et al., 1993; Palsbøll et al., 1995).

CONSERVATION STATUS. *Megaptera novaeangliae* is listed as endangered by both the U.S. Endangered Species Act and the International Union for the Conservation of Nature. Similarly, it is classified in Appendix I of the Convention on International Trade in Endangered Species.

The present status of this species is difficult to determine, given its wide-ranging nature and the difficulty of providing adequate sampling coverage across ocean basins. As a result, we regard most absolute estimates of abundance for *M. novaeangliae* (or any other large whale) as unreliable. Nonetheless, evidence from a variety of studied populations in both hemispheres indicates that strong recovery is occurring in most areas, including the North Atlantic and several regions of the Southern Ocean (Bannister et al., 1991; Barlow and Clapham, 1997; Best, 1993; Palsbøll et al., 1997; Paterson et al., 1994).

The North Atlantic population was recently estimated from genetic tagging data collected in the breeding range by Palsbøll et al. (1997) at 4,894 males (95% *CI* 3,374–7,123) and 2,804 females (95% *CI* 1,776–4,463). Since the sex ratio in this population is known to be even (Palsbøll et al., 1997), the excess of males is presumed to be a result of sampling bias, lower rates of migration among females, or sex-specific habitat partitioning in the West Indies; whatever the reason, the combined total is an underestimate of overall population size in this ocean. The status of the humpback whale in the northeastern North Atlantic is unclear, although Øien (1990) estimated from sighting survey data that there were 1,100 humpback whales in the Barents Sea region.

Calambokidis et al. (1997) applied mark-recapture techniques to photographic data to estimate the North Pacific population at ca. 6,000 animals. However, the low sampling effort in the western part of this ocean makes it likely that this is an underestimate.

Although many populations appear to be recovering, exceptions exist. Best (1993) notes that no significant increase is apparent among the humpback population that migrates past New Zealand to Tonga, where a substantial native fishery persisted until 1978. Historically important breeding grounds in the Cape Verde Islands and the southeastern Caribbean, once the focus of significant 19th century fisheries (Mitchell and Reeves, 1983), now appear to host relatively few whales (Mattila et al., 1994; Reiner et al., 1996). The population which feeds off the California coast is currently estimated at ca. 600 animals (Barlow, 1995; Calambokidis and Steiger, 1995), but analysis of catch data from the 1920s suggests that this is well below the pre-exploitation size (Clapham et al., 1997).

Known threats to this species include entanglement in fishing gear and ship strikes (Lien, 1994; Whitehead, 1987; Wiley et al., 1995), although it is questionable whether the mortality involved in either is significant at the population level. Existing data suggest that baleen whales, including *M. novaeangliae,* do not carry high contaminant burdens (O'Shea and Brownell, 1994), although the potential impact of transgenerational accumulation remains unstudied. There is only a single known instance of a mass mortality in this species, an event in which at least 15 humpback whales died off Cape Cod, Massachusetts, over a six-week period in 1987–1988. The cause appears to have been saxitoxin poisoning from ingested mackerel (Geraci et al., 1989).

REMARKS. The genus name *Megaptera* derives from the Greek *mega* for "large" and *pteron* for "wing", and refers to the humpback's huge flippers. The specific epithet *novaeangliae* refers to New England, where the type specimen was described. There are no commonly used vernacular names in English except humpback whale. *M. novaeangliae* was the first animal species to be the subject of a study to use genetic markers as the primary means of identifying individuals in a large population (Palsbøll et al., 1997).

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