

Megaptera novaeangliae. By Phillip J. Clapham and James G. Mead.

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Megaptera Gray, 1846a

- Megaptera* Gray, 1846a:83. Type species is *Megaptera longipinna* (= *Balaena longimana* Rudolphi 1832 = *Balaena novaeangliae* Borowski 1781) by monotypy.
- Perqualus* Gray, 1846b: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, 1864a:207. Subgenus of *Megaptera* Gray 1846a. Included species *Balaena lalandii* Fischer 1829 (= *Balaena novaeangliae* Borowski, 1781), *Megaptera novae-zelandiae* Gray, 1864b: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, 1846a:83. Type locality unknown.
- Megaptera poeppok* Gray, 1846b:17. Type locality "Cape of Good Hope."
- Megaptera americana* Gray, 1846b:17. Type locality unknown.
- Balaena allamack* Gray, 1846b: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, 1864a: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 longimana 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 keporhak* 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, 1864a) 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 protuberances (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

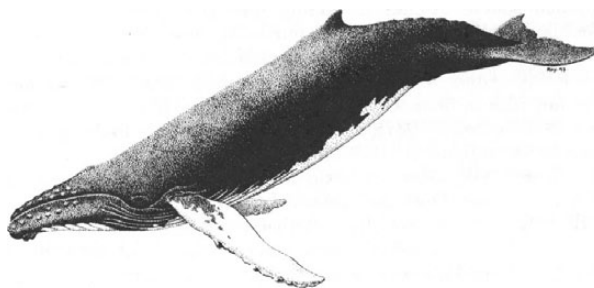


FIG. 1. The humpback whale, *Megaptera novaeangliae*. Illustration by Roxy Corbett.

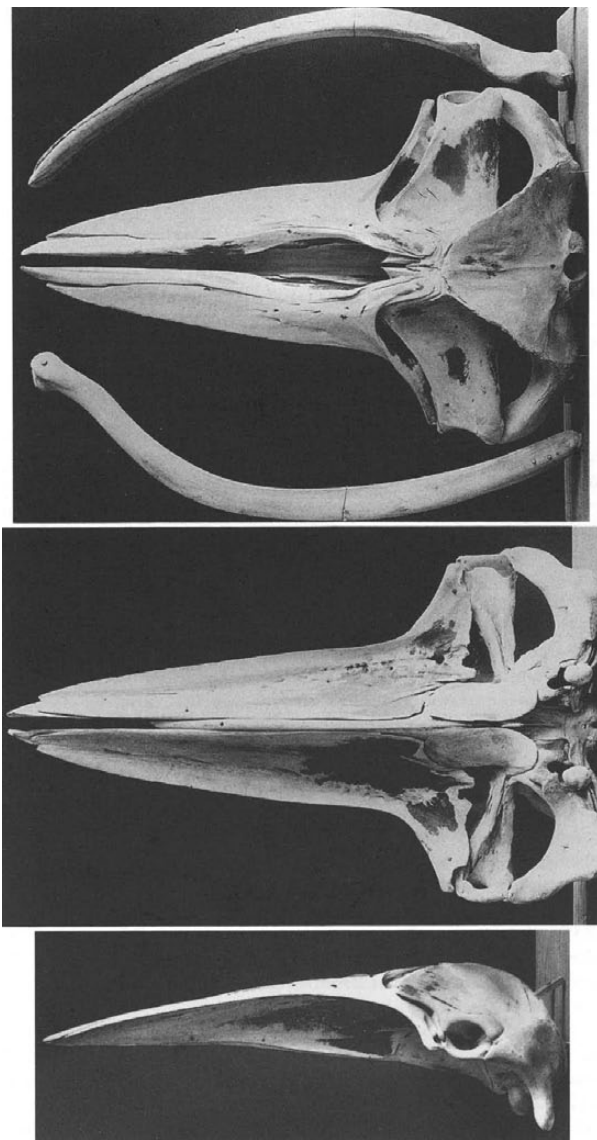


FIG. 2. Dorsal view of cranium and mandibles and ventral and lateral views of cranium of *Megaptera novaeangliae* (USNM 16252, immature female killed April 1879 off Provincetown, Massachusetts). Greatest length of skull is 231 cm. Photographs courtesy of National Museum of Natural History.

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 ex-

treme 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 Antinaja, 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., 1993a; 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

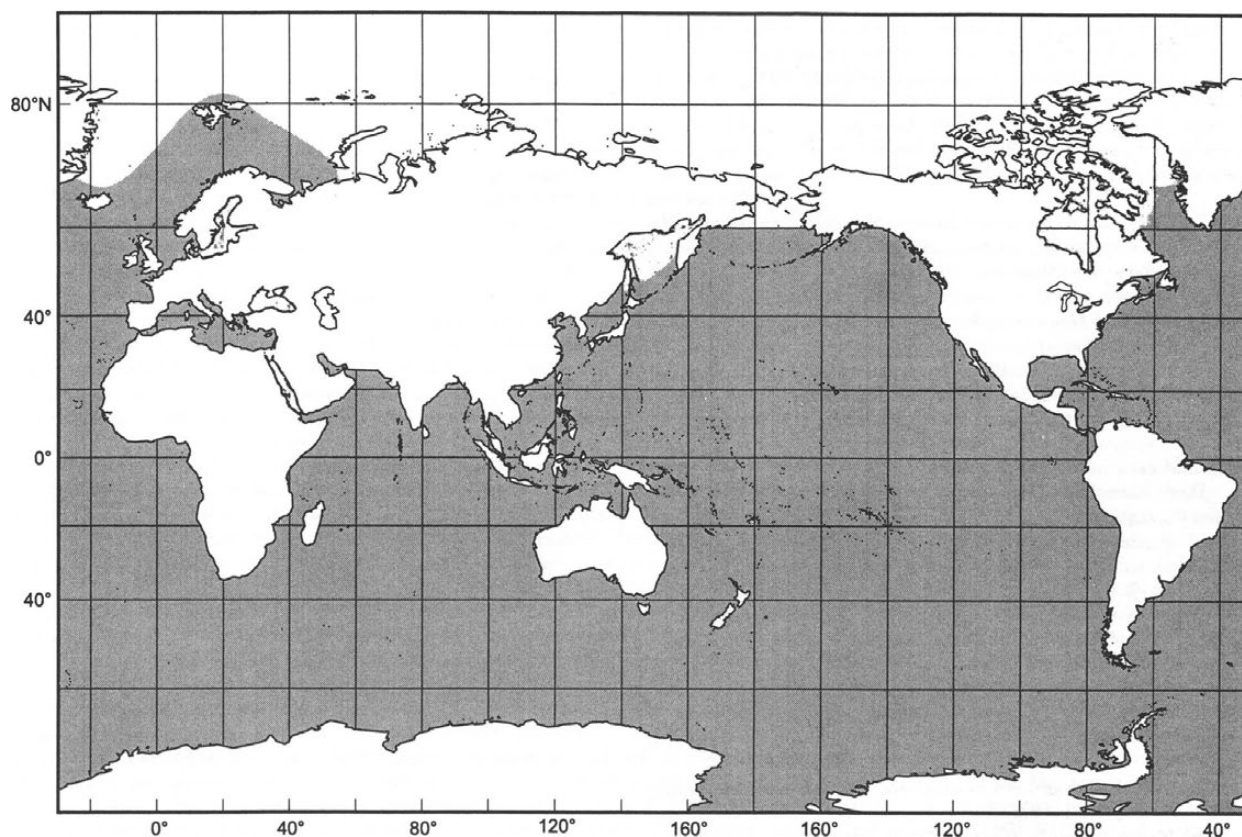


FIG. 3. Geographic distribution of *Megaptera novaeangliae*.

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 (1864b) 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 × 10⁶ 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 Antinaja, 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*, *Thysanoessa* 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, 1987a). *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., 1993b; 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., 1993a; 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 Revillagigedo 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 Revillagigedo 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., 1995b; 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 commercial 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., 1995a).

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, 1987b). 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, 1987b). 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), flippers (slapping one or both pectoral fins on the water surface), and lob-tailing (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., 1993b; Katona and Beard, 1990) appears to 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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LITERATURE CITED

- ACUILAR, A. 1985. Aboriginal whaling off Pagalu (Equatorial Guinea). Reports of the International Whaling Commission, 35: 385–386.
- . 1989. A record of two humpback whales, *Megaptera novaeangliae*, in the western Mediterranean Sea. Marine Mammal Science, 5:306–309.
- ANDREWS, R. C. 1914. Monographs of the Pacific Cetacea. I: The California gray whale (*Rhachianectes glaucus* Cope). Memoirs of the American Museum of Natural History, New Series, 1(v): 227–287.
- . 1916. The sei whale (*Balaenoptera borealis*). Memoirs of the American Museum of Natural History, New Series, 1(6): 289–388.
- BAKER, C. S., AND L. M. HERMAN. 1984. Aggressive behavior between humpback whales (*Megaptera novaeangliae*) wintering in Hawaiian waters. Canadian Journal of Zoology, 62:1922–1937.
- BAKER, C. S., L. M. HERMAN, A. PERRY, W. S. LAWTON, J. M. STRALEY, AND J. H. STRALEY. 1985. Population characteristics and migration of summer and late season humpback whales (*Megaptera novaeangliae*) in southeastern Alaska. Marine Mammal Science, 1:304–323.
- BAKER, C. S., ET AL. 1986. Migratory movement and population structure of humpback whales (*Megaptera novaeangliae*) in the central and eastern North Pacific. Marine Ecology Progress Series, 31:105–119.
- . 1993. Abundant mitochondrial DNA variation and worldwide population structure in humpback whales. Proceedings of the National Academy of Sciences, 90:8239–8243.
- BANNISTER, J. L., G. P. KIRKWOOD, AND S. E. WAYTE. 1991. Increase in humpback whales off Western Australia. Reports of the International Whaling Commission, 41:461–465.
- BARAFF, L. S., AND M. T. WEINRICH. 1993. Separation of humpback whale mothers and calves on a feeding ground in early autumn. Marine Mammal Science, 9:431–434.
- BARLOW, J. 1995. The abundance of cetaceans in California waters. Part I: ship surveys in summer and fall 1991. Fishery Bulletin, 93:1–14.
- BARLOW, J., AND P. J. CLAPHAM. 1997. A new birth-interval approach to estimating demographic parameters of humpback whales. Ecology, 78:535–546.
- BAYLIS, H. A. 1920. Observations on the genus *Crassicauda*. American Magazine of Natural History, 9:410–419.
- BEST, P. B. 1993. Increase rates in severely depleted stocks of baleen whales. ICES Journal of Marine Science, 50:169–186.
- BONNATERRE, J. P. 1789. Tableau encyclopédique et méthodique des trois règnes de la nature, dédié et présenté à M. Necker, ministre d'état, et directeur général des finances. Cétologie. Panckoucke, Paris, pp. i–xli, 1–28, pl. 1–12. Encyclopédie Méthodique, vol. 183.
- BOROWSKI, G. H. 1781. Gemeinnützige Naturgeschichte des Thierreichs. Gottlieb August Lange, Berlin, 1:1–21.
- BRODIE, P. F. 1975. Cetacean energetics: an overview of intraspecific size variation. Ecology, 56:152–161.
- BROWN, M., AND P. CORKERON. 1995. Pod characteristics of migrating humpback whales (*Megaptera novaeangliae*) off the East Australian coast. Behaviour, 132:163–179.
- BROWN, M. R., P. J. CORKERON, P. T. HALE, K. W. SCHULTZ, AND M. M. BRYDEN. 1995. Evidence for a sex-segregated migration in the humpback whale (*Megaptera novaeangliae*). Proceedings of the Royal Society of London Part B, 259:229–234.
- CALAMBOKIDIS, J., AND G. H. STEIGER. 1995. Population estimates of humpback and blue whales made through photo-identification from 1993 surveys off California. Final report to the Southwest Fisheries Science Center, La Jolla, California. 31 pp.
- CALAMBOKIDIS, J., ET AL. 1996. Interchange and isolation of humpback whales off California and other North Pacific feeding grounds. Marine Mammal Science 12:215–226.
- . 1997. Population abundance and structure of humpback whales in the North Pacific basin. Final report to Southwest Fisheries Science Center, La Jolla, California. 67 pp.
- CHITTLEBOROUGH, R. G. 1953. Aerial observations on the humpback whale, *Megaptera nodosa* (Bonnaterre), with notes on other species. Australian Journal of Marine and Freshwater Research 4:219–226.
- . 1954. Studies on the ovaries of the humpback whale, *Megaptera nodosa* (Bonnaterre), on the eastern Australian coast. Australian Journal of Marine and Freshwater Research 5:35–63.
- . 1958. The breeding cycle of the female humpback whale, *Megaptera nodosa* (Bonnaterre). Australian Journal of Marine and Freshwater Research 9:1–18.
- . 1965. Dynamics of two populations of the humpback whale, *Megaptera novaeangliae* (Borowski). Australian Journal of Marine and Freshwater Research 16:33–128.
- CHRISTENSEN, I., T. HAUG, AND N. ØIEN. 1992. Seasonal distribution, exploitation and present abundance of stocks of large baleen whales (Mysticeti) and sperm whales (*Physeter macrocephalus*) in Norwegian and adjacent waters. ICES Journal of Marine Science, 49:341–355.
- CHU, K. C. 1988. Dive times and ventilation patterns of singing humpback whales (*Megaptera novaeangliae*). Canadian Journal of Zoology, 66:1322–1327.
- CLAPHAM, P. J. 1992. The attainment of sexual maturity in humpback whales. Canadian Journal of Zoology, 70:1470–1472.
- . 1993. Social organization of humpback whales on a North Atlantic feeding ground. Symposia of the Zoological Society of London, 66:131–145.
- . 1994. Maturation changes in patterns of association among male and female humpback whales. Journal of Zoology (London), 234:265–274.
- . 1996. The social and reproductive biology of humpback whales: an ecological perspective. Mammal Review 26:27–49.
- CLAPHAM, P. J., AND D. K. MATTILA. 1990. Humpback whale songs as indicators of migration routes. Marine Mammal Science, 6: 155–160.
- CLAPHAM, P. J., AND C. A. MAYO. 1987. Reproduction and recruitment of individually identified humpback whales, *Megaptera*

- novaeangliae*, observed in Massachusetts Bay, 1979–1985. Canadian Journal of Zoology, 65:2853–2863.
- . 1990. Reproduction of humpback whales, *Megaptera novaeangliae*, observed in the Gulf of Maine. Reports of the International Whaling Commission, Special Issue 12:171–175.
- CLAPHAM, P. J., AND P. J. PALSBOELL. 1997. Molecular analysis of paternity shows promiscuous mating in female humpback whales (*Megaptera novaeangliae*, Borowski). Proceedings of the Royal Society of London Part B, 264:95–98.
- CLAPHAM, P. J., M. C. BERUBE, AND D. K. MATTILA. 1995b. Sex ratio of the Gulf of Maine humpback whale population. Marine Mammal Science, 11:227–231.
- CLAPHAM, P. J., D. K. MATTILA, AND P. J. PALSBOELL. 1993a. High-latitude-area composition of humpback whale competitive groups in Samana Bay: further evidence for panmixis in the North Atlantic population. Canadian Journal of Zoology, 71:1065–1066.
- CLAPHAM, P. J., S. LEATHERWOOD, I. SZCZEPANIAK, AND R. L. BROWNELL, JR. 1997. Catches of humpback and other whales from shore stations at Moss Landing and Trinidad, California, 1919–1926. Marine Mammal Science, 13:368–394.
- CLAPHAM, P. J., E. LEIMKUEHLER, B. K. GRAY, AND D. K. MATTILA. 1995a. Do humpback whales exhibit lateralized behavior? Animal Behaviour, 50:73–82.
- CLAPHAM, P. J., P. J. PALSBOELL, D. K. MATTILA, AND O. VÁSQUEZ. 1992. Composition and dynamics of humpback whale competitive groups in the West Indies. Behaviour, 122:182–194.
- CLAPHAM, P. J., ET AL. 1993b. Seasonal occurrence and annual return of humpback whales in the southern Gulf of Maine. Canadian Journal of Zoology, 71:440–443.
- COPE, E. D. 1865. Note on a species of humpback whale. Proceedings of the Academy of Natural Sciences, Philadelphia, 1865:178–181.
- . 1867. A young species of whale, known as the Bahia finner. Proceedings of the Academy of Natural Sciences, Philadelphia, 1867:32.
- . 1869. On the cetaceans of the western coast of North America. Proceedings of the Academy of Natural Sciences, Philadelphia, 1869:13–63.
- . 1871. On *Megaptera bellicosa*. Proceedings of the American Philosophical Society, 12:103–108.
- CUVIER, F. 1836. De l'histoire naturelle des Cétacés, ou recueil et examen des faits dont se compose l'histoire naturelle de ces animaux. Librairie Encyclopedique de Roret, Paris, 1836, 416 pp.
- DARLING, J. D., AND S. CERCHIO. 1993. Movement of a humpback whale (*Megaptera novaeangliae*) between Japan and Hawaii. Marine Mammal Science, 9:84–89.
- DARLING, J. D., AND K. MORI. 1993. Recent observations of humpback whales (*Megaptera novaeangliae*) in Japanese waters off Ogasawara and Okinawa. Canadian Journal of Zoology, 71:325–333.
- DARLING, J. D., ET AL. 1996. Movements of a humpback whale (*Megaptera novaeangliae*) from Japan to British Columbia and return. Marine Mammal Science, 12:281–287.
- DAWBIN, W. H. 1966. The seasonal migratory cycle of humpback whales. Pp. 145–170, in Whales, dolphins and porpoises (K. S. Norris, ed.). University of California Press, Berkeley, 789 pp.
- . 1997. Temporal segregation of humpback whales during migration in southern hemisphere waters. Memoirs of the Queensland Museum, 42:105–138.
- DOLPHIN, W. F. 1987a. Observations of humpback whale, *Megaptera novaeangliae*-killer whale, *Orcinus orca*, interactions in Alaska: comparison with terrestrial predator-prey relationships. Canadian Field Naturalist, 101:70–75.
- . 1987b. Dive behavior and estimated energy expenditure of foraging humpback whales in southeast Alaska. Canadian Journal of Zoology, 65:354–362.
- DUFFIELD, D. A., J. CHAMBERLIN-LEA, J. C. SWEENEY, D. K. ODELL, E. D. ASPER, AND W. G. GILMARTIN. 1987. Use of corneal cell culture for R-band chromosome studies on stranded cetaceans. In Proceedings of the Second Marine Mammal Stranding Workshop (J. E. Reynolds and D. K. Odell, eds.), 3–5 December 1987, Miami, FL, pp. 181–202.
- D'VINCENT, C. G., R. M. NILSON, AND R. E. HANNA. 1985. Vocalization and coordinated feeding behavior of the humpback whale is southeastern Alaska. Scientific Reports of the Whales Research Institute, 36:41–47.
- ESCHRICHT, D. F. 1849. Undersøgelser over hvaldyrene. Kongelige Danske Videnskabernes Selskabs Skrifter, Naturvidenskabelige og Mathematisk Afhandlinger, København, 5 række, 1: 87–188.
- FABRICIUS, O. 1780. Fauna Groenlandica, systematice sistens animalia Groenlandiae occidentalis hactenus indigata, quoad nomen specificum, triviale, vernaculumque; synonyma auctorum plurium, descriptionem, locum, victum, generationem, mores, usum, capturamque singuli, prout detegendi occasio fuit, maximaque parte secundum proprias observationes Othonis Fabricii, Ministri Evangelii, quondam Groenlandis ad Coloniam Friderichshaab, posthac Norvagus Drangedeliae, nunc vero Danis hopunti iutiae, Membri Societatis Scientiarum quae est Hafniae. Hafniae et Lipsiae [Copenhagen and Leipzig], Ioanis Gottlob Rothe, 452 pp.
- FELTS, W. J. L. 1966. Some functional and structural characteristics of cetacean flippers and flukes. Pp. 255–276, in Whales, dolphins, and porpoises (K. S. Norris, ed.). University of California Press, Berkeley, 789 pp.
- FISCHER, J. B. 1829. Synopsis mammalium. Stuttgart, J. G. Cottae, 1829, 528 pp.
- FISH, F. E., AND J. BAITLE. 1995. Hydrodynamic design of the humpback whale flipper. Journal of Morphology, 225:51–60.
- FLÓREZ-GONZÁLEZ, L. 1991. Humpback whales *Megaptera novaeangliae* in the Gorgona Island, Colombian Pacific breeding waters: population and pod characteristics. Memoirs of the Queensland Museum, 30:291–295.
- FLÓREZ-GONZÁLEZ, L., J. J. CAPELLA, AND H. C. ROSENBAUM. 1994. Attack of killer whales (*Orcinus orca*) on humpback whales (*Megaptera novaeangliae*) on a South American Pacific breeding ground. Marine Mammal Science, 10:218–222.
- FRAZER, J. F. D., AND A. ST. G. HUGGETT. 1973. Specific foetal growth rates of cetaceans. Journal of Zoology (London), 169:111–126.
- GERACI, J. R., ET AL. 1989. Humpback whales (*Megaptera novaeangliae*) fatally poisoned by dinoflagellate toxins. Canadian Journal of Fisheries and Aquatic Science, 46:1895–1898.
- GERVAIS, H. F. P. 1883. Sur une nouvelle espèce du genre mégaptère provenant de la Baie de Bassora (Golfe Persique). Comptes Rendus de l'Académie des Sciences, Paris, 97:1566–1569.
- GLOCKNER, D. A. 1983. Determining the sex of humpback whales (*Megaptera novaeangliae*) in their natural environment. In Behaviour and communication of whales (R.S. Payne, ed.). AAAS Selected Symposium, Westview Press, Boulder, Colorado, 76:447–464.
- GLOCKNER-FERRARI, D. A., AND M. J. FERRARI. 1990. Reproduction in the humpback whale (*Megaptera novaeangliae*) in Hawaiian waters, 1975–1988: the life history, reproductive rates and behaviour of known individuals identified through surface and underwater photography. Reports of the International Whaling Commission, Special Issue 12:161–169.
- GRAY, J. E. 1843. List of mammalia hitherto recorded as found in New Zealand. In Travels in New Zealand; with contributions to the geography, geology, botany, and natural history of that country (Diffenback, E. ed.). J. Murray, London, 2:181–185.
- . 1846a. On the British cetacea. Annals and Magazine of Natural History, Series 1, 17:82–85.
- . 1846b. On the cetaceous animals. Pp. 13–53, in Mammalia of Richardson, J. and Gray, J. E. (eds.), The zoology of the voyage of H.M.S. Erebus and Terror, under the command of Captain Sir James Clark Ross during the years 1839 to 1843. By authority of Lords Commissioners of the Admiralty. Longmans, Brown, Green and Longmans, London, 1 (part III).
- . 1850. Catalogue of the specimens of mammalia in the collection of the British Museum. Part I: Cetacea. British Museum, London, 153 pp.
- . 1864a. On the cetacea which have been observed in the seas surrounding the British Islands. Proceedings of the Zoological Society of London, 1864(2):195–248.
- . 1864b. Notes on the whalebone-whales; with a synopsis of the species. Annals and Magazine of Natural History, 3rd Series, 14(83):345–353.
- . 1866. Catalogue of seals and whales in the British Museum. Second ed. British Museum, London, 402 pp.
- HAIN, J. H. W., G. R. CARTER, S. D. KRAUS, C. A. MAYO, AND H.

- E. WINN. 1982. Feeding behaviour of the humpback whale, *Megaptera novaeangliae*, in the western North Atlantic. *Fishery Bulletin*, 80:259–268.
- HAIN, J. H. W., ET AL. 1995. Apparent bottom-feeding behavior by humpback whales on Stellwagen Bank. *Marine Mammal Science*, 11:464–479.
- HERMAN, L. M. 1979. Humpback whales in Hawaiian waters: a study in historical ecology. *Pacific Science*, 33:1–15.
- HERMAN, L. M., AND R. C. ANTINOJA. 1977. Humpback whales in the Hawaiian breeding waters: population and pod characteristics. *Scientific Reports of the Whales Research Institute*, 29: 59–85.
- HURDIS, J. L. 1897. Rough notes and memoranda relating to the natural history of the Bermudas. R. H. Porter, London, 408 pp.
- INTERNATIONAL WHALING COMMISSION. 1995. Southern hemisphere catch data coding: position at 1 July 1994. *Reports of the International Whaling Commission*, 45:129–130.
- IVASHIN, M. V. 1958. O sistematicheskoy polozhenii gorbatogo kita (*Megaptera nodosa lalandii* Fischer) yuzhnogo polushariya [On the systematic position of the humpbacked whale in the southern hemisphere]. *Byulleten' Sovetskoi Antarkticheskoi Ekspeditsii*, 3:77–78 (in Russian).
- JACQUINOT, H., AND J. PUCHERAN. 1853. Mammifères et oiseaux. Volume 3 in d'Urville, D., 1841–54 *Voyage au Pôle Sud et dans l'Océanie sur les corvettes l'Astrolabe et la Zélée: exécuté par ordre du roi pendant les années 1837-1838-1839-1840—sous le commandement de M. J. Dumont d'Urville, capitaine de vaisseau, publié par ordonnance de Sa Majesté; sous la direction supérieure de M. Jacquinot, capitaine de vaisseau, commandant de la Zélée; Histoire du voyage par M. Dumont d'Urville*, Paris.
- JURASZ, C. M., AND V. P. JURASZ. 1979. Feeding modes of the humpback whale, *Megaptera novaeangliae*, in southeast Alaska. *Scientific Reports of the Whales Research Institute*, 31:69–83.
- KATONA, S. K., AND J. C. BEARD. 1990. Population size, migrations and feeding aggregations of the humpback whale (*Megaptera novaeangliae*) in the western North Atlantic Ocean. *Reports of the International Whaling Commission, Special Issue 12*: 295–305.
- KATONA, S. K., AND H. P. WHITEHEAD. 1981. Identifying humpback whales using their natural markings. *Polar Record*, 20:439–444.
- KATONA, S. K., P. M. HARCOURT, J. S. PERKINS, AND S. D. KRAUS. 1980. Humpback whales: a catalogue of individuals identified in the western North Atlantic Ocean by means of fluke photographs. *College of the Atlantic, Bar Harbor, Maine*, 78 pp.
- KAUFMAN, G. D., M. A. SMULTEA, AND P. H. FORESTELL. 1987. Use of lateral body pigmentation patterns for photo-identification of East Australian (Area V) humpback whales. *Cetus*, 7:5–13.
- KELLOGG, R. 1922. Description of the skull of *Megaptera miocaena*, a fossil humpback whale from the Miocene diatomaceous earth of Lompoc, California. *Proceedings of the United States National Museum*, 61:1–18.
- KLINOWSKA, M. 1986. Diurnal rhythms in Cetacea: a review. *Reports of the International Whaling Commission, Special Issue 8*:75–88.
- LAMBERTSEN, R. H. 1992. Crassicaudosis: a parasitic disease threatening the health and population recovery of large baleen whales. *Reviews of the Scientific and Technical Office of International Epizootics*, 11:1131–1141.
- LAMBERSTEN, R. H., C. S. BAKER, D. A. DUFFIELD, AND J. CHAMERLIN-LEA. 1988. Cytogenetic determination of sex among individually identified humpback whales (*Megaptera novaeangliae*). *Canadian Journal of Zoology*, 66:1243–1248.
- LARSEN, A. H., J. SIGURJÓNSSON, N. ØIEN, G. VIKINGSSON, AND P. J. PALSBOÛLL. 1996. Population genetic analysis of mitochondrial and nuclear genetic loci in skin biopsies collected from central and northeastern North Atlantic humpback whales (*Megaptera novaeangliae*): population identity and migratory destinations. *Proceedings of the Royal Society of London Part B*, 263:1611–1618.
- LEATHERWOOD, S., D. K. CALDWELL, AND H. E. WINN. 1976. Whales, dolphins, and porpoises of the western North Atlantic—a guide to their identification. *NOAA Technical Report NMFS CIRC-396*, 176 pp.
- LESSON, R. P. 1828. Cétacés. Pg. 372, in Lesson, R. P. 1828–1844 *Histoire naturelle, générale et particulière des mammifères et des oiseaux découverts depuis 1788 jusqu'à nos jours*. Baudouin Frères, Éditeurs, Paris, 1.
- . 1842. *Nouveau tableau du règne animal. Mammifères*. A. Bertrand, Paris, 204 pp.
- LIEN, J. 1994. Entanglement of large cetaceans in passive inshore gear in Newfoundland and Labrador (1979–1990). *Reports of the International Whaling, Special Issue 15*:149–157.
- LILLIE, D. G. 1915. Cetacea. *Natural history of the British Antarctic Terra Nova Expedition 1910*, 1:85–124.
- MACKINTOSH, N. A. 1942. The southern stocks of whalebone whales. *Discovery Reports*, 22:197–300.
- MATE, B. R., S. L. NIEUKIRK, AND S. D. KRAUS. 1997. Satellite-monitored movements of the northern right whale. *Journal of Wildlife Management*, 61:1393–1405.
- MATTHEWS, L. H. 1937. The humpback whale, *Megaptera nodosa*. *Discovery Reports*, 17:7–92.
- MATTILA, D. K., L. N. GUINEE, AND C. A. MAYO. 1987. Humpback whale songs on a North Atlantic feeding ground. *Journal of Mammalogy*, 68:880–883.
- MATTILA, D. K., P. J. CLAPHAM, O. VÁSQUEZ, AND R. BOWMAN. 1994. Occurrence, population composition and habitat use of humpback whales in Samana Bay, Dominican Republic. *Canadian Journal of Zoology*, 72:1898–1907.
- MCSWEENEY, D. J., K. C. CHU, W. F. DOLPHIN, AND L. N. GUINEE. 1989. North Pacific humpback whale songs: a comparison of southeast Alaskan feeding ground songs and Hawaiian wintering ground songs. *Marine Mammal Science*, 5:116–138.
- MIKHALEV, Y. A. 1997. Humpback whales *Megaptera novaeangliae* in the Arabian Sea. *Marine Ecology Progress Series*, 149:13–21.
- MITCHELL, E., AND R. R. REEVES. 1983. Catch history, abundance and present status of northwest Atlantic humpback whales. *Reports of the International Whaling Commission, Special Issue 5*:153–212.
- MOBLEY, J. R., AND L. M. HERMAN. 1985. Transience of social affiliations among humpback whales (*Megaptera novaeangliae*) on the Hawaiian wintering grounds. *Canadian Journal of Zoology*, 63:763–772.
- MÜLLER, A. 1863. Über das Bruchstück vom Schädel eines Finnwales, *Balaenoptera syncondylus*, welches im Jahre 1860 von der Ostsee an die kurische Nehrung geworfen wurde. *Königliche Physikalisch-Oekonomische Gesellschaft zu Königsberg, Schriften*, 4:38–78.
- NISHIWAKI, M. 1959. Humpback whales in Ryukyuan waters. *Scientific Reports of the Whales Research Institute*, 14:49–87.
- . 1966. Distribution and migration of the larger cetaceans in the North Pacific as shown by Japanese whaling results. Pp. 171–191 in *Whales, dolphins and porpoises* (K. S. Norris, ed.). University of California Press, Berkeley, 789 pp.
- ØIEN, N. 1990. Sighting surveys in the northeast Atlantic in July 1988: distribution and abundance of cetaceans. *Reports of the International Whaling Commission*, 40:499–511.
- OMURA, H. 1953. Biological study on humpback whales in the Antarctic whaling Areas IV and V. *Scientific Reports of the Whales Research Institute*, 8:81–102.
- O'SHEA, T. J., AND R. L. BROWNELL, JR. 1994. Organochlorine and metal contaminants in baleen whales: a review and evaluation of conservation implications. *Science of the Total Environment*, 154:179–200.
- PALSBOÛLL, P. J., ET AL. 1995. Distribution of mtDNA haplotypes in North Atlantic humpback whales: the influence of behavior on population structure. *Marine Ecology Progress Series*, 116:1–10.
- PALSBOÛLL, P. J., ET AL. 1997. Genetic tagging of humpback whales. *Nature*, 388:767–769.
- PALUMBI, S. R., AND C. S. BAKER. 1994. Contrasting population structure from nuclear intron sequences and mtDNA of humpback whales. *Molecular Biology and Evolution*, 11:426–435.
- PATERSON, R., P. PATERSON, AND D. H. CATO. 1994. The status of humpback whales *Megaptera novaeangliae* in East Australia thirty years after whaling. *Biological Conservation*, 70:135–142.
- PAYNE, P. M., J. R. NICOLAS, L. O'BRIEN, AND K. D. POWERS. 1986. Distribution of the humpback whale, *Megaptera novaeangliae*, on Georges Bank and in the Gulf of Maine in relation

- to densities of the sand eel, *Ammodytes americanus*. Fishery Bulletin, 84:271–277.
- PAYNE, R. S., AND L. N. GUINEE. 1983. Humpback whale, *Megaptera novaeangliae*, songs as an indicator of "stocks." In Communication and behavior of whales (R. S. Payne, ed.). AAAS Selected Symposia Series, Westview Press, Boulder, Colorado, 76:333–358.
- PAYNE, R. S., AND S. MCVAY. 1971. Songs of humpback whales. Science, 173:585–597.
- PERRIN, W. F. 1975. Variation of spotted and spinner porpoise (genus *Stenella*) in the eastern tropical Pacific and Hawaii. Bulletin of the Scripps Institution of Oceanography, 21:1–206.
- PERRY, A., C. S. BAKER, AND L. M. HERMAN. 1990. Population characteristics of individually identified humpback whales in the central and eastern North Pacific: a summary and critique. Reports of the International Whaling Commission, Special Issue 12:307–317.
- PIKE, G. C. 1953. Colour pattern of the humpback whales from the coast of British Columbia. Journal of the Fisheries Research Board of Canada, 17:1–54.
- REINER, F., M. E. DOS SANTOS, AND F. W. WENZEL. 1996. Cetaceans of the Cape Verde archipelago. Marine Mammal Science, 12: 434–443.
- RICE, D. W. 1963. Progress report on biological studies of the larger cetacea in the waters off California. Norsk Hvalfangsttidende, 7:181–192.
- ROMER, A. S. 1966. Vertebrate paleontology. Third ed. University of Chicago Press, Chicago, 468 pp.
- ROSENBAUM, H., ET AL. 1995. Variations in ventral fluke pigmentation of humpback whales, *Megaptera novaeangliae*, worldwide. Marine Ecology Progress Series, 124:1–7.
- ROWNTREE, V. J. 1996. Feeding, distribution, and reproductive behavior of cyamids (Crustacea: Amphipoda) living on humpback and right whales. Canadian Journal of Zoology, 74:103–109.
- RUDOLPHI, D. K. A. 1832. Über *Balaena longimana*. Abhandlung der Königs Akademie der Wissenschaften zu Berlin, 1829 (1832), pp. 133–144.
- SCARFF, J. E. 1986. Occurrence of the barnacles *Coronula diadema*, *C. reginae* and *Cetopirus complanatus* (Cirripedia) on right whales. Scientific Reports of the Whales Research Institute, 37:129–153.
- SMITH, A. 1835. An epitome of African zoology: or, a concise description of the objects of the animal kingdom inhabiting Africa, its islands and seas. South African Quarterly Journal, 2: 234–243.
- STONE, G. S., L. FLOREZ-GONZALEZ, AND S. KATONA. 1990. Whale migration record. Nature, 346:705.
- STRUTHERS, J. 1889. Memoir on the anatomy of the humpback whale *Megaptera longimana*. MacLachlan and Stewart, Edinburgh, [iv] + 188 = [1], 6 pls. Reprinted from the Journal of Anatomy and Physiology, 1887–89.
- TOMILIN, A. G. 1946. Thermoregulation and the geographical races of cetaceans. Academie des Sciences de l'URSS, Comptes Rendus (Doklady), 54(5):465–468.
- . 1957. Zveri SSSR prilozhashchikh stran Zveri vostochnoi Evropy i severnoi azii [Animals of the USSR and adjacent countries] (in Russian). Volume 9: Kitoobraznye. Izdatel'stvo Akademi Nauk SSSR, Moscow. Translated in 1967 as Mammals of Eastern Europe and adjacent countries. Volume 9, Cetacea. Israeli Program for Scientific Translations, Jerusalem, 717 pp.
- TRUE, F. W. 1904. The whalebone whales of the western North Atlantic. Smithsonian Institution Press, Washington, District of Columbia, 332 pp.
- TURNER, W. 1912. The marine mammals in the Anatomical Museum of the University of Edinburgh. Macmillan and Co., London, 207 pp.
- TYACK, P. 1981. Interactions between singing Hawaiian humpback whales and conspecifics nearby. Behavioral Ecology and Sociobiology, 8:105–116.
- TYACK, P., AND H. WHITEHEAD. 1982. Male competition in large groups of wintering humpback whales. Behaviour, 83:1–23.
- VALSECCHI, E., ET AL. 1997. Microsatellite genetic distances between oceanic populations of the humpback whale (*Megaptera novaeangliae*). Molecular Biology and Evolution, 14:355–362.
- VAN BENEDEN, P. J. 1868. Les squelettes de Cétacés-et les Musées qui les renferment. Bulletin de l'Académie Royale de Belgique, Classe de Sciences, Bruxelles, 25:88–125.
- . 1882. Une baleine fossile de Croatie, appartenant au genre *Mesocete*. Mémoire de l'Académie Royale de Belgique, 45:1–29.
- VAN LENNEP, E. W., AND W. L. VAN UTRECHT. 1953. Preliminary report on the study of the mammary glands of whales. Norsk Hvalangsttidende, 42:249–258.
- WATKINS, W. A., AND W. E. SCHEVILL. 1979. Aerial observation of feeding behavior in four baleen whales. Journal of Mammalogy, 60:155–163.
- WEINRICH, M. T. 1991. Stable social associations among humpback whales (*Megaptera novaeangliae*) in the southern Gulf of Maine. Canadian Journal of Zoology, 69:3012–3019.
- WEINRICH, M. T., AND A. E. KUHLBERG. 1991. Short-term association patterns of humpback whales (*Megaptera novaeangliae*) groups on their southern Gulf of Maine feeding grounds. Canadian Journal of Zoology, 69:3005–3011.
- WEINRICH, M. T., J. BOVE, AND N. MILLER. 1993. Return and survival of humpback whale (*Megaptera novaeangliae*) calves born to a single female in three consecutive years. Marine Mammal Science, 9:325–328.
- WEINRICH, M.T., M. R. SCHILLING, AND C. R. BELT. 1992. Evidence for acquisition of a novel feeding behaviour: lobtailing feeding in humpback whales, *Megaptera novaeangliae*. Animal Behaviour, 44:1059–1072.
- WHITEHEAD, H. P. 1981. The behaviour and ecology of Northwest Atlantic humpback whales. Ph.D. thesis. University of Cambridge, Cambridge, 256 pp.
- . 1983. Structure and stability of humpback whale groups off Newfoundland. Canadian Journal of Zoology, 61:1391–1397.
- . 1985. Humpback whale breaching. Investigations on Cetacea, 17:117–155.
- . 1987. Updated status of the humpback whale, *Megaptera novaeangliae*, in Canada. Canadian Field Naturalist, 101: 284–294.
- WHITEHEAD, H. P., AND C. GLASS. 1985. Orcas (killer whales) attack humpback whales. Journal of Mammalogy, 66:183–185.
- WHITEHEAD, H. P., AND M. J. MOORE. 1982. Distribution and movements of West Indian humpback whales in winter. Canadian Journal of Zoology, 60:2203–2211.
- WILEY, D. N., R. A. ASMUTIS, T. D. PITCHFORD, AND D. P. GANNON. 1995. Stranding and mortality of humpback whales, *Megaptera novaeangliae*, in the mid-Atlantic and southeast United States, 1985–1992. Fishery Bulletin, 93:196–205.
- YABLOKOV, A. V. 1994. Validity of whaling data. Nature, 367:108.
- ZEMSKY, V. A., A. A. BERZIN, Y. A. MIKHALIEV, AND D. D. TOMOSOV. 1995. Soviet Antarctic pelagic whaling after WWII: review of actual catch data. Reports of the International Whaling Commission, 46:131–135.

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