



The Humpback Whale

Introduction

The humpback whale, *Megaptera novaeangliae* Borowski 1781, is a member of the Balaenopteridae family, a group of baleen whales commonly known as rorquals. The humpback whale is of medium size relative to the other large whales, reaching a length of 15 m and a weight of about 34 metric tons (t) at maturity. Humpback whales are characterized by wing-like pectoral flippers that are from one-fourth to one-third their total body length, heads covered in bumps known as tubercles, and tail flukes with individually identifiable trailing-edge patterns (Fig. 15). Like other balaenopterids, they have fringed baleen plates instead of teeth which allow for the filtering of small crustaceans and fish. Deep grooves on the ventral surface allow for throat expansion, increasing the volume of water that can be engulfed and then filtered through the baleen.

Humpback whales display a wide range of above-water behaviors, such as whole-body breaches, lob-tailing, and lunging. These behaviors are usually associated with breeding and feeding activities (Ward, 1995) (Fig. 16). These

whales also have a distinctive and varied acoustic repertoire consisting of complex “songs” that may last several hours and contain phrases which are distinct between individuals and vary among geographic areas.

In general, most humpback whales spend the summer feeding in high-latitude waters and then migrate long distances into low-latitude tropical waters for the winter where they breed and calve. Calving takes place in shallow coastal waters along continental shelves and off some oceanic islands.

Distribution and Migration

Humpback whales inhabit all major ocean basins from the equator to sub-polar latitudes (Fig. 17). They generally follow a predictable migratory pattern in both hemispheres, feeding during the summer in the higher near-polar latitudes and then during the winter migrating to the lower latitudes where calving and breeding takes place. Their migratory movements have been traced through recovery of Discovery tags³⁸ during commercial whaling operations. More recently, comparisons of photographs, songs, and genetic material between different geographical areas have

led scientists toward a better understanding of the stock structure of these whales.

North Pacific

The IWC has designated one stock of humpback whales in the North Pacific Ocean (Donovan, 1991). These whales range widely across the entire North Pacific during the summer months—south to Point Conception, Calif., and north into the Bering Sea (Johnson and Wolman, 1984).

Recent, on-going photo-identification and genetic studies reveal what may be separate stocks of humpback whales within the North Pacific basin that are not apparent from any geographical separation. There are known calving and breeding grounds off Mexico, among the Hawaiian Islands, and off Japan. Known feeding grounds exist off California, Oregon, and Washington (CA/OR/WA), in the Bering Sea, along the Aleutian Islands, and in southeastern Alaska (Fig. 4). Barlow (1994b) lists four separate migratory stocks of humpback whales in the North Pacific based on current resightings, genetic analysis, and historical whaling records (Table 8).

Calambokidis et al. (1996) have shown through photographic mark-recapture analysis that the summer feeding aggregations off the western United

Table 8.—North Pacific humpback whale stocks.

Winter areas (breeding/calving)	Summer areas (feeding)	Source
Mexico (Mainland, Baja California, Gulf of California), Costa Rica	CA/OR/WA	Steiger et al., 1991; Barlow et al., 1997; Clapham et al., 1997
Offshore Mexico-Islas Revillagigedo	Unknown	Medrano-Gonzalez et al., 1995
Central North Pacific-Hawaii	Alaska-Prince William Sound to British Columbia	Baker et al., 1994; Barlow et al., 1997
Western North Pacific-Japan, Taiwan	Bering Sea, Aleutian Islands-west of Kodiak Archipelago	Darling et al., 1996

³⁸ Discovery tags were shot into individual whales during whaling operations. The tag was a steel rod 23 cm in length and 1.5 cm in diameter with a lead tip and was fired from a modified 12-gauge shotgun. Such marking began in 1949, although it was geographically limited to the Southern Hemisphere (until 1979) and North Pacific (until 1980) (Brown, 1981; Ivashin, 1983).

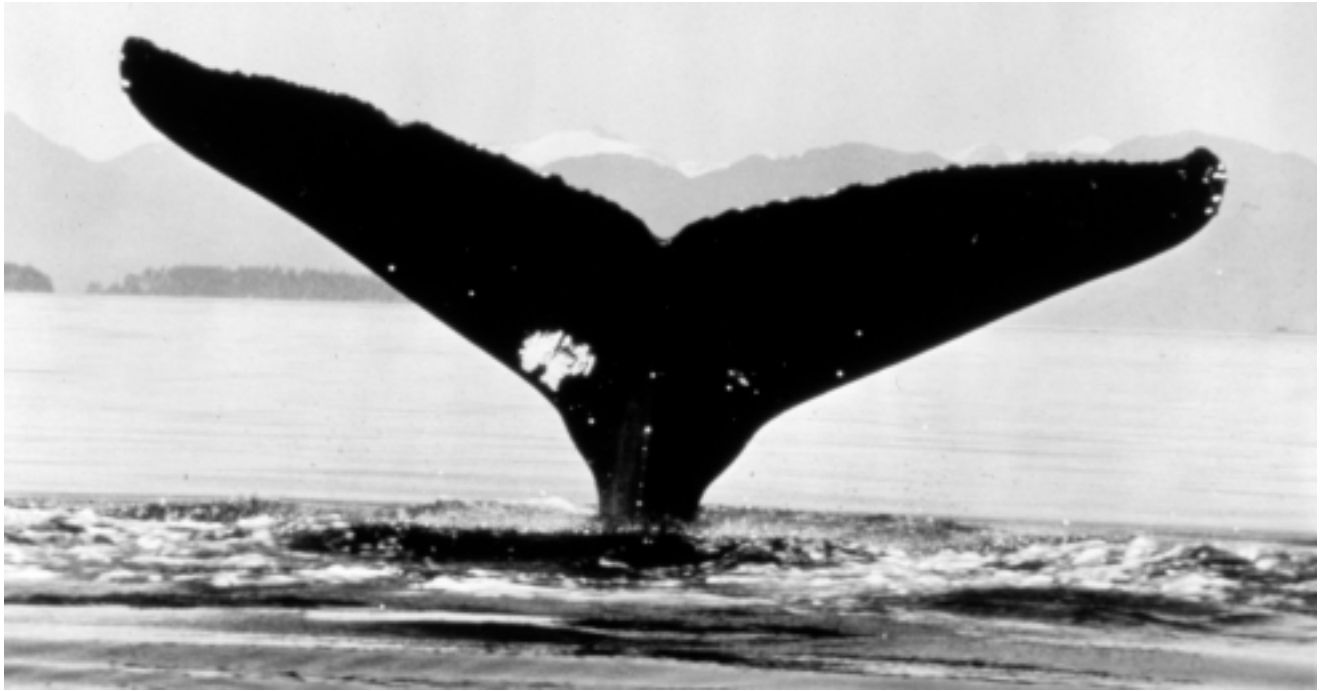


Figure 15.—The tail flukes of a humpback whale in southeast Alaska. The pattern of notches and scars along the trailing edge (top of the tail in this photograph) varies among individuals. J. Reinke, NMML Collection.

States (CA/OR/WA stock) may be a distinct population with only limited interchange between feeding areas in British Columbia and Alaska. British Columbia appears to serve as a geographical boundary between feeding populations (Calambokidis et al.³⁹). In addition, genetic differences between California and Alaska feeding groups based on mitochondrial DNA and nuclear DNA analysis have been detected (Baker et al., 1990, 1993, 1994). The genetic exchange rate between these two feeding aggregations is estimated at less than one female per generation; however, the sample size used for this analysis was too small to make formal conclusions about the segregation between these two areas (Baker et al., 1994; Baker⁴⁰). Baker⁴⁰ found fewer



Figure 16.—A humpback whale off Sunset Island, Alaska, breaks the water's surface. This strange image is the result of complete deflation of the throat pleats and the whale pushing water through its baleen and out the sides of its mouth. A. Wolman, NMML Collection.

³⁹ Calambokidis, J., G. H. Steiger, and J. R. Evenson. 1993. Photographic identification and abundance estimates of humpback and blue whales off California in 1991-92. Final contr. rep. 50ABNF100137 to NMFS Southwest Fisheries Science Center, P.O. Box 271, La Jolla, CA 92038, 67 p.

⁴⁰ Baker, C. S. 1992. Genetic variability and stock identity of humpback whales, world-wide. Final contr. rep. to the IWC, Camb., U.K., 45 p.

genetic differences between whales on the Mexico and Hawaii wintering grounds, which suggests a maternally

directed fidelity to specific summering grounds. Genetic studies have also shown that the humpback whales which

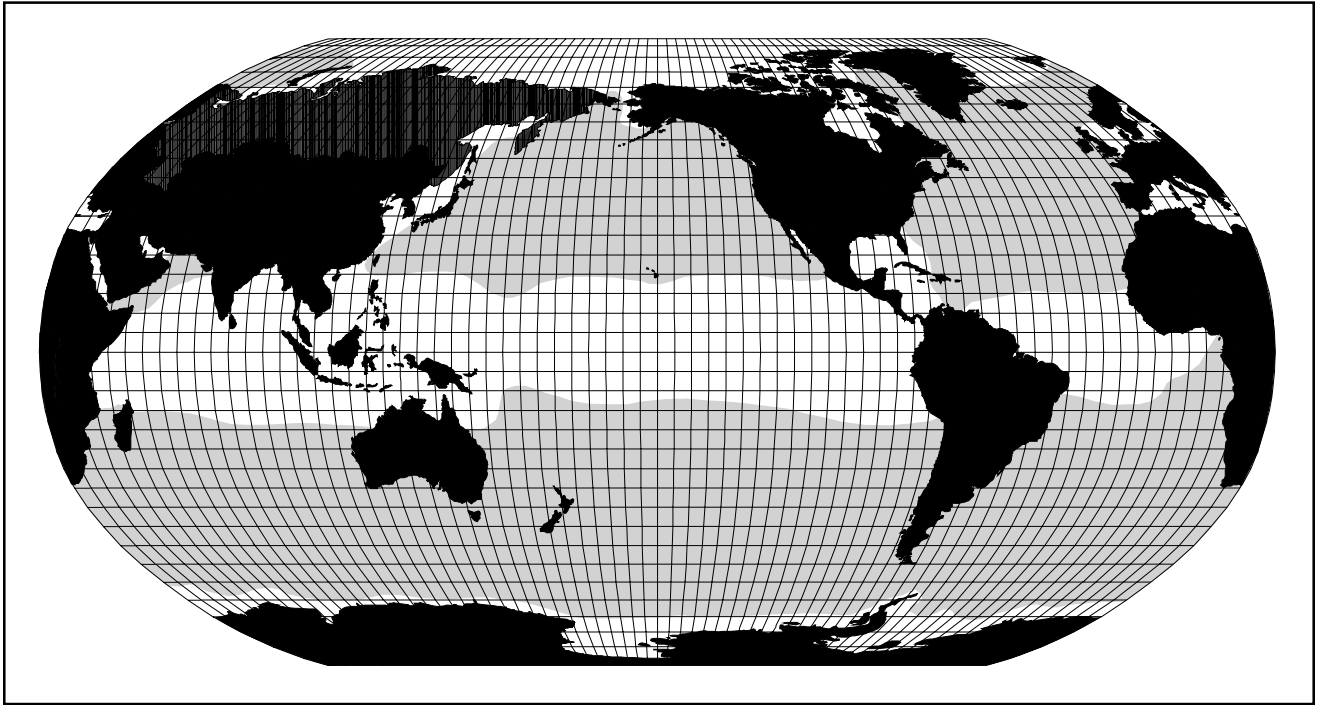


Figure 17.—Worldwide humpback whale distribution. Adapted from Johnson and Wolman (1984).

breed and calve off the Revillagigedo Islands, Mex., are significantly different from the humpback whales found along Baja California and coastal Mexico (Fig. 4)(Medrano-Gonzalez et al., 1995). Currently, the feeding area(s) of the whales wintering off the Revillagigedo Islands is unknown.

The central North Pacific migratory stock of humpback whales travels from Hawaiian wintering grounds to summering areas in southeast Alaska each year. In inside waters off southeastern Alaska (i.e. Glacier Bay and Frederick Sound), photo-identification studies appear to show that humpback whales utilize discrete, geographically isolated feeding areas which individual whales return to year after year (Straley⁴¹). There has been little documented exchange in individual animals between Prince William Sound and Kodiak Island areas, and between Kodiak Island

and southeast Alaska feeding areas, suggesting that this type of movement occurs, but is reasonably uncommon (von Zeigesar et al., 1994; Perry et al., 1990; Waite et al.⁴²).

The western North Pacific migratory stock of humpback whales is known to calve and breed off Japan during the winter and spring, but their feeding areas during the summer are still in question (Darling et al., 1996; Darling⁴³). Darling and Mori (1993) and Miyashita et al. (1996) document the occurrence of these whales in shallow coastal waters (usually within 10 km of shore) around the Ogasawari (Bonin) Islands (lat. 24–26°N, long. 141°E) and Kerama Islands (lat. 26–27°N, long. 127°E) during winter (Fig. 5). Darling⁴³ and Darling et al. (1996) provide evidence of resightings between whales in Japanese waters and

whales found in the Bering Sea, Aleutian Islands, Hawaiian Islands, and off British Columbia in the summer months.

North Atlantic

The IWC Scientific Committee recognizes one stock of humpback whales in the North Atlantic Ocean (Donovan, 1991). However, historical whaling documents and recent research in the western North Atlantic have revealed distinct areas of seasonal concentration for the eastern and western halves of this ocean basin (Johnson and Wolman, 1984). From early 1992 to 1995, a large-scale ocean-wide study of humpback whales in the North Atlantic, called the Years of the North Atlantic Humpback project (YoNAH) (Allen et al.⁴⁴), was conducted. Photo-identifications and genetic samples from this study are cur-

⁴¹ Straley, J. M. 1994. Seasonal characteristics of humpback whales (*Megaptera novaeangliae*) in southeastern Alaska. M.S. thesis, Univ. Alaska, Fairbanks, 121 p.

⁴² Citation updated in proof: see Waite et al., 1998 in literature cited.

⁴³ Darling, J. D. 1991. Humpback whales in Japanese waters, Ogasawara and Okinawa: Fluke identification catalog 1987-1990. Final contr. rep., World Wide Fund for Nature, Japan, 22 p.

⁴⁴ Allen, J., P. Clapham, P. Hammond, S. Katona, F. Larsen, J. Lien, D. Mattila, N. Øien, P. Palsbøll, J. Sigurjonsson, and T. Smith. 1993. Years of the North Atlantic Humpback (YoNAH): progress report. Int. Whal. Comm. unpubl. doc. SC/45/NA6.

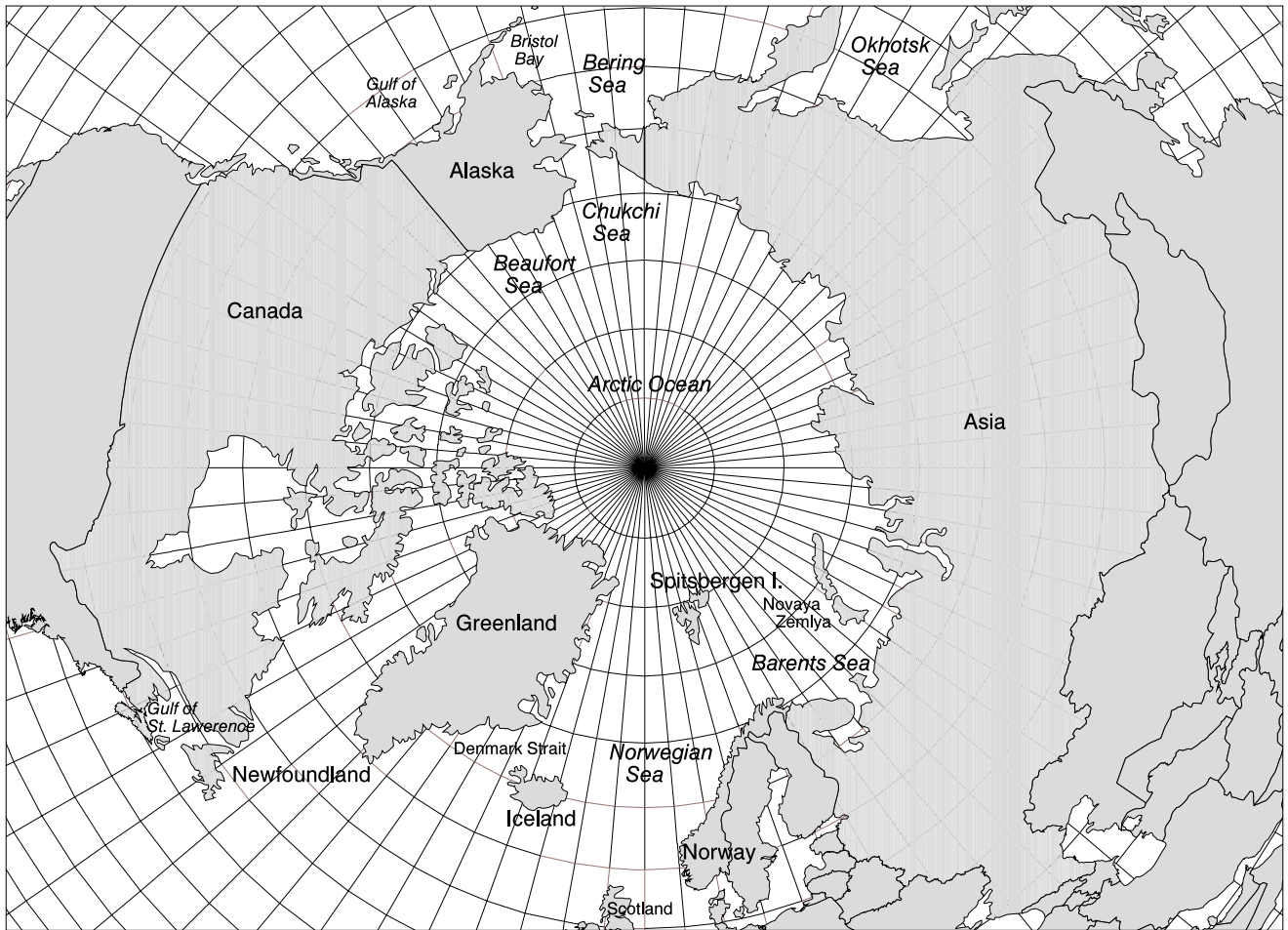


Figure 18.—Arctic region.

rently being analyzed in order to better determine the current population status and genetic relationships of North Atlantic humpback whales.

In the eastern North Atlantic, humpback whales are found in the summer off west and southwest Iceland; Scotland; Spitsbergen, Norway; and Novaya Zemlya in the Barents Sea (Fig. 18) (Sigurjónsson and Gunnlaugsson, 1990). In winter, the only documented concentration of humpback whales in the eastern North Atlantic is found off the Cape Verde Islands off western Africa (Fig. 7) (Kellogg, 1929).

In the western North Atlantic, the whales are found in five separate feeding aggregations between lat. 42°N and 78°N (Fig. 6) (Katona and Beard, 1990; Johnson and Wolman, 1984):

- 1) Iceland-Denmark Strait,
- 2) Southwest Greenland,
- 3) Southern Labrador and east of Newfoundland,
- 4) Gulf of St. Lawrence, and
- 5) Gulf of Maine/Nova Scotia region.

During summer, humpback whale distribution and shifts in distribution on New England feeding grounds have been correlated with the abundance and distribution of the whale's principal prey species (e.g. herring and sand-lance) (Payne et al., 1986a, b; Fogarty et al., 1991; Weinrich et al., 1997). Recent photo-identification research indicates that the majority of whales from all five of these feeding areas migrate to Caribbean waters during winter for breeding and calving (Matilla et al.,

1994). Approximately 85% of the humpback whales migrating between higher latitudes on the western side of the North Atlantic to lower latitudes can be found in winter on Silver and Navidad Banks off the northern coast of the Dominican Republic. The remainder of the whales, with resightings from the higher latitudes during summer, are found in the eastern part of Samana Bay, Dominican Republic (Matilla et al., 1994), the northwest coast of Puerto Rico, the Virgin Islands, and along the eastern Antilles south to Venezuela (Fig. 13) (Katona and Beard, 1990). In addition, there are reports of humpback whales found during winter off Greenland, Norway, Newfoundland, in the southern Gulf of Maine, and Bermuda (Fig. 6, 7) (Katona et al., 1994).

These reports from higher latitudes during winter suggest that not all whales migrate each year, perhaps taking advantage of unusual prey occurrences or demonstrating year-round, regional site fidelity (Clapham et al., 1993).

In addition to photo-identification studies, genetic research into the influence of seasonal migration on the geographic distribution of mitochondrial DNA haplotypes revealed what appears to be a maternally directed site fidelity to specific feeding grounds (Baker et al., 1990), as in the North Pacific. However, resightings have shown that interbreeding could be occurring during winter, when whales that were segregated on the summer feeding grounds (Clapham et al., 1992; Katona, 1986) congregate in the tropical latitudes.

Northern Indian Ocean

The humpback whale population in the Arabian Sea (Fig. 14), unlike other populations, does not migrate to temperate waters as part of their annual cycle. Instead, they both feed and breed in tropical waters (Mikhailiev, 1997). However, little or no research has been conducted on this unique population, so information on their current abundance and trends does not exist.

Southern Hemisphere

The six baleen whale areas designated by the IWC (Donovan, 1991) for stock management purposes are also used to separate Southern Hemisphere humpback whale stocks (Fig. 9). These areas loosely correspond to known humpback whale wintering and summering areas from sighting and mark-recapture data (Mackintosh, 1942). In the austral winter, the whales are found along the tropical and western sides of each continent, along eastern coastlines, and around island groups. One such wintering area exists off Brazil on Abrolhos Bank (Siciliano, 1995). During the austral summer months, they are found in South Georgia, the South Shetlands, and along the west and east coasts of Africa, Australia, and South America (Dawbin, 1966). Most migratory paths for the southern humpback whales are unknown. Movements of humpback whales along the South Af-

rican coasts from Antarctic summering grounds to wintering grounds have been summarized in Best et al. (1995). One path takes the whales from the Antarctic region, past western South Africa, to wintering grounds off Angola, the Congo, or Gabon. The other path takes them past eastern South Africa to wintering grounds off Mozambique (Fig. 19).

Japanese Sighting Vessel (JSV) and International Whaling Commission/International Decade of Cetacean Research (IWC/IDCR) surveys of Antarctic waters from lat. 60°S to the pack-ice edge indicate that concentrations of humpback whales occur in Areas III and IV (at long. 10–30°E, 50–60°E, and 90–100°E) during the austral summer. These concentrations make up well-defined feeding areas spread over a wide range of latitudes in which the whales show little longitudinal dispersal during the entire summer season (Kasamatsu et al., 1996). These areas correspond with observed concentrations of humpback whales during the 1930's period of modern whaling operations.

Findlay et al. (1994) reviewed the distribution of humpback whales along the Mozambique coast (Area III) during late winter through early spring and found that high densities of humpback whales were recently found in the region between long. 33° and 35°E, south of lat. 24°S (between Maputo and Ponta Zavora), and north of lat. 18°S. Their distribution indicates a highly mobile population, with an extended northern range which is not suggested in the modern whaling records. The waters in which the whales were found are characterized by shallow banks and the strong offshore flow of the Mozambique Current. A suspected calving/nursery area exists on northern Solfala Bank (Fig. 19).

During the same months that humpback whales are found off Mozambique, areas of concentration are also found in the southern coastal waters of Madagascar (Area III) (Best et al., 1996). According to anecdotal evidence, these whales are widely dispersed and highly mobile like the whales along the African coast (see above). The catch data from 19th century American whaling logbooks indicated humpback whale concentrations off Madagascar in the

southwest near Tulear, the northeast near Baie du Antongil, and scattered along the central west coast at around lat. 20°S during August and September (Fig. 19) (Townsend, 1935).

Off Western Australia (Area IV), there is a possible area of calving/breeding off Cape Leveque (approx. lat. 17°S, long. 123°E) (Jenner and Jenner, 1994). However, the migratory movements between Antarctic waters and Australia are still not certain, and further research, such as continued shore-based monitoring projects (Paterson, 1991; Bryden et al., 1990), is needed.

Current and Historical Abundance North Pacific

Currently, there are no statistically reliable estimates of humpback whale population abundance for the entire North Pacific Ocean. Calambokidis et al.⁴⁵ used photo-identification methods to estimate approximately 6,000 humpback whales in the entire North Pacific; but, considering statistical biases and separate regional estimates, the true abundance is likely to be higher. The IWC does not recognize any total population estimates as statistically accurate at this time (IWC, 1995a).

The most recent population estimates for the western U.S. (CA/OR/WA stock) feeding groups and central North Pacific stock are summarized in Table 9. Sighting cruises during winter 1993 through winter 1995 encountered only 56 individuals in areas of the western North Pacific and eastern South China Sea (Miyashita et al., 1996). The most recent estimate for the western North Pacific is 394 (CV = 0.084) whales based on photo-identification methods applied to data collected between 1991 and 1993 (Calambokidis et al.⁴⁵). In the central North Pacific, Calambokidis et

⁴⁵ Calambokidis, J., G. H. Steiger, J. M. Straley, T. Quinn, L. M. Herman, S. Cerchio, D. R. Salden, M. Yamaguchi, F. Sato, J. R. Urbán, J. Jacobsen, O. von Ziegesar, K. C. Balcomb, C. M. Gabriele, M. E. Dahlheim, N. Higashi, J. K. B. Ford, Y. Miyamura, P. L. de Guevara, S. A. Mizroch, L. Schlender, and K. Rasmussen. 1997. Abundance and population structure of humpback whales in the North Pacific basin. Final contr. rep. conducted by Cascadia Research Collective under Contr. 50ABNF500113 for NMFS Southwest Fisheries Science Center, La Jolla, Calif., 72 p.

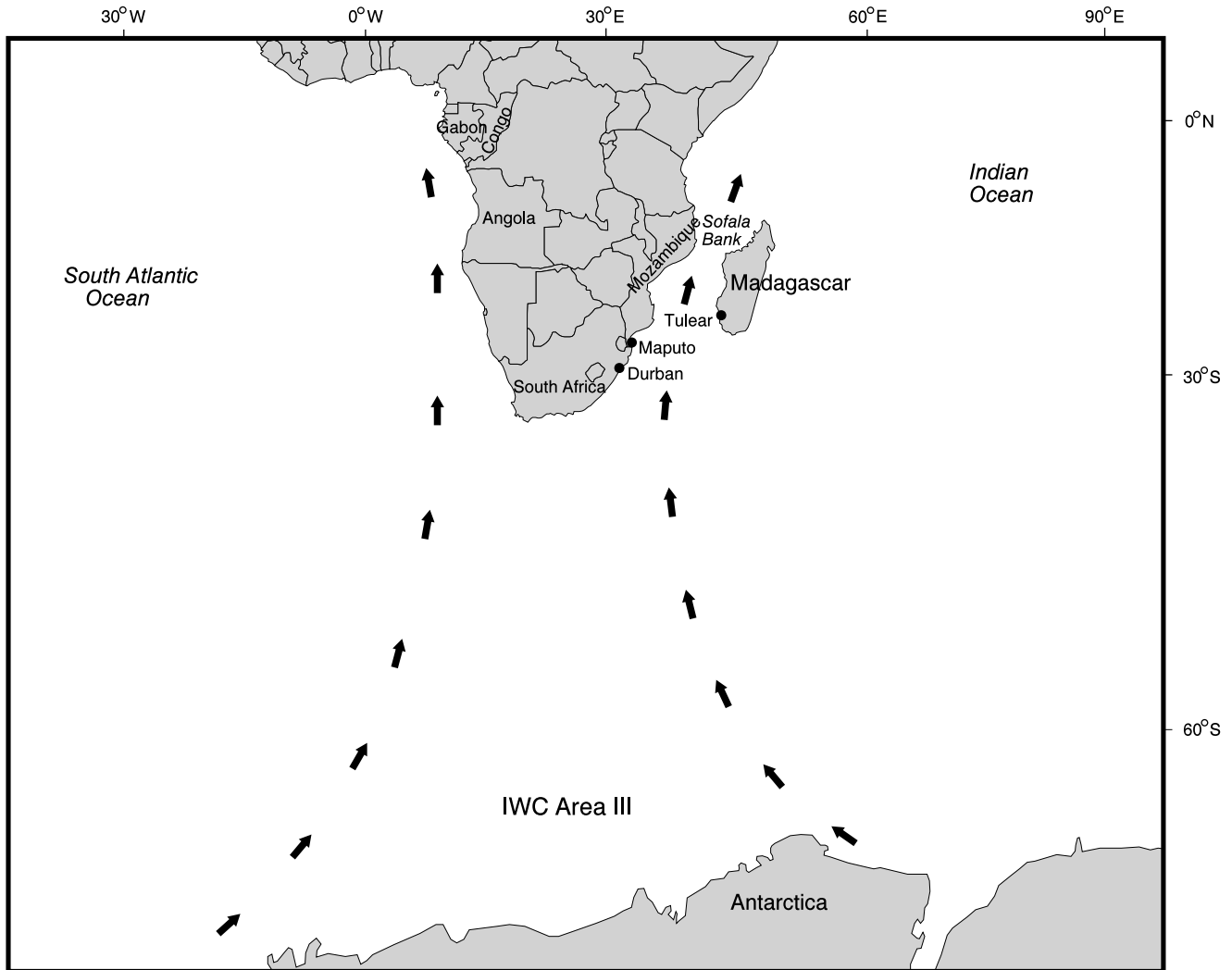


Figure 19.—Possible humpback whale migratory paths around southern Africa. Adapted from Best et al. (1995).

al.⁴⁵ used the same photo-identification methods applied to the western North Pacific whales and arrived at an estimate of 4,005 (CV = 0.095) in this region.

Before 1905, there were an estimated 15,000 humpback whales in the entire North Pacific (Rice, 1978a). After heavy exploitation, in 1966 this population was estimated at between 1,000 (Rice, 1978a) and 1,200 animals (Johnson and Wolman, 1984), although it is not clear whether these estimates represent the entire North Pacific or only the eastern North Pacific.

North Atlantic

Current estimates of North Atlantic humpback whale abundance are sum-

marized in Table 9 by geographic area. In 1986, the IWC recognized a current “best” estimate of 5,561 (S.E. = 570, CV = 0.103) whales for the North Atlantic west of Iceland (IWC, 1986b). In contrast, Gunnlaugsson and Sigurjónsson (1990) estimated from sighting surveys west and southwest of Iceland, that less than 2,000 humpback whales inhabited those waters. Smith et al.⁴⁶ summarized some of the main findings from the YoNAH project, as well as

⁴⁶ Smith, T. D., P. S. Hammond, N. Friday, and P. J. Clapham. 1997. Status of information on the North Atlantic humpback whale. Unpubl. doc. SC/49/NA8, submitted to Rep. Int. Whal. Comm., 4 p.

other regionally based studies in the North Atlantic. For example, Palsbøll et al. (1997) used genetic data to estimate 7,698 humpback whales in the eastern North Atlantic. In the Smith et al.⁴⁶ summary, it is suggested that the new data generated by the YoNAH project may provide a solid base for a comprehensive assessment of the North Atlantic humpback whale’s status by the IWC’s Scientific Committee. In 1999, Smith et al.¹¹ arrived at an estimate of 10,600 (CV=0.067) humpback whales in the North Atlantic based on mark-recapture analysis of photographically identified animals.

An initial population estimate of 4,700 whales was derived from all whal-

Table 9.—Abundance estimates for humpback whale stocks worldwide (N.e. = no published estimate).

Area	Population estimate	Coefficient of variation	95% confidence interval	Source ¹
North Pacific				
Total	6,000–8,000	N.e.	N.e.	Calambokidis et al. ⁴⁵
CA/OR/WA	2,250	N.e.	N.e.	Calambokidis et al. ⁴⁵
Central	1,407	N.e.	1,113–1,701	Baker and Herman, 1987; Anonymous, 1991b
Central	4,005	0.095	N.e.	Calambokidis et al. ⁴⁵
Western	394			
	(1991–1993)	0.084	N.e.	Calambokidis et al. ⁴⁵
North Atlantic				
Total	10,600	0.067	N.e.	Smith et al. ¹¹
Western (west of Iceland)	5,543	0.16	N.e.	Katona et al., 1994
	(1979–1990)			
Western	>2,000	N.e.	N.e.	Gunnlaugsson and Sigurjónsson, 1990
Cape Hatteras, North Carolina to Nova Scotia	294	0.45	N.e.	CeTAP ⁷⁰
	(1978–1982)			
Eastern	7,698			Palsbøll et al., 1997
Southern Hemisphere				
South of 60°S	4,660	0.193	N.e.	IWC, 1996a
Area II				
Abrolhos Bank, Brazil	1,556	N.e.	815–3,260	Bethlem et al. ⁴⁸
	(1989–1995)			
Abrolhos Bank, Brazil	1,100	N.e.	553–2,350	Bethlem et al. ⁴⁸
	(1995–1996)			
Area III				
South Africa (northward migration)	1,711	0.122–0.114	N.e.	Findlay and Best, 1996
Mozambique	1,954	0.38	N.e.	Findlay et al., 1994
Madagascar	2,532	0.27	N.e.	Best et al., 1996
Area IV				
Western Australia	3,878	N.e.	1,319–14,108	Jenner and Jenner, 1994

¹ Source footnote numbers refer to text footnote numbers.

ing catches during the 1865 season from Davis Strait, Iceland, and south to the West Indies (Mitchell and Reeves, 1983). This is the only available historic abundance estimate from North Atlantic waters.

Southern Hemisphere

The IWC Scientific Committee has recognized data from IWC/IDCR and JSV surveys of the Antarctic Ocean as valid for population estimation south of lat. 60°S (IWC, 1996a; Butterworth et al.⁴⁷). From these data, a total Southern Hemisphere population estimate of 19,851 humpback whales was calculated for the years 1978 through 1988. However, the Scientific Committee also recognizes this estimate as statistically unreliable (IWC, 1996a). Current esti-

mates have been calculated for the concentrations of whales found in Areas III and IV— off South Africa, Mozambique, Madagascar, and Western Australia, respectively (Table 9). In the western South Atlantic, Bethlem et al.⁴⁸ estimated the number of humpback whales from Abrolhos Bank, off Bahia, Brazil, from 7 years of photo-identification studies (1989–96). Using the Bailey-modified Petersen estimation method, they estimated 1,556 individuals for the period 1989–94 and 1995 (95% CI 815–3260) and 1,100 individuals for the period 1995–96 (95% CI 553–2350) (Bethlem et al.⁴⁸).

The initial preexploitation population size of the entire Southern Hemisphere has been estimated at 100,000 whales (Gambell, 1976). In western Australian waters, there were an estimated 800 whales at the end of 1962. By 1963, this estimate had dropped to only 568 (Banister, 1964; Chittleborough, 1965).

⁴⁷ Butterworth, D. S., D. L. Borchers, S. Chalis, and J. B. DeDecker. 1995. Estimation of abundance for Southern Hemisphere blue, fin, sei, humpback, sperm, killer, and pilot whales from the 1978/79 to 1990/91 IWC/IDCR sighting survey cruises, with extrapolations to the area south of 30° for the first five species based on Japanese scouting vessel data. Unpubl. doc. SC/46/SH24 submitted to Rep. Int. Whal. Comm., 54 p.

⁴⁸ Bethlem, C. B. P., P. G. Kinan, M. H. Engel, and A. C. S. Freitas. 1997. Abundance estimates of humpback whales wintering off Abrolhos Bank, Bahia, Brazil. Unpubl. doc. SC/49/SH31 submitted to Rep. Int. Whal. Comm., 6 p.

Trends in Abundance

Comparison of current population estimates with analysis of historical whaling data from the U.S. west coast suggest that the California/Oregon/Washington stock of humpback whales may be below its preexploitation size (Clapham et al., 1997). More recent photographic capture-recapture data has led to higher estimates of abundance for the California/Oregon/Washington and central North Pacific humpback whale stocks (Table 9) (Calambokidis et al.⁴⁵). However, this apparent increase should be viewed with caution, as it may only be an artifact of increased survey effort and shifts in the distribution of individual whales. Until more identification photos are collected and there are more complete demographic records from the entire North Pacific Ocean, there is no conclusive evidence as to whether these stocks are declining, increasing, or stationary.

At this time, there are insufficient data to produce reliable estimates of trends in the total North Atlantic humpback population (Waring et al., 1998). However, Katona and Beard (1990) and Sigurjónsson and Gunnlaugsson (1990)

have suggested annual rates of increase from 9.0% to 14.8%, respectively. Barlow and Clapham (1997) used birth intervals to estimate a population growth rate of 6.5% (± 1.2) for the Gulf of Maine humpback whale population. Estimated rates of net increase range from 3.9% to 11.8% for the western North Atlantic (Whitehead, 1982).

Trends in abundance in the Southern Hemisphere show an annual rate of increase in both western Australia (Bannister et al., 1991; Bannister, 1994) and southern Madagascar (Best et al., 1996). The western Australian population's recovery has been well documented, with a "best" estimate of annual rates of increase at 8.8% ($\pm 5.8\%$) for the years 1963–76, and at 10.9% ($\pm 3.0\%$) for the years 1963–91. Within Areas IV and V, annual rates of increase have been estimated at 8.9% and 56.6%, respectively, for the years 1988–96 (IWC, 1996a). The Southern Hemisphere Area IV stock has shown rates of increase between 10.3% and 13.1% since the mid 1960's (Chittleborough, 1965). All of these rates are considered unreliable pending greater accuracy in determining age at sexual maturity and exact calving intervals for this species.

Historic Exploitation Patterns

North Pacific

Prior to 1900, an unknown number of humpback whales were taken both in aboriginal whaling and early hand-harpoon commercial operations. Modern operations in the western North Pacific began in 1889 and in the eastern North Pacific in 1905. From 1905 through 1960, there were 23,000 humpback whales taken in modern whaling operations (Johnson and Wolman, 1984)(Fig. 20). From 1960 to 1965, over 5,000 whales were taken, reducing the North Pacific humpback whale population to around 1,000 animals by the end of 1965 (Rice, 1978a). On a more regional scale, a total of 1,871 humpback whales were taken ashore in California's Moss Landing and Trinidad whaling stations (Clapham et al., 1997). In 1965, the IWC banned the commercial hunting of humpback whales in the Pacific Ocean; however, Soviet whal-



Figure 20.—A humpback whale being rowed towards a whaling station platform in Port Hobron, Alaska, circa 1930. University of Washington Special Collections, Lagen Collection, negative UW18184.

ers continued their take of whales until 1980 (Zemsky et al., 1995).

Eastern North Atlantic

From 1868 through 1955, at least 1,579 humpback whales were taken as part of the eastern North Atlantic and Arctic whaling operations. The number of humpback whales taken from the Faeroe Islands in the years 1868 to 1909 is unknown (Johnson and Wolman, 1984). The IWC granted this stock "Protected Status" in 1955. Nonetheless, 11 animals were still taken for local consumption between 1955 and 1967 in Norway, the Faeroe Islands, and Madiera (Brown, 1976). There are no data on the number of whales taken during Spanish and Portuguese whaling operations from the mid 1800's through the mid 1950's.

Western North Atlantic

Whaling operations for humpback whales off West Greenland began in 1886 and ended in 1976, with a total take of 522 whales (Kapel, 1979). Off Nova Scotia, Newfoundland, and Labrador, 1,397 whales were taken from 1903 to 1970 (Mitchell, 1974c). Between 1977 and 1982, there was a sub-

sistence catch off West Greenland of 81 animals, which exceeded the IWC's recommended quota of 10 whales per year in 1978 through 1982 (IWC, 1980a).

Southern Hemisphere

There were three phases of commercial whaling for humpback whales in the Southern Oceans (Tønnessen and Johnsen, 1982; Findlay and Best, 1996). The first phase was a pre-1917 coastal operation centered around the Falkland Dependencies (1904–16) and off the coast of South Africa (1908–17), with smaller operations off Australia and New Zealand (1912–16). During this period (1904–17), an estimated 43,000 humpback whales were taken (Chittleborough, 1965), of which 25,000 were taken in the South African coastal (or bay) operations (Best, 1994b), about 3,500 were taken off the eastern coast of Africa (Best, 1994b), and about 3,157 were taken in Mozambique coastal operations (Findlay and Best, 1996).

The second phase of whaling took place in the pelagic waters of the Antarctic from 1917 to 1938, with about 28,000 humpback whales taken there during 1923–38. In 1938, the IWC began regulating catches in these south-

ern waters (Findlay and Best, 1996; Mizroch et al.⁴⁹).

The third phase of whaling in the Southern Hemisphere was marked by post-1938 coastal whaling operations. These operations were centered in Australian and New Zealand waters, where approximately 22,000 humpback whales were taken. From 1937 to 1950, there were 5,019 humpback whales taken off southern Madagascar (Best et al., 1996;

⁴⁹ Mizroch, S. A., D. W. Rice, and S. Larson. 1992. Distribution of rorquals in the Southern Ocean: an atlas based on pelagic catch data. Unpubl. doc. SC/44/SHB17 submitted to Rep. Int. Whal. Comm., 40 p.

Table 10.—Total number of whales killed in the North Atlantic from 1988 to 1995 (IWC Ann. Rep., 1988–89 to 1994–95)

North Atlantic stocks	Humpback	Fin	Sei
Denmark	4		
West Greenland	1	103	
East Greenland			2
Iceland ¹		136	10
St. Vincent and the Grenadines	4		
Total strikes	9	239	12
Total kills	8	239	12

¹ Iceland did not report to the IWC after the 1989–90 season.

Findlay and Best, 1996). From 1953 to 1963, the pelagic whaling operations in the Antarctic were limited to only 4 days per year by IWC regulations (Findlay and Best, 1996; Mizroch et al.⁴⁹).

Current Exploitation

Table 10 summarizes the North Atlantic take of humpback whales in the seasons 1988–89 to 1994–95. During this period, there were reports of eight humpback whales taken and one struck and lost in the western North Atlantic for subsistence purposes⁵⁰ off West and East Greenland and St. Vincent and The Grenadines (IWC, 1996a).

Worldwide protection of humpback whales began in 1966, although by 1963 the IWC had already given these whales “Protected Status” in the Southern Hemisphere. Despite the official end to Southern Hemisphere whaling for humpback whales in 1963, some takes still occurred until 1980. In 1978, there was an aboriginal catch of 12 animals, including 3 calves, in the western South

⁵⁰ The IWC defines “subsistence” as the use of whale meat and products exclusively for local consumption as human or animal food.

Pacific (Tonga). Most significant, however, was the unreported take by Soviet whaling vessels in the Antarctic from 1947 to 1980. In 1995, former Russian whaling captains revealed that 48,477 humpback whales had been taken during this time—only 2,710 of which were originally reported to the IWC (Zemsky et al., 1995; IWC, 1995a). The majority of these whales were taken in Area V (Eastern Australia), followed by Area II, Area IV, Area VI, Area III, and Area I (Fig. 9) in descending order of number of whales taken (Tormosov, 1995; IWC, 1995a).

Life History and Ecology

Feeding

Humpback whales in the Northern Hemisphere could be classified as generalists when it comes to their diet. They have been known to prey upon krill (euphausiids); copepods; juvenile salmonids, *Oncorhynchus* spp.; Arctic cod, *Boreogadus saida*; walleye pollock, *Theragra chalcogramma*; pollock, *Pollachius virens*; pteropods; and some cephalopods (Johnson and Wolman, 1984). In New En-



A group of humpback whales feeding in southeast Alaska. L. Gerber.

gland waters of the North Atlantic, 95% of their diets consist of fish species. The most common prey item is the Atlantic sandlance, *Ammodytes dubius*; with Atlantic herring, *Clupea harengus*; capelin, *Mallotus villosus*; Atlantic mackerel, *Scomber scombrus*; and other schooling species also found in their diets (Kenney et al., 1985). On the Alaska feeding grounds in the North Pacific, krill, herring, and capelin make up the majority of prey items in the stomachs of humpback whales (Bryant et al., 1981; Dolphin and McSweeney, 1983). In contrast, Southern Hemisphere humpback whales feed almost exclusively on Antarctic krill, *Euphausia superba* (Kawamura, 1994).

Humpback whales generally do not feed when on their wintering grounds (Slijper, 1962; Lockyer, 1981). However, there have been some documented events in low-latitude waters of whales exhibiting their characteristic feeding behaviors both in the Dominican Re-

public (Baraff et al., 1991) and Hawaii (Salden⁵¹). Feeding on wintering grounds seems to be opportunistic and is considered a rare event.

Humpback whales utilize a wide range of feeding techniques, at times involving more than one individual and resembling a form of cooperative participation. The two most observable techniques are lob-tail feeding (Weinrich et al., 1992) and bubble-cloud feeding (Fig. 21) (Ingebrigtsen, 1929; Jurasz and Jurasz, 1979a; Hain et al., 1982). Recently, there has also been documentation of bottom-feeding by humpback whales on Stellwagen Bank off Massachusetts and near the mouth of Chesapeake Bay (Swingle et al., 1993; Hain et al., 1995).

⁵¹ Salden, D. R. 1989. An observation of apparent feeding by a sub-adult humpback whale off Maui, Hawaii (Abstr.) In Proceedings of the eighth biennial conference on the biology of marine mammals, 1989, Pacific Grove, Calif.

Reproduction

In the Northern Hemisphere, calving takes place between January and March (Johnson and Wolman, 1984) and in the Southern Hemisphere between April and September in warm, low-latitude waters. Age at sexual maturity has been estimated to range from 4 to 9 years in females, but there is no reliability associated with these estimates (Clapham and Mayo, 1987). The calving interval is also variable. A range of 2–3 years has been given (Clapham, 1990); however, there is some evidence of calving by females in consecutive years (Clapham and Mayo, 1987; Clapham, 1990; Weinrich et al., 1993; Glockner-Ferrari and Ferrari⁵²). In a study looking at various reproductive parameters and survival rates, Wiley and Clapham (1993) concluded that a longer calving interval resulted in superior maternal condition. This conclusion needs further study to be considered valid for all individuals. Gestation averages around 12 months, and lactation lasts close to a year (Rice, 1967). The majority of calves are weaned at 1 year, but the specific timing of separation is still unknown (Clapham, 1992)(Fig. 22).

In the North Pacific, separate annual reproductive rates have been estimated from information collected in wintering and summering areas. In the winter areas the rate was 0.58 calves per year, and in the summer areas this rate was only 0.38 calves per year (Baker et al., 1987). In the North Atlantic, an annual reproductive rate of 0.41 calves per year has been calculated (Clapham and Mayo, 1987).

Natural Mortality

Natural mortality rates have rarely been estimated for humpback whales, and the causes of natural mortality in this species are not well known. However, Buckland (1990) used photo-identification data to estimate an annual survival rate of 0.951 (± 0.010) for North Atlantic whales photographed in the Gulf of Maine.

⁵² Glockner-Ferrari, D. A., and M. J. Ferrari. 1985. Individual identification, behavior, reproduction, and distribution of humpback whales, *Megaptera novaeangliae*, in Hawaii. U.S. Mar. Mammal Comm., Wash., D.C., Rep. MMC-83/06, 35 p. NTIS PB85-200772.



Figure 21.—An aerial view of a bubble net created by feeding humpback whales off Cape Fanshaw, Alaska. J. Olson, NMML Collection.



Figure 22.—Humpback whale mother and calf in clear Hawaiian waters. J. Hudnall, NMML Collection.

Killer whale, *Orcinus orca*, attacks on humpback whales do occur, although they are observed at a relatively low frequency on known wintering and summering areas (Dolphin, 1987; Whitehead, 1987). Humpback whales bear the scars of such attacks, as evidenced in 33% of photographically identified whales in the western North Atlantic (Katona et al.⁵³) and 15–20% of photographically identified whales in Alaska (Dolphin, 1987). It seems most likely that younger animals during migration—when group size is lowest—may be most susceptible to this form of harassment and mortality (Dolphin, 1987; Whitehead, 1987).

Humpback whales are known to harbor many varieties of commensal and parasitic organisms (Tomilin, 1967; Matthews, 1978). Lambertsen (1992) describes infestations of the giant nematode, *Crassicauda boopis*, which causes inflammation of the renal arteries and, in severe cases, complete kidney failure. Due to particularly high levels of crassicaudosis in calves and juveniles, Lambertsen (1992) cites these infesta-

tions as a potential factor in limiting the recovery of humpback whales.

In 1987 and 1988, 14 humpback whales died from ingesting dinoflagellate saxitoxin-infected Atlantic mackerel (Blaylock et al., 1995). To what extent this type of poisoning occurs and what effects it has on the species is unknown.

From 1985 through 1998, there was an increase in the occurrence of strandings and sightings along the U.S. middle Atlantic and southeast Atlantic coasts (Swingle et al., 1993; Wiley et al., 1995). How much of this may be attributed to increased search effort and public awareness is unknown. However, some researchers have speculated that these coastal areas may be increasingly important habitat for juvenile humpback whales.

Human-related Mortality

Worldwide, humpback whales are vulnerable to a broad range of human-caused disturbances. These include vessel movements and noise on their restricted wintering grounds and fisheries activities and pollution on their feeding grounds.

Fisheries Interactions

In 1990, there were thought to be fewer than three humpback whale mor-

talities annually in U.S. waters due to commercial fishing operations. More recent NMFS observer data (1990–95) from the Bering Sea, Aleutian Islands, and Gulf of Alaska groundfish trawl, longline, and pot fisheries revealed no humpback mortalities in the western North Pacific stock (Hill et al., 1997). For the central North Pacific stock, the NMFS data through 1995 (i.e. observers, MMPA logbook reports, strandings) from the Hawaii and southeastern Alaska areas were used to calculate an estimated minimum mortality rate incidental to commercial fishing operations of 0.8 humpback whales per year (Hill et al., 1997). Barlow et al. (1997) report an estimated minimum mortality rate of 1.21 humpback whales per year from the California/Oregon/Washington stock, but there is no information on fisheries-related mortality when these whales are in Mexican waters during winter. Given that the PBR level³⁷ for whales found off California, Oregon, and Washington is estimated to be 0.5 whales per year (Barlow et al., 1995b), fisheries-related mortality off the U.S. Pacific coast may pose a threat to the recovery of this North Pacific stock. In other areas of the North Pacific (Japan, Russia, etc.) there is no information to estimate fisheries-related mortality.

In the western North Atlantic between 1975 and 1990, a minimum of 51 humpback whales were recorded as entrapped in fishing gear (i.e. bottom gillnets, lobster gear, weirs, longlines, purse seines) off the northeastern U.S. coast (Anonymous³³). Of those entrapped whales, seven died. Total average annual estimated mortality and serious injury in fisheries under the NMFS monitoring programs (observer programs) was 0.6 whales (CV = 0.22) from 1992 to 1996 (Waring et al., 1998). Reports from other unobserved U.S. fisheries involving mortality and serious injury to humpback whales from 1991 to 1996 were found in the records of the NMFS Northeast Regional Office. These records contained 23 additional cases of mortality and serious injury related to fisheries (Waring et al., 1998). Regionally, the average number of entanglements, and thus mortalities,

⁵³ Katona, S. K., P. Harcourt, J. Perkins, and S. D. Kraus. 1980. Humpback whales: a catalogue of individuals identified in the western North Atlantic by means of fluke photographs. Coll. Atl., Bar Harbor, Maine, 169 p.



The NOAA research vessel, *John N. Cobb*, with a humpback whale off its port side. J. Waite, NMML Collection.

may be even greater. For example, in the 1980's, 50 (range 26–66) whales per year were entangled in Canadian waters, especially in Newfoundland (Lien et al.⁵⁴). Given the information currently available on fishing interactions in the western North Atlantic and the current levels of PBR³⁷ set by the NMFS (Table 3), commercial fishing activities may pose a significant threat to the status of this stock. In other regions with known humpback whale occurrence, such as Iceland and the Denmark Strait, southwest Greenland, and southern Labrador, fisheries interaction data are scarce.

Like other baleen species, the humpback whale's distribution and health relies upon the distribution, abundance, and health of their prey. This means whale distributions shift depending on the cyclical abundance and distribution of prey items (Weinrich et al., 1997).

⁵⁴ Lien, J., W. Ledwell, and J. Naven. 1988. Incidental entrapment in inshore fishing gear during 1988: A preliminary report to the Newfoundland and Labrador Department of Fisheries and Oceans, Canada, 15 p.

The details of these biological/environmental changes should be a factor in their conservation status and affect the steps that are taken towards proactive management. One documented example of such an environmental change occurred in Newfoundland waters during the late 1970's when a shift in the distribution of capelin stocks caused a redistribution of humpback whales into inshore waters, where they encountered fishing gear for Atlantic cod, *Gadus morhua*, and the incidence of entanglements increased (Lien and Whitehead⁵⁵).

Vessel Collisions

Direct ship strikes are a significant source of mortality in humpback whale stocks along the western U.S. coast

⁵⁵ Lien, J., and H. Whitehead. 1983. Changes in humpback (*Megaptera novaeangliae*) abundance off northeast Newfoundland related to the status of capelin (*Mallotus villosus*) stocks (Abstr.). In Proceedings of the Fifth Biennial Conference on the Biology of Marine Mammals, Nov. 1983, Boston, Mass.

(CA/OR/WA) and in the western North Atlantic. In California/Oregon/Washington feeding areas, there are an average 0.6 whales killed by ship strikes per year (Barlow et al., 1997). In the North Atlantic, 6 out of 20 humpback whales stranded along the Mid Atlantic coast between 1990 and 1994 showed signs of major ship strike injuries (Wiley et al., 1995). According to Waring et al. (1998), an annual average of 1.3 humpback whale mortalities in U.S. waters of the North Atlantic (between 1991 and 1996) could be attributed to vessel strikes. There is little information on the number of ship strikes occurring outside of U.S. waters.

Noise Disturbance

Continued coastal development and oil exploration and drilling may lead to avoidance of areas by the whales. Studies to date have shown that humpback whales exposed to playbacks of noise from drillships, semisubmersibles, drilling platforms, and production platforms do not exhibit avoidance behaviors at

levels up to 116 dB (Malme et al.⁵⁶). However, two whales were found dead near the site of repeated subbottom blasting in a Newfoundland inlet. Studies showed no signs of avoidance or disturbance from the noise pulses, but both whales suffered severe mechanical damage to their ears (Ketten et al., 1993; Lien et al., 1993; Ketten, 1995).

Humpback whales appear most responsive to moving sound sources, such as whale-watching vessels, fishing vessels, recreational vessels, and low-flying aircraft (Anonymous, 1987; Atkins and Swartz, 1989; Beach and Weinrich, 1989; Clapham et al., 1993; Tinney⁵⁷; Green and Green⁵⁸). Responses to noise are variable, and the level and type of response exhibited by whales has been correlated to group size and composition and apparent behaviors at the time of possible disturbance (Watkins et al., 1981; Krieger and Wing, 1986; Glockner-Ferrari, 1990; Herman et al.⁵⁹; Glockner-Ferrari and Ferrari⁵²).

There is the possibility that long-term displacement may have resulted from vessel noise disturbance in the central North Pacific stock, where researchers have noted a decline in the use of Glacier Bay, Alaska, during feeding seasons (Jurasz and Jurasz⁶⁰; Dean et al.⁶¹) and avoidance of near-shore waters by mothers and calves in Hawaii (Salden, 1988; Glockner-Ferrari, 1990; Glockner-Ferrari and Ferrari⁵²). Humpback whales may also become habituated to vessel traffic and its associated noise (Watkins, 1986; Belt et al.⁶²), which may leave them more vulnerable to vessel strikes (Swingle et al., 1993; Wiley et al., 1995). In Hawaii, regulations prohibit boats from approaching within 91 m of adult whales and within 274 m in areas designated mother/calf areas (Anonymous, 1987). Likewise, in Alaska, the number of cruise ships entering Glacier Bay has been limited to reduce possible disturbance (Baker et al., 1988).

Classification Status

The humpback whale was listed as endangered under the ESA in 1973 and designated as depleted under the MMPA. Endangered status is applied to

all stocks in U.S. waters (Anonymous, 1994b). In addition, all stocks are classified as "Protected Stocks" by the IWC. Under this designation, the IWC recognizes that these whales are 10% or more below their maximum sustainable yield (MSY) levels (IWC, 1995b).

All humpback whale stocks in U.S. waters are adversely affected by human activities (Table 3, 11) (Barlow et al., 1997; Hill et al., 1997; Waring et al., 1998). There is no information on the extent of the effects of human activity on humpback whale stocks in the eastern North Atlantic, western North Pacific, Mexico, and Southern Hemisphere.

With a few notable exceptions (see below), there has been little advance in the accuracy and availability of population parameters, abundance, or stock identity worldwide since Braham's 1991 status review³. Forthcoming results of the YoNAH project should help resolve some uncertainties about genetic stock structure and the distribution of humpback whales in the North Atlantic (Allen et al.⁴⁴). Genetic analysis holds promise in distinguishing between biological stocks, but at this time the number of whales sampled is too small to be of statistical value (Baker et al., 1994; IWC, 1995a). A second phase of the YoNAH project is being discussed. These further studies would provide population trend data.

During a recent (1997) workshop on the reevaluation of North Pacific humpback whale classification, Gerber and DeMaster⁶³ reported that the partici-

⁵⁶ Malme, C. I., P. R. Miles, P. Tyack, C. W. Clark, and J. E. Bird. 1985. Investigation of the potential effects of underwater noise from petroleum industry activities on feeding humpback whale behavior. Rep. from BBN Labs Inc., Cambridge, Mass., for U.S. Minerals Manage. Serv., Anchorage, Alaska. BBN Rep. 5851; OCS Study MMS 85-0019.

⁵⁷ Tinney, R. T., Jr. 1988. Review of information bearing upon the conservation and protection of humpback whales in Hawaii. Rep. for U.S. Mar. Mammal Comm., Wash., D.C., 56 p. NTIS PB88-195359.

⁵⁸ Green, M. L., and R. G. Green. 1990. Short-term impact of vessel traffic on the Hawaiian humpback whale (*Megaptera novaeangliae*), 9 p. Pres. at Annu. Meet. Anim. Behav. Soc., June 1990, Buffalo, N.Y.

⁵⁹ Herman, L. M., P. H. Forestell, and R. C. Antinjoja. 1980. The 1976/1977 migration of humpback whales into Hawaiian waters: composite description. Rep. MMC-77/19 for the U.S. Mar. Mammal Comm., Wash., D.C., 55 p. NTIS PB80-162332.

⁶⁰ Jurasz, C. M., and V. P. Jurasz. 1979. Ecology of humpback whales. Contr. cx-9000-7-0045. Draft rep. for U.S. Natl. Park Serv., Anchorage, Alaska, 118 p.

⁶¹ Dean, F. C., C. M. Jurasz, V. P. Palmer, C. H. Curby, and D. L. Thomas. 1985. Analysis of humpback whale (*Megaptera novaeangliae*) blow interval data/Glacier Bay, Alaska, 1976-1979, 224 p., 2 vol. Rep. from Univ. of Alaska, Fairbanks, for U.S. Natl. Park Serv., Anchorage, Alaska.

⁶² Belt, C. R., M. T. Weinrich, and M. R. Schilling. 1989. Behavioral development of humpback whales in the southern Gulf of Maine (Abstr.). In Proceedings of the eighth biennial conference on the biology of marine mammals, 1989, Pacific Grove, Calif.

⁶³ Gerber, L. R., and D. P. DeMaster. 1997a. Report on workshop to develop Endangered Species Act classification criteria for North Pacific humpback whales. Natl. Mar. Mammal Lab., NMFS, NOAA, 7600 Sand Point Way N.E., Seattle, WA 98115. Unpubl. rep., 16 p.

Table 11.—Factors possibly influencing the recovery of humpback whales under the ESA (1973)§4(a)(1), 1992 Amend. (eastern North Atlantic and Southern Hemisphere data are not available).

Factor	North Pacific	Western North Atlantic
1. Present or threatened destruction or modification of habitat	Central stock: Vessel traffic; oil and gas exploration	Vessel traffic; channel dredging; oil and gas exploration; coastal development
2. Overutilization for commercial, subsistence, recreational, scientific, or educational purposes	Central stock: Whale watching, scientific research, photography, and associated vessel traffic	Whale watching, scientific research, photography, and associated vessel traffic; West Greenland, St. Vincent and the Grenadines harvests
3. Disease or predation	Unknown	Saxitoxin
4. Other natural or man-made factors	Central stock: Entanglement in fishing gear	Vessel collisions; entanglement in fishing gear (e.g. bottom gillnets, lobster gear, weirs, longlines, purse seines); human depletion of fish stocks

pants had concluded that the criteria used to classify humpback whales should incorporate uncertainties from the available data (e.g. abundance, trends in abundance) and be flexible enough to accommodate multiple population structure scenarios. Gerber and DeMaster⁶⁴ developed classification criteria based on abundance, trends in abundance, changes in distribution, and

⁶⁴ Gerber, L. R., and D. P. DeMaster. 1997b. An approach to Endangered Species Act classification of North Pacific humpback whales. Avail. from Leah Gerber, Natl. Mar. Mammal Lab., NMFS, NOAA, 7600 Sand Point Way N.E., Seattle, WA 98115.

regulatory status. Trends in population abundance over time were used to generate a probability distribution around the population's underlying rate of change, which could be used to designate potential thresholds for endangered and threatened status. According to thresholds generated by their model, a recommendation to downlist to threatened the central North Pacific humpback whale stock would be warranted. However, they also noted that more accurate information on life history parameters, trends in abundance, sex ratio, environmental variability, and stock structure must continue to be collected

and applied to such classification models in order to make accurate status determinations. Reliable abundance estimates exist for the central North Pacific humpback whale stock, and there are indications of its continued growth.

Assuming that abundance levels are accurate and continue to increase, anthropogenic threats are reduced, adequate monitoring plans are developed and implemented, and information on population trends continue to be collected, the western North Atlantic and central North Pacific stocks should be considered for downlisting to threatened status.