

# Migration of a humpback whale (*Megaptera novaeangliae*) between the Cape Verde Islands and Iceland

B. JANN\*, J. ALLEN<sup>+</sup>, M. CARRILLO<sup>#</sup>, S. HANQUET<sup>§</sup>, S.K. KATONA<sup>+</sup>, A.R. MARTIN<sup>\*\*</sup>, R.R. REEVES<sup>++</sup>, R. SETON<sup>+</sup>, P.T. STEVICK<sup>+</sup> AND F.W. WENZEL<sup>###</sup>

Contact e-mail: Frederick.Wenzel@noaa.gov

## ABSTRACT

The movements of individual humpback whales (*Megaptera novaeangliae*) can be tracked by matching photographs of the distinctive markings on the ventral sides of their tail flukes. During the winter-spring seasons of 1990, 1991, 1995, 1996, 1999, 2000, 2001 and 2002 a total of 42 individual humpbacks were identified by fluke photographs from the waters of the Cape Verde Islands. These were compared with photographs taken elsewhere in the North Atlantic. One match was made with a whale previously photographed in the Denmark Strait off Iceland, providing the first direct evidence of a link between the humpbacks in tropical waters of the eastern North Atlantic and a high-latitude feeding ground. This finding is consistent with the mitochondrial DNA evidence of at least two distinct breeding populations of humpback whales in the North Atlantic. The presence of cows with young calves as well as singers during the humpback mating and calving season implies that waters surrounding the Cape Verde archipelago constitute a breeding and calving ground for an eastern North Atlantic population of humpback whales.

KEYWORDS: HUMPBACK WHALE; REPRODUCTION; HABITAT; ATLANTIC OCEAN; BREEDING GROUNDS; PHOTO-ID; MIGRATION; FEEDING GROUNDS

## INTRODUCTION

The population of humpback whales (*Megaptera novaeangliae*) in the North Atlantic Ocean is one of the best-studied populations of large whales in the world (see review in IWC, 2002; 2003). Since the 1970s, extensive photo-identification effort has yielded much information on population structure and migratory movements (Katona and Whitehead, 1981; Katona and Beard, 1990; Clapham and Mead, 1999; Smith *et al.*, 1999). Genetic tagging has also been used to determine connections between whales in different areas of the North Atlantic (Palsbøll *et al.*, 1995; 1997; Larsen *et al.*, 1996; Valsecchi *et al.*, 1997).

It is clear from previous studies that humpback whales feed during the summer in a number of relatively discrete grounds, including: Gulf of Maine; Newfoundland/Labrador; Gulf of St Lawrence; Greenland; Iceland; and Norway. Fidelity to these summer feeding areas is strong and apparently maternally directed; genetic analyses suggest that it is maintained on an evolutionary timescale (Larsen *et al.*, 1996; Palsbøll *et al.*, 1997). Despite the low level of movement between the various feeding grounds, photo-identification and genotyping has shown that some individuals from all of the identified high-latitude areas migrate long distances (in some instances more than 8,000km) to common winter breeding grounds in the West Indies (Martin *et al.*, 1984; Stevick *et al.*, 1998; 1999b; 2003) where they mix spatially and genetically. The great majority of humpback whales in the North Atlantic appear to use West Indies wintering areas, with large concentrations in the northern Antilles, especially on or near Silver Bank (Winn *et al.*, 1975; Clapham and Mead, 1999; Smith *et al.*, 1999).

During the 19<sup>th</sup> century, American open-boat whalers rarely reported taking humpbacks in the northern Antilles. Instead, their humpback whaling effort focused on portions of the southeastern Caribbean and on the Cape Verde Islands (Mitchell and Reeves, 1983; Reeves *et al.*, 2001; 2002; Reeves and Smith, 2002). Today, densities of humpbacks in these two historic breeding areas are comparatively low (Jann and Wenzel, 2001; Swartz *et al.*, 2003). A photographic match was made recently between the southeastern Caribbean and Fyllas Bank off West Greenland (Stevick *et al.*, 1999a), suggesting that at least some of the whales that winter in the southern portion of the West Indies have migratory habits similar to those of the whales that winter in the northern Antilles. The summer feeding range of the humpback whales that winter in the Cape Verde Islands has remained uncertain.

This paper reports the first match of an individually identified humpback whale from the Cape Verde Islands to a northern feeding ground (Iceland), and discusses the implications for population structure.

## METHODS AND MATERIALS

### Study area

The Cape Verde Islands are situated in the eastern North Atlantic between 14°48'–17°22'N and 22°44'–25°22'W, 460–830km west of Senegal, West Africa (Hazevoet, 1995). The ten islands and several islets are of volcanic origin, with steep shores, arising from a marine bottom more than 3,000m deep. Only the islands of Maio, Boavista and Sal have a continental platform, while the northwestern islands of Sao Vicente, Santa Lucia, Branco and Raso have limited

\* Swiss Whale Society, via Nolgio 3, CH-6900 Massagno, Switzerland.

<sup>+</sup> College of the Atlantic, 105 Eden St., Bar Harbor, Maine 04609, USA.

<sup>#</sup> La Laguna, Tenerife, Canaries, Spain.

<sup>§</sup> Los Cristianos, Tenerife, Canaries, Spain.

<sup>\*\*</sup> British Antarctic Survey, High Cross, Madingley Road, Cambridge, CB3 0ET, UK.

<sup>++</sup> Okapi Wildlife Associates, 27 Chandler Lane, Hudson, Quebec, Canada, J0P 1H0.

<sup>###</sup> National Marine Fisheries Service, Northeast Fisheries Science Center, 166 Water St., Woods Hole, MA 02543, USA.

amounts of water less than 100m deep (Fig.1). Most research effort since 1990 has been in the eastern sector of the archipelago around the islands of Sal, Boavista and Maio.

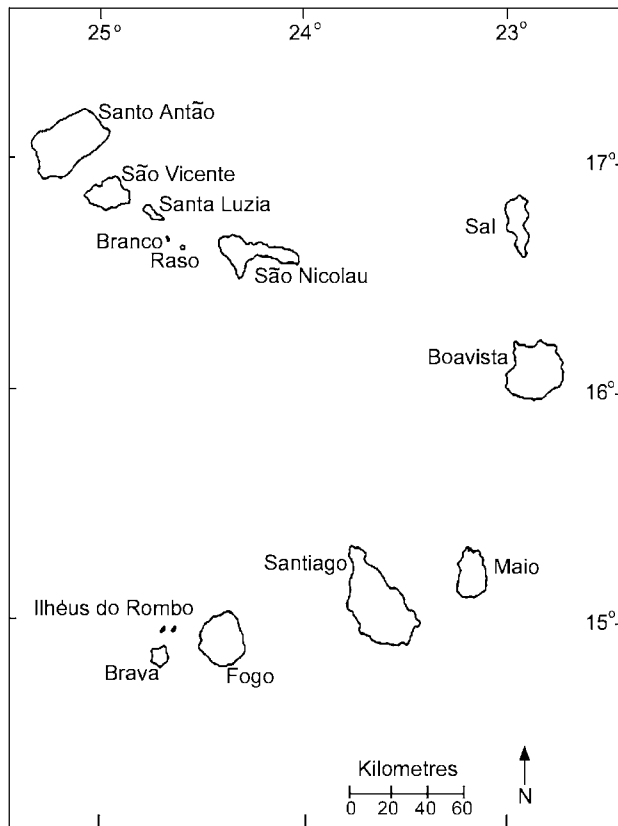


Fig. 1. Map of the Cape Verde Islands, as in Hazevoet (1995), with permission of the author.

These waters are known for strong trade winds, rough seas and sand storms, often making navigation around the islands difficult and hazardous and producing less than ideal conditions for mariners and whale researchers. This helps explain the low number of fluke photographs and limited amount of information on cetaceans from this region (Reiner *et al.*, 1996; Hazevoet and Wenzel, 2000; Jann and Wenzel, 2001; Jann *et al.*, 2002).

### Data collection

Searches for humpback whales in the Cape Verde Islands were conducted from February to May in 1990, 1991, 1995 and 1996 aboard a 5m inflatable boat around the islands of Sal and Boavista (Reiner *et al.*, 1996; Hazevoet and Wenzel, 2000). The searches in 1999 (26 February – 8 April) were made from a 50m steel-hulled motor ship; in 2000 (27-29 February, 30 March – 4 April) and 2001 (31 March – 2 May) from a 37m schooner; and in 2002 (22 March – 2 May) from a 20m sailboat. During 2000-2002, a 5m inflatable boat was deployed from the larger vessels when humpbacks were observed and sea state permitted. More humpback fluke photographs were obtained in the 1999-2002 seasons than in previous years, presumably because of the advantages associated with using larger vessels in the types of sea-state conditions that prevail in these waters.

For each cetacean sighting, the time, GPS position, group size and composition, and behaviour were noted. Photographs were taken for identification purposes and

acoustic recordings were made during approaches to humpback whales. The photographs were taken with a 35mm single lens reflex camera equipped with a 75-300mm zoom lens using 400 ASA black and white and/or colour print film.

### Photo comparison

There are two major projects involving individual identification of humpback whales that include geographical coverage over much of the North Atlantic Ocean: the North Atlantic Humpback Whale Catalogue (NAHWC) and the collection from the Years of the North Atlantic Humpback Whale (YoNAH) project. Both humpback catalogues (NAHWC and YoNAH) are maintained at Allied Whale, College of the Atlantic, 105 Eden St., Bar Harbor, Maine 04609, USA.

The NAHWC is a central curator facility for photographs of humpback whales from throughout the North Atlantic Ocean. Photographs date from 1952 to 2002, though few are available from years prior to 1978. The NAHWC project is collaborative and photographs have been submitted by more than 350 contributors. Photographs have been obtained opportunistically, so temporal and spatial coverage is highly variable. Most photographs were taken on the western North Atlantic feeding grounds (Tables 1 and 2).

Table 1

Numbers of identified individuals in the two photograph collections (as of 31 December 2002) to which the Cape Verde Islands photographs were compared. Individuals identified in both a feeding and breeding region are included only in the number for the feeding region and not also in that for the breeding region. Western and eastern feeding areas are divided at the longitude just east of Cape Farewell, Greenland (40W longitude). No photographic matches have been found between the western and eastern feeding areas.

Collection	NAHWC	YoNAH
Feeding grounds, western	3,431	1,398
Feeding grounds, eastern	158	260
West Indies	1,647	1,324
Cape Verde Islands	42	0
Non-feeding/breeding regions: US coast south of Cape Cod, Bermuda and Mediterranean	122	0
Total	5,400	2,982

Table 2

Numbers of individuals in the NAHWC and the YoNAH collections identified in both a feeding and a breeding ground.

	West Indies	Cape Verde Is.
<b>NAHWC</b>		
Feeding grounds, western	564	0
Feeding grounds, eastern	15	1
<b>YoNAH</b>		
Feeding grounds, western	163	0
Feeding grounds, eastern	21	0

The YoNAH project, an extensive study of humpback whales in the North Atlantic, was conducted during 1992 and 1993. It did not include the waters of the Cape Verde Islands, the Irish Sea and other parts of the eastern North Atlantic. As part of that study, identification photographs were obtained in all of the known major feeding grounds and in the West Indies, using standardised protocols. Due to logistical considerations, sampling intensity in Icelandic and Norwegian waters, while considerably greater than during any previous effort, was less than that in the western North

Atlantic feeding areas (i.e. Greenland, eastern Canada and northeastern United States (Gulf of Maine) (Smith *et al.*, 1999). No YoNAH sampling was conducted in the Cape Verde Islands (Tables 1 and 2).

Since 1994, it has not been possible to manually compare all photographs within the (growing) NAHWC with the YoNAH catalogue. While the YoNAH collection has not been systematically compared to the NAHWC, due to resource and time limitations, nearly 800 individual humpback whales have been identified in both collections (J. Allen, unpublished data). All identification photographs from the Cape Verde Islands were compared to both the NAHWC and the YoNAH collections using methods described by Katona and Whitehead (1981), Katona and Beard (1990) and Smith *et al.* (1999).

## RESULTS

### Photographic match

A total of 42 individual humpback whales have been identified thus far in the Cape Verde Islands. The first Cape Verde fluke photographs were obtained in 1991 ( $n=2$ ), and numbers thereafter were 1 in 1995, 22 in 1999, 1 in 2001 and 16 in 2002. No individual has been identified in more than one year.

A single individual, NAHWC#4504, photographed on 10 March 1999 in the Bay of Sal Rei, Boavista, at 16°02'N, 23°02'W, had previously been photographed in the Denmark Strait west of Iceland, at 65°16'N, 27°30'W, in July 1982 (Fig. 2a-2b). No other photographic re-identifications of this animal were recorded during the 18 years between the 1982 and 1999 sightings.

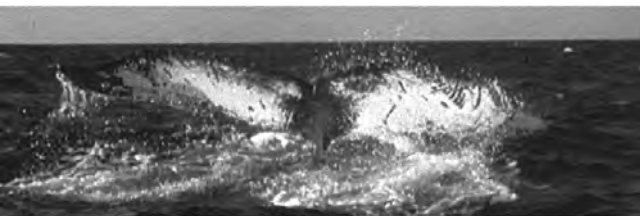


Fig. 2a and 2b. Fluke photographs of NAHWC#4504, from the Denmark Strait west of Iceland at 65°16'N, 27°30'W in July of 1982 and again photographed on March 10 1999 in the Bay of Sal Rei, Boavista, Cape Verde Islands at 16°02'N, 23°02'W.

### Presence of mother-calf pairs

Mother-calf pairs of humpback whales have been observed at the Cape Verde Islands as early as 23 February (in Baía de Mordeira, Sal, in 1995 and in the Bay of Sal Rei, Boavista, in 2002) and as late as 5 June (at Punta Preta, Sal; Robert Mannink, pers. comm.). A calf was defined as: < 5m in total length; often of grey body colouration; and remaining most of the time within one body length of the female (see

Clapham *et al.*, 1999; Clapham and Mead, 1999). Most observed calves had floppy dorsal fins and foetal folds on the sides of the body. Some had wrinkles reminiscent of a pickle. Nearly all encounters with mother-calf pairs were in waters < 15m deep (see Smultea, 1994).

### Presence of singers

Humpback whale songs have been described in detail by many authors (see Payne and Guinee, 1983; Payne and McVay, 1971; Winn and Winn, 1978; Noad *et al.*, 2000). Winn *et al.* (1981) compared humpback whale songs between the West Indies and the Cape Verde Islands. The small sample size from the Cape Verde Islands ( $n=1$  individual) and a couple of hours of recordings (13 songs) were compared to 10 songs from a probable 7 individuals from the West Indies. Winn *et al.* (1981) stated that by aligning similar themes it was clear that the thematic composition of the Cape Verde Island song format followed that of the West Indies songs, the only differences being in the number of 'groans' emitted within each theme and minor variations in phase structure. Winn *et al.* (1981), based on their sample size of one, stated that the songs from the Cape Verde Islands and the West Indies were 'essentially equivalent'.

Humpback whale songs have been recorded during every field season, between February and May, especially around the islands of Sal and Boavista (Reiner *et al.*, 1996; Carrillo *et al.*, 1999; Hazevoet and Wenzel, 2000; Jann and Wenzel, 2001). The earliest song recording was on 17 February (1990) (Reiner *et al.*, 1996) and the latest was on 12 May (1996) (Hazevoet and Wenzel, 2000). It is assumed that by mid-May most humpbacks have started their northward migration to the feeding grounds. Unfortunately, to date no additional song comparisons have been undertaken to evaluate the validity of the conclusions of Winn *et al.* (1981) with regard to intra-ocean variability.

## DISCUSSION

Over the years, several authors have suggested the existence of two breeding stocks of humpback whales in the North Atlantic, one along the western and another along the eastern margin of the basin, separated roughly at Cape Farewell, Greenland (Ingebrigtsen, 1929; Kellogg, 1929). However, the degree of separation, overlap and limits of the two proposed stocks have often been discussed and questioned (Mitchell and Reeves, 1983; Palsbøll *et al.*, 1995; 1997; Larsen *et al.*, 1996; Valsecchi *et al.*, 1997; Smith *et al.*, 1999; Stevick *et al.*, 1999b; IWC, 2002).

Two spatially distinct tropical regions of the North Atlantic are known to have been used traditionally by humpback whales during the winter calving/breeding season – one in the West Indies (assuming a continuous distribution from the Greater Antilles to Venezuela) and one in the Cape Verde Islands. The recent sightings of mothers with young calves, recordings of humpback songs, and observations of surface-active groups establish that the waters around the Cape Verde Islands are currently used as a breeding and calving habitat during the boreal winter and spring.

The photographic match with Iceland is the first evidence of a feeding-ground destination for humpback whales from the Cape Verde Islands. As animals photo-identified off Iceland have also been observed in the West Indies (Martin *et al.*, 1984; Smith *et al.*, 1999; Stevick *et al.*, 2003), this match is consistent with the hypothesis that there is overlap on the feeding grounds between animals from the West Indies and Cape Verde Islands. Moreover, the failure to

match any of the photo-identified animals from the Cape Verde Islands with those on western feeding grounds or on the West Indies breeding ground is consistent with the hypothesis that humpbacks from the Cape Verde Islands constitute a distinct breeding population that feeds preferentially or exclusively in eastern feeding areas. Such a model is supported by the existence of mitochondrial DNA differences between eastern and western feeding areas (Palsbøll *et al.*, 1995; 1997; Larsen *et al.*, 1996; Valsecchi *et al.*, 1997).

It is difficult to interpret effort for the NAHWC by region and years. The NAHWC humpback fluke catalogue has grown enormously over the last 30 years, and YoNAH was a limited two-year study (1992 and 1993). However, the low match rate (1) strongly suggests that most of the whales that winter in the Cape Verde Islands use one or more eastern North Atlantic summer feeding area where there has been little or no recent sampling effort. When one considers how limited the photo-identification effort has been in the eastern feeding areas over the last 20 years, it is not particularly surprising that only one match has been made with a Cape Verde Islands fluke photograph, or that there has been an 18-year interval between the photographs of that individual.

## CONCLUSIONS

Research effort in the Cape Verde Islands has been modest in comparison to that in the West Indies and many other parts of the western North Atlantic (Reiner *et al.*, 1996; Carrillo *et al.*, 1999; Hazevoet and Wenzel, 2000; Jann and Wenzel, 2001). The first long-distance match, reported in this paper, should stimulate increased photo-identification effort not only in the Cape Verde Islands, but also at sites along the likely migratory route to the north (e.g. Canary Islands, Madeira) and on potential eastern North Atlantic feeding grounds (e.g. the Irish Sea). It should also give impetus to intensified efforts to obtain biopsies and song recordings from whales in Cape Verdean waters for comparative genetic and acoustic analyses. From a local perspective, it is desirable to improve understanding of habitat use patterns, residency times and site fidelity of individual humpbacks within the Cape Verde archipelago, and to determine whether numbers are increasing in this part of the species' range as they have been elsewhere in the North Atlantic (Sigurjónsson and Gunnlaugsson, 1990; Barlow and Clapham, 1997; Smith *et al.*, 1999).

## ACKNOWLEDGMENTS

We wish to acknowledge the Captains and crews of the ships *Holland*, *Corvette* and *Sodade*, especially Luis and Carlos Albrecht, Captain Luis A. Lopez, Captain Kees Roll, Captain Robert Mannink, Sonia Elsy Merino, The Instituto Nacional de Desenvolvimento da Pesca (INDP), and the volunteers who made this research possible through their very often enthusiastic participation, in particular Doris Vetsch and Walter Heckenthaler. Partial funding support for the 2002 cruise and the photograph matching at the College of the Atlantic was through the International Whaling Commission. In previous years, funding support was provided by the Whale and Dolphin Conservation Society (UK) and Cetacean Society International (USA). A number of friends and reviewers greatly assisted us with earlier drafts of this manuscript. Special thanks to Tim Smith, Phil Clapham, Per Palsbøll, Phil Hammond, Kees Hazevoet, Melissa Alexander, Gwilym Jones, Northeastern University,

David Senn, Karl Zbinden, Daniel Zbinden, Chris Schlegel and Durant Hembree for their years of encouragement regarding humpback whale research in the eastern North Atlantic, especially at the Cape Verde Islands and Iceland. We thank Finn Larsen and one anonymous reviewer for comments and suggestions which improved this manuscript.

## REFERENCES

- Barlow, J. and Clapham, P.J. 1997. A new birth-interval approach to estimating demographic parameters of humpback whales. *Ecology* 78(2):535-46.
- Carrillo, M., Jann, B., Seton, R. and Wenzel, F. 1999. Present status of humpback whales in the Cape Verde Islands. Presented at the 13th Biennial Conference on the Biology of Marine Mammals, Maui, Hawaii, December 1999. [Poster]. [Available from [Frederick.Wenzel@noaa.gov](mailto:Frederick.Wenzel@noaa.gov)].
- Clapham, P.J. and Mead, J.G. 1999. *Megaptera novaeangliae*. *Mamm. Species* 604:1-9.
- Clapham, P.J., Wetmore, S.E., Smith, T.D. and Mead, J.G. 1999. Length at birth and at independence in humpback whales. *J. Cetacean Res. Manage.* 1(2):141-6.
- Hazevoet, C.J. 1995. *The Birds of the Cape Verde Islands – BOU Checklist No.13*. British Ornithologists' Union, Tring, Herts, UK. 192pp.
- Hazevoet, C.J. and Wenzel, F.W. 2000. Whales and dolphins (Mammalia, Cetacea) of the Cape Verde Islands, with special reference to the humpback whale (*Megaptera novaeangliae*) (Borowski, 1781). *Contrib. Zool.* 69(3):197-211.
- Ingebrigtsen, A. 1929. Whales caught in the North Atlantic and other seas. *Rapp. P.-V. Réun. Cons. Int. Explor. Mer* 56(2):1-26.
- International Whaling Commission. 2002. Report of the Scientific Committee. Annex H. Report of the Sub-Committee on the Comprehensive Assessment of North Atlantic Humpback Whales. *J. Cetacean Res. Manage. (Suppl.)* 4:230-60.
- International Whaling Commission. 2003. Report of the Scientific Committee. Annex H. Report of the Sub-Committee on the Comprehensive Assessment of humpback whales. *J. Cetacean Res. Manage. (Suppl.)* 5:293-323.
- Jann, B. and Wenzel, F. 2001. Humpback whales in the Cape Verde Islands. Paper SC/53/NAH19 presented to the IWC Scientific Committee, July 2001, London (unpublished). [Paper available from the Office of this Journal].
- Jann, B., Wenzel, F.W. and Reeves, R.R. 2002. Humpback whales (*Megaptera novaeangliae*, Borowski 1781 Cetacea, Mysticeti) of the Cape Verde Islands: Past and Present. Presented to the Flora and Fauna Conference of the Atlantic Islands, Praia, Cape Verde Islands, September 2002. [Available from [Frederick.Wenzel@noaa.gov](mailto:Frederick.Wenzel@noaa.gov)].
- Katona, S.K. and Beard, J.A. 1990. Population size, migrations and feeding aggregations of the humpback whale (*Megaptera novaeangliae*) in the western North Atlantic Ocean. *Rep. int. Whal. Commn* (special issue) 12:295-305.
- Katona, S.K. and Whitehead, H.P. 1981. Identifying humpback whales using their natural markings. *Polar Rec.* 20:439-44.
- Kellogg, R. 1929. What is known of the migration of some of the whalebone whales. *Smithsonian Institution. Annual Report of the Board of Regents, 1928* :467-94+2pls.
- Larsen, A.H., Sigurjónsson, J., Øien, N., Vikingsson, G. and Palsbøll, P.J. 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. *Proc. R. Soc. Lond. Ser. B.* 263:1611-8.
- Martin, A.R., Katona, S.K., Mattila, D., Hembree, D. and Waters, T.D. 1984. Migration of humpback whales between the Caribbean and Iceland. *J. Mammal.* 65(2):330-3.
- Mitchell, E. and Reeves, R.R. 1983. Catch history, abundance, and present status of northwest Atlantic humpback whales. *Rep. int. Whal. Commn* (special issue) 5:153-212.
- Noad, M.J., Cato, D.H., Bryden, M.M., Jenner, M.N. and Jenner, K.C.S. 2000. Cultural revolution in whale songs. *Nature, Lond.* 408:537.
- Palsbøll, P.J., Clapham, P.J., Mattila, D.K., Larsen, F., Sears, R., Siegismund, H.R., Sigurjónsson, J., Vasquez, O. and Arctander, P. 1995. Distribution of mtDNA haplotypes in North Atlantic

- humpback whales: the influence of behavior on population structure. *Mar. Ecol. Prog. Ser.* 116:1-10.
- Palsbøll, P.J., Allen, J., Bérubé, M., Clapham, P.J., Feddersen, T.P., Hammond, P.S., Hudson, R.R., Jørgensen, H., Katona, S., Larsen, A.H., Larsen, F., Lien, J., Mattila, D.K., Sigurjónsson, J., Sears, R., Smith, T., Sponer, R., Stevick, P. and Øien, N. 1997. Genetic tagging of humpback whales. *Nature, Lond.* 388:767-9.
- Payne, R. and Guinee, L.N. 1983. Humpback whale (*Megaptera novaeangliae*) songs as an indicator of 'stocks'. pp. 333-58. In: R. Payne (ed.) *Communication and Behavior of Whales*. AAAS Selected Symposium 76. Westview Press, Colorado. xii+643pp.
- Payne, R. and McVay, S. 1971. Songs of humpback whales. *Science* 173:585-97.
- Reeves, R.R. and Smith, T.D. 2002. Historical catches of humpback whales in the North Atlantic Ocean: an overview of sources. *J. Cetacean Res. Manage.* 4(3):219-34.
- Reeves, R.R., Swartz, S.L., Wetmore, S.E. and Clapham, P.J. 2001. Historical occurrence and distribution of humpback whales in the eastern and southern Caribbean Sea, based on data from American whaling logbooks. *J. Cetacean Res. Manage.* 3(2):117-29.
- Reeves, R.R., Clapham, P.J. and Wetmore, S.E. 2002. Humpback whale (*Megaptera novaeangliae*) occurrence near the Cape Verde Islands, based on American 19th century whaling records. *J. Cetacean Res. Manage.* 4(3):235-53.
- Reiner, F., Dos Santos, M.E. and Wenzel, F.W. 1996. Cetaceans of the Cape Verde archipelago. *Mar. Mammal Sci.* 12(3):434-43.
- Sigurjónsson, J. and Gunnlaugsson, T. 1990. Recent trends in abundance of blue (*Balaenoptera musculus*) and humpback whales (*Megaptera novaeangliae*) off west and southwest Iceland, with a note on occurrence of other cetacean species. *Rep. int. Whal. Commn* 40:537-51.
- Smith, T.D., Allen, J., Clapham, P.J., Hammond, P.S., Katona, S., Larsen, F., Lien, J., Mattila, D., Palsbøll, P.J., Sigurjónsson, J., Stevick, P.T. and Øien, N. 1999. An ocean-basin-wide mark-recapture study of the North Atlantic humpback whale (*Megaptera novaeangliae*). *Mar. Mammal Sci.* 15(1):1-32.
- Smultea, M.A. 1994. Segregation by humpback whale (*Megaptera novaeangliae*) cows with a calf in coastal habitat near the island of Hawaii. *Can. J. Zool.* 72(5):805-11.
- Stevick, P.T., Øien, N. and Mattila, D.K. 1998. Migration of a humpback whale (*Megaptera novaeangliae*) between Norway and the West Indies. *Mar. Mammal Sci.* 14(1):162-6.
- Stevick, P.T., Carlson, C.A. and Balcomb, K.C. 1999a. A note on migratory destinations of humpback whales from the eastern Caribbean. *J. Cetacean Res. Manage.* 1(3):251-54.
- Stevick, P.T., Øien, N. and Mattila, D.K. 1999b. Migratory destinations of humpback whales from Norwegian and adjacent waters: evidence for stock identity. *J. Cetacean Res. Manage.* 1(2):147-52.
- Stevick, P.T., Allen, J., Berube, M., Clapham, P.J., Katona, S.K., Larsen, F., Lien, J., Mattila, D.K., Palsbøll, P.J., Robbins, J., Sigurjónsson, J., Smith, T.D., Øien, N. and Hammond, P.S. 2003. Segregation of migration by feeding ground origin in North Atlantic humpback whales (*Megaptera novaeangliae*). *J. Zool., London.* 259:231-37.
- Swartz, S.L., Cole, T., McDonald, M.A., Hildebrand, J.A., Oleson, E.M., Martinez, A., Clapham, P.J., Barlow, J. and Jones, M.L. 2003. Acoustic and visual survey of humpback whale (*Megaptera novaeangliae*) distribution in the Eastern and Southeastern Caribbean Sea. *Caribb. J. Sci.* In press.
- Valsecchi, E., Palsbøll, P., Hale, P., Glockner-Ferrari, D., Ferrari, M., Clapham, P., Larsen, F., Mattila, D., Sears, R., Sigurjónsson, J., Brown, M., Corkeron, P. and Amos, W. 1997. Microsatellite genetic distances between oceanic populations of the humpback whale (*Megaptera novaeangliae*). *Mol. Biol. Evol.* 14:355-62.
- Winn, H.E. and Winn, L.K. 1978. The song of the humpback whale *Megaptera novaeangliae* in the West Indies. *Mar. Biol.* 47(2):97-114.
- Winn, H.E., Edell, R.K. and Taruski, A.G. 1975. Population estimate of the humpback whale (*Megaptera novaeangliae*) in the West Indies by visual and acoustic techniques. *J. Fish. Res. Bd Can.* 32(4):499-506.
- Winn, H.E., Thompson, T.J., Cummings, W.C., Hain, J., Hundnall, J., Hays, H. and Steiner, W.W. 1981. Songs of the humpback whale — population comparisons. *Behav. Ecol. Sociobiol.* 8:41-6.

Date received: March 2003.

Date accepted: July 2003.