

Current Knowledge on the Distribution and Relative Abundance of Humpback Whales (*Megaptera novaeangliae*) off the Cape Verde Islands, Eastern North Atlantic

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Abstract

During the winter/spring months from 1990 to 2009, 13 cetacean surveys were conducted around the Cape Verde Islands off West Africa. The main target species was the humpback whale (*Megaptera novaeangliae*). Study periods varied from 14 to 90 d in duration. Study platforms included a 5-m inflatable boat, a 12-m catamaran, and/or 15-m sailing or motor vessels. Collectively, we obtained 88 individual humpback fluke photographs from this region. These fluke photographs have been compared to over 6,500 individual fluke photographs maintained in the *North Atlantic Humpback Whale Catalogue*. Based on photo-identification, humpbacks in the Cape Verde Islands have a relatively high interannual resight rate (> 22%) compared to other studied breeding locations in the West Indies. While this is partly due to increased probability of detection in a small population, this result nonetheless suggests strong site fidelity to this breeding ground.

Three photo-identified individuals from the Cape Verde Islands had been previously photographed on high-latitude feeding grounds off Bear Island, Norway, and Iceland. One Cape Verdean humpback was resighted in the Azores, possibly en route to the northern feeding grounds. These findings are consistent with the belief that the Cape Verde Islands represent a breeding ground for northeastern Atlantic humpback whales.

Tourism activities in the Cape Verde Islands are rapidly increasing. A balance is needed whereby conservation, whale watching guidelines, habitat preservation, and enforcement are fully enacted in order to provide protection to both this species and

its habitat. In addition, further research is required to clarify the importance of this small population and its breeding ground.

Key Words: humpback whale, *Megaptera novaeangliae*, Cape Verde Islands, breeding grounds, eastern North Atlantic, photo-identification

Introduction

Humpback whales (*Megaptera novaeangliae*) in the North Atlantic Ocean constitute one of the best-studied populations of large whales in the world. Since the 1970s, extensive photo-identification effort has yielded considerable information on abundance and migratory movements (Katona et al., 1979; Katona & Whitehead, 1981; Katona & Beard, 1990; Clapham & Mead, 1999; Smith et al., 1999). Genetic tagging has been used to determine stock structure as well as the whales' migratory destinations and fidelity to specific regions of the North Atlantic (Palsbøll et al., 1995, 1997; Larsen et al., 1996; Valsecchi et al., 1997; Berube et al., 2004).

It is clear from previous studies that humpback whales feed during the summer in a number of relatively discrete regions, including the Gulf of Maine, Newfoundland/Labrador, the Gulf of St. Lawrence, Greenland, Iceland, and Norway. Fidelity to these summer feeding areas is strong and is apparently maternally directed, with genetic analyses suggesting that the fidelity 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

have shown that some individuals from all of the identified high-latitude areas migrate long distances (in some instances more than 8,000 km) to common winter breeding grounds in the West Indies (Martin et al., 1984; Stevick et al., 1998, 1999a, 2003), where they mix spatially and genetically. The great majority of humpback whales in the North Atlantic appear to use the West Indies wintering areas, with the largest concentrations in the northern Antilles, especially on or near Silver Bank, Dominican Republic (Winn et al., 1975; Clapham & Mead, 1999; Smith et al., 1999; Clapham et al., 2005). Photographic matches of identified individual humpbacks were recently made between the southeastern Caribbean and Fyllas Bank off West Greenland (Stevick et al., 1999b), and between St. Vincent (southeastern Caribbean) and the Gulf of Maine (Robbins et al., 2006). A genetic match was also made between the southeastern Caribbean and Norway (Berube et al., 2004). Together, these matches suggest that at least some of the whales that winter in the southeastern West Indies have migratory habits similar to those whales found in the major breeding grounds of the northern Antilles.

During the 19th century, American open-boat whalers rarely reported killing humpbacks in the northern Antilles. Most of their whaling efforts were focused on portions of the southeastern Caribbean and the Cape Verde Islands. The large historical catches of humpbacks in the eastern North Atlantic (Norway and Cape Verde) may be responsible for this population's slow recovery (Ingebrigtsen, 1929; Kellogg, 1929; Mitchell & Reeves, 1983; Reeves et al., 2001, 2002; Reeves & Smith, 2002; Smith & Reeves, 2003).

In this paper, we report photographic resightings of identified humpback whales from the Cape Verde Islands to northern feeding grounds (Iceland and Bear Island, Norway) and along the migratory corridor, the Azores. A relatively high interannual return rate of humpbacks to Cape Verdean waters suggests strong site fidelity to this breeding ground. We also discuss the implications for this northeastern Atlantic breeding population of recent increases in on-the-water tourism activities in the Cape Verde Islands.

Materials and Methods

The Cape Verde Islands (CVI) are situated in the eastern North Atlantic between 14° 48'-17° 22' N and 22° 44'-25° 22' W, 460 to 830 km west of Senegal, West Africa. The ten islands and several islets are of volcanic origin, with steep shores arising from an ocean floor more than 3,000 m deep. Only the islands of Maio, Boavista, and Sal have a continental platform, while the northwestern

islands of São Vicente, Santa Luzia, Branco, and Raso have limited amounts of water less than 100 m deep surrounding them (Figure 1). Since 1990, most of the research effort has been in the eastern sector of the archipelago, focused near the islands of Sal, Boavista, and Maio.

These Cape Verdean waters are known for strong winter trade winds, rough seas, and sand storms, often making navigation around the islands difficult and hazardous as well as producing less than ideal conditions for mariners and whale researchers. These weather conditions help explain the low number of humpback whale fluke photographs and the limited amount of cetacean information from this region (Reiner et al., 1996; Hazevoet & Wenzel, 2000; Jann & Wenzel, 2001; Jann et al., 2002, 2003; Wenzel et al., 2004, 2005).

Data Collection

Marine mammal surveys in the CVI were conducted from February to May in 1990, 1991, 1995, and 1996 from a 5-m inflatable boat around the islands of Sal and Boavista (Reiner et al., 1996; Hazevoet & Wenzel, 2000). The research effort in 1999 (26 February to 8 April) was made from a 50-m steel-hulled motor ship; in 2000 (27 to 29 February, 30 March to 4 April) and 2001 (31 March to 2 May), from a 37-m schooner; and from 2002 to 2007, from a 20-m sailboat during March and April. Two simultaneous marine mammal surveys in the Cape Verde archipelago were conducted by sail boats during 2003 and 2006. During 2008 and 2009, all data were collected from a 12-m whale watching catamaran between mid-March and mid-May. More humpback fluke photographs were obtained in the 1999, 2002, 2003, and 2006 seasons than in previous years, largely because of the advantages associated with using larger vessels in the types of sea-state conditions which prevail in these waters. Several research cruises have been made in the western portion of the Cape Verde archipelago, with very little success in locating humpbacks in that region. For each cetacean sighting, the time, GPS position, group size and composition, and behaviour were noted. Fluke photographs, which are used to identify individual humpbacks from the unique pattern of pigmentation and scars on the ventral surface, were obtained with a 35-mm digital camera. Only those fluke photographs for which quality and individual distinctiveness was 3- or better were used in this analysis (Friday et al., 2000, 2008).

Photo Comparison

The *North Atlantic Humpback Whale Catalogue* (NAHWC) is the primary curator for humpback whale fluke photographs from throughout the North Atlantic Ocean. Photographs date from 1952

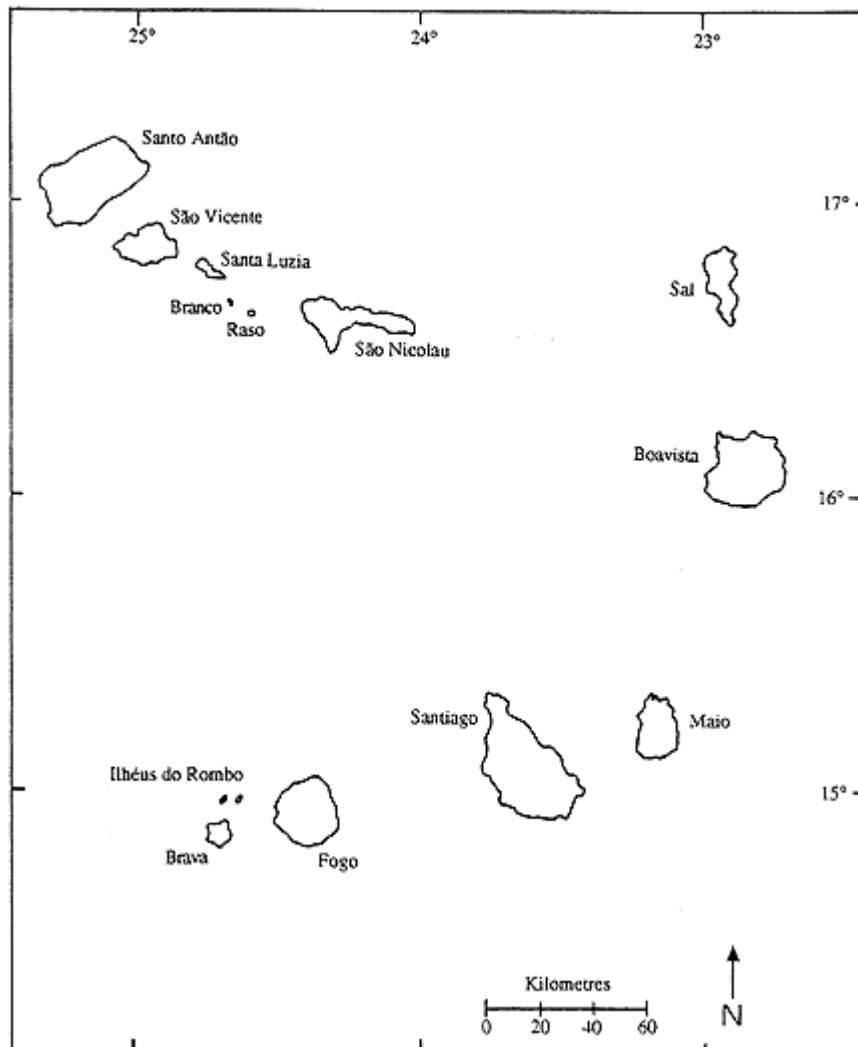


Figure 1. Map of the Cape Verde Islands

to 2009, though few fluke photographs are available from years prior to 1978. The *NAHWC* project is collaborative, and photographs have been submitted by more than 400 international 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. Recently, there has been an increase in the contribution of humpback fluke photos from the eastern North Atlantic, including the waters off Ireland, the Azores, and Iceland.

Three North Atlantic Ocean projects have involved the photo-identification of humpback whales: (1) *NAHWC*, (2) the Years Of the North Atlantic Humpback (*YONAH*) project, and (3) the *MOre* North Atlantic Humpbacks (*MONAH*)

project. The *YONAH* project was an extensive study of humpback whales in the North Atlantic conducted during 1992 and 1993. This photo-identification project was conducted in all of the known major northern feeding grounds and the breeding grounds of the West Indies (Smith et al., 1999). Due to logistical considerations, sampling intensity in Icelandic and Norwegian waters, while considerably greater than any previous effort, was less than that in the western North Atlantic feeding areas such as Greenland, eastern Canada, and the Gulf of Maine (Smith et al., 1999). *YONAH* did not include the waters of the CVI, the Celtic Sea, and other parts of the eastern North Atlantic.

The *MONAH* collection of biopsy samples and fluke photographs occurred during the winters

of 2004 and 2005 on Silver Bank, Dominican Republic, and during the summer months in the Gulf of Maine and on the Scotian Shelf, eastern Canada. The comparison of MONAH whale fluke photographs and the genetic analysis of biopsy samples are currently underway (Clapham et al., 2005; P. Palsbøll, pers. comm.).

All North Atlantic humpback fluke catalogues have been merged under the *NAHWC* (1952 to 2009). This includes photos from whale-watching enthusiasts, researchers, and dedicated and opportunistic platforms from across the North Atlantic. The *NAHWC* is maintained at Allied Whale, College of the Atlantic, 105 Eden Street, Bar Harbor, Maine 04609, USA (www.coa.edu/html/alliedwhale.htm).

CVI humpback fluke photographs were catalogued and compared to the *NAHWC* using methods described by Katona & Whitehead (1981), Katona & Beard (1990), and Smith et al. (1999).

Results – Photographic Analysis

A total of 88 individual humpback whales have been identified thus far in the CVI. There have been 20 resighted individuals. Twenty (22.7%) of the 88 individuals were recorded in the CVI in more than one year; these include 15 humpbacks recorded two different years, four humpbacks recorded in three different years, and one individual in four different years (Table 1). Unfortunately, years with strong winter trade winds (2000, 2001, 2005, and 2007) produced a low number of sightings, fewer acoustic recordings, and fewer humpback fluke photographs and resights (Tables 1 & 2).

One 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° 66' N, 27° 30' W, in July 1982 (Jann et al., 2002, 2003). A second individual, NAHWC #4810, photographed on 4 April 2004, off Boavista had previously been photographed off Bear Island, Norway, on 9 September 1984. The third whale, NAHWC #4820, was photographed on 4 April 2008 (Bay of Sal Rei, Boavista) and had last been observed and photographed on 10 July 1995 off Bear Island, Norway. A fourth individual, photographed in the Azores on 1 June 2006, matched an individual photographed in the CVI on 14 April 2009, NAHWC #4795. No additional photographic resightings of these four whales have been documented (Figures 2, 3, 4 & 5).

The frequency of Cape Verdean humpback photo-identification recapture within the same year was very low, with almost all individuals recaptured within a week of their initial sighting. One humpback was resighted 15 d apart and nearly 100 km away.

Discussion

Two spatially distinct tropical regions of the North Atlantic are known to have been traditionally used 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 (CVI). The sightings of mature females with newborn calves, recordings of humpback songs, and observations of competitive groups (related to mating; Clapham et al., 1992) have established that the waters around the CVI represent breeding and calving habitat during the boreal winter and spring (Hazevoet & Wenzel, 2000; Jann et al., 2003).

The photographic matches between the CVI and Iceland and Bear Island, Norway, are the first evidence of feeding ground destinations for humpback whales from the CVI. It seems likely that a photographic match also might be found among the islands of the eastern North Atlantic (Azores and Cape Verde) due to their proximity and potential migratory corridor, increased

Table 1. Number of years photographically captured

| | 1 y | 2 y | 3 y | 4 y | Total |
|-------------------|-----|-----|-----|-----|-------|
| Between 1990-2009 | 68 | 15 | 4 | 1 | 88 |
| Total | 68 | 30 | 12 | 4 | 114 |

Table 2. Humpback whales of the Cape Verde Islands

| Year | 1991 | 1995 | 1999 | 2000 | 2001 | 2002 | 2003 | 2004 | 2005 | 2006 | 2007 | 2008 | 2009 | Total |
|---|------|------|------|------|------|------|------|------|------|------|------|------|------|-------|
| n (Flukes obtained per year – CVI) | 2 | 1 | 21 | 0 | 1 | 15 | 19 | 12 | 2 | 22 | 0 | 9 | 10 | 114 |
| Resightings from previous CVI years | 0 | 0 | 0 | 0 | 0 | 0 | 7 | 3 | 0 | 8 | 0 | 4 | 3 | 25 |
| # of NEW identified individuals | 2 | 1 | 21 | 0 | 1 | 15 | 12 | 9 | 2 | 14 | 0 | 4 | 7 | 88 |
| Humpbacks matched to portions of the <i>NAHWC</i> | -- | -- | 1 | -- | -- | -- | -- | 1 | -- | -- | -- | 1 | 1 | 4 |

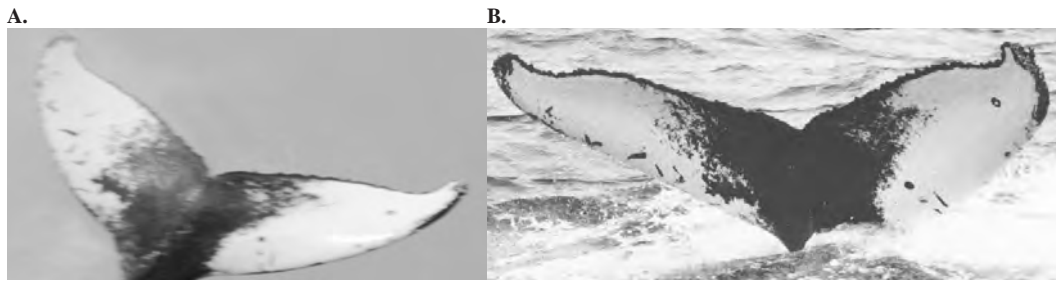


Figure 2. A: HWC #4820 observed 4 April 2008, Sal Rei, Boavista, CVI; B: 10 July 1995 off Bear Island, Norway

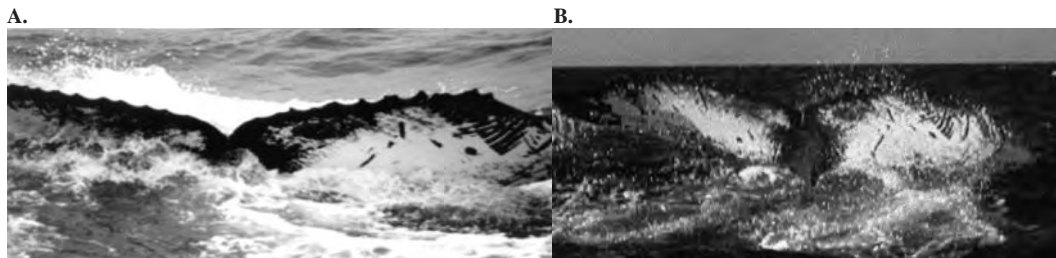


Figure 3. Fluke photographs of NAHWC #4504 from the Denmark Strait west of Iceland at 65° 40' N, 27° 30' W in July of 1982 and again photographed on 10 March 1999 in the Bay of Sal Rei, Boavista, CVI, at 16° 02' N, 23° 02' W

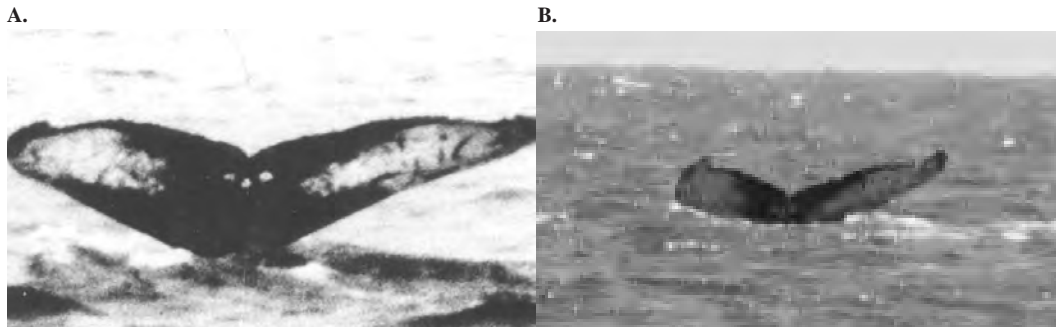


Figure 4. Fluke photographs of NAHWC #4810 from Bear Island, Norway (in 1984) and Sal Rei, Boavista, CVI (in March 2004) (Wenzel *et al.*, 2005)

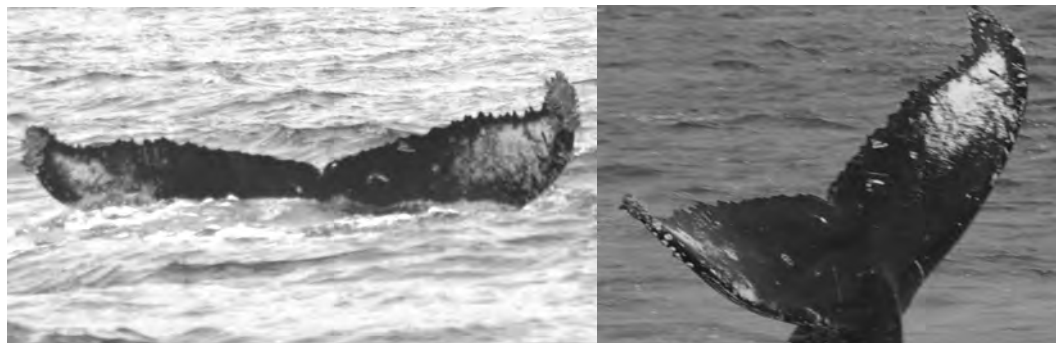


Figure 5. Fluke photographs of NAHWC #4795 from the Azores (1 June 2006) and Sal Rei, Boavista, CVI (14 April 2009)

whale watching, and marine mammal research activities.

Humpbacks photo-identified and biopsied off Iceland (Martin et al., 1984; Smith et al., 1999; Stevick et al., 2003) and Norway (Stevick et al., 2003; Berube et al., 2004) have also been observed in the West Indies but at a significantly lower expected match rate (Brooks et al., 2009) when compared to the entire *NAHWC* and the genetic catalogue of identified individuals (P. Palsbøll, pers. comm.). These findings are consistent with the hypothesis that there is overlap on the eastern North Atlantic feeding grounds between whales which migrate to the West Indies and those which migrate to the CVI. Significant is the failure to match any of the photo-identified animals from the CVI with those on western North Atlantic feeding grounds or to the West Indies breeding ground, despite the huge sample size from both of these regions. This is consistent with the hypothesis that humpbacks from the CVI constitute a distinct breeding population that feeds preferentially or exclusively in northeastern Atlantic feeding areas. Such a model is supported by the existence of nuclear DNA differences between humpbacks from the eastern and western North Atlantic (Larsen et al., 1996; Palsbøll et al., 1995, 1997; Valsecchi et al., 1997; Berube et al., 2009).

The interannual resighting rate of 22.7% is high relative to that observed on the major breeding grounds of the West Indies (e.g., Silver Bank, Dominican Republic) where thousands of whales are present at one time (Mattila et al., 1987) or Hawaii (Cerchio, 1998), but not as high as Revillagigedos (Pacific Ocean, west coast of Mexico) (Urban et al., 1999). It may well be that humpback whales also return at similar rates to major breeding grounds like Silver Bank but are simply lost in the crowd and not rephotographed.

Nonetheless, the CVI population is clearly small; individuals demonstrate strong fidelity to this breeding area, therefore the probability of an individual being resighted is high. Either way, the CVI appear to represent an important breeding habitat for some eastern North Atlantic humpback whales.

The *NAHWC* has grown enormously over the last 30+ y, and it is difficult to interpret effort by region and/or by year. However, the low match rate of four whales between the CVI and the entire *NAHWC* strongly suggests that most humpbacks that winter in the CVI use one or more eastern North Atlantic high-latitude summer feeding areas from where less sighting effort and fewer fluke photographs currently exist. Considering the limited photo-identification effort in the eastern North Atlantic over the last 30 y, it is not particularly surprising that there are only four matches to

the CVI, or that there is a 20-y interval between some resightings and photographs. It is surprising that none of the humpback fluke photographs collected under YONAH matched any of the Cape Verdean humpbacks. However, this should not be construed as providing an actual estimate for the eastern North Atlantic humpback population.

Conclusions

Over the years, several authors have suggested the existence of two or more breeding stocks of humpback whales in the North Atlantic: one western and another on the eastern margin of the North Atlantic basin. The high-latitude range of these putative breeding stocks was separated roughly at Cape Farewell, Greenland (Ingebrigtsen, 1929; Kellogg, 1929). However, the degree of separation, overlap, and limits of the two proposed stocks are often discussed and questioned (Mitchell & Reeves, 1983; Larsen et al., 1996; Palsbøll et al., 1995, 1997; Valsecchi et al., 1997; Smith et al., 1999; Stevick et al., 1999a). It is believed that some humpbacks may not migrate far from this region in winter (Ingebrigtsen, 1929; Christensen et al., 1992) and the reports of singing humpbacks year-round in the northeast Atlantic potentially supports this (Charif et al., 2001). In the northeast Atlantic, winter whaling records reported catches of adult female humpbacks carrying full-term fetuses, suggesting a nearby calving region in addition to those currently known in the tropical Cape Verde Islands and West Indies (Ingebrigtsen, 1929). In actuality, there might be more than two humpback whale stocks in the North Atlantic (Punt et al., 2006, 2007).

Research efforts in the CVI have been modest in comparison to those in the West Indies and many other parts of the western North Atlantic. These long-distance matches have stimulated an increased photo-identification effort at sites along the likely eastern North Atlantic migratory corridor (e.g., the Azores, Canary Islands, Madeira, Ireland) and on potential eastern North Atlantic feeding grounds—for example, Celtic Sea (Strietman et al., 2008), Mediterranean Sea (Frantzis et al., 2004), North Sea (Camphuysen, 2007), and Iceland (E. Wald, pers. comm.). It should also provide impetus to intensify efforts to obtain biopsies and additional humpback fluke photographs in Cape Verdean waters for comparative genetic and photo analyses. From a local perspective, it is desirable to improve our understanding of habitat use patterns, residency times, and site fidelity. Most important is to determine the growth in population within the Cape Verde archipelago, and elsewhere in the eastern North

Atlantic (Sigurjonsson & Gunnlaugsson, 1990; Smith et al., 1999).

The high resighting rate on the CVI humpback breeding ground suggests a low abundance of humpbacks (Tables 1 & 2). However, research efforts for this CVI humpback population have been problematic. Wind, weather, and funding are providing limitations to a long-term dedicated effort. It is plausible that the apparent low abundance in this breeding area indicates a slow recovery of this eastern North Atlantic humpback breeding population (Ingebrigtsen, 1929; Kellogg, 1929; Reeves et al., 2001, 2002; Reeves & Smith, 2002; Smith & Reeves, 2003; Punt et al., 2006, 2007). However, it is also possible that the CVI is today only a minor breeding ground for eastern North Atlantic animals, which migrate to some other, currently unknown, wintering area.

Analysis of 19th-century whaling logs indicates that the CVI were more important for humpbacks as a historical breeding ground than it seems to be today (Reeves et al., 2002; Reeves & Smith, 2002); and that there is a major disparity between the numbers of whales seen in the CVI and in the eastern North Atlantic feeding grounds. Put simply, there are too many whales in the high latitudes of the central and eastern North Atlantic to account for the number of whales observed in the CVI. This implies that most eastern North Atlantic humpbacks are going somewhere else to winter—not only to the CVI.

During this Cape Verde project, the probability of capture has also varied due to differences in sampling effort and survey platforms as is the case in many studies of free-ranging cetaceans (Hammond, 1986, 1990; Hammond et al., 1990).

During the last two decades, tourism has significantly increased around the CVI. The rise in tourism has also brought about an increase in hotel construction and in large ships delivering food, cement, construction materials, and amenities for these temporary residents in the CVI. Hotel construction along the sandy beaches has produced pollution as well such as plastic bags, construction noise, packing materials, and debris washing into the protective bays. During the early 1990s, humpbacks were regularly observed off Santa Maria, Sal, CVI. Unfortunately, coinciding with the dramatic increase of tourist maritime activities over the last 20 y, there have been no recent humpback sightings near Santa Maria (P. James, pers. comm.). This increase in tourism has also generated a loss of sea turtle nesting habitat as hotel lights and tourists ravaging the beaches with four-wheel ATVs have not been sea turtle friendly. There has also been an increase in on-the-water recreational activities such as wind surfers and jet skis. A balance is needed whereby conservation, whale watching guidelines,

habitat preservation, and enforcement are fully enacted in order to provide protection to both cetaceans and marine habitat.

Acknowledgments

We wish to acknowledge the Captains and crews of the ships *Iceni Queen*, *Holland*, *Corvette*, and *Sodade*, especially Luis and Carlos Albrecht, Captain Luis A. Lopez, Captain Kees Roll, Captain Robert Mannink, Sonia Elsy Merino, 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 research cruises and the photograph matching at the College of the Atlantic was through the International Whaling Commission, Whale Dolphin Conservation Society (UK), and Cetacean Society International (USA). A number of friends, colleagues, and reviewers greatly assisted us with earlier drafts of this manuscript. Special thanks to Fred Serchuk, Richard Merrick, Richard Pace, Tim Smith, Phil Clapham, Per Palsbøll, M. Berube, R. Reeves, Zelinda Evora, Peter Stevick, Durant Hembree, Jon Lien, Elke Wald, Virginia Brook, Gale McCullough, and Anthony R. Martin as well as our anonymous reviewers for their helpful comments. Special thanks to Vanda Monteiro and Óscar Melício, Instituto Nacional de Desenvolvimento das Pescas (INDP), Republic of Cape Verde, for research permits and support within Cape Verdean waters. We want to dedicate this paper to the late Rebecca Clark, who helped greatly in the search for Cape Verde humpbacks but did not live to see the results of her efforts.

Literature Cited

- Berube, M., Øien, N., Robbins, J., Vikingsson, G., Jorgensen, H., Sellas, A., et al. (2009). It is not what you know, but what you don't know: Genetic analyses reveal a small unknown eastern North Atlantic breeding population of humpback whales. *Abstract of the 18th Biennial Conference on the Biology of Marine Mammals*, Quebec, Canada.
- Berube, M., Rew, M. B., Cole, T., Swartz, S. L., Zolman, E., Øien, N., et al. (2004). Genetic identification of an individual humpback whale between the eastern Caribbean and the Norwegian Sea. *Marine Mammal Science*, 20(3), 657-663.
- Brooks, V., Allen, J., Cecchetti, A., Sewall, R., Stevick, P. T., Vikingsson, G., et al. (2009). Migration rate of humpback whales feeding off Iceland to the breeding and calving grounds of the West Indies. *Abstract of the 18th Biennial Conference on the Biology of Marine Mammals*, Quebec, Canada.
- Camphuysen, C. J. (2007). Foraging humpback whale (*Megaptera novaeangliae*) in the Marsdiep area (Wadden

- Sea), May 2007 and a review of sightings and strandings in the southern North Sea, 2003-2007. *Lutra*, 50(1), 31-42.
- Cerchio, S. (1998). Estimates of humpback whale abundance off Kauai, 1989-1993: Evaluation biases associated with sampling the Hawaiian Islands breeding assemblage. *Marine Ecology Progress Series*, 175, 23-34.
- Charif, R. A., Clapham, P. J., & Clark, C. W. (2001). Acoustic detections of singing humpback whales in deep waters off the British Isles. *Marine Mammal Science*, 17(4), 751-768.
- Christensen, I., Haug, T., & Øien, N. (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(3), 341-355.
- Clapham, P. J., & Mead, J. G. (1999). *Megaptera novaeangliae*. *Mammalian Species*, (604), 1-9. Published by the American Society of Mammalogists.
- Clapham, P. J., Palsbøll, P. J., Mattila, D. K., & Vasquez, O. (1992). Composition and dynamics of humpback whale competitive groups in the West Indies. *Behaviour*, 122(3-4), 182-194.
- Clapham, P. J., Barco, S., Jann, G., Martinez, A., Mattila, D. K., Nelson, M., et al. (2005). *Update on a new assessment of North Atlantic humpback whales* (Paper SC/57/AWMP9). Cambridge, UK: Scientific Committee of the International Whaling Commission.
- Frantzis, A., Nikolaou, O., Bompar, J. M., & Cammedda, A. (2004). Humpback whale (*Megaptera novaeangliae*) occurrence in the Mediterranean Sea. *Journal of Cetacean Research and Management*, 6(1), 25-28.
- Friday, N., Smith, T. D., Stevick P. T., & Allen, J. (2000). Measurement of photographic quality and individual distinctiveness for the photographic identification of humpback whale (*Megaptera novaeangliae*). *Marine Mammal Science*, 16(2), 355-374.
- Friday, N., Smith, T. D., Stevick, P. T., Allen, J., & Fernald, T. (2008). Balancing bias and precision in capture-recapture estimates of abundance. *Marine Mammal Science*, 24(2), 253-275.
- Hammond, P. S. (1986). Estimating the size of naturally marked whale populations using capture-recapture techniques (SC/37/PS27). *Report of the International Whaling Commission* (Special Issue 8), 253-282.
- Hammond, P. S. (1990). Heterogeneity in the Gulf of Maine? Estimating humpback whale population size when capture probabilities are not equal. *Report of the International Whaling Commission* (Special Issue 12), 135-139.
- Hammond, P. S., Mizroch, S. A., & Donavon, G. P. (Eds.). (1990). Individual recognition of cetaceans: Use of photo-identification and other techniques to estimate population parameters. *Report of the International Whaling Commission* (Special Issue 12), 440 pp.
- Hazevoet, C. J., & 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). *Contributions to Zoology*, 69(3), 197-211.
- Ingebrigtsen, A. (1929). Whales caught in the North Atlantic and other seas. *Rapports et Procès-verbaux des reunions, Conseil Permanent International pour l'Exploration de la Mer*, 56(2), 1-26.
- Jann, B., & Wenzel, F. W. (2001). *Humpback whales in the Cape Verde Islands* (Paper SC/53/NAH19). Presented to the Scientific Committee of the International Whaling Commission. (Unpublished report). 7 pp.
- Jann, B., Wenzel, F. W., & Reeves, R. R. (2002). Humpback whales (*Megaptera novaeangliae*, Borowski 1781 Cetacea, Mysticeti) of the Cape Verde Islands: Past and present. *Proceedings of the Flora and Fauna Conference of the Atlantic Islands*, Praia, Cape Verde Islands.
- Jann, B., Allen, J., Carrillo, M., Hanquet, S., Katona, S. K., Martin, A. R., et al. (2003). Migration of a humpback whale between the Cape Verde Islands and Iceland. *Journal of Cetacean Research and Management*, 5(2), 125-129.
- Katona, S. K., & Beard, J. A. (1990). Population size, migrations and feeding aggregations of the humpback whale (*Megaptera novaeangliae*) in the western North Atlantic Ocean. *Report of the International Whaling Commission* (Special Issue 12), 295-305.
- Katona, S. K., & Whitehead, H. (1981). Identifying humpback whales using their natural markings. *Polar Record*, 20, 439-444.
- Katona, S. K., Baxter, B., Brazier, O., Kraus, S., Perkins J., & Whitehead, H. (1979). Identification of humpback whales by fluke photography. In H. E. Winn & B. L. Olla (Eds.), *Behavior of marine mammals* (Vol. 3, pp. 33-44). New York: Plenum Press.
- Kellogg, R. (1929). What is known of the migrations of some of the whalebone whales. In *Annual report of the Board of Regents 1928* (pp. 467-494). Washington, DC: Smithsonian Institution.
- Larsen, A. H., Sigurjonsson, J., Øien, N., Vikingsson, G., & 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. *Proceedings of the Royal Society of London, Series B*, 263, 1611-1618.
- Martin, A. R., Katona, S. K., Mattila, D. K., Hembree, D., & Waters, T. D. (1984). Migration of humpback whales between the Caribbean and Iceland. *Journal of Mammalogy*, 65, 330-333.
- Mattila, D. K., Guinee, L. N., & Mayo, C. A. (1987). Humpback whale songs on the North Atlantic feeding grounds. *Journal of Mammalogy*, 68, 880-883.
- Mattila, D. K., Clapham, P. J., Vasquez, O., & Bowman, R. S. (1994). Occurrence, population composition, and habitat use of humpback whales in Samana Bay, Dominican Republic. *Canadian Journal of Zoology*, 72(11), 1898-1907.
- Mitchell, E., & Reeves, R. R. (1983). Catch history, abundance and present status of Northwest Atlantic humpback whales. *Report of the International Whaling Commission* (Special Issue 5), 153-212.

- Palsbøll, P. J., Allen, J., Berube, M., Clapham, J., Feddersen, T. P., Hammond, P. S., et al. (1997). Genetic tagging of humpback whales. *Nature*, 388, 767-769.
- Palsbøll, P. J., Clapham, P. J., Mattila, D. K., Larsen, F., Sears, R., Siegmund, H. R., et al. (1995). Distribution of mtDNA haplotypes in North Atlantic humpback whales: The influence of behaviour on population structure. *Marine Ecology Progress Series*, 116, 1-10.
- Punt, A. E., Friday, N. A., & Smith, T. D. (2006). Reconciling data on the trends and abundance of North Atlantic humpback whales within a population modelling framework. *Journal of Cetacean Research and Management*, 8(2), 145-159.
- Punt, A. E., Friday, N. A., & Smith, T. D. (2007). Reconciling historical catches and current abundance of North Atlantic humpback whales. *Journal of Cetacean Research and Management*, 9(2), 145-160.
- Reeves, R. R., & Smith, T. D. (2002). Historical catches of humpback whales in the North Atlantic Ocean: An overview of sources. *Journal of Cetacean Research and Management*, 4(3), 219-234.
- Reeves, R. R., Clapham, P. C., & Wetmore, S. E. (2002). Humpback whale (*Megaptera novaeangliae*) occurrence near the Cape Verde Islands based on American 19th century whaling records. *Journal of Cetacean Research and Management*, 4(3), 235-253.
- Reeves, R. R., Swartz, S. L., Wetmore, S. E., & Clapham, P. C. (2001). Historical occurrence and distribution of humpback whales in the eastern and southern Caribbean Sea based on data from American whaling logbooks. *Journal of Cetacean Research and Management*, 3(2), 117-129.
- Reiner, F., Dos Santos, M. E., & Wenzel, F. W. (1996). Cetaceans of the Cape Verde archipelago. *Marine Mammal Science*, 12(3), 434-443.
- Robbins, J., Allen, J. M., Clapham, P. J., & Mattila, D. K. (2006). Stock identity of a humpback whale taken in a southeastern Caribbean hunt. *Journal of Cetacean Research and Management*, 8(1), 29-31.
- Sigurjonsson, J., & Gunnlaugsson, T. (1990). Recent trends in abundance of blue (*Balaenoptera musculus*) and humpback whale (*Megaptera novaeangliae*) off west and southwest Iceland, with a note on occurrence of other cetacean species. *Report of the International Whaling Commission*, 40, 537-552.
- Smith, T. D., & Reeves, R. R. (2003). Estimating American 19th century catches of humpback whales in the West Indies and Cape Verde Islands. *Caribbean Journal of Science*, 39, 286-297.
- Smith, T. D., Allen, J., Clapham, P. J., Hammond, P. S., Katona, S. K., Larsen, F., et al. (1999). An ocean basin-wide mark-recapture study of the North Atlantic humpback whale (*Megaptera novaeangliae*). *Marine Mammal Science*, 15(1), 1-32.
- Stevick, P. T., Carlson, C. A., & Balcomb, K. C. (1999b). A note on migratory destinations of humpback whales from the eastern Caribbean. *Journal of Cetacean Research and Management*, 1(2), 251-254.
- Stevick, P. T., Øien, N., & Mattila, D. K. (1998). Migration of a humpback whale between Norway and the West Indies. *Marine Mammal Science*, 14(1), 162-166.
- Stevick, P. T., Øien, N., & Mattila, D. K. (1999a). Migratory destinations for humpback whales from Norwegian and adjacent waters: Evidence for stock identity. *Journal of Cetacean Research and Management*, 1(2), 147-152.
- Stevick, P. T., Allen, J., Berube, M., Clapham, P. J., Katona, S. K., Larsen, F., et al. (2003). Segregation of migration by feeding ground origin in North Atlantic humpback whales (*Megaptera novaeangliae*). *Journal of Zoology, London*, 259, 231-237.
- Strietman, W. J., Whooley, P., Ryan, C., Camphuysen, K., Seton, R., Berrow, S., et al. (2008). *First international humpback whale match in European waters*. Twenty-Second Annual Conference of the European Cetacean Society, Egmond aan Zee, The Netherlands.
- Urban, J. R., Alvarez, C. F., Salinas, M. Z., Jacobsen, J., Balcomb, K. C., Jaramillo, A. L., et al. (1999). Population size of humpback whale, *Megaptera novaeangliae*, in the waters off the Pacific coast of Mexico. *Fishery Bulletin*, 97, 1017-1024.
- Valsecchi, E., Palsbøll, P., Hale, P., Glockner-Ferrari, D., Ferrari, M., Clapham, P. J., et al. (1997). Microsatellite genetic distances between oceanic populations of the humpback whale (*Megaptera novaeangliae*). *Molecular Biology and Evolution*, 14(4), 355-362. Retrieved 25 November 2009 from <http://mbe.oxfordjournals.org/cgi/content/abstract/14/4/355>.
- Wenzel, F. W., Allen, J., Berrow, S., Jann, B., & Seton, R. (2005). Humpbacks whales (*Megaptera novaeangliae*) of the Cape Verde Islands. *Abstract of the 16th Biennial Conference on the Biology of Marine Mammals*, San Diego, CA.
- Wenzel, F. W., Allen, J., Berrow, S., Jann, B., Lien, J., Martin, A. R., et al. (2004). Humpback whales (*Megaptera novaeangliae*) of the Cape Verde Islands. Fifth Symposium on Fauna & Flora of Atlantic Islands, Dublin, Ireland. (Published September 2006).
- Winn, H. E., Edel, R. K., & Taruski, A. G. (1975). Population estimate of the humpback whale (*Megaptera novaeangliae*) in the West Indies by visual and acoustic techniques. *Journal of the Fisheries Research Board of Canada*, 32(4), 499-506.