Humpback Whales (*Megaptera novaeangliae*) in the Cape Verde Islands: Migratory Patterns, Resightings, and Abundance

Frederick W. Wenzel, Fredrik Broms, Pedro López-Suárez, Katia Lopes, Nadia Veiga, Kate Yeoman, Manuel Simão Delgado Rodrigues, Judy Allen, Thomas W. Fernald, Peter T. Stevick, Lindsey Jones, Beatrice Jann, Laurent Bouveret, Conor Ryan, Simon Berrow, And Peter Corkeron and Peter Corkeron

¹NOAA, National Marine Fisheries Service, Northeast Fisheries Science Center,
166 Water Street, Woods Hole, MA 02543, USA
Frederick.Wenzel@noaa.gov
²North Norwegian Humpback Whale Catalogue (NNHWC), Straumsvegen 238, N-9105 Kvaløya, Norway
³Bios, CV, Sal-Rei, Boa Vista, Republic of Cape Verde
¹Naturalia, Sal Rei, Boa Vista, Republic of Cape Verde
²College of the Atlantic, 105 Eden Street, Bar Harbor, ME 04856, USA
°Swiss Whale Society, Via Inera, CH-6999 Astano, Switzerland
²Observatoire des Mammifères Marins de l'Archipel Guadeloupéen, Route Hégésippe Legitimus,
Beauport, 97117 Port-Louis, Guadeloupe, FWI

*Song of the Whale, Marine Conservation Research, 94 High Street, Kelvedon, Essex, CO5 9AA, UK
*Marine and Freshwater Research Centre, Galway-Mayo Institute of Technology, Dublin Road, Galway, Ireland
"Irish Whale and Dolphin Group, Merchants Quay, Kilrush County Clare, Ireland
"Anderson Cabot Center for Ocean Life, New England Aquarium, Central Wharf, Boston, MA 02110, USA

Abstract

Effective conservation of the endangered North Atlantic humpback whale (Megaptera novaeangliae) which breeds in the eastern North Atlantic around the Cape Verde Islands off West Africa requires information about their spatio-temporal distribution, population size, and migratory patterns. Understanding temporal distribution is particularly important as annually only a portion of this population migrates between high-latitude summer feeding grounds and their breeding grounds. During the winter/spring months between 1990 and 2018, we conducted cetacean surveys targeting humpback whales. Survey periods varied from 30 to 90 days in duration. Collectively, we obtained fluke photographs from 267 individually recognizable humpback whales from this region. These fluke photographs have been compared and included in the North Atlantic Humpback Whale Catalogue, which has nearly 11,000 individual flukes photographed from throughout the North Atlantic. Photo-identified individuals from the Cape Verde Islands population have been previously photographed/recaptured on high-latitude feeding grounds in northern Norway (including the Barents Sea and Svalbard archipelago), Iceland, Azores, Tenerife, Canary Islands, and Guadeloupe (southeast Caribbean). Those whales

resighted off Azores and the Canary Islands were most often observed in May/June and were presumably en route to their northern feeding grounds. The largest number of recaptures from high-latitude feeding grounds were 44 individual humpbacks (44/267 = 16.4%) identified in both Cape Verdean and Norwegian waters. Twelve humpbacks (12/267 = 4.5%) were identified in the Cape Verde Islands and Iceland. Based on photo-identification of humpbacks in the Cape Verde Islands, we report a high interannual resighting rate with 131 whales observed in more than one year (131/267 = 49.1%). While this is partly due to high probability of detection in a small population, these results nonetheless also suggest strong site fidelity to this breeding ground. The estimated total number of individual whales occurring in this eastern North Atlantic breeding area between 2010 and 2018 was 272 (SE 10).

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

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 efforts have yielded substantial information on the abundance and migratory movements of this species (Katona et al., 1979; Katona & Whitehead, 1981; Katona & Beard, 1990; Clapham & Mead, 1999; Smith et al., 1999). Genetic tagging has also been used to determine humpback whale migratory destinations, stock identity, and fidelity to specific regions of the North Atlantic (Palsbøll et al., 1995, 1997; Larsen et al., 1996; Valsecchi et al., 1997; Bérubé et al., 2004; Robbins et al., 2006).

North Atlantic 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, including Svalbard. 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 feeding grounds, both photo-identification and genotyping have demonstrated that some individuals from all of the identified high-latitude areas migrate long distances to the recognized major winter breeding grounds on Silver Bank, Dominican Republic, where it is assumed that this spatial overlap corresponds to genetic mixing (Winn et al., 1975; Martin et al., 1984; Clapham et al., 1992, 2005; Stevick et al., 1998, 1999a, 1999b, 2003; Clapham & Mead, 1999; Smith et al., 1999). The only other known breeding area for North Atlantic humpbacks is a smaller humpback population utilizing the southeastern Caribbean in the waters near and around the French island of Guadeloupe (Stevick et al., 2016, 2018).

Photographic sighting history and migratory patterns are reported in this article, and an updated population estimate of identified humpbacks from the Cape Verde Islands is provided. The population of humpbacks breeding in the Cape Verde Islands likely represent the remnants of a historically larger population breeding around the Cape Verde Islands and off northwestern Africa (Reeves et al., 2002). A recent review of the worldwide status of humpback whales (Bettridge et al., 2015) determined that this Cape Verde population comprises a "Distinct Population Segment" (DPS) under the U.S. Endangered Species Act. The DPS designation was based upon genetic evidence that suggested a second breeding ground occupied by humpback whales that feed primarily off Norway and Iceland. Loss of this DPS unit would result in a loss of this unique breeding population as well as a significant number of whales that feed in Iceland and Norway (Bettridge et al., 2015). Our primary objective is to better understand

how the Cape Verde humpbacks are connected to the other known North Atlantic breeding areas. Recent research discoveries have identified some exchange between both the Cape Verde Islands and the Guadeloupe breeding grounds (Stevick et al., 2016, 2018).

Methods

The Cape Verde Islands (CVI) are situated in the eastern North Atlantic between 14° 48' to 17° 22' N and 22° 44' to 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 shallow areas less than 100 m deep surrounding them (Figure 1). Since 1990, most cetacean research effort has been in the eastern sector of the archipelago, focused near the islands of Maio, Boavista, and Sal.

The Cape Verdean waters are known to experience a harmattan season, which is a very dry, dusty easterly or northeasterly wind from the West African coast, occurring from December to mid/late March. This often makes maritime navigation around the islands difficult and hazardous as well as produces less than ideal conditions for mariners and whale researchers. These weather conditions

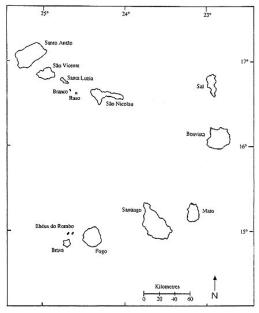


Figure 1. Map of the Cape Verde Islands (CVI) (Republic of Cape Verde)

may help explain the low number of humpback whale sightings and fluke photographs, and the limited amount of cetacean information from this region (Reiner et al., 1996; Hazevoet & Wenzel, 2000; Jann et al., 2003; Wenzel et al., 2009; Berrow et al., 2015a, 2015b).

Data Collection

Marine mammal surveys were conducted during the winter/spring months (January to June) between 1990 and 2018. Surveys varied from 30 to 90 days in duration (see Reiner et al., 1996; Hazevoet & Wenzel, 2000; Jann et al., 2003; Wenzel et al., 2009). Two simultaneous marine mammal surveys occurred in the Cape Verde archipelago via sailing vessels during 2003 and 2006. Ryan et al. (2013a, 2014) conducted small (5 m) boat research, including biopsy and photo-identification efforts, during the 2011-2012 seasons. Since 2008, most data were collected from whale-watching vessels from early March to late May. Additional research has been conducted around the Cape Verde archipelago focusing on Southern Hemisphere humpback whales that may breed there during the austral breeding season (Hazevoet et al., 2011; Berrow et al., 2015a, 2015b; Ryan et al., 2019). However, in this article, we are only reporting on humpbacks found during the boreal breeding season (January to June).

In recent years, more humpback sightings and fluke photographs were obtained due to increased effort with larger vessels offering whale-watching activities in Sal Rei and Boa Vista, as well as via citizen science from 2010 to 2018. Several research excursions were conducted 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 behavior were noted. Fluke photographs—used to identify individual humpbacks from the unique pattern of pigmentation and scars on the ventral surface-were obtained with a 35-mm DSLR camera. Fluke photographs were graded for photo quality and individual distinctiveness (1 – Excellent, 2 – Good, 3 – Fair, and 3- – Poor photo quality and no individual distinctiveness). Only fluke photographs graded better than 3- were used in this analysis (Friday et al., 2006, 2008).

Photo Comparison

The North Atlantic Humpback Whale Catalogue (NAHWC) is the primary repository for humpback whale fluke photographs from throughout the North Atlantic. Photographs date from 1976 to the present. The NAHWC is collaborative, and photographs have been submitted by more than 700 international contributors. Fluke photographs were most often obtained opportunistically, so temporal and spatial

coverage is highly variable. Most photographs were obtained from the western North Atlantic feeding grounds. Recently, there has been a significant increase in the collection of humpback fluke photos from the eastern North Atlantic, including the waters off Norway, Ireland, Azores, and Iceland, and these are compared/merged in the NAHWC.

Most photographic data came from two largescale North Atlantic Ocean projects involving the photo-identification of humpback whales: (1) the Years Of the North Atlantic Humpback (YONAH) project (1992 and 1993) and (2) the More North Atlantic Humpbacks (MONAH) project (2004-2005). The YONAH project was an extensive study of North Atlantic humpback whales in all known major northern feeding grounds and the breeding grounds of the Dominican Republic (Smith et al., 1999). The YONAH project did not include the waters of the CVI, Azores, or other parts of the eastern North Atlantic. The MONAH project focused on Silver Bank, Dominican Republic, and Gulf of Maine populations. All aforementioned North Atlantic humpback fluke collections have been merged under the NAHWC. The NAHWC contains approximately 11,000 individual fluke photographs from the entire 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). Humpback whales are uniquely identifiable based primarily on the ventral side of their flukes (Katona & Whitehead, 1981). Identification can sometimes be augmented by other features such as dorsal fin shape, scars, and genetic data (Smith et al., 1999).

The probability of capture/recapture frequently 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). CVI humpback fluke photographs have all been compared and catalogued within the NAHWC using methods described by Katona & Whitehead (1981), Katona & Beard (1990), and Smith et al. (1999).

Abundance Estimation

A Jolly-Seber open population model was fit to the data from CVI using *Rcapture*, Version 1.4-2 (Rivest & Baillargeon, 2014), using *R*, Version 3.5.3 (R Core Team, 2019), to estimate abundance from the photo-identification mark-recapture. Prior to 2010, there was less effort, and fewer whales were photo-identified annually (Tables 1 & 2), so only the non-calf data collected during 2010 to 2018 were used to estimate the abundance of non-calf humpback whales. Because there were too few individual whales that were identified to sex, the abundance analyses were conducted on the pooled dataset. Note that not all parameters

Table 1. From 1990 to 2018, the number of individual humpback whales (*Megaptera novaeangliae*) identified per year in the Cape Verde Islands (CVI)

Inter-annual observations	1 year	2 years	3 years	4 years	5 years	6 years	7 years	8 years	9 years	10 years	11 years	Total
Number of individuals	136	52	27	22	12	6	4	5	2	0	1	267

Table 2. Inter-annual recapture history of individual CVI humpbacks (via fluke photographs)

Years	1991	1995	1999	2000	2001	2002	2003	2004	2005	2006	2007	2008	2009	2010	2011	2012	2013	2014	2015	2016	2017	2018	Summary
No. of individual flukes obtained	2	1	21	0	1	15	19	15	2	16	0	9	10	33	41	45	63	57	59	58	60	69	596
No. of resightings to previous years	0	0	0	0	0	0	7	3	1	7	0	4	3	16	22	25	32	40	35	46	48	40	329
NEW individuals	2	1	21	0	1	15	12	12	1	9	0	5	7	17	19	20	31	17	24	12	12	29	267

for all years can be estimated using Joly-Seber modeling (Rivest & Baillargeon, 2014), so the estimated parameters for the first and final year of data have no estimates.

Assumptions of the log-linear form of the Jolly-Seber open population model implemented in *Rcapture* are those of the standard Jolly-Seber model (Rivest & Baillargeon, 2014). The main assumptions (Williams et al., 2002) are as follow:

- Individuals retain their individual identifiers through the sampling period; these are not overlooked, and identifiers are recognized correctly.
- Sampling periods are (relatively) instantaneous.
- Fates of all individuals with respect to capture and survival is independent of all other individuals.
- Every individual whale, whether it is identifiable or not, has the same probability of being resighted and the same probability of survival between sampling periods.
- Figures were produced using the 'ggplot2' package (Wickham, 2016).

Results

Photo-Identifications

There are 1,038 fluke photo-identified sighting records logged in the CVI database (based solely on fluke photographs) from 1990 to 2018 that were ranked as 3 or better in accordance with the photo-quality guidelines and determinations

by Friday et al. (2006, 2008). These records identify 267 individual humpback whales (as of 1 January 2019) on this breeding ground. This includes 27 males whose sex determination was based on one or more of the following methods: whale identified as a singer, genetic verification, photograph of genital area, and identified as the primary escort of a female with newborn calf. Thirty-two females were identified with the determination based on one of more of the following methods: observation of a whale with a newborn calf, genital photograph, and genetic verification; and there were 208 individuals whose sex is unknown (see Ryan et al., 2013a, 2013b, 2014). Of the 267, 131 (49%) were photographed in more than one year. A recent count of the minimum number of whales identified for any one year on this breeding ground was 69 (2018; based on fluke photographs) and does not include newborn calves.

Calf flukes and ½ fluke photos were excluded unless the calf was re-identified via another full fluke photograph obtained one year or more after its initial capture. There have been 12 calves identified via fluke photographs (of excellent photo quality) collected in the waters of the CVI since 2006. Three of these calves have returned to the CVI waters more than a year after their initial (calf year) photo capture and are included in the results.

Resightings of Individuals

Male humpback NA04950 (aka NNHWC-200) has been resighted in the Cape Verde archipelago 11 different years (from 2002 to 2018) and is always sighted between 2 April and 20 May. It was resighted (photo recaptured) numerous times, with a residency

time exceeding 30 days in 2012 and 37 days in 2014 and 2016. This whale was also identified near Tromsø, Norway, in 2012 and 2014 (F. Broms, pers. comm.). The within-year frequency of Cape Verdean humpback photo-identification recaptures varied as most individuals were only captured once per year/season. One humpback (sex unknown) was resighted 15 days apart and nearly 100 km away within the CVI archipelago. One male humpback (NA04750) was resighted numerous times between 18 March and 12 May 2010, remaining in the region for 61 days. Female humpbacks without calves were most often sighted once within the year. A few females, observed with a newborn calf, maintained an extended residency of over a month. Female humpback NA04906 was observed with a newborn calf between 6 April and 12 May 2010 (36 d), and between 13 April and 4 May 2018 (21 d) with another calf. Female humpback NA04968 was resighted with a newborn calf numerous days from 10 March to 10 April 2017 (31 d).

There have been a few anecdotal observations of humpbacks documented from shore in January and as late as early June. Those humpbacks observed between August and October are assumed to be Southern Hemisphere humpbacks (Hazevoet et al., 2011; Berrow et al., 2015a, 2015b; Ryan et al., 2019). Humpbacks generally arrive in late February/early March with consistency, and the last observations are at the end of May. The frequency of sightings and photographic identifications tend to peak in mid- to late April, with the mean (across all years) corresponding with 17 April (Table 3). Our earliest photo-identification capture was 29 February 2016, and the latest photo identification capture was on 26 May 2018.

The largest number of recaptures from eastern North Atlantic high latitude feeding grounds was 44 individual humpbacks (44/267 = 16.5%) identified in both the Cape Verdean and Norwegian waters, followed by 12 humpbacks (12/267 = 4.5%) identified in the CVI and Iceland. Fifteen humpbacks were sighted in both the CVI and Azores, with seven of these whales also having Norwegian sightings. There has been one resighting between Cape Verde and Tenerife, Canary Islands, and there have been five resightings of Cape Verde-identified humpbacks observed in different years in the southeast Caribbean, around the French West Indies island of Guadeloupe one of these whales has also been photographed near Tromsø, Norway (Stevick et al., 2016).

Abundance

Between 2010 and 2018 (inclusive), 228 individuals were identified. During this time period, there were too few individual whales (29 females, 27 males, and 172 unknown) for which sex was

Table 3. All CVI fluke photo captures (1990-2018) by 2-wk periods

Dates	Fluke captures
February 15-29	2
March 1-15	84
March 16-31	155
April 1-15	269
April 16-30	240
May 1-15	221
May 16-30	67
	1,038

Note: On 29 February 2016, there were two fluke captures.

known to analyze the data separately by sex. The discovery curve of identifications (Figure 2) did not show an asymptote. A model with no "trap effect" with an Akaike information criterion (AIC) of 590.6 provided a better fit to the data than one that included a trap effect (AIC 599.2). This means that all identifiable individuals were equally likely to be sampled throughout the study. The fitted model included the probabilities of capture and survival, both varying by sampling period (i.e., annually). Annual capture probabilities (Table 4) varied from 0.277 (Standard Error [SE] 0.037) in 2015 to 0.4067 (SE 0.091) in 2011.

Estimates of the number of new arrivals between years were highly variable, ranging from 0 to 31 (SE 25) (Figure 2). Estimates of annual abundances ranged from 101 (SE 19) in 2011 to 213 (SE 16) in 2015 (Figure 3). The estimate of the total number of individual whales that occurred in the study area between 2010 and 2018 was 272 (SE 10). As calves are not photo-identified (and as sightings of calves are not independent from sightings of their mothers, and so inappropriate for mark-recapture analysis), these population estimates are for non-calf animals.

Discussion

Two spatially distinct tropical regions in the North Atlantic are known to have been traditionally used by humpback whales (and whalers) during the winter calving/breeding season: (1) the southeastern Caribbean and (2) the Cape Verde Islands (Reeves et al., 2001, 2002; Smith & Reeves, 2003, 2010; Cabral & Hazevoet, 2011). Reeves et al. (2001) suggested a population shift from the southeastern to the northern West Indies based on the lack of historical records

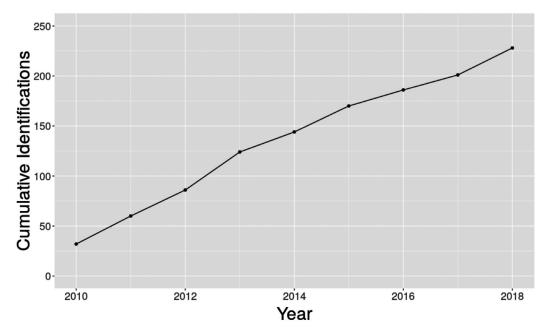


Figure 2. Cumulative tally of individual humpback whales (Megaptera novaeangliae) identified photographically, 2010 to 2018

of 19th-century whaling from the Dominican Republic. Kennedy & Clapham (2017) suggest it may have been an inability of the whalers to obtain the necessary licenses to hunt humpback whales in the Dominican Republic rather than an absence of whales in this region. Today, the largest concentrations of North Atlantic breeding humpbacks are observed on Silver, Navidad, and Mouchoir Banks (north of Hispaniola, Dominican Republic), as well as in Samaná Bay in the northeast Dominican Republic (Winn et al., 1975; Smith et al., 1999).

The documentation of the inter-annual migratory exchange between the southeast Caribbean and the CVI sparks new interest in the relationship between these two regions (Palsbøll et al., 2017). Four thousand kilometers separate these two breeding habitats, and five individuals have been photo-documented in both regions (Stevick et al., 2016, 2018).

There have been no photographic matches between any of the Cape Verde humpback whales and those on western North Atlantic feeding grounds or to the West Indies/Dominican Republic breeding ground despite the huge sample size that exists from both of those regions (Jann et al., 2003; Wenzel et al., 2009; Stevick et al., 2016, 2018). This further supports the hypothesis that humpbacks from the CVI constitute a Distinct (breeding) Population Segment (DPS) that feeds exclusively in northeastern Atlantic waters. This model

Table 4. Estimates of annual probability of capture of individual humpback whales in the CVI study area, 2011 to 2017, derived from a Jolly-Seber open population model fit to the data using *Reapture* (Rivest & Baillargeon, 2014). Where parameter estimates cannot be identified in the model, the estimates are replaced with --.

*	1	
Year	Point estimate	Standard error
2010		
2011	0.4072	0.0907
2012	0.3338	0.0620
2013	0.3177	0.0458
2014	0.3409	0.0497
2015	0.2769	0.0373
2016	0.2890	0.0531
2017	0.3826	0.0753
2018		

is supported by the existence of both nuclear and mitochondrial DNA differences between hump-backs from the eastern and western North Atlantic (Palsbøll et al., 1995, 1997, 2017; Larsen et al., 1996; Valsecchi et al., 1997). Further support may be found in the disparity in the timing of migrations and peak relative abundance on the breeding

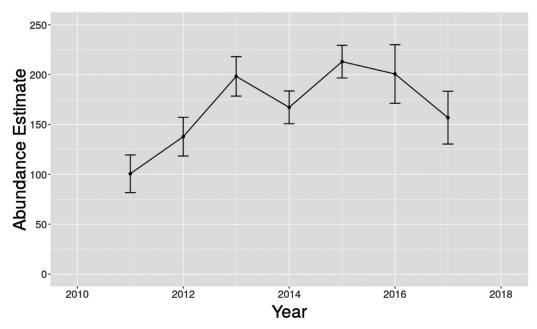


Figure 3. Estimates of annual abundance of humpback whales in the CVI study area, 2011 to 2017, derived from a Jolly-Seber open population model fit to the data using *Reapture* (Rivest & Baillargeon, 2014). Bars show plus or minus one standard error.

grounds across the North Atlantic: earlier in the west and later in the east (Stevick et al., 2016). We suspect that in animal populations with high resight and extended residency, as observed here, site fidelity is similar to route fidelity in that both refer to the repeated utilization of migratory destinations (Horton et al., 2017).

Mark-recapture estimates of humpback whale abundance in the CVI show that this population has been, and remains, very small. Previous estimates ranged from 99 (CV = 0.23) in 1999 to 2005 (Punt et al., 2006) to 170 to 260 (CV = 0.02) in 2010 to 2013 (Ryan et al., 2014). In this study, we estimated that there were 272 (SE 10) individual, non-calf whales using the CVI between 2010 and 2018, with a maximum of 213 whales (SE 16) in 2015. Although Figure 3 shows annual abundance estimates for 2011 to 2017, the overall estimate of the number of humpback whales using the CVI is for all years' data (i.e., 2010 to 2018). Because of the constraints of the Jolly-Seber model (Rivest & Baillargeon, 2014), not all years' annual abundances can be estimated. We recognize that our abundance estimate is likely biased, but our dataset was too sparse to run more complex models to address some of these biases. For example, there are too few individuals of known sex (29 females and 27 males) in the 2010 to 2018 dataset to derive sex-segregated abundance estimates. As not all

female humpback whales migrate each year (e.g., Brown et al., 1995), their likelihood of detection (capture) each year is different from that of males. Indeed, Ryan et al. (2013b) determined a significant genetically determined male:female bias in a very small sample of biopsied whales (n = 26)of 1.9:1. We cannot address this sex bias with the data on hand and acknowledge this caveat in our study. Furthermore, since individual whales have discrete ranges within the Cape Verde archipelago, their likelihood of detection in the study area may differ as data were collected from a small portion of the island group. However, running the test for a trap effect (i.e., individual differences in likelihood of detection of whales) demonstrated that a model without a trap effect fitted the data better than a model with a trap effect. That being so, these biases, if they exist, are insufficient to affect the acceptability of our modeling assumptions and so do not detract from the primary message of the mark-recapture analysis. The population of humpback whales occurring in the CVI is at very low abundance.

The low abundance of humpback whales in this breeding area probably indicates a slow recovery (or even lack thereof) of this eastern North Atlantic humpback breeding population (Ingebrigtsen, 1929; Kellogg, 1929; Reeves et al., 2001, 2002; Reeves & Smith, 2003; Smith & Reeves, 2003, 2010; Punt

et al., 2006; Ryan et al., 2014). Analysis of 19thcentury whaling logs indicates that the CVI historically hosted a much larger population of humpbacks than it does today (Reeves et al., 2002; Reeves & Smith, 2003). Although there are no recent markrecapture estimates for the eastern North Atlantic feeding aggregations, there are, for example, over 900 individual humpback whales photo-identified in the northern Norwegian humpback whale catalog (2011 to 2018; www.hvalid.no/catalogue/browse) as of 31 December 2018 (F. Broms, pers. comm.). There are sightings/resightings of humpbacks migrating from the eastern North Atlantic (Norway and Iceland) to the Dominican Republic and the southeast Caribbean (Martin et al., 1984; Stevick et al., 1998, 2003, 2016, 2018); however, there are too many whales in the high latitudes of the central and eastern North Atlantic for the humpback whales observed in the CVI to represent the only breeding population from the eastern North Atlantic.

The CVI population of humpback whales arrive and depart 6 to 8 wks later in the winter breeding season than do humpbacks found in the waters off the Dominican Republic (Balcomb & Nichols, 1982; Whitehead, 1982; Whitehead & Moore, 1982; Mattila et al., 1994). Stevick et al. (2018) demonstrated that the southeast Caribbean humpbacks are on a similar reproductive schedule, arriving and departing 6 to 8 wks later than those in the Dominican Republic, There is a marked cline from west to east in the arrive/peak relative abundance/ departure time of whales. This may be attributed to the shorter distance traveled for humpbacks migrating from the western North Atlantic feeding grounds (Gulf of Maine and eastern Canada) to the Dominican Republic compared to the migration (distance traveled) from the eastern North Atlantic feeding grounds of Iceland and northern Norway to the CVI. Future studies should address how temporal, in addition to spatial, separation may maintain DPSs across the North Atlantic breeding areas.

Conclusion

This study confirms previous findings (Punt et al., 2006; Ryan et al., 2014) that the population of humpback whales using the waters off the Cape Verde Islands is extremely small and still numbers fewer than 300 individuals. Only the Arabian Sea subpopulation of humpback whales, comprising less than 100 individuals (Minton et al., 2011), is smaller. Unlike several other populations (Thomas et al., 2016), the humpbacks found off the CVI are not increasing rapidly. Effective monitoring efforts can provide insight into potential changes/ trends within this whale population and are, therefore, a necessity. Put together, these findings generate concern for the conservation status of humpbacks in the Cape Verdean waters, indicating that

strong, local conservation measures for whales and their habitat should be considered by the Republic of Cape Verde.

Importantly, this study provides further support for the idea that the Cape Verde humpback subpopulation is not reproductively isolated and that additional genetic and photo-identification research is required. The large influx of animals estimated to have occurred on three separate occasions indicates that immigration from elsewhere must be occurring. Photographic matches to the southeast Caribbean indicate that one source of immigrants is from there, but we cannot rule out the possibility that there is at least one other breeding area in the North Atlantic that has yet to be discovered. Similarly, there may be northern feeding areas that are not being adequately surveyed or photographically and genetically sampled. Finally, this work adds to the evidence (Stevick et al., 2018) that the West Indies DPS recognized under the U.S. Endangered Species Act (Bettridge et al., 2015) comprises at least two reproductively distinct groups of whales.

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, Martin Wenger and the R/V Wanda, Joe Aston, Fiacc O'Brolchain, and the volunteers who made this research possible through their enthusiastic participation—in particular, R. Clark, C. Carlson, G. Cascella, D. Craig, Z. Evora, B. Gravanita, E. Magileviciute, A. Ramirez, A. Cecchetti, A. Ricard, S. Vieira, L. Steiner, S. Hanquet, V. Chosson, A. Kennedy, K. Zbiden, M. Versluis, F. Hennicke, A. Hennicke, C. Rinaldi, R. Rinaldi, M. van der Linde, G. Karbus, C. Broechner Jespersen, G. Nicolas, R. Peres dos Santos, L. Rudin, A. F. Aston, M. Aston, I. Enlander, L. Lysaght, J. O'Brien, M. O'Connell, D. Wall, T. Whelan, J. Wilson, P. Whooley, D. B. Nuno, L. Steiner, C. Schmidt, D. Vetsch, and W. Heckenthaler. Partial funding support for research cruises and the photograph matching at the College of the Atlantic was through the Whale Dolphin Conservation Society (UK), S. Mackenzie and Cetacean Society International (USA), Island Foundation (USA), Heritage Council, Bord Iascaigh Mhara, Cape Verde Development (Ireland), and Karl Mayer Stiftung (Liechtenstein). Special thanks to P. Clapham, P. Palsbøll, M. Bérubé, R. Reeves, F. Larsen, J. Lien, E. Wald, V. Brooks, M. A. Rasmussen, and A. R. Martin for numerous discussions over the years on this subject; to D. Palka and two anonymous reviewers for their helpful comments; and to S. Ratao and R. Moreno, Maio Biodiversity Foundation, S. Correia, Instituto Nacional de Desenvolvimento das Pescas

(INDP), Republic of Cape Verde, and the General Directorate of Environment for research permits and support of Sónia Araujo and Liza Lima within Cape Verdean waters.

Literature Cited

- Balcomb, K. C., & Nichols, G. (1982). Humpback whale censuses in the West Indies. Report of the International Whaling Commission, 32, 401-406.
- Berrow, S., López, P., Jann, B., O'Brien, J., Palsbøll, P. J., Bérubé, M., & Ryan, C. (2015a). *Cape Verde:* A new breeding site for both Northern and Southern Hemisphere humpback whales? 29th Conference of the European Cetacean Society, Malta.
- Berrow, S., López Suárez, P., Jann, B., O'Brien, J., Ryan, C., Varela, J., & Hazevoet, C. J. (2015b). Recent and noteworthy records of Cetacea from the Cape Verde Islands. Zoologia Caboverdiana, 5(2), 111-115.
- Bérubé, M., Rew, M. B., Cole, T., Swartz, S. L., Zolman, E., Øien, N., & Palsbøll, P.J. (2004). Genetic identification of an individual humpback whale between the eastern Caribbean and the Norwegian Sea. *Marine Mammal Science*, 20(3), 657-663. https://doi.org/10.1111/j.1748-7692.2004.tb011 85.x
- Bettridge, S., Baker, C. S., Barlow, J., Clapham, P. J., Ford, M., Gouveia, D., . . . Wade, P. R. (2015). Status review of the humpback whale (Megaptera novaeangliae) under the Endangered Species Act (NOAA Technical Memorandum NOAA-TM-NMFS-SWFSC-540). Silver Spring, MD: National Oceanic and Atmospheric Administration. 240 pp.
- Brown, M. R., Corkeron, P. J., Hale, P. T., Schultz, K. W., & Bryden, M. M. (1995). Evidence for a sex-segregated migration in the humpback whale (Megaptera novaeangliae). Proceedings of the Royal Society of London, Series B: Biological Sciences, 259, 229-234. https://doi. org/10.1098/rspb.1995.0034
- Cabral, J. J., & Hazevoet, C. J. (2011). The last whale: Rise and demise of shore-based whaling in the Cape Verde Islands. *Zoologia Caboverdiana*, 2(1), 30-36. Retrieved from www.scvz.org
- Clapham, P. J., & Mead, J. G. (1999). Megaptera novaeangliae. Mammalian Species, Issue 604, 1-9.
- 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. https://doi.org/10.1163/156853992X00507
- Clapham, P. J., Barco, S., Jann, G., Martinez, A., Mattila, D. K., Nelson, M., . . . Wenzel, F. (2005). *Update on a new assessment of North Atlantic humpback whales* (Paper SC/57/AWMP9). Cambridge, UK: Scientific Committee of the International Whaling Commission.
- Friday, N., Smith, T. D., Stevick, P. T., & Allen, J. (2006). Measurement of photographic quality and individual distinctiveness for the photographic identification of humpback whale (*Megaptera novaeangliae*). Marine Mammal Science, 16(2), 355-374. https://doi.org/10.11 11/j.1748-7692.2000.tb00930.x

- Friday, N., Smith, T. D., Stevick, P. T., Allen, J., & Fernald, T. (2008). Balancing bias and precision in capturerecapture estimates of abundance. *Marine Mammal Science*, 24(2), 253-275. https://doi.org/10.1111/j.1748-7692.2008.00187.x
- 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. https://doi. org/10.1163/18759866-06903004
- Hazevoet, C. J., Gravanita, B., López-Suárez, P., & Wenzel, F. W. (2011). Seasonality of humpback whale *Megaptera novaeangliae* (Borowski, 1781) records in Cape Verde seas: Evidence for the occurrence of stocks from both hemispheres? *Zoologia Caboverdiana*, 2(1), 25-29.
- Horton, T. W., Hauser, N., Zerbini, A. N., Francis, M. P., Domeier, M. L., Andriolo, A., . . . Clapham, P. J. (2017). Route fidelity during marine megafauna migration. *Frontiers of Marine Science*, 4, 422. https://doi. org/10.3389/fmars.2017.00422
- 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., Allen, J., Carrillo, M., Hanquet, S., Katona, S. K., Martin, A. R., Wenzel, F. W. (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. https://doi.org/10.1017/S0032247 40000365X
- 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. https://doi.org/10.1007/978-1-4684-2985-5_2

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.

- Kennedy, A. S., & Clapham, P. J. (2017). From whaling to tagging: The evolution of North Atlantic humpback whale research in the West Indies. *Marine Fisheries Review*, 79(2), 23-37. https://doi.org/10.7755/MFR.79.2.2
- 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: Biological Sciences, 263, 1611-1618. https://doi.org/10.1098/rspb.1996.0236
- 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. Retrieved from https://www.jstor.org/stable/1381174; https://doi.org/10.2307/1381174
- Mattila, D. K., Clapham, P. J., Vásquez, O., & Bowman, R. (1994). Occurrence, population composition and habitat use of humpback whales in Samana Bay, Dominican Republic. *Canadian Journal of Zoology*, 72, 1898-1907. https://doi.org/10.1139/z94-258
- Minton, G. T. J. Q., Collins, T., Findlay, K. P., Ersts, P. J., Rosenbaum, H. C., Berggren, P., & Baldwin, R. (2011). Seasonal distribution, abundance, habitat use and population identity of humpback whales in Oman. *Journal of Cetacean Research and Management* (Special Issue on Southern Hemisphere Humpback Whales), 3, 185-198.
- Palsbøll, P. J., Allen, J., Bérubé, M., Clapham, J., Feddersen, T. P., Hammond, P. S., . . . Øien, N. (1997). Genetic tagging of humpback whales. *Nature*, 388, 767-769. https:// doi.org/10.1038/42005
- Palsbøll, P., Bérubé, M., Ryan, C., Lópes-Suárez, P., Robbins, J., Mattila, D., . . . Berrow, S. D. (2017). A post-whaling legacy: Differential post-whaling recovery rates resulting in the genetic extinction of native Cape Verde humpback whales. 22nd Biennial Conference on the Biology of Marine Mammals, Halifax, Nova Scotia.
- Palsbøll, P. J., Clapham, P. J., Mattila, D. K., Larsen, F.,
 Sears, R., Siegismund, H. R., . . . Arctander, P. (1995).
 Distribution of mtDNA haplotypes in North Atlantic humpback whales: The influence of behaviour on population structure. *Marine Ecology Progress Series*, 116, 1-10. https://doi.org/10.3354/meps116001
- 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.
- R Core Team. (2019). The *R* project for statistical computing. R, *Version 3.5.3*. Retrieved from https://www.r-project.org Reeves, R. R., & Smith, T. D. (2003). 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. https://doi.org/10.11 11/j.1748-7692.1996.tb00595.x
- Rivest, L. P., & Baillargeon, S. (2014). RCapture: Loglinear models for capture-recapture experiments. R package, Version 1.4-2. Retrieved from http://CRAN.R-projectorg/package=Rcapture
- 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.
- Ryan, C., Wenzel, F. W., López Suárez, P., & Berrow, S. D. (2014). An abundance estimate for humpback whales, *Megaptera novaeangliae* breeding around Boa Vista, Cape Verde Islands. *Zoologia Caboverdiana*, 5(1), 20-28.
- Ryan, C., Romagosa, M., Boisseau, O., Moscrop, A., & McLanaghan, R. (2019). Humpback whale (*Megaptera novaeangliae*) song detected at the Cape Verde Islands during boreal and austral spring. *Marine Mammal Science*, 35(1), 336-344. https://doi.org/10.1111/mms.12523
- Ryan, C., Craig, D., López Suárez, P., Vazquez Perez, J., O'Connor, I., & Berrow, S. D. (2013a). Breeding habitat of poorly studied humpback whales (Megaptera novaeangliae) in Boa Vista, Cape Verde. Journal of Cetacean Research and Management, 13(2), 175-180.
- Ryan, C., McHugh, B., Boyle, B., McGovern, E., Bérubé, M., López-Suárez, P., . . . Clapham, P. J. (2013b). Levels of persistent organic pollutants in eastern North Atlantic humpback whales. *Endangered Species Research*, 22(3), 213-223. https://doi.org/10.3354/esr00545
- 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., & Reeves, R. R. (2010). Historical catches of humpback whales, *Megaptera novaeangliae*, in the North Atlantic Ocean: Estimates of landings and removals. *Marine Fisheries Review*, 72(3), 1-43.
- Smith, T. D., Allen, J., Clapham, P. J., Hammond, P. S., Katona, S. K., Larsen, F., . . . Øien, N. (1999). An ocean basin-wide mark-recapture study of the North Atlantic humpback whale (Megaptera novaeangliae). Marine Mammal Science, 15(1), 1-32. https://doi.org/10.1111/j.1748-7692.1999.tb00 779.x

- Stevick, P. T., Carlson, C. A., & Balcomb, K. C. (1999a).
 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. https://doi. org/10.1111/j.1748-7692.1998.tb00701.x
- Stevick, P.T., Øien, N., & Mattila, D. K. (1999b). 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., Bérubé, M., Clapham, P. J., Katona, S. K., Larsen, F., . . . Hammond, P. S. (2003). Segregation of migration by feeding ground origin in North Atlantic humpback whales (*Megaptera novae-angliae*). *Journal of Zoology, London*, 259, 231-237. https://doi.org/10.1017/S0952836902003151
- Stevick, P. T., Bouveret, L., Gandilhon, N., Rinaldi, C., Rinaldi, R., Broms, F., . . . Wenzel, F. W. (2016). There and back again: Multiple and return exchange of humpback whales between breeding habitats separated by an ocean basin. *Journal of the Marine Biological Association of the UK*, 1, 1-6. https://doi.org/10.1017/S0025315416000321
- Stevick, P. T., Bouveret, L., Gandilhon, N., Rinaldi, C., Rinaldi, R., Broms, F., . . . Wenzel, F. W. (2018). Migratory destinations and timing of humpback whales in the southeastern Caribbean differ from those off the Dominican Republic. *Journal of Cetacean Research and Management*, 18(1), 127-133.
- Thomas, P. O., Reeves, R. R., & Brownell, R. L., Jr. (2016). Status of the world's baleen whales. *Marine Mammal Science*, 32(2), 682-734. https://doi.org/10.1111/mms. 12281

- Valsecchi, E., Palsbøll, P., Hale, P., Glockner-Ferrari, D., Ferrari, M., Clapham, P. J., . . . Amos, B. (1997). Microsatellite genetic distances between oceanic populations of the humpback whale (Megaptera novaeangliae). Molecular Biology and Evolution, 14(4), 355-362. https://doi.org/10.1093/oxfordjournals.molbev.a025771
- Wenzel, F. W., Allen, J., Berrow, S., Hazevoet, C. J., Jann, J., Seton, R. E., . . . Whooley, P. (2009). Current knowledge on the distribution and relative abundance of humpback whales (*Megaptera novaeangliae*) off the Cape Verde Islands, eastern North Atlantic. *Aquatic Mammals*, 35(4), 502-510. https://doi.org/10.1578/AM.35.4.2009.502
- Whitehead, H. (1982). Populations of humpback whales in the northwest Atlantic. *Report of the International Whaling Commission*, 32, 345-353.
- Whitehead, H., & Moore, M. J. (1982). Distribution and movements of West Indian humpback whales in winter. *Canadian Journal of Zoology*, 60(9), 2203-2211. https:// doi.org/10.1139/z82-282
- Wickham, H. (2016). ggplot2 Elegant graphics for data analysis (2nd ed.). New York: Springer-Verlag. 260 pp. Retrieved from www.springer.com/gp/book/ 9783319242750
- Williams, B. K., Nichols, J. D., & Conroy, M. J. (2002).
 Analysis and management of animal populations.
 San Diego, CA: Academic Press. 817 pp.
- 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. https://doi.org/10.1139/f75-061