There and back again

Stevick, P. T.; Berrow, Simon D.; Berube, Martine; Bouveret, Laurent; Broms, Fredrik; Jann, Beatrice; Kennedy, Amy; Suarez, Pedro Lopez; Meunier, Marine; Ryan, Conor

Published in:
Journal of the Marine Biological Association of the United Kingdom

DOI:
10.1017/S0025315416000321

Journal of the Marine Biological Association of the United Kingdom, 2016, 96(4), 885–890.
doi:10.1017/S0025315416000321

There and back again: multiple and return exchange of humpback whales between breeding habitats separated by an ocean basin

PETER T. STEVICK[1], SIMON D. BERROW[2,3], MARTINE BÉRUBÉ[4], LAURENT BOUVERET[5], FREDRIK BROMS[6], BEATRICE JANN[7], AMY KENNEDY[8], PEDRO LÓPEZ SUÁREZ[9,10], MARINE MEUNIER[5], CONOR RYAN[2,3,11] AND FREDERICK WENZEL[12]

[1]College of the Atlantic, 105 Eden St, Bar Harbor, ME 04856, USA, [2]Irish Whale and Dolphin Group, Merchant's Quay, Kilrush, Co. Clare, Ireland, [3]Department of Life Sciences, Marine and Freshwater Research Centre, Galway-Mayo Institute of Technology, Dublin Road, Galway, Ireland, [4]Marine Evolution and Conservation, Centre for Ecological and Evolutionary Studies, University of Groningen, PO Box 11103, Groningen, the Netherlands, [5]Observatoire des Mammifères Marins de l'Archipel Guadeloupéen, Route Hégésippe Legitimus, Beauport, 97117 Port-Louis, Guadeloupe, FWI, [6]Akvaplan-niva AS, Fram Centre, P.O. Box 6606 Langnes, Tromsø, Norway, [7]Swiss Whale Society, CH-6900 Massagno, Switzerland, [8]NOAA, National Marine Fisheries Service, National Marine Mammal Laboratory, Alaska Fisheries Science Center, 7600 Sand Point Way Northeast, Seattle, WA 98115, USA, [9]Bios.CV, Sal-Rei. Boa Vista, Republic of Cape Verde, [10]Naturalia Capa Verde Lda. Sal-Rei. Boa Vista, Republic of Cape Verde, [11]Current address: Hebridean Whale and Dolphin Trust, 28 Main Street, Tobermory, Isle of Mull, PA75 6RF, UK, [12]NOAA, National Marine Fisheries Service, Northeast Fisheries Science Center, 166 Water Street, Woods Hole, MA 02543, USA

In species that aggregate for reproduction, the social and fitness costs of movement between groups frequently lead to restricted exchange between breeding areas. We report on four individual humpback whales identified in both the Cape Verde Islands and Guadeloupe; locations separated by an ocean basin and >4000 km. This rate of exchange is rarely encountered between such geographically discrete breeding areas. Two individuals returned to the area where they were originally identified. In contrast, no individuals from the Cape Verde Islands were resighted to the much larger sample from the Dominican Republic, though the migratory distances from the feeding areas are comparable between these areas. The social factors driving the stark difference between groups that is observed here are not clear. Effective conservation requires an understanding of the extent and pattern of movement between population units. The findings presented here suggest that there may well be more than one behaviourally distinct group within the West Indies. More broadly, they argue that considerable caution is warranted in assumptions made regarding the number, boundaries and status of population units based solely on spatial separation or proximity.

Keywords: breeding aggregation, breeding habitat choice, philopatry, photo-identification, humpback whale, *Megaptera novaeangliae*

Submitted 30 March 2015; accepted 17 February 2016; first published online 17 March 2016

INTRODUCTION

In species that aggregate for reproduction, the location and boundaries of aggregations, the distribution of animals within these, and movement within and between aggregation sites are the result of both the ecological characteristics of the available habitat and of social factors (Reynolds, 1996; Coulson, 2002; Krause & Ruxton, 2002). While the specific factors that influence seasonal migration and habitat selection patterns in humpback whales (*Megaptera novaeangliae*, Borowski, 1871) are not well understood, these animals aggregate during winter months in areas where mating-related behaviour and calving is observed (Clapham & Mead 1999). The physical characteristics common to the known preferred habitats include tropical and sub-tropical waters, typically with temperatures of 24–28°C, depths of <100 m and low slopes (Zerbini *et al.*, 2004; Rasmussen *et al.*, 2007; Oviedo & Solís, 2008). Locations that have this combination of oceanographic characteristics are frequently separated by wide expanses that are of a dramatically different nature from that typically used by humpbacks for breeding.

Social factors, including male display and female mate choice, frequently lead to a high local density of individuals and give the humpback whale mating system many of the characteristics of a lek (Clapham, 1996, 2000). These factors may result in a small number of areas with high whale density, even within broad areas of suitable habitat (Reeves *et al.*, 2001; Matthiopoulos *et al.*, 2005). Relatively low levels of small-scale fidelity have been shown within breeding

Corresponding author:
P.T. Stevick
Email: ptstevick@gmail.com

habitats, with considerable short-term, small-scale movements (Mattila *et al.*, 1994; Cerchio *et al.*, 1998; Wenzel *et al.*, 2009; Kennedy *et al.*, 2013). However, in spite of the absence of physical barriers and the low apparent cost of transit, on a larger scale some limitation in exchange has been observed even between breeding areas that are segregated by only a few hundred kilometres (Urbán *et al.*, 2000). Few individuals have been documented using breeding grounds that are separated by more than hundreds of kilometres, resulting, in many cases, in genetically distinct populations (Olavarría *et al.*, 2007; Rosenbaum *et al.*, 2009; Baker *et al.*, 2013). However, a small number of cases of such inter-breeding-ground exchange have been reported globally (Chittleborough, 1959, 1965; Darling & McSweeney, 1985; Darling & Cerchio, 1993; Salden *et al.*, 1999; Calambokidis *et al.*, 2001; Pomilla & Rosenbaum, 2005; Stevick *et al.*, 2010, 2014; Kaufman *et al.*, 2011).

We report on four instances of individuals identified in both the Cape Verde Islands and in Guadeloupe in the south-eastern Caribbean. These two breeding and calving sites are separated by an ocean basin and >4000 km.

Breeding aggregations in the North Atlantic

Within the North Atlantic there are two generally recognized winter mating and calving areas for humpback whales. The vast majority of individuals winter off the West Indies. While the entire arc of suitable habitat spans about 2000 km from the Turks and Caicos to Aruba, there are no obvious discontinuities in habitat or distribution (Swartz *et al.*, 2003). Thus, this area is generally considered to represent a single breeding population (NMFS, 1991; Palsbøll *et al.*, 1997; Smith *et al.*, 1999).

The most heavily used habitats are in the waters of the Dominican Republic (Whitehead & Moore, 1982; Mattila *et al.*, 1989; Mattila *et al.*, 1994). Humpback whales are also found in lower concentrations off Puerto Rico and throughout the Lesser Antilles south to Venezuela and the Leeward Dutch Antilles, though considerably less is known about the distribution, abundance and movement patterns of humpback whales in these waters (Mattila & Clapham, 1989; Debrot *et al.*, 1998; Mignucci-Giannoni, 1998; Romero *et al.*, 2002; Swartz *et al.*, 2003; Acevedo *et al.*, 2008; Debrot *et al.*, 2013).

On the eastern margin of the North Atlantic basin the only known winter breeding area is associated with the Cape Verde Islands (Reiner *et al.*, 1996; Hazevoet & Wenzel, 2000; Wenzel *et al.*, 2009; Ryan *et al.*, 2014). Prior to the work reported here, no individual had been observed to occur in both areas.

METHODS

Humpback whales were identified by natural markings on the ventral surface of the flukes (Katona *et al.*, 1979). Photo comparison was done using standard methods (Katona & Beard, 1990; Allen *et al.*, 2011). Comparison of identification photographs was made by the North Atlantic Humpback Whale Catalogue (NAHWC), an internationally collaborative central database for fluke identification photographs collected throughout the North Atlantic Ocean (Katona & Beard, 1990).

For this analysis, individuals from two areas in the West Indies were treated separately. Most of the individuals identified in the south-eastern Caribbean region have been photographed off Guadeloupe. Individuals identified from the Cape Verde Islands were compared with these whales from Guadeloupe, and also from the largest concentration areas in the West Indies, located in the waters of the Dominican Republic.

Photographs from the Cape Verde Islands were collected primarily by an international collaboration that included dedicated sampling surveys and collection of photographs from ecotourism vessels. The majority of photographs from Guadeloupe were taken by ecotourism operators and recreational boaters. A small proportion was taken during dedicated research operations. Photographs from the Dominican Republic have come from extensive, dedicated research efforts and from ecotourism.

Skin biopsy samples were collected using standard methods (Ryan *et al.*, 2013). DNA was extracted by a silica-based method using filter purification, following the manufacturer's protocol (DNeasy kit for blood and tissue, Qiagen, Valencia, CA, USA). Sex was determined from extracted DNA as described by Bérubé & Palsbøll (1996a, b).

RESULTS

Photographs of 195 individual whales identified in the Cape Verde Islands, mostly in the vicinity of Boa Vista, were compared with those of 242 collected off Guadeloupe and 2377 collected from the Dominican Republic. The Cape Verde sample was collected between 1991 and 2014, though only three individuals were identified prior to 1999. The Guadeloupe sample was collected between 2004 and 2014 and the Dominican sample from 1973 to 2014. While the samples from Boa Vista and Guadeloupe largely overlap in time, the majority of the Dominican sample is from earlier decades. Given the open population, this may influence the probability of resightings. However, 414 individuals were identified from the Dominican Republic during the decade corresponding to the Guadeloupe sample.

The mean sighting date for the individuals photographed off the Cape Verde Islands is 11 April, and for Guadeloupe 3 April. Few whales are seen in either area before March. In contrast, abundance of whales in the Dominican Republic peaks during February, declining through March, with few animals remaining by April (Whitehead & Moore, 1982; Mattila *et al.*, 1994).

Four individuals were identified in both the Cape Verde Islands and off Guadeloupe (Table 1). None of the resighted individuals were in both areas during the same year. The resighted individuals were all photographed within about 60 km of one another in Guadeloupe. Individuals that were seen in more than 2 years (na4756 and na4933) made a return movement from the Cape Verde Islands to Guadeloupe. In both cases the animal was seen in the Cape Verde Islands in the year following the sighting in the Eastern Caribbean, in one case it was also seen in the Cape Verde Islands during the preceding year. No individuals from the Cape Verde Islands were resighted in the Dominican Republic, despite the sample size being an order of magnitude larger there than in Guadeloupe.

One of the resighted individuals, na4933, was also photographed in the feeding area off Tromsø, Norway. The great-circle transit distances from Tromsø to Guadeloupe and to Samana Bay in the Dominican Republic are nearly identical

Table 1. Sighting histories of humpback whales identified in both the Cape Verde Islands and off Guadeloupe.

Whale id	Date	Location
na4474	9 April 2010	Off Boa Vista, CVI
	13 April 2011	Pointe Des Chateaux, Guadeloupe
na4756	22 April 2009	Off Boa Vista, CVI
	7 April – 4 May 2011	Off Boa Vista, CVI
	19 April 2012	Off Guadeloupe
	2–15 May 2013	Off Boa Vista, CVI
	5–22 May 2014	Off Boa Vista, CVI
na4918	18 March 1999	CVI
	24 March 2012	la Vigie, Guadeloupe
na4933	21 March 1999	CVI
	4 April 2003	CVI
	26 April 2009	Petite Terre, Guadeloupe
	13 April 2010	Off Boa Vista, CVI
	4–9 May 2012	Off Boa Vista, CVI
	23 January 2014	Northern Norway

at 7900 km. The corresponding distance to the largest concentration in Silver Bank, Dominican Republic is 7770 km. In contrast, the migratory distance from Tromsø to Boa Vista is 6600 km.

Two of the whales are classified as males. One was confirmed to be male by molecular results from a skin biopsy sample. That and another individual were seen in competitive groups and one of these was identified as a singer, both roles associated with males (Clapham *et al.*, 1992; Darling *et al.*, 2006).

DISCUSSION

The level of exchange that occurs between breeding habitats represents a balance of the fitness costs that result from leaving an established, familiar area, including missed mating opportunities, energy expended in searching and transit, and the exposure to greater risk (Danchin & Cam, 2002; Bonte *et al.*, 2012), and the benefits, including accessing superior resources (Clapham & Zerbini, 2015), the discovery of superior habitats and the avoidance of close inbreeding (Rabouam *et al.*, 1998; Schjorring, 2002; Delgado *et al.*, 2014). In this instance we observe very different patterns in individuals from the Dominican Republic and Guadeloupe, two breeding concentrations that are separated by less than 1000 km, with comparable distances to migratory destinations and between which there is a nearly contiguous area of suitable habitat. There is virtually no information available on movement between the south-eastern Caribbean and other habitats within the West Indies. The results of a comprehensive comparison examining movement rates between the south-eastern Caribbean and other parts of the West Indies are not yet available. The single published observation is an individual identified in both Dominica and Puerto Rico (Stevick *et al.*, 1999).

Most previous findings of inter-breeding-area exchange in humpback whales are based on only a single instance, often from large samples, and have represented undeniably rare events. Three cases were documented between Japan and Hawaii during a single study (Calambokidis *et al.*, 2001). However, those results included resightings between individuals from widely separated regions off both Hawaii and Japan, contrasting with the small scale of the re-sighting locations reported here, and were based on a much larger sample of identified individuals (Salden *et al.*, 1999; Calambokidis *et al.*, 2001).

The resightings reported here contrast to the lack of resightings discovered between the Cape Verde Islands and the Dominican Republic, in spite of the order of magnitude larger sample size from that area. Even in species with long lifespans, the resighting rate will be influenced by changing population, and many of the whales identified in the Dominican Republic were photographed decades before those in Guadeloupe. However, about 200 more whales were identified in the Dominican Republic than Guadeloupe during the 10 years covered by the Guadeloupe sample.

Humpback whales of both sexes have previously been observed to move between distant breeding sites (Darling & Cerchio, 1993; Salden *et al.*, 1999; Pomilla & Rosenbaum, 2005; Stevick *et al.*, 2010, 2014), though a male bias in gene flow has been noted (Rosenbaum *et al.*, 2009; Baker *et al.*, 2013). Thus having two of these whales identified as males in behavioural roles associated with reproductive activity is not unexpected.

It seems highly unlikely that an individual would take the time during the height of the breeding season to swim directly between these breeding areas in the same year. Rather, this almost certainly reflects a difference in choice in migratory destination in the different years. Canada is the only migratory destination that has previously been documented for a humpback whale from Guadeloupe (Rinaldi *et al.*, 2009). In addition, two satellite-tagged humpback whales from Guadeloupe were tracked on migration towards feeding areas in the eastern North Atlantic (Kennedy *et al.*, 2013). The few migrations documented from other parts of the south-eastern Caribbean include movement to the Gulf of Maine, Canada, Greenland and Norway (Stevick *et al.*, 1999; Bérubé *et al.*, 2004; Robbins *et al.*, 2006). All whales from the Cape Verde Islands that have been identified in a northern feeding area to date have migrated to Norway or Iceland (Jann *et al.*, 2003; Wenzel *et al.*, 2009). The sighting of one of these individuals in Norwegian waters, coupled with the tag results from Guadeloupe and the previous identification of a whale from the south-eastern Caribbean off Norway (Bérubé *et al.*, 2004) suggests some possibility of migratory affinity of individuals from Guadeloupe to eastern North Atlantic feeding areas. The later mean sighting dates in Guadeloupe than in the Dominican Republic also suggest an affinity for eastern feeding destinations, as whales from these regions have been identified later in the season in the Dominican Republic (Stevick *et al.*, 2003).

The social factors driving this difference between groups are not clear. The migratory distance from these feeding grounds does not provide an obvious explanation for the use of Guadeloupe rather than the Dominican Republic by individuals that also use the Cape Verde Islands. Humpback whales do not necessarily migrate between seasonal habitats that are closest, nor to those that are most similar in longitude (Robbins *et al.*, 2011). The shortest migration route from foraging sites off Norway and Iceland to Guadeloupe is nearly identical to, or very slightly longer than, the corresponding distance to the major habitats in the Dominican Republic, providing no particular incentive for whales from Norway to migrate to one of these locations rather than the other,

especially when the shorter distance would bring whales to an area with a higher density of conspecifics.

These four instances of change in individual migratory destination between the Eastern Caribbean and the Cape Verde Islands, and in some cases return, especially from modest sample sizes, have implications for management of humpback whales across the region. Both the Cape Verde Islands and the south-eastern Caribbean were sites of extensive 19th century whaling (Reeves *et al.*, 2001, 2002), and the whales in these area are relatively under-studied today.

Designing effective conservation efforts and interpreting the conservation implications of observed abundance and distribution patterns requires an understanding of population units and the extent and patterns of movement between these (Taylor, 1997; Clapham & Zerbini, 2015). Based on analogy from other areas, the aggregation sites on the eastern and western margins of the ocean basin would be anticipated to represent discrete population units, with few if any individuals switching migratory destination between these areas. There are genetic markers in humpback whales from the eastern North Atlantic that are not known from the Dominican Republic (Valsecchi *et al.*, 1997), which could support this contention. Humpback whales have been identified in varying numbers in a nearly continuous band extending from the Turks and Caicos to South America, and the animals that aggregate for breeding in the entire West Indies chain are currently treated as a single population (NMFS, 1991; Smith *et al.*, 1999).

The differences in movement patterns of individuals from Guadeloupe and the Dominican Republic observed here, however, are at odds with the idea that the West Indies region is used by a common group of individuals with similar movement patterns. These findings suggest that there may well be more than one behaviourally distinct population group within the West Indies with boundaries as yet not known, and potentially a higher level of exchange between the Cape Verde Islands and some portion of the West Indies than other parts. More broadly, they argue that considerable caution is warranted in any assumptions regarding the number, boundaries and status of population units based on spatial separation or proximity alone.

ACKNOWLEDGEMENTS

This study would not be possible without the hard work and dedication of the numerous researchers who collaborate on humpback whale study in the North Atlantic Ocean. Hundreds of photographers have pooled their data to make the NAHWC possible, and countless staff and students have spent untold hours comparing photographs. The assistance of J. Allen and T. Fernald was invaluable. Fieldwork in the Cape Verde Islands was conducted under permit from the General Directorate of Environment (DGA) and with logistical support from the National Institute of Fisheries (INDP) of Cape Verde. Special thanks to P. Whooley for his contribution to field work. Naturalia provided photographs from Boa Vista, and both Seaturtle Sailing Catamarans and Scubacaribe provided logistics and facilitated humpback whale monitoring activities off Boa Vista since 2010. More than 35 individuals contributed photographs to the OMMAG network in Guadeloupe. Dedicated tagging studies that made a critical contribution to field data collection from Guadeloupe were conducted under the direction of N. Gandilhon. N. Ward has provided enthusiastic encouragement for humpback whale studies in the Eastern Caribbean over many years.

FINANCIAL SUPPORT

The NAHWC is funded by donors and an anonymous foundation. IWDG research in Cape Verde was supported by the Karl Meyer and Island Foundations, Bord Ischaigh Mhara, Heritage Council, Crossing the Line Films and Cape Verde Development. Field work in Guadeloupe was funded by the Université des Antilles et de la Guyane (Guadeloupe), The BREACH Association (Guadeloupe), Biologie des Organismes Aquatiques et Ecosystèmes (UMR BOREA), the Centre de Neurosciences (Université Paris Sud, Paris) and the National Marine Mammal Laboratory (NOAA, USA).

REFERENCES

Acevedo R., Oviedo L., Silva N. and Bermudez-Villapol L. (2008) A note on the spatial and temporal distribution of humpback whales (*Megaptera novaeangliae*) off Venezuela, southeastern Caribbean. *Journal of Cetacean Research and Management* 10, 73–79.

Allen J., Carlson C.A. and Stevick P.T. (2011) A description and summary of the Antarctic Humpback Whale Catalogue. *Journal of Cetacean Research and Management Special Issue* 3, 95–99.

Baker C.S., Steel D., Calambokidis J., Falcone E., Gonzalez-Peral U., Barlow J., Burdin A.M., Clapham P.J., Ford J.K.B., Gabriele C.M., Mattila D., Rojas-Bracho L., Straley J.M., Taylor B.L., Urban R.J., Wade P.R., Weller D., Witteveen B.H. and Yamaguchi M. (2013) Strong maternal fidelity and natal philopatry shape genetic structure in North Pacific humpback whales. *Marine Ecology Progress Series* 494, 291–306. doi: 10.3354/meps10508.

Bérubé M. and Palsbøll P.J. (1996a) Identification of sex in cetaceans by multiplexing with three ZFX and ZFY specific primers. *Molecular Ecology* 5, 283–287.

Bérubé M. and Palsbøll P.J. (1996b) Erratum of identification of sex in cetaceans by multiplexing with three ZFX and ZFY specific primers. *Molecular Ecology* 5, 602.

Bérubé M., Rew M.B., Cole T., Swartz S.L., Zolman E., Oien N. and Palsbøll P.J. (2004) Genetic identification of an individual humpback whale between the eastern Caribbean and the Norwegian sea. *Marine Mammal Science* 20, 657–663.

Bonte D., Van Dyck H., Bullock J.M., Coulon A., Delgado M., Gibbs M., Lehouck V., Matthysen E., Mustin K., Saastamoinen M., Schtickzelle N., Stevens V.M., Vandewoestijne S., Baguette M., Barton K., Benton T.G., Chaput-Bardy A., Clobert J., Dytham C., Hovestadt T., Meier C.M., Palmer S.C.F., Turlure C. and Travis J.M.J. (2012) Costs of dispersal. *Biological Reviews* 87, 290–312. doi: 10.1111/j.1469-185X.2011.00201.x.

Calambokidis J., Steiger G.H., Straley J.M., Herman L.M., Cerchio S., Salden D.R., Urbán R.J., Jacobsen J., vonZiegesar O., Balcomb K.C., Gabriele C.M., Dalheim M.E., Uchida S., Ellis G., Miyamura Y., Ladrón de Guevara P., Yamaguchi M., Sato F., Mizroch S.A., Schendler L., Rasmussen K., Barlow J. and Quinn T.J.I. (2001) Movements and population structure of humpback whales in the North Pacific. *Marine Mammal Science* 17, 769–794.

Cerchio S., Gabriele C.M., Norris T.F. and Herman L.M. (1998) Movements of humpback whales between Kauai and Hawaii: implications for population structure and abundance estimation in the Hawaiian Islands. *Marine Ecology Progress Series* 175, 13–22.

Chittleborough R.G. (1959) Intermingling of two populations of humpback whales. *Norsk Hvalfangst-tidende* 48, 510–521.

Chittleborough R.G. (1965) Dynamics of two populations of the humpback whale, *Megaptera novaeangliae* (Borowski). *Australian Journal of Marine and Freshwater Research* 16, 33–128.

Clapham P.J. (1996) The social and reproductive biology of humpback whales: an ecological perspective. *Mammal Review* 26, 27–49.

Clapham P.J. (2000) The humpback whale: seasonal feeding and breeding in a baleen whale. In Mann J., Tyack P.L., Connor R. and Whitehead H. (eds) *Cetacean societies*. Chicago, IL: University of Chicago Press, pp. 173–196.

Clapham P.J. and Mead J.G. (1999) *Megaptera novaeangliae*. *Mammalian Species* 604, 1–9.

Clapham P.J. and Zerbini A.N. (2015) Are social aggregation and temporary immigration driving high rates of increase in some Southern Hemisphere humpback whale populations? *Marine Biology* 162, 625–634.

Clapham P.J., Palsbøll P.J., Mattila D.K. and Vásquez O. (1992) Composition and dynamics of humpback whale competitive groups in the West Indies. *Behaviour* 122, 182–194.

Coulson J.C. (2002) Colonial breeding in seabirds. In Schreiber E.A. and Burger J. (eds) *Biology of marine birds*. Boca Raton, FL: CRC Press, pp. 87–113.

Danchin E. and Cam E. (2002) Can non-breeding be a cost of breeding dispersal? *Behavioral Ecology and Sociobiology* 51, 153–163.

Darling J.D. and Cerchio S. (1993) Movement of a humpback whale (*Megaptera novaeangliae*) between Japan and Hawaii. *Marine Mammal Science* 9, 84–89.

Darling J.D. and McSweeney D.J. (1985) Observations on the migrations of North Pacific humpback whales (*Megaptera novaeangliae*). *Canadian Journal of Zoology* 63, 308–314.

Darling J.D., Jones M.E. and Nicklin C.P. (2006) Humpback whale songs: do they organize males during the breeding season? *Behaviour* 143, 1051–1102.

Debrot A.O., De Meyer J.A. and Dezentjé P.J.E. (1998) Additional records and a review of the cetacean fauna of the Leeward Dutch Antilles. *Caribbean Journal of Science* 34, 204–210.

Debrot A.O., Esteban N., Bervoets T., Hoetjes P.C. and Scheidat M. (2013) Marine mammals of the north-eastern Caribbean Windward Dutch Islands: Saba, St Eustatius, St Maarten, and the Saba Bank. *Caribbean Journal of Science* 47, 159–172.

Delgado M.M., Bartoń K.A., Bonte D. and Travis J.M.J. (2014) Prospecting and dispersal: their eco-evolutionary dynamics and implications for population patterns. *Proceedings of the Royal Society B: Biological Sciences* 281. doi: 10.1098/rspb.2013.2851.

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). *Contributions to Zoology* 69, 197–211.

Jann B., Allen J., Carrillo M., Hanquet S., Katona S.K., Martin A.R., Reeves R.R., Seton R., Stevick P.T. and Wenzel F.W. (2003) Migration of a humpback whale (*Megaptera novaeangliae*) between the Cape Verde Islands and Iceland. *Journal of Cetacean Research and Management* 5, 125–129.

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. *Reports of the International Whaling Commission, Special Issue* 12, 295–305.

Katona S.K., Baxter B., Brazier O., Kraus S., Perkins J. and Whitehead H. (1979) Identification of humpback whales by fluke photographs. In Winn H.E. and Olla B.L. (eds) *The behavior of marine animals. Volume 3, Cetacea*. New York, NY: Plenum Press, pp. 33–44.

Kaufman G., Coughran D., Allen J.M., Burns D., Burton C., Castro C., Childerhouse S., Constantine R., Franklin T., Franklin W., Forestell P., Gales R., Garrigue C., Gibbs N., Jenner C., Paton D., Noad M.J., Robbins J., Slooten E., Smith F. and Stevick P. (2011) Photographic evidence of interchange between East Australia (BS E-1) and West Australia (BS – D) humpback whale breeding populations. Paper SC/63/SH11 presented to the Scientific Committee of the International Whaling Commission. May 2011.

Kennedy A.S., Zerbini A.N., Vásquez O.V., Gandilhon N., Clapham P.J. and Adam O. (2013) Local and migratory movements of humpback whales (*Megaptera novaeangliae*) satellite-tracked in the North Atlantic Ocean. *Canadian Journal of Zoology* 92, 8–17. doi: 10.1139/cjz-2013-0161.

Krause J. and Ruxton G.D. (2002) *Living in groups*. Oxford: Oxford University Press.

Matthiopoulos J., Harwood J. and Thomas L.E.N. (2005) Metapopulation consequences of site fidelity for colonially breeding mammals and birds. *Journal of Animal Ecology* 74, 716–727. doi: 10.1111/j.1365-2656.2005.00970.x.

Mattila D.K. and Clapham P.J. (1989) Humpback whales, *Megaptera novaeangliae*, and other cetaceans on Virgin Bank and in the northern Leeward Islands, 1985 and 1986. *Canadian Journal of Zoology* 67, 2201–2211.

Mattila D.K., Clapham P.J., Katona S.K. and Stone G.S. (1989) Population composition of humpback whales, *Megaptera novaeangliae*, on Silver Bank, 1984. *Canadian Journal of Zoology* 67, 281–285.

Mattila D.K., Clapham P.J., Vásquez O. and Bowman R.S. (1994) Occurrence, population composition, and habitat use of humpback whales in Samana Bay, Dominican Republic. *Canadian Journal of Zoology* 72, 1898–1907.

Mignucci-Giannoni A.A. (1998) Zoogeography of cetaceans off Puerto Rico and the Virgin Islands. *Caribbean Journal of Science* 34, 173–190.

NMFS (1991) *Recovery plan for the humpback whale (Megaptera novaeangliae)*. Silver Springs, MD: National Marine Fisheries Service.

Olavarría C., Baker C.S., Garrigue C., Poole M., Hauser N., Caballero S., Flórez-González L., Brasseur M., Bannister J.L., Capella J., Clapham P., Dodgemont R., Donoghue M., Jenner C., Jenner M-N., Moro D., Oremus M., Paton D., Rosenbaum H.C. and Russell K. (2007) Population structure of South Pacific humpback whales and the origin of the eastern Polynesian breeding grounds. *Marine Ecology Progress Series* 330, 257–268.

Oviedo L. and Solís M. (2008) Underwater topography determines critical breeding habitat for humpback whales near Osa Peninsula, Costa Rica: implications for Marine Protected Areas. *Revista de Biología Tropical* 56, 591–602.

Palsbøll P.J., Allen J., Bérubé M., Clapham P.J., Feddersen T.P., Hammond P.S., Hudson R.R., Jorgensen 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, London* 388, 767–769.

Pomilla C. and Rosenbaum H.C. (2005) Against the current: an inter-oceanic whale migration event. *Biology Letters* 1, 476–479.

Rabouam C., Thibault J. and Bretagnolle V. (1998) Natal philopatry and close inbreeding in Cory's shearwater (*Calonectris diomedea*). *The Auk* 115, 483–486.

Rasmussen K., Palacios D.M., Calambokidis J., Saborío M.T., Dalla Rosa L., Secchi E.R., Steiger G.H., Allen J.M. and Stone G.S. (2007) Southern Hemisphere humpback whales wintering off Central America: insights from water temperature into the longest

mammalian migration. *Biology Letters* 3, 302–305. doi: 310.1098/rsbl.2007.0067.

Reeves R.R., Clapham P.J. and Wetmore S.E. (2002) American humpback whaling and humpback whale occurrence in the Cape Verde Islands, eastern Atlantic Ocean. *Journal of Cetacean Research and Management* 4, 235–253.

Reeves R.R., Swartz S., 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. *Journal of Cetacean Research and Management* 3, 117–129.

Reiner F., dos Santos M.E. and Wenzel F.W. (1996) Cetaceans of the Cape Verde archipelago. *Marine Mammal Science* 12, 434–443.

Reynolds J.D. (1996) Animal breeding systems. *Trends in Ecology and Evolution* 11, 68–72. doi: http://dx.doi.org/10.1016/0169-5347(96)81045-7.

Rinaldi C., Sears R., Stevick P.T. and Carlson C. (2009) First resighting of a humpback whale between the French Lesser Antilles and the North Atlantic feeding grounds off Canada. Paper IWC/SC61/013 presented to the Scientific Committee of the International Whaling Commission, June 2009. 4 pp.

Robbins J., Allen J.M., Clapham P.J. and Mattila D.K. (2006) Stock identity of a humpback whale taken in a southeastern Caribbean hunt. *Journal of Cetacean Research and Management* 8, 29–31.

Robbins J., Dalla Rosa L., Allen J.M., Mattila D.K., Secchi E.R., Friedlaender A.S., Stevick P.T., Nowacek D.P. and Steel D. (2011) Return movement of a humpback whale between the Antarctic Peninsula and American Samoa: a seasonal migration record. *Endangered Species Research* 13, 117–121. doi: 10.3354/esr00328.

Romero A., Hayford K.T. and Romero J. (2002) The marine mammals of Grenada, WI, and their conservation status. *Mammalia* 66, 479–494.

Rosenbaum H.C., Pomilla C., Mendez M., Leslie M.S., Best P.B., Findlay K.P., Minton G., Ersts P.J., Collins T., Engel M.H., Bonatto S.L., Kotze D.P.G.H., Meÿer M., Barendse J., Thornton M., Razafindrakoto Y., Ngouessono S., Vely M. and Kiszka J. (2009) Population structure of humpback whales from their breeding grounds in the South Atlantic and Indian Oceans. *PLoS ONE* 4, e7318. doi: 7310.1371/journal.pone.0007318.

Ryan C., McHugh B., Boyle B., McGovern E., Bérubé M., Lopez-Suárez P., Elfes C.T., Boyd D.T., Ylitalo G.M., Van Blaricom G.R., Clapham P.J., Robbins J., Palsbøll P.J., O'Connor I. and Berrow S.D. (2013) Levels of persistent organic pollutants in eastern North Atlantic humpback whales. *Endangered Species Research* 22, 213–223. doi: 10.3354/esr00545.

Ryan C., Wenzel F.W., López Suárez P. and Berrow S.D. (2014) An abundance estimate for humpback whales, *Megaptera novaeangliae*, breeding around Boa Vista, Cape Verde Islands. *Zoologia Caboverdiana* 5, 20–28.

Salden D.R., Herman L.M., Yamaguchi M. and Sato F. (1999) Multiple visits of individual humpback whales (*Megaptera novaeangliae*) between the Hawaiian and Japanese winter grounds. *Canadian Journal of Zoology* 77, 504–508.

Schjorring S. (2002) The evolution of informed natal dispersal: inherent versus acquired information. *Evolutionary Ecology Research* 4, 227–238.

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*). *Marine Mammal Science* 15, 1–32.

Stevick P.T., Allen J., Bérubé 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*). *Journal of Zoology, London* 259, 231–237.

Stevick P.T., Allen J.M., Engel M.H., Félix F., Haas B. and Neves M.C. (2014) Inter-oceanic movement of an adult female humpback whale between Pacific and Atlantic breeding grounds off South America. *Journal of Cetacean Research and Management* 13, 159–162.

Stevick P.T., Carlson C.A. and Balcomb K.C. (1999) A note on the migratory destinations of humpback whales from the eastern Caribbean. *Journal of Cetacean Research and Management* 1, 251–254.

Stevick P.T., Neves M.C., Johansen F., Engel M.H., Allen J., Marcondes M.C.C. and Carlson C. (2010) A quarter of a world away: female humpback whale moves 10,000 km between breeding areas. *Biology Letters* 7, 299–302. doi: 10.1098/rsbl.2010.0717.

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. *Caribbean Journal of Science* 39, 195–208.

Taylor B.L. (1997) Defining "population" to meet management objectives for marine mammals. In Dizon A.E., Chivers S.J. and Perrin W.F. (eds) *Molecular genetics of marine mammals*. Lawrence, KS: Marine Mammal Science Special Publication, Volume 33, pp. 49–65.

Urbán R.J., Jaramillo L.A., Aguayo L.A., Ladrón de Guevara P.P., Salinas Z.M., Alvarez F.C., Medrano G.L., Jacobsen J.K., Balcomb K.C., Claridge D.E., Calambokidis J., Steiger G.H., Straley J.M., vonZiegesar O., Waite J.M., Mizroch S.A., Dalheim M.E., Darling J.D. and Baker C.S. (2000) Migratory destinations of humpback whales wintering in the Mexican Pacific. *Journal of Cetacean Research and Management* 2, 101–110.

Valsecchi E., Palsbøll P.J., Hale P., Glockner-Ferrari D.A., Ferrari M., Clapham P., Larsen F., Mattila D., Sears R., Sigurjónsson J., Brown M., Corkeron P. and Amos B. (1997) Microsatellite genetic distances between oceanic populations of the humpback whale (*Megaptera novaeangliae*). *Molecular Biology and Evolution* 14, 355–362.

Wenzel F.W., Allen J., Berrow S.D., Hazevoet C.J., Jann B., Seton R.E., Steiner L., Stevick P.T., López Suárez P. and 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, 502–510.

Whitehead H. and Moore M.J. (1982) Distribution and movements of West Indian humpback whales in winter. *Canadian Journal of Zoology* 60, 2203–2211.

and

Zerbini A.N., Andriolo A., Da Rocha J.M., Simões-Lopes P.C., Siciliano S., Pizzorno J.L., Waite J.M., DeMaster D.P. and VanBlaricom G.R. (2004) Winter distribution and abundance of humpback whales (*Megaptera novaeangliae*) off Northeastern Brazil. *Journal of Cetacean Research and Management* 6, 101–107.

Correspondence should be addressed to:
Peter T. Stevick
College of the Atlantic, 105 Eden St, Bar Harbor, ME 04856, USA
email: ptstevick@gmail.com