# Migratory destinations and timing of humpback whales in the southeastern Caribbean differ from those off the Dominican Republic

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ABSTRACT

Humpback whales wintering in the entire West Indies chain are widely treated as comprising a single breeding population. However, most areas outside of Silver Bank and Samana Bay, Dominican Republic, are poorly and sporadically studied. Data is presented on the timing and movement patterns of 262 whales from the southeastern Caribbean, extending from Antigua in the north to Trinidad and Tobago in the south. Whales from the area were re-sighted in all of the major North Atlantic feeding grounds. However, of the 43 individuals re-sighted in feeding areas, animals from eastern feeding grounds were significantly over-represented, while those from western feeding areas were under-represented. This is in direct contrast to the pattern previously demonstrated in the Dominican Republic. Supporting this finding, the proportion of whales showing visible scarring on the flukes from non-lethal attack by killer whales was similar to that previously shown for Norway; yet lower than that presented from western feeding areas. The seasonal pattern of distribution in the southeastern Caribbean shows a peak of occurrence about six weeks later than in the Dominican Republic, and there is little overlap in the periods of greatest use. Sightings are uncommon before February. The peak in abundance occurs during March and April, declining during May, with some sightings extending into June. This is consistent with the pattern of sightings from historical whaling records in the southeastern Caribbean. These results suggest that the humpbacks mating and calving in this region are not a representative subset of those that winter in the Dominican Republic. Further studies will be needed to examine the spatial nature of the pattern shown here and define the nature and limits of this group, but these results suggest that some part of this breeding area represents a previously un-described distinct population segment within the North Atlantic. Given this, the widely held idea that there is a single West Indies humpback whale distinct population segment is in need of reconsideration.

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

## INTRODUCTION

Historically, a substantial mating and calving area for humpback whales (*Megaptera novaeangliae*) in the North Atlantic Ocean appears to have been located around the islands of the southern Lesser Antilles (Reeves *et al*., 2001a). The greatest number of humpback whale catches in the 19th and early 20th century were made in the waters from Guadeloupe south to the coast of Venezuela (Romero and Hayford, 2000; Reeves *et al.,* 2001a; 2001b; Reeves *et al.,* 2004). Whale densities in these southeastern Caribbean waters today appear to be low, and limited dedicated work has been done there (Winn *et al.,* 1975; Levenson and Leapley, 1978; Swartz *et al.,* 2003). The vast majority of the humpback whales in the North Atlantic now winter off the Dominican Republic and Puerto Rico (Smith *et al.,* 1999; Fleming and Jackson, 2011).

The entire West Indies chain (Fig. 1) extending from Cuba and the Turks and Caicos to Venezuela is widely treated as comprising a single breeding population (Fleming and Jackson, 2011; Bettridge *et al.,* 2015). Animals that aggregate for breeding are likely to concentrate at a small number of sites, even where other suitable habitat is available (Matthiopolous *et al.,* 2005). Given the social structure of humpback whales, in which aggregation with conspecifics plays a primary role, it has been proposed that changes in distribution since early whaling represent a shift in the principal part of the habitat in which whales concentrate rather than reflecting population changes or divisions (Reeves *et al.,* 2001a; Clapham and Zerbini, 2015). However, for the total available habitat in the West Indies (crescent-shaped group of islands more than 3,200km long), humpback distribution within it is patchy and often sparse (Swartz *et al.,* 2003), and for most areas outside of Silver Bank and Samana Bay, Dominican Republic, they are poorly and sporadically studied, so the dynamics in most areas are not known.

Previous work has shown movement from the northern end of the Leeward Islands, notably the Virgin Islands, Anguilla and Saba Banks, to several feeding areas in the western North Atlantic and to the major breeding and calving areas off the Dominican Republic and Puerto Rico (Mattila and Clapham, 1989; Stevick *et al.,* 1999a). Information on the movement patterns and stock identity of individuals from the waters from Antigua south to South America, the heart

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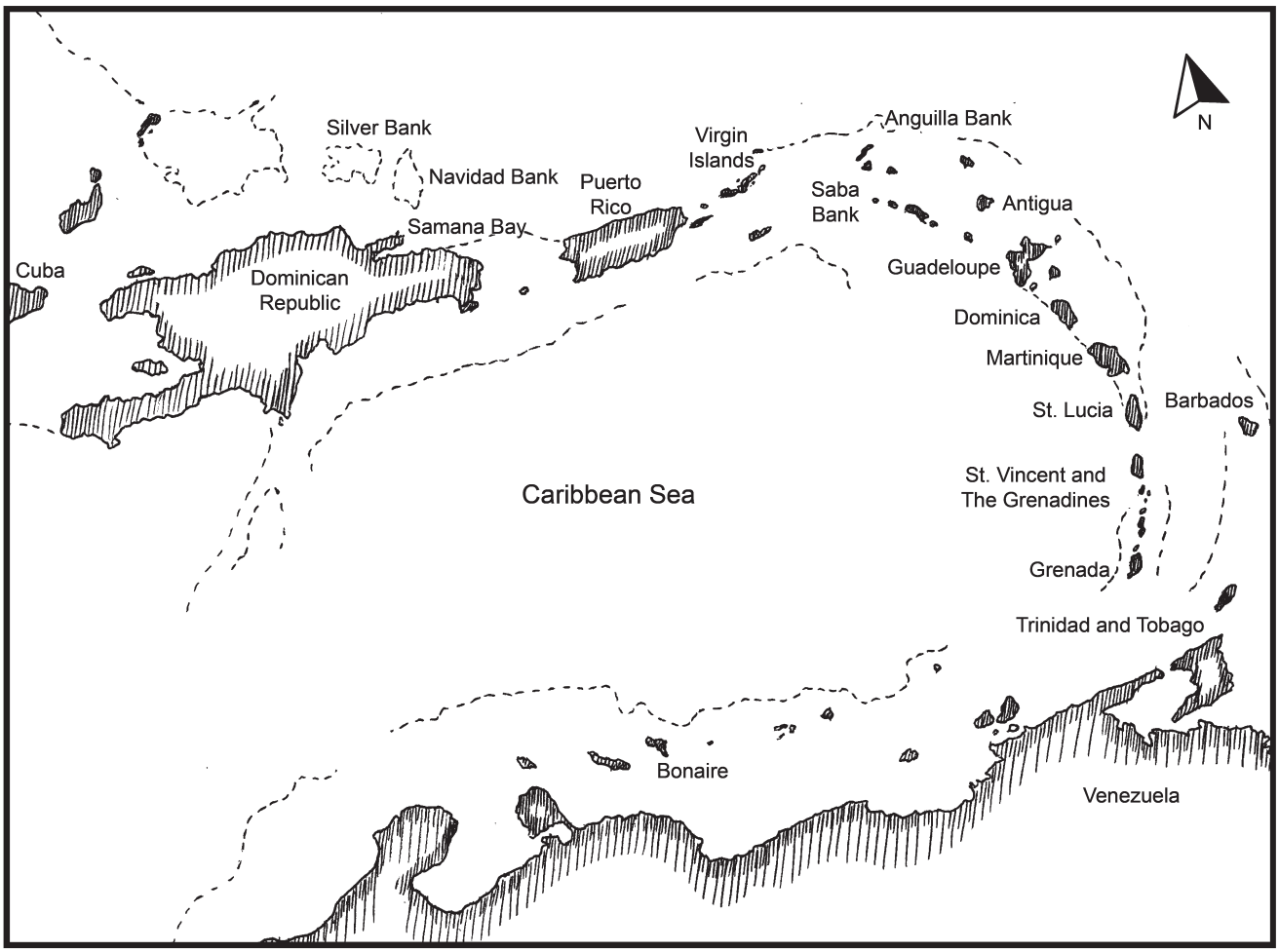


Fig. 1. The major habitats known to be used by humpback whales in the West Indies chain. Locations referred to in the text are labelled.

of the historic whaling distribution, has previously been limited. Four whales have been identified moving from these waters to feeding areas, with one each identified in the Gulf of Maine, Canada, Greenland, and Norway (Stevick *et al.,* 1999b; Bérubé *et al.,* 2004; Robbins *et al.,* 2006; Rinaldi *et al*., 2009). However, the small sample has not provided adequate grounds for comparison with other parts of the breeding range. More recently, tagging studies showed migratory movement by three whales tagged off Guadeloupe (Kennedy *et al.,* 2013). One of these travelled to the waters just east of the Faroe Islands before the tag failed.

Over the past decade, larger numbers of individuals have been photographically identified in these waters. In particular, more than 200 individuals have been identified near Guadeloupe over the past five years, providing an opportunity to examine the patterns of movement from these waters in greater detail. We present data on the migratory timing and movement patterns of whales from the southeastern Caribbean showing that these patterns are substantially dissimilar to those of whales from the Dominican Republic.

## METHODS

The study area extended from Antigua (17°10'N, 61°50'W) south to the Venezuelan coast of South America (Fig. 2). While there are published data on movements of individuals to the north and west of Antigua (Mattila and Clapham, 1989; Stevick *et al.*, 1999a), very few individuals have previously been identified from the current study area and little is known about it. This area was also selected as it coincides with the highest concentration of 19th and early 20th century catches (Romero and Hayford, 2000; Reeves *et al*., 2001a).

Between 1972 and 2014, 262 humpback whales were identified by fluke pattern in the study area. Of these, all except eight have been photographed in the year 2000 or more recently. The great majority (232) were photographed off the Guadeloupe archipelago. Photographs were also obtained from St. Vincent and the Grenadines (11), Martinique (5), Dominica (5), Trinidad and Tobago (3), Grenada (2), Barbados (2), Bonaire (1) and Antigua (1). Ten of the individuals identified from St Vincent and the Grenadines were whales killed in the hunt at Bequia.

Photographs of the ventral surface of the flukes were collected from opportunistic and dedicated sources, by academic and government research teams, NGOs, commercial tour operators and members of the public. Photographs were collected and analysed using standard methods (Katona and Beard, 1990; Allen *et al.*, 2012). Individual whales from the southeastern Caribbean were compared to those of 9,326 individuals contained in the North Atlantic Humpback Whale Catalogue (NAHWC) database to identify re-sightings (Katona and Beard, 1990). Records in the NAHWC represent whales that have been identified throughout all of the major habitats in the North Atlantic,

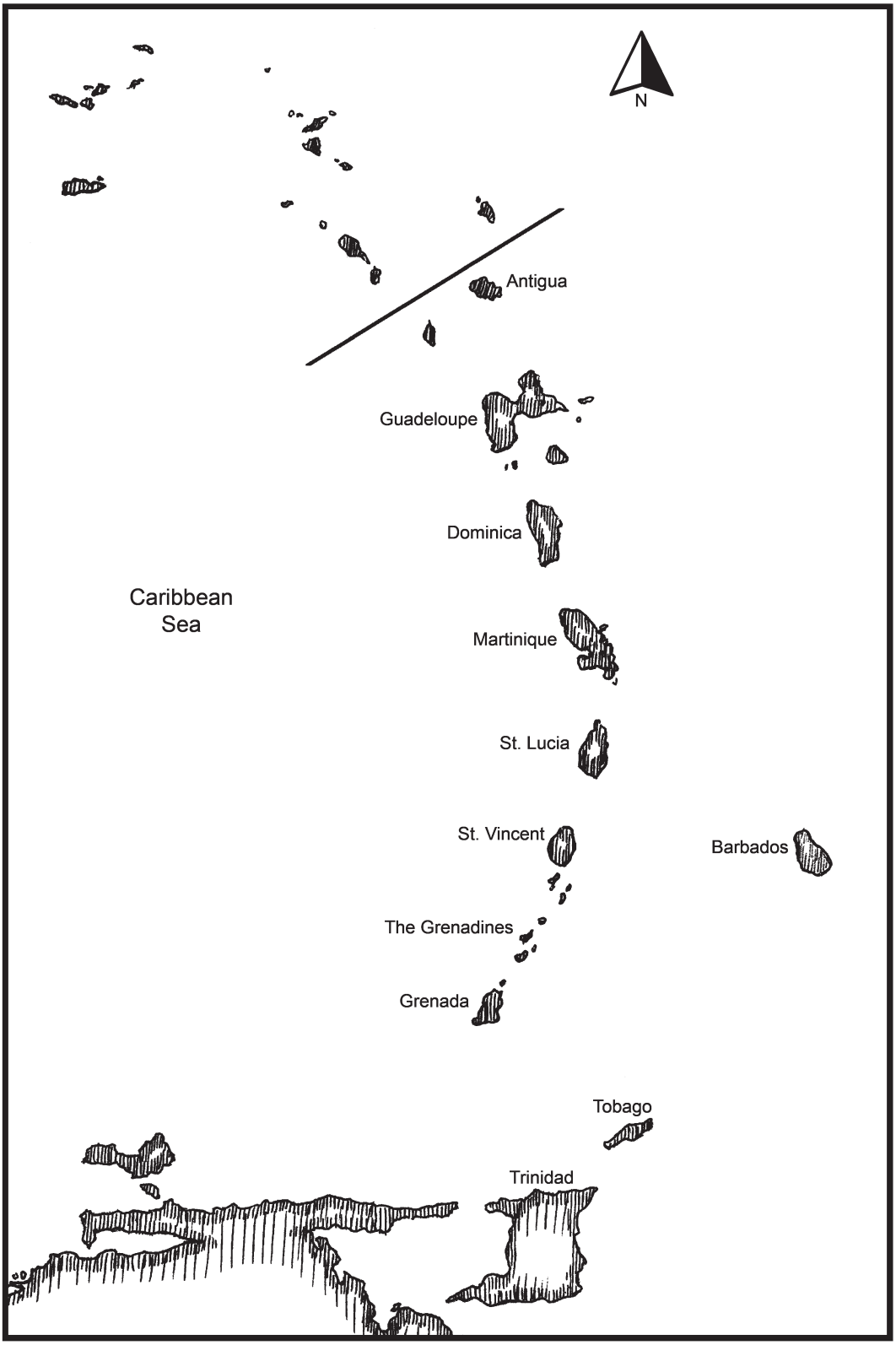


Fig. 2. The southeastern Caribbean. This study encompasses sightings made south of the line at Antigua.

including 6,690 individuals with sightings in feeding areas. Photographs were also compared to > 400 additional whales included in the Northern Norway Humpback Whale Catalogue (NNHWC), a collection from the feeding ground off northern Norway. Not all of the individuals from the NNHWC have been integrated into the NAHWC.

Multinomial exact tests for goodness-of-fit were calculated using R package XNomial. The feeding ground sample sizes of identified individuals were used for expected distribution and the log-likelihood ratio was used for assessing fit. Binomial confidence intervals for proportions were determined by the adjusted Wald method (Sauro and Lewis, 2005; Lewis and Sauro, 2006).

The presence of visible scars on the flukes caused by non-lethal interactions with killer whales has been shown to differ significantly between North Atlantic feeding grounds,

presumably reflecting ecological variation between groups of killer whales (McCordic *et al.*, 2014). All 262 whales from the southeastern Caribbean were coded for killer whale scarring. The proportion of whales in the sample showing killer whale scars was compared with published rates for the five principal high-latitude feeding grounds (from McCordic *et al.*, 2014). This was supplemented with an additional sample of individuals from Norway ($n$ = 820) from the NNHWC. Whales were coded as having killer whale scars if they had three or more parallel lines and/or corresponding injuries on their flukes consistent with encounters with killer whales (McCordic *et al.*, 2014). Although successful predation will not result in whales surviving with scars, the proportion of scarred whales in an area may indicate the frequency of predatory pressure of killer whales on various subpopulations of humpback whales around the world (Schoener, 1979; Mehta *et al.,* 2007).

The timing of presence in the area was determined from directed sighting and acoustic surveys along the leeward shore of Basse Terre island, Guadeloupe conducted from 1998 to 2009 by Association Evasion Tropicale (AET). Approximately 7,700 hours of survey effort were conducted including 200 hours or more from each month of the year (Rinaldi and Rinaldi, 2011). Results are presented as sightings or acoustic detections per hundred hours of survey effort. Sightings were collected from waters around the Guadeloupe archipelago by a network of observers organized by the Observatoire des Mammifères Marins de l'Archipel Guadeloupeen (OMMAG). While there are no effort data associated with these sightings, the network also tracks resident cetacean species year round and many participants are operating in these waters throughout the year. The dates that sightings of whales identified by fluke photographs were made were also investigated for evidence of seasonal presence. Finally, the dates of reported humpback whale catches from 19th Century whaling logbooks compiled by Reeves *et al.* (2001a) are included for comparison.

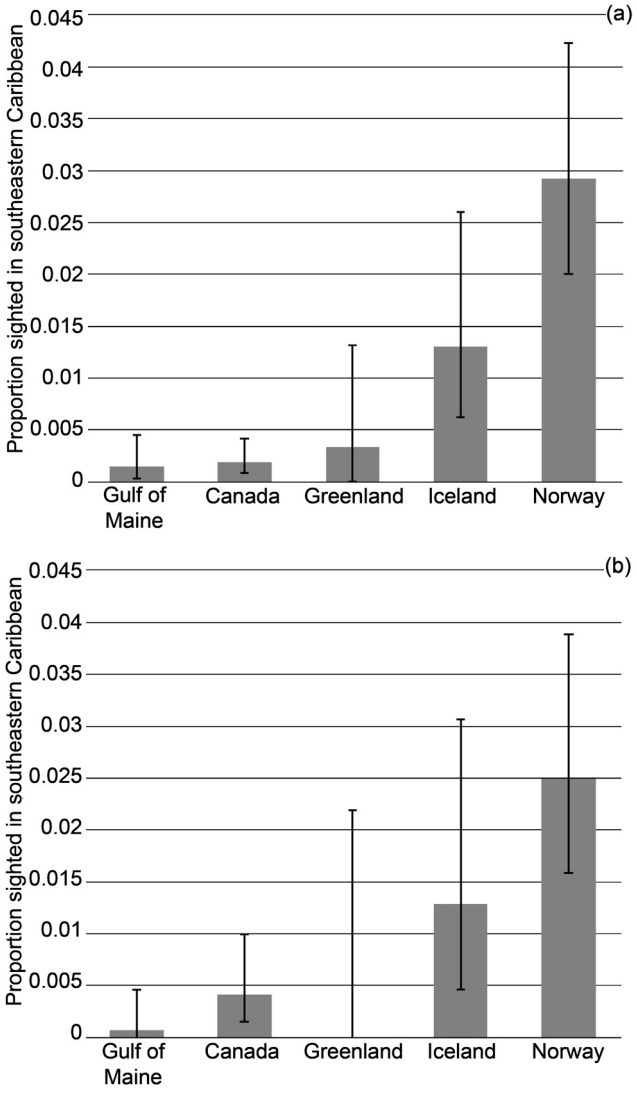


Fig. 3. The proportion of whales (with 95% CI) from each of the high-latitude feeding areas that also have been sighted in the southeastern Caribbean. 3a includes all individuals identified in the high latitude feeding areas. 3b includes only those records from the high latitude feeding areas that are more recent than year 2000.

## RESULTS

Whales from the southeastern Caribbean were re-sighted in all of the major feeding grounds, with 43 individuals re-sighted on the feeding grounds. However, the proportion of re-sightings to the different feeding areas differed significantly ($p = 1.41 \times 10^{-12}$ Multinomial exact test; Fig. 3a). The major difference was between the feeding grounds along the eastern and western margins of the North Atlantic. The number of re-sightings to Norway was nine times that to the Gulf of Maine. The 95% confidence intervals for the Gulf of Maine and Canada did not overlap with those from Iceland and Norway.

As the data spans multiple decades, and the probability of making a resighting will decline with increasing time between samples in an open population, the samples from the feeding grounds were restricted to individuals identified since 2000 to more closely correspond with the time when most samples were collected from the southeastern Caribbean. While this reduced precision, the overall pattern of resightings changed little ($p = 7.02 \times 10^{-8}$ Multinomial exact test; Fig. 3b).

The proportion of whales in the southeastern Caribbean showing visible scarring on the flukes from non-lethal attack by killer whales was 0.0345 (95% CI 0.017–0.065; Fig. 4). This proportion is nearly identical to that from Norwegian waters observed in the NNHWC (0.0366 95% CI 0.026–0.052) and quite similar to the substantially less precise figure previously reported for whales feeding in Norwegian waters (0.027; McCordic *et al.*, 2014). The scarring rate differed significantly from that reported in each of the western feeding areas (Gulf of Maine, $p = 9.98 \times 10^{-4}$; Canada, $p = 2.5 \times 10^{-11}$; Greenland, $p = 2.3 \times 10^{-4}$; Fisher's exact tests; feeding area results from McCordic *et al.*, 2014). The comparison with Iceland is somewhat more ambiguous. The Fisher's exact test demonstrates a significant difference between the number of individuals in these areas that have visible scarring ($p = 0.043$). However, the upper bound of the Wald confidence intervals for the proportion from the southeastern Caribbean overlaps with the lower bound previously reported from Iceland (0.051; McCordic *et al.*, 2014). The proportions of humpbacks with killer whale scars for Iceland and Norway are lower than those for the same regions reported by Mehta *et al.* (2007). The sample size has increased substantially and the additional whales included in

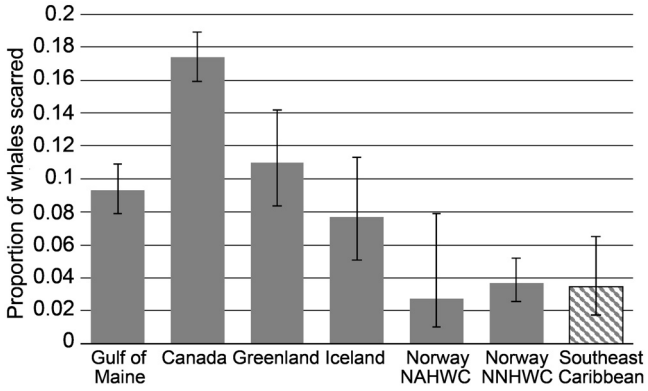


Fig. 4. The proportion of whales (with 95% CI) from each of the high-latitude feeding areas (from McCordic *et al.,* 2014), the Northern Norway Humpback Whale Catalogue and the southeastern Caribbean that have visible killer whale scarring on the flukes.

the more recent work are likely to make it a more accurate representation of scar rates. There may also be slight differences in how coding was conducted for the two studies. However, the analyses presented by Mehta *et al.* (2007) represent a similar trend, with the lowest proportion being found on whales from Norway and a low scarring rate also from Iceland. In all cases Iceland and Norway have the smallest samples among the high-latitude feeding grounds and are therefore the least precise.

The timing of presence in the area shown by the two effort-corrected data sets (sighting and acoustic survey) agrees well with the two uncorrected data sets (sighting network and identifications) and with the humpback whaling catches (Fig. 5). While sightings have been reported as early as November, humpback whales are seen in only low numbers in the southeastern Caribbean before the beginning of February. The peak in sightings occurs during March and April, declining rapidly during May, with some sightings extending into June. Acoustic detections peak earlier than sightings. Surveys are conducted throughout the year, but no humpback whales have been reported from July through October. The seasonal pattern in the non-effort-corrected data sets closely matches that from the survey data. The median sighting date for animals identified by fluke photograph from Guadeloupe is 3 April, with more than 80% of identified whales being sighted in March or April.

## DISCUSSION

These data show two ways in which the humpback whales in the southeastern Caribbean differ from those off the Dominican Republic. While migration has been documented to all of the major feeding areas, the results presented here demonstrate a strong tendency for whales from the southeastern Caribbean to migrate to feeding areas in the eastern North Atlantic. This observation is supported by the much lower incidence of killer whale scarring seen on whales in the southeastern Caribbean than on whales from the western feeding grounds. Within the eastern feeding areas, the higher rate of re-sightings to Norway than to Iceland and the greater similarity in killer whale scarring with Norway than with Iceland may suggest a stronger migratory affinity for Norwegian waters. The over-representation of whales from Iceland and Norway in these data is in direct contrast to the pattern reported from the Dominican Republic. Individuals feeding in the eastern North Atlantic were previously shown to be under-represented in a sample of 1,080 individuals collected from the Dominican Republic and Puerto Rico (Stevick *et al.*, 2003).

The seasonal pattern of humpback whale presence in the southeastern Caribbean is also in stark contrast to that for sightings reported in the Dominican Republic. The observed timing in the southeastern Caribbean is consistent with historical patterns, as whales were killed in the area primarily during February through May (Reeves *et al.*, 2001a; 2004).

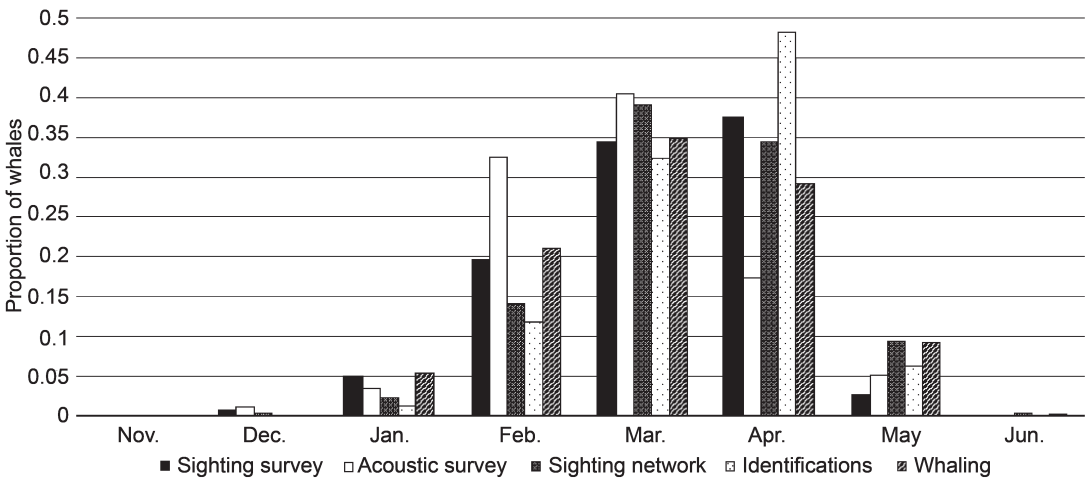


Fig. 5. Seasonal occurrence of humpback whales in the southeastern Caribbean. The sighting survey represents the number of whales sighted per hundred hours of sighting effort, 1998–2009, while acoustic survey represents the number of whales detected acoustically per hundred hours of acoustic monitoring, 2001–2009. Both were conducted off the leeward coast of Basse Terre island, Guadeloupe by AET. Surveys were conducted throughout the year, but only months when humpback whales were seen or heard are included here. Identifications represent the dates of all sightings in the NAHWC database. The sighting network represents 2,390 sightings reported to the OMMAG sighting program in the Guadeloupe archipelago from 2010 to 2014. Neither of these are corrected for effort. The dates of humpback whale records from 19th Century whaling logbooks (whaling) are included for comparison (using data from table 2 in Reeves *et al.,* 2001a). Most are from the waters between Guadeloupe and Trinidad, though there are also some records from other regions. These also do not account for effort.

However, whales on Silver and Navidad Banks, Dominican Republic, appear in early January, and are at their peak densities in February and early March, with few animals remaining by early April (Balcomb and Nichols, 1982; Whitehead and Moore, 1982; Whitehead, 1982). The pattern is very similar in Samana Bay, Dominican Republic, with the greatest sighting per unit of effort observed in February and early March (Mattila *et al.*, 1994).

As such, the peak of distribution in the southeastern Caribbean is about six weeks later than in the Dominican Republic, and there is little overlap in the periods of greatest use. Some of the highest densities occur during April and May, which is well after humpbacks are essentially absent from the Dominican Republic (Whitehead and Moore, 1982; Whitehead, 1982; Mattila *et al.*, 1994). This also overlaps with the peak migratory season for northbound whales at Bermuda, where most sightings occur during April (Stone *et al.*, 1987) and continues after whales have begun arriving on some of the feeding grounds. For example, in the Gulf of Maine, humpback whales are numerous enough to support commercial whale watch operations by mid-April (Clapham, 1993). On the Stellwagen Bank National Marine Sanctuary (Gulf of Maine), humpback songs occurred from mid-March through early-June with a peak in singing activity in the middle of April (Vu *et al.,* 2012; Stanistreet *et al.,* 2013). This timing difference may be related to the feeding ground origin/destination of these whales, as it has been previously demonstrated that humpback whales from eastern feeding areas are sighted in the Dominican Republic significantly later than are those with feeding area sightings in the western North Atlantic (Stevick *et al*., 2003). Based on what we currently know, the Swartz *et al.* (2003) research survey of the southeast Caribbean in 2001 was most likely too early in the season and may have missed the peak in humpback sightings, which would have been several weeks later.

Other work provides additional support for an eastern North Atlantic connection to the southeastern Caribbean. In a recent tagging study, all three tagged humpback whales were able to be tracked on at least part of their migration. All were observed to travel in a direction consistent with a feeding ground destination in the eastern North Atlantic, and one of these was tracked to waters west of the Faroe Islands (Kennedy *et al.,* 2013). Furthermore, four individual humpback whales from Guadeloupe have also been identified in the Cape Verde Islands, some 4,000km to the east, including one whale that was also identified off Norway (Stevick *et al.,* 2016). Also, a whale from Trinidad was identified genetically off Norway (Bérubé *et al.,* 2004).

In conclusion, the whales mating and calving in this southeastern Caribbean region do not seem to be a representative subset of those that winter in the Dominican Republic. Most of the whales considered in this study were in the vicinity of Guadeloupe, and studies to the north and south will be needed to examine the spatial nature of this pattern, and define the nature and limits of this group. However, it is clear that some of the whales using the southeastern Caribbean represent a previously un-described distinct population segment within the North Atlantic. Given this, the widely-held idea that there is a single West Indies breeding population (Bettridge *et al.,* 2015) is in need of reconsideration.

**ACKNOWLEDGEMENTS**

This study would not have been 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. Particular thanks to the many researchers from the feeding areas to which these whales were compared. We extend special appreciation to E. Aaseth, H. Baer, S. Barnaby, C. Bertulli, Blue Ocean Society for Marine Conservation, Center for Coastal Studies, K. Chater, Coastal Research and Education Society of Long Island, A. Debrot, S. Gero, R. Etcheberry, A. Erven, Greenland Institute of Natural Resources, C. Graeme, B. Gretz, F. Hester, J. Horrocks, Húsavík Research Center, Húsavík Whaling Museum, Institute of Marine Research (Norway), M. Kilmer, R. Kempen, Marine Research Institute (Iceland), Memorial University of Newfoundland, C. Lecroy, Mingan Island Cetacean Study, Ocean Research and Education Society, C. Price, J. Rambally, D. Snow, Whale and Dolphin Conservation, Whale Center of New England, H. Whitehead, H. Winn and D. Young. Countless staff and students have spent untold hours comparing photographs. L. Jones, L. Crowe and O. Bolus contributed to the recent comparison from the southeastern Caribbean. A. St. Onge assisted with the scar coding. M. Messina prepared the maps. We are particularly grateful for the assistance of J. Allen, T. Fernald and R. Seton. Dozens of individuals contributed sightings and photographs to the research effort in Guadeloupe. The NAHWC is funded by donors and an anonymous foundation. This project has been made possible with support of the Stellwagen Bank National Marine Sanctuary (US Office of National Marine Sanctuaries) and Yarari Marine Mammal Sanctuary (Caribbean Netherlands). The North Atlantic Humpback Whale Sister Sanctuary Program; A project under the framework of the United Nations Caribbean Environment Programmes Specially Protected Areas and Wildlife Programme partners (Stellwagen Bank National Marine Sanctuary and the Caribbean Netherlands marine mammal initiative) who provided invaluable additional support for these analyses. Comparison of photos from Norway was made possible by funding through the Fram Centre 'Fjord & Coast Flagship' funding scheme and National Geographic Society grant GEF (GEFNE130-14). There were many conversations that took place around the workshop on Current Developments in North Atlantic Humpback Whale Research, held in Malta in March 2015 in conjunction with the European Cetacean Society meeting, which helped substantially in developing these ideas. Special thanks to P. Corkeron, S. Hayes and M. Simpkins (NOAA, NMFS, NEFSC) and to R. Reeves, P. Clapham and an anonymous reviewer for their review and productive comments to earlier versions of this manuscript.

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