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

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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

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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; Orviedo & 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., 2003; Matthiopoulos et al., 2005). Relatively low levels of small-scale fidelity have been shown within breeding
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., 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.

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 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.
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., 2011). 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.

<table>
<thead>
<tr>
<th>Whale id</th>
<th>Date</th>
<th>Location</th>
</tr>
</thead>
<tbody>
<tr>
<td>na4474</td>
<td>9 April 2010</td>
<td>Off Boa Vista, CVI</td>
</tr>
<tr>
<td>na4756</td>
<td>13 April 2011</td>
<td>Pointe Des Chateaux, Guadeloupe</td>
</tr>
<tr>
<td>na4918</td>
<td>22 April 2009</td>
<td>Off Boa Vista, CVI</td>
</tr>
<tr>
<td></td>
<td>7 April – 4 May 2011</td>
<td>Off Boa Vista, CVI</td>
</tr>
<tr>
<td></td>
<td>19 April 2012</td>
<td>Off Guadeloupe</td>
</tr>
<tr>
<td></td>
<td>2–15 May 2013</td>
<td>Off Boa Vista, CVI</td>
</tr>
<tr>
<td></td>
<td>5–22 May 2014</td>
<td>Off Boa Vista, CVI</td>
</tr>
<tr>
<td>na4933</td>
<td>18 March 1999</td>
<td>CVI</td>
</tr>
<tr>
<td></td>
<td>24 March 2012</td>
<td>la Vigie, Guadeloupe</td>
</tr>
<tr>
<td>na4935</td>
<td>21 March 1999</td>
<td>CVI</td>
</tr>
<tr>
<td></td>
<td>4 April 2003</td>
<td>CVI</td>
</tr>
<tr>
<td></td>
<td>28 April 2009</td>
<td>Petite Terre, Guadeloupe</td>
</tr>
<tr>
<td></td>
<td>13 April 2010</td>
<td>Off Boa Vista, CVI</td>
</tr>
<tr>
<td></td>
<td>4–9 May 2012</td>
<td>Off Boa Vista, CVI</td>
</tr>
<tr>
<td></td>
<td>23 January 2014</td>
<td>Northern Norway</td>
</tr>
</tbody>
</table>

**Table 1.** Sighting histories of humpback whales identified in both the Cape Verde Islands and off Guadeloupe.
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 (Valsecchi et al., 1997), which extends from the eastern North Atlantic that are not known from the Cape Verde Islands and some portion of the West Indies 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.

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REFERENCES


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