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Migratory preferences of humpback whales between feeding and breeding grounds in the eastern South Pacific

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Abstract

Latitudinal preferences within the breeding range have been suggested for Breeding Stock G humpback whales that summer in different feeding areas of the eastern South Pacific. To address this hypothesis, humpback whales photo-identified from the Antarctic Peninsula and the Fueguian Archipelago (southern Chile) were compared with whales photo-identified from lower latitudes extending from northern Peru to Costa Rica. This comparison was performed over a time span that includes 18 austral seasons. A total of 238 whales identified from the Antarctic Peninsula and 25 whales from the Fueguian Archipelago were among those photo-identified at the breeding grounds. Our findings showed that humpback whales from each feeding area were resighted unevenly across the breeding grounds, which suggests a degree of spatial structuring in the migratory pathway. Humpback whales that feed at the Antarctic Peninsula were more likely to migrate to the southern breeding range between northern Peru and Colombia, whereas whales that feed at the Fueguian Archipelago were more likely to be found in the northern range of the breeding ground off Panama. Further photo-identification efforts and genetic sampling from poorly sampled or unsampled areas are recommended to confirm these reported connectivity patterns.

Key words: *Megaptera novaeangliae*, migratory destinations, Breeding Stock G, photo-identification, feeding ground, Antarctic Peninsula, Fueguian Archipelago.

Humpback whales (*Megaptera novaeangliae*) undertake long-distance seasonal migrations between high-latitude regions, where they feed during summer and part of autumn, and low-latitude regions, where they breed during winter (Dawbin 1966). In certain cases, this migration can reach one-way distances of ~8,000–8,500 km (*e.g.*, Stone *et al.* 1990, Rasmussen *et al.* 2007). In the Southern Hemisphere, the International Whaling Commission (IWC) has defined seven breeding populations (Breeding Stocks A to G) for management purposes (IWC 1998). Although these breeding grounds are geographically separated by landmasses or wide ocean basins, physical barriers to dispersal are absent in high-latitude regions; therefore, individuals from different breeding stocks may intermingle while feeding in Antarctic waters. Thus, a one-to-one connection does not necessarily occur between their feeding grounds and their respective breeding grounds (Chittleborough 1965; Pomilla and Rosenbaum 2005; Forestell and Urbán 2007; Stevick *et al.* 2010, 2013; Kaufman *et al.* 2011; Robins *et al.* 2011; Schmitt *et al.* 2014).

In the eastern South Pacific, humpback whales primarily breed along the coasts of northern Peru (~4°S) to Costa Rica (~12°N) (Flórez-González 1991, Acevedo-Gutiérrez and Smultea 1995, Félix and Haase 1997, Scheidat *et al.* 2000, Rasmussen *et al.* 2007, Best 2008, Pacheco *et al.* 2009, Guidino *et al.* 2014) and migrate to three discrete feeding areas: two in southern Chile and one off the Antarctic Peninsula (Mackintosh 1942, Gibbons *et al.* 2003, Acevedo 2005, Acevedo *et al.* 2006, Haro 2009, Hucke-Gaete *et al.* 2013). This humpback whale population is named Breeding Stock G (BSG, IWC 1998).

Previous studies involving photo-identification (Stone *et al.* 1990, Stevick *et al.* 2004, Rasmussen *et al.* 2007, Dalla Rosa *et al.* 2012, Guzmán *et al.* 2015) and genetic analyses (Caballero *et al.* 2001, Engel *et al.* 2008, Félix *et al.* 2012) provided

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evidence of the connectivity between specific wintering sites of BSG and the Antarctic Peninsula feeding area. In recent years, additional studies based on photo-identification have also yielded evidence of the connectivity of certain whales between the Fueguian Archipelago feeding area (~53°40′S) and wintering sites of BSG (Acevedo *et al*. 2007, Capella *et al*. 2008); however, this connectivity has not been as clearly demonstrated in molecular studies (Olavarría *et al*. 2006, Félix *et al*. 2012).

Current photo-identification and genetic data suggest a level of population structuring between feeding areas (Olavarría *et al*. 2006, Acevedo *et al*. 2013) and genetic structuring between breeding and feeding areas of BSG (Félix *et al*. 2012). Additionally, preliminary evidence shows latitudinal differences in the migratory connectivity within BSG and suggests that the southern area of the breeding range appears to serve primarily as a migratory corridor for whales that feed in the Fueguian Archipelago feeding area (Acevedo *et al*. 2007). This hypothesis is supported in part by an individual that was observed in three consecutive seasons in the Fueguian Archipelago feeding area and in both interceding winters in Panama, whereas seven other whales known to feed in the Fueguian Archipelago have only been sighted once in Ecuador and Colombia, and may represent animals in transit to or from more northern breeding sites (Acevedo *et al*. 2007).

Although important insights into the migratory connectivity of BSG have been reported, potential latitudinal preferences in the migratory destinations for breeding from a particular feeding area have yet to be examined. To address this topic, latitudinal preferences in the migratory connectivity of humpback whales between their feeding areas and low-latitude breeding areas spanning the Pacific coast of South and Central America were examined based on large samples of photo-identified humpback whales. The photographs were collected from 1986 to 2013 as part of a broadscale collaboration among scientists conducting studies in the eastern Pacific, from Costa Rica to the Antarctic Peninsula. Understanding the potential latitudinal variability in the migratory connectivity of humpback whales within this population could yield insights into the regional differences in migratory behavior related to a north and south feeding region, and provide important information for future assessments of the dynamic population of BSG.

Materials and Methods

A data set of individual humpback whale fluke photographs was assembled from 14 independent research teams working throughout the eastern South Pacific. Photographs of flukes were collected from systematic surveys, whale-watching operations, and other opportunistic platforms from late May to late October/November, when humpback whales are known to use the low-latitude region for breeding, and from December to May, when humpback whales are known to use the high-latitude region for foraging. Whales were identified by the natural coloring patterns, marks, and permanent scars on the underside of their tail flukes (Katona *et al*. 1979). A total of 6,605 whales were identified, however, because of the extent of this collaboration, considerable spatial and temporal variations exist in the number of photographs.

Prior to the analysis, the four Antarctic Peninsula catalogues were visually compared to exclude duplicated individuals (n = 100). For certain breeding areas where two or more catalogues were available for the same location, duplicate individuals obtained during the same winter season were discarded (n = 52). A total of 1,187 identified whales in the Antarctic Peninsula and 137 identified whales in the

Fueguian Archipelago feeding areas was compared with 4,802 identified whales in the breeding ground of the eastern South Pacific. Photo-identification catalogs of the Antarctic Peninsula and Fueguian Archipelago feeding areas were also compared. To examine the differences in the migratory connectivity within the breeding grounds, the sample was stratified into nine breeding sites from northern Peru to Costa Rica. Each breeding site corresponded to the location where the research effort was applied (Table 1, Fig. 1). Only photographs that provided a good visual resolution of the marks were used for the comparisons. All matches were independently re-confirmed by members of the respective research teams that provided the matching photographs. Each match was considered an independent "event."

Because whales can be resighted more than once in the same breeding site in different years or in two or more places in one year or across several years, the "events" were arranged as follows: (1) if individuals were sighted at a single or multiple sites in different years (*e.g.*, one site each year), each breeding site was assumed to represent their final migratory destination; (2) if individuals were sighted at more than one breeding area during the same year, the northernmost breeding site was assumed to be their final migratory destination and the previous breeding site was considered part of their transit zones, with the latter excluded from the posterior analysis.

To test the hypothesis of latitudinal migratory differences of the whales identified in each feeding area, we made inferences based on the probability of transitioning between each feeding area and specific sites of the breeding ground (ψ) *via* multistate models. Accordingly, ψ_{FB} is defined as the probability that a whale alive in region F (feeding area) at time t will be in region B (breeding area) at time t + 1; P_F is defined as the probability that a whale alive in region F in year t will be sighted; and f_F is defined as the probability that a whale alive in year t in region F will survive over the interval (t, t + 1). The regions F and B are feeding and breeding grounds, respectively. Three geographic states were defined for the multistate models: feeding areas (F), southern breeding sites (Bs) from northern Peru to Gorgona Island in Colombia, and the northern breeding sites (Bn) from Coqui Cove/Gulf of Tribugá in Colombia to Drake Bay/Dulce Gulf in Costa Rica. The southern and northern breeding sections have a similar length (~1,103–1,222 km of coast). A set of models was developed that corresponded to our best *a priori* hypothesis. We used the lowest adjusted Akaike information criterion (AICc) (Burnham and Anderson 2002) to select the model that provided the most parsimonious description of the variation in the data. We also used the weighted (w) AICc as a measure of relative support for each model (Burnham and Anderson 2002). All of the computations were conducted using program MARK version 8.0 (White and Burnham 1999), and the sin link function available from MARK was used. Estimates of the SE and 95% confidence interval (95% CI) were obtained directly from MARK. Goodness of fit (GOF) tests of multistate models were calculated using the U-CARE version 2.3 program (Choquet *et al*. 2005, 2009). Data overdispersion was measured by summing the tests WBWA, 3G.SR, 3G.Sm, M.ITEC, and M.LTEC (Choquet *et al*. 2009). Significant differences (*i.e.*, $P < 0.05$) indicated that overdispersions should be corrected (Choquet *et al*. 2005, 2009).

The proportion of white and black coloration on the underside of the tail flukes was also examined. Of the 6,098 flukes, a total of 5,591 were ranked in values ranging from 1 (all white) to 5 (all black) (Rosenbaum *et al.* 1995). The variations in the photographs were ranked by two trained observers, and the average values of the coloration rank were used for each area in the analysis. Differences in the frequency of the coloration categories between a feeding area and nine breeding sites were assessed

Table 1. Number of humpback whales from each study area that were identified and examined.

Ground	Area	Sampling years	Number of whales: Total	Number of whales: Examined	Curator
Feeding	Antarctic Peninsula (region includes: Bransfield and Gerlache Straits, Grandidier Channel, and South Orkney Islands).	1985–2010	1,316	1,187	Projeto Baleias/PROANTAR, INACH Project 163, College of the Atlantic, Fundación CEQUA and other contributors
	Fueguian Archipelago, Chile.	2003–2013	147	137	Fundación CEQUA
Breeding	Los Órganos, northern Peru	2009–2013	311	308	Pacific Adventures
	Salinas and Machalilla National Park, Ecuador	1991–2010	3,310	3,095	Museo de Ballenas and Pacific Whales Foundation-Ecuador
	Esmeraldas and Machalilla National Park, Ecuador	1996–2012	337	323	Project Cetacea USFQ
	Gorgona Islands National Park, Coqui Cove, Colombia	1986–1994, 2003 2000–2002	438	397	Fundación Yubarta
	Gulf of Tribugá, Colombia	2010, -2013	194	153	Fundación Macuáticos Colombia
	Las Perlas Archipelago/Gulf of Panama, Panama	2003–2009, 2012	145	145	Smithsonian Tropical Research Institute and other contributors
	Chiriqui Gulf, Panama	2002–2004, 2006–2013	343	318	Panacetacea
	Drake Bay/Dulce Gulf, Costa Rica	1993, 1995, 1999, 2001–2003, 2007–2008	64	63	Panacetacea and Asociación Ambiental Vida
			6,605	6,098	

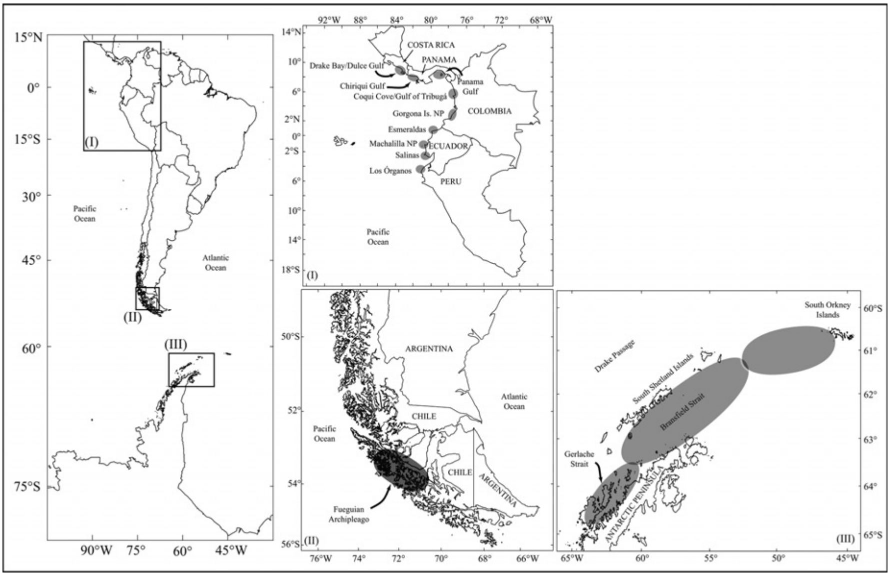

Figure 1. Geographic areas of the examined and identified whales, including details of each sampling area at the breeding (I) and feeding grounds (II, III). Shaded circles and ellipses delimit the main areas where photo-identification was conducted.

using a chi-square test under the hypothesis of uniform distribution. In addition, a hierarchical cluster analysis using an unweighted pair-group average (UPGMA) was performed to display areas with similar coloration frequencies.

Results

Connectivity among Feeding and Breeding Grounds

A total of 377 matches were found between 263 identified whales photographed in both the Antarctic Peninsula and Fueguian Archipelago feeding areas and whales identified in the breeding ground of the eastern South Pacific (Table 2). No matches were found between the photo-identification catalogs of the Antarctic Peninsula and Fueguian Archipelago feeding areas.

From the Antarctic Peninsula feeding area, 238 whales were matched on 336 occasions with at least one breeding site from northern Peru to Costa Rica. Twenty-two of these whales were resighted in the same year between the Antarctic Peninsula and the breeding ground, whereas the remaining whales (90.7%) were resighted between both seasonal habitats (feeding-breeding) in intervals ranging from 1 to 26 yr after their first sighting. The observed matches show that 176 whales were sighted only once in one breeding site. The vast majority of these whales were matched off Ecuador (60.7%) and Colombia (22.7%), and fewer were matched off Panama (7.9%) and Costa Rica (3.9%). Of the whales that were matched across years ($n = 62$), 19 individuals were resighted at the same breeding site during two or three consecutive years or at intervals of 2–7 yr, with Ecuador showing the highest percentage of matches

Table 2. Summary of the observed and expected (in parenthesis) events, the overall events and the events from any single feeding area. Abbreviations: (LO) Los Órganos; (SA) Salinas; (MNP) Machalilla National Park; (ES) Esmeraldas; (GI) Gorgona Island National Park; (CC/GT) Coqui Cove and Gulf of Tribugá; (LPA) Las Perlas Archipelago; (CHG) Chiriqui Gulf; and (DB/DG) Drake Bay and Dulce Bay.

	Peru ($n = 308$)	Ecuador ($n = 3,418$)			Colombia ($n = 550$)		Panama ($n = 463$)		Costa Rica ($n = 63$)	
Country/locality	LO	SA	MNP	ES	GI	CC/GT	LPA	CHG	DB/DG	All breeding sites ($n = 4,802$)
All feeding areas ($n = 1,324$)	12 (24)	67 (138)	163 (122)	12 (10)	58 (29)	17 (12)	17 (11)	18 (25)	12 (5)	377
Antarctic Peninsula ($n = 1,187$)	11 (22)	53 (114)	155 (109)	11 (9)	50 (26)	14 (11)	17 (19)	14 (23)	11 (4)	336
Fueguian Archipelago ($n = 137$)	1 (3)	14 (15)	8 (13)	1 (1)	8 (3)	3 (1)	0 (1)	5 (3)	1 (1)	41

(25.8%). Moreover, only one whale was observed in two consecutive winter seasons in Ecuador (2003–2004) and one interceding summer (2004) in the Antarctic Peninsula. The remaining whales (n = 43) were all resighted at multiple breeding sites across different years. The vast majority of these whales were matched between the Ecuador sites (41.8%) and the Ecuador-Colombia sites (18.6%).

From the Fueguian Archipelago feeding area, 25 individuals (based on 41 matches) were resighted at eight of the nine breeding sites. The observed matches show that 17 whales were sighted only once at one breeding site, mostly at the Ecuador sites (13 whales), followed by Colombia (two whales) and Panama (two whales). However, the two Panama whales were observed in consecutive summer seasons (2007–2008) and the interceding winter (2007), and they displayed a complete migratory cycle. Of the whales that matched the different breeding sites across years (n = 8), one whale was resighted between northern Peru and southern Ecuador and two other whales were sighted between two Ecuadorian sites as well as between Ecuador and northern Colombia (with three events). Finally, an additional three whales were sighted at multiple sites, and Panama and Costa Rica were the northern sites. Of the latter, one whale was also sighted in consecutive summer seasons in the Fueguian Archipelago starting in 2003 and the interceding winters in Panama in 2003, 2004, and 2013.

Goodness of Fit (GOF)

The observed resightings were significantly different from a uniform distribution, both for the overall resightings ($\chi^2 = 102.06$, df = 8, $P < 0.05$) and the resightings at any single feeding area ($\chi^2_{FA} = 16.92$, df = 8, $P < 0.05$; $\chi^2_{AP} = 108.83$, df = 8, $P <$ 0.05), which suggests that individuals from different feeding areas have a preference for migrating to specific breeding sites. The observed number of whales from the different feeding areas was smaller than expected at four breeding sites (Table 2).

The GOF test indicated that model JMV (Jolly-Move model) fit the data well for the Fueguian Archipelago feeding area ($\chi^2_{FA} = 11.38$, df = 27, $P > 0.99$) but not for the Antarctic Peninsula feeding area ($\chi^2_{AP} = 175.05$, df = 134, $P < 0.05$). Therefore, a correction factor ($\hat{c}$) of 1.103 was applied to correct for overdispersions. Based on the resighting histories, the most parsimonious multistate models assumed an estimate ($\hat{E}S$) of the probability of movement that was different for each feeding area. For humpback whales observed at the Antarctic Peninsula feeding area, the model-average movement estimates (ψ_{FB}) were higher for the southern ($\hat{E}S = 0.78 \pm 0.04$, 95% CI = 0.67–0.86) than the northern breeding areas ($\hat{E}S = 0.05 \pm 0.02$, 95% CI = 0.02–0.11), whereas for humpback whales observed at the Fueguian Archipelago feeding area, the movement estimates (ψ_{FB}) were slightly higher for the northern ($\hat{E}S = 0.23 \pm 0.06$, 95% CI = 0.13–0.38) than the southern breeding sites ($\hat{E}S$ = 0.17 ± 0.05, 95% CI = 0.09–0.29). The probability of movement of humpback whales from the Fueguian Archipelago to the Antarctic Peninsula feeding area was 0.01, and the likelihood of matching at least one migrant between these regions based on a modification of the Lincoln-Petersen estimate was <0.008.

Fluke Coloration Patterns

The average fluke coloration values from all sampled areas ranged between 2.13 and 2.74. Within the eastern South Pacific breeding ground, the average fluke coloration values showed an increasing trend from south to north, and this trend was also observed between both feeding areas (Fig. 2). The whitest average coloration was found at Machalilla National Park (Ecuador), and the darkest coloration was observed at Chiriqui Gulf (Panama). Significant differences in the frequencies of fluke pigmentation classes were observed between each of the breeding sites and the Antarctic Peninsula ($\chi^2 = 61.02$, df = 44, $P < 0.05$) and the Fueguian Archipelago feeding areas ($\chi^2 = 75.96$, df = 44, $P < 0.05$). These differences in the distribution of pigmentation classes were observed for flukes that were 75% black ($\chi^2_{AP} = 30.54$ and $\chi^2_{FA} = 41.30$, df = 9,

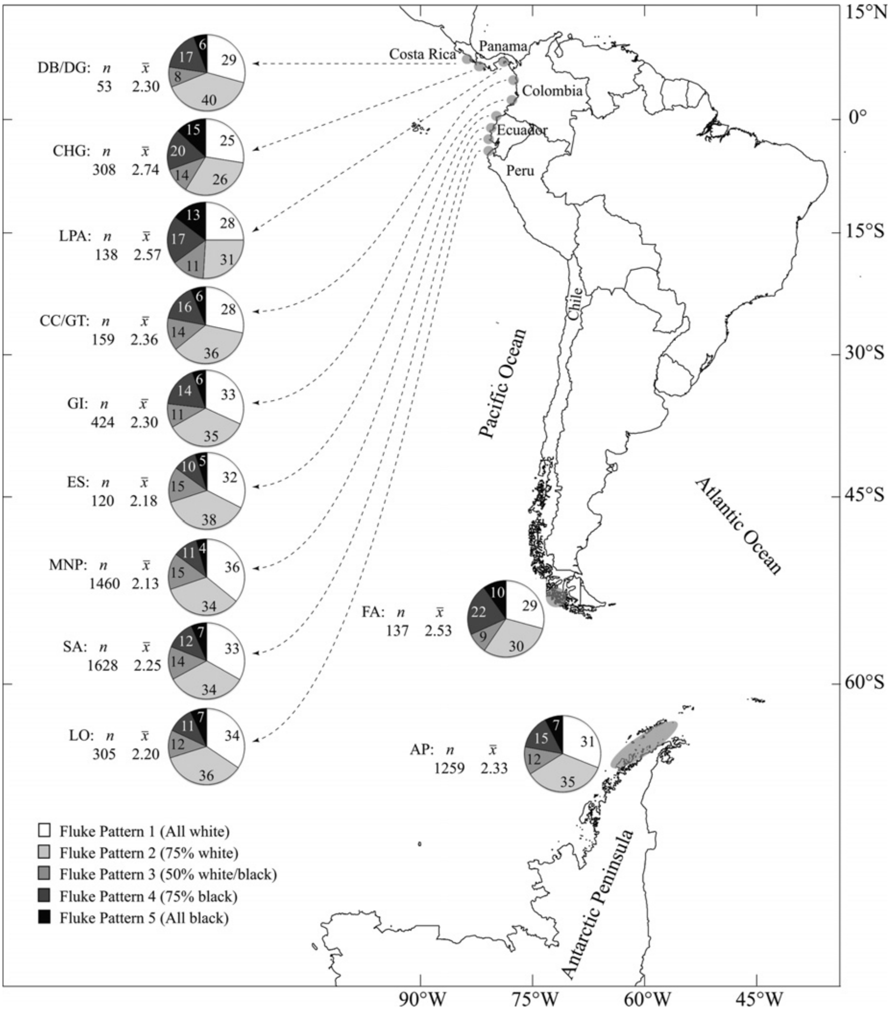

Figure 2. Frequencies of fluke coloration for each area in this study. The frequency assigned-rank values are shown inside each graph. n = number of photographs assessed and $\bar{x}$ = average fluke coloration. Abbreviations: (LO) Los Órganos; (SA) Salinas; (MNP) Machalilla National Park; (ES) Esmeraldas; (GI) Gorgona Island National Park; (CC/GT); Coqui Cove and Gulf of Tribugá; (LPA) Las Perlas Archipelago; (CHG) Chiriqui Gulf; (DB/DG) Drake Bay and Dulce Bay; (FA) Fueguian Archipelago; and (AP) Antarctic Peninsula.

$P < 0.05$) and all black ($\chi^2_{AP} = 70.73$, $\chi^2_{FA} = 71.65$, df = 9, $P < 0.05$). For the Antarctic Peninsula feeding area, the differences in the frequencies of fluke pigmentation classes for the breeding sites Gorgona Island (Colombia), Las Perlas Archipelago and Chiriqui Gulf (Panama) and Drake Bay/Dulce Gulf (Costa Rica) were observed for 75% black and all black flukes. For the Fueguian Archipelago feeding area, the highest differences for the breeding sites from northern Peru to Ecuador were observed for the 75% black fluke category, and from northern Peru to Coqui Cove/Gulf of Tribugá (Colombia) and Costa Rica were observed for the all black fluke category.

The cluster analysis identified two primary groups (correlation: 0.85). The first was composed of similar fluke colorations between whales from the Fueguian Archipelago feeding area and the two breeding sites off Panama (Las Perlas Archipelago and Chiriqui Gulf) (correlation: 0.98), and the second one was composed of whales from the Antarctic Peninsula feeding area and the breeding sites from northern Peru to Coqui Cove/Gulf of Tribugá (Colombia) and Costa Rica (correlation: 0.99) (Fig. 3). However, in this second group, the breeding sites of Coqui Cove/Gulf of Tribugá and

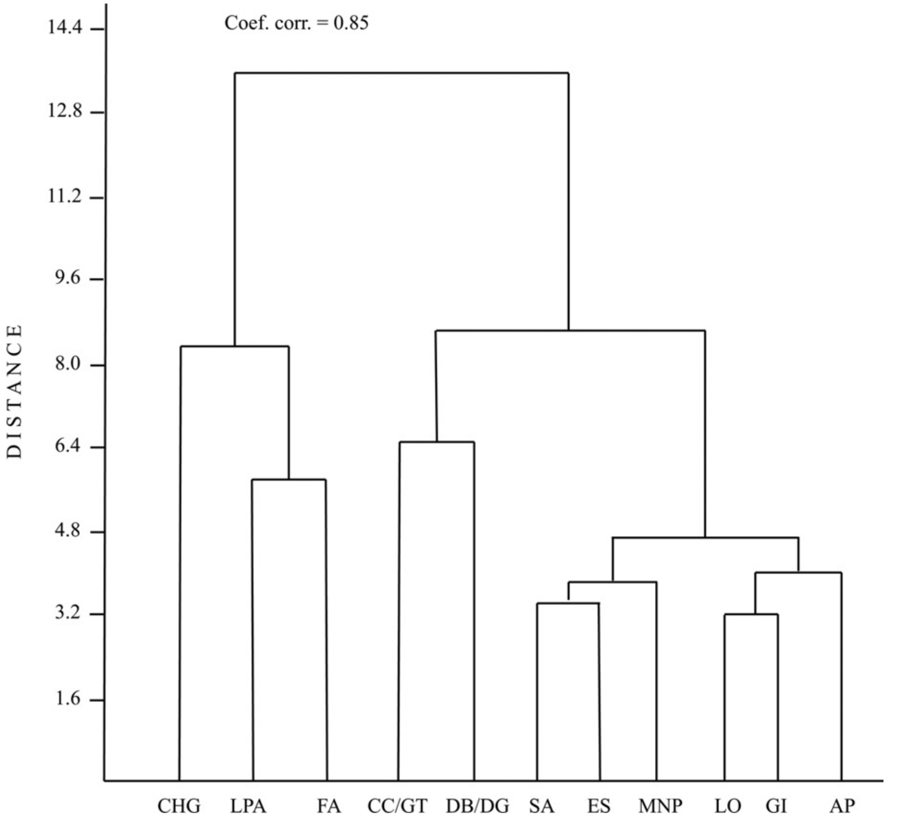

Figure 3. Dendrogram of the hierarchical cluster analysis of the fluke coloration frequencies. Abbreviations: (LO) Los Órganos; (SA) Salinas; (MNP) Machalilla National Park; (ES) Esmeraldas; (GI) Gorgona Island National Park; (CC/GT) Coqui Cove and Gulf of Tribugá; (LPA) Las Perlas Archipelago; (CHG) Chiriqui Gulf; (DB/DG) Drake Bay and Dulce Bay, (FA) Fueguian Archipelago; and (AP) Antarctic Peninsula.

Drake Bay/Dulce Gulf (Costa Rica) formed a distinct subgroup from the main group of Antarctic Peninsula humpback whales, although the position of the breeding site off Costa Rica should be interpreted with caution because the number of available and evaluated photographs was small ($n = 63$).

Discussion

This study identified a substantial number of new resightings between the breeding and feeding areas of BSG and provides further evidence for previously reported movement patterns, as well as new insights into latitudinal preferences. The observed matches between each feeding area and the common breeding grounds of BSG largely confirm the connectivity reported in previous studies that have used photo-identification data (Stone *et al.* 1990, Stevick *et al.* 2004, Acevedo *et al.* 2007, Rasmussen *et al.* 2007, Guzmán *et al.* 2015), and provide the first evidence that the whales that summer in the Antarctic Peninsula migrate to northern Peru. However, our main focus was to provide new insights into the spatial structuring of BSG humpback whales by testing the hypothesis of potential latitudinal preferences in their migratory behavior.

The portion of whales that match one or multiple breeding sites can provide insights into the latitudinal preferences of these whales for breeding grounds. Humpback whales from the Antarctic Peninsula feeding area were mostly matched with southern breeding sites, and the highest overall match rate was observed in Ecuador and Colombia, with a lower percentage of overall matches observed in the northern breeding sites, such as the Panama and Costa Rica sites. For whales identified at the Fueguian Archipelago feeding area, the matches also showed that a greater number of animals were resighted in Ecuador (all sighted only once in these areas); however, certain animals displayed complete migration cycles ($n = 5$) between the Fueguian Archipelago and the northern breeding sites (Chiriqui Gulf, Panama). These findings suggest that whales from the southernmost feeding area (Antarctic Peninsula) are more likely to migrate to the southern breeding range (northern Peru to middle Colombia), whereas whales from the northernmost feeding area (Fueguian Archipelago) are more likely to migrate to the northern region of the breeding range. Although a portion of humpback whales from both feeding areas could have been captured in the more southerly areas during their transit to the more northerly breeding region, our inferences based on the probability of transition of movement (multistate models) and the analyses of site-specific fluke pigmentation are consistent with the evidence of latitudinal preferences in the winter migratory connectivity from each feeding area in the BSG.

These latitudinal preferences in the migratory connectivity are consistent with a previous analysis of genetic studies. Humpback whales that breed in the BSG are known to migrate to three feeding areas; however, the highest genetic similarity is found between individuals feeding around the Antarctic Peninsula and individuals breeding off Ecuador (Salinas) and Colombia (Gorgona Island) (Caballero *et al.* 2001, Félix *et al.* 2012). This genetic similarity is not as obvious for humpback whales from the Fueguian Archipelago feeding area with those same breeding sites (Olavarría *et al.* 2006, Félix *et al.* 2012), although no genetic samples from Peru, Panama, and Costa Rica have been included in these analyses. Despite this latitudinal pattern, a degree of mixing also occurs within the breeding ground as reflected in the matches documented here. Thus, although whales from the Antarctic Peninsula feeding area show the greatest connection with the southern breeding region, certain whales will migrate to the northern breeding region, which is explained by the levels of interchange detected in the multistate model.

Our results are also consistent with the absence of resightings between the Antarctic Peninsula and Fueguian Archipelago humpback whales as previously observed *via* photo-identification records (Acevedo *et al.* 2007, 2013), which support the distinctiveness of both feeding areas. This lack of resightings and lower probability of interchange detected with the Antarctic Peninsula feeding area can be explained by the high site fidelity of the humpback whales, especially for the individuals that migrate to the Fueguian Archipelago feeding area (74.8%, Acevedo *et al.* 2014). Moreover, although the Fueguian Archipelago humpback whales share some common mtDNA haplotypes with the Antarctic Peninsula whales, striking differences in the regional frequencies of mtDNA haplotypes are documented between both feeding areas (Olavarría *et al.* 2006, Félix *et al.* 2012).

This latitudinal pattern of interchange between seasonal habitat has also been reported for the eastern North Pacific humpback whale population, where whales feeding in the northern areas (*e.g.*, Washington) migrate primarily to mainland Mexico (northern breeding range) and those feeding in the southern area (*e.g.*, south of California) migrate primarily to Central America (southern breeding range) (Calambokidis *et al.* 2000, 2001, 2008; Barlow *et al.* 2011). This structure in the BSG migratory connectivity might be partially reflected in the regional differences in behavioral and migratory patterns (coastal *vs.* oceanic); however, data on the migratory behavior and routes and the short-range movement pattern within the BSG are scarce (*e.g.*, Félix and Guzmán 2014, Guzmán *et al.* 2015) and remains to be investigated. These latitudinal preferences may also reflect the differences in regional maternal fidelity and natal philopatry, which play important roles in the formation of the genetic structure of whale populations (Baker *et al.* 1990, 1994; Medrano-González *et al.* 1995; Palumbi and Baker 1994; Pardini *et al.* 2001; Lee *et al.* 2007; Baker *et al.* 2013; Carvalho *et al.* 2014). For most whales, the early maternally inherited experiences of calves during the first year of life provide a direct mechanism for the learned fidelity to breeding and feeding habitats and represent the basis for the cultural inheritance of migratory destinations (Clapham *et al.* 2008, Baker *et al.* 2013).

Our comparison used the more extensive photo-identification samples available for BSG (n = 6,098 flukes); however, our resightings between the seasonal habitats are relatively low (263 whales of 4,802 flukes photographed in the breeding ground or 1,324 flukes photographed in both feeding areas), and the migratory connectivity remains unknown for many whales. This gap is likely to remain because most of the efforts to photo-identify individuals are concentrated in specific coastal areas. Assuming that all humpback whales migrate seasonally from low-latitude to high-latitude regions, the sample size for the latter represents only 27.5% of all whales identified at the breeding ground, which suggests that certain components of the population are underrepresented or missing (unsampled). The number of whales identified at the Fueguian Archipelago feeding area (n = 137) that was used here is slightly lower than the estimated population size based on an extensive capture-recapture effort (153 individuals; 95% CI: 147–160 in 2012, Gende *et al.* 2014). However, our comparison set for the Antarctic Peninsula represents an underestimated sample of the real population size (~3,500 individuals, Branch 2011). Although many whale surveys have been conducted around the Antarctic Peninsula, the photo-identification effort has been mainly concentrated between the South Shetland Islands and the western coast of the Antarctic Peninsula, which represents a small fraction of all humpback whales feeding along the Antarctic Peninsula (Secchi *et al.* 2011). In addition, historical and recent studies provide evidence that humpback whales from the BSG can reach a latitudinal extent of up to 69°S (Rayner 1953, Curtice *et al.* 2015), between 73°W (Rayner 1953) and 110°W (Mackintosh 1942) in the western extension, and up to 40°W (Dalla Rosa *et al.* 2012) and as far as 27°W in more eastward areas (Castro *et al.* 2015). Nonetheless, the absence of these regions likely did not influence the conclusions of this study; although we recognize that further effort is required to cover the latter area to provide more robust data. There is also some degree of interchange of whales between different populations, which could decrease the proportion of resightings. However, this decrease is likely negligible in our analysis because only four matches have been documented between BSG whales and other breeding populations (Dawbin 1964, Robbins *et al.* 2011, Stevick *et al.* 2013).

A similar situation is observed in the BSG whales in the low latitudes because our samples are overrepresented in certain areas and underrepresented in other areas, such as Costa Rica, where southern humpback whales have been known to occur since the early 1990s (Acevedo-Gutiérrez and Smultea 1995); however, this area remains relatively unsampled. There have also been scarce sampling efforts focused on open waters or around oceanic islands, such as the Galapagos Islands off Ecuador (*e.g.*, Palacios and Salazar 2002, Castro and Merlen 2009, Félix *et al.* 2011), Coco Island off Costa Rica (Acevedo-Gutiérrez and Smultea 2005), Lobos de Tierra Island in northern Peru[3] and Juan Fernandez Archipelago and Eastern Island off Chile (Aguayo-Lobo *et al.* 1998). In addition, although the few winter sightings of humpback whales suggest that they might be uncommon near these oceanic islands, the lack of photo-identification survey efforts in such areas is acknowledged as a likely reason.

Finally, our results presented here show that BSG whales have more complex migratory dynamics than previously reported, with individuals distributed in the southernmost feeding area to be mostly observed in the southern breeding range (northern Peru to middle Colombia) and individuals localized to the northernmost feeding area to be mostly observed in the more northern region of the common breeding ground. This migratory pattern could be particularly important for conservation and management purposes and future assessments, particularly for the Fueguian Archipelago humpback whale aggregation as demonstrated by the relatively low abundance and growth rate (Gende *et al.* 2014), significant differentiation in mtDNA haplotypes (Olavarría *et al.* 2006, Félix *et al.* 2012), high site fidelity (Acevedo *et al.* 2006, 2014) and preference for breeding in the northerly region. These particular characteristics would satisfy the preliminary criteria for the recognition of distinct "management units" (Moritz 1994, Taylor 2005) or "distinct population segments" (DPS, Waples 2006). However, defining differentiated population segments requires further photo-identification efforts in open waters and around oceanic islands in both low and high latitudes, additional genetic samples from poorly sampled or unsampled areas, and satellite telemetry efforts, which may provide new evidence on the structure of humpback whales throughout the BSG range and help to clarify patterns of connectivity between breeding grounds and feeding areas.

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