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Short Note

Movements and Timing of Humpback Whales (*Megaptera novaeangliae*) Within the Breeding Region of the Eastern South Pacific

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Eastern South Pacific humpback whales (*Megaptera novaeangliae*) (Breeding Stock G, according to the International Whaling Commission [IWC], 1998) migrate from feeding grounds located mainly in the surroundings of the Antarctic Peninsula (Dalla Rosa et al., 2008) and to a lesser extent in the Magellan Strait (Gibbons et al., 2003; Acevedo et al., 2006, 2013) and Golfo de Corcovado in southern Chile (Hucke-Gaete et al., 2013) to their breeding region off northern Peru, Ecuador, Colombia, Panama, and Costa Rica (Flórez-González, 1991; Flórez-González et al., 1998; Félix & Haase, 2001; Rasmussen et al., 2007; Pacheco et al., 2009; Guidino et al., 2014; Guzmán et al., 2015). The connectivity between some feeding and breeding grounds has been demonstrated through photo-identification (Stone et al., 1990; Stevick et al., 2004; Acevedo et al., 2007; Capella et al., 2008; Rasmussen et al., 2007) and to a lesser extent with genetics (Caballero et al., 2001; Félix et al., 2012). In addition, regional movements of five individuals and a migratory path used by one humpback whale from the breeding region to feeding grounds has been recently characterized via satellite tracking (Félix & Guzmán, 2014). Although important information on connectivity and migration at the geographical scale that has been generated, little is known about the movement patterns at the regional or mesoscale.

Humpback whales tend to have a continuous distribution throughout coastal areas of the breeding region (Zerbini et al., 2004; Félix & Haase, 2005; Van Waerebeek et al., 2013). However, residence patterns and movements within the breeding region may vary within and between seasons (Baker & Herman, 1981; Calambokidis et al., 2001; Smith et al., 2012; Guzmán et al., 2015). Understanding the movement patterns within the breeding area may provide valuable information about the migration timing and habitat use by whales along the breeding grounds (e.g., Guzmán & Félix, 2017). This information may help to identify potential risks to humpback whales caused by human activities such as interaction with gillnets (García-Godos et al., 2013), and seismic and whale-watching operations (Pacheco et al., 2011); and it may provide the understanding to address them.

Previous photo-identification studies in the eastern South Pacific revealed the connectivity between sites within the breeding region—Ecuador, Colombia, Panama, and Costa Rica (Flórez-González et al., 1998; Castro et al., 2008; Félix et al., 2009). Northern Peru was considered in those studies, but the sample size was rather low (no more than 20 photographs). Research efforts in the region have increased progressively in the last 20 y (Floréz-González et al., 2007), and more sites within the breeding region have been surveyed (Pacheco et al., 2009; Castro et al., 2011; Rojas et al., 2014). These studies support the notion that this population has a continuous distribution along the eastern South Pacific from northern Peru to southern Costa Rica during the austral winter/spring breeding season.

Information on variability in abundance may provide some insights about timing and movements of eastern South Pacific humpback whales within the breeding region. Thus, an apparent relationship would exist between whale abundance and latitude. Whale abundance peaks off Panama in August and September (Guzmán et al., 2015) and off Colombia in August (Flórez-González et al., 1998); while off Ecuador, it is reported in July (Scheidat et al., 2000; Félix & Haase, 2001). In northern Peru, the peak is observed towards the end of the breeding season in September and October (Pacheco et al., 2009; Santillán, 2011; Guidino et al., 2014). This variability in abundance suggests that whales have an offshore path arriving first to Ecuador in July, then moving up north to Colombia, and finally moving further north to Panama. The peak of abundance later in the season (September and October) in northern Peru would indicate that this southern region constitutes a migratory corridor for humpback whales returning to feeding areas via neritic waters. This belief is also supported by whaling statistics from Paita (*ca.* 5° S), northern Peru, which show the landing peak for humpback whales in October (Ramírez, 1988).

Herein, we tested the prediction that humpback whales would primarily use northern destinations early in the breeding season—first to Ecuador and then to Panama, and then move towards the south via northern Peru. To study this prediction, we compared photo-identified humpback whales (i.e., photographs of the ventral side of the flukes [see Katona et al., 1979] and also the dorsal fin in some cases) coming from the neritic zones of northern Peru with those of central Ecuador and Panama, thus covering the major extension of the breeding region (Figure 1).

Photographs were taken between June and October during the 1991 to 2014 study period, principally during whale-watching excursions but also during studies of humpback whale distribution and population dynamics (Table 1). For the comparison, photographs were simultaneously visualized using a double screen and examined by the naked eye. Photographs with poor resolution, bad quality, and duplicates were discarded. Catalogs were compared in the following sequence: Peru vs Ecuador, Peru vs Panama, and Ecuador vs Panama.

A total of 2,999 unique photo-identified humpback whales were compared yielding 39 matches (19 photographs were discarded due to poor resolution; see Table 1). Only five matches were detected within the same season In 2010, two individuals sighted in Ecuador in July were resighted in northern Peru—one in August and one in October. A third animal was sighted off Ecuador on 8 September and seen 4 d later off northern Peru (Table 2). (Photographs of the total matches are available on the *Aquatic Mammals* website: www.aquaticmammalsjournal.org/index.php?option=com_content&view=article&id=10&Itemid=147). The estimated time elapsed between locations was 34.9 d (SD = 21.2) on average. Another within-season resighting was made in 2008: an individual sighted in Panama in July was resighted in Ecuador in August. Finally, an individual sighted in Panama in August 2013 was resighted in northern Peru in September (Table 2). The estimated time between locations was 45 and 36 d, respectively. Of the 34 between-years matches, 30 were between Ecuador and Peru, and four were between Panama and Ecuador (Table 2). The timing of sighting and resighting in these cases was similar as in the within-seasons analysis. Individuals were sighted first in Ecuador and/or Panama during June, July, and August, and then whales were resighted in northern Peru after variable times ranging from 2 wks to 3 mo during August, September, and October (Table 2). The longest estimated time interval was between 17 July to 30 October. Only five resightings showed the opposite timing (Table 2). A chi square test comparing the timing of recaptures between Peru and Ecuador provided statistical significance to the observed tendency of sighting whales early in the season in Ecuador and late in Peru ($\chi^2 = 29.9$; df = 4, $p < 0.05$). No statistical comparison was made with Panama due to the low number of recaptures.

Although humpback whales arrive first to Ecuador and then to Panama, matches indicated that most individuals moved in the opposite direction (south) as the season progresses. Persistent and directional movement seems to be a common characteristic for humpback whales in breeding areas. For example, Baker & Herman (1981) reported a southeast to northwest movement pattern in the breeding area at the Hawaiian Archipelago. Smith et al. (2012) modeled the habitat used by breeding humpback whales in eastern Australia and suggested that whales arrive first to neritic waters at northern breeding destinations and then move southwards closer to the coast. Indeed, southern locations were considered migratory corridors.

A plausible explanation of such distribution within breeding grounds could be a consequence of population stratification, with humpback whales arriving first to the breeding destination,

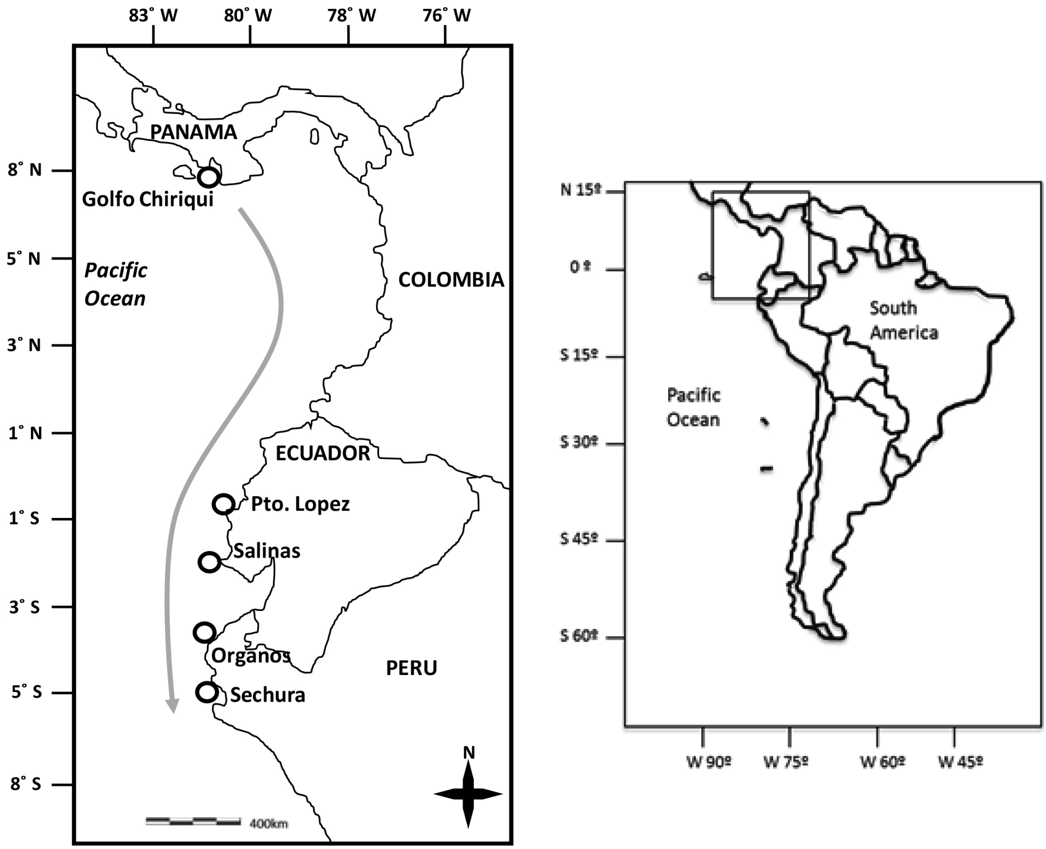

Figure 1. The map on the right shows the breeding region for humpback whales (*Megaptera novaeangliae*) of the eastern South Pacific. The map on the left indicates the locations (open dots) where photographic surveys were conducted. The grey arrow highlights the main north to south movement revealed in this study (see "Results" for details).

Table 1. Number of humpback whales (*Megaptera novaeangliae*) identified by photographs of flukes at the different study sites along the breeding region

	No. of photographs						
Institutions	Available	Examined	Years	Sightings*	Observation time†	Location	Country
Panacetacea	445	441	2002-2013	946	1,188	Golfo de Chiriqui	Panamá
MBS	222	218	1991-1997	180	94	Puerto López 1° 24' S, 80° 55' W	Ecuador
MBS	1,898	1,890	2001-2013	1,907	855	Salinas 2° 13' S, 80° 57' W	Ecuador
Pacífico Adventures	440	437	2009-2014	1,602	372	Los Organos 4° 10' S, 81° 8' W	Perú
CEPEC	13	13	2009-2010	43	82	Sechura 5° 34' S, 80° 57' W	Perú
Total	3,018	2,999		4,678	2,591		

CEPEC = Centro Peruano de Estudios Cetologicos, MBS = Museo de Ballenas de Salinas, * = total number of sighted whales, and † = total number of observation hours.

Table 2. Photograph matches among humpback whales from Peru, Ecuador, and Panama along the eastern South Pacific breeding region. The numbers in the first column are the time intervals between matches in days; the first five rows are within-year recaptures followed by the rest of the between-years matches.

	Perú				Ecuador		Panamá	
	Sechura		Los Organos		Salinas/Pto López		Chiriqui	
Time	ID	Date	ID	Date	ID	Date	ID	Date
20			PAO#0026	8 Aug. 2010	MBS#1687	18 July 2010		
103	SE 09-4	30 Oct. 2010			MBS#1870	17 July 2010		
4			PAO#0004	12 Sept. 2010	MBS#1949	8 Sept. 2010		
45					MBS#1414	30 Aug. 2008	PAN#1106	15 July 2008
36			PAO#0305	27 Sept. 2013			PAN#1321	21 Aug. 2013
6			PAO#0392	16 Sept. 2014	MBS#0116	22 Sept. 1996		
8			PAO#0106	11 Aug. 2012	MBS#0748	3 Aug. 2010		
7					MBS#2104	3 Aug. 2012	PAN#1182	10 Aug. 2007
9			PAO#0013	29 Aug. 2009	MBS#0059	20 Aug. 1995		
13			PAO#0004	15 Aug. 2009	MBS#2009	2 Aug. 2008		
14					MBS#1527	31 July 2009	PAN#1076	14 Aug. 2007
14			PAO#0031	14 Aug. 2010	MBS#0771	31 July 2006		
15			PAO#0164	19 Sept. 2012	MBS#1440	4 Sept. 2008		
17			PAO#0127	27 Aug. 2012	MBS#0181	10 Aug. 2010		
49			PAO#0050	5 Sept. 2010	MBS#0988	16 July 2006		
19			PAO#0023	5 Aug. 2010	MBS#0739	16 July 2006		
20			PAO#0282	18 Sept. 2013	MBS#0947	29 Aug. 2006		
21			PAO#0109	15 Aug. 2012	MBS#0391	6 Sept. 2003		
26			PAO#0051	14 Sept. 2010	MBS#1155	19 Aug. 2007		
27			PAO#0074	26 Aug. 2011	MBS#0948	29 July 2006		
29			PAO#0010	9 Aug. 2009	MBS#0253	8 Sept. 2008		
66			PAO#0279	13 Sept. 2013	MBS#0517	7 July 2004		
37			PAO#0014	14 Sept. 2009	MBS#0453	7 Aug. 2004		
38			PAO#0314	30 Sept. 2013	MBS#1904	22 Aug. 2010		
42			PAO#0015	14 Sept. 2009	MBS#0592	2 Aug. 2005		
42			PAO#0318	13 Oct. 2013	MBS#1193	1 Sept. 2007		
44			PAO#0055	19 Sept. 2010	MBS#1095	5 Aug. 2008		
44			PAO#0059	30 Sept. 2010	MBS#0011	16 Aug. 1992		
44			PAO#0077	24 Aug. 2011	MBS#1488	10 July 2009		
45			PAO#0006	21 Aug. 2009	MBS#0255	6 July 2002		
47			PAO#0245	19 Sept. 2010	MBS#1270	2 Aug. 2007		
48			PAO#0056	19 Aug. 2010	MBS#1155	1 July 2009		
48			PAO#0257	3 Sept. 2013	MBS#1683	15 July 2008		
52					MBS#1630	14 Sept. 2010	PAN#1287	22 July 2007
53			PAO#0009	10 Sept. 2013	MBS#1002	17 July 2010		
57					MBS#1658	11 July 2010	PAN#1365	8 Sept. 2013
60			PAO#0173	22 Sept. 2012	MBS#0752	22 July 2006		
63			PAO#0323	12 Oct. 2013	MBS#0372	9 Aug. 2003		
66	SE09-10	30 Oct. 2010			MBS#0168	24 Aug. 1997		

following an offshore path, and then being resighted in the southern areas by the end of the season (September-October) once the southern coastal migration has started. This change to a coastal distribution is more evident in females with calves (Félix & Botero-Acosta, 2011; Guidino et al., 2014), a behavior that is maintained by migrating females after leaving the breeding area (Félix & Guzmán, 2014). Recently generated information on movements of whales that were satellite-tagged in Panama and Ecuador supports stratification in this population at breeding grounds (Guzmán & Félix, 2017) as well as the low number of matches in a large sample as in our study.

We are aware that migration is a complex process with different timing and overlapping stages (Dawbin, 1966; Craig et al., 2003), and spatial segregation according to the whale's age/class (Félix & Haase, 2005; Félix & Botero-Acosta, 2011; Rasmussen et al., 2012; Guidino et al., 2014), which increases uncertainty and precludes reaching definitive conclusions from the available data. In the same line, we suggest caution with between-years matching results. Although these results point to a consistent movement pattern, we cannot unequivocally account for the explanatory processes behind this since whale behavior may also vary between years due to environmental variability. Other factors must also be considered such as short residence time and the relatively large home range (between 25,000 and 60,00 km^2; *sensu* Guzmán & Félix, 2017) which may not be covered entirely during photographic surveys. In addition, it may be difficult to distinguish between the absence of an individual in a group and the failure to capture it photographically, and the low probability of capture of fluke-up which is lower in breeding areas with respect to feeding areas. Moreover, the photographic effort may vary throughout the breeding area as research teams do not necessarily survey humpback whales simultaneously across their study region during the whole breeding season. Nevertheless, our comparison and previous studies (e.g., Castro et al., 2008; Félix et al., 2009) call attention to this north-to-south movement pattern because of the implications in population estimate studies using mark-recapture models since such heterogeneity may affect whales' probability of capture (Félix et al., 2011). This study highlights the importance of monitoring movements of humpback whales within the breeding area of the eastern South Pacific as in other regions. In future studies, we recommend including photographs from Colombia to cover the entire breeding area as well as to increase telemetry studies, which would enhance our understanding of humpback whale movements during the breeding season.

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