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Movements and Habitat Use by Southeast Pacific Humpback Whales (*Megaptera novaeangliae*) Satellite Tracked at Two Breeding Sites

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Abstract

Satellite tags were deployed on 47 humpback whales (*Megaptera novaeangliae*) in Panama and Ecuador between 2009 and 2015 to monitor both short- and long-distance movements within the breeding season. Ultimately, data from 37 animals (23 mothers with a calf and 14 unsexed adults) were included in the assessment. Transmissions were filtered and behavior states defined using a Bayesian state-space model. Mean tag longevity was 14.2 d (SD = 12.43; range: 1 to 70 d), and longevity was significantly longer in mothers (53%) than in unsexed individuals (t test = 2.43, p = 0.02). Based on the extent of their movements, two different habitat use patterns were recognized and referred to as short range (SR) and long range (LR). SR movements were associated mainly with slow, area-restricted movements (ARM) and short periods of fast, directed movement (FDM). LR movements were related mainly to FDM and, in some cases, with short ARM periods. We found significant differences in the proportion of time spent in each behavioral mode and in swim speed between mothers and unsexed individuals ($p < 0.01$, in all cases). Mothers displaying SR movements stayed in relatively small areas with back and forth movements up to 350 km along the coast; the 95% home range (kernel density) was estimated to be 61,105 km^2 in whales from Panama and 26,331 km^2 in whales from Ecuador. In mothers displaying LR movements, distribution range was seven times greater in Panama and up to 2.5 times greater in Ecuador. Since tag longevity was not significantly different between SR and LR movements in females (t test = 0.063, $p >$ 0.05), a shift from the nursing to migration phase is a plausible explanation for this increased range. Information from unsexed animals is inconclusive because of the short tracking periods. Mothers were distributed closer to shore than other tagged unsexed individuals, but both types of whales swam into deeper waters mainly during migration. Our results confirm maternal-biased stratification in this population along the entire breeding range. These findings have important implications for coastal management, including reduction of risk posed by human activities such as bycatch, ship strikes, and whale watching.

Key Words: satellite tracking, breeding grounds, habitat use, spatial-state switching model, Southeast Pacific, population structure, Panama, Ecuador, humpback whale, *Megaptera novaeangliae*

Introduction

Most baleen whale species carry out seasonal movements between low latitude breeding grounds and high latitude feeding grounds. However, variability in large-scale movements among species is recognized. Some species, such as blue whales (*Balaenoptera musculus*) (Branch et al., 2007), distribute widely in open waters in response to dynamic oceanographic processes, whereas others, such as humpback whales (*Megaptera novaeangliae*) (Dawbin, 1966) and gray whales (*Eschrichtius robustus*) (Rice & Wolman, 1971), tend to concentrate in the same coastal areas season after season either for breeding or feeding. With the exception of a few cases (e.g., Kennedy et al., 2013; Zerbini et al., 2015), fine-scale movements and habitat use within destination sites is poorly understood for some migratory baleen whales.

Because the distance traveled by whales in a single day and the inability to follow the animals at night limit continuous monitoring using conventional means, satellite telemetry has become a widespread technique to study movement patterns at both broad and fine spatial scales. Most studies using satellite telemetry to date have focused on defining migration routes and habitat use (Mate et al., 1998; Zerbini et al., 2006, 2015; Dalla Rosa et al., 2008; Lagerquist et al., 2008; Garrigue et al., 2010; Hauser et al., 2010; Kennedy et al., 2013; Félix & Guzman, 2014; Guzman et al., 2015).

The humpback whale is a migratory species that concentrates around tropical oceanic islands or continental coasts during the breeding season, usually in waters less than 200 m deep over the continental shelf (Dawbin, 1966; Herman & Antinoja, 1977; Ersts & Rosenbaum, 2003; Félix & Haase, 2005). Reasons for such a coastal distribution are not sufficiently clear. The use of traditional places would facilitate social interactions and breeding encounters, but it would also make the species predictable and, therefore, vulnerable to predators (Pitman et al., 2014) and to whaling in the past (Townsend, 1935). In addition, coastal distribution along continental shelves exposes humpback whales to a number of human activities such as interactions with fishing gear, increased risk of ship strikes, and habitat degradation (Robbins & Mattila, 2001; Van Waerebeek et al., 2007; Félix et al., 2011b; Guzman et al., 2013).

Spatial analyses have been conducted to model the humpback whale habitat at breeding grounds using presence data in combination with environmental variables such as depth, distance from shore, slope, tide, bottom type, and wind speed (Ersts & Rosenbaum, 2003; Oviedo & Solis, 2008; Félix & Botero, 2012; Bruce et al., 2014; Craig et al., 2014). These studies have consistently demonstrated that depth is the most important predictor of humpback whale distribution at breeding grounds. Within the breeding area, individual whales show some level of spatial segregation according to age and sex class, with mother/calf pairs distributed closer to the coast while adults and immature whales prefer deeper waters (Glockner & Venus, 1983; Smultea, 1994; Ersts & Rosembaum, 2003; Félix & Haase, 2005; Rasmussen et al., 2011; Bruce et al., 2014; Oña et al., 2016). However, movements of individual humpback whales within breeding grounds are poorly known. Some studies reported that most individuals seem to distribute widely with low site fidelity (e.g., Mattila et al., 1994; Craig et al., 2001; Félix & Haase, 2001), although extended resighting intervals of up to 67 d in Ecuador (Félix & Botero, 2012) and up to 76 d in Hawaii (Craig et al., 2001) have been described. Reports of whales leaving and returning to core areas within a few days also exist (Guzman et al., 2015). Differences in residency level between age classes, with higher fidelity by mothers with calves, also have been reported (Glockner & Venus, 1983; Capella et al., 1995; Félix & Botero, 2012). Photo-identification (photo-ID) and genetic studies have demonstrated high variability in spatial and temporal structuring at the population level in different breeding areas (Rosenbaum et al., 2009; Félix et al., 2012; Baker et al., 2013; Carvalho et al., 2014) due to maternal fidelity and natal philopatry (Baker et al., 2013).

In the Southeast Pacific, humpback whales from Breeding Stock G (International Whaling Commission [IWC], 1998) reproduce offshore of northwestern South America and southwestern Central America (4° S to 12° N) along the coasts of five countries: Peru, Ecuador, Colombia, Panama, and Costa Rica (Flórez-González et al., 1998; Rasmussen et al., 2007). Photo-ID studies have demonstrated connectivity between different sites within this extended breeding area (Flórez et al., 1998; Félix et al., 2009) but also some level of population stratification (Acevedo et al., 2007; Félix et al., 2011a). Because photo-ID matching and genetic sampling (Félix et al., 2012) provide limited information in time and space, ecological questions related to site fidelity and habitat use remain largely unanswered in this population. To address such issues properly and to determine the extent of local movements, continuous following up of individuals during the breeding season is necessary.

Satellite tagging of humpback whales off Panama and Ecuador has been conducted during the breeding season since 2009 to monitor both short- and long-distance movements. Information about collision risk and migratory movements derived from this study has been published elsewhere (Guzman et al., 2013, 2015; Félix & Guzman, 2014). Herein, we focused our analysis on local movements within breeding areas to assess habitat use and movement patterns by different sex classes in two breeding sites, and we have added several new unpublished tracks.

Methods

Study Site

This study was conducted at two sites within the breeding area of the Southeast Pacific humpback whale population: (1) Las Perlas Archipelago in Panama (8.41° N, 79.02° W) and (2) Salinas in Ecuador (2.20° S, 80.97° W) (Figure 1). These sites are located at the northern and southern borders of the breeding area and are separated by about 1,200 km in a straight line. Three whales tagged off Costa Rica were pooled with Panama's because of the short distance (50 km) between the countries. These tracked whales traversed the Gulf of Chiriquí (northwestern Panama); thus, the entire Pacific coast of Panama was covered in this study for the first time.

Las Perlas Archipelago is located in the Gulf of Panama 60 km southwest of Panama City. It includes 250 basaltic rock islands and islets. The archipelago is the fourth largest coastal marine protected area of Panama and covers 1,688 km^2 (Guzman et al., 2008). The Gulf of Panama experiences an upwelling period during the dry season (January through April) that results in high marine productivity, whereas the Gulf of Chiriquí is not affected by seasonal upwelling (D'Croz & O'Dea, 2007). The archipelago is located within the 50 m isobaths, with shallow water averaging 15 m depth. Waters of the Las Perlas Archipelago have been a natural wintering area for humpback whales mainly from the Southern Hemisphere, but part of the northeastern Pacific wintering humpback whale population overlaps in southern Central America (Costa Rica and Panama) during different seasons (Flórez-González et al., 1998; Guzman et al., 2015). In the Gulf of Chiriquí, whales are commonly observed in the shallow areas of the Paridas, Secas, and Coiba Archipelagos (Rasmussen et al., 2011).

Salinas is located at the tip of the Santa Elena Peninsula in the westernmost point of Ecuador and is the northern limit of the Gulf of Guayaquil. A narrow shelf surrounds the peninsula, and depth gradually increases westward from the peninsula and reaches 100 m to 13 km offshore, at which point the slope increases by one order of magnitude. The shallow area is wider north of the peninsula than to the south, and sandy and rocky bottoms characterize this zone. The geographic characteristics of the site allow rapid access to researchers along the whales' migratory corridor (Félix & Haase, 2005). This area is also characterized by seasonal influence of the cold, productive Humboldt Current from the south and warm tropical waters of the Panama Bight from the north where the Equatorial Front is formed (Cucalón, 1996).

Tagging Procedures
Satellite transmitters were deployed on humpback whales off Salinas (2013 and 2014), around the Las Perlas Archipelago (2009, 2013, and 2014), and in Golfo Dulce in southern Costa Rica (2015) during the peak breeding season (August through October). Wildlife Computers SPOT5 tag models (AM-S193) were used (Guzman et al., 2013; Félix & Guzman, 2014). For the tagged whales from Costa Rica, only track data from Punta Burica at the border between Costa Rica and western Panama (8.02° N, 82.88° W; 58 km from tagging site) were included in the analyses. The tag-derived positions from Argos satellite location classes 3, 2, 1, 0, A, and B were used with the range of errors in accuracy estimated at between

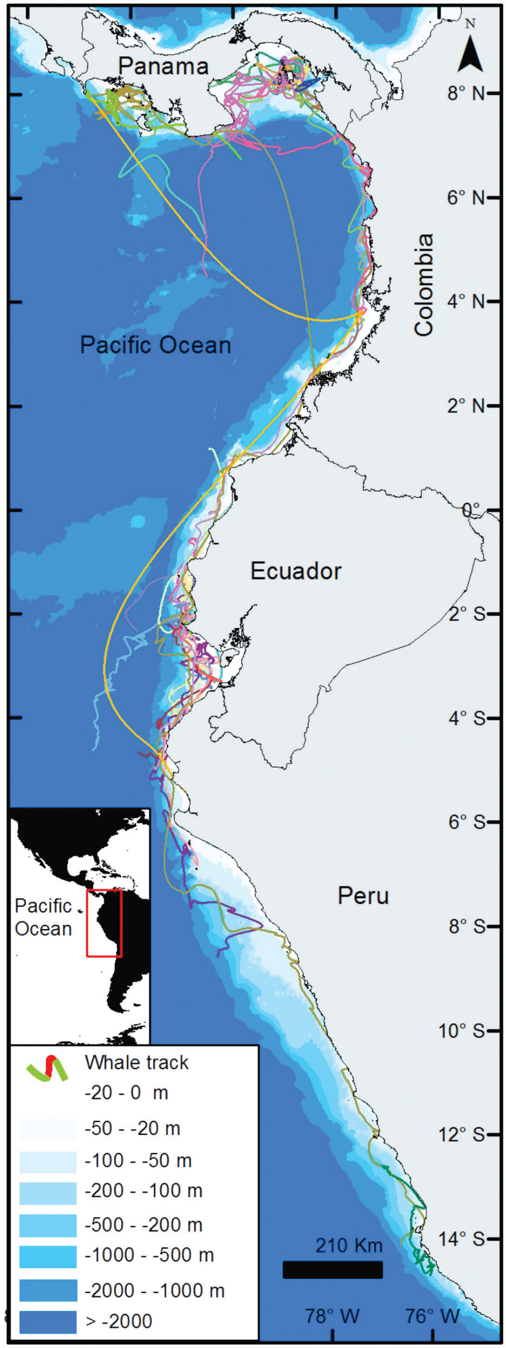

Figure 1. The study area showing the tagging sites in Panama (Las Perlas) and Ecuador (Salinas) along the depth gradient; whale tracks obtained during the study period are shown in colors (n = 34).

150 m and 5 km radius for plotting general filtered whale movements (see Vincent et al., 2002; Tougaard et al., 2008; Costa et al., 2010; Douglas et al., 2012; Guzman et al., 2013).

Factory transmitters consisted of a 2-cm diameter stainless steel tube case, 17.5 cm in length, coupled to a custom-made stainless steel spear with a 3-cm triangular double-edged blade tip containing one to three pairs of 5-cm barbs placed at 90° to each other (Guzman et al., 2013). We tagged whales from 5-m-long fiberglass or inflatable boats at a distance of 3 to 5 m from the whale. Tags were deployed using an ARTS pneumatic line-thrower (Restech Inc., Bodø, Norway) coupled to a LK-carrier (developed by LKARTS, Bodø, Norway). A detailed description of the tagging procedure is provided elsewhere (Guzman et al., 2013). The transmitters were attached to the whales about 20 cm below and in front of the dorsal fin on either the right or left side. Tags were chemically sterilized and plastic wrapped in the laboratory. In the field, the tag/spear was sprayed with Neomycin Sulfate – Clostebol Acetato (Neobol®) before deployment. Only adult animals were tagged, which included mothers accompanied with a newborn calf and unsexed animals. The Animal Care and Use Committee of the Smithsonian Tropical Research Institute approved the tagging procedure.

Data and Statistical Analyses

Satellite data were initially processed using the *Satellite Tracking Analysis Tool* software (Coyne & Godley, 2005) and filtered using the Kalman algorithm (Lopez et al., 2014). Filtering of Argos-acquired satellite tracking location data and behavioral state pattern estimations were obtained using the Bayesian state-space switching model (SSSM) with codes available for *R* software; the methodology is explained in detail elsewhere (Jonsen et al., 2003, 2005, 2013). In particular, we chose the hierarchical switching model (hDCRWS) for location filtering and estimating the different behaviors with two states across multiple animals (Jonsen et al., 2003, 2005, 2007). The switching behaviors analysis can discriminate between two movement behaviors (Jonsen et al., 2007), described as "latent resident (slow, area-restricted movements, or ARM) and transient (fast, directed movement, hereafter FDM) behavioral states" (see Block et al., 2011). These two discrete behavioral modes (b_t) from position data are values defined or rounded as 1 or 2, and they are obtained by adopting cut-offs at 1.25 and 1.75; mean estimates between 1.25 and 1.75 are considered to be uncertain (Jonsen et al., 2005, 2007). However, we adopted cut-off 1.1 and 1.9 of mean estimated values to define behavioral modes 1 and 2 (M1 and M2) because once mean estimated values reach such thresholds, they become less variable. Values in between were defined as behavioral mode 3 (M3), which is an intermediate behavior between ARM (M2) and FDM (M1) that could involve different combinations of speed and direction adopted by whales at any time.

Whales' distribution ranges were calculated from the filtered data using the kernel density estimator to generate surface values indicating higher or lower utilization of the space by whales. Data derived from satellite transmissions included location, date, distance from tagging place, estimated speed, and depth. Kernel density 95% and 50% home ranges were calculated using the *Spatial Analyst* tool in *ArcGis*, Version 10.2.2. Kernel density analyses were conducted separately for mothers and for individuals of undetermined sex. Kernel values were extracted from raster files for each transmission point. The area (km^2) where 50 and 95% of the points with higher raster values were located was determined by reclassifying kernel raster values into these two categories and then transforming such files into polygons using the raster conversion tool from the same software. Tag longevity (d) and whale swim speed (km d^{-1}) were compared between mothers and unsexed animals with a *t* test after log transformation of the data.

To describe whale distribution as a function of depth, bathymetric data from transmission sites were obtained from archives at SRMT30+ V11 (http://topex.ucsd.edu/WWW_html/srtm30_plus.html), which are available from the Satellite Geodesy Research Group at the Scripps Institution of Oceanography, University of California–San Diego (see Becker et al., 2009). Depth data ranges were divided into eight arbitrary depth categories, and each modeled transmission was assigned to one of these ranges. A total of 1,015 georeferenced records was incorporated into the analysis.

Results

Tagged Whales

Forty-seven satellite tags were deployed on adult Southeast Pacific humpback whales (25 in Panama and 22 in Ecuador). Eight of those tags did not transmit. Tags on two whales started transmission during migration well south of the study area; therefore, data from these two tags were left out of this analysis (Table 1). An unsexed animal with Tag No. 585 transmitted for the first 7 d and then stopped; transmission started again 57 d later from the Antarctic (see details in Félix & Guzman, 2014). For this tag only, the first 7-d period was included in this analysis. Thus, 37 tags that transmitted for at least 1 d after attachment were used

Table 1. Summary information of modeled data for 37 humpback whales tagged in Panama (Pa) and Ecuador (Ec) between 2009 and 2015. F = mothers and U = unsexed animals. Movement pattern: SR = short range and LR = large range.

Tag no.	Country	Tagging date (d/mo/y)	Sex	Longevity (d)	Distance (km)	Type of movement
721	Pa	27/8/2009	F	19	1,039	SR
723	Pa	25/8/2009	U	12	2,001	SR
725	Pa	27/8/2009	F	8	1,228	LR
726	Pa	25/8/2009	U	2	326	
727	Pa	25/8/2009	F	2	36	
731	Pa	25/8/2009	U	2	71	
734	Pa	26/8/2009	F	9	823	LR
736	Pa	26/8/2009	F	9	471	SR
738	Pa	25/8/2009	U	12	1,180	LR
739	Pa	23/8/2009	F	6	184	SR
740	Pa	26/8/2009	F	25	2,023	SR
741	Pa	27/8/2009	U	12	680	SR
742	Pa	23/8/2009	U	7	271	SR
743	Pa	23/8/2009	U	14	740	SR
202[1]	Pa	9/9/2014	F	26	1,386	SR
203[1]	Pa	9/9/2014	F	26	1,959	LR
214[1]	Pa	17/9/2014	F	19	632	SR
455[2]	Pa	8/9/2015	F	69	5,433	SR & LR
456[2]	Pa	12/9/2015	F	10	633	SR
459[2]	Pa	8/9/2015	F	24	1,947	LR
264	Ec	10/8/2013	F	11	645	SR
267	Ec	14/8/2013	U	5	338	
268	Ec	14/8/2013	F	22	1,078	SR
271	Ec	13/8/2013	U	11	920	LR
272	Ec	12/8/2013	F	5	347	SR
273	Ec	13/8/2013	F	28	1,703	SR
275	Ec	11/8/2013	F	15	438	SR
276	Ec	16/9/2013	U	8	877	SR
584	Ec	17/9/2013	F	24	524	SR
585[3]	Ec	14/8/2013	U	8	698	LR
586	Ec	18/9/2013	F	15	1,088	LR
587	Ec	13/8/2013	U	16	708	LR
588	Ec	24/8/2013	F	11	1,416	LR
589	Ec	13/8/2013	U	3	222	
206	Ec	11/8/2014	F	5	66	SR
207	Ec	14/8/2014	U	4	27	
590	Ec	18/9/2013	F	12	1,907	LR & SR

[1]Transmissions from these three whales were interrupted on the same date and time, apparently due to electronic failure of the tags and not to detachment.

[2]Tagged in Costa Rica but only data from Panama were analyzed.

[3]Included only the transmission time within the breeding area.

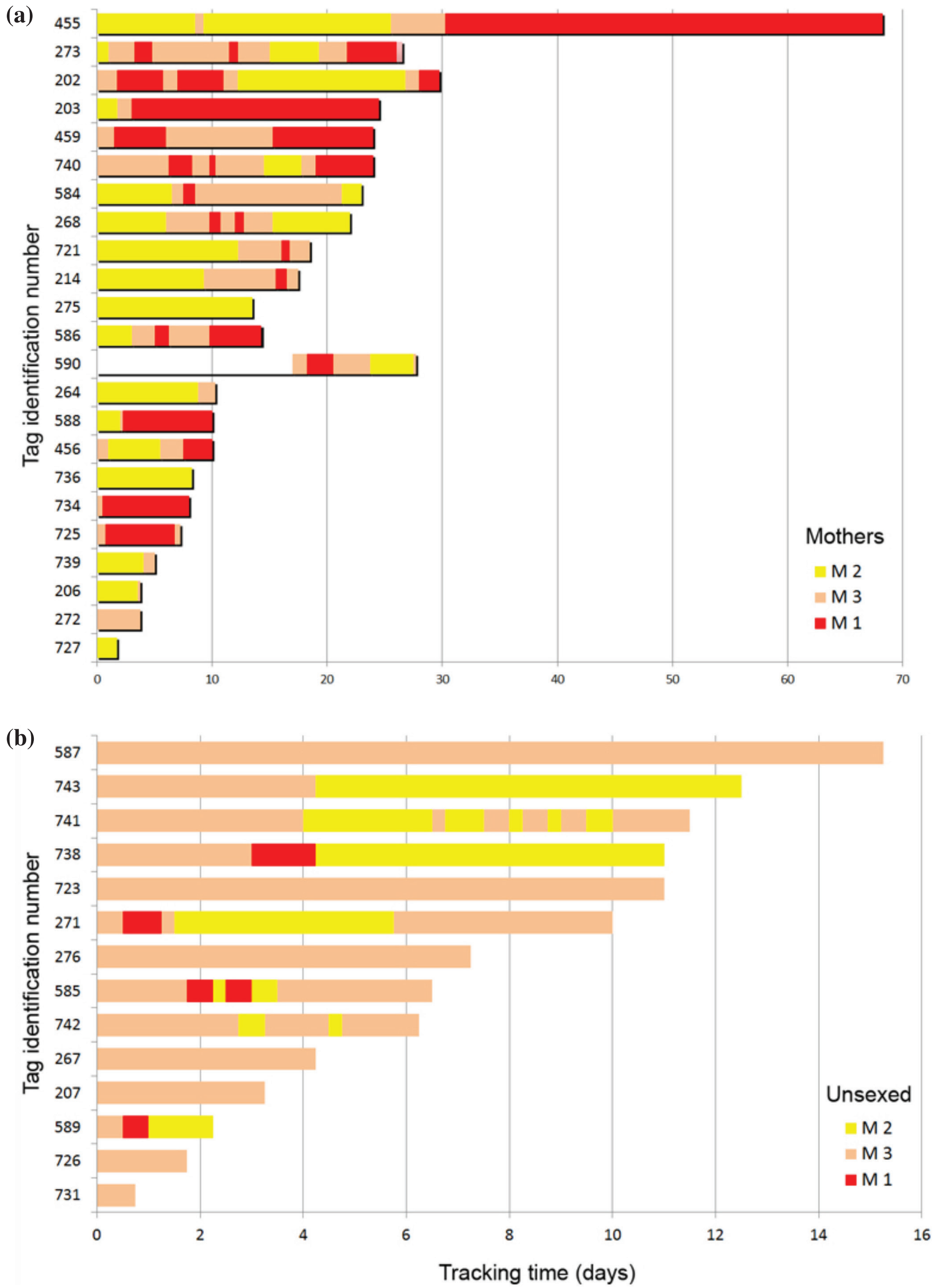

Figure 2. Dynamic of behavioral modes (1, 2, and 3) recorded in humpback whales (*Megaptera novaeangliae*) during the tracking period according to whale type. Behavior M1 is related to fast, directed movements (FDM); and behavior M2 is associated with slow, area-restricted movements (ARM). M3 is an intermediate behavioral state between M1 and M2. Top panel (a) = mothers (M), and bottom panel (b) = unsexed animals (U).

for the analysis. The tag attachments were on 23 mothers accompanied by a newborn calf and 14 unsexed animals (including two whales escorting mother and calf pairs) (Figure 1; Table 1).

Tag longevity averaged 14.2 d (SD = 12.43; range: 1 to 69 d). Mean longevity in mothers with calves from Panama (18.9 d; SD = 17.5; range: 2 to 69 d) was not significantly different from mothers with calves in Ecuador (16.4 d; SD = 8.8; range: 3 to 28 d) (t test = –0.40, $p = 0.68$, $df = 19$). Mean tag longevity for unsexed whales was also not significantly different between the two groups (8.8 d, SD = 5.8 in Panama; and 7.7 d, SD = 4.5 in Ecuador) (t test = –0.39, $p = 0.7$, $df = 8$). However, mean tag longevity was significantly longer (53%) for mothers with calves than for unsexed whales (t test = 2.43, $p = 0.02$, $df = 26$).

Behavioral Modes and Speed

Time spent by humpback whales in each of the three behavioral modes was estimated for each whale type separately (Figure 2). Thirteen of the 23 mothers (56%) exhibited all three behavioral modes at some time during their tracking period vs four of the 14 unsexed animals (28.5%) engaging in all three modes. Behaviors M2 and M3 were the most common behavioral modes recorded in mothers ($n = 19$, 62.6%). All unsexed animals exhibited behavior M3, but only seven within this group exhibited behavior M2 (50%). Behavior M1 was observed more in mothers with calves ($n = 16$, 69.5%) than in unsexed animals ($n = 4$, 28.5%). Overall, the proportion of time spent in the three behavioral modes was highly significantly different between the two whale group types ($X^2_2 = 93.9$, p < 0.01).

In mothers with > 10 d of tracking data, behavior M1 was observed either in short periods lasting hours to a few days separated by periods of behavior M3 (Tag Nos. 273, 202, 740, 584, 268, 721, 214, 586, and 590) or at the end of the tracking period, which would be associated with migration (Tag Nos. 455, 203, 459, 588, and possibly 734 and 725) (Figure 2a). In contrast, only a few unsexed animals spent short periods in M1 (Figure 2b). The short periods spent in behavior M1 in both types of whales may be related to fast travel between areas or to periods of increased activity and not necessarily related to migration. Time spent in behavior M2 was common in mothers (82.6%) but only in 50% of unsexed animals. Behavior M2 may be related to resting or to singing in the case of males. Extended periods in behavior M3 were common in unsexed animals and only in a few mothers, which suggests less predictable movements within breeding grounds in the former class.

Although the vector describing behavioral modes has two components—(1) speed and (2) direction, only speed could be accurately estimated between position data (every 6 h) after modeling. Swim speeds were compared by animal class, tagging site, and behavioral mode (Table 2). Average speed of mothers was not significantly different between Panama-Costa Rica and Ecuador in M1 and M2 but did differ in M3. In the case of unsexed animals, average speeds in M1 and M3 were not significantly different, but they were for M2. When data were pooled by whale class, the average speeds of mothers in M1 and M2 were significantly lower than those of unsexed whales in both cases (81 and 32 km d^{-1}

Table 2. Summary data for average speed (km d^{-1}) values by whale class (M = mothers and U = unsexed animals), tagging site (Pa = Panama and Ec = Ecuador), and behavioral mode (M1, M2, and M3) as described in the "Methods" section. Values in bold indicate statistically significant differences.

	M1	M2	M3
Class/site	Speed (SD)	Speed (SD)	Speed (SD)
M Pa	80.5 (33.9)	32.33 (21.1)	41.1 (25.7)
M Ec	83.49 (36.24)	31.47 (26.52)	36.78 (28)
	$t = 0.9$, $p = 0.34$	$t = –1.7$, $p = 0.78$	$t = –4.4$, $\mathbf{p < 0.001}$
U Pa	136.2 (36.1)	42.5 (28.6)	47.81 (32.73)
U Ec	129.9 (48.7)	132.65 (48.24)	45.49 (32.59)
	$t = 1.1$, $p = 0.26$	$t = –4.2$, $\mathbf{p < 0.001}$	$t = 1.1$, $p = 0.23$
M Ec-Pa	81 (34.31)	32 (23.35)	41.1 (25.78)
U Ec-Pa	132.2 (43.26)	67.13 (48.24)	45.5 (32.68)
	$t = –6.4$, $\mathbf{p < 0.001}$	$t = –2.8$, $\mathbf{p = 0.009}$	$t = –0.8$, $p = 0.39$

vs 132.2 and 67.13 km.d^{-1}, respectively), but average speeds did not differ significantly for M3 (Table 2).

Movement Patterns

Based on the extent of whale movements, two different patterns were distinguished and are herein referred as to short range (SR) and long range (LR). Whales that stayed around the tagging area moving back and forth performed SR movements that lasted up to 30 d in mothers and up to 15 d in unsexed animals. LR movements were identified in animals that either continued moving in a straight direction after tagging (southbound in all but one case) or started a straight southbound direction after some days of SR movements.

SR movements in mothers were associated with M2 and M3 and with short periods in M1 (most animals in Figure 2a). LR movements in mothers were associated mainly with M1 and to a lesser extent with M3. Mothers that showed LR movements shortly after tagging included Tag Nos. 203, 459, 586, 588, 734, and 725 (Figure 2a). One mother (Tag No. 455) spent the first 30 d in SR movement and then exhibited LR movement until the end of the tracking period on Day 70. Another mother's tag (Tag No. 590) started transmission on Day 18 around 2,000 km south of the tagging area in Ecuador and recorded SR movement during 11 d off central Peru (Figure 2b). Mothers with Tag Nos. 203 and 455, tagged in Panama, that changed from LR to SR movement when they arrived south of Colombia, displayed similar behavior.

All 14 of the unsexed animals exhibited only SR movements. Panamanian whales showed increased movements off the Gulf of Panama but mainly stayed along the coast of Colombia. Ecuadorian whales moved north, south, and southwest (offshore) of the tagging area (Figure 1). Several whales (Tag Nos. 738, 271, 585, and 738) moved straight southbound in a pattern similar to that of LR mothers but apparently without accomplishing the speed and direction threshold defined by the SSSM algorithm to be considered LR. Unfortunately, the short tracking period precluded further analysis of movements in this whale class (see "Discussion").

Kernel Analysis

Probabilistic kernel density maps of whale distribution showing 50% core range and 95% home range were generated for SR and LR groups by tagging site and whale class (Figures 3, 4 & 5). The home range areas for mothers showing SR movements in Panama and Ecuador were estimated to be 61,105 and 26,331km^2, respectively (Figure 3). Ecuadorian mothers concentrated in a nucleus area located between 1º 20 and 3.5º S, where they moved back and forth 250 to 300 km along the coast during the SR phase. A secondary nucleus was present off central Peru. As mentioned above, the mother with Tag No. 590 remained in this area and exhibited ARM after a migration period (probably as FDM). In Panama-Costa Rica, SR mothers were distributed at two sites: (1) within the Gulf of Panama and (2) within the Gulf of Chiriquí (Figure 4). However, they also occurred off central Colombia and off the southwest coast of Colombia, where whales using the offshore migration route remained for a few days with lower speed movements.

These findings indicate that mothers remain in a relatively small area where they move back and forth along 250 to 300 km of the coastline during the nursing period. They then start the southbound migration but make stops lasting days before restarting migration. Mothers from Panama-Costa Rica used two routes during the southbound migration: (1) a coastal one along the Panama and Colombian coasts and (2) another shorter offshore route connecting central and west Panama with the south of Colombia.

In Ecuador, mothers that exhibited LR movements had an estimated home range that was 2.5 times larger than that of SR mothers (26,331 vs 64,082 km^2). It extended north of the tagging site up to 1º N north off Ecuador and south of the tagging site to 8º 30' S off north Peru around 1,000 km of coast (Figure 3). The home range of mothers that exhibited LR movements in Panama was seven times greater than that of SR mothers (61,105 km^2 vs 441,605 km^2). In some cases, whales moved along the entire breeding area from Panama to north Peru and further south to mid Peru (Figure 4). The presence of mothers migrating offshore would be the cause of this huge difference.

The estimated home range of unsexed animals in Panama (20,980 km^2) was 65% smaller than that of SR mothers. In Ecuador, the home range of unsexed animals (36,108 km^2) was 37% larger than that of SR mothers but 55% smaller than that of LR mothers. Considering that the tracking period of unsexed whales was on the average 55% shorter and the number of animals 35% lower than in mothers, it was not possible to obtain conclusive information from this whale class.

Depth Distribution Analysis

Depths at transmission sites were used to define whales' distribution with respect to bathymetry (Table 3). Most mothers showing SR movements were distributed mainly over the shelf along both the Panama-Costa Rica and Ecuador areas. They spent ~67% of their time in waters < 200 m deep. However, SR mothers with calves also made

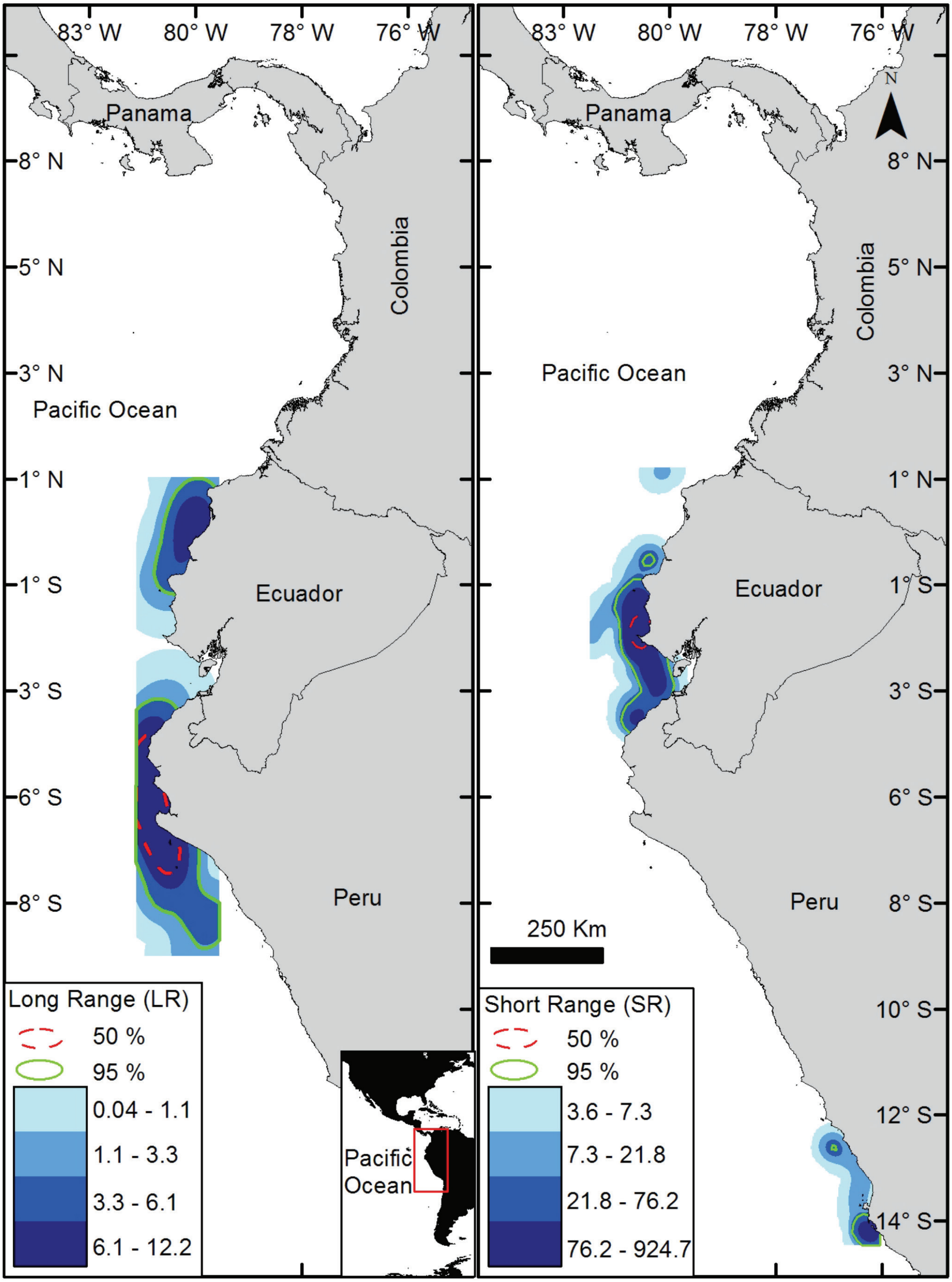

Figure 3. Kernel distribution analysis of mother humpback whales tagged off Ecuador; dashed red line includes 50% of home range, and green line includes 95% of home range. Left side = distribution of whales labeled as long range (LR), and right side = distribution of whales labeled as short range (SR). Tagging period: 2009 to 2015.

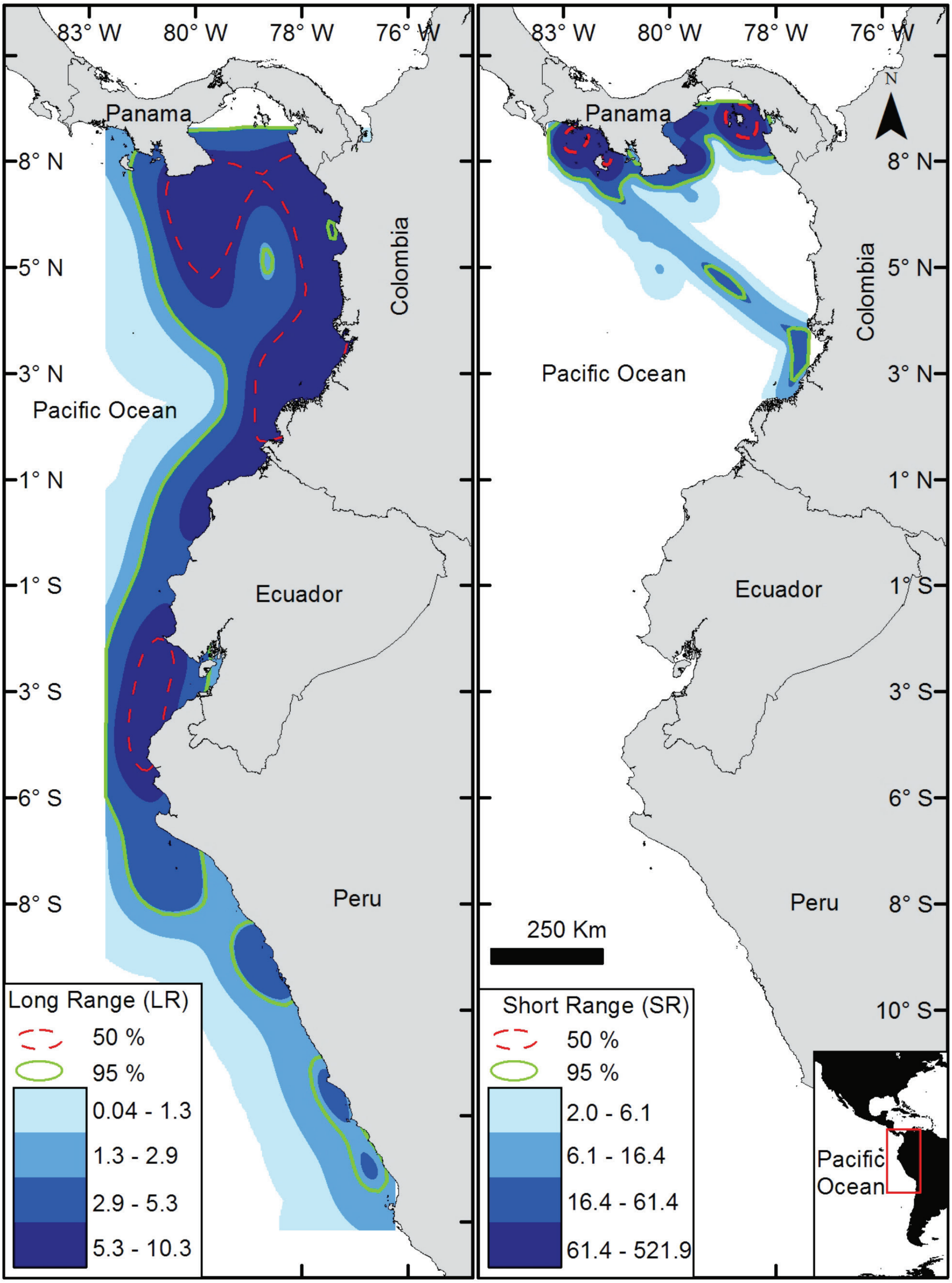

Figure 4. Kernel distribution analysis of mother humpback whales tagged off Panama; dashed red line includes 50% of home range, and green line includes 95% of home range. Left side distribution = whales labeled as LR, and right side distribution = whales labeled as SR. Tagging period: 2009 to 2015.

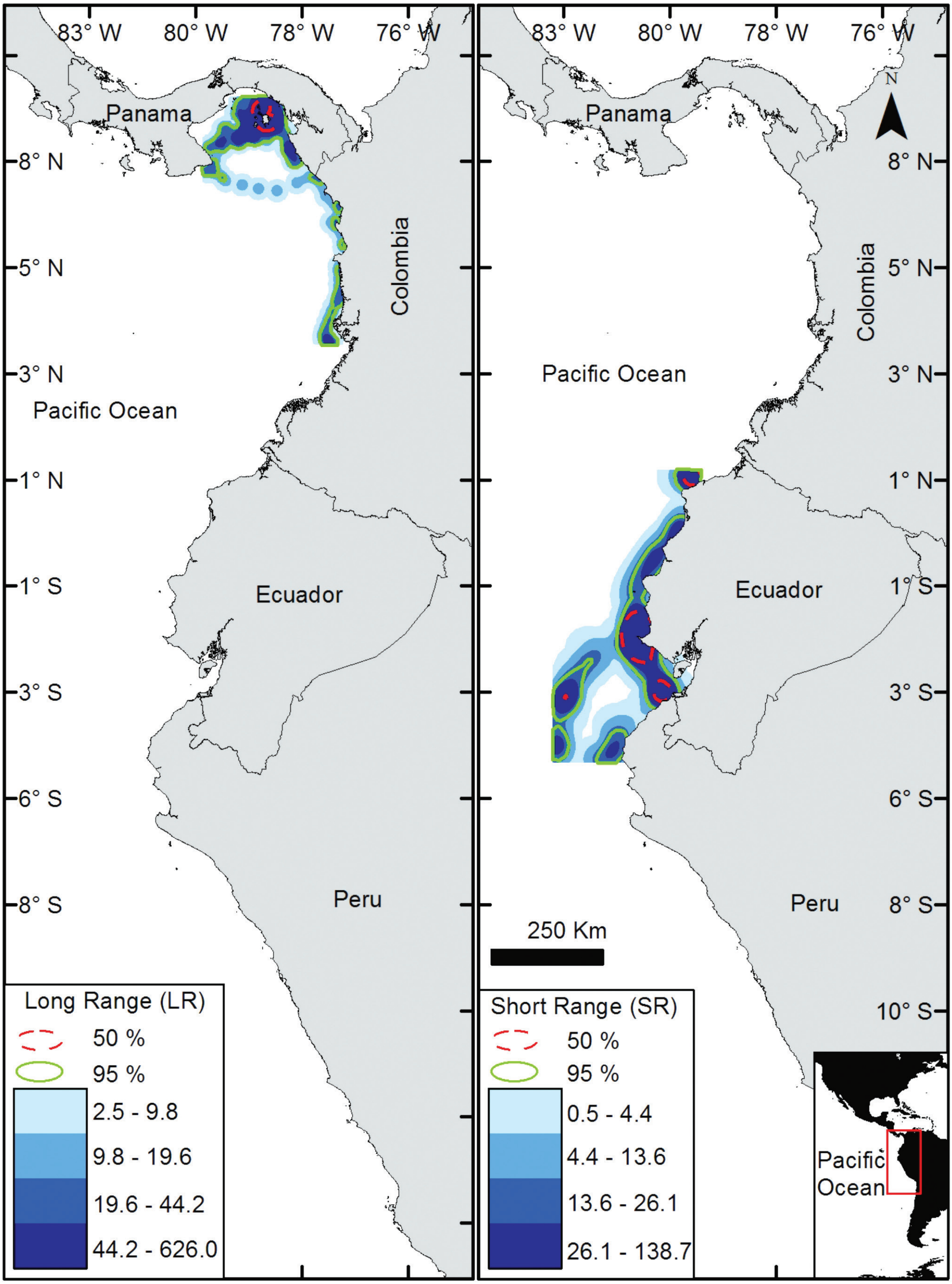

Figure 5. Kernel distribution analysis of unsexed animals labeled as SR humpback whales tagged off Panama (left) and Ecuador (right); dashed red line includes 50% of home range, and green line includes 95% of home range. Tagging period: 2009 to 2015.

Table 3. Percentage of whales' distribution area with respect to depth (m), movement extent (SR = short range and LR = long range), and class (mothers and unidentified sex whales) as estimated by kernel density 95% home range. Bold numbers indicate significant differences ($p > 0.01$) between whales tagged in Panama (Pa) vs Ecuador (Ec).

	Mothers (%)				Unidentified sex (%)	
Depth (m)	Pa LR	Ec LR	Pa SR	Ec SR	Pa SR	Ec SR
> 2,000	53.1	16.9	10.2	3.1	0.6	28
1,000-2,000	10.5	14.9	9.9	8.1	1.5	7
500-1,000	6.0	11.1	7.2	8.3	6	4.7
200-500	**4.7**	**13.5**	10.5	12.8	11.2	4.6
100-200	7.3	16.2	10.4	15.4	14.4	8.5
50-100	10.0	14.6	28.1	24.4	43	20.1
20-50	4.6	7.9	16.1	16.1	17.2	15.4
0-20	3.8	4.9	7.6	11.8	6.2	11.6

incursions into deeper waters as 27% of transmissions from Panama-Costa Rica and 19.5% from Ecuador occurred in water deeper than 1,000 m. The proportion of SR mothers' transmissions from depths > 2,000 m was significantly higher in Panama-Costa Rica than in Ecuador ($X^2_7 = 32.27$, $p > 0.01$).

Higher variability with respect to depth was found in LR mothers compared to SR mothers. Only 25.7% of LR mothers' transmissions from Panama-Costa Rica were made in water < 200 m deep contrary to 43.6% from Ecuador, despite its shallower shelf. A significantly greater proportion of LR mothers' transmissions were produced in water deeper than 2,000 m in Panama-Costa Rica as compared to Ecuador (53 vs 16.9%, respectively). But in Ecuador, a significantly higher proportion of LR mothers' transmissions were made in the 200 to 500 m depth range (13.5 vs 4.7% in Panama-Costa Rica) ($X^2_7 = 31.9$, $p < 0.01$). For unsexed animals, comparisons were limited to SR movements. Significant differences were found between whales in Panama-Costa Rica and Ecuador for > 2,000 m (0.6% Panama-Costa Rica vs 28% Ecuador).

Discussion

Satellite tracking has provided valuable information about the extent of movements by Southeast Pacific humpback whales within breeding grounds, thereby offering new insights about habitat use on a finer scale than was previously available, including information on the extent of distribution ranges by adults of different breeding condition and migration behavior. However, our study was limited by a relatively short tracking period (14.2 d on average), particularly in unsexed adults for which the average was 53% shorter than in mothers with calves. Such a difference could be associated with differences in breeding behavior displayed by both types of whales, with adult animals participating in competitive groups characterized by bouts of intense activity and male aggression (Tyack & Whitehead, 1983; Clapham et al., 1992; Félix & Novillo, 2015), which leads to the risk of breaking the antenna or having the tag expulsed being higher than in mothers nursing calves.

Although the SSSM was originally developed to evaluate movements of other marine vertebrates such as sea turtles and seals (Jonsen et al., 2005, 2007), it has been successfully applied to whale studies, particularly to differentiate feeding from transit and migration periods (Bailey et al., 2009; Kennedy et al., 2014; Zerbini et al., 2015). In general, this model allowed us to differentiate between the behavioral states of breeding humpback whales based on the way animals changed speed and direction, but it did not provide sufficient information to differentiate with precision the behavioral conditions in all cases, particularly in behavior M3. For instance, we noticed significant differences in speed between mothers and unsexed animals in behaviors M1 and M2, but the same behavioral mode could have a completely different function for mothers vs unsexed animals. New prediction models in which environmental and behavioral data are incorporated into the SSSM framework could help to differentiate behavioral states among age and sex classes as suggested by Jonsen et al. (2007).

Based on fidelity of whales to the tagging area, we defined two basic movement patterns exhibited by tracked whales: (1) short range (SR) and (2) long range (LR). A whale showed either pattern and, in a few cases, both if the second phase, the SR phase, always preceded the LR phase. When displaying the SR pattern, whales moved back and forth, traveling between 200 and 350 km along the coast with short excursions into deep water. The SR pattern was associated with more restrained movements and was recorded in both mothers and unsexed animals, despite behavioral states being different in both types of whales. Mothers with SR movements were mainly associated with the behavioral M2 state (ARM) and covered distribution ranges between 26,000 and 61,000 km^2 in Ecuador and Panama, respectively. Such differences in the level of residence among mothers could be attributed to the availability of appropriate sites for nursing around the tagging site, animals being tagged during different phases of the migratory cycle, or mothers that lost the calf and then changed breeding status. With respect to different phases of the migratory cycle, mothers displaying LR movements could be those that arrived and gave birth earlier (June-July) and were tagged during migration or just before starting migration (e.g., Tag Nos. 203, 459, and others). Although the birthing peak in Southern Hemisphere humpback whales occurs in August, when half of the total number of mothers with calves was tagged, some mothers in the Southern Hemisphere give birth as early as the end of June (Chittleborough, 1958; Félix & Haase, 2001). If a female lost her calf, then she might ovulate within the same breeding period (Chittleborough, 1958) and presumably start acting as a receptive adult female for mating or she may migrate back to feeding grounds. SR movements in unsexed animals are presumed to be more variable than in mothers because they were mostly associated with behavior M3—a behavioral state that the model was unable to provide a characterization for other than as an intermediate state between behavioral M1 and M2 states. Thus, the model confirms behavioral differences between both classes during the SR phase likely associated with their breeding condition.

LR movements displayed by whales immediately after tagging or adopted days later during a SR period were associated with a behavioral M1 state (FDM) and is more suggestive of migration. For both locations, mothers with LR movements had a considerably larger distribution range (441,000 and 64,000 km^2 in Panama and Ecuador, respectively). This difference would have two explanations: (1) some whales from Panama were tracked longer, and (2) some Panama whales used an alternative offshore migratory path (which also illustrates variability among mothers nursing at the same breeding site). The speed of mothers with LR movements matched the speed range estimated for migrating animals recorded in other studies (65 to 128 $km.d^{-1}$) (Mate et al., 1998; Zerbini et al., 2006; Félix & Guzman, 2014). LR movements were not recorded from unsexed animals, probably because of the short tracking period.

In summary, during the breeding season, humpback whales, independent of where they arrive, show an SR pattern in the first weeks, concentrating activity in relatively small areas and then increasing their speed and distribution area in a southerly direction once they start migration. Restrained seasonal residency found in SR humpback whales breeding off Panama and Ecuador support the notion of latitudinal population structure at breeding grounds as occurs in other populations (e.g., Medrano-González et al., 1995; Calambokidis et al., 2000; Rosembaum et al., 2009; Carvalho et al., 2014). Population stratification in Southeast Pacific humpback whales would explain why animals feeding in the Magellan Strait, which is located at the northernmost border of these feeding grounds, might have a higher exchange with whales breeding off Panama, located in the northern part of the breeding area, than with whales from Ecuador or Colombia (Acevedo et al., 2007). Stratification also explains why the population estimated in Ecuador in 2006 (6,500, CV = 0.21) (Félix et al., 2011a) is six times higher than the population estimated in Panama in 2009 (1,041 whales; credible interval 664 to 1,546) (Guzman et al., 2015), where only a fraction of this population would arrive for breeding. Female-biased stratification also explains differences in haplotype proportions found between males and females in whales breeding off Ecuador and Colombia (Félix et al., 2012).

We also confirmed that mothers with calves were distributed closer to shore than other tagged adults (unsexed animals). However, mothers showing SR and LR movements were also found in deep water, particularly off Panama, where 20% of transmissions by mothers with SR movements were in depths > 1,000 m (and the proportion increased up to 60% in LR animals). These findings were rather unexpected as previous reports of the distribution of humpback whales breeding off northwestern South America indicated a more coastal distribution of the species (Félix & Haase, 2005; Oviedo & Solis, 2008; Félix & Botero, 2012), which could be the result of coastal sampling bias. Incursions into deep water are commonly reported in humpback whales breeding within oceanic archipelagos such as Hawaii and the West Indies, where whales move between islands (Cerchio et al., 1998; Kennedy et al., 2013). The narrow continental shelf along the west coast of South America and the (potential) offshore shortcut used by some migrating animals between Panama and Colombia could be causes for this relatively deep distribution of the species in the Southeast Pacific.

Management Implications

Population Structure—The overlapping distribution of whales showing either SR or LR movements at tagging sites could explain why some photo-ID and genetic analyses of population structure at breeding grounds seem inconclusive (Valsecchi et al., 2010; Félix et al., 2012; Carvalho et al., 2014), even when large samples are used (Rosenbaum et al., 2009; Baker et al., 2013). Because migration is a continuous process with a succession of group classes arriving and leaving the breeding area at different times during the season (Dawbin, 1966; Craig et al., 2003), sampling heterogeneity will always be present. This is particularly true in areas such as Salinas in Ecuador because whales breeding in Colombia and Panama must pass by here during northbound and southbound migration. In light of the complex and not well-understood structure of humpback whale populations, particularly in the Southern Hemisphere, Baker et al. (2013) noted the necessity of re-evaluating management strategies for this species on both breeding and feeding grounds to incorporate population management as an alternative to how the International Whaling Commission (1998) currently divides whales into stocks. Future efforts should include tissue biopsies of tagged individuals to differentiate maternal lineages to help define such management units.

Human Activities—A variety of human activities overlap the distribution of humpback whales off Panama and Ecuador, including fishing, maritime traffic, and tourism (Félix & Haase, 2005; Guzman et al., 2013). Increasing coastal infrastructure in the region, such as oil/gas terminals, offshore platforms, new ports, and marina facilities, as well as different forms of pollution, add pressure to whales during a key stage of their life cycle.

Our findings also have implications for whale watching. Because of their high resident level and shallower distribution pattern, mothers with calves would be the class with the highest potential to be recurrently sighted by whale-watching vessels during the season. Therefore, it is necessary to modify the current regulations to reduce the time and number of encounters with mother/calf pairs by establishing exclusion areas where the probability is high of finding mothers with calves as demonstrated by spatial analysis (Ersts & Rosenbaum, 2003; Félix & Botero, 2012; Bruce et al., 2014).

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