Aquatic Mammals 2014, *40*(4), 329-340, DOI 10.1578/AM.40.4.2014.329

Satellite Tracking and Sighting Data Analyses of Southeast Pacific Humpback Whales (*Megaptera novaeangliae*): Is the Migratory Route Coastal or Oceanic?

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Abstract

This paper presents an analysis of the migration movements of Southeast Pacific humpback whales (*Megaptera novaeangliae*) based on satellite and sighting data. We used information obtained from six humpback whales tagged off the coast of Ecuador between August and September 2013, and sighting information from oceanographic cruises and seismic prospection studies. Tagged humpback whales were followed along the west coast of South America, and in one case off the Antarctic Peninsula, for between 11 and 72 d. Distance covered by tracked whales was between 920 and 8,670 km. While available sighting data indicated that humpback whales follow a coastal route, satellite tracking data show that single adults use a more direct offshore route and mother/calf pairs tend to follow the longer coastal route. A 4-d period of irregular movements by a mother with a calf off central Peru suggested foraging behavior in this area characterized by intense upwelling processes. On the other hand, the humpback whale that reached Antarctic waters by mid-October quickly moved 200 km off the Antarctic Peninsula, probably because the zone was still covered by ice. We also found differences in travel speed between age/sex classes of humpback whales with mother/calf pairs traveling about 30% slower than single adults. The average humpback whale swim speed ranged between 65.5 and 169 km.d^{-1}. Our information provides a first examination of potential routes used by this whale population and highlights the need for a regional approach in appropriately addressing the migratory behavior and threats to the species during its annual migration.

Key Words: migratory route, Southeast Pacific, Breeding Stock G, humpback whale, *Megaptera novaeangliae*

Introduction

The Southeast Pacific humpback whale (*Megaptera novaeangliae*) population, which the International Whaling Commission refers to as Breeding Stock G, is one of the seven stocks of this species inhabiting the South Pacific (International Whaling Commission [IWC], 1998). Early descriptions of the migrations of humpback and other large whales in this region were based on the logbooks of Yankee and British whalers from the 17th through early 20th centuries (Kellogg, 1929; Mackintosh, 1942). These reports included general descriptions of the sites where baleen whales concentrated in breeding areas in the tropics and feeding areas in Antarctic waters. From these data, the migration path of humpback whales along the western South American coast was inferred.

In the last 20 y, studies on humpback whales in the Southeast Pacific have focused on whale concentration at both breeding and feeding areas. Thus, it has been determined that the breeding area extends from north of Peru (5° S) to central Costa Rica (12° N) (Félix & Haase, 2001; Rasmussen et al., 2007; Pacheco et al., 2009), and the feeding areas are located mainly west of the Antarctic Peninsula and southern Chile (Acevedo et al., 2007; Dalla Rosa et al., 2008; Hucke-Gaete et al., 2013). The link between these sites has been demonstrated via matching photo-identified animals (Stone et al., 1990; Stevick et al., 2004; Acevedo et al., 2007; Rasmussen et al., 2007) and genetics (Caballero et al., 2001; Olavarría et al., 2007; Félix et al., 2012). The Southeast Pacific populations undertake the longest migration of all stocks of this species in the world; they travel a round trip of more than 16,000 km (Stone et al., 1990; Rasmussen et al., 2007).

While important advances in our knowledge about the migratory destinations of this population have been made, some gaps remain regarding the migratory path (i.e., coastal or oceanic) that whales follow between these sites. Addressing the migratory route gap was prioritized as a research topic in a recent initiative focused on modeling the humpback whale habitat in the Southeast Pacific because the available information was biased toward the coastal area (Comisión Permanente del Pacífico Sur [CPPS], 2014). In the 20th century, humpback whales were taken infrequently by whalers from land-based stations along the coast of Chile and Peru; this led Clarke (1962) to suggest that humpback whales migrate off the Humboldt Current in oceanic and warmer waters until reaching Ecuador. This is consistent with whaling records from the mid-1960s for the water north of Peru (Ramírez, 1988) and also recent coastal studies in this area (Pacheco et al., 2009; Santillán, 2011).

The use of satellite telemetry is useful to unravel the migratory paths used by humpback whales between breeding and feeding grounds (e.g., Mate et al., 1998; Zerbini et al., 2006; Gales et al., 2010; Hauser et al., 2010; Kennedy et al., 2013). In general, humpback whales seem to take the shortest and most direct routes even in high seas or following the mainland profile (Gales et al., 2010). However, there are some populations whose breeding areas include both oceanic and continental waters. This is the case for the North Pacific humpback whale stock breeding off Mexico, Central America, and in the oceanic Revillagigedo Archipelago. Humpback whales breeding at Revillagigedo follow a more direct oceanic route than humpback whales breeding along the mainland (Calambokidis et al., 2008; Lagerquist et al., 2008). In the Southeast Pacific, some humpback whales breed in an oceanic archipelago, the Galapagos Islands, 1,000 km off Ecuador, but in significantly lower numbers than along mainland South America (Félix et al., 2011b). Considering the long migration of Southeast Pacific humpback whales, it is expected that whales of this population will take the shortest route, in this case a combination of coastal waters north of Peru and south of Chile, with an oceanic excursion to avoid the sinuous profile of the central west coast of South America. Humpback whales breeding at Galapagos are expected to take a completely oceanic route as no evidence of longitudinal movements between the continent and the Galapagos has been recorded (Félix et al., 2012).

In this article, we present a tracking analysis of humpback whales tagged with satellite transmitters off Ecuador during the breeding season. Sighting data obtained off the coasts of Chile and Peru over the past 40 y complemented the analysis. The information presented here aims to identify conservation needs for the species in a broader regional context and to encourage research on the species beyond the coastal zone where the effort is currently concentrated.

Methods

Study Area

The Southeast Pacific extends 8,000 km along the west coast of South America (Figure 1). It includes a diversity of ecosystems such as mangroves and estuarine areas in the tropics, upwelling areas in subtropical and temperate regions, and sub-Antarctic fjords in southern Chile. The South American continent's southernmost tip is located approximately 1,000 km north of the Antarctic Peninsula, where the main feeding areas of the Southeast Pacific humpback whale population are located (Dalla Rosa et al., 2008). The ocean circulation is dominated by the Southeast Pacific anticyclonic gyre that originates the Humboldt or Peruvian Current System (HCS). The HCS originates between 40º and 50º S from the Antarctic Circumpolar Current, heading north along the west coast of South America (Wyrtky, 1975). The Southeast Pacific is a highly productive area due to both the Humboldt Current and local upwelling processes along the coast of Peru and north of Chile (Thiel et al., 2007; Heileman et al., 2008).

The Southeastern Pacific is characterized in its northern area by warm tropical waters from the southern gyre of the Equatorial Countercurrent reaching the Gulf of Guayaquil at approximately 3° S where it meets the Humboldt Current and diverges west, forming the South Equatorial Current. Both currents collide and form the Equatorial Front, which moves north or south off Ecuador depending on the strength of the Southeast Pacific anticyclonic winds (Wyrtky, 1975; Cucalón, 1996). For this study, we define the edge of the shelf (200 m) as the limit between the coastal and offshore oceanic realms.

Satellite Tagging

Only adult humpback whales were the focus of this study. Two classes of animals were identified based on their relative size and social condition at the time of tagging—single adults and females with calves—but class designation could change during the study if a female in a late stage of pregnancy was tagged and later had a calf or if an adult female lost her calf.

Twenty-one satellite tags were deployed on humpback whales off Salinas, Ecuador (2° 10' S, 81° W), between August and September 2013. Satellite transmitters Wildlife Computers SPOT5 Model AM-S193C with two AA lithium batteries were used for this study. Transmission parameters included no time limitations to allow for constant transmissions. The maximum number of transmissions per day was set at 200, allowing unused transmissions to be used the next day. For transmissions to reach the satellite when the animal surfaced, fast and slow repetition rates (seconds) were set by the manufacturer at ranges of 41.5 to 47.5 s and 86.5 to 92.5 s, respectively. The tag-derived positions from Argos location classes 3, 2, 1, 0, A, and B were used with a range of errors in accuracy estimated at between 150 m and 5 km radius for plotting general whale movements (see Costa et al., 2010; Douglas et al., 2012; Guzmán et al., 2012).

Factory transmitters consisted of a 2-cm-diameter stainless steel tube case, 7.5-cm-long, coupled to a custom-made stainless steel spear with a 3-cm triangular double-edged blade tip containing three pairs of 5-cm barbs placed at 90º to each other (modified from Guzmán et al., 2012). Total tag weight (transmitter and spear) was 380 g. We tagged humpback whales from a 5-m-long fiberglass boat at a distance of 2 to 5 m from the whale. Tags were deployed using a modified pneumatic line-thrower (Model ARTS, Restech Inc., Norway) fitted with a ZOS Universal waterproof and fogproof 1 × 40 riflescope. Air pressure ranged from 10 to 15 bars (10.2 to 15.3 kg.cm^{-1}). Before deployment, tags (transmitter and spear) were coupled to a LK-carrier developed by LKARTS-Norway; the carrier consisted of a 50-cm-long by 3-cm-diameter PVC pipe with three 19 × 3.5-cm plastic fletching vanes in the rear. The transmitters were attached to the whales about 20 to 40 cm below and in front of the dorsal fin, in a thick layer of blubber, to minimize injury to the animals. Some animals reacted initially to tagging, but all continued in the same area for hours and days without changing normal behavior, site, or trajectory overall. In order to reduce the likelihood of infection, spears and 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. Track distances were processed using STAT–MAPTOOL (Satellite Tracking Analysis Tool) (Coyne & Godley, 2005).

Sighting Data

Sighting data on humpback whales off the west coast of South America were obtained from two major sources: (1) oceanographic cruises by National Oceanic and Atmospheric Administration (NOAA) fisheries during marine mammal assessments conducted between 1991 and 2004 (Hill et al., 1991; Kinzey et al., 1999, 2000, 2001; Jackson et al., 2004), and (2) data contained in the Regional System on Marine Biodiversity and Protected Areas of the Southeast Pacific (SIBIMAP), compiled by the Permanent Commission for the South Pacific (CPPS) (www.sibimap.net). This online database contains more than 16,000 geo-referenced records without information on sighting effort for 34 cetacean species in the Eastern Pacific since 1959, including 4,619 records of humpback whales.

The information extracted from SIBIMAP for this analysis includes opportunistic data from oceanographic cruises carried out by the Peruvian Institute of Fisheries (IMARPE) (Bello et al., 1997; Sánchez & Arias-Schreiber, 1998; Sánchez et al., 1998; Márquez & Arias-Schreiber, 2000), unpublished information from seismic prospection surveys off Peru (Geolab, 2010; Walsh Peru, 2011), and the Cetacean Sighting Network of the Chilean Navy directly submitted to SIBIMAP. The geographic area of the data used in this analysis included the area between 4° S (north of Peru) and 60º S (300 km north of the Antarctic Peninsula). Data from the main breeding areas north of Peru and from land-based studies north of Peru and south of Chile were not included because it was not possible to distinguish when migrating whales were from the destination breeding/feeding assemblies, thus reducing the bias toward coastal sightings in the dataset. In addition, it is recognized that sighting data reported to SIBIMAP may include potential errors associated to misidentified species at sea.

Results

Satellite Information

Transmissions were dominated by Argos location classes 0, A, and B (Table 1). Of the 21 humpback whales tagged off Ecuador, three tags never transmitted, six whales started the feeding migration to the Antarctic, and 15 remained in the breeding area during the transmission period and were not included in this analysis. Since none of the humpback whales that crossed the 4º S parallel returned to the north, we assumed that all whales moving south of this point started the migration. Migrating humpback whales included three mothers with calves and three adults of unknown sex (Table 1 & Figure 1). Three humpback whales were tagged in mid-August (Nos. 71, 85, and 88) and the other three in mid-September (Nos. 86, 90, and 91). The transmission time of these tags was between 11 and 72 d ($\bar{x}$ = 29.5 d, SD = 23.6). The distance traveled by the whales ranged between 920 and 8,670 km. For three cases, transmission was continuous (Nos. 71, 86, and 88) but brief (11 to 15 d). For No. 85, the signal was lost on day 7 and retransmitted on day 63 from the Antarctic Peninsula. No. 90 started transmission on day 19 and transmitted for 10 d.

The tagged humpback whales showed different behavior with respect to their of onset of

Table 1. Data summary for six humpback whales (*Megaptera novaeangliae*) tagged off Ecuador during the 2013 southerly migration, with three adult females with calf (MC) and three adult (A) animals of unknown sex; relevant information for Argos transmission location classes is presented for each tag along with the tracking period.

Variable/ID	No. 71	No. 85	No. 86	No. 88	No. 90	No. 91	Total	Mean (SD)
Tagging date	13 Aug	14 Aug	18 Sept	13 Aug	18 Sept	16 Sept		--
Class/sex	A	A	MC	MC	MC	A		--
Tag longevity (d)	11	72	15	11	29	39	177	29.5 (23.6)
Total distance (km)	920	8,670	1,088	1,416	1,907	4,343	18,344	3,057 (3,020.5)
Speed average (km.d^{-1})	83.6	120.4	72.5	128.7	65.7	111.3		97.03 (26.5)
Transmission data								
Received	143	229	118	113	95	136	834	--
LC 3	0	4	3	0	0	1	8	--
LC 2	2	12	4	0	3	2	23	--
LC 1	4	25	6	1	5	4	45	--
LC 0	1	15	2	2	1	0	21	--
LC A	16	34	18	10	13	26	117	--
LC B	104	134	78	88	68	97	569	--
Used	127	224	111	101	90	130	783	--

migration, travel speed, and routes. A summary of individual movements for each of the six humpback whales is provided below:

- *No. 71* – Adult animal, unknown sex, observed in a competitive group with three other conspecific whales. This whale spent 2 d north of the tagging site and then started moving southwest (offshore) and continued south. The last transmission occurred when the whale was about 120 km off Paita in northern Peru. This whale moved at an average speed of 83.6 km.d^{-1}.
- *No. 85* – Adult animal, unknown sex, found in a competitive group. Like No. 71, after 2 d this animal started moving south into the Gulf of Guayaquil, from a few kilometers north of the tagging area. The whale continued southbound but transmissions stopped on day 7 when the whale was about 92 km offshore of Paita, Peru (4.7º S). Transmission restarted on day 63 when the whale was about 300 km southwest of the Shetland Islands off the Antarctic Peninsula (Figure 1). The distance in a straight line from the last transmission off the north of Peru on 21 August to this point was 6,747 km. Thus, at a minimum, this whale covered this distance in 56 d with an average speed of 120.48 km.d^{-1}. In Antarctic waters, the whale transmitted for another 8 d, moving northeast for 1,263 km at an average speed of 158 km.d^{-1} (Figure 1).
- *No. 86* – Mother with calf stayed about 30 to 40 km north of the tagging site near the coast for 6 d and then started moving south. The whale continued south in the shallow waters of the Gulf of Guayaquil and along the north coast of Peru, transmitting for 15 d over 1,088 km with an average speed of 72.5 km.d^{-1}. The last transmission was south of Bahía Sechura (6° S), 50 km offshore.
- *No. 88* – Mother with calf moved southward after tagging. They remained in the central part of the Gulf of Guayaquil for 4 d and then started moving south along the coast. South of Bahía Sechura (6° S), the whale was about 120 km offshore and then approached the coast again at 8° S. This whale was followed for 11 d and swam at an average speed of 128.7 km.d^{-1}.
- *No. 90* – Mother with calf started transmission on day 19 near mid-Peru (12° S), 1,255 km south of the tagging site. This whale transmitted for 11 d. During transmission time, the whale remained within 30 km of the coast off Paracas traveling 712 km at an average speed of 65 km.d^{-1}.
- *No. 91* – Adult, unknown sex, observed in a competitive group. The whale started transmission on day 23 from the southern part of Peru, approximately 400 km offshore. On average, the whale swam at a speed of 111 km.d^{-1}, but during the 16 d of transmission, the whale moved 2,706 km, heading south at an average speed of 169 km.d^{-1}. Of the six tagged animals, this was the whale recorded farthest offshore. It

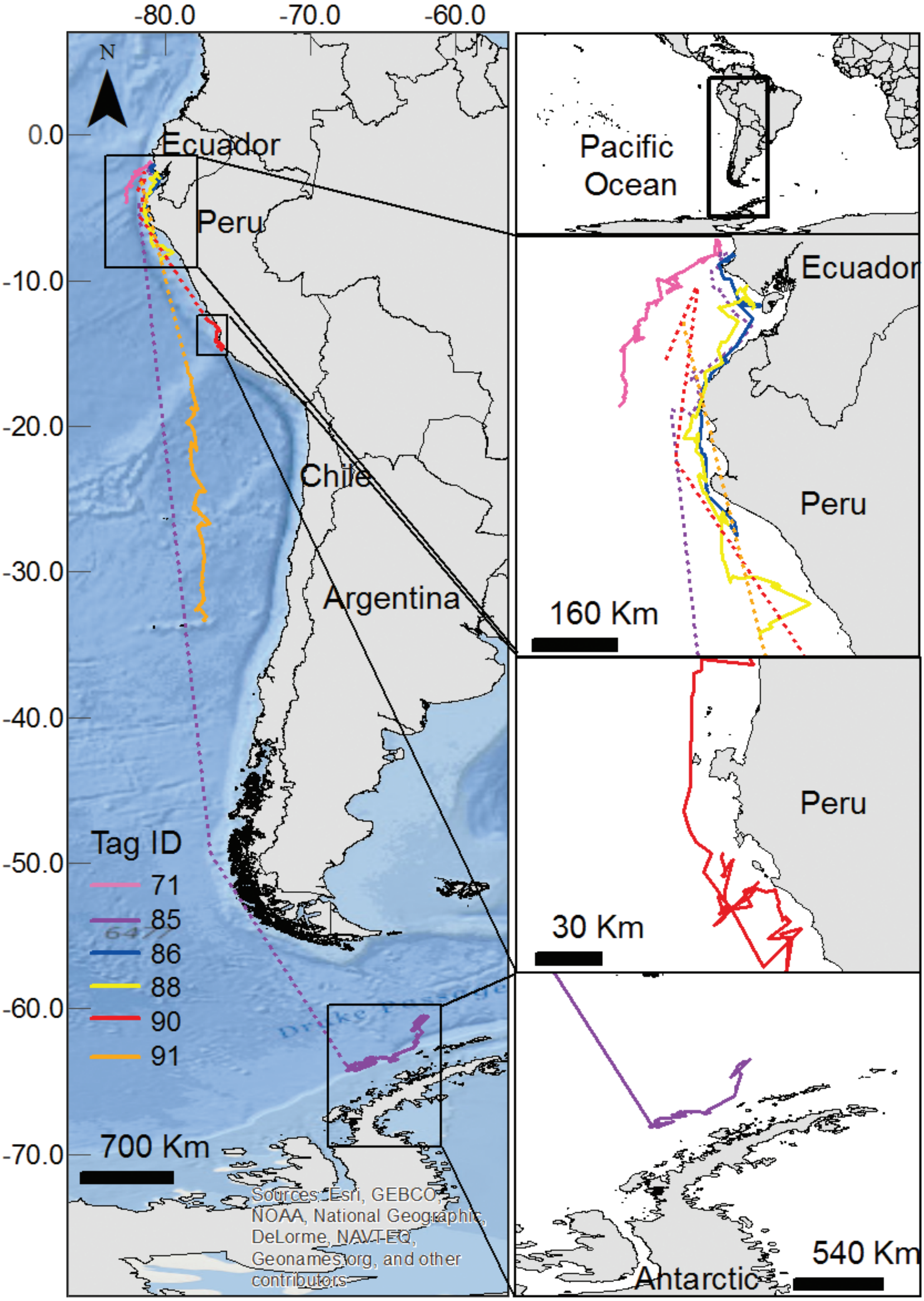

Figure 1. Tracks of six humpback whales (*Megaptera novaeangliae*) tagged off Ecuador en route to the Antarctic; dashed straight lines represent the sites where transmission was lost. Insert maps show the detailed movements of the whales (color coded) at different latitudes from Ecuador to western Antarctic Peninsula.

traveled about 800 km off the northern coast of Chile (Figure 1).

Sighting Data

Available sighting data from SIBIMAP included 241 records of migrating humpback whales off Chile and Peru (Figure 2). In order to determine differences in sighting distribution counts and depths between northbound or southbound migrations, the dataset was divided into two periods: February 16 to August 15 ($n = 110$) for the breeding migration from the Antarctic to the tropics and August 16 to February 15 ($n = 131$) for the feeding migration from the tropics toward the Antarctic. The difference was not significantly different ($X^2 = 1.83$, $p > 0.05$). Sighting data show a continuous coastal distribution of the species along Peru and north and central Chile, with few records offshore ($n = 13$, 5.4 %). The same pattern was observed in both periods, which was expected given the fact that the sampling effort was biased toward the coast. The few available offshore records were made off the central part of Chile, mainly around the Juan Fernández Archipelago and even further offshore.

Migration Time and Routes

Based on the six tracks of humpback whales that started migration, there seems to be two migratory routes—one more straight and offshore as that taken by No. 91 and likely Nos. 85 and 71, and another path bordering the coast profile taken by adult females with calves. We estimated

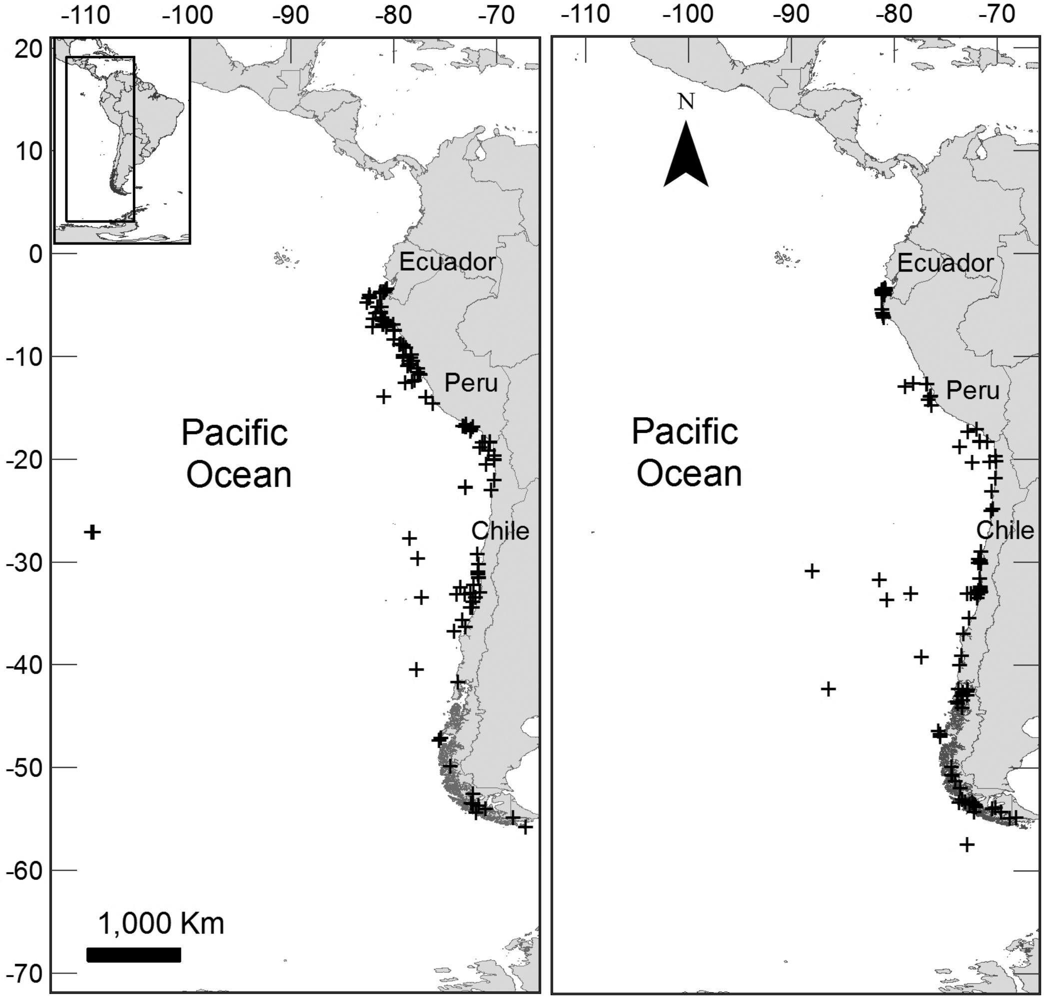

Figure 2. Opportunistic sightings of humpback whales (+) from the period 1994 to 2012 obtained during the migration along the coast of Chile and Peru available from the SIBIMAP database; sightings were divided in two periods: 16 February to 15 August during the northbound migration (left) and 16 August to 15 February during the southbound migration (right).

the offshore route from 4º S to the point of the first transmission by No. 85 from the Antarctic Peninsula (64.19º S, 67.52º W) as 6,816 km and the larger, coastal route as 7,264 km; this latter route is *ca.* 6.2% longer. Based on the average speed estimates, the migration of single whales would last on average 66.4 d (SD = 13.25) if using the offshore route and 70.8 d (SD = 14.12) along the coastal route. For adult females with calves, assuming they maintain the average speed as recorded in the first part of the migration, the offshore migration would last 83.6 d (SD = 26.9), while the coastal route would take 89 d (SD = 28.7). However, if No. 91 could maintain the same speed along the entire migratory route as we recorded during continuous tracking off southern Peru and Chile (169 km.d^{-1}), the migration would last only 40 d. For No. 85, if its migration speed was the same as what was recorded in Antarctic waters (158 km.d^{-1}), the migration period would be 46 d along the coastal route and 43 d via the offshore route.

Discussion

Transmission location classes were typical for marine mammals with short-surface intervals (Costa et al., 2010; Douglas et al., 2012). The accuracy of those location classes may not be defined within specific limits, but they provided useful tracking information at the resolution of our analyses (see Vincent et al., 2002). This is the first study to preliminarily analyze the potential migration routes of humpback whales in the Southeast Pacific. Our analysis indicates that this population uses both coastal and offshore routes for migration, depending on the reproductive status of the animals. Single adults seem to take a shorter, offshore route, while mother/calf pairs seemed to prefer the longer, coastal route. This difference has not been identified in other populations of humpback whales likely because most satellite tracking studies on the species have been conducted on stocks breeding in oceanic archipelagos, such as Hawaii, Abrolhos, the Caribbean, and the South Pacific, where whales of all age and both sex classes migrate through open waters (e.g., Mate et al., 1998; Zerbini et al., 2006; Hauser et al., 2010; Kennedy et al., 2013). Humpback whales that migrate along both coasts of Australia seem to follow the shortest route along the coast and then head south toward the Antarctic (see maps in Gales et al., 2010). The reasons why adult females with calves in the Southeast Pacific undertake a longer migratory route near the coast despite traveling slower than without a calf is unknown, but this could be related to predator avoidance (e.g., orcas) or the potential for feeding in coastal upwelling areas off Peru and Chile during migration (see below).

In addition to the different migration routes, Southeast Pacific whales showed differences in migration speed according to age and sex classes in ways similar to those reported elsewhere (e.g., Zerbini et al., 2006; Kennedy et al., 2013). Two of the three adult females with calves (Nos. 86 and 90) showed the lowest swim speeds, 65 and 72 km.d^{-1}, respectively, which is about a third less on average than single adults; however, adult female No. 88 presented the highest average speed of the six humpback whales (128 km.d^{-1}). No. 88 started migrating shortly after being tagged in mid-August, which was unusual for an adult female with a calf to leave the breeding area after the other age/sex classes (see Dawbin, 1966). Mate et al. (1998) also recorded an adult female from the Hawaii group that moved faster (average of 150 km.d^{-1}) than other age/sex classes. Zerbini et al. (2006) tracked a mother with calf to the feeding zone in the South Atlantic that moved at an average speed of 92 km.d^{-1} for 3,700 km. This indicates that mothers with calves could move at speeds similar to single adult whales and, in some cases, even faster during migration than other whale classes. For No. 88, because of her early migration time and her speed, we suspect this whale might have lost her calf and therefore left the breeding area earlier than expected. It is not possible to be sure about the fate of calves in these cases, but it is reasonable to suppose that adult females who lost calves early on breeding grounds might have migratory behavior more similar to that of single adults, which would explain why No. 88's speed was closer to that of single adult whales recorded for the longest distances (No. 85, 120 km.d^{-1}, and No. 91, 111 km.d^{-1}) rather than for other mother/calf pairs.

The speed of the three individual adult whales (between 83 and 120 km.d^{-1}) was consistent with rates of migrating humpback whales recorded in other locations in both the Southern and Northern Hemispheres (Gabriele et al., 1996; Mate et al., 1998; Zerbini et al., 2006; Kennedy et al., 2013). Interestingly, the speed of No. 85 in Antarctic waters averaged 60% faster (158 km.d^{-1}) than during the 7 d of travel from Salinas to the north of Peru when transmission stopped the first time (99.7 km.d^{-1}). Studies of humpback whales off the Antarctic Peninsula show that humpback whales generally move more slowly when feeding, covering less than 50 km.d^{-1} with an irregular pattern, and only increasing speed when moving between feeding areas (Dalla Rosa et al., 2008). This suggests that No. 85 did not start feeding during the tracking period. We speculate that No. 85 stayed 200 km off the Antarctic Peninsula, moving northeast and not within the coastal area where the whales usually feed (Dalla Rosa et al., 2008) because the coastal area still would have been covered with ice on the date of arrival (mid-October).

The behavior of whale No. 85—leaving the breeding area early—is consistent with what is known to occur with pregnant females who leave the breeding area earlier than other classes for an extended feeding season (Chittleborough, 1958; Dawbin, 1966). Because no tag transmissions were received during No. 85's migration, it is not possible to know whether this animal used the offshore route nor No. 85's arrival date and time in Antarctic waters before transmissions restarted. Since the reason to return to the Antarctic so soon after becoming impregnated would be to maximize feeding to store sufficient energy to raise a calf (Dawbin, 1966), we speculate the shortest route could seem the best option. It was estimated that if No. 85 used the offshore route, it arrived in Antarctica in 56 d; and if the coastal path was followed, then 60 d would be maximum. Notwithstanding, the speed of Nos. 85 and 91 increased in the last part of the tracking period, which suggests that humpback whales might be able to sustain higher speeds during long periods, reducing considerably the migration time to as low as 40 to 50 d.

Humpback whales could use ocean currents or other oceanographic variables, such as the presence of thermal fronts, during migration along the Southeast Pacific. While Clarke (1962) suggested that humpback whales avoid the cold waters of the Humboldt Current on their way to the tropics, migrating with the current would help them conserve energy, especially considering that this current flows north for about 6,000 km. Still, the Humboldt Current System (HCS) is formed by a series of microcurrents and gyres interacting in a complex pattern, including two important branches along the coast and offshore, separated by a warmer subsurface countercurrent from the north (Wyrtky, 1975). Therefore, the HCS provides an unusual condition for humpback whales, with northerly and southerly flows that could be used during migration. It is unknown, however, the incidence of the thermal structure of the HCS in the energetic budget of migrating humpback whales. Since oceanographic conditions may change every year, which would be unpredictable for the whales, it seems more likely that humpback whales prioritize the shorter, although colder, over the longer, even if warmer, route during migration.

The high productivity found along the HCS could eventually provide feeding opportunities for humpback whales during the migration. Although there are no confirmed records of humpback whales feeding en route, it has been suggested that the abundance of small pelagic fish, such as anchovies and sardines, could be taken by humpback whales along the way as occasionally occurs elsewhere (see Papastavrou & Van Waerebeek, 1994). Feeding while migrating might compensate the energetic costs of both lactation and the longer migratory route seemingly favored by adult females when accompanied by a calf. The longer route crosses coastal zones off central Peru where the most intense upwelling processes occur in the HCS (Heileman et al., 2008). This may explain why an adult female with a calf (No. 90) remained in a small area off Paracas, Peru (14º S), for 4 d before her signal was lost, moving back and forth within 30 km of the shore (see Figure 1). Her behavior over shallower waters resembles that reported for satellite tagged humpback whales during feeding episodes off the Antarctic Peninsula (Dalla Rosa et al., 2008) and the Bering Sea (Kennedy et al., 2014). The short duration and uniqueness of this record precludes a detailed behavioral analysis.

The intermittent transmission of No. 85, as well as the late transmission of No. 90, could be related to a combination of migration speed and prevailing oceanic conditions, which did not permit enough "dry" time to intercept the satellites for transmission. Similar problems of intermittent or delayed transmissions have been reported elsewhere (e.g., Hauser et al., 2010; Kennedy et al., 2013).

Satellite Data vs Sighting Data

Satellite data indicate that the migration corridor extends from the coast to at least 800 km offshore, although there are sighting records (albeit limited) as far as 1,500 km offshore. These records suggest the actual migration corridor could be much wider than is described in this paper. Nonetheless, sighting data from SIBIMAP, most of which are opportunistic, favor the impression that humpback whales migrate mostly along the coast as less than 5% of the available records were located in offshore waters. On the other hand, the six satellite tracks shown in this paper suggest that only mother/calf pairs use the coastal route since all adult females with a calf began their migration(s) close to the coast. In contrast, single adults, such as individuals Nos. 71 and 75, initiated their migrations offshore after having left Ecuador. Despite the limited number of tracks, it seems reasonable to assume that only part of the population is migrating along the continental profile from Ecuador to Antarctic, mostly females with calves, which might represent around 20% of the population according to the maximum plausible reproductive rate in humpback whales (11.8%) (sensu Zerbini et al., 2010). The SIBIMAP database, however, showed the same sighting distribution pattern during north- and southbound migrations, suggesting that both routes are used during the northbound migration as well. Further investigations to appropriately address the lack of information about migration routes used by this species are required with a larger sample of tagged animals.

Management Implications

This preliminary analysis has shown that despite the availability of a large amount of sighting data for this region (e.g., SIBIMAP database), although valuable, it may not be representative of the species distribution or suitable for robust habitat modeling. Indeed, a recent habitat suitability modeling exercise wrongly suggested that Southeastern Pacific humpback whales were nearly restricted to coastal areas with less emphasis on oceanic areas due to the coastal-biased nature of the surveys along the South American coast (CPPS, 2014). Ongoing satellite tracking data may improve modeling exercises like this, providing more realistic information on the migratory routes of the species.

A better understanding of migratory routes will allow a comprehensive assessment of anthropogenic threats faced by humpback whales during their migration, providing the basis for implementing effective and dynamic regional management and conservation measures. Gill nets and ship strikes have been identified as the main threats in coastal areas for this species in the region (Van Waerebeek et al., 2007; Félix et al., 2011a; Guzmán et al., 2012). The risk would be even higher for adult females with calves that migrate along the coast due to the intense use of those areas by small-scale fishermen (Steward et al., 2010) and commercial ships (Guzmán et al., 2012) in the Eastern Pacific countries.

Acknowledgments

The authors thank Catalina Gomez, Carlos Guevara, and Gabriela Escobar for preparing maps. Ben Haase, Xavier Avalos, Karla Pozo, and Miguel Jaramillo participated during fieldwork. The Permanent Commission for the South Pacific allowed us access to the SIBIMAP database. We thank the SEATURTLE Organization (www.seaturtle.org) and the Marine Research Turtle Group for permission to use the Satellite Tracking and Analysis Tool program. The Animal Care and Use Committee of the Smithsonian Tropical Research Institute approved tagging procedures. Two anonymous reviewers made valuable comments to improve an earlier version of this paper. This study was conducted under research permit No. 011-IC-FA-DPSE-MA–2013, issued by the Provincial Department of Environment of Santa Elena. This study was partially financed by the Smithsonian Tropical Research Institute, Secretaría Nacional de Ciencia y Tecnología de Panamá (SENACYT), The International Community Foundation, and The Whale Museum.

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