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Distribution and behaviour of humpback whale mother–calf pairs during the breeding season off Ecuador

Fernando Félix[1,*], Natalia Botero-Acosta[2]

[1]Museo de Ballenas, Salinas, Ecuador, and PO Box 0906-2370, Guayaquil, Ecuador
[2]Fundación Macuáticos Colombia, Calle 27, No. 79-167, Medellín, Colombia

ABSTRACT: Data on distribution and behaviour of mother–calf pairs of humpback whales *Megaptera novaeangliae* obtained during the breeding season (June to October) off Ecuador were analysed. The study was carried out between 2001 and 2009 aboard whale-watching boats. A total of 187 groups containing mother–calf pairs were recorded: 124 pairs alone (MC), 44 with an escort whale (MCE) and 18 with 2 or more whales (MC + n). Five environmental variables were used to assess mother–calf distribution with a principal component analysis (PCA). Two variables, depth and time of day, were sufficient to explain heterogeneity. Average depths increased significantly with group size from MC to MC + n groups ($p < 0.001$), showing that mother–calf social condition would be a function of the depth at which they moved. MC groups were distributed in shallower waters during afternoon hours ($p = 0.035$), indicating a preference for shelter areas when sea conditions worsened. The proportion of the 3 female–calf group classes remained fairly constant during the season. In 2 MCE groups, the same escort accompanied the pair after 1 and 4 d, indicating some level of stability and/or guarding behaviour. Twenty resightings of 14 different mother–calf groups were recorded, 90% of resightings occurred within 10 d, showing low site fidelity. In coastal waters, a lower proportion of mother–calf pairs was associated with competitive groups than in other breeding areas located in oceanic archipelagos. This is probably because whales breeding in continental shores do not have to enter oceanic waters when moving between sites within the breeding area. Coastal distribution exposes mother–calf pairs to a greater extent than other age classes to anthropogenic activities in coastal waters, which must be taken into account when considering coastal management.

KEY WORDS: Humpback whales · Breeding behaviour · Spatial distribution · Conservation · Southeastern Pacific

INTRODUCTION

The humpback whale *Megaptera novaeangliae* is a cosmopolitan species that carries out extensive breeding and feeding migrations on an annual basis (Mackintosh 1942, Dawbin 1966). In winter, after feeding during the austral summer (December to April) in waters around the Antarctic Peninsula and southern Chile, humpback whales in the southeast Pacific Ocean, referred to as Breeding Stock G by the International Whaling Commission (IWC 2006), migrate to low latitudes for breeding and calf rearing in warm coastal waters off Ecuador, Colombia, Panama and Costa Rica (Flórez-González 1991, Félix & Haase 2001, Stevick et al. 2004, Acevedo et al. 2007, Flórez-González et al. 2007, Rasmussen et al. 2007). The size of this stock was estimated in 2006 at 6500 individuals (coefficient of variation [CV] = 0.21) (Félix et al. in press). Mother–calf pairs are typically observed in this zone in early August, but they can be sighted as early as the end of

*Email: fefelix90@hotmail.com

May and as late as November and even December (Félix & Haase 2001, Flórez-González et al. 2007).

During the breeding season in the southeast Pacific Ocean, the species exhibits a heterogeneous distribution according to their age class and breeding state (Félix & Haase 2005). While most individuals maintain a neritic distribution in waters < 200 m in depth, mother–calf pairs prefer shallower waters close to shore (Félix & Haase 2005, Flórez-González et al. 2007, Rasmussen et al. 2007), similar to that found in other breeding areas (e.g. Dawbin 1966, Winn et al. 1975, Glockner & Venus 1983, Smultea 1994, Ersts & Rosenbaum 2003, Morete et al. 2007). It is unclear, however, what social and environmental conditions motivate the segregation of females and calves within the shallowest zones of their winter distribution, but it may be in response to ecological and social pressures such as predation risk (Chittleborough 1953, Herman & Antinoja 1977), harassment by males (Chittleborough 1958, Smultea 1994, Craig et al. 2002, Cartwright & Sullivan 2009) and energy conservation (Whitehead & Moore 1982, Elwen & Best 2004).

In ways similar to that seen in some land mammals that have a polygynous or promiscuous breeding system, female humpback whales are not monopolised by males at breeding grounds. Instead males range widely in search of oestrus females, including mothers with newborn calves (Clapham 1996, Darling 2001, Cerchio et al. 2005). Even though humpback whales display a solitary female parental care behaviour independent of other adult helpers, some adult individuals identified as males and referred to as escorts associate temporarily with mother–calf pairs during the calving period (Herman & Antinoja 1977, Glockner 1983, Clapham et al. 1992). The reason for this association remains speculative as males do not have responsibilities for calf rearing in this species (Darling 2001). However, a male escort could provide some benefits for the pair, such as defence and protection from predators and other adult males (Chittleborough 1953, Herman & Antinoja 1977, Herman & Tavolga 1980). On the other hand, adult males joining a mother–calf pair would increase the energetic budget of the pair owing to an increase in the time spent travelling and a decrease in the time spent at rest (Cartwright & Sullivan 2009). Also, the presence of males could disrupt nursing, cause injuries to the calf or even be responsible for the separation of a calf from its mother because of the aggressive behaviour that males exhibit during the mating process (Smultea 1994).

Given the constraints inherent to the study of highly mobile animals in the marine environment and the complexity of the humpback whale reproductive behaviour, further specialized fieldwork is required to improve our understanding of this critical stage. In addressing such a daunting task, individual variability and environmental factors are fundamental to understanding the reproductive behaviour of a species (Clutton-Brock 1989, Reynolds 1996).

This article describes the spatial distribution and behaviour of mother–calf pairs of humpback whales during the breeding season off Ecuador. We attempted to identify the social and environmental variables that would explain their presence in shallow areas and to determine how behavioural patterns are affected when other whales join the mother–calf pair. Our results show similarities with other more intensively studied humpback whale breeding areas, such as near Hawaii and in the Caribbean Sea, but also show some differences that could be related to particular geographic and environmental features of the studied area. This study, besides contributing to the understanding of the reproductive behaviour of this species, provides baseline information for conservation efforts and coastal management.

MATERIALS AND METHODS

Study area. The study area covered 120 km^2 around the coast of the Santa Elena Peninsula in south-central Ecuador (2° 10′ S, 81° 00′ W). The area is located in the southern part of the breeding grounds of the southeast Pacific humpback whale stock, which extends about 3000 km from the north of Peru (6° S) to the south of Costa Rica (8° N) (Flórez-González et al. 2007, Félix et al. 2009).

Our base was Salinas, a major tourist village on the northeastern tip of the Peninsula. The Santa Elena Peninsula is the westernmost point of Ecuador (extending into the Pacific Ocean) and is surrounded by a narrow shelf (Fig. 1). Ocean depth gradually increases westward from the tip of the peninsula and reaches 100 m in depth 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; sandy and rocky bottoms characterize this zone. The geographic characteristics of the site allow rapid access to the whales' migratory corridor (Félix & Haase 2005).

The area is also characterised by the seasonal influence of the cold and productive Humboldt Current from the south and warm tropical waters of the Panama Bight from the north, where the Equatorial Front is formed. The front moves from north to south along the coast of Ecuador depending on the strength of the southeast Pacific anticyclonic winds (Cucalón 1996). During the breeding season of the humpback whales the Equatorial Front is located in its northernmost position off the central part of Ecuador, causing the sea surface temperature in this zone to vary between 22 and 25°C.

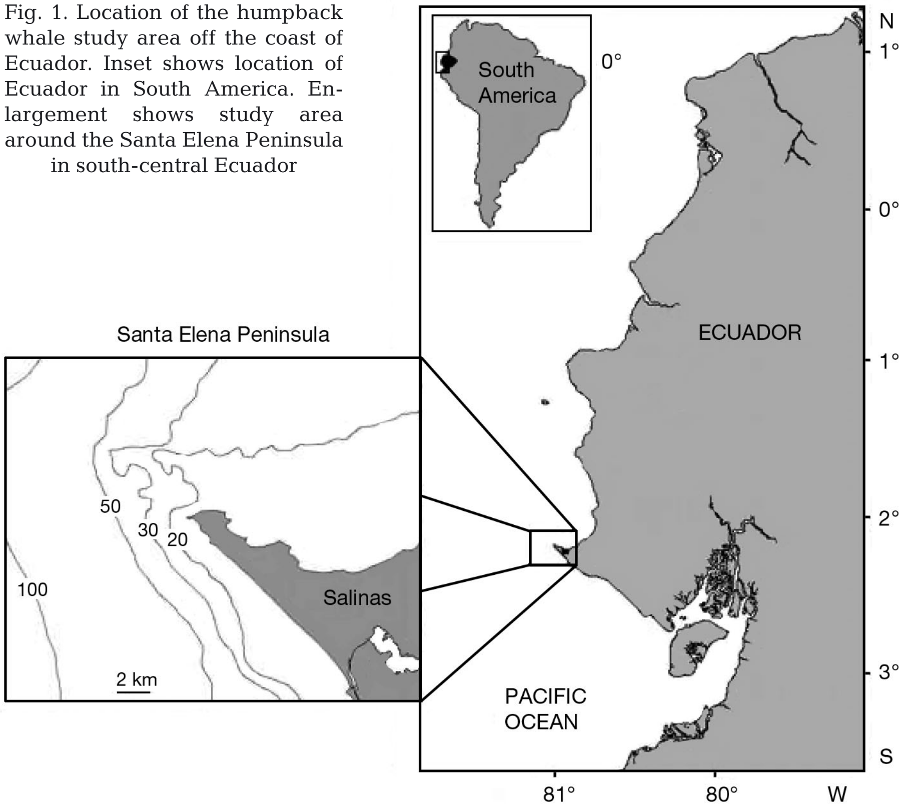

Fig. 1. Location of the humpback whale study area off the coast of Ecuador. Inset shows location of Ecuador in South America. Enlargement shows study area around the Santa Elena Peninsula in south-central Ecuador

Boat trips. Trips around the tip of Santa Elena Peninsula to study humpback whales during the breeding season (June to October) were conducted between 2001 and 2009 aboard whale-watching boats as part of a long-term study of this population along the coast of Ecuador (see Félix & Haase 2001, 2005). During the study, 18 different boats between 8 and 15 m in length with capacities ranging from 10 to 30 passengers were used. Boats usually departed in the morning between 09:00 and 10:00 h and returned to port 2 or 3 h later. No specific route was taken for the trip; it was the skippers' choice. When leaving port boats headed offshore between north and west. The search for whales started soon after leaving port, as did the communication with other boats that provided information as to where sightings had occurred. Usually 1 trip per day was made, but in the peak of the season (late July to early September) 2 and sometimes 3 trips a day were conducted. The research team regularly consisted of 2 people, but depending on the boat size and availability of space onboard the number varied from 1 to 4.

During the study period 676 trips were made, 1426 humpback whale groups were approached and 1047 h were spent at sea. However, as a consequence of the heterogeneous coverage during the season, the information obtained during June as well as from late September onward is probably underrepresented in the data set.

Data collection. Whales were usually approached at a distance of 50 to 100 m. Information on group size, composition, behaviour, dive time, heading and oceanographic conditions was recorded during the sighting period, and started when we first approached the whales (200 to 300 m). Sighting time was variable; on average the observation period lasted 30.26 min (SD = 17.40; range, 1 to 83 min). Additionally, group positions were determined with GPS. The first position was recorded at the beginning of the observation and then every 15 min until the boat left the whales, when a final position was taken. Group speed was estimated by dividing the total distance covered along a single track (i.e., distance between two track points) by the time elapsed. The GPS had been programmed to get a track point every time the boat changed course. Only speeds estimated in those groups tracked for at least 10 min were used for statistical comparisons.

Photographs to identify individual whales were taken with 35 mm film cameras with ISO 200 slide film in the first 3 yr and in subsequent years with digital SLR cameras of 6 to 10 megapixel capacity equipped with 70 to 300 mm zoom lenses. Identification was based on the colouration pattern of the ventral side of the flukes (see Katona et al. 1979), as well as the shape of dorsal fins. The latter was more effective in the case of mother–calf pairs, because mothers usually do not raise their flukes out of the water before diving. A catalogue of mother–calf dorsal fins was created with good quality photographs that allowed the fins to be clearly distinguished. The combination of the 2 dorsal fins in 1 photograph (mother and calf) facilitated the comparison process and reduced the mismatching error. Dorsal fins were used, however, only for identification within the same season.

Groups. A group was defined as all individuals present within a radius of 100 m that moved in the same direction and generally maintained a coordinated breathing pattern. Data were collected on groups containing all age classes, but groups that did not contain a mother–calf pair were omitted from this analysis. A mother–calf pair was defined as 2 individuals in close association, one of them was visually estimated to be significantly smaller and thinner and was referred to as the calf, and the larger of the pair was presumed to be its mother. A total of 187 groups containing a mother–calf pair were recorded, which represents 12.5% of the total number of groups followed during the study period. Some calves were very small and greyish coloured and frequently raised their heads to breathe, which indicated that they were newborn and the birth probably occurred within the study area or nearby. However, as the season progressed, calves grew in length and girth; by the end of the season, the ability to assign mother–calf pairs required time and expertise. We defined 3 types of groups containing a mother with a calf: those consisting of only the mother–calf pair (referred to as MC), the mother–calf pair and an escort (referred as to MCE) and those in which at least 2 more whales accompanied the mother–calf pair (referred to as MC + n). We assumed that in MCE and MC + n groups, the individual that remained in closer association to the calf was its mother.

Spatial distribution and environment data. Whale distribution data were analysed with the GIS software DIVA GIS 4.0 (Hijman et al. 2004) with the first position taken during the approach phase. Five quantitative environmental variables were then subsequently associated with this point: depth, distance to shore, time of day, wind speed and tide height. These were simultaneously evaluated with a principal component analysis (PCA) with the statistical software PAST 1.96 (Hammer et al. 2001). The correlation matrix created allowed us to explore the relationship among quantitative variables associated with each type of group containing mother–calf pairs (nominative variables).

Sighting depths were approximated using the data set: Topography, SRTM30 + v. 6.0, with a resolution of 30 arc-second (1 km^2) (Becker et al. 2009, Sandwell & Smith 2009), downloaded by the Environmental Research Division's Data Access Program (ERDDAP) of NOAA. Data on tide heights were obtained from the tide tables produced by the National Oceanographic Institute of the Ecuadorian Navy (INOCAR) for port La Libertad (10 km north of Salinas) and available on line (www.inocar.mil.ec). Average daily tide amplitude was 1.63 m with a maximum of 2.7 m. Information on wind speed was directly requested from the Marine Science Department of INOCAR for the oceanographic station off La Libertad. Southwest winds prevailed during the season with an average speed of 3.07 m s^{-1} (range, 0.04 to 6 m s^{-1}). Data on tide and wind speed were interpolated to the sighting hour as only 4 measures per day were available.

Statistical analysis. Both the 1-way ANOVA test and the unequal variance *t*-test (Ruxton 2006) were used to compare the central tendency of several data sets with the standard Microsoft Excel data analysis provided in the Microsoft Office 2007 package.

Other considerations. We caution about the potential biases introduced in our study because of the use of data obtained from whale-watching boats, where we had little control on most aspects related to the navigation, approach and sighting processes. Some important issues include different sighting distances, the diversity of boats used and the different degree of expertise of the skippers. The searching effort was probably biased toward groups of whales with coastal distribution or higher surface activity and, therefore, the study area was not randomly or homogeneously surveyed. In addition, the presence of whale-watching boats could affect the whales' behaviour that could cause an increase in their average speed, a change of direction or changes in their breathing–diving patterns (Bauer et al. 1993, Bauer 1995, Corkeron 1995, Au & Green 2000, Scheidat et al. 2000). The extent of such biases and how they could influence the results of this study is unclear. Most studies on ecology and behaviour conducted so far on humpback whales have been made either from boats destined specifically for that purpose or from land, and thus may or may not be completely comparable with ours.

RESULTS

Groups recorded

Approximately two-thirds of the 187 groups containing a mother with calf comprised the mother–calf pair alone (MC) (n = 124, 66.7%). In 44 groups (23.6%) the mother–calf pair was accompanied by an escort (MCE) and in 18 groups (9.7%) the mother–calf pair was with 2 or more whales (MC + n). The occurrence of the MC + n groups decreased with the number of whales present. Thus, there were 8 MC + 2 groups (44.4%), 5 MC

+ 3 groups (27.8%), 2 MC + 4 groups (11.1%), 1 MC + 5 (5.6%) group and 2 MCE + 6 groups (11.1%). Because of the low frequency in some categories, for purposes of subsequent comparisons, all mother–calf pairs accompanied by 2 or more whales were included in a single category (MC + n). Of 18 MC + n groups, 7 (38.9%) were considered to be competitive groups according to the behaviour observed during the sighting period (see Tyack & Whitehead 1983 and Baker & Herman 1984 for detailed descriptions of this behaviour). Because sighting time onboard whale-watching boats was limited (30 min per group on average) it was not possible to determine whether the other 11 groups of mother–calf pairs were in a less active stage of competition or were engaged in a different social activity when they were recorded.

Distribution

Environment data analysis

The results of the PCA including the eigenvalues and the correlation among the 5 variables assessed within each principal component (PC) are shown in Table 1. The 2 first PCs with eigenvalues >1 were retained for interpretation; both PCs accounted for 63.9% of the cumulated variance. PC1 showed a high positive correlation between distance from shore and depth. PC2 showed a high positive correlation between wind speed and time of day, indicating that the wind was stronger in the afternoon hours. Because of the high correlation existing in 2 variables in both PC1 and PC2, assessing one of them would be sufficient to explain the heterogeneous distribution of mother–calf groups in the study area. Thus, depth and time of day were the variables chosen for subsequent analysis.

Table 1. Eigenvalue analysis of the correlation matrix of the 5 environmental variables used to compare the spatial distribution of *Megaptera novaeangliae* mother–calf groups in the study area. Eigenvalues higher than 1 as well as strongly positively correlated variables in the first 2 components (PC1 and PC2) are highlighted in **bold** text for visibility

	PC1	PC2	PC3	PC4	PC5
Eigenvalue	**1.8145**	**1.3822**	0.8925	0.6869	0.2236
Proportion	0.3629	0.2764	0.1785	0.1373	0.0447
Cumulative	0.3629	0.63.93	0.8178	0.9552	0.9999
Variable					
Distance	**0.8962**	0.2783	0.0935	0.0315	−0.3311
Depth	**0.9152**	0.2018	0.0320	−0.1024	0.3319
Tide height	−0.2727	0.4555	0.8454	0.0488	0.0323
Wind speed	−0.1538	**0.7421**	−0.3313	0.5604	0.0435
Time of day	−0.2753	**0.7113**	−0.2414	−0.5992	−0.0307

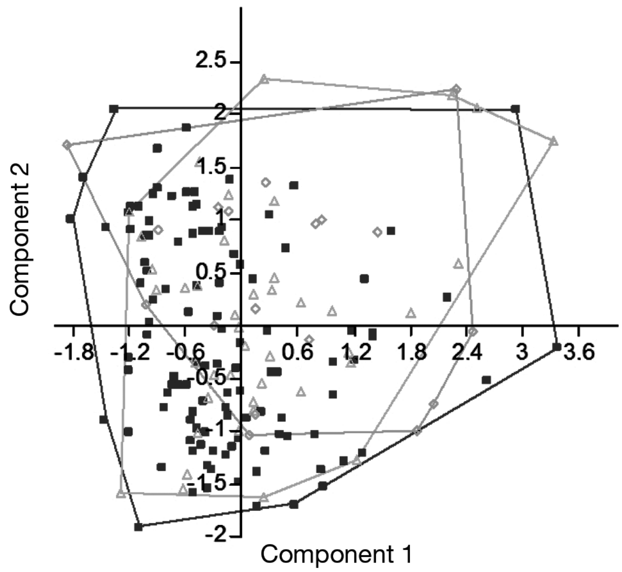

Fig. 2. Results of the principal component analysis showing the projections of the observations of each humpback whale group type on the principal components 1 and 2. ■: MC (mother + calf); △: MCE (mother + calf + escort); ◇: MC + n (mother + calf + ≥2 whales)

A bi-dimensional graph of the cloud of points showed that it was not possible to discriminate between mother–calf groups, indicating that all 3 group types contributed to a similar extent to each first 2 principal components (Fig. 2).

Depth data analysis

After the PC analysis, sightings were plotted on a chart with depth profiles to obtain a spatial visualization by group class (Fig. 3). Most groups were found within a radius of 9 km around the peninsula tip in waters < 50 m in depth. Although some overlap in depths between the 3 group classes was evident, average depths showed a progressive but significant increase with group size from MC to MC + n groups ($F_{2,175}$ = 7.41, p < 0.001) (Table 2). Additional individual analysis showed highly significant differences in depths between MC and MCE (t = –2.33, p = 0.022) and between MC and MC + n (t = –3.01, p = 0.006), but not between MCE and MC + n (t = –1.33, p = 0.19). No significant differences were found when depths were compared by months (July to September) ($F_{2,172}$ = 0.646, p = 0.524).

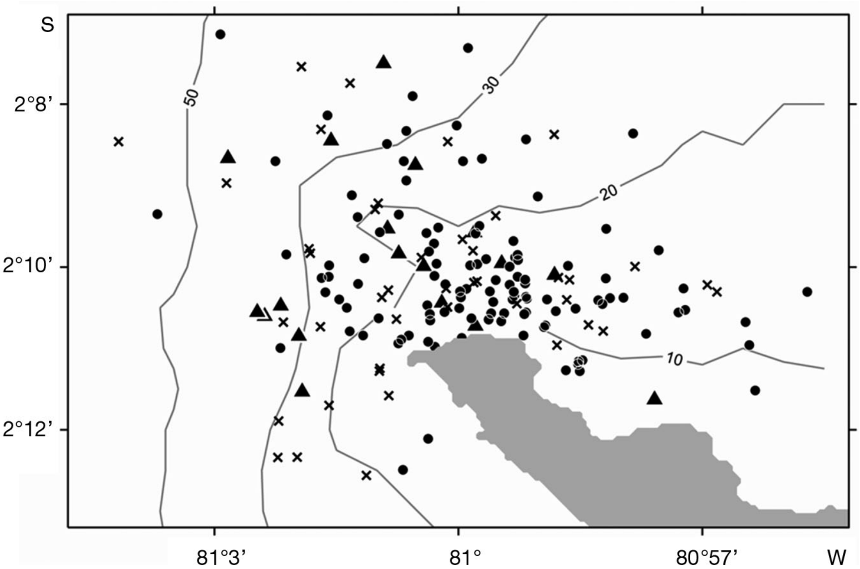

Fig. 3. Distribution of humpback whale mother–calf pairs (MC, ●), mother–calf and escort (MCE, ×) and mother–calf with 2 or more whales (MC + n, ▲) with respect to depth (m) around Santa Elena Peninsula from 2001 to 2009

Table 2. Average values of depth (m) by humpback whale group type. See Fig. 3 for group abbreviations. ANOVA analysis: $F_{2,175}$, 7.41; p < 0.001

Group type	Depth (m)	SD	n
MC	17.68	8.49	117
MCE	21.74	10.36	50
MC + n	25.94	11.32	11

Time of day data analysis

In a second analysis, sightings were pooled into 2 periods: morning (08:00 to 12:59 h) and afternoon (13:00 to 18:00 h) and then depths were compared between the 3 group classes. Significant differences in depths were found only within MC groups, which were distributed in shallower waters by afternoon hours (*t*-test = –2.13, p = 0.035) (Table 3).

Seasonality

The occurrence of the 3 group classes during the breeding season is shown in Fig. 4. MC groups prevailed almost throughout the entire season except during the last 5 d period when MCE groups were more abundant. In the first 30 d, few mother–calf groups were recorded, and most of them were MC groups. The first MCE group was recorded on Day 16 and the first MC + n group on Day 23. The presence of the 3 group classes increased as the season progressed, although with different intensity. MC groups peaked between Days 45 to 49 and remained fairly constant until Days 70 to 74 and then decreased abruptly. Another short peak was recorded on Days 80 to 84. MCE groups showed a short peak on Days 50 to 54, which was on average 5 d later than for the MC groups, and had a higher peak on Days 60 to 64, and then numbers maintained a constant but low value until the end of the season. MC + n groups were less common than MCE groups during the first half of the season and then peaked around Days 50 to 54, which was in the same period of the first MCE peak, and then sightings steadily decreased until Days 85 to 89 when the last of this group class was recorded.

Site fidelity and social condition change (resighting analysis)

Twenty within-year resightings of 14 different mother–calf pairs allowed us to estimate the fidelity of mother–calf pairs in the study area. Within-season resightings ranged between 1 and 4 (Table 4). Eighteen resightings (90%) occurred within 10 d, indicating that mother–calf pairs did not stay long in the study area. The longest interval between sightings was 61 d. The 3 longest intervals involved only MC groups.

Of the 10 groups first sighted as MC, 3 were resighted as MCE and on 1 occasion as MC + n. Of the 4 first groups sighted as MCE, 2 were resighted as MC. The other 2 groups first sighted as MCE remained with the same escort when resighted; in one case, the interval was 1 d, and in the second case 4 d. Another MCE

Table 3. Average depths (m) of mother–calf groups in morning (08:00 to 12:59 h) and afternoon (13:00 to 18:00 h) and results of the *t*-test comparison by humpback whale group type. See Fig. 3 for group abbreviations. Significant p-value is in **bold** text

Group type	Morning			Afternoon			*t*-value	p-value
	Mean	SD	n	Mean	SD	n		
MC	18.89	8.92	74	15.60	7.32	43	–2.133	**0.035**
MCE	21.31	9.96	26	22.41	11.23	17	–0.430	0.669
MC + n	28.56	8.59	9	23.33	13.53	9	1.165	0.268

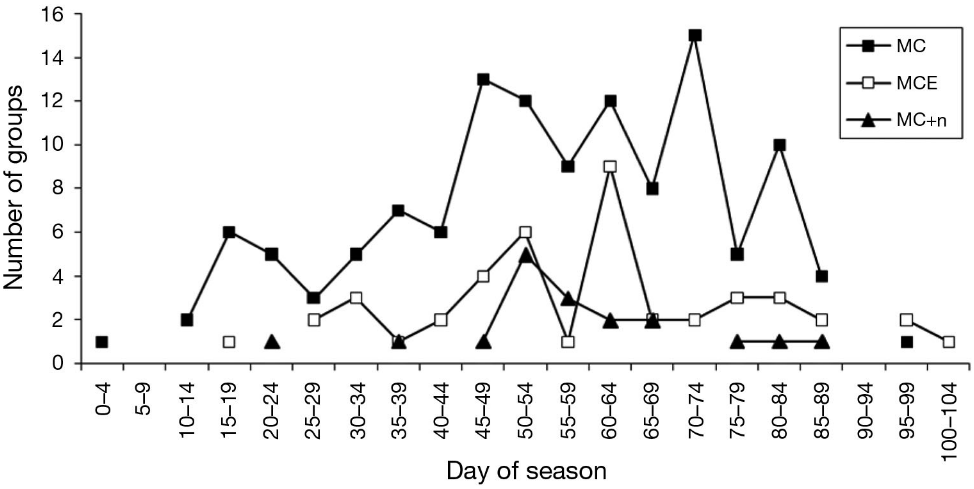

Fig. 4. Seasonal occurrence of humpback whale groups containing mother–calf pairs during the period from 2001 to 2009 around the Santa Elena peninsula. The beginning of the birthing season (Day 0) was set on 30 June of each year because it was the earliest date in which a mother with calf was recorded (2005). ■: mother–calf pairs alone (MC); □: mother–calf pairs escorted (MCE); ▲: mother–calf pairs with 2 or more other whales (MC + n). Breaks in the plots correspond to periods without records

Table 4. Humpback whale mother–calf pairs resighted within the same season. Data include the dates of the sighting and subsequent resightings, the time between sightings (d), and the type of group (MC, MCE or MC + n; see Fig. 4 for abbreviations)

Identification	Date 1st sighting	Group type	Date 2nd sighting	Group type	Date 3rd sighting	Group type	Date 4th sighting	Group type	No. of days (d)
NN1	25 Sep 04	MCE	26 Sep 04	MCE					1
NN2	12 Jul 04	MC	11 Sep 04	MC					61
NN3	30 Aug 06	MC	08 Sep 06	MC					9
NN4	31 Jul 06	MC	06 Aug 06	MCE					6
NN5	29 Aug 07	MCE	02 Sep 07	MCE					4
No. 1165	23 Aug 07	MC	25 Aug 07	MC + 5					2
No. 1447	17 Aug 08	MC	06 Sep 08	MC					20
No. 1421	31 Aug 08	MCE	31 Aug 08	MC	02 Sep 08	MCE			2
NN6	18 Jul 09	MC	19 Jul 09	MC	23 Jul 09	MC	28 Jul 09	MC	10
NN7	18 Jul 09	MC	21 Jul 09	MC	24 Jul 09	MC			6
NN8	6 Aug 09	MC	09 Aug 09	MC	10 Aug 09	MCE			4
NN9	10 Aug 09	MC	14 Aug 09	MCE	16 Aug 09	MC			6
NN10	10 Aug 09	MCE	19 Aug 09	MC					9
NN11	24 Aug 09	MC	29 Aug 09	MCE					5

group changed to MC in the same day and then was recorded again as MCE 2 d later with a different escort.

Speed

Groups moved with an average speed of 6.16 km h^{-1} (SD = 2.01; range, 2.32 to 10.7 km h^{-1}, n = 115). Although an increase in speed of around 10% was noticed in MC + n groups, the difference was not significant with respect to the other 2 groups (Table 5).

DISCUSSION

In this study, we confirm the preference of humpback whales mother–calf pairs for shallow, coastal waters off Salinas, Ecuador. We also noticed differences with respect to habitat use and behaviour when the mother–calf pair was alone or accompanied by 1 whale or more. Such differences could be a result of social, ecological and/or environmental pressures that we attempted to establish. While coastal areas in the tropics with sea surface temperatures of around 25°C have been attributed as the major environmental variable influencing the distribution of humpback whales

Table 5. Average speed of humpback whale mother–calf groups. See Fig. 4 for abbreviations. ANOVA analysis: $F_{2,112}$, 0.493; p = 0.611

Group type	Speed (km/h)	SD	N
MC	6.13	1.97	73
MCE	6.02	2.01	31
MC + n	6.77	2.21	11

at breeding grounds (Dawbin 1966, Rasmussen et al. 2007), our finer-scale study shows that the interaction of social condition and environment variables would be a key aspect in understanding distribution of mother–calf pairs during the nursing period.

The exploratory analyses from the PCA showed that 2 of the 5 environmental variables assessed — depth and time of day — were sufficient to explain the heterogeneous distribution of mother–calf groups in the study area. In general, a correlation between group size and depth was established, with MC groups distributed in the shallowest zone, MCE at mid depths and MC + n groups in the deepest part. Our results indicate that mother–calf social condition is mainly a function of the depth in which the pair moves, which is concordant with the belief that water depth would be a major constraint for the association of mother–calf pairs with others whales since shallow waters limit the movements of courting males within the water column (Smultea 1994, Ersts & Rosenbaum 2003). Avoiding deep waters where the mother–calf pair is easily joined by males would have a positive impact on the offspring survival, as seen in right whales *Eubalaena australis* off South Africa, where the stranding rate of neonates increased in areas dominated by non-cow individuals (Elwen & Best 2004). The authors suggested this could be caused by inexperienced mothers failing to avoid those sites or their inability to deal with harassment by males.

Diurnal movements of MC groups toward shallower waters in afternoon hours were recorded. While avoiding the highest breeding activities and aggression by adult whales in the afternoon could be a plausible explanation for such diurnal movements (see Helweg & Herman 1994, Smultea 1994, Ersts & Rosenbaum 2003), the PCA showed also a positive correlation between time of day and wind speed, which suggests that mother–calf pairs approach the coast more often in afternoon hours off Salinas to avoid rough seas. Coastal protected waters may provide shelter to mother–calf pairs during rough seas helping to save energy (Whitehead & Moore 1982, Elwen & Best 2004). Alternatively, such a difference could be attributed to smaller quieter MC groups that would be harder to see in the rougher waters offshore in the afternoon.

An important difference in the proportion of escorted versus non-escorted groups in Ecuador was found in comparison with the Hawaiian breeding area, where the number of escorted and multi-adult humpback whale groups is twice as high as MC groups (Glockner & Venus 1983, Baker & Herman 1984, Smultea 1994). Cartwright & Sullivan (2009) even suggested that the association with 1 male could be a strategy of Hawaiian humpback whale mother–calf pairs to reduce harassment by males in competitive groups. In that sense, the Salinas breeding area shows similarities with the Caribbean and the Abrolhos Archipelago, Brazil, where mother–calf pairs participate less frequently in competitive groups (Clapham et al. 1992, Morete et al. 2007). Clapham et al. (1992) proposed that differences in post-partum oestrus between populations would explain such a phenomenon, but differences in environmental features such as depth of the surveyed areas would seem a more plausible explanation. Ersts & Rosenbaum (2003) suggested that whales join mothers with calves when the pair is in transit between shallow areas; our data support that assertion. In contrast to the Hawaiian Islands archipelago, where mother–calf pairs enter into deeper waters when moving widely between islands (Cerchio et al. 1998, Darling 2001), in the southeast Pacific female–calf pairs can move continuously along continental shallow zones. Conversely, in the Caribbean, the breeding population is concentrated in 2 shallow areas, the Silver and Navidad banks (Winn et al. 1975), and in Brazil in the Abrolhos Archipelago where the maximum water depth is 20 m (Morete et al. 2007).

Our study provides additional information about the social role of the escort whale when it joins mother–calf pairs; the 2 cases in which we found mother–calf pairs with the same escort after 1 and 4 d confirm that some males were performing a type of guarding behaviour (Mobley & Herman 1985, Brown & Corkeron 1995, Clapham 1996). It is possible that males increase mating probabilities by reducing competition with other males by moving toward shallow waters and joining a mother–calf pair (Craig et al. 2002, Cerchio et al. 2005). It has been stated that females with the best reproductive potential become scarce as the season progresses as, once impregnated, they leave the breeding area, and males then turn their attention to females with calves (Craig et al. 2002, Cerchio et al. 2005). Still, there is no evidence that the proportion of escorted female–calf pairs increased as the season progressed in Ecuador. Our data show that escorting is a temporary condition probably driven by water depth that could be reverted anytime. Furthermore, MC groups off Salinas would not associate with other whales during relatively long periods and would maintain their social condition for weeks. All these factors may indicate that whales of distant breeding grounds develop different reproductive strategies in response to social (e.g. sexual competition and tolerance to escorting) and environment conditions.

Mother–calf pairs either alone or with other whales stayed around the Santa Elena Peninsula for only a few days, indicating that whales move continuously within a larger area of unknown extent. A similar low residence level has also reported in other areas off Ecuador (Scheidat et al. 2000, Félix & Haase 2001) and seems to be common to other breeding grounds as well (see Mattila et al. 1994, Mate et al. 1998, Cerchio et al. 1998), although Craig et al. (2001) suggested that whales would favour some areas within the Hawaiian Islands archipelago. Such extensive movements, even when the calf is small, demonstrate that they can cover large distances easily and could help to prepare the calf for migration (Darling 2001). The maximum span of time recorded for a cow–calf pair in Ecuador (61 d) is similar than that recorded for other age classes (67 d, authors' unpubl. data) and is comparable to what has been reported for the Hawaiian breeding area (76 d) (Craig et al. 2001).

The delay of 5 d in the peak of abundance of MC versus MCE and MC + n groups suggests that mother–calf pairs segregate in the first days after giving birth, reducing interactions with conspecifics (Herman & Antinoja 1977, Herman & Tavolga 1980, Smultea 1994). During this period the pair would not conduct extensive movements but stay around the birthing site. Once calves mature, escorts and other whales may join the mother–calf pair, but will still avoid other mother–calf pairs (Darling et al. 1983 Mobley & Herman 1985, Smultea 1994, Craig et al. 2002). Alternatively, males would not be interested in mothers during this period, as ovulation would occur around 1 mo after giving birth and only in a low proportion of females (Chittleborough 1958).

Mothers with calves traveled off Salinas with similar speed regardless of their social condition (between 6.1 and 6.7 km h^{-1}). Similar speed between groups of mothers and calves was also reported by Cartwright & Sullivan (2009) in Hawaii but with lower speeds (3.3 to 4.3 km h^{-1}). Glockner & Venus (1983) reported an even lower average speed of mother–calf pairs in Hawaii (1.9 km h^{-1}). While a temporary increase in the average speed could be attributed to a reaction to the whale-watching boats (see Heckel et al. 2001, Bejder & Samuels 2003, Scheidat et al. 2004), such an impact could not be measured from a mobile platform used for this study. As boats did not move exactly as the whales did or reacted late when whales surfaced after a long dive, estimated speeds in our study are most probably slightly overestimated due to continuous corrections in the boat's course made to adjust to that of the whales. However, humpback whale mother–calf pairs are able to maintain a speed of 6.2 km h^{-1} for several days and move faster than other classes (Mate et al. 1998).

Due to their preferential use of the shallow habitat, mother–calf pairs are vulnerable to human-related disturbances, such as tourism, fisheries, shipping, pollution (chemical and noise) and habitat degradation. As a consequence of all these activities, there is a risk of mother–calf pairs abandoning traditional coastal habitats if uncontrolled coastal activities increase (e.g. Salden 1988, Rowntree et al. 2001, Findley & Vidal 2002). This risk needs to be addressed with responsibility in environmental impact studies and coastal conservation and management plans (Salden 1988, Smultea 1994, Corkeron 1995, Ersts & Rosenbaum 2003). On 23 September 2008, a surface area of 47 274.3 ha around the tip of the Santa Elena Peninsula was declared as a marine protected area (MPA) by the Ministry of Environment of Ecuador (Ministerial Decree No. 1476). Such a designation provides an additional tool to regulate maritime activities around the Santa Elena Peninsula. Considering the diversity of local stakeholders, authorities face a colossal challenge in implementing management measures in this MPA.

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LITERATURE CITED

Acevedo J, Rasmussen K, Félix F, Castro C and others (2007) Migratory destinations of the humpback whales from Magellan Strait feeding ground, Chile. Mar Mamm Sci 23: 453–463

Au WWL, Green M (2000) Acoustic interaction of humpback whales and whale-watching boats. Mar Environ Res 9: 469–481

Baker CS, Herman LM (1984) Aggressive behavior between humpback whales (*Megaptera novaeangliae*) wintering in Hawaiian waters. Can J Zool 62:1922–1937

Bauer GB (1995) An overview of the effects of vessel approaches on humpback whale behavior in Hawaii. In: Payne PM, Phillips B, Nitta ET (compilers) Report of the workshop to assess research and other needs and opportunities related to humpback whale management in the Hawaiian Islands, 26–28 April 1995, Maui, HI. NOAA Tech Memo NMFS-OPR-11, p 68–73

Bauer GB, Mobley, JR, Herman LM (1993) Responses of wintering humpback whales to vessel traffic. J Acoust Soc Am 94:1848

Becker JJ, Sandwell DT, Smith WHF, Braud J and others (2009) Global bathymetry and elevation data at 30 arc seconds resolution: SRTM30_PLUS. Mar Geodesy 32: 355–371. Available at http://coastwatch.pfeg.noaa.gov/erddap/griddap/index.html

Bejder L, Samuels A (2003) Evaluating the effect of nature-based tourism on cetaceans. In: Gales N, Hindell M, Kirkwood R (eds) Marine mammals: fisheries, tourism and management issues. CSIRO Publishing, Collingwood, p 229–256

Brown M, Corkeron P (1995) Pod characteristics of migrating humpback whales (*Megaptera novaeangliae*) off the east Australian coast. Behaviour 132:163–179

Cartwright R, Sullivan M (2009) Associations with multiple male groups increase the energy expenditure of humpback whale (*Megaptera novaeangliae*) female and calf pairs on the breeding grounds. Behaviour 146:1573–1600

Cerchio S, Gabriele CM, Norris TF, Herman LM (1998) Movements of humpback whales between Kauai and Hawaii: implications for population structure and abundance estimation in the Hawaiian Islands. Mar Ecol Prog Ser 175: 13–22

Cerchio S, Jacobsen JK, Cholewiak DM, Falcone EA, Merriwether DA (2005) Paternity in humpback whales, *Megaptera novaeangliae*: assessing poligyny and skew in male reproductive success. Anim Behav 70:267–277

Chittleborough RG (1953) Aerial observations on the humpback whale *Megaptera nodosa* (Bonnaterre), with notes on other species. Aust J Mar Freshw Res 4:219–226

Chittleborough RG (1958) The breeding cycle of the female humpback whale *Megaptera nodosa* (Bonnaterre). Aust J Mar Freshw Res 9:1–18

Clapham PJ (1996) The social and reproductive biology of humpback whales: an ecological perspective. Mammal Rev 26:27–49

Clapham PJ, Palsbøll PJ, Matilla DK, Vasquez O (1992) Composition and dynamics of humpback whale competitive groups in the West Indies. Behaviour 122:182–194

Clutton-Brock TH (1989) Mammalian mating systems. Proc R Soc Lond B Biol Sci 236:339–372

Corkeron PJ (1995) Humpback whales (*Megaptera novaeangliae*) in Hervey Bay, Queensland: behaviour and responses to whale-watching vessels. Can J Zool 73: 1290–1299

Craig AS, Herman LM, Pack AA (2001) Estimating residence times of humpback whales in Hawaii. Report to Hawaiian Islands Humpback Whale National Marine Sanctuary. NOAA Office of National Marine Sanctuaries and the Department of Land and Natural Resources, Honolulu, HI

Craig AS, Herman LM, Pack AA (2002) Male mate choice and male–male competition coexist in the humpback whale (*Megaptera novaeangliae*). Can J Zool 80:745–755

Cucalón E (1996) Primera parte: oceanografía y sistemas físicos. In: Sistemas biofísicos en el Golfo de Guayaquil. Comisión Asesora Ambiental CAMM, Ecuador, p 1–109

Darling JD (2001) Characterization of behavior of humpback whales in Hawaiian waters. Report to Hawaiian Islands Humpback Whale National Marine Sanctuary. Honolulu, HI

Darling JD, Gibson KM, Silber GK (1983) Observations on the abundance and behavior of humpback whales (*Megaptera novaeangliae*) off West Maui, Hawaii, 1977–79. In: Payne R (ed) Communication and behavior of whales. Westview Press, Boulder, CO, p 201–222

Dawbin WH (1966) The seasonal migratory cycle of humpback whales. In: Norris KS (ed) Whales, dolphins and porpoises. University of California Press, Berkeley, CA, p 145–170

Elwen SH, Best PB (2004) Female southern right whales *Eubalaena australis*: Are there reproductive benefits associated with their coastal distribution off South Africa? Mar Ecol Prog Ser 269:289–295

Ersts PJ, Rosenbaum HC (2003) Habitat preference reflects social organization of humpback whales (*Megaptera novaeangliae*) on a wintering ground. J Zool 260:337–345

Félix F, Haase B (2001) The humpback whale off the coast of Ecuador, population parameters and behavior. Rev Biol Mar Oceanogr 36:61–74

Félix F, Haase B (2005) Distribution of humpback whales along the coast of Ecuador and management implications. J Cetacean Res Manag 7:21–31

Félix F, Rasmussen K, Garita F, Haase B, Simonis A (2009) Movements of humpback whales between Ecuador and Central America, wintering area of the Breeding Stock G. Paper SC/61/SH18 presented to the 61 Scientific Committee of the International Whaling Commission, June 2009, Madeira

Félix F, Castro C, Laake J, Haase B, Scheidat M (in press) Abundance and survival estimates of the Southeastern Pacific humpback whale stock from 1991–2006 photo-identification surveys in Ecuador. J Cetacean Res Manag (Spec Issue)

Findley LT, Vidal O (2002) The gray whale, *Eschrichtius robustus*, at calving sites in the Gulf of California, México. J Cetacean Res Manag 4:27–40

Flórez-González L (1991) Humpback whales *Megaptera novaeangliae* in the Gorgona Island, Colombian Pacific breeding waters: population and pod characteristics. Mem Queensl Mus 30:291–295

Flórez-González L, Ávila IC, Capella J, Falk P and others (2007) Estrategia para la conservación de la ballena jorobada del Pacífico Sudeste. Lineamientos para un plan de acción regional e iniciativas regionales. Fundación Yubarta, Cali

Glockner DA (1983) Determining the sex of humpback whales (*Megaptera novaeangliae*) in their natural environment. In: Payne R (ed) Communication and behavior of whales. Westview Press, Boulder, CO, p 447–464

Glockner DA, Venus SC (1983) Identification, growth rate and behavior of humpback whales (*Megaptera novaeangliae*) cows and calves in the waters of Maui, Hawaii, 1977–79. In: Payne R (ed) Communication and behavior of whales. Westview Press, Boulder, CO, p 223–258

Hammer Ø, Harper DAT, Ryan PD (2001) PAST: paleontological statistics software package for education and data analysis. Paleontol Electron 4(1):1–9

Heckel G, Reilly SB, Sumich JL, Espejel I (2001) The influence of whalewatching on the behavior of migrating gray whales (*Eschrichtius robustus*) in Todos Santos Bay and surrounding waters, Baja California, Mexico. J Cetacean Res Manag 3:227–237

Helweg DA, Herman LM (1994) Diurnal patterns of behaviour and group membership of humpback whales (*Megaptera novaeangliae*) wintering in Hawaiian waters. Ethology 98:298–311

Herman LM, Antinoja RC (1977) Humpback whales in their Hawaiian breeding waters: population and pod characteristics. Sci Rep Whales Res Inst 29:59–85

Herman LM, Tavolga WN (1980) The communication systems of cetaceans. In: Herman LM (ed) Cetacean behavior: mechanisms and functions. Wiley Interscience, New York, NY, p 149–209

Hijman RJ, Guarino L, Bussink C, Mathur P, Cruz M, Barrantes I, Rojas E (2004) DIVA GIS, Versión 4.0. Sistema de Información Geográfica para el análisis de distribución de especies. Manual. Available at www.gbif.es/ficheros/Taller_nichos_10/DIVA-GIS4_manual_Esp.pdf

International Whaling Commission (2006) Annex H. Report of the sub-committee on other Southern Hemisphere whale stocks. J Cetacean Res Manag 8(Suppl):151–170

Katona S, Baxter B, Brazier O, Kraus S, Perkins J, Whitehead H (1979) Identification of humpback whales by fluke photographs. In: Winn HE, Olla BL (eds) Behavior of marine animals, Vol 3. Cetaceans. Plenum Press, New York, NY, p 33–34

Mackintosh NA (1942) The southern stocks of whalebone whales. Discov Rep 22:197–300

Mate BR, Gisiner R, Mobley J (1998) Local and migratory movements of Hawaiian humpback whales tracked by satellite telemetry. Can J Zool 76:863–868

Matilla DK, Clapham PJ, Vasquez O, Bowman R (1994) Occurrence, population composition and habitat use of humpback whales in Samana Bay, Dominician Republic. Can J Zool 72:1898–1907

Mobley JR Jr, Herman LM (1985) Transience of social affiliations among humpback whales (*Megaptera novaeangliae*) on the Hawaiian wintering grounds. Can J Zool 63:762–772

Morete ME, Bisis TL, Rosso S (2007) Temporal pattern of humpback whale (*Megaptera novaeangliae*) group structure around Abrolhos Archipelago breeding region, Bahia, Brazil. J Mar Biol Assoc UK 87:87–92

Rasmussen K, Palacios DM, Calambokidis J, Saborio MT and others (2007) Southern Hemisphere humpback whales wintering off Central America: insights from water temperature into the longest mammalian migration. Biol Lett 3:302–305

Reynolds JD (1996) Animal breeding systems. Trends Ecol Evol 11:68–72

Rowntree VJ, Payne R, Schell DM (2001) Changing patterns of habitat use by southern right whales (*Eubalaena australis*) on their nursery ground at Península Valdés, Argentina, and in their long-range movements. J Cetacean Res Manag 2(Spec Issue):133–143

Ruxton DR (2006) The unequal variance *t*-test is an underused alternative to Student's *t*-test and the Mann-Whitney *U* test. Behav Ecol 17:688–690

Salden DH (1988) Humpback whale encounter rates offshore of Maui, Hawaii. J Wildl Manag 52:301–304

Sandwell DT, Smith WHF (2009) Global marine gravity from retracked Geosat and ERS-1 altimetry: ridge segmentation versus spreading rate. J Geophys Res 114, B01411, doi:10.1029/2008JB006008

Scheidat M, Castro C, Denkinger J, González J, Adelung D (2000) A breeding area for humpback whales (*Megaptera novaeangliae*) off Ecuador. J Cetacean Res Manag 2: 165–171

Scheidat M, Castro C, González J, Williams R (2004) Behavioural responses of humpback whales (*Megaptera novaeangliae*) to whalewatching boats near Isla de la Plata, Machalilla National Park, Ecuador. J Cetacean Res Manag 6:63–68

Smultea MA (1994) Segregation by humpback whale (*Megaptera novaeangliae*) cows with a calf in coastal habitat near the Island of Hawaii. Can J Zool 72:805–811

Stevick P, Aguayo-Lobo A, Allen J, Ávila IC and others (2004) A note on the migrations of individually identified humpback whales between the Antarctic Peninsula and South America. J Cetacean Res Manag 6:109–113

Tyack P, Whitehead H (1983) Male competition in large groups of wintering humpback whales. Behaviour 83:132–154

Whitehead H, Moore MJ (1982) Distribution and movements of West Indian humpback whales in winter. Can J Zool 60: 2203–2211

Winn HE, Edel RK, Taruski AG (1975) Population estimate of the humpback whale (*Megaptera novaeangliae*) in the West Indies by visual and acoustic techniques. J Fish Res Board Can 32:499–506

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