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What do humpback whales *Megaptera novaeangliae* (Cetartiodactyla: Balaenopteridae) pairs do after tagging?

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ABSTRACT. The social structure of humpback whales in their tropical wintering grounds is very fluid. To date, no information has been published for cases in which two whales were both satellite-tagged while in association. Here, we report the movements of four humpback whale pairs tagged together off the coast of Brazil. Fieldwork and satellite tagging of humpback whales was conducted between 2003 and 2008 along the eastern coast of Brazil, between 20°S and 8°S. Movement was monitored while whales were still in their breeding ground. A switching state space model was applied to the filtered data of each humpback whale to standardize telemetry data and allow direct comparison of each individual track. GIS was used to plot model-predicted locations and to visually compare animal movements. The results confirm the short-lived nature of associations between breeding humpback whales, and shows that individuals differ widely in their movements.

KEY WORDS. Cetacean; large whale; satellite telemetry; social behavior; SSSM.

Humpback whales, *Megaptera novaeangliae* (Borowski, 1781), occur in all major oceans of the world. They are one of the most well studied large whale species, but much remains unknown about their behavioral ecology. In the Southern Hemisphere the species typically migrates from summer feeding grounds in the Antarctic to mating and calving grounds in tropical and subtropical coastal waters (Dawbin 1956, Chittleborough 1965, Mackintosh 1965, Zerbini *et al*. 2006, 2011). Humpbacks move through ocean waters during migration (e.g., Zerbini *et al*. 2006), or during residency in feeding areas (e,g., Dalla Rosa *et al*. 2008).

The International Whaling Commission (IWC) afforded Humpback whales virtually complete protection in the mid 1960s, and currently recognizes seven humpback whale breeding grounds in the Southern Hemisphere with corresponding feeding areas in high-latitude Antarctic waters (IWC 1998, 2005). Breeding Stock 'A' (BSA) corresponds to whales wintering off Brazil. In this region, the species typically occur from the northern portion of the South America (~5°S) to Cabo Frio area (~23°S) in the state of Rio de Janeiro (Andriolo *et al*. 2010). Occasional records have been observed along the South American continent and near oceanic islands (Pinedo 1985, Lodi 1994, Siciliano 1997, Pizzorno *et al*. 1998), but it is not yet clear whether these regions correspond to the regular range of the species.

An aerial survey conducted in 2005 constituted the first systematic effort to confirm that the southern limit of the breeding ground of Humpback whales on the continental shelf corresponded to the coast of Rio de Janeiro state (~23°S) (Andriolo *et al*. 2010). Results from this study were further supported by satellite telemetry (Zerbini *et al*. 2006). The Abrolhos Bank (16°40' to 19°30'S) corresponds to the main breeding habitat of the species in the western South Atlantic Ocean (Siciliano 1997, Martins *et al*. 2001, Morete *et al*. 2003, Andriolo *et al*. 2006, 2010), with some individuals showing relatively high site-fidelity to this region (Wedekin *et al*. 2010). Humpback whales that reproduce off Brazil migrate to summer feeding grounds to the west of the South Scotia Sea, near the South Georgia and the South Sandwich Islands (Zerbini *et al*. 2006, 2011, Stevick *et al*. 2006, Engel & Martin 2009). Animals that overwinter at the Abrolhos Bank may occasionally feed opportunistically in the waters of the western South Atlantic (Danilewicz *et al*. 2009, Alves *et al*. 2009).

The social structure of humpback whales in tropical waters is very fluid (Herman & Antinoja 1977, Mobley & Herman 1985, Mattila *et al*. 1989). With the exception of mothers and calves, long-term associations are relatively uncommon. The groups are usually small, but lager groups are formed in association with aggressive intrasexual competition among males (Tyack & Whitehead 1982, Bakes & Herman 1984, Clapham *et al*. 1992). Observations of individuals in breeding ground suggest that humpbacks are not territorial (Tyack 1981, Clapham 2000). Stable associations between paired whales have been noted (Clapham 2000), even among larger groups in feeding grounds (Perry *et al*. 1990).

Humpback whales appear to be polygynous, with similarities to a lek mating system. Clapham (1996) has proposed the category of 'floating lek' for this species. Genetic analysis of paternity has shown that females mate with multiple males, at least from one year to the next (Clapham & Palsboll 1997). Cypriano-Souza *et al.* (2010) found that individuals distributed along the Brazilian coast belong to a single population, without evidence of substructure (spatial or temporal differentiation).

Satellite tracking is an important tool to study the behavior and movements of marine mammals (e.g., Jouventin & Weimerskirch 1990, Polovina *et al*. 2004) and has been applied to humpback whales, providing information on the habitat use, movements and migrations of individual whales (Mate *et al*. 1998, Zerbini *et al*. 2006, 2011, Dalla-Rosa *et al*. 2008, Mate & Best 2008). To date, however, there is no published information on the fate of individuals that were both satellite tagged while in association. Here, we report the movements of four pairs of humpback whales tagged together off the coast of Brazil.

MATERIAL AND METHODS

The breeding ground for humpback whales in this population was defined as the area within the continental shelf (depth <200 m) along the Brazilian coast between 5°S and 23°S (Andriolo *et al*. 2010). Fieldwork and satellite tagging of humpback whales was conducted between 2003 and 2008 along the northeastern coast of Brazil, between 20°S and 8°S (Fig. 1).

Daily searches for humpback whales were undertaken during good weather conditions (Beaufort sea state ≤ 3) from a 10m-long fiberglass speedboat and two inflatable boats. Transmitter models and configurations differed among the survey years, but were basically the Wildlife Computers SPOT3, 4 and 5 housed in "mini-can" and "implantable" configurations (Table I). Deployment of the tags, biopsy sample collection followed the methods described by Heide-Jørgensen *et al.* (2006) and Zerbini *et al.* (2006).

Group categories were defined as follows (Clapham 1993, Mattila *et al.* 1994, Clapham 2000): a) singleton – a lone individual (SIN); b) mother and calf pair (MOC) – for two individuals, being one adult and one individual less than half the size of the adult; c) mother and calf pair plus one escort (MOCE) – for a mother and calf pair (as defined above) plus one escort; d) pair – for two individuals; e) >pair, for three or more individuals.

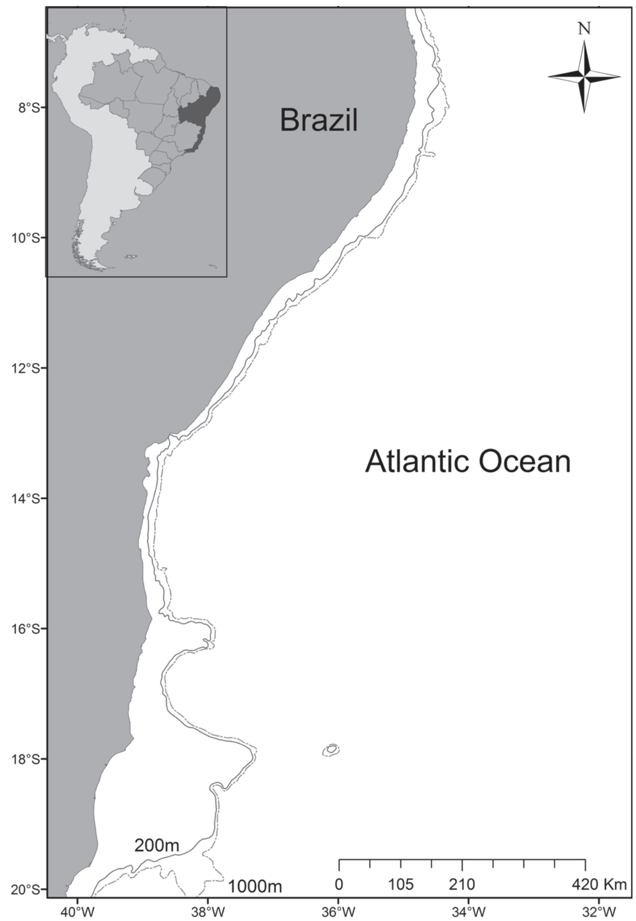


Figure 1. Northeastern coast off Brazil at breeding ground where humpback whales were satellite instrumented between 2003 and 2008. The light gray lines represent the 200 and 1000m isobaths.

The social role of the tagged individuals were based on the position of the animal in the group composition: a) mother (MO); b) calf (C); c) escort (E) – a third whale accompanying a mother and calf, d) principal escort (PE) – whale closest to nuclear animal (MOC) in groups larger than three individuals and e) Other – animal with position not clearly identifiable. The group composition was defined at the moment of tagging. Groups with four different compositions were considered in this study: one competitive group (female and principal escort tagged), a mother with a female companion; a male-female pair, and another pair consisting of one male and one animal of unknown sex. Except for the latter animal, the sex of each individual was determined using methods described by Bruford *et al.* (1992) and Bérubé & Palsbøll (1996). Table I summarizes information of the pairs considered in the analysis.

Movement was monitored after tag deployment while whales were still on the breeding grounds. Locations were obtained from Service Argos, Inc. (Argos 1990). Location quality

(LC) of each tag transmission was coded A, B, 0, 1, 2 or 3 in increasing order of position accuracy. Argos locations were filtered considering an alternative algorithm, based on swimming speed, distance between successive locations, and turning angles (Freitas *et al.* 2008).

A switching-state space model (SSSM, Jonsen *et al.* 2005) was applied to the filtered data of each humpback whale individual. Modeling was conducted in open-source software packages, R (R Core Team 2011) and WinBugs (Lunn *et al.* 2000). The SSM allows location estimates to be inferred from observed data (satellite locations) by accounting for errors (measurement equation) and from dynamics of the movement process (transition equation) (Patterson *et al.* 2008). Predicted locations were estimated at 6-hour time intervals. Although the SSSM provides the states, for this study we were interested only in the predicted latitude and longitude, in order to be able to compare both animals in each tagged pair. Because the time of the interpolated positions matched across all individuals, precise distances were computed for individuals within the pair. The speed of each animal was calculated as an average of the distances between two consecutive predicted locations divided by six hours. Animal tracks were plotted in a Geographic Information System (GIS) Package (ArcGIS 9) for visual inspection of animal movements. The Mann-Whitney Test was used to compare the speed between the two whales in the pair.

RESULTS

Between 2003 and 2008, four pairs of animals tagged while in association provided data to investigate the duration of their associations. The overall results of each pair are summarized in Table II. Except when associated with a mother and calf, males were on average faster than females (Table II).

Pair A consisted of a mother with a calf and an escort (MOCE). During the tagging period, two more individuals joined the group. The female was tagged first (21162) and the escort 55 minutes later (27259). Both tagged whales followed a similar track for five days (until October 24th) (Fig. 2); then, on October 25th, the distance between them began to increase (Fig. 10). The male moved in a convoluted pattern, remaining in the same general area for seven days, while the female with the calf moved more linearly southwest along the continental shelf. The female traveled at a higher average speed than the male (Table II) ($U = 1288.00$, $p = 0.014$).

Table I. Spatial and temporal data for humpback whale pairs A, B, C and D tagged on the Brazilian breeding grounds between 2003 and 2008. Year, tag number, transmitter type, sex, social role, group composition at the moment of deployment is presented for each pair.

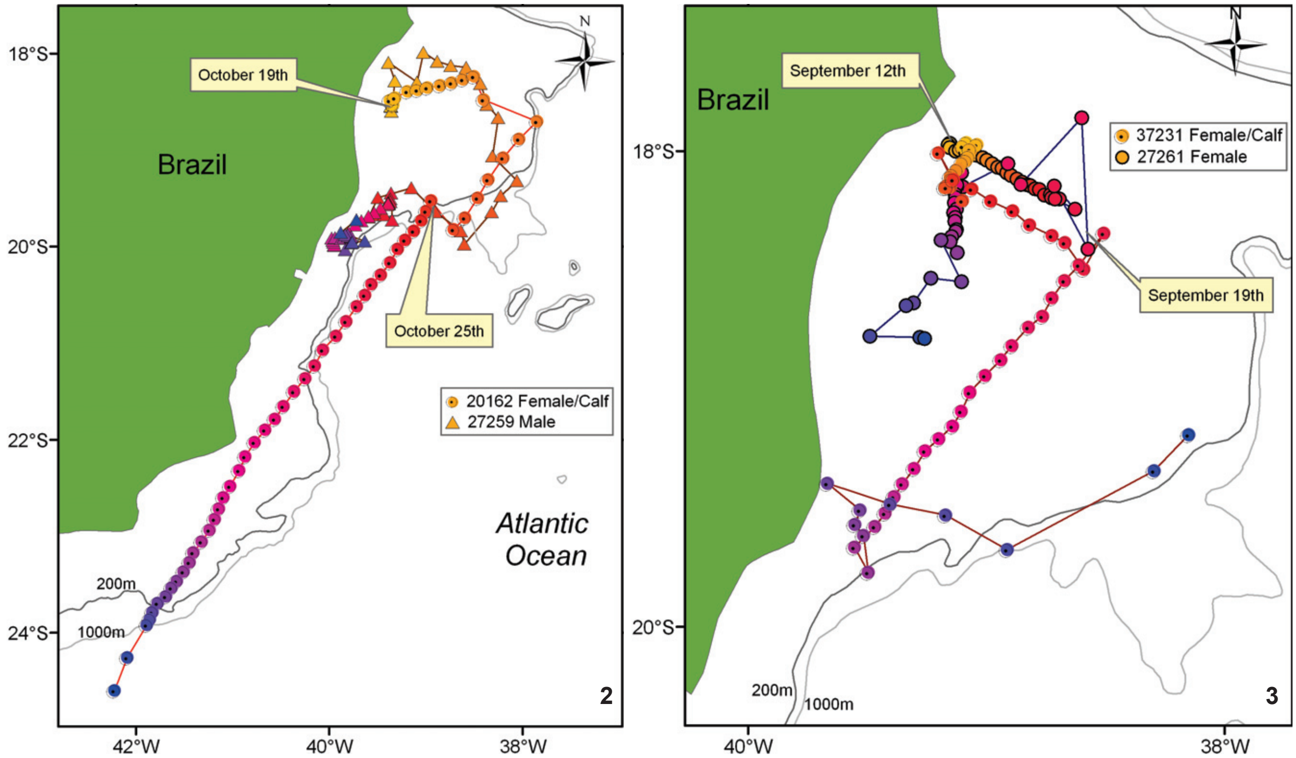
Pair	Year	Tag number	Transmitter type	Tagging date time	Latitude	Longitude	Sex	Social role	Group composition
A	2003	27259	CAN	10/19/2003 11:33	-18.48	-39.37	M	PE	MOC+PE+2O
		20162	CAN	10/19/2003 10:38	-18.52	-39.36	F	MO	MOC+PE+2O
B	2007	37231	IMP	9/12/2007 10:32	-17.98	-39.09	F	MO	MOC+O
		27261	IMP	9/12/2007 10:51	-17.98	-39.08	F	O	MOC+ O
C	2008	87765	IMP	9/7/2008 13:25	-10.74	-36.51	F	MO	MOC+5O
		87766	IMP	9/7/2008 13:41	-10.73	-36.53	M	O	MOC+5O
D	2008	87761	IMP	8/28/2008 16:10	-15.32	-38.77	M	O	Pair
		87760	IMP	8/28/2008 14:58	-15.36	-38.76	nd	O	Pair

(Nd) Not determined, (M) male, (F) female, (MOC) mother and calf pair, (MOCE) mother and calf pair plus one escort, (Pair) for two individuals, (E) escort, (PE) principal escort, (O) other.

Table II. Satellite-monitored pairs of tagged humpback whales on the Brazilian breeding grounds between 2003 and 2008. (ND) Not determined.

Pair	Tag number	Sex	Argos Positions	SSSM Positions	Longevity (days)*	Distance Monitored (km)	Average speed (km/h)	Pair Minimum Distance (km)	Pair Average Distance (km)	Pair Maximum Distance (km)
A	27259	Male	51	60	14.5	848.46	2.39 ± 2.13	2.41	185.64	583.95
	20162	Female	11			1026.23	2.89 ± 1.62			
B	37231	Female	10	57	14.0	595.69	1.77 ± 1.81	3.59	61.69	154.43
	27261	Female	41			399.98	1.19 ± 1.79			
C	87765	Female	263	82	20.3	1543.53	3.17 ± 1.97	1.63	100.49	214.27
	87766	Male	88			1946.46	4.00 ± 2.22			
D	87761	Male	203	123	30.5	3280.20	4.48 ± 2.04	0.20	260.52	727.50
	87760	ND	258			3257.27	4.44 ± 1.75			

* Longevity is the period in days that the pair was monitored.

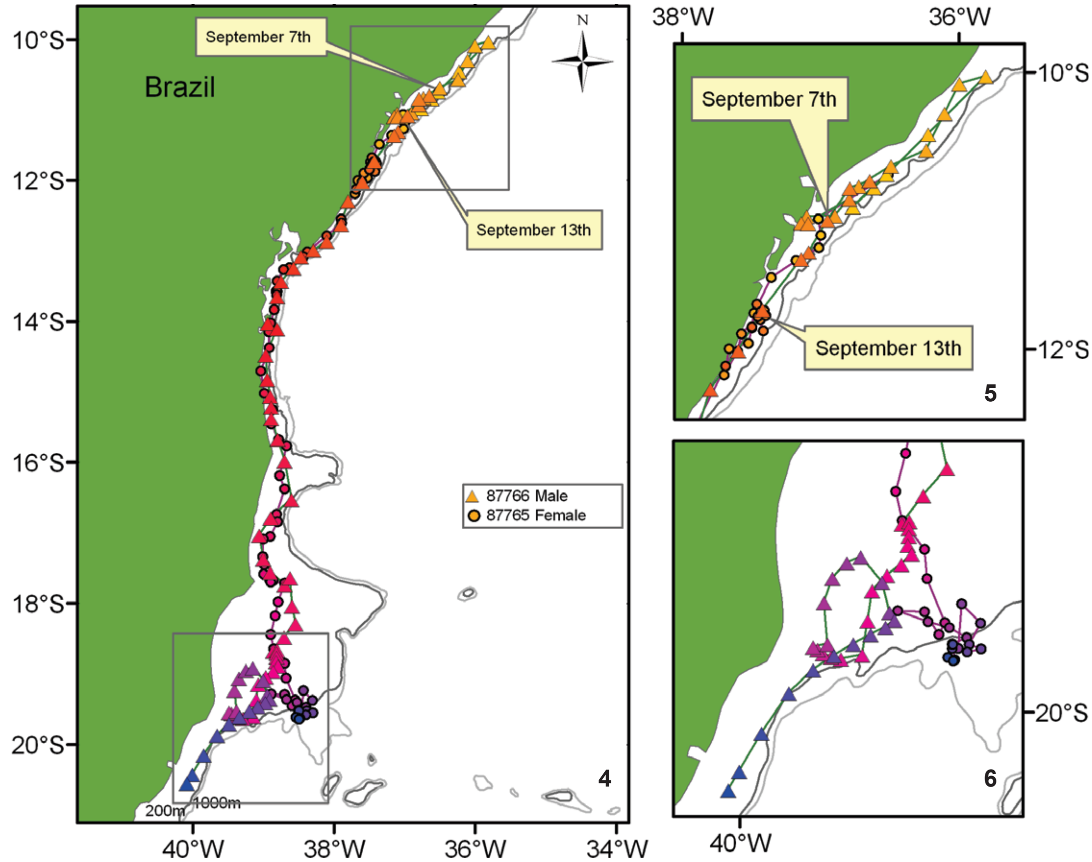


Figures 2-3. Movements of humpback whale Pairs A (2) and B (3), tagged on the Brazilian breeding grounds. The same colors correspond to the same dates for each individual.

The two members of Pair B, a mother (27261) with a calf and an adult (37231), identified as female by DNA analysis, were tagged 19 minutes apart. On September 19th, seven days after tagging, the distance between them began to increase (Figs 3 and 11). The mother with the calf moved slower (Table II) than the other female (U = 3.49, $p < 0.001$).

Pair C, consisted of an adult male (87766) and an adult female (87765) (Fig. 4). Both were part of a group of six individuals, which included a calf. After tag deployment, the male moved north, while the female traveled in the opposite direction (towards the South) along the coast. At 125.3 km from the tagging position, the male turned back and headed south (Fig. 5). The female was at 175.1 km south of the tagging position on September 10th, when she turned north, swimming 51.7 km; after this, she exhibited a convoluted movement beginning on September 11th and ending on September 13th when she headed south again (Fig. 5). At the same time, late on September 13th, the male was passing by the same area and at one point the two whales were within 1.9 km of each other (Fig. 12). On the next day, September 14th, the distance between them began to increase (Fig. 12). The male moved ahead; remarkably, the female followed the same track as the male, even where the continental shelf became larger. Close to the end of the monitored period, the male made a loop and continued along the coast, while the female exhibited a more convoluted movement (Fig. 6). The male moved at a higher average speed than the female (Table II) (U = 2508.00, p = 0.009).

Pair D was composed of two adults, one male (87761) and another individual (87760) of unidentified sex (Fig. 7). The male headed north for 454.8 km and subsequently turned south on September 2nd (Fig. 8). The other whale (87760) headed south after deployment (Fig. 8). On September 4th they reached the greatest distance apart, 727.50 km (Fig. 13). At this moment both whales were on the southern portion of the continental shelf enlargement known as the Abrolhos Bank. Whale 87760 went further south along the coast and then on September 8th made a turn and returned to the Abrolhos Bank, heading to the principal point from which humpback whales begin the migration to high-latitude feeding grounds. Whale 87761 crossed the Abrolhos Bank on its eastern side and initiated its southbound migration. On September 12th, after crossing the 500 m isobath, the predicted locations of the two whales were just 0.208 km apart (Fig. 13). Subsequently, whale 87760 swam southwards and male 87761 followed approximately the same track until the end of the monitoring period (Fig. 13. There was no difference in the average speed of the two whales (Table II) (U = 7561.0, p = 0.822).



Figures 4-6. Movements of humpback whale Pair C tagged on the Brazilian breeding grounds: (4) overview of the tracks; (5) tracks after deployment; (6) shows the end of the monitoring period. The same colors correspond to the same dates for each individual.

DISCUSSION

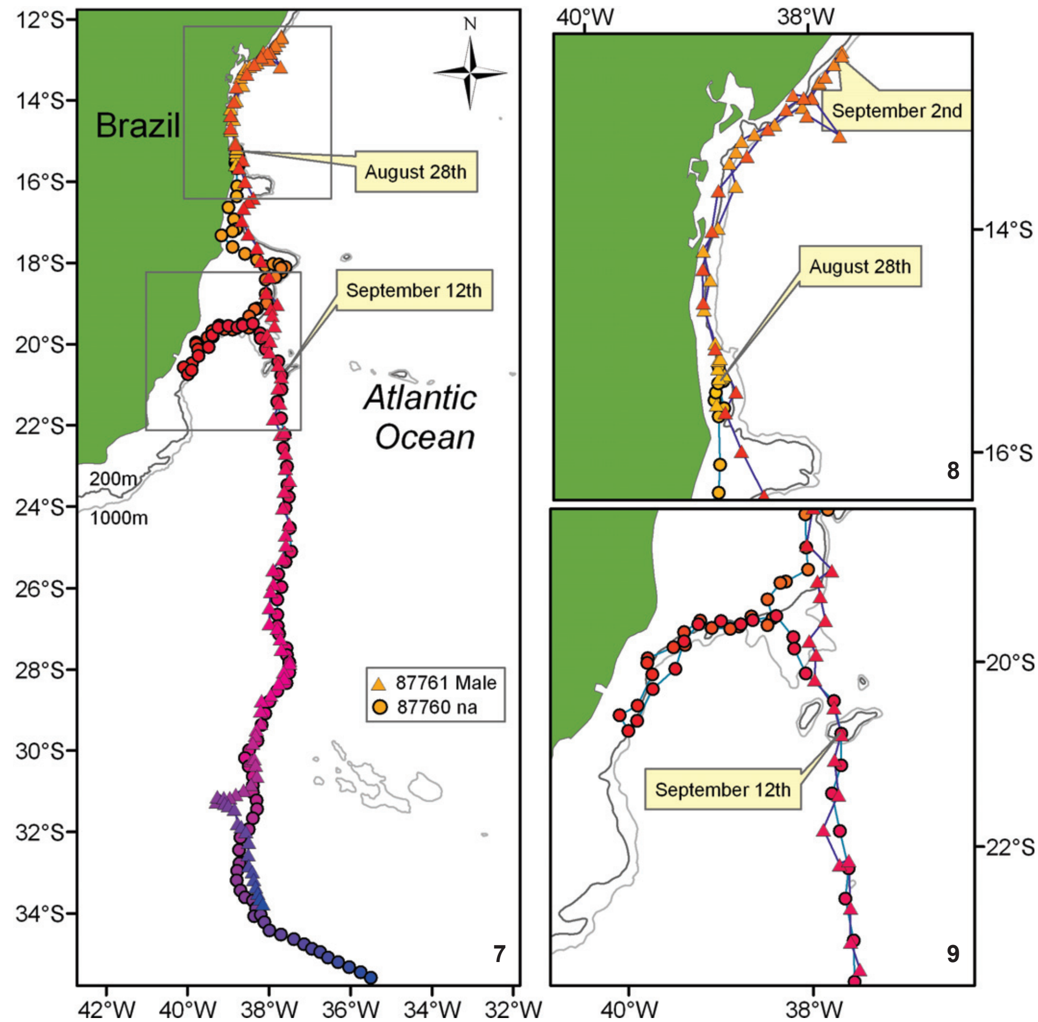
The humpback whales tagged in association separated at different times after tagging and sometimes traveled in opposite directions. This study confirms reports in the general literature that humpback whale associations in the wintering (Herman & Antinoja 1977, Mobley & Herman 1985, Mattila *et al*. 1989, Clapham 1996) and feeding grounds (Weinrich & Kulberg 1991) are ephemeral. However, there have been reports of stable social association in feeding grounds (Weinrich 1991).

The social structure of mysticets is poorly understood due to the difficulties in identifying and defining the associations among individuals. While observations sometimes allow scientist to categorize these associations it is difficult to ascertain how long they last after the observations stop. We considered that pair A remained associated from the moment of tagging until October 24th based on the distance between the two whales that did not increase significantly during that time. This would indicate that this pair remained in close proximity for at least 5 days. A similar pattern was observed for pairs B (length of association of four days) and D (length of association of one day).

The stable association between humpbacks at feeding areas has been classified as 'continuous' (individual whales associated for at least seven consecutive days) or 'recurring' (individuals associate at least five times within a 6-week period), although most groups were together for only brief periods (Weinrich 1991, Weinrich & Kuhlberg 1991). Under this classification, the associations between the pairs monitored by us would not be considered stable, as the individuals were only together for brief periods.

The male of pair A was the escort of a female/calf pair. In this social role it was possibly waiting for mating opportunities (Clapham 1996), and it would be expected to stay with the female for as long as possible, until the female became receptive for mating, or until it found another female. The average speed of the female in this pair was higher than the male's.

Both individuals from pair D presented similar average speeds, which were higher than the speed of individuals in the other pairs. Whales moved linearly, a fact that reinforces the

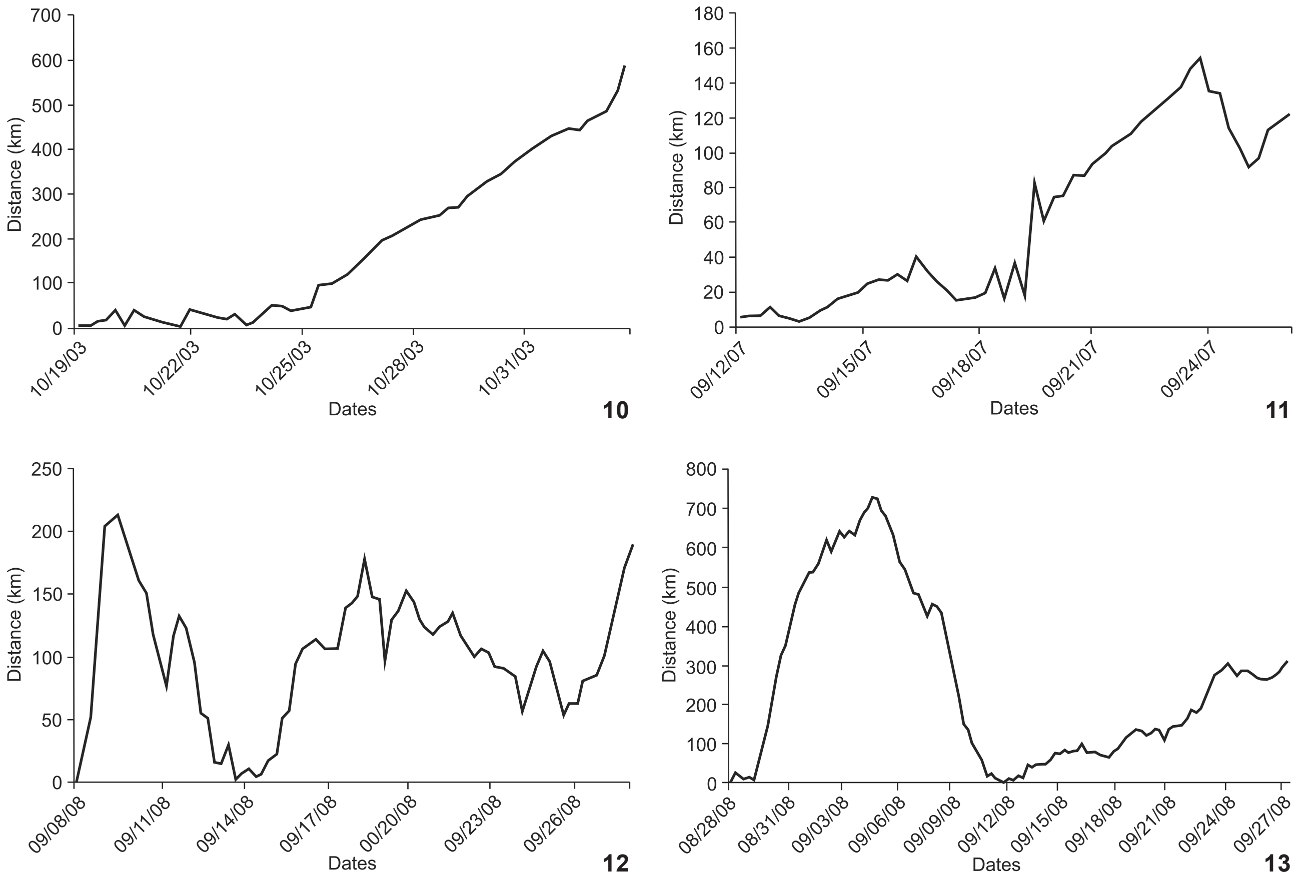


Figures 7-9. Movements of humpback whale Pair D tagged at the Brazilian breeding ground. (7) overview of the tracks; (8) tracks after deployment; (9) shows the end of the monitoring period. The same colors correspond to the same dates for each individual.

possibly that group D was composed of two males that were not competing for a mate. The movement pattern observed for this pair was not compatible with competition for mates. After being 15 days and 700 km far apart, it is notable that they approximated each other in the principal area where humpback whales begin the migration to high-latitude feeding grounds (Zerbini *et al*. 2006).

The social structure of humpback whales is very fluid in tropical waters (Herman & Antinoja 1977, Mobley & Herman 1985, Mattila *et al.* 1989). Despite the fluidity of the associations, the results indicate that whale associations on their breeding area are nonrandom. The pairs are not stable during the reproductive season, permitting females to join other males. In two cases (Pairs C and D), the tracks of tagged whales converged after being separated for periods of six and 15 days. Usual methods for behavioral studies (e.g., direct observation, photo identification and genetics) are based on an instantaneous sampling. Given the population sizes, the fluidity of groups and the distance between the individuals, such methodologies have a low probability of resighting the same individuals in association. Long-term satellite monitoring, however, may be able to locate possible reunions of previously associated whales.

The results presented here highlight two hypotheses that should be further investigated: 1) the whales recognize each other individually and 2) whales communicate far apart. In addition, our results are in accordance with the promiscuous mating in female Humpback whales (Clapham & Palsboll 1997), confirm the short-lived nature of their breeding associations, and corroborate that individuals differ widely in their movements.



Figures 10-13. Calculated distance between the individuals humpback whales belonging to the same pair: (10) Pair A; (11) Pair B; (12) Pair C; (13) Pair D.

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