Marine Mammal Science

MARINE MAMMAL SCIENCE, 26(4): 787–802 (October 2010)

DOI: 10.1111/j.1748-7692.2010.00387.x

Site fidelity and movements of humpback whales (*Megaptera novaeangliae*) on the Brazilian breeding ground, southwestern Atlantic

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ABSTRACT

Site fidelity and movements were studied for humpback whales photo-identified from 1989 to 2006 in the Abrolhos Bank, southwestern Atlantic, Brazil. A total of 2,612 individuals were identified, 374 of which were observed on more than one occasion. The cumulative number of identified whales has increased since 1989. Recapture rate was low and varied among different years. A total of 33 whales was observed using the Abrolhos Bank for longer than 10 yr, up to a maximum of 16 yr. Our data suggest that different whales show distinct movement rates. Some whales used a large extent of the Abrolhos Bank region. Opportunistic photo-identification data (on the scale of the Brazilian coast from 4° to 23°S) revealed important information about stock identity. The longest distance between within-season resightings was over 600 km, while one whale was observed in two locations separated by more than 1,400 km in different years. Long-range movements within and between seasons support the single stock hypothesis for humpback whales wintering off the Brazilian coast.

Key words: humpback whale, *Megaptera novaeangliae*, Abrolhos Bank, occupancy, residency, site fidelity, breeding stock A, Brazil.

Site fidelity may be defined as the tendency of an animal to occupy an area or to return to a previously occupied area over some period of time (White and Garrot

1990). Site fidelity has also been described as an area-restricted space use behavior and has important consequences for many ecological processes (see Börger *et al.* 2008). Different degrees of site fidelity have been documented for many animal taxa (see Switzer 1993, Janmaat *et al.* 2009), including toothed whales and dolphins (*e.g.*, Simões-Lopes and Fabian 1999, Bräger *et al.* 2002, Rossi-Santos *et al.* 2007, Baird *et al.* 2008) and baleen whales (*e.g.*, Dorsey *et al.* 1990, Best 2000, Calambokidis *et al.* 2001) and has important implications for management and conservation strategies of a species. Strong site fidelity may be one important biological characteristic that caused local extinction of large whales in heavily exploited areas such as South Georgia (Clapham *et al.* 2008) during whaling times. Information about site fidelity may also help in the design of effective marine protected areas for the conservation of cetacean species (Bräger *et al.* 2002).

For baleen whales, site fidelity has been studied in migratory species on both feeding and breeding grounds (Dorsey *et al.* 1990, Craig and Herman 1997, Best 2000, Acevedo *et al.* 2006). Humpback whales (*Megaptera novaeangliae* Borowski, 1781) undertake annual migrations between tropical winter breeding grounds and circumpolar summer feeding grounds (Kellogg 1929), and show different degrees of site fidelity to the breeding and feeding grounds. High annual return rates to feeding grounds have been demonstrated (up to 90%; Clapham *et al.* 1993, Acevedo *et al.* 2006) and this fidelity is maternally directed (Clapham and Mayo 1987). In contrast, breeding grounds appear to be more fluid, with whales roaming widely during the winter (Matilla *et al.* 1994). Calambokidis *et al.* (2001) conducted an extensive comparison between photo-identified humpback whales from feeding and breeding grounds in the North Pacific and found that fidelity to feeding grounds is indeed higher than to breeding grounds.

Humpback whales from breeding stock A (IWC 1998, 2005) spend winter on the eastern and northeastern Brazilian coast (Siciliano 1997, Martins *et al.* 2001) and feed in the waters around South Georgia and South Sandwich Islands (Stevick *et al.* 2006, Zerbini *et al.* 2006*a*, Engel *et al.* 2008, Engel and Martin 2009). Within the species' known breeding range in Brazil, most whales concentrate in the shallow waters of the Abrolhos Bank (Andriolo *et al.* 2006*a*). Groups containing mother and calf are the most frequent social category observed in the Abrolhos Bank (Martins *et al.* 2001, Morete *et al.* 2007*b*). Relative abundance around the Abrolhos archipelago increases continually from early July, reaching a peak around the end of August and beginning of September, and then decreases until late November, when most whales have already returned to the feeding grounds (Morete *et al.* 2008).

Photo-identification of individual whales through their natural marks is one of the main techniques used in long-term studies of humpback whales (see review by Clapham 2000). Ventral fluke pigmentation varies from all white to all black with several intermediate patterns (Katona and Whitehead 1981). Over the years, these studies have provided important information about population structure (*e.g.*, Calambokidis *et al.* 2001), demographic parameters (*e.g.*, Clapham and Mayo 1987), site fidelity and occupancy (*e.g.*, Matilla *et al.* 1994, Craig and Herman 1997), and migration (*e.g.*, Baker *et al.* 1986).

Despite being the most studied baleen whale species in the world, many aspects of humpback whale biology remain poorly understood in the Southern Hemisphere (IWC 2006). Clapham (2000) affirmed that "a reasonable understanding of the movements and residency of humpback whales in winter requires greater field effort than has been invested to date." We present information about site fidelity, occupancy, and movements of humpback whales resulting from a long-term study in the Abrolhos

Bank breeding ground, eastern Brazil, from 1989 to 2006. Additionally, we report on resighting data within the species' breeding range along the Brazilian coast.

Material and Methods

Study Area

The continental shelf of the northeastern and eastern Brazilian coast is generally narrow, usually varying from 20 to 50 km in width, and has a steep edge (Ekau and Knoppers 1999). One of the few exceptions is the Abrolhos Bank (16°40′–19°30′S, 37°25′–39°45′W), where the continental shelf widens out to 220 km. In the present study, systematic research covered the area mainly around the Abrolhos archipelago and the Abrolhos National Marine Park. Occasionally, research cruises covered areas as far north as Porto Seguro (16°27′S) and as far south as Barra do Riacho (19°48′S).

Data Collection and Analysis

Photo-identification data were collected between 1989 and 2006, onboard systematic research cruises departing weekly from Caravelas during the humpback whale breeding season, from July to November, the austral winter and spring. Approximately 6,780 h of observation effort were undertaken during the 18 yr of study in the Abrolhos Bank (annual mean = 376 h, SD = 115, range = 172–573). Diesel powered boats, 14–18 m in length, were used. Weekly cruises lasted 3–5 d and were carried out when the weather conditions permitted (sea state below Beaufort 4 and absence of rain). Observations started in early morning and ended around sunset. Groups of whales were followed for a maximum period of 50 min. Group size and composition, behavior and geographical position were registered. Whenever a group of humpback whales was approached, individual identification through photographs of the ventral surface of the flukes was attempted. From 1989 to 2003 photographs were taken with film cameras (see Freitas *et al.* 2004) and since 2004, digital cameras have been used.

The Abrolhos Bank humpback whale photo-identification catalog was compared to three other catalogs held by Instituto Baleia Jubarte (IBJ) assembled in different areas—Praia do Forte, southeastern and northeastern Brazilian coast—in order to broaden the spatial scale of movement and breeding range analysis (Table 1). Excluding the oceanic islands off the Brazilian coast, these catalogs correspond to the main breeding distribution of humpback whales along the Brazilian coast (see Andriolo *et al.* 2006*b*), with a latitudinal range varying from 4° to 23°S. The catalog for Praia do Forte was gathered between 2000 and 2006, during systematic 1-d research

Table 1. Catalogs of identified humpback whales used in the comparisons, covering the known breeding distribution of the species on the Brazilian coast.

Region	IDs	Years	Latitude range	Effort (nmi)
Abrolhos Bank (AB)	2,612	1989–2006	16°–19°S	~30,000
Praia do Forte (PF)	685	2000–2006	12°–14°S	9,739
Northeastern coast of Brazil (NE)	14	2004	4°–11°S	1,700
Southeastern coast of Brazil (SE)	25	2005	19°–23°S	2,000

cruises conducted throughout the breeding seasons (July–October) departing from Praia do Forte (see Rossi-Santos *et al.* 2008). The northeastern coast of Brazil was surveyed during a dedicated expedition from September to November 2004, when 55 d were spent searching for whales. The southeastern coast of Brazil was surveyed during another expedition, with a total of 56 d of effort during two periods: June 2005 and November–December 2005 (see Lodi *et al.* 2008).

Only good quality photographs of individual whales (sharp focus, near vertical and perpendicular angle of the fluke, and adequate photometry, *i.e.*, black and white pigmentation visibility) were included in the catalogs. New individuals were classified into one of five distinguishable patterns according to the percentage of white pigmentation in the fluke (1 = all white, to 5 = all black) (Rosenbaum *et al.* 1995). Each new individual photograph was compared by an experienced team (two researchers) to all whales of the same pattern and both adjacent patterns (inferior and superior). Sightings with geographical position were plotted using the software Arcview 3.1 (ESRI, Redland, CA, USA) in a digitized nautical chart of the Brazilian coast. Straight distances between resightings were measured using Arcview.

Definitions

Recapture rate—Calculated as the number of recaptures in the year divided by the total number of identifications in the year. The recapture rate has been referred to elsewhere as annual return (*e.g.*, Clapham *et al.* 1993).

Occupancy—Number of days between the first and last sightings of an individual whale within a season (Clapham *et al.* 1993). It has also been referred to as residency (Matilla *et al.* 1989). It is not assumed that whales remained the whole period in the study area.

Movement—Any resighting (with geographical positions recorded) of a whale within the same breeding season. The distance between a resighting may be regarded as the minimum distance traveled by the whale.

RESULTS

Sample and Catalog

From 1989 to 2006, 10,875 whales were sighted in the Abrolhos Bank, 1,748 of which were calves (16.1%). A total of 2,612 humpback whales were individually photo-identified. The number of identified whales progressively increased from the beginning of the study in 1989 until 1997. Thereafter, the number of whales identified each year and the number of new individuals remained constant, with a slight increase in the last 4 yr (Fig. 1). Most of the identified whales were sighted only once (n = 2,238, 85.7%), while 374 individuals were sighted on two or more occasions (14.3%). Identified whales were resighted most frequently between seasons (n = 267), while 59 whales were resighted only within the same season, and 48 whales were resighted both within and between seasons. Most whales that were resighted in different years (between season) were observed in 2 yr (n = 230, 73%), followed by 3 yr (n = 55, 17.5%), 4 yr (n = 19, 6%), 6 yr (n = 7, 2.2%), and 5, 7, 8, and 9 yr with one whale each.

The within-season resightings were more frequent in the middle of the study period (1995–2000) and less frequent after 2003 and in the beginning of the study

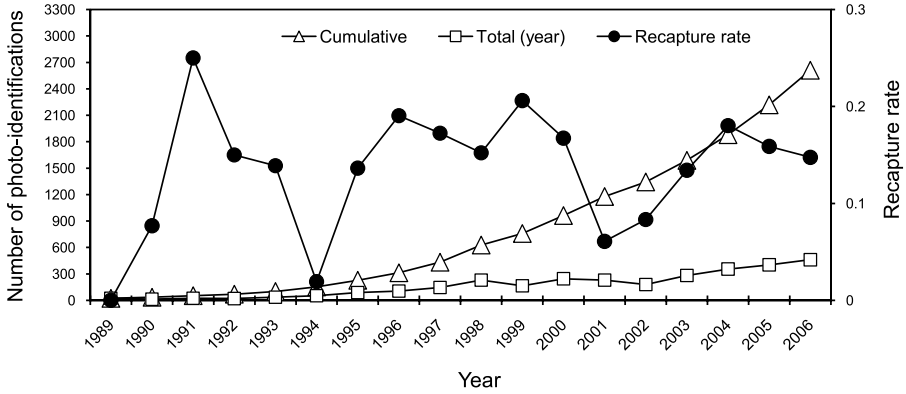

Figure 1. Cumulative curve of photo-identified humpback whales in the Abrolhos Bank, total number of photo-identifications each year, and recapture rate.

period (Table 2). Recapture rate varied among different years, with a 13% mean from 1989 to 2006 (range = 2%–25%). Recapture rate was not correlated with sampling effort (Pearson correlation: $r = 0.1$, df = 15, $P > 0.05$).

Movements and Occupancy

During the study period occupancy ranged from 1 to 71 d (mean = 15.4, SD = 16.7, $n = 74$) and mean movement distance was 35.5 km (SD = 43.1, range = 0.5–291.8, $n = 74$). Some individuals used a large portion of the Abrolhos Bank and adjacencies, but resightings were concentrated around the Abrolhos Archipelago, where most of the field effort was aimed at (Fig. 2).

Mean rate of movement (which may also be regarded as the mean travel speed) of identified whales was 7.8 km/d (SD = 11.9, range = 0.2–62.5, $n = 74$), but different values were observed among individuals (Fig. 3). Some traveled more than 100 km in a period shorter than 5 d, while others were sighted in practically the same area after 70 d. The correlation between interval of days and distance of resightings within the same season was not significant (Pearson correlation: $r = 0.1$, df = 71, $P > 0.05$). The longest displacement observed for the Abrolhos Bank data was of more than 290 km in 13 d (Whale #1885). Additionally, another three long-range movements of more than 600 km were recorded between Abrolhos and Praia do Forte when comparing these catalogs. Whales #1035 (2001), #1198 (2003), and #0719 (2006) were sighted in both areas within an interval of 6, 56, and 17 d, respectively.

Site Fidelity

The most frequent interval observed for between-season resightings was 1 yr (30%), followed by 2 yr (24%) (Fig. 4A). The interval between first and last sighting (excluding within-season resightings) varied from one to a maximum of 16 yr (whales #2, #11, #24, and #27) (Fig. 4B). A total of 33 whales were observed in the Abrolhos Bank over a period longer than 10 yr.

Table 2. Number of humpback whales identified and number of unique whales identified each year, and resightings within (marked with *) and between seasons in the Abrolhos Bank.

Year	Total IDs	Unique IDs	1989	1990	1991	1992	1993	1994	1995	1996	1997	1998	1999	2000	2001	2002	2003	2004	2005	2006
1989	23	12	*6**	1	4	1	1	0	3	2	3	3	3	3	0	0	0	2	2	0
1990	13	4		*0**	2	0	1	1	1	3	2	3	3	3	1	0	0	2	1	2
1991	24	12			*2**	3	2	0	1	2	2	3	3	1	1	0	0	2	2	0
1992	20	7				*0**	2	1	3	1	1	4	1	1	2	1	2	1	2	2
1993	36	15					*3**	0	6	6	6	7	4	5	2	3	2	4	1	3
1994	52	35						*1**	2	3	3	2	4	2	1	0	2	1	2	0
1995	89	54							*10**	9	10	8	4	9	2	3	3	4	3	2
1996	105	59								*8**	8	16	7	7	5	2	7	9	6	8
1997	145	92									*8**	13	14	9	4	2	7	10	7	6
1998	230	164										*25**	11	12	5	4	12	10	7	8
1999	165	109											*11**	13	5	4	6	10	8	7
2000	245	178												*14**	7	6	4	12	12	8
2001	230	192													*8**	5	9	12	7	9
2002	180	150														*8**	7	5	8	12
2003	283	219															*3**	14	13	14
2004	355	272																*1**	16	16
2005	403	330																	*4**	17
2006	461	393																		*9**

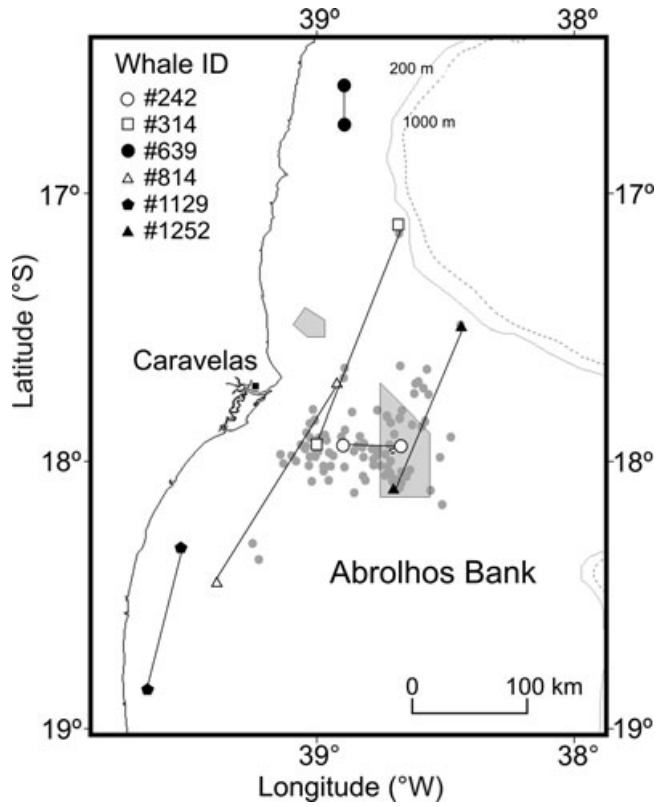

Figure 2. Within-season resightings of humpback whales in the Abrolhos Bank (light gray dots) and the National Marine Park of Abrolhos (dark gray poligons). Movements of some whales were shown with lines.

Mean distance of between-season resightings was 39.2 km (SD = 48.9, range = 2.1–337.7, $n = 231$) and a similar value was found for within-season resightings (Kruskal-Wallis test: $H = 1.34$, df = 1, $P > 0.05$). All whales, with no exception, had a wider individual breeding range than the limits of the Abrolhos National Marine Park.

Comparisons among different catalogs of photo-identified whales (AB, PF, NE, and SE) revealed a low interchange among different sectors of the Brazilian coast. Resightings from different regions showed the use of a large latitudinal breeding range on the Brazilian coast by some whales (Fig. 5). The comparison of catalogs from the two systematic study areas (AB and PF) revealed 17 matches (corresponding to approximately 0.5% of the whales from the Abrolhos and Praia do Forte catalogs). The furthest between-season resightings were observed for whale #1364. It was observed for the first time in the Abrolhos Bank in 2002, then near João Pessoa in 2004, more than 1,400 km to the north, and finally near Praia do Forte in 2005. Whale #1545 was observed on the Abrolhos Bank in 2003, and 2 yr later (2005), more than 550 km to the south, near Búzios.

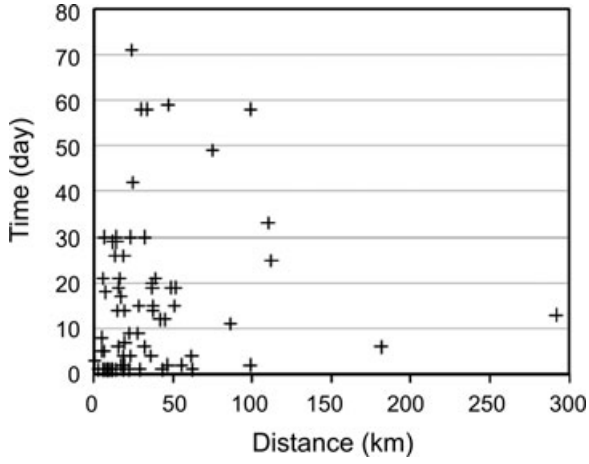

Figure 3. Minimum distance traveled and number of days between within-season resightings of identified humpback whales in the Abrolhos Bank, from 1989 to 2006.

Discussion

Movements and Occupancy

The occupancy observed for humpback whales in the Abrolhos Bank was longer than observed in other breeding grounds in the Caribbean (mean = 6 d, maximum = 33 d, Matilla *et al.* 1994; mean = 9 d, maximum = 30 d, Matilla *et al.* 1989), Ecuador (mean = 13 d, maximum = 30 d, Scheidat *et al.* 2000), Camiguin Island (40 d, Acebes *et al.* 2007), and Maui (34 d, Baker and Herman 1981). This could be possibly explained by the shorter sampling periods of those studies (approximately 2–3 mo/yr) when compared to this one (5 mo/yr). Thus, most occupancy periods are probably underestimated.

Rates of movement, though, estimated through photo-identification in the Abrolhos Bank, were lower than those observed through satellite telemetry studies

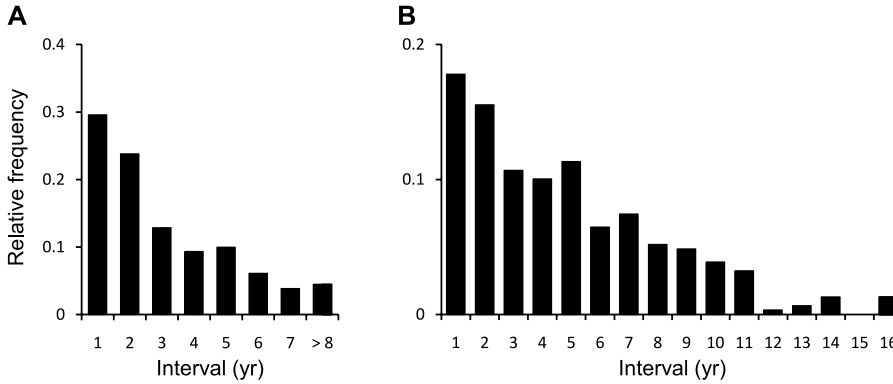

Figure 4. Interval of between-season resightings of identified humpback whales (A) and interval between first and last sighting (B) in the Abrolhos Bank.

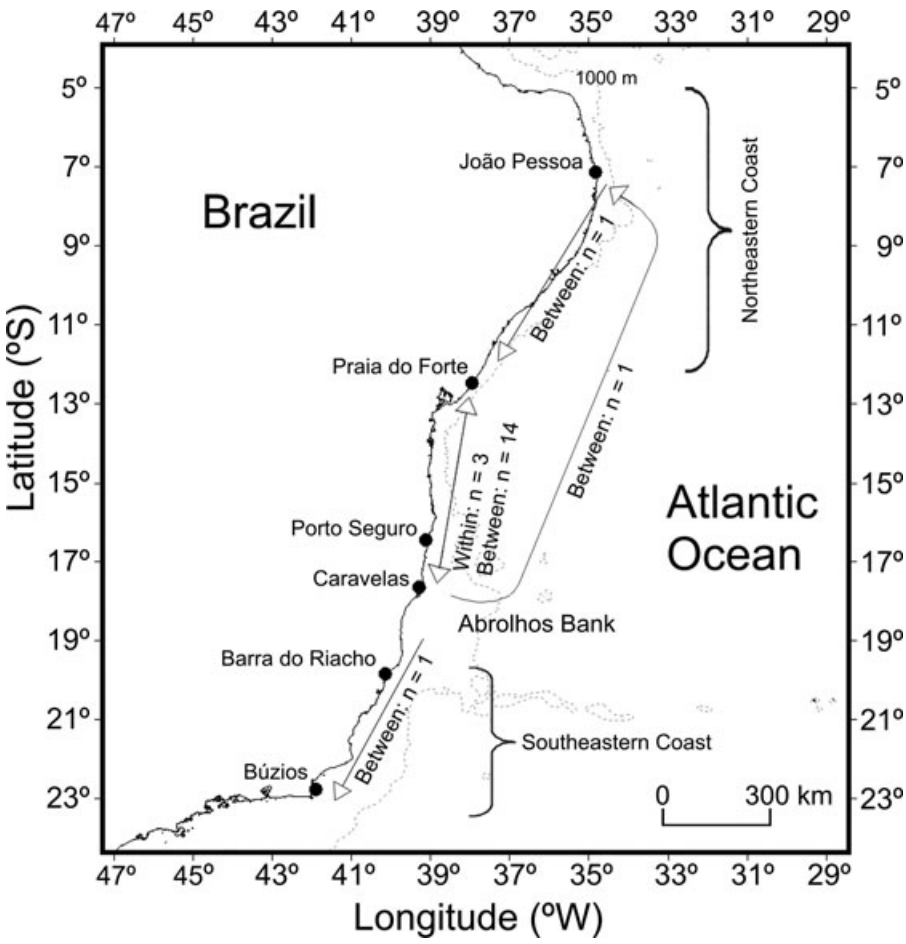

Figure 5. Study area in the Brazilian coast showing interchange of identified humpback whales among areas (within and between-season resightings).

(excluding migrating animals) carried out on the same breeding ground (mean = 42 km/d in Abrolhos Bank, $n = 5$; Zerbini *et al.* 2006*a*) and on the Hawaiian breeding ground (mean = 113 km/d in Hawaii, $n = 3$; Mate *et al.* 1998). Considering that the movements of whales observed through photo-identification are fragmented and certainly underestimated, it is not possible to assess whether a particular individual stayed in the region for a long period of time or whether it moved around and was resighted just when it happened to be close to where it was first sighted. This must certainly be taken into account when interpreting the results of this study.

In this study, some whales were resighted in the same area across many weeks, while others moved over 100 km in just a few days. Similarly, daily rates of movement varied from less than 1 km to more than 60 km. These findings are consistent with those observed in other feeding and breeding grounds (Zerbini *et al.* 2006*a*, Dalla-Rosa *et al.* 2008, Lagerquist *et al.* 2008). Matilla *et al.* (1989) suggested that "most

whales are relatively transient in a particular area of the breeding range." This high mobility is typical of baleen whales, and the relative cost involved in such movements is probably low (see Corkeron and Connor 1999). Humpback whales utilize a large home range within their breeding ground and rarely remain in one area long enough to allow identified individuals to be continuously observed (Baker and Herman 1981). The longest documented movement of a humpback whale in the breeding season was between two different breeding sites, separated by 4,700 km, in the same year (Forestell and Urbán 2007). In the present study, the mean distance between within-season resightings corresponded grossly to the radius of the area where sampling effort was concentrated (30–35 km) around the Abrolhos Archipelago. We observed displacements of up to 600 km within a breeding season, supporting the view that the population ranges over a much broader area than the study site.

Site Fidelity

Few reports on site fidelity exist for humpback whales in the Southern Hemisphere, yet low site fidelity was observed for the whales in the Abrolhos Bank and other breeding grounds alike, with a low proportion of the humpback whales identified being observed over more than 1 yr (Northern Hemisphere—Baker *et al.* 1986, Matilla *et al.* 1994, Craig and Herman 1997; Southern Hemisphere—Flórez-González *et al.* 1998). Likewise, on a Western Australia breeding ground a 9-yr interval between the first and last marking was observed (Chittleborough 1965), and Craig and Herman (1997) reported few whales that were observed to use the Hawaiian breeding ground for more than 10 yr. In our study, less than 2% (1.26) of the identified whales were observed using the Abrolhos Bank breeding ground for more than 10 yr. However, the longest interval recorded between resightings corresponded to the span of the study, suggesting long-term site fidelity.

Many factors may account for the low and variable annual recapture rates for humpback whales in the Abrolhos Bank. Capture probability of an individual may vary according to sampling effort and the behavior of the whales. Rates of interannual resightings reflect the size of the population being sampled besides the degree of site fidelity (Calambokidis *et al.* 2001). The latest (2005) abundance estimate for the population wintering in Brazil was 6,251 individuals (CV = 0.16) (Andriolo *et al.* 2006*b*) and it is increasing at an estimated rate of 7.4% per year (Ward *et al.* 2006). The population is undergoing a period of exponential growth following the rapid decline during the whaling period (Zerbini *et al.* 2006*b*). Thus, hundreds of new individuals are accruing in the population each year and only a proportion of the population that uses the Abrolhos Bank has been captured by photographs. Following a better coverage of the population through photo-identification and the stabilization of the population growth, an increase in the recapture rate is expected. Additionally, the fact that some females do not undertake the winter migration, remaining throughout the year in the feeding ground (Brown *et al.* 1995, Craig and Herman 1997) may also contribute to this pattern of low recapture. This migration pattern results in the whole population being present on the feeding ground in the summer, and only a fraction of the population present on the breeding ground in the winter (Brown *et al.* 1995). Moreover, many individuals may frequent different breeding grounds in different years (Darling and McSweeney 1985, Darling and Cerchio 1993, Salden *et al.* 1999, Garrigue *et al.* 2002).

Besides behavior and population characteristics, methodological variables may also influence recapture rates. The sampling area was grossly the same throughout the years, with an expansion since 2001, when a decline in the recapture rates and intra-annual resightings was observed. On the other hand, after the adoption of digital cameras since 2004, the total number of photo-identifications has apparently increased. The biological and methodological variables described above may result in the underestimation of true site fidelity.

Management Implications

The comparison of two humpback whale photo-identification catalogs, obtained during systematic studies along the eastern Brazilian coast (Abrolhos Bank and Praia do Forte, separated by 600 km), revealed relatively few matches. The low interchange among individuals of these two regions suggests that the whales do not exchange freely between the two areas and show some degree of fidelity to subregions of the Brazilian breeding ground. Possible mechanisms, which underlie this segregation, could be the separation by age, different migration routes for different individuals (*e.g.*, the existence of an offshore route), and/or habitat barriers or discontinuities along the breeding range. Genetic analyses, however, demonstrated no evidence of spatial differentiation among the breeding populations from Praia do Forte and the Abrolhos Bank, as well as no temporal differences across years, supporting the hypothesis that the southwestern Atlantic humpback whale is a single breeding population (Cypriano-Souza 2008). Using 10 microsatellite loci, this study compared samples from Praia do Forte ($n = 39$) and Abrolhos Bank ($n = 235$). Thus, possibly a minor proportion of "wandering" whales (see Darling and Cerchio 1993, Salden *et al.* 1999) are responsible for maintaining the panmictic population as suggested by genetics. However, although data are indicative of a single breeding population in Brazil, further studies are needed to confirm this hypothesis due to the sparseness of photo-identification and genetics data. Photo-identification efforts covering a wider geographical area, including oceanic islands off the Brazilian coast (see IWC 2006), and a larger genetic sample, are recommended to adequately study this population structure.

In the Abrolhos Bank, short-term behavioral changes have been observed for humpback whales approached by tourism vessels (Morete *et al.* 2007*a*, Sousa-Lima 2007). Behavioral changes included song disruption by male singers (Sousa-Lima 2007) and evasion by females with calves from resting areas (Morete *et al.* 2007*a*). Whale watching in the Abrolhos Bank area has been mainly opportunistic during tourism trips to the Abrolhos National Marine Park (Morete *et al.* 2000). But although the overall number of visitors to the National Marine Park is decreasing, the number of visitors during the "whale season" has increased over the last years (*in litt*., ICMBio–National Marine Park Authority). The apparently high transient characteristic of whales in our study area is both positive and negative for the conservation of whales. Transience certainly minimizes the negative impacts from exposure to whale watching, diluting the negative effects over the whole population that uses or passes through the Abrolhos Bank and not concentrating the impacts on resident individuals. On the other hand, transience may raise the chances of whales encountering and getting entangled in fishing gear, which is also a potential threat to the whales in the Abrolhos Bank (Zambonim *et al.* 2009; IBJ, unpublished data).

A considerable portion of the population seems to travel long distances within the same or different seasons, using multiple sites along the Brazilian coast. Although the proportion of such whales is unknown, and could be restricted to few "wandering" whales, the breeding range of these individuals may be as extensive as the eastern and northeastern Brazilian coasts, where whales are subject to several human threats such as shipping, fishing, oil and gas exploration, among others. Additionally, the movement range of humpback whales on the Abrolhos National Marine Park was generally wider than the limits of the Park. Considering that this marine-protected area was created, among other things, to protect humpback whales during their breeding season, its effectiveness remains questionable. To enhance present protection, we propose the creation of a buffer zone, encompassing a wider area, adjusted to the scale of the movements of the whales within the breeding ground. Such a buffer zone would also warrant vital protection for coral reefs from damages caused by potential oil spills, and has already been proposed by other authors (Marchioro *et al.* 2005). This measure is recommended in order to effectively protect a critical breeding habitat of the humpback whale in the southwestern Atlantic.

Acknowledgments

This article is part of a doctoral thesis by the first author in Zoology at Universidade Federal do Paraná, Brazil. We wish to thank: Luiza Godoy, Ana Freitas, and Grazyela F. Lima for photo-identification data organization and management in early years; Thatiana Faget for data entry; Sandra Ferreira and Fernando Fontes for catalog comparisons; all the people who somehow helped to collect data along more than 20 yr of research—for reasons of saving space and paper we will omit the long list; the crew members of Tomara and other research boats used in the long-term study in the Abrolhos Bank; ICMBio–National Marine Park of Abrolhos Authority for logistic support; PETROBRAS, IFAW, CENPES—PETROBRAS, and many other institutions for essential financial support. P. C. Simões-Lopes received a research grant from the Brazilian Research Bureau (Conselho Nacional de Desenvolvimento Científico e Tecnológico CNPq/PQ, proc: 304698/2006-7); Daryl Bonness, Douglas Nowacek, James Darling, Luena Fernandes, and two anonymous reviewers for constructive comments and suggestions on the manuscript.

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Received: 9 December 2008
Accepted: 29 November 2009