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Satellite-monitored movements of humpback whales *Megaptera novaeangliae* in the Southwest Atlantic Ocean

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ABSTRACT: Southern Hemisphere humpback whales *Megaptera novaeangliae* migrate from wintering grounds in tropical latitudes to feeding areas in the Antarctic Ocean. It has been hypothesized that the population wintering off eastern South America migrates to feeding grounds near the Antarctic Peninsula (ca. 65° S, 60° W) and/or South Georgia (54° 20′ S, 36° 40′ W), but direct evidence to support this has never been presented. Between 19 and 28 October 2003, 11 humpback whales (7 females and 4 males) were instrumented with satellite transmitters off Brazil (ca. 18° 30′ S, 39° 30′ W) to investigate their movements and migratory destinations. Mean tracking time for the whales was 39.6 d (range = 5 to 205 d) and mean distance travelled was 1673 km per whale (range = 60 to 7258 km). Movements on the wintering ground showed marked individual variation. Departure dates from the Brazilian coast ranged from late October to late December. Whales migrated south through oceanic waters at an average heading of 170° and travelled a relatively direct, linear path from wintering to feeding grounds. Two whales were tracked to feeding grounds in offshore areas near South Georgia and in the South Sandwich Islands (58° S, 26° W) after a 40 to 60 d long migration. Historical catches and current sighting information support these migratory routes and destinations. This study is the first to describe the movements of humpback whales in the western South Atlantic Ocean.

KEY WORDS: *Megaptera novaeangliae* · Migration · Satellite telemetry · Wintering grounds · Feeding grounds · South Atlantic Ocean · South Georgia · South Sandwich Islands

INTRODUCTION

Long-distance seasonal migration is typical of some baleen whales. Many species forage in productive, high-latitude areas in the summer and migrate to temperate or tropical waters, where mating and calving occur during winter and spring. Studies of whale movements can provide information on their behaviour, habitat use, migration routes, and migratory destinations (e.g. Chittleborough 1965, Baker et al. 1986, Best et al. 1993, Mate et al. 1998, 2000, Calambokidis et al. 2001, Heide-Jørgensen et al. 2003). Such studies are also useful for clarifying population structure (e.g. Calambokidis et al. 2001, Heide-Jørgensen

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et al. 2003, 2006) and for understanding the ecology of the whales (e.g. Laidre et al. 2003).

Humpback whales *Megaptera novaeangliae* inhabit all major ocean basins and undertake the longest migrations of any mammal (Stone et al. 1990, Stevick et al. 2003). Currently, 7 geographically separated populations (labelled breeding stocks A to G) are recognized by the International Whaling Commission (IWC) in the wintering grounds in the Southern Hemisphere (IWC 1998). These stocks are connected to feeding areas in the IWC Management Areas I to VI in the Antarctic (e.g. Donovan 1991). Movement patterns, migratory corridors, and feeding destinations are unknown for some populations, such as that wintering off the eastern coast of South America (breeding stock A). Humpback whales spend the winter breeding season in eastern Brazil from about 21°S to the northeast tip of the South American continent (~5°S) (e.g. Mackintosh 1965, Williamson 1975, Martins et al. 2001, Zerbini et al. 2004a). Additional winter records have been made to the north and west of 5°S (Furtado-Neto et al. 1998) and near oceanic islands in the Southwest Atlantic Ocean (SWA) (Lodi 1994), but it is unclear whether these areas correspond to the typical range of the species.

The movement patterns of humpback whales wintering off Brazil are poorly known and their summering grounds have not yet been determined. Historically, it was suggested that this population migrated to feeding areas near the Antarctic Peninsula (AP) and/or South Georgia (SG) (e.g. Slijper & van Utrecht 1959, Slijper 1962, 1965, Mackintosh 1965). However, no direct evidence was provided to substantiate these proposed migratory connections. In recent years, studies involving sighting surveys, photo-identification, and molecular genetics have been conducted on the humpback whale wintering ground off Brazil and the presumed high-latitude feeding grounds near SG and the AP (Moore et al. 1999, Rosenbaum et al. 2000, Stevick et al. 2004). These studies were also unable to determine migratory connections of whales wintering off Brazil.

Satellite telemetry has proven to be an important tool in the study of behaviour and movements of marine vertebrates (e.g. Jouventin & Weimerskirch 1990, Polovina et al. 2004). This technique has been successfully applied to cetaceans in recent years (e.g. Mate et al. 1998, 2000, Heide-Jørgenesen et al. 2001), particularly when the use of other research techniques is difficult or whales inhabit areas of limited human access. In October 2003, satellite transmitters were deployed on humpback whales in the wintering ground off the coast of Brazil with the purpose of investigating their (1) movements, (2) migration routes, and (3) migratory destinations in the western SA. Results of this 2003 study are reported here.

MATERIALS AND METHODS

Study area. Tagging operations were conducted from Conceição da Barra (18°30′S, 39°30′W), northern Espírito Santo State, southeastern Brazil, between 19 and 28 October 2003. Daily searches for humpback whales were undertaken during good weather conditions (Beaufort sea state ≤3) from a 10 m long fiberglass speedboat and 2 inflatable boats, over an area of approximately 100 km^2. This area had the highest density of humpback whales in the wintering ground off the eastern coast of South America (Andriolo et al. in press).

Transmitter configuration. Two configurations of the SPOT3 satellite transmitters (Wildlife Computers) were used: 'Mini-can' (n = 7) and 'implantable' (n = 4) tags (Table 1). Mini-can tags consisted of an epoxy cylinder glued to a cup-shaped stainless steel base and mounted to a stainless steel spear with 3 sets of barbs and either a sharp-pointed tip or a triangular double-edged blade. The transmitters were the same as those used in bowhead whale *Balaena mysticetus* studies in Baffin Bay (Heide-Jørgensen et al. in press) except that the spear was shorter. Implantable tags were steel cylinders connected to a spear with 1 set of barbs and a triangular double-edged blade. Duty cycling and programming varied by tag. Five tags were duty cycled to transmit every other day while the remainder transmitted every day. Programming for frequency of emissions, total number of emissions d^{-1} and transmission time were variable for mini-can tags, but were equal for all implantable tags (Table 1).

Tag deployment and biopsy sampling. When a whale was observed, only the inflatable boats approached it for instrumentation. Tags were deployed using an 8 m long fiberglass pole at about 4 to 5 m from the whale as described by Heide-Jørgensen et al. (2003). The tag-delivery system was designed such that a biopsy skin sample was collected simultaneously when a whale was tagged. Biopsies were used for DNA extraction and sex determination of each individual as described by Bruford et al. (1992) and Bérubé & Palsbøll (1996).

Data analysis. Locations were obtained from Service Argos (1990). Location quality (LQ) was coded A, B, 0, 1, 2, or 3 in increasing order of position accuracy. Positions 1 to 3 are presumably of higher accuracy. Service Argos (1990) predicts that 68% of classes 1, 2, and 3 are within 1.0, 0.35, and 0.15 km of the true location respectively. It does not provide error predictions for location classes 0, A, and B. However, satellite tracking of pinnipeds has shown that error may range from 3.8 km (SD 2.6) for class 0 positions, 18.8 km (SD 42.6) for class A positions, to 22.8 km (SD 43.9) for class B locations (Boyd et al. 1998).

Throughout this paper, the regions where whale locations were received are categorised by 'wintering ground', 'feeding grounds', and 'migratory corridors'. The wintering ground is defined as the area within the continental shelf (depth < 200 m) along the Brazilian coast north of 25°S, whereas feeding grounds are defined as the habitat south of the northern limit of the Antarctic Convergence in the SA (~50°S) (e.g. Deacon 1986). Migratory corridors lie between the wintering and the feeding grounds.

Distance and rate of travel for each whale was calculated using daily average positions. Because of the relatively high associated errors with locations 0, A, and B, only good quality locations were used to calculate daily averages when examining short-range movements on the 'wintering' and 'feeding grounds'. All quality locations were used to calculate daily average positions for long-range movements in the 'migratory corridors'. Distance and rate of travel were calculated for each 24 or 48 h period for tags transmitting every day or every other day, respectively.

RESULTS

We tagged 11 humpback whales (Table 1). Molecular sex identification was obtained for 9 whales: 3 males and 6 females. The gender of the remaining 2 whales, 1 female (Whale #24642, the mother in a mother-calf pair) and 1 male (Whale #20162, the escort in a mother-calf-escort group), was inferred based upon role within the observed group. Apart from 1 individual (Whale #20162), probably a sub-adult, all other whales were considered adults as judged by their relatively large size.

A total of 1691 locations was received, but only 858 were used to calculate daily averages. Mean tracking time for the 11 whales was 39.6 d (range = 5 to 205 d) and distance travelled varied from 60 to 7258 km with a mean of 1673 km (Table 1).

Movements and habitat use on the wintering ground

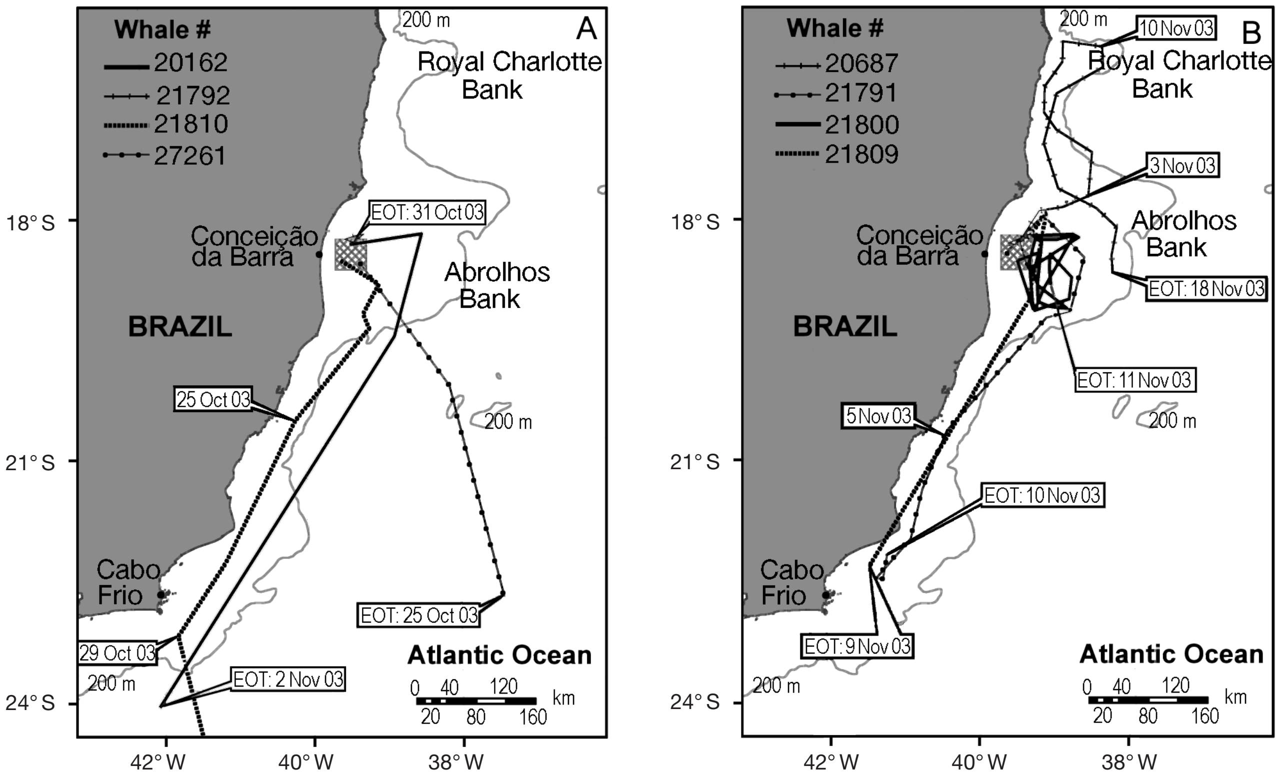
All whales were tagged in approximately the same general area within a period of 10 d (Table 1). Subsequent movement of these whales on the wintering ground showed marked individual variation (Fig. 1). Of the 4 males, 3 moved south within a few days after tagging. Whale #20162 moved 100 km offshore 2 d after tagging and then moved 750 km south-southwest along the coast (Fig. 1A). Whale #21810 followed a similar route. It moved 740 km southwest in about 11 d, before traveling offshore (Fig. 1A). Whale #27261 also left the area right after tag deployment, but followed a slightly different route. It moved 540 km southeast through offshore waters within the 6 d it was tracked (Fig. 1A). The fourth male tracked during this study (Whale #21792) remained near the tagging area for the 5 d period during which the transmitter provided locations (Fig. 1A).

All other whales tracked were females and all, except Whale #24640, were accompanied by calves when transmitters were deployed. Whale #20687 moved northeast in the first days after tagging and then moved north towards the Royal Charlotte Bank, ca. 350 km north of the tagging location. It remained there for 4 d and then moved south again for another 300 km to Abrolhos Bank (Fig. 1B). Whale #21791 headed north after tagging and then turned around and moved nearly 620 km south along the coast in about 9 d. It stayed in that region (at approximately

Table 1. *Megaptera novaeangliae.* Transmitters deployed on humpback whales off the coast of Brazil in October 2003. MC, mini-can; IMP, implantable. Spear type: N, needle; T, triangular blade. eod: tags programmed to transmit every other day

Whale ID no.	Sex	Tag type	Spear type	Duty cycling	Daily emissions	Transmission time (h)	Tagging date (2003)	Tag longevity (d)	No. of locations received	No. of locations used	Distance travelled (km)
20162	M[a]	MC	N	eod	300	6–21	19 Oct	13	10	8	850
20687	F	MC	N	none	500	0–23	27 Oct	23	319	229	933
21791	F	MC	N	none	500	0–23	28 Oct	14	166	86	743
21792	M	MC	N	none	500	0–23	27 Oct	5	52	24	60
21800	F	MC	N	none	500	0–23	28 Oct	31	287	99	965
21809	F	MC	N	none	500	0–23	27 Oct	14	51	6	598
21810	M	IMP	T	eod	300	6–21	18 Oct	76	84	52	4383
24640	F	IMP	T	eod	300	6–21	19 Oct	8	24	8	337
24642	F[b]	IMP	T	eod	300	6–21	27 Oct	205	624	324	7258
27259	F	MC	N	none	300	6–21	19 Oct	39	51	20	2315
27261	M	IMP	T	eod	300	6–21	18 Oct	8	5	2	516
Total								436	1673	858	18958

[a]Assumed to be male because it was an escort in a triad with a mother and a calf
[b]Assumed to be a female because it was the adult individual in a cow-calf pair



22° 30′ S) for 3 d before transmissions ceased (Fig. 1B). A similar movement pattern was observed for Whale #21809 (Fig. 1B). The movement paths of these 2 individuals were similar to those exhibited by male Whales #20162 and #21810.

Whales #21800 and #24642 showed limited north-south and inshore-offshore movements between 18 and 20°S. The former remained there for the 30 d during which locations were received (Fig. 1B), while the latter stayed in the area for 49 d, before moving south towards the feeding grounds (Fig. 1C).

Movement patterns on the wintering ground were typically restricted to the continental shelf. Except for Whale #27259, which briefly left the shelf for 1 d (Fig. 1C), locations for all other individuals were within the 200 m isobath. Satellite locations showed that all whales used the shelf near the Abrolhos Bank area as far south as Cabo Frio (~23°S) and that the whales never moved further north than Royal Charlotte Bank (~16°S).

Departure points and timing

Tracks for most individuals indicated that once whales have moved into deep waters, beyond the continental slope, they begin to migrate. No reverse movement was recorded for any whale that moved into

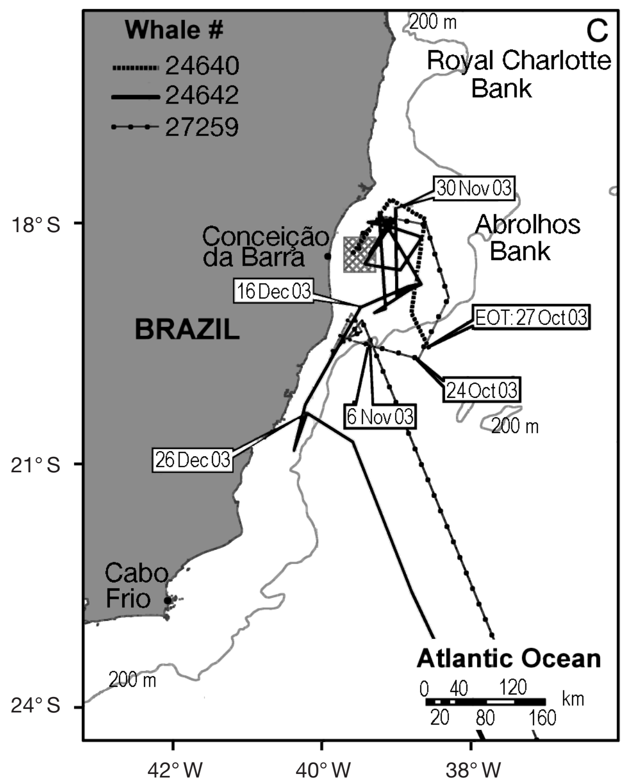


Fig. 1. *Megaptera novaeangliae*. Tracks of tagged whales in the wintering grounds off eastern Brazil (A: males; B, C: females). Shaded squares represent the area where tag deployment was carried out. EOT: end of transmissions

these areas. Five individuals were tracked after they left the wintering ground and no preferential departure point was observed (Fig. 1). Whales #20162 and #21810 moved south past Cabo Frio before venturing into offshore waters and Whale #24642 moved into deep waters near 20° 30′ S, south of the Abrolhos Bank. Whales #24642 and #27261 departed from the south-southeastern portion of Abrolhos Bank.

All 3 males left the wintering ground by the end of October, 1 female departed on 6 November and another on 26 December 2003.

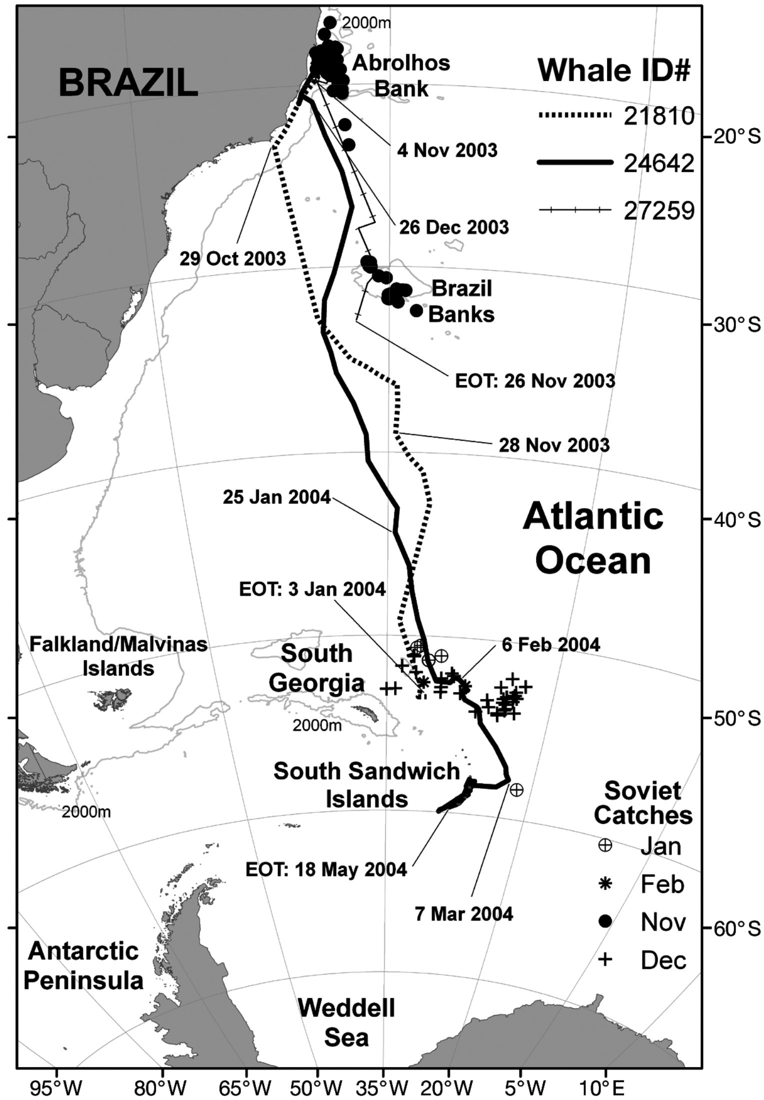


Fig. 2. *Megaptera novaeangliae*. Migratory routes and summer destinations of 3 humpback whales wintering off the coast of Brazil and locations of historical humpback whale Soviet catches from the 'Yuri Dolgorukiy' fleet (EOT: end of transmissions)

Migration routes and migratory destinations

Tracks of 3 whales provided details of their migration route (Fig. 2). Whale #27259 was tracked for approximately one-third of the route, while Whales #21810 and #24642 were tracked until they reached the (presumed) feeding grounds. The migration path was consistent among the whales irrespective of sex and departure time. Departure timing varied for a period of 2 mo and none of the whales travelled together. Nonetheless, their tracks intersected and were never more than 500 km apart (Fig. 2). Whales travelled a relatively direct, linear path and gradually moved away from the South American continent as they migrated to higher latitudes. They followed approximately the same route southwards at an average geographic heading of 170° (Fig. 2). Whales #27259 and #24642 travelled towards an area known as the 'Brazil Banks' (ca. 31° S, 35° W), a former whaling ground off the eastern South American coast (e.g. Townsend 1935). It is not possible to evaluate whether Whale #21810 also migrated through that area because no positions were received from this whale while it travelled between 24 and 33° S.

Whales #21810 and #24642 migrated to an area 270 to 400 km northeast of SG (54° 20′ S, 36° 40′ W), some 3500 km southeast of the wintering ground (Fig. 2). Whale #21810 departed from the coast of Brazil on 29 October 2003 and was north of SG on 28 December, having travelled 3640 km at an average speed of 63 km d^{-1}. In the following 6 d, this whale travelled only 109 km at an average speed of 18 km d^{-1}. During that period, its movements were erratic and it stayed in the same general region. Transmissions from this whale ended on 3 January 2004.

Whale #24642 left the wintering ground on 26 December 2003 and arrived on the feeding grounds in the same area as Whale #21810 on 6 February 2004. During that period, it travelled 3720 km at an average speed of 92 km d^{-1}. Average swimming speed of Whale #24642 diminished when it reached 52° 30′ S, 30° 40′ W, nearly 400 km northeast of SG. It continued moving slowly westward in an erratic fashion for 22 d, until it reached 53° 53′ S, 26° 32′ W (Fig. 2). This whale's movement rate during this period averaged 24 km d^{-1}. It then increased speed (average = 52 km d^{-1}) and moved to its westernmost position (57° 45′ S, 22° 30′ W) on 7 March 2004, where it turned east and moved towards the South Sandwich Islands (SSIs) (~58° S, 26° W). The whale reached those islands on 11 March 2004 and continued moving erratically around the southern portion of the South Sandwich Archipelago until transmissions ceased on 18 May 2004.

DISCUSSION

Movements and habitat use on the wintering ground

There is little information on movement patterns and habitat use of humpback whales on their SWA wintering ground. Considerable individual variation was observed in the direction and extension of whale tracks, suggesting much heterogeneity in movement patterns. Most whales moved south after tag deployment. This was expected, considering that tagging operations occurred relatively late in the season (mid- to late October), when many whales should be departing to the feeding areas in higher latitudes. Martins et al. (2001) showed that the peak abundance of humpback whales on the Abrolhos Bank is September. By late October and November abundance declines, but some individuals can be found there in December. In the present study, some individuals remained in the area where they were tagged and showed limited north-south and inshore-offshore movements. Only 1 whale (#20687, a female) moved further north (350 km) relative to its tagging position. While differences in movement patterns of humpback whales may be related to sex, age and reproductive condition, the present study suggests that they also vary on an individual basis. However, additional sampling is needed to better understand the importance of age- and sex-specific movements relative to inherent variability among individuals.

Wide variation in the movement patterns of humpback whales on the wintering ground has important implications for mark-recapture studies. Population estimates have been derived from analysis of photo-identified whales on the Abrolhos Bank (e.g. Kinas & Bethlem 1998). However, these estimates were based on incomplete coverage of the wintering range of the humpback whale population on the Bank and upon the assumption of constant capture probability of individual whales. The present study showed that the residency pattern of whales on the Bank varies substantially. While some whales remained in relatively small areas for long periods, others moved around the Bank or further south along the coast. Such movements provide direct evidence that the probability of recapturing individuals in mark-recapture studies is not constant on the Abrolhos Bank. This is an important point to consider in future studies because heterogeneity in capture probabilities usually causes negative bias in mark-recapture-based estimates of abundance (e.g. Hammond 1990).

Departure points and timing

Data presented in this study indicate that there were no preferential departure points for humpback whales leaving the wintering ground off Brazil. The observed whale tracks show that individuals departed from the wintering ground from within a 500 km region, ranging from the southern portion of Abrolhos Bank south to the area of Cabo Frio.

The timing of migration of the whales tracked in this work is consistent with studies conducted in other regions. Out of 4 males monitored, 3 left the coast of Brazil by late October, whereas females with calves departed later. Elsewhere, humpback whales departing from wintering grounds show temporal segregation by sex and reproductive condition (e.g. Chittleborough 1965). Dawbin (1997) observed that the first whales to depart are non-calving (newly pregnant) females and immature whales of both sexes. They are followed by mature males and, subsequently, lactating females. This migration pattern is similar to that observed for North Pacific humpback whales (Craig et al. 2004).

Migratory routes and migratory destinations

Two non-exclusive migration routes between wintering and summering grounds in the SWA were proposed. Slijper & van Utrecht (1959) and Slijper (1962) suggested that migration from the Antarctic Peninsula (AP) and perhaps Falkland Islands to the eastern coast of South America was restricted to coastal waters, while Slijper (1962, 1965) and Mackintosh (1965) hypothesised that whales feeding near SG would move north/northwest into deep waters until reaching tropical latitudes close to the eastern South American coast. The southbound migration would follow approximately the same route back to SG. Mackintosh (1965, Table 3, p. 85) further suggested that summer feeding grounds for animals found in coastal waters of Brazil probably included the SSIs.

The migratory connections proposed above were based on the coincidental collapse of humpback whaling in the AP, SG and South America (IWC 2005). Whaling began in 1904 in SG and 1905 near the AP and focused mainly on humpback whales (Tønnessen & Johnsen 1982). Catches were small and the population had already been considerably depleted in both areas by 1915 (e.g. Matthews 1931, Tønnessen & Johnsen 1982, Findlay 2001). The catch history off Brazil is much less complete, but off Costinha (7° S) humpback whales were taken in relatively high numbers from 1910 to 1914 (average = 280 whales yr^{-1}), much lower numbers from 1924 to 1928 (average = 45 whales yr^{-1}), and even more rarely afterwards (average = 11 whales yr^{-1} from 1948–1963) (Williamson 1975). Small catches made from 1960 to 1963 (average = 2.5 whales yr^{-1}) at another Brazilian whaling station in Cabo Frio (23° S) (Williamson 1975) are also consistent with the depleted status of this population.

No direct evidence (e.g. observation of marked individuals) has ever been presented to support the migratory connections proposed above. In recent years, sighting surveys, photo-identification and genetic studies have been carried out on the humpback whale wintering ground off Brazil and the presumed high-latitude feeding grounds near SG and the AP, but they have been unable to provide evidence for migratory connections among these areas. Since 1979, sighting cruises and shore-based observations conducted in the summer in offshore areas to the west and in nearshore waters to the north and northeast of SG showed that the current density of humpback whales has been very low in these former whaling grounds (Moore et al. 1999, T. Martin pers. comm.). The paucity and lack of recovery of humpback whales near SG today contrasts with the relatively high and increasing abundance of the population wintering off Brazil (Martins et al. 2001, Zerbini et al. 2004a, Andriolo et al. in press), suggesting that whales from this population may not migrate into coastal areas off SG. Likewise, genetic and photo-identification studies conducted near the AP and off Brazil have not shown migratory connections between these 2 areas (Rosenbaum et al. 2000, Stevick et al. 2004).

In conjunction with modern whaling, Discovery marks were fired into free-ranging whales and were later recovered when carcasses were processed (e.g. Rayner 1940). These studies were successful for some populations of humpback whales in the Southern Hemisphere (e.g. those wintering off eastern and western Australia; Chittleborough 1965), but not for whales in the SWA. Only 1 Discovery mark from a whale tagged in the South Pacific on 16 Dec 1957 was recovered in the western South Atlantic on 14 Apr 1962 (IWC 1998, p. 181–182), suggesting a possible migratory connection between these 2 areas. The reported recovery position of that whale (28° S, 48° W) does not correspond to the catch position. This individual was actually killed somewhere in the Antarctic sector of the South Pacific but the mark was not found until the ship's cooker was cleaned (in the reported position) off eastern South America, during the voyage back to the fleet's homeport (Y. Mikhalev pers. comm., March 2005).

In the present study, 2 individuals were tracked to the feeding grounds and another whale provided the heading towards the feeding grounds. Despite the small sample, they provided the first direct evidence of migratory routes and destinations of humpback whales wintering off Brazil. Whales moved through offshore deep waters in the SWA to the northeast of SG and near the SSIs. This movement pattern and migratory destinations are consistent with the hypotheses of Slijper (1962, 1965) and Mackintosh (1965).

Catch records from the latest years of humpback whaling in the Southern Hemisphere further support the use of these (offshore) migration routes. Catch locations in the presumed humpback whale migration paths in the SWA are available for 1 of the 4 Soviet fleets (the 'Yuri Dolgorukiy') whaling in the Southern Hemisphere (Zemsky et al. 1996). From 31 October to 13 November 1967, this fleet operated off the Brazilian coast, taking whales in coastal waters off the Abrolhos Bank and then further south and offshore near the Brazil Banks (Fig. 2). The timing and location of the catches are similar to the tracks of some whales monitored in this study. For example, Whale #27259 migrated through the Brazil Banks between 20 and 24 November, which almost coincides with the period when whales were taken in the late 1960s.

Individuals tracked until their departure moved into oceanic waters to migrate, providing no support for a coastal (i.e. along the continental shelf) migration route towards the Falkland Islands and the AP, as proposed by Slijper & van Utrecht (1959) and Slijper (1962). Stranding and sighting data are also consistent with these findings. Despite substantial research effort in recent years, strandings of humpback whales are scarce along the coasts of southern Brazil, Uruguay and Argentina (e.g. Lichter & Harris 1992, Siciliano 1997). Also, sighting surveys conducted off the southern coast of Brazil (21 to 34° S) in 1996 and 1997 did not record humpback whales over the continental shelf or shelf break to the south of 25° S (Zerbini et al. 2004b). In fact, whales feeding in the AP migrate to the western coast of South America to winter off the coasts of Colombia, Costa Rica and Ecuador (Stone et al. 1990, Flórez-Gonzáles et al. 1998, Olavarría et al. 2000, Stevick et al. 2004).

The present results suggest that humpback whales migrate to areas not far from SG. The 2 individuals monitored to the feeding grounds remained offshore, not moving into the former whaling grounds in coastal areas. The offshore occurrence of humpback whales near SG is also supported by Soviet catches and sighting data. The 'Yuri Dolgorukiy' fleet operated in high latitudes in the SWA in 1965, 1966 and 1973 and captured humpback whales 125 to 500 km off the east-northeast coast of SG (between 22 and 35° W, Fig. 2 and see also Mikhalev 1998). Kasamatsu et al. (1996) reported relatively high humpback whale encounter rates between 20° and 40° W and 54° and 58° S during ship surveys conducted in the austral summer from 1976 and 1988. Also, a joint research cruise of the IWC and the Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR) recorded several humpback whale sightings about 400 km northeast of SG in January to February 2000 (Reilly et al. 2004).

SG was one of the most important historical humpback whaling grounds in the SWA (Tønnessen & Johnsen 1982). Matthews (1931) observed that whales were plentiful close to shore, even within some bays where whaling stations were sited, in the early 20th century. In the 1910s, whales were taken off the northeastern coast of the island usually 30 to 50 km offshore, but on occasions, up to 100 km from shore (Hinton 1915, E. Lea unpubl. data). The former whaling grounds are likely a suitable whale habitat, where food availability (e.g. krill *Euphausia superba*) seems to be high (e.g. Murphy et al. 2004). Yet, humpback whale density seems to be lower there (Moore et al. 1999, T. Martin pers. comm.) than in more offshore habitats (Kasamatsu et al. 1996) through which whales tracked by satellite telemetry moved. Even though this study's sample size is small, results presented here, associated with catch and sighting data, point to a few possible hypotheses for this nearshore/offshore difference in density. These deserve further investigation.

The present low coastal abundance and relatively higher offshore abundance suggest that humpback whales inhabiting coastal waters near SG were nearly extirpated by commercial whaling (Tønnessen & Johnsen 1982, Clapham & Hatch 2000), but whales exploiting offshore habitats were less depleted. It is not clear how, or indeed whether, these 2 habitats are connected. It is possible that some sub-structuring of the humpback whale population exists and the whales tracked in this study correspond to a sub-population with affinity for the SSIs and for offshore areas to the northeast of SG. This is expected because if 'coastal' whales were heavily depleted and most of the remnant population corresponds to 'offshore' whales, the latter have a higher probability of being tagged in the wintering grounds. The alternative is that whales in this area belong to the same population. While the bulk of the Soviet catches taken around the SG in the 1960s came from offshore areas, some whales were killed as close as 125 km from shore (Fig. 2). Due to the proximity between the Soviet catch locations and the coastal whaling grounds (20 to 100 km offshore, Hinton 1915, E. Lea unpubl.) whales may have had a continuous pre-whaling distribution in this region. The currently observed nearshore low densities could result from differential exploitation of coastal and offshore elements of the population, implying distinct feeding ground fidelity. If the remnant population inhabiting offshore areas near SG is still small, it may not have yet expanded its range to reoccupy nearshore habitats. Current assessments estimated that this population is small relative to its pre-exploitation size (Johnston & Butterworth 2004, Zerbini 2004, IWC 2005). It is possible that, as the population increases, whales will expand their distribution towards the historical coastal whaling grounds.

Changes in environmental conditions and/or trophic structure near SG may also explain the absence of humpback whales in their historical coastal whaling grounds. The depletion of large whale stocks around SG in the early 20th Century (Mackintosh 1965, Tønnessen & Johnsen 1982) should have left a considerable surplus of krill production that would maintain this as an attractive area for the re-establishment of whale populations. However, if this area was occupied by other top predators (e.g. birds, pinnipeds and other baleen whales), foraging pressure in coastal waters would be higher than in offshore areas, making the latter more advantageous for feeding humpback whales. Pinnipeds (e.g. Antarctic fur seal *Arctocephalus gazella*) were hunted to near-extinction at SG in the 19th century and recovered to unprecedented levels (Croxall 1987) during the early to mid- 20th century, a period when whale populations were being heavily exploited. In addition, some of the present foraging areas of Antarctic fur seals in the SG overlap with the former coastal whaling grounds (Boyd et al. 2002), suggesting the potential for competition for krill.

Whale #24642 not only travelled through an area to the northeast of SG, but also moved south-southeast towards the SSIs. The slow, erratic movement pattern observed near SG, followed by a faster, more direct swimming towards the SSIs (Fig. 2) suggests a seasonal shift in distribution within the summering grounds. The occurrence of humpback whales near the SSIs is poorly documented. A floating factory and 2 catcher boats operated near the Archipelago in 1911–12 and took only 28 whales, including 13 humpback whales (Tønnessen & Johnsen 1982, data from the IWC database — Allison & Smith 2004). Tønnessen & Johnsen (1982) indicated that this small catch was a failure and no further attempts to hunt whales there were pursued. The small catches reflected poor weather conditions limiting operations in the region rather than low whale densities (Tønnessen & Johnsen 1982). Whale #24642 remained near the SSIs for 68 d, which suggests that the feeding grounds of humpback whales wintering off Brazil extend to the area around this Archipelago. Krill density near the SSIs is high (Mackintosh 1973, Hewitt et al. 2004), suggesting this might be a suitable whale foraging habitat.

Results of this study are relevant in helping to clarify population identity of SWA humpback whales. The population wintering off Brazil (breeding stock A) has been linked to feeding grounds between 20° W (west of the SSIs) and 70° W (west of the AP) in the IWC Management Areas I and II (IWC 1998). Whales tracked in this study do not indicate any migration to the southwest, towards the AP or other areas west of SG (e.g. the Falkland Islands). Whales migrated to 32 to 33° W (east of SG) and 1 individual moved as far west as 22° 30′ W, supporting the proposition that the eastern boundary of the feeding grounds for this population should be near 20° W. The limits of the western boundary have been recently discussed by the IWC (IWC 1998, 2005). Genetic and photo-identification data (Olavarría et al.

2000, Stevick et al. 2004) provide evidence that it should be moved to the east. Further data are required for a firm conclusion to be reached in this respect, but the data presented here provide additional evidence that the feeding grounds of humpback whales wintering off Brazil are located to the east of the AP.

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