Migration and summer destinations of humpback whales (*Megaptera novaeangliae*) in the western South 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. In 2003 and 2005, satellite transmitters were deployed on humpback whales on their wintering grounds off the eastern coast of South America (Breeding Stock A). Seven whales were tracked for a period of 16 to 205 days travelling between 902 and 7,258km. The tracks of these whales provided partial or full information on the migratory schedule, migration routes and location of the feeding ground in the Southern Oceans. Whales departed from the coast of Brazil from late October to late December between 20˚ and 25˚S and gradually moved away from the South American coast as they moved towards high latitudes. They followed a somewhat direct, linear path, with an approximate geographic heading of 170˚. Satellite telemetry data indicated that the migratory corridors are restricted to a relatively narrow (~500–800km) strip in the South Atlantic Ocean. Migration speed to the feeding grounds averaged 80.2km/day and lasted from 40–58 days. Four individuals arrived at the feeding ground located to the north of the South Sandwich Islands, where they were tracked up to 102 days. Movements in this area were erratic at a mean travelling speed of 22.3km/day. Satellite telemetry data indicate that the main feeding grounds for the population wintering off eastern South America lie between 22˚W and 33˚W and in the southern South Atlantic Ocean south of the Antarctic Convergence but north of 60˚S. This is only partially consistent with the currently proposed stock boundaries for this population on the feeding grounds.

KEYWORDS: HUMPBACK WHALE; MOVEMENTS; MIGRATION; FEEDING GROUNDS; SATELLITE TELEMETRY; SOUTH ATLANTIC OCEAN; SOUTHERN HEMISPHERE

INTRODUCTION

Seasonal migration between winter/breeding and summer/feeding areas is typical of humpback whales (*Megaptera novaeangliae*) (Clapham and Mead, 1999). In the Southern Hemisphere most populations migrate from coastal, low-latitude regions where mating and calving occur, to Antarctic waters for feeding (e.g. Dawbin, 1966; Mackintosh, 1942). The stock inhabiting the western South Atlantic Ocean (WSA) has been termed Breeding Stock 'A' (BSA) by the International Whaling Commission (IWC, 1998). The wintering grounds of this population are relatively well known; whales occur in the winter and spring off the coast of Brazil between the northeastern tip of the South American continent (~5˚S) south towards Cabo Frio (23˚S) (Andriolo *et al.*, 2010; Martins *et al.*, 2001; Pizzorno *et al.*, 1998; Zerbini *et al.*, 2004b). Despite this relatively wide latitudinal range, nearly 85% of the population is concentrated in the Abrolhos Bank (~18˚30'S, 38˚30'W) (Andriolo *et al.*, 2010; Siciliano, 1995).

The migration routes and feeding grounds of BSA are poorly known. Until recently, there was no evidence of the migratory destinations of whales wintering off eastern South America. Historically, it was suggested that this population migrated to areas near the Antarctic Peninsula (AP) (~60˚S, 64˚W) and/or South Georgia (SG) (54˚20'S, 36˚40'W) and the Scotia Sea, in the Antarctic sector of the Atlantic Ocean (Mackintosh, 1965; Slijper, 1962; 1965; Slijper and Utrecht, 1959). Studies involving Discovery marks, sighting surveys, photo-identification and molecular genetics conducted on the presumed feeding grounds of BSA (e.g. Moore *et al.*, 1999; Rayner, 1940; Rosenbaum *et al.*, 2000; Stevick *et al.*, 2004), were unable to provide evidence that whales using these regions actually migrated to eastern South America. The first migratory connection between wintering and summering grounds of whales from BSA was obtained in 2003/04 when two individuals monitored by satellite telemetry migrated from the coast of Brazil to offshore waters to the northeast of SG and to the South Sandwich Islands (SSIs) (Zerbini *et al.*, 2006). Subsequently, individuals photo-identified near Shag Rocks (53˚33'S, 42˚02'W), to the west of SG, and near the SSI, were matched with whales wintering off Brazil (Engel and Martin, 2009; Stevick *et al.*, 2006).

In 2005, new satellite transmitters were deployed off the coast of Brazil. This paper combines data from the 2003 and 2005 satellite tagging seasons and provides additional information on the migratory routes and summer destinations of humpback whales in the western South Atlantic Ocean.

METHODS

Field work was conducted in October 2003 and 2005 off the eastern coast of Brazil, in the southern portion of the Abrolhos Bank. In 2003 and 2005, tagging operations were carried out, respectively, from Conceição da Barra (18˚30'S, 39˚30'W), Espírito Santo State (ES), and from Nova Viçosa (17˚53'S, 37˚22W), Bahia State (BA). Daily searches for humpback

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whales were undertaken during good weather conditions (Beaufort Sea state ≤3) from a 10m-long fibreglass speedboat and two inflatable boats. Transmitter models and configurations differed between the two seasons. In 2003, 'can' (n = 7) and 'implantable' (n = 4) version of the Wildlife Computers (WC) SPOT 3 transmitters were used (Zerbini *et al.*, 2006). In 2005, only implantable versions of the WC SPOT 5 transmitter were available in two configurations: the 'short implantable' (n = 13), with the same dimensions as for the transmitters used in 2003 and a 'long implantable' (n = 2), which accommodated an additional AA-cell. Deployment of the tags, biopsy sample collection, and data analysis followed the methods described by Heide-Jørgensen *et al.* (2006) and Zerbini *et al.* (2006). Biopsies were used for DNA extraction and sex determination of each individual as described by Bruford *et al.* (1992) and Bérubé and Palsbøll (1996).

Locations were obtained from Service Argos, Inc. (ARGOS, 1990). Location quality (LC) 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 0.15km, respectively. Argos does not provide error predictions for location classes 0, A, and B, but errors may range from 3.8km (LC 0) to 23km (LC B) (e.g. Boyd *et al.*, 1998). Distance and rate of travel for each whale was calculated using daily average positions as described in Zerbini *et al.* (2006). Movement was monitored after tag deployment while whales were still on the wintering grounds, but in this paper, only data from whales tracked during part of or the total spring migration, and while on the summer feeding grounds are included. Table 1 summarises information on transmitter configuration and duty cycling for these individuals.

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 <200m) along the Brazilian coast north of 25˚S, while the feeding ground is defined as the habitat south of the northern limit of the Antarctic Convergence in the South Atlantic Ocean (~50˚S) (e.g. Deacon, 1984). The migratory corridor connects the wintering and the feeding ground.

RESULTS

Seven humpback whales had their migration or partial migration monitored through satellite telemetry (Table 1). Sex identification was obtained through molecular methods for two individuals and was inferred based upon role within the observed group of whales for another five. A total of 1,148 locations were received, tracking days for the whales ranged from 16 to 205 days, and distance travelled varied from 902 to 7,258km (Table 1).

Tracks of the seven individuals monitored during the migration are shown in Fig. 1. Two individuals were monitored for about one quarter to one third of their migration (whales Id no. 27259 [03] and No.26712 [05]). Another (whale Id no. 37274 [05]) was monitored through half of the migration while the remaining four individuals were tracked to the feeding grounds. The migratory path was remarkably consistent among all individuals, irrespective of their departure time and sex. Whales departed from the wintering ground from 19 October to 26 December (Table 1) between the latitudes of 20–25˚S. Individuals gradually moved away from the coast of the South American continent as they moved toward higher latitudes. All individuals followed a relatively direct, linear, path with an average geographic heading of 170˚. Despite different departure times from the wintering grounds (from late October to late December), some individuals followed almost the same route to their feeding destinations. For example, whale Id no. 10946 (05) left the Abrolhos Bank area nine days before whale Id no. 24641 (05), but their tracks greatly overlapped for nearly half of their migration. Movement rate was also relatively consistent during the migration. Whales travelled at an average rate of 80.2km/day (range = 62.7–92.6km/day) and the migration was completed in an average of 50 days (range = 40–58 days) (Table 2).

Four individuals were tracked to the feeding ground some 3,700km southeast of the wintering grounds (Fig. 1). Arrival was inferred by a change in swimming speed and behaviour in which the linear direction and relatively fast rate of movement was replaced by a slower, more erratic movement pattern. The average speed of travel (22.3km/day, range = 18.0–29.1km/day, Table 2) of whales tracked on the feeding grounds was much lower than in the migratory corridor. This change in behaviour occurred when humpback whales were just south of 50˚S, a region regarded to correspond to the northern boundary of the Antarctic Convergence (Deacon, 1984). Whales remained in offshore waters 250–750km northeast of SG and 300km north of the SSIs, in a region bounded by the 51˚ and the 55˚S parallels and the 22˚ and the 33˚W meridians (Fig. 1). Whale Id no. 21810 (03) was tracked for only six days (late December and early January) after its arrival on the feeding grounds, but the remaining individuals were monitored for another 36–102 days. Whale

Table 1

Whales tracked through satellite telemetry in the western South Atlantic Ocean in 2003/04 and 2005/06.

Whale ID no. (year)	Sex	Duty cycling	Daily transmission allowance	Transmission time	Tagging date	Tag longevity (days)	No. of locations received	Distance traveled (km)
21810 (03)	M	eod[2]	300	6–21hr	18 Oct 2003	76	84	4,383
24642 (03)	F[1]	eod	300	6–21hr	27 Oct 2003	205	624	7,258
27259 (03)	M	none	300	6–21hr	19 Oct 2003	39	51	2,315
10946 (05)	F[1]	Oct/Nov – eod, Dec/Jul – e4d[3]	300	7–22hr	19 Oct 2005	80	150	4,895
24641 (05)	F[1]	Oct/Nov – none Dec/Jul – e4d	300	7–22hr	19 Oct 2005	112	185	5,023
26712 (05)	F[1]	Oct/Nov – none Dec/Jul – e4d	300	7–22hr	11 Oct 2005	16	27	902
37234 (05)	F[1]	Oct/Nov – eod, Dec/Jul – e4d	300	0–23hr	19 Oct 2005	32	27	3,445
Total						560	1148	28,221

[1]Assumed to be a female because it was the adult individual in a cow-calf pair; [2]eod = every other day; [3]e4d = every fourth day.

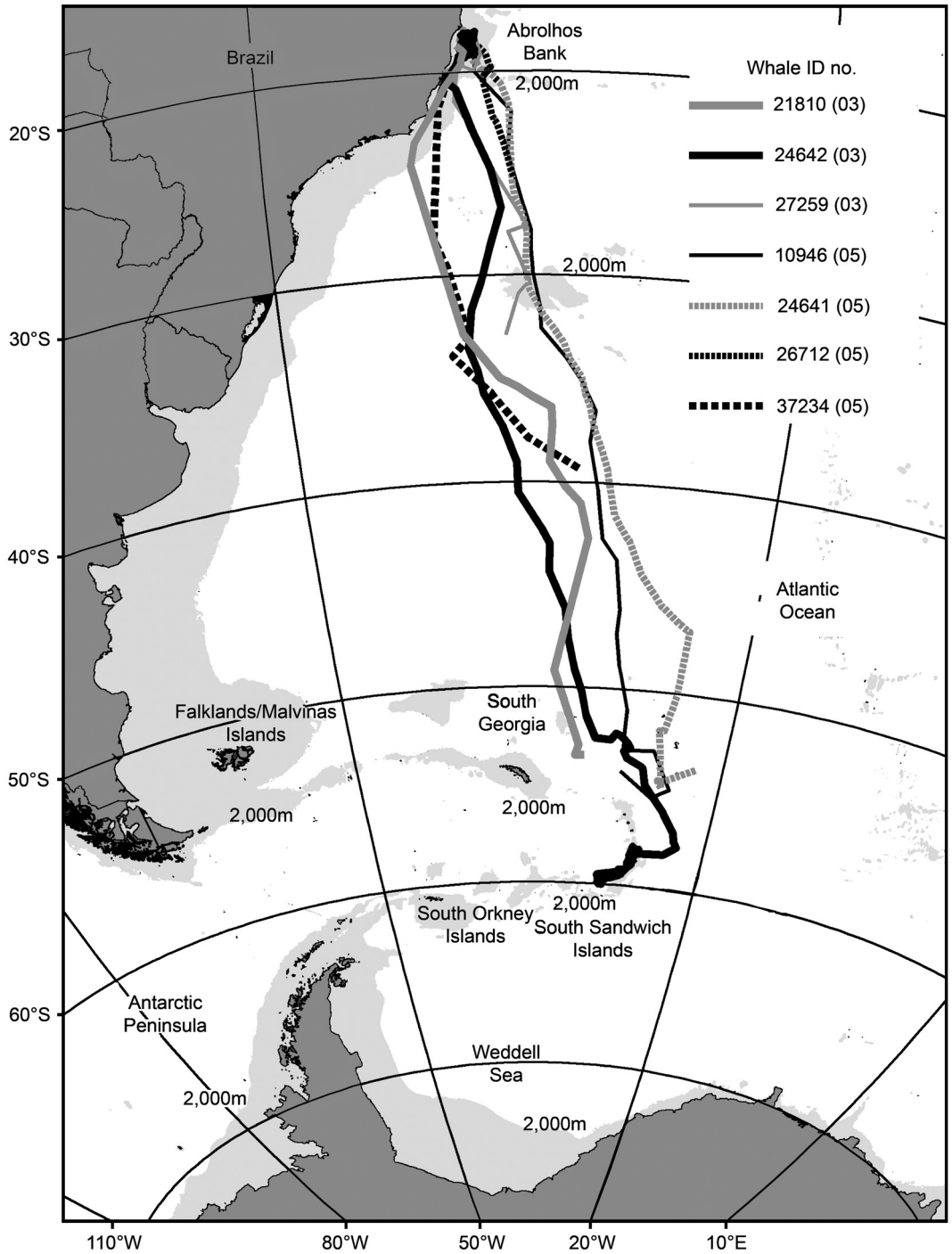

Fig. 1. Southbound migratory routes and summer destinations of humpback whales in the western South Atlantic Ocean.

Id no. 10946 (05) and Id no. 24641 (05) stayed in the same general area, to the north of the SSIs, for the period they were tracked (36–44 days) in the months of December, January and February. Whale Id no. 24642 (03) remained in this same area for about 35 days, after its arrival in February. Subsequently, in March, it moved southeast, and finally moved back west towards the SSIs. This individual remained in the southern sector of the Islands for about 68 days (from mid March to mid May), until transmissions ceased.

DISCUSSION

Migratory schedule, routes and summer destination of whales monitored during the 2003–2004 season were described by Zerbini *et al.* (2006), but sample size was relatively small. The migration of three new individuals was monitored in 2005–2006, but only two were tracked until they reached the feeding ground. The partial or full migration of the additional whales reported here is consistent with and strengthen the conclusions of the previous study. Results confirm that departure from the wintering grounds occur when whales move south of the Abrolhos Bank and along the southeastern coast of Brazil between 20˚ and 25˚S. Despite within-season differences in the onset of the southbound migration, the migratory schedule, path and destination was remarkably consistent among individuals. Departure dates from the wintering ground ranged over a period of two months and none of the whales monitored

Table 2
Travelling distances and movement speed of humpback whales on their migratory routes and feeding grounds in the southwest Atlantic Ocean.

	Migratory corridor				Feeding grounds			
Whale ID no. (year)	Departure date	Distance travelled (km)	Days monitored	Average speed	Arrival date	Distance travelled (km)	Days monitored	Average speed
21810 (03)	31 Oct 2003	3,639	58	62.7 km/day	28 Dec 2003	108	6	18 km/day
24642 (03)	26 Dec 2003	3,733	44	84.8 km/day	8 Feb 2004	2,376	102	23.3 km/day
27259 (03)	9 Nov 2003	1,507	18	83.7 km/day	–	–	–	–
10946 (05)	23 Oct 2005	3,691	40	92.3 km/day	2 Dec 2005	1,048	36	29.1 km/day
24641 (05)	30 Oct 2005	3,692	57	64.8 km/day	26 Dec 2005	817	44	18.6 km/day
26712 (05)	19 Oct 2005	727	9	80.7 km/day	–	–	–	–
37234 (05)	23 Oct 2005	2,317	25	92.6 km/day	–	–	–	–
Average				80.2 km/day				22.3 km/day

travelled together. However, their tracks intersected to a great extent, never being more than 800km apart, and usually much less (300–500km). Migration occurred through deep offshore waters in the WSA and the direction of migration (geographic bearing) and rate of travel were also relatively similar across all whales.

Migratory routes between wintering and feeding grounds of BSA humpback whales remained questionable for nearly 100 years. Two main hypotheses were previously proposed: (1) whales migrated to/from the Antarctic Peninsula (AP) and perhaps the Falkland Islands from/to the eastern coast of South America using coastal waters over the continental shelf (Slijper, 1962; Slijper and Utrecht, 1959); and (2) whales migrated through deep waters from/to tropical latitudes off eastern South America to/from feeding grounds near SG and SSIs (Mackintosh, 1965; Slijper, 1962; 1965). Migratory connections had been proposed based on the coincidental collapse of humpback whaling in the AP, SG and eastern South America in the early 1900s (IWC, 2005) and as an analogy with other Southern Hemisphere humpback whale populations, which seemed to migrate to feeding areas located directly south of their wintering grounds (Dawbin, 1966; Mackintosh, 1942).

Results of telemetry studies were consistent with hypothesis (2) above. Individuals monitored through satellite telemetry migrated to offshore areas in the WSA and the four individuals tracked while in the feeding grounds arrived and remained in waters near SG and the SSI (Zerbini *et al.*, 2006, see Results). This migratory connection was subsequently supported by photo-identification studies. Stevick *et al.* (2006) reported that a whale photographed in December 2004 near Shag Rocks, west of SG, had been previously recorded in August 2000 in the Bank of Abrolhos. In addition, three individuals photographed near the SSIs in January 2006 had also been seen in Brazil, one in each of the years 1999, 2001 and 2002 (Engel and Martin, 2009). Existing data provided little support for the hypothesis that humpback whales wintering off Brazil migrate through coastal waters to the AP. In fact, extensive photo-identification and genetic studies have shown that whales feeding near the Peninsula migrate to the western coast of South America (Olavarria *et al.*, 2007; Rasmussen *et al.*, 2007; Stevick *et al.*, 2004). In addition, humpback whales are rare in coastal waters over the continental shelf south of the wintering grounds in Brazil (e.g. Zerbini *et al.*, 2004a), or in Uruguay and Argentina (Bastida and Rodriguez, 2005; Lichter, 1992).

Certainly, SG was an important historical feeding ground (see Findlay, 2001; Tønnessen and Johnsen, 1982). Humpback whales were heavily exploited in the vicinities of the island (over 25,000 individuals were taken there between 1904 and 1916, Allison, 2006), causing a rapid collapse of this population. Contemporary data indicate that the species has not recovered on the former whaling grounds in coastal waters near SG (Moore *et al.*, 1999, A.R. Martin, pers. comm.). This contrasts with the relatively high abundance of humpback whales off Brazil and provides additional evidence that whales from this population migrate elsewhere, as shown by satellite telemetry. Reasons for low densities of humpback whales in the former whaling grounds of SG are not known, but may be related to complete extirpation of the population using those nearshore waters, competition with other krill predators and/or shifts in distribution resulting from temporal changes in environmental conditions in nearshore waters off SG (Clapham *et al.*, 2008; Zerbini *et al.*, 2006).

All the individuals monitored to the feeding ground migrated to open ocean waters in a region located to the northeast of SG and north of SSI (between approximately 51–55˚S, 22–33˚W; Fig. 1). Whales remained in this area between December and February. Geographical and monthly distribution of these individuals overlapped with existing Soviet catch data from the late 1960s (Mikhalev, 1998; Zemsky *et al.*, 1995) and with sighting data from the 1980–2000s (Hedley *et al.*, 2001; Kasamatsu *et al.*, 1996; Reilly *et al.*, 2004). Consistency among catch, sighting and telemetry data provides strong evidence that the primary feeding ground of humpback whales wintering off Brazil is located to the north of the SSIs from December to February. Except for one individual, locations were not received from whales later in the summer and therefore information on whether whales remain in this area or move to other possible feeding areas explored by whales from BSA is relatively limited. Interestingly, the only whale tracked during late summer and part of autumn (Whale Id no. 24642 [03]) left the area to the north of SSIs in early March, moving southwest and then east towards the South Sandwich Archipelago, where it stayed until May (Fig. 1). This whale departed from the wintering ground (in late December) and arrived on the feeding ground much later (in early February) than the other three individuals. It is unclear what caused this shift in habitat, but one possibility is that foraging opportunities further north are reduced later in the season, forcing whales to look for areas closer to the ice edge, where food availability may be greater.

Despite being monitored for 35–102 days while on the feeding ground, none of the whales moved further south than 60˚S. This suggests that most individuals of this population do not venture into the Weddell Sea and adjacent areas. This is further supported by contrasting estimates of abundance on the feeding grounds south of 60˚S and those obtained on

wintering grounds. The abundance in 1997/98 south of 60˚S was estimated to be 200 (CV = 0.64) whales on the feeding ground presumed to be occupied by BSA whales (3rd circumpolar survey of the IDCR/SOWER surveys; Branch, 2011). If a growth rate of ~7%/year is assumed for this stock (Ward *et al.*, 2011), the population size south of 60˚S in 2005 should be nearly 350 whales. This number does not match the much higher abundance estimate of 6,400 (CV = 0.12) whales on the wintering ground off the Brazilian coast (Andriolo *et al.*, 2010), indicating that the majority of the population is likely distributed further north.

Understanding movements and habitat use of whales is important to better define stock structure. The IWC Scientific Committee proposed a number of core feeding grounds associated with the various Southern Hemisphere humpback whale breeding stocks for management and catch allocation purposes (IWC, 1998; 2006). The northern and southern boundaries of these feeding grounds are the 40˚S parallel and the Antarctic continent, respectively. Longitudinal boundaries are vertical lines placed at different meridians. Originally, longitudinal boundaries of the feeding grounds associated with BSA corresponded to the 70˚W meridian in the west and the 20˚W meridian in the east (IWC, 1998). These boundaries encompassed former humpback whaling grounds in the AP, Weddell Sea and the Scotia Sea (SG, SSIs and the South Orkney Islands). The western boundary was shifted to 60˚W once it became clear that humpback whales feeding along the Antarctic Peninsula used the breeding grounds in the eastern South Pacific (Breeding Stock G-BSG) (IWC, 2001; Stevick *et al.*, 2004). Subsequently, it was shown that whales photographed west of 55˚S were also associated with the AP (Dalla Rosa *et al.*, 2004; Stevick, 2005) and the western boundary was changed to its current position at 50˚W (IWC, 2006).

Information presented in this study partially supports the current boundaries of the feeding grounds associated with BSA. Telemetry data indicated that humpback whales wintering off Brazil migrated to the eastern Scotia Sea and remained between the latitudes of 54˚S and 60˚S and the longitudes of 22˚W and 33˚W for the period they were monitored (Fig. 1). This is consistent with an eastern boundary of 20˚W (IWC, 1998; 2006), but provides little evidence to support a western 50˚W boundary. Perhaps more importantly, however, was the finding that no whales moved south of 60˚S, suggesting that humpback whales from BSA may not venture into the higher latitudes of the Antarctic Ocean and Weddell Sea. Results from satellite telemetry were further corroborated by photo-identification. Photographic matches also indicated whales from BSA were using the SSIs during the summer (Engel and Martin, 2009). In addition, the re-sighting of a whale previously seen in Brazil and later photographed near Shag Rocks (53˚33'S 42˚02'W) (Stevick *et al.*, 2006) indicated that at least some individuals from BSA also occurred west of SG, but still nearly 500km to the east of 50˚W. Photo-identification and telemetry studies also indicated that some individuals summering near the AP (BSG) ventured into waters near or west of the current western boundary of BSA (Dalla Rosa *et al.*, 2004; 2008). A whale photographed to the southeast of the South Orkney Islands (at the position 61˚50'S, 38˚48'W) was observed a year later just to the northeast of the Antarctic Peninsula (at the position 62˚11S, 52˚51'W) (Dalla Rosa *et al.*, 2004; 2008). In addition, an individual tagged off the western AP (Gerlache Strait, ~64˚S, 61˚W) moved northeast to the pack-ice in the Weddell Sea (~63˚S) close to the 50˚W meridian (Dalla Rosa *et al.*, 2008).

Although additional studies are clearly needed due to relatively low research effort and small sample sizes, the above data provide preliminary evidence that a review of the boundary between the feeding grounds associated with BSA and BSG (50˚W) is needed (see also discussion by Dalla Rosa *et al.*, 2008). In addition, and perhaps more importantly, these data indicate the potential for a latitudinal separation of whales from these two stocks. Whales from BSA were not photographed or tracked south of ~60˚S, whereas individuals from the AP moving into the Weddell Sea area were only seen south of ~62˚S. Further studies will allow a better description of the areas used by whales from BSA and BSG in their feeding grounds and a more precise description of stock structure in the Antarctic sector of the South Atlantic Ocean.

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