

# Movements of satellite-monitored humpback whales on their feeding ground along the Antarctic Peninsula

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Received: 15 August 2007 / Revised: 4 January 2008 / Accepted: 9 January 2008 / Published online: 6 February 2008  
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**Abstract** Humpback whales were instrumented with satellite transmitters off the western Antarctic Peninsula in January of 2004–2006 to examine their movement patterns and habitat use. Whales were tracked from 4 to 80 days (mean = 36.5 days). Distance and travel rate estimates for nine individuals ranged from 223 to 4,356 km and from 17 to 75 km/day, respectively. Considerable individual variation was observed in direction, speed and range of movements. The overall pattern was characterized by short- and

long-distance movements between presumed foraging areas with relatively short residency times. Travel rates were lower at these sites, characterized by erratic movements, than during traveling between them. Area usage for six individuals based on the 95% fixed kernel home range with least squares cross-validation ranged from 2,771 to 172,356 km<sup>2</sup>. The management boundary between the feeding grounds associated with Breeding Stocks G and A needs revision, as current available data suggest it should be located to the east of 50°W. This study is the first to present detailed information on the movements of humpback whales in the Southern Ocean.

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**Keywords** Humpback whale · Satellite telemetry ·  
Movements · Antarctic Peninsula

## Introduction

The humpback whale, *Megaptera novaeangliae*, is a highly migratory species found in all major oceans, from low latitude breeding and calving grounds in the winter to temperate and high latitude feeding grounds between spring and fall (Dawbin 1966). Its migration is the longest of any mammal (Stone et al. 1990; Stevick et al. 2004; Rasmussen et al. 2007).

In the Southern Hemisphere, seven geographically isolated humpback whale Breeding Stocks (A–G) are recognized by the International Whaling Commission (IWC 1998, 2006). Waters in the western Antarctic Peninsula have been identified as feeding grounds for the eastern South Pacific (Peru, Ecuador, Colombia, Panama and Costa Rica) population based on photo-identification and molecular genetic data (Stone et al. 1990; Stevick et al. 2004; Rasmussen et al. 2007; Olavarria et al. 2000). On the other

hand, the lack of photographic matches between whales from the Antarctic Peninsula and the breeding grounds off Brazil (Stevick et al. 2004; Dalla Rosa et al. 2004) indicate the western Antarctic Peninsula region is not used as a feeding ground by whales from the western South Atlantic, as previously hypothesized (e.g., Slijper 1962; IWC 1998). In fact, satellite telemetry studies have recently demonstrated that whales wintering off Brazil migrate to feeding destinations in the Scotia Sea, near South Georgia and the South Sandwich Islands (Zerbini et al. 2006a, b).

Photo-identification studies have also shown that humpback whales have strong site fidelity to the Antarctic Peninsula region (Dalla Rosa et al. 2001, 2004), and that at least part of the population wintering in the eastern South Pacific does not migrate to the Antarctic, but feeds in the Magellan Strait area (Acevedo et al. 2007). However, despite extensive research effort in the area around the Antarctic Peninsula (e.g., Secchi et al. 2001, 2006; Thiele et al. 2004; Williams et al. 2006), virtually nothing is known about the movement patterns of humpback whales in this area. Dalla Rosa et al. (2001) reported two within-season resightings of humpback whales in 1998. The first was photographed off King George Island on 22 January, and the second was photographed in Bismarck Strait (southern end of Gerlache Strait) on 27 January. Both individuals were photographed together in Gerlache Strait on 7 March, 335 and 71 km away, respectively, from their previous sighting locations. Knowledge of such movements has important ecological and management implications, as it can provide insights into how whales use their feeding habitat and assist in defining stock boundaries and in designing proper surveys for stock assessment.

Satellite telemetry has been successfully used to investigate behavior (e.g., Laidre et al. 2003), associations with environmental features (e.g., Baumgartner and Mate 2005; Etnoyer et al. 2006), habitat use, migration and movement patterns (e.g., Mate et al. 1998, 1999; Heide-Jørgensen et al. 2003; Zerbini et al. 2006a, b), home range (Heide-Jørgensen et al. 2002) and stock discreteness (Heide-Jørgensen et al. 2006) of cetacean species.

In this paper we investigate the movement patterns and habitat use of humpback whales instrumented with satellite transmitters in Gerlache Strait and Dallman Bay (63.8°S to 65°S; 61°W to 63.5°W), Antarctic Peninsula in January of 2004–2006.

## Materials and methods

Tags consisted of Wildlife Computers' SPOT3 (2004), SPOT4 (2005) and SPOT5 (2006) satellite-linked radio transmitters housed in a surface-mounted stainless steel can ('mini-can' or MC) or in an implantable (IM) stainless steel

cylinder. The transmitters were attached to a titanium or stainless steel anchoring system equipped with foldable barbs and a triangular sharp tip. The tags used in 2004 were programmed to transmit every day, and the ones used in 2005 and 2006 were duty-cycled to transmit every fourth day, and every other day, respectively. The number of transmissions was limited to 300 per day in all tags, and transmission time was between 0:00 and 23:00 hours for the mini-can and 7:00–22:00 hours for the implantable tags. The expected total number of transmissions for each tag was about 20,000 based on the battery configurations used: 2xM1 for mini-can and 1xAA for implantable tags.

Tag deployment was conducted from an inflatable boat with a wood-mounted standing platform using an 8 m long fiberglass pole. Whales were approached with caution by first observing their surface activity patterns. Tagging was only attempted on large individuals and when they were parallel to the boat from about a 4–5 m distance. A skin sample was collected simultaneously with tag deployment by a biopsy tip attached to the pole or, alternatively, with a crossbow and a modified dart. Skin samples were used for DNA extraction and sex determination following methods described in Sambrook et al. (1989), Bérubé and Pasbøll (1996) and Shaw et al. (2003). Fluke and dorsal fin photographs of the tagged animals were taken for individual identification.

Locations were obtained using the Argos System (ARGOS 1990). Each location was coded by Service Argos according to predicted accuracy. In order of increasing quality, location classes (LC) B, A and 0 have no associated error prediction, and LC 1, 2 and 3 are predicted to be within 1, 0.35 and 0.15 km of the true position, respectively. Locations used for analyzing movement patterns and distance traveled were selected based on the following criteria: (1) only good quality locations (LC 1–3) were selected, (2) daily average positions were calculated when good locations were not available, and (3) locations were removed from the data set if travel speed between two consecutive locations exceeded 12 km/h. This value was selected based on maximum speeds reported for humpback whales (e.g., Tyack 1983; Bauer 1986; Frankel et al. 1995). Straight great-circle distances between consecutive points were transformed into minimum distances around land masses if underestimation was noticeable from tracks over land, particularly for the duty-cycled tags. The rate of travel (km/day) was calculated as the total distance traveled between locations divided by the number of days elapsed between locations. Individual mean speeds (km/h) were also computed for the two whales with daily transmissions (and therefore with larger sample sizes) using only segments between consecutive LC 2 or 3 that were at least 20 min and no more than 4 h apart for improved accuracy.

The area usage was investigated by estimating the 95% fixed kernel home range with least squares cross-validation and the minimum convex polygon (MCP) using the Home Range Tools extension (Rodgers et al. 2005) in ArcGIS 9.1 (ESRI, Redlands, CA). When more than one good quality position was available per day, average daily positions were used to minimize autocorrelation bias in home range calculations (e.g., Heide-Jørgensen et al. 2002). Since this procedure reduced sample size considerably, individual area usage could only be estimated for six individuals with more than 30 days of tracking. Furthermore, for the kernel estimates of whales with duty-cycled tags, one pseudo-location (e.g., Frydman and Gales 2007) was added midway along the track between each pair of every other day locations assuming constant speed and straight line of travel between them. This method places data in the same temporal resolution (one daily position) allowing for better comparisons among individuals and partially reducing the bias in kernel estimation due to sample size differences. Also, considering the long distances that humpback whales may travel on a single day, it adds biological significance to the lower resolution data by taking into account information present in their tracks. The kernel smoothing should help reduce biases associated with likely deviations from straight-line tracks. Two pseudo-locations for one individual were added on a path around land. Pseudo-locations were not included in the MCP home ranges as they would not have any effect on these estimates. An overall summer area usage combining all individual ranges overlaid was also computed to give an idea of minimum area use for this population. Areas where land

overlapped with the home range were subtracted from the estimates.

The coastline data were extracted from the Antarctic Digital Database version 4.1 (Scientific Committee on Antarctic Research 2003). Regional sea ice concentration maps using data from the Advanced Microwave Scanning Radiometer (AMSR-E) with the ARTIST sea ice algorithm (ASI version 5.2) (Spren et al. 2007) were obtained from the Institute of Environmental Physics, University of Bremen (<http://www.iup.uni-bremen.de>).

## Results

We tagged eleven humpback whales in January 2004–2006 (Table 1). Sex was determined for six individuals of which five were females. Whales with IM tags and with MC tags were tracked for 4–20 days and for 32–80 days, respectively. One tag never transmitted. A total of 3,951 locations were received, of which 1,295 were used to analyze movement patterns. Estimates of traveled distances for nine individuals ranged from 223 to 4,356 km (mean = 1,415 km, SD = 1,343 km). Travel rates ranged from 17 to 75 km/day (mean = 32 km/d, SD = 16). The mean speed and standard error using only small segments between LC 2–3 was  $2.26 \pm 0.17$  km/h ( $n = 85$ ) for whale 20683 and  $4.03 \pm 0.27$  km/h ( $n = 51$ ) for whale 20689 ( $P < 0.001$ ;  $Z$  test;  $Z = -5.52$ ).

Marked individual variation was observed in direction, speed and range of movements. All whales tagged in Gerlache Strait (GS) between  $63^{\circ}59'S$  and  $64^{\circ}45'S$  left this

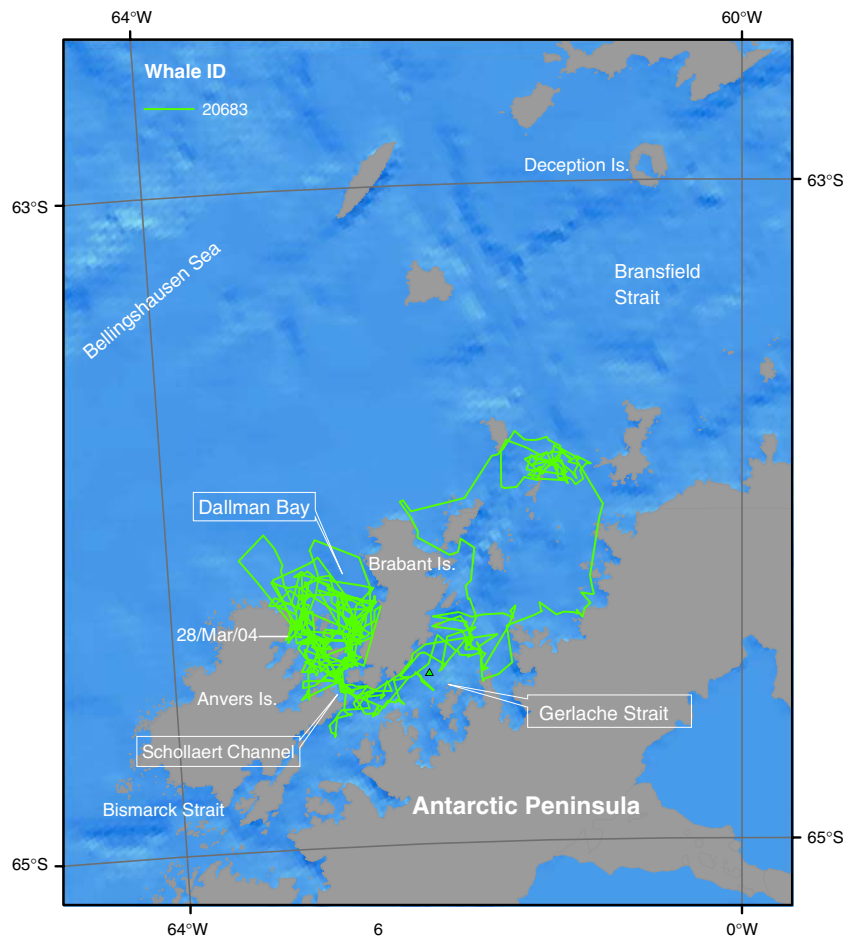
**Table 1** Satellite transmitters deployed on humpback whales, *Megaptera novaeangliae*, in Gerlache Strait, Antarctic Peninsula, between 2004 and 2006

Whale ID (Tag no.)	Sex	Tag type	Duty cycling	Deployment date	Tagging location	Tag longevity (day)	No. of locations received	No. of locations used	Distance traveled (km)	Speed (km/day)
20683	–	MC	None	17 Jan 04	64°28.61'S 62°11.90'W	72	1,931	612	2,733	39
20689	–	MC	None	17 Jan 04	64°31.86'S 62°16.92'W	59	1,021	306	4,356	75
20691	–	MC	None	17 Jan 04	64°35.27'S 62°32.37'W	–	–	–	–	–
21809	–	IM	e4d	19 Jan 05	64°09.55'S 61°22.04'W	13	26	8	312	28
24639	–	IM	e4d	23 Jan 05	64°44.44'S 63°01.67'W	13	43	24	223	19
24640	F	IM	e4d	24 Jan 05	63°59.56'S 61°18.46'W	20	32	15	418	23
26715	F	IM	e4d	20 Jan 05	64°23.00'S 62°54.60'W	4	5	1	–	–
63375	F	MC	eod	24 Jan 06	64°25.68'S 62°04.75'W	39	206	61	636	18
63376	M	MC	eod	26 Jan 06	64°32.11'S 62°32.84'W	33	86	20	1,235	40
63377	F	MC	eod	27 Jan 06	64°33.91'S 62°12.50'W	32	173	56	525	17
63378	F	MC	eod	27 Jan 06	64°35.86'S 62°11.02'W	80	428	192	2,298	29
Total						365	3,951	1,295	12,736	
Mean (SD)						36.5 (24.8)			1,415 (1,343)	32 (16)

Distances and speeds were rounded to the closest integer

MC 'mini can', IM implantable, e4d every fourth day, eod every other day

**Fig. 1** Track of humpback whale # 20683 tagged in the Gerlache Strait in January 2004. *Triangle* indicates tagging location



area within 3–10 days, and all except two moved initially north to Bransfield Strait (BS). Only two whales returned to GS at some point during their monitored period.

Whale 20683 stayed near the tagging location, in the northern section of GS for the first 10 days, and then it moved north to the boundary with BS, where it stayed for a week (Figs. 1, 2). Finally, it traveled back through GS and Schollaert Channel into Dallman Bay and its open-sea section, where it moved erratically the remaining 47 days of the tracking period, except for two days when it ventured back into mid-GS. Whale 20689, on the other hand, left GS three days after the instrumentation and moved north nearby to Deception Island, in BS, before traveling south to the Bischoe Archipelago, where it stayed for five days (Fig. 2). Then it traveled 1,300 km to the southwest in 12 days (at an average 108 km/day) reaching its southernmost position at 71°30.7'S, 81°58.7'W on 16 February 2004, near an area with patches of sea-ice. After 9 days in this area, it moved on a round clockwise turn towards the Marguerite Bay area, where it spent 8 days before starting to move southwest along the shore, 3 days prior to the end of transmissions. The speed of whale 20689 averaged 43 km/day at presumed foraging patches characterized by

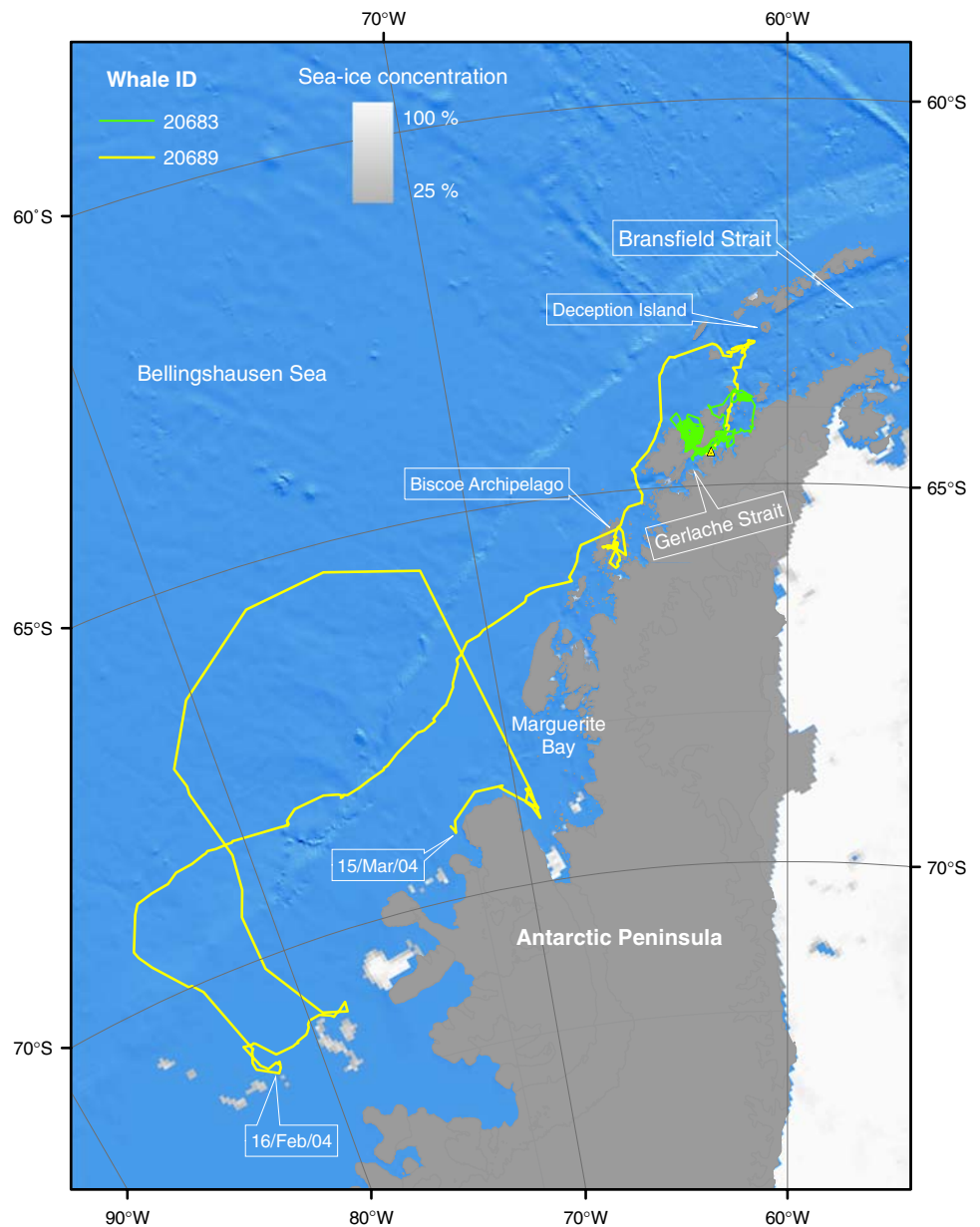
erratic movements and 109 km/day during travel between these sites.

Whale 21809, tagged in northern GS, was in the middle of BS about 60 km east of Deception Island four days later (Fig. 3). Whale 24639, on the other hand, was tagged in southern GS and moved out into an open area in the Bellingshousen Sea (Fig. 3). It was the only whale to exit GS through its southern section, but also the only one tagged in this area of the strait. Whale 24640, tagged in northern GS, moved south around the west side of Brabant and Anvers Islands, then traveled through Bismarck Strait and back north through GS until transmissions ended about 28 km from its tagging location (Fig. 3). Whale 26715 was the only individual tagged outside of GS and it was still inside Dallman Bay four days after tag deployment, when it stopped transmitting (Fig. 3).

Whales 63375 and 63377, which were tagged 3 days and 16.5 km apart, moved into BS with a time lag of about 6 days (Fig. 4). However, both individuals followed a very similar path until they were north of Deception Island. Their time lag was only 2 days near this island, but increased again to 6 days near Livingston Island. Whale 63377 was about 70 km south of King George Island when



**Fig. 2** Track of humpback whale # 20689 tagged in the Gerlache Strait in January 2004. The track of whale # 20683 is also included to better represent the difference in the range of movements between the two whales. Sea-ice concentration on 16 February 2004 is shown along with the whale location on that date. *Triangle* indicates tagging location

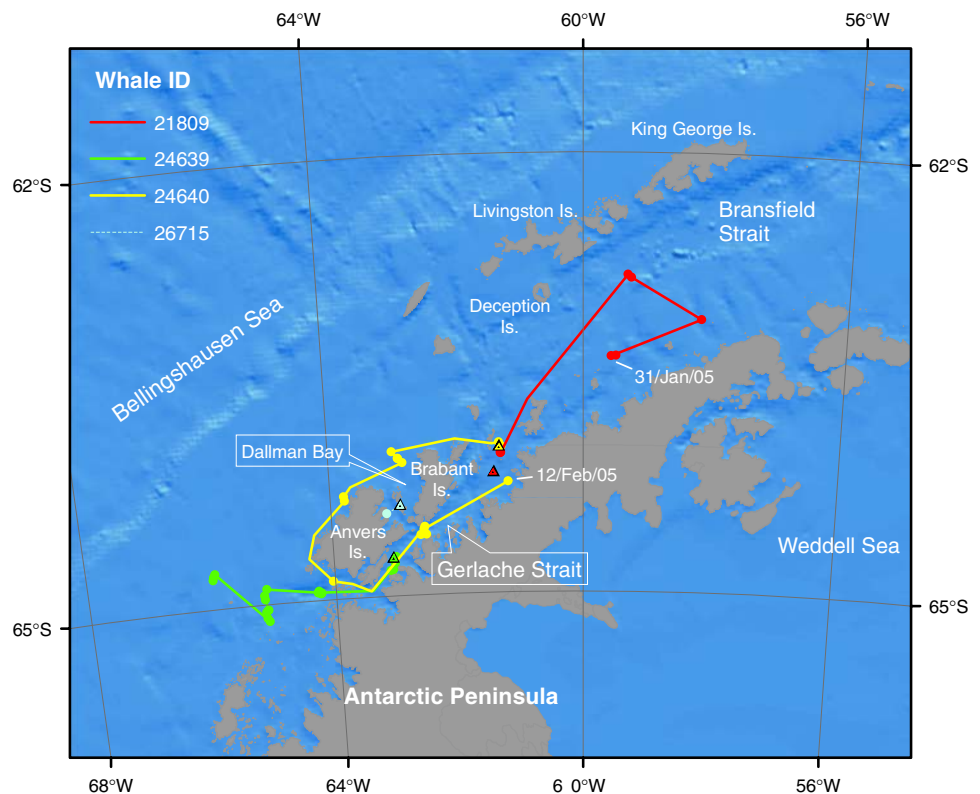


transmissions ended, while whale 63375 was very close to continental land in the southeast section of BS when transmissions ceased almost a week later. Whale 63376 left GS about 7–8 days after being tagged, and once it reached an area close to the Peninsula in BS, it traveled 637 km northeast across the strait and east into the Weddell Sea to a location ( $63^{\circ}09'S$ ;  $50^{\circ}14'W$ ) near an area covered by sea-ice (Fig. 5) in 16 days (40 km/day). This individual then returned to an area near the eastern side of the Antarctic Peninsula 4 days later, when transmissions ceased. Whale 63378 traveled north into southern BS about 9 days after it was tagged, then it moved to an area north of Brabant Island, where it stayed for 8 days, and after that it reached an area off Dallmann Bay for 10 days (Fig. 5). On 5 March 2006 it started traveling south at a speed of 42 km/day

reaching its southernmost position 849 km later on 25 March at the entrance of Marguerite Bay ( $68^{\circ}43'S$ ;  $69^{\circ}47'W$ ). This whale started moving back northwards 6 days later and it may have attempted to pass through 'The Gullet' channel between Adelaide Island and the mainland. However, sea-ice images suggest that the channel was closed during that period, perhaps forcing the whale to turn around and contour Adelaide Island to head straight to the Biscoe Archipelago area, where it stayed from 8 April to the end of transmissions on 16 April 2006 (Fig 5).

The area usage based on the MCP estimator varied from 4,782 to 407,583 km<sup>2</sup> with a mean of 97,709 km<sup>2</sup> and a total overlaid area of 480,825 km<sup>2</sup>. The 95% kernel calculations ranged from 2,771 to 172,356 km<sup>2</sup> with a mean of 48,193 km<sup>2</sup> and a total area of 239,501 km<sup>2</sup> (Table 2). The

**Fig. 3** Tracks of humpback whales tagged with satellite transmitters in the Gerlache Strait and Dallmann Bay in January 2005. *Triangles* indicate tagging location



wide variation in these estimates, which in part is caused by differences in sample size and the complex coastline, is still present after estimates are rated by the number of tracking days, indicating individual variation in area use. The limited movements of whale 20683, which had the second-longest tracking period, resulted in the smallest area usage by far. And the broad movements of whale 20689 resulted in very large estimates when compared to the other individuals.

## Discussion

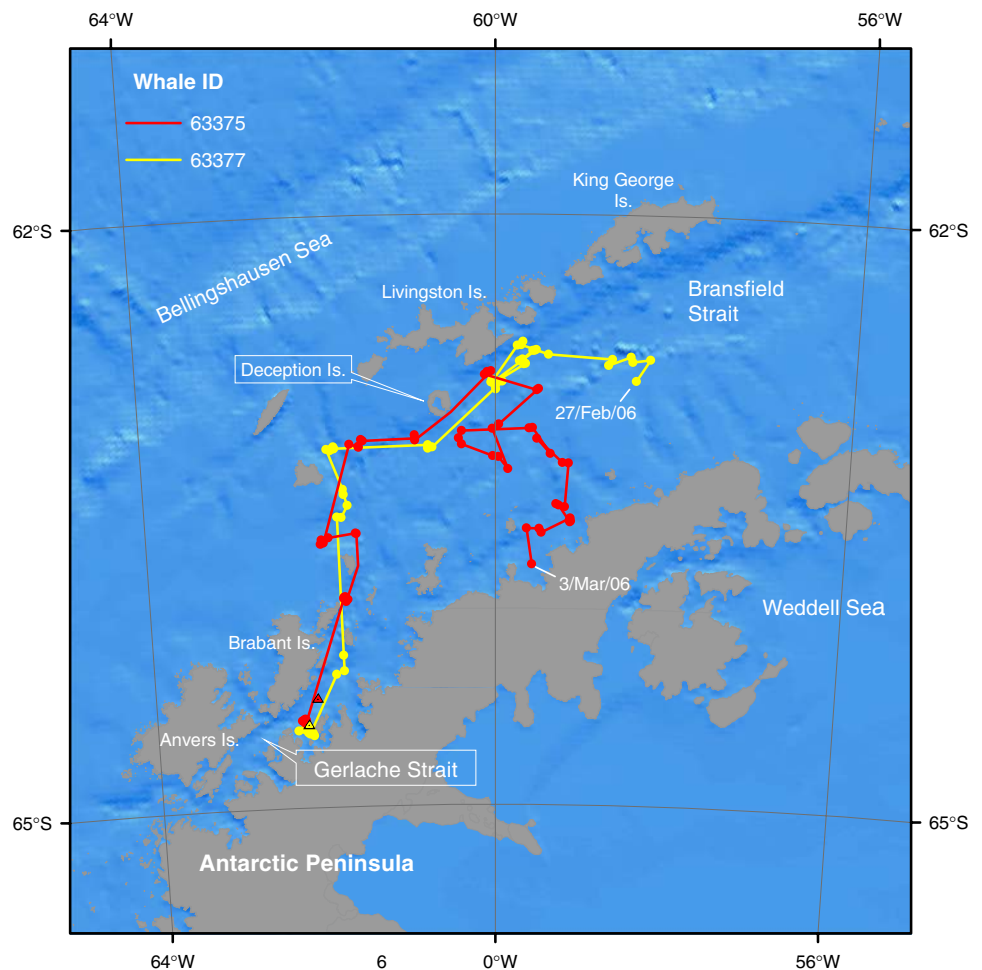
The longevity of MC tags was greater than that of IM tags in the present study. Nevertheless, IM tags were expected to last longer since they were duty-cycled to transmit at longer intervals, therefore saving battery, and also because they were designed to cause less drag when whales moved. We believe they fell off sooner because they were not properly attached to the whales.

The observed individual variation in the movement pattern of humpback whales suggests important individual differences in foraging strategies. Except for whale 20683, residency time in specific areas was limited (up to 10 days), possibly reflecting the depletion of local krill patches below a required threshold or some other dynamic process that might affect prey fields and influence the animal's decision on whether to stay longer in an area or not. That includes

GS, an important feeding area for humpback whales, where site fidelity is demonstrated by several inter-annual resightings, some within a few kilometers of each other (Dalla Rosa et al. 2004), and where high encounter rates are commonly found (e.g., Secchi et al. 2001). Therefore, in general, humpback whales do not stay in the same place for extended periods of time, but rather present fluid movements. This observation is also evident from a similar study in the Northern Hemisphere, where satellite telemetry was used to observe movement patterns of humpback whales on their feeding ground in West Greenland (see Heide-Jørgensen and Laidre 2008). Movements between foraging sites involve adjacent patches (commuting) or more distant regions with a different set of oceanographic conditions (ranging) (see Stern 2002). The short-range movements between northern GS and southwestern Bransfield Strait (BS) and the long-distance movements between southwestern BS and Marguerite Bay and other distant sites are examples of these two types of displacements.

Most whales moved initially north to BS instead of south through Bismarck Strait or west through Schollaert Channel, suggesting a common pattern. The wider north exit of GS and the influence of waters from the Bellingshausen and Weddell Seas (Hofmann et al. 1996; Garcia et al. 2002) which turn northern GS and southwestern BS into highly productive areas (e.g., Ross et al. 1996; Lorenzo et al. 2002) might be driving this pattern. All the four whales tagged in GS in 2006 moved into BS within 9 days of being

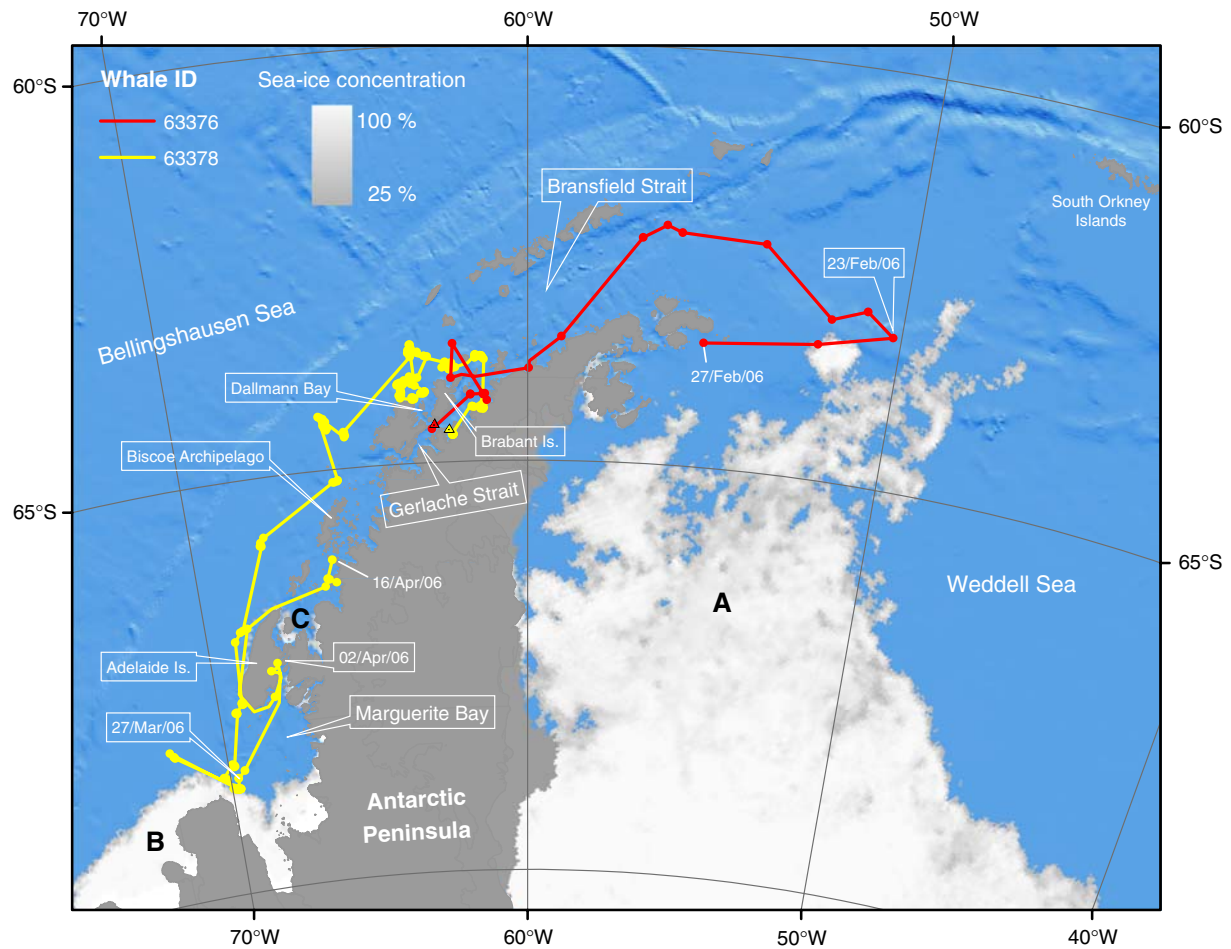
**Fig. 4** Tracks of humpback whales (#63375 and 63377) tagged in the Gerlache Strait in January 2006. *Triangles* indicate tagging location



tagged, between 28 January and 5 February. This period coincides with the higher encounter rate of humpback whales observed in BS as compared to GS between late January and early February 2006 (Secchi et al. 2006). The similar routes taken by whales 63375 and 63377 into BS seem to be associated with the bathymetry of the region, i.e., both tracks followed the deep channel connecting GS and BS and the deeper basins of BS. This region is characterized by a northward surface flow of the GS current that meets the BS current flowing northeastward along the southern continental margin of the South Shetland Islands (Zhou et al. 2002). An analysis of the distribution and movements of the tagged humpback whales with respect to environmental variables should help to characterize their foraging habitat and to interpret some of these observations.

The distances traveled and travel rates obtained from the Argos locations correspond to minimum estimates. Long directional movements, such as those characteristic of migrating whales, yield better estimates than the more erratic movements of feeding animals. This is particularly true for the tracks with coarser resolution from whales with duty-cycled tags. Nevertheless, satellite telemetry can provide better estimates than other methods previously used

(e.g., discovery marks, photo-identification and genotyping). Travel rates estimated from photo-identification/genotype matches typically lack precise information on departure and arrival dates to specific locations, while speeds measured on site either from shore-based observations or by following animals with a boat correspond to short temporal and fine spatial scales, and, in the latter case, potentially distressed animals. As expected, whales with wider ranges yielded proportionally larger distance and speed estimates, which were also affected by the duty cycling frequency. The distance traveled by whale 20689 seems remarkable for a whale in the feeding grounds, and its average travel rate of 75 km/day is comparable to that of migrating whales. Travel rates ranging from 63 to 100 km/day were reported for humpback whales that migrated southward in the South Atlantic (Zerbini et al. 2006a, b), although these same individuals traveled between 18 and 30 km/day in the feeding grounds. The average speed of 108 km/day maintained by whale 20689 during a 12-day period traveling offshore is also similar to the average of 120 km/day reported by Mate et al. (1998) for three North Pacific humpback whales tracked for up to 15 days during their initial migration from Hawaii. However, when we



**Fig. 5** Tracks of humpback whales (# 63376 and 63378) tagged in the Gerlache Strait in January 2006. Sea-ice fields correspond to the following dates with nearby whale locations: **a** 23 February 2006, **b** 27 March 2006; and **c** 2 April 2006. *Triangles* indicate tagging location

**Table 2** Estimates of area usage ( $\text{km}^2$ ) based on the minimum convex polygon (MCP) and the 95% fixed kernel home range with least squares cross-validation (95% kernel) for six humpback whales satellite monitored near the Antarctic Peninsula in 2004–2006

Whale ID	MCP	$n_1$	95% Kernel	$n_2 = d$	MCP/day	95% Kernel/day
20683	4,782	69	2,771	72	66	38
20689	407,583	57	172,356	59	6,908	2,921
63375	15,763	19	20,024	37	426	541
63376	71,669	16	57,647	31	2,312	1,860
63377	16,723	16	5,851	31	539	189
63378	69,735	40	30,508	79	883	386
All overlaid	480,825		239,501			

Rates of area usage ( $\text{km}^2/\text{day}$ ) and an estimate of summer area usage combining all individual home ranges overlaid are also provided  $n_1$  and  $n_2$  number of average daily positions used in the MCP and 95% kernel estimates, respectively,  $d$  number of days between first and last transmission

partition whale 20689's track into presumed foraging sites and traveling between these sites, the difference in effective movement is clearly shown in the corresponding travel rate estimates (43 and 109  $\text{km}/\text{day}$ , respectively). In this case, the lower value approaches those estimated for whales 20683 (predominantly erratic movements) and 63376

(more directional movements but lower resolution data). Average daily speeds between 10 and 55  $\text{km}/\text{day}$ , with considerably higher speeds during long-distance or offshore movements, were recorded for satellite-monitored humpback whales in the feeding grounds of West Greenland (Heide-Jørgensen and Laidre 2008).



The mean swimming speeds computed for whales 20683 and 20689 using only segments between the best quality locations represent more accurate estimates and reflect well the difference in the range of movements of both animals. Again, the mean speed of whale 20689 is consistent with other reported humpback whale speeds. An average migratory speed of 4.74 km/h was estimated for the fastest documented migration in the North Pacific (Gabriele et al. 1996), and an average swimming speed of 4.44 km/h was calculated from shore-based observations in Hawaiian wintering grounds (Bauer 1986). The mean speeds of migrating humpback whales estimated from acoustic and visual observations off the east coast of Australia were 2.5 and 4.0 km/h for singing and non-singing whales, respectively (Noad and Cato 2007). These estimates are similar to the mean speed of whales 20683 (2.26 km/h) and 20689 (4.03 km/h). From these comparisons, our results suggest that swimming speeds of humpback whales vary according to individual behavioral patterns and not necessarily to common patterns differing among migratory corridors and breeding and feeding grounds.

Movements of humpback whales monitored during this study have implications for stock structure. The Antarctic Peninsula is located directly to the south of South America, so populations wintering on either side of this continent could potentially feed near the Peninsula. In 1997, the IWC Scientific Committee suggested that the stock boundary separating the feeding grounds associated with Breeding Stocks A (wintering off Brazil) and G (wintering off western Central and South America) should be placed at 60°W (IWC 1998). Subsequently, in light of new genetic and photo-identification data (e.g., Olavarría et al. 2000; Dalla Rosa et al. 2004), this boundary was moved east to 50°W (IWC 2006). The tracks of one whale tagged in 2005 and three in 2006 crossed the 60°W longitude, confirming the lack of a biological meaning for the previous boundary. In addition, one individual (whale 63376), a male, traveled eastward of the Antarctic Peninsula nearly to 50°W, the new proposed boundary. This individual was on an eastward path and apparently turned around when it reached a sea-ice fringe, so it is reasonable to assume that it would have probably continued further east had it not found a physical barrier. In this respect, it is noteworthy that the easternmost tracking position of whale 63376 (63°09.1'S, 50°13.7'W) is located 172 km southeast of the resighting location (62°11.1'S, 52°51.1'W), in February 2001, of a humpback whale first photographed in February 2000 in a position 732 km to the east (61°50.5'S, 38°48.8'W) (Dalla Rosa et al. 2004). This resighting, therefore, suggests that some individuals may cross the new proposed 50°W boundary. Furthermore, there were no matches between 15 and 983 individuals photo-identified in the Weddell Sea and off Brazil, respectively (Dalla Rosa et al. 2004).

Satellite-monitored humpback whales wintering off Brazil migrated southeastwards to 32–33°W, east of South Georgia, and one whale reached as far south as the South Sandwich Islands (~58°S, 26°W), where it remained for several months (Zerbini et al. 2006a). None of the whales tracked by Zerbini et al. (2006a, b) migrated towards the Antarctic Peninsula or the Weddell Sea. Results from satellite telemetry were further supported by photo-identification as individuals seen near South Georgia and the South Sandwich Islands were matched to whales wintering off Brazil (e.g., Stevick et al. 2006). While further investigation is necessary due to sample sizes, we hypothesize from the above information that the Weddell Sea area south of the South Orkney Islands (60°36'S, 45°32'W) and west of ~35°W is occupied by whales from Breeding stock G, and that whales from Breeding stock A are unlikely to use this area, or rarely do so. Alternative hypotheses include a partial overlap between these two stocks in the feeding grounds in the Weddell Sea, around the 50°W boundary and further east, or a spatial but not temporal overlap in this region either within or between seasons. However, there are currently no data to support or reject either of these hypotheses.

Low densities of humpback whales have been observed in the Weddell Sea (Projeto Baleias/PROANTAR, unpublished data), possibly as a consequence of the variable sea-ice conditions characteristic of the region (Venegas and Drinkwater 2001). Humpback whales may be common near ice margins (e.g., Thiele et al. 2004), but they avoid entering the pack ice. Sea-ice coverage in the Weddell Sea often reaches 60°S and the west tip of the Peninsula during the feeding season, creating a natural barrier to the whales. As a result, use of this area by humpback whales may vary within and between seasons, depending on sea-ice extent.

The accuracy of home range estimates is affected by sample size and sampling interval (Kernohan et al. 2001). Therefore, considering differences in the number of locations used and that the whale-tracking periods did not cover their whole feeding season, our home range calculations are only intended to represent individual area use during the tracking period and a minimum estimate of summer home range. Autocorrelation between sequential average daily positions was detected in our analyses of area use by indexes based on time to independence (TTI) (see Swihart and Slade 1997). Sub-sampling data to a larger interval of one location every 4 days did not result in independent observations either. However, we must note that the TTI test has little value when animal movements are not centered around one focal use area (Kernohan et al. 2001), as this will produce unrealistically long TTI (McNay et al. 1994). In addition, although autocorrelation may lead to underestimation of home range size, the use of statistically independent intervals that result in loss of important biological information

may also underestimate home range, in which case autocorrelated data may provide a more accurate estimate (Reynolds and Laundré 1990). The use of pseudo-locations allowed us to include areas used by the whales that otherwise would be missed in the kernel density calculations. Rates of area usage per tracking day provided a better idea of area use given the variable tagging duration and suggested that the estimates for whales 20689 and 63376 are likely positively biased, in particular the MCP estimates.

## Conclusions

Our study shows that humpback whales can travel extensive distances in the feeding grounds as part of their foraging strategy, and that individual movement patterns are highly variable near the Antarctic Peninsula. While photo-identification data suggest that site fidelity to the Gerlache Strait is high, our telemetry data indicate that use of area may be fluid, with short residency times and frequent movements of whales between neighboring or distant feeding sites. Travel rate estimates are lower at presumed foraging sites, characterized by erratic movements, than during traveling between these sites. We also show that humpback whales may travel from the western Antarctic Peninsula to the Weddell Sea, and we suggest, based on available information, that the current boundary between the feeding grounds associated with Breeding Stocks A and G should be reconsidered.

**Acknowledgments** We are greatly indebted to the crew of the NApOc *Ary Rongel* and to P. G. Kinas, C. A. E. Garcia and M. M. Mata for giving support to our study. M. Bassoi and A. F. Azevedo assisted in the field. M. V. Jensen conducted tag deployment in 2004. H. Cunha (LBM-UFRJ) and J. W. Gonçalves (LBM-Unisinos) kindly helped with the gender determination. We also thank the administrative assistance from S. C. Moreira and A. Andriolo, and software assistance from A. R. Rodgers. Valuable comments and suggestions to improve this manuscript were provided by D. Thiele and an anonymous reviewer. Funding for the Projeto Baleias/GOAL/Brazilian Antarctic Program was provided by the Brazilian Council for Scientific and Technological Development (CNPq), the Ministry of the Environment (MMA) and the Inter-ministerial Commission for the Resources of the Sea (CIRM). Tags used in 2005 and additional funding for 2006 were acquired through the establishment of a collaborative project with the Projeto de Monitoramento de Baleias por Satélite (PMBS). Funding for PMBS was provided by Shell Brasil S.A. L. Dalla Rosa was supported by the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES; Grant BEX1339/02-8).

## References

- Acevedo J, Rasmussen K, Félix F, Castro C, Llano M, Secchi ER, Saborío MT, Aguayo-Lobo A, Haase B, Scheidat M, Dalla Rosa L, Olavarría C, Forestell P, Acuña P, Kaufman G, Pastene L (2007) Migratory destinations of the humpback whales from Magellan Strait feeding ground, Chile. *Mar Mamm Sci* 23(2):453–463. doi:10.1111/j.1748-7692.2007.00116.x
- Argos (1990) User's manual. Service Argos, Landover, 267pp
- Bauer GB (1986) The behavior of humpback whales in Hawaii and modifications of behavior induced by human interventions. PhD Dissertation, University of Hawaii, Hawaii (unpublished)
- Baumgartner MF, Mate BR (2005) Summer and fall habitat of North Atlantic right whales (*Eubalaena glacialis*) inferred from satellite telemetry. *Can J Aquat Sci* 62:527–543
- Bérubé M, Palsbøll P (1996) Identification of sex in cetaceans by multiplexing with three ZFX and ZFY specific primers. *Mol Ecol* 5:283–287
- Dalla Rosa L, Secchi ER, Kinas PG, Santos MCO, Martins MB, Zerbini AN, Bethlem CBP (2001) Photo-identification of humpback whales, *Megaptera novaeangliae*, off the Antarctic Peninsula from 1997/98 to 1999/2000. *Mem Queensl Mus* 47(2):555–561
- Dalla Rosa L, Freitas A, Secchi ER, Santos MCO, Engel MH (2004) An updated comparison of the humpback whale photo-id catalogues from the Antarctic Peninsula and the Abrolhos Bank, Brazil. Paper SC/56/SH16 presented to the IWC Scientific Committee (unpublished)
- Dawbin WH (1966) The seasonal migratory cycle of humpback whales. In: Norris K (ed) Whales, dolphins and porpoises. University of California Press, Berkeley, pp 145–170
- Etnoyer P, Canny D, Mate BR, Morgan LE, Ortega-Ortiz JG, Nichols WJ (2006) Sea-surface temperature gradients across blue whale and sea turtle foraging trajectories off the Baja California Peninsula, Mexico. *Deep Sea Res II* 53(3–4):340–358
- Frankel AS, Clark CW, Herman LM, Gabriele CM (1995) Spatial distribution, habitat utilization, and social interactions of humpback whales, *Megaptera novaeangliae*, off Hawaii, determined using acoustic and visual techniques. *Can J Zool* 73(6):1134–1146
- Frydman S, Gales N (2007) HeardMap: tracking marine vertebrate populations in near real time. *Deep-Sea Res II* 54:384–391
- Gabriele CM, Straley JM, Herman LM, Coleman RJ (1996) Fastest documented migration of a North Pacific humpback whale. *Mar Mamm Sci* 12(3):457–464
- García MA, Castro CG, Ríos AF, Doval MD, Rosón G, Gomis D, López O (2002) Water masses and distribution of physico-chemical properties in the Western Bransfield Strait and Gerlache Strait during Austral summer 1995/96. *Deep-Sea Res II* 49:585–602
- Heide-Jørgensen MP, Dietz R, Laidre KL, Richard P (2002) Autumn movements, home ranges, and winter density of narwhals (*Monodon monoceros*) tagged in Tremblay Sound, Baffin Island. *Polar Biol* 25(5):331–341
- Heide-Jørgensen MP, Dietz R, Laidre KL, Richard P, Orr J, Schmidt HC (2003) The migratory behaviour of narwhals (*Monodon monoceros*). *Can J Zool* 81(8):1298–1305
- Heide-Jørgensen MP, Laidre KL, Jensen MV, Dueck L, Postma LD (2006) Dissolving stock discreteness with satellite tracking: bow-head whales in Baffin Bay. *Mar Mamm Sci* 22(1):34–45
- Heide-Jørgensen MP, Laidre KL (2008) Autumn space-use patterns of humpback whales (*Megaptera novaeangliae*) in West Greenland. *J Cetacean Res Manage* (in press)
- Hofmann EE, Klinck JM, Lascara CM, Smith DA (1996) Hydrography and circulation west of the Antarctic Peninsula and including Bransfield Strait. In: Ross R, Hofmann E, Quetin L (eds) Foundations for ecological research west of the Antarctic Peninsula. *Am Geophys Union Antarctic Res Ser* 70:61–80
- International Whaling Commission (1998) Annex G—report of the sub-committee on comprehensive assessment of Southern Hemisphere humpback whales. *Rep int Whal Commn* 48:170–182
- International Whaling Commission (2006) Report of the Workshop on the Comprehensive Assessment of Southern Hemisphere Humpback Whales. Document SC/58/Rep 5 (unpublished)

- Kernohan BJ, Gitzen RA, Millspaugh JJ (2001) Analysis of animal space use and movements. In: Millspaugh JJ, Marzluff JM (eds) Radio tracking and animal populations. Academic Press, San Diego, pp 125–166
- Laidre KL, Heide-Jørgensen MP, Dietz R, Hobbs RC, Jørgensen OA (2003) Deep-diving by narwhals *Monodon monoceros*: differences in foraging behavior between wintering areas? *Mar Ecol Prog Ser* 261:269–281
- Lorenzo LM, Arbones B, Figueiras FG, Tilstone GH, Figueroa FL (2002) Photosynthesis, primary production and phytoplankton growth rates in Gerlache and Bransfield Straits during Austral summer: cruise FRUELA 95. *Deep-Sea Res II* 49:707–721
- Mate BR, Gisiner R, Mobley J (1998) Local and migratory movements of Hawaiian humpback whales tracked by satellite telemetry. *Can J Zool* 76(5):863–868
- Mate BR, Lagerquist BA, Calambokidis J (1999) Movements of North Pacific blue whales during the feeding season off southern California and their southern fall migration. *Mar Mamm Sci* 15(4):1246–1257
- McNay RS, Morgan JA, Bunnell FL (1994) Characterizing independence of observations in movements of Columbian black-tailed deer. *J Wildl Manage* 58:422–429
- Noad MJ, Cato DH (2007) Swimming speeds of singing and non-singing humpback whales during migration. *Mar Mamm Sci*. doi:10.1111/j.1748-7692.2007.02414.x
- Olavarría C, Baker CS, Medrano L, Aguayo A, Caballero S, Flórez-González L, Capella J, Rosenbaum HC, Garrigue C, Greaves J, Jenner M, Jenner C, Bannister JL (2000) Stock identity of Antarctic Peninsula Humpback whales inferred from mtDNA variation. Paper SC/52/IA15 presented to the IWC Scientific Committee (unpublished)
- Rasmussen K, Palacios DM, Calambokidis J, Saborío MT, Dalla Rosa L, Secchi ER, Steiger GH, Allen JM, Stone GS (2007) Southern Hemisphere humpback whales wintering off Central America: insights from water temperature into the longest mammalian migration. *Biol Lett*. doi:10.1098/rsbl.2007.0067
- Reynolds TD, Laundré JW (1990) Time intervals for estimating pronghorn and coyote home ranges and daily movements. *J Wildl Manage* 54(2):316–322
- Rodgers AR, Carr AP, Smith L, Kie JG (2005) HRT: home range tools for ArcGIS. Ontario Ministry of Natural Resources, Centre for Northern Forest Ecosystem Research, Thunder Bay
- Ross RM, Quetin LB, Lascara CM (1996) Distribution of Antarctic krill and dominant zooplankton west of the Antarctic Peninsula. In: Ross R, Hofmann E, Quetin L (eds) Foundations for Ecological Research West of the Antarctic Peninsula. Am Geophys Union, Antarctic Res Ser 70:199–217
- Sambrook J, Fritsch EF, Maniatis T (1989) Molecular cloning: a laboratory manual, 2nd edn. Cold Spring Harbor Lab Press, New York
- Secchi ER, Dalla Rosa L, Kinas PG, Santos MCO, Zerbini AN, Bassoi M, Moreno IB (2001) Encounter rates of whales around the Antarctic Peninsula with special reference to humpback whales, *Megaptera novaeangliae*, in the Gerlache Strait: 1997/98 to 1999/2000. *Mem Queensl Mus* 47(2):571–578
- Secchi ER, Dalla Rosa L, Kinas PG, Nicolette RF, Azevedo AF, Maia YG (2006) Abundance of humpback whale, *Megaptera novaeangliae*, in the Gerlache and Bransfield Straits, Antarctic Peninsula region. Paper SC/A06/HW43 presented to the IWC Scientific Committee (unpublished)
- Shaw CN, Wilson PJ, White BN (2003) A reliable molecular method of gender determination for mammals. *J Mamm* 84(1):123–128
- Slijper EJ (1962) Whales. Hutchinson & Co., London
- Spren G, Kaleschke L, Heygster G (2007) Sea ice remote sensing using AMSR-E 89 GHz channels. *J Geophys Res*. doi:10.1029/2005JC003384
- Stern SJ (2002) Migration and movement patterns. In: Perrin WF, Würsig B, Thewissen JGM (eds) Encyclopedia of marine mammals. Academic Press, San Diego, pp 742–748
- Stevick PT, Aguayo A, Allen J, Avila IC, Capella J, Castro C, Chater K, Dalla Rosa L, Engel MH, Félix F, Florez-Gonzalez L, Freitas A, Haase B, Llano M, Lodi L, Muñoz E, Olavarria C, Secchi ER, Scheidat M, Siciliano S (2004) Migrations of individually identified humpback whales between the Antarctic Peninsula and South America. *J Cetacean Res Manage* 6(2):109–113
- Stevick PT, Pacheco de Godoy L, Mcosker M, Engel MH, Allen J (2006) A note on the movement of a humpback whale from Abrolhos Bank, Brazil to South Georgia. *J Cetacean Res Manage* 8(3):297–300
- Stone GS, Florez-Gonzalez L, Katona S (1990) Whale migration record. *Nature* 346:705
- Swihart RK, Slade NA (1997) On testing for independence of animal movements. *J Agricult Biol Environ Stat* 2:48–63
- Thiele D, Chester ET, Moore SE, Širovic A, Hildebrand JA, Friedlander AS (2004) Seasonal variability in whale encounters in the Western Antarctic Peninsula. *Deep-Sea Res II* 51:2311–2325
- Tyack P (1983) Differential response of humpback whales, *Megaptera novaeangliae*, to playback of song or social sounds. *Behav Ecol Sociobiol* 13:49–55
- Venegas SA, Drinkwater MR (2001) Sea ice, atmosphere and upper ocean variability in the Weddell Sea, Antarctica. *J Geophys Res Oceans* 106(C8):16747–16765
- Williams R, Hedley SL, Hammond PS (2006) Modeling distribution and abundance of Antarctic baleen whales using ships of opportunity. *Ecol Soc* 11(1):1. [online] url: <http://www.ecologyandsociety.org/vol11/iss1/art1/>
- Zerbini AN, Andriolo A, Heide-Jørgensen MP, Pizzorno JL, Maia YG, Vanblaricom GR, Demaster DP, Simões-Lopes PC, Moreira S, Bethlem C (2006a) Satellite-monitored movements of humpback whales *Megaptera novaeangliae* in the southwest Atlantic Ocean. *Mar Ecol Prog Ser* 313:295–304
- Zerbini AN, Andriolo A, Heide-Jørgensen MP, Moreira S, Pizzorno JL, Maia YG, Bethlem C, Vanblaricom GR, Demaster DP (2006b) What does satellite telemetry tell us about the stock identity and feeding grounds of humpback whales in the western South Atlantic Ocean? Paper SC/A06/HW46 presented to the IWC Scientific Committee (unpublished)
- Zhou M, Niiler PP, Hu J-H (2002) Surface current in the Bransfield and Gerlache Straits measured by surface Lagrangian drifters. *Deep-Sea Res I* 46:267–280