

Foraging movements of Magellanic Penguins *Spheniscus magellanicus* in the Beagle Channel, Argentina, related to tide and tidal currents

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Abstract This study investigates the movements of Magellanic Penguins *Spheniscus magellanicus* breeding on Isla Martillo during the early chick-rearing period. Foraging paths were reconstructed using GPS loggers that registered the penguins' geographic position, water temperature and depth at regular intervals. The relationship between penguins' movements and search strategies, tide and tidal currents were assessed. Mean trip duration was on average 14.7 ± 6.9 h (33% overnight), and the maximum distance reached was 24 ± 10 km. All penguins studied foraged to the east of the colony. We identified three phases based on the sinuosity and speed of the trajectory: transit, central and return. Foraging effort was higher during the central phase, followed by the transit phase, and lower in the return phase. Foraging success, measured as the percentage of time at the bottom during each phase, was also highest during the central phase. In all birds

studied, the central phase of the foraging trip took place during ebb tide, and birds travelled to the foraging areas with flow tide running in the same direction of displacement. Our study suggests that penguins take advantage of tidal currents to facilitate their movements to and from the main foraging area, thereby reducing the energy expended. Moreover, we suggest that piscivorous diving birds may enhance their catch rate during ebb tide when fish are more concentrated near the channel bed.

Keywords *Spheniscus magellanicus* · Foraging movements · Search strategy · Tide and tidal currents

Introduction

Seabirds are mobile species that depend on a spatially and temporally heterogeneous environment (Hunt 1999). As a consequence seabirds exhibit considerable variation in their foraging behaviour or at-sea distribution. Prey availability is related to the physical and biological properties of the ocean, such as depth (Hastie et al. 2003), hydrological structure (Charrassin and Bost 2001), and substrate type (Tollit et al. 1998) and, in near-shore waters, tidal effects (Chen et al. 1999; Holm and Burger 2002; Zamon 2003). Therefore, habitat utilisation by predators is assumed to reflect the quality and availability of resources in an area (Davoren et al. 2003; Laidre et al. 2004). Predators must make optimal decisions about where and how to forage to maximise both their efficiency and, ultimately, their fitness (Stephens and Krebs 1986). Seabirds are thought to follow complex scale-driven strategies when searching for food (Weimerskirch et al. 2007; Fritz et al. 2003). Establishing the factors driving the movements of free-ranging seabirds is then crucial for a better understanding of their

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dependence on the marine environment and hence for the conservation of optimal feeding habitats.

Foraging patterns and search strategies have been studied in many seabirds from albatrosses and petrels (Weimerskirch et al. 1997; Fritz et al. 2003; Pinaud and Weimerskirch 2005; Weimerskirch et al. 2007) to cormorants (Grémillet et al. 1999; Frere et al. 2002; Gandini et al. 2005) and penguins (Bost et al. 1997; Lescroël and Bost 2005; Cotté et al. 2007; Mattern et al. 2007; Boersma et al. 2009). Studies conducted so far have revealed species- and site-specific behavioural strategies, for example, area restricted search (i.e., Pinaud and Weimerskirch 2007), or travel to and from a preferred foraging area almost directly (Cotté et al. 2007; Mattern et al. 2007, Boersma et al. 2009), and movements according to tidal phases (Hunt et al. 1998; Holm and Burger 2002; Zamon 2003). Studies in restricted near-shore maritime environments such as estuaries, channels and straits have shown spatially temporal concentration of zooplankton related with tidal currents (Forward and Tankersley 2001; Zamon 2002; Cotté and Simard 2005). Several authors have acknowledge that the interaction between tidal currents and plankton distribution creates predictable changes in food availability for planktivore seabirds (Hunt et al. 1998; Holm and Burger 2002; Zamon 2003) and hence predators such as seabirds that prey on planktivorous fishes (Zamon 2003). However, this was mainly proved for flying seabirds that took advantage of fish becoming more disperse in the water column during flood tides (Zamon 2003).

Inter-colony differences in diet composition for Magellanic Penguin *Spheniscus magellanicus* have been previously described over the species' latitudinal range in Argentina (Frere et al. 1996; Scolaro et al. 1999; Wilson et al. 2005). Also, it has been shown that foraging trip lengths from different colonies along the Patagonian coast differ, and hence the distance to the colony given the location of their main prey (Wilson et al. 2005, Boersma et al. 2009). In Tierra del Fuego, the Magellanic Penguin *Spheniscus magellanicus* feeds mainly on Fuegian Sprat *Sprattus fuegensis*, and to a lesser extent on Lobster Krill *Munida gregaria* and some other nototheniid fish (Schiavini et al. 2005). In this area penguins forage in a narrow water passage, the Beagle Channel, which has the particular characteristics of a coastal marine habitat. The colony offered the opportunity to study the foraging movements in a restricted spatial environment: an inner channel with open waters located about 40 nm from the colony.

The objectives of this research were: (1) to analyse the foraging trip organisation and strategies of Magellanic Penguins *Spheniscus magellanicus* brooding small chicks, (2) to characterise the foraging areas of Magellanic Penguins *Spheniscus magellanicus* in terms of their physical features and (3) to assess whether penguins synchronise the

timing of their foraging trips according to local hydrography. We tested the hypothesis proposed by Cotté et al. (2007) that penguins would swim in the same direction as the current (in this case tidal current) en route to foraging spots as a mechanism to reduce travel cost. Finally, we tested the "tidal-coupling" hypothesis (Zamon 2003) where current-coastline interactions may create temporally and spatially predictable rips and jets, which in turn favour zooplankton development and, as a consequence top-predators' main prey aggregation.

Materials and methods

The study was conducted at the Magellanic Penguin *Spheniscus magellanicus* breeding colony on Isla Martillo, Tierra del Fuego, Argentina (54°54'S, 67°23'W). This hammer-shaped island is part of a group of small islands located in the eastern section of the shallow Argentinean waters of the Beagle Channel. The island is 2,000 m long on its NW-SE axis and up to 750 m wide. The colony of Magellanic Penguins *Spheniscus magellanicus* has developed during the past 30 years and has about 2,000 active nests to date (Schiavini et al. 2005).

GPS tracking of Magellanic Penguins *Spheniscus magellanicus*

Global positioning systems (GPS) equipped with temperature and pressure sensors (GPS-TDlog, Earth & OCEAN Technologies, Kiel, Germany) were deployed between 3 and 7 December 2006 on four male and four female Magellanic Penguins *Spheniscus magellanicus* breeding at Martillo Island. One of the female's devices did not work, and one of each sex performed two trips. Subsequently, data from nine foraging trips were obtained and analysed in order to determine foraging locations and diving behaviour.

The loggers use an active patch antenna to record GPS positions to 0.001 min of latitude and longitude, with an absolute accuracy of ca. 5 m in continuous GPS mode and 20 m in intermittent mode (when the device is programmed to switch on at preselected intervals; see Ryan et al. 2004 for further details). Devices were programmed at two sampling intervals: continuous mode (four devices, six trips) and 20-min intermittent mode (three devices, three trips). The GPS-TDlog also recorded penguin dive depth accurate to 0.03 bar every 2 s, allowing accurate measurement of dive profiles, and temperature to 5 mK. Data were stored in a 2-Mbyte flash memory. Each logger had a hydrodynamic, waterproof housing measuring 96 × 39 × 27 mm and with a total mass of 75 g corresponding to ca. 1.7% of the mean Magellanic Penguin *Spheniscus magellanicus* body mass, and to ~6.5% of the cross-sectional

area of the bird. The housing protected the device against mechanical impact, and the electronics against water pressures of up to 16 bar (*ca.* 160-m water depth). An O-ring-sealed cap allowed access to the logger for data retrieval and battery exchange. The temperature sensor protruded from the rear of the housing on a 1-cm-long flexible probe, allowing immediate response to changing environmental temperature.

Attachment procedure

Adult Magellanic Penguins *Spheniscus magellanicus* raising chicks 10–15 days old were captured by the legs in their burrow with a hook. Mean body mass of males (4.8 ± 0.4 kg) and females (4.1 ± 0.2 kg) at departure did not differ significantly ($U = 16$, $P > 0.01$). In order to minimise the hydrodynamic drag the devices were attached on the mid-line of the back using black tape (Tesa, Beiersdorf AG, Hamburg, Germany) according to the method described by Wilson et al. (1997) and positioned on the middle back so as not to compromise the penguins' balance (Chiaradia et al. 2005). The whole process took less than 10 min per bird.

Trip organisation

We recorded trip duration and maximum distance to the colony. Travelling speed was calculated by dividing the minimum distance between two consecutive locations by the time interval between the locations. For each penguin trip, we identified three phases using running speed averages per hour and compared these running averages to the mean swimming speed for the whole trip. In doing so, we assumed that Magellanic Penguins *Spheniscus magellanicus* would decrease their travelling speed to actively forage, i.e., they would decrease their horizontal (displacements) activity while they increased their vertical (diving) activity (in accordance with Bost et al. 1997; Pütz et al. 1999; Charrassin et al. 2002; Cotté et al. 2007; for King Penguins *Aptenodytes patagonica*; Boersma et al. 2009 for Magellanic Penguins *Spheniscus magellanicus*). These three phases were defined as (I) the *Transit Phase*, i.e., travel between the colony and the central phase, where the running averages of swimming speeds were higher than the mean speed of the whole trip. (II) The *Central Phase*, which began at the first episode of *slowing* down, where the running averages were below the mean speed. (III) The *Return Phase*, where running averages of swimming speed were again higher than the overall mean speed. Path sinuosity was defined for each phase as the ratio of the total displacement for the phase (sum of the distances of each track for the whole phase) to the actual displacement (distance between the first and last position in each phase).

Several parameters were compared between phases, in terms of (i) foraging effort such as time spent in each phase, mean diving depth, time spent underwater and at the surface; trip organisation (horizontal distance travelled and mean maximum distance reached during the foraging trip, vertical distance covered per hour and (ii) index of foraging success, such as time spent at the bottom per foraging trip (bottom time %), and bottom time.

Foraging trip strategy

Time of departure and arrival were analysed with respect to the tidal flow patterns during the study period. Bearing deviations between penguins and underlying current directions, varying from 0° to 360° , were also investigated. In the study area the tide regime is semidiurnal, and tidal currents differed between spring and neap tides. During spring tides the current flows 9 h to the east and three to the west between high tides, whereas during neap tides the current flows always to the east. The study period took place during spring tides. A bearing deviation of 0° to 90° and 270° to 360° indicated similar directions for a penguin and the tide current (positive rheotaxis), while a bearing deviation of 90° to 270° corresponded to opposing directions (negative rheotaxis) (Ream et al. 2005). The relative use of the water by penguins was calculated and plotted as follows. A 1×1 -km grid was superimposed over each penguin track in a geographical information system, ArcGIS 9.1 (ESRI, Redland, CA) and analysed using Spatial Analyst. A line was drawn connecting two sequential locations of the bird. The time lapse between these two locations was allocated to the length of the line. The portion of a line falling within a grid square became a proportion of the time interval, and this increment of “penguin time” was thus assigned to the grid square. The procedure was repeated for each penguin, and maps of the relative time spent for all the penguins and for long and short trips during the study period were drawn.

We analysed diving data using MultiTrace (Jensen Software, Kiel, Germany). Diving activity was analysed in terms of foraging effort (distance covered: vertical distance travelled in meters per hour) and foraging success as percentage of bottom time and time spent during the bottom phase of a dive. Given that Magellanic Penguins *Spheniscus magellanicus* feed mostly on Fuegian Sprat *Sprattus fuegensis* at this location and that this fish species is distributed during the day in depths between 20 and 70 m and at night in depths between 5 and 10 m (Casarsa 2005), dives were separated into foraging dives (>5 m) and travelling dives (<5 m), and the proportion of each dive type between phases was compared. Bathymetric data were overlapped with the grid of time spent and penguins' positions in ArcGIS 9.1, and the relationship between

penguins' movements and local topography was analysed using Spatial Analyst. Statistical analyses were performed using Minitab 13. Data are given as mean \pm SD unless otherwise noted.

Results

A total of nine foraging trips were recorded from four males and three females given that one of each sex performed two trips. The two sexes did not differ in terms of foraging trip duration (15.4 ± 5.5 h and 15.1 ± 9.2 h for males and females, respectively; $U = 20$, $P > 0.01$) and maximum foraging range from the colony (23.6 ± 7.5 km and 24.3 ± 13.9 km for males and females, respectively; $U = 19$, $P > 0.01$) (Table 1). Three out of nine trips took place overnight and were performed by both sexes

(Table 1). Maximum distance to the colony was correlated with foraging trip duration ($r^2 = 0.78$, $P < 0.05$). Maximum distance to the colony ranged from 14.7 to 45.1 km and trip duration from 7.9 to 28.9 h.

At-sea movements

Penguins departed either early in the morning or early in the afternoon (Table 1), while arrival times were either late at night or early in the afternoon (the latter, in particular, for the penguins that started the trip early in the morning). Regarding the tide, all penguins departed and with two exceptions also returned during flood (two penguins returned from an overnight trip during ebb).

Almost all penguins left the island towards the east except for two birds that departed east southeast and one east northeast (Fig. 1). Bearing deviations during commuting to

Table 1 Summary of data from Magellanic penguins with attached GPS and characteristics of their foraging trips

Bird	Sex	Trip	Start day	Start time	Trip duration (h)	Distance to colony (km)	Night
137_3dic	M	1	03/12/2006	15:50:15	7.96	14.93	No
137_3dic	M	2	04/12/2006	14:29:55	9.67	18.07	No
91_3dic	F	1	03/12/2006	16:39:55	28.94	45.14	Yes
94_3dic	F	1	04/12/2006	03:41:35	10.25	18.87	No
94_3dic	F	2	05/12/2006	03:25:45	9.63	18.75	No
93_3dic	F	1	04/12/2006	03:09:10	11.56	14.7	No
91_5dic	M	1	06/12/2006	03:14:50	15.29	34.29	No
93_5dic	M	1	06/12/2006	14:12:55	18.59	25.53	Yes
137_5dic	M	1	06/12/2006	16:57:15	20.76	25.55	Yes

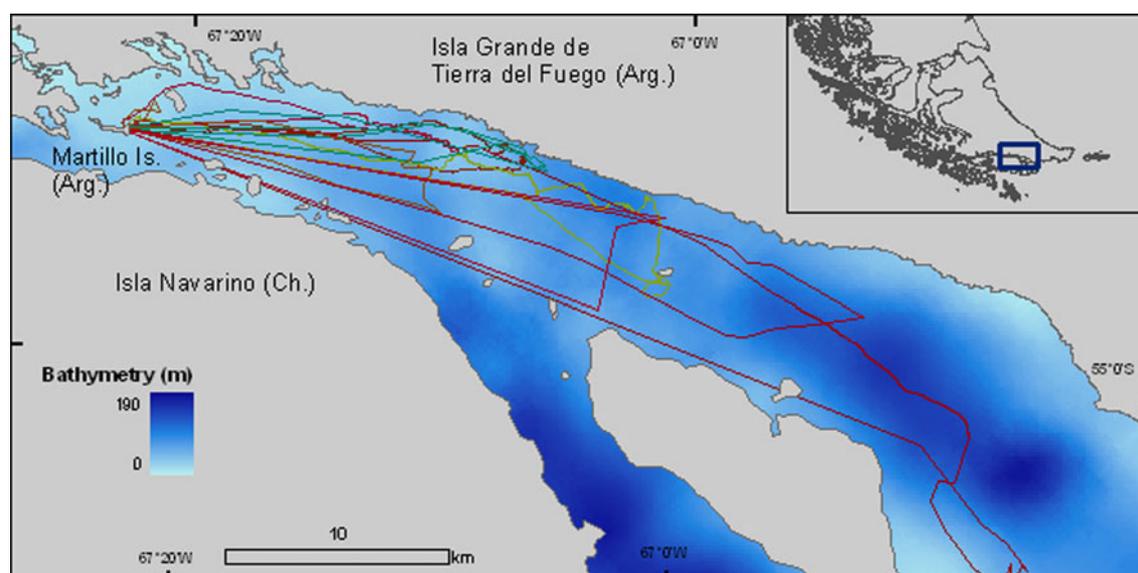


Fig. 1 Foraging tracks of Magellanic penguins from Isla Martillo in the Beagle Channel, Tierra del Fuego, Argentina, during the breeding season

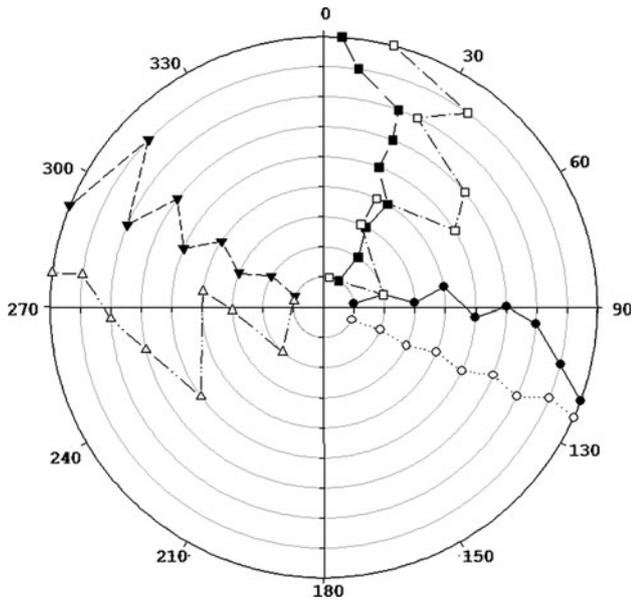


Fig. 2 Direction of departing (filled circle) and returning penguins (inverted filled triangle), tidal current during departure (open circle) and return (open triangle), and bearing deviations between penguins and the underlying current direction during departure (filled square) and return (open square)

and from the central foraging area were evaluated in relation to contemporaneous tidal currents. The mean tide current direction was 113°, and the penguins' direction at departure was 91°, while penguins returned from a mean direction of 262° while the main direction of the current was 298°. In both cases the bearing deviations were between 0 and 90°, which indicates the penguins travelled in the direction of the tide current (Fig. 2).

Trip orientation

The transit and return phases of the trip were characterised by a higher speed and lower sinuosity index (i.e., the penguins travelled almost in a straight line), while in the central phase penguins slowed down and had a higher sinuosity index (i.e., the penguins travelled on a zig-zagging course; Table 2; Fig. 3). However, time spent in each phase, horizontal distance travelled, time underwater, time at the surface and water temperature did not vary significantly between phases (Table 2). Most time was spent in a small area at a distance of ca. 15 km from the colony during the central phase, while the same amount of time was spread over a larger area during the commuting phases of the trip (Table 2; Fig. 4a, b). Importantly, the central phase of the foraging trips for all penguins occurred during ebb tide.

There was a significant difference in the type of dives during each phase, with a higher percentage of foraging dives during the transit and central phases and more

Table 2 Mean diving and movement parameters during the three different phases (transit, central and return) during the foraging trips of Magellanic penguins

	Transit	Central	Return	<i>H</i>	<i>P</i>
Travelling speed (km/h)	3.73	1.365	3.79	13.52	0.001
Sinuosity	1.07	4.39	1.23	13.30	0.001
Time spent in each phase (%)	0.27	0.4	0.3	5.86	0.053
Horizontal distance (%)	0.41	0.21	0.34	2.66	0.264
Horizontal distance (km)	16.54	12.16	18.44	2.21	0.332
Temperature (°C)	8.33	8.41	8.46	1.15	0.562
Time underwater (%)	0.25	0.35	0.32	1.37	0.505
Time at the surface (%)	0.74	0.65	0.67	1.37	0.505
Mean maximum depth dive (m)	15.48	17.28	8.58	8.27	0.0016
Foraging dives (%)	59.4	60.3	24.7	10.04	0.007
Travelling dives (%)	40.5	38.8	75.31	10.04	0.007
Dive rate (dives/h)	14	18	12	3.61	0.165
Distance covered(m/h)	481	780	303	9.26	0.01
Bottom time (s/h)	217	318	191	2.77	0.251
Mean Bottom time (s)	48.9	57.5	47.2	2.58	0.275
Bottom time/trip dur (%)	25.2	58	22	8.35	0.015

Kruskal-Wallis statistics and their correspondent *P*-value for the differences in each parameter between phases are given. Significant differences are marked in bold

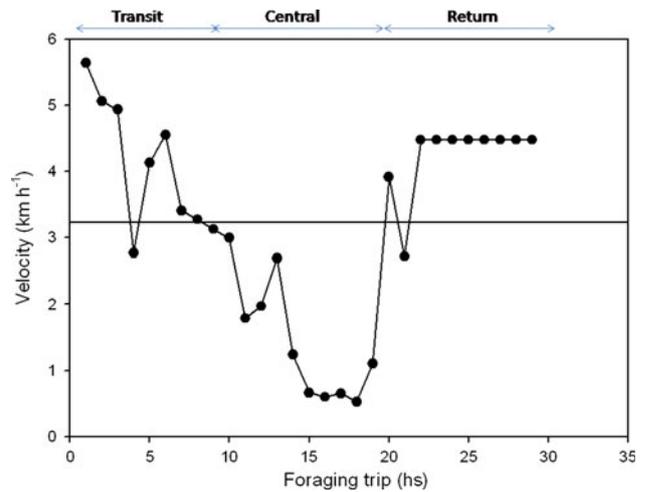


Fig. 3 Magellanic penguin travelling velocity versus time into foraging trip (solid line indicates the mean travelling speed for the entire foraging trip)

travelling dives during the return phase (Fig. 5). The mean dive depth of penguins was thus shallower during the return phase (Table 2). In terms of foraging effort, there was no significant difference in the dive rate (dives per hour) between the phases, but significant differences occurred with respect to distance covered (vertical distance travelled per hour), which was highest during the central

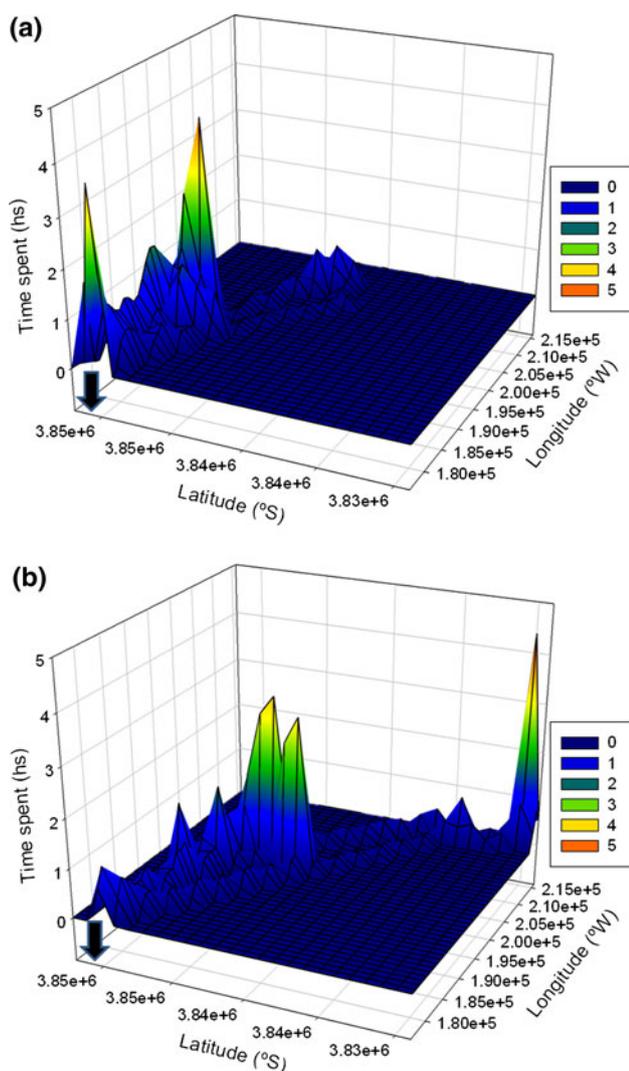


Fig. 4 The relative amount of time spent in the Beagle Channel area for Magellanic penguins performing (a) daily and (b) overnight trips pooled together. The arrow indicates the location of the colony

phase. Regarding the foraging success, the percentage of the total bottom time in each phase was higher during the central phase compared with the commuting phases; however, mean bottom time duration was similar between phases (Table 2). During overnight trips birds reduced their diving activity at night, and no dives were performed between 01:00 and 02:00 am (sunrise 4.31 h, sunset 9.37 h, and dawn and dusk were at 12.17 and 1.47, on 7 December following the nautical definition).

Foraging habitat

Bathymetry in the study area varied from 5 to 130 m water depth. Penguins consistently foraged over shallow waters as 48% of the positions corresponded to water depths of less than 30 m. Bathymetry did not differ between central (35 ± 13 m)

and transit areas (43 ± 18 m) ($\chi^2 = 2.28$, $P = 0.131$, Fig. 6). The bathymetry slope ranged from 0 to 3° in the study area, and there was no difference between transit and foraging areas ($0.56^\circ \pm 0.35^\circ$ and $0.44^\circ \pm 0.24^\circ$, respectively, $\chi^2 = 0.41$, $P = 0.524$). Temperature was homogeneous (8–9°C) throughout transit and foraging areas, and a mixing of waters occurred with less than half a degree difference from the surface down to 60 m water depth.

Discussion

In this study, the foraging trip organisation and strategy of Magellanic Penguins *Spheniscus magellanicus* feeding in a restricted marine environment were investigated. Moreover, the study has highlighted the influence of tides on penguins' foraging activity in a coastal environment.

Studies of marine birds have shown that their foraging movements are likely to reflect behavioural adjustments to both prey distribution and climatic conditions, and that they are also influenced by both small- and large-scale oceanographic features. For example, several studies on the adjustment of foraging movements in marine predators such as Wandering Albatrosses *Diomedea exulans* (Fritz et al. 2003; Weimerskirch et al. 2007), Antarctic Petrels *Thalassoica antarctica* (Fauchald and Tveraa 2003), Yellow-Nosed Albatrosses *Thalassarche carteri* (Pinaud and Weimerskirch 2005) and also Magellanic Penguins *Spheniscus magellanicus* (Wilson et al. 2001; Boersma et al. 2009) have revealed some relationships to large-scale oceanographic parameters such as oceanographic fronts and shelf breaks. However, much less is known about the driving forces in a restricted and/or near-shore environment (Hunt et al. 1998; Radl and Culik 1999; Frere et al. 2002; Zamon 2003; Gandini et al. 2005).

Oceanic predators use large-scale predictable oceanographic features (shelf slope, fronts, etc.) and focus their foraging activity on a smaller scale. For example, sub-meso to small-scale domains characterised by different water masses defined the movements of King Penguins *Aptenodytes patagonica* and Rockhopper Penguins *Eudyptes chrysocome* (Charrassin and Bost 2001; Charrassin et al. 2002; Raya Rey et al. 2007), while topographic features influenced the movements of Yellow-Eyed Penguins *Megadyptes antipodes* (Mattern et al. 2007). In coastal waters, seabirds appear to adjust their movements according to tidal currents; however, this was mainly studied in flying seabirds (Holm and Burger 2002; Zamon 2003; Gandini et al. 2005).

At-sea movements

During the central phase, Magellanic Penguins *Spheniscus magellanicus* foraged at a particular distance (i.e., 24 ± 10 km) from the colony while mainly travelling

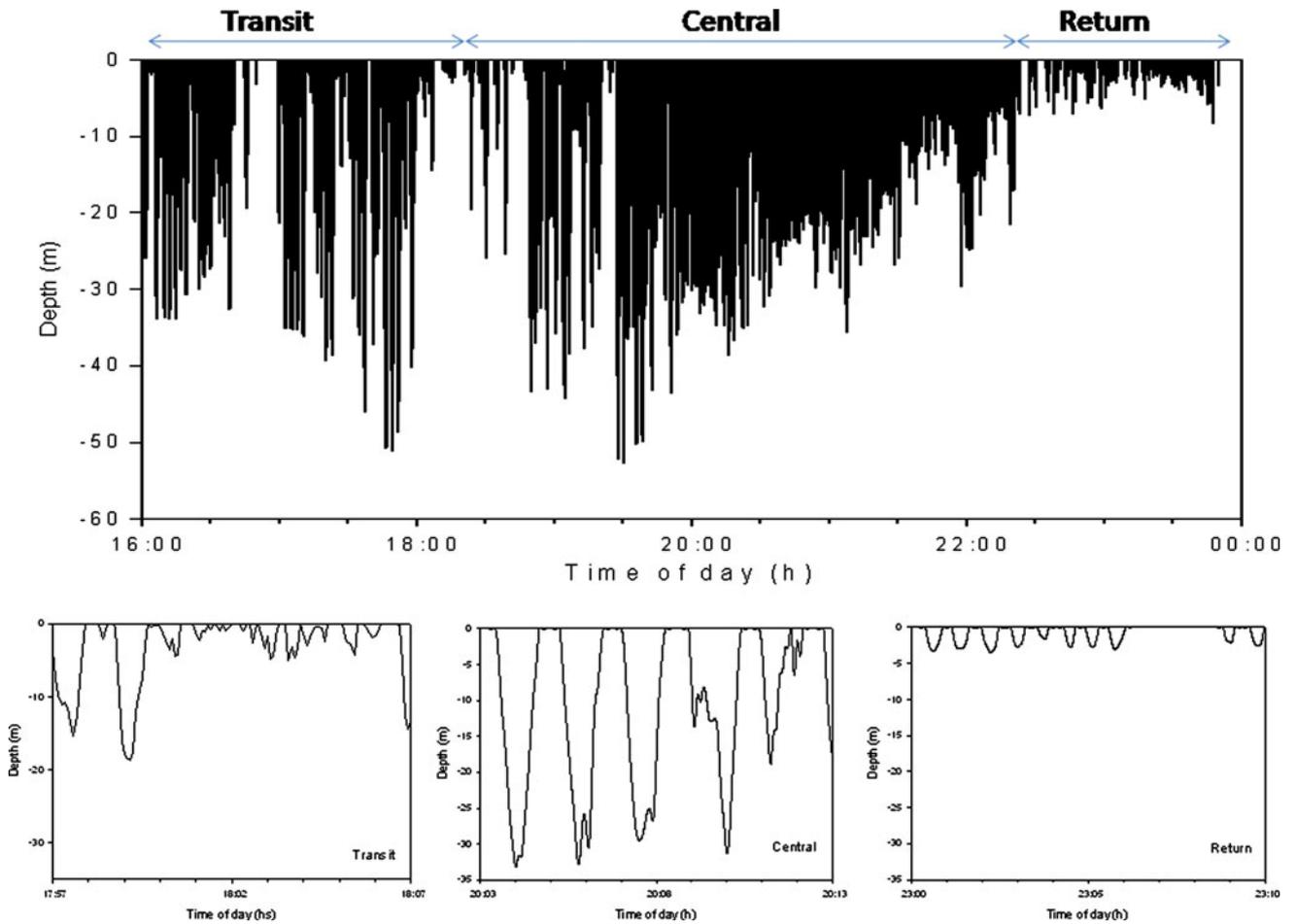


Fig. 5 Dive profile during the three different phases of one individual foraging trip

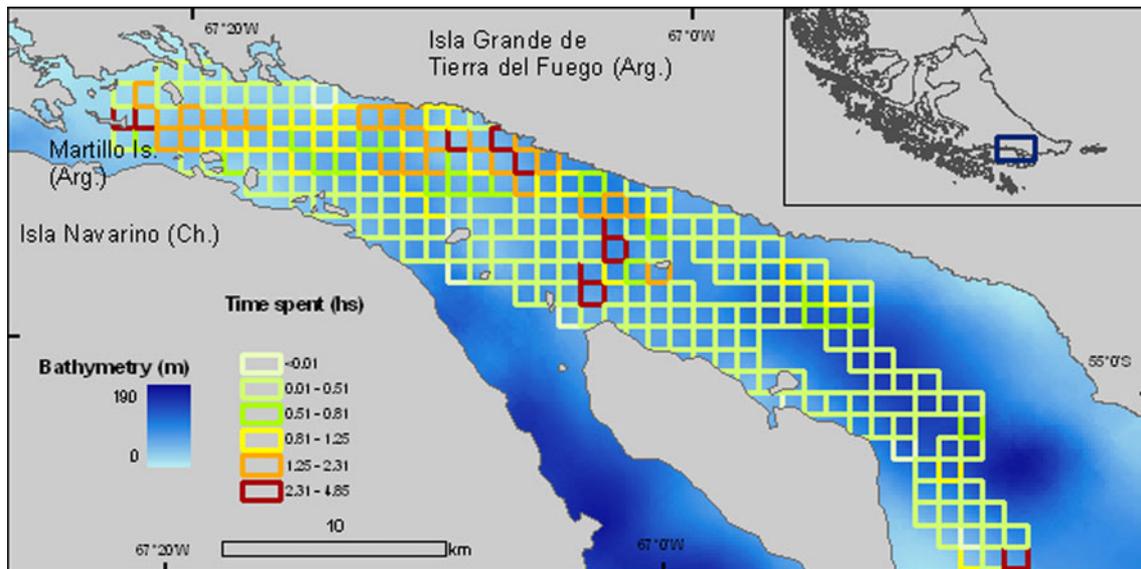


Fig. 6 The relative amount of time spent in 1 × 1-km grid squares by foraging Magellanic penguins in relation to bathymetry in the Beagle Channel area

during the outgoing and incoming phases. However, dive parameters and sinuosity during both travelling stages differed. Penguins exhibited more travelling dives when returning to the colony while performing searching and foraging dives also during the inward, transit phase, and a similar pattern was described for Yellow-Eyed Penguins *Megadyptes antipodes* (Mattern et al. 2007). During the return phase, where diving rate and food intake decreased drastically (Bost et al. 1997; Charrassin et al. 2002), penguins swam rapidly back to the colony because of breeding constraints, i.e., to relieve the partner on the nest or provision the chick with food (Cotté et al. 2007; Boersma et al. 2009). Given this strategy it appears that birds could either be foraging for themselves during the transit phase and for the chicks during the central phase where food is more abundant, or searching for food during the transit phase and so performing deep dives. The former has already been suggested for Magellanic Penguins *Spheniscus magellanicus* from mainland Patagonia (Wilson et al. 2004). Wilson et al. (2004) using stomach temperature loggers showed that temperature drops faster during the first half of the trip and generally that drop slows down during the second half. The authors suggested a pattern of ingestion and digestion for the adult at the beginning, followed by a period where the adult is foraging for the chick.

Influence of tidal activity

Environmental factors are known to influence the movements of animals (e.g., currents or tidal movements for marine animals, topography for terrestrial animals) (Fritz et al. 2003). In our study, it appears that penguins benefited from both tide and tidal currents. Tide and tidal currents have been shown to be used by marine birds as a way to facilitate transport (Hays et al. 1999; Pütz et al. 2003; Cotté et al. 2007) and/or enhance availability of prey items (Holm and Burger 2002; Zamon 2003; Gibson 2003; Gandini et al. 2005). On one hand it could be shown that penguins adjust the onset of and return of a foraging trip to a time when the tide is flowing in the preferred direction. Our results support the hypothesis proposed for Rockhopper Penguins *Eudyptes chrysocome* and King Penguins *Aptenodytes patagonica* (Pütz et al. 2003; Cotté et al. 2007), but also suggested for turtles (Hays et al. 1999), that penguins may take advantage of current flow to increase their speed without increasing their energetic costs. Tidal current in the area during the study period (spring tides) was 0.8 to 1.1 knots to the east and 0.4 knots to the west. Wilson et al. (2001) showed that Magellanic Penguins *Spheniscus magellanicus* from San Julian modify their commuting behaviour according to perceived currents by minimising the time spent swimming against strong currents and maximising the time spent swimming with

currents flowing in their preferred direction. However, penguins at that location apparently do not time their foraging trips so as to be commuting only during periods of favourable current flow. According to Wilson et al. (2005), speed is a particularly important and confounding element for the energy expenditure and thus oxygen use of a penguin, since these increase as a cubed function of speed (Culik et al. 1994; Luna-Jorquera and Culik 2000). Also, Wilson et al. (1986) proved that the amount of food ingested was proportional to the distance travelled. In our study, travelling time is reduced, helped by the currents, and as a result penguins are able to increase time spent at the central phase of the foraging trips, thereby maximising the time and/or distance covered in the preferred area with higher prey abundance or availability. This is particularly important when feeding small chicks as they need more frequent meals (Williams et al. 1992).

The availability of prey to seabirds is often more important than their abundance (Croxall and Prince 1980; Hunt et al. 1998). The role of tidal processes in trophic transfer is enhanced by spatial and temporal predictability of prey availability, which permits predators to anticipate when and where prey will be available (Hunt et al. 1998). As previously suggested for other seabird species (Zamon 2003), we can assume that the responses of penguins to tidal currents would be linked to the relative sensitivity of their prey types to these currents. Many studies have documented tidally generated concentrations of zooplankton (i.e., Hunt 1997; Hunt et al. 1998; Cotté and Simard 2005), but few have reported tidally forced aggregations of fish (Aldredge and Hamner 1980; Hoffman et al. 1981). In our study, the time when foraging success was highest, as confirmed by the percentages of bottom time and proportion of foraging dives, corresponded to ebb tide. In general, piscivorous birds have been shown to take advantage of flood tide when prey is more dispersed in the water column (Holm and Burger 2002; Zamon 2003). However, the species studied were flying seabirds that may benefit from fish being more dispersed and closer to the surface.

Seabird foraging behaviour can indicate short-term prey availability given that they must forage efficiently to sustain themselves and their chick (Cairns 1987; Grémillet et al. 2004; Piatt et al. 2007). Detailed knowledge about seabird movements also help in understanding factors affecting prey distribution, especially in monophagic species (Ichii et al. 2007; Bost et al. 2008). Magellanic Penguins *Spheniscus magellanicus* breeding at Martillo Island feed exclusively on Fuegian Sprat *Sprattus fuegensis* in years of abundance, which was the case during the study period, while relying on other prey species when sprats are scarce (Schiavini et al. 2005; Scioscia et al., unpublished data). Sprat distribution is thought to be related to water masses ranging between 9

and 12°C (Sanchez et al. 1995), which could be confirmed by the temperature profile recorded during the trips in our study (between 8 and 9°C), while in poor sprat years the temperatures range between 6 and 7°C (Raya Rey unpublished data, breeding season 2007/2008). Furthermore, waters in the Beagle Channel were well mixed, evident from only little variation (<0.5°C) in the temperature depth profiles obtained (Antezana 1999; this study) Also, sprats seem to be concentrated in certain areas of the Beagle Channel, although bathymetry was not found to be a key feature explaining sprat distribution, which coincided with the previous knowledge from an acoustic survey (Casarsa 2005). Sprats fed on zooplankton (copepods and decapods crustaceans) along the coasts of Santa Cruz and Tierra del Fuego (Sabatini et al. 2001). Although the movements and patterns of sprats' schools were not investigated in relation with their prey movements, Casarsa (2005) found compact sprat schools as well as fish in scattered layers, and he suggested that this could be related with their foraging behaviour. Our results suggest that Magellanic Penguins *Spheniscus magellanicus* could benefit from fish being more concentrated during ebb tide while not actively foraging. Gandini et al. (2005) found that Red-Legged Cormorants *Phalacrocorax gaimardi* fed mainly when the tide is falling, and they suggested these were the optimal conditions to acquire food faster and reduce diving costs.

Finally, daily and overnight trips were recorded in Magellanic Penguins *Spheniscus magellanicus* from Martillo Island. During overnight trips, penguins exploited prey patches twice as distant as during the daily ones. Overnight trips have been reported in other penguin species (Chinstrap Penguins *Pygoscelis antarctica*, Jansen et al. 1998) as well as in Magellanic Penguins *Spheniscus magellanicus* from southern Chile (Radl and Culik 1999), and are assumed to be related to a higher energetic gain. Considering the twilight periods, important at the latitude of the colony, night time duration is only 90 min at the study area. Hence, penguins at the study colony would have enough light to forage successfully as was suggested for Rockhopper Penguins *Eudyptes chrysocome* from a nearby colony (Schiavini and Raya Rey 2004).

In conclusion, our study strongly suggests that penguins use tide and tidal currents in a restricted oceanic environment, such as the narrow waterway of the Beagle Channel, in order to maximise their foraging success. Penguins may take advantage of tidal currents to facilitate their movements to and from the main foraging area by reducing the energy needed for travel. On the other hand, we suggest that piscivorous, diving, non-flying birds may enhance their catch rate during ebb tide when fish are more concentrated in compact schools.

Zusammenfassung

Bewegungen von Nahrung suchenden Magellanpinguinen im Beagle-Kanal, Argentinien, in Beziehung zu Gezeiten und Gezeitenströmen

Diese Studie untersucht die Bewegungen von auf der Isla Martillo brütenden Magellanpinguinen *Spheniscus magellanicus* während der frühen Kükenaufzuchtphase. Nahrungssuchrouten wurden mit Hilfe von GPS-Datenloggern rekonstruiert, welche die geographische Position der Pinguine, die Wassertemperatur und die Tiefe in regelmäßigen Abständen registrierten. Die Beziehung zwischen den Bewegungen und Suchstrategien der Pinguine, Gezeiten und Gezeitenströmen wurde abgeschätzt. Die mittlere Tripdauer betrug im Durchschnitt $14,7 \pm 6,9$ h (33% über Nacht) und die maximal erreichte Entfernung 24 ± 10 km. Alle untersuchten Pinguine suchten im Osten der Kolonie nach Nahrung. Wir haben drei Phasen identifiziert, basierend auf Sinusität und Geschwindigkeit der Bewegungsbahn: Transit-, Zentral- und Rückkehrphase. Die Nahrungssuchaktivität war höher während der Zentralphase, gefolgt von der Transitphase, und niedriger während der Rückkehrphase. Der Nahrungssucherefolg, gemessen als der Zeitanteil am Meeresboden während jeder Phase, war ebenfalls während der Zentralphase am höchsten. Bei allen untersuchten Vögeln fand die Zentralphase des Nahrungssuchtrips während der Ebbe statt, und die Vögel gelangten zu den Nahrungssuchgebieten mit dem Gezeitenstrom. Unsere Studie deutet darauf hin, dass die Pinguine die Gezeitenströme ausnutzen, um ihre Bewegungen zu und von ihrem Hauptnahrungssuchgebiet zu erleichtern, indem sie die aufgewendete Energie reduzieren. Außerdem schlagen wir vor, dass fischfressende Tauchvögel ihre Fangrate während der Ebbe erhöhen könnten, wenn die Fische stärker in der Nähe des Kanalbetts konzentriert sind.

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