

Foraging under contrasting oceanographic conditions: the gentoo penguin at Kerguelen Archipelago

Amélie Lescroël*, Charles-André Bost

Centre d'Etudes Biologiques de Chizé, CNRS, UPR 1934, 79360 Villiers en Bois, France

ABSTRACT: Coastal seabirds are bound to be dependent on local marine resources. We hypothesize that the localization of the breeding colony will influence the foraging patterns of such predators. The foraging behavior of gentoo penguins *Pygoscelis papua* was investigated in contrasting marine environments at Kerguelen Archipelago over the 2002–03 and 2003–04 breeding seasons. Using time-depth recorders (TDRs) and satellite transmitters, we describe the at-sea distribution and diving behavior of gentoo penguins breeding in 2 colonies facing the open sea (Open Sea 1 and Open Sea 2) and 1 colony protected in a closed bay (Closed Sea). The foraging behavior varies extensively across the Kerguelen Archipelago, almost as much as it does over the entire range of the species. Different foraging strategies emerge, depending on the local conditions: large foraging ranges, long trips, long benthic dives on demersal fish at Open Sea colonies versus small foraging ranges, short trips, short pelagic dives on swarming crustaceans at Closed Sea, for a same foraging effort. The diving behavior of the gentoo penguin therefore varies as a function of the locality and the site, closely related to prey availability. This study demonstrates the importance of foraging plasticity as a fundamental aspect of life history in coastal marine predators.

KEY WORDS: *Pygoscelis papua* · Foraging strategy · Diving behavior · At-sea distribution · Behavioural plasticity · Geographic variation · Prey availability · Marine predator

—Resale or republication not permitted without written consent of the publisher—

INTRODUCTION

Marine top predators are highly mobile species exploiting a spatially and temporally heterogeneous environment (Hunt et al. 1999). In response to this heterogeneity, many marine birds and mammals can exhibit considerable variation in their foraging behaviour or at-sea distribution (e.g. Croxall et al. 1988, Wilson 1995, Boyd 1996, Weimerskirch 1998, Rodary et al. 2000, Charassin & Bost 2001, Beauplet et al. 2004, Grémillet et al. 2004a).

For the last 20 yr, the development of microprocessor-based time-depth recorders (e.g. Kooyman et al. 1992, Croxall et al. 1993, Wilson 1995, Boyd et al. 2004), satellite transmitters and global positioning systems (e.g. Jouventin & Weimerskirch 1990, McConnell et al. 2002, Weimerskirch et al. 2002) has

allowed us to gain considerable knowledge about the foraging behavior and energetics of diving species. Recently, it has appeared that individuals of the same species can adapt their behavioral responses, via different foraging modes, to changes in prey availability (Boyd et al. 1994, McCafferty et al. 1998, Ropert-Coudert et al. 2002). The response of any one species will differ according to several parameters such as season, breeding stage and abiotic conditions (Salamolard & Weimerskirch 1993, Hunt et al. 1999, Charassin & Bost 2001, Charassin et al. 2002). Hence, the effects of biotic and abiotic factors on foraging strategies are difficult to discriminate. One way to cope with this difficulty is to adopt a comparative approach on a small spatial scale. The study, during a given year and breeding stage, of several populations of the same species, living in habitats which are geographi-

*Email: lescroel@cebc.cnrs.fr

cally close to each other but different in terms of marine resources, should eliminate the majority of the confounding abiotic factors. Until now, few studies (Kirkwood & Robertson 1997, Radl & Culik 1999) have followed this approach.

A particularly well-suited model is the gentoo penguin *Pygoscelis papua*, which is one of the main avian benthic consumers of the sub-Antarctic area (e.g. Croxall & Prince 1980a, Ridoux 1994, Woehler 1995). Gentoo penguins are inshore opportunistic feeders as illustrated by their diet varying greatly both with locality (see review in Bost & Jouventin 1990) and breeding colony (Hindell 1989, Lescroël et al. 2004). Despite the large distribution range of the gentoo penguin from the Antarctic Peninsula (63° 15' to 65° 05' S) to the northernmost sub-Antarctic islands (Crozet Archipelago, 46° 00' S), only 2 studies (Hindell 1989, Lescroël et al. 2004) have focused on the spatial variation of the gentoo penguin diet. No study has investigated the spatial variation of the diving behavior of the gentoo penguin. Furthermore, the at-sea distribution and movements of the gentoo penguin have rarely been directly determined (i.e. by satellite telemetry or geolocation: Wilson et al. 1998, during summer; Clausen & Pütz 2003, Tanton et al. 2004, during winter) and their diving behavior has been described in only 4 (Croxall et al. 1988, Williams et al. 1992, Bost et al. 1994, Wilson et al. 1996) of the 9 breeding localities (Bost & Jouventin 1990), and was never carried out on more than 1 colony.

Almost 40 000 pairs of gentoo penguins (12% of the world's population) breed annually on Kerguelen Archipelago (Bost & Jouventin 1990). They are scattered in small colonies along the indented coast, experiencing a wide range of oceanographic conditions. As gentoo penguins are neritic foragers during the breeding period (Wilson 1995), they are bound to be dependent on local marine resources. We therefore hypothesize that the localization of the breeding colony will strongly influence their foraging patterns. In this study, conducted on a small spatial scale, our objectives were (1) to describe the foraging characteristics, diving behavior and feeding areas of the gentoo penguin at Kerguelen Archipelago, (2) to compare its foraging behavior in contrasting marine environments at Kerguelen Archipelago, between colonies facing the sea and a sheltered colony, and (3) to study how local oceanographic conditions may affect the foraging ecology of a marine top predator.

This is the first study to investigate the foraging behavior of the gentoo penguin on the Kerguelen plateau, which is the largest submarine plateau of the Southern Ocean and one of the most productive areas of sub-Antarctic localities (Duhamel 1987, Blain et al. 2001). It also provides the first comparative study of diving behavior in penguins that takes into account environmental variability on a small spatial scale during the whole breeding cycle (from incubation to chick crèche). This study was conducted over 2 consecutive years at several sites, from winter to summer each year, and encompassed 2 breeding seasons.

MATERIALS AND METHODS

Study sites. The study took place during the 2002–03 and 2003–04 austral summers (hereafter called 2002 and 2003) at Kerguelen Archipelago. We chose 3 study colonies (120 to 200 breeding pairs) localized in contrasting habitats, 20 to 55 km apart (Fig. 1); 1 colony in the largest sheltered bay of the Archipelago and 2 colonies exposed to the open sea, northeast and southeast of the Archipelago (Estacade and Antarctic Cove, hereafter called Open Sea 1 and Open Sea 2, respectively). Located close to the Polar Front, the open sea colonies have direct access to the rich benthic ichthyofauna of the shelf's neritic waters (Duhamel 1987).

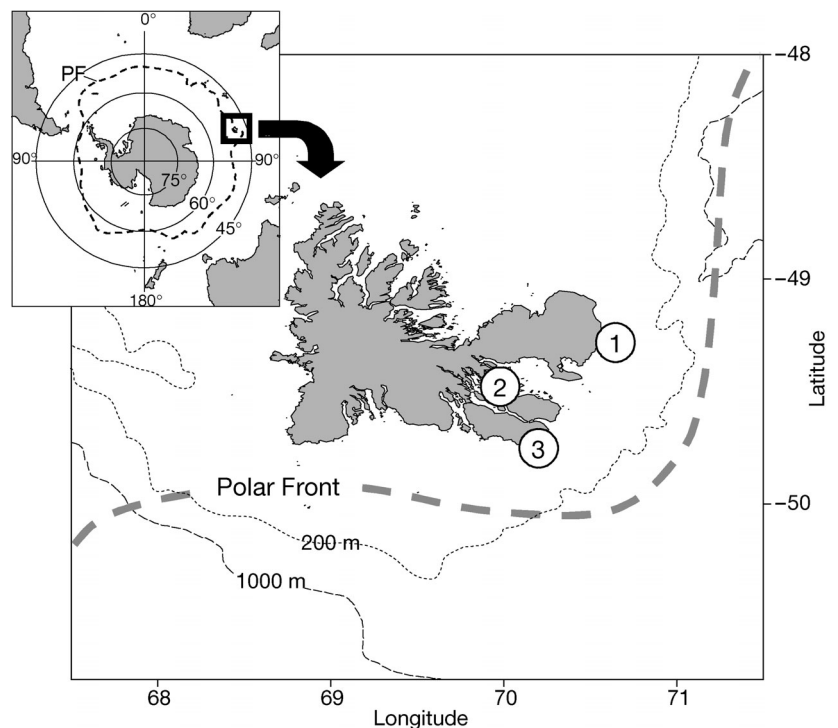


Fig. 1. Kerguelen Archipelago (48° 45' to 50° 00' S, 68° 45' to 70° 58' E) showing the 3 study sites: (1) Open Sea 1 (Estacade), (2) Closed Sea (Longue Island, Morbihan Gulf), (3) Open Sea 2 (Antarctic Cove). PF: Polar Front

Open Sea 1 and Open Sea 2 differ by their distance to the Polar Front and to oceanic waters, and by their terrestrial environment (a flat peninsula surrounded by sandy beaches and steep cliffs broken by deep sandy valleys, respectively) (Lescroël et al. 2004). The Closed Sea colony, Longue Island, is located in the western part of the Morbihan Gulf, a sheltered bay of about 700 km² with kelp belts, muddy sand and low tidal amplitude. The Morbihan Gulf is a productive ecosystem, which supports important populations of meso- and macrozooplankton (Razouls et al. 1997, Bocher et al. 2001).

Foraging behaviour. During the 2002 and 2003 breeding seasons, a total of 46 breeding gentoo penguins were equipped with time-depth recorders (TDRs) to study their diving behavior. We used 2 models of TDR (Wildlife Computers) which recorded depth (resolution of 0.5 m), temperature and light level every 5 s: (1) Mk7 (86 mm × 20 mm × 11 mm, 27 g) and (2) Mk9 (67 mm × 17 mm × 17 mm, 30 g). A total of 11 breeding gentoo penguins were equipped with a platform terminal transmitter (PTT, Kiwisat 101, 130 mm × 28 mm × 14 mm, 77 g) during the 2002 breeding season to study their at-sea distribution. The cross-sectional areas of Mk7, Mk9 and PTTs were equivalent to 1.0, 1.3 and 1.7% of the cross-sectional area of a gentoo penguin, respectively. We equipped the same number of males and females with each device.

The devices were streamlined to reduce hydrodynamic drag (Culik et al. 1994). Breeding birds were captured on the beach at their departure to the sea using a landing net. The devices were attached to feathers in the midline of the lower back so as to minimize drag (Bannasch et al. 1994) using a cyanoacrylate glue (Loctite 401) and plastic cable ties. Birds were weighed, measured, marked with serial numbers painted on the breast with picric acid and then released towards the sea. Care was taken to minimize stress after the capture by covering the bird's head with a hood while they were being handled (10 to 15 min). Birds were recaptured after 1 foraging trip and the devices were subsequently redeployed on different individuals. All devices were recovered, except for one on a female from the Open Sea 1 group during crèche 2002 that did not come back to the colony before our departure.

Satellite data analysis. The Argos system assigned locations to 7 classes on the basis of positional accuracy. The accuracy of locations was classified as follows: Class 3 was accurate to within 150 m, Class 2 to 350 m, Class 1 to 1 km; Classes 0, A and B have no assigned accuracy; and Class Z indicates an invalid location. Because of the low number of daily locations, all classes except Class Z were included in the analysis. Locations were filtered so that those that gave

transit speeds ≥ 2.8 m s⁻¹ over half an hour (i.e. the maximum measured velocity, Robinson & Hindell 1996) or ≥ 2.0 m s⁻¹ over an hour or more (i.e. the maximum velocity measured for an extended period, Wilson et al. 1989) were discarded. Then, using homemade software (CROZARG, author: T. Zorn), we calculated the maximal range from the colony, the swimming speed to this maximum distance (i.e. the outward swimming speed calculated as the mean of all the swimming speeds between locations from the departure to the point of maximal range) and the return swimming speed to the colony (mean of all the swimming speeds between locations from the point of maximal range to the return to the colony). We also calculated an index of sinuosity, which is the cumulated distance traveled to the point of maximal range divided by the distance of maximal range (Haggett & Chorley 1969, Grémillet et al. 2004b). Due to the low number of locations obtained for 2 birds from Open Sea 1 (i.e. 5 locations versus 11 to 76 locations for the other equipped birds), we discarded them from the calculations of swimming speed and sinuosity.

Dividing data analysis. Dive parameters were analyzed using dedicated dive analysis software (Multi-Trace, Jensen Software Systems) to determine the dive depth, dive duration, bottom time (i.e. the time spent around the maximum depth, defined by the period spent at a depth equal to at least 60% of the maximum depth with a vertical speed smaller than 0.3 m s⁻¹, which corresponds to the inflexion point of the dive before and after reaching the maximum depth), total way vertical at the bottom (i.e. the vertical distance travelled during bottom time), and the duration and vertical velocity of the descent and ascent phases. The determination of each parameter was visually verified for each dive. According to the depth resolution of TDRs, a dive was deemed to occur when the maximum depth was ≥ 1 m.

The dives were visually classified by dive profile into 6 categories (Fig. 2). We calculated the diving efficiency (bottom time/[dive duration + post-dive interval duration], Ydenberg & Clark 1989) for U- and W-dives, excluding dives with an extended post-dive interval ≥ 325 s (bout-ending criterion, Gentry & Kooyman 1986).

To compare parameters of general foraging behavior (e.g. total trip duration, number of dives) between colonies, we used individual averages recorded for each bird. For 3 of the birds, these parameters were considerably lower compared to the other birds, indicating that they did not perform foraging trips. They were not included in further analysis. We used the total dive rate, i.e. the vertical distance travelled per foraging trip, and the daily dive rate, i.e. the vertical distance travelled per 24 h, as indices of foraging effort.

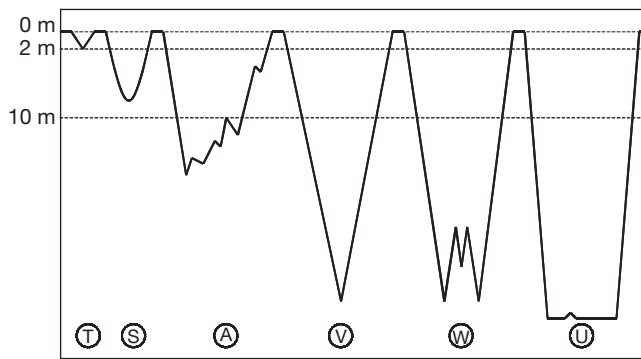


Fig. 2. *Pygoscelis papua*. Stylized profiles of dive types performed by gentoo penguins at Kerguelen Archipelago. T: travelling dives, occurring at depths ≤ 2 m; S: searching dives, occurring at depths between 2 and 10 m with no irregularities in the smooth descent/ascent patterns; A: asymmetrical feeding dives performed at depths > 2 m with a distinct descent phase and then a ragged ascent phase (or the opposite); V: pelagic feeding dives, i.e. symmetrical dives performed at depths > 10 m with no bottom phase; W: symmetrical feeding dives with pronounced ragged bottom; U: benthic feeding dives performed at depths > 10 m with flat bottom (Le Boeuf et al. 1988, Williams et al. 1992, Wilson 1995, Kirkwood & Robertson 1997)

Temperature data were used to determine the beginning and end of each foraging trip. Depending on the air temperature, the logger temperature could drop sharply when the bird entered the water to attain the water temperature (the sea-surface temperature at Kerguelen Archipelago during winter is about 3°C , Park et al. 1993). We defined the onset of this temperature drop as the beginning of the foraging trip. The end of the foraging trip was indicated by a rapid temperature increase and strong fluctuations.

For comparison of specific dive parameters (e.g. maximum depth, dive duration), dives were treated independently. In order to take into account the partial autocorrelation of dives (Hurlbert 1984) and to give all birds an equal statistical weight, we randomly selected 50 dives per bird except for 1 bird (69 feeding dives, 40 dives selected). The maximum depth of foraging dives actually lost correlation after 2 successive dives and

the lowest number of foraging dives recorded for 1 individual was around 100. This resulted in a 2090 dives data set (1150, 800 and 250 at Open Sea 1, Closed Sea and Open Sea 2, respectively). As the maximum depth reached during a dive influenced all other dive parameters (Wilson et al. 1996, 1997, Cherel et al. 1999), the data were standardized (Sokal & Rohlf 1995) by depth class to compare normal deviates of dive parameters independently of depth (Tremblay & Cherel 2000).

Feeding frequency and effect of instrumentation.

We estimated the effect of the instrumentation by comparing foraging trip duration between instrumented and non-instrumented birds. For that, we painted the sides of 30 incubating birds in Open Sea 1 and Closed Sea without catching them, using a brush with a long handle. We were then able to know at a distance, which one of the mates (marked or not) was at sea and which one was on the nest. Hence, foraging trip duration of non-instrumented birds was visually assessed by 3 observations per day during incubation and chick guard for 1 wk.

During crèche, both parents may forage at sea at the same time and bird departures or returns often occurred during periods of darkness. Consequently, direct observation of shift duration was by far more difficult and we used 10 VHF transmitters ($60\text{ mm} \times 26\text{ mm} \times 14\text{ mm}$, 36 g; i.e. 1.6% of the cross-sectional area of a gentoo penguin, Sirtrack) in Open Sea 1, Open Sea 2 and Closed Sea to assess the feeding frequency. The transmitters were attached using Loctite 401 and remained on the birds for 3 to 6 d, providing information on 2 to 7 trip durations per bird. The presence or absence of the birds at the colony was assessed by scanning the VHF frequencies every 2 h, day and night, using a multidirectional Yaggi antenna coupled to a VHF receptor. For analysis, we used individual averages for each bird.

Statistics. Data were analyzed statistically using Systat 7.0. Values are given as means \pm SD unless stated otherwise. Comparisons of general foraging parameters between the study sites and breeding

Table 1. *Pygoscelis papua*. Foraging trip duration (d) of gentoo penguins at Kerguelen Archipelago (mean \pm SD). n = number of pairs successfully followed. Data for incubation and chick guard are from the 2002 breeding season and data for crèche from the 2003 breeding season. Values in the same horizontal row not sharing a common superscript are significantly different between sites for the same breeding stage (Student *t*-test and ANOVA). TDR: time-depth recorder

Set	Incubation		Chick guard		Crèche		
	Open Sea 1	Closed Sea	Open Sea 1	Closed Sea	Open Sea 1	Open Sea 2	Closed Sea
Non-instrumented birds	3.16 ± 1.00^a n = 29	2.08 ± 1.15^b n = 24	1.50 ± 0.76^a n = 28	0.98 ± 0.19^b n = 12	–	–	–
VHF birds	–	–	–	–	1.17 ± 0.54^a n = 10	1.07 ± 0.47^a n = 9	0.69 ± 0.26^a n = 9
TDR birds	2.15 ± 0.97^a n = 6	2.03 ± 0.74^a n = 6	0.96 ± 0.37^a n = 6	0.95 ± 0.55^a n = 6	2.53 ± 1.19^a n = 5	$1.40 \pm 1.14^{a,b}$ n = 5	0.83 ± 0.63^b n = 4

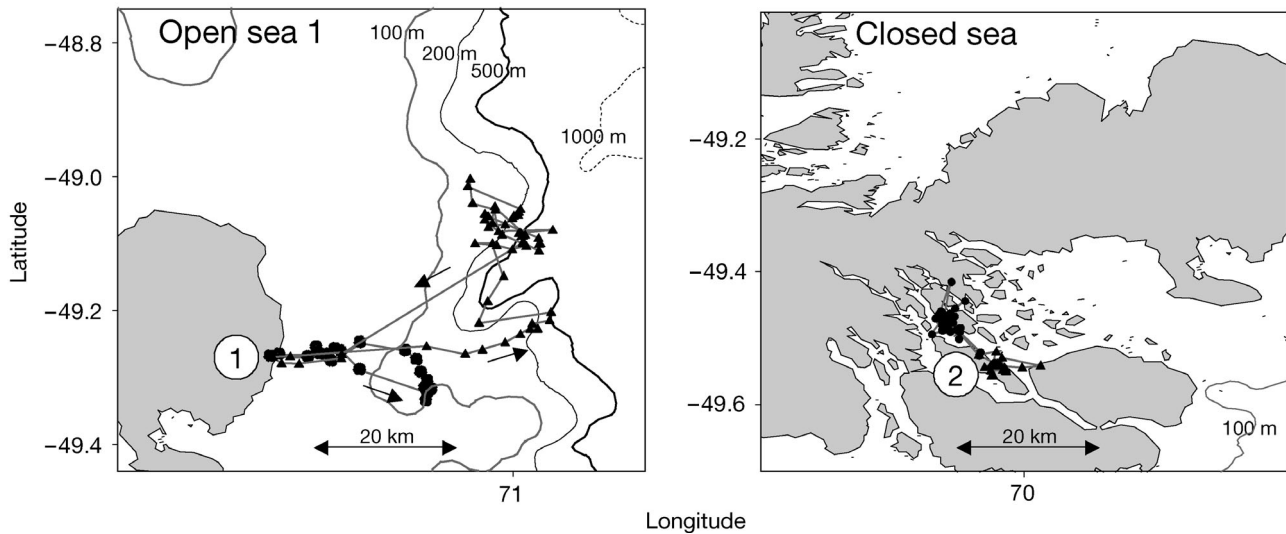


Fig. 3. *Pygoscelis papua*. Tracks of gentoo penguins during the incubation stage at Open Sea 1 and Closed Sea. At each site, 2 tracks from 2 different birds (1 trip per bird) are plotted and represented by 2 different symbols. 1: Open Sea 1 colony; 2: Closed Sea colony

stages were made using a Student's *t*-test or ANOVA. Dive parameters were compared between sites with respect to the breeding stage using a nested ANOVA with the factor 'bird' nested into 'site'. ANOVAs were followed by the Tukey post hoc test when necessary. Normality and homoscedasticity were tested before using parametric tests. Significance was assumed for $p < 0.05$.

RESULTS

Foraging trip duration

Instrumented and non-instrumented birds

The foraging trip duration did not differ significantly between instrumented and non-instrumented birds ($F_{1,154} = 1.939$, $p = 0.166$ for all 3 sites) (Table 1).

Among sites

After being equipped in late afternoon, birds departed to sea mainly at the end of the subsequent night at Open Sea 1 and Open Sea 2 (81 and 80% of departures, respectively) and at dawn (31%) or during the day after (44%) at Closed Sea. At all sites, they returned mainly during the day (57, 60 and 94% at Open Sea 1, Open Sea 2 and Closed Sea, respectively).

Gentoo penguins from Open Sea 1 made significantly longer foraging trips than birds from Closed Sea

during incubation and chick guard (Table 1, $F_{1,53} = 13.232$, $p = 0.001$ and $F_{1,40} = 5.228$, $p = 0.028$, respectively, data from non-instrumented birds). Concerning the crèche period, birds from Open Sea 1 and Open Sea 2 also tended to forage longer than birds from Closed Sea ($F_{1,28} = 3.055$, $p = 0.065$, data from VHF birds).

Among breeding stages

At both Open Sea 1 and Closed Sea, trip duration was significantly longer during incubation than during other breeding stages ($F_{2,95} = 32.895$, $p < 0.0001$ at Open Sea 1 and $F_{2,45} = 11.589$, $p < 0.0001$ at Closed Sea) (Table 1).

Satellite tracking data

A total of 7 birds were tracked during incubation, 4 at Open Sea 1 and 3 at Closed Sea (Fig. 3). Absence from the colony ($t_{3,7} = -0.589$, $p = 0.598$) and the at-sea trip duration ($t_{2,7,7} = -0.776$, $p = 0.499$) did not differ among sites, nor did the number of locations obtained ($t_{4,2,7} = -0.232$, $p = 0.828$). However, Open Sea 1 gentoo penguins foraged farther out than Closed Sea ones (Table 2, $t_{2,7,7} = 2.781$, $p = 0.039$). At Open Sea 1, all birds headed towards the plateau slope (100 to 200 m isobaths) with 1 bird foraging above the 500 m isobath, more than 46 km away from the breeding colony. At Closed Sea, birds were extremely coastal, remaining inside the Morbihan Gulf at a maximum distance of 11.6 km from the colony.

Table 2. *Pygoscelis papua*. Satellite tracking data (mean \pm SD) at 2 sites of the Kerguelen Archipelago in 2002. $n = 4$ birds at Open Sea 1 and 3 birds at Closed Sea during incubation and $n = 4$ birds at Open Sea 1 during chick guard. Values in the same horizontal row not sharing a common superscript are significantly different (Student t -test)

2002	Incubation		Chick guard Open Sea 1
	Open Sea 1	Closed Sea	
Deployment period	17–30 Sep 2002	05–12 Oct 2002	19–23 Oct 2002
Absence duration (d)	2.53 \pm 1.68 ^a	3.65 \pm 2.94 ^a	2.32 \pm 1.13 ^a
At sea trip duration (d)	2.21 \pm 1.45 ^a	3.65 \pm 2.94 ^a	2.20 \pm 0.95 ^a
Number of locations	41.30 \pm 30.00 ^a	38.00 \pm 33.90 ^a	22.50 \pm 18.10 ^a
Maximum foraging range (km)	28.30 \pm 14.10 ^a	8.30 \pm 4.20 ^b	30.80 \pm 8.10 ^a

Open Sea 1 gentoo penguins swam faster than those at Closed Sea during the outward journey (Fig. 4, $t_{2,7,6} = 5.143$, $p = 0.018$). Return swimming speed ($t_{2,5,6} = 1.824$, $p = 0.186$), outward sinuosity index ($t_{2,5,6} = -1.646$, $p = 0.218$) and return sinuosity index ($t_{2,1,6} = -0.479$, $p = 0.677$) did not differ significantly for birds of both sites, despite a trend for a lower speed and higher sinuosity values at Closed Sea.

In the same way, the evolution of foraging range with trip duration illustrated differences among sites in foraging patterns. At Open Sea 1, the foraging range increased quickly during the first 20% of the foraging trip duration, reaching its maximum around the middle of the foraging trip and then decreasing gradually on the way back, forming circular tracks (Fig. 5A). At Closed Sea, the foraging range showed a totally different pattern, with low variations and a maximum range reached at around 70% of the foraging trip duration (Fig. 5B). This suggests that Closed Sea birds foraged nearly at the same distance from the breeding colony

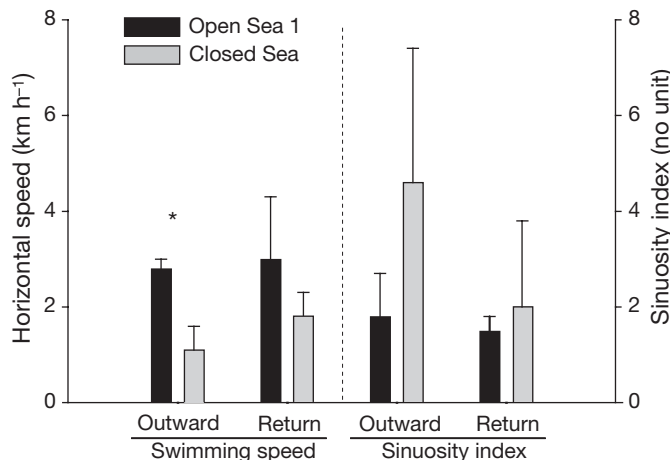


Fig. 4. *Pygoscelis papua*. Outward and return swimming speeds and sinuosity index of foraging trips performed by gentoo penguins at Open Sea 1 and Closed Sea. Data from satellite tracking ($n = 3$ for each site). * $p < 0.05$

all along the trip or that they came and went near the shore several times, which is supported by the tracks forming 'stars' in contrast to 'loops' at Open Sea 1 (Fig. 3).

None of the foraging characteristics collected by satellite tracking at Open Sea 1 differed between the incubation and chick guard periods (Table 2).

Dive types

Open Sea gentoo penguins performed a higher proportion of traveling dives, as opposed to foraging dives, than Closed Sea birds. The difference was statistically significant during incubation (39.2% at Open Sea 1 versus 15.8% at Closed Sea, $t_{7,8,12} = 2.677$, $p = 0.029$) and crèche (44.3% at Open Sea 1 and 46.9% at Open Sea 2 versus 27.9% at Closed Sea, $F_{2,14} = 9.683$, $p = 0.004$) but not during chick guard (39.3% at Open Sea 1 versus 30.6% at Closed Sea).

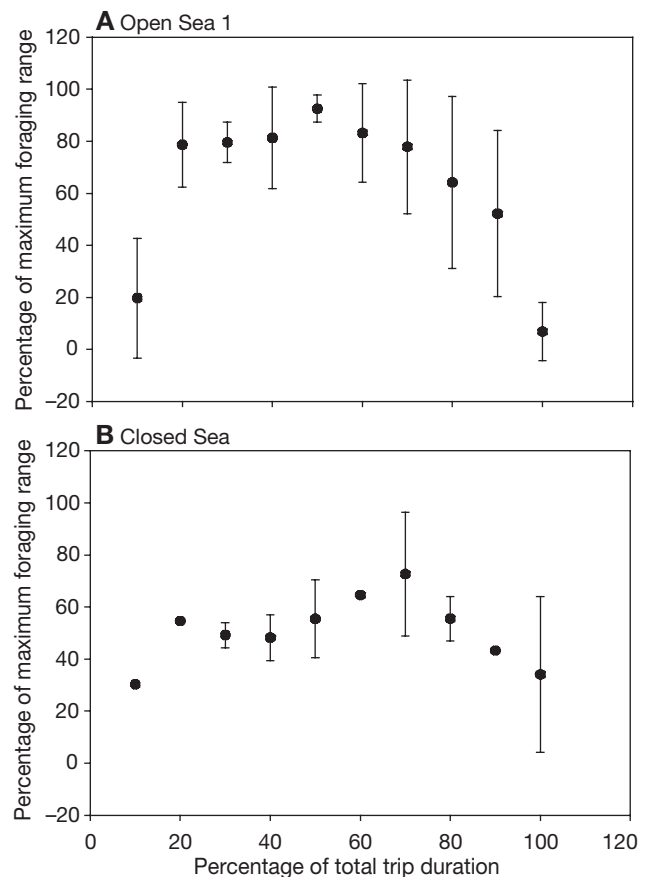


Fig. 5. *Pygoscelis papua*. Evolution of the foraging range during the foraging trip of gentoo penguins at (A) Open Sea 1 ($n = 8$) and (B) Closed Sea ($n = 3$). Data from satellite tracking

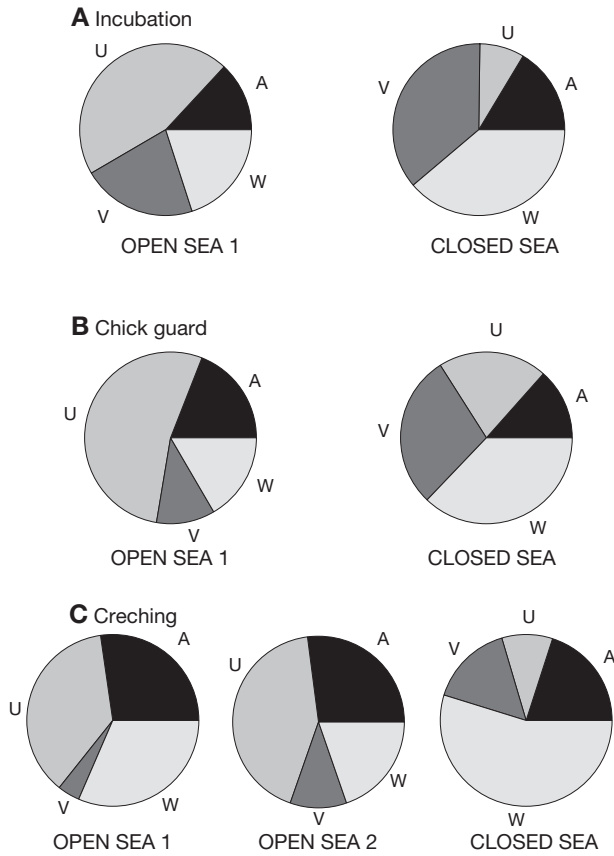


Fig. 6. *Pygoscelis papua*. Use of dive types by gentoo penguins at 3 sites (Open Sea 1, Open Sea 2 and Closed Sea) throughout the breeding season (A) during the incubation stage, (B) during the chick guard stage and (C) during the crèche stage. A: asymmetrical dives; V: pelagic dives; W: symmetrical dives with ragged bottom; U: benthic dives. Data are from time-depth recorders

Gentoo penguins were not only diurnal foragers. A small proportion of shallow foraging dives (<15 m depth) was performed during the night. This occurred more often at Open Sea 1 (16.4, 16.8 and 13.2% during

incubation, chick guard and crèche, respectively) than at other sites (3.2, 5.3 and 11.9% during incubation, chick guard and crèche at Closed Sea, respectively and 4.2% during crèche at Open Sea 2).

During their foraging trips, gentoo penguins from Open Sea 1 performed a majority of benthic dives (U-dives), whereas those from Closed Sea performed a majority of pelagic dives (V- and W-dives, Fig. 6). Whatever the breeding stage, the most common dive types were U-dives (from 37.1 to 53.3% at Open Sea) and W-dives (from 37.1 to 54.8% at Closed Sea); A- and V-dives were used less (from 13.1 to 27.3% and 4.2 to 36.4%, respectively).

Diving patterns: the scale of the trip

Among sites

During incubation and chick guard, TDR birds from Open Sea 1 and Closed Sea exhibited the same general characteristics in their foraging trips, except for dive frequency during incubation and time spent at the bottom during chick guard (Table 3). During incubation, the average number of dives conducted per hour by Closed Sea penguins was nearly twice that recorded at Open Sea 1. During chick guard, the time spent daily at the bottom by Closed Sea birds was only 52% that recorded at Open Sea 1. However, in both cases, the total and daily dive rates were equal: birds from Open Sea 1 and Closed Sea exhibited the same foraging effort during incubation and chick guard.

During crèche, differences between sites were more marked (Table 4). At the end of the breeding period, Closed Sea birds differed from Open Sea 1 birds in almost all their characteristics and from Open Sea 2 birds in exhibiting a higher dive frequency and a lower total dive rate. Foraging behavior of gentoo penguins

Table 3. *Pygoscelis papua*. Characteristics of foraging trips (means ± SD) from 28 gentoo penguins instrumented with TDRs at Kerguelen Archipelago in 2002. n = the number of birds instrumented. Values in the same horizontal row not sharing a common superscript are significantly different between sites for a same breeding stage (Student t-test)

2002	Incubation		Chick guard		Crèche
	Open Sea 1	Closed Sea	Open Sea 1	Closed Sea	Open Sea 1
n	6	6	6	6	4
Deployment period	16 Sep–1 Oct	04–8 Oct	17–20 Oct	25–27 Oct	19–22 Nov
Absence duration (d)	2.15 ± 0.97 ^a	2.03 ± 0.74 ^a	0.96 ± 0.37 ^a	0.95 ± 0.55 ^a	1.01 ± 0.82
At-sea trip duration (d)	2.00 ± 1.01 ^a	1.25 ± 0.46 ^a	0.91 ± 0.37 ^a	0.67 ± 0.29 ^a	0.94 ± 0.70
Travelling time (h)	2.77 ± 2.49 ^a	0.58 ± 0.44 ^a	1.24 ± 0.67 ^a	0.80 ± 0.67 ^a	1.17 ± 1.13
Foraging time (h)	23.69 ± 8.76 ^a	19.63 ± 6.83 ^a	13.46 ± 2.99 ^a	11.14 ± 4.19 ^a	14.28 ± 10.75
Dive frequency (dive h ⁻¹)	9.66 ± 3.11 ^a	17.17 ± 4.84 ^b	12.27 ± 2.97 ^a	16.29 ± 3.53 ^a	13.39 ± 6.29
Time spent at the bottom (h d ⁻¹)	4.42 ± 1.68 ^a	2.98 ± 1.33 ^a	6.89 ± 2.69 ^a	3.59 ± 1.59 ^b	7.99 ± 2.92
Total dive rate (km trip ⁻¹)	52.50 ± 21.13 ^a	43.98 ± 21.96 ^a	25.28 ± 15.30 ^a	29.42 ± 9.67 ^a	30.09 ± 28.31
Daily dive rate (km d ⁻¹)	25.01 ± 7.07 ^a	20.99 ± 4.00 ^a	26.57 ± 13.85 ^a	34.89 ± 9.47 ^a	25.82 ± 8.18

Table 4. *Pygoscelis papua*. Characteristics of foraging trips (means \pm SD) from 14 gentoo penguins instrumented with TDRs at Kerguelen Archipelago in 2003. n = the number of birds instrumented. Values in the same horizontal row not sharing a common superscript are significantly different between sites (1-way ANOVA followed by a Tukey post hoc test)

2003	Crèche		
	Open Sea 1	Open Sea 2	Closed Sea
n	5	5	4
Deployment period	06–9 Jan	20–28 Nov	28–30 Nov
Absence duration (d)	2.53 \pm 1.19 ^a	1.40 \pm 1.14 ^{a,b}	0.83 \pm 0.63 ^b
At-sea trip duration (d)	2.16 \pm 0.99 ^a	1.40 \pm 1.14 ^{a,b}	0.53 \pm 0.41 ^b
Traveling time (h)	4.19 \pm 2.39 ^a	2.49 \pm 2.02 ^{a,b}	0.48 \pm 0.37 ^b
Foraging time (h)	28.16 \pm 12.70 ^a	15.69 \pm 10.53 ^b	8.43 \pm 6.70 ^b
Dive frequency (dive h ⁻¹)	11.51 \pm 6.12 ^a	9.74 \pm 3.86 ^a	15.03 \pm 3.30 ^b
Time spent at the bottom (h d ⁻¹)	4.90 \pm 0.74 ^a	5.22 \pm 2.21 ^a	4.02 \pm 0.76 ^a
Total dive rate (km trip ⁻¹)	61.27 \pm 33.03 ^a	35.94 \pm 29.64 ^a	18.31 \pm 15.96 ^b
Daily dive rate (km d ⁻¹)	22.77 \pm 10.07 ^a	24.65 \pm 4.20 ^a	26.16 \pm 13.05 ^a

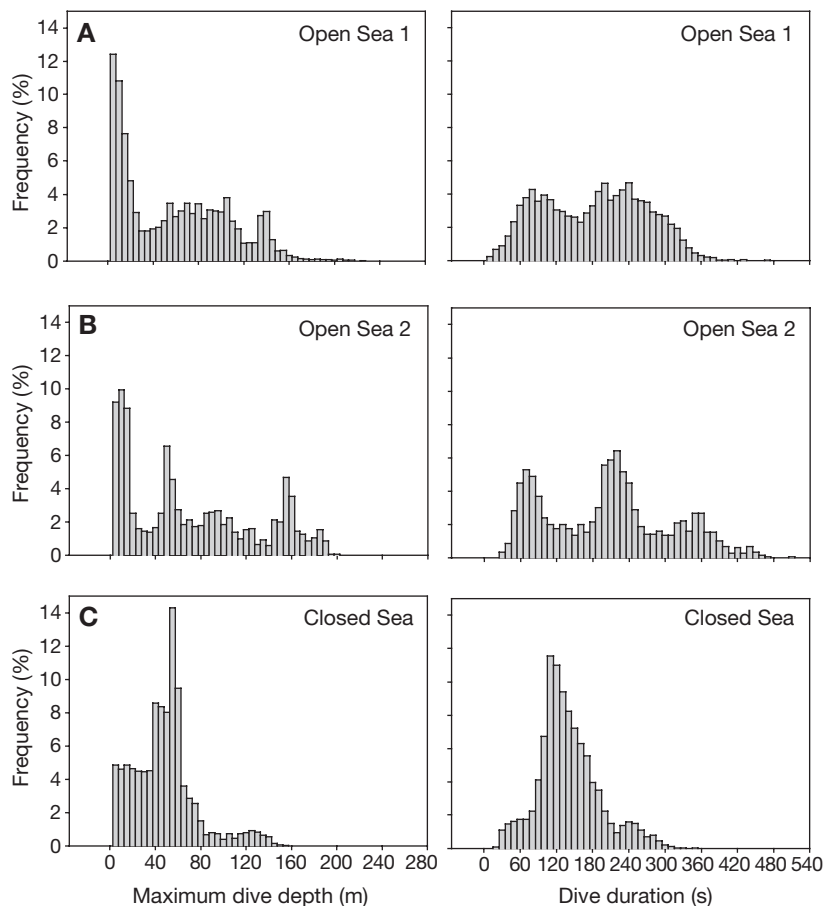


Fig. 7. *Pygoscelis papua*. Frequency distribution of dive depth and dive duration (excluding travelling dives) at (A) Open Sea 1 (n = 8343 dives), (B) Open Sea 2 (n = 1495 dives) and (C) Closed Sea (n = 5508 dives). Data are from time-depth recorders

from Open Sea 1 and Open Sea 2 did not differ during crèche except for the foraging time, which was greater at Open Sea 1. Due to their much shorter foraging trips and despite their higher dive frequency, Closed Sea birds exhibited a lower total dive rate. Nevertheless, the daily dive rate did not differ among the 3 sites, so birds would make about the same foraging effort even during crèche.

Among breeding stages

At both Open Sea 1 and Closed Sea sites, most parameters remained identical between stages (Tables 3 & 4). Closed Sea birds, however, reduced their foraging time ($t_{10,12} = -2.596$, $p = 0.027$) and increased their foraging effort through their daily dive rate ($t_{6,7,12} = 3.312$, $p = 0.014$) between incubation and chick guard.

Among years

At Open Sea 1, foraging trips undertaken by TDR birds lasted longer during crèche in 2003 than crèche in 2002 (Tables 3 & 4). This was reflected by longer absences ($t_{7,9} = -2.457$, $p = 0.044$), at-sea trip durations ($t_{7,9} = -3.287$, $p = 0.013$), and travelling ($t_{6,9} = -2.914$, $p = 0.027$) and foraging ($t_{7,9} = -2.591$, $p = 0.036$) times in 2003. Nevertheless, there was no difference in dive frequency, total time spent daily at the bottom, or total or daily dive rate.

Diving patterns: the scale of the dive

Gentoo penguins from Open Sea 1, Open Sea 2 and Closed Sea performed a total of 8343, 1495 and 5508 feeding dives (A-, U-, W- and V-dives), respectively. Among those, the deepest dives reached 225.0, 198.5 and 153.5 m, and the longest dives lasted 470, 545 and 345 s, respectively.

Gentoo penguins exhibited large differences among sites in terms of depth use and dive duration (Fig. 7).

Table 5. *Pygoscelis papua*. Characteristics of feeding dives from the randomly selected data set (see 'Materials and methods') depending on site and stage at Kerguelen Archipelago in 2002. Values in italics represent standardized data. n = the number of analyzed dives. Values in the same horizontal row not sharing a common superscript are significantly different between sites (nested ANOVA with 'bird' nested into 'site', incubation and chick guard data only). For diving efficiency (bottom time/[dive duration + post-dive interval duration]), only U- and W-dives with post-dive intervals ≤ 325 s were taken into account

2002	Incubation		Chick guard		Crèche
	Open Sea 1	Closed Sea	Open Sea 1	Closed Sea	Open Sea 1
n	300	300	300	300	200
Dive depth (m)	59.15 \pm 41.65 ^a	39.32 \pm 17.28 ^b	60.82 \pm 41.01 ^a	61.72 \pm 40.71 ^a	61.01 \pm 46.64
Dive duration (s)	180.85 \pm 72.49 ^a <i>0.04 \pm 0.86^a</i>	130.33 \pm 42.99 ^b <i>-0.50 \pm 0.98^a</i>	192.61 \pm 70.92 ^a <i>0.27 \pm 0.88^a</i>	155.50 \pm 63.10 ^b <i>-0.64 \pm 0.83^b</i>	201.45 \pm 100.60 <i>0.60 \pm 1.15</i>
Bottom time (s)	75.82 \pm 52.70 ^a <i>0.01 \pm 1.00^a</i>	41.60 \pm 38.30 ^b <i>-0.44 \pm 0.90^b</i>	90.06 \pm 54.36 ^a <i>0.29 \pm 0.97^a</i>	42.24 \pm 36.14 ^b <i>-0.62 \pm 0.83^b</i>	104.61 \pm 71.02 <i>0.53 \pm 1.03</i>
Post-dive interval duration (s)	39.12 \pm 39.93 ^a <i>-0.38 \pm 1.05^a</i>	38.42 \pm 37.05 ^a <i>-0.03 \pm 1.18^a</i>	35.79 \pm 34.90 ^a <i>-0.42 \pm 1.06^a</i>	38.83 \pm 39.10 ^a <i>-0.40 \pm 1.10^a</i>	51.20 \pm 57.74 <i>0.39 \pm 1.57</i>
Descent rate (m s ⁻¹)	1.09 \pm 0.50 ^a <i>0.02 \pm 1.06^a</i>	0.97 \pm 0.35 ^a <i>-0.03 \pm 0.97^a</i>	1.15 \pm 0.52 ^a <i>0.23 \pm 1.04^a</i>	1.07 \pm 0.47 ^a <i>-0.17 \pm 1.15^a</i>	1.08 \pm 0.56 <i>0.20 \pm 0.95</i>
Ascent rate (m s ⁻¹)	-1.03 \pm 0.60 ^a <i>-0.01 \pm 1.10^a</i>	-0.87 \pm 0.40 ^b <i>-0.09 \pm 0.92^a</i>	-1.10 \pm 0.61 ^a <i>0.10 \pm 0.92^a</i>	-1.00 \pm 0.49 ^a <i>-0.15 \pm 1.04^a</i>	-1.11 \pm 0.71 <i>0.31 \pm 1.11</i>
Total way vertical at the bottom (m)	8.44 \pm 7.99 ^a <i>-0.28 \pm 0.81^a</i>	10.10 \pm 9.18 ^a <i>-0.16 \pm 1.06^a</i>	9.05 \pm 8.07 ^a <i>-0.20 \pm 0.75^a</i>	8.97 \pm 8.18 ^a <i>-0.24 \pm 0.92^a</i>	9.53 \pm 8.13 <i>-0.13 \pm 0.84</i>
Diving efficiency	0.42 \pm 0.15 ^a <i>0.06 \pm 1.07^a</i>	0.33 \pm 0.12 ^b <i>-0.62 \pm 0.90^b</i>	0.46 \pm 0.13 ^a <i>0.41 \pm 0.87^a</i>	0.32 \pm 0.12 ^b <i>-0.58 \pm 0.91^b</i>	0.45 \pm 0.10 <i>0.43 \pm 0.82</i>

Throughout the breeding cycle, gentoo penguins from Open Sea performed longer dives (nested ANOVA: $F_{1,12} = 19.540$, $p = 0.001$ for incubation, $F_{1,12} = 7.777$, $p = 0.019$ for chick guard and $F_{2,14} = 4.885$, $p = 0.030$ for crèche) and spent more time at the bottom ($F_{1,12} = 11.375$, $p = 0.007$ for incubation, $F_{1,12} = 21.982$, $p = 0.001$ for chick guard and $F_{2,14} = 9.032$, $p = 0.005$ for crèche) than birds from Closed Sea (Tables 5 & 6). The dives performed at Open Sea 1 were significantly deeper ($F_{1,12} = 109.555$, $p = 0.000$) than those recorded at Closed Sea only during incubation. Gentoo penguins from Open Sea also exhibited a higher dive efficiency during incubation ($F_{1,12} = 4.981$, $p = 0.049$) and brooding ($F_{1,12} = 10.939$, $p = 0.008$).

For the same site, most of the dive parameters did not differ significantly between breeding stage or year. At Closed Sea only, birds dived deeper during brooding than during incubation ($F_{1,12} = 8.279$, $p = 0.016$).

Dive cycle of feeding dives

Since maximal depth reached during a dive may influence the other dive parameters, we examined the stan-

dardized data in order to compare the sites in a rigorous way. For the same depth, the diving efficiency was significantly higher at Open Sea throughout the breeding season (nested ANOVA: $F_{1,12} = 5.119$, $p = 0.047$ during incubation, $F_{1,12} = 13.212$, $p = 0.005$ during

Table 6. *Pygoscelis papua*. Characteristics of feeding dives from the randomly-selected data set (see 'Materials and methods') depending on site and stage at Kerguelen Archipelago in 2003. Values in italics represent standardized data. n = the number of analyzed dives. Values in the same horizontal row not sharing a common superscript are significantly different between sites (nested ANOVA with 'bird' nested into 'site'). For diving efficiency, only U- and W-dives with post-dive intervals ≤ 325 s were taken into account

2003	Crèche		
	Open Sea 1	Open Sea 2	Closed Sea
n	250	250	190
Dive depth (m)	68.02 \pm 49.57 ^a	66.86 \pm 54.93 ^a	45.71 \pm 28.72 ^a
Dive duration (s)	202.72 \pm 86.22 ^a <i>0.33 \pm 0.90^a</i>	201.69 \pm 99.71 ^a <i>0.35 \pm 0.91^a</i>	148.41 \pm 42.88 ^b <i>-0.21 \pm 0.68^a</i>
Bottom time (s)	90.79 \pm 51.35 ^a <i>0.25 \pm 0.85^a</i>	97.49 \pm 60.82 ^a <i>0.38 \pm 0.97^a</i>	58.87 \pm 29.65 ^b <i>-0.07 \pm 0.77^a</i>
Post-dive interval duration (s)	50.11 \pm 44.65 ^a <i>-0.22 \pm 1.13^a</i>	46.65 \pm 40.45 ^a <i>-0.28 \pm 1.23^a</i>	39.87 \pm 39.80 ^a <i>-0.16 \pm 1.41^a</i>
Descent rate (m s ⁻¹)	1.08 \pm 0.47 ^a <i>-0.13 \pm 0.78^a</i>	1.08 \pm 0.54 ^a <i>0.02 \pm 0.95^a</i>	0.94 \pm 0.35 ^a <i>-0.14 \pm 0.82^a</i>
Ascent rate (m s ⁻¹)	-1.04 \pm 0.60 ^a <i>-0.13 \pm 0.90^a</i>	-1.11 \pm 0.65 ^a <i>0.20 \pm 1.02^a</i>	-0.85 \pm 0.40 ^a <i>-0.21 \pm 0.81^a</i>
Total way vertical at the bottom (m)	16.81 \pm 14.00 ^a <i>0.46 \pm 1.12^a</i>	14.42 \pm 12.48 ^a <i>0.40 \pm 1.17^a</i>	15.02 \pm 10.35 ^a <i>0.29 \pm 0.86^a</i>
Diving efficiency	0.41 \pm 0.11 ^a <i>0.09 \pm 0.83^{a,b}</i>	0.44 \pm 0.12 ^a <i>0.41 \pm 0.92^a</i>	0.36 \pm 0.13 ^a <i>-0.37 \pm 0.82^b</i>

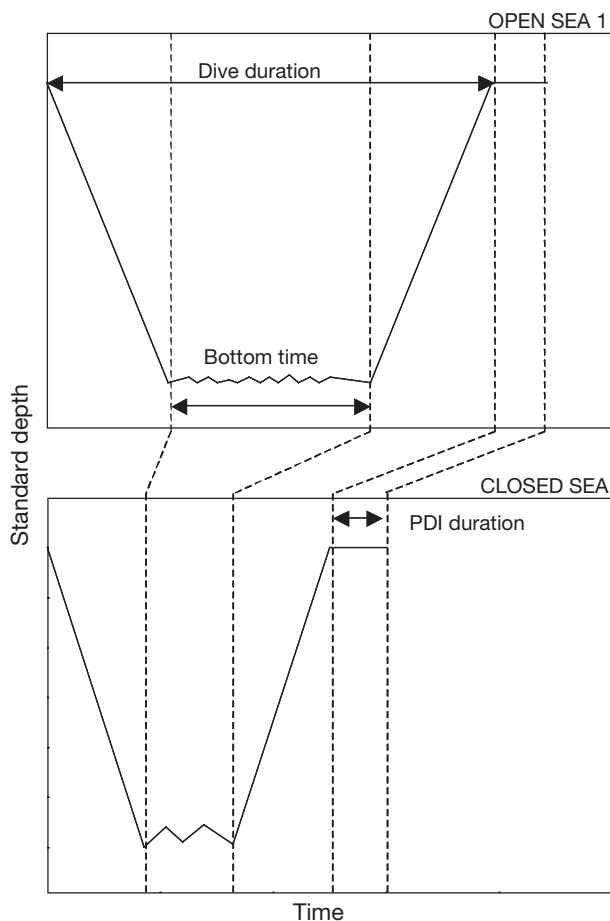


Fig. 8. *Pygoscelis papua*. Schematic representation of typical dive cycles for a foraging dive performed during the chick guard stage at Open Sea 1 and Closed Sea. Dives are longer at Open Sea 1, with a longer bottom time, for a same post-dive interval (PDI) duration than at Closed Sea

chick guard and $F_{2,14} = 4.837$, $p = 0.031$ during crèche) (Tables 5 & 6). This was the consequence of a longer total dive duration ($F_{1,12} = 24.796$, $p = 0.001$ during chick guard and $F_{2,14} = 3.257$, $p = 0.077$ during crèche) and a longer bottom time ($F_{1,12} = 5.029$, $p = 0.049$ during incubation, $F_{1,12} = 16.077$, $p = 0.002$ during chick guard) at Open Sea compared to Closed Sea, for the same post-dive interval. Thus, gentoo penguins showed a differential management of time during a dive cycle between the 2 types of site (Fig. 8). For the same site, standardized dive parameters did not differ significantly between breeding stage or year.

DISCUSSION

Device effect

Remote-sensing devices are essential tools for the study of at-sea behavior. Unfortunately, they may

adversely affect energetics, diving behavior and breeding success of equipped penguins (Wilson et al. 1986, Culik & Wilson 1991, Hull 1997, Ropert-Coudert et al. 2000, Taylor et al. 2001). Hence, inversely related to the cross-sectional area of the devices, the drag effect may reduce swimming speed or increase the cost of transport in water (Wilson et al. 1986, Culik & Wilson 1991, Boyd et al. 1997). Foraging trips consequently last longer for the same foraging success. In our study, we did not find any significant effect of the devices on trip duration. However, birds fitted with PTTs (the biggest of our devices at 1.7% of the birds' cross-sectional area) tended to undertake longer trips, particularly at Closed Sea where the gentoo penguins are smaller in size (Bost et al. 1992). This may be due to the device size or to the additional drag effect of the antenna (Wilson et al. 2004). Extra energy costs induced by externally attached devices may also affect the diving behavior, particularly in increasing the recovery duration after a deep dive (Ropert-Coudert et al. 2000). Nevertheless, as our devices were hydrodynamically shaped, were placed in the most caudal position and accounted for a small proportion of the birds' cross-sectional area, we assume that the drag effect was minimized (Bannasch et al. 1994) and did not significantly affect the behavior of the birds.

Inter-locality variability

Our study found an unexpectedly large variation in the foraging behavior of gentoo penguins, which varied almost as much among Kerguelen colonies as it does over the entire range of the species (Table 5).

Trip duration

Overall, the foraging trips of Kerguelen gentoo penguins are among the longest in comparison to other localities. At Open Sea 1, the trip duration during incubation was the longest ever mentioned in the literature. Lasting more than 2 d during incubation and more than 1 d during chick-rearing, the trip duration at Open Sea can be compared to that at Crozet Islands or Macquarie Island (Table 7). This may be related to abundant but distant resources. The Open Sea 1 colony faced the large Kerguelen shelf, and the proximity of the Polar Front allowed the penguins access to a large area of particularly productive shallow, neritic waters (Blain et al. 2001). According to the central place foraging theory (Orians & Pearson 1979), birds would perform longer trips and return with larger meals when food is abundant (Watanuki et al. 1997).

Table 7. *Pygoscelis papua*. Foraging characteristics and diet of the gentoo penguin at different breeding localities, from north to south of the breeding range (mean with maximal values in parentheses). Rearing = Chick guard + Crèche. For the diet, we indicated the dominant taxon by mass. Cr: Crustaceans; Fi: Fish; Cr/Fi: mixed diet dominated by crustaceans; Fi/Cr: mixed diet dominated by fish

Breeding stage	Locality	Trip duration (d)	Foraging range (km)	Dive frequency (dive h ⁻¹)	Dive depth (m)	Dive duration (s)	Diet	Source ^a
Incubation	Crozet Is.	2.4	(130)	–	–	–	Cr	A
	Marion Is.	1–2	(54–108)	–	–	–	Fi/Cr	B
	Kerguelen Is.							C
	Open Sea 1	3.16	28.3 (46.0)	9.7	59.1 (225)	181 (345)	Fi	
	Closed Sea	2.08	8.3 (11.6)	17.2	39.3 (108)	130 (275)	Cr	
	Falkland Is.	–	–	–	–	–	Fi/Cr	D
	South Georgia Is.	1.4	(76)	–	–	–	Cr or Fi	E
Antarctic Peninsula	1.8	50 (200)	–	–	–	Cr	F	
Chick guard	Crozet Is.	1.2	(65)	–	25.3 (210)	203	Cr/Fi	A
	Marion Is.	0.34–0.99	7	–	–	–	Fi/Cr	B
	Kerguelen Is.							C
	Open Sea 1	1.5	30.8 (37.6)	12.3	60.8 (187)	193 (344)	Fi	
	Closed Sea	0.98	–	16.3	61.7 (153)	155 (295)	Cr	
	Heard Is.	–	–	–	–	–	Fi	G
	Macquarie Is.	0.52–1.70	12.7–39.1	9.5	89 (212)	210 (384)	Fi	H
	South Georgia Is.	0.26–0.50	2.4–4.1 (35)	10.9	71.4–98.2 ^b	144–168	Cr or Fi	E
South Shetland Is.	0.19–0.52	17 (24)	14.7	–	128	Cr	I	
Antarctic Peninsula	0.08–0.29	5 (16)	18.2	34.7 (107)	(225)	Cr	F	
Crèche	Kerguelen Is.							C
	Open Sea 1	1.17	–	12.4	65 (213)	202 (470)	Fi	
	Open Sea 2	1.07	5.5–21	9.7	66.9 (198)	202 (440)	Fi/Cr	
	Closed Sea	0.69	–	15.0	45.7 (146)	148 (278)	Cr	

^aKey to sources. A: Bost & Jouventin (1990), Bost et al. (1994), Ridoux (1994); B: Van Zinderen Bakker (1971), Adams & Brown (1983), Adams & Klages (1989), Brown et al. (1990); C: Lescroël et al. (2004), this study; D: Clausen & Pütz (2002); E: Croxall & Prince (1980b, 1987), Croxall et al. (1988), Kato et al. (1991), Williams (1991), Williams et al. (1992), Wilson et al. (1998); F: Cordier et al. (1983), Wilson et al. (1996); G: Klages et al. (1990); H: Robinson & Hindell (1996); I: Volkman et al. (1980), Trivelpiece et al. (1986, 1987)

^bMean depth was calculated by the authors for dives deeper than 30 m

The shorter trips at Closed Sea are halfway between those exhibited at the northern and southern localities. Closed Sea birds indeed foraged for 2 d during incubation but then performed daily trips during chick guard (0.98 d) and crèche (0.69 d), whereas birds from the Antarctic Peninsula, South Georgia and South Shetland Islands made even shorter trips, from 2 to 12 h (Table 7). The short trips performed by Closed Sea birds were probably due to the proximity of abundant macrozooplankton species (Bocher et al. 2001). For instance, *Parathemisto gaudichaudii* occurs in high densities in the Morbihan Gulf, and particularly in its western part (Bocher et al. 2001, Bost et al. 1994); therefore, around the Closed Sea colony. In this way, the strong dependence shown at Closed Sea on 2 crustacean species *Euphausia vallentini* and *P. gaudichaudii* (Lescroël et al. 2004) is similar to that observed at Antarctic localities on Antarctic krill *Euphausia superba*.

At-sea distribution

In foraging nearly 20 km away from their breeding grounds and as far as 46 km away, Open Sea birds are halfway between those from Macquarie Island, and those from Crozet and Marion Islands (Table 7). Gentoo penguins from Closed Sea, however, exhibited the smallest incubation range of all localities (3.6 to 11.6 km), being similar to those at the southernmost localities during chick rearing (Antarctic Peninsula, South Shetland and South Georgia Islands) (Table 7).

Diving behavior

During their trips, Open Sea birds dived as frequently as birds from Macquarie and South Georgia Islands, i.e. around 10 dives per hour. Closed Sea birds dived more often, around 15 dives per hour as at the

Antarctic Peninsula and South Shetland Islands. At Open Sea 1, we recorded the deepest (225 m) and the longest (470 s) dives ever reported for a gentoo penguin.

There was a large variation in the foraging behavior at Kerguelen Archipelago with Open Sea penguins tending to behave like those from the northern localities, whereas Closed Sea penguins behaved more like those from the southern localities. Interestingly, Open Sea penguins fed predominantly on fish while the Closed Sea ones favored crustaceans most of the time (Table 7). Thus, the foraging behavior of the gentoo penguin is not strictly set for the species and may vary as a function of locality and probably of prey availability.

Intra-locality variability

Such diversity on the scale of the Kerguelen Archipelago may be linked to the high diversity of the oceanographic conditions in the penguin feeding areas. Since the foraging ecology of the gentoo penguin was investigated at several sites during the same season following the same methodology, we can therefore exclude any year-season confounding effect in our intersite comparisons.

At-sea distribution

At the Open Sea sites, gentoo penguins departed before the end of the night, possibly to arrive at their remote feeding grounds when the luminosity enables them to dive deeply. Accordingly, most of the tracked birds arrived near their maximal foraging range between 11:00 and 14:00 h (local time). They foraged much farther than Closed Sea birds, as reflected by the high proportion of travelling dives, and swam faster to get to their feeding areas. At Open Sea 1, gentoo penguins undertook direct circular tracks towards the shelf slope where they found a predictable resource, namely nototheniid fish and the Icefish *Champscephalus gunnari*. These species are preferentially located on the eastern part of the shelf (Duhamel 1987, 1993), known to be an area of high fish abundance (Guinet et al. 2001), and form the main items in the gentoo penguin diet at Open Sea 1 (Lescroël et al. 2004). At Open Sea 2, we did not collect data on the penguin at-sea distribution but birds frequently dived deeper than 150 m depth, which corresponds to at least 21 km away from the colony. Thus, Open Sea 2 penguins probably also foraged on the shelf slope (data from the Service Hydrographique et Océanographique de la Marine, France).

Closed Sea birds departed later, mainly during daylight hours, to undertake short sinuous trips in the

vicinity of the colony. They took much more sinuous tracks, traveling around the colony in search of their main prey, the very mobile and patchy swarms of *Euphausia vallentini* and *Parathemisto gaudichaudii* (Lescroël et al. 2004).

Short foraging trips such those performed at Closed Sea are only possible when prey availability near the colony is sufficiently high (Wilson 1995). This tactic was possible because of the high productivity of the Morbihan Gulf (Razouls et al. 1997). Available crustacean biomass is indeed particularly high in this bay, and dominated in all seasons by *Parathemisto gaudichaudii* (Bocher et al. 2001, P. Mayzaud pers. comm.). Birds may also have been limited by landmasses but this is unlikely to occur as the open ocean was located <15 km away from the colony. On the other hand, the greater distances travelled by Open Sea penguins may be a consequence of (1) the exploitation of distant but abundant and predictable resources or (2) the depletion of resources or the competition for resources around the breeding colony (Ashmole & Ashmole 1967). Due to the influence of the Polar Front (Fig. 1), the east of the archipelago is a very productive area (Blain et al. 2001) where other top predators, like black-browed albatrosses and fur seals, forage intensively (Guinet et al. 2001, Pinaud & Weimerskirch 2002). Furthermore, the Icefish *Champscephalus gunnari* and the nototheniid *Lepidonotothen squamifrons*, 2 important species in the gentoo penguin diet at Open Sea (Lescroël et al. 2004), are preferentially and abundantly located on the eastern part of the shelf (Duhamel 1993). Since all equipped gentoo penguins headed their trips towards the eastern shelf slope, the first hypothesis is likely to be valid. However, we cannot exclude an additional effect of competition because, although our study colonies had similar sizes, the density of gentoo penguins is higher on the northeastern coast of the archipelago than inside the Morbihan Gulf (around 175 versus 11 individuals per kilometer of coast, respectively) (C. A. Bost & A. Lescroël unpubl. data). In this latter case, increased distances would increase the probability of prey encounters (Wilson & Wilson 1990). Nevertheless, there are also numerous colonies of potential competitors such as the Rockhopper penguins *Eudyptes chrysocome filholi* and Kerguelen shags *Phalacrocorax atriceps verrucosus* in the Morbihan Gulf, which are missing around Open Sea 1 (Weimerskirch et al. 1989).

Diving behaviour

Penguins are mainly visual predators (Wilson 1995). Accordingly, the birds from both Open Sea and Closed Sea confined most of their diving activity to the day-

Table 8. *Pygoscelis papua*. Characteristics of the foraging ecology at 3 breeding sites of the Kerguelen Archipelago. Dietary data are from Lescroël et al. 2004

Site	Prospected area	Dive type	Diet (% by mass)			
			Fish	Crustaceans	Cephalopods	Annelids
Open Sea 1	Plateau slope	U/W	71	13	10	6
Open Sea 2	Plateau slope	U/A	38	28	20	14
Closed Sea	Neritic zone	W/V	13	84	0	3

light hours but also dived at very shallow depths during the night, as reported at Macquarie Island (Robinson & Hindell 1996). However, at Open Sea 1, gentoo penguins performed dives much more frequently at night than at the other 2 sites. This observation can easily be explained by the longer trip duration, at least during incubation and chick guard, leading to more frequent overnight trips. Thus, the proportion of these night dives at Open Sea 1 tended to decrease between chick guard and crèche. Whether night diving may represent an additional constraint for visual predators, shallow dives during the night may allow the birds to catch pelagic prey such as squids, near the surface, during their nyctemeral migration (Weimerskirch et al. 1986, Weimerskirch & Wilson 1992, Croxall & Prince 1994).

The differential use of dive types by penguins of the 3 sites may be interpreted by feeding upon distinct prey types (Table 8). At the Open Sea sites, gentoo penguins fed mainly on demersal and semipelagic fish species (Lescroël et al. 2004), which have a highly predictable vertical distribution. In this case, maximizing the time spent at the bottom, by the use of U-dives, will greatly increase the probability of encountering prey (Williams et al. 1992, Wilson et al. 1996). At the Closed Sea site, gentoo penguins fed mainly on swarming crustaceans, which have a variable and therefore more unpredictable, horizontal and vertical distribution (Perissonotto 1989). A successful foraging strategy might therefore consist of performing a high proportion of exploratory dives (as may be some of the V-dives, Wilson et al. 1996) and dives which maximize the exploration of the water column (A- and W-dives). This is the case at Closed Sea, and probably also at South Georgia and the Antarctic Peninsula where gentoo penguins feed on Antarctic krill (Williams et al. 1992, Wilson et al. 1996). The higher dive frequency of Closed Sea birds also allowed them to maximize the time spent scanning the water column. The Rockhopper penguin *Eudyptes chrysocome filholi*, breeding at the same Closed Sea site at Kerguelen, seems to adopt another strategy and perform a substantial proportion of benthic dives (about 40%) on pelagic crustaceans trapped on the sea floor (Tremblay & Cherel 2000). Hence, the diving efficiency of the Rock-

hopper penguin is higher than that of the Closed Sea gentoo penguins but similar to that of the Open Sea ones (0.45, 0.32 and 0.46, respectively during chick guard). We suggest that competition for food resources during the summer season may have reinforced the ecological partitioning of the water column in sympatrically-breeding species.

Furthermore, the differential use of the water column by Open Sea and Closed Sea penguins is also shown by the frequency distribution of dive depth. Open Sea birds performed a high proportion of deep dives as they fed on the shelf slope above the 100 to 200 m isobaths, whereas Closed Sea birds dived mainly at depths <65 m, following the bathymetry of the Morbihan Gulf, i.e. shallow waters around 50 m depth with some deeper pits such as the Prince Albert sill (180 m depth) just in front of the Closed Sea colony (data from the Service Hydrographique et Océanographique de la Marine, France). These observations are consistent with the broad pattern observed among Antarctic species, with krill-eating species diving shallower overall than fish-eating ones (Croxall et al. 1988, McCafferty et al. 1998).

To summarize, the foraging behavior of the gentoo penguin is likely to vary as a function of prey availability, in terms of taxonomic composition, density, and distribution. Hence, following our current knowledge of the gentoo penguin's prey distribution and behavior at Kerguelen, there is strong evidence that the spatial distribution of prey particularly influences the diving behavior of these penguins. Fish-eating gentoo penguins increased their foraging effort horizontally, i.e. travelling farther and longer, and spending more time at the bottom. On the other hand, crustacean-eating penguins increased their effort vertically with frequent pelagic dives. At Open Sea 2, gentoo penguins had a more mixed diet (with crustaceans, annelids and cephalopods but always dominated by fish, Lescroël et al. 2004) and sometimes showed intermediary diving characteristics. Overall, as indicated by their daily dive rates, birds from all 3 sites exhibited the same foraging effort.

Seasonal variations

As in all other localities, Kerguelen gentoo penguins reduced their trip duration between the incubation and the chick-rearing periods, ensuring regular food supplies to their chicks (Table 5). All seasonal variations in the foraging behavior occurred between the incubation and chick guard periods, when penguins needed

to adjust the amount of food needed to feed chicks, which was obviously higher than for self-maintenance. There was no discernable adjustment of trip duration between rearing young versus older chicks as was found at Macquarie Island (Robinson & Hindell 1996). Nevertheless, during the crèche stage, both parents foraged at the same time and no longer relieved each other, potentially increasing the feeding frequency of their chicks (Trivelpiece et al. 1987).

At Closed Sea, gentoo penguins increased their daily dive rate compared to the incubation period by diving deeper during chick guard for a same dive frequency. At Open Sea 1, gentoo penguins tended to increase their dive frequency between incubation and chick guard. Thus, at both sites, birds increased their foraging effort, mainly in the vertical dimension. This may be related to the decrease of the proportion of fish in the penguin diet at both Open Sea 1 and Closed Sea sites during a period of probable high abundance of sub-Antarctic krill (Lescroël et al. 2004). Hence, gentoo penguins might adapt to changes in the relative abundance of food sources.

CONCLUSIONS

Opportunism appears to be a key feature of the gentoo penguin's foraging ecology. This inshore feeding species is able to adapt to local oceanographic conditions to utilize available prey species. Other penguin species, such as Rockhopper *Eudyptes chrysocome*, Emperor *Aptenodytes forsteri* or Adélie *Pygoscelis adeliae* penguins, exhibit flexible chasing tactics (Watanuki et al. 1993, Wienecke & Robertson 1997, Tremblay & Cherel 2003), but none of them shows such a degree of plasticity both in the foraging dimensions (i.e. distance from the colony, horizontal and vertical components of the water column during diving) and in the diet, especially at a small spatial scale.

At Kerguelen Archipelago, gentoo penguins showed at least 2 foraging strategies that depended on the local conditions: large foraging ranges, long trips, long benthic dives on demersal fish at colonies facing the open sea versus small foraging ranges, short trips and short pelagic dives on swarming crustaceans at the more enclosed site, for the same foraging effort. This result emphasizes the importance of behavioral plasticity when living in heterogeneous, highly variable environments like coastal habitats compared to oceanic ones (Ropert-Coudert et al. 2002). Consequently, caution must be exercised in extrapolating information gathered at a specific site, breeding stage or year, especially concerning coastal species.

Ecological adaptations to local oceanographic conditions have been reported in some other marine apex

predators like shags or cormorants (Grémillet et al. 1998, Wanless et al. 1998, Kato et al. 1991, 2000), Rockhopper penguins (Tremblay & Cherel 2003) and fur seals (Boyd et al. 1994, McCafferty et al. 1998, Beuaplet et al. 2004) but remain understudied. Yet, such studies might provide original information on the local availability and characteristics of marine prey populations (Ridoux 1988) and help to monitor coastal marine ecosystems (Boyd & Murray 2001).

Acknowledgements. This work was supported by the Institut Polaire Paul Emile Victor (IPEV, Programme No. 394), the Terres Australes et Antarctiques Françaises and the Centre National de la Recherche Scientifique. We thank A. Lamalle and the members of the 52nd, 53rd and 54th missions at Kerguelen, and especially V. Chartendraul, E. Pettex, C. Marteau, J. L. Chill and F. Le Bouard for their help in the field. The authors are also grateful to A. Schmidt for his help in the analysis of TDR data and to J. Lage who provided his software. We thank N. D. Holmes, G. Beuaplet and 4 anonymous reviewers for their helpful comments on the manuscript. Finally, many thanks to A. Pape who improved the English.

LITERATURE CITED

- Adams NJ, Brown CR (1983) Diving depths of the gentoo penguin (*Pygoscelis papua*). *Condor* 85:503–504
- Adams NJ, Klages NT (1989) Temporal variation in the diet of the gentoo penguin *Pygoscelis papua* at sub-Antarctic Marion Island. *Colon Waterbird* 12:30–36
- Ashmole NP, Ashmole MJ (1967) Comparative feeding ecology of sea birds of a tropical oceanic island. *Bull Peabody Mus Nat Hist, Yale Univ* 24:1–131
- Bannasch R, Wilson RP, Culik BM (1994) Hydrodynamic aspects of design and attachment of a back-mounted device in penguins. *J Exp Biol* 194:83–96
- Beuaplet G, Dubroca L, Guinet C, Cherel Y, Dabin W, Gagne C, Hindell M (2004) Foraging ecology of sub-Antarctic fur seals *Arctocephalus tropicalis* breeding on Amsterdam Island: seasonal changes in relation to maternal characteristics and pup growth. *Mar Ecol Prog Ser* 273:211–225
- Blain S, Tréguer P, Belviso S, Bucciarelli E and 7 others (2001) A biogeochemical study of the island mass effect in the context of the iron hypothesis: Kerguelen Islands, Southern Ocean. *Deep-Sea Res I* 48:163–187
- Bocher P, Cherel Y, Labat JP, Mayzaud P, Razouls S, Jouventin P (2001) Amphipod-based food web: *Themisto gaudichaudii* caught in nets and by seabirds in Kerguelen waters, southern Indian Ocean. *Mar Ecol Prog Ser* 223: 261–276
- Bost CA, Jouventin P (1990) Evolutionary ecology of the gentoo penguin *Pygoscelis papua*. In: Davis L, Darby J (eds) *Penguin biology*. Academic Press, San Diego, CA, p 85–112
- Bost CA, Jouventin P, Pincson Du Sel N (1992) Morphometric variability on a microgeographical scale in two inshore seabirds. *J Zool* 226:135–149
- Bost CA, Pütz K, Lage J (1994) Maximum diving depth and diving patterns of the gentoo penguin *Pygoscelis papua* at the Crozet Islands. *Mar Ornithol* 22:237–244

- Boyd IL (1996) Temporal scales of foraging in a marine predator. *Ecology* 77:426–434
- Boyd IL, Murray WA (2001) Monitoring a marine ecosystem using responses of upper trophic level predators. *J Anim Ecol* 70:747–760
- Boyd IL, Arnould JPY, Barton T, Croxall JP (1994) Foraging behaviour of Antarctic fur seals during periods of contrasting prey abundance. *J Anim Ecol* 63:703–713
- Boyd IL, McCafferty DJ, Walker TR (1997) Variation in foraging effort by lactating Antarctic fur seals: response to simulated increased foraging costs. *Behav Ecol Sociobiol* 40:135–144
- Boyd IL, Kato A, Ropert-Coudert Y (2004) Bio-logging science: sensing beyond the boundaries. In: Naito Y (ed) *Bio-logging science: Proc Int Symp Bio-logging Science*, National Institute of Polar Research, Tokyo, Mar 17–21, 2003. *Memoirs of National Institute of Polar Research, Special Issue 58*, National Institute of Polar Research, Tokyo
- Brown CR, Klages NT, Adams NJ (1990) Short and medium-term variation in the diets of penguins at Marion Island. *S Afr Antarct Res* 20:13–20
- Charassin JB, Bost CA (2001) Utilisation of the oceanic habitat by king penguins over the annual cycle. *Mar Ecol Prog Ser* 221:285–297
- Charassin JB, Park YH, Le Maho Y, Bost CA (2002) Penguins as oceanographers unravel hidden mechanisms of marine productivity. *Ecol Lett* 5:317–319
- Cherel Y, Tremblay Y, Guinard E, Georges JY (1999) Diving behaviour of female northern rockhopper penguins, *Eudyptes chrysocome moseleyi*, during the brooding period at Amsterdam Island (Southern Indian Ocean). *Mar Biol* 134:375–385
- Clausen A, Pütz K (2002) Recent trends in diet composition and productivity of Gentoo, magellanic and rockhopper penguins in the Falkland Islands. *Aquat Conserv* 12:51–61
- Clausen A, Pütz K (2003) Winter diet and foraging range of gentoo penguins (*Pygoscelis papua*) from Kidney Cove, Falkland Islands. *Polar Biol* 26:32–40
- Cordier JR, Mendez A, Mougou JL, Visbeek G (1983) Les oiseaux de la baie de l'Espérance, Péninsule Antarctique (63° 24' S, 56° 59' W). *L'Oiseau R.F.O* 51:147–160
- Croxall JP, Prince PA (1980a) Food, feeding ecology and ecological segregation of seabirds at South Georgia. *Biol J Linn Soc* 14:103–131
- Croxall JP, Prince PA (1980b) The food of gentoo penguin *Pygoscelis papua* and Macaroni penguin *Eudyptes chrysolophus* at South Georgia. *Ibis* 122:245–253
- Croxall JP, Prince PA (1987) Seabirds as predators on marine resources, especially krill, at South Georgia. In: Croxall JP (ed) *Seabirds: feeding ecology and role in marine ecosystems*. Cambridge University Press, Cambridge, p 347–368
- Croxall JP, Prince PA (1994) Dead or alive, night or day: How do albatrosses catch squid? *Antarct Sci* 6:155–162
- Croxall JP, Davis RW, O'Connell MJ (1988) Diving patterns in relation to diet of gentoo and macaroni penguins at South Georgia. *Condor* 90:157–167
- Croxall JP, Briggs DR, Kato A, Naito Y, Watanuki Y, Williams TD (1993) Diving pattern and performance in the macaroni penguin *Eudyptes chrysolophus*. *J Zool* 230: 31–47
- Culik BM, Wilson RP (1991) Swimming energetics and performance of instrumented Adélie penguins (*Pygoscelis adeliae*). *J Exp Biol* 158:355–368
- Culik BM, Bannasch R, Wilson RP (1994) External devices on penguins: How important is shape? *Mar Biol* 118: 353–357
- Duhamel G (1987) Ichtyofaune des Secteurs Indien Occidental et Atlantique Oriental de l'océan austral: Biogéographie, cycles biologiques et dynamique des populations. PhD thesis, Université Pierre et Marie Curie, Paris
- Duhamel G (1993) Distribution, abondance et principales caractéristiques biologiques des espèces de la ZEE des îles Kerguelen en 1987 et 1988. In: Duhamel G (ed) *Campagnes SKALP 1987 et 1988 aux îles Kerguelen à bord des navires 'SKIF' et 'KALPER'*. *Rapp Camp Mer Publ IFRT* 93-01:194–251
- Gentry RL, Kooyman GL (1986) Methods of dive analysis. In: Gentry RL, Kooyman GL (eds) *Fur seals: maternal strategies on land and at sea*. Princeton University Press, Princeton, NJ, p 28–40
- Grémillet D, Argentin G, Schulte B, Culik BM (1998) Flexible foraging techniques in breeding Cormorants *Phalacrocorax carbo* and shags *Phalacrocorax aristotelis*: benthic or pelagic feeding? *Ibis* 140:113–119
- Grémillet D, Kuntz G, Delbart F, Mellet M and 6 others (2004a) Linking the foraging performance of a marine predator to local prey abundance. *Funct Ecol* 18:1–7
- Grémillet D, Dell'Omo G, Ryan PG, Peters G, Ropert-Coudert Y, Weeks SJ (2004b) Offshore diplomacy, or how seabirds mitigate intra-specific competition: a case study based on GPS tracking of Cape gannets from neighbouring colonies. *Mar Ecol Prog Ser* 268:265–279
- Guinet C, Dubroca L, Lea MA, Goldsworthy SD, Cherel Y, Duhamel G, Bonadonna F, Donnay JP (2001) Spatial distribution of foraging in female Antarctic fur seals *Arctocepalus gazella* in relation to oceanographic variables: a scale-dependent approach using geographic information systems. *Mar Ecol Prog Ser* 219:251–264
- Haggett P, Chorley R (1969) *Network analysis in geography*. Edward Arnold, London
- Hindell MA (1989) The diet of gentoo penguins *Pygoscelis papua* at Macquarie Island: winter and early breeding season. *Emu* 89:71–78
- Hull C (1997) The effect of carrying devices on breeding Royal penguins. *Condor* 99:530–534
- Hunt GL, Mehlum F, Russell RW, Irons D, Decker MB, Becker PH (1999) Physical processes, prey abundance, and the foraging ecology of seabirds. In: Adams NJ, Slotow RH (eds) *Proc 22 Int Ornithol Congr Durban*. BirdLife South Africa, Johannesburg
- Hurlbert SH (1984) Pseudoreplication and the design of ecological field experiments. *Ecol Monogr* 54:187–211
- Jouventin P, Weimerskirch H (1990) Satellite tracking of wandering albatrosses. *Nature* 343:746–748
- Kato A, Williams TD, Barton TR, Rodwell S (1991) Short-term variation in the winter diet of gentoo penguins *Pygoscelis papua* at South Georgia during July 1989. *Mar Ornithol* 19:31–38
- Kato A, Watanuki Y, Nishiumi I, Kuroki M, Shaughnessy P, Naito Y (2000) Variation in foraging and parental behavior of King Cormorants. *Auk* 117(3):718–730
- Kirkwood R, Robertson G (1997) The foraging ecology of female Emperor Penguins in winter. *Ecol Monogr* 67(2): 155–176
- Klages NTW, Pemberton D, Gales RP (1990) The diets of King and gentoo penguins at Heard Island. *Aust Wildl Res* 17: 53–60
- Kooyman GL, Cherel Y, Le Maho Y, Croxall JP, Thorson PH, Ridoux V, Kooyman CA (1992) Diving behavior and energetics during foraging cycles in king penguins. *Ecol Monogr* 62:143–163

- Le Boeuf BJ, Costa DP, Huntley AC, Feldkamp SD (1988) Continuous, deep diving in female northern elephant seals, *Mirounga angustirostris*. Can J Zool 66:446–458
- Lesacroël A, Ridoux V, Bost CA (2004) Spatial and temporal variation in the diet of the gentoo penguin (*Pygoscelis papua*) at Kerguelen Islands. Polar Biol 27:206–216
- McCafferty D, Boyd IL, Walker TR, Taylor RI (1998) Foraging responses of Antarctic fur seals to changes in the marine environment. Mar Ecol Prog Ser 166:285–299
- McConnell BJ, Fedak MA, Burton HR, Englehard GH, Reijnders P (2002) Movements and foraging areas of naive, recently weaned southern elephant seal pups. J Anim Ecol 71:65–78
- Orians GH, Pearson NE (1979) On the theory of central place foraging. In: Horm DJ, Mitchell RD, Stairs GR (eds) Analysis of ecological systems. Ohio University Press, Columbus, OH, p 157–177
- Park YH, Gambéroni L, Charriaud E (1993) Frontal structure, water masses, and circulation in the Crozet basin. J Geophys Res 97:12361–12385
- Perissinotto R (1989) The structure and diurnal variations of the zooplankton of the Prince Edwards Islands: implications for the biomass build-up of higher trophic levels. Polar Biol 9:505–510
- Pinaud D, Weimerskirch H (2002) Ultimate and proximate factors affecting the breeding performance of a marine top-predator. Oikos 99:141–150
- Radl A, Culik BM (1999) Foraging behaviour and reproductive success in Magellanic penguins (*Spheniscus magellanicus*): a comparative study of two colonies in southern Chile. Mar Biol 133:381–393
- Razouls S, De Bovée F, Delille D, Fiala M, Mayzaud P (1997) Temporal variability of bacteria, phytoplankton and zooplankton assemblages of the sub-Antarctic Morbihan Bay (Kerguelen Archipelago). In: Battaglia B, Valencia J, Walton DWH (eds) Antarctic communities, species, structure and survival. Cambridge University Press, Cambridge, p 86–92
- Ridoux V (1988) Subantarctic krill *Euphausia vallentini* preyed upon by penguins around Crozet Islands (Southern Indian Ocean): population structure and avian cycle. J Plankton Res 10:675–690
- Ridoux V (1994) The diets and dietary segregation of seabirds at the subantarctic Crozet Islands. Mar Ornithol 22: 1–192
- Robinson SA, Hindell MA (1996) Foraging ecology of gentoo penguins *Pygoscelis papua* at Macquarie Island during the period of chick care. Ibis 138:722–731
- Rodary D, Bonneau W, Le Maho Y, Bost CA (2000) Benthic diving in male emperor penguins (*Aptenodytes forsteri*) foraging in winter. Mar Ecol Prog Ser 207:171–181
- Ropert-Coudert Y, Bost CA, Handrich Y, Bevan RM, Butler PJ, Woakes AJ, Le Maho Y (2000) Impact of externally attached loggers on the diving behaviour of the King Penguin. Physiol Biochem Zool 73:438–445
- Ropert-Coudert Y, Kato A, Bost CA, Rodary D, Sato A, Le Maho Y, Naito Y (2002) Do Adélie penguins modify their foraging behaviour in pursuit of different prey? Mar Biol 140:647–652
- Salamolard M, Weimerskirch H (1993) Relationship between foraging effort and energy requirement throughout the breeding season in the Wandering albatross. Funct Ecol 7: 643–652
- Sokal RR, Rohlf FJ (1995) Biometry: the principles and practice of statistics in biological research. Freeman, New York
- Tanton JL, Reid K, Croxall JP, Trathan PN (2004) Winter distribution and behaviour of gentoo penguins *Pygoscelis papua* at South Georgia. Polar Biol 27:299–303
- Taylor SS, Leonard ML, Boness DJ, Majluf P (2001) Foraging trip duration increases for Humboldt Penguins tagged with recording devices. J Avian Biol 32:369–372
- Tremblay Y, Cherel Y (2000) Benthic and pelagic dives: a new foraging behaviour in rockhopper penguins. Mar Ecol Prog Ser 204:257–267
- Tremblay Y, Cherel Y (2003) Geographic variation in the foraging behaviour, diet and chick growth of rockhopper penguins. Mar Ecol Prog Ser 251:279–297
- Trivelpiece WZ, Bengston JL, Trivelpiece SG, Volkman NJ (1986) Foraging behavior of gentoo and chinstrap penguins as determined by new radiotelemetry techniques. Auk 103:777–781
- Trivelpiece WZ, Trivelpiece SG, Volkman NJ (1987) Ecological segregation of Adélie, gentoo and chinstrap penguins at King George Island, Antarctica. Ecology 68:351–361
- Van Zinderen Bakker EM Jr (1971) A behavior analysis of the gentoo penguin *Pygoscelis papua* Forster in Marion and Prince Edward Islands. In: Van Zinderen Bakker EM Sr, Winterbottom JM, Dyer RA (eds) Report on the South African biological and geological expedition 1965–1966. Balkema, Cape Town, p 251–272
- Volkman NJ, Jazdzewski K, Kittel W, Trivelpiece WZ (1980) Diets of *Pygoscelis* Penguins at King George Island, Antarctica. Condor 82:373–378
- Wanless S, Grémillet D, Harris MP (1998) Foraging activity and performance of Shags *Phalacrocorax aristotelis* in relation to environmental characteristics. J Avian Biol 29(1):49–54
- Watanuki Y, Kato A, Mori Y, Naito Y (1993) Diving performance of Adélie penguins in relation to food availability in fast sea-ice areas: comparison between years. J Anim Ecol 62:634–646
- Watanuki Y, Kato A, Robertson G (1997) Diving and foraging behaviour of Adélie penguins in areas with and without fast sea-ice. Polar Biol 17:296–304
- Weimerskirch H (1998) Foraging strategies of Indian Ocean albatrosses and their relationships with fisheries. In: Robertson G, Gales R (eds) Albatross biology & conservation. Surrey Beatty & Sons, Chippington North, p 168–179
- Weimerskirch H, Wilson RP (1992) When do wandering albatrosses *Diomedea exulans* forage? Mar Ecol Prog Ser 86: 297–300
- Weimerskirch H, Jouventin P, Stahl JC (1986) Comparative ecology of the six albatross species breeding on the Crozet Islands. Ibis 128:195–213
- Weimerskirch H, Zotier R, Jouventin P (1989) The avifauna of the Kerguelen Islands. Emu 89:15–29
- Weimerskirch H, Bonnadona F, Bailleul F, Mabile G, Dell'Omo G, Lipp HP (2002) GPS tracking of foraging albatrosses. Science 295:1259
- Wienecke BC, Robertson G (1997) Foraging space of emperor penguins *Aptenodytes forsteri* in Antarctic shelf waters in winter. Mar Ecol Prog Ser 159:249–263
- Williams TD (1991) Foraging ecology and diet of gentoo penguins *Pygoscelis papua* at South Georgia during the winter and an assessment of their winter prey consumption. Ibis 133:3–13
- Williams TD, Briggs DR, Croxall JP, Naito A, Kato A (1992) Diving pattern and performance in relation to foraging ecology in the gentoo penguin, *Pygoscelis papua*. J Zool 227:211–230
- Wilson RP (1995) The foraging ecology of penguins. In: Williams T (ed) Penguins. Oxford University Press, Oxford, p 81–106
- Wilson RP, Wilson MP (1990) Foraging ecology of breeding

- Spheniscus* penguins. In: Davis LS, Darby JT (eds) Penguin biology. Academic Press, San Diego, CA, p 181–206
- Wilson RP, Grant WS, Duffy DC (1986) Recording devices on free-ranging animals: Does measurement affect foraging performance? *Ecology* 67:1091–1093
- Wilson RP, Nagy KA, Obst BS (1989) Foraging ranges of penguins. *Polar Rec* 25:303–307
- Wilson RP, Culik BM, Peters G, Bannasch R (1996) Diving behaviour of gentoo penguins, *Pygoscelis papua*: factors keeping dive profiles in shape. *Mar Biol* 126:153–162
- Wilson RP, Bost CA, Pütz K, Charrassin JB, Culik BM, Adelung D (1997) Southern rockhopper penguin *Eudyptes chrysocome chrysocome* foraging at Possession Island. *Polar Biol* 17:323–329
- Wilson RP, Alvarez B, Latorre L, Adelung D, Culik B, Bannasch R (1998) The movements of gentoo penguins *Pygoscelis papua* from Ardley Island Antarctica. *Polar Biol* 19:407–413
- Wilson RP, Kreye JM, Lucke K, Urquhart H (2004) Antennae on transmitters on penguins: balancing energy budgets on the high wire. *J Exp Biol* 207:2649–2662
- Woehler E (1995) Consumption of southern ocean marine resources by penguins. In: Dann P, Norman I, Reilly P (eds) The penguins: ecology and management. Surrey Beatty & Sons, Chippington North, p 266–294
- Ydenberg RC, Clark CW (1989) Aerobiosis and anaerobiosis during diving by western grebes: an optimal foraging approach. *J Theor Biol* 139:437–449

Editorial responsibility: Otto Kinne (Editor-in-Chief), Oldendorf/Luhe, Germany

*Submitted: February 8, 2005; Accepted: May 11, 2005
Proofs received from author(s): October 13, 2005*