INTRODUCTION


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-
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).
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) (Lescoët 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 creche 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.

**Diving data analysis.** Dive parameters were analyzed using dedicated dive analysis software (MultiTrace, 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.
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 mm × 26 mm × 14 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 ± SD unless stated otherwise. Comparisons of general foraging parameters between the study sites and breeding sites for the same breeding stage (Student t-test and ANOVA). TDR: time-depth recorder.

![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)](image)

Table 1. *Pygoscelis papua*. Foraging trip duration (d) of gentoo penguins at Kerguelen Archipelago (mean ± 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.

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<tr>
<th>Set</th>
<th>Incubation</th>
<th>Chick guard</th>
<th>Crèche</th>
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<tr>
<td></td>
<td>Open Sea 1</td>
<td>Open Sea 1</td>
<td>Open Sea 1</td>
</tr>
<tr>
<td>Non-instrumented</td>
<td>3.16 ± 1.00</td>
<td>1.50 ± 0.76</td>
<td>1.17 ± 0.54</td>
</tr>
<tr>
<td>birds</td>
<td>n = 29</td>
<td>n = 28</td>
<td>n = 12</td>
</tr>
<tr>
<td>VHF birds</td>
<td>2.08 ± 1.15</td>
<td>0.98 ± 0.19</td>
<td>1.07 ± 0.47</td>
</tr>
<tr>
<td></td>
<td>n = 24</td>
<td>n = 12</td>
<td>n = 10</td>
</tr>
<tr>
<td>TDR birds</td>
<td>2.15 ± 0.97</td>
<td>0.95 ± 0.55</td>
<td>2.53 ± 1.19</td>
</tr>
<tr>
<td></td>
<td>n = 6</td>
<td>n = 6</td>
<td>n = 5</td>
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</table>
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.

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 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).

Table 2. Pygoscelis papua. Satellite tracking data (mean ± 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).

<table>
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<tr>
<th>2002</th>
<th>Incubation</th>
<th>Chick guard</th>
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<tr>
<td></td>
<td>Open Sea 1</td>
<td>Closed Sea</td>
</tr>
<tr>
<td></td>
<td>Open Sea 1</td>
<td>Closed Sea</td>
</tr>
<tr>
<td>Absence duration (d)</td>
<td>2.53 ± 1.68*</td>
<td>3.65 ± 2.94*</td>
</tr>
<tr>
<td>At sea trip duration (d)</td>
<td>2.21 ± 1.45*</td>
<td>3.65 ± 2.94*</td>
</tr>
<tr>
<td>Maximum foraging range (km)</td>
<td>28.30 ± 14.10*</td>
<td>8.30 ± 4.20*</td>
</tr>
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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). *\( p < 0.05 \)

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.
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

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<th>Incubation</th>
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<th>Crèche</th>
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<td></td>
<td>Open Sea 1</td>
<td>Closed Sea</td>
<td>Open Sea 1</td>
</tr>
<tr>
<td>Absence duration (d)</td>
<td>2.15 ± 0.97a</td>
<td>2.03 ± 0.74a</td>
<td>0.96 ± 0.37a</td>
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<tr>
<td>At-sea trip duration (d)</td>
<td>2.00 ± 1.01a</td>
<td>1.25 ± 0.46a</td>
<td>0.91 ± 0.37a</td>
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<tr>
<td>Travelling time (h)</td>
<td>2.77 ± 2.49a</td>
<td>0.58 ± 0.44a</td>
<td>1.24 ± 0.67a</td>
</tr>
<tr>
<td>Foraging time (h)</td>
<td>23.69 ± 8.76a</td>
<td>19.63 ± 6.83a</td>
<td>13.46 ± 2.99a</td>
</tr>
<tr>
<td>Dive frequency (dive h⁻¹)</td>
<td>9.66 ± 3.11a</td>
<td>17.17 ± 4.84b</td>
<td>12.27 ± 2.97a</td>
</tr>
<tr>
<td>Time spent at the bottom (h d⁻¹)</td>
<td>4.42 ± 1.68a</td>
<td>2.98 ± 1.33a</td>
<td>6.89 ± 2.69a</td>
</tr>
<tr>
<td>Total dive rate (km trip⁻¹)</td>
<td>52.50 ± 21.13a</td>
<td>43.98 ± 21.96a</td>
<td>25.28 ± 15.30a</td>
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<tr>
<td>Daily dive rate (km d⁻¹)</td>
<td>25.01 ± 7.07a</td>
<td>20.99 ± 4.00a</td>
<td>26.57 ± 13.85a</td>
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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.

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).
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 \((t_{9,9} = –2.591, p = 0.036)\) 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 \((A-, U-, W-\text{ and } V\text{-dives})\), 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.

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<th>2002</th>
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<td></td>
<td>Open Sea 1</td>
<td>Open Sea 1</td>
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<tr>
<td>n</td>
<td>300</td>
<td>300</td>
<td>300</td>
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<tr>
<td>Dive depth (m)</td>
<td>59.15 ± 41.65&lt;sup&gt;a&lt;/sup&gt;</td>
<td>39.32 ± 17.28&lt;sup&gt;b&lt;/sup&gt;</td>
<td>60.82 ± 41.01&lt;sup&gt;a&lt;/sup&gt;</td>
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<tr>
<td>Dive duration (s)</td>
<td>180.85 ± 72.49&lt;sup&gt;a&lt;/sup&gt;</td>
<td>130.33 ± 42.99&lt;sup&gt;b&lt;/sup&gt;</td>
<td>192.61 ± 70.92&lt;sup&gt;a&lt;/sup&gt;</td>
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<td>Bottom time (s)</td>
<td>75.82 ± 52.70&lt;sup&gt;a&lt;/sup&gt;</td>
<td>41.60 ± 38.30&lt;sup&gt;a&lt;/sup&gt;</td>
<td>90.06 ± 54.36&lt;sup&gt;a&lt;/sup&gt;</td>
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<td>Post-dive interval duration (s)</td>
<td>0.01 ± 1.00&lt;sup&gt;a&lt;/sup&gt;</td>
<td>–0.44 ± 0.90&lt;sup&gt;b&lt;/sup&gt;</td>
<td>0.29 ± 0.97&lt;sup&gt;a&lt;/sup&gt;</td>
</tr>
<tr>
<td>Descent rate (m s&lt;sup&gt;−1&lt;/sup&gt;)</td>
<td>–0.38 ± 1.50&lt;sup&gt;a&lt;/sup&gt;</td>
<td>–0.10 ± 0.40&lt;sup&gt;b&lt;/sup&gt;</td>
<td>0.15 ± 0.52&lt;sup&gt;a&lt;/sup&gt;</td>
</tr>
<tr>
<td>Ascent rate (m s&lt;sup&gt;−1&lt;/sup&gt;)</td>
<td>–0.13 ± 1.10&lt;sup&gt;a&lt;/sup&gt;</td>
<td>–0.87 ± 0.40&lt;sup&gt;b&lt;/sup&gt;</td>
<td>–1.10 ± 0.61&lt;sup&gt;a&lt;/sup&gt;</td>
</tr>
<tr>
<td>Total way vertical at the bottom (m)</td>
<td>8.44 ± 7.99&lt;sup&gt;a&lt;/sup&gt;</td>
<td>10.10 ± 9.18&lt;sup&gt;a&lt;/sup&gt;</td>
<td>9.05 ± 8.07&lt;sup&gt;a&lt;/sup&gt;</td>
</tr>
<tr>
<td>Diving efficiency</td>
<td>0.42 ± 0.15&lt;sup&gt;a&lt;/sup&gt;</td>
<td>0.30 ± 0.12&lt;sup&gt;b&lt;/sup&gt;</td>
<td>0.46 ± 0.13&lt;sup&gt;a&lt;/sup&gt;</td>
</tr>
<tr>
<td></td>
<td>0.06 ± 1.07&lt;sup&gt;a&lt;/sup&gt;</td>
<td>–0.62 ± 0.90&lt;sup&gt;b&lt;/sup&gt;</td>
<td>0.41 ± 0.87&lt;sup&gt;a&lt;/sup&gt;</td>
</tr>
</tbody>
</table>

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 standardized 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 chick guard and \( F_{2,14} = 253, p = 0.008 \) at crèche). 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.

<table>
<thead>
<tr>
<th>2003</th>
<th>Incubation</th>
<th>Chick guard</th>
<th>Crèche</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Open Sea 1</td>
<td>Open Sea 2</td>
<td>Closed Sea</td>
</tr>
<tr>
<td>n</td>
<td>250</td>
<td>250</td>
<td>190</td>
</tr>
<tr>
<td>Dive depth (m)</td>
<td>68.02 ± 49.57&lt;sup&gt;a&lt;/sup&gt;</td>
<td>66.86 ± 54.93&lt;sup&gt;a&lt;/sup&gt;</td>
<td>45.71 ± 28.72&lt;sup&gt;a&lt;/sup&gt;</td>
</tr>
<tr>
<td>Dive duration (s)</td>
<td>202.72 ± 86.22&lt;sup&gt;a&lt;/sup&gt;</td>
<td>201.69 ± 99.71&lt;sup&gt;a&lt;/sup&gt;</td>
<td>148.41 ± 42.88&lt;sup&gt;b&lt;/sup&gt;</td>
</tr>
<tr>
<td>Bottom time (s)</td>
<td>90.79 ± 51.35&lt;sup&gt;a&lt;/sup&gt;</td>
<td>97.49 ± 60.82&lt;sup&gt;a&lt;/sup&gt;</td>
<td>58.87 ± 29.65&lt;sup&gt;a&lt;/sup&gt;</td>
</tr>
<tr>
<td>Post-dive interval duration (s)</td>
<td>–0.22 ± 1.13&lt;sup&gt;a&lt;/sup&gt;</td>
<td>–0.28 ± 1.23&lt;sup&gt;a&lt;/sup&gt;</td>
<td>–0.16 ± 1.41&lt;sup&gt;a&lt;/sup&gt;</td>
</tr>
<tr>
<td>Descent rate (m s&lt;sup&gt;−1&lt;/sup&gt;)</td>
<td>1.08 ± 0.47&lt;sup&gt;a&lt;/sup&gt;</td>
<td>1.08 ± 0.54&lt;sup&gt;a&lt;/sup&gt;</td>
<td>0.94 ± 0.35&lt;sup&gt;a&lt;/sup&gt;</td>
</tr>
<tr>
<td>Ascent rate (m s&lt;sup&gt;−1&lt;/sup&gt;)</td>
<td>–1.04 ± 0.60&lt;sup&gt;a&lt;/sup&gt;</td>
<td>–1.11 ± 0.65&lt;sup&gt;a&lt;/sup&gt;</td>
<td>–0.85 ± 0.40&lt;sup&gt;a&lt;/sup&gt;</td>
</tr>
<tr>
<td>Total way vertical at the bottom (m)</td>
<td>16.81 ± 14.90&lt;sup&gt;a&lt;/sup&gt;</td>
<td>14.42 ± 12.48&lt;sup&gt;a&lt;/sup&gt;</td>
<td>15.02 ± 10.35&lt;sup&gt;a&lt;/sup&gt;</td>
</tr>
<tr>
<td>Diving efficiency</td>
<td>0.41 ± 0.11&lt;sup&gt;a&lt;/sup&gt;</td>
<td>0.44 ± 0.12&lt;sup&gt;a&lt;/sup&gt;</td>
<td>0.36 ± 0.13&lt;sup&gt;a&lt;/sup&gt;</td>
</tr>
<tr>
<td></td>
<td>0.09 ± 0.83&lt;sup&gt;b&lt;/sup&gt;</td>
<td>0.41 ± 0.92&lt;sup&gt;a&lt;/sup&gt;</td>
<td>–0.37 ± 0.82&lt;sup&gt;b&lt;/sup&gt;</td>
</tr>
</tbody>
</table>
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).

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.
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 (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 swim 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 *Champsocephalus 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 *Champsocephalus 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 north-eastern 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 chrysolophus 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-
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 creche. 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 Rockhopper 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

<table>
<thead>
<tr>
<th>Site</th>
<th>Prospected area</th>
<th>Dive type</th>
<th>Diet (% by mass)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Open Sea 1</td>
<td>Plateau slope</td>
<td>U/W</td>
<td>71 13 10 6</td>
</tr>
<tr>
<td>Open Sea 2</td>
<td>Plateau slope</td>
<td>U/A</td>
<td>38 28 20 14</td>
</tr>
<tr>
<td>Closed Sea</td>
<td>Neritic zone</td>
<td>W/V</td>
<td>13 84 0 3</td>
</tr>
</tbody>
</table>

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**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.
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, Beauplet 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).

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