

# Foraging strategies of chinstrap penguins at Signy Island, Antarctica: importance of benthic feeding on Antarctic krill

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**ABSTRACT:** Chinstrap penguins *Pygoscelis antarctica* are one of the major consumers of Antarctic krill *Euphausia superba* in the Southern Ocean. To examine their foraging strategy, we studied foraging trip patterns and diving behaviour of chinstrap penguins breeding at Signy Island, Antarctica, using time-depth recorders. Foraging trips of penguins could be divided into 2 groups, short diurnal (7.8 h) and longer overnight (19.9 h) trips, with diurnal trips (74 %) being dominant in number (263 out of 355 trips). The diving depths of our study birds were much deeper (to 179 m) than previous studies on this species, with modal maximum dive depth at around 90 to 100 m. Diving patterns and profiles included typical pelagic dives, but also included series of consecutive square-wave shaped dives reaching similar maximum depth, the typical characteristics of benthic dives. These benthic-type dives were more abundant in diurnal foraging trips than overnight trips. Analysis of stomach contents showed that penguins on both types of trip fed almost exclusively on Antarctic krill. There was a positive relationship between indices of the proportion of benthic feeding and of foraging efficiency (stomach content mass divided by foraging trip duration). These results highlight the potential importance of benthic feeding on Antarctic krill, the first such recorded instance for chinstrap penguins. This previously undescribed foraging strategy by one of the major avian consumers of Antarctic krill provides a new insight into the predator-prey interactions of the Antarctic coastal marine ecosystem.

**KEY WORDS:** Chinstrap penguins · Antarctic krill · Diving behaviour · Foraging efficiency · Benthic dive · Signy Island

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## INTRODUCTION

Chinstrap penguins *Pygoscelis antarctica* are one of the major consumers of Antarctic krill in the Southern Ocean marine ecosystem (Croxall & Lishman 1987, Wilson 1995). They are the second most numerous penguin species with an estimated total population of 7.5 million breeding pairs (Woehler 1995). As major consumers of krill, knowledge of their predator-prey interactions is an important component in understanding and monitoring the Antarctic marine ecosystem (Croxall et al. 1988, Reid & Croxall 2001). This is especially important in the Scotia Sea and Antarctic Peninsula regions, as populations are mainly located in these areas (Williams

1995), and this is where the local climate change associated with global warming has been particularly marked (Vaughan et al. 2001), including effects on marine ecosystems (Fraser et al. 1992, Loeb et al. 1997, Smith et al. 1999). Accordingly, the diet and foraging habitat of this species have been studied in the Scotia Sea and Antarctic Peninsula region. These studies have shown that chinstrap penguins: (1) feed mainly on krill *Euphausia superba* and *E. crystallophias* (Lishman 1985a, Trivelpiece et al. 1990, Jansen et al. 1998), and (2) that they forage inshore during the breeding season (Trivelpiece et al. 1987, Wilson & Peters 1999, Jansen et al. 2002, Lynnes et al. 2002). Diving behaviour has also been studied, and the species is characterized as a

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typical pelagic diver utilizing mainly shallow water (<40 m) (Bengtson et al. 1993, Mori 1997, Wilson & Peters 1999), although 2 of these studies examined only a small number of individuals (4 birds in Bengtson et al. 1993; 2 birds in Mori 1997).

The benthic marine environment is important as a foraging habitat for some seabirds and marine mammals (Wilson & Wilson 1988, Hindell et al. 1991, Gales & Mattlin 1997, Kato et al. 1998, Martin et al. 1998, Grémillet et al. 1999, Rodary et al. 2000). Such animals usually target benthic prey at or near the sea floor, although there is some evidence that prey may also include epipelagic zooplankton near the sea floor (Coyle et al. 1992, Hunt et al. 1996). Such prey may be concentrated by local bottom topography or by current flow, and may be an attractive foraging target for predators (Coyle et al. 1992, Hunt et al. 1996). The importance of benthic foraging on pelagic organisms by marine predators has rarely been examined. However, a recent study has highlighted that benthic dives are an important element of foraging for rockhopper penguins feeding on the euphausiid *Euphausia vallentini* in coastal areas of the Kerguelen Archipelago (Tremblay & Cherel 2000).

Chinstrap penguins breeding at Signy Island, South Orkney Islands, Antarctica, feed mainly inshore (within 60 km of the colony) compared to sympatric Adélie penguins that forage further offshore (Lynnes et al. 2002). The proximity of their foraging site to the coast may enable chinstrap penguins at Signy Island to use the benthic marine environment. In the present paper, we examine the diving behaviour of chinstrap penguins at Signy Island, to determine: (1) the possible

use of the benthic environment, (2) if found, the relative importance of benthic feeding in the foraging ecology of chinstrap penguins at Signy Island, and (3) possible mechanisms influencing the foraging efficiency of benthic and pelagic dives.

## MATERIALS AND METHODS

**Study site.** The study was carried out at Gourlay Peninsula on Signy Island, South Orkney Islands (60° 72' S, 45° 36' W) (Fig. 1) during January 2002. The breeding population of chinstrap penguins on Signy Island is approximately 50 000 pairs, of which 13 000 breed at Gourlay Peninsula (Lynnes et al. 2002). The breeding biology, diet and foraging range of the species on Signy Island is described in Lishman (1985a,b) and Lynnes et al. (2002).

**Study birds and deployment of devices.** We collected diving data from 2 types of deployments. The first were deployments of 3 wk duration (20 birds from 10 pairs); these are referred to as 'monitor birds'. The second were deployments of a single foraging trip ('trip birds'): stomach contents were collected from these birds after their trip (26 birds from 26 pairs). This allowed us to examine diving behaviour during multiple trips made by individual birds (from monitor birds) as well as during single trips in relation to diet and stomach content mass (from trip birds).

Monitor birds were captured opportunistically in the breeding colony between 10 and 13 January 2002, when they were about to go to sea after completing a

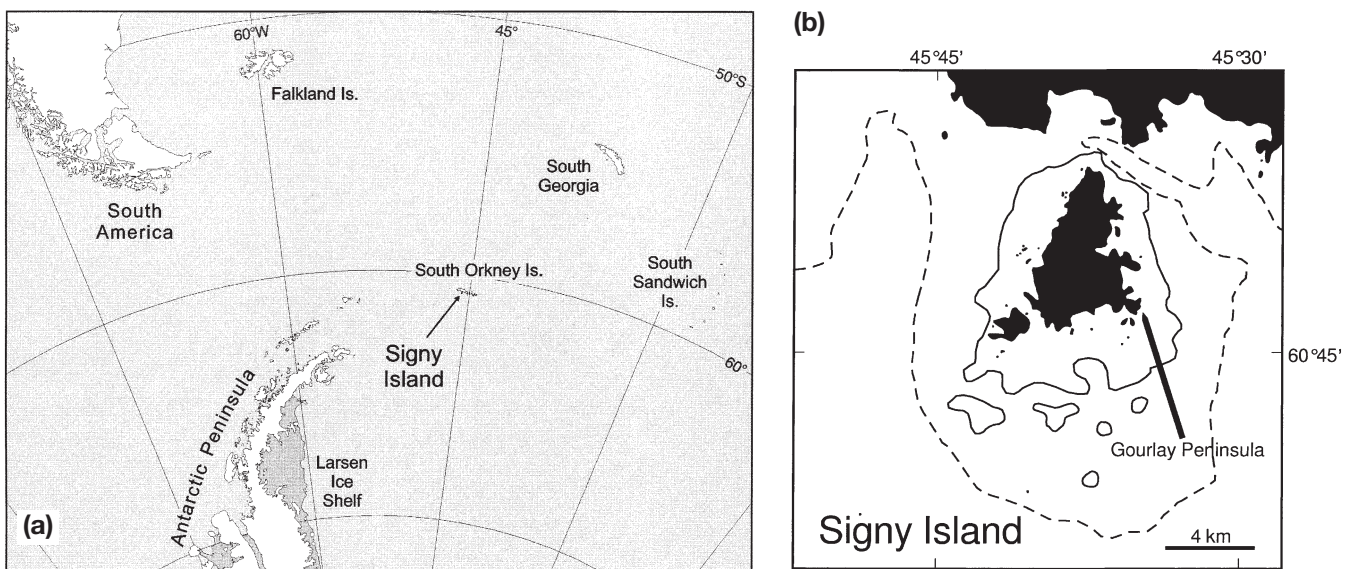


Fig. 1. Map showing the location of Signy Island (a) and the bathymetry around Signy Island (b). The solid and dashed lines indicate 20 fathom (36 m) and 100 fathom (180 m) contours, respectively

period of chick guarding. A time-depth recorder (TDR) (UME-DT, a cylindrical container with a domed top: 15 mm diameter, 50 mm length, mass 14 g including battery; Little Leonardo) was attached to the lower medial portion of the back of the penguin using Tesa tape, plastic cable ties and quick-set epoxy resin following the methods described by Wilson et al. (1997). The TDRs recorded depth every 3 s (with accuracy to within 1 m, resolution of 0.05 m), and temperature every 30 s (with accuracy to within 0.1°C). Each bird was marked on the chest with hair dye. The attachment procedure took about 30 min per bird, after which the penguins were released close to their nest sites. The instrumented birds began their foraging trip within 10 min of being returned to their nest. On their return after completing their trip, their partner was captured and instrumented in exactly the same way. From 31 January, instrumented birds were recaptured and TDRs retrieved. The data were downloaded from the logger to a portable laptop computer.

Trip birds were captured opportunistically in the breeding colony on 18 and 28 January 2002, when they were about to go to sea after switching guard duties with their partner. The birds were captured throughout the day, to fully cover the diurnal patterns of foraging trips. A TDR (UME-DT or UWE-PDT) was attached in the same way as previously described above. The UME-DTs were set to record depth and temperature every 1 s. The UWE-PDTs (20 mm diameter, 102 mm length, mass 50 g including battery; Little Leonardo) were set to record depth and swim speed every 1 s, and temperature every 30 s. On their return from the sea after a foraging trip, the birds were captured near their nest site before feeding their chicks. The stomach content of the bird was collected using the water-offloading technique (CCAMLR 1997). The diet composition was analyzed following the methods described in CCAMLR (1997). The total length of krill in the stomach samples was estimated from the carapace length using the methods in Hill (1990).

**Effect of devices.** To evaluate the effects of attached devices, we compared the growth rates of chicks from monitor birds with those from 10 control pairs without devices from the same colony. Chicks of both the monitor pairs and the control pairs were weighed every 5 d during the study period (11 to 31 January). Growth rates of the chicks were calculated from the slope of the linear regression of chick mass against date. To examine the effect of devices on trip birds, we compared foraging trip durations between trip birds and 8 un-instrumented control birds. The control birds were captured before their departure on a foraging trip, and marked on the chest with hair dye. The departure and arrival time at the colony were monitored by observation of the nest sites at least every 30 min

between dawn and dusk; transiting outside these periods has previously shown to be very rare (Lishman 1985a, Jansen et al. 1998).

**Data analysis.** Dive-depth data were analyzed using custom-written software (LOG TOOLS, Marine Micro Technology) and Igor Pro (Wave Metrics). The dive depth, dive duration, bottom time (the time between the start and end of the time when birds showed depth change of 0 m), descent and ascent rate, diving efficiency (bottom time/[dive duration + post-dive intervals]; only dives <200 s post-dive interval) were determined for each dive. A dive was deemed to occur when the maximum depth was >1 m, as dive recording units of less than 1 m were within the error range of the recorders.

Since birds tended to dive serially to a specific depth zone, consecutive dives that returned within the same depth zone were called intra-depth zone (IDZ) dives (cf. Tremblay & Cherel 2000). The IDZ was defined as the maximum depth reached by the preceding dive  $\pm 5\%$  (e.g.  $100 \pm 5$  m for a 100 m dive). Although Tremblay & Cherel (2000) used a definition for intra-depth zone as the depth of  $\pm 10\%$  to examine the benthic feeding behaviour of rockhopper penguins, we chose 5% as a criterion for our chinstrap penguins because they dive deeper than rockhopper penguins (Tremblay & Cherel 2000), and a 10% margin would produce wide limits for deep dives.

A visual inspection of dive profiles showed a variety of 'shapes' for individual dives, including square-wave shaped dives. We therefore calculated a time allocation at depth (TAD) index (Fedak et al. 2001) to compare the dive shape between dives from different foraging trips. The TAD index is designed to utilize relevant information from dive profiles and highlight where the diver centres its activity with respect to depth during a dive. The TAD index is expressed as:

$$\text{TAD index} = \frac{\{\sum_{i=2}^n [(d_i + d_{i-1})/2] \times t - A_t\}}{[(D \times T) - 2A_t]}$$

where  $A_t = D^2/S$ ,  $d$  = individual depth readings from the TDR during the dive,  $i$  = sequence of depth readings within the dive,  $t$  = sampling time interval of the TDR,  $D$  = maximum depth of the dive,  $T$  = total duration of the dive,  $S$  = a predefined average rate of change of depth. For our analyses,  $S$  was set to  $2.6 \text{ m s}^{-1}$ ; this is similar to the minimum cost of transport for chinstrap penguins ( $2.4 \text{ m s}^{-1}$ ; Culik et al. 1994), which is in line with the recommendation made by Fedak et al. (2001), who suggested that the TAD index would be close to 0.5 for V-shaped dives and close to 1 for square-wave shaped dives.

**Statistics.** Data were analysed statistically using Minitab (Version 13, Minitab) and Statview (Version 5.0, SAS) software. Values are mean  $\pm$  SD, with significance set at the 0.05 level.

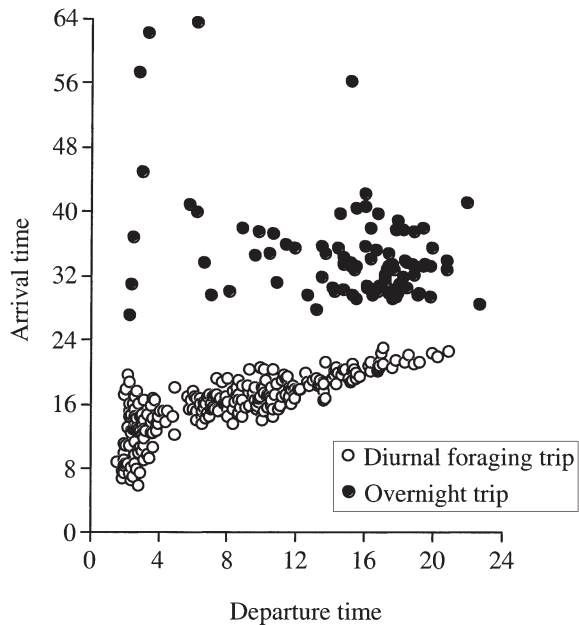


Fig. 2. *Pygoscelis antarctica*. Patterns of departure and arrival time for foraging trips from 18 birds

## RESULTS

### Device recovery and instrument effects

Of the 20 monitor birds, 18 birds were recaptured. The other 2 birds probably deserted their nests on Days 18 and 19 after deployment, respectively. One chick died after 15 d of instrument deployment on its parents; no chicks died in the un-instrumented control pairs. Chick survival rate was 86.3% during the same period at the long-term monitoring colonies on Signy Island (British Antarctic Survey unpubl. data), suggesting the loss of 1 chick would be within a natural variability range. Growth rates of the chicks did not differ between those of instrumented (19 chicks) and un-instrumented pairs (20 chicks) ( $87.4 \pm 15.4$  vs  $93.3 \pm 11.7$  g d<sup>-1</sup>; ANOVA, df = 1,37,  $F = 1.806$ ,  $p = 0.19$ ).

Of the 26 trip birds, 1 bird could not be recaptured. Another 3 birds were recaptured on Day 8 (2 birds) and Day 16 (1 bird) after deployment. These birds probably went on unusually long foraging trips. The foraging trip duration of the other 22 birds did not differ from those of 8 un-instrumented birds ( $13.6 \pm 8.2$  vs  $13.9 \pm 7.3$  h; ANOVA, df = 1,28,  $F = 0.012$ ,  $p = 0.91$ ). Of these 22 birds, we failed to recover stomach contents from 6 birds. This was because the study colony was close to the sea, and some birds had already started to feed their chicks before we found them. Consequently, we have both food and dive data for 16 trip birds. We believe that the device effects were small enough

to allow the analysis of foraging behaviour for both monitor and trip birds.

### Characteristics of foraging trip

From the depth and temperature data, we determined the departure (start of first dive) and arrival (end of last dive) times of 355 foraging trips from 18 monitor birds. The departure and arrival times of these birds showed clear patterns in relation to time of day (Fig. 2), with no departures or arrivals around midnight. The foraging trips were classified into either diurnal or overnight foraging trips. Diurnal foraging trips were dominant in number (263 trips or 74%). The duration of diurnal trips was shorter than overnight trips, when all foraging trips from 18 birds were combined ( $7.8 \pm 2.9$  vs  $19.9 \pm 9.6$  h; ANOVA, df = 1,353,  $F = 336.8$ ,  $p < 0.01$ ). Although 2 out of 18 birds exhibited only diurnal trips, 16 birds exhibited both diurnal and overnight foraging trips. There were significant differences in trip duration between diurnal and overnight trips in these 16 birds, together with significant between-individual differences (2-way ANOVA, trip type: df = 1287,  $F = 392.3$ ,  $p < 0.01$ ; individual effect: df = 15,287,  $F = 8.4$ ,  $p < 0.01$ ; interaction: df = 15,287,  $F = 5.1$ ,  $p < 0.01$ ).

### Dive patterns and profiles

A total of 163 115 dives were recorded from the 355 foraging trips of the 18 monitor birds. Two types of dives were typically recorded (Fig. 3): (1) shallow and short duration dives and (2) deeper and longer duration dives, similar to previous dive records for chinstrap

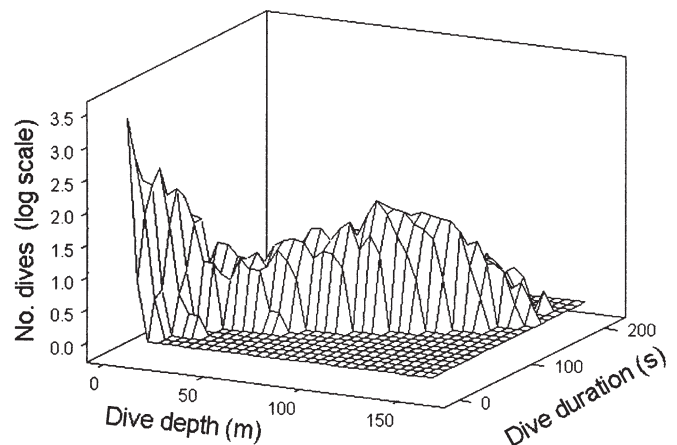


Fig. 3. *Pygoscelis antarctica*. Frequency distribution by depth and duration for all dives made by 1 chinstrap penguin. Note that the z-axis is a logarithm scale

penguins, e.g. Bengtson et al. (1993). We concentrated our analyses mostly on dives deeper than 5 m in depth or longer than 20 s in duration (called foraging dives hereafter); dives <5 m and <20 s may be considered as dives for travelling (Bengtson et al. 1993), these consist mostly of porpoising (Yoda et al. 1999) and are dives without feeding activity (Ropert-Coudert et al. 2001) in congeneric Adélie penguins. On average, the contribution of these travelling dives (<5 m and <20 s) to the total dives for each bird was 51.1% by number, but only 7.2% in total dive duration. Thus, analyses of foraging dives represent most of the foraging activity. A frequency distribution of dive parameters for foraging dives showed a peak around 90 to 95 m for maximum dive depth (Fig. 4a) and peaks at 20 to 30 s and 110 to 120 s for dive duration (Fig. 4b). The deepest dive was to 179 m, and the longest dive was 219 s in duration.

Visual inspection of dive profiles indicated diving variability between foraging trips (Fig. 5). Some trips showed variable dive profiles, with dives reaching different maximum depths (Figs. 5a,b & 6a). These dive patterns have been considered to reflect pelagic dives in previous studies in chinstrap penguins (Bengtson et al. 1993, Wilson & Peters 1999) as well as other species of penguin (Chappell et al. 1993, Cherel et al. 1999) and other seabirds (Grémillet et al. 1999). In contrast, some foraging trips showed consecutive dives to the same depth, with no deeper dives in the series for some or most of the trip (Fig. 5c,d). The profiles of individual dives within these series showed a square-wave shape (Fig. 6b). Dives with these patterns have been reported as benthic dives in rockhopper penguins (Tremblay & Cherel 2000), Adélie penguins (Ropert-Coudert et al. 2002) and some marine mammals (Hindell et al. 1991, Gales & Mattlin 1997, Martin et al. 1998).

Our results showed that there was diel variation in diving behaviour. The timing of civil sunrise and sunset for the latitude and longitude of Signy Island varied during the study; the nighttime (with the sun below the horizon) was 21:24 to 02:54 h at the shortest and 20:39 to 03:53 h at the longest. The dive depth of foraging dives was shallower at nighttime (21:00 to 03:00 h), and showed little variation during the daytime (Fig. 7a). The frequency of foraging dives tended to be lower between 17:00 and 21:00 h (Fig. 7b), probably because birds tend to spend this time at the breeding colony following the peak arrival period between 15:00 and 20:00 h (Fig. 2).

### Diving efficiency

The calculated TAD index for each dive appeared to represent the dive shape well (Fig. 6a,b), as previously shown by Fedak et al. (2001). Foraging dives with a

TAD index higher than 0.85 corresponded to square-wave shaped dives (benthic dives); dives with a TAD index below this were more variable and were mostly pelagic dives. The diving efficiency was higher in square-wave shaped dives than in other dives for all birds (ANOVA,  $p < 0.01$  for all 18 birds); on average,  $0.179 \pm 0.019$  for square-wave shaped dives and  $0.112 \pm 0.016$  for other dives ( $n = 18$  birds). Square-wave shaped dives were deeper than other dives (for example, average dive depth of 91.8 and 44.2 m, respectively, for Bird A), but because diving efficiency is known to be depth dependent (Cherel et al. 1999, Tremblay & Cherel 2000), we further restricted the comparison to dives between 80 and 100 m depth. With this restriction, square-wave shaped dives still had a higher diving efficiency than other dives for all birds

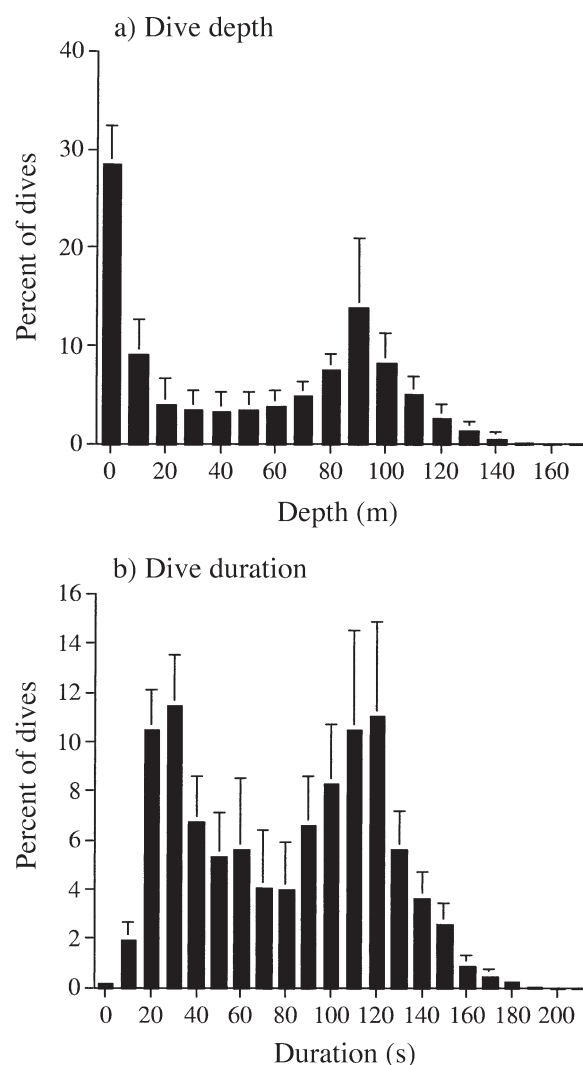


Fig. 4. *Pygoscelis antarctica*. Frequency distribution of (a) dive depth and (b) dive duration for foraging dives (dives >5 m or >20 s). Means + SD are shown, calculated using individual bird data ( $n = 18$ )

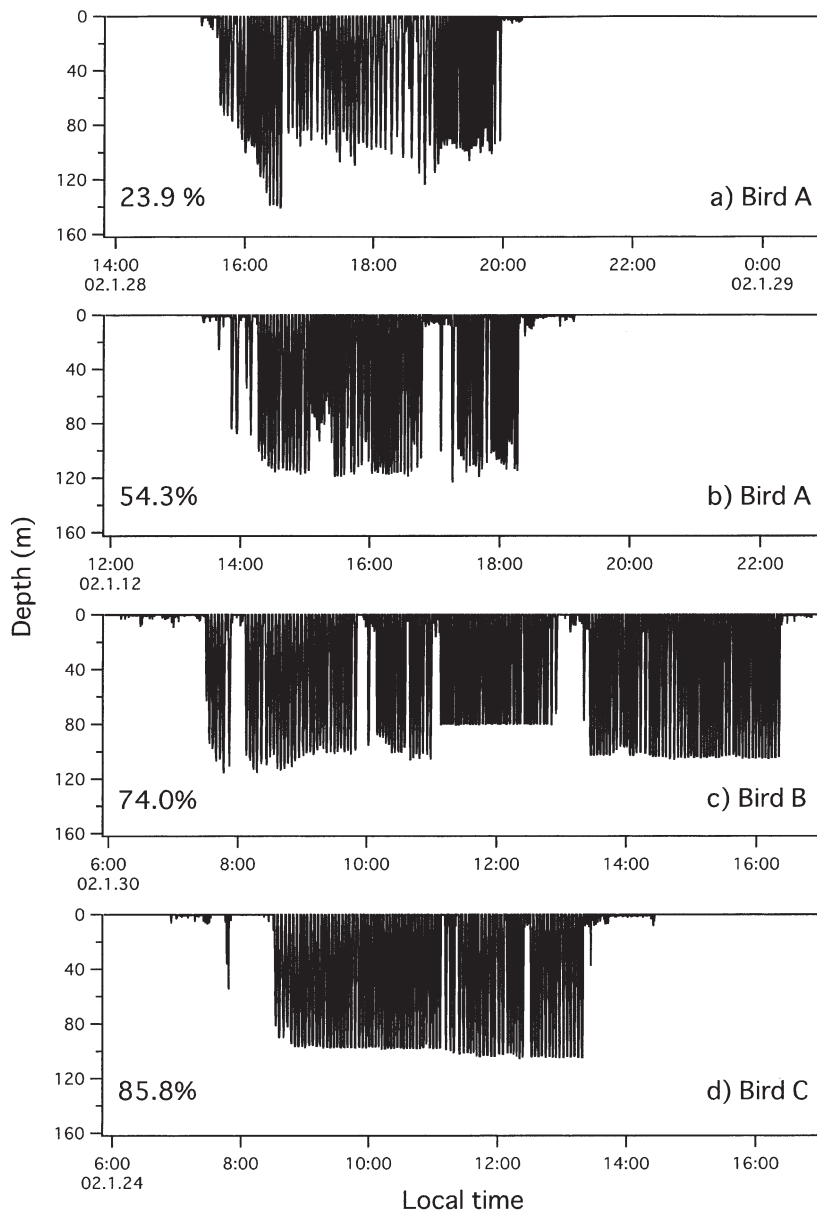


Fig. 5. *Pygoscelis antarctica*. Diving records from 4 foraging trips from 3 individual penguins. The proportion of intra-depth zone (IDZ) dives is shown as a percentage for each trip. Note that the value of the IDZ index is higher as the dive profiles within a trip become more flat

(ANOVA,  $p < 0.01$  for all 18 birds); on average,  $0.167 \pm 0.014$  for square-wave shaped dives and  $0.106 \pm 0.017$  for other dives ( $n = 18$  birds).

#### Intra-depth zone (IDZ) dives

For each foraging trip, the proportion of time spent diving in IDZ dives was calculated to quantify the tendency of birds to dive to similar depths in consecutive

dives. We calculated the proportion of the time spent in IDZ dives instead of the percent number of IDZ dives as calculated by Tremblay & Cherel (2000); the latter may be biased in our birds due to the high contribution of very shallow dives to total dive numbers. As a high proportion of the IDZ dive duration appeared to correspond with a flat dive profile, the IDZ index may be an approximate index for the amount of benthic diving (Fig. 5). The average proportion of IDZ dive duration among the 355 recorded foraging trips was  $51.8 \pm 16.3\%$ , and was higher in diurnal ( $57.5 \pm 15.0\%$ ) than in overnight ( $36.0 \pm 6.0\%$ ) foraging trips (Fig. 8). There were no seasonal trends in the IDZ value for diurnal trips, indicating the occurrence of benthic dives throughout the study period (from 10 to 31 January; Spearman's rank correlation,  $\rho = 0.09$ ,  $p = 0.16$ ).

To determine whether the increased 'flatness' of dive patterns (the value of the IDZ index) over a foraging trip indicates a higher proportion of square-wave shaped dives within the trip, the relationship between the IDZ index and an index of dive shape (TAD index) were examined. The average value of the TAD index for foraging dives within a foraging trip varied from 0.66 to 0.88. There was a significant positive relationship between the average value of the TAD index of dives (dive shape) and the proportion of IDZ dive durations (flatness of dive profiles within a whole foraging trip) both for all trips combined ( $n = 355$  trips,  $R^2 = 0.469$ ,  $p < 0.0001$ ) and among trips for each individual bird ( $n = 8$  to 30 trips,  $R^2 = 0.403\text{--}0.787$ ,  $p < 0.05$  for all individuals). This indicates that the higher the proportion of square-wave shaped dives in the trip, the higher the IDZ dive proportion in a foraging trip.

#### Diet and meal mass

The analysis of the 16 stomach contents samples from the trip birds showed that the prey items were exclusively Antarctic krill *Euphausia superba*, except for 1 amphipod (<1 g). The average wet mass of the stomach contents was 344.3 g. We calculated an index of foraging efficiency for each bird as the stomach content mass divided by the corresponding foraging trip duration. The index varied from 6.8 to 65.3  $\text{g h}^{-1}$  among

the study birds and it was correlated with the proportion of IDZ dive durations during the corresponding foraging trip: thus, the greater the contribution of IDZ dives, the higher the index of foraging efficiency (Fig. 9). The relationship was significant for diurnal foragers ( $y = 0.64x + 18.4$ ;  $n = 10$ ,  $R^2 = 0.65$ ,  $p < 0.01$ ), although the average value of the foraging efficiency index differed between diurnal foragers (10 birds:  $45.4 \pm 13.9 \text{ g h}^{-1}$ ) and overnight foragers (6 birds:  $16.7 \pm 7.1 \text{ g h}^{-1}$ ) (ANOVA,  $df = 1, 14$ ,  $F = 21.5$ ,  $p < 0.01$ ). Changes in bird body mass before and after the foraging trip (after accounting for the mass of stomach contents) could indicate the amount of digested food at sea. There was no relationship between body mass change of birds and proportion of IDZ dive durations of corresponding foraging trips (for all birds:  $n = 16$ ,  $R^2 = 0.003$ ,  $p = 0.84$ ; for diurnal foragers:  $n = 10$ ,  $R^2 = 0.001$ ,  $p = 0.94$ ), indicating that the amount of digested food at sea is independent of IDZ dive frequency.

The mean total length of krill varied from 44.1 to 50.0 mm among stomach content samples. There was no relationship between the proportion of IDZ dive duration and mean total length of krill from the stomach samples ( $n = 16$ ,  $R^2 = 0.05$ ,  $p = 0.39$ ).

## DISCUSSION

### Occurrence of benthic dives during the foraging trip

One of the striking results from this study is the occurrence of square-wave shaped dives, invariably appearing as a series of consecutive dives to similar dive depths (Figs. 5c,d & 6b). Tremblay & Cherel (2000) reviewed and presented 6 criteria to characterize the benthic diving behaviour in air-breathing vertebrates. According to these criteria, benthic dives: (1) have a typical square-wave dive profiles, (2) are consecutive dives varying little in their maximum depth, (3) have no dives reaching a deeper depth within a series, indicating that the sea floor limits the depth to which animals dive, (4) generally show no diurnal patterns in depth, duration and frequency, suggesting that animals do not feed on pelagic organisms performing daily vertical migration. In addition to these 4 criteria, (5) bathymetry in the foraging area and (6) a diet containing benthic prey can also be used

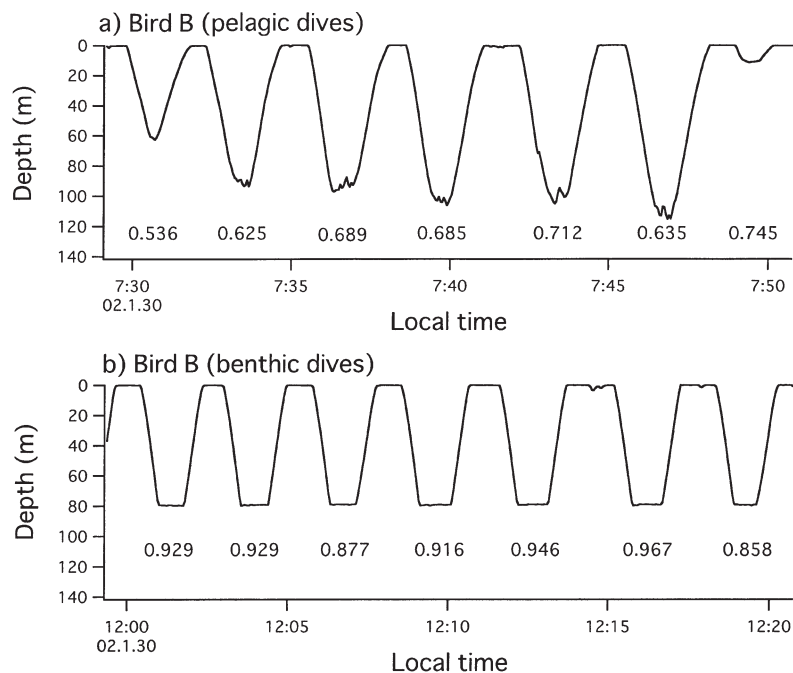


Fig. 6. *Pygoscelis antarctica*. Extended dive records of Bird B from Fig. 5 to show various dive profiles. The top panel illustrates pelagic dives and the bottom panel shows benthic dives with square-wave shape dives. The values of the time allocation at depth index (TAD index) are shown for each dive

as criteria for determining the occurrence of benthic dives.

The diving profiles of chinstrap penguins presented in this study are in close agreement with the first 3 criteria. Substantial numbers of dives showed square-wave profiles, with consecutive dives to similar depths (usually around 90 to 100 m), and without any dives to depths deeper than this (Fig. 5c,d). These results indicate that the sea floor probably limited diving behaviour for these penguins.

Data on the foraging range of chinstrap penguins and bathymetry around Signy Island appear to meet these criteria. Lynnes et al. (2002) examined the foraging location of chick-rearing chinstrap penguins using satellite telemetry in January and February of 2000 and 2001, though there are no analogous data for 2002. In both 2000 and 2001, there was a high concentration of foraging near Signy Island (<15 km south of the island), although there was also another area of high foraging activity at about 60 km south west of the island in 2000, a year with lower reproductive success (Lynnes et al. 2002). The foraging trip duration was similar during 2001 and 2002, but differed in 2000 (24.2, 14.4 and 11.0 h on average in 2000, 2001 and 2002, respectively), indicating that foraging distances for penguins in 2002 were probably close to the island, as in 2001. There is a shallow shelf between 36 m

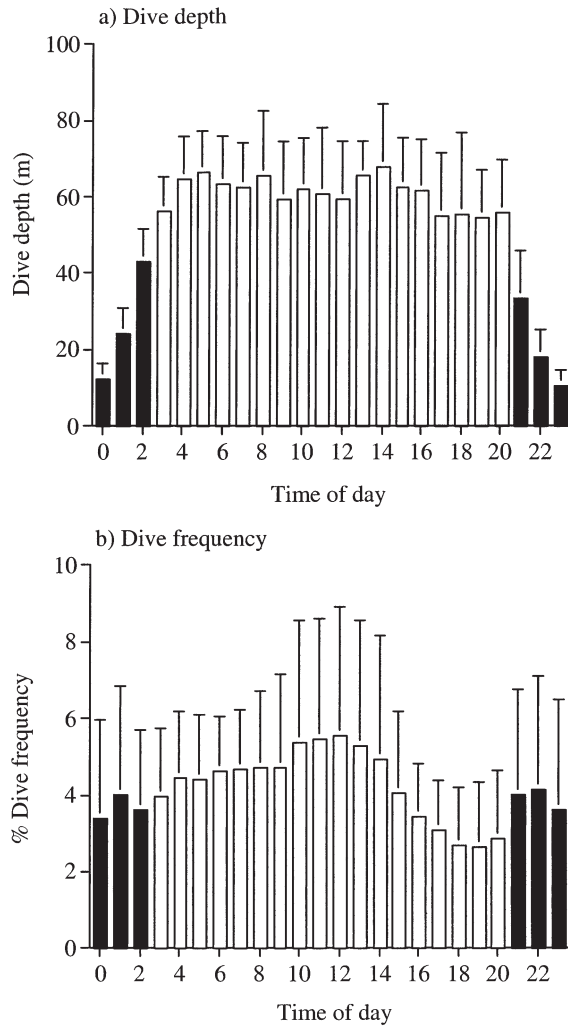


Fig. 7. *Pygoscelis antarctica*. Diel variation of (a) dive depth and (b) dive frequency distribution. Means + SD are shown, calculated using individual bird data (18 birds for dive frequency but 14 to 18 birds for dive depth as some birds did not dive at some hours). The open and closed columns show daytime and nighttime, respectively

(20 fathoms) and 180 m (100 fathoms) depth contour at the south of Signy Island (<10 km) (Fig. 1). This is where high foraging activity was located during 2001. Thus, the diving behaviour, foraging area and bathymetry data suggest that these birds could reach the sea floor in nearshore regions around the island.

The analysis of stomach contents indicates that chinstrap penguins at Signy Island fed almost exclusively on Antarctic krill in the austral summer of 2002; this was similar to previous studies at Signy Island (Lishman 1985a, Lynnes et al. 2002) as well as in the Antarctic Peninsula region (Trivelpiece et al. 1990, Jansen et al. 1998, see also Williams 1995 for a review). This seems to be inconsistent with the occurrence of benthic

dives among study birds, as Antarctic krill usually occur pelagically in the water column between the sea surface and a depth of about 100 m (Godlewska 1996). However, previous examples of the occurrence of benthic aggregations of Antarctic krill have been reported (Gutt & Siegel 1994), and a recent study showed the importance of benthic feeding on diatoms by krill in coastal waters of the Antarctic Peninsula (Ligowski 2000). Diet of demersal fish in Antarctic shelf waters also indicates that these fish opportunistically feed on Antarctic krill, which might descend to the bottom (Kock 1985, Takahashi & Iwami 1997). Thus, benthic aggregations of Antarctic krill would provide a foraging opportunity for higher predators in the Antarctic coastal marine ecosystem.

Our results indicate that chinstrap penguins at Signy Island opportunistically feed on Antarctic krill at the sea floor; this is a previously undescribed foraging strategy for krill-dependent penguin species.

#### Importance of benthic dives in the foraging ecology of penguins

There was a positive relationship between the proportion of IDZ dives within a foraging trip and the index of foraging efficiency (meal mass divided by foraging trip duration) (Fig. 9). This indicates that benthic dives could be a more efficient way to feed on krill than pelagic dives for chinstrap penguins breeding at Signy Island. Feeding on pelagic euphausiids at or near the sea floor has been reported for murres *Uria* spp. (Coyle et al. 1992) and short-tailed shearwaters *Puffinus*

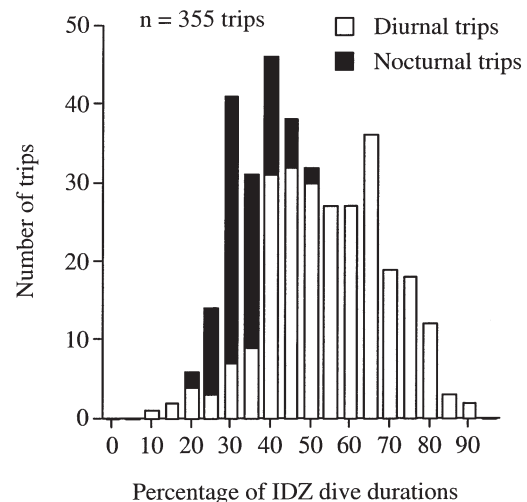


Fig. 8. *Pygoscelis antarctica*. Frequency distribution of the proportion of intra-depth zone dives in 355 foraging trips made by 18 birds. Note that diurnal trips had a higher but more variable extent of intra-depth zone (IDZ) dives



*tenuirostris* (Hunt et al. 1996) in Alaska, and rockhopper penguins *Eudyptes chrysocome filholi* in the Kerguelen Archipelago (Tremblay & Cherel 2000), although only the study by Tremblay & Cherel (2000) indicated that benthic feeding was more efficient than pelagic feeding.

In order to determine why feeding on krill at the sea floor is more efficient than feeding on krill pelagically, we suggest that 2 factors may be important: (1) predictability of prey distribution and (2) differences in krill behaviour in the pelagic and benthic habitat. First, predictability of prey aggregation between dives may be higher in the benthic environment as the vertical movement of prey is restricted by the sea floor. This may enable penguins to locate and re-locate prey more easily during consecutive dives, as the prey would remain near the sea floor at the same depth. The predictable diving depth would contribute to the higher time-use efficiency of benthic dives, through changes in diving behaviour, for example, efficient oxygen loading during surface time between dives (Wilson et al. 2002). Tremblay & Cherel (2000) also found higher dive efficiency in benthic dives than in pelagic dives for rockhopper penguins. Furthermore, Zamon et al. (1996), by studying the fine-scale 3-dimensional prey field of chinstrap penguins, suggested that the encounter probability, rather than the density of prey, is an important factor for chinstrap penguins when they select krill patches to feed on. Hunt & Harrison (1990) showed that planktivorous auklets prefer to forage where prey was concentrated at the thermocline off St. Lawrence Island, Alaska, and suggested that the concentration of prey in the vertical dimension may be important for foraging by diving seabirds.

Second, pelagic crustaceans may be restricted by the horizontal as well as the vertical features of complex bottom topography in shallow shelf waters, making them potentially more vulnerable to predation (Perissinotto & McQuaid 1992, Hunt et al. 1996). The depth changes of penguins at the bottom phase of benthic dives are very small, suggesting that they were feeding on dense and relatively static patches of prey, which might increase the efficiency of foraging. The swim speed of Adélie penguins during flat-bottom dives slow down to less than  $0.5 \text{ m s}^{-1}$  and sometimes to  $0.0 \text{ m s}^{-1}$  (Ropert-Coudert et al. 2002), similar to the movement of chinstrap penguins from Signy Island (A. Takahashi unpubl. data). This would also support the idea that they were feeding on relatively static patches of prey.

Previous studies on the diving behaviour of chinstrap penguins using time-depth recorders have been conducted at Seal Island (Bengtson et al. 1993, Mori 1997) and at Ardley Island (Wilson & Peters 1999) in the Antarctic Peninsula region. These studies did not report

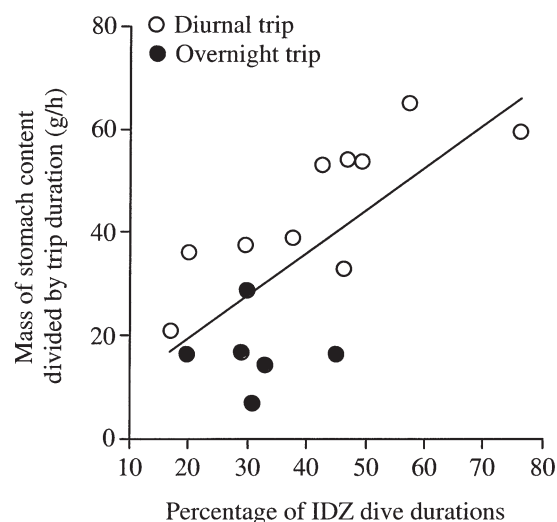


Fig. 9. *Pygoscelis antarctica*. Foraging efficiency index (mass of stomach content divided by foraging trip duration) in relation to the percentage of intra-depth zone (IDZ) dives during the corresponding foraging trip. Regression equation is  $y = 0.83x + 3.25$  ( $n = 16$ ,  $R^2 = 0.48$ ,  $p < 0.01$ )

any sign of benthic dives and showed that chinstrap penguins mainly foraged in shallow waters; i.e. mean dive depth of foraging dives ( $>5 \text{ m}$  in depth or  $>20 \text{ s}$  duration) was  $31.0 \text{ m}$  (Bengtson et al. 1993) and 80% of all dives ( $>2 \text{ m}$ ) had a depth maxima of less than  $30 \text{ m}$  (Wilson & Peters 1999). This contrasts with our results, which showed the occurrence of both benthic and deeper dives (Figs. 4 & 5). It is difficult to interpret the differences in diving patterns between these studies, as there are some confounding factors; for example, differences in the size of TDR devices used and in sampling intervals of TDR, which may influence the dive shape (Wilson et al. 1995). However, if the difference in the foraging environment is the principal cause, then birds from Signy Island may have the opportunity to feed on benthic aggregations of krill, which may not be an option for birds in the Antarctic Peninsula. Hunt et al. (1996) showed that shearwaters feeding on euphausiids near the Pribilof Islands, Alaska, took advantage of tidal currents that apparently push the prey to shallow depths. The bathymetry and current flow around Signy Island could concentrate prey near to shore regions, and so requires further study.

An implication from our study is the importance of the inshore marine habitat at Signy Island. Our results showed that the proportion of benthic feeding within the trip influenced the foraging efficiency of our study birds. The foraging efficiency index used in this study (stomach content mass divided by trip duration) would directly relate to the chick-provisioning rate. As the

potential areas of high-efficiency foraging appear to be limited to relatively shallow areas near the island, these inshore areas may be important for the reproductive performance of chinstrap penguins.

In conclusion, the present study showed that chinstrap penguins breeding at Signy Island fed opportunistically on Antarctic krill at the sea floor. Feeding at the sea floor under the circumstances of this study appeared to be an efficient way of foraging compared to pelagic feeding. This previously undescribed foraging strategy by one of the major avian consumers of Antarctic krill provides a new insight into the predator-prey interactions of the Antarctic coastal marine ecosystem.

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