

Utilisation of the oceanic habitat by king penguins over the annual cycle

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ABSTRACT: The distribution and behaviour of foraging seabirds depend on the physical features of the ocean at different time and space scales, but little is known for penguins. We investigated the foraging behaviour of king penguins in relation to oceanographic features over the birds' complete annual cycle. A total of 44 birds was followed between 1994 and 1997 at the Crozet Islands to monitor foraging habitat, diving behaviour, and sea temperature of the water column, using satellite-tracking and time-temperature-depth recorders (TDR) carried by the birds. The study included breeding in summer, the winter period of chick raising, and the post-moult period in spring. King penguins foraged in 2 specific regions in response to the seasonal changes in local prey availability. In summer, satellite-tracked birds during the incubating and brooding stages ($n = 14$) preferentially exploited the polar front located 340 to 450 km to the south of their breeding site. TDR-equipped birds ($n = 12$) also foraged at the polar front in summer as indicated by the vertical temperature profiles. In autumn and winter, satellite tracks ($n = 8$) and sea temperature measurements of TDR-equipped birds ($n = 8$) showed that birds with crèching chicks instead foraged in antarctic waters, with 70% of individuals reaching the latitude of the pack-ice limit (1600 km from the colony). This suggests better prey availability than in the polar frontal zone at that time. When the birds were at the latitude of the polar front, the thickness of the surface mixed layer (SML) ranged from 80 m in summer to 140 m in winter, the SML temperature was $\sim 4^{\circ}\text{C}$ and the thermocline had a mean maximum gradient of -0.5°C for each 10 m depth. When the birds were at their most southerly position, the depth of the SML ranged from 100 m in autumn to ~ 150 m in winter, while its temperature ranged from -0.8 to 2°C . The temperature gradient of the thermocline showed an inversion in autumn, and this gradient was positive in winter (mean maximum gradient of 0.3°C for each 10 m depth). Except for spring birds ($n = 4$) and for 1 winter bird, where the SML exceeded the diving range, all TDR-equipped penguins ($n = 19$) dived preferentially in and below the depth of the thermocline, thereby minimising diving in the SML. Therefore, their prey may have been predictably concentrated below the SML through oceanographic processes. In king penguins, the strategy of going south could then have evolved in relation to the thinning of the SML towards the south at any time of the year.

KEY WORDS: Habitat use · Foraging · King penguins · Diving · Sea temperature · Thermocline · Predictability · Southern Ocean

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INTRODUCTION

The foraging behaviour of seabirds largely depends on the distribution and predictability of

their prey. The distribution of the prey species is correlated to various degrees with the physical and biological features of the ocean. According to their foraging range and mode, at-sea distribution of seabirds is related to physical processes at different geographic and temporal scales (Hunt & Schneider 1987, Ainley & DeMaster 1990, Hunt et al. 1999).

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For nearshore species of the northern hemisphere such as alcsids, physical processes at small geographic scales and over shallow waters (such as the interaction of bottom topography and tidal current) influence the concentration of plankton and make it available to birds near the surface (Hunt 1991). Off-shore, volant species such as those inhabiting the Southern Ocean may rely on bathymetric features or on mesoscale physical features of the deep, open ocean. Evidence comes from studies on individual albatrosses, which are concentrated at edges of island shelves or at oceanic fronts at certain periods of their annual cycle (Rodhouse et al. 1996, Weimerskirch 1997). While their ability to travel at a low cost allows them to take advantage of localised prey concentrations, they appear to explore the surface ocean essentially at random, with the probability of finding prey increasing with the area covered (Weimerskirch et al. 1994).

In contrast, diving seabirds such as penguins generally travel more slowly than volant birds and travel at a much higher energy cost. In addition, prey are not visible from a distance as they are for other birds. Therefore, diving birds should rely particularly on prey showing a predictable spatial distribution (Brown 1980, Wilson & Wilson 1990, Costa 1991, Gaston & Jones 1998).

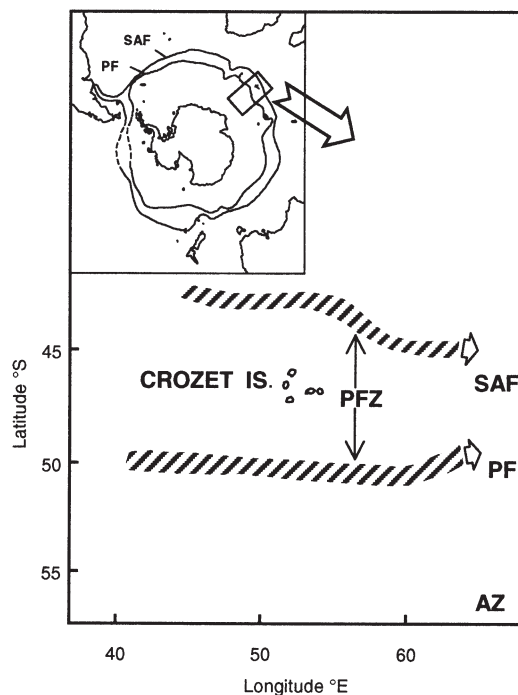


Fig. 1. Study area and major oceanographic structures of the Crozet sector. AZ: Antarctic zone; PF: Polar front; PFZ: Polar frontal zone; SAF: Sub-antarctic front. Data from Park et al. (1991, 1997), Belkin & Gordon (1996)

Studies of the horizontal movement of some oceanic penguin species have revealed that they indeed forage preferentially at large-scale physical features such as oceanic fronts (Bost et al. 1997, Hull et al. 1997). However, although these predators spend nearly 50% of their time underwater (Charrassin et al. 1998), whether and how penguins use hydrographic features in the vertical dimension remains virtually unknown. Ship-based studies of emperor penguins have suggested that they may rely on subsurface fronts while foraging over the shelf break, but records of the diving behaviour at such sites are not available (Ainley et al. 1998). Studying the relation between individual diving behaviour of penguins and the local hydrology appears essential, therefore, for understanding how oceanographic features affect foraging patterns in terms of prey predictability. Such studies are now possible because animals can readily carry miniaturised sampling instruments that record both behavioural and environmental parameters (e.g. Wilson et al. 1994, Campagna et al. 2000, Georges et al. 2000, Koudil et al. 2000).

King penguins *Aptenodytes patagonicus* are exceptional among diving seabirds. They travel considerable distances at sea, commonly more than 400 km from the colony (Bost et al. 1997). They are also the best avian divers apart from emperor penguins *A. forsteri* since they frequently dive to depths >300 m (Kooyman et al. 1992, Charrassin et al. 1998, Pütz et al. 1998). King penguin foraging habitat and diving behaviour have been studied extensively in summer (Kooyman et al. 1992, Jouventin et al. 1994, Bost et al. 1997, Charrassin et al. 1998, Pütz et al. 1998), but information is sparse for other seasons (Jouventin et al. 1994, Moore et al. 1999). Interestingly, the distribution of their main prey, myctophid fish, depends on the water temperature (Hulley 1981), which makes this parameter potentially important for the penguin hunting strategy. We address here 2 main questions: (1) what are the main foraging areas of king penguins throughout their annual cycle, including during the winter period of chick rearing and the post-moult stage in spring; and (2) what is the importance of the local hydrographic features, including those in the vertical dimension, for the diving patterns throughout the year?

METHODS

Study area. The study was conducted from 1994 to 1997 at 'La Grande Manchotière' colony, Possession Island, Crozet Archipelago (46° 25' S, 51° 45' E), where about 40 000 pairs of king penguins breed. The whole Crozet Archipelago (1 million pairs) has ~50% of the

world population (Guinet et al. 1995). The Crozet Archipelago (mean annual air temperature 8°C) lies in the polar frontal zone (PFZ), which is the northern boundary of the antarctic zone (Fig. 1). The PFZ is the area between the sub-antarctic front (located at ~43°S) and the polar front (at ~50°S in April) (Park et al. 1993), which are major fronts of the Southern Ocean (Fig. 1). The polar front is defined by the northernmost extent of the subsurface 2°C temperature minimum, which corresponds to a sea surface temperature (SST) of 4 to 5°C (Park et al. 1993, 1998). The antarctic zone lies south of the polar front down to the antarctic continent.

The distribution of the summer properties of the surface mixed layer (SML) and of the underlying layer in the study area is shown in Fig. 2. These 2 layers are separated by a vertical temperature gradient (or thermocline). In the Southern Ocean, the temperature of the SML is lowest during winter. In summer, a seasonal warming occurs in the upper part of the SML, while a part of the previous winter's mixed layer persists below (characterised by the minimum temperature attained during the previous winter). These underlying waters constitute in summer the subsurface temperature minimum and define the 'winter water' (Park et al. 1998). The SML and winter water temperatures decrease towards the south, as do the SML thickness and the winter water depth (Fig. 2).

Birds and study periods. Forty-four birds were studied and equipped so that king penguins were represented over their complete annual cycle (Fig. 3). Horizontal movements at sea were monitored in 23 birds during the 1994, 1996 and 1997 breeding seasons, and diving behaviour was monitored in 21 birds during the 1995 and 1996 breeding seasons. Brooding birds were tending a 1 to 3 wk-old chick and birds at the autumn and winter crèche stage were caring for an emancipated chick (i.e. older than 6 wk). Birds at the post-moult stage (spring 1996) were unsuccessful breeders from 1995.

Deployment of satellite transmitters. The movements of penguins at sea were tracked by satellite (CLS Argos, Toulouse, France). Birds were fitted with platform transmitter terminals (PTT; Toyocom T2038, Tokyo, Japan, and Telonics ST-10, Mesa, AZ). The transmission interval was 90 s with either a continuous emission or an on-off interval (6 or 12 h). The transmitters had a cylindrical form and a cross sectional area of 4.9 cm² (ST-10 model, length 180 mm, weight 270 g) or 7.0 cm² (T2038 model, length 224 mm, weight 208 g). At the incubating and brooding stages, birds were caught before departure to sea after having been relieved on the nest by their partner. At the crèche stages, penguins were captured after their parental link with a chick had been ascertained. In order to

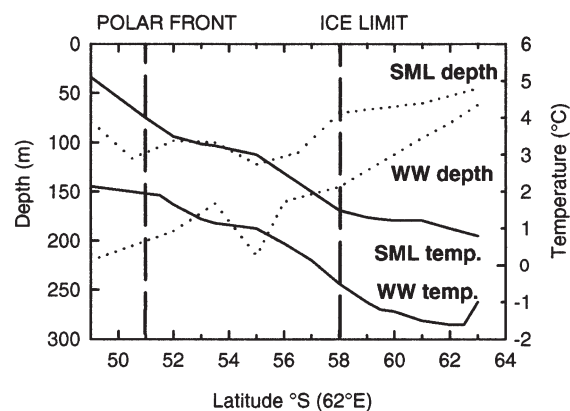


Fig. 2. Summer distribution of the surface mixed layer (SML) and winter water (WW) properties (depth and temperature) along the 62°E section (adapted from Fig. 5 of Park et al. 1998). The ice limit is defined as the northernmost extent of the pack-ice

reduce drag (Bannasch et al. 1994) the PTTs were hydrodynamically shaped and fitted to the lower back with the antennae posterior. The devices were attached with cable-ties to a small metal grid glued (with fast epoxy) to the feathers of the back or fixed directly to the feathers with a cyanoacrylate adhesive (Loctite 420). Birds were flipper marked with coloured tape. Care was taken to reduce handling stress (by covering birds' eyes with a dark hood). The equipping procedure took ca 40 min. After the equipment was attached, the birds were released in the colony.

Time-temperature-depth recorder deployment and sampling procedure. Twenty-one king penguins were observed for diving behaviour and sea water temperature during 24 foraging trips using time-temperature-depth recorders (TDRs). All foraging trips monitored were performed by different birds except for 3 birds whose foraging activity was studied at the incubating and brooding stages consecutively on the same animals (Fig. 3). Birds at the post-moult stage were randomly captured just after moult in the earliest cohort of moulting penguins. TDRs (Wildlife Computers, Redmond, WA) were fitted using the same method as for the PTTs. TDRs deployed in summer, autumn, and winter were Mk5 3.0 (95 × 38 × 15 mm) and those used at the post-moult stage were Mk5 3.3 (110 × 38 × 15 mm). The hydrodynamics of the instruments were improved by adding a small resin nose cone in the frontal position. All instruments had a 512 kbyte memory.

The MK5s logged hydrostatic pressure with 2 m depth resolution over a range of 0 to 500 m and sea water temperature to the nearest 0.1°C. To minimise the response time of the temperature sensor, the TDRs were modified so that the temperature probe protruded slightly from the unit. The time constant was

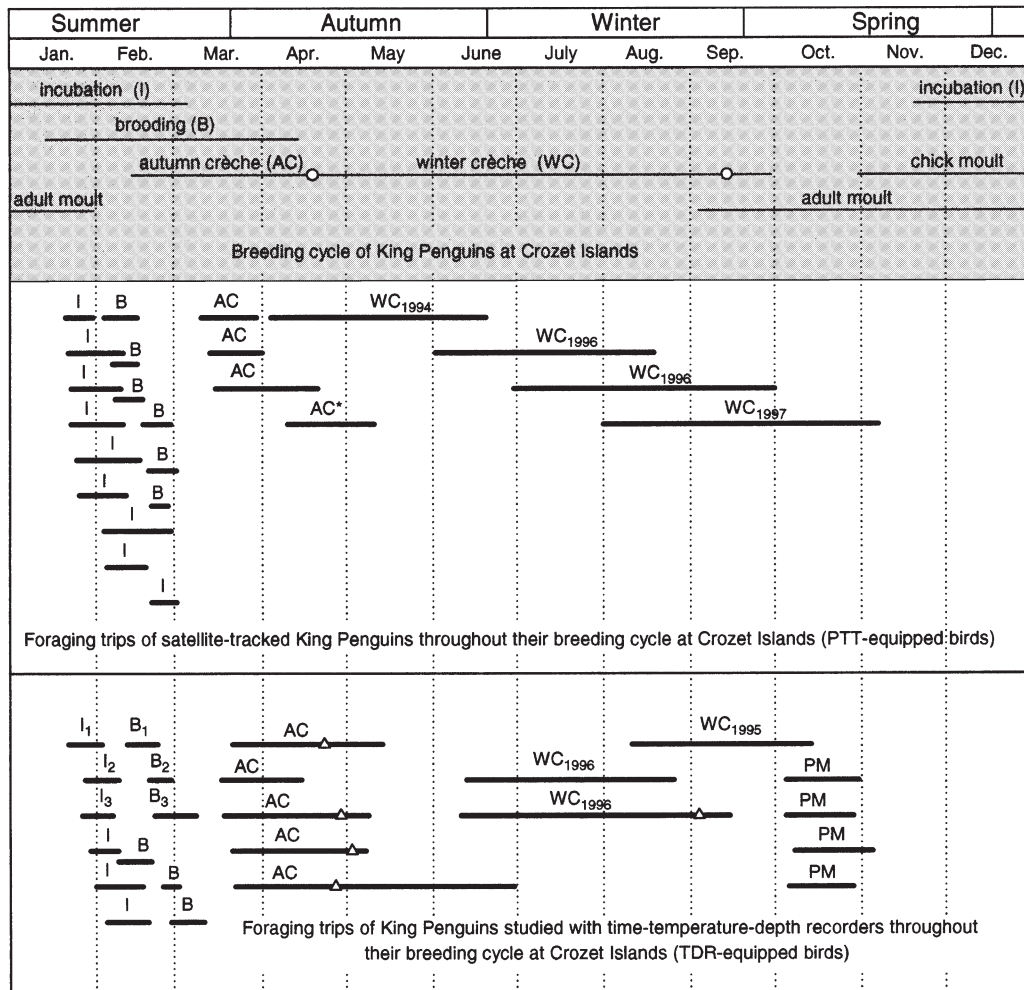


Fig. 3. Phenology of breeding in king penguins at Crozet Islands (thin horizontal lines); (o) beginning and end of the winter fast (data from Weimerskirch et al. 1992). Foraging trips of king penguins throughout the annual cycle (heavy horizontal lines), studied with platform transmitter terminals (PTTs) or time-temperature-depth recorders (TDRs). Each trip corresponds to a single individual except for the incubating and brooding trips showing the same subscript (1,2,3) that were studied consecutively on the same animal, with each subscript corresponding to one individual. For PTT-equipped birds, incubating and brooding, autumn crèche, and winter crèche stages were studied in 1994–96, 1994, and 1994–96–97, respectively. One autumn crèche bird (*) was not followed over the complete trip because of an early failure of PTT batteries and was not seen again at the colony. For TDR-equipped birds, incubating and brooding stages were studied in 1995; trips at other stages were recorded in 1996 except for 1 winter crèche bird obtained in 1995. PM: post-moult stage of adults. Sampling started when birds entered the water. (Δ) End of sampling by TDR (memory full) if it occurred before the bird returned to the colony

6 s, and when a TDR was moved between 2 water baths at different temperatures, 95% of the total temperature change was attained in less than 20 s. King penguins have a maximum vertical velocity of 1.5 m s⁻¹ (Pütz et al. 1998) and may thus travel ~30 m vertically in 20 s. In the study area the maximum vertical temperature gradient is ~0.04°C m⁻¹ (Park et al. 1998), corresponding to a 1.2°C change over 30 m. Thus, at depths with strong temperature gradients, a maximum difference of 1.2°C is expected between recorded and 'real' values. This deviation may not be uniform during descent and ascent phases of the dives, but should be biased to an over-estimation of the actual temperature

during the descent phase of the dives and an underestimation during the ascent phase. As our vertical temperature profiles have been calculated by averaging temperatures from both ascent and descent phases of the dives, we believe that much of the errors induced by the response time of our probes were essentially cancelled out.

Depth was recorded every 5 s in summer and every 10 s during autumn, winter, and post-moulting periods to allow for complete coverage of long trips. For the same reason, depth and sea water temperature were measured every second day in the winter crèche group. Sea water temperature was recorded every

20 to 60 s when depth was >40 m, with the sampling maintained for 40 s during ascent above 40 m to record the SST. In the following analysis, we take SST as the mean water temperature from 0 to 10 m.

Analysis of foraging zones (PTT-equipped birds).

Locational data were processed and analysed with customised software. Locations with 7 classes of accuracy are provided by the Argos system (Argos 1996). The classes 0, A, B, and Z were filtered following Wienecke & Robertson (1997). The travelling speed at a given position was determined by averaging the speeds found between 2 consecutive positions over a period including the 2 previous and the 2 next locations of this given position. We rejected data giving an average swimming speed higher than 14 km h^{-1} since this value has been found to be the mean maximum swimming velocity for king penguin (Kooyman & Davis 1987). When data were incomplete due to battery failure, the total distance covered included the direct-line distance from the last point only if the bird was engaged in the return journey. Results from birds tracked during summer 1994 (Bost et al. 1997) have been included in this study. Contemporaneous, monthly data on SST were obtained from the Lamont-Doherty Earth Observatory at Columbia University (USA) and the Integrated Global Ocean Service System (IGOSS). The extension of the pack-ice was obtained from monthly ERS data (CERSAT, IFREMER, France).

Analysis of diving behaviour in relation to water temperature at depth (TDR-equipped birds). Using custom-made software (Jensen Software Systems, Laboe, Germany), depth data were corrected for the drift in the surface measurements. Only dives ≥ 4 m were analysed because dives < 4 m were considered unresolvable by the TDR. Dives and SST were studied daily. We examined the diving behaviour in relation to the thermal structure of the water column by plotting the depth-temperature profiles during the different phases of the foraging trips. Two days of the central and transit phases of the trips were chosen for this purpose, during which temperature values were averaged for every 10 m depth interval and the frequency distributions of dive depth (10 m depth interval) were obtained. These periods were chosen as follows: (1) Central phase: We studied all groups during the 2 d when SST was the coldest, i.e. when birds were at the most southerly position of their trip. (2) Transit phase: We studied the autumn crèche, winter crèche, and post-moult groups during the 6th and 7th day after departure, i.e. during a period comparable with the central phase of birds foraging during summer (incubating and brooding stages) by being at similar distances from the colony (6 to 7 foraging days) but that occurred well before the most southerly position of the trips was reached.

Foraging range of TDR-equipped birds. The foraging latitudes of TDR-equipped penguins during the transit and the central phases of the trips were inferred from the temperature-depth profiles recorded for the birds. For this, based on the known distribution of the water layer properties (Park et al. 1998 and Fig. 2), winter water temperature recorded from the penguins in spring, summer, and autumn (or extrapolation of the SML temperature in winter) were extrapolated to give the approximate foraging latitudes of the birds. Data were also compared with the corresponding weekly SST maps from IGOSS. For all of the study, means are given \pm SE.

Effect of instruments on foraging behaviour. The effect of instruments on foraging was examined by comparing the trip durations of our equipped penguins with those of device-free conspecifics. Trip durations of TDR-equipped (10.7 ± 1.3 d, $n = 6$) and PTT-equipped (10.0 ± 0.7 d, $n = 6$) birds at the brooding stage were similar ($U = 14$, $p > 0.05$). Trip durations of both TDR- and PTT-equipped brooding birds were longer than those of control birds (6.8 ± 0.7 d, $n = 8$) ($U = 7$ vs TDR-equipped birds, $p = 0.031$, and $U = 5$ vs PTT-equipped birds, $p = 0.015$). At the winter crèche stage, trip durations of both TDR-equipped (78.0 ± 9.5 d, $n = 3$) and PTT-equipped birds (86.8 ± 5.4 d, $n = 4$) were also longer than for control birds (50.1 ± 7.7 d, $n = 10$) (Mann-Whitney $U = 10$, $p = 0.017$ when TDR- and PTT-equipped birds were pooled to be compared with the control group). However, because we compared instrumented birds at several stages of the annual cycle, differences found among groups in our study were mostly due to the stage of the annual cycle rather than to the instrumentation itself.

RESULTS

Seasonal changes in foraging areas (PTT-equipped birds)

Summer (incubating and brooding stages)

The foraging areas varied substantially according to season. During summer (January to mid-March), king penguins exploited mostly the PFZ, covering a total area of $265\,815 \text{ km}^2$. Generally the trips were oriented towards the antarctic polar front, although 1 bird foraged to the northeast, i.e. towards the sub-antarctic front (Fig. 4a). During incubation, mean maximum foraging ranges were generally greater than during the brooding period ($U = 7$, $p < 0.05$, Table 1), with birds of both groups reaching the polar front area (48.3° to 50.3° S) before going back to the colony.

Table 1. Characteristics of the tracks of foraging platform transmitter terminal (PTT) -equipped king penguins at Crozet Islands for the different breeding stages. The maximum foraging distances among groups differed significantly ($H_3 = 17.1$, $p < 0.001$, Kruskal-Wallis test). See also Fig. 3

Breeding stage	Bird	Locations received (n)	Maximum foraging range	
			Coordinates (°)	Distance (km)
Incubating (PTT, 1994)	315-1 ^a	21	50.52 S–52.18 E	456
	238-2 ^a	29	49.15 S–52.26 E	304
	239-1 ^a	49	50.07 S–51.81 E	405
	Mean ± SE	49 ± 10		448 ± 40
Incubating (PTT, 1996)	570-1	20	48.51 S–56.44 E	415
	597-1	53	50.02 S–52.38 E	402
	598-1	115	52.31 S–52.29 E	655
	599-1	69	50.64 S–55.78 E	550
	600-1	63	52.19 S–52.68 E	644
	890-1	25	51.35 S–53.40 E	560
	Mean ± SE	49 ± 10		448 ± 40
	Mean ± SE	29 ± 6		338 ± 29
Brooding (PTT, 1994)	238-1	47	49.77 S–54.74 E	428
	240-1	37	49.21 S–51.35 E	318
	240-2	38	49.91 S–52.30 E	397
	316-1	19	45.72 S–55.43 E	295
	316-2	24	49.30 S–53.60 E	356
	317-2 ^b	9	48.47 S–51.18 E	236
	Mean ± SE	29 ± 6		338 ± 29
Autumn crèche (PTT, 1994)	238-3	66	49.89 S–58.15 E	605
	316-3	33	53.42 S–55.23 E	815
	317-3	39	57.27 S–58.11 E	1279
	239-3 ^b	148	59.44 S–59.41 E	1532
	Mean ± SE	46 ± 10		900 ± 199
Winter crèche (PTT, 1994–96–97)	316-4	119	60.67 S–47.65 E	1608
	598-2	34	62.13 S–42.01 E	1856
	315H	154	59.50 S–45.93 E	1475
	570H	53	59.76 S–55.17 E	1495
	Mean ± SE	90 ± 28		1609 ± 88

^aBost et al. (1997); ^bPremature battery failure prevented following the whole trip

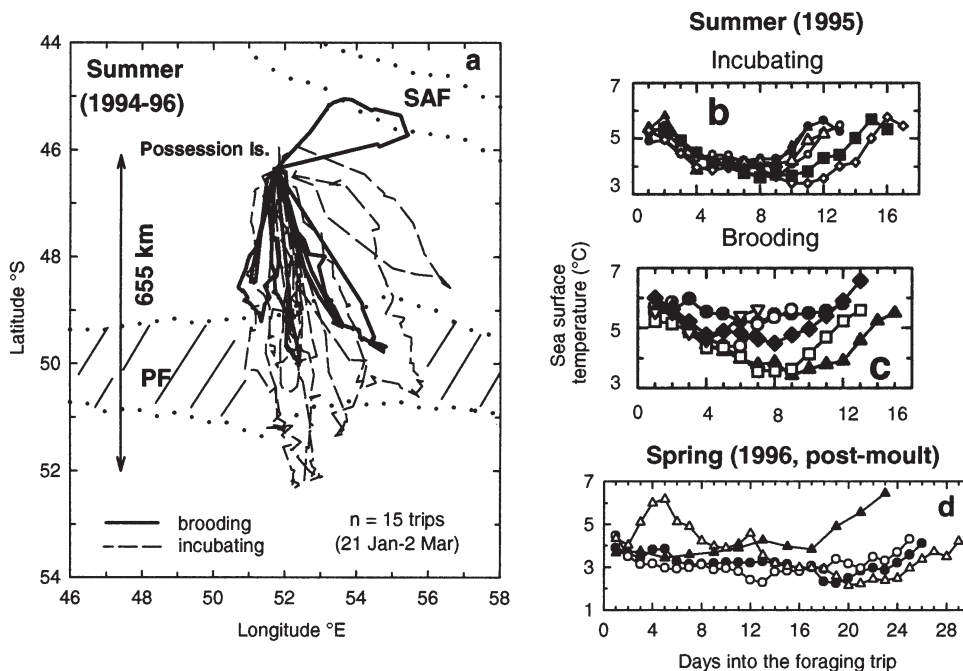


Fig. 4. (a) Tracks of PTT-equipped king penguins from Possession Island (Crozet Archipelago) during summer (incubating and brooding stages). The mean position of the PF and the SAF (Park et al. 1993) during the study period were obtained from Integrated Global Ocean Service System (IGOSS) data. Daily changes in sea surface temperature for TDR-equipped king penguins during the (b) incubating and (c) brooding stages, and (d) at the post-moult stage (spring). Within each group, each symbol pertains to 1 individual

Autumn crèche

From mid-March, the maximum foraging range and distance covered increased dramatically, in agreement with the prolonged absences from the colony (Fig. 5a, Table 1). In April, the birds continued to head southeast, up to 1532 km from the colony, and stopped in waters with SST between 3 and 1°C (Fig. 5a).

Winter crèche

During winter, the distances covered and the foraging ranges were the highest, the total area encompassed (1128205 km²) being up to 4 times the area used in summer, even though the number of birds sam-

pled was smaller. After departure, the birds headed directly south, crossing the northern limit of the light pack-ice (56 to 62° S, Fig. 6a). After crossing this limit, the birds stayed in this zone for between 14 and 43 d (mean 18 ± 9 d, n = 4) before traveling directly back to the colony.

Hydrographic features of the foraging habitat (TDR-equipped birds)

Changes in daily SST during the foraging trips

The mean SST encountered by birds typically decreased to a minimum on the outward phase of the trip before rising gradually to near initial values as the

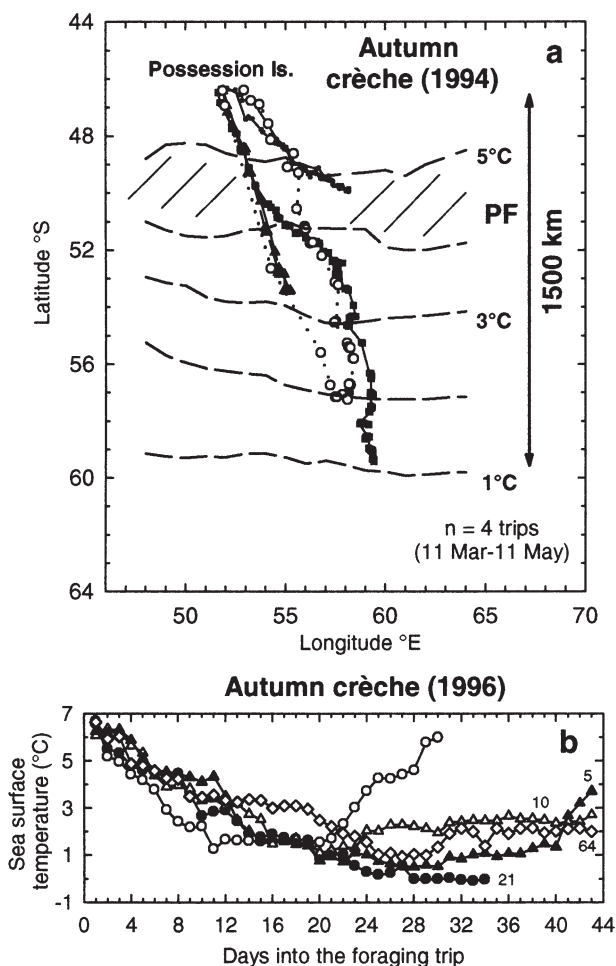


Fig. 5. (a) Tracks of PTT-equipped king penguins from Crozet Islands at the autumn crèche stage (mean sea surface isotherms corresponding to April 1994; IGOSS data). (b) Daily changes in sea surface temperature for TDR-equipped king penguins during the autumn crèche stage. The number of days before return is indicated on the SST curves if sampling stopped before the end of the trip

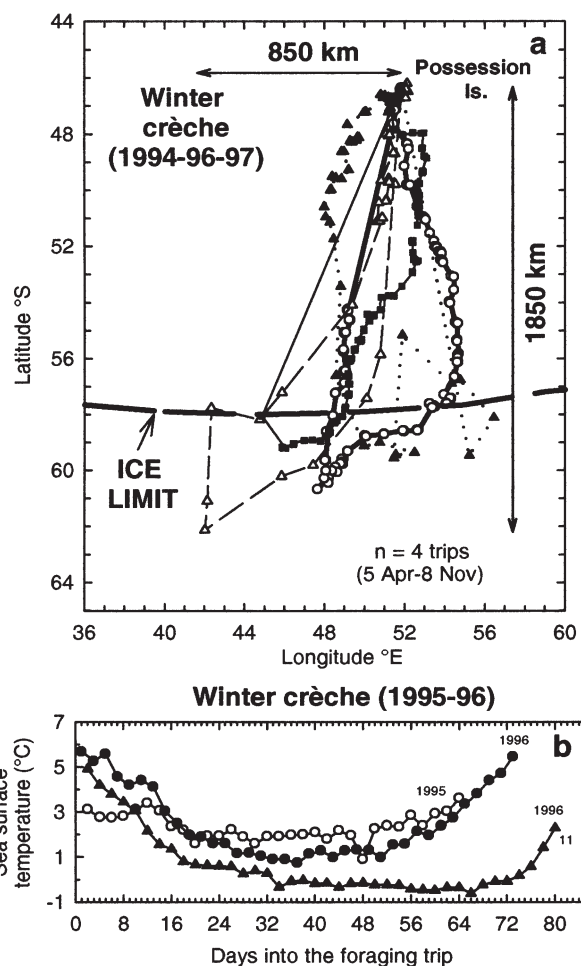


Fig. 6. (a) Tracks of PTT-equipped king penguins from Crozet Islands during the winter crèche stage with the mean limit of the pack-ice (ice density index 1 to 3) in August 1994–96–97 (CERSAT data, IFREMER). (b) Daily changes in sea surface temperature for TDR-equipped king penguins at the winter crèche stage

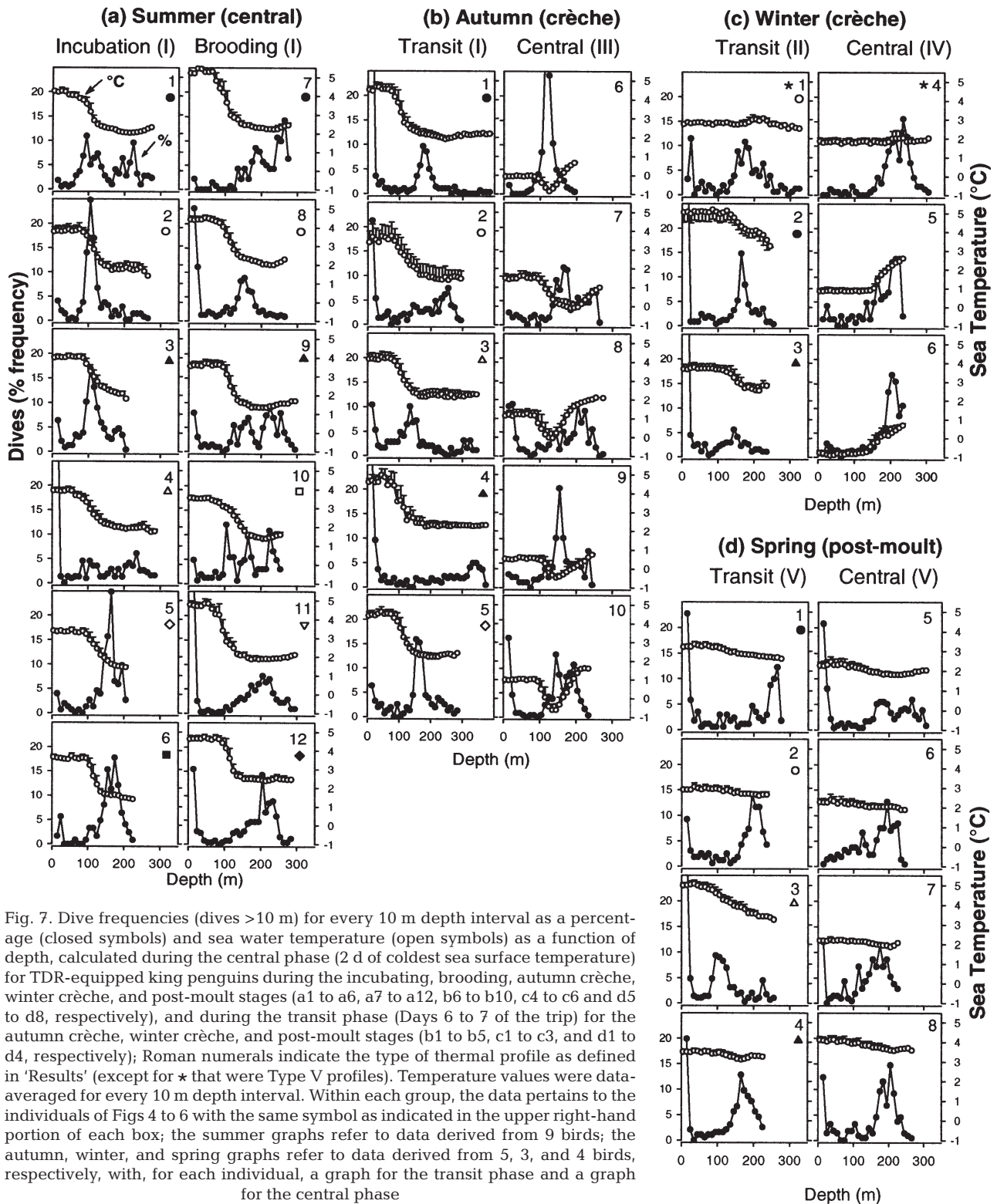


Fig. 7. Dive frequencies (dives >10 m) for every 10 m depth interval as a percentage (closed symbols) and sea water temperature (open symbols) as a function of depth, calculated during the central phase (2 d of coldest sea surface temperature) for TDR-equipped king penguins during the incubating, brooding, autumn crèche, winter crèche, and post-moult stages (a1 to a6, a7 to a12, b6 to b10, c4 to c6 and d5 to d8, respectively), and during the transit phase (Days 6 to 7 of the trip) for the autumn crèche, winter crèche, and post-moult stages (b1 to b5, c1 to c3, and d1 to d4, respectively); Roman numerals indicate the type of thermal profile as defined in 'Results' (except for * that were Type V profiles). Temperature values were data-averaged for every 10 m depth interval. Within each group, the data pertains to the individuals of Figs 4 to 6 with the same symbol as indicated in the upper right-hand portion of each box; the summer graphs refer to data derived from 9 birds; the autumn, winter, and spring graphs refer to data derived from 5, 3, and 4 birds, respectively, with, for each individual, a graph for the transit phase and a graph for the central phase

birds returned (Figs 4b–d, 5b & 6b). Average mean SSTs at departure were 5.2, 5.6, 6.4, 4.6, and 4.1°C for incubating, brooding, autumn crèche, winter crèche, and post-moult groups, respectively, reflecting the sea-

sonal changes in SST at Crozet Islands. Averages of the minimum SSTs of the trips were lower during the autumn and winter trips (0.7 and 0.6°C, respectively) than during the spring and summer trips (2.5, 3.8, and

4.3°C in post-moulting, incubating, and brooding birds, respectively).

Vertical temperature profiles

Five types of thermal profiles were identified from sea temperature data obtained with TDR-equipped penguins: (1) Type I, rapid temperature decline (Fig. 7a,b1 to b5): For incubating and brooding birds during the central phase, and for autumn birds during the transit phase, temperature profiles were characterised by an SML thickness of 80 m on average (range 60 to 100 m) with a temperature of 3.5 to 5°C, followed by a rapid decline to ~2°C at 130 to 230 m (average of maximum temperature gradients -0.5°C every 10 m) where temperature leveled out. (2) Type II, low temperature decline (Fig. 7c2,c3): This was found during the transit phase of winter birds, and resembles Type I, although the SML was thicker (~140 m) and the temperature drop below the SML was less abrupt (maximum temperature gradients -0.3°C every 10 m). (3) Type III, temperature inversion (Fig. 7b6 to b10) and (4) Type IV, temperature rise (Fig. 7c5,c6): For autumn and winter crèche birds during the central phase, the SML was cold (-0.8 to 1.8°C) and had an average thickness of 100 m in autumn and 145 m in winter. Temperatures then either dropped (with a mean maximum temperature of -0.35°C every 10 m) to an average of 0.3°C (range -0.9 to 0°C) before rising (with a mean maximum temperature gradient of 0.35°C every 10 m) to 1 to 2°C at 200 to 300 m in autumn (Type III) or increased directly to 1 to 2°C at 200 to 300 m in winter (with a maximum temperature gradient of 0.35°C every 10 m) (Type IV). For 1 winter bird (Fig. 7c1,c4), however, the thermal profiles resembled Type V (see below) with a temperature of 2°C during the central phase. (5) Type V (deep SML) (Fig. 7d): For birds at the post-moult stage, the SML reached 250 to 300 m. The SML temperatures were ~3.5°C and 2.2 to 2.5°C for the transit and the central phases, respectively, except for 1 bird that encountered an SML at 4°C during the central period of its trip (Fig. 7d8).

Seasonal changes in foraging areas inferred from thermal profiles

The Type I thermal profile found in incubating and brooding birds (central phase) and during the transit phase of autumn crèche birds corresponds to the polar front area with an SST of 4 to 5°C and a subsurface temperature minimum of 2°C at 200 m (Fig. 2). This is in good agreement with the foraging

areas of satellite-tracked birds at the same breeding stages.

Subsurface minima (winter water) ranging from -0.9 to 0°C in autumn and SML temperatures ranging from -0.8 to 1.8°C in winter indicate that TDR-equipped birds foraged at latitudes ranging from 57 to 59° S and from 52 to 59° S in autumn and winter, respectively (Fig. 2). All autumn TDR-equipped birds reached latitudes where the pack-ice was apparently in formation (winter SML having not yet been established; Type III). In winter, 1 bird reached the pack-ice limit (Type IV, Fig. 7c6). If PTT-equipped birds are included, 7 out of 9 birds reached the ice limit region in autumn (before ice formation) and 5 out of 7 foraged at the pack-ice limit in winter. In spring, the Type V profile was typical of the area north of 50 to 51° S (Fig. 2). The birds' positions obtained in this way were also confirmed by contemporaneous SST satellite maps.

Diving behaviour in relation to thermal profiles (TDR-equipped birds)

If traveling dives (≤ 20 m) are excluded, the frequency distribution of dive depths for most of the birds was clearly skewed towards depths greater than 70 m (Fig. 7). Dive depths (averages of individual mean dive depths for dives >70 m) were greatest during the transit phase in autumn crèche birds (204 ± 18 m) and during the central phase of winter crèche birds (204 ± 16 m). They were shallowest during the central phase of incubating (161 ± 13 m) and autumn crèche birds (167 ± 12 m), and were intermediate during the central phase of brooding birds (192 ± 9 m) and during the transit (177 ± 16 m) and central (183 ± 11 m) phases of post-moulting birds.

Comparison of the frequency distribution of dive depths with the thermal profile recorded simultaneously indicates that in most cases birds avoided diving in the part of the water column corresponding to the SML (Fig. 7). Instead, they dived either in parts of the water column characterised by large temperature gradients (thermocline depths) or in the underlying deep layer. During incubation, 3 birds out of 6 dived mainly in the thermocline (Fig. 7a2,a4 & a5). At the brood stage, the birds mainly dived at the base of the thermocline (Fig. 7a8,a10) or in the deep layer. This was also observed during the transit phase in autumn (Fig. 7b1 to b5) and for winter crèche birds (Fig. 7c2,c3). During the central part of their trips, autumn birds typically dived at the depth of the temperature inversion below the SML (Fig. 7b6 to b10), and winter birds dived in the deep positive thermocline (Fig. 7c5,c6). At the post-moult stage in spring, the temperature was homogeneous in the water column and preferred diving depths were generally greater than 150 m.

DISCUSSION

Ours is the first study to examine the 3-dimensional exploitation of the water mass in relation to hydrographic features by diving seabirds throughout their complete annual cycle. King penguins did not forage randomly, but utilised specific oceanic areas and adjusted their foraging activity to the water mass explored.

Foraging at the polar front in summer

The present work has elucidated the extent of the foraging habitat of king penguins, with the importance of the polar front being well confirmed. Most of the PTT- and all of the TDR-equipped birds headed south towards the polar front, where they ended their outward trip, with the trips ranging on average 340 and 450 km at the brooding and incubating stages, respectively (PTT-equipped birds). The same daily decreases of SST recorded after a bird's departure to minimum values of $\sim 4^{\circ}\text{C}$ typical of the polar front (TDR-equipped birds) were also obtained from remote-sensed SST data interpolated from tracks of satellite-tracked king penguins (Guinet et al. 1997). The importance of the polar front for king penguins was first suggested by Jouventin et al. (1994), being strongly backed by data of Bost et al. (1997), Guinet et al. (1997), and Pütz et al. (1998) in telemetric studies. The consistency of this pattern over several years of study shows that the PFZ is the main summer foraging habitat of king penguins of the South Indian Ocean. Interestingly, those king penguins breeding south of the polar front (South Georgia and Heard Island) forage north of their colony in the area of the polar front (Rodhouse et al. 1998, Moore et al. 1999), as did sympatric volant predators, grey-headed albatrosses (*Diomedea chrysotoma*, Rodhouse et al. 1996). In the southern Pacific Ocean, royal penguins *Eudyptes schlegeli* were also dependent on the polar front located south of the Macquarie Islands in summer (Hull et al. 1997). It appears, therefore, that this oceanic structure is a key foraging area for predators able to travel large distances during breeding. It is known that frontal areas are privileged places of biological activity due to mechanical concentration of phytoplankton or increased *in situ* production through enhanced availability of nutrients (Franks 1992, Laubscher et al. 1993, Pakhomov et al. 1994). Consequently, abundance of zooplankton secondary consumers is enhanced (Pakhomov et al. 1994), which in turn results in locally increased seabird densities (Pakhomov & McQuaid 1996, Rodhouse et al. 1996).

Foraging at the ice-edge area in autumn and winter

In autumn and winter king penguins undertook non-random migrations towards areas located as far south as the pack-ice region. All PTT-equipped birds headed south in trips characterised by ranges increasing substantially from autumn to winter. Similar foraging habitats were used by TDR-equipped birds, as inferred from the SST typically decreasing after their departure and by the characteristic thermal profiles at their most southerly positions. Most birds (77%) studied with both types of equipment reached the ice limit region in autumn (before ice formation) and foraged at the pack-ice limit in winter (71%). In terms of foraging range, our data agree well with those found in autumn and in early winter and winter at Crozet Islands (Jouventin et al. 1994) and at Heard Island (Moore et al. 1999). The light pack-ice area is thus a major foraging ground in winter for the king penguin populations of the Indian Ocean sector of the Southern Ocean. Among other penguins, such distant trips from the colony (>1000 km) compare only with those of juvenile emperor penguins *Aptenodytes forsteri* (Kooyman et al. 1996) and Adélie penguins *Pygoscelis adeliae* during their non-breeding winter migrations (Davis et al. 1996). Utilisation of antarctic waters in autumn and winter by king penguins strongly suggests a drastic drop in prey availability in the PFZ at the end of March. Despite reduced trophic activity of pelagic ecosystems in winter, the ice edge's physical features increase biological production. Primary production is greater at the ice edge than within the pack-ice because of a higher light level. The water column at the ice edge is also probably more stable vertically than in open waters, which favours primary production (Knox 1994). Through zooplankton, this enhanced biological activity may make the ice edge an attractive spot for top predators (Hopkins et al. 1993). Consistent with this idea, high densities of marine birds and mammals have been observed at the ice edge in winter (Ainley et al. 1991, Ribic et al. 1991).

Diving behaviour and vertical temperature profiles

We show that the diving behaviour of king penguins depends strongly on the hydrothermal structure of the water column, with penguins avoiding the SML during most of their annual cycle.

In summer, depth-temperature profiles observed for incubating and brooding birds have shown that king penguins dived substantially in and below the thermal discontinuity separating the SML and the underlying waters. This strategy may be related to the physical properties of the water strata explored. In diving

predators, such preference for thermocline depths has been described only in southern elephant seals (Boyd & Arnborn 1991). Thermal gradients in oceans are generally accompanied by salinity and density gradients (Park et al. 1998). Discontinuities in physical properties of the water column may result in enhanced biological activity because of the 'barrier effect' of the density gradients leading to a concentration of sinking matter (Boyd & Arnborn 1991). These nutrient-rich water layers may attract prey such as mesopelagic myctophid fish. The 2 main prey of king penguins from the Crozet Islands during summer are the myctophids *Electrona carlsbergi* and *Krefflichthys anderssoni* (Cherel & Ridoux 1992, Bost et al. 1997), which are opportunistic mesozooplankton consumers (Pakhomov et al. 1996). Despite the important role of myctophids in pelagic ecosystems (Sabourenkov 1991), detailed information on their vertical distribution is lacking (Duhamel 1998). Our penguin dive data may indicate that a substantial part of myctophids were distributed in and below the thermocline, perhaps due to interactions with their prey. In addition, the temperature in the lower part of the thermocline is close to the thermal optimum for myctophids (2.6 to 5°C) consumed in summer by king penguins (Hulley 1981).

In autumn, king penguins dived deeper in the polar front area (transit phase) than in summer, suggesting that prey were less accessible in the PFZ. It is known that the summer prey of king penguins (e.g. *Electrona carlsbergi*) migrate to great depths at the end of the summer, probably to follow their own zooplankton prey, which overwinter in deep waters (Kozlov et al. 1991). Presumably as a response to this drop in prey availability in the PFZ, king penguins continued towards the south. At their southernmost position (57 to 59° S), they consistently dived in waters with typical strong temperature inversions at relatively shallow depths (~130 m, Fig. 7b6 to b10). If prey actually concentrate at water column discontinuities, birds may be able to exploit the thermocline at shallower depths by heading south. Indeed, at any time of the year, the SML thickness decreases at higher latitudes (Fig. 2).

In winter, king penguins foraged deep and consistently in the thermocline all along their foraging trip. The SML reaches its greatest extent in winter (corresponding to the winter water depth, Fig. 2). Since there is a good correlation between the thermocline depths and penguins' diving behaviour, the lower depths of prey in winter may have been partly related to the descending thermocline in winter. Because long trip durations result in complete digestion that prevents prey identification (Cherel et al. 1993, 1996), there is little information on prey eaten in the pack-ice area by king penguins. The myctophid *Electrona antarctica* may be an important part of their winter diet, since it is

the main myctophid species in the marginal sea-ice zone and an important winter prey of seabirds in this region (Ainley et al. 1991, Lancraft et al. 1991). Our dive data show a productive depth strata at 200 to 250 m, to which most dives were directed, and which may be indicative of the daily winter vertical distribution of *E. antarctica* in this region. Overall, for penguins foraging in winter, and as suggested for autumn birds, prey may be located at shallower depths in antarctic waters than in the PFZ due to the decrease of SML thickness towards the south. Therefore, at any time of the year, penguins tend to find prey at shallower depths by heading south rather than by staying at lower latitudes.

In spring, king penguins used a rather different foraging strategy from that in other seasons. The foraging ranges of TDR-equipped birds inferred from SST and thermal profiles indicate that they did not go further south than the latitudes where the polar front lies in summer. Prey were thus abundant enough to prevent trips to remote antarctic areas as in autumn and winter. This pattern agrees with the only data available to date taken from the Crozet Islands (Jouventin et al. 1994), showing that king penguins made south-eastward trips in spring that did not take them farther south than in the summer. At Heard Island, king penguins foraging in spring also showed foraging ranges that appeared less than in summer (Moore et al. 1999). In spring, king penguins resumed intense feeding on the same myctophid species as before winter (Cherel et al. 1993, Raclot et al. 1998), but little is known of the spring distribution of myctophids. The data suggest that they reenter the penguins' diving range in the PFZ, probably through a general upward migration to track the seasonal upward migration of zooplankton (Kozlov et al. 1991). In comparison with autumn and winter, changes in the hydrothermal structure encountered by the birds over their trip in spring were small, probably due to the reduced latitudinal displacements of the birds at this time. In addition, the thick SML provided a constant water temperature over the whole penguin diving range, without gradients that favour prey concentration (Franks 1992, Laubscher et al. 1993). Therefore, in spring birds foraged without apparent hydrographic cues for prey that were probably more randomly distributed than in other seasons.

In conclusion, our study shows that for birds travelling by swimming in the marine environment, hydrographic features on both short and large scales are important components of the foraging strategy. By diving king penguins can take advantage of the thermal discontinuities below the SML. As long-distance foragers, they exploit remote, but predictable, areas of the ocean (polar front, ice edge) according to seasonal changes in local prey availability. Such long trips may

be efficient because penguins can continuously use the thermal gradients found at depth thanks to their deep diving ability. For king penguins, the strategy of heading south when prey availability decreases in the PFZ may have evolved in relation to the thinning of the SML towards the south. Such strategy allows them to exploit mesopelagic resources all year round. Whether king penguins either directly use thermal gradients at depth as cues to find prey or feed opportunistically on prey predictably concentrated through hydrographic process is a fascinating topic for future research.

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