

Feeding of diving predators and diel vertical migration of prey: King penguins' diet versus trawl sampling at Kerguelen Islands

C. A. Bost^{1,*}, T. Zorn¹, Y. Le Maho¹, G. Duhamel²

¹Centre d'Ecologie et Physiologie Energétiques, 23 rue Becquerel, 67087 Strasbourg Cedex 2, France

²Muséum National d'Histoire Naturelle, Laboratoire d'Ichtyologie Générale et Appliquée, 43 rue Cuvier, 75231 Paris Cedex 05, France

ABSTRACT: The diving behavior and diet composition of King penguins were examined during summer 1995 at Kerguelen Islands. This was in relation to real-time estimations of diel prey availability during 2 sampling sessions totaling 10 d at sea. During daylight hours King penguins performed medium to deep dives of 120–250 m. At night, they dived no deeper than 60 m. Daytime, dusk and night-time sampling of prey was performed in the depth ranges corresponding to the depths of the penguins' dives in this study. The diversity in mesopelagic fish was found to be highest during the night at 0–50 m (15 vs 9 species during the day), and their number was up to 20-fold higher at these depths at night than during the day at the 150–250 m depth layer. The 3 myctophid species *Electrona antarctica*, *Gymnoscopelus fraseri* and *G. braueri* which were present in large sub-surface numbers during the night were virtually absent from the penguins' diet. The 2 species dominant in their diet, *Muraenolepis marmoratus* and *Krefftichtys anderssoni* (56.5 and 32.9% by number, 30.3 and 31.6% by biomass, respectively), were scarcely detected in the penguins' diving range during the night. In contrast, these 2 species, of which only the latter is bioluminescent, were significantly present during the day in the 0–300 m depth range (16.5 and 30.0% of the diurnal catches by number, respectively). In terms of biomass, these 2 prey types constituted only 6.3 and 12.6% of the total daylight trawls, which were dominated by the genus *Protomyctophym* (38.6% of the catches). The overlap between the penguins' diet and trawl content was the most significant with daylight sampled data. King penguin feeding success seems mostly dependent on deep dives during the day, despite lower prey availability than during the night. Ambient light levels, which were found to be higher at deeper depths (150–180 m) during the day compared to the sub-surface (0–60 m) at night-time, therefore appear to better determine King penguin foraging success than diel migration of prey to shallow depths.

KEY WORDS: King penguins · Diet · Diel vertical migration · Myctophids · Foraging behavior

Resale or republication not permitted without written consent of the publisher

INTRODUCTION

The way in which seabirds obtain food at sea remains poorly understood despite scientific advances (e.g. Weimerskirch et al. 1994, Nevitt et al. 1995, Charassin et al. 2001, Ropert-Coudert et al. 2001, Wilson et

al. in press). Among surface feeders, albatrosses seem to depend on light intensity and therefore forage mostly during daylight (Weimerskirch & Wilson 1992). It is usually assumed that penguins rely on vision to detect and pursue their prey during underwater foraging. This idea is supported by their eye structure (Martin & Young 1984, Martin 1999) and the close relationship between their foraging activities and the daily light cycle (Wilson et al. 1993, Cannell & Cullen 1998).

*E-mail: charles.bost@c-strasbourg.fr

During breeding, most penguin species have diurnal foraging patterns, leaving their colony at dawn to go to sea and returning to land before nightfall. For species spending more than one day at sea, trips rarely start or finish at night. Penguins also show a marked diel pattern in diving activity. Thus deep dives generally occur during daylight, with maximum depths recorded around midday. During the night, they usually dive less and their diving depths are much shallower (Wilson 1995).

Among those species performing long foraging trips, King penguins exhibit especially intriguing diel patterns, with very deep dives during the day (<323 m) and numerous shallow dives (0–30 m) at night (Kooyman et al. 1992, Pütz et al. 1998). King penguins are highly dependent on myctophids especially during summer (Cherel & Ridoux 1992). These small schooling fish contribute most to the biomass of mesopelagic fish of the Southern Ocean (Lancraft et al. 1989, Pakhomov et al. 1996). Myctophids are vertically migrating bioluminescent prey (Tett & Kelly 1973, Zasel'sliy et al. 1985). During the daytime, myctophids appear to be distributed at depths of over 100 m. At night, they undergo a vertical migration towards the surface, where they are dispersed in the upper water column (Zasel'sliy et al. 1985, Perissinotto & McQuaid 1992, Duhamel 1998). Recently, some studies based on changes in stomach temperatures have provided indirect evidence that King penguins feed much more efficiently during the day than at night (Pütz & Bost 1994, Pütz et al. 1998). However, to date, no concurrent information has been available on circadian prey availability. Additionally, the sensitivity of the stomach temperature sensor device may have been inadequate due to diving hypothermia (Handrich et al. 1997). Whether foraging is more successful during the day or at night still remains to be clarified.

In this study, we have examined the diving behavior and diet composition of King penguins in comparison to simultaneous sampling of diel prey availability using a research vessel. As part of a long-term study on King penguin foraging ecology and prey availability at Kerguelen Islands, our objectives here were (1) to compare the diet and diving patterns of the penguins with the diel variation in the abundance of their potential prey in the same depth range and (2) to check the assumption that King penguins are diurnal foragers. This follows Duhamel et al. (2000) whose work studied the mesopelagic fish community off the Kerguelen Islands.

MATERIALS AND METHODS

The field study was carried out during the austral summer, from 28 February to 20 March 1995, in the Ker-

guelen Archipelago (48° 45'–50° 00' S, 68° 45'–70° 58' E, Southern Indian Ocean). King penguin feeding activity was studied at the Ratmanoff Colony on the eastern side of Kerguelen (~50 000 pairs, Weimerskirch et al. 1988). Most of the birds were foraging to feed chicks (1 mo old), which were left unattended during trips lasting 3 to 13 d.

Prey sampling and penguin foraging area. In order to acquire simultaneous data on the prey available to the penguins, trawling surveys were conducted off the study colony using the 25 m scientific vessel 'La Curieuse'. Details of the sampling protocol are given in Duhamel (1998). To summarize, these surveys occurred during 2 field sessions, each of 5 d (1 to 5 March and 9 to 13 March), overlapping the study on King penguin feeding patterns. In this work, we considered stations which enabled research to be conducted from the deep oceanic zone to the limit of the shelf break. At each station, standardised trawls of 30 min were performed at 4 depths (50, 150, 250 and 300 m), including a sequence of both night and day trawls. We considered daylight, dusk and night stations corresponding to penguin depth ranges observed during these time periods for this study. Daylight stations occurred at 50 (n = 7), 150 (n = 6), 250 (n = 7), and 300 m (n = 7) depth. Dusk stations were at 50 (n = 2) and 150 m (n = 1) depth. Night stations were located at the sub-surface (0–50 m depth; n = 5). The sampling gear was an IYGPT net (International Young Gadoid Pelagic Trawl; opening: 12 × 7 m) with a 10 mm mesh size in the codend towed at 3 knots. In the present analysis of trawl content, only fish species potentially caught by King penguins were considered (see Olsson & North 1997). Avoidance reactions and trawl size could not be evaluated here. As 10 mm mesh size has been known to collect fish larvae, bias in sampling via trawls according to fish size seems limited. In the Southern Ocean, there are potentially no large fish in the deep oceanic zone which are able to escape the towed trawl except the rare *Alepisaurus brevirostris* and *Lampis immaculatus* (Gon & Heemstra 1990).

The foraging area of King penguins was determined simultaneously by satellite tracking on 9 breeding birds (mean maximal foraging range 267 ± 88 km; 129–409 km; Fig. 1). Argos transmitters (ST-10, Telonics) were used for this purpose, and a total of 224 locations was obtained. The classes 0, A, B and Z were filtered following Wienecke & Robertson (1997). Average speed was determined by taking the root mean square of the 2 previous and 2 following locations of a given position. We rejected data that gave an average swimming speed higher than 14 km h⁻¹, a value which corresponded to the mean maximal swimming velocity of King penguin (Kooyman & Davis 1987).

Comparison of spatial co-occurrence (presence-absence) between trawl stations and penguins' at-sea

location was performed after plotting the locations of the birds and stations on blocks of 0.2° latitude by 0.2° longitude (Fig. 1). This block size was considered a compromise of the distribution of the sampled zones and penguin locations in relation to the local oceanic features (C.A.B. unpubl. data). Because of logistic constraints of rough seas and the limitation of the sampling periods, there was a partial spatial overlap between penguins' foraging area and trawl sampling (Fig. 1). Trawling occurred more in the area visited by penguins during their outward journey (i.e. in the north portion of the penguin foraging area) than in the area crossed on return (12.8% of the outward area sampled vs 9.7% of the return area, chi-squared test for spatial co-occurrence = 32.6, $p < 0.01$).

Dividing activity. Data on diving behavior were collected from 5 breeding penguins fitted with MK5 time-depth recorders (TDR) (Wildlife Computer, Woodinville, WA, USA), which recorded pressure at a resolution of ± 2 m. A 5 s sampling rate was used. The birds were caught when leaving the colony and then fitted with instruments, which were glued dorsally and secured around the feathers by 2 cable ties as for satellite-tracked birds. All instrumented penguins used in the study were successfully recovered and data was obtained for the entire foraging cycle. Trip duration was 34% longer by comparison with the control birds ($p < 0.05$). No significant difference was found in mean daily body mass gain between the 2 groups (132 ± 166 and 68 ± 97 g respectively, $U = 13$, $p > 0.05$).

Dive analysis was made on a total of 15 853 dives using custom-made software (Jensen Software, Laboe, Germany). We retained all dives ≥ 4 m for the present analysis, because dives < 4 m were considered indistinguishable from the surface. Circadian patterns in diving activity were compared for daytime, twilight and night-time. The twilight periods (dawn and dusk) were defined as the time when the angle of the sun was between the horizon and 6° (Annuaire du Bureau des Longitudes 1995). A light level index at depths visited by the penguins was estimated by records from the MK5 light sensors (sampling rate \sim every 20 s). As the system recorded a logarithmic value of light level (light level index), data provided by each logger were calibrated adequately with a Roline luxmeter.

The relation found between light intensity (*Lux*) and light level recorded was:

$$Lux = 14\,800 \times 10^{[(LL_r - hLL_r)/20]} \quad (1)$$

where LL_r is the recorded light level and hLL_r the highest light level recorded.

As King penguins foraged as far as 400 km from their colony, the twilight periods of TDR-equipped birds were calculated to correspond with their estimated at-sea locations. For this, we considered that

the birds had traveled along a 71 to 76° longitudinal gradient, at 50° S, a latitude representative of the central foraging range. Thereafter, the hours of sunrise and sunset were determined for each day of the trip, assuming that the birds had traveled continuously at a speed of 2 m s^{-1} (Ropert-Coudert et al. 2000) to their most distant location before coming back. The day corresponding to the most distant location was assumed to correspond to the minimal temperature recorded, as King penguin foraging trips at Kerguelen are generally associated with a decrease in sea surface temperature during the outward journey up to the maximal foraging distance. Temperature-depth records obtained from TDR-equipped penguins indicated that the birds had generally foraged in a south-eastward direction, overlapping the range of penguins fitted with satellite transmitters, except for one having foraged farther south (see Koudil et al. 2000).

Diet sampling and analysis. Diet analysis of penguins was performed from stomach contents sampled using the water off-loading technique (Wilson 1984). A total of 22 samples were recovered from 2 to 20 March 1995, from birds of known breeding status and trip duration, captured on arrival at the colony. Determination and quantification of the prey were made according to Cherel & Ridoux (1992). Measurements of otoliths were made only for those enclosed in the cranium or undamaged. These measurements allowed calculation of fish standard length and mass from allometric equations provided by Gon & Heemstra (1990),

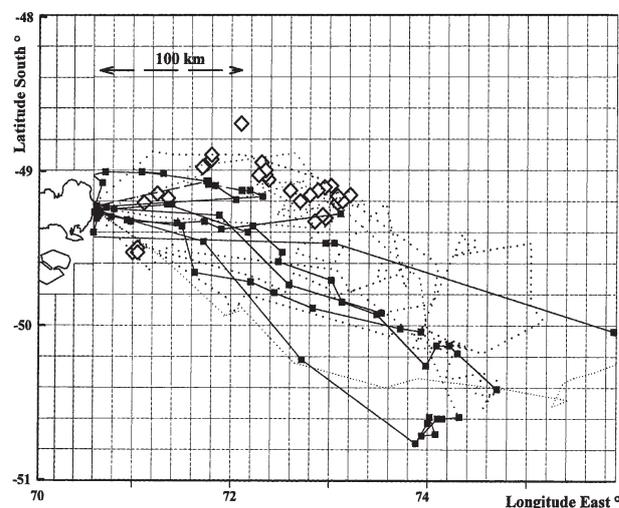


Fig. 1. Position of trawl stations (\diamond) and foraging trips of satellite-tracked King penguins during the study period (March 1995) on a $0.2 \times 0.2^\circ$ map of the East coast of Kerguelen. The outward journey of each trip is shown as a dotted line and the return journey as a continuous line. (\blacksquare) Locations of birds at sea during the return journey

Williams & McEldowney (1990), and personal reference collections. The otoliths found for one of the main prey, the eel cod *Muraenolepis marmoratus*, were mostly from juvenile specimens. We estimated their reconstituted mass from the mean mass of items found in the 150–300 m daylight trawls (0.41 g, mean SL 44 mm, G.D. unpubl. data), as size estimation of juvenile fish is especially difficult to calculate from otoliths.

To compare the similarity in the diversity and importance of prey caught by trawls and penguins, we used the Morisita index as modified by Horn (1966). This relative measure, which varies between 0 (no overlap) and 1 (total similarity), depends on the number of prey categories, taking into account information on the number of individuals as well as species recovered by 2 distinct sampling methods (Adams & Brown 1989, Gaston & Bradstreet 1993).

For a comparison of the size distribution of prey, statistics were calculated using Systat (Version 8.0, SPSS). When data were normally distributed, analysis of variance (1-way ANOVA) was performed (Sokal & Rohlf 1981). When this was not possible, we used Mann-Whitney *U*-test for 2-sample comparisons. Proportions were tested by a χ^2 test. To compare the length-frequency distributions of fish caught by penguins and trawls, we used a Kolmogorov-Smirnov 2-sample test (Sokal & Rohlf 1981).

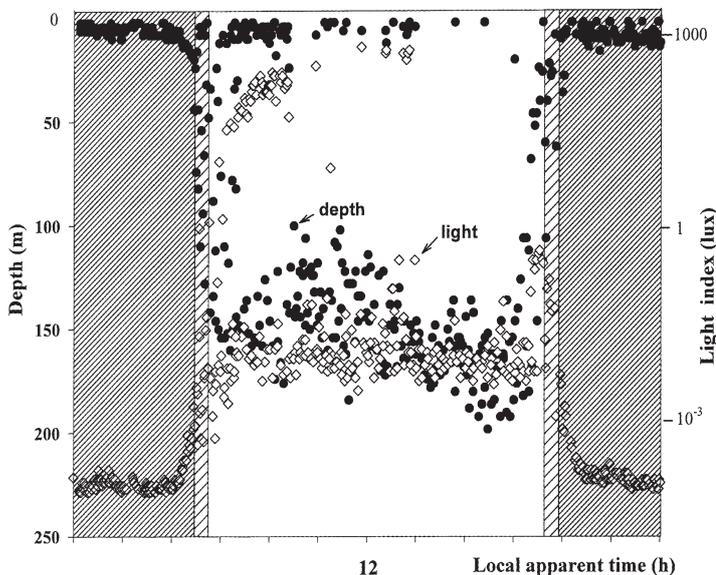


Fig. 2. Maximum diving depths (●) of King penguins at different times of the day at Kerguelen Islands (1 to 3 March, $n = 2$ birds). (◇) Light-level index recorded at the corresponding dive depth. The lightly-shaded sections correspond to dawn and dusk periods and the heavily shaded sections correspond to the night period (see 'Materials and methods')

RESULTS

Diving activity

A systematic diel foraging rhythm was observed during the dive cycles (Fig. 2). During the night, the penguins spent a reduced amount of their time below the surface (22 vs 50.4 % during daylight) and their median diving depth was 12 m (maximum diving depth 60 m, mean dive frequency 6.9 ± 8.5 dives h^{-1} ; Fig. 2). At dawn, the diving depth quickly increased and was positively correlated with the light level at maximal depth (m) ($r^2 = 0.54$, $p < 0.05$) according to a log-normal function where:

$$m = (118.1) \exp\{-0.5[\ln(\text{light level recorded}/857.1) (\log \text{lux})/1.51]^2\} \quad (2)$$

Thereafter diving depth stabilized ~5 h after sunrise at medium to deep depth (120–250 m, 42.6 % of the dives). During the course of the day, the light level index recorded at such depths was always higher than the sub-surface levels at night (Fig. 2). The birds clearly avoided diving in the 20–100 m depth range (2.8 % of the dives) during daylight. The median diving depth was 148 m (maximum diving depth 264 m, mean dive frequency 7.5 ± 2 dives h^{-1} , $n = 15853$ dives). At the time of highest sunlight, diving depth was inversely correlated to light levels ($r^2 = -0.375$, $p < 0.01$). About 1 h before sunset, the maximum diving depth abruptly decreased (Fig. 2). No significant relationship was found for that time between the diving depth and the light intensity index ($r^2 = 0.26$, $p > 0.01$).

Composition of King penguin diet

The fish component in the diet exceeded 95.3 % of the prey by number found in stomach samples of King penguins. Two species constituted the bulk of the diet, the eel-cod *Muraenolepis marmoratus* and the myctophidae *Krefftichtys anderssoni* (56.5 and 32.9 % by number, 30.1 and 31.6 % by biomass, respectively). Three other species of myctophids of the genus *Protomyctophum*, *P. bolini*, *P. tenisoni* and *P. andriashevi*, constituted almost all of the residual part, (5.7, 2.2 and 1.2 % by number, 13.7, 4.1, and 2.6 % by biomass, respectively; Fig. 3, Table 1).

Comparison with trawl samples composition

King penguin diet differed from that of trawl composition in terms of species and relative importance by number and biomass (Fig. 3, Table 1). The similarity in number between penguin diet and trawl composition in

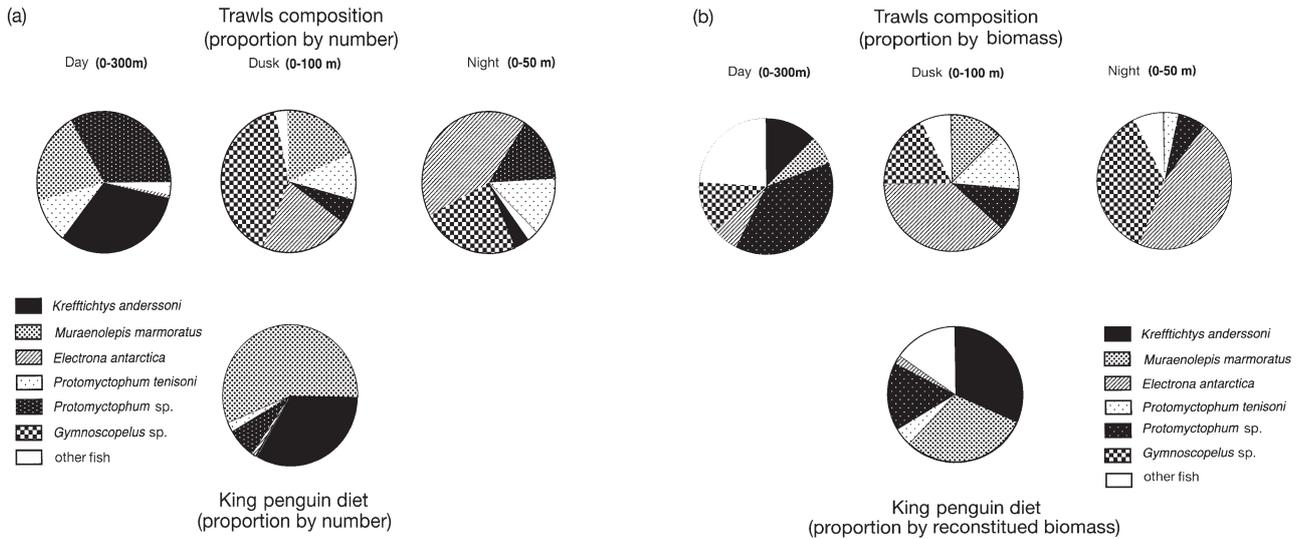


Fig. 3. Comparison of King penguin diet species composition by numbers and reconstituted biomass (percentage of relative proportions of prey item numbers, n = 22 samples) with trawl composition by number and biomass during the day (n = 27 stations), dusk (n = 3 stations) and night (n = 5 stations). Comparison by (a) number and (b) by biomass

the penguins' depth range was high for sampling performed during the day, and low when performed during dusk hours (Morisita index = 0.73 and 0.37, respectively). Virtually no overlap was found with the trawls performed at night (Morisita index = 0.06).

Circadian pattern in prey availability

Prey availability changed drastically in terms of diversity and abundance in the depth range of the penguins over the circadian cycle. Generally, the prey biomass was always higher by night at the sub-surface (0–50 m) than during the day, regardless of the depth layer considered (50, 150, 250 and 300 m) (Wilcoxon

Mann-Whitney test, $p < 0.05$; Table 2). The number of prey species and their abundance in trawls were the highest at night at sub-surface (15 prey species, mean abundance: 946 fish per station, n = 5 sampling stations) and the lowest during the day between the surface and 50 m (2 species, mean abundance 2 fish per station, n = 7 sampling stations).

Daylight trawls

Although the mean abundance of prey increased from the 150 m layer (41 fish per station) to the 300 m layer (93 fish per station), no significant difference among catches was found whatever the horizon

Table 1. Percentage composition by number and biomass of fish caught by trawls at day, dusk and night with regard to King penguin diet at Kerguelen (March 1995). For each prey species considered, the comparison between the composition of penguin diet and trawls differed significantly in terms of numbers and biomass regardless of sample time (χ^2_1 , $p < 0.001$) except when indicated by an asterisk (* $p > 0.05$)

Fish species	% by number				% by biomass			
	Day	Dusk	Night	Penguins	Day	Dusk	Night	Penguins
<i>Muraenolepis marmoratus</i>	16.5	16.4	0.3	56.5	6.1	10.7	0.1	30.1
<i>Krefftichtys anderssoni</i>	30.1	0	2.6	32.9	12.6	0	0.1	31.6
<i>Protomyctophum bolini</i>	21.1	7.7*	10.7	5.7	15.8	8.2	6.7	13.7
<i>Protomyctophum tenisoni</i>	4.9	16.6	11.8	2.2	1.3	11.4	3.3	4.1
<i>Protomyctophum andriashevi</i>	16.1	0	0	1.2	17.6	0	0	2.6
<i>Protomyctophum spp.</i>	0.7	0.4*	0.1*	0.2	2.3*	1.7*	0.1	0.7
<i>Gymnoscopelus spp.</i>	2.8	37.9	29.6	0	11.5	15.1	36.7	0
<i>Electrona antarctica</i>	5.3	18.9	43.8	0.9	6.1	31.0	44.7	2.1
<i>Electrona carlsbergi</i>	2.5	0	0	0.2	20.8	0	0	7.5
Other fish	0.3*	1.8	1.1	0.3	6.3*	21.9	8.2*	8.0

Table 2. Mean abundance and biomass of King penguin prey caught by trawls at Kerguelen Islands (March 1995) in relation to depth sampled at night and in daylight

Depth sampled (m)	Night		Daylight		
	50 (n = 5)	50 (n = 7)	150 (n = 6)	250 (n = 7)	300 (n = 7)
Mean abundance \pm SD (n/30 min trawling)	946.4 \pm 650 (39–2105)	2.5 \pm 2.3 (0–6)	41.5 \pm 51 (3–128)	46.7 \pm 6.6 (2–164)	93.4 \pm 108 (0–279)
Mean biomass \pm SD (g/30 min trawling)	1850.6 \pm 128 (1102–4132)	1.6 \pm 1.8 (0–4)	22.7 \pm 25.4 (0.4–621)	102.4 \pm 230.6 (0.4–621)	195.7 \pm 225.6 (5–489)

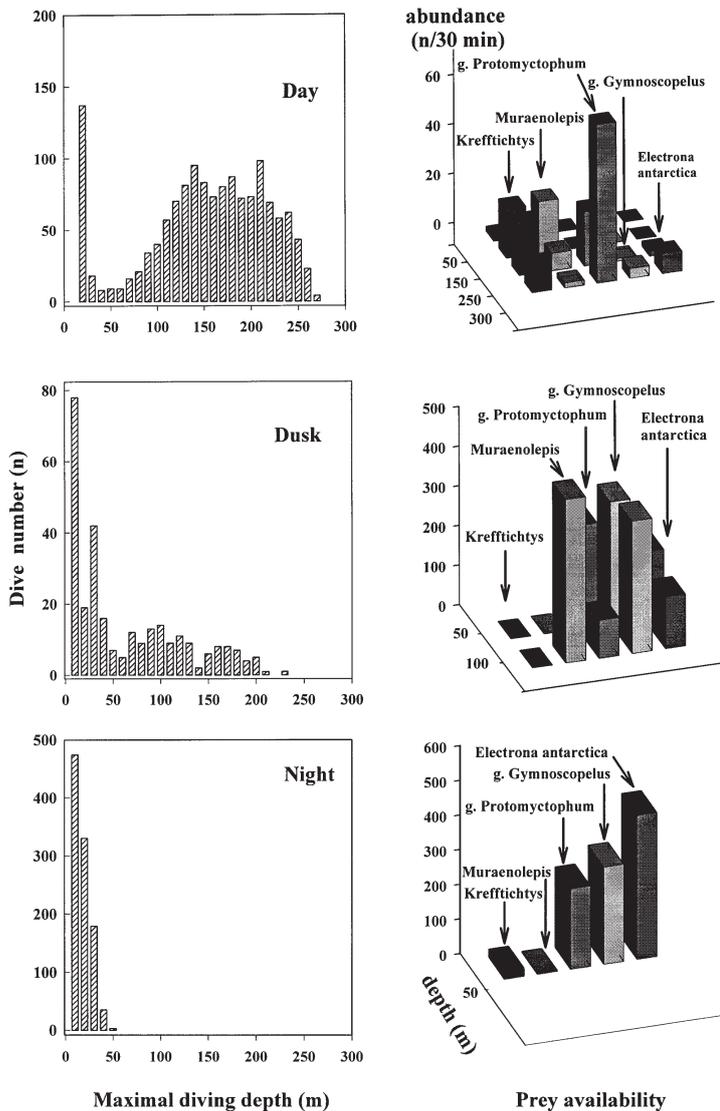


Fig. 4. Circadian pattern in maximum diving depths in relation to the availability of dominant prey species sampled (n/30 min) in the corresponding depth range of the penguin dives during daylight, dusk and night. The dive frequency graph corresponding to daylight (top) does not include shallow dives between 0 and 10 m

sampled (1-way ANOVA, $F_{3,20} = 2.4$, $p > 0.05$). The 2 dominant species in the penguins' diet (*Muraenolepis marmoratus* and *Krefftichtys anderssoni*) were among the 3 prey categories significantly present during the day in the 0–300 m depth range (constituting 16.5 and 30.1%, respectively, of the diurnal catches by number, all sampling depths considered). In terms of biomass, these 2 prey constituted only 6.1 and 12.6%, respectively, of the total daylight trawls, in contrast to the abundance of the species of the genus *Protomyctophum* (42.8% of catches; Fig. 3, Table 1). *M. marmoratus* and *K. anderssoni* were mostly caught at 150 m depth, i.e. at about the median diving depth of penguins during the day (52.0 and 47.6%, respectively, of the catches at the 150 m horizon; Fig. 4).

Night trawls

Muraenolepis marmoratus and *Krefftichtys anderssoni* were rarely found in the trawls at night within the depth range utilised by the penguins (0.3 and 2.6%, respectively, number of the total catches, 0.2% biomass; Figs 3 & 4). Two other prey species, *Protomyctophum tenisoni* and *P. bolini* constituted 22.5% of prey caught by the trawls (9.9% biomass). The catches were dominated by 3 other myctophid species, *Electrona antarctica*, *Gymnoscopelus fraseri* and *Gymnoscopelus braueri* (62% number and totaling 82% biomass; Fig. 4), which were found virtually absent from the penguins' diet (Fig. 3, Table 1). Overall, the mean biomass of potential prey found within the penguins' depth range was 1850 g per station (n = 5 stations, horizon sampled: 50 m), i.e. 6 times higher that the value obtained for the 4 sampled during the day (50, 150, 250, 300 m, Table 2).

Dusk trawls

The values reported were intermediate in terms of species diversity and biomass (Fig. 4, Table 1).

Muraenolepis marmoratus was caught only at 150 m depth, and *Krefflichthys anderssoni* was absent in the depth range used by the penguins during dusk hours.

Prey size

For a comparison of the size distribution of prey, *Krefflichthys anderssoni* was the only species found in sufficient numbers in both the stomach contents and trawl samples for the depth corresponding to the penguins' dive range to allow statistical comparisons.

There was no significant difference between the size distribution of *Krefflichthys anderssoni* measured from daylight trawl samples and the data from the penguins' diet (Kolmogorov-Smirnov 2-sample test, $D = 0.161$, $p > 0.05$). No quantitative data about *K. anderssoni* caught by night at sub-surface (50 m) were available to allow such comparison. However data from night trawls performed at 150 m depth indicated an absence of significant difference with the size distribution from penguin diet (Kolmogorov-Smirnov 2-sample test, $D = 0.065$, $p > 0.05$; Fig. 5).

DISCUSSION

Validity of the comparison between predator and trawl data

Studies relating predator foraging activities and prey depth distribution must ensure that both data sets are temporally and spatially compatible (Croxall et al. 1985, Wilson et al. 1993). However, in Southern Ocean localities it remains very difficult to assess predator feeding activity with simultaneous estimations of prey availability because of rough conditions and logistic constraints. The task is further complicated with diving predators like penguins using the 3 dimensions of the marine environment, as it necessitates sampling surveys at different depth levels throughout the circadian cycle.

Although the sampling periods were limited in duration, this work provides one of the first insights into the changes in diving depth of a southern pelagic predator in relation to simultaneous estimations of the diel prey availability. Furthermore, it has been possible to perform these prey estimations at the preferential depth levels of the penguins in this study, and to compare them with the diet composition at the same time of year.

We assume that the results of day/night trawling reflect the prey species potentially available to the penguins in the corresponding depth range and on the

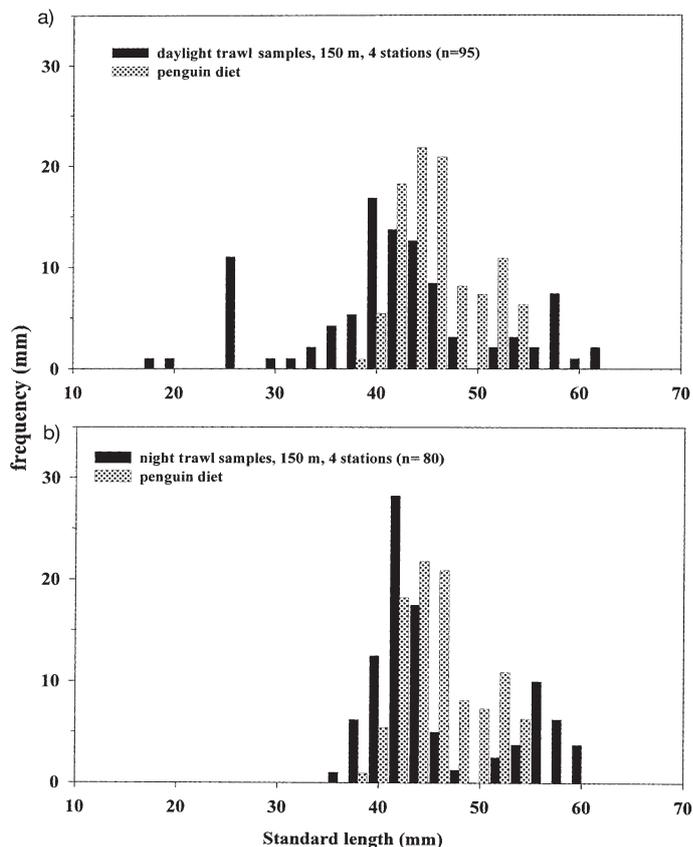


Fig. 5. Length-frequency distribution of *Krefflichthys anderssoni* from King penguin diet (8 birds, $n = 110$) and trawls conducted at Kerguelen Island in March 1995 in (a) daylight and (b) at night (150 m depth)

same spatial scale. Mesopelagic fish are patchily distributed and highly mobile (Zemsky & Zozulya 1991, Duhamel et al. 2000). Since myctophids are dispersed at night, trawls may then give a better estimation of mesopelagic fish biomass than by day because of the patchiness of the daytime shoals. This especially concerns the associated pelagic species *Krefflichthys anderssoni*, *Muraenolepis marmoratus* and the genus *Protomyctophum* that may form dense shoals in upper layers of the water column during the day (Duhamel et al. 2000). However, when considering the species composition of trawls in relation to depth, the differences between day and night were so contrasted that a major bias seems unlikely.

Analysis of penguin diet from prey remnants may be subject to several sources of error (Robertson et al. 1994). Nevertheless it seems improbable that digestion in the stomach before sampling could have induced a notable overrepresentation of certain fish size categories since most of the fish items recovered were small-sized species (Gon & Heemstra 1990).

Diet recomposition from land-based stomach lavages may not correspond to what penguins feed on during the central part of their trip, and provide only information about the last meals before the return to the colony (Kooyman & Kooyman 1995). During the study period, the return journey of tracked King penguins from their distant foraging trip lasted generally less than 3 d (C.A.B. unpubl. data). As the digestion rate is unknown, it cannot be determined here whether the analysis of penguin stomach contents reflected the prey caught during the last hours at sea or rather the prey caught at the furthest point of the trip.

Although the spatial overlap between penguin return journeys and trawl stations was reduced, the sampling area was nonetheless representative of the physical and biotic characteristics of the oceanic zone crossed by the penguins during their foraging trip (Duhamel et al. 2000). As the composition of the trawls varies little off the shelf break in terms of species diversity, it ensures that the prey caught by the birds during their last days at sea were potentially sampled. Consequently, these observations lead us to consider that our comparative analysis of diet and trawl composition is not very different from the real situation.

Foraging behavior and diel changes in prey availability

At Kerguelen, the diving activities of King penguins showed a marked diel pattern, with maximum dive depth recorded during daylight and only shallow dives at night. This situation is consistent with those already reported for the other breeding colonies during the summer (Kooyman et al. 1992, Pütz et al. 1998, Moore et al. 1999).

Several hypotheses have been debated to interpret this pattern in diving activity. The first is that according to vertical prey migration, optimal feeding time should be at night because of the ascension of the prey towards the surface. Penguins would look for their prey at the sub-surface, taking advantage of their bioluminescence. During the day, they would have to track their prey much deeper, possibly with a lower yield (Kooyman et al. 1992). The ambient light hypothesis instead proposes that dive depth and efficiency of prey capture are dependent on light availability, i.e. on the time of day and diving depth. Feeding efficiency should be higher during the day, when the birds perform deeper dives due to a greater visual acuity. At night, the foraging success would be much reduced because of a light level which is too low (Wilson et al. 1993, Pütz et al. 1998). A third hypothesis concerns changes in prey density and behavior

between day and night. During the day, resting myctophids usually occur in dense shoals (Zasel'sliyi et al. 1985, Perissinotto & McQuaid 1992). During the night they disperse to feed actively on mesozooplankton (Perissinotto & McQuaid 1992, Pakhomov et al. 1996).

The comparison between diet and day/night trawl composition has provided some evidence supporting the assumption that King penguins feed essentially during their diurnal deep dives. Indeed the 2 key prey species at Kerguelen (*Mureanoleopis marmoratus* and *Krefflichys anderssoni*) were also among the dominant prey sampled in daylight trawls within the 150–300 m depth range. Their preferential depth of 150 m also corresponded to the average maximum depth of King penguin dives at Kerguelen during the day. The prey sampling performed at night provided other direct evidence. The 2 key prey species represented a negligible part of the total mesopelagic fish biomass sampled at night at the sub-surface, i.e. in the nocturnal depth range of the penguins. Concerning *M. marmoratus*, the abundance by day at 150 m (i.e. considering only 1 sampling horizon) was found to be 7 times higher than by night at 50 m. The abundance found for *K. anderssoni* at 50 m was about the same magnitude than for each of the 3 sampling horizons performed during the day between 150 and 300 m. The total number of these prey items was probably much higher in the entire depth range of the penguins during the day. In addition, despite a huge increase of prey biomass in the upper level from dusk to night-time, none of the dominant myctophid species sampled at that time (*Electrona antarctica*, *Gymonoscopelus* spp., *Protomyctophum* spp.) were found to be significant in penguins' diet.

During darkness, the penguins continued to search for their prey as shown by the numerous shallow dives of between 10 and 40 m, which can only be interpreted as traveling dives (Wilson 1995, Pütz et al. 1998). However, the low occurrence of nocturnal species in the diet suggests that the prey capture rate at night was reduced at this time of the year. Even if a dispersal of myctophids' schools occurs at the sub-surface, the number of fish caught by the trawls in the 0–50 m depth range was much larger (up to 25 times) than at any depth level in the 0–300 m range sampled during daylight. It seems unlikely that the virtual absence of such abundant nocturnal species in the diet would result from a selection of prey of different sizes and/or energetic values according to the needs of the chick. Available data on energy content of mesopelagic fish from other localities indicate that *Krefflichys anderssoni*, the most frequently preyed upon myctophid by King penguins at Kerguelen, has about the same calorific content (8 kJ g⁻¹ wet mass, Cherel & Ridoux

1992) than those measured for 2 species found among the most abundant fish during night trawls (*Electrona antarctica* and *Gymnoscopelus braueri*, Donnelly et al. 1990). Furthermore, these species are also of larger size (individual mass 2 and 7 times larger, respectively, than *K. anderssoni*) and therefore potentially provide a highly profitable prey resource for penguins foraging off Kerguelen.

Timing of feeding of King penguins and visual prey detection

The most likely explanation of the absence in the diet of nocturnal migrating species is that visually guided King penguins mostly fail to detect and catch their prey at night, at least during the summer period. Importantly, the light level index recorded at 0–30 m at night was always lower than the value recorded between 150 and 200 m during daylight in Kerguelen waters. Despite the fact that all the myctophids found at Kerguelen have photophores (Gon & Heemstra 1990), our results show indirectly that King penguins cannot rely on the bioluminescence of these fish to exploit them efficiently, despite their massive rise to the surface at night.

One role of the light level at depth has been shown in captive little penguins, whose foraging is less effective below a certain light threshold (Cannell & Cullen 1998). In King penguins, a rapid increase in diving depths occurs at dawn in relation to the increase in light intensity. During a narrow 'window', the birds might then take advantage of the rise in light to exploit the descending migration of myctophids. At dusk, no positive relationship was found between light level index and diving depth. This suggests that the penguins may forage more erratically, prevented from foraging in the most productive stratas because of the reduced light intensity. The exact timing and duration of the myctophids' ascent could not be determined in this work. An average rate of ascent of 0.5 m min^{-1} has been estimated for *Electrona carlsbergi* in the Southern Atlantic, whose ascending migration from 80 to 120 m starts about 1 h before sunset (Zasel'sliy et al. 1985). If a similar timing exists in Kerguelen waters, this may suggest that the ascent of such potential prey occurred at a very low light level, preventing efficient predation by the penguins.

How King penguins detect their prey at such depths remains a subject of debate. Their eye structure and retinal visual field facilitate vision at low light levels, but the attenuation of the spatial resolution at depths deeper than 100 m are major constraints (Martin 1999). Despite this, based on the present study, King penguins may not necessarily rely on bioluminescence of

their prey, even at deeper depths of 150 to 250 m, since one of its major prey species, *Muraenolepis marmoratus*, does not possess photophores (Gon & Heemstra 1990). Some other prey detection mechanism may be used, such as the counter-shade effect experienced when looking upwards to visualize the silhouette of prey, although the mechanisms of such visual guidance still remain elusive.

To conclude, King penguins appear to be primarily diurnal predators, and the ambient light level, already low during the day in the deep, seems more decisive in their feeding success than the abundance of their prey, whether bioluminescent or not. However, we cannot exclude that another potentially important factor is the density of prey *per se*. It would become more profitable to feed in dense patches of resting myctophids than on dispersed and active prey, even if closer to the surface. As there is variation of both changes in light levels and theoretical prey density during the day, the importance of the prey density still remains obscure. Nevertheless, the rapid increase in diving depths at dawn, in relation to the increase in light intensity, points out the importance of the level of light for foraging penguins, independently of a possible prey aggregation at depth during their descent.

Nocturnal feeding on myctophids has been reported in chinstrap penguins foraging off the Antarctic Peninsula (60°59' S) during summer (Jansen et al. 1998) but at this time of the year the darkness is less pronounced at these latitudes (Wilson et al. 1989) than in the sub-Antarctic zones where King penguins forage. Macaroni penguins breeding at Heard Island (53°06' S) have a diet composed almost only of *Kreff-tichtys anderssoni* at the end of summer. These predators dive essentially between dawn and dusk to depths of 10 to 60 m, with maximal diving depths scarcely exceeding 90 m (Green et al. 1998). It is unlikely that *K. anderssoni* occur in abundance at this depth during daylight by analogy to the situation observed at Kerguelen (~500 km away). Consequently it can be hypothesized that macaroni penguins succeed best in catching these prey during their descent and ascent, i.e. when the prey are available in the diving range.

Clearly, diving predators have several ways to exploit the same prey category and there is a complex relationship between the diel prey migration and the predators' foraging tactics. Future studies based on deployment of multi-data recorders (accurate prey ingestion recorders, sensitive light meters for different wavelengths, diving depth) in different seasons, in conjunction with prey estimation surveys as performed in this study, offer promise for understanding predator foraging tactics.

Acknowledgements. This study was supported by the Institut Français pour la Recherche et la Technologie Polaires (IFRTP) and Terres Australes et Antarctiques Françaises (TAAF) and a grant from the Programme Environnement, Vie et Société du CNRS). We are especially indebted to the Captain of La Curieuse, D. Rochard, and his crew, and to A. Lamalle for logistical support. We are grateful to S. Eudes for his help in the field study, and R. Seyller and J. P. Gendner for their contributions to the data management. Y. Cherel, D. Gremillet and V. Ridoux are thanked for providing useful suggestions on the manuscript, and A. Pape for help with the English. Three anonymous referees provided constructive comments that greatly improved the manuscript.

LITERATURE CITED

- Adams NJ, Brown CR (1989) Dietary differentiation and trophic relationships in the sub-Antarctic penguin community at Marion Island. *Mar Ecol Prog Ser* 57:249–258
- Annuaire du Bureau des Longitudes (1995) Ephémérides astronomiques. Masson, Paris
- Cannell BL, Cullen LM (1998) The foraging behaviour of little penguins (*Eudyptula minor*) at different light levels. *Ibis* 140:467–471
- Charrassin JB, Kato A, Handrich Y, Sato K and 6 others (2001) Feeding behaviour of free-ranging penguins determined by oesophageal temperature. *Proc R Soc Lond B* 268: 151–157
- Cherel Y, Ridoux V (1992) Prey species and nutritive value of food fed during summer to King penguin (*Aptenodytes patagonica*) chicks at Possession Island, Crozet Archipelago. *Ibis* 134:118–127
- Croxall JP, Everson I, Kooyman GL, Ricketts C, Davis RW (1985) Fur seal diving behaviour in relation to vertical distribution of krill. *J Anim Ecol* 54:1–8
- Donnelly J, Torres JJ, Hopkins TL, Lancraft TM (1990) Proximate composition of Antarctic mesopelagic fish. *Mar Biol* 106:13–23
- Duhamel G (1998) The pelagic fish community of the Polar Frontal zone off Kerguelen Islands. In: Di Prisco G, Pisano E, Clarke A (eds) *Fishes of Antarctica: a biological overview*. Springer, Berlin, p 63–74
- Duhamel G, Koubbi P, Ravier C (2000) Day and night mesopelagic fish assemblages off the Kerguelen Islands (Southern Ocean). *Polar Biol* 23:106–112
- Gaston AJ, Bradstreet MSW (1993) Intercolony difference in the summer diet of Thick-billed Murres in the eastern Canadian Arctic. *Can J Zool* 71:1831–1840
- Gon O, Heemstra PC (1990) *Fishes of the Southern Ocean*. JLB Smith Institute of Ichthyology, Grahamstown
- Green K, Williams R, Green MG (1998) Foraging ecology and diving behaviour of macaroni penguins (*Eudyptes chrysolophus*) at Heard Island. *Mar Ornithol* 26:27–34
- Handrich Y, Bevan R, Charrassin JB, Butler PJ, Pütz K, Lage J, Woakes A, Le Maho Y (1997) Hypothermia in foraging King penguin. *Nature* 388:64–67
- Horn H (1966) Measurement of 'overlap' in comparative ecological studies. *Am Nat* 100:419–424
- Jansen JK, Boveng PL, Bengtson J (1998) Foraging modes of chinstrap penguins: contrasts between day and night. *Mar Ecol Prog Ser* 165:161–172
- Kooyman GL, Davis RW (1987) Diving behavior and performance, with special reference to penguins. In: Croxall JP (ed) *Seabirds, feeding ecology and role in marine ecosystems*. Cambridge University Press, Cambridge, p 63–75
- Kooyman GL, Kooyman TG (1995) Diving behavior of Emperor Penguins nurturing chicks at Coulman Island, Antarctica. *Condor* 97:536–549
- Kooyman GL, Cherel Y, Le Maho Y, Croxall JP, Thorson PH, Ridoux V, Kooyman CA (1992) Diving behavior and energetics during foraging cycles in King penguins. *Ecol Monogr* 62:143–163
- Koudil M, Charrassin JB, Le Maho Y, Bost CA (2000) Seabirds as monitors of upper-ocean thermal structure. King penguins at the Antarctic Polar Front, Kerguelen sector. *C R Acad Sci Ser III Life Sci* 323:377–384
- Lancraft TM, Torres JJ, Hopkins TL (1989) Micronekton and macrozooplankton in the open waters near the Antarctic ice edge zones (AMERIEZ 1983 and 1986). *Polar Biol* 9: 225–233
- Martin GR (1999) Eye structure and foraging in King penguins. *Ibis* 141:444–450
- Martin GR, Young SR (1984) The eye of the Humboldt penguin (*Spheniscus Humboldtii*): visual fields and schematic optics. *Proc R Soc Lond B* 223:197–222
- Moore GJ, Wienecke B, Robertson G (1999) Seasonal change in foraging areas and dive depths of breeding King penguins at Heard Island. *Polar Biol* 21:376–384
- Nevitt GA, Veit RR, Karelva P (1995) Dimethyl sulphide as a foraging cue for Antarctic Procellariiform seabirds. *Nature* 376:680–682
- Olsson O, North AW (1997) Diet of the King penguin (*Aptenodytes patagonicus*) during three austral summers at South Georgia. *Ibis* 139:504–513
- Pakhomov EA, Perissinotto R, McQuaid CD (1996) Prey composition and daily rations of myctophid fishes in the Southern Ocean. *Mar Ecol Prog Ser* 134:1–14
- Perissinotto R, McQuaid CD (1992) Land-based predator impact on vertically migrating zooplankton and micronekton advected to a Southern Ocean Archipelago. *Mar Ecol Prog Ser* 80:15–27
- Pütz K, Bost CA (1994) Feeding behavior of free-ranging King penguins (*Aptenodytes patagonicus*). *Ecology* 75: 489–497
- Pütz K, Wilson RP, Charrassin JB, Raclot T and 5 others (1998) Foraging strategy of King penguins (*Aptenodytes patagonicus*) during summer at the Crozet Islands. *Ecology* 79: 1905–1921
- Robertson G, Williams R, Green K, Robertson L (1994) Diet composition of emperor chicks *Aptenodytes forsteri* at two Mawson colonies, Antarctica. *Ibis* 136:19–31
- Ropert-Coudert Y, Sato K, Kato A, Charrassin JB, Bost CA, Le Maho Y, Naito Y (2000) Preliminary investigations of prey pursuit and capture by King penguins at sea. *Polar Biosci* 13:101–112
- Ropert-Coudert Y, Kato A, Baudat J, Bost CA, Le Maho Y, Naito Y (2001) Feeding strategies of free-ranging Adelie penguins (*Pygoscelis adeliae*) analysed by multiple data recording. *Polar Biol* 24:460–466
- Sokal RR, Rohlf FJ (1981) *Biometry*, 2nd edn. Freeman and Co., San Francisco
- Tett PB, Kelly MG (1973) Marine bioluminescence. *Oceanogr Mar Biol Annu Rev* 11:89–173
- Weimerskirch H, Wilson RP (1992) When do wandering albatross (*Diomedea exulans*) forage? *Mar Ecol Prog Ser* 86: 297–300
- Weimerskirch H, Zotier R, Jouventin P (1988) The avifauna of Kerguelen Islands. *Emu* 89:15–29
- Weimerskirch H, Doncaster P, Cuenot-Chaillet F (1994) Pelagic seabirds and the marine environment: foraging patterns of wandering albatrosses in relation to prey availability and distribution. *Proc R Soc Lond B* 255:91–97
- Wienecke BC, Robertson G (1997) Foraging space of Emperor

- Penguins (*Aptenodytes forster*) in Antarctic shelf waters in winter. *Mar Ecol Prog Ser* 159:249–263
- Williams R, McEldowney A (1990) A Guide to the fish otoliths from water off the Australian Antarctic Territory, Heard and Macquarie Islands. *ANARE Res Notes* 75:1–173
- Wilson RP (1984) An improved stomach pump for penguins and other seabirds. *J Field Ornithol* 55:109–112
- Wilson RP (1995) Foraging ecology. In: Williams TD (ed) *The penguins*. Oxford University Press, Oxford, p 81–106
- Wilson RP, Culik B, Coria NR, Adelung D, Spairani HJ (1989) Foraging rhythms in adelic penguins (*Pygoscelis adeliae*) at Hope Bay, Antarctica: determination and control. *Polar Biol* 10:161–165
- Wilson RP, Pütz K, Bost CA, Culik BM, Bannasch R, Reins T, Adelung D (1993) Diel dive depth in penguins in relation to diel vertical migration of prey: whose dinner by candlelight? *Mar Ecol Prog Ser* 94:101–104
- Wilson RP, Grémillet D, Syder J, Kierspel MA and 7 others (in press) Remote-sensing systems and seabirds: their use, abuse and potential for measuring marine environmental variables. *Mar Ecol Prog Ser*
- Zasel'sliy VS, Kudrin BD, Poletayev VA, Chechenin SC (1985) Some features of the biology of *Electrona carlsbergi* (Tanin) (Myctophidae) in the Atlantic sector of the Antarctic. *J Ichthyol* 25:163–166
- Zemsky AV, Zozulya SA (1991) A functional division of *Electrona carlsbergi* (Tanin 1932) area of habitat in relation to the latitudinal zonation of the southern ocean. *Selec Sci Pap Com Cons Ant Liv Res* 1990:369–395, CCAMLR, Hobart, Australia

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

*Submitted: August 14, 2000; Accepted: June 5, 2001
Proofs received from author(s): January 28, 2002*