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Summer diet of king penguins (*Aptenodytes patagonicus*) at the Falkland Islands, southern Atlantic Ocean

Received: 22 April 2002 / Accepted: 23 July 2002 / Published online: 20 September 2002
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Abstract The diet of king penguins (*Aptenodytes patagonicus*) brooding chicks was investigated during February 2001 at the Falkland Islands, where a small but increasing population is located at the limit of the breeding range of this species. Fish was the most important food source by number (98.0%) and reconstituted mass (97.8%), squids accounting for the remainder. Myctophid fishes represented the main part of the diet (97.7% by number and 96.6% by reconstituted mass), *Protomyctophum choriodon* being by far the main prey item (84.2% and 88.1%, respectively). Four other myctophids and one squid species each contributed to more than 1% of the diet by number: *Krefflichthys anderssoni* (4.8%), *Electrona carlsbergi* (4.6%), *Gymnoscopelus nicholsi* (2.2%) and *Protomyctophum tenisoni* (1.8%), together with small juveniles of *Gonatus antarcticus* (1.8%). Twelve squid species were identified from accumulated lower beaks, including the ommastrephid *Martialia hyadesi* (48.3% by number), the onychoteuthids *Moroteuthis ingens* (15.6%), *Kondakovia longimana* (10.5%) and *Moroteuthis knipovitchi* (7.3%), and *Gonatus antarcticus* (9.2%). The stable-carbon and stable-nitrogen isotopic composition of chick food and adult blood differed in a way that suggests that, during the same trip, adult birds fed for themselves in distant foraging grounds, and fed for their chicks on their way

back to the colony. The study emphasizes that king penguins are specialist myctophid eaters throughout their breeding range in summer, and highlights the importance of *Protomyctophum choriodon* as a link between zooplankton and top predators in the pelagic ecosystem of the southwestern Atlantic Ocean.

Introduction

The king penguin (*Aptenodytes patagonicus*) is the largest subantarctic penguin, breeding in large numbers on islands located in the Polar Frontal Zone (PFZ: the area located between the Subantarctic Front in the north and the Polar Front in the south), and to a lesser extent on two islands located further south in Antarctic waters: Heard Island and South Georgia (Woehler 1993). The king penguin is especially abundant in the southern Indian Ocean, where the majority of its world population breeds (Woehler 1993). Extralimitally, a small breeding colony occurs also in the Falkland Islands (Bingham 1998), with a currently increasing population of around 700 breeding pairs at the main colony located at Volunteer Beach (East Falkland) in February 2001 (Y. Cherel, K. Pütz, unpublished data).

Its total biomass makes the king penguin a major marine predator. At Crozet and Kerguelen (southern Indian Ocean), it was estimated that this species consumes annually about 1 million tonnes of resources (Guinet et al. 1996). Throughout its range, king penguins are specialist feeders, targeting almost exclusively myctophid fish during the summer months (Adams and Klages 1987; Hindell 1988; Cherel and Ridoux 1992; Olsson and North 1997; Moore et al. 1998; Bost et al. 2002). In winter, it is a more opportunistic predator, shifting to a more diverse diet including a significant amount of squid at some localities (Adams and Klages 1987; Cherel et al. 1996; Moore et al. 1998). While the diet of king penguin has now been investigated at all other breeding localities, no information is available for

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the small population from the Falkland Islands, except for the recent analysis of its squid prey in winter (Piatkowski et al. 2001).

The main goal of the study was to document the food of king penguins at the limit of its breeding range in the Falkland Islands. The work was devoted to the food and feeding ecology of the species in summer, which included both the description of its prey (present work) and its behaviour at sea (K. Pütz, Y. Cherel, unpublished data). Comparison is made with the food of king penguins at other localities, and with that of other penguin species breeding at the Falkland Islands. Finally, together with prey biogeography, the stable-isotope measurement technique of carbon and nitrogen (Hobson et al. 1994; Kelly 2000) was used to gain information on the trophic level and feeding grounds of birds foraging in a complex area characterized by various water masses and fronts (Peterson and Whitworth 1989). A hypothesis can be made on birds performing long foraging trips (as king penguins do during the brooding stage) that adult birds feed for themselves in the middle of the trip in distant areas, and feed for the chicks on the way back to the colony. This could induce different isotopic signatures in the chicks' food and adult blood, because Antarctic plankton food bases tend to be depleted in ^{13}C compared to those in lower-latitude waters (Goericke and Fry 1994).

Materials and methods

Study site and birds

Fieldwork was conducted in February 2001 at Volunteer Beach, East Falkland (51°29'S, 57°50'W). Low prey diversity in king-penguin diet at a given locality during summer (Cherel and Ridoux 1992), together with the small size of the colony at the Falkland Islands (Bingham 1998), initiated the collection of ten stomach contents during the brooding period, using the water offloading technique described by Wilson (1984). This small sample size precludes any generalization to the whole breeding period, especially to winter, which is characterized by marked dietary changes (Adams and Klages 1987; Cherel et al. 1996; Moore et al. 1998). Food samples were taken from five males and five females returning to relieve their mate and feed their single chick. Sexes were determined from the long calls (Derenne et al. 1979) that occur during the chick change-over ceremony. Additionally, a 2-ml blood sample was taken from a flipper vein of each king penguin with a heparinized syringe, before the bird was flushed two to three times to collect its stomach content.

Dietary analysis

In the field, food samples were drained to remove the excess water, and kept a few days at ambient temperature. They were then deep-frozen at Stanley, Falkland Islands. For analysis, each sample was thawed overnight, drained and placed in a large flat-bottomed tray. Items that accumulate over time (squid beaks and stones) were subsequently removed. Accumulated beaks were analysed separately from fresh items, and they were not considered when calculating the reconstituted proportion by mass in the diet of the different prey species. Fresh remains were divided into broad prey classes (fish and cephalopods), which were weighed to calculate their proportion by fresh mass in the diet.

Identification of prey relied almost entirely on the examination of otoliths and bones for fish, and chitinous lower beaks for cephalopods. Items were identified by comparison with material held in our own collection and by reference to the available literature (Clarke 1986; Williams and McEldowney 1990; Reid 1996). Length of uneroded or slightly eroded otoliths (OL) and dentary bones (ML for mandible length) of fish, and lower rostral length (LRL) of squid beaks were measured with a vernier caliper or using an ocular scale in a binocular microscope. Fish standard length (SL), cephalopod dorsal mantle length (DML) and prey body masses (M) were calculated using our own and published regression equations (Clarke 1986; Adams and Klages 1987; Hindell 1988; Rodhouse and Yeatman 1990; Rodhouse et al. 1990; Williams and McEldowney 1990; Thompson 1994; Jackson 1995; Olsson and North 1997; Jackson et al. 2000; dos Santos and Haimovici 2000; Piatkowski et al. 2001). For the few species where no relationships were available, length and mass were estimated using equations for closely related species or for species with a similar morphology. The reconstituted mass of each taxon for each sample was calculated from the mean wet body mass for the species in the sample. The value was then multiplied by the number of individuals in the sample, and the resulting value was pooled with those calculated for the same taxon in the other samples. The calculated masses for all the different taxa were consequently pooled, and the reconstituted proportion by mass of each taxon then calculated as the percentage it represented in the total reconstituted mass.

Stable-isotope analysis

After centrifuging in the field to separate plasma and cellular fractions, plasma, blood cells and a subsample of each stomach content were kept in 70% ethanol until analysis. Plasma and cellular fractions of blood, and food samples were dried in an oven at 60°C. Food samples were then ground to a fine powder in an analytical mill, and lipids were removed using a Soxhlet apparatus with chloroform solvent for 4–6 h.

Stable-carbon and stable-nitrogen isotope assays were performed on 1-mg subsamples of homogenized materials by loading into tin cups and combusting at 1800°C in a Europa Robo-Prep elemental analyser. Resultant CO_2 and N_2 gases were then analysed using an interfaced Europa 20:20 continuous-flow isotope ratio mass spectrometer (CFIRMS) with every 5 unknowns separated by 2 laboratory standards. Stable-isotope abundances were expressed in δ -notation as the deviation from standards in parts per thousand (‰) according to the following equation:

$$\delta X = [(R_{\text{sample}}/R_{\text{standard}}) - 1] \times 1000$$

where X is ^{13}C or ^{15}N and R is the corresponding ratio $^{13}\text{C}/^{12}\text{C}$ or $^{15}\text{N}/^{14}\text{N}$. The R_{standard} values were based on the Pee Dee Belemnite (PDB) for ^{13}C and atmospheric N_2 (air) for ^{15}N . Replicate measurements of internal laboratory standards (albumen) indicate measurement errors of $\pm 0.1\text{‰}$ and $\pm 0.3\text{‰}$ for stable-carbon and stable-nitrogen isotope measurements, respectively.

Statistics

Data were statistically analysed using SYSTAT 9.0 for WINDOWS (Wilkinson 1999). Values are means \pm SD.

Results

The mean mass of the 10 stomach contents obtained from adult king penguins was $1,271 \pm 225$ g (range = 1,010–1,730 g). They included both accumulated items (mainly stones and squid beaks) and fresh items (1.5% and 98.5% of the total mass for all the 10 samples pooled, respectively). Overall (all the samples

pooled), fish was the most important food source by wet mass (99.1%), reconstituted mass (97.8%), and by number (98.0%), cephalopods accounting for the remainder (0.9%, 2.2% and 2.0%, respectively). Fish and cephalopods occurred in all individual samples, and fish dominated by wet mass ($99.1 \pm 1.8\%$) and by number ($97.4 \pm 5.0\%$) in all of them. Crustaceans, mainly calanoid copepods, euphausiids and the hyperiid amphipod *Themisto gaudichaudii*, were also common but were apparently fish prey secondarily ingested by penguins. It was noticeable that the occurrence of the parasitic copepod, *Sarcotretes scopeli*, was in fairly large numbers in all the stomach contents ($n=2,020$ for the pooled samples).

No significant difference in any parameter was found between dietary samples collected from male and female king penguins. Data from both sexes were consequently pooled for subsequent analysis.

Fish and cephalopod species and prey size

A total of 4,706 fresh prey items was recovered from the 10 stomach contents (4,611 fish and 95 squid) (Table 1). Eighteen species or species groups of prey were identified, including 12 species of fish and 6 of squid.

Myctophid fishes represented the main part of the diet (97.7% by number and 96.6% by reconstituted mass). By far, the most important prey species was *Protomyctophum choriodon*, which dominated both by number and by mass in all the samples (84.2% and 88.1% by number and reconstituted mass, respectively). Other significant items were the myctophids, *Electrona carlsbergi*, *Gymnoscopelus nicholsi* and *Krefflichthys anderssoni* (Table 1). King penguins fed on one size class of *Protomyctophum choriodon* (mean: 70 mm SL; Table 2) and *Electrona carlsbergi* (mean: 70 mm SL), but they preyed on a largest range in size of *Gymnoscopelus nicholsi* (Fig. 1). The size of *Protomyctophum choriodon* was, overall, different among individual penguins (ANOVA, $F_{9,284}=4.53$, $P<0.0001$), mainly because 1 bird fed on smaller fish (9.5 vs 9.9–10.4 mm ML; post-hoc Tukey HSD multiple comparison test).

The only significant fresh squid prey was *Gonatus antarcticus*, which was found in all the samples and accounted for 1.8% and 1.2% by number and reconstituted mass, respectively. Twelve different species of squids were identified from accumulated lower beaks (Table 3). The ommastrephid, *Martialia hyadesi*, ranked first (48.3% by number), followed by *Moroteuthis ingens* (15.6%), *Kondakovia longimana* (10.5%), *Gonatus antarcticus* (9.2%) and *Moroteuthis knipovitchi* (7.3%).

Table 1 Frequency of occurrence, numbers and reconstituted mass of fresh prey items identified from ten stomach contents of king penguins during summer at the Falkland Islands

Species	Occurrence in stomachs		Number		Reconstituted mass	
	(n)	(%)	(n)	(%)	(g)	(%)
Fish	10	100	4611	98.0	21282.9	97.8
Bathylagidae						
<i>Bathylagus</i> sp.	1	10	1	<0.1	14.6	<0.1
Paralepididae						
<i>Notolepis coatsi</i>	3	30	4	<0.1	244.2	1.1
Myctophidae						
<i>Electrona carlsbergi</i>	5	50	215	4.6	1032.8	4.7
<i>Gymnoscopelus nicholsi</i>	8	80	105	2.2	421.9	1.9
<i>Krefflichthys anderssoni</i>	4	40	224	4.8	275.0	1.3
<i>Protomyctophum andriashevi</i>	2	20	3	<0.1	5.3	<0.1
<i>Protomyctophum choriodon</i>	10	100	3961	84.2	19159.8	88.1
<i>Protomyctophum tenisoni</i>	7	70	87	1.8	121.5	0.6
<i>Protomyctophum</i> sp.	2	20	3	<0.1	6.1	<0.1
Gadidae						
<i>Micromesistius australis</i>	1	10	1	<0.1	0.3	<0.1
Unidentified postlarvae	2	20	5	0.1	0.8	<0.1
Osteichthyes sp. A	2	20	2	<0.1	0.6	<0.1
Squid	10	100	95	2.0	469.3	2.2
Ommastrephidae						
<i>Martialia hyadesi</i>	1	10	1	<0.1	156.7	0.7
Onychoteuthidae						
<i>Moroteuthis knipovitchi</i>	1	10	1	<0.1	0.4	<0.1
<i>Kondakovia longimana</i>	1	10	2	<0.1	22.0	0.1
Brachioteuthidae						
<i>Brachioteuthis ?riisei</i>	1	10	1	<0.1	1.9	<0.1
Gonatidae						
<i>Gonatus antarcticus</i>	10	100	86	1.8	269.5	1.2
Neoteuthidae						
<i>Alluroteuthis antarcticus</i>	2	20	4	<0.1	18.9	<0.1
Total			4706	100.0	21752.2	100.0

Table 2 Measured fish mandible length (*ML*), otolith length (*OL*) and squid lower rostral length (*LRL*), and estimated fish standard length (*SL*), squid dorsal mantle length (*DML*) and body mass (*M*) of the prey identified from stomach contents of adult king penguins during brooding at the Falkland Islands. Values are means \pm SD with ranges in parentheses

Species	<i>n</i>	Measured parameters		SL/DML (mm)	M (g)
		Parameters	Values (mm)		
Fish					
<i>Bathylagus</i> sp.	1	ML	7.0	126	15
<i>Notolepis coatsi</i>	3	ML	17.0 \pm 3.8 (13.9–21.3)		
	1	OL	2.6	341	61
<i>Electrona carlsbergi</i>	40	ML	12.3 \pm 0.6 (11.0–13.6)	70 \pm 5 (60–80)	5.0 \pm 1.1 (3.0–7.7)
<i>Gymnoscopelus nicholsi</i>	43	ML	14.3 \pm 1.4 (12.4–17.8)	73 \pm 8 (63–92)	4.2 \pm 1.5 (2.5–8.4)
<i>Krefflichthys anderssoni</i>	21	ML	7.0 \pm 0.7 (5.0–8.0)	49 \pm 4 (36–55)	1.2 \pm 0.3 (0.4–1.8)
<i>Protomyctophum andriashevi</i>	2	OL	2.1–2.2	52–54	1.7–1.8
<i>Protomyctophum choriodon</i>	294	ML	10.1 \pm 0.6 (8.5–11.9)	70 \pm 4 (59–82)	4.8 \pm 1.0 (2.6–9.3)
<i>Protomyctophum tenisoni</i>	15	ML	7.4 \pm 0.3 (7.0–8.0)	51 \pm 3 (44–56)	1.4 \pm 0.2 (0.8–1.9)
<i>Micromesistius australis</i>	1	OL	2.3	35	0.3
<i>Osteichthyes</i> sp. A	1	OL	1.8		
Squid^a					
<i>Martialia hyadesi</i>	51	LRL	4.1 \pm 0.7 (2.8–5.3)	223 \pm 20 (184–259)	194 \pm 62 (86–322)
<i>Illex argentinus</i>	1	LRL	5.8	310	558
<i>Moroteuthis ingens</i>	1	LRL	2.8	131	71
<i>Moroteuthis knipovitchi</i>	2	LRL	0.8–5.7	5–232	0.4–413
<i>Kondakovia longimana</i>	7	LRL	2.6 \pm 0.8 (1.8–4.0)	75 \pm 30 (44–128)	19 \pm 19 (4.3–58)
<i>Brachioteuthis ?riisei</i>	5	LRL	1.9 \pm 0.6 (1.1–2.7)	55 \pm 13 (38–71)	4.5 \pm 2.0 (1.9–7.1)
<i>Gonatus antarcticus</i>	107	LRL	1.7 \pm 0.7 (0.7–6.0)	47 \pm 24 (25–215)	6.9 \pm 27.1 (0.4–206)
<i>Histioteuthis eltaninae</i>	9	LRL	3.1 \pm 0.2 (2.7–3.5)	55 \pm 5 (46–63)	67 \pm 12 (49–87)
<i>Histioteuthis atlantica</i>	1	LRL	1.6	22	15
<i>Alluroteuthis antarcticus</i>	2	LRL	1.1–2.0	35–66	4.7–26
<i>Loligo gahi</i>	14	LRL	1.9 \pm 0.3 (1.6–2.4)	134 \pm 18 (109–165)	47 \pm 15 (28–76)

^aIncluding both fresh and accumulated lower beaks

Noticeable was the presence of the loliginid squid of commercial interest, *Loligo gahi*, which accounted for 3.4% of total number of lower beaks. King penguins fed mainly on juvenile squids (including both fresh and accumulated items), as indicated by the level of darkening of their beaks. *Gonatus antarcticus* were mostly small specimens (mean: 43 mm DML), while *Martialia hyadesi* juveniles were of larger size (mean: 223 mm DML) (Fig. 2, Table 2). The largest and heaviest penguin prey was one adult of the ommastrephid squid, *Illex argentinus* (310 mm DML, 558 g).

Stable isotopes

Food, plasma and blood cells of king penguins were segregated by their stable-isotope values (MANOVA, Wilk's Lambda, $F_{4,52} = 40.07$, $P < 0.0001$) (Table 4). $\delta^{13}\text{C}$ values were different overall, being higher in food than in plasma and blood cells. $\delta^{15}\text{N}$ values were also different overall, being 1.3‰ higher in plasma and blood cells than in food (Table 4). $\delta^{15}\text{N}$ values were positively and linearly related to $\delta^{13}\text{C}$ values, regression lines being significant for food and plasma, but not for blood cells (Fig. 3). Interestingly, the dietary sample having the lowest $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values corresponded to that containing *Protomyctophum choriodon* of smaller size (see above).

Discussion

King-penguin diet at the Falklands

King penguins from the Falkland Islands are mainly fish eaters during summer, the myctophid fish *Protomyctophum choriodon* being their staple food at that time. *Protomyctophum choriodon* matures sexually from about 77 mm SL (Hulley 1981), indicating that king penguins fed mostly on subadult fish. This prey species is mesopelagic with a subantarctic pattern (Hulley 1981), and it was also previously taken by bottom trawls in slope waters (Hulley 1981; Konstantinova et al. 1994). Other myctophid prey of king penguins have either a subantarctic pattern (species living between the Subtropical Front and the Antarctic Polar Front: *Electrona carlsbergi*, *Protomyctophum andriashevi*) or a broadly Antarctic pattern (species living from the Subtropical Front to south of the Antarctic Polar Front: *Krefflichthys anderssoni*, *Gymnoscopelus nicholsi*, *Protomyctophum tenisoni*) (Hulley 1981, 1990). Fish biogeography together with location of water masses in the southern Atlantic Ocean (Peterson and Whitworth 1989) therefore suggest king penguins foraged for their chicks in summer in slope waters and nearby oceanic waters of the PFZ, located northeast, east and south of the Falkland Islands (Peterson and Whitworth 1989).

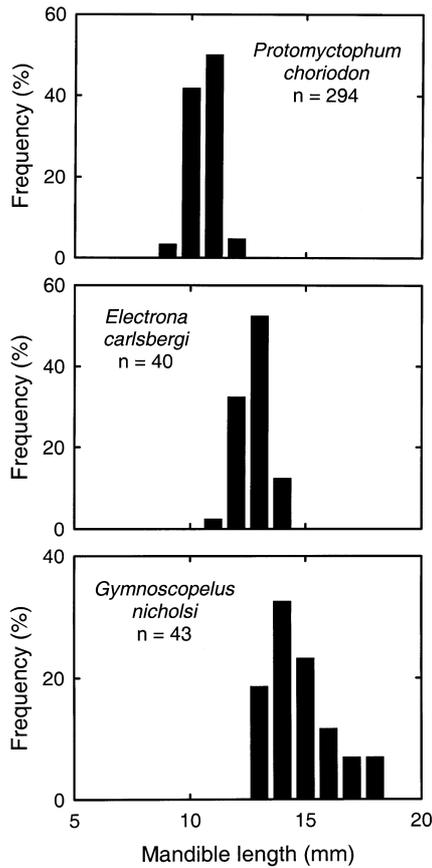


Fig. 1 Length-frequency distribution of the main myctophid prey of king penguins at the Falkland Islands in summer

Cephalopod prey of king penguins at the Falklands was recently investigated during the austral winter (Piatkowski et al. 2001). Basically, king penguins fed on the same squid species both in winter and summer, but

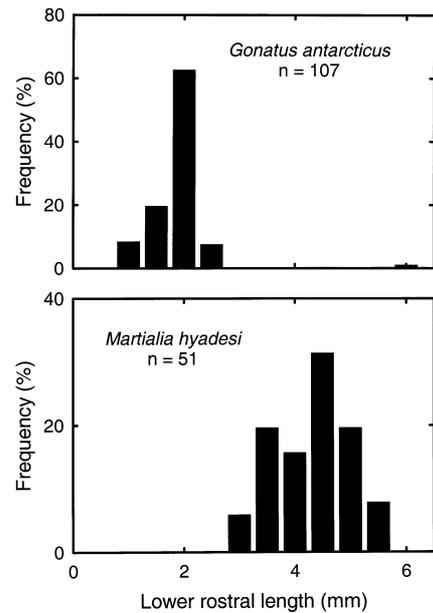


Fig. 2 Length-frequency distribution of the two main squid prey of king penguins at the Falkland Islands in summer

in different proportions. *Martialia hyadesi* and *Kondakovia longimana* were commoner, and *Moroteuthis knipovitchi*, *Moroteuthis ingens* and *Loligo gahi* rarer in summer than in winter (Piatkowski et al. 2001; present study). In addition, birds fed on larger *Loligo gahi*, but on smaller *Martialia hyadesi* and *Gonatus antarcticus* in summer than in winter (Piatkowski et al. 2001; present study). All the squid species have been recorded before on the Patagonian shelf and/or in southern waters around South Georgia and in the Scotia Sea: small juveniles of *Gonatus antarcticus* are associated with subantarctic and PFZ waters and are abundant over the

Table 3 Frequency of occurrence and numbers of accumulated lower beaks of squids identified from ten stomach contents of king penguins during summer at the Falkland Islands

Species	Occurrence in stomachs		Number	
	(n)	(%)	(n)	(%)
Ommastrephidae				
<i>Martialia hyadesi</i>	8	80	211	48.3
<i>Illex argentinus</i>	1	10	1	0.2
Onychoteuthidae				
<i>Moroteuthis ingens</i>	9	90	68	15.6
<i>Moroteuthis knipovitchi</i>	7	70	32	7.3
<i>Moroteuthis</i> sp. B (Imber)	5	50	7	1.6
<i>Kondakovia longimana</i>	7	70	46	10.5
Brachioteuthidae				
<i>Brachioteuthis ?riisei</i>	3	30	4	0.9
Gonatidae				
<i>Gonatus antarcticus</i>	7	70	40	9.2
Histioteuthidae				
<i>Histioteuthis eltaninae</i>	3	30	10	2.3
<i>H. atlantica</i>	1	10	1	0.2
Neoteuthidae				
<i>Alluroteuthis antarcticus</i>	2	20	2	0.5
Loliginidae				
<i>Loligo gahi</i>	4	40	15	3.4
Total			437	100.0

Table 4 Stable carbon and nitrogen isotope concentrations (mean \pm SD‰) in dietary samples and in blood cells and plasma of breeding adult king penguins at the Falkland Islands, and results of one-way ANOVA for differences among groups for each isotope. Values in the same column not sharing a common superscript letter are significantly different (post-hoc Tukey HSD multiple comparison test $P < 0.05$)

Sampling group	<i>n</i>	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$
Food	10	$-21.8 \pm 1.1^{\text{a,c}}$	$8.4 \pm 0.5^{\text{a}}$
Plasma	10	$-23.2 \pm 0.9^{\text{b}}$	$9.7 \pm 0.4^{\text{b}}$
Blood cells	10	$-22.5 \pm 0.4^{\text{b,c}}$	$9.7 \pm 0.3^{\text{b}}$
ANOVA		$F_{2, 27} = 6.99$ $P = 0.004$	$F_{2, 27} = 32.90$ $P < 0.0001$

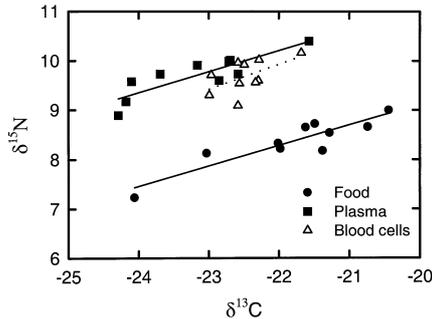


Fig. 3 Relationship between $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ in king-penguin food samples, plasma and blood cells. Equations of regression lines are $y = 0.41x + 17.39$ ($r = 0.91$, $F = 37.46$, $P < 0.0001$), $y = 0.43x + 19.60$ ($r = 0.86$, $F = 23.40$, $P = 0.001$) and $y = 0.51x + 21.10$ ($r = 0.57$, $F = 3.75$, $P = 0.089$) for food samples, plasma and blood cells, respectively

eastern shelf around the Falklands (Rodhouse et al. 1992a); *Moroteuthis ingens* and *Loligo gahi* are among the commonest squids of the area (Jackson et al. 1998a; Piatkowski et al. 2001); juvenile *Martialia hyadesi* are found both in slope and oceanic waters of the PFZ (Rodhouse 1997), and *Kondakovia longimana* and *Moroteuthis knipovitchi* are known from waters of both the PFZ and Antarctic Zone (Cherel and Weimerskirch 1999; Xavier et al. 1999). Thus, prey biogeography again suggests king penguins foraged in slope and oceanic waters east of the Falklands.

Among the penguin community from the Falkland Islands, king penguins segregate from the other species by being a specialist consumer targeting myctophid fish. By contrast, all three other penguin species during summer are opportunistic predators feeding on a mixture of fish, squid and crustaceans, with large spatial and temporal variations (Pütz et al. 2001). The diet of gentoo penguins (*Pygoscelis papua*) consists mainly of neritic fish, that of magellanic penguins (*Spheniscus magellanicus*) of neritic fish, squids and lobster krill (*Munida gregaria*), and that of rockhopper penguins (*Eudyptes chrysocome*) mainly of crustaceans (Thompson 1993; Pütz et al. 2001). All penguin species, however, feed on juvenile *Gonatus antarcticus*; it is a major item for the more inshore feeders, gentoo, magellanic and rockhopper penguins (Thompson 1994), but only a minor prey

for the more offshore-feeding king penguin (present study). Other marine predators from the Patagonian region preying on the same community of organisms as king penguins include the southern opah (*Lampris immaculatus*) (Jackson et al. 2000), and the squids *Illex argentinus* (Ivanovic and Brunetti 1994), and probably *Martialia hyadesi* (Rodhouse et al. 1992b¹; Gonzalez and Rodhouse 1998; Ivanovic et al. 1998) and *Moroteuthis ingens* (Jackson et al. 1998b; Phillips et al. 2001). However, the king penguin is, to our knowledge, the only species relying almost exclusively on *Protomyctophum choriodon* during the summer months.

Comparison with other localities

A review of the food of king penguins at various localities clearly shows that the species is a specialist myctophid eater throughout its breeding range (Table 5). In summer, myctophids form the bulk of its food in colonies located in the PFZ, the core of king-penguin distribution, including the Prince Edward Islands (Adams and Klages 1987), Crozet (Cherel and Ridoux 1992; Raclot et al. 1998), and Macquarie (Hindell 1988). Myctophids were also the main prey of king penguins breeding south of the Polar Front, at Heard Island (Klages et al. 1990; Moore et al. 1998) and South Georgia (Olsson and North 1997), and our study indicates that they also constitute the staple food of king penguins at the Falkland Islands. The only exception is the Kerguelen Islands where the species preys heavily upon juvenile eel cods (*Muraenolepis marmoratus*), together with myctophid fish (Bost et al. 2002). The main species of myctophids (>10% by number) vary among islands and are probably related to water masses (Table 5). At colonies located in the PFZ, birds prey upon *Electrona carlsbergi*, *Krefflichthys anderssoni* and *Protomyctophum tenisoni* (Adams and Klages 1987; Hindell 1988; Cherel et al. 1993). *Krefflichthys anderssoni* dominates the myctophid diet at colonies located at the Polar Front (Bost et al. 2002) and in Antarctic waters (Olsson and North 1997; Moore et al. 1998), and the Falkland Islands are the only locality where *Protomyctophum choriodon* is the main prey (present study).

Protomyctophum choriodon also accounts for a significant number of fish prey of king penguins at South Georgia (Olsson and North 1997). Among other sub-antarctic and Antarctic air-breathing predators, *Protomyctophum choriodon* was found previously to be a common prey only of Antarctic fur seals (*Arctocephalus gazella*) at South Georgia (Reid and Arnould 1996). The importance of *Protomyctophum choriodon* in the diet of top predators thus suggests it is an abundant species in slope/oceanic waters around the Falklands and South Georgia. Since the species feeds on copepods, amphipods and euphausiids (Oven et al. 1990), our study

¹Figure 4c of that article refers to an eroded otolith from *Protomyctophum choriodon* misidentified as *Electrona carlsbergi*.

Table 5 Percentage composition by number (%) of food samples from king penguins breeding at different localities throughout the Southern Ocean

Prey species	Marion Summer	Crozet Summer	Kerguelen Summer	Heard Annual	Macquarie Annual	South Georgia Summer	Falklands Summer
Fish	96.6	99.6	95.3	96.8	99.1	Main prey	98.0
Myctophidae	96.6	94.1	43.3 ^a	96.4	98.0	96.9 ^a	97.7
<i>Electrona carlsbergi</i>	33.4	44.6	<1.0 ^a	<1.0	48.5	9.4 ^a	4.6
<i>Krefflichthys anderssoni</i>		42.7	32.9 ^a	92.6	48.1	35.0 ^a	4.8
<i>Krefflichthys anderssoni</i> / <i>Protomyctophum tenisoni</i>	57.0						
<i>Protomyctophum tenisoni</i>		<1.4	2.2 ^a	3.1			1.8
<i>Protomyctophum choriodon</i>	3.9 ^b	1.0 ^b	<1.0 ^a	<1.0 ^b		9.1 ^a	84.2
Other fish	<1.0	5.5	56.5 ^a	<1.0	1.1	3.1 ^a	<1.0
Squid	3.5	<1.0	Minor prey	2.4	<1.0	Minor prey	2.0
Reference	Adams and Brown (1989)	Cherel and Ridoux (1992)	Bost et al. (2002)	Moore et al. (1998)	Hindell (1988)	Olsson and North (1997)	This study

^aNumber of fish only

^bMisidentified as *Protomyctophum normani*

demonstrates the importance of *Protomyctophum choriodon* as a key link between zooplankton and top predators in the pelagic ecosystem and food web of the Southwest Atlantic.

Stable isotopes and king-penguin feeding ecology

Stable-nitrogen and stable-carbon isotope ratios were strongly correlated in food samples; they were less, but still significantly, correlated in plasma, and the correlation was not significant for blood cells (Fig. 3). Hobson et al. (2000) suggested that decoupling of the carbon and nitrogen isotope correlation in consumer proteinaceous tissues could result from carbon and nitrogen sources to proteins differing in their metabolic pathways. In this case, it is possible that the long-term dietary transfer (as indicated by the cellular blood fraction) of carbon and nitrogen to blood cells differed whereas those for more recent diets (as indicated by plasma) were similar or identical. Should lipid-derived carbon from diet or body stores be mobilized and contribute to blood cellular composition while nitrogen sources are derived from dietary protein, such decoupling of carbon and nitrogen isotope signatures could take place. This explanation gains some credibility from the fact that penguins fasted during the incubation period, a time when lipid stores were likely mobilized to the body carbon pool and can be used for protein synthesis. Clearly, more information is needed about the importance of carbon of lipid origin in biochemical pathways of amino-acid synthesis and hence protein in seabirds (Thompson et al. 2000).

Variance in both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values (higher in food, medium in plasma, lowest in blood cells) is likely to result from different temporal dietary integration among food and tissues. Experimental evidence indicates that the half-life for dietary-derived ^{13}C and ^{15}N in

plasma is about 3–4 days, while it is much longer, about 1 month, in blood cells (Hobson and Clark 1993; Hilderbrand et al. 1996). Consequently, integration over time increases greatly from food to plasma (7–10 days) and blood cells (2 months). Concerning penguin biology, food samples represented the last meal only, while plasma proteins integrated meals ingested during the whole foraging trip (about 1 week in brooding king penguins; Weimerskirch et al. 1992), and proteins of blood cells integrated food ingested over the last part of the incubation period (together with fasting) and the beginning of the chick-rearing period. Thus, $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values in blood cells represent mean values over many meals, which dampen differences observed between individual meals and in tissues with very high protein turnover rates, such as blood plasma. Conversely, the high consistency in prey type among dietary samples, together with the reduced variance in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values in blood fractions, indicate king penguins also fed on myctophid fish on their last foraging trip and during the weeks preceding blood sampling. This is in agreement with data obtained with the use of the fatty acid-signature technique, indicating that adult king penguins are myctophid eaters both when they feed for themselves and for their chicks in summer (Raclot et al. 1998).

Stable-nitrogen isotope ratios of blood fractions showed enrichment relative to food amounting to 1.3‰ (Table 4). This diet-tissue fractionation value is close to those found in captive penguins (Y. Cherel, K.A. Hobson, unpublished data), and it is lower than in other studies on captive birds (2.2–3.0‰) (Hobson and Clark 1992; Haramis et al. 2001). By contrast, lower $\delta^{13}\text{C}$ values in plasma than in food (Table 4) did not match with previous results showing almost no changes or positive increases in $\delta^{13}\text{C}$ values between the diet of birds, including penguins, and their blood (Hobson and

Clark 1992, 1993; Haramis et al. 2001; Y. Cherel, K.A. Hobson, unpublished data). There are two plausible explanations for these discrepancies, one related to metabolism and the other to feeding ecology. As noted, if stored or dietary lipids were incorporated significantly into protein synthesis in penguins, then their blood protein $\delta^{13}\text{C}$ values would be more negative than if they were derived exclusively from proteins. Such an effect would result in lower and possibly negative fractionation factors between diet and tissue $\delta^{13}\text{C}$ values. A more parsimonious explanation, however, is that adult king penguins fed for themselves on different prey and/or in isotopically different areas than when they fed for their chicks. Given that Antarctic plankton food bases tend to be depleted in ^{13}C to those in lower-latitude waters (Goericke and Fry 1994), and that king penguins always prey on myctophid fish in summer (see above), the likely explanation is that adult birds fed for themselves on myctophids in more southern (isotopically depleted foodweb) waters in the middle of their trips, and that they fed for their chicks on their way back to the colony, including slope waters off the Patagonian shelf where *Protomyctophum choriodon* is known to be abundant (Oven et al. 1990). Such different feeding areas were previously suspected for king penguins at the Crozet Islands in winter, when adult birds forage up to the pack ice, but feed their offspring with prey taken in the vicinity of the islands (see Cherel et al. 1996 for discussion). This strategy is probably common in birds performing long trips during the chick-rearing period, and the stable-isotope technique has the potential to give new insights on the foraging location and trophic levels of these adult birds when they are far away from their breeding grounds and build up energy reserves.

Acknowledgements Logistical and financial support was partly provided by Falklands Conservation. We are grateful to Jenny and George Smith, and to Sasha Arkhipkin and people from the Fisheries Department for their generous hospitality in the field and at Stanley, respectively. Patricia Healy performed preparations of samples for stable isotope analyses which were conducted by David Harris at the University of California (Davis).

References

- 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
- Adams NJ, Klages NT (1987) Seasonal variation in the diet of the king penguin (*Aptenodytes patagonicus*) at sub-Antarctic Marion Island. *J Zool Lond* 212:303–324
- Bingham M (1998) The distribution, abundance and population trends of gentoo, rockhopper and king penguins in the Falkland Islands. *Oryx* 32:223–232
- Bost CA, Zorn T, Le Maho Y, Duhamel G (2002) Feeding of diving predators and diel vertical migration of prey: king penguins' diet versus trawl sampling at Kerguelen Islands. *Mar Ecol Prog Ser* 227:51–61
- 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
- Cherel Y, Weimerskirch H (1999) Spawning cycle of onychoteuthid squids in the southern Indian Ocean: new information from seabird predators. *Mar Ecol Prog Ser* 188:93–104
- Cherel Y, Verdon C, Ridoux V (1993) Seasonal importance of oceanic myctophids in king penguin diet at Crozet Islands. *Polar Biol* 13:355–357
- Cherel Y, Ridoux V, Rodhouse PG (1996) Fish and squid in the diet of king penguin chicks, *Aptenodytes patagonicus*, during winter at sub-Antarctic Crozet Islands. *Mar Biol* 126:559–570
- Clarke MR (1986) A handbook for the identification of cephalopod beaks. Clarendon Press, Oxford
- Derenne M, Jouventin P, Mougin JL (1979) Le chant du Manchot royal (*Aptenodytes patagonica*) et sa signification évolutive. *Gerfaut* 69:211–224
- Goericke R, Fry B (1994) Variations of marine plankton $\delta^{13}\text{C}$ with latitude, temperature, and dissolved CO_2 in the world ocean. *Global Biogeochem Cycles* 8:85–90
- Gonzalez AF, Rodhouse PG (1998) Fishery biology of the seven star flying squid *Martialia hyadesi* at South Georgia during winter. *Polar Biol* 19:231–236
- Guinet C, Cherel Y, Ridoux V, Jouventin P (1996) Consumption of marine resources by seabirds and seals in Crozet and Kerguelen waters: changes in relation to consumer biomass 1962–85. *Antarct Sci* 8:23–30
- Haramis GM, Jorde DG, Macko SA, Walker JL (2001) Stable-isotope analysis of canvasback winter diet in upper Chesapeake Bay. *Auk* 118:1008–1017
- Hilderbrand GV, Farley SD, Robbins CT, Hanley TA, Titus K, Servheen C (1996) Use of stable isotopes to determine diets of living and extinct bears. *Can J Zool* 74:2080–2088
- Hindell MA (1988) The diet of the king penguin *Aptenodytes patagonicus* at Macquarie Island. *Ibis* 130:193–203
- Hobson KA, Clark RG (1992) Assessing avian diets using stable isotopes. II. Factors influencing diet-tissue fractionation. *Condor* 94:189–197
- Hobson KA, Clark RG (1993) Turnover of ^{13}C in cellular and plasma fractions of blood: implications for nondestructive sampling in avian dietary studies. *Auk* 110:638–641
- Hobson KA, Piatt JF, Pitocchelli J (1994) Using stable isotopes to determine seabird trophic relationships. *J Anim Ecol* 63:786–798
- Hobson KA, McLellan BN, Woods JG (2000) Using stable-carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) isotopes to infer trophic relationships among black and grizzly bears in the upper Columbia River Basin, British Columbia. *Can J Zool* 78:1332–1339
- Hulley PA (1981) Results of the research cruises of FRV "Walther Herwig" to South America. LVIII. Family Myctophidae (Osteichthyes, Myctophiformes). *Arch Fischereiwiss* 31:1–300
- Hulley PA (1990) Family Myctophidae. In: Gon O, Heemstra PC (eds) Fishes of the Southern Ocean. JLB Smith Institute of Ichthyology, Grahamstown. pp 146–178
- Ivanovic ML, Brunetti NE (1994) Food and feeding of *Illex argentinus*. *Antarct Sci* 6:185–193
- Ivanovic ML, Brunetti NE, Elena B, Rossi GR (1998) A contribution to the biology of the ommastrephid squid *Martialia hyadesi* (Rochebrune and Mabille, 1889) from the South-West Atlantic. *S Afr J Mar Sci* 20:73–79
- Jackson GD (1995) The use of beaks as tools for biomass estimation in the deepwater squid *Moroteuthis ingens* (Cephalopoda: Onychoteuthidae) in New Zealand waters. *Polar Biol* 15:9–14
- Jackson GD, George MJA, Buxton NG (1998a) Distribution and abundance of the squid *Moroteuthis ingens* (Cephalopoda: Onychoteuthidae) in the Falkland Islands region of the South Atlantic. *Polar Biol* 20:161–169
- Jackson GD, McKinnon JF, Lallas C, Ardern R, Buxton NG (1998b) Food spectrum of the deepwater squid *Moroteuthis ingens* (Cephalopoda: Onychoteuthidae) in New Zealand waters. *Polar Biol* 20:56–65
- Jackson GD, Buxton NG, George MJA (2000) Diet of the southern opah *Lampris immaculatus* on the Patagonian Shelf; the sig-

- nificance of the squid *Moroteuthis ingens* and anthropogenic plastic. *Mar Ecol Prog Ser* 206:261–271
- Kelly JF (2000) Stable isotopes of carbon and nitrogen in the study of avian and mammalian trophic ecology. *Can J Zool* 78:1–27
- Klages NTW, Pemberton D, Gales RP (1990) The diets of king and gentoo penguins at Heard Island. *Aust Wildl Res* 17:53–60
- Konstantinova MP, Remeslo AV, Fedulov PP (1994) The distribution of myctophids (Myctophidae) in the Southwest Atlantic in relation to water structure and dynamics. *J Ichthyol* 34:151–160
- Moore GJ, Robertson G, Wienecke B (1998) Food requirements of breeding king penguins at Heard Island and potential overlap with commercial fisheries. *Polar Biol* 20:293–302
- Olsson O, North AW (1997) Diet of the king penguin *Aptenodytes patagonicus* during three summers at South Georgia. *Ibis* 139:504–512
- Oven LS, Konstantinova MP, Shevchenko NF (1990) Aspects of reproduction and feeding of myctophids (Myctophidae) in the Southwest Atlantic. *J Ichthyol* 30:115–127
- Peterson RG, Whitworth T (1989) The Subantarctic and Polar Fronts in relation to deep water masses through the Southwestern Atlantic. *J Geophys Res* 94:10817–10838
- Phillips KL, Jackson GD, Nichols PD (2001) Predation on myctophids by the squid *Moroteuthis ingens* around Macquarie and Heard Islands: stomach contents and fatty acid analyses. *Mar Ecol Prog Ser* 215:179–189
- Piatkowski U, Pütz K, Heinemann H (2001) Cephalopod prey of king penguins (*Aptenodytes patagonicus*) breeding at Volunteer Beach, Falkland Islands, during austral winter 1996. *Fish Res* 52:79–90
- Pütz K, Ingham RJ, Smith JG, Croxall JP (2001) Population trends, breeding success and diet composition of gentoo *Pygoscelis papua*, magellanic *Spheniscus magellanicus* and rockhopper *Eudyptes chrysocome* penguins in the Falkland Islands. *Polar Biol* 24:793–807
- Raclot T, Groscolas R, Cherel Y (1998) Fatty acid evidence for the importance of myctophid fishes in the diet of king penguins, *Aptenodytes patagonicus*. *Mar Biol* 132:523–533
- Reid K (1996) A guide to the use of otoliths in the study of predators at South Georgia. British Antarctic Survey, Cambridge
- Reid K, Arnould JPY (1996) The diet of Antarctic fur seals *Arctocephalus gazella* during the breeding season at South Georgia. *Polar Biol* 16:105–114
- Rodhouse PG (1997) Large and meso-scale distribution of the ommastrephid squid *Martialia hyadesi* in the Southern Ocean: a synthesis of information relevant to fishery forecasting and management. *Korean J Polar Res* 8:145–154
- Rodhouse PG, Yeatman J (1990) Redescription of *Martialia hyadesi* Rochebrune and Mabile, 1889 (Mollusca: Cephalopoda) from the Southern Ocean. *Bull Br Nat Hist Zool* 56:135–143
- Rodhouse PG, Prince PA, Clarke MR, Murray AWA (1990) Cephalopod prey of the grey-headed albatross *Diomedea chrysostoma*. *Mar Biol* 104:353–362
- Rodhouse PG, Symon C, Hatfield EMC (1992a) Early life cycle of cephalopods in relation to the major oceanographic features of the southwest Atlantic Ocean. *Mar Ecol Prog Ser* 89:183–195
- Rodhouse PG, White MG, Jones MRR (1992b) Trophic relations of the cephalopod *Martialia hyadesi* (Teuthoidea: Ommastrephidae) at the Antarctic Polar Front, Scotia Sea. *Mar Biol* 114:415–421
- Santos RA dos, Haimovici M (2000) The argentine short-finned *Illex argentinus* in the food webs of southern Brazil. *Sarsia* 85:49–60
- Thompson DR, Phillips RA, Stewart FM, Waldron S (2000) Low $\delta^{13}\text{C}$ signatures in pelagic seabirds: lipid ingestion as a potential source of ^{13}C -depleted carbon in the Procellariiformes. *Mar Ecol Prog Ser* 208:265–271
- Thompson KR (1993) Variation in magellanic penguin *Spheniscus magellanicus* diet in the Falkland Islands. *Mar Ornithol* 21:57–67
- Thompson KR (1994) Predation on *Gonatus antarcticus* by Falkland Islands seabirds. *Antarct Sci* 6:269–274
- Weimerskirch H, Stahl JC, Jouventin P (1992) The breeding biology and population dynamics of king penguins *Aptenodytes patagonica* on the Crozet Islands. *Ibis* 134:107–117
- Wilkinson L (1999) SYSTAT 9 for Windows. SPSS, Chicago
- Williams R, McEldowney A (1990) A guide to the fish otoliths from waters 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* 55:9–12
- Woehler EJ (1993) The distribution and abundance of Antarctic and subantarctic penguins. Scientific Committee on Antarctic Research, Cambridge
- Xavier JC, Rodhouse PG, Trathan PN, Wood AG (1999) A Geographical Information System (GIS) atlas of cephalopod distribution in the Southern Ocean. *Antarct Sci* 11:61–62