Marine Biology (1998) 130: 335–344

Y. Cherel · G. L. Kooyman

Food of emperor penguins (*Aptenodytes forsteri*) in the western Ross Sea, Antarctica

Received: 20 May 1997 / Accepted: 8 October 1997

Abstract The diet of the emperor penguin *Aptenodytes forsteri* in the western Ross Sea during spring was investigated by analysis of stomach contents sampled at three different localities. At Cape Washington, emperor penguins feeding chicks consistently preyed on fishes (89 to 95% by mass) and crustaceans (5 to 11%) over the four spring seasons examined. By far the commonest prey was the Antarctic silverfish *Pleuragramma antarcticum* (89% of the fish prey); the remainder of fish prey were mainly unidentified juveniles of different species of channichthyid fishes. Three species dominated the crustacean part of the diet, i.e. the gammarid amphipods *Abyssorchomene rossi/plebs* (30% of the crustacean prey) and *Eusirus microps* (22%), together with the euphausiid *Euphausia crystallorophias* (24%). At Coulman Island and Cape Roget, fishes, mainly *P. antarcticum*, formed the bulk of the food (88 and 93% by mass, respectively), crustaceans were minor prey (2.5 and 0.4%), and the squid *Psychroteuthis glacialis* accounted for a small but significant part of the food (3.5 and 0.8%). This study emphasizes the importance of the small, shoaling pelagic fish *Pleuragramma antarcticum* as a key link between zooplankton and top predators, including seabirds, in the food web and marine ecosystem of the Ross Sea.

Introduction

The emperor penguin *Aptenodytes forsteri* is the most southerly penguin species. The total population of about 200 000 breeding pairs is distributed in 42 colonies along the coast of the Antarctic continent (Woehler 1993). Six colonies are located in the western Ross Sea (Kooyman 1993). Of these, the smallest is Cape Crozier (a few hundred pairs); the largest – Cape Washington and Coulman Island (>20 000 pairs) – are also the two largest colonies in the world (Kooyman and Mullins 1990; Kooyman 1993). In the western Ross Sea, there are a minimum of 60 000 pairs of this species (Kooyman and Mullins 1990).

Birds of the genus *Aptenodytes* are the heaviest penguins and the deepest divers among seabirds (Kooyman et al. 1992; Kooyman and Kooyman 1995). The emperor penguin reaches depths of 400 to 500 m (Ancel et al. 1992; Kooyman and Kooyman 1995; Robertson 1995; Kirkwood and Robertson 1997). Their diving capabilities, therefore, allow emperor penguins to forage in the whole water column over the Antarctic shelf.

Previous dietary studies at five colonies located outside the Ross Sea indicated that emperor penguins nurturing chicks feed on fishes, squid and crustaceans. Fishes, mainly the Antarctic silverfish *Pleuragramma antarcticum*, is always a main component of the diet; this species forms the bulk of the food by mass in Amanda Bay (Gales et al. 1990) and probably also in Adélie Land (small "nototheniids": Offredo and Ridoux 1986). Unlike fishes, the dietary importance of cephalopods and crustaceans varies according to locality. Squid, mainly *Psychroteuthis glacialis* and *Alluroteuthis antarcticus*, dominate the diet at Taylor and Auster glaciers (Robertson et al. 1994), while the Antarctic krill *Euphausia superba* is the main prey at Drescher Inlet (Klages 1989).

The emperor penguin is an important top predator in the marine environment of Antarctica. For example, it was recently estimated that each pair of penguins consumes about one metric tonne of food during the chick-rearing period (Robertson and Newgrain 1996). Surprisingly, however, little is known about the prey of this species in the Ross Sea, where at least 30% of the world's population breeds. Anecdotal dietary data include the occurrence of squid beaks in the stomachs of dead chicks at Cape Crozier (Kooyman et al. 1971), and

Communicated by S.A. Poulet, Roscoff

Y. Cherel (✉)
Centre d'Etudes Biologiques de Chizé,
UPR 4701 du Centre National de la Recherche Scientifique,
F-79360 Villiers-en-Bois, France

G.L. Kooyman
Center for Marine Biotechnology and Biomedicine,
Scripps Institution of Oceanography,
University of California, San Diego,
California 92093-0204, USA

adult emperor penguins preying on the fish *Pagothenia borchgrevinki* in McMurdo Sound (Kooyman et al. 1989). The main goal of this study, therefore, was to investigate the food of the emperor penguin in the Ross Sea. Food samples were collected over four spring seasons at Cape Washington and during one season at two other localities, Coulman Island and Cape Roget, thus, allowing a comparison between large breeding colonies.

Materials and methods

Fieldwork was carried out at Cape Washington (165°22′E; 74°39′S) in November/early December 1986, 1989, 1990 and 1992, and at Coulman Island (169°38′E; 73°20′S) and Cape Roget (170°31′E; 71°59′S) in late October/November 1993. Samples were collected from *Aptenodytes forsteri* by the stomach-pumping method of Wilson (1984) using warm water, or in the case of Coulman Island and Cape Roget by the collection of frozen-vomit samples. To minimize bird disturbance, penguins were flushed only one time and, consequently, only incomplete stomach contents were recovered. Food samples were then drained to remove excess water, and stored at −20 °C until analysis.

In the laboratory, samples were thawed, drained a second time, and placed in a large flat-bottomed tray. Food was analysed as described by Cherel and Ridoux (1992). Briefly, items that accumulate over time (stones, squid beaks) were sorted first. Fresh fish, squid and crustacean components were thereafter weighed. Identification of fishes and squids relied almost totally on the examination of otoliths, mandibles, vertebrae, opercular bones (Iwami 1985; Hecht and Hecht 1987; Williams and McEldowney 1990), and of upper and lower beaks (Clarke 1986), respectively, because the digested condition of the samples prevented the use of any external features. Fish numbers were estimated either from eye-lens or mandible counts. Only uneroded otoliths and mandibles were measured. Fish lengths and masses were calculated using previously determined regressions (Hecht and Hecht 1987; Williams and McEldowney 1990) or unpublished data (R. Williams personal communication). The length of unidentified channichthyid fishes was estimated using mandible length (MaL) and assuming that lower jaws account for 18% of fish standard length (SL), as calculated from drawings (Gon and Heemstra 1990) of channichthyids living in the Ross Sea. Lower rostral length (LRL) of the squid *Psychroteuthis glacialis* was measured, and dorsal mantle length (ML) and body mass were estimated using the equations in Lu and Williams (1994).

Crustaceans were identified from their external features using keys in Baker et al. (1990), Ledoyer (1990) and Bowman (1973) for euphausiids, mysids and hyperiid amphipods, respectively. The total lengths (TL) of undigested crustaceans were measured following Ridoux (1994).

Data were compared for statistically significant differences using the Peritz' *F*-test. Values in the text are expressed as means ± SE unless otherwise stated.

Results

General diet composition

Fishes contributed 89 to 95% by mass of the diet of *Apteno-dytes forsteri* at Cape Washington during the 4 yr study (Table 1). Crustaceans ranked second (5 to 11% by mass), and no fresh squid was found. No significant interannual variations were detected. A comparison of percentages by mass and number for both unpooled and pooled samples (Table 1, Fig. 1) clearly shows that fishes were more important by mass than by number (92 vs 47%); the opposite trend was true for crustaceans (8 vs 53%).

Fishes also comprised the bulk of the food of emperor penguins at Coulman Island and Cape Roget (Table 1). Two differences emerged, however, from the comparison of the diet at these two localities with that at Cape Washington. First, crustaceans accounted for lower percentages both by mass and by number at Coulman Island and Cape Roget. Second, squid were a small but significant part of the food at the latter two locations, while no fresh remains of squid occurred in the Cape Washington samples (Table 1, Fig. 1).

Fishes

Ten fish taxa were identified in the samples from Cape Washington (Table 2). Both the frequency of occurrence and percentage by number clearly indicated that the nototheniid *Pleuragramma antarcticum* together with unidentified channichthyids comprised most of the fish diet (99% by number). *P. antarcticum* alone occurred in 95% of the samples, and accounted for 89% by fish number (Table 2) and for 38% of the total number of

Table 1 *Aptenodytes forsteri*. Composition (means ± SE) by wet mass of general prey classes and numbers of prey items in diet of emperor penguins in western Ross Sea. Values within same vertical column *not* sharing common superscript letter are significantly different ($P < 0.05$) (*nd* no data)

Location, Year	(*n*)	Percentage by mass of:			Percentage by number of:		
		Fishes	Squid	Crustaceans	Fishes	Squid	Crustaceans
Cape Washington							
1986	(14)	94.9 ± 1.5[a]	0	5.1 ± 1.5[a]	nd	nd	nd
1989	(9)	91.0 ± 2.6[a]	0	9.0 ± 2.6[a]	nd	nd	nd
1990	(7)	93.9 ± 1.1[a]	0	6.1 ± 1.1[a]	nd	nd	nd
1992	(10)	88.6 ± 2.6[a]	0	11.4 ± 2.6[a]	38.2 ± 6.8[a]	0	61.8 ± 6.8[a]
Coulman Island							
1993	(7)	88.0 ± 9.1[a]	11.6 ± 9.2[b]	0.4 ± 0.2[b]	94.0 ± 2.3[b]	3.5 ± 2.6[b]	2.5 ± 0.9[b]
Cape Roget							
1993	(4)	93.3 ± 2.7[a]	6.6 ± 2.7[b]	0.1 ± 0.01[b]	98.9 ± 0.5[b]	0.8 ± 0.2[b]	0.4 ± 0.3[b]

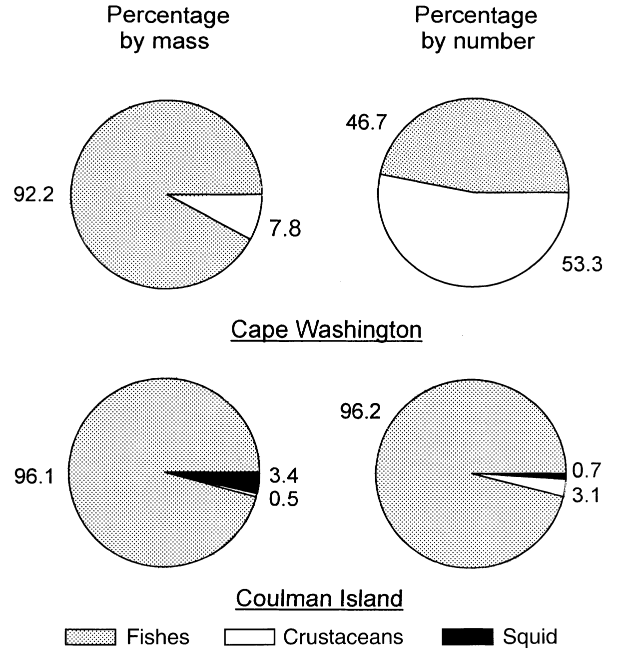

Fig. 1 *Aptenodytes forsteri*. Percentages by wet mass and numbers of broad prey classes in pooled samples collected at Cape Washington in 1992 (n = 10) and at Coulman Island in 1993 (n = 7)

prey at Cape Washington. *P. antarcticum* was also by far the major penguin food at Coulman Island and Cape Roget. It was found in all the samples and constituted 97% of the fish diet. Three size classes of *P. antarcticum* were revealed by MaL measurements (Fig. 2). A discrete mode in MaL occurred at 4 to 5 mm (SL = 28 mm; mass = 0.11 g). This mode was underestimated because it was very difficult to sort such small mandibles from the well-digested food samples. The second and third modes were at 7 to 8 and 15 to 16 mm MaL (Fig. 2); these corresponded to 48 and 104 mm SL, and body masses of 0.7 and 7.7 g, respectively. *P. antarcticum* eaten by emperor penguins reached a maximum of 144 mm SL (mass = 22.0 g).

Only a few identifiable otoliths of channichthyid fishes were found in the samples. They allowed the determination of individuals of large size from five species (Table 2), including one specimen of *Dacodraco hunteri* (otolith length = 1.74 mm; SL = 173 mm) in a regurgitation from Coulman Island. The use of jaws was the only way to count channichthyid fishes. Numerical distributions of MaL and SL showed that most of these fishes were small, with a main mode at 12 to 15 mm MaL. The latter corresponds to a mean SL of 75 mm (Fig. 3). MaL and SL ranged from 8.9 to 74.2 mm, and from 50 to 412 mm, respectively. We were unable to identify channichthyid species from the morphology of jaws only. Distinctive features of opercular bones (Iwami 1985) and the presence of an antrorse rostral spine at the tip of the snout (Gon and Heemstra 1990), however, indicated that two species formed a significant part of the small channichthyids: *Chaenodraco wilsoni* and *Pagetopsis* sp.

Squid

All but two of the cephalopods identified were *Psychroteuthis glacialis*. The two other species were *Gonatus antarcticus* and *Alluroteuthis antarcticus*, with only one eroded beak for each species. Both the latter were found

Table 2 *Aptenodytes forsteri*. Frequency of occurrence, numbers and length of fishes in diet of emperor penguins at Cape Washington, Ross Sea, Antarctica. Values are means ± SD

Prey item	Occurrence		Numbers		Total/standard length	
	(n)[b]	%	(n)[c]	%	(n)[d]	mm
Nototheniidae						
Pagothenia borchgrevinki	(2)	4.9	(11)	0.3	(4)	143 ± 54
Pleuragramma antarcticum	(39)	95.1	(3875)	88.6	(429)	75 ± 32
Trematomus lepidorhinus	(1)	2.4	(1)	< 0.1	(1)	180
T. newnesi	(3)	7.3	(7)	0.2	(4)	184 ± 17
Bathydraconidae						
Gerlachea australis	(1)	2.4	(1)	< 0.1	(1)	201
Channichthyidae						
Unidentified Channichthyidae[a]	(26)	63.4	(468)	10.7	(205)	~122 ± 79
Chaenodraco wilsoni	(1)	2.4	(1)	< 0.1	(1)	275
Chionodraco hamatus	(2)	4.9	(2)	< 0.1	(2)	297–336
Neopagetopsis ionah	(2)	4.9	(2)	< 0.1	(2)	402–422
Pagetopsis sp.	(3)	7.3	(3)	0.1	(3)	177 ± 10
Osteichthyes sp. A	(5)	12.2	(5)	0.1	(–)	nd
Total	(–)	–	(4376)	100.0	(–)	–

[a] Mainly small individuals of several species including *Chaenodraco wilsoni* and *Pagetopsis* sp. (see "Results – Fishes")
[b] No. of penguin samples examined
[c] No. of individuals identified for each prey species
[d] No. of individuals measured for each prey species

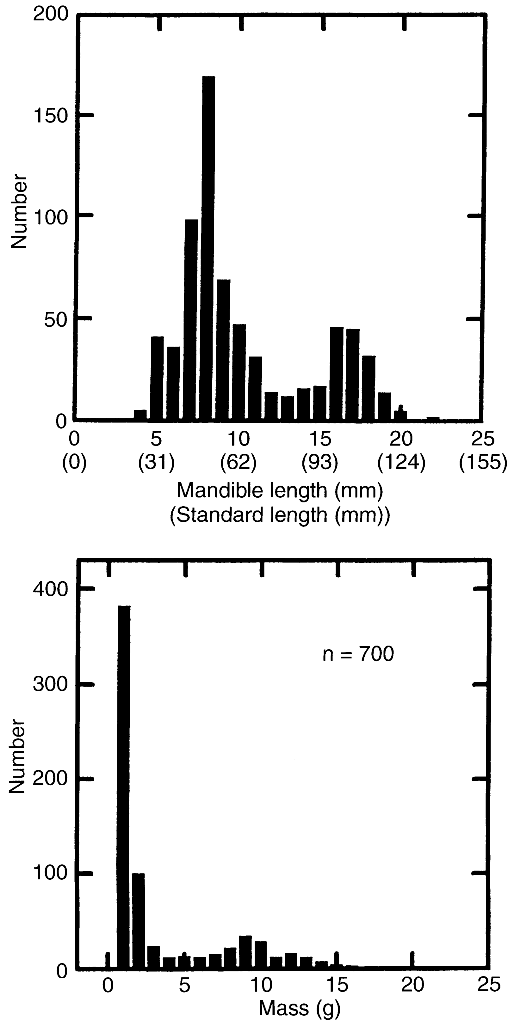

Fig. 2 *Aptenodytes forsteri.* Numerical distribution of mandible length, standard length and body mass of nototheniid fish *Pleuragramma antarcticum* in diet of emperor penguins from western Ross Sea (*n* number of measurements)

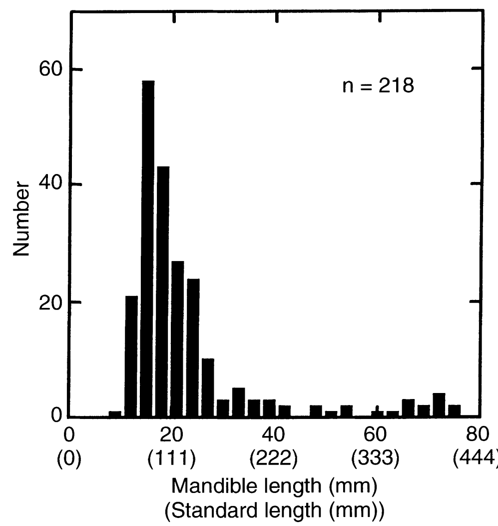

Fig. 3 *Aptenodytes forsteri.* Numerical distribution of mandible length and standard length of unidentified channichthyid fish in diet of emperor penguins from western Ross Sea

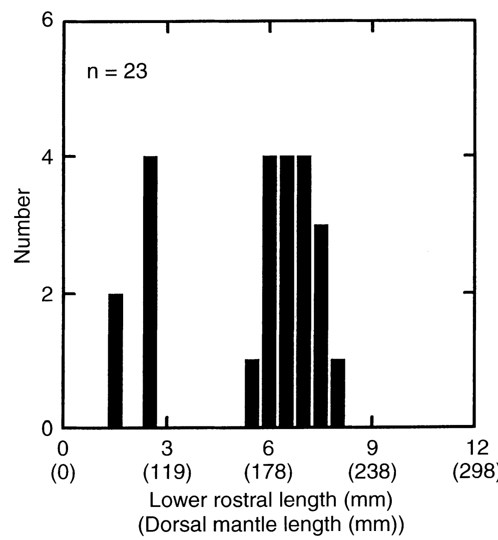

Fig. 4 *Aptenodytes forsteri.* Numerical distribution of lower rostral length and dorsal mantle length of cephalopod *Psychroteuthis glacialis* in diet of emperor penguins at Coulman Island and Cape Roget (combined data)

in samples from Cape Washington. No fresh squid remains occurred in food samples from that colony, but 30 accumulated lower beaks of *P. glacialis* were found in three stomach contents. All the beaks were very eroded, thus precluding LRL measurements and indicating that squids had been ingested several weeks/months ago (Pütz 1995).

Squids were more important prey at Coulman Island and Cape Roget than at Cape Washington. Fresh remains and/or hardly eroded accumulated beaks were found in all but one food sample. Of the 23 measured beaks of *Psychroteuthis glacialis* (8 fresh and 15 accumulated), two distinct size classes were apparent (Fig. 4), one with a mean LRL of 1.9 ± 0.4 mm (ML = 97 mm, mass = 18 g; $n = 6$), and the other with a mean LRL of 6.5 ± 0.7 mm (ML = 187 mm, mass = 127 g; $n = 17$). Minimum and maximum LRL values were 1.3 and 7.6 mm, corresponding to specimens with a ML of 84 and 209 mm and a mass of 9 and 163 g, respectively.

Crustaceans

Ten species of crustaceans were identified from the Cape Washington samples (Table 3). The most diverse and important taxon was Amphipoda, with four gammarid and two hyperiid species. Taken together, amphipods accounted for 75% of the total number of crustaceans, including four abundant species: *Abyssorchomene rossi/plebs* (30%), *Eusirus microps* (22%), *Epimeriella macronyx* (11%) and *Hyperia macrocephala* (9%) (Table 3). Careful examination of 68 specimens of the genus *Abyssorchomene* (Hurley 1965; Nagata 1986) in eight 1992 samples indicated that *A. rossi* predominated (84 vs 16%) in the diet over the closely related species *A. plebs*.

Table 3 *Aptenodytes forsteri*. Frequency of occurrence, numbers and length of crustaceans in diet of emperor penguins at Cape Washington, Ross Sea, Antarctica. Values are means ± SD (*n* as in footnotes to Table 2)

Prey item	Occurrence		Numbers		Total length	
	(*n*)	%	(*n*)	%	(*n*)	mm
Mysidacea						
Mysidae						
Antarctomysis ohlinii	(5)	12.2	(13)	0.2	(3)	47.0 ± 2.2
Amphipoda						
Epimeriidae						
Epimeriella macronyx	(37)	90.2	(675)	11.4	(17)	22.7 ± 4.1
Eusiridae						
Eusirus microps	(40)	97.6	(1324)	22.3	(30)	35.2 ± 6.4
Eusirus propeperdentatus	(29)	70.7	(119)	2.0	(1)	40.0
Lysianassidae						
Abyssorchomene rossi/plebs	(40)	97.6	(1801)	30.3	(128)	22.3 ± 5.6
Uristes gigas	(14)	34.1	(18)	0.2	(4)	23.3 ± 5.1
Hyperiidae						
Hyperia macrocephala	(23)	56.1	(516)	8.7	(72)	24.0 ± 3.4
Hyperiella macronyx	(5)	12.2	(15)	0.3	(2)	6.3–6.8
Euphausiacea						
Euphausiidae						
Euphausia superba	(4)	9.8	(48)	0.8	(0)	–
Euphausia crystallorophias	(31)	75.6	(1406)	23.7	(10)	25.4 ± 3.8
Unidentified *Euphausia*	(3)	7.3	(4)	0.1	(0)	–
Unidentified Crustacea	(1)	2.4	(1)	< 0.1	(0)	–
Total	(–)	–	(5940)	100.0	(-)	–

Most of the amphipods were >20 mm TL, the largest species being *Eusirus* spp. (Table 3, Fig. 5). The small species *Hyperiella macronyx* was secondarily ingested as a fish prey, some of the individuals being found in fish stomachs.

Euphausiacea was the second important crustacean taxon in the emperor penguin diet at Cape Washington (Table 3). *Euphausia crystallorophias* alone accounted for 24% of the total number of crustaceans, while the Antarctic krill *E. superba* was only a minor prey (< 1%). Finally, a few individuals of the mysid shrimp *Antarctomysis ohlinii* were also positively identified. It was not possible to measure their total length because they were always broken in several pieces and partially digested. However, nine specimens were sexed (4 males and 5 females), including three females carrying Larval Stages III (Crescenti et al. 1994) in their marsupium. Most specimens of *A. ohlinii* therefore were mature individuals, i.e. they probably had a TL of >45 mm (Siegel and Mühlenhardt-Siegel 1988).

Only a few crustaceans occurred in food samples collected at Coulman Island and Cape Roget. No hyperiids, no *Eusirus microps* and no *Euphausia superba* were found in these stomach contents.

Discussion

Stomach samples recovered from the emperor penguin *Aptenodytes forsteri* were highly digested, thus inducing some biases in analysis. The most important bias was probably an underestimation of the number of small fishes in the diet. In some cases, the only evidence of fishes was their flesh and eye lenses; species determination was possible only from a few recognisable lower jaws. In this study, such bias has induced an underestimation of the smallest cohorts of Antarctic silverfish, and probably of juvenile channichthyid fishes. On the other hand, an underestimation of crustaceans was unlikely to occur because exoskeletons, especially those of amphipods, resist digestion better than flesh and bones of small fishes. However, some crustaceans, such as the euphausiid *Euphausia crystallorophias*, were probably secondarily ingested by the fishes preyed upon by the emperor penguins.

Comparison with other studies

Fishes dominated the diet (>85% by mass) of emperor penguins, not only in the western Ross Sea, but also in Adélie Land and in Amanda Bay (Table 4). At other localities, fishes were also an important component of the diet, accounting for 27 to 55% of the food by mass (Table 4). The nototheniid *Pleuragramma antarcticum* is the main fish prey in the Ross Sea (present study), Amanda Bay (Gales et al. 1990) and the eastern Weddell Sea (Klages 1989), and probably in Adélie Land – most of the fish prey there being small unidentified "nototheniids" (Offredo and Ridoux 1986). Length at sexual maturity of the Antarctic silverfish is ~125 mm SL; it attains a maximum length of ~250 mm SL (Gon and Heemstra 1990). In the Ross Sea, emperor penguins mainly fed on three cohorts of juvenile fishes, with only

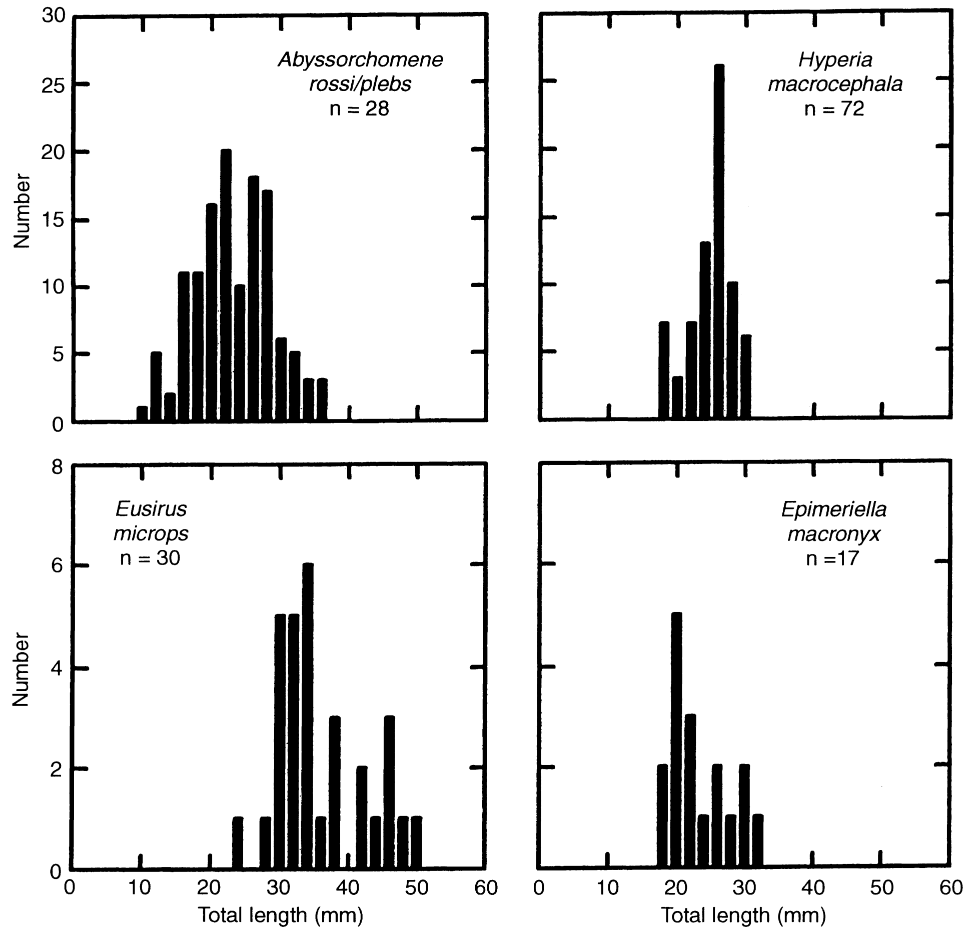

Fig. 5 *Aptenodytes forsteri.* Numerical distribution of total length of crustaceans in diet of emperor penguins from western Ross Sea

a few adults taken (Fig. 2). Juveniles dominated by number at other colonies investigated, but birds from the eastern Weddell Sea (Klages 1989) and the Mawson Coast (Robertson et al. 1994) also preyed on adult fishes (167 and 150 mm SL, respectively).

Pleuragramma antarcticum also predominated in the diet of emperor penguins from the Mawson Coast in winter 1993 (Kirkwood and Robertson 1997), but birds mainly ate the larger nototheniid *Trematomus eulepidotus* during the spring 1988 (Robertson et al. 1994). Fishes other than the Antarctic silverfish were generally found in small numbers in the food of emperor penguins, the commonest being nototheniids (*Pagothenia borchgrevinki* and *Trematomus* spp.) and channichthyids (*Chionodraco* spp. and *Pagetopsis* spp.), including a few specimens of large size (length >400 mm SL) (Green 1986; Offredo and Ridoux 1986; Klages 1989; Gales et al. 1990; Williams and McEldowney 1990; Robertson et al. 1994; Pütz 1995; present study). One distinctive otolith of *Dacodraco hunteri* occurred in a food sample from Coulman Island. To our knowledge, this is the first positive identification of this rare channichthyid fish in the Ross Sea, where its presence was previously suspected but not proved (Gon and Heemstra 1990).

Squid generally accounts for a low percentage by mass (< 12%) in the diet of emperor penguins feeding chicks, except at Taylor and Auster glaciers where squid forms the major component of the diet (45 to 69%, Table 4). Cephalopods, however, account for >99% by mass of the food of birds caught at sea in autumn and winter (Ainley et al. 1991), suggesting that they may be major prey of adult emperor penguins outside the chick-rearing period. Our finding that *Psychroteuthis glacialis* is by far the commonest cephalopod eaten agrees with previous works on both fresh and accumulated squid remains in the emperor penguin food (41 to 99% by number: Offredo et al. 1985; Klages 1989; Gales et al. 1990; Ainley et al. 1991; Piatkowski and Pütz 1994; Robertson et al. 1994). Penguins generally prey upon both juvenile and adult *P. glacialis*, as indicated by the bimodal distribution of beak sizes (Offredo et al. 1985; Gales et al. 1990; Piatkowski and Pütz 1994), except in the eastern Weddell Sea and Mawson Coast where they only feed on juveniles (Klages 1989; Robertson et al. 1994).

The only species of crustaceans previously reported to account for a significant part of the diet (25 to 70% by mass) of the emperor penguin is the Antarctic krill *Euphausia superba* at Auster Glacier in winter and at the Drescher Inlet (Table 4). In the Ross Sea, *E. superba* is rare, and it is replaced by the dominant neritic species *E. crystallorophias* (Smith and Schnack-Schiel 1990). Accordingly, *E. superba* and *E. crystallorophias* amount to < 1 and 24% of the number of crustaceans at Cape

Table 4 *Aptenodytes forsteri*. Composition of diet of emperor penguins at various antarctic breeding colonies (? = some crustaceans in diet but not quantified)

Locality	Season	Frequency of occurrence (%)			Number (%)			Mass (%)			Source
		Fishes	Squid	Crustaceans	Fishes	Squid	Crustaceans	Fishes	Squid	Crustaceans	
Dronning Maud Land											
Drescher Inlet	spring	73	80	93	17	3	80	38	10	52	Klages (1989)
Drescher Inlet	summer	93	0	93	17	0	83	~75	0	~25	Pütz (1995)
Princess Elizabeth Land											
Taylor Glacier	winter/spring	29	55	87	27	73	?	31	69	?	Robertson et al. (1994)
Auster Glacier	winter/spring	74	58	82	52	48	?	55	45	?	Robertson et al. (1994)
Auster Glacier	winter	100	41	88	4	< 1	96	27	3	70	Kirkwood and Robertson (1997)
Wilkes Land and Adélie Land											
Amanda Bay	winter/spring	86	36	> 41	83	4	13	97	3	< 1	Gales et al. (1990)
Pointe Géologie	spring	100	93	> 82	65	1	34	95	3	2	Offredo and Ridoux (1986)
Ross Sea											
Cape Roget	spring	100	100	25	99	1	< 1	93	7	< 1	Present study
Coulman Island	spring	100	86	86	94	3	3	88	12	< 1	Present study
Cape Washington	spring	100	0	100	38	0	62	89–95	0	5–11	Present study

Washington, respectively (Table 3). *E. crystallorophias* nevertheless is a minor component of the diet in the western Ross Sea, a few specimens appearing in food samples from Coulman Island and Cape Roget.

The most unusual prey of emperor penguins identified in this study were amphipods at Cape Washington. They were generally barely digested and accounted for almost all of the crustacean portion of the diet by mass (5 to 11%) and number (75%) (Table 1). To date, this feature appears unique and characteristic of the emperor penguin diet at Cape Washington, because (1) they consistently occurred in the food samples over the 4 yr study and (2) they were rare or absent from the penguin diet at other localities (Green 1986; Offredo and Ridoux 1986; Klages 1989; Gales et al. 1990; Robertson et al. 1994; Pütz 1995; present study). The species found in the diet at Cape Washington were previously identified as prey of emperor penguins but in small numbers (Offredo and Ridoux 1986); the only amphipod found in substantial amounts in previous works was the hyperiid *Cyllopus lucasii* (Pütz 1995).

Prey biology and foraging ecology

The Antarctic silverfish *Pleuragramma antarcticum* is a small, shoaling fish living in Antarctic shelf areas (Gon and Heemstra 1990; Eastman 1993); *Euphausia superba* is an open-water euphausiid found in oceanic and slope regions (Lomakina 1966; Smith and Schnack-Schiel 1990); and the squid *Psychroteuthis glacialis* mainly inhabits the upper shelf break (Lu and Williams 1994). Emperor penguins feeding chicks prey on the Antarctic silverfish when breeding colonies are in the vicinity of extended neritic areas (Gales et al. 1990; present study). Satellite tracking has clearly shown that adult emperor penguins from Cape Washington remain within the Ross Sea while foraging for their chicks (Ancel et al. 1992). On the other hand, the presence of large numbers of *E. superba* and/or squid, together with *Pleuragramma antarcticum* in the diet, strongly suggests that emperor penguins feed in deeper waters where the Antarctic continental shelf is narrow (Offredo and Ridoux 1986; Klages 1989; Piatkowski and Pütz 1994; Robertson et al. 1994; Kirkwood and Robertson 1997).

The major prey of emperor penguins identified in this study is pelagic organisms, except for the epibenthic nototheniid *Trematomus lepidorhinus* (Eastman 1993). Some species are mainly pelagic, i.e. *Pleuragramma antarcticum* (Eastman 1993), juvenile channichthyids (Gon and Heemstra 1990), euphausiids, the mysid shrimp *Antarctomysis ohlinii* (Siegel and Mühlenhardt-Siegel 1988), and the amphipods *Eusirus properdentatus*, *Hyperia macrocephala* and *Hyperiella macronyx* (Bowman 1973; Andres 1979). Other prey may be found also near the bottom (benthopelagic species): channichthyid fishes (Gon and Heemstra 1990), *Trematomus newnesi* (Eastman 1993), the squid *Psychroteuthis glacialis* (Lu and Williams 1994; Piatkowski and Pütz 1994), and the amphipods *Epimeriella macronyx*, *Eusirus microps* and *Uristes gigas* (Andres 1979; C. De Broyer personal communication). Lastly, some prey species live in close association with the undersurface of sea ice such as the nototheniid *Pagothenia borchgrevinki* (Eastman 1993) and sometimes Antarctic euphausiids (O'Brien 1987). Note that the gammarids *Abyssorchomene rossi/plebs* live in the whole water column, but are mainly located both under the ice and near the bottom (Andres 1979; Kaufmann et al. 1995).

The predominance of pelagic species in food samples agrees well with the diving behavior of emperor penguins recently described in the Ross Sea (Kooyman and Kooyman 1995) and the Mawson coast (Robertson 1995; Kirkwood and Robertson 1997). The majority of dives are < 200 m, with many at 20 to 180 m (Kooyman and Kooyman 1995; Robertson 1995; Kirkwood and Robertson 1997). These dives occur in mid-water, where penguins probably feed on euphausiids and juvenile Antarctic silverfish, which both form dense swarms at these depths (Lomakina 1966; Gon and Heemstra 1990).

Our data suggest that during deep dives, emperor penguins in the Ross Sea target the mysid *Antarctomysis ohlinii* and the large fishes *Trematomus lepidorhinus*, *Gerlachea australis*, *Chaenodraco wilsoni*, *Dacodraco hunteri*, and adults and subadult *Pleuragramma antarcticum*, all consistently occurring in depths below 200 m (Siegel and Mühlenhardt-Siegel 1988; Gon and Heemstra 1990; Eastman 1993). Flat dive-record profiles at the maximum depth, the uniform depth of successive dives and bathymetry of the foraging area all suggest that some deep dives of emperor penguins extend to the bottom or near to it (Ancel et al. 1992; Kooyman and Kooyman 1995; Robertson 1995; Kirkwood and Robertson 1997). The presence of various benthopelagic species in the food of emperor penguins (see foregoing paragraphs) together with the almost total absence of truly benthic animals support the view of foraging throughout the water column but not in close association with the bottom.

Shallow dives (< 20 m) are very common in emperor penguins. They are interpreted as non-foraging dives, travelling dives, or part of the recovery from an oxygen debt (Kooyman and Kooyman 1995; Kirkwood and Robertson 1997). However, Robertson (1995) indicates that some emperor penguins performed many shallow dives of long duration consistent with foraging under the fast ice. The occurrence of the cryopelagic species *Pagothenia borchgrevinki* and of *Euphausia superba* and scavenger amphipods in food samples (Offredo and Ridoux 1986; Klages 1989; Pütz 1995; present study) supports the assumption that some shallow dives are probably feeding dives under the ice. Moreover, many surface or shallow-depth foraging seabirds in the Ross sea feed on *Pleuragramma antarcticum*, *Psychroteuthis glacialis* and the various crustaceans evident in the emperor penguin diet (Ainley et al. 1984; Mund and Miller 1995). Thus, there is no reason to believe that emperor penguins would not find prey at shallow depths as well.

A serious limitation in the dietary predictions based on food samples is that a foraging trip of emperor penguins lasts several days and even weeks, while the corresponding stomach content represents only the prey swallowed during its final stage (Kooyman and Kooyman 1995; Kirkwood and Robertson 1997). The diving patterns of birds from Coulman Island in spring 1993 clearly show that emperor penguins stopped very deep diving and performed continuous dives concentrated at midwater depths during the last 2 to 3 days of the foraging trip (Kooyman and Kooyman 1995). Accordingly, the pelagic fish *Pleuragramma antarcticum* formed the bulk of the food at that time (95% of the total number of items), the only identified deep-water prey being 13 specimens of the midwater mysid *Antarctomysis ohlinii* and one individual of the channichthyid *Dacodraco hunteri* (present study). In this context, the occurrence of large numbers of amphipods (genus *Abyssorchomene*) in the food of birds from Cape Washington suggests that at least some of the last foraging dives occur either in shallow water under the ice or in very deep water near the bottom. It is possible that there is a switch in foraging habitat between the mid-part of a foraging trip and the last day or two before returning to the colony.

Comparison with other predators in the Ross Sea

In the Ross Sea, Adélie penguins feed on the same community of prey as emperor penguins, including *Pleuragramma antarcticum*, small unidentified channichthyids, amphipods [mainly *Abyssorchomene* (= *Orchomenella*) *rossi/plebs*] and *Euphausia crystallorophias* (Emison 1968). However, emperor penguins feed more on fishes, while Adélie penguins feed more on krill (Emison 1968; Ainley et al. 1984; Van Heezik 1988), except in recent years, which have been marked by a dietary shift to *P. antarcticum* as the main prey (Ainley and Wilson personal communication). Any trophic segregation results from different feeding strategies. Adélie penguins are shallow divers, the bulk of foraging activity taking place at depths of < 30 m (Chappell et al. 1993; Watanuki et al. 1993), where dense and large concentrations of krill occur (Lomakina 1966; O'Brien 1987). Emperor penguins dive deeper where adult krill is less abundant and large fishes more available.

In the Ross Sea, *Euphausia crystallorophias* make up the bulk of food of other important air-breathing divers, i.e. the minke whale and the crabeater seal (Ainley and DeMaster 1990), while the deep-diving Weddell seal, like the emperor penguin, preys heavily on the Antarctic silverfish (Green and Burton 1987; Castellini et al. 1992). *Pleuragramma antarcticum* is also a main item in stomach contents of various surface-feeding seabirds, including the South polar skua, snow petrel and antarctic petrel (Ainley et al. 1984; Mund and Miller 1995). It is a major component of the diet of several squids (Lu and Williams 1994) and fishes such as channichthyids and the large nototheniid *Dissostichus mawsoni* (Takahashi and Nemoto 1984; Eastman 1985).

The Antarctic silverfish is the dominant fish in both the Ross and Weddell Seas, where it feeds on copepods and *Euphausia crystallorophias* (Gon and Heemstra 1990; Eastman 1993). *Pleuragramma antarcticum* therefore acts as a link between plankton and the community of top predators in the shelf waters surrounding the Antarctic continent, being especially important in the marine ecosystem and food web of large neritic areas such as Prydz Bay and the Ross and the Weddell Seas (Williams 1989; Ainley and DeMaster 1990).

Acknowledgements We are especially grateful to V. Ridoux and C. Trouvé for their help in food-sample analysis, to C. de Broyer for amphipod determination, and to R. Williams for giving us allometric equations for *P. antarcticum*. The authors thank D. Ainley for his helpful comments on the text. We had important assistance in the field by P. Ponganis, M. Horning, C. Kooyman, T. Kooyman, G. Robertson and R. Van Dam. A part of this study was performed in the Centre d'Ecologie et de Physiologie Energétiques at Strasbourg, France. This work was supported by National Science Foundation, Office of Polar Programs Grant 9219872.

References

Ainley DG, DeMaster DP (1990) The upper trophic levels in polar marine ecosystems. In: Smith WO (ed) Polar oceanography. Part B. Academic Press, San Diego, pp 599–630

Ainley DG, Fraser WR, Smith WO, Hopkins TL, Torres JJ (1991) The structure of upper level pelagic food webs in the Antarctic: effect of phytoplankton distribution. J mar Syst 2: 111–122

Ainley DG, O'Connor EF, Boekelheide RJ (1984) The marine ecology of birds in the Ross Sea, Antarctica. Orn Monogr 32: 1–97

Ancel A, Kooyman GL, Ponganis PJ, Gendner JP, Lignon J, Mestre X, Huin N, Thorson PH, Robisson P, Le Maho Y (1992) Foraging behaviour of emperor penguins as a resource detector in winter and summer. Nature, Lond 360: 336–338

Andres HG (1979) Gammaridea (Amphipoda, Crustacea) der Antarktisexpedition 1975/76. Auswertung der Dauerstation südlich von Elephant Island. Meeresforsch Rep mar Res 27 (Sonderbd): 88–102 (Ber dt wiss Kommn Meeresforsch)

Baker A de C, Boden BP, Brinton E (1990) A practical guide to the euphausiids of the world. Natural History Museum Publications, London

Bowman E (1973) Pelagic amphipods of the genus *Hyperia* and closely related genera (Hyperiidea: Hyperiidae). Smithson Contr Zool 136: 1–76

Castellini MA, Davis RW, Kooyman GL (1992) Annual cycles of diving behavior and ecology of the Weddell seal. Bull Scripps Instn Oceanogr (New Ser) 28: 1–54

Chappell MA, Shoemaker VH, Janes DN, Bucher TL, Maloney SK (1993) Diving behavior during foraging in breeding Adélie penguins. Ecology 74: 1204–1215

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

Clarke MR (1986) A handbook for the identification of cephalopod beaks. Clarendon Press, Oxford

Crescenti N, Costanzo G, Guglielmo L (1994) Developmental stages of *Antarctomysis ohlinii* Hansen, 1908 (Mysidacea) in Terra Nova Bay, Ross Sea, Antarctica. J Crustacean Biol 14: 383–395

Eastman JT (1985) *Pleuragramma antarcticum* (Pisces, Nototheniidae) as food for other fishes in McMurdo Sound, Antarctica. Polar Biol 4: 155–160

Eastman JT (1993) Antarctic fish biology. Evolution in a unique environment. Academic Press, San Diego

Emison WB (1968) Feeding preferences of the Adelie penguin at Cape Crozier, Ross Island. Antarct Res Ser 12: 191–212

Gales NJ, Klages NTW, Williams R, Woehler EJ (1990) The diet of the emperor penguin, *Aptenodytes forsteri*, in Amanda Bay, Princess Elizabeth Land, Antarctica. Antarctic Sci 2: 23–28

Gon O, Heemstra PC (1990) Fishes of the Southern Ocean. JLB Smith Institute of Ichthyology, Grahamstown

Green K (1986) Food of the emperor penguin *Aptenodytes forsteri* on the Antarctic fast ice edge in late winter and early spring. Polar Biol 6: 187–188

Green K, Burton HR (1987) Seasonal and geographical variation in the food of Weddell seals. *Leptonychotes weddellii*, in Antarctica. Aust Wildl Res 14: 475–489

Hecht T, Hecht A (1987) A guide to the otoliths of Southern Ocean fishes. S Afr J antarct Res 17: 1–87

Hurley DE (1965) A common but hitherto undescribed species of *Orchomenella* (Crustacea Amphipoda: family Lysianassidae) from the Ross Sea. Trans R Soc NZ Zool 6: 107–113

Iwami T (1985) Osteology and relationships of the family Channichthyidae. Mem natn Inst polar Res, Tokyo E 36: 1–69

Kaufmann RS, Smith KL Jr, Baldwin RJ, Glatts RC, Robison BH, Reisenbichler KR (1995) Effects of seasonal pack ice on the distribution of macrozooplankton and micronekton in the northwestern Weddell Sea. Mar Biol 124: 387–397

Kirkwood R, Robertson G (1997) The foraging ecology of female emperor penguins in winter. Ecol Monogr 67: 155–176

Klages N (1989) Food and feeding ecology of emperor penguins in the eastern Weddell Sea. Polar Biol 9: 385–390

Kooyman GL (1993) Breeding habitats of emperor penguins in the western Ross Sea. Antarctic Sci 5: 143–148

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: 143–463

Kooyman GL, Drabek CM, Elsner R, Campbell WB (1971) Diving behavior of the emperor penguin, *Aptenodytes forsteri*. Auk 88: 775–795

Kooyman GL, Kooyman TG (1995) Diving behavior of emperor penguins nurturing chicks at Coulman Island, Antarctica. Condor 97: 536–549

Kooyman GL, Mullins JL (1990) Ross Sea emperor penguin breeding populations estimated by aerial photography. In: Kerry KR, Hempel G (eds) Antarctic ecosystems. Ecological change and conservation. Springer Verlag, Berlin Heidelberg, pp 169–176

Kooyman GL, Ponganis PJ, Castellini MA, Ponganis E, Eckert S, Le Maho Y (1989) Physiology of diving in emperor penguins and Weddell seals. Antarctic J US 24: p. 204

Ledoyer M (1990) Mysidacea (Crustacea) de la Campagne "EPOS 3" en Mer de Weddell, Antarctique. Mésogée 50: 37–44

Lomakina NB (1966) The euphausiid fauna of the Antarctic and notal regions. In: Andriashev AP, Ushakov PV (eds) Biological reports of the soviet Antarctic expedition 1955–58. Israel Programme for Scientific Translations, Jerusalem, pp 260–342

Lu CC, Williams R (1994) Contribution to the biology of squid in the Prydz Bay region, Antarctica. Antarctic Sci 6: 223–229

Mund MJ, Miller GD (1995) Diet of the south polar skua *Catharacta maccormicki* at Cape Bird, Ross Island, Antarctica. Polar Biol 15: 453–455

Nagata K (1986) Amphipod crustaceans found near Syowa Station, Antarctica. Mem natn Inst polar Res, Tokyo (Spec Issue) 40: 249–258

O'Brien DP (1987) Direct observations of the behavior of *Euphausia superba* and *Euphausia crystallorophias* (Crustacea: Euphausiacea) under pack ice during the Antarctic spring of 1985. J Crustacean Biol 7: 437–448

Offredo C, Ridoux V (1986) The diet of emperor penguins *Aptenodytes forsteri* in Adelie land, Antarctica. Ibis 128: 409–413

Offredo C, Ridoux V, Clarke MR (1985) Cephalopods in the diets of Emperor and Adelie penguins in Adelie Land, Antarctica. Mar Biol 86: 199–202

Piatkowski U, Pütz K (1994) Squid diet of emperor penguins (*Aptenodytes forsteri*) in the eastern Weddell Sea, Antarctica during late summer. Antarctic Sci 6: 241–247

Pütz K (1995) The post-moult diet of emperor penguins (*Aptenodytes forsteri*) in the eastern Weddell Sea, Antarctica. Polar Biol 15: 457–463

Ridoux V (1994) The diets and dietary segregation of seabirds at the subantarctic Crozet Islands. Mar Orn 22: 1–192

Robertson GG (1995) The foraging ecology of emperor penguins (*Aptenodytes forsteri*) at two Mawson Coast colonies, Antarctica. ANARE Rep 138: 1–139

Robertson G, Newgrain K (1996) The food and energy intake rates of adult emperor penguins (*Aptenodytes forsteri*) rearing chicks. Antarctic Sci 8: 37–44

Robertson G, Williams R, Green K, Robertson L (1994) Diet composition of emperor penguin chicks *Aptenodytes forsteri* at two Mawson coast colonies, Antarctica. Ibis 136: 19–31

Siegel V, Mühlenhardt-Siegel U (1988) On the occurrence and biology of some Antarctic Mysidacea (Crustacea). Polar Biol 8: 181–190

Smith SL, Schnack-Schiel SB (1990) Polar zooplankton. In: Smith WO (ed) Polar oceanography, Part B. Academic Press, San Diego, pp 527–598

Takahashi M, Nemoto T (1984) The food of some Antarctic fish in the western Ross Sea in summer 1979. Polar Biol 3: 237–239

Van Heezik Y (1988) Diet of Adélie penguins during the incubation period at Cape Bird, Ross Island, Antarctica. Notornis 35: 23–26

Watanuki Y, Kato A, Mori Y, Naito Y (1993) Diving performance of Adélie penguins in relation to food availability in fast sea-ice areas: comparison between years. J Anim Ecol 62: 634–646

Williams R (1989) Australian research on Antarctic bird and seal diets. Sel scient Pap scient Comm Conserv antarct mar living Resour 1988(2): 231–249

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 Fld Ornithology 55: 109–112

Woehler EJ (1993) The distribution and abundance of antarctic and subantarctic penguins. Scientific Committe on Antarctic Research, Cambridge