POLISH POLAR RESEARCH
vol. 24, no. 2, pp. 133–142, 2003

Diet of the Adélie penguin during three consecutive chick rearing periods at Laurie Island

Marcela M. LIBERTELLI[1], Nestor CORIA[1] and Germán MARATEO[2]

[1] *Departamento de Ciencias Biológicas, Instituto Antártico Argentino, Cerrito 1248, (C1010AAZ) Buenos Aires, Argentina*
<aguara 35@hotmail.com>

[2] *División Zoología Vertebrados, Sección Ornitología, Museo de Ciencias Naturales, Paseo del Bosque s/n1, (1900) La Plata, Argentina*

ABSTRACT: The diet of the unsexed breeding Adélie penguin (*Pygoscelis adeliae* Hombron *et* Jacquinot, 1841) was investigated during three consecutive chick rearing periods, from 1996–97 to 1998–99, on Laurie Island, South Orkney Islands (60˚46'S, 44˚42'W), Antarctica. This analysis showed that during the whole sampling period, Antarctic krill (*Euphausia superba* Dana, 1852) represented the predominant prey in terms of frequency of occurrence, mass, and number. The hyperiid amphipod *Themisto gaudichaudii* (Guerin-Méneville, 1825) was present in small amounts. *Electrona antarctica* (Gunter, 1878), *Trematomus newnesi* (Boulenger, 1902) and larval stages of Nototheniidae constituted the bulk of the fish portion, particularly during the 1997/98 and 1998/99 breeding periods. This study is the first examination of the Adélie penguin diet at Laurie Island. It is important to recognize, however, the importance of knowing the sex of the penguins being sampled and that prey composition may vary during the breeding season and from one year to the next.

Key words: Antarctic, South Orkney Islands, Adélie penguin, diet.

Introduction

Penguins (Spheniscidae) are major consumers of Southern Ocean marine resources, mainly feeding on planktonic crustaceans, small fishes and squids (Croxall and Lishman 1987). Adélie penguins (*Pygoscelis adeliae* Hombron et Jacquinot, 1841) have circumpolar range, breeding from Cape Royds (77˚ S) in the Ross Sea, along the entire coast of the Antarctic continent, the west coast of Antarctic Peninsula, the islands of the Scotia Arc, and north to South Sandwich Islands and Bouvet Island (Williams 1995). This penguin is the most abundant of the pygoscelid penguins, with a total population estimated as at least 2.44 million breeding pairs (Woehler 1993) and 10 million immatures (Croxall 1984). Thus,

this penguin plays a major role in the food webs in the South of the Southern Ocean (Ainley *et al.* 1984; Trivelpiece *et al.* 1990).

Several studies on the diet of the Adélie penguin have been carried out in the vicinity of the Antarctic Peninsula (Trivelpiece *et al*. 1983, Lishman 1985, Jabłoński 1985, Coria *et al.* 1995) and, as observed for these penguins at other localities (van Heezik 1988, Puddicombe and Johnstone 1988, Green and Johnstone 1988, Ridoux and Offredo 1989), Antarctic krill were by far the most important prey.

Monitoring of Adélie penguins has been conducted at Laurie Island as part of the Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR) Ecosystem Monitoring Program (CEMP) since 1993–94. However, dietary data have been collected since the 1996–97 season. In order to learn the diet composition of this bird, we analysed stomach contents of *Pygoscelis adeliae* collected during 3 post-hatching periods at Point Martin, Laurie Island, South Orkney Islands, an area where there has existed little information on this topic since Lishman's studies (Lishman 1985).

Material and methods

Field work was carried out during the austral summers of 1997, 1998 and 1999 at Point Martin, Laurie Island, and the South Orkney Islands (60° 46´ S, 44° 42´ W), Antarctica. In this area Adélie penguin arrive ashore to breed in early October, eggs are laid in the first week of November, and chicks hatch from early December and fledge in February (personal observation). Approximately 26,000 Adélie pairs breed at Point Martin (N. Coria, unpubl. data). Forty seven stomach samples of *Pygoscelis adeliae* were obtained from 14 December 1996 to 14 January 1997, 42 stomach contents from 24 December 1997 to 19 January 1998 and 35 from 2 to 19 January 1999. At the initial dates of sampling, about 50 to 80% of chicks were already hatched. Sampling continued, whenever possible, until fledging. Collection of stomach contents was made between 12:00 and 18:00 hours (local time), obtaining between four to nine penguins per sampling date.

Samples were collected by the stomach-flushing method of Wilson (1984). Following Gales (1987), two flushes were done to each individual, in order to insure collection of the entire stomach content. All samples were packed, labelled, frozen (–20° C) and returned to Argentina for analysis. In the laboratory all samples were unfrozen, and then entire samples were placed into trays and non-food (pebbles) were removed. The samples were then rinsed with fresh water and strained through sieves of 0.25 and 0.10 mm, meshed, blotted dry and weighed to the nearest 0.1 g.

Prey items were separated into different categories (krill, fish, amphipods and other minor components) and each was weighed separately. The number of individual prey items (krill eyes, fish otoliths or eye-lenses) were counted for each taxon in the entire sample. Measurements of krill length from telson to anterior tip

of rostrum were taken to the nearest 0.1 mm. For broken individuals, the carapace length of each specimen was measured from the tip of the rostrum to the posterior dorsal median margin in order to determine body length using the formula X= 11.6 + 2.44 Y (Hill 1990), where X is the body length and Y the carapace length. A total of 5854 *Euphausia superba* individuals were measured. The minimum number of fish represented in the samples was determined by counting eye lenses or otoliths. The otoliths recovered from the samples were assigned to species using illustrations and descriptions in Hecht (1987) and Williams and McEldowney (1990). The otoliths belonging to each species were sorted into right and left, the most abundant being considered as the number of individuals from that species present in the sample. The length and mass of the individuals identified were estimated from otolith's length (OL) using the equations of Hecht (1987) and Williams and McEldowney (1990). Amphipods could sometimes be identified to species level.

Results

Overall period

The mean mass of the samples collected were significantly different among the breeding seasons considered (one way ANOVA $F_{2, 124}$= 51.51, P < 0.0001). The mean mass of the stomach content in the first period was significantly higher than the 1997–98 and 1998–99 breeding seasons (Table 1).

Table 1

Variation in the mean mass of stomach contents of the Adélie penguin (*Pygoscelis adeliae*) sampled at Laurie Island, South Orkney Islands, throughout the three breeding seasons.

Breeding season	n	Mean (g)	SD	Range (g)
1996–1997	47	453.5[a]	116.9	227.6–729.2
1997–1998	42	200.3[b]	109.0	37.5–507.4
1998–1999	35	290.0[c]	134.1	112.8–709.0

[a, b, c] Means not sharing a common superscript (a, b, c) are significantly different at p < 0.05, Tukey Test.

Diet composition showed significant differences between the three breeding seasons in terms of frequency of occurrence, importance by number and mass of the main prey groups (c^2_6 = 31.6, P < 0.001; c^2_6 = 1311.9, P < 0.0001; c^2_6 = 140.9, P < 0.0001, respectively).

The analysis of the stomach contents showed that Antarctic krill, *Euphausia superba*, were by far the largest component of the diet of the Adélie penguin, followed by amphipods and fish (Table 2). This importance of krill remained relatively constant throughout the study, and the non-krill prey was more frequent during the 1997–98 breeding season. The mean total length of krill showed significant differences between 1996–97 (41.6 mm ± 6.8), 1997–98 (45.8 mm ± 5.0) and

Table 2

The composition of the diet of Adélie penguin at Point Martin (Laurie Island), as reflected by the analysis of stomach contents during three breeding seasons. Percentage frequencies of occurrence (F%), number (N%) and mass (M%) sample sizes in parentheses. ++ = traces.

	1996/97 (n = 47)			1997/98 (n = 42)			1998/99 (n = 35)		
	F%	N%	M%	F%	N%	M%	F%	N%	M%
Krill	100	99.9	99.9	100	98.0	99.3	100	99.5	99.8
Amphipods	31.9	< 0.1	< 0.1	64.3	2.0	0.4	34.3	0.2	++
Fish	2.1	++	++	21.4	< 0.1	0.2	54.3	0.3	0.2
Others	17.0	++	< 0.1	4.8	++	< 0.1	8.6	< 0.1	++

Table 3

Size of fish (estimated from otolith lengths) in stomach contents of chick rearing Adélie penguins at Laurie Island. Data from the 1996–1997, 1997–1998 and 1998–1999 summers are combined.

Taxa	n	Otolith length	Total length	Total weight
		Mean ± s.d. (mm)	Mean ± s.d. (mm)	Mean ± s.d. (g)
Myctophidae				
Electrona antarctica	5	1.75 ± 0.18	58.55 ± 6.62	2.76 ± 0.89
Protomyctophum normani	2	2.47 ± 0.03	78.6 ± 0.9	–
Protomyctophum choriodon	1	2.36	74.7	–
Nototheniidae				
Trematomus newnesi	2	1.87 ± 0.11	93.4 ± 4.4	17.01 ± 1.71

1998–99 (43.7 mm ± 5.1) (Kruskal-Wallis Test $P < 0.0002$). Amphipods were frequently found in the samples (> 40%), however in terms of mass they were insignificant (< 1%). The bulk of krill eaten were mature or gravid females in each year of the study. One sample also contained *Thysanoessa macrura* Tattersall, 1908 (two individuals in December 1996). The hyperiid *Themisto gaudichaudii* Guerin-Méneville, 1825, as well as unidentified gammarids, were found in a few stomach samples. The remains of marine algae, isopods and trochiid snails in the stomach contents were negligible.

Fish constituted a low proportion of the total prey recovered from 124 stomach contents: from 29 containing fish remains, only 10 individual fish were identified belonging to 2 *Trematomus newnesi* Boulenger, 1902 and 8 myctophids (5 *Electrona antarctica* Gunter, 1878, 2 *Protomyctophum normani* Taning, 1932 and 1 *P. choriodon* Hulley, 1981) (Table 3). The otoliths from the remaining 13 specimens in the 1998–99 breeding season were unidentifiable to species, as they were broken or strongly eroded. Another 35 fish, in the same season, were classified as juvenile nototheniids. Others, representing 35 fish, all of them also recovered from the samples of 1998–99, were too small to be accurately identified, but probably belonged to early stages of a notothenid species of the genus *Trematomus*.

Table 4

Mean mass of stomach contents collected for guard and crèche periods during the three breeding seasons at Laurie Island, South Orkney Islands.

Breeding season	(n)	Mean (g)	SD	Range
1996–1997				
Guard period	24	394.3	103.7	227.6–615.8
Crèche period	23	528.6[a]	113.0	330.0–729.2
1997–1998				
Guard period	11	142.2	97.8	52.3–374.4
Crèche period	31	220.9[b]	106.7	37.5–507.4
1998–1999				
Crèche period	30	290.8[b]	137.7	112.8–709.0

[a, b, c] Means not sharing a common superscript (a, b, c) are significantly different at $p < 0.05$; Tukey Test.

Table 5

Mean length of E*uphausia superba* caught by Adélie penguins over three seasons at Laurie Island, South Orkney Islands.

Breeding seasons	N (krill)	Mean (mm)	SD	Range
1996–1997				
Guard period	703	40.3	5.0	31.6–50.8
Crèche period	692	43.6	3.6	36.4–50.3
1997–1998				
Guard period	326	42.4	2.2	37.2–46.6
Crèche period	1120	46.7	2.8	38.5–50.3
1998–1999				
Crèche period	3013	43.8	1.9	37.9–47.4

Guard and crèche periods

There were significant differences in the mean mass of stomach contents between the 1996–97 guard and crèche periods (ANOVA $F_{1, 47} = 18.05$, $P < 0.0001$). The same comparison also resulted significantly in the 1997–98 guard and crèche periods (ANOVA $F_{1, 42} = 4.61$, $P < 0.04$). Only five samples were collected for the guard period of 1998–99, which were not taken into account for statistical analysis because of their low number and the near collection date from crèche period samples. The mean mass of stomach contents between the 1996–97 and 1997–98 guard periods showed significant differences (Mann-Whitney Test, $U = 12.00$, $P < 0.0001$). The mean mass of crèche period of stomach contents collected were significantly different during the three periods considered (ANOVA $F_{2, 84} = 45.68$, $P < 0.0001$). The mean mass of stomach contents in the 1996–97 crèche was significantly higher than the other crèche periods (Table 4).

There were significant differences in the mean size of krill taken between the guard and crèche periods in two of the seasons studied: 1996–97 and 1997–98

(Kruskal-Wallis Test, H = 6.09, P = 0.01; H= 14.81, P = 0.0001 respectively) (Table 5). The same comparison also resulted significantly among the three crèche periods considered (Kruskal-Wallis Test, H= 21.76, p = 0.0001). Significant differences were found in the mean krill length taken between guard periods (1996–97 and 1997–98) (Mann-Whitney Test, U = 12.00, P < 0.0001).

Discussion

Adélie penguins breeding at the Antarctic Peninsula and on Antarctic islands consume mainly Antarctic krill, *E. superba* (Volkman *et al.* 1980, Lishman 1985, Trivelpiece *et al.* 1990, Coria *et al*. 1995), although those breeding in the Antarctic continental area feed either on a variety of organisms such as *E. superba*, *E. crystallorophias* Holt et Tatterstall, 1906 and fish (Emison 1968, Puddicombe and Johnstone 1988, Ridoux and Offredo 1989, Kerry *et al.* 1994, Kent *et al*. 1998). This regional variation has been attributed to the species difference in krill distribution patterns with *E. superba* occurring offshore of the continental shelf break and *E. crystallorophias* limited to inshore coastal waters (Ridoux and Offredo 1989, Knox 1994, Rodary *et al.*, 2000).

The results reported here are fully coincident with the regional trend previously reported. The proportion of Antarctic krill (nearly to 100%) by mass at Laurie Island was comparable to those reported in other breeding places of the South Orkney Islands, Signy Island (Lishman 1985).

In the 1997 season stomach content weights were significantly larger than in 1998 and 1999 (Table 1). Such differences could be explained by more rapid rates of digestion of prey items (Wilson *et al.* 1985, Duffy and Jackson 1986, Jackson and Ryan 1986) and perhaps by local differences in the availability of food, but other explanations are possible. Adélie penguins confronted different climatic conditions in the three years. In the 1997/98 breeding season pack ice broke on January 29 (*Orcadas* Base Meteorological Station). At Laurie Island in the preceding three breeding seasons the date of pack ice break-off varied between the first days of October and late November (*Orcadas* Base Meteorological Station). During the 1998/99 breeding season the pack did not form, so penguins had free access to the sea from their colonies. Rombolá *et al*. (2002), working with Adélie and chinstrap (*Pygoscelis antarctica* (Forster, 1781)) penguins at the same area, suggested that sea conditions had opposite effects on the two species. It was found that late pack ice break-off in 1998 resulted in lower reproductive success than in 1999 for chinstrap, while Adélie penguin parameters were rather insensitive. This species has shown to be able to cope with this environmental factor, as suggested by its circumpolar and more southerly range (Wilson *et al.* 2001). Rombolá *et al.* (2003) also suggested that the plasticity of *P. adeliae* allowed this species to breed successfully in the 1997/98 and 1998/99 seasons, making clear that the observed

interannual changes involving CEMP parameters (stomach content weight and reproductive success) were due to environmental factors and not to changes in prey abundance. The results reported here are for three breeding seasons only. In order to establish whether the low weight of the stomach contents of Adélie penguins in the 1997/98 are representative of other years, when the fast-ice persists longer than usual, diet studies have to be carried out over several seasons.

The size of *E. superba* taken by Adélie penguins at Laurie Island was greater than that reported at nearby Signy Island (both in the South Orkney Islands) by Lishman (1985). At Signy these birds preyed upon krill of 36.7 mm in overall mean length. Lishman (1985) found that Adélie penguins caught large numbers of juvenile krill and suggested that these euphausiids are associated with the ocean current confluence. The data presented here comes from an area where krill is abundant (Jackowski 2002), but unfortunately we are not aware of any adequate surveys of krill distribution in the study area during the Adélie chick rearing periods to compare our data on diet composition with krill abundance. However, this difference in the size of krill eaten by Adélie penguins on the South Orkney Islands may be due to (1) differences in the distribution of krill age classes; (2) differences in foraging areas; or (3) differences in the krill recruitment, perhaps caused by variations in sea-ice coverage (Frazer and Trivelpiece 1996)

During 1997–98 the diet was more diverse, which is reflected by the frequency of occurrence of non-krill prey (Table 2). The occurrence of the pelagic *Themisto gaudichaudii* in the records of the guard period at Laurie Island was similar to that observed at *Esperanza* (Hope Bay, Antarctic Peninsula) in the 1987–88 breeding season (Coria *et al.* 1995). These findings suggest a local phenomena of differential availability of this prey and/or a different foraging strategy during the guard period, when the sea ice conditions in 1997–98 restricted access to krill. *T. gaudichaudii*, usually found in large swarms, is the most common and abundant hyperiid amphipod in the Southern Ocean (Jażdżewski 1982). While this species may have been targeted prey, it is likely that some of the other crustacean consumed were incidental prey, present in swarms of targeted species such as *E. superba*, or secondary prey taken for fish.

The small fish component in the diet of Adélie penguins at Laurie Island was dominated by pelagic species, particularly the myctophid *Electona antarctica*. This species is circumpolar in distribution in Antarctica, feeds largely on krill and other invertebrates, and often occurs in shallow waters, especially at night (Gon and Heemstra 1990). *E. antarctica* seems to be well distributed around the South Orkney Islands, where it has been reported as a frequent prey of other top predators (Daneri and Coria 1993, Coria *et al.* 1997, Casaux *et al.* 1998, Ferretti *et al.* 2001). Other fish taxa also appear as important in penguin diet. *T. newnesi* is circumpolar in distribution in Antarctica (Gon and Heemstra 1990). It consumes largely krill and possibly is taken by penguins when foraging in krill swarms. In contrast, other studies had reported *Pleuragramma antarcticum* Boulenger, 1902, as forming the

bulk of the fish portion. Thus this nototheniid was the most frequent fish species in East Antarctica (Puddicombe and Johnstone 1988, Ridoux and Offredo 1989, Clarke *et al.* 1998, Kent *et al.* 1998, Wienecke *et al.* 2000). Information on the occurrence of fish in the diet of the Adélie penguins indicates that *P. antarcticum* is the most important fish in the area of the Antarctic Peninsula (Jabłoński 1985, Coria *et al.* 1995). *P. antarcticum* is perhaps the most abundant fish in Antarctica (Radtke *et al.* 1993), where it occurs in pelagic regions at depths from the surface to 728 m (Miller 1993). It has a circumpolar distribution and has been reported in the diet of several top predators in Antarctica (Gon and Heemstra 1990). Surprisingly, *P. antarcticum* was not present in our diet samples, nor in the diet of two *P. antarcticum*-feeders, Cape petrels (Coria *et al.* 1997) and Snow petrels (Ferretti *et al.* 2001) at Laurie Island. This could be associated with the poor availability of this nototheniid fish in the South Orkneys area during this sampling period.

Intraspecific differences in dietary composition have been demonstrated in Adélie penguins on the South Shetland Islands by Volkman *et al.* (1980), who found that male birds consumed significantly smaller krill than did females. The study of Chapell *et al.* (1993), carried out at Anvers Island (Antarctic Peninsula), indicates that sex differences in foraging strategies of Adélie penguins may be widespread amongst the species, even in locations where their diet consists almost exclusively of krill. Consistent sex differences in dietary preference were demonstrated at two localities in East Antarctica over several breeding seasons (Clarke *et al.* 1998). Unfortunately, the data on diet reported in this paper come almost exclusively from unsexed birds. The present study is the first examination of Adélie pengun diet at Laurie Island. It is important to recognize, however, the importance of knowing the sex of the penguins being sampled, and that prey composition may vary during the breeding season and from one year to the next.

Acknowledgements. — We wish to thank the members of *Orcadas* Station for their logistic help, and R. Salazar, M. Gray, C. Vazquez, G. Soave, V. Ferretti and G. Leotta for field assistance. We are also grateful to R. Casaux for his help in the identification of fish otoliths.

References

AINLEY D.G., O'CONNOR E.F. and BOEKELHEIDE R.J. 1984. The marine ecology of birds in the Ross Sea, Antarctica. Ornithological Monographs, American Ornithologists Union, Washington, DC. 32: 1–97

CASAUX R., SOAVE G. and CORIA N. 1998. Lanternfish (Myctophidae) in the diet of the Cape Petrel *Daption capense* at the South Shetland and South Orkney Islands, Antarctica. Polar Biology 20: 364–366

CHAPELL M.A., JANES D.N., SHOEMAKER V.H., BUCHER T.L. and MALONEY S.K. 1993. Reproductive effort in Adélie penguins. Behaviour Ecological Sociobiology 33: 173–182.

CLARKE J., MANLY B., KERRY K.. GARDNER H., FRANCHI H., CORSOLONI S. and FOCARDI S. 1998. Sex differences in Adélie penguin foraging strategies. Polar Biology 20: 248–258.

CORIA N.R., SPAIRANI H., VIVEQUIN S. and FONTANA R. 1995. Diet of Adélie penguins *Pygoscelis adeliae* during the post-hatching period at Esperanza Bay, Antarctica, 1987/88. Polar Biology 15: 415–418.

CORIA N., SOAVE G. and MONTALTI D. 1997. Diet of the Cape Petrel *Daption capense* during the post-hatching period at Laurie Island, South Orkney Islands, Antarctica. Polar Biology 18: 236–239.

CROXALL J.P. 1984. Seabirds. *In:* R.M. Laws (ed.), Antarctic Ecology, Vol. 2, Academic Press, London; 533–619.

CROXALL J.P. and LISHMAN G.S. 1987. The food and feeding ecology of penguins. *In*: Croxall JP (ed). *Seabirds: feeding ecology and role in marine ecosystems.* Cambridge University Press: Cambridge, 101–133.

DANERI G. and CORIA N.R. 1993. Fish prey of Antarctic fur seals, *Arctocephalus gazella*, during the summer-autumn period at Laurie Island, South Orkney Islands. Polar Biology 13: 287–289.

DUFFY, D.C. and. JACKSON S. 1986. Diets of seabirds: a review of methods. Colonial Waterbirds 9: 1–17.

EMISON W.B. 1968. Feeding preferences of the Adélie penguin at Cape Crozier, Ross Island. Antarctic Research Series 12: 191–212.

FERRETTI V., SOAVE G.E., CASAUX R. and CORIA N. 2001. Diet of Snow Petrel, *Pagodroma nivea,* at Laurie Island, Antarctic, during the 1997/98 breeding season. Marine Ornithology. 29: 71–73

FRASER W.R. and TRIVELPIECE W.Z. 1996. Factors controlling the distribution of seabirds: winter-summer heterogeneity in the distribution of Adélie penguin populations. Foundations for ecological research west of the Antarctic Peninsula. Antarctic Research Series 70: 257–272.

GALES R.P. 1987. Validation of the stomach-flushing technique for obtaining stomach contents of penguins. Ibis 129: 335–343.

GON O. and HEEMSTRA P.C. 1990. Fishes of the Southern Ocean. J. L. B. Smith Institute of Ichthyology, Grahamstown, 462pp.

GREEN K. and JOHNSTONE G.W. 1988. Changes in the diet of Adélie penguins breeding in East Antarctica. Australian Wildlife Research 15: 103–110.

HECHT T. 1987. A guide to the otoliths of Southern Ocean fishes. South African Journal of Antarctic Research 17: 1–87.

HILL H.J. 1990. A new method for the measurement of Antarctic krill, *Euphausia superba* Dana, from predator food samples. Polar Biology 10: 300–317.

JABŁOŃSKI B. 1985. The diet of penguins on King George Island, South Shetland Islands. Acta Zoologica Cracoviensia 29: 117–186.

JACKOWSKI E. 2002. Distribution and size of Antarctic krill (*Euphausia superba* Dana) in Polish commercial catches taken in the Atlantic Sector of the Southern Ocean from 1997 to 1999. CCAMLR Science 9: 83–105.

JACKSON S. and RYAN P.G. 1986. Differential digestion rates of prey by White-chinned Petrels (*Procellaria aequinoctialis*). Auk 103: 617–619.

JAŻDŻEWSKI K. 1982 (1981). Amphipod crustaceans in the diet of pygoscelid penguins of the King George Island, South Shetland Islands, Antarctica. Polish Polar Research 2: 133–144.

KENT S., SEDDON J., ROBERTSON G. and WIENECKE B.C. 1998. Diet of Adélie penguins at Shirley Island, East Antarctica, January 1992. Marine Ornithology 26: 7–10.

KERRY K.R., CLARKE J.R., BROWN S., LAWLESS R., YOUNG K. and JOHNSTON J. 1994. Adélie penguin as consumers of fish and zooplankton communities. Document WG-CEMP-94/33. CCAMLR, Hobart.

KNOX G.A. 1994. The biology of the Southern Ocean. Cambridge. Cambridge University Press, 444 pp.

LISHMAN G.S. 1985. The food and feeding ecology of Adelie penguins (*Pygoscelis adeliae*) and chinstrap penguins (*P. antarctica*) at Signy Island, South Orkney Islands. Journal of Zoology, London (A) 205: 245–263.

MILLER R.G. 1993. History and atlas of the fishes of the Antarctic Ocean. Foresta Institute for Ocean and Mountain Studies, Carson City, Nevada.

PUDDICOMBE H.A. and JOHNSTONE G.W. 1988. The breeding season diet of Adélie penguins at the Vestfold Hills, East Antarctica. Hydrobiologia 165: 239–253.

RADTKE R.L., HUBOLD G., FOLSOM S.D. and LENZ P.H.1993. Otolith structural and chemical analyses the key to resolving age and growth of the Antarctic silverfish, *Pleuragramma antarcticum.* Antarctic Science 5: 51–62.

RIDOUX V. and OFFREDO C. 1989. The diets of five summer breeding seabirds in Adélie Land, Antarctica. Polar Biology 9: 137–145.

RODARY D., WIENECKE B.C. and BOST C.A. 2000. Diving behaviour of Adélie penguins (*Pygoscelis adeliae*) at Dumont D'Urville, Antarctica: nocturnal patterns of diving and rapid adaptations to changes in sea-ice condition. Polar Biology 23: 113–120.

ROMBOLA E., MARSCHOFF E. and CORIA N.R. 2003. Comparative study of the effects of the late pack ice break-off on Chinstrap and Adélie penguins diet and reproductive success at Laurie Island, South Orkneys Islands, Antarctica. Polar Biology 26: 41–48.

TRIVELPIECE W.Z., TRIVELPIECE S.G., VOLKMAN N.J and WARE S.H. 1983. Breeding and feeding ecologies of Pygoscelid penguins. Antarctic Journal of the United States 18: 209–210.

TRIVELPIECE W.Z., TRIVELPIECE S.G., GEUPEL G.R., KJELMYR J. and VOLKMAN N.J. 1990. Adélie and chinstrap penguins: their potential as monitors of the southern ocean marine ecosystem. *In*: Kerry K.R., Hempel G. (eds), *Antarctic ecosystems: ecological change and conservation*.. Springer, Berlin Heidelberg New York; 191–202.

VAN HEEZIK Y. 1988. Diet of Adélie Penguins during the incubation period at Cape Bird, Ross Island, Antarctica. Notornis 35: 23–27.

VOLKMAN N.J., PRESLER P. and TRIEVELPIECE W. 1980. Diets of Pygoscelid penguins at King George Island, Antarctica. Condor 82: 373–378.

WIENECKE B.C., LAWLESS R., RODARY D., BOST C.-A., THOMSON R., PAULY T., ROBERTSON G., KERRY K.R. and LEMAHO Y. 1997. Adélie penguins foraging behaviour and krill abundance along the Wilkes and Adélie land coasts, Antarctica. Deep Sea Research II 47: 2573–2587.

WILLIAMS R. and MCELDOWNEY A. 1990. A guide to the fish otoliths from waters of the Australian Antarctic Territory, Heard and Macquarie Islands. ANARE Research Note 75: 1–173.

WILLIAMS T.D. 1995. The Penguins. Oxford University Press. 295 pp.

WILSON P.R., AINLEY D.G., NUR N., JACOBS S.S., BARTON K.J., BALLARD G. and COMISO J.C. 2001. Adélie penguin population change in the Pacific sector of Antarctica: relation to sea-ice extent and the Antarctic Circumpolar Current. Marine Ecology Progress Series 213: 301–309.

WILSON R.P. 1984. An improved stomach pump for penguins and other seabirds. Journal of Field Ornithology 55: 109–112.

WILSON R.P., La COCK G.D., WILSON M.P. and. MOLLAGEE F. 1985. Differential digestion of fish and squid in Jackass Penguins *Spheniscus demersus*. Ornis Scandinavica 16: 77–79.

WOEHLER E.J. 1993. The distribution and abundance of Antarctic and Subantarctic penguins. Scientific Committee on Antarctic Research (SCAR), Cambridge.

Received 15 January 2003
Accepted 25 June 2003