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A 1000-year record of Adélie penguin diets in the southern Ross Sea

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Abstract: Non-krill prey remains were recovered from ornithogenic sediments at three active Adélie penguin colonies on Ross Island, to assess long-term dietary trends in this species. Radiocarbon dates place the age of these deposits from a maximum of 947 years ago to the present. We identified 12 taxa of fish and two of squid with the Antarctic silverfish (*Pleuragramma antarcticum*) as the most abundant prey species represented at all sites. In addition, silverfish have decreased in importance in Adélie penguin diet over the past 600 years, perhaps in response to climate change since the onset of the Little Ice Age, though it remains much more abundant in current penguin diet in the Ross Sea than in the Antarctic Peninsula. Other prey taxa reflect the diversity of prey selection by Adélie penguins in Antarctica.

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Introduction

In the Ross Sea region, krill, especially *Euphausia crystallorophias* Holt & Tattersall, is a major component of Adélie penguin (*Pygoscelis adeliae* Hombron & Jacquinot) diet, comprising 44–99% of their summer prey (by mass), depending on the time of the breeding cycle in which breeding adults were sampled (Emison 1968, Paulin 1975, van Heezik 1988). In the most recent and complete dietary analysis of the three colonies (Cape Royds, Cape Crozier, and Cape Bird) on Ross Island (77°30'S, 168°00'E), krill was only 25% of the total diet (wet mass), while fish (primarily *Pleuragramma antarcticum* Boulenger) made up the other 75% (Ainley *et al*. 1998). Ainley *et al*. also noted that, during some years, fish comprised a smaller part of the total diet at Cape Bird than at other colonies on Ross Island, which the authors attributed to pack-ice conditions.

The proportion of prey items in past Adélie penguin diets in the Antarctic Peninsula appears to have varied with climate change (Emslie *et al.* 1998, Emslie & McDaniel 2002). However, detailed information on prey fluctuations in the Ross Sea region is lacking. Adélie penguin diet in the southern Ross Sea was investigated, with excavations of ornithogenic soils at three active colonies in 2001. Recent studies in the Antarctic Peninsula have shown that these soils can yield considerable dietary information on non-krill prey from the excellent preservation of remains found within them (Emslie *et al.* 1998, Emslie & McDaniel 2002). These studies also have confirmed that fish (*Pleuragramma antarcticum* and *Electrona antarctica* Günther) and squid (*Psychroteuthis glacialis* Thiele) are important components in Adélie penguin diets.

Study area and methods

Excavations of ornithogenic soils were undertaken at Cape Royds, Cape Bird, and Cape Crozier, Ross Island, East Antarctica (Fig. 1) during the 2000/01 summer. These sites were sampled late in the season, after penguin chicks had formed crèches, to minimize disturbance to the colonies. Methodology followed that of Emslie *et al*. (1998) and Emslie & McDaniel (2002). At each site, 1 x 1 m test pits (TP) were excavated in 5 cm arbitrary (non-stratigraphical) levels until sterile beach sediments were encountered. The volume of sediments excavated from each level was

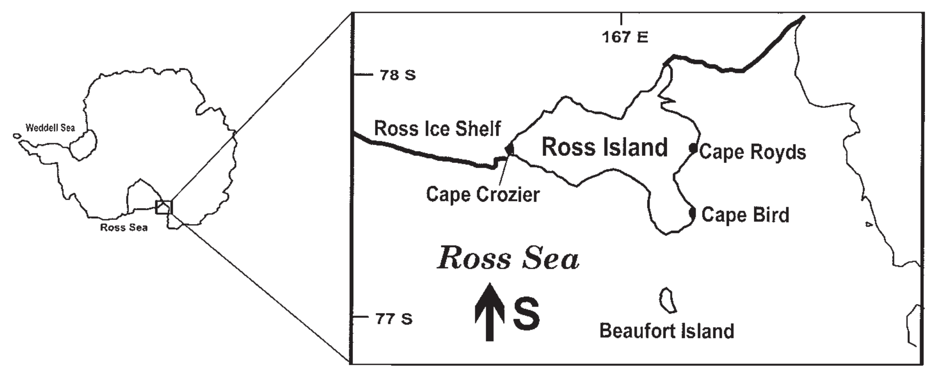

Fig. 1. Map of the southern Ross Sea (inset) with detail showing the location of active penguin colonies on Ross Island at Cape Royds, Cape Bird, and Cape Crozier.

Table I. The major prey taxa identified from beaks and otoliths recovered from all modern penguin colonies sampled at Ross Island, Antarctica. Sediment volume, the total number of identifiable specimens, and the minimum number of individuals (MNI; in parentheses) represented are provided for each taxon by stratigraphical level; an asterisk (*) indicates those samples where the MNI was estimated from sorting only 15–22% (by mass) of the sediments from the No. 60 sieve (see text).

Site/ Provenience	Sediment volume (l)	*Psychroteuthis glacialis*	*Pleuragramma antarcticum*
Cape Crozier			
TP 1, Level 1	28	5 (3)	683 (289)
TP 1, Level 2	26	5 (3)	1037 (430)
TP 1, Level 3	24	9 (6)	695 (866*)
TP 1, Level 4	16	8 (5)	854 (949*)
TP 1, Level 5	19	17 (11)	711 (1229*)
TP 2, Level 1	28	3 (2)	473 (198)
TP 2, Level 2	28	19 (12)	664 (279)
TP 2, Level 3	28	8 (4)	1145 (479)
TP 2, Level 4	28	12 (6)	1034 (1355*)
Cape Bird			
Area D, TP 1, Level 1	28		146 (291*)
Area D, TP 1, Level 2	28	3 (2)	197 (297*)
Area D, TP 1, Level 3	28	2 (2)	1004 (447)
Area D, TP 1, Level 4	28	3 (2)	249 (404*)
Area D, TP 1, Level 6	14	1 (1)	
Area D, TP 1, Level 7	20		
Cape Royds			
TP 1, Level 1	28	1 (1)	142 (259*)
TP 1, Level 2	28		185 (318*)

determined using 14 litre buckets. Due to limitations in field logistics, the total amount of sediment sampled at these sites was limited to a maximum of 28 l per level. TP locations were determined by surveying the active areas and choosing sites near the middle of the colonies where sediments appeared to be deepest. Two TPs were completed at Cape Crozier while one each was excavated at Cape Bird and Cape Royds. All pits were backfilled with pebbles and rocks after excavations were completed.

Sediments were transported to the laboratory where they were washed through three nested screens with mesh sizes of 0.64, 0.32, and 0.025 cm² and dried. Organic material trapped in the top two screens was sorted and recovered by eye or with a low power magnifying lamp. The fine sediments in the 0.025 cm² screen was sorted again using two geology sieves of 1.0 mm (No. 18) and 0.25 mm (No. 60) mesh. Material in these sieves was sorted using a low-power stereomicroscope. All sediments from the No. 18 sieve were sorted in this manner. However, due to high sample volume and the large amount of time necessary to completely sort and process fine sediments from the No. 60 sieve, we subsampled this fraction by sorting only 15–22% (by dry mass) in nine of the samples and extrapolating the data to estimate the total number of prey items represented (see below).

Identification of otoliths and cephalopod remains were completed at the National Marine Mammal Laboratory, Seattle, Washington. The Minimum Number of Individuals (MNI) represented for fish taxa found in each level was determined by counting the most common side (right or left) of complete saggital otoliths present. Otolith fragments of unknown side were counted and this number was halved to estimate the number of whole otoliths represented. This number was halved again to give a conservative estimate of the total number of right and left otoliths. The higher number of either right or left otoliths was summed from these two categories to give a total MNI for each level.

For those nine levels in which only a subsample of the sediments from the No. 60 sieve was sorted (see Table I), MNIs were estimated for Antarctic silverfish by multiplying the MNI represented from the subsample by the total mass (g) of the sample and then dividing by the mass of sediments in the subsample. The resulting estimated MNI from the No. 60 sieve was then added to those found in the No. 25 sieve to calculate a total MNI for each level. MNIs were determined for squid species by counting the most abundant beak element (upper or lower) represented, partial and complete. Temporal changes in MNI per litre of sediments by site were statistically analyzed using a Chi-square test at $P < 0.05$. Expected values were calculated as the mean of the total MNI for all litres of sediment from all levels per pit.

Accelerated mass spectrometry (AMS) dating of penguin remains was completed by the Rafter Radiocarbon Laboratory, New Zealand, in collaboration with Dr David Lambert, Massey University. Samples consisted of bone when possible, but eggshell or feathers were also used. Radiocarbon dates of organic remains were corrected for the marine-carbon reservoir effect and upwelling of old water in the Southern Ocean by using a $\Delta R = 750 \pm 50$ BP (see Emslie 1995, 2001). Calibrations were completed with the Calib 4.2 software program and the 98MARINE database (Stuiver & Reimer 1993, Stuiver *et al*. 1998). All dates are reported in 2σ calibrated ranges in calendar years before present (BP). The relative age of levels without radiocarbon dates was assumed to follow stratigraphical chronology, with older levels occurring at greater depth in the deposits.

Results

A total of 427 l of sediments was excavated from four TPs from the three colonies on Ross Island. One of the test pits (TP 2 at Cape Crozier) was in a recently abandoned breeding area. In addition, TP 1 in Area D (centre of the northern colony, see Heine & Speir 1989) at Cape Bird had ornithogenic sediments through level 4, but deeper levels contained primarily feather remains and few pebbles or prey remains. These deeper levels may have formed when the area was used as a moulting site by Adélie penguins and were not included in the dietary analyses. Similarly, TP 1 level 3 at Cape Royds was composed primarily of non-ornithogenic sediments and was not included in our

Table II. Other prey taxa identified from beaks and otoliths recovered from the No. 18 geology sieve from Adélie penguin colonies, Ross Island. The total number of identifiable specimens and minimum number of individuals (MNI; in parentheses) are provided for each taxon by colony. These results reflect total specimens found in sorted sediments and do not include estimated MNIs calculated from the nine subsamples where only 15–22% by mass of the sediments were sorted.

Taxon	Cape Crozier	Cape Bird D	Cape Royds
Cephalopoda: Teuthoidea			
Brachioteuthis sp.	3 (2)	2 (1)	
Unident. oegopsid beak fragments	112	44	1
Unident. Octopod	2		
Osteichthyes:			
Family Nototheniidae			
Nothothenia cf. *N. neglecta*		1 (1)	
Nothothenia sp.	11 (8)	12 (8)	11 (8)
Trematomus cf. *T. eulepidotus*			2 (1)
Trematomus sp.	32 (23)	45 (32)	7 (5)
Pagothenia cf. *P. bernachii*	5 (2)	5 (4)	1 (1)
Pagothenia sp.	14 (10)	12 (8)	9 (5)
Aethotaxis cf. *A. mitopteryx*			1 (1)
Family Harpagiferidae (unident.)			1 (1)
Family Channichthyidae			
Champsocephalus sp.		1 (1)	
Pagetopsis maculatus	52 (36)	7 (6)	
Pagetopsis sp.	4 (4)	13 (8)	2 (2)
Chionodraco sp.	10 (8)		4 (2)
Unident. Channichthyidae		4 (2)	
Unident. Nothothenoidei	64 (45)	28 (16)	33 (22)
Unident. Nothothenoidei	7	49	40
Family Myctophidae			
Protomyctophum bolini		1 (1)	
Family Macrouridae (unident.)		12 (6)	1 (1)
Family Gempylidae			
Paradiplospinus gracilis	1 (1)		
Unident. lapillae (utricular) otoliths	525	60	27
Unident. saggital otolith fragments	654	204	179

analyses, though one radiocarbon date was obtained from this level.

Dietary remains identified from all sites consisted of two major prey taxa, squid (*Psychroteuthis glacialis*) and Antarctic silverfish, that were quantified by level at each site (Table I). Other prey remains that were identified in the samples include another squid, *Brachioteuthis* sp., and 11 taxa of fish (Table II). *Pleuragramma antarcticum* is the most abundant prey species in the samples and varies in MNI per litre of sediments between the three sites (Table I). Moreover, at Cape Crozier, this species decreases significantly in relative abundance from older to younger levels in the deposits ($\chi^2 > 50.9$, $P < 0.001$; Fig. 2) in both test pits. However, it should be noted that the levels in TP 2 at this site are slightly older than comparable levels in TP 1 (Table III), though both follow the same trends. At Cape Bird and Cape Royds, *P. antarcticum* shows no variation in abundance with stratigraphical level ($\chi^2 < 2.35$, $P < 0.5$).

Nine radiocarbon dates provide an estimate for the occupation history of Ross Island (Table III). Except for those from Cape Royds, all dates reflect increasingly greater age with depth in the TPs. These dates are reversed at Cape Royds, with the oldest in level 2 and the younger in level 3, perhaps due to mixing of specimens in the sediments or other factors. The date from level 2 indicates that Adélie penguins began occupying Cape Royds at approximately 947–653 BP (2σ calibrated range) while other dates signify that Cape Bird and Cape Crozier were not occupied by breeding birds until 500 to 600 BP; Cape Bird probably was

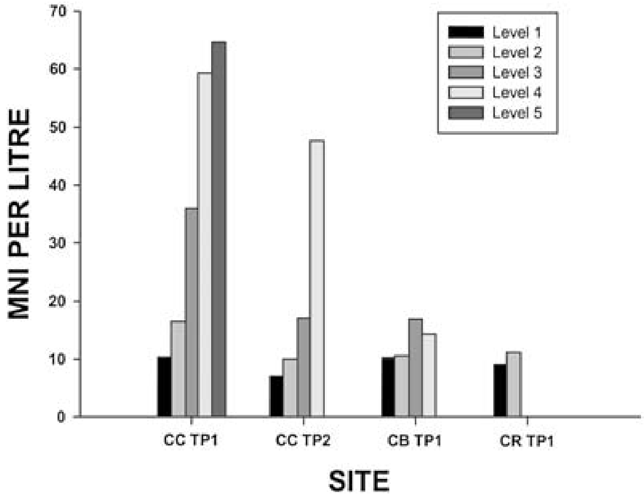

Fig. 2. Relative abundance (MNI, minimum number of individuals) of *Pleuragramma antarcticum* by stratigraphical level in test pits (TP) excavated at Cape Crozier (CC TP1 and TP2), Cape Bird (CB TP1), and Cape Royds (CR TP1). The decrease in abundance from older to younger levels at Cape Crozier is significant ($\chi^2 > 50.9$, $P < 0.001$). See Table I for sample sizes.

Table III. Radiocarbon dates completed on Adélie penguin bone, eggshell, or feather fragments from active colonies on Ross Island, Antarctica. Conventional dates (in radiocarbon years BP) were corrected with a $\Delta R = 750 \pm 50$ years and calibrated using the Calib 4.2 software program and the MARINE98 database (see Stuiver & Reimer 1993) to yield a 2σ calibrated range (in calendar years BP), or 95% confidence interval, for the true age of the sample.

Site/Provenience	Material	Lab. no.	Conventional date	2σ Calibrated range
Cape Crozier				
TP 1, Level 3	Bone	NZA 13201	1272 ± 65	307–0
TP 1, Level 4	Bone	NZA 13202	1323 ± 65	401–0
TP 1, Level 5	Eggshell	NZA 13313	1397 ± 95	492–0
TP 2, Level 3	Bone	NZA 13203	1463 ± 80	510–139
Cape Bird				
Area D, TP 1, Level 4	Bone	NZA 13366	1580 ± 55	551–304
Area D, TP 1, Level 6	Bone	NZA 13367	1547 ± 55	534–286
Area D, TP 1, Level 7	Feather	NZA 13374	1856 ± 65	797–530
Cape Royds				
TP 1, Level 2	Bone	NZA 13368	2007 ± 60	947–653
TP 1, Level 3	Eggshell	NZA 13369	1241 ± 55	281–0

used as a moulting site only up to 797 years ago (Table III). These results are comparable to other published dates on penguin remains from Cape Bird and Cape Crozier (Lambert *et al*. 2002).

Discussion

The radiocarbon chronologies presented here and elsewhere (Lambert *et al*. 2002) indicate that breeding Adélie penguins have been active on Ross Island since approximately 1000 years ago, at least at Cape Royds. Data from Cape Crozier and Cape Bird provide a dietary record spanning the last 510 to 551 years. Dates for the occupation of Cape Bird are much younger than suggested by Speir & Cowling (1984) and Heine & Speir (1989) who obtained two dates on penguin bones at the middle colony at Cape Bird that indicated ages of 8080 ± 160 and 7070 ± 180, respectively. However, these dates are considered to be incorrect based on evidence for a much younger age for the beach terraces where these samples were taken (Dochat *et al*. 2000). Other penguin dates completed by Dochat *et al*. (2000) at Cape Bird are from bones deposited in raised beach, rather than ornithogenic sediments, and are not associated with breeding occupation in the past.

Fish remains

Three of the five most abundant prey taxa identified from all the ornithogenic soils examined in this study are nototheniid fish. These include the predominant taxa, *Pleuragramma antarcticum*, as well as *Trematomus*, *Notothenia*, and *Pagothenia* species. Ainley (2002) proposed that Adélie penguins mix nototheniid fish with *Euphausia crystallorophias* when feeding over the continental shelf. Radiotelemetry studies have shown that Adélie penguins from Ross Island colonies forage throughout McMurdo Sound and over the continental shelf (Sadleir & Lay 1990, Ribic *et al*. 1998).

Pleuragramma antarcticum is circum-Antarctic in distribution and accounts for over 80% of numbers and biomass of fishes in the Ross Sea (Gon & Heemstra 1990). Larval and juvenile *P. antarcticum* occur within the maximum foraging depth (170 m) of Adélie penguins (Williams 1995) and this fish has long been recorded as a dietary component of this species (Emison 1968, Paulin 1975, van Heezik 1988, Ainley *et al*. 1998), as well as for emperor penguins (*Aptenodytes forsteri* Gray; Cherel & Kooyman 1998) and Weddell seals (*Leptonychotes weddellii* Lesson; Plötz *et al*. 1991) in the southern Ross Sea.

Despite the abundance of *Pleuragramma antarcticum* in the Ross Sea, our data indicate that this prey species has decreased in importance in Adélie penguin diets over the past 600 years at Cape Crozier. A similar decrease is reflected in the data from Cape Bird and Cape Royds, though the trends are not statistically significant. These trends may not necessarily indicate a decrease in *P. antarcticum* in the Ross Sea, but may simply reflect changes in foraging conditions (e.g. amount of open water) and prey selection by Adélie penguins. Ainley *et al*. (1998) found that Adélie penguins may switch between krill and fish depending on pack-ice conditions. During years with extensive sea-ice coverage, krill is more available while fish, especially *P. antarcticum*, is taken more so when less ice is present.

Although climatic factors may be responsible for the decrease in *Pleuragramma antarcticum* in penguin diets at Cape Crozier, the radiocarbon and palaeoclimatic records lack the resolution for correlation over such a relatively short time period. Data from the Dry Valleys indicate that a warming trend and an increase in lake levels began in this region at about 1200 to 1000 years ago (Lyons *et al*. 1998, 1999). This trend was interrupted by cooling during the Little Ice Age (LIA) from about 450 to 100 years ago (Grove 1988) when conditions in East Antarctica are known to have been colder than today (Mosely-Thompson *et al*. 1990). Although radiocarbon dates presented here overlap extensively, rendering it too difficult to determine the exact timing for silverfish abundance in past penguin diet, the stratigraphical chronology of the samples at Cape Crozier begins in conjunction with the onset of the LIA. It is possible that silverfish were more important in Adélie penguin diet at that time, and then became less important as conditions cooled from 450 to 100 years ago. Further studies, including isotopic analyses of the otoliths, are needed to test this hypothesis.

Dietary trends for Adélie penguins follow a different pattern in the Antarctic Peninsula where krill, especially *Euphausia superba* Dana, is the dominant prey in open waters and in pack ice (Ainley *et al*. 1992). In addition, these authors found that fish (especially *Electrona antarctica*) and squid became more important prey items in winter. Although Ainley *et al*. (1992) did not recover *Pleuragramma antarcticum* in their penguin stomach samples, data from ornithogenic sediments at Palmer Station (64°04'W, 64°46'S), Anvers Island, and Rothera Point (67°34'S, 68°08'W), Adelaide Island, indicate it was an important prey species (with *Psychroteuthis glacialis*) for Adélie penguins in the past (Emslie *et al*. 1998, Emslie & McDaniel 2002). *Pleuragramma antarcticum* abundance in the sediments also appears to correlate with cooling periods, presumable when more sea ice would be present, in the Antarctic Peninsula region (Emslie *et al*. 1998), a pattern opposite that of the Ross Sea.

Other nototheniids represented in the sediments at Ross Island, *Trematomus* and *Notothenia* species, are also circum-Antarctic in their distributions and known to feed on krill (Miller 1993). These species are found well within the foraging depth of Adélie penguins (Williams 1995), especially *N. neglecta* Nybelin juveniles, which occur within 1–10 m of the surface (Miller 1993). These nototheniids perhaps are taken when penguins are foraging in krill swarms.

Squid remains

The mesopelagic squid *Psychroteuthis glacialis* was the most abundant cephalopod prey identified in the ornithogenic soils. Though there are few records of cephalopod predation by Adélie penguins, one study in Adélie Land found that *P. glacialis* comprised 3% of the diet by mass in some adult penguins (Offredo *et al*. 1985). Even though *P. glacialis* is considered a common, circum-Antarctic species (Lu & Williams 1994), little is known concerning its distribution in the Ross Sea. *P. glacialis* does comprise a small but significant part of emperor penguin and other seabird diets in the Ross Sea (Ainley *et al*. 1984, Cherel & Kooyman 1998), though it has not been identified as a component of Adélie penguin diet in this region (Emison 1968, Paulin 1975, van Heezik 1988, Ainley *et al*. 1998). Larval squid possibly could be taken opportunistically while Adélie penguins are foraging in krill swarms. In the Antarctic Peninsula, *P. glacialis* may comprise up to 44% by mass of Adélie penguin diet in winter (Ainley *et al*. 1992).

Our data on relative abundance of prey species can be compared to similar data from the Antarctic Peninsula region (Emslie *et al*. 1998, Emslie & McDaniel 2002). In sites of the same age as those in the Ross Sea, *Pleuragramma antarcticum* is almost four times as abundant (26.95 MNI per litre; Cape Crozier, Test Pit 1, Levels 1–4) in sediments from Ross Island than those from Rothera Point, Adelaide Island (6.80 MNI per litre; Emslie & McDaniel 2002). This pattern agrees with a review of diet samples throughout Antarctica by Ainley (2002) that indicates *P. antarcticum* is more important in Adélie penguin diet in the southern Ross Sea than in the Antarctic Peninsula where krill (*Euphausia superba*) is the primary prey.

Conversely, *Psychroteuthis glacialis* is much more prevalent (more than seven times) in similar aged sediments from Rothera Point (1.38 MNI per litre; Emslie & McDaniel 2002) than in those from Ross Island (0.18 MNI per litre). Squid also appears to be a more important component of Adélie penguin diet near Palmer Station than at Ross Island, though this comparison cannot be easily quantified (Emslie *et al*. 1998). If Adélie penguins in the Antarctic Peninsula are foraging over deeper water than those in the southern Ross Sea as suggested by Ainley (2002), penguins in the former region could have greater opportunities to prey on *P. glacialis* when it rises from depth. Additional data from ornithogenic soils throughout Antarctica will help verify these regional dietary trends.

Conclusions

Results from several studies (Emslie *et al*. 1998, Emslie & McDaniel 2002, Ainley 2002) demonstrate how climate change, bathymetry, and other factors are important in determining the prey available to foraging Adélie penguins. Ainley (2002) argues that Adélie penguins, like many seabirds, are generalists. This suggests that a perceived change in the abundance of fish in Adélie penguin diet, if not an artefact of penguin physiology (e.g. increase in metabolic activities) or other factors, reflects either the relative availability of the prey species in the marine environment or changes in environmental conditions (i.e., amount of sea ice). If true, and if the relative abundance of krill and fish in penguin diet varies proportionally, assumptions may be made on past marine conditions based on non-krill prey in ornithogenic sediments. Further studies of the ornithogenic soils in the southern Ross Sea region, coupled with tools such as stable-isotope analyses, may help resolve this issue.

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