

Steven D. Emslie · Jennifer D. McDaniel

Adélie penguin diet and climate change during the middle to late Holocene in northern Marguerite Bay, Antarctic Peninsula

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Abstract We investigated one active and three abandoned Adélie penguin (*Pygoscelis adeliae*) colonies in northern Marguerite Bay, Antarctic Peninsula, during austral summer 2000. Extinct colonies were located by ground survey on small islands and recognized by concentrations of nest pebbles. The colonies were excavated to recover organic remains from ornithogenic soils. Radiocarbon dates on penguin bone and eggshell provided a 6,000-year occupation history after correction for the marine-carbon reservoir effect; this history was compared to the paleoclimate record (ice cores and marine sediments) to assess patterns in occupation by penguins with episodes of climate change. We quantified prey remains recovered from the sites to examine potential dietary shifts by penguins with climatic change. Two species, Antarctic silverfish (*Pleuragramma antarcticum*) and squid (*Psychroteuthis glacialis*), were most commonly represented in the sediments. The data indicate that silverfish may have been exploited more during cool, and squid in warm climatic intervals in the past.

Introduction

Investigations of abandoned penguin colonies have been providing considerable information on the occupation history and paleobiology of penguins in Antarctica since ornithogenic soils that characterize these sites were first recognized and described by Syroechkovsky (1959). Summaries of these investigations (see Campbell and Claridge 1987; Tatur 1989; Emslie et al. 1998) indicate the wealth of paleoecological data that can be obtained from these sites. Here, we excavated ornithogenic soils at one modern and three abandoned Adélie penguin

(*Pygoscelis adeliae*) colonies near Rothera Point, Adelaide Island, in northern Marguerite Bay in the Antarctic Peninsula. Our objective was to determine the occupation history and diet of Adélie penguins that once bred there.

Adélie penguins feed primarily on krill (*Euphausia superba*; Williams 1995) and probably did so in the past. However, other prey taxa appear to vary in importance in penguin diet, perhaps in relation to climate and marine conditions. These taxa include fish and squid and can account for up to 32.3 and 0.4% of the diet by weight, respectively, in Adélie penguins (Williams 1995). Moreover, it is likely that squid are more important in the penguin diet than indicated by these data. One of the more common species identified in the diet of Antarctic seals and seabirds, *Psychroteuthis glacialis*, is a mesopelagic species that may not be available to foraging penguins until larval forms occur near the surface in late summer (Offredo et al. 1985; Lu and Williams 1994). Since most diet studies of penguins are conducted during the chick-rearing period, the role of squid in penguin diet may be under-represented. In addition, previous investigations at Palmer Station, Anvers Island, have indicated that Adélie penguins may have altered the relative abundance of fish and squid in their diet over the past 700 years in relation to climate change (Emslie et al. 1998).

We completed radiocarbon dates on penguin bones and eggshell fragments recovered from ornithogenic soils at Rothera to determine an occupation history for this region. This history was compared to the paleoclimatic record to correlate penguin occupation periods with warming and cooling events in the past. We also quantified prey remains recovered from the colonies to determine if shifts in the relative abundance of specific prey taxa could be correlated with climate events. We assume that long-term changes in penguin populations result ultimately from climate change, although other short-term factors can be important (e.g., predation, changes in direction of prevailing winds; Emslie et al. 1995; Fraser and Patterson 1997).

S.D. Emslie (✉) · J.D. McDaniel
Department of Biological Sciences,
University of North Carolina, Wilmington,
NC 28403, USA
E-mail: emslied@uncwil.edu

Materials and methods

Rothera Point (67°34'S, 68°07'W) is located on the southeast coast of Adelaide Island (Fig. 1). It was first visited by personnel of the British Antarctic Survey in 1974–1975 and construction of the station began in 1976 (British Antarctic Survey 1995). No active penguin colonies were reported in the area at that time or since. The closest colonies include a large concentration of Adélie penguins at Avian and Ginger Islands, 60 km to the south, and a small emperor penguin (*Aptenodytes forsteri*) colony on the Dion Islands (Woehler 1993). Smith (1996) reported potential ornithogenic soils on Rothera Point and nearby islands, but no sampling of these soils was completed.

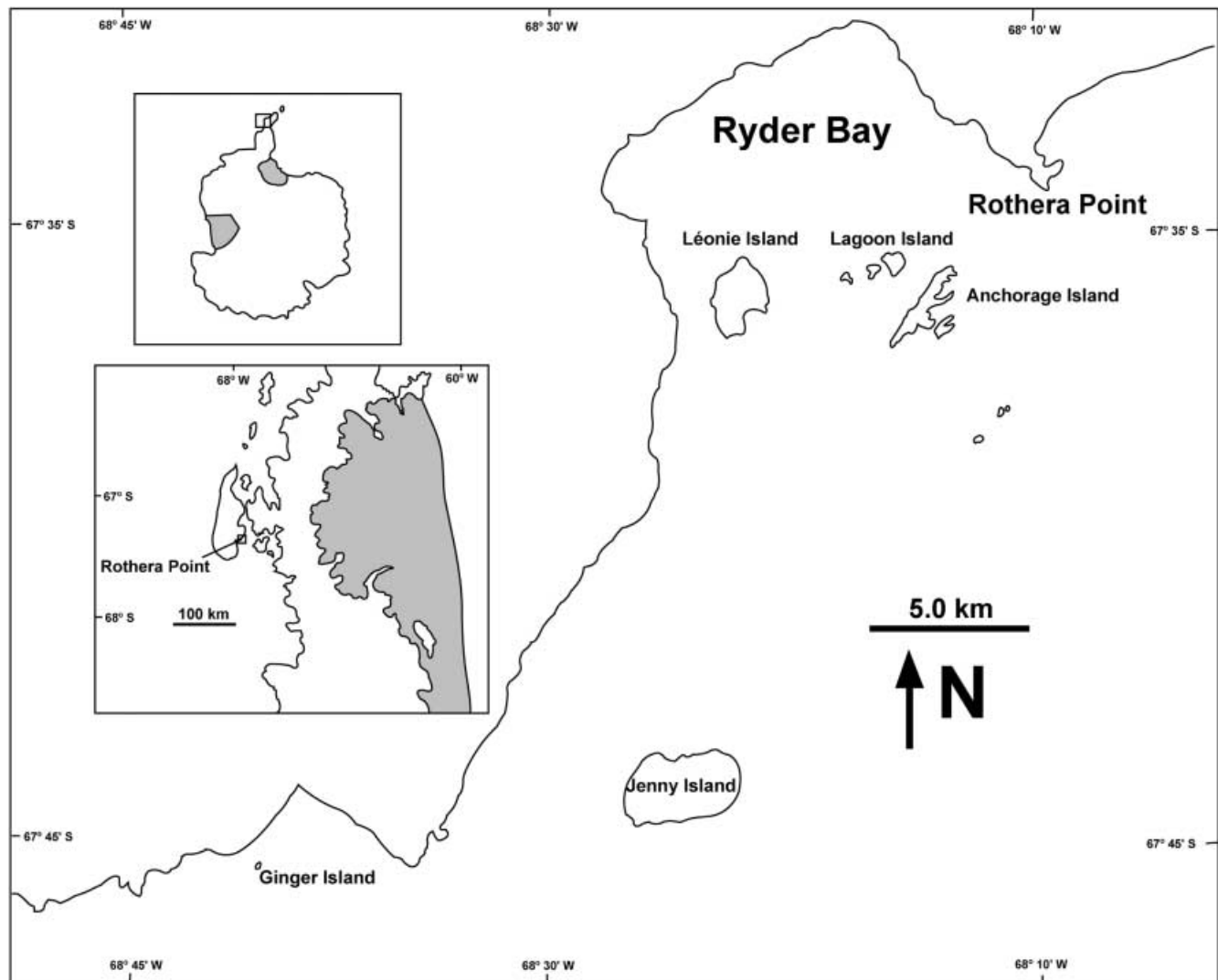
We conducted research at Rothera Station in January and February 2000. Six islands in Ryder Bay were visited by zodiac to complete ground surveys: Anchorage, Lagoon (3 islands in group), Leonie, and Killingbeck (Fig. 1). In addition, we accessed Ginger Island (67°45'S, 68°41'W) by ship. Surface surveys on most islands were hampered by unusually persistent snow cover during summer 2000. However, we were able to locate four sites on the largest and

northwest island of the Lagoon Island group. These sites were excavated to recover organic remains preserved in ornithogenic soils, and were designated as sites 1–4.

Each site was excavated by establishing a 1 × 1 m test pit. Loose surface pebbles (designated as level 1) were removed and sorted in the field to recover bones and other organic remains. The depth of these pebbles ranged from 5 to 10 cm. Excavations began below these loose pebbles where ornithogenic soils, characterized by a reddish-brown color, were first encountered. The test pit was excavated in 5-cm levels; all sediments from each level were quantified by volume using 16-l buckets and washed through 3 screens with mesh sizes of 0.64, 0.32, and 0.025 cm². These sediments were rewashed in the laboratory, dried, and sorted using a low-power binocular microscope to recover all organic remains. Each test pit was backfilled with pebbles and rocks at the completion of excavations.

Most penguin bones from the sites were too fragmentary for identification and all are assumed to represent Adélie penguin, as the nearest current breeding sites of chinstrap (*Pygoscelis antarctica*) and gentoo (*Pygoscelis papua*) penguins, the two closest species to Adélies in size and morphology, are approximately 210–370 km to the north (Woehler 1993). Four bone samples from sites 2 (level 2) and 3 (level 5) from Lagoon Island were submitted to D. Lambert (Massey University, New Zealand) for DNA extraction and identification. These samples were processed using primers L-12SE and H-12SF2 (D. Lambert, personal communication).

Fig. 1 Map showing the location of Rothera Point on Adelaide Island (*inset*) with detail of Ryder Bay and islands discussed in the text. The three abandoned penguin colonies (sites 2–4) are on Lagoon Island (largest and most western Island in group)



Radiocarbon analyses were completed on small fragments of penguin bone from selected stratigraphic levels at Ginger Island and sites 2, 3, and 4 on Lagoon Island. Site 1, an apparent molting site based on the high concentration of bones and feathers found in the sediments but no eggshell fragments, was not dated. Each sample was weighed and subjected to Accelerator Mass Spectrometry (AMS) analysis at Beta Analytic, Miami. Conventional dates (in ^{14}C years BP) were corrected by subtracting a predetermined ΔR value of 700 ± 50 BP (see Emslie 1995 for determination of this value) and calibrated using the MARINE98 database of Stuiver and Reimer (1993) and Stuiver et al. (1986, 1998) and the Pretoria/Beta Analytic calibration program at Beta Analytic. The resulting calibrated dates are reported in calendar years before present (BP). Gaps in the stratigraphic record colony sediments, based on radiocarbon analyses, are assumed to represent periods of abandonment by breeding penguins.

Prey remains from ornithogenic soils (otoliths and squid beaks) were identified by W. Walker, using comparative collections at the National Marine Mammal Laboratory, Seattle, Washington. We quantified by the total number of identifiable specimens and the minimum number of individuals (MNI) represented for each taxon. The MNI was calculated for fish species by counting the number of complete otoliths of known side (right or left) and using the greater value of the two sides. In addition, fragmentary otoliths of unknown side were quantified by first dividing their number in half to obtain a conservative estimate for total number of whole otoliths. This latter number was halved again to further estimate the number of right and left sides represented. This value was then added to the MNI determined from complete otoliths to yield a total MNI for the sample. For squid, MNI was determined from the larger number of upper or lower mandibles, partial and complete, representing each species. MNIs from similarly aged stratigraphic levels were combined and treated as one sample unit, rather than analyzed by each level. To compare the relative importance of prey taxa in Adélie penguin diet from different-aged stratigraphic deposits, it was necessary to correct for the amount of sediment excavated at each site. Accordingly, we calculated the relative density of prey taxa by dividing MNI values by the volume (in liters) of sediments from each sample unit.

Results

Of 4 DNA samples, only 1 from site 3, level 5 on Lagoon Island could be identified to species and represents

Adélie penguin. The other three samples produced no or low yield DNA, or were contaminated (D. Lambert, personal communication). Twelve radiocarbon dates from the three abandoned colonies on Lagoon Island (sites 2, 3, 4), and four from the active colony at Ginger Island provide an estimate for the occupation history of Adélie penguins in this region (Table 1). Seven occupation periods based on stratigraphic sample units, including modern, are represented among the sites (Table 2). These dates indicate that penguins first occupied Lagoon Island at approximately 6,000 BP. The island appears to have been abandoned by 5,000 BP, and then reoccupied by penguins from 4,000 to 3,265 BP. At that time, the island was again abandoned, with a subsequent occupation occurring from 2,750 to 1,715 BP at site 3, and 1,490 to 1,220 BP at site 4. Another gap in the radiocarbon chronology is present until the final occupation of site 2 on Lagoon Island from 895 to 650 BP (Table 1). At Ginger Island, Adélie penguins apparently occupied this site as early as 2,275 BP, but may have abandoned it between 1,900 and 720 BP. Reoccupation of this island occurred from 720 to 405 BP and perhaps has been continuous since that time. However, the top 3 levels from this site were analyzed separately as modern in age based on 1 date from level 3 that was too young for a calibrated range (Table 1).

Dietary remains were quantified from all sites based on this occupation history (Table 3). These data indicate considerable diversity in prey represented from these sites, especially at Ginger Island. Two taxa of squid, *Psychroteuthis glacialis* and *Brachioteuthis* sp., are well represented in the younger deposits while primarily only unidentifiable fragments occur in the older sites. Eight families and 32 taxa of fish are represented, also with greater numbers and diversity in the younger deposits, with the exception of *Pleuragramma antarcticum*. This species varies in abundance, both in MNIs

Table 1 Radiocarbon dates (in either ^{14}C or calendar years BP) from penguin bone and eggshell from Ginger and Lagoon Islands, Antarctic Peninsula

Site/Provenience	Species	Material	Lab. no.	Conventional date (^{14}C years BP)	Corrected date (^{14}C years BP)	Calibrated range (2σ) (cal. years BP)
Ginger Island						
TP 1, level 3	<i>Pygoscelis adeliae</i>	Bone	Beta 141904	1090 ± 40	390 ± 60	—
TP 1, level 4	<i>P. adeliae</i>	Bone	Beta 141905	1580 ± 50	880 ± 70	615–405
TP 1, level 5	<i>P. adeliae</i>	Bone	Beta 141906	1770 ± 40	1070 ± 60	720–535
TP 1, level 7	<i>P. adeliae</i>	Bone	Beta 144171	3130 ± 40	2430 ± 65	2275–1900
Lagoon Island						
Site 2, TP 1, level 2	<i>Pygoscelis</i> sp.	Bone	Beta 141907	1910 ± 40	1210 ± 60	895–650
Site 2, TP 1, level 3	<i>Pygoscelis</i> sp.	Bone	Beta 141908	4440 ± 50	3740 ± 70	3835–3470
Site 2, TP 1, level 4	<i>Pygoscelis</i> sp.	Bone	Beta 141909	4390 ± 50	3690 ± 70	3800–3435
Site 2, TP 1, level 5	<i>Pygoscelis</i> sp.	Bone	Beta 141910	4550 ± 50	3850 ± 70	3975–3625
Site 2, TP 1, level 6	<i>Pygoscelis</i> sp.	Bone	Beta 141911	4240 ± 50	3540 ± 70	3585–3265
Site 3, TP 1, level 2	<i>Pygoscelis</i> sp.	Bone	Beta 141912	2980 ± 50	2280 ± 70	2050–1715
Site 3, TP 1, level 3	<i>Pygoscelis</i> sp.	Bone	Beta 141913	3510 ± 70	2810 ± 90	2750–2315
Site 3, TP 1, level 4	<i>Pygoscelis</i> sp.	Bone	Beta 141914	5610 ± 80	4910 ± 95	5460–4950
Site 3, TP 1, level 5	<i>Pygoscelis</i> sp.	Bone	Beta 141915	5920 ± 50	5220 ± 70	5715–5450
Site 3, TP 1, level 5	<i>Pygoscelis</i> sp.	Bone	Beta 141916	6080 ± 50	5380 ± 70	5900–5590
Site 4, TP 1, level 2	<i>Pygoscelis</i> sp.	Bone	Beta 141917	2490 ± 50	1790 ± 70	1490–1220
Site 4, TP 1, level 4	<i>Pygoscelis</i> sp.	Eggshell	Beta 144170	5550 ± 40	4850 ± 65	5305–4950

Table 2 Volume of matrix (in liters) excavated from modern and abandoned penguin colonies at Lagoon and Ginger Islands, 2000. The matrix is separated by site level and age as determined from the radiocarbon chronology (Table 1). Site acronyms are: *GI L1–3* Ginger Island levels 1–3; *GI L4–5* Ginger Island levels 4 and 5; *La2 L2* Lagoon Island site 2 level 2; *La4 L2* Lagoon Island site 4 level 2; *La3 L2–3* Lagoon Island site 3 levels 2 and 3; *GI L7* Ginger Island level 7; *La2 L3–6* Lagoon Island site 2 levels 3–6; *La3 L4–5* Lagoon Island site 3 levels 4 and 5

Time period	Site	Age (BP)	Matrix volume (l)
Modern	GI L1–3	Modern	71
1	GI L4–5	405–720	66
2	La2 L2	650–895	45
3	La4 L2	1220–1490	32
4	La3 L2–3, GI L7	1715–2750	98
5	La2 L3–6	3265–3975	160
6	La3 L4–5, La4 L4	4950–5900	96

and MNIs per liter of sediments, among the occupation periods while squid declines in abundance with older ages (Fig. 2). Other fish that are well represented in the fauna include *Trematomus* sp., *Notothenia* sp., and *Electrona antarctica*.

Discussion

The occupation history of Adélie penguins in northern Marguerite Bay coincides with the paleoclimatic record. This record, based on studies of ice cores and marine sediments, is summarized by Björck et al. (1993, 1996) and Ingólfsson et al. (1998) and indicates that a warming event and glacial retreat occurred in the Antarctic Peninsula at approximately 6,000 BP. This retreat coincides with the first occupation of Lagoon Island by Adélie penguins. It is likely that the island was covered with ice or snow prior to this event, or extensive sea ice blocked access to the island, but it then became accessible as ice-free terrain to nesting penguins by 6,000 BP. This occupation lasted for approximately 1,000 years when another glacial advance is recorded at 5,000 BP. Adélie penguins abandoned Lagoon Island at that time, perhaps due to increased snow or ice cover on the island. A gap in the occupation history extended from 4,950 to 3,975 BP before site 2 on Lagoon Island was occupied. At that time, another warming event, known as the “penguin optimum” due to increased occupation of sites in the Ross Sea from approximately 3,000 to 4,000 BP (Baroni and Orombelli 1994), or the Holocene optimum in the Antarctic Peninsula (Björck et al. 1993, 1996), probably re-exposed terrain for nesting penguins at Rothera.

A briefer gap in the occupation history occurs from 3,265 to 2,750 BP after which site 3 is reoccupied on Lagoon Island. In addition, Ginger Island is first occupied at 2,275 BP, implying that favorable conditions for nesting penguins continued until 1,715 BP. By that time, all sites were again abandoned until reoccupation of site 2 at 895 BP and Ginger Island at 720 BP. The climatic

record is less clear during these occupation cycles. This period of the Holocene had a series of glacial advances and retreats and it is likely that the occupations again correlate with glacial retreats. Additional data, however, are needed to refine the paleoclimatic record. Ginger Island may have been abandoned by 405 BP until the modern occupation began. This abandonment corresponds with the onset of the Little Ice Age (LIA, 1,500–1,850 AD; Grove 1988) and it is possible that snow and ice cover again prevented occupation of this island. Occupation of Lagoon Island also ended before the LIA at 650 BP. Additional comparisons of Adélie and chinstrap penguin occupation of the Antarctic Peninsula with climate change during the late Holocene are discussed by Emslie (2001).

This occupation history can be compared with relative changes in prey taxa, other than krill, that occur in the ornithogenic sediments at each site. The diversity of fish and squid taxa identified from these prey remains is relatively high, especially at Ginger Island (Table 3). The high diversity of prey at this latter site may be related to its younger age where diagenetic processes have not affected the preservation of organic remains as much as at older sites. This preservation bias is particularly evident with the squid remains. Although it is possible that squid has been important in the diet of penguins only within the past 720 years, it is more likely that the chitonous beaks are crushed and fragmented by freeze-thaw actions through time, more so than otoliths, which remain well represented in the older deposits. The large number of beak fragments recovered from deposits dating to two warming events at 5,900–4,950 and 2,750–1,715 BP (calendar years, Tables 1 and 3) support this conclusion and suggest that squid may have been important in penguin diet during these periods.

The most common species of squid represented at Rothera, *Psychroteuthis glacialis*, has a circumantarctic distribution and is probably one of the more common squid in the Southern Ocean (Offredo et al. 1985; Gröger et al. 2000). It is mesopelagic and occurs at depths from 200 to 700 m (Sweeney et al. 1992). However, Lu and Williams (1994) found larval forms (4–18 mm length) of this species in Prydz Bay at shallow depths (exact depth not specified) while larger specimens were caught only in the bottom trawls at depths of 430–530 m. Diet studies of Adélie penguins indicate that squid is rare or absent as a prey item, at least during the breeding season. Cephalopods compose only <0.4% of the diet by weight at Adélie Land and Davis, Antarctica (Williams 1995). Ornithogenic soils at Palmer Station, however, also contained an abundance of squid remains (especially *Psychroteuthis glacialis*) indicating that this species has been, and continues to be an important component of Adélie penguin diet (Emslie et al. 1998). *Psychroteuthis glacialis* also has been reported in the diet of elephant seals, as well as other seabirds in Antarctica (Lubimova 1985; Rodhouse et al. 1992; Sweeney et al. 1992; Croxall and Prince 1994; Slip 1995; Williams 1995; Danieri et al. 2000).

Table 3 Squid and fish taxa identified from beaks and otoliths recovered from modern and abandoned colonies of Adelie penguins, northern Marguerite Bay. Total number of identifiable specimens and minimum number of individuals (*MNI*; in parentheses) are provided for each taxon by dated stratigraphic deposits (see Table 2); for *Psychroteuthis glacialis* and *Pleuragramma antarcticum*, the second row of data gives the ratio of MNI per liter of sediments excavated from the dated deposits (see Table 2)

Taxon	GI L1–3 Modern	GI L4–5 720–405	La2L2 895–650	La4L2 1490–1220	La3L2–3, GI L7 2750–1715	La2L3–6 3975–3265	La3L4–5, La4L4 4950–5900
Cephalopoda: Teuthioidea							
<i>Psychroteuthis</i>	202 (98)	233 (123)	39 (26)	7 (3)	3 (2)	3 (3)	0 (0)
<i>glacialis</i>	1.38	1.86	0.58	0.09	0.02	0.02	0
<i>Psychroteuthis</i>	100	55	1				
<i>glacialis</i> fragments							
Unident. beak	250	77	55	11	3 (3)		
fragments (probably <i>P. glacialis</i>)							
<i>Brachioteuthis</i> sp.	28 (15)	26 (11)			1 (1)	1 (1)	
Unident. beak	23	76		1	1	1	59 (59)
fragments							
Unident. Oegopsid			1		80	13	9 (9)
fragments							
Unident. Octopoda		1		1	1		
Osteichthyes: Nototheniidae							
<i>Pleuragramma</i>	1022 (483)	3198 (1161)	2201 (707)	3670 (1230)	5141 (1802)	1422 (487)	1433 (540)
<i>antarcticum</i>	6.80	17.59	15.71	38.44	18.57	3.04	5.63
<i>Pleuragramma</i>			1500+	378	330	90	60
<i>antarcticum</i> fragments							
<i>Trematomus newnesi</i>		4 (3)	4 (3)	1 (1)	26 (14)	2 (2)	
<i>Trematomus</i> cf.	5					1 (1)	
<i>T. newnesi</i>							
<i>Trematomus</i> cf.		1 (1)					
<i>T. eulepidotus</i>							
<i>Trematomus</i> sp.	48 (26)	184 (92)	19 (10)	10 (7)	110 (52)	21 (14)	39 (24)
<i>Notothenia nudifrons</i>	2 (1)						
<i>Notothenia</i> cf.	14 (9)						
<i>N. nudifrons</i>							
<i>Notothenia</i> cf.	34 (18)						
<i>N. kempfi</i>							
<i>Notothenia</i> sp.	13 (7)	30 (21)	13 (8)	9 (7)	20 (12)	4 (4)	10 (7)
Unident.	310 (155)	2 (2)	10 (8)		2 (2)	2 (1)	
Nototheniidae							
Unident.				13 (7)			
Nototheniidae							
(probably							
<i>Trematomus</i> sp.)							
Unident.		79	24		9		
Notothenioidei							
fragments							
Family Harpagiferidae							
<i>Harpagifer</i> sp.		1 (1)					
Family Bathydraconidae							
<i>Cygnodraco mawsoni</i>			2 (1)				
Family Channichthyidae							
<i>Champscephalus</i> cf.	7 (4)						
<i>C. gunnari</i>							
<i>Champscephalus</i> sp.		1 (1)		1 (1)			(1)
<i>Pagetopsis</i> cf.	10 (6)						
<i>P. maculatus</i>							
cf. <i>Pagetopsis</i> sp.		4 (3)					
<i>Chionodraco</i> cf.		1 (1)					
<i>C. wilsoni</i>							
<i>Chionodraco</i> sp.	7 (5)				1 (1)	1 (1)	
<i>Channichthys</i> sp.	3 (2)						
Unident.	5 (4)	5 (3)		8 (4)	3 (9)	1 (1)	
Channichthyidae							
Unident.	118 (60)	119 (36)	23 (6)	91 (26)	92 (23)	31 (13)	28 (10)
Notothenioidei							

Table 3 (Contd.)

Taxon	GI L1–3 Modern	GI L4–5 720–405	La2L2 895–650	La4L2 1490–1220	La3L2–3, GI L7 2750–1715	La2L3–6 3975–3265	La3L4–5, La4L4 4950–5900
Family Myctophidae							
<i>Electrona antarctica</i>	19 (10)	11 (9)	1 (1)	32 (18)	11 (7)		
<i>Electrona carlsbergi</i>	3 (2)	1 (1)					
<i>Protomyctophum bolini</i>	6 (4)			2 (2)			
<i>Gymnoscopelus braueri</i>					1 (1)		
<i>Gymnoscopelus fraseri</i>		1 (1)					
<i>Lampanyctus</i> sp.					1 (1)		
Unident. Myctophidae	37 (19)	2 (1)			1 (1)	1 (1)	
Family Gempylidae							
<i>Paradiplospinus</i> cf. <i>P. gracilis</i>	2 (2)						
Family Zoarcidae	1 (1)				1 (1)		
Family Macrouridae	3 (3)				5 (3)		2 (1)
Unident. teleost	18	80	38	7	285	8	26
Non-sagittal otoliths (lapillae)	46	71	22	43	62	11	26

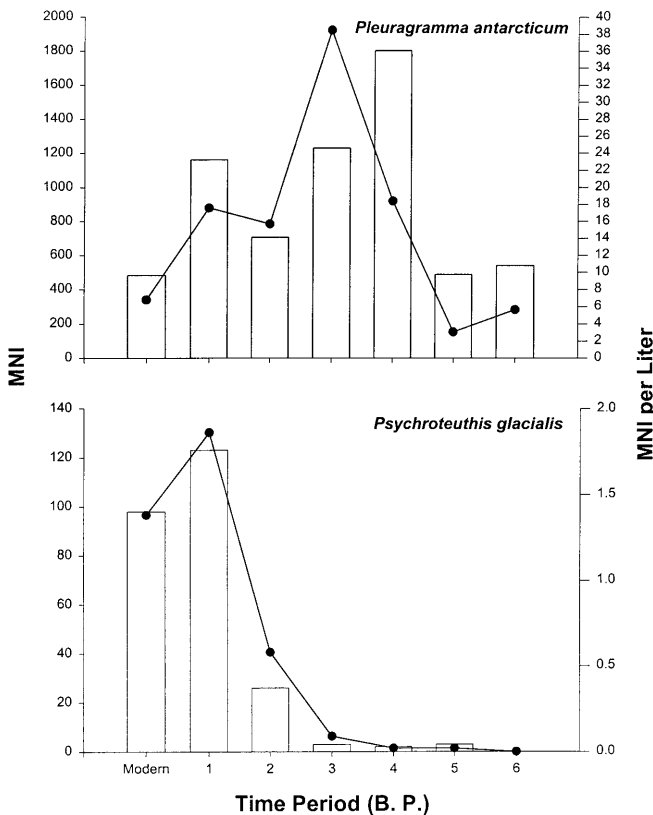


Fig. 2 The relative abundance of *Pleuragramma antarcticum* and *Psychroteuthis glacialis* in ornithogenic soils at Rothera Point. Both Minimum Number of Individuals (MNI, bars) and MNIs per liter of sediments (line) are graphed by time periods (in calendar years before present, BP) ranging from modern to six periods as defined in Table 2

The Antarctic silverfish (*Pleuragramma antarcticum*) appears to have been important in Adélie penguin diet in northern Marguerite Bay from 720 to 405 BP, as well as from 2,750 to 1,220 BP. This latter period follows the “penguin optimum” indicating that silverfish are depredated more during cooler intervals. This cooling interval extended until approximately 1,400 BP (Ingólfsson et al. 1998) and corresponds with the peaks in silverfish abundance at Lagoon Island (Fig. 2). There is additional evidence that another cooling period and glacial advance occurred in the South Shetland Islands at about 1,240 AD (Ingólfsson et al. 1998, citing Birkemajer 1981), corresponding with the increase in silverfish abundance in Adélie diet at Lagoon Island from 720 to 405 BP. Moreover, at Palmer Station silverfish was most abundant, and squid less so, in deposits dating to the LIA (Emslie et al. 1998).

Pleuragramma 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 circumantarctic distribution and has been reported in the diet of fur seals and whales, as well as other seabirds, in Antarctica (Gon and Heemstra 1990; Miller 1993; Radtke et al. 1993). Studies of Adélie penguins have indicated that fish compose < 4% by weight of the diet, but it was as high as 18% at Terre Adélie (Offredo et al. 1985). The larval and post-larval fish (< 30 mm length) and juveniles (30–110 mm), suitable for consumption by penguins, occur only in depths of less than 135 m and 50–400 m, respectively in Antarctica (Gon and Heemstra 1990; Miller 1993), well within the diving capabilities of Adélie penguins, which

are known to forage as deep as 170 m (Williams 1995). In the Weddell Sea, post-larval silverfish (8–25 mm in length) were more common near the surface than in deeper waters (Hubold 1984).

Other fish taxa also appear important in penguin diet. *Trematomus newnesi* is circumpolar in distribution in Antarctica (Miller 1993). It feeds largely on krill (*Euphausia superba*) and perhaps is taken by penguins while foraging in krill swarms. *Notothenia* cf. *N. kemp*i and *N. nudifrons* are well represented in the modern sediments at Ginger Island. *Notothenia* species feed on a variety of marine invertebrates, including krill, and *N. kemp*i has been reported from the South Shetland Islands (Miller 1993). *Electrona antarctica* is represented in sediments at Rothera dating back to 2,750 BP. This species also is circumpolar in distribution, feeds largely on krill and other invertebrates, and is often in shallow waters (<100 m depth), especially at night (Gon and Heemstra 1990). This last species, with *Pleuragramma antarcticum*, also was well represented in the ornithogenic sediments at Palmer Station (Emslie et al. 1998).

The importance of these other prey taxa recovered from these sites in the penguin diet is equivocal. At Ginger Island, where prey diversity is highest and the deposits are youngest in age, blue-eyed shags (*Phalacrocorax atriceps*) also nest. It is possible that otoliths from their prey have been deposited within the ornithogenic soils as these birds can wander into the penguin colony during or after the breeding period. However, contamination by these and other species is probably minimal since many of these fish taxa also have been identified in the diet of living pygoscelid penguins (Williams 1995) and in the sediments at other abandoned colonies (Emslie et al. 1998). In addition, diet studies of *Phalacrocorax atriceps* have indicated a preference for *Notothenia* (especially *N. coriiceps*) and *Harpagifer antarcticus* (Green et al. 1990; Favero et al. 1998), species absent or less well represented in the sediments at Ginger Island. Additional data from ornithogenic soils in Antarctica are needed to verify patterns in dietary shifts in penguins with climate change.

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