Antarctic Science 10 (3): 257–268 (1998)

Abandoned penguin colonies and environmental change in the Palmer Station area, Anvers Island, Antarctic Peninsula

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Abstract: Six abandoned colonies of Adélie penguin (*Pygoscelis adeliae*) were excavated near Palmer Station, Anvers Island, Antarctic Peninsula, to investigate the occupation history of this species. Sediments from each site yielded abundant fish bones and otoliths and squid beaks that represent prey remains deposited by penguins during the nesting period. Radiocarbon analyses indicate that colony occupation began prior to the Little Ice Age (LIA; 1500–1850 AD), with the oldest site dating to 644 yrs before present (BP; average reservoir-corrected date with 1s range, 603–679 yr BP). Food remains indicate that the non-euphausiid prey of penguins consisted primarily of a mesopelagic squid (*Psychroteuthis glacialis*) and two species of fish (*Pleuragramma antarcticum* and *Electrona antarctica*). The relative abundance of the first two prey taxa varied significantly among six sites ($\chi^2 > 34.6$; df = 10; $P < 0.001$) with colonies dating prior to the LIA having greater representation of squid, and less of silverfish, than those occupied during the LIA. Data from control excavations at three modern colonies indicate a diet similar to that of the pre-LIA sites. These results suggest that Adélie penguins may have changed their diet in response to warming and cooling cycles in the past. In addition, only Adélie penguins are known to have nested in the Palmer Station area prior to the 1950s; gentoo (*Pygoscelis papua*) and chinstrap (*P. antarctica*) penguins now breeding in this region have expanded their ranges southward in the Peninsula within the past 50 yrs, in correlation with pronounced regional warming.

Received 2 January 1998, accepted 29 May 1998

Key words: abandoned colonies, Adélie penguins, climate change, palaeodiet, palaeoecology

Introduction

Abandoned penguin colonies are becoming increasingly important for palaeoenvironmental research in Antarctica. The excellent preservation of organic remains in ornithogenic soils (formed from bird guano) in these sites can provide significant amounts of information on the palaeoecology and palaeoclimatology of this ecosystem. Previous investigations of abandoned colonies have provided information on nutrient cycling and soil chemistry and ecology in the Antarctic ecosystem (Ugolini 1972, Speir & Heine 1982, Speir & Cowling 1984, Speir & Ross 1984, Myrcha *et al.* 1985, Tatur 1987, 1989, Heine & Speir 1989, Tatur & Myrcha 1989, Myrcha & Tatur 1991, Tatur *et al.* 1997). Bones and other remains of penguins are well preserved at the sites and can provide further information on the age and palaeoecology of the species that once occupied them (Harrington & McKellar 1958, Spellerberg 1970, Stonehouse 1970, Bochenski 1985, Moors *et al.* 1988, Baroni & Orombelli 1991, 1994, Zale 1994, Emslie 1995).

Although studies of abandoned colonies in East Antarctica have provided data on past fluctuations in penguin populations related to climate change (Baroni & Orombelli 1991, 1994), detailed investigations in the Peninsula region are lacking (Emslie 1995). Our studies at Palmer Station, Anvers Island (64°04'W; 64°46'S), western Antarctic Peninsula, indicate that abandoned colonies contain a wealth of information not only on the occupation history of penguins, but also on their past diet and foraging strategies. Moreover, Fraser *et al.* (1992) proposed that populations of Adélie and chinstrap penguins (*Pygoscelis antarctica*) have fluctuated over the past 50 yrs in response to changing sea-ice conditions concurrent with a regional warming of 4–5°C. Data from abandoned rookeries may reflect similar responses by these species with climate change in the past.

Three species of penguins currently breed near Palmer Station. The most abundant species is the Adélie penguin (*Pygoscelis adeliae*) which has been studied in this region since 1973 (Parmelee 1992). In 1957, chinstrap penguins (*P. antarctica*) were recorded breeding in small colonies on the Joubin Islands (35 nests) and at Dream Island (2 nests); no gentoo penguins (*P. papua*) were known in the vicinity of Palmer Station until 1975 (Parmelee 1992). Both gentoo and chinstrap penguins have been increasing in this area since those first sightings, while Adélie penguins have declined (Fraser & Patterson 1997). The former two species may be expanding their breeding populations southward in the Antarctic Peninsula in response to climate change and a warming trend over the past 50 yrs that has increased the average mid-winter surface air temperature in this region by up to 4–5°C (Fraser *et al.* 1992, Smith *et al.* in press). If so, evidence for similar population responses may be found in the occupation record at abandoned penguin colonies. To address this question, six abandoned and three modern colonies were excavated in the Palmer Station area in summer 1996–97. Here, we present the results of the excavations with interpretations of the late Holocene environmental history of the region. The data also provide information on past diets and ecological responses by penguins to climatic change.

Methods

Nine abandoned penguin colonies were located in the Palmer Station area by ground surveys (Fig. 1). Areas rich in vegetation and/or where concentrations of pebbles were apparent were considered sites most likely to be former breeding colonies. Vegetation (moss, lichens, and grass) often grows more densely in former colonies, because of soil nutrient enrichment from penguin guano, than in areas that were not used by penguins (Tatur 1989, Myrcha & Tatur 1991, Tatur *et al.* 1997). Pebbles (used in nests) and bone concentrations on the surface also characterize the sites (Fig. 2). Areas meeting the criteria were tested by probing beneath the surface to locate additional evidence for a former colony (concentrated organic remains including bones, feathers, and eggshell fragments).

Once an abandoned colony was identified, a 1x1 m test pit was established within the site and excavated in 5–10 cm arbitrary levels, or by natural stratigraphical layers where apparent, until underlying bedrock was reached (Fig. 3). Volumetric measurement of all excavated sediments from each site was accomplished using 20-l buckets; the sediments were then washed through three nested screens with mesh sizes of 0.64, 0.32, and 0.025 cm^2. Organic material trapped in the top two screens was sorted and collected in the field; matrix in the 0.025 cm^2 mesh screen was dried, weighed to the nearest 0.1 g, and sorted under a low-power (x 5–10) binocular microscope. In this manner, most organic remains preserved

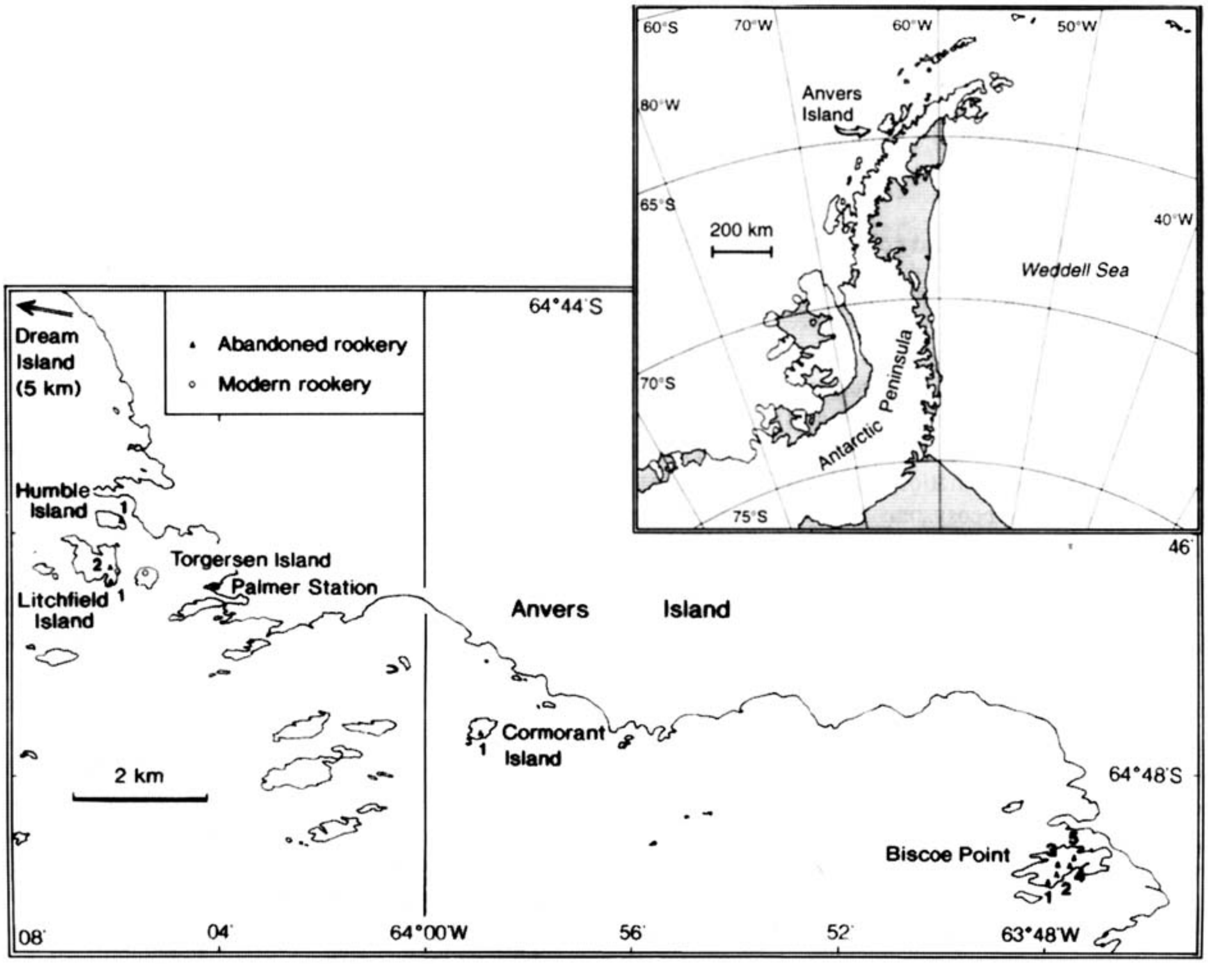

Fig. 1. Map of the Palmer Station area, Anvers Island, showing the location of islands and abandoned penguin colonies discussed in the text.

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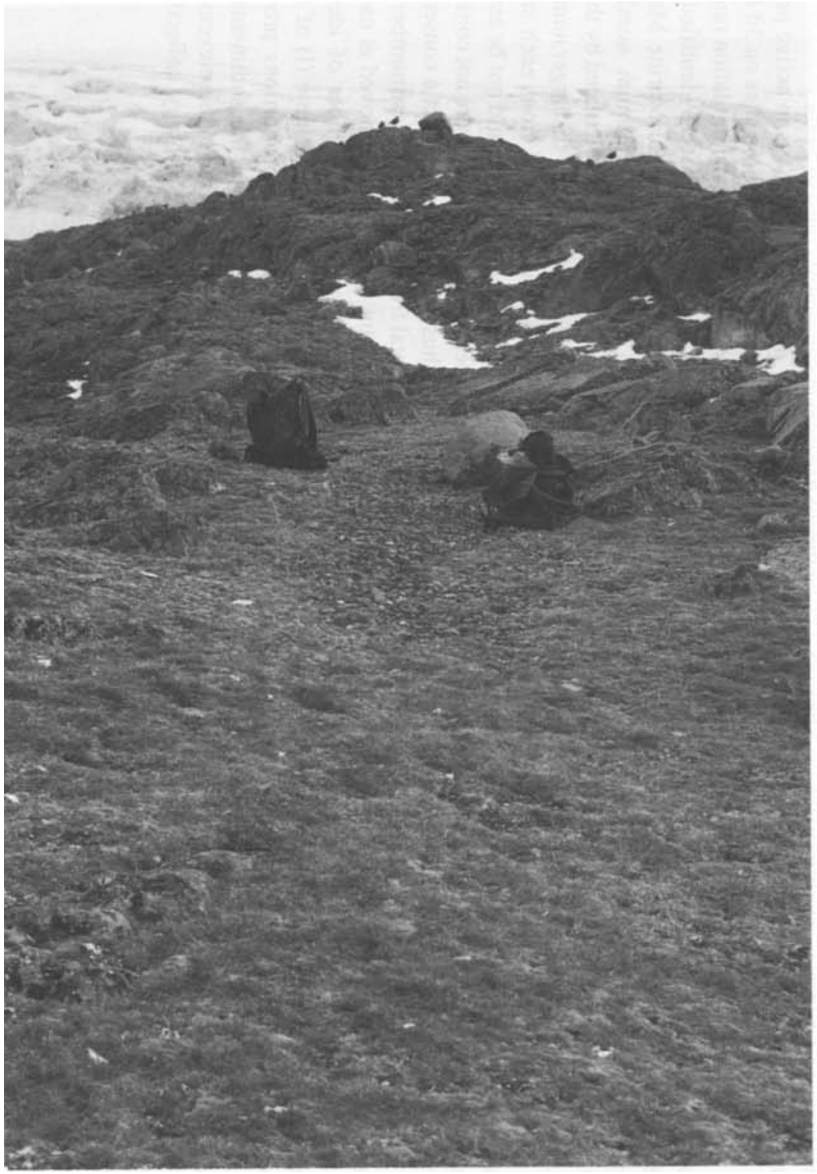

Fig. 2. View of the abandoned penguin colony at Site 3, Biscoe Point. Note the concentration of pebbles on the surface near the backpack, and the vegetation covering most of the site.

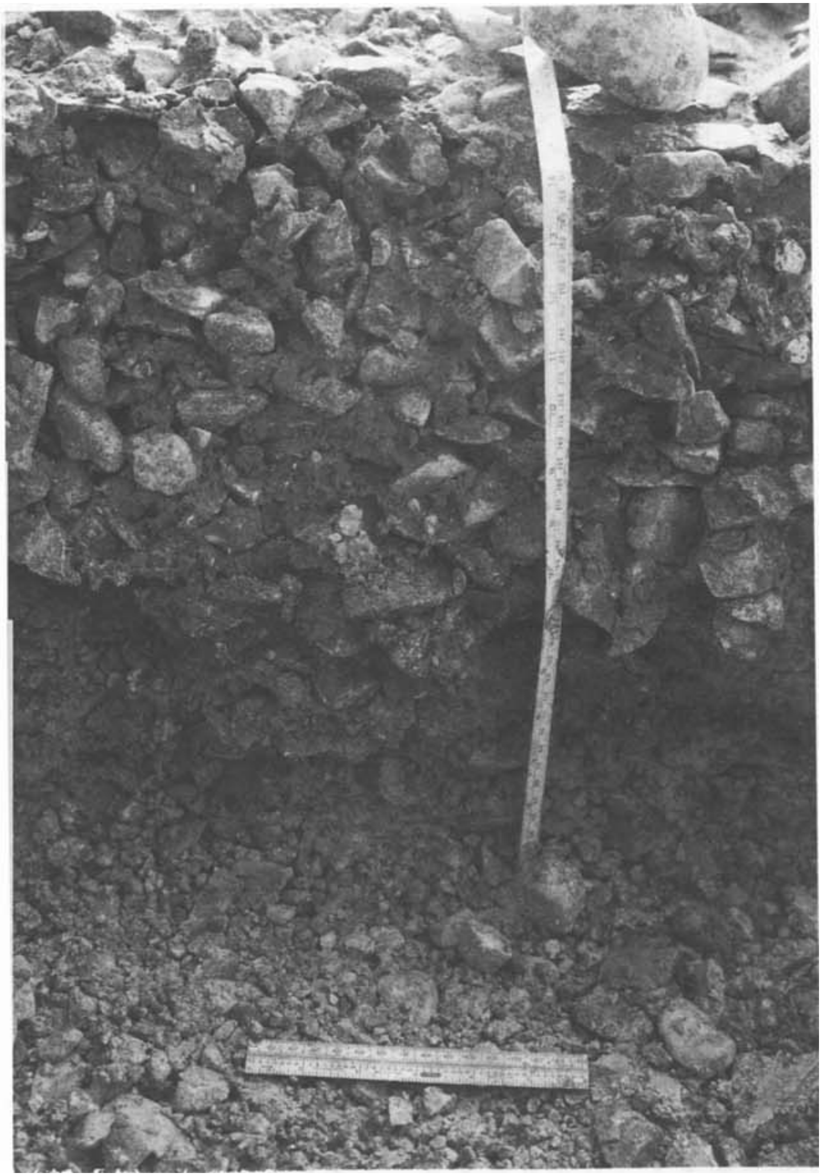

Fig. 3. Profile of Test Pit 1 at the modern Adélie penguin colony on Litchfield Island. Ornithogenic soils, comprised of pebbles and dark organic sediments, extended to a depth of 30 cm before greyish, finer-grained sediments and angular gravel were reached. Scales in centimetres.

in the sediments, including penguin bones, feathers, eggshell fragments, fish bones, scales, otoliths, and squid beaks, were recovered. All test pits were backfilled, and any surface vegetation replaced, at the conclusion of the excavations.

Three modern colonies also were excavated using similar techniques to act as controls against the number and kinds of organic remains recovered from the abandoned sites. These modern colonies were excavated late in the breeding season, after nesting birds had departed, so that no disturbances to occupied nests occurred. In addition, four sites in marine terraces away from any abandoned or modern colonies were excavated to act as additional controls on the amount and kinds of organic remains that accumulate in sediments outside of penguin colonies. The terraces were selected for their current heavy use by southern elephant seals (*Mirounga leonina*) and Antarctic fur seals (*Arctocephalus gazella*) to assess potential contamination of abandoned colonies by the activities of these species. The peak censuses for these animals on Litchfield Island in the summers of 1996–97 and 1997–98 ranged from 36–47 elephant seals and 83–261 fur seals. The six abandoned colonies that were excavated were located on Humble Island (1 site), Litchfield Island (2), and Cormorant Island (1), and at Biscoe Point (2). Modern colonies were excavated on Dream Island (1 chinstrap colony), Litchfield Island (1 recently abandoned Adélie penguin colony), and Torgersen Island (1 Adélie penguin colony; Fig. 1). Four samples from two marine terraces were collected on Litchfield Island.

Penguin bones recovered from the excavations were identified using the collections at the Florida Museum of Natural History (FLMNH), Gainesville. Species identifications were based on osteological characters described by Emslie (1995). Juvenile and adult individuals were also determined based on bone development, size, and porosity (Emslie 1995). Small portions (< 2 g) of bone were removed from identified elements from each site for accelerator mass spectrometry (AMS) radiocarbon analysis. These specimens were submitted to the University of Colorado Radiocarbon Laboratory, Boulder, where they underwent pretreatment and preparation for this analysis. All radiocarbon dates were corrected for the marine carbon-reservoir effect using the Calib 3.0 computer program that incorporates a calibration curve for the world ocean (Stuiver & Reimer 1993). A regional offset value (ΔR) of 700 ± 50 yr BP for the calibration curve was applied in this program as previously determined for the Antarctic Peninsula region (see Emslie 1995). All radiocarbon dates reported here are with the reservoir correction and a 1s range as calculated by the Calib program.

Accumulation rates of organic remains on modern penguin colonies were assessed by placing three 1x1 m fine-mesh (0.025 cm^2) screens in active colonies on Litchfield and Torgersen Islands. These screens were placed under a clean layer of pebbles in Colony 7B (525 breeding pairs in 1997) and Colony 14 (1059 breeding pairs) on Torgersen Island, and in Colony 7 (111 breeding pairs) on Litchfield Island, on 14 April 1997 after breeding birds had left their sites. One control screen was placed on an abandoned colony on Litchfield Island (see below). The screens were collected and washed on 30 March 1998, and all organic remains captured by these screens were sorted from the accumulated debris using a low-power binocular microscope. These data provide a means to assess accumulation rates of squid beaks, otoliths, and fish bones over a period of 381 days in active penguin colonies. Screens were replaced on these sites on 30 March 1998 to continue monitoring annual accumulation rates.

Fish bones, otoliths and squid beaks were identified using the reference collections at the National Marine Mammal Laboratory, Seattle, Washington. Minimum number of individuals (MNI) for each taxon was calculated by the total number of otoliths divided by two, or by the larger number of upper or lower squid beaks recovered from each sample. Fragmentary otoliths and beaks which could not be assigned to left or right or upper or lower portions were not considered in this calculation; thus, the numbers reflect a conservative estimate of the true total from each site. These numbers were corrected for the amount of sediment removed at each site (sample size) by dividing the total number of identified specimens and the MNI by the total volume (l) of matrix excavated per site. The resulting proportions provide a relative abundance of each taxon in the sediments from different sites. All specimens collected in these excavations are housed in the vertebrate palaeontology collections at FLMNH.

Table I. Matrix excavated from modern and abandoned penguin colonies in the Palmer Station area.

Site	Matrix volume (l)	Fine Sediments dry weight (g)
HI	80	1035
LI-1	160	593
LI-2	140	1131
*LI	220	1629
CI	140	1283
BP-1	80	3335
BP-2	120	1862
*DI	80	171
*TI	120	791
BT-1	40	975
BT-2	40	4448
BT-3	40	1473
BT-4	40	5003

Total volume of matrix in litres; dry weight (in grams) of sediments washed and trapped in the fine-mesh (0.025 cm^2) screen. Site acronyms are: HI, Humble Island; LI, Litchfield Island; CI, Cormorant Island; BP, Biscoe Point; TI, Torgersen Island; DI, Dream Island; BT, Beach Tests 1–4 on Litchfield Island. Numbers refer to site numbers of abandoned colonies. An asterisk (*) designates modern colonies that were excavated.

https://doi.org/10.1017/S0954102098000352 Published online by Cambridge University Press

Results

The total volume of sediments excavated from each modern and abandoned colony is presented in Table I with the dry weight of sediments trapped in the fine-mesh screen (0.025 cm²). The following is a brief description of each excavated site.

Humble Island

One abandoned colony was located on a rocky exposure on the north-east shore of the island. The site consisted of exposed and eroded pebble concentrations emerging beneath grass and other vegetation extending over an area of approximately 10 m in diameter. The vegetation was more extensive in previous years, but much has been removed over the past few years by the activities of fur and elephant seals now using the island. The sediments at this site were relatively shallow (10–20 cm depth) and, because of the rocky terrain, it was not possible to establish a 1x1 m test pit to sample the site. Instead, sediments were excavated laterally across the site until a sufficient sample had been removed for screening.

Litchfield Island

Two abandoned colonies were located and excavated on the south-east side of the island. The first site (Site 1) consisted of two pebble concentrations located on small hummocks, each approximately 5 m in diameter and 15 m apart. A 0.5 x 0.5 m test pit (TP 1) was placed in the southern hummock and excavated in two levels to a depth of 20 cm. The sediments consisted of pebbles and ornithogenic soils with organic debris throughout. The bottom of the pit was characterized by greyish fine sediment and angular gravel.

Test Pit 2 (1 x 1 m) was placed on the northern pebble concentration and produced more bone and organic remains than TP 1. It was also excavated in two 10 cm levels to bedrock with the sediments similar in characteristics as those of TP 1; only material from level 1 was analysed in detail and is presented here.

Site 2 was located approximately 35 m north of Site 1 and consisted of a pebble concentration surrounding a small rocky outcrop 10 m in diameter. A 1 x1 m test pit (TP 1) was placed on the south side of the pebble concentration and excavated in two 10 cm levels. A second test pit (TP 2) was placed adjacent to TP 1 to the south and only the first level (10 cm) was excavated. On 14 April 1997, a 1x1 m screen trap was placed on this site as a control against similar traps placed on active colonies.

A modern, recently abandoned (within the past 10 yrs) Adélie penguin colony was sampled on the east side of the island, 20 m east of Site 2, as a control site. A 1 x 1 test pit was excavated in three levels to a depth of 27–30 cm where greyish fine sediments and gravel were encountered. These latter sediments continued to bedrock at a depth of 60 cm; a clear break in soil colour and pebble content was apparent at the boundary between the ornithogenic soils and these lower sediments at 27–30 cm (Fig. 3).

Control excavations were also made at four locations in two marine terraces on this island. Forty litres of matrix were excavated from each of the four locations, designated as Beach Tests (BT) 1–4, two of which were on the south side of the island, and two on the east side. The sediments lacked the high concentration of pebbles and ornithogenic soils that characterized the colonies, and had a higher proportion of finer particles (sand, silt) as indicated by higher dry weights of the fine-screen concentrate compared to the colony sediments (Table I).

Cormorant Island

One abandoned colony was located near the centre of the island and consisted of a dense pebble concentration 10–15 m in diameter around a small, rocky outcrop. A single 1 x 1 m test pit was placed near the center of the pebble concentration and excavated in two levels to a depth of 20–22 cm until greyish fine sediments and gravel (similar to those on Litchfield Island discussed above) were encountered. Very few bones were recovered from the site, but abundant squid beaks and otoliths were preserved in the sediments.

Biscoe Point

Survey of this area revealed at least five abandoned colonies as recognized by small, dense pebble concentrations and penguin bones in the subsurface. The colonies were located across Biscoe Point (actually an island as exposed by retreating ice), from the tip to its base, as well as on marine terraces near the shore to the tops of high ridges or moraines near the center of the island. Two sites, one on a terrace above the south shore (Site 1) and one on the highest moraine in the centre (Site 5), were selected for excavation. Site 1 consisted of a 20 m-long pebble concentration that was so dense that no fine sediment, but only pebbles with some bones, were encountered in the top 10–15 cm of a 1 x 1 m test pit placed at the west end of the site. Level 2 consisted of fine sediment and pebbles to a depth of 20–25 cm before beach gravels and bedrock were reached. Dietary remains were recovered only from Level 2 sediments.

Site 5, located approximately 50 m above sea level, was similar to Site 1 in being characterized by a dense concentration of pebbles, but the area of the site was smaller (5–10 m diameter). As with Site 1, the first level of a 1 x 1 m test pit consisted only of pebbles and some bones. Level 2 extended to a depth of 20 cm and comprised pebbles and fine sediment from which dietary remains could be sifted. Excavations of Level 3, also with fine sediment and pebbles, were terminated when a fine greenish silt and gravel was encountered at a depth of approximately 30 cm.

Table II. Squid and fish identified from beaks and otoliths recovered from measured volumes of matrix excavated from abandoned colonies of Adélie penguin, Palmer Station area.

Taxon	Site HI	LI-1	LI-2	CI	BP-1	BP-5
Cephalopoda						
Psychroteuthis glacialis	26 (18)	205 (160)	303 (232)	371 (305)	261 (163)	306 (150)
	0.325 (0.225)	1.28 (1.0)	1.68 (1.29)	2.65 (2.18)	3.26 (2.04)	2.55 (1.25)
cf. *Psychroteuthis*	24	105	181	222	64	133
	0.3	0.66	1.01	1.59	0.8	1.11
Galiteuthis glacialis	1 (1)	2 (2)	2 (2)			1 (1)
Alluroteuthis antarctica			6 (6)	6 (6)		
Brachioteuthis sp.		9 (6)	4 (3)	12 (12)	1 (1)	3 (2)
cf. *Kondakovia* sp.				2 (1)		
Cranchiidae, indet.			1			2
Teuthoidea, indet.		1051	1622	83	575	
Eledonine octopod				56 (34)		
Octopoda, indet.				1		
Osteichthyes: Teleostei						
Pleuragramma antarcticum	41 (21)	84 (42)	223 (112)	7 (4)	6 (3)	11 (6)
	0.51 (0.26)	0.53 (0.26)	1.24 (0.62)	0.05 (0.029)	0.075 (0.038)	0.092 (0.05)
Electrona antarctica	3 (2)	6 (3)	21 (11)	2 (1)	11 (6)	18 (9)
	0.04 (0.025)	0.04 (0.02)	0.12 (0.061)	0.014 (0.01)	0.138 (0.075)	0.15 (0.075)
Krefftichthys anderssoni	1 (1)					
Gymnoscopelas braueri			1 (1)			
Gymnoscopelas cf. *G. nicholsi*		2 (1)	21 (11)			
Trematomus cf. *T. newnesi*			3 (2)			
Notothenia sp.			2 (1)			
Nototheniidae, indet.	14	15	30	5	1	3
Channichthyidae, indet.			3			
Myctophidae, indet.			1		1	
Teleostei, indet.	58	13	144	4	13	2
Vertebrae	76	145	1908	702	98	483

Total number of identifiable specimens and minimum number of individuals (MNI; in parentheses) represented for each taxon at each site is provided; for *Psychroteuthis glacialis*, cf. *Psychroteuthis*, *Pleuragramma antarcticum*, and *Electrona antarctica*, second line of data refers to ratios of total number of specimens and MNI's l^{-1} of sediments excavated at each site (see Table I). Site acronyms as for Table I.

Dream Island

A modern chinstrap colony on a rocky point on this island has been increasing in size since it was first discovered in 1957 (2 nests; Parmelee 1992) and now consists of over 250 breeding pairs. It was excavated by collecting guano, pebbles, and sediments deposited on and near nest sites. Most of the sediments consisted of fresh guano in shallow pockets (< 10 cm deep) above the rocky substrate.

Torgersen Island

A modern Adélie penguin colony was excavated on the north side of this island by placing a 1 x 1 m test pit within a dense pebble concentration. The pit was excavated in one level, to a depth of 15 cm, before encountering bedrock. Sediments consisted of pebbles and dark, ornithogenic soil throughout. The bottom of the pit was characterized by a thin lens (1 cm thick) of greyish fine sediment and gravel (similar to that of sites on Litchfield and Cormorant Islands described above) directly overlying the bedrock.

Identification and analysis of organic remains

All penguin bones recovered from the abandoned colonies were identified as *Pygoscelis* sp. or *P. adeliae*; no bones of *P. antarctica* or *P. papua* were recognized. The majority of bones from each site represented juvenile individuals, recognized by their incomplete ossification and porous surface, as would be expected at a breeding site (Emslie 1995).

Taxa of cephalopods and fish identified from abandoned colonies and control sites are given in Tables II & III. The most abundant taxa identified from all sites are a single species of squid (*Psychroteuthis glacialis*), Antarctic silverfish (*Pleuragramma antarcticum*), and lantern fish (*Electrona antarctica*). The number of identifiable specimens and MNI's for the first two of these taxa vary significantly between the abandoned colonies ($\chi^2 > 34.6$; df = 10; $P < 0.001$), but lantern fish do not ($\chi^2 < 16.1$; df = 10; $P < 0.1$). In contrast, the modern Adélie penguin colonies at Litchfield and Torgersen islands show no difference in numbers or MNI between sites for squid and lantern fish ($\chi^2 < 4.4$; df = 2; $P < 0.05$); only the total number of specimens (and not MNI) of silverfish is significantly different between these two sites (χ^2 = 8.3;

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Table III. Squid and fish identified from beaks and otoliths recovered from measured volumes of matrix excavated from modern colonies of Adélie and chinstrap penguin, and beach terraces, Palmer Station area.

	Site						
Taxon	LI	TI	DI	BT-1	BT-2	BT-3	BT-4
Cephalopoda							
Psychroteuthis glacialis	292 (215)	144 (108)	7 (5)	15 (12)	6 (4)		1 (1)
	1.33 (0.98)	1.20 (0.90)	0.09 (0.063)	0.38 (0.3)	0.15 (0.1)		0.03 (0.025)
cf. *Psychroteuthis*	185	64	3	18			
	0.84	0.53	0.038	0.45			
Galiteuthis glacialis	2 (2)	2 (2)	1 (1)				
Alluroteuthis antarctica	5 (5)						
Gonatus antarcticus			1 (1)				
Brachioteuthis sp.	1 (1)						
Kondakovia longimana				1 (1)			
Teuthoidea, indet.	1000	511			12	5	7
Osteichthyes: Teleostei							
Pleuragramma antarcticum	27 (14)	31 (16)	28 (14)	1 (1)			
	0.12 (0.064)	0.26 (0.13)	0.35 (0.2)	0.03 (0.03)			
Electrona antarctica	15 (8)	8 (4)	11 (6)				
	0.07 (0.04)	0.07 (0.03)	0.14 (0.08)				
Dissostichus cf. *D. mawsoni*		1 (1)					
Gymnoscopelas cf. *G. nicholsi*		2 (1)	6 (3)				
Lampanyctus sp.	1 (1)						
Nototheniidae, indet.	35	7	12				
Bathydraconidae, indet.	2						
Channichthyidae, indet.	2						
Myctophidae, indet.	1						
Teleostei, indet.	24	12	29				
Vertebrae	520	143	647	18	6		

Total number of identifiable specimens and minimum number of individuals (MNI; in parentheses) represented for each taxon at each site are provided; for *Psychroteuthis glacialis*, cf. *Psychroteuthis*, *Pleuragramma antarcticum*, and *Electrona antarctica*, second line of data refers to ratios of total number of specimens and MNI's l^{-1} of sediments excavated at each site (see Table I). Site acronyms as for Table I.

df = 2; $P < 0.025$). When these two sites are compared to prey remains from the chinstrap colony on Dream Island, all three prey taxa (number of specimens and MNI) vary significantly between sites ($\chi^2 > 13.4$; df = 4; $P < 0.01$).

The proportion of prey taxa based on the amount of sediments excavated may explain the significant variations in number of specimens and MNI's from each site. These data (Table II) indicate much higher proportions of *Psychroteuthis glacialis*, and lower of *Pleuragramma antarcticum*, from Cormorant Island and Sites 1 & 5 on Biscoe Point compared to Humble Island and Sites 1–2 on Litchfield Island. The two modern Adélie penguin colonies on Torgersen and Litchfield Island show few differences in the proportions of squid and fish represented at each. Both these sites also have a much higher proportion of squid, and lower of fish, compared to the modern chinstrap colony at Dream Island (Table III).

Except for Beach Test 1, control samples from marine terraces show much lower proportions of squid and fish remains (total number of specimens and MNIs per taxon) than in the modern and abandoned colonies. BT 1 had the highest proportion of *Psychroteuthis* in the sediments, similar to data from the abandoned colony on Humble Island, and higher than the modern chinstrap colony on Dream Island (Tables II & III). However, the total number of specimens of squid and silverfish remained significantly higher at Humble Island compared to BT 1 ($\chi^2 > 4.9$; df = 2; $P < 0.05$); though the MNI of squid did not ($\chi^2 = 3.6$; df = 1; $P < 0.1$).

Table IV. Squid and fish identified from beaks and otoliths from screen traps in active Adélie penguin colonies, 14 April 1997–30 March 1998 (381 d).

	Site			
Taxon	TI-7B	TI-14	LI-7	LI-C
Cephalopoda				
Psychroteuthis glacialis	32 (14)	7 (3)	2 (2)	1 (1)
Teuthoidea, indet.				
Fragments of beaks	48	13	5	2
Osteichthyes: Teleostei				
Pleuragramma antarcticum	1 (1)	1 (1)		
Electrona antarctica	3 (2)			
Gymnoscopelas sp.		1 (1)		
Myctophidae, indet.	1 (1)			
Vertebrae	53	5	2	
Other fragments	128	9	12	4

Total number of identifiable specimens and minimum number of individuals (MNI; in parentheses) represented in each sample are provided. Acronyms refer to: Torgersen Island Colony 7B (TI-7B) and 14 (TI-14), Litchfield Island Colony 7 (LI-7) and a control site (C) placed outside of active colonies.

Table V. Uncorrected and reservoir-corrected radiocarbon dates on penguin bones and squid beaks recovered from excavations of abandoned colonies of Adélie penguin, Palmer Station area.

Site/Provenence	Material	Lab. no. (CAMS)	Uncorrected date (BP)	Corrected date (BP)	Range (1 s) yr BP
Litchfield Island					
Site 1, TP 2, Level 1	Bone	42001	1380± 50	296	261 – 403
	Bone	42380	1300±50	257	136 – 291
Site 1, TP 2, Level 2	Bone	42002	1330±50	271	227 – 310
Site 2, TP 1, Level 1	Bone	41997	1230±60	136	0 – 261
Site 2, TP 1, Level 2	Bone	41998	1540±40	471	425 – 507
Site 2, TP 2, Level 1	Bone	41999	1360±50	286	251 – 359
Site 2, TP 2, Level 2	Bone	42000	1240±50	147	56 – 262
Modern TP 1, Level 3	Bone	42011	1170±60	–	–
Humble Island					
Site 1, Level 1	Bone	42003	1400±50	309	271 – 421
	Bone	42004	1360±40	286	254 – 334
	Bone	42005	790±50	–	–
	Bone	42006	1160±50	–	–
Biscoe Point					
Site 1, TP 1, Level 1	Bone	42007	1540±50	471	420 – 510
	Bone	42370	1530±50	465	411 – 505
Site 1, TP 1, Level 2	Bone	42371	1790±40	644	603 – 679
Site 2, Level 2	Bone	42377	1650±50	529	493 – 598
Site 3, Level 2	Bone	42378	1460±50	412	302 – 466
Site 4, Level 2	Bone	42379	1460±50	412	302 – 466
Site 5, TP 1, Level 1	Bone	42372	1350±50	281	245 – 329
	Bone	42373	1180±50	74	0 – 209
Site 5, TP 1, Level 2	Bone	42374	1600±40	504	468 – 538
	Bone	42375	1580±50	494	450 – 530
	Squid beak	38709	1580±50	494	450 – 530
Site 5, TP 1, Level 3	Bone	42376	1600±50	504	464 – 542
	Squid beak	38708	1650±50	529	493 – 598
Cormorant Island					
Site 1, TP 1, Level 2	Bone	42008	1700±50	558	518 – 636
	Bone	42009	1760±60	630	547 – 669
Torgersen Island					
Modern Colony, TP1,	Bone	42010	1190±40	92	0 – 221
Level 1, Lower Layer	Squid beak	38710	1280±50	246	120 – 281

All squid beaks are *Psychroteuthis glacialis* and all bones are *Pygoscelis adeliae*. Radiocarbon dates were corrected using a ΔR = 700±50 yrs as the calibration offset value for the Antarctic Peninsula region (see Emslie 1995) and the Calib 3.0 computer program of Stuiver & Reimer (1993).

Species richness of cephalopods was lowest from the abandoned colony at Humble Island (three taxa) and highest at Site 2 on Litchfield Island (six taxa); fish species richness also was highest at the latter site (nine taxa; Table II). In the modern colonies, species richness of cephalopods (five taxa) and fish (seven taxa) was highest at Litchfield Island, and similar between Torgersen and Dream islands (Table III).

Data from the screen traps on modern colonies further indicate that modern Adélie penguin diet includes squid and fish, especially at Colony 7B on Torgersen Island (Table IV). This latter colony is only half the size of Colony 14, but produced a much larger sample. Colony 7 on Litchfield Island produced the smallest sample of dietary remains in an active colony. As expected, the control screen on an abandoned colony captured the fewest organic remains.

Radiocarbon analyses

Uncorrected and corrected radiocarbon dates on penguin bones and squid beaks provide an occupation history of Adélie penguins in the Palmer Station area for at least the past 644 yrs (Table V, based on average reservoir-corrected dates). The oldest dates are from the lower strata at Site 1 on Biscoe Point and Cormorant Island. Multiple dates from two sites (Site 1 on Litchfield and Cormorant Islands) suggest a relatively brief occupation period. Site 1 at Humble Island produced two dates that also suggest a relatively brief period of occupation at 254–421 BP, and two modern dates (Table V). The last two dates may represent another brief occupation period in the more recent past, or may be intrusive specimens that were mixed within the shallow sediments at this site. Site 5 at Biscoe Point is similar in having an older occupation period in the lower strata, with dates ranging from 450–598 BP, as well as a younger occupation from 329 BP to the present

(Table V). Site 2 at Litchfield Island exhibits the greatest range in dates and penguin occupation from 507 BP to the present, though it is unknown if these dates represent a single or multiple occupation period(s). Radiocarbon dates on squid beaks were similar to those on penguin bones from the same stratigraphic level at Biscoe Point Site 5 and the modern colony at Torgersen Island, indicating correspondence in age of penguin bones and prey remains in the colony sediments.

Discussion

Occupation history

The presence of bones of adult and juvenile Adélie penguins at all sites except on Cormorant Island, and the absence of bones that could be verified as other pygoscelid species, suggests that these colonies were occupied in the past only by the former species. Future excavation and recovery of identifiable penguin bones from these and other abandoned colonies in the Palmer Station area will serve to test this hypothesis.

The radiocarbon chronology by site, and by stratigraphic levels within each site, indicates that all abandoned penguin colonies in the Palmer region were occupied either before (> 450 yrs old) or during (100–450 yrs ago) the Little Ice Age (LIA, 1500–1850 AD; Grove 1988). The former category includes Sites 1, 2, and 5 on Biscoe Point and Site 1 on Cormorant Island whereas the latter includes Site 1 on Humble Island, Sites 3 and 4 on Biscoe Point (and perhaps a more recent occupation of Site 5) and Sites 1 and 2 on Litchfield Island (Table V). Osteological identifications further indicate that all abandoned sites, except for Site 1 on Cormorant Island, were occupied by Adélie penguins. No bones identifiable to species were recovered from Cormorant Island and it is assumed that this site was used by Adélie penguins.

The results allow comparison of ecological responses by Adélie penguins to past climatic fluctuations as evinced by ice-core and marine sediment records. In the Antarctic Peninsula these records indicate that, prior to the LIA, climate was warmer than today (Mosley-Thompson *et al.* 1990, Leventer *et al.* 1996, Smith *et al.* in press). Cool and warm periods occurred throughout the LIA (with more of the latter than the former) with temperatures steadily rising again over the past 50 yrs (Mosley-Thompson *et al.* 1990, Leventer *et al.* 1996, Smith *et al.* in press). Moreover, the warming over the past three decades is the most pronounced that has occurred in over four centuries as shown by a 480-yr ice-core record from Dyer Plateau (Thompson *et al.* 1994, Smith *et al.* in press).

Abandoned colonies exhibiting the greatest temporal range of occupation are those located on Biscoe Point. Thar area, currently occupied by Adélie and gentoo penguins, appears to have been colonized first by the former species beginning approximately 603–679 yrs ago (Site 1; Table V). Sites 2 & 5 were colonized shortly after Site 1, if not at the same time, and were occupied up to 598 yrs ago. The occupation history denotes that Biscoe Point was ice-free prior to the LIA, but was largely abandoned by 302 yr BP (Sites 2 & 3; Table V); Site 5 may have been reoccupied by 245 yr BP. The cause for abandonment is unknown. The area may have become too snow- or ice-covered for occupation by breeding birds. In recent years, a piedmont glacier covered the base of Biscoe Point, but has been retreating over the past 20 years in concert with current warming trends in the Antarctic Peninsula region. If this piedmont glacier once covered the Point, occupation by breeding penguins would not have been possible. Other causes for abandonment may have included changes in marine food availability and/or sea-ice conditions that precluded breeding penguins from existing in the area (see Fraser *et al.* 1992).

The remaining abandoned sites on Humble and Litchfield islands were occupied primarily during the LIA, or within the past 300 yrs, with Site 1 on Humble island abandoned by 254 yr BP (Table V). As with Biscoe Point, those islands may have been too snow or ice-covered for occupation by breeding birds prior to the LIA (though one older date of 425–507 yr BP was obtained from Site 2 at Litchfield Island). A single date from the lower level of a modern colony excavated on Litchfield Island indicates occupation of the site began up to 158 yrs ago. In contrast, a modern colony on the nearby Torgersen Island has an occupation history beginning 281 yrs ago. Thus, it is unknown if Humble Island was abandoned for climatic or other reasons by 254 yr BP while Torgersen Island remained occupied by breeding birds from 281 yr BP to the present.

The radiocarbon chronology of penguin bones so far indicates that only Adélie penguins have bred in the Palmer region beginning up to 603–679 yrs ago (corrected average, 644 yr BP, Biscoe Point Site 1; Table V) and that only recently have gentoo and chinstrap penguins expanded their breeding distribution to this region. It is possible that the relatively rapid regional warming now occurring in the Antarctic Peninsula has favoured the expansion of these species southward, while the Adélie penguin has declined (Fraser *et al.* 1992, Smith *et al.* in press). The absence of gentoo and chinstrap penguins in the Palmer Station area prior to 1957 supports this hypothesis.

These and other data gathered in the Antarctic Peninsula on abandoned penguin colonies (Emslie 1995, Tatur *et al.* 1997) indicate that the sites are relatively young compared to other regions of the Antarctic. Baroni & Orombelli (1994) reported colonies as old as 13 000 yr BP in the Ross Sea region and Goodwin (1993) obtained a corrected age of 3290 yr BP on an Adélie penguin skull at the Windmill Islands, Budd Coast, East Antarctica. The absence of sites of that age or older in the Antarctic Peninsula is not easily explained. Tatur *et al.* (1997) speculated that erosion may have destroyed most of these older sites. It is also possible that climatic cycles in the Antarctic Peninsula caused glacial advances that scoured the terrain to the extent that few or no abandoned colonies older than the past 600–700 yrs now remain. Additional ground surveys and sampling of Antarctic Peninsula sites are needed to address this question.

Palaeodiet

In addition to the occupation history, significant variations in prey species richness and relative abundance represented in the colony sediments suggest that Adélie penguins may have changed their diet during different occupation intervals, or that diet varies by colony. That these differences probably are not due to diagenetic processes is indicated by the similar quality of preservation of organic material from each site, despite the disparity in site ages. Moreover, all sites are subject to similar weathering processes. Given the relatively similar age of the abandoned colonies within the past 600–700 yrs, it is assumed that differential preservation has not been a major factor in determining the relative amount of prey remains represented at each site. For sites that differ in age by thousands of years, however, these processes may bias the recoverable sample of organic remains.

Dietary remains recovered from the lower levels (Levels 2 & 3) at two sites excavated at Biscoe Point (Site 1 and 5) indicate a greater relative abundance of squid (*Psychroteuthis glacialis*) represented at Site 1, but few differences otherwise (Table II). Interestingly, one other site of similar age at Cormorant Island also produced a relatively high abundance and species richness of squid remains in the sediments (Table II). These results suggest that Adélie penguins consumed a greater proportion of squid from 679 to 450 yr BP, or prior to the LIA, perhaps due to greater squid availability (especially *P. glacialis*) over other prey taxa at that time.

Dietary remains from colonies that were occupied during the LIA on Litchfield and Humble Islands indicate that a lower proportion of squid was consumed, especially at Site 1 on Humble Island, but that fish species richness and abundance were significantly higher in these sites compared to pre-LIA sites on Cormorant Island and Biscoe Point (Table II). The data further suggest that Adélie penguins may have changed their diet from more squid prior to the LIA to more fish during the LIA, perhaps in response to warming and cooling cycles that may have affected prey abundance.

Comparison of dietary remains recovered from the three modern penguin colonies that were excavated indicate that the relative abundances of squid and lantern fish remains are similar between the two Adélie penguin colonies on Torgersen and Litchfield islands (Table III). However, when food remains from these sites are compared to those from the Chinstrap penguin colony on Dream Island, it appears that squid is less important, and fish more so, in the diet of chinstrap compared to Adélie penguins (Table III). Additional data are needed to verify if these dietary differences currently exist between these two species of penguins at these colonies.

The high abundance of squid beaks in the sediments of the modern Adélie penguin colonies also is of interest as squid are rarely encountered in stomach samples from living Adélie penguins (Williams 1995). A low frequency of *Pyschroteuthis glacialis* has been reported in Adélie penguin diet at Adélie Land, but only from samples gathered late in the breeding season (Offredo *et al.* 1985). Those authors speculate that this squid species may move to shallower depths in February and therefore become accessible to predation by penguins only late in the breeding season. If so, a similar response may be occurring in the Palmer Station area. Diet samples collected from Adélie penguins in January over the past 10 years failed to produce any substantial remains of squid, yet squid beaks are common in the colony sediments. The samples from the three screen traps placed on the modern colonies (Table IV) verify that the penguins presently are feeding on squid at some point during occupation or attendance of their breeding sites. The results suggest that the penguins must be taking squid early or late in the season, while they are still occupying their breeding sites, but feed primarily on krill (and some fish) during the chick-rearing season as shown by the stomach samples. Additional research is needed to determine the importance of squid in Adélie penguin diet and the environmental circumstances in which this prey species is taken.

Conclusions

Our investigations of abandoned colonies have provided an occupation history of Adélie penguins in the Palmer Station area over the past 644 years. In addition, this research raises new questions on the ecological response by penguins, especially dietary shifts, to changing environmental conditions, e.g., do the proportions of various prey species change with warming and cooling trends in a predictable pattern in Adélie penguin diet? Additional information on modern penguin diet throughout the entire breeding season also is needed, and is being gathered with the use of screen traps placed in the active Adélie penguin colonies.

Investigation of abandoned colonies also may provide information on sea-level and ice-margin changes in the past (Goodwin 1993). Adélie penguins require ice-free terrain for their nesting sites. Excavations indicated that sediments below ornithogenic soils were deposited either from glacial meltwater or on marine terraces at or near sea-level in the past. Thus, radiocarbon dates on organic debris in the ornithogenic soils immediately above the glacial or marine deposits can provide a minimum age for the retreat of the ice margin or lowering of sea-level. Radiocarbon dates at the bottom of ornithogenic soils in the modern Adélie penguin colony on Torgersen Island (Fig. 3) suggest that ice-free terrain became available for breeding on the island up to 281 yrs ago (Table V).

Other potential information to be gained from investigations of abandoned colonies includes isotopic analyses of eggshells from colony sediments that may provide supportive evidence for shifts in penguin diet over time. Analyses of $^{15}N/^{14}N$ in seabird eggshells, for example, reflect the relative role of prey from different trophic levels in seabird diet (e.g. krill vs squid vs fish; Schaffner & Swart 1991, Hobson & Welch 1992, Rau *et al.* 1992, Hobson *et al.* 1994, Hobson 1995, Gould *et al.* 1997, Sydeman *et al.* 1997). In addition, isotopic analyses of squid beaks from abandoned colonies may reflect fluctuations in ocean temperatures through changes in O^{16}/O^{18} ratios in the chitin.

Acknowledgements

This research was funded by a supplementary grant to the authors to NSF Grant OPP 96-32763. We give special thanks for the enthusiastic assistance in the field and/or laboratory by Neijla Bouziane, Ralph Bovard, Sharon Delsack, Janice Jones, Donna Patterson, Lizann Rucker, Craig Seeman, Michele Sewolt, Karie Sines, and T. Verry. Randy Sliester assisted with boat operations. Pretreatment of radiocarbon samples was completed at the University of Colorado by Dr Thomas Stafford and Jocelyn Turnbull. The manuscript was improved with comments from L. Davis and P. Berkman. We thank C. Pudsey for drafting Fig. 1.

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