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A 9000-year record of Adélie penguin occupation and diet in the Windmill Islands, East Antarctica

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Abstract: We investigated 17 abandoned Adélie penguin (*Pygoscelis adeliae*) colonies in the Windmill Islands, East Antarctica, in summer 2002/03. Forty radiocarbon dates on penguin bones and eggshells from 13 of these sites indicate a near continuous occupation by breeding penguins in this region for over 9000 years. These dates refine the recent geological record in this region and indicate that deglaciation of the northern islands occurred much earlier than previously suggested. Dietary remains from these sites include at least 23 taxa of cephalopods and teleost fish. Quantification of these remains indicates significant fluctuations in the relative abundance of two of the more common major prey taxa. The Antarctic silverfish (*Pleuragramma antarcticum* Boulenger) was the most common teleost prey during all time periods represented by the ages of the sites, but preservational factors may explain a gradual decrease in the remains of this species in increasingly older sites. The most common cephalopod in the sediments was the squid, *Psychroteuthis glacialis* Thiele, which occurred in low numbers in most sites except one (Site 75). An unusually high number of squid beaks preserved in Site 75, dating to approximately 5700–6100 cal. yr BP, does not correlate with a decrease in fish prey at that time. The high number of abandoned penguin colonies (> 200) in the Windmill Islands may be due to population cycles in the past in association with low nest-site fidelity and movement by breeding penguins to new sites within this region.

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Key words: abandoned colonies, deglaciation, palaeodiet, *Pleuragramma antarcticum*, *Psychroteuthis glacialis*, *Pygoscelis adeliae*

Introduction

Adélie penguins (*Pygoscelis adeliae* Hombron & Jacquinot) have been known to breed in the Windmill Islands, East Antarctica, since at least the late 1950s, when humans first visited this region (Woehler *et al*. 1991). The breeding population is currently estimated at *c.* 105 000 pairs at 14 locations (Woehler, unpublished data). Compared to initial surveys in the 1950s and 1960s, this estimate indicates the population has increased by over 300% since that time (Woehler *et al*. 1991). However, while the overall population has increased, specific colonies and especially those near human habitation have decreased (Woehler *et al*. 1994).

In addition to the current breeding population of penguins, a high number of relict, or abandoned colonies also have been identified in the Windmill Islands (Goodwin 1993). Investigation of abandoned colonies has been shown to be an effective means to gather data on the occupation history of penguins in a given region, their palaeodiet, and the climatic conditions that prevailed during the occupation period(s) (Baroni & Orombelli 1994, Emslie 2001, Emslie & McDaniel 2002, Emslie *et al*. 2003a). Previously, Goodwin (1993) completed a series of radiocarbon dates on peat from lake and pond sediments in the Windmill Islands, and on one Adélie penguin skull found 20 cm below the surface in a gully between abandoned colonies. These dates indicated that the southern Windmill Islands were deglaciated by 8000 corr. yr BP (years before present, corrected for the marine-carbon reservoir effect), while the northern islands (those north of Robinson Ridge, 66°22'S, see Fig. 1) did not become ice free until 5500 corr. yr BP. However, the exact extent of penguin occupation of the region was not investigated.

Here, we report on a preliminary study of abandoned colonies in the Windmill Islands to characterize further the occupation history and diet of Adélie penguins in this region. We concentrated primarily on colonies located in the northern islands, as defined by Goodwin (1993), with some limited work conducted at Robinson Ridge and Peterson Island in the south. We compare these records to the palaeoclimatic history of this region of East Antarctica, as evinced by previously published ice core and sedimentary data, to refine the geological history of this region. Finally, we address the question as to why so many abandoned colonies exist in the Windmill Islands using historic and recent photographic and census data.

Study area and methods

The Windmill Islands extend for over 130 km along the

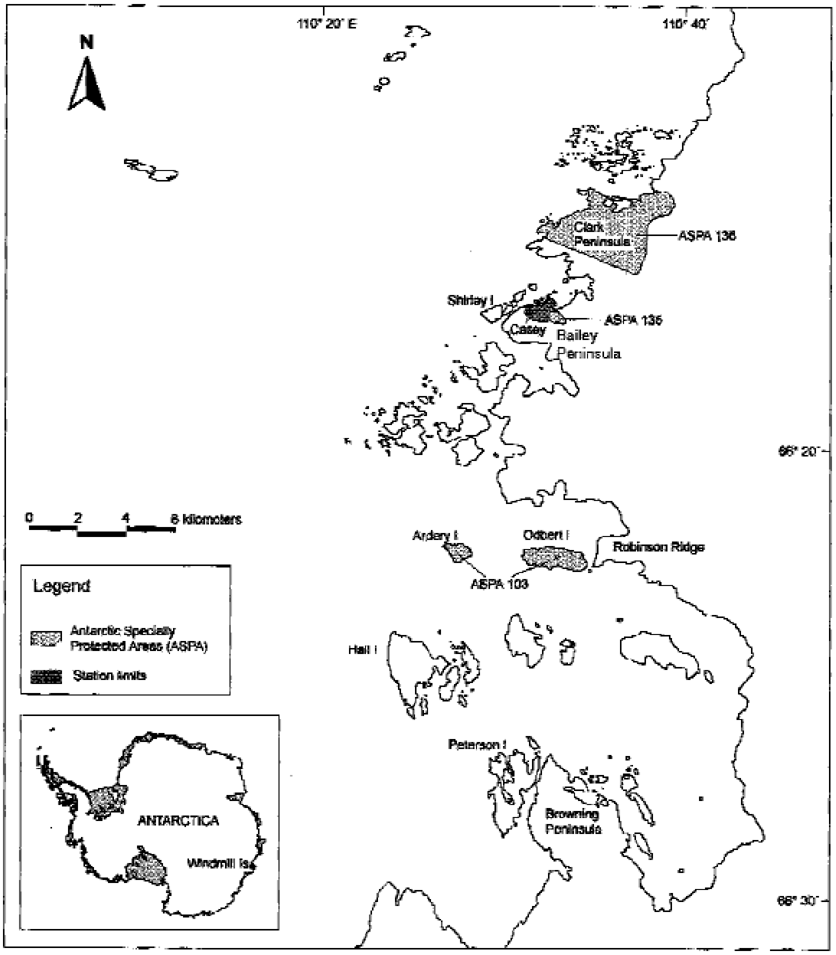

Fig. 1. Map showing the location of the Windmill Islands in Antarctica (bottom left) and the locations of major geographic features where abandoned penguin colonies were located (see Table I for GPS locations of the 17 sites discussed in the text).

coast of East Antarctica between 66°12'–66°30'S (Fig. 1). Numerous ice free shorelines, islands, and marine terraces occur within this region with active Adélie penguin colonies located on Clark and Bailey peninsulas to the north, and extending to Peterson Island to the south (Woehler *et al.* 1991). Even though numerous abandoned pebble mounds occur within one geographic area (e.g. Bailey Peninsula), we refer to each of the abandoned mounds as 'colonies', and not 'subcolonies' as defined by Ainley (2002). We use this more general terminology for our sites since each mound could represent a different occupation period from others in a given region. Thus, there would be no true subcolonies (*sensu* Ainley 2002) if all the mounds were occupied at different times and designating each one as a colony is therefore more logical

Ground surveys were conducted in January and February 2003 to locate and map abandoned colonies and subcolonies using Global Positioning System (GPS). While incomplete, these surveys resulted in the identification of hundreds of abandoned colonies, especially near extant colonies. Not all of the abandoned colonies that were mapped were numbered and only 17 were excavated (Table I). These sites include 11 on Bailey Peninsula, two each at Robinson Ridge, Clark Peninsula, and at Peterson Island (Fig. 1). In addition, modern penguin guano was sampled at two active colonies on Clark Peninsula and Shirley Island.

Excavations were conducted by establishing 1 x 1 m pits near the centre of each abandoned colony. Loose surface pebbles not mixed with sediments were removed as level 1 in each pit to a depth where ornithogenic sediments were first encountered, usually 5–15 cm below the present surface. Thereafter, the pit was excavated in 5 cm levels until bedrock or the bottom of the ornithogenic sediments (recognized by a distinct change in colour and texture) was reached. At the conclusion of the excavations, each pit was backfilled with rock and pebbles; surface pebbles with vegetation were replaced so that little or no evidence of the pit was visible on the surface.

The amount of all excavated sediments was quantified using 14 litre buckets to measure the total volume removed from each level, so that data could be quantified between levels of different ages in the same and different pits. These sediments were then washed through three stacked sieves with square mesh sizes of 0.64, 0.32, and 0.025 cm^2. Organic remains (bone and feather) from the top sieve were sorted and removed during the washing process. Sediments from the middle screen were dried and sorted in the lab. The finer sediments from the bottom screen were dried and re-

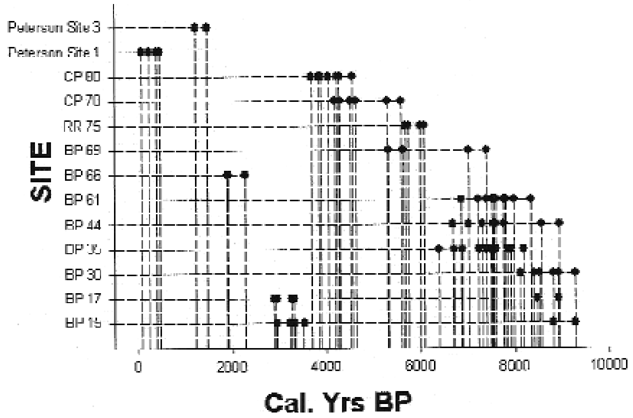

Fig. 2. Distribution of 40 calibrated radiocarbon dates on penguin remains from the Windmill Islands, East Antarctica. Two points are plotted to show the 2σ range in cal. yr BP for each dated sample from 13 sites (see Table II). Site acronyms are: BP = Bailey Peninsula, CP = Clark Peninsula, RR = Robinson Ridge.

screened through 1 mm and 0.25 mm geology sieves, then sorted under a low-power stereomicroscope to recover fish bones, otoliths, squid beaks and other dietary remains. In most cases, the large amount of this fine sediment necessitated that only a subsample of this sediment could be sorted in the lab. In those cases, the proportion sorted (a minimum of 15%) was quantified by dry mass for comparison to other samples.

Dietary remains (otoliths and squid beaks) were identified by W. Walker, National Marine Mammal Laboratory, Seattle. These remains are quantified by total number of identifiable specimens and by the minimum number of individuals (MNI) per taxon per excavated level. MNI was

Table I. Abandoned penguin colonies excavated in the Windmill Islands, East Antarctica, giving GPS locations, depth of excavations, and total dry mass of screened sediments (1 mm and 0.25 mm screens).

Site	GPS position (lat./long.)	Depth (cm)	Sediment mass (g)
Bailey Peninsula			
Site 2	66°17'0.03"S/110°31'45.0"	12	5959
Site 4	66°17'02.6"S/110°31'43.4"	15	7295
Site 7	66°16'48.3"S/110°31'05.4"	18	14588
Site 15	66°16'53.1"S/110°30'46.9"	53	21701
Site 17	66°16'51.7"S/110°30'44.2"	40	20444
Site 30	66°17'09.8"S/110°29'54.8"	64	17467
Site 35	66°17'11.9"S/110°30'04.5"	53	11444
Site 44	66°17'11.7"S/110°29'55.4"	46	15794
Site 61	66°17'07.2"S/110°30'24.0"	48	16525
*Site 66	66°16'56.6"S/110°32'24.5"	50	10488
*Site 69	66°16'58.0"S/110°32'30.0"	35	12227
Robinson Ridge			
Site 72	66°22'14.0"S/110°35'06.4"	36	5833
Site 75	66°22'04.6"S/110°35'04.9"	40	24759
Clark Peninsula			
**Site 78	66°15'17.6"S/110°33'51.3"	38	8322
**Site 80	66°15'07.8"S/110°33'28.7"	27	9140
Peterson Island			
Site 1	66°26'59.7"S/110°30'12.6"	30	8878
Site 3	66°26'51.0"S/110°30'29.5"	45	29233

*Denotes sites within Antarctic Specially Protected Area 135.
**Denotes sites within Antarctic Specially Protected Area 136.

Table II. Radiocarbon dates (in yrs BP) on Adélie penguin (*Pygoscelis adeliae*) bone collagen and eggshell carbonates from abandoned penguin colonies in the Windmill Islands, East Antarctica. Conventional dates were corrected and calibrated for the marine-carbon reservoir effect using a ΔR = 750 ± 50 years (see Emslie 1995) and the MARINE98 database of Stuiver & Reimer (1993). The laboratory number (NZA, Rafter Radiocarbon Lab, New Zealand), conventional date (in ^{14}C yr BP), mean calibrated date (in cal. yr BP), and calibrated 2σ range (95% confidence interval, in cal. yr BP) also are provided.

Site/provenience		Material	Lab. no.	Conventional date	Calibrated mean	Calibrated range (2σ)
Peterson Island						
Site 1	Level 4	Bone	NZA 18038	1356 ± 40	266	396–78
	Level 5	Bone	NZA 18079	1433 ± 40	305	460–238
Site 3	Level 8	Bone	NZA 18080	2539 ± 40	1316	1476–1229
Casey station area						
Site 15	Level 2	Bone	NZA 18075	4054 ± 40	3153	3321–2949
	Level 6	Eggshell	NZA 17711	4242 ± 40	3364	3520–3225
	Level 9	Eggshell	NZA 17710	9182 ± 55	8925	9284–8802
Site 17	Level 2	Bone	NZA 18076	4009 ± 40	3074	3259–2887
	Level 3	Bone	NZA 18035	4042 ± 40	3137	3313–2939
	Level 7	Eggshell	NZA 17712	8952 ± 60	8690	8921–8475
Site 30	Level 6	Eggshell	NZA 17696	8562 ± 55	8290	8400–8113
	Level 9	Eggshell	NZA 17695	8969 ± 50	8717	8924–8517
	Level 10	Eggshell	NZA 17694	9168 ± 50	8917	9277–8800
Site 35	Level 2	Bone	NZA 17802	6869 ± 45	6541	6709–6392
	Level 4	Bone	NZA 17699	7310 ± 45	7081	7233–6889
	Level 5	Eggshell	NZA 17690	7954 ± 85	7658	7853–7493
	Level 7	Eggshell	NZA 17692	7761 ± 45	7498	7607–7403
	Level 8	Eggshell	NZA 17691	8343 ± 50	8023	8178–7916
Site 44	Level 2	Bone	NZA 17805	7138 ± 45	6853	7011–6684
	Level 4	Eggshell	NZA 17709	7719 ± 65	7458	7598–7316
	Level 7	Eggshell	NZA 17708	7926 ± 45	7640	7754–7541
	Level 8	Eggshell	NZA 17697	9012 ± 55	8789	8950–8557
Site 61	Level 3	Eggshell	NZA 17689	7755 ± 50	7492	7607–7392
	Level 4	Eggshell	NZA 17688	7289 ± 50	7024	7222–6860
	Level 7	Eggshell	NZA 17687	7957 ± 50	7660	7793–7555
	Level 8	Eggshell	NZA 17685	8461 ± 60	8162	8339–7975
		Eggshell	NZA 17686	7921 ± 50	7633	7756–7508
Site 66	Level 4	Bone	NZA 18037	3179 ± 40	2061	2271–1901
	Level 5	Bone	NZA 18078	3197 ± 40	2093	2286–1923
Site 69	Level 4	Eggshell	NZA 17693	5910 ± 45	5553	5642–5327
	Level 5	Bone	NZA 17804	7451 ± 60	7236	7392–7029
Site 75	Level 5	Bone	NZA 17803	6225 ± 50	5873	5984–5677
		Bone	NZA 17905	6292 ± 40	5912	6089–5755
Site 78	Level 1	Bone	NZA 17682	5012 ± 40	4384	4521–4178
	Level 3	Bone	NZA 17683	5085 ± 40	4439	4625–4288
	Level 5	Bone	NZA 17698	5081 ± 40	4435	4619–4284
	Level 6	Bone	NZA 17684	5849 ± 50	5460	5592–5293
Site 80	Level 2	Bone	NZA 18036	4780 ± 45	4059	4234–3852
	Level 3	Bone	NZA 18077	4641 ± 40	3849	4050–3681
	Level 4	Eggshell	NZA 17713	5037 ± 40	4403	4557–4225
		Bone	NZA 18134	4812 ± 45	4084	4280–3892

Table III. Age category and 2σ range in age (in cal. yr BP) of dated levels of active and abandoned Adélie penguin colonies excavated in the Windmill Islands, East Antarctica. Dated sites/levels are grouped by similar ages with total dry mass (g) of sorted sediments and the percent sorted of total dry mass of all sediments (1 mm and 0.25 mm screens).

Age category	Range (cal. yr BP)	Site/levels	Sorted mass (g)	% Total mass
0	Modern	Active colonies	862	100
1	100–500	Peterson Site 1, Level 4–5	2494	50
2	1900–2300	Site 66, Level 4–5	1063	26
3	2900–3500	Site 15, Level 2–6; Site 17, Level 2–3	9006	34
4	3700–4200	Site 80, Level 2–3	2237	50
5	4200–4600	Site 78, Level 1–5; Site 80, Level 4	3767	41
6	5300–5600	Site 69, Level 4; Site 78, Level 6	919	15
7	5700–6100	Site 75, Level 5	1819	21
8	6400–7000	Site 35, Level 2; Site 44, Level 2	978	15
9	6900–7600	Site 35, Level 4; Site 44, Level 4	3503	25
10	7400–8300	Site 35, Level 5–7; Site 44, Level 7; Site 61, Level 7-8	3112	30
11	7900–8200	Site 30, Level 6; Site 35, Level 8	1240	49
12	8500–9300	Site 15, Level 9; Site 17, Level 7 Site 30, Level 9-10; Site 44, Level 8	2970	38

determined for each identified fish species by counting the most abundant side (right or left) of whole otoliths. Otolith halves of unknown side were counted and divided by two, then divided by two again to provide a conservative MNI estimate that was added to that based on whole otoliths to obtain a total MNI for each species and level. MNI for squid were calculated by counting the most abundant portion (upper or lower beak) plus the number of upper or lower halves divided by two.

To assess changes in penguin diet through time, data from specific dated levels from each site were grouped by similar ages and assigned an arbitrary age category from 0 (modern) to 12 (oldest). MNIs of fish and squid taxa were summed from all levels within each of these age categories. To normalize the data against variable amounts of sediments excavated and sorted from each site, all MNIs of the two most common prey taxa, Antarctic silverfish (*Pleuragramma antarcticum* Boulenger) and squid (*Psychroteuthis glacialis* Thiele), were divided by the proportion of dry sediments that were sorted in each age category. These data were then plotted by age category and analysed using a contingency table and Chi square. Correlation analyses of dietary trends between these two prey taxa were performed using Kendall Tau and Spearman Rank tests using JMP IN software version 3.2.1 (SAS Institute Inc.).

Radiocarbon dates on penguin bone and eggshell were completed using accelerator mass spectrometry (AMS). Forty samples were submitted to Massey University and the Rafter Radiocarbon Laboratory, New Zealand, and the resulting dates are reported with NZ numbers assigned by this lab. All dates were corrected and calibrated using a ΔR = 750 ± 50 years and the CALIB 4.1 program (Stuiver & Reimer 1993, see also Emslie *et al*. 2003a for a discussion of this method) and are reported here in calendar years before present (cal. yr BP). A 2σ range for each date also is provided to give a 95% confidence interval that the true age of the specimen falls within this range.

Results

A summary of each excavated site, its location, and the depth of excavation is provided in Table I. Except for small fragments, very little bone was recovered from most of the sites and organic remains within the ornithogenic sediments were limited primarily to hundreds of eggshell fragments and dietary remains (otoliths and squid beaks). When present, bone was preferentially used for radiocarbon dating; eggshell was used when bone was absent or insufficient for obtaining a reliable date. Forty radiocarbon dates (21 bone, 19 eggshell) from 13 of the 17 excavated sites indicate a range in penguin occupation in the Windmill Islands beginning at approximately 9000 cal. yr BP and extending to the present (Fig. 2 and Table II). When dated levels are grouped by age categories (Table III), gaps of approximately 100 to 600 years occur between the 2σ range of some of these categories and suggest brief periods of abandonment of the Windmill Islands by breeding Adélie penguins. However, since only 17 of hundreds of abandoned colonies were sampled in this study, we interpret our existing data as indicating a probable continuous

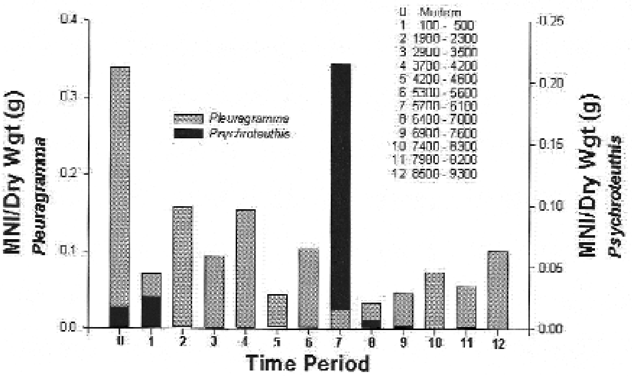

Fig. 3. Graph showing trends in the relative abundance (MNI/dry mass) in the two most abundant prey taxa, *Pleuragramma antarcticum* (left scale) and *Psychroteuthis glacialis* (right scale), from ornithogenic sediments grouped into 13 time periods from modern (0) to approximately 9300 cal. yr BP (see Table III for sites/levels assigned to each time period).

Table IV. Squid and fish taxa identified from beaks and otoliths recovered from modern and abandoned colonies of Adélie penguins, Windmill Islands, East Antarctica. Total number of identifiable specimens and minimum number of individuals (MNI; in parentheses) are provided for each taxon by dated grouped deposits (see Table I); for *Psychroteuthis glacialis* and *Pleuragramma antarcticum*, the second row of data gives the ratio of MNI per dry mass of sediments sorted from the dated deposits (see Table I). Systematics follow that of Gon & Heemstra (1990) and Miller (1993).

Taxon	Modern	1	2	3	4	5	6	7	8	9	10	11	12
Cephalopoda: Teuthiodea													
Psychroteuthis glacialis	27 (15)	115 (65)	3 (2)	7 (5)	2 (1)	12 (8)	1 (1)	693 (391)	23 (7)	26 (11)	1 (1)	3 (2)	
	0.017	0.026	0.002	0.001	0.0004	0.002	0.001	0.215	0.01	0.003	0.0003	0.002	
P. glacialis fragments	6	13				1		830					
Galiteuthis glacialis								1 (1)					
Brachioteuthis sp.		1 (1)		1 (1)									
Unident. Oegopsid fragments	2	17		1	2	15	14	878	4	130	6		2
Unident. Octopoda fragments						1							
Osteichthyes: Paralepididae													
Notolepis coatsi											2 (2)		
Notolepis sp.									1 (1)				
Family Myctophidae													
Electrona antarctica	1 (1)	1 (1)		2 (2)		1 (1)	1 (1)			1 (1)	3 (2)	7 (7)	2 (2)
Gymnoscopelus braueri										1 (1)	1 (1)		
Family Macrouridae													
Cynomacrurus piriei				1 (1)		2 (1)					1 (1)		
Unident. Macrouridae													1
Family Ophidiidae													
Unident. Ophidiidae						3							1
Family Nototheniidae													
Pleuragramma antarcticum	590(292)	355(179)	327(167)	1701(846)	676(345)	383(162)	308(95)	112(56)	57(33)	354(168)	426(230)	111(69)	608(301)
	0.338	0.072	0.157	0.094	0.154	0.043	0.103	0.031	0.03	0.05	0.07	0.06	0.10
P. antarcticum fragments	6						67						
Lepidonotothen sp.	2 (2)							1	1	3	2		1
Lepidonotothen cf. *L. kempi*	1 (1)				1 (1)						1 (1)		
Trematomus newnesi	19 (14)		2 (1)	6 (3)	7 (4)	1 (1)	1 (1)			1 (1)	2 (2)	1 (1)	
Trematomus nicolai				1 (1)									
Trematomus eulepidotus			3 (3)		2 (2)								
Trematomus bernacchii				7 (5)	3 (2)								
Trematomus cf. *T. newnesi*	4 (2)		8 (6)	4 (4)		2 (1)				3 (3)	1 (1)		11 (8)
Trematomus cf. *T. nicolai*											1 (1)	1 (1)	
Trematomus cf. *T. eulepidotus*	1 (1)		1 (1)	10 (1)	1 (1)	1 (1)				4 (3)	1 (1)		6 (4)
Trematomus cf. *T. bernacchii*				5 (4)	3 (2)	1 (1)				2 (2)			
Trematomus cf. *T. hansoni*								1 (1)					
Trematomus sp.	23		3	17		20	24	1		3	7	2	11
Pagothenia borchgrevinki		1 (1)	2 (2)	2 (2)						1 (1)	2 (2)		
Pagothenia sp.			1	5		1	1			1			3
Notothenia sp.			1	9									
Paranotothenia sp.					1								
cf. *Paranotothenia* sp.	2												
Unident. Nototheniidae	1		2	8						1			
Unident. Notothenioidei	4	2		31	2	9	33	5	1	24	7		6
Family Artedidraconidae													
Artedidraco sp.				2 (1)									
Unident. Artedidraconidae				1									
Family Bathydraconidae													
Unident. Bathydraconidae	2									6			
Family Channichthyidae													
Pagetopsis maculatus		1 (1)		1 (1)	1 (1)								
Pagetopsis cf. *P. maculatus*										2 (1)			
Pagetopsis sp.				9		1	2						
Chaenodraco wilsoni				1 (1)	2 (2)		1 (1)	1 (1)					
Chaenodraco cf. *C. wilsoni*		4 (4)		3 (2)									
Chaenodraco sp.	3												
Chionodraco sp.	7		2	2	1	1							1
Unident. Channichthyidae				2					1				
Unident. otolith fragments	8			64	8	38			1			2	5

occupation of the Windmill Islands over the past 9000 years.

Dietary remains from all dated levels indicate considerable diversity in prey selection, with at least three species of cephalopods and 23 taxa of teleost fish represented (Table IV). Most of the prey, however, are relatively rare in the samples and only two taxa, the Antarctic silverfish (*Pleuragramma antarcticum*) and the squid (*Psychroteuthis glacialis*), are extremely common. These two taxa vary significantly in their relative abundance in the sediments among all time periods (Fig. 3; $\chi^2 > 1098$; df = 12; $P < 0.001$). *Pleuragramma* is also well represented in modern penguin guano and its importance in the past fluctuates through time. In general, remains of this prey decrease in increasingly older sites, but the variation in MNIs by time period remains significant even when the modern sample is removed from the analysis ($\chi^2 = 487$; df = 11; $P < 0.001$). Squid are less represented at most sites except during time period 7 (5700–6100 cal. yr BP) when they are quite abundant. Only one site, Site 75 from Robinson Ridge, dates within this period and the high number of squid beaks preserved in the sediments there is unusual. When this site is removed from the analysis, squid MNIs still vary significantly by time period ($\chi^2 = 445.6$; df = 11; $P < 0.001$). In addition, no correlation occurs between the dietary trends of *Pleuragramma* and *Psychroteuthis* with time period (Kendall Tau and Spearman rho, df = 12, $P > 0.14$).

Discussion

Penguin occupation history and palaeoclimate

The glacial and climatic records for the Windmill Islands indicate that this region was glaciated until the early Holocene, when the southern islands were first exposed, followed by the northern islands by the mid-Holocene (Goodwin 1993). A recent study by Kirkup *et al.* (2002) in the southern Windmill Islands adds new information to these interpretations. Using data from a marine sediment core at Peterson Island, these authors found evidence for a mid-Holocene climatic optimum or warming at about 4000 cal. yr BP that resulted in open water and high biogenic production at that time. At the time of their study, only one radiocarbon date was known from penguin remains in this region (Goodwin 1993) which placed the minimum occupation for breeding Adélie penguins in the Windmill Islands at approximately 3290 ± 250 cal. yr BP. This date corresponds with the mid-Holocene climatic optimum identified by Kirkup *et al*. (2002).

The mid-Holocene warming at ~4000 BP also has been identified in marine and lake sediment cores in the Windmill Islands. Using diatom assemblages from marine sediment cores, Cremer *et al.* (2001, 2003a, 2003b) identified a warming period or climatic optimum from 4000–1000 cal. yr BP. In addition, Roberts *et al.* (2004) analysed diatoms from a sediment core from Beall Lake and recognized a warming period from 4800–2900 corr. yr BP.

The 40 new dates on penguin remains from the Windmill Islands reported here help refine these geological interpretations. These dates now indicate that breeding Adélie penguins have probably been continuously present in the Windmill Islands since 9000 cal. yr BP, and that deglaciation in the northern islands took place much earlier than first proposed by Goodwin (1993). Though these penguin dates are presented in calibrated calendar years, and the geological dates are in corrected radiocarbon years, we do not consider this a problem as discrepancies between them are minimal for dates as old as the early to middle Holocene (Stuiver *et al*. 1998). Thus, it appears from this evidence that Adélie penguins began breeding in the Windmill Islands soon after deglaciation following the LGM and exposure of ice free terrain.

The 40 dates on penguin remains also suggest patterns in occupation that require additional investigation (Fig. 2). For example, the oldest dates ranging from approximately 9000–7000 cal. yr BP cluster from sites on Bailey Peninsula. After abandonment of this peninsula, only Site 69 appears to have been reoccupied for a brief period between 6000–5000 cal. yr BP, with Sites 15, 17, and 66 reoccupied from 2000–1000 cal yr. BP. Site 75 on Robinson Ridge and Site 78 on Clark Peninsula also were occupied from about 6000–5000 cal. yr BP. Perhaps after a period of abandonment, Site 78 was reoccupied and Site 80 occupied, on Clark Peninsula at about 4500–3500 cal. yr BP. Finally, Sites 1 and 3 on Peterson Island were colonized from 2000–1000 cal. yr BP.

If these occupation patterns are real, they would fit with palaeoclimatic data from lake and marine sediments in the Windmill Islands and Bunger Hills. For example, Melles *et al.* (1997), Kulbe *et al.* (2001), and Verkulich *et al.* (2002) recognized a cooling trend between 9000–5500 cal. yr BP (dates vary slightly by authors and whether or not dates are reported as cal. yr or ^{14}C yr BP), based on diatoms from marine and lake sediment cores. The peak of this cooling period occurs at about 7000 cal. yr BP, when the penguin colonies on Bailey Peninsula were abandoned. The reoccupation of one site (Site 69) on this peninsula, plus the initial occupation of sites on Clark Peninsula and Robinson Ridge, at 6000–5000 cal. yr BP further corresponds with warming trends at that time. Last, the occupation of sites at Peterson Island and reoccupation of Bailey Peninsula at 2000–1000 cal. yr BP matches a warming period identified by Verkulich *et al*. (2002).

Precise determination on whether or not the dates on abandoned colonies represent a pattern in occupation and reoccupation in the Windmill Islands with climate change requires additional testing. Many undated penguin colonies remain to be sampled in the area and dates on these sites could fill in gaps within this chronology. However, the pattern emerging so far suggests that the earliest occupation of the area occurred only on Bailey Peninsula, and that mid to late Holocene warming trends stimulated additional occupation and reoccupation of specific locations in the Windmill Islands.

The sites on Clark Peninsula also are of interest as they are located on a high ridge distant from the present coastline and above a valley that may have been submerged during the occupation of these sites, thus allowing easy access to this area. Since the occupation of these sites corresponds with the onset of a mid-Holocene warming trend at about 4000 cal. yr BP, it is possible that this scenario is correct. Again, additional sites need to be excavated in this area of the Windmill Islands to test this hypothesis.

Palaeodiet

The diversity and relative abundance of prey taxa identified in the ornithogenic sediments are similar to other regions in the Antarctic. Similar diversity has been apparent in remains from abandoned penguin colonies in the Antarctic Peninsula (Emslie & McDaniel 2002, Emslie *et al*. 2003b) and Ross Sea (Polito *et al*. 2002) regions, as well as in the high representation of *Pleuragramma* and *Psychroteuthis* in these remains. Both of these taxa have circum-Antarctic distributions and appear to be the preferred prey, other than *Euphausia* spp., of Adélie penguins throughout Antarctica (Williams 1995, Ainley 2002). Of particular interest here is that both these prey species fluctuate in their relative abundance in dated ornithogenic sediments from 9000 cal. yr BP to the present. The overall decrease in *Pleuragramma* from younger to increasingly older sites (Fig. 2) may be due more to preservational factors rather than an increase in the importance of this prey to Adélie penguins. The large increase in *Pleuragramma* in the modern guano compared to the fossil sediments supports this suggestion of a preservational effect on the otoliths in older deposits.

Of the other teleost prey that have been identified in the ornithogenic sediments, most are either circum-Antarctic in distribution and occur in continental shelf waters, including in East Antarctica (Gon & Heemstra 1990, Williams & McEldowney 1990, Miller 1993). One species, *Cynomacrurus piriei* Dollo, is more bathypelagic than the others reported here, occurring in deeper waters off the continental shelf in Antarctica. It is represented in three time periods (Table IV), but in very low numbers. All the specimens were well preserved and represented small juveniles or post-larval forms that probably fed in the upper water column (W. Walker, personal communication 2003), where they were subject to predation by diving penguins. The most abundant fish prey in the sediments, other than *Pleuragramma*, include *Trematomus newnesi* Boulenger, *T. eulepidotus* Regan, and *T. bernacchii* Boulenger (in addition to a number of otoliths identified only as *Trematomus* sp.). All three species occur in shelf waters in East Antarctica and are known to include euphausiids in their diet (Miller 1993).

As with the otoliths, the preservation and abundance of squid beaks in these deposits also are equivocal. In a previous study (Emslie & McDaniel 2002), it was found that otoliths preserved well, but squid beaks less so, in ornithogenic sediments dating up to 6000 years old at Adelaide Island (67°15'S, 68°30'W). Bone in these sediments also was extremely reduced and worn, indicating that continuous freeze/thaw action through time caused considerable erosion and loss of organic remains. Similar erosional effects in the Windmill Islands probably accounts for the absence of bone in many of the sites, although the abundance of squid beaks (including numerous intact specimens) at Site 75, dating up to 6000 years old (time period 7; Table III), is in contrast with these conclusions. It is possible that local conditions within the soil or other factors prevented erosion of organic remains at this site compared to others in this region. Thus, the extremely high abundance of squid at Site 75, with relatively few remains identified in other sites, may be an artefact of preservation, but additional sampling of similarly-aged sites is needed to test this hypothesis. If the high abundance in squid during time period 7 is real, and represents a period of increased consumption of this species by penguins, it could indicate an episode of prey switching due to lack of other preferred prey and/or an increase in numbers of squid in the marine environment. Such an increase might occur during warm climatic intervals, as has been identified in the Bunger Hills between 6000 to 5000 years ago discussed above. In addition, if the relative abundance of *Pleuragramma* and *Psychroteuthis* varied in the marine environment with climate change, a negative correlation could be expected between the dietary trends in these taxa through time, but no such correlation exists in the samples from the Windmill Islands in this study.

The results of this palaeodietary analysis can also be compared to a study on the current diet of Adélie penguins in the Windmill Islands. Kent *et al*. (1998) collected and identified stomach samples from 41 penguins at Shirley Island in January 1992. Their results indicated that the penguins consumed primarily fish (nearly 49% by mass), with *Pleuragramma antarcticum* as the most abundant prey (41.9% by mass), and krill (*Euphausia superba* Dana, 39.7%, and *E. crystallorophias* Holt and Tattersall, 8.5%, by mass). Other teleost prey included *Trematomus newnesi* and *T. bernacchii*, species also identified in the palaeodiet (Table IV). In addition, Kent *et al*. (1998) identified two cephalopods among the prey, the squid *Mesonychoteuthis hamiltoni* Robson, which did not occur in the fossil sediments, and *Psychroteuthis glacialis*. Both these taxa occurred in very low numbers in the penguin stomach contents. Overall, the results of this study are in accord with the fossil data, in that the preferred non-krill prey by Adélie

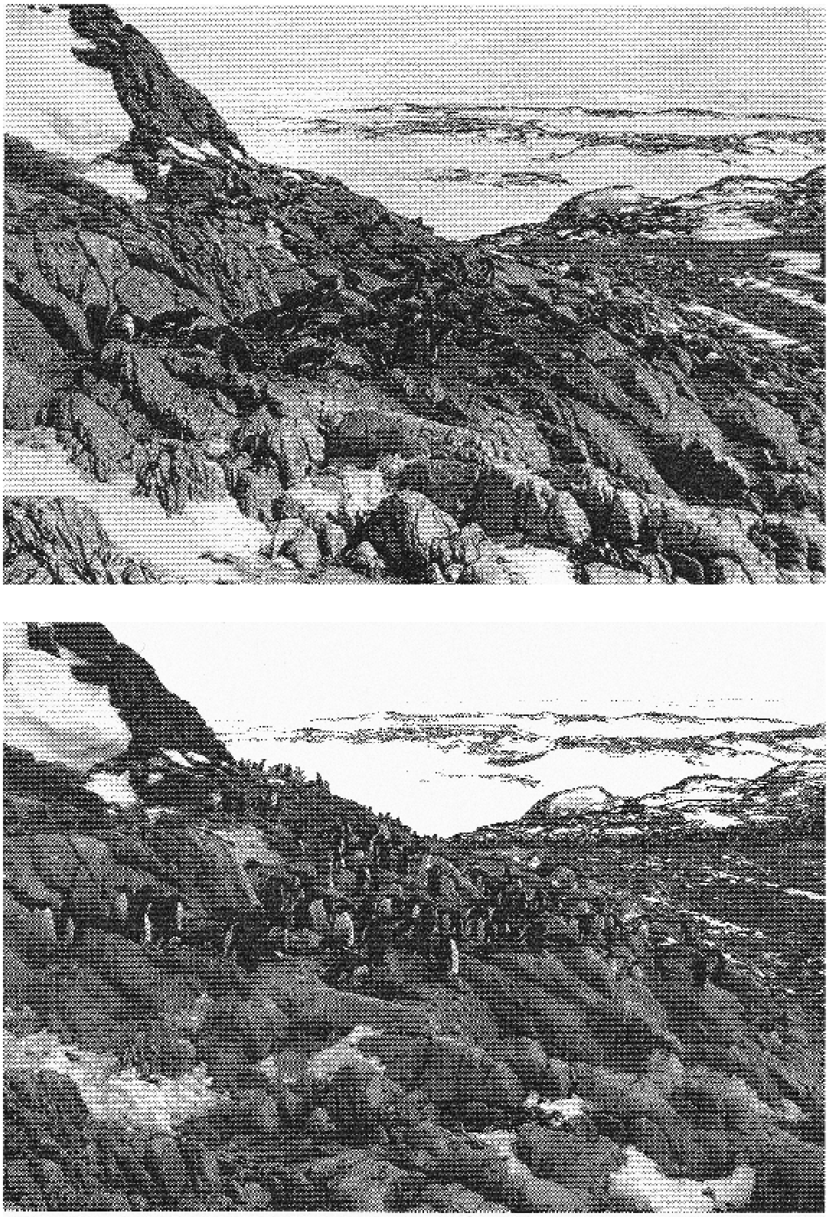

Fig. 4. Adélie penguin (*Pygoscelis adeliae*) colony at Whitney Point, Wilkes Land, East Antarctica in 1963 (top) and 2003 (bottom). The colony in the foreground has increased while a colony that established in the 1980s (seen in the background) continues to increase. Top photograph © Australian Antarctic Division archives, bottom photograph © Eric Woehler, AAD.

penguins in the Windmill Islands has remained stable for the past 9000 years.

Abandoned colonies and nest-site fidelity

Another characteristic of abandoned colonies in the Windmill Islands of interest is the very high number of these colonies that are present. Over 200 abandoned colonies have been located and mapped, but this is a minimal estimate as not all that are known to exist have been mapped by GPS. This extensive record of occupation and abandonment is currently unknown elsewhere in the Antarctic. It may be due simply to the large amount of ice free terrain in the Windmill Islands compared to other regions, with numerous access beaches for penguins, but similar terrain on the Victoria Land Coast, Ross Sea, lacks the density of sites found in this study.

Historic photographs of penguin colonies taken in the 1960s in the Windmill Islands offer one possible explanation for the high number of abandoned sites here (Fig. 4). These photos, compared with more recent images and surveys at the same locations, indicate that some recently established colonies are now declining, while other colonies are being occupied and growing rapidly. The abandonment is occurring over 1–2 decades, or faster than would be expected with natural attrition due to mortality of aging adults, even with low offspring recruitment back to the colony. Moreover, the occupation of nearby mounds by breeding penguins at the same time that others are abandoned has maintained a large penguin population in the

Windmill Islands that has increased since the 1950s, not decreased as might be expected if attrition was causing site abandonment.

We hypothesize that small subcolonies of Adélie penguins breeding in one location are moving to new breeding sites, rather than abandoning old sites due to attrition. Such behaviour is rare in Adélie penguins that have been studied in other regions of the Antarctic, and where banded, known-age individuals can be tracked from year to year. Studies on nest-site fidelity in this species range from 62–98.9% for males (Williams 1995, Ainley 2002), but these studies do not indicate whether the movements that occurred were within or between colonies. If Adélie penguins in the Windmill Islands are showing lower site fidelity than in other regions of the Antarctic where this species breeds, it would help explain the high number of abandoned colonies found throughout the region. However, we have no explanation for why penguins would move their breeding sites to a nearby location as abandoned and newly occupied mounds are in the same area and exposed to the same local environmental conditions. Additional study using marked birds would be necessary to fully address this question.

An alternate hypothesis that might explain the high number of abandoned colonies would be that penguin populations in the Windmill Islands were much larger in the past compared to today. If so, simultaneous occupation of most of the now abandoned mounds would need to be demonstrated through radiocarbon analyses. In our sample of 17 sites discussed here, we found a large range in dates for their occupation throughout the Holocene. Thus, it is unlikely that most of the remaining undated sites were occupied at the same time and we believe that low site fidelity is a more likely explanation for the large number of these abandoned sites in the Windmill Islands.

This preliminary study of abandoned penguin colonies in the Windmill Islands has provided a greater resolution to the palaeoclimatic record for this region. The continuous occupation by breeding Adélie penguins over the past 9000 years is unmatched in any other region of the Antarctic. More detailed investigations of these sites are warranted to further document this occupation history, especially in comparison to other locations in East Antarctica (e.g. Vestfold Hills) where similar colonies and colony density may exist.

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