LATE-HOLOCENE PENGUIN OCCUPATION AND DIET AT KING GEORGE ISLAND, ANTARCTIC PENINSULA

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Twelve abandoned and two active colonies of Adélie (*Pygoscelis adeliae*), Chinstrap (*P. antarctica*), and Gentoo penguin (*P. papua*) were excavated on King George Island, Antarctic Peninsula, in January/February 2002. Ancient DNA was extracted from nine samples of penguin bone from five abandoned colonies to verify species identifications. Thirty-six radiocarbon dates on penguin remains from these sites, including the first to be completed on *P. papua* from an abandoned colony in Antarctica, indicate that these three penguin species began occupying this region 500 to 600 years ago, agreeing with similar trends found at other abandoned colonies in the northern Antarctic Peninsula. This colonization event corresponds with warming trends in the Antarctic Peninsula during the Little Ice Age (A.D. 1500–1850), based on previously published isotope records from the Siple Dome ice core. Non-krill dietary remains recovered from the ornithogenic sediments at the 12 abandoned colonies indicate a high diversity of cephalopod and fish prey. Guano samples from the two active colonies further indicate that Chinstrap and Adélie penguins differ in their non-krill diet with the former species preferring lantern fish (*Electrona antarctica*) and the latter Antarctic silverfish (*Pleuragramma antarcticum*).

INTRODUCTION

Three species of pygoscelid penguins currently breed on King George Island in the Antarctica Peninsula: the Adélie (*Pygoscelis adeliae*), Chinstrap (*P. antarctica*), and Gentoo penguin (*P. papua*). Although considerable information is now known on the ecology and population biology of these species at this location [e.g., *Volkman et al.*, 1980; *Trivelpiece et al.*, 1986, 1987, 1990], little is known on their occupation history in the northern Antarctic Peninsula. *Emslie* [1995] investigated abandoned colonies of Chinstrap and Adélie penguins on King George Island and other locations. These and subsequent investigations [*Emslie*, 2001] have indicated that no colonies older than approximately 540 years before present (B.P.) have been found in the northern Antarctic Peninsula. Although colonies as old as 5000 to 6000 years have been identified in more southern regions of the peninsula [*Emslie and McDaniel*, 2002], the absence of old colonies in the northern region remains an enigma.

In 2002, the senior author returned to King George Island to resample relict penguin colonies in the Admiralty Bay region and survey for additional abandoned colonies that might indicate older occupations by pygoscelid penguins. Active colonies also were sampled

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to determine their age and to recover dietary remains from fresh guano. Twelve abandoned and two active penguin colonies were sampled during this study and include the first known excavations of abandoned Gentoo penguin colonies in Antarctica. Radiocarbon dates were obtained on penguin remains recovered from all sites and ancient DNA was extracted from penguin bones to verify species identification. The results of these investigations are presented here with identification of dietary remains.

METHODS

All active and abandoned colonies sampled in this study are located on the west side of Admiralty Bay and within Site of Special Scientific Interest (SSSI) No. 8 (Figures 1–2). Excavations were conducted at five areas within this SSSI at, from north to south, Rakusa Point, Llano Point, Uchatka, Blue Dyke, and Patelnia (Figure 2A-C). The two active colonies that were sampled included one of Chinstrap penguins at Patelnia (Area D) and one of Adélie penguins at Cascade Head, Llano Point. Area D and Cascade Head refer to colony names assigned by W. Trivelpiece for specific locations within a larger colony complex. Abandoned Chinstrap penguin colonies were located at Patelnia, Blue Dyke, and Uchatka Point, while two Gentoo and seven Adélie Penguin colonies were sampled at Llano Point and Rakusa Point. Geographic Positioning System (GPS) coordinates and approximate elevation above mean sea level (± 1 m) were determined with a handheld Brunton MNS MultiNavigator for each site (Table 1).

Each site was sampled by excavating a 1x1 m test pit (TP) in 5-cm arbitrary levels, with level 1 at the top. Excavations ceased when either the bottom of the ornithogenic sediments (recognized by change in soil texture and color) or bedrock was reached. All sediments removed during excavations were quantified by level and volume, washed through three nested screens (mesh sizes, from top to bottom, of 0.64, 0.32, and 0.025 cm^2), and dried and sorted following the methods of *Emslie et al.* [1998, 2002] and *Emslie and McDaniel* [2002]. Sediments recovered from the middle and lower screens were dried, weighed, and resorted in the laboratory through No. 18 (1 mm) and No. 60 (0.25 mm) sieves. These sediments were then sorted under a low-power stereomicroscope to recover organic remains (bones, otoliths, squid beaks). If no or few remains were encountered after sorting > 10% of the sample by dry weight, the remainder of the sample was left unsorted. Total dry weights (in grams) and percent sorted are provided in Table 1.

All bones were saved from each excavated level. Penguin bones were identified to species following the methods of *Emslie* [1995]; these identifications were used to determine which species formerly occupied the abandoned colony. Dietary remains (otoliths and squid beaks) recovered from the sorted sediments were identified by W. Walker, National Marine Mammal Laboratory, Seattle, WA. For each taxon, the total number of complete and partial otoliths or squid beaks was tabulated. Minimum number of individuals (MNI) represented for each taxon was calculated following the methods of *Polito et al.* [2002] and are reported here for both partially and completely sorted samples. MNIs were corrected for amount of sediments excavated by dividing MNI values with the total liters of sediments excavated and screened from each test pit. This method was applied only to the two most abundant species of fish, *Pleuragramma antarcticum* and *Electrona antarctica*, recovered from the modern guano samples. A Chi-square analysis was used to test for significant differences in these corrected MNIs using an even distribution of MNIs between sites as the expected values.

Radiocarbon dates were obtained from penguin bone, feather, or egg membrane recovered from each site and from the 5-cm arbitrary levels. All dates were corrected and calibrated for the marine-carbon reservoir effect using the Calib 4.2 software program and the 98MARINE database [*Stuiver and Reimer*, 1993; *Stuiver et al.*, 1998] using a $\Delta R = 700 \pm 50$ B. P. [see *Emslie*, 1995, 2001]. All dates are reported in 2σ calibrated ranges in calendar years B. P. and were assigned NZA (Rafter Radiocarbon Laboratory code) numbers.

Ancient DNA was extracted from sub-fossil bones in a dedicated laboratory following the procedures of *Lambert et al.* [2002]. To construct standards for taxonomic identification, DNA was also extracted from blood samples of *P. adeliae*, *P. antarctica* and *P. papua*.

A 445 base pair (bp) portion of the mitochondrial DNA 12S rRNA gene was PCR-amplified from the three *Pygoscelis* reference samples using the primers L-12SA (5'-AAACTGGGATTAGATACCCCACTAT-3') and H-12SB (5'-GAGGGTGACGGGCGGTATGT-3'). A 193 bp sequence of the same portion was amplified from the ancient DNA samples using the PCR primers L-12SE (5'-CCCACCTAGAGGAGCCTGTTC-3') and H-12SF (5'-AAATGTAGCCCATTTCTTCC-3'). The amplified products were sequenced using the ABI PRISM® BigDye™ Terminator Cycle Sequencing kit (Applied

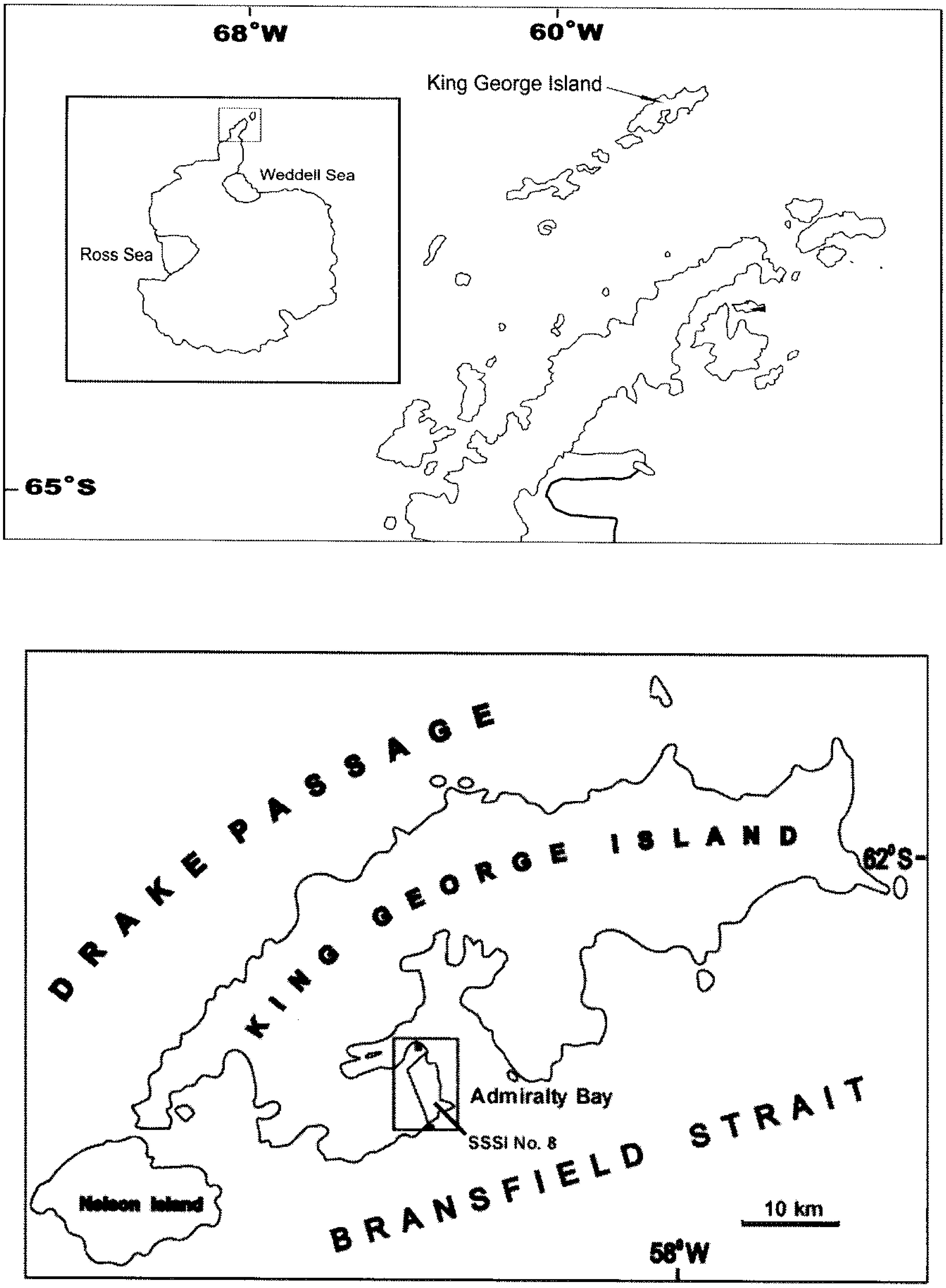

Fig. 1. Location of King George Island, South Shetland Islands, in the Antarctic Peninsula (top) and detail of King George Island (bottom) showing the location (in box) of SSSI No. 8 where abandoned and active penguin colonies were sampled.

Biosystems) and analyzed on a ABI 377A automated sequencer. The resulting DNA sequences were aligned by eye and the sub-fossil bones were identified by comparison to the reference sequences.

RESULTS

Identifiable bones of penguins, primarily juveniles, were recovered from most of the abandoned sites and indicated that three of these colonies were formerly occupied by Chinstrap, two by Gentoo, and six by Adélie penguins (Table 1). Two other abandoned sites (Sites 5 and 6 at Rakusa Point) lacked identifiable remains and are presumed to represent Adélie penguin occupations based on other sites of this species nearby. Results of the 36 radiocarbon dates are presented in Table 2. One date from Copa Site 3 Level 2 (NZA 15411) was too young to provide a valid age for calibration using the Calib 4.2

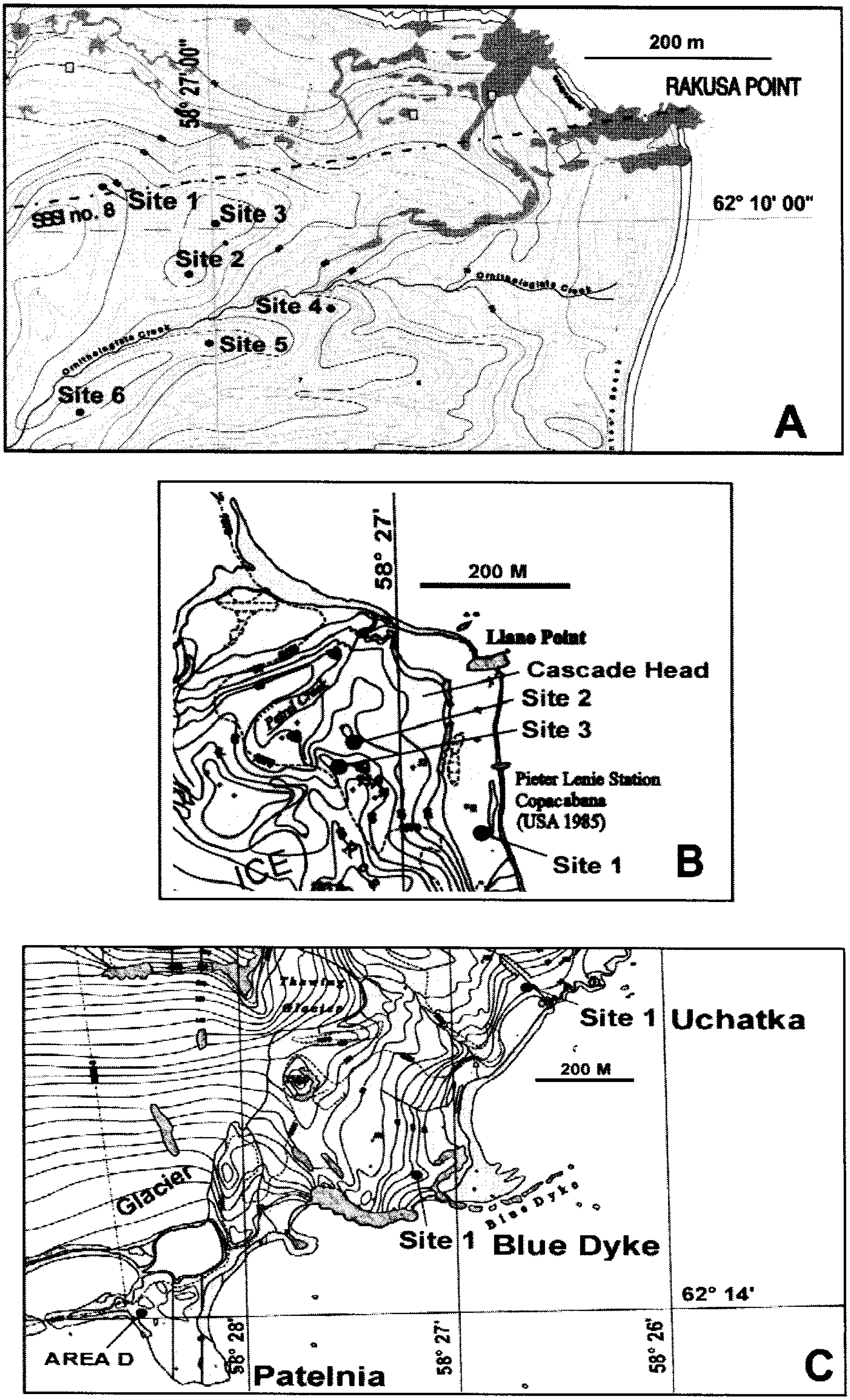

Fig. 2. A. Detail of Rakusa Point near Arctowski Station (Poland) showing the locations of Sites 1–6. B. Detail of Llano Point with Copacabana Field Station showing the locations of Sites 1–3. D. Detail of Uchatka, Blue Dyke and Patelnia showing the location of sites excavated at these areas. All maps are modified from *Padelko* [2002].

software program. All other dates except one indicate that penguin occupation in this region did not begin until approximately 500 to 600 B.P. The one exception (NZA 15300) from Rakusa Point Site 4, Level 4, is much older than any other date from all sites in this area, including four other dates from the same test pit and/or level, and is considered to be anomalous (Table 2).

The DNA sequences for the three *Pygoscelis* standards have been deposited in GenBank under the accession numbers AY234841, AY234842, and AY236364. There was 3.7–4.3% sequence difference among the three reference sequences and the DNA sequences that were retrieved from each sub-fossil bone could easily be assigned to a *Pygoscelis* species. This analysis confirmed the species identification at five of the abandoned sites (Tables 1 and 2).

Dietary remains were identified from all but two sites. Despite the apparent poor preservation of these remains at most sites, five taxa of cephalopods and 14 fish were identified in the sediments and are summarized by combining data from all levels from each test pit at each site (Table 3). At Rakusa Point, prey remains were scarce or absent and are summarized for Sites 1–4 combined; no prey remains were recovered from Sites 5–6 at this location.

Of the total prey identified, *Psychroteuthis glacialis*, *Galiteuthis glacialis*, *Pleuragramma antarcticum*, *Electrona antarctica*, and *Gymnoscopelus* cf. *G. nicholsi* were most abundant from most sites. Dietary remains recovered from guano samples from the two active colonies, Patelnia (Area D) and Cascade Head, were richer and better preserved than those from the abandoned sites. These remains allowed comparison of the modern diet in Chinstrap and Adélie penguins. Calculations of MNIs of two of the most abundant taxa represented from these sites, *Pleuragramma antarcticum* and *Electrona antarctica* (Table 3), indicate that the former species is more abundant in Adélie (MNI 0.52 per liter of sediment) compared to Chinstrap penguin (MNI 0.36 per liter) guano samples. In addition, *E. antarctica* is over three times more abundant in Chinstrap (MNI 2.8 per liter) compared to Adélie penguin (MNI 0.8 per liter) guano samples. However, these differences are not statistically significant ($\chi^2 < 1.094$, df = 1, $P < 0.9$).

DISCUSSION

Emslie [2001] reviewed all previous radiocarbon dates on penguin remains from the Antarctic Peninsula. A total of 63 dates from 21 abandoned colonies indicated that no sites older than approximately 540 B. P. existed in the northern peninsula. The absence of older sites may be due to late-Holocene glacial scouring of ornithogenic soils, solifluction, or an absence of penguins in the peninsula until the past 500–600 years. However, penguin bones and guano have been recovered and dated from raised beaches and lake sediments on King George Island that indicate these birds were present in the region during the middle Holocene [*Bocheński*, 1985; *Barsch and Mäusbacher*, 1986; *Tatur et al.*, 1997, *Sun et al.*, 2000)].

Results of 36 radiocarbon dates on Adélie, Gentoo, and Chinstrap penguin remains presented here support earlier findings that no pygoscelid penguin colonies existed in the northern Antarctic Peninsula until the late Holocene. Only one date from Site 4 (NZA 15300; Table 2) at Rakusa Point provides an older age. However, four other dates from this site, including one from the same level, all converge on a calibrated age ranging from 0 to 533 B.P. In addition, all other sites excavated at Rakusa Point had similar depositional characteristics in the depth and color of the ornithogenic soils. Thus, the simplest explanation for this older date is that it is anomalous. If an earlier occupation did occur in the middle Holocene, as suggested by guano deposits in lake cores at King George Island and Hope Bay [*Zale*, 1994a, b; *Sun et al.*, 2000], then ornithogenic soils from that occupation period have not been preserved or have not yet been located in this region.

Five of the 36 dates presented here, ranging in age from 619 B. P. to the present (based on 2σ calibrated ranges), are the first known on Gentoo penguin bones from ornithogenic sediments in Antarctica. While much more needs to be done on the paleohistory of Gentoo penguins, the two abandoned sites in Admiralty Bay indicate a similar late occupation history by this species as with Chinstrap and Adélie penguins and that all three species have been contemporaneous in the Admiralty Bay region for at least the past 500 to 600 years.

The radiocarbon dates from Rakusa Point also provide a minimum age for the formation of the glacial moraines that characterize this area. Two small abandoned colonies (Rakusa Point Sites 5 and 6) are located on the top of an old lateral moraine on the north side of Ecology glacier (Figure 1) and range in age from 550–265 B. P. Although *Birkenmajer* [1997] postulated that this moraine is less than 100 years old based on lichen growth, the penguin dates indicate a much older age for their formation prior to occupation by small groups of breeding penguins.

Dietary remains from most of these sites, while sparse, demonstrate the diversity of prey consumed by

TABLE 1. Abandoned and active penguin colonies excavated on King George Island with their excavation units, GPS location, approximate elevation above mean sea level (± 1 m), total sediments excavated in liters with dry weight (in parentheses) of all sediments recovered from the 0.32 and 0.025 cm^2 mesh screens after washing, and total percent dry weight of the last sorted for dietary remains. The *Pygoscelis* species identified by bones recovered at each site, when present, also is given; identification confirmed with DNA analysis of bone are indicated by an asterisk (*).

Site	Species	Excavation units	GPS Location	Elev. (m)	Total Sediments liters (grams)	Total Sorted (%)
Uchatka	**P. antarctica*	TP 1, Levels 1-5	62° 13' 15.1" S; 58° 26' 29.5"	20	143 (10,652)	69.4
		TP 2, Levels 1-4		22	114 (8452)	30.2
Blue Dyke	**P. antarctica*	TP 1, Levels 1-4	62° 13' 37.6" S; 58° 26' 59.5" W	28	151 (6276)	58.9
Patelnia Area D	*P. antarctica*	TP 1, Levels 1-5	62° 14' 05.9" S; 58° 28' 16.9" W	7	138 (3644)	100
Patelnia Area D	*P. antarctica*	Modern surface	62° 14' 05.9" S; 58° 28' 16.9" W	7	25 (120)	100
Copa Site 1	*P. papua*	TP 1, Levels 1-4	62° 10' 45.2" S; 58° 26' 43.5" W	3	159 (13,812)	11.4
Cope Site 2	*P. adeliae*	TP 1, Levels 1-3	62° 10' 29.6" S; 58° 27' 03.9" W	36	82 (3951)	16.9
Copa Site 3	**P. papua*	TP 1, Levels 1-3	62° 10' 30.7" S; 58° 27' 07.7" W	44	84 (3627)	19.2
Cascade Head	*P. adeliae*	Modern surface	62° 10' 31.6" S; 58° 26' 54.0" W	22	42 (475)	100
Rakusa Point Site 1	**P. adeliae*	TP 1, Levels 1-3	62° 09' 48.6" S; 58° 28' 07.0" W	48	80 (7253)	13.7
Rakusa Point Site 2	*P. adeliae*	TP 1, Levels 1-5	62° 09' 51.7" S; 58° 28' 02.2" W	50	140 (15,601)	12.7
Rakusa Point Site 3	*P. adeliae*	TP 1, Levels 1-3	62° 09' 49.9" S; 58° 28' 00.3" W	46	84 (10,744)	14.8
Rakusa Point Site 4	**P. adeliae*	TP 1, Levels 1-4	62° 09' 53.1" S; 58° 27' 51.6" W	31	108 (5970)	18.3
Rakusa Point Site 5	*P. adeliae*	TP 1, Levels 1-3	62° 09' 54.0" S; 58° 27' 59.7" W	48	66 (8301)	13.9
Rakusa Point Site 6	*P. adeliae*	TP 1, Levels 1-2	62° 09' 55.1" S; 58° 28' 05.1" W	49	44 (6168)	12.2

TABLE 2. Radiocarbon dates (in years B.P.) on penguin (*Pygoscelis* sp.) bone and eggshell membrane tissue from 12 abandoned colonies on King George Island. Stratigraphic position for each date is provided by site, test pit (TP) number, and 5-cm level. Conventional dates were corrected and calibrated for the marine-carbon reservoir effect using a $\Delta R = 700 \pm 50$ years [see *Emslie* 1995] and the MARINE98 database of *Stuiver and Reimer* (1993). The conventional date, $\delta^{13}C$ (‰) value, mean corrected date (both in radiocarbon years B. P.), and calibrated 2σ range(s) (95% confidence interval in calendar years B. P.) are provided for each sample. Multiple 2σ ranges are provided for corrected dates that intersected two or more regions of the calibration curve. All bones were identified by osteological comparison to reference skeletal material; an asterisk (*) denotes specimens further identified by DNA extraction.

Site/Provenience	Species	Material	Lab. No.	$\delta^{13}C$	Conventional Date	Calibrated Range (2σ)
Uchatka						
TP 1 Level 4	**P. antarctica*	Bone	NZA 15416	−22.42	1420 ± 65	502–238
TP 1 Level 5	*P. antarctica*	Bone	NZA 15417	−19.13	1490 ± 65	535–273
TP 2 Level 3	**P. antarctica*	Bone	NZA 15418	−18.40	1380 ± 60	478–141
TP 2 Level 4	**P. antarctica*	Bone	NZA 15419	−22.92	1260 ± 55	320–0
Blue Dyke						
TP 1 Level 3	**P. antarctica*	Bone	NZA 15414	−19.24	1420 ± 65	502–239
TP 1 Level 4	**P. antarctica*	Bone	NZA 15415	−20.08	1300 ± 65	420–0
Patelnia						
Area D Level 5	*P. antarctica*	Bone	NZA 15412	−20.71	1440 ± 60	506–253
	P. antarctica	Bone	NZA 15413	−21.50	1420 ± 60	498–243
Copa						
Site 1 TP 1 Level 1	*P. papua*	Bone	NZA 15406	−21.20	1450 ± 55	509–264
Site 1 TP 1 Level 2	*P. papua*	Bone	NZA 15539	−22.36	1580 ± 55	616–376
Site 1 TP 1 Level 3	*P. papua*	Bone	NZA 15407	−19.77	1580 ± 55	619–391
Site 1 TP 1 Level 4	*Pygoscelis* sp.	Bone	NZA 15408	−19.78	1530 ± 60	555–299
Site 1 TP 1 Level 4	*Pygoscelis* sp.	Bone	NZA 15409	−20.74	1400 ± 70	497–142
Site 2 TP 1 Level 2	*P. adeliae*	Bone	NZA 15410	−22.18	1340 ± 70	461–65 or 6 – 0
Site 2 TP 1 Level 3	*Pygoscelis* sp.	Feather	NZA 15613	−23.74	1350 ± 55	445–115
Site 3 TP 1 Level 2	**P. papua*	Bone	NZA 15411	−18.78	740 ± 55	Invalid age for calibration
Site 3 TP 1 Level 3	*Pygoscelis* sp.	Feather	NZA 15614	−22.09	1360 ± 55	459–133
Rakusa Point						
Site 1 TP 1 Level 2	*P. adeliae*	Bone	NZA 15285	−21.89	1380 ± 65	478–132
Site 1 TP 1 Level 3	**P. adeliae*	Bone	NZA 15286	−21.60	1500 ± 55	511–266
	P. adeliae	Bone	NZA 15287	−22.77	1430 ± 60	504–251
Site 2 TP 1 Level 1	*P. adeliae*	Bone	NZA 15288	−22.13	1410 ± 55	490–243
Site 2 TP 1 Level 2	*P. adeliae*	Bone	NZA 15289	−20.11	1370 ± 65	473–127
Site 2 TP 1 Level 3	*P. adeliae*	Bone	NZA 15290	−23.77	1500 ± 65	545–281
Site 2 TP 1 Level 4	*P. adeliae*	Bone	NZA 15291	−16.89	1490 ± 60	536–280
Site 2 TP 1 Level 5	*P. adeliae*	Bone	NZA 15292	−22.54	1670 ± 60	665–458
	P. adeliae	Feather	NZA 15612	−22.50	1460 ± 55	514–269
Site 3 TP 1 Level 1	*P. adeliae*	Bone	NZA 15293	−21.87	1480 ± 65	534–271
Site 3 TP 1 Level 2	*P. adeliae*	Bone	NZA 15294	−18.80	1360 ± 55	456–131
Site 3 TP 1 Level 3	*P. adeliae*	Bone	NZA 15295	−23.68	1450 ± 60	510–258
Site 4 TP 1 Level 1	**P. adeliae*	Bone	NZA 15296	−21.87	1290 ± 55	401–0
Site 4 TP 1 Level 2	*P. adeliae*	Bone	NZA 15297	−23.12	1480 ± 65	533–271
Site 4 TP 1 Level 3	**P. adeliae*	Bone	NZA 15298	−23.53	1310 ± 65	433–0
Site 4 TP 1 Level 4	*P. adeliae*	Bone	NZA 15299	−22.78	1340 ± 55	444–113
	P. adeliae	Bone	NZA 15300	−21.19	8380 ± 60	8318–7954
Site 5 TP 1 Level 2	*P. adeliae*	Egg mem	NZA 15317	−21.83	1530 ± 55	550–303
Site 6 TP 1 Level 2	*P. adeliae*	Egg mem	NZA 15318	−21.42	1450 ± 55	510–265

TABLE 3. Taxa of cephalopods and fish identified from abandoned penguin colonies on King George Island compared to remains identified from Patelnia and Cascade Head, the active Chinstrap and Adélie Penguin colonies, respectively. The total number of identifiable specimens (including fragments) and minimum number of individuals (MNI, in parentheses) of prey (based on whole and fragmentary remains summed by level) are provided for all levels of each test pit (TP); data are combined from TP 1 and 2 at Uchatka and from Sites 1–4 at Rakusa Point.

Taxon	Uchatka TP 1-2	Blue Dyke TP 1	Patelnia Area D	Copa Site 3	Rakusa Point Sites 1-4	Patelnia (Chinstrap)	Cascade Head (Adélie)
Cephalopoda (squid and octopus)							
Psychroteuthis glacialis	7 (6)	19 (12)	15 (5)		1 (1)	1 (1)	1 (1)
Brachioteuthis sp.			2 (2)				
Galiteuthis glacialis	13 (11)	13 (8)	9 (8)		2 (2)	1 (1)	
Pholidoteuthis sp.			1 (1)				
Unident. oegopsid beak frags.	19	21	17		2	7	1
cf. Parelodone sp.			1 (1)				
Osteichthyes: Teleostei (bony fish)							
Dissostichus sp.				1 (1)			
Paranotothenia sp.			1 (1)				
Notothenia sp.			1 (1)				
Trematomus sp.	1 (1)		3 (2)				
Pleuragramma antarcticum	12 (8)	10 (5)	18 (14)		2 (2)	15 (9)	33 (22)
Harpagifer cf. H. georgianus			1 (1)				2 (2)
Pagetopsis cf. P. maculatus							
Pagetopsis sp.			2 (2)				
Chaenodraco cf. C. wilsoni		3 (3)				8 (4)	
Chaenodraco sp.			2 (2)				
Notolepis coatsi	1 (1)	1 (1)	1 (1)				
Protomyctophum bolini	1 (1)						
Electrona antarctica	254 (138)	330 (179)	512 (145)		10 (8)	140 (70)	60 (34)
Electrona carlsburgi			3 (2)			3 (3)	1 (1)
Gymnoscopelus braueri	3 (2)						
Gymnoscopelus cf. G. braueri	3 (2)	2 (1)					
Gymnoscopelus cf. G. nicholsi	27 (4)	73 (9)	59 (7)		1 (1)	4 (1)	
Unident. Notothenoidei	1		13			2	1
Unident. Channichthyidae			13				
Unident. Paralepididae	1						
Unident. Myctophidae	244	171	246		1	23	14
Unident. otolith fragment		2	172	1	1		18

pygoscelid penguins. Although krill is by far the dominant prey of choice by these species at King George Island today, fish are consumed in small to large quantities and are an important component of their diet [*Williams*, 1995]. The data from the modern samples also suggest that Chinstrap penguins prefer lantern fish (*Electrona* spp.) over Antarctic silverfish (*Pleuragramma antarcticum*) while Adélie penguins are the reverse, though these patterns from these small samples are not statistically significant. Preferences by these species for these prey previously have not been documented in stomach sampling or other dietary studies in this region [*Volkman et al.*, 1980; *Williams*, 1995]. However, additional investigation is needed to determine if a significant difference in non-krill prey selection does occur between these species at King George Island.

Last, the absence of older penguin colonies in the northern Antarctic Peninsula remains an enigma and additional research in other regions of King George Island and at other islands, including those in the Weddell Sea, are needed to determine if this occupation pattern is real or an artifact of sampling or other factors. It is possible that the northern peninsula was abandoned by penguins by the mid to late Holocene and that the record for this earlier occupation (i.e., ornithogenic sediments) has been erased by glacial scouring or other processes; only limited evidence for this occupation remains from guano deposits in lakes. If so, this abandonment was followed by reoccupation of the region beginning approximately 500 to 600 years ago, near the beginning of the Little Ice Age [LIA, A.D. 1500–1850; *Grove*, 1988]. At that time, the Antarctic Peninsula was thought to have experienced more warming than cooling periods based on the ice core record from Siple Dome [*Mosely Thompson et al.*, 1990]. However, recent evidence from marine sediments in the Palmer Deep suggest otherwise [*Warner and Domack*, 2002; see also *Domack et al.* and *Hjort et al.*, this volume].

If the LIA was characterized by colder conditions in the Antarctic Peninsula compared to today, then it is difficult to reconcile the penguin record with the climatic record. A colder period presumably would be less favorable for penguin colonization, especially if extensive sea ice and/or glacial expansion and persistent snow cover blocked access to ice-free terrain along the coast. It is possible that conditions varied throughout the peninsula during the late Holocene so that some areas, such as King George Island, were accessible to breeding penguins beginning about 600 B.P. Additional paleoenvironmental data are needed from a diversity of locations in the Antarctic Peninsula to fully address this problem.

Modern warming trends in the peninsula over the past two decades have been causing a decrease in Adélie penguins [*Smith et al., 1999*] that may lead to abandonment of this region in the future. Conversely, Gentoo penguins, which prefer warmer, sub-Antarctic regions, have been expanding farther southward in the Antarctic Peninsula over the past 20 years than they have in any period prior to this [*Smith et al.*, 1999]. Although our data indicate that Adélie, Chinstrap, and Gentoo penguins have been contemporaneous in Admiralty Bay for the past 500–600 years, their current relative population sizes and ranges are rapidly shifting with climate change. This trend could result in a new geographic distribution of pygoscelid penguins in the Antarctic Peninsula, and a loss of sympatry among these species that apparently has existed in this region for the past 600 years.

Acknowledgments. This research was funded by grants from the National Science Foundation (OPP 9909274) and the National Geographic Society (NGS Grant #7040-01). Field assistance was provided by R. Hollingshead, M. Polito, M. Romano, J. Smykla, C. Thiessen, and W. Trivelpiece. I thank S. Rakusa-Suszczewski and the Polish Academy of Sciences for their cooperation and assistance at Arctowski Station, and W. Trivelpiece for use of facilities at the Copacabana Field Station. W. Walker provided identifications of otolith and squid remains and R. Pudelko allowed use of digital maps. All radiocarbon dates were completed at the Rafter Radiocarbon Laboratory, New Zealand. The paper was improved with comments from A. Clarke, E. Domack, C. Hjort and one anonymous reviewer.

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