

Holocene elephant seal distribution implies warmer-than-present climate in the Ross Sea

B. L. Hall*^{†‡}, A. R. Hoelzel[§], C. Baroni[¶], G. H. Denton*^{†||}, B. J. Le Boeuf**[†], B. Overturf*, and A. L. Töpfer[§]

*Climate Change Institute and [†]Department of Earth Sciences, University of Maine, Orono, ME 04469; [§]School of Biological and Biomedical Sciences, University of Durham, Durham DH1 3HP, United Kingdom; [¶]Dipartimento di Scienze della Terra, Istituto di Geoscienze e Georisorse, Università di Pisa and Consiglio Nazionale delle Ricerche, 56126 Pisa, Italy; and ^{**}Institute of Marine Studies and Department of Biology, University of California, Santa Cruz, CA 95064

Contributed by G. H. Denton, May 15, 2006

We show that southern elephant seal (*Mirounga leonina*) colonies existed proximate to the Ross Ice Shelf during the Holocene, well south of their core sub-Antarctic breeding and molting grounds. We propose that this was due to warming (including a previously unrecognized period from $\approx 1,100$ to $2,300$ ^{14}C yr B.P.) that decreased coastal sea ice and allowed penetration of warmer-than-present climate conditions into the Ross Embayment. If, as proposed in the literature, the ice shelf survived this period, it would have been exposed to environments substantially warmer than present.

Antarctica | southern elephant seals

With the warming climate of the past decades, rapid break-ups (caused by pooling of surface melt, seepage into crevasses, and wedging through the ice shelf) have destroyed several small, thin ice shelves fringing the Antarctic Peninsula (1, 2). Removal of ice-shelf back pressure has resulted in a marked increase in the seaward flow of glaciers discharging into the now abandoned embayments (i.e., ref. 3). With continued warming, this mechanism potentially could spread southward and affect the huge Ross and Ronne–Filchner Ice Shelves, the disintegration of which could result in accelerated ice-stream flow, catastrophic thinning of the West Antarctic Ice Sheet (WAIS), and global sea-level rise (4, 5). Several studies have suggested a time frame that could lead to disintegration of the Ross Ice Shelf over decades within this century (1, 4, 5).

We present Holocene climate data, which result from our discovery of abandoned southern elephant seal colonies along the Victoria Land Coast (VLC) (Fig. 1), that may bear on the question of Ross Ice Shelf susceptibility to warmer-than-present climate. The southern elephant seal has a circumpolar distribution today, typically breeding in sub-Antarctic latitudes on isolated islands. It is the largest of the phocid seals. They parturate and breed annually (after delayed implantation of the embryo) and spend the rest of the year foraging. Relatively few elephant seals have been observed in Antarctica, and these consist primarily of seals on foraging excursions or isolated molting groups (6), although some breeding takes place at Palmer Station and in the Windmill Islands (7, 8). The closest extant rookery to the VLC occurs in the sub-Antarctic 3,400 km to the north on Macquarie Island. Although a few southern elephant seals forage in the Ross Sea today, there are no breeding colonies or molting sites in the region and less than a dozen seals have been noted on the beaches since the discovery of Victoria Land in 1841 (9).

Results

We collected seal skin and hair from Holocene raised beaches (Fig. 2). Small pieces were found in nearly every excavation and, in places, were in roughly equal proportions to sand and gravel. Both visual inspection and DNA analysis confirm that the material is from southern elephant seals. We identified nine individuals from five sites, ranging in age from 266 to $2,864$ ^{14}C yr B.P., as *M. leonina*, based on mtDNA amplification and

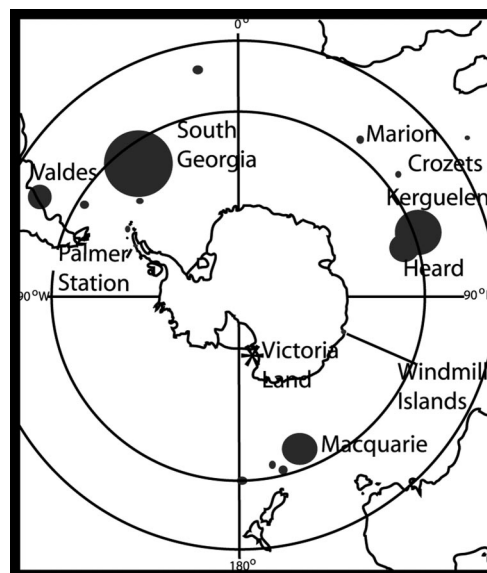


Fig. 1. Map showing the present distribution of *M. leonina* (circles) and the former VLC colonies (asterisk) (6).

sequence comparison with modern samples and all closely related local species. There were eight haplotypes among the nine ancient samples and all fit into the southern elephant seal lineage (Fig. 3). All but one of the ancient haplotypes was new [compared against modern haplotypes (10)]; therefore, they could not be the result of contamination. In addition to molted skin, mummified southern elephant seal tissue encasing essentially complete skeletal remains were found, totaling six adults and two pups.

Fifty radiocarbon dates of the seal remains ranged from 266 to $6,065$ ^{14}C yr B.P., after correction for the marine reservoir effect (see Table 1, which is published as supporting information on the PNAS web site, and Figs. 2 and 4). Initial colonization began $\approx 6,000$ ^{14}C yr B.P. at Inexpressible Island. More southerly sites (Marble and Gneiss Points, and Dunlop Island) were occupied by $\approx 4,500$ ^{14}C yr B.P. Seals were present at Gneiss Point, Cape Ross, and Campbell Glacier only briefly, probably because suitable access was absent after glacio-isostatic rebound. In addition, the record at Depot Island (Peninsula) also is short because of only limited reconnaissance. We exclude these sites

Conflict of interest statement: No conflicts declared.

Abbreviation: VLC, Victoria Land Coast.

[†]To whom correspondence may be addressed at: University of Maine, 303 Bryand, Orono, ME 04469. E-mail: brendah@maine.edu.

^{||}To whom correspondence may be addressed. E-mail: debbies@maine.edu.

© 2006 by The National Academy of Sciences of the USA

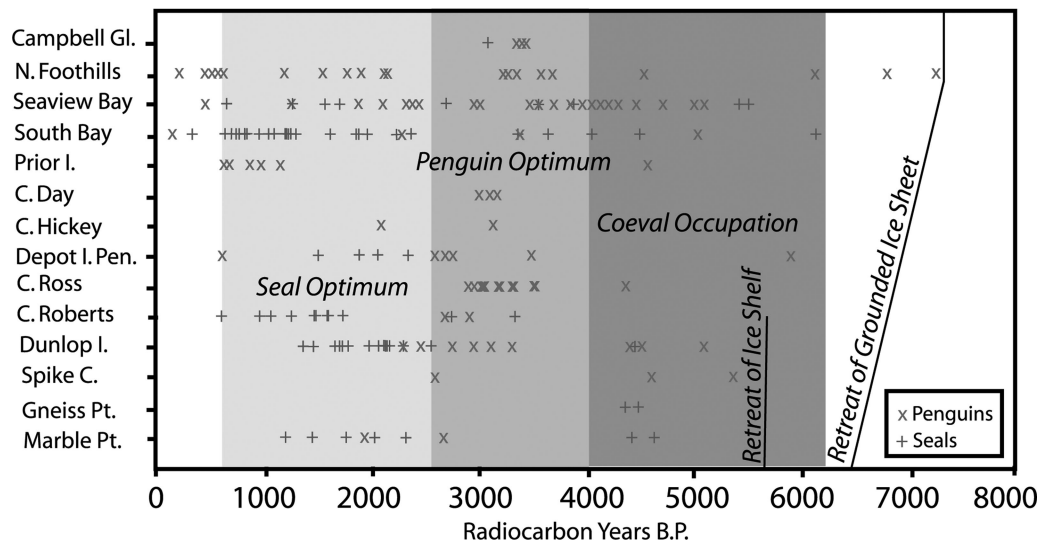


Fig. 4. Diagram showing the distribution of radiocarbon dates for elephant seal (“+”) and Adélie penguin (“x”) samples from each site listed from south (bottom) to north (top).

record comes from Inexpressible Island, which, because of its northern location and adjacent polynya, may be the most favorable site in the study area. In contrast, southern locations (Marble Point and Dunlop Island) with little open-water access today have the shortest habitation records of any of the major sites (Figs. 2 and 4). Because elephant seals have a predominantly sub-Antarctic distribution and a known propensity to haul out adjacent to open water, we conclude that expansion of land-fast, perennial sea ice, probably coupled with increased pack ice, may have prevented access to haul-out sites and resulted in colony demise. Moreover, the former presence of seal colonies indicates that unlike today at least seasonally open water must have been present along the VLC in the middle to late Holocene. If these sites were used for both breeding and molting, as we have suggested, open water would have had to be present from early spring through to the autumn.

If the seals had only been found near the Terra Nova Bay polynya or on Ross Island (Fig. 1), a viable alternative explanation would be that katabatic winds controlled the sea-ice extent rather than temperature. However, seals were found over the entire length of the Scott Coast, including areas that are relatively sheltered from katabatic winds. In general, the areas where we found the seals are almost always locked in fast ice today despite the occasional presence of open water a few tens of kilometers to the east. Icebergs today sometimes locally increase the thickness and duration of sea ice. However, the widespread distribution of seal remains reduces substantially the likelihood that it was icebergs rather than temperature controlling sea ice that affected the seals’ use of the area. Past seal distribution also could have been affected by prey distribution, but because elephant seals feed in this region today, and often breed and molt far from where they feed, we do not think prey access is likely the factor that controlled their historical use of the area for breeding and/or molting. Taken together the data best support the hypothesis that sea-ice distribution controlled by temperature changes is what affected elephant seal use of the area.

Relict Adélie penguin rookeries along the VLC also have been used as sea-ice indicators (13). Comparison of the seals and penguins indicates that the timing of occupation at southern sites and possibly at southern Inexpressible Island appears to have been mutually exclusive, with little overlap between the species (Fig. 4). This relationship is not surprising, because today the

habitats of these two species overlap only rarely. During the climate warming (and sea-ice decrease) of the last three decades, Adélie penguins have declined 70% in the vicinity of Palmer Station (thought to be related to reduced sea ice; Fig. 1), whereas elephant seals increased 300% (14, 15) (W. Fraser, personal communication). Whereas southern elephant seals favor open water, pack ice is important to the breeding success of Adélie penguins, offering one of the few reliable zones of prey concentration during spring (16, 17). Thus, these penguins tend to live south of the pack-ice limit year round. However, excessive, intact sea ice negatively impacts a colony by increasing distance to open water and delaying arrival at the nest sites (18). Adélie penguins, therefore, occupy a narrow zonal habitat optimum between insufficient and excessive sea ice (16, 19).

Between $\approx 4,000$ and $6,000$ ^{14}C yr B.P., the two species coexisted along the VLC, indicating less sea ice than at present (a requirement for elephant seal colonies) but still sufficient regional pack ice for Adélie penguins. Land-fast ice must have been at a minimum, and seasonally open water must have persisted right up to the shore. Between 2,300 and 4,000 ^{14}C yr B.P., a decline and even possible disappearance of elephant seals suggest that sea ice returned. The penguin colonies spread, perhaps because an increase in pack ice resulted in more favorable foraging ecology. However, ice still must have been less severe than at present along the VLC (where penguins cannot survive today) and may have resembled conditions seen today adjacent to northern Ross Island (Fig. 2).

The period between 1,100 and 2,300 ^{14}C yr B.P., marked by significant expansion of elephant seal colonies and a disappearance of Adélie penguins, represents the greatest sea-ice decline (and probably the warmest ocean and air temperatures) in the Ross Sea in the last 6,000 yr. This was followed by an increase in sea ice and the development of land-fast ice $\approx 1,000$ yr ago on the VLC, which we propose led to the abandonment of seal colonies. The ice regime remains too severe for either elephant seals or penguins to occupy the southern VLC today. Integration of southern elephant seal and Adélie penguin data affords a distinctly different record of Holocene sea-ice change than that previously derived from penguin data alone. For example, the disappearance of penguins from the southern VLC ($\approx 2,500$ ^{14}C yr B.P.), originally thought to reflect severe ice (13), is now interpreted as indicating a period of sea-ice reduction so great that Adélie penguins no longer were a viable population. Al-

though our new reconstruction differs from some previous interpretations (13, 20, 21), it is consistent with late Holocene atmospheric circulation intensity records from Siple Dome (22) and with methanesulfonic acid data from nearby Newall Glacier that suggest expanded sea ice between 300 and 1,250 yr B.P. (23). In addition, our “seal optimum” is coeval with a significant accumulation rate increase at Taylor Dome, which may have resulted from sea-ice reduction and greater moisture availability (24). The disappearance of elephant seals from the VLC is broadly contemporaneous with the onset of Little Ice Age climatic conditions in the Northern Hemisphere and with glacier advance near Terra Nova Bay (25).

Our reconstruction implies that during parts of the middle and late Holocene, sea ice was less extensive, the warm season was likely longer, and the environment was more like the sub-Antarctic than at present in the Ross Embayment. Our data on seal distribution cannot inform us about the fate of the Ross Ice Shelf during these periods. However, the lack of coastal landforms, such as beaches south of the present calving front (unpublished observation), and the dates of marine organisms on the adjacent McMurdo Ice Shelf both suggest that the Ross Ice Shelf has been continuously present over the last 7,000 yr (26). Domack *et al.* (27) recently showed that the Larsen B ice shelf survived warm conditions in the mid-Holocene, even though it recently collapsed catastrophically. They infer from their data (based on oxygen isotope measurements in planktonic foraminifera) that the Larsen B ice shelf has been thinning throughout the Holocene and suggest that this, together with recent warming, led to the collapse. If the Ross Ice Shelf did survive, it too may have been thinning throughout the middle and late Holocene in response to grounding-line retreat (28). However, the critical parameter for recent ice-shelf collapse is thought to be an increase in the intensity and length of the summer melt season with ice shelves on the Antarctic Peninsula becoming susceptible to rapid breakup when January temperatures have exceeded -1.5°C (1). The presence of southern elephant seal colonies (which today exclusively occupy areas where the mean January temperature exceeds 0°C , usually by considerable margins), the disappearance of ice-obligate penguins, and the inferred significant reduction in sea ice, both in intensity and seasonal duration, suggest that the front of the Ross Ice Shelf could have been subject to January temperatures that surpassed the -1.5°C threshold during two long periods at $\approx 1,000$ – $2,300$ and $4,000$ – $6,000$ ^{14}C yr B.P. It may be that the environment, although warmer than present, did not reach the critical temperature over a sufficiently large portion of the ice shelf necessary to initiate rapid collapse, or that a steep climate gradient left much of the shelf in a stable zone. In addition, pinning points, such as Ross Island, may have contributed to its stability.

Materials and Methods

Field Methods. We collected samples (see Table 1) from hand-dug excavations within raised beaches from sea level to ≈ 30 m elevation, the marine limit. All raised beaches in the study area were examined. Samples were obtained by careful examination of excavated sediment and extraction with trowels and tweezers. Seal skin and hair were abundant in most locations, although collection required careful searching. Mummified remains were identified as elephant seals based on skeletal morphology and pelage. Adult males (five of the six adults) could be identified by their distinctive canine teeth and body length. Two adult mummies were from Marble Point, one was from Cape Ross, and three adults and two pups were from Inexpressible Island.

Sample Preparation and DNA Extraction. Ancient DNA extractions were carried out in a laboratory physically separated from the

main building and exclusively dedicated to ancient DNA manipulation. Seven of the nine samples amplified are indicated in Table 1 (the samples that were dated). PCR and post-PCR analyses were carried out in the main laboratory. In addition, a one-way (from the ancient laboratory to the PCR laboratory) procedure was always followed to avoid the imperceptible carrying of DNA aerosols on clothes or skin into the ancient DNA laboratory (29). All plastic-ware was double autoclaved, and the PCR setup was done in a laminar flow hood. To detect possible contamination, extraction, PCR, and carrier negative controls were undertaken every 10 samples. No southern elephant seal DNA had ever been in the building housing the ancient laboratory prior to this study. Replications were done from a different piece of the same skin sample.

Dried skin pieces (from which the hairs had been plucked) were incubated overnight at 55°C with 3 ml of lysis buffer (0.5 M EDTA, pH 8.0/0.5% SDS) and 50 μl of proteinase K (20 mg/ml). Samples were centrifuged for 3 min at high speed, and aliquots of 500 μl of supernatants were transferred to clean tubes. Five volumes of QIAquick PB buffer (Qiagen) were added and thoroughly mixed. A 700- μl aliquot of this solution was loaded into a QIAquick PCR purification column (Qiagen) and centrifuged at high speed for 45 sec. The flow-through was discarded, and the process repeated until all of the extract was passed through the column. DNA binding to the silica filter was washed by adding 750 μl of QIAquick PE buffer and centrifuged for 1 min at high speed. The flow-through was discarded, and the samples were centrifuged for another 2 min to eliminate any trace of ethanol. DNA was eluted in 35 μl of EB buffer (TE-based buffer; Qiagen). Samples were centrifuged at maximum speed for 30 sec, and the DNA solution was collected in a clean tube. The DNA solution was kept at 4°C for 3 days and then stored at -20°C until being used for the PCR.

Primer Design and PCR Amplification. Primers were designed across a segment of mtDNA 5' control region sequence that showed both indel and sequence variation among Antarctic phocids, including four fixed differences between the southern elephant seal and each of the other Antarctic phocid species (*Leptonychotes weddellii*, *Ommatophoca rossii*, *Lobodon carcinophaga*, and *Hydrurga leptonyx*). The sequence also included fixed differences between the southern and northern elephant seal (*Mirounga angustirostris*) species, and extensive differentiation between Antarctic phocids and otariids. The primer sites showed no differentiation among 41 haplotypes [from screening 128 seals (10)] for the southern elephant seal. To facilitate amplification from ancient DNA, the fragment was designed to be short (209 bp including primers), from which 144 bp could be reliably sequenced (omitting sequence near the forward primer used for sequencing but including all fixed difference sites). The following primers were used: SESanc3f, 5'-GCTGACATTCTACTTA-ACT-3', and SESanc3r, 5'-ATGTACATGCTTATATGCAT-3'. Each 25- μl PCR contained 0.2 pM/ μl each primer, 0.2 mM each dNTP, Platinum 1X High Fidelity Buffer [60 mM Tris- SO_4 , pH 8.9/18 mM $(\text{NH}_4)_2\text{SO}_4$ (Invitrogen)], 15 mM MgCl_2 , 0.08 $\mu\text{g}/\mu\text{l}$ BSA, and 1 unit of Taq High Fidelity DNA polymerase (Invitrogen). PCR conditions were as follows: 95°C for 8 min (enzyme activation); 45 cycles of 94°C for 45 sec, 52°C for 1.5 min, and 72°C for 1.5 min; and a final extension at 72°C for 5 min. Results were confirmed by repeated amplification from independent samples.

DNA Sequencing and Phylogenetic Analysis. PCR products were purified with Qiagen PCR purification columns and sequenced directly by using the ABI dye-terminator method on an ABI 377 automated sequencer (Applied Biosystems). DNA sequences were aligned by using CLUSTALX (30) and saved as a NEXUS file for input into PAUP (31). A neighbor-joining tree was constructed

