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Widespread southern elephant seal occupation of the Victoria Land Coast implies a warmer-than-present Ross Sea in the mid-to-late Holocene

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Abstract

Prediction of future ice-sheet behavior in Antarctica and its contribution to sea-level rise depends on accurate understanding of ice-sheet response to a warm climate. Examination of how the ice sheet reacted to past warm episodes affords a means of assessing its tolerances to climate change. The West Antarctic Ice Sheet (WAIS), in particular, is thought to be highly susceptible to variations in ocean temperature at its grounding lines. Yet, detailed records of past ocean temperatures close to the continent are rare. Here, we present a record of past relative ocean-temperature and sea-ice change derived from the presence and then eventual abandonment of southern elephant seal (*Mirounga leonina*) occupation sites along the Victoria Land Coast (VLC) of the western Ross Embayment. Our results suggest greatly reduced landfast and likely pack ice, as well as potentially the incursion of relatively warm modified Circum-Polar Deep Water from ~7100-500 yr BP, with the greatest reduction in ice/warmest water temperatures at ~5200 and ~2300-1800 yr BP. These changes in ocean conditions would have had a strong influence on VLC marine-terminating glaciers through variations in buttressing sea ice and melt rates on the underside of floating ice. Independent data suggest that these glaciers had restricted extent in the mid-Holocene, consistent with our inference of warm ocean temperatures and low sea ice. The glaciers subsequently expanded within the last millennium, coincident with the disappearance of southern elephant seals from the coast and the inferred return to icy conditions. Our relative sea-ice and ocean-temperature reconstruction also is consistent with the hypothesized retreat of the WAIS inland of its present position in the mid to late Holocene, although the distance between our sites and the current WAIS grounding lines is large (600-1000 km), and thus any linkage is speculative at present. Finally, limited pre-Holocene southern elephant seal data support the existence of warm ocean temperatures immediately prior to and perhaps even during build-up to the Last Glacial Maximum (LGM) ice position. If this could be confirmed, it would suggest that factors other than ocean temperatures, such as lowered sea level, might have been critical in causing ice-sheet advance in the Ross Embayment at the LGM.

Key Words *Mirounga leonina*; southern elephant seals; Ross Sea; ocean temperatures; sea ice, West Antarctic Ice Sheet

1. Introduction

The future stability of the marine-based West Antarctic Ice Sheet (WAIS) remains one of the greatest uncertainties in sea-level projections for the next century. Indications of its past behavior, particularly during times of climate warming, afford insight into the range of possible ice-sheet responses to rising temperatures (Hall et al., 2015; Neuhaus et al., 2021). However, our current understanding of WAIS response to former warm periods, including the Holocene thermal optimum (~7-4 ka), remains inadequate (e.g., Johnson et al., 2022). Moreover, the number and variety of local (Antarctic) temperature records with which to compare ice-sheet behavior, are still relatively limited.

Recent work shows the importance of ocean temperature in controlling melt rates along marine ice-sheet margins (Shepherd et al., 2004; Pritchard et al., 2012; Milillo et al., 2019; Holland et al., 2020). Because much of the WAIS lies on topography with a reverse bed slope (i.e., it becomes deeper inland), processes that cause grounding-line recession, such as increased melt, lead ice to retreat into progressively deeper water, a phenomenon that promotes marine ice-sheet instability (Hughes, 1973; Weertman, 1974). Under future global warming, warm subsurface ocean waters and thus melt likely will increase around Antarctica due to southward movement of the westerlies and enhanced meltwater production (e.g., Bronselaer et al., 2020) or stronger polar easterlies (e.g., Naughten et al., 2022), both of which have been suggested to promote relatively warm Circum-Polar Deepwater penetration to glacier grounding lines.

Comparison of prior glacier fluctuations with past ocean temperatures allows assessment of the resilience of the WAIS and its huge buttressing ice shelves to a warming ocean. Yet, well-constrained records of ocean-temperature change are uncommon close to the Antarctic continent. Here, we present a ~7000 yr record of relative ocean temperature change derived from the past occurrence of southern elephant seals (SES, *Mirounga leonina*) along the Victoria Land coast (VLC; Fig. 1) of the western Ross Embayment. We use this record to improve understanding of Holocene ocean temperatures in the Ross Sea and to assess the tolerances of the extensive Ross Ice Shelf and WAIS grounding lines to a warming ocean.

2. Background

Located along the western margin of the Ross Embayment, the VLC (Fig. 1) displays numerous small ice-free islands and peninsulas interspersed with outlet glaciers and local ice piedmonts. Perennial, landfast sea ice characterizes most of the region, particularly south of Drygalski Ice Tongue. Terra Nova Bay, a coastal polynya, is a notable exception. A northward-flowing cold current, derived from sub-ice shelf water, contributes to maintaining icy conditions along the western shore of the Ross Sea, particularly adjacent to McMurdo Sound (Barry and Dayton, 1988).

Holocene-age coastal landforms and sediments elevated by isostatic rebound dominate the low-lying ice-free areas. These features (≤ 32 m elevation) are as old as ~8000 yr BP (Baroni and Hall, 2004; Hall et al., 2004). Despite extensive present-day landfast sea ice, ancient landforms display features indicative of persistent open water at the shore, such as pocket beaches, spits, tombolos, and well-rounded clasts (Nichols, 1968; Hall and Denton, 2000). These contrast with many modern beaches, which have been produced by ice push.

Today, the beaches are largely free of marine mammals and birds; skuas (*Stercorarius maccormicki*) are the most widespread species. Along the southern coast, penguins are absent, although small Adélie (*Pygoscelis adeliae*) rookeries existed in the past (i.e., Baroni and Orombelli, 1991, 1994a; Emslie et al., 2007). Adélies also occur adjacent to Terra Nova Bay at Adélie Cove and Inexpressible Island. Solitary or small groups of Weddell seals (*Leptonychotes weddellii*) occasionally haul out on the VLC. No other seals use these beaches at present.

In 2006, we suggested a pre-historic presence of SES on the Ross Sea VLC (Hall et al., 2006). Based on our initial, but limited dataset, we proposed that these seals may have been present during the Holocene and that extensive sea ice led to their exclusion from the present-day coast. Here, we present a more comprehensive dataset of radiocarbon-dated molted skin/hair, mummified and skeletal remains, and whiskers covering ~7000 yrs and at least 73-78° S latitude. These data show the widespread presence of SES along the VLC, which we attribute to the reduction or absence of landfast ice, as well as warmer ocean temperatures over much of the Holocene compared to today.

The presence of abundant SES remains on the VLC is unexpected. Today, this species is based largely on subantarctic islands, such as South Georgia, Kerguelen, and Macquarie (Fig. 2). A few hundred sub-adult males from subantarctic colonies molt on the East Antarctic coast near Vincennes and Prydz Bays polynyas (~66° S; Gales and Burton, 1989; van den Hoff et al., 2003), and SES currently are expanding their range along the Antarctic Peninsula as climate warms and sea ice disappears (Siniff et al., 2008; Hindell et al., 2016). A few dozen individuals molted on Ross Island, adjacent to the Ross polynya, in the early 1970s (Brownell and Ainley, 1976), but there currently are not, nor have there been in historic times, any molting or breeding colonies along the VLC. Nor do tracking studies provide evidence for substantial foraging on the continental shelf in the western Ross Sea along the VLC, despite foraging by adult male and female SES on the adjacent Wilkes Land coast (e.g., Hindell et al., 2017). We are aware of only a few anecdotal sightings of a live SES along the coast in the entire historic era.

3. Methods

We carried out extensive, systematic foot surveys of all significant coastal islands and peninsulas from Butter Point (77.70° S, 163.91° E) to Cape Phillips (73.07° S, 169.62° E), looking for both mummified/skeletal remains and molted skin and hair (Figs. 1, 3). We conducted repeat, late-summer surveys in multiple years for most locations to examine the coast under different snow conditions. Permanent or semi-permanent snowbanks are known to cover seal remains, and thus the likely extent of the remains is greater than presented here. In prior work, we obtained key body-size metrics for mummified and skeletal remains (Koch et al., 2019), as well as ancient DNA (aDNA) for species verification and population dynamics (e.g., de Bruyn et al., 2009, 2014). Here, we focus on the chronology and patterns of SES occupation on the VLC, as well as on Ross Island, constrained by 305 radiocarbon dates of remains (289 from the VLC, the remainder from Cape Bird on Ross Island). We then explore the paleoclimatic and glaciologic implications of this occupation history.

We located shed skin and hair by flipping over partially embedded, medium-sized boulders on raised beaches to reveal skin and hair pressed beneath (e.g., Hall and Denton, 1999). The flat, pressed nature of these pieces under the centers of the rocks suggests that this material was buried when rocks were deposited on the beaches. Alternatively, the skin and hair may have ended up beneath the rocks because of elephant seal turbation. Surfaces probably were covered by shed skin and hair during the molt, but only that reworked beneath clasts by subsequent beach augmentation and/or by crawling seals was preserved from the wind. We also examined recently deglaciated terrain where melting ice has revealed surfaces covered with molted skin and hair. Finally, we also searched for skin and hair in hand-dug excavations within beach sediments.

We produced a chronology for seal remains using radiocarbon dating. Samples were rinsed with ultrapure water and dried overnight. Cleaned samples were processed at the National Oceanic Sciences Accelerator Mass Spectrometry (NOSAMS) laboratory at Woods Hole Oceanographic Institution using standard procedures. We converted radiocarbon dates to calendar years, using Marine20 (Heaton et al., 2020) and the Ross Sea Holocene marine reservoir correction of Hall et al. (2010), recalculated for use with Marine20 (delta R = 610 +/- 110 yr; Hall et al., 2010; Braddock et al., 2022). Although Marine20 is not optimal for polar regions (Heaton et al., 2020), it is considered satisfactory for Holocene samples such as ours (Heaton et al., 2022) and has been used previously for Holocene-age Antarctic marine records (e.g., Braddock et al., 2022; Gao et al., 2022). The local delta R correction is derived from independently dated Victoria Land Coast corals (Hall et al., 2010) that span the Holocene.

4. Results

4.1 Locations and types of remains found

SES remains are abundant and widespread along the VLC (Figs. 1, 3) from Edmonson Point (74.34° S) to Explorers Cove (77.57° S). They are also present on Ross Island at Cape Bird (77.25° S). We did not find evidence of the species south of Explorers Cove, nor did we locate any remains between Edmonson Point and Cape Phillips (73.07° S). This latter coastline is glaciated extensively today with narrow recent ice-push and storm beaches; any older beach deposits would be covered by ice. In addition, given its cliffed nature, only a very limited number of potential haul-out sites would be possible in this region.

SES remains fall into three categories: mummified and skeletal remains (including teeth), molted pelage (skin and hair), and whiskers (Fig. 4). Koch et al. (2019) described 47 individuals represented by mummies (30), frozen carcasses (6), and scattered bones (11) from Terra Nova Bay south to Marble Point. SES mummies and nearly complete skeletons are easily distinguished from other species by their great size (snout-to-tail lengths more than 3.5 m for mummified adult males, skull half-widths of as much as 19 cm; Koch et al., 2019), robust bones, and diagnostic molars. Species identification of less-complete specimens was determined by aDNA (Koch et al., 2019).

Mummified SES remains cluster largely on the beaches of Inexpressible Island. In contrast, frozen SES remains buried in the beaches or (in one case) emerging from beneath a retreating glacier have a greater geographic distribution. We found these by chance, and it is likely that more such individuals exist. At Cape Ross, an adult male skeleton held together loosely by rotting tendons emerged from a semi-permanent snowbank during only one of at least six late-summer visits. A frozen SES carcass, an adult male also at Cape Roberts, was exposed by retreat of the Wilson Piedmont Glacier in the early 2000s. Farther south, on Dunlop Island, what appears to be a large frozen adult male with flesh and internal organs intact is buried in a raised beach (Fig. 4E). Finally, there are two frozen SES carcasses from Marble Point - one excavated accidentally in the 1950s by bulldozer (Nichols, 1968), the other partially buried in a beach swale and exposed during low snow cover in 1996. Scattered surface finds of bones from SES also show a wide geographic distribution from Inexpressible Island to Explorers Cove but are not common, possibly because the cancellous nature of the bones leads to quick degradation.

Because the presence of animals too small to have swum from sites outside of the Ross Sea would be evidence of breeding females on the VLC, we describe the remains of four small individuals. The smallest is known only from a mandible that melted out of a snowbank at Cape Roberts measuring ~7 cm in length. Although incomplete, it would not have been more than a few cm longer when the animal was alive. A second isolated mandible, also from Cape Roberts, measured 15.2 cm long. A third specimen, a nearly complete mummy at Cape Roberts, was <150 cm long (~100 cm long plus broken skull which prevented accurate measurement). Because it was mummified, the only available bone measurements are of the left tibia (14.4 cm long) and femur (5.8 cm long). A final individual was a nearly complete, but highly fractured carcass (skeletal and mummified components) at South Bay, Inexpressible Island. No measurements were made at the time and an estimate of 190 cm snout-to-tail length is based on comparison with a scale in the photograph. Bones were thin and fragile compared to other skeletal remains. Species has been confirmed by aDNA. Based on comparisons to measurements made on museum specimens and from publications, Koch et al. (2019) concluded that these individuals were under two years of age, and the smallest individual may have been a newborn or even fetal sample. Even adding 4 cm to its reconstructed length, this mandible would be smaller than the mandible from a South Georgia Island individual labeled by collectors as a neonate. While this smallest specimen is intriguing, we cannot rule out that the other individuals were sea-going animals capable of reaching VLC beaches from breeding colonies further north if land-fast ice was absent and the pack ice was not dense.

Molted pelage is far more common than carcass remains and occurs abundantly both in and on the beaches from Edmonson Point to Explorers Cove (Fig 1). It is present within beaches of all ages, except for the storm beaches of the past few hundred years. The shed skin and hair rarely occur more than a couple hundred meters from coeval sea level, in keeping with the observed limited mobility of the species ashore. Concentrations of skin and hair, including large (~20-30 cm diameter) sheets, are present in muddy swales, which likely served as wallows. Other concentrated deposits occur in relatively flat, gravelly locations, with north-facing aspect and wind protection, sites that probably were appealing to seals undergoing the molt. However, we also located remains at more rocky sites and, in some areas at certain times, even the most unfavorable-looking locales were occupied. Finally, at Cape Roberts retreat of the Wilson Piedmont Glacier between 2002 and 2005 uncovered a ~500 m^2 area that displays nearly continuous cover of well-preserved molted pelage (e.g., Fig. 4C) and at least two whiskers in between high points on the bedrock and boulders. One additional whisker was found in association with sealskin on Inexpressible Island.

4.2 Age of southern elephant seal remains

SES remains adjacent to the Ross Embayment range from ~7100 to ~450 yr BP (Tables 1, S1; Fig. 5; Supplemental Information). The oldest evidence of the seals comes from Inexpressible Island in northern Victoria Land (Fig. 3), where seal hairs and skin dating to 7070 ± 160 yr BP (AA-48518) occur within a raised beach. In contrast, the earliest record of seals along the southern VLC is nearly a thousand years later, 6240 ± 150 yr BP (AA-73383), at Gneiss Point. Nearly all sampled sites show evidence of SES in the last ~3000 years. However, of the 289 dated VLC samples, only five fall within the last 500 years and none from the past few hundred years (Table 1). Four of these samples (one from Edmonson Point, three from Inexpressible Island) cluster around 400 yr BP, whereas the age of the remaining sample, from Explorers Cove, is 500 yr BP. Of the 16 additional dated samples on Cape Bird (Ross Island), only two are <500 yr old (440 and 480 yr BP).

In addition to the Holocene SES remains, we found three samples that predate the last glaciation. All were buried deep in raised beaches in deposits recognized stratigraphically and by the presence of pre-last glaciation penguin bones (Gardner et al., 2006) to differ from the Holocene sediments that make up the beach surfaces. At Cape Ross, one sample yielded a calibrated age of 24,790 ± 290 yr BP (AA-42213). Farther south at Dunlop Island, we dated two samples from within an excavation in the upper beach. One afforded repeat ages of 31,830 ± 520 and 38,270 ± 830 yr BP (same sample dated twice; AA-73372); the other produced an age of 42,040 ± 190 yr BP (OS-66600).

5. Geographic and temporal distribution of Ross Sea southern elephant seals

5.1 Influence of taphonomic processes and sampling bias

Taphonomic processes and related sampling biases affect the SES age distribution. Mummified seals undergo gradual wind abrasion, and complete mummies and even bones > 2000 yr BP are rare (Koch et al., 2019). In contrast, shed skin in raised beaches is well-preserved and, as shown by our oldest samples, can last tens of thousands of years. However, processes immediately after the molt influence the survival of such material. Initially, beach surfaces and swales likely were covered with shed pelage, with the amount related to the numbers of seals present. Much of this material probably blew away within a short time. Thus, the amount preserved is heavily dependent upon the speed at which it was reworked into the sediments (by seals or beach construction) or protected from the wind by the formation of permanent snowbanks the following winter. Most sealskin incorporated during beach construction lies at depth within the sediments and thus is secure from further disturbance. Near-surface samples, however, are subject to reworking and destruction by subsequent seal movements and periglacial activity. Thus, samples near beach surfaces (e.g., those buried under rocks) tend to have a younger age distribution than those deep within the sediments, although old sealskin occurs near the surface in some locations.

Sampling bias exacerbates the complication of sample disturbance and destruction. Near-surface samples are easier to locate than those deeply buried, particularly given time and weather constraints. Excavation in commonly bouldery beach deposits is time consuming and without certain success of finding SES remains, although in our experience most excavations yielded some skin. Thus, sample collection inevitably is biased toward the younger, surface or near-surface remains. Later decisions about which samples to date help to alleviate this complication.

Another complicating factor when considering SES population size is the relationship between amount of shed skin and hair and the number of seals. Larger seals produce more molted material than pups. Thus, there is a possibility of inferring multiple seals from the shed skin from a single individual. However, we are not attempting to assess changes in the size of the sampled population with a high level of precision. Rather, we are examining in a general way whether the number of samples and, more important, the geographic area over which they occur, has changed. Moreover, in the 223 samples analyzed for aDNA so far, we recovered 177 unique control region (mtDNA) haplotypes (de Bruyn et al., 2009), suggesting limited potential resampling of the same individual and that the number of samples is a broad reflection of the number of seals ashore (not multiple samples from single individuals), with the taphonomic caveats discussed above.

Given all of these potential biases, generating robust estimates of relative SES population size from changes in sample numbers is complicated. At a minimum, it would require controlling for sampling effort, the area sampled, the extent of snow cover, and model(s) of the expected taphonomic loss of materials. Such an exercise is beyond the scope of this paper. Below, we discuss shifts in relative population size in a general way, focusing especially on variations in dated samples within a site over a relatively short time interval, especially where sample numbers drop approaching recent times (contrary to the expectation of taphonomic loss). We also consider expansion or contraction of range (i.e., more or fewer sites occupied along the VLC) as indicators of relative population variations.

5.2 Interpretation of age data

The recovered samples indicate that a large, genetically diverse (de Bruyn et al., 2009) population of SES hauled out and molted at every feasible site over nearly 400 km of coastline during the Holocene. They also were present prior to the LGM. Based on the number and geographic spread of locations where SES remains were found (Fig. 5), we infer that the greatest concentrations of animals (and the longest occupation times) were in the Terra Nova Bay region (especially at South and Seaview Bays on Inexpressible Island), Cape Roberts, Dunlop Island, and Marble Point. All these sites have large expanses of low-gradient coastline with raised beaches. Inexpressible Island is adjacent to the open water of the Terra Nova Bay polynya. Farther south, sea ice breaks out on occasion at Cape Roberts under present-day climate but does so less commonly at Dunlop Island and Marble Point. At their southern range (Explorers Cove, Cape Bernacchi), remains are rare. The entire coast has experience isostatic rebound throughout the Holocene (e.g., Baroni and Hall, 2004; Hall et al., 2004), and thus not only the area, but also the topography has been changing through time. For example, the existence of cliffs near sea level at some sites (e.g., Edmonson Point, Adélie Cove, Cape Ross, Gneiss Point, Cape Bernacchi) limited the interval of the Holocene during which seals could haul out, because the coastline was too steep.

Post-glacial SES remains suggest occupation of the northern coast by ~7100 yr BP, the age of the oldest dated sample at Inexpressible Island. As we likely did not find the oldest SES remains and deglaciation was not complete in this area until ~8000 yr BP

[Baroni and Hall, 2004; recalculated as per Methods; Gao et al., 2022], SES may have migrated into the region as the ice sheet retreated. The oldest age from the southern VLC is about 900 years younger than that at Inexpressible Island. This age difference may reflect delayed seal occupation at southern sites due to an ice shelf that lingered in the McMurdo Sound region immediately after retreat of grounded ice (Hall and Denton, 1999).

SES occupied at least parts of the VLC, particularly near Terra Nova Bay, nearly continuously between ~7000 and 500 yr BP, although occupation was discontinuous at many southern sites. Samples prior to ~5500 yr BP are scarce, possibly because of low population but also likely because of sampling and preservation biases mentioned above. However, a distinct uptick in dated seal remains occurred at ~5400 yr BP, suggesting that some of the low sample numbers immediately prior to this time may have been due to small population size (Figs. 5, 6). This increase in dated SES remains is most noticeable at Terra Nova Bay (Campbell Glacier, ~5200-4800 yr BP, n=5; South Bay, 5900-4600 yr BP, n=11; Whisker Cove, 5200 yr BP, n=1), Dunlop Island (5400-5100 yr BP, n=7), Gneiss Point (5300-5000 yr BP, n=4), and Marble Point (5400-5200 yr BP, n=2).

There are spatial differences in numbers of SES remains after ~5000 yr BP. On the northern coast, elephant seals occupied available areas from Edmonson Point to Inexpressible Island continuously from ~5500 to 500 yr BP. (Note: beaches at Edmonson Point and Adélie Cove did not emerge from the sea until 2000 yr BP; Baroni and Hall, 2004). However, there are variations in sample numbers that may reflect population-size changes, such as a decline between ~3900 and ~3300 yr BP at South and Seaview Bays. The number of recovered remains rises sharply at ~3300 yr BP but then declines again. At the two locations with the most remains (South and Seaview Bays), the greatest number (77 altogether) date to 2300-500 yr BP. The seals show an expanded range at ~1000 yr BP, spreading to beaches at Edmonson Point, Campbell Glacier, and Adélie Cove. A precipitous decline in sample numbers and in the number of sites occupied in the last millennium, particularly after 500 yr BP, cannot be attributed to sampling bias or taphonomic issues, both of which would be expected to favor greater numbers of more recent samples. We interpret this drop to a population crash, which resulted in the eventual abandonment of this segment of coastline by SES. This interpretation is supported by Bayesian skyline analyses of ancient DNA that indicate a precipitous population decline starting at about 1000 yr BP (de Bruyn et al., 2009).

Farther south, in the central part of our field area (Depot Peninsula to Dunlop Island), there is a gap in dated SES remains (with only one sample found) between ~5000 and

~3800 yr BP (Fig 5). Following this interval, remains became more common and document the only known postglacial occupation of Cape Ross (3840-3160 yr BP), as well as the presence of SES at Cape Roberts and Dunlop Island. Based on the dated remains, both Cape Roberts and Dunlop Island likely had nearly continuous subsequent occupation until ~650 yr BP. However, we did not find SES younger than 3160 yr BP at Cape Ross nor older than 3000 yr BP at nearby Depot Peninsula, suggesting that seals may have relocated as the Cape Ross coast steepened during rebound. Depot Peninsula was either abandoned or not commonly used after ~1400 yr BP. This time may correspond with a coeval gap in samples at Dunlop Island from 1240-650 yr BP. As along the northern coast, SES remains increased significantly in the late Holocene, reaching a peak at Cape Roberts at ~1600 yr BP and at Dunlop Island by ~2300 yr BP. Sample numbers dropped precipitously at ~1000 yr BP at Cape Roberts, similar to (although a few centuries earlier than) the decline at sites adjacent to Terra Nova Bay. Unlike at other major sites, the number of dated SES remains at Dunlop Island began to decline as early as ~2000 yr BP. The last large peak in seal remains seen at every major site elsewhere along the VLC at ~1000 yr BP apparently does not occur at Dunlop Island. Instead, the reduction in remains at ~2000 yr BP at Dunlop Island more closely resembles the pattern seen at many of the smaller sites, particularly those along the southern and central coasts, where SES declined or disappeared after ~2000 yr BP and geographic range contracted (Fig. 5). We have no satisfactory explanation at present for this apparent early reduction in seals on Dunlop Island but speculate that it may have been a marginal site (today surrounded by landfast ice with a glacier nearby). When coastal ice conditions began to deteriorate, it became less feasible for SES occupation. There is no evidence of SES on the central coast after ~600 yr BP.

SES occupation of the southern coast (Spike Cape to Explorers Cove) appears to have been discontinuous (Fig. 5). Following the brief, but distinct SES occupations at ~5400-5000 yr BP, the coastline may have been abandoned or visited only rarely until after 3000 yr BP. There are only two samples dating to this period, one of which (from Gneiss Point) may be in error (see Supplemental Information). Spike Cape shows the presence of SES again by ~2900 yr BP and the more southerly Marble Point and Cape Bernacchi by ~2500 yr BP and Gneiss Point by ~2400 yr BP. SES appear to have expanded their range at 2500-2000 yr BP, when every possible site on the southern coast was occupied. This increase in SES remains on the southern VLC matches that seen at most sites farther north.

Although Marble Point still had SES after 2000 yr BP, most southern sites record only limited or even a lack of SES between at least 2000-1280 yr BP. Other than at Marble

Point (n=5), the only evidence of SES at southern sites after 1280 yr BP comes from a cluster of remains dating to ~1280-860 yr BP at Spike Cape (n=5), one skin sample at Bernacchi Bay (1280 yr BP), and an isolated bone at Explorers Cove (500 yr BP).

Cape Bird is distinct in that it is located on an offshore island adjacent to the Ross Polynya rather than on the VLC. It experiences open water in most summers under modern conditions. Beaches on Cape Bird began forming ~4000 yr ago (Dochat et al., 2000; Hall et al., 2004; with ages recalibrated for Marine2020 and the updated marine reservoir correction of Hall et al., 2010), thus providing available haul out locations by that time. However, existing data do not afford evidence for the presence of SES prior to ~2000 yr BP (Fig. 5). Rather, the data show a late-Holocene peak in remains (1900-1300 yr BP) followed by the decline seen elsewhere. The youngest SES sample dates to 440 yr BP.

In summary, initial occupation occurred on the northern coast by 7100 yr BP and on the southern coast by 6200 yr BP (Fig. 5). After a mid-Holocene increase in both remains and geographic extent at ~5200 yr BP, SES remains declined and the colony contracted until at least 3800 yr BP, particularly along the central and southern coast (where the decline lasted longer). There also may have been an increase along the central and northern coasts at 3300-2800 yr BP, which is not found in the southern region (Fig. 6). All areas show increasing SES sample numbers and extent, and thus likely population size beginning ~2500 yr BP (Fig. 5). We infer that populations along the southern coast and at Dunlop Island started to decline after ~2000 yr BP, with decreasing sample numbers and fewer sites being occupied. However, evidence for SES presence remained steady or even increased on Inexpressible Island and Cape Bird. Both of these latter sites are near polynyas, known to be favorable locations for male foraging (Johnstone et al., 1973; Labrousse et al., 2018). Across all sites, there is a precipitous drop in the number and geographic extent of SES remains within the last millennium, with only few samples dating to <600 yr BP and none to <~400 yr BP.

The general pattern of seal distribution is in accord with aDNA analysis of SES remains from this region. De Bruyn et al. (2009, 2014) found that VLC seals represented a distinct breeding population (breeding either along the VLC or at unsampled sites farther north), genetically distinct from any modern SES. This Victoria Land population may have been founded by seals that migrated from Macquarie Island during deglaciation and established a permanent occupation that rapidly increased in diversity (de Bruyn et al., 2014). De Bruyn et al. (2009, 2014) moreover proposed that the VLC population expanded rapidly until about 1000 yr BP, when it underwent a significant, irreversible population crash and loss of diversity. Effective population size prior to the collapse was approximately 200,000 individuals, much greater than the reconstructed size of the coeval Macquarie population (de Bruyn et al., 2014). Upon eventual abandonment of the VLC, genetic evidence suggests that some VLC seals migrated to Macquarie Island, and their maternally inherited genetic markers (mitochondrial haplotypes) are still present in that population.

6. Climate and Ice-Sheet Implications

6.1 Elephant seal sea-ice tolerances

SES were a key part of the western Ross Sea ecosystem for much of the Holocene. Today, the species has a circum-polar, generally subantarctic distribution with all major breeding and molting sites (Fig. 2) lying close to the polar front. SES life history is dominated by two periods of extended onshore haul out for breeding and molting separated by lengthy feeding excursions, which can take the seals hundreds, if not thousands of kilometers from their home colonies (Biuw et al., 2007). Elephant seals show strong fidelity to their birth colony and generally return to the same area for breeding (LeBoeuf and Laws, 1994). Molting can take place in the same location or at different sites and commonly is segregated by sex and age. On Macquarie Island, which hosts the colony geographically nearest and most genetically related to the VLC population, breeding takes place in September through November, peaking in late October (Hindell and Burton, 1988). Juveniles and sub-adult males haul out to molt in December-January, females in January to early February, and adult males in February to April (Hindell and Burton, 1988). Thus, seals are ashore nearly continuously from September to April.

Seasonal haul outs are limited both by available substrate (preference for low-gradient, sandy shorelines) and by the presence/absence of landfast sea ice during the breeding and molting timeframe. Crawling over ice is energetically expensive, and thus landfast sea ice is thought to be a key factor in limiting the southern extent of breeding and molting colonies (e.g., Laws, 1956, 1960; Tierney, 1977; Burton, 1985; Gales and Burton, 1989; Hall et al., 2006). In areas where coastal sea ice is decreasing, elephant seals have expanded their molting and breeding range in recent decades (Siniff et al., 2008).

Despite the limiting effect of landfast ice on SES haul out, some SES, largely adult males (e.g., Borneman et al., 2000; Bailleul et al., 2007; Hindell et al., 2021; Allegue et al., 2022), forage in the pack ice on Antarctic shelves. Females, who tend to prefer open-ocean foraging, move north as pack ice expands in the fall (e.g., Labrousse et al, 2015; Hindell et al., 2016), and extensive winter pack ice is thought to result in poor foraging performance (McMahon et al., 2017; although see Labrousse et al., 2017, where Kerguelen females are thought to benefit from early pack-ice expansion and its positive effect on krill). Allegue et al. (2022) attributed habitat selection in part to sex, age, breeding status, and personality ("boldness"), and noted that females, breeding males, and subadult males tended to move north in the winter to avoid becoming trapped in the ice. Non-breeding adult males stayed later in the pack ice, often feeding in winter in highly productive coastal polynyas (e.g., Labrousse et al., 2018; Allegue et al., 2022). Such behavior may be a cost-benefit trade-off between productive foraging vs. risk of entrapment and substantial interannual variability in habitat accessibility due to sea-ice density (Hindell et al., 2021; Allegue et al., 2022).

Tracking data for Macquarie Island SES (currently limited to adult females) indicate that some individuals feed on the highly productive outer Ross Sea shelf, whereas others feed on and off the narrow Wilkes Land continental shelf, and still others forage in subantarctic pelagic waters (Hindell et al., 2017). Of 101 tracked animals, just one penetrated onto the extensive Ross Sea continental shelf, though well offshore from Victoria Land. In addition, pack-ice expansion (both in duration and extent) in the Ross Sea over the last several decades (Comiso et al., 2011; Stammerjohn et al., 2008, 2012; Turner et al., 2015, 2016) has been linked to reduced female foraging in this region, consequent low weaning weights and survival of pups, and ultimately the decline of the Macquarie Island population (McMahon et al., 2000; van den Hoff et al., 2014; Hindell et al., 2016, 2017; Clausius et al., 2017; Volzke et al., 2021). Thus, sea ice has a large effect on SES populations not only by limiting their ability to access haul-out sites (through the presence/absence of summer landfast ice), but also through impacts on foraging success (because of pack-ice density, particularly for juveniles and females; e.g., Bester, 1988).

Satellite imagery shows the density of end-of-summer landfast ice along the coast is substantial, despite open water and pack ice tens of kilometers to the east (Fig. 1). Because of the propensity of SES to favor open coasts, we attribute the lack of these seals today to the development of summer landfast ice in the late Holocene. In addition, recent work summarized above linking decline of the Macquarie colony to expansion of pack ice in the Ross Sea points to possible additional effects. Namely, VLC females encountering denser and more extensive pack ice may have become less successful in foraging. Any juveniles and pups also may have struggled, because successful use of pack ice for foraging may be linked to large body size (Bailleul et al., 2008). Such seals, as well as females, could have been excluded from high-quality local foraging areas as sea ice spread in the Ross Sea. In summary, we conclude that growth of perennial landfast sea ice, possibly accompanied by pack-ice expansion, led to the decline and eventual abandonment of the VLC, with the decline beginning earlier at southern sites.

Did SES both breed and molt on the VLC? Or were the haul-out sites used only for molting? This question bears on the length of time open water would be required along the VLC. Based on an analysis of mummified remains, Koch et al. (2019) found 14 adult males (with some of beachmaster size with large proboscises), three that were either adult or sub-adult males, six sub-adult males, four juveniles <2 years old (including one very small individual, possibly fetal), and one possible female. Mummified remains, however, may not afford a complete assessment of the population over its history, due to factors such as robustness of skeletons (which affect preservation potential), time of year when animals died (which determines the sex and age group ashore), and temporal evolution of the occupation. For example, sites that began as breeding colonies may have transitioned to adult-male, molting-only sites as climate deteriorated and sea ice may have excluded females (e.g., Bester, 1988). Given that most mummies are relatively recent and do not reflect the entire temporal duration of the colony, Koch et al. (2019) inferred that the majority may document a “last stand” cohort of animals dominated by molting males.

DNA evidence, predominantly represented by hair rather than mummies, indicates that the VLC population was genetically distinct from that at Macquarie Island or any other extant population (de Bruyn et al., 2009, 2014). Thus, they must represent an independent breeding colony (or colonies). But whether that breeding took place at the sites we examined as opposed to VLC sites farther north (e.g., Cape Hallett, Cape Adare) or on islands even farther north (e.g., Possession Islands, Campbell Island) yet to be examined, remains uncertain. The presence of pups too small to have arrived from subantarctic colonies would afford direct evidence for breeding. Based on comparative analysis (Laws, 1953; Carrick et al., 1962; Koch et al., 2019), we infer that the four smallest individuals were <2 yrs old, with the smallest possibly being fetal. Today, young animals (<14 months old) from Macquarie Island do not travel south of the southern limb of the Antarctic Circumpolar Current into the Ross Sea (van den Hoff et al., 2002; McConnell et al., 2002). Thus, we consider the most likely option is that these small individuals were born on the VLC or farther north on an Antarctic coast. However, further work is needed to confirm (or not) the presence of breeding at these high southern latitudes.

Regardless of whether breeding was occurring in our field area or to the north, the presence of SES on these beaches indicates significantly reduced landfast sea ice relative to today. Taking the present-day annual cycle of Macquarie Island seals as a guide (Hindell and Burton, 1988), the remains imply open water at or close to the shore from at least December to March/April (in the case of a male-only molting haul out) or from September-April (in the case of breeding as well). This scenario assumes that the Antarctic population kept to a similar schedule as the seals on Macquarie, something that appears supported by similar breeding and molting seasons in the South Shetland Islands (Fudala and Bialik, 2020) and the male molting season of January-April in the Windmill Islands (Fig. 1; van den Hoff et al., 2003). Even the molting-only scenario requires about four months of open access to land in areas that today experience little to no open water in spring and summer at the shore (excluding South and Seaview Bays by the Terra Nova Bay polynya). Thus, we infer that landfast sea ice extent and duration in coastal regions of the western Ross Sea were significantly less for much of the Holocene than they are at present. Growth of persistent summer landfast sea ice and cooling of the western Ross Sea over the last millennium likely caused the SES population crash shortly after 1000 yr BP and the abandonment of the VLC a few centuries later. Disappearance of the SES cannot be attributed to human-induced causes, such as overfishing of the Southern Ocean (e.g. Ainley and Blight, 2009), because the seals left the area centuries before the Ross Sea or its productive fishing grounds near the polar front were discovered.

6.2 Millennial-scale variability

Spatial and temporal fluctuations in SES numbers suggest smaller, millennial-scale climate and sea-ice variations superimposed on overall reduced sea ice and warmer ocean conditions during the Holocene. For example, many sites from Campbell Glacier in the north to Marble and Gneiss Points in the south, record a jump in extent and number of SES remains just prior to ~5000 yr BP, suggesting that conditions may have been favorable (low sea ice, relatively warm water) along the entire coast at that time. During some of the relatively cool periods, southern sites were abandoned temporarily or went into decline. For example, after 5000 yr BP, SES may have been rare or absent along the southern and central coast until ~3800 yr BP, while the northern coast continued to be occupied. Shortly after 2300 yr BP, the number and geographic range of SES remains increased significantly, suggesting colony expansion. This may have been the most productive and perhaps warmest period of the mid-late Holocene in the Ross Sea, with greatly reduced summer landfast and pack ice.

6.3 Comparison to other Ross Sea region climate records

Relatively few other records of Holocene sea ice and ocean temperatures exist for the Ross Sea region. The most extensive of these come from reconstructions of Adélie penguin rookeries (e.g., Baroni and Orombelli, 1991, 1994a; Hall et al., 2006; Hu et al., 2013; Emslie et al., 2018). Such penguins require pack ice for feeding but are affected adversely by long-duration landfast ice. These tolerances led to the concept of a "penguin optimum" (~4800-2800 yr BP; Fig. 7), a time of increase in the size and number of colonies, particularly along the southern coast (Baroni and Orombelli, 1994a). The southern coast, which never supported large numbers of birds, was abandoned after that time. Comparison with our dataset indicates that the penguin optimum coincided with SES expansion in the Terra Nova Bay region, but with relatively low seal numbers along the central and southern coast. We infer that land fast ice returned to the southern coast between 5000-2700 yr BP sufficient to deter SES colonization, but not heavy enough to exclude Adélie penguins, an ice-obligate species. Loss of penguins on the southern coast coincided with SES re-expansion into these areas at ~2500 yr BP. Hall et al. (2006) speculated that the absence of landfast ice at the time favored SES but coeval reduced pack ice was insufficient to support Adélie penguins. If true, this time may record some of the lowest landfast and pack-ice extent of the Holocene in the western Ross Sea. We infer that the documented population crash and abandonment of the entire coast by SES after ~1000-500 yr BP was due to return of heavy sea ice (particularly summer landfast ice), the greatest of the postglacial period, and likely cold ocean temperatures. We speculate that these conditions also may have resulted in contraction of the Cape Adare Adélie penguin "super colony" (Emslie et al., 2018), as well as the disappearance of this species at Cape Irizar (Emslie, 2021); the latter site also may have been affected by advance of the Drygalski Ice Tongue. Persistent coastal sea ice also may have caused penguin migration to sites close to polynyas (e.g., Hu et al, 2013; Yang et al., 2017), where wind-driven upwelling of nutrient-rich water would have led to highly productive foraging.

Other proxies of past sea-ice extent and ocean temperatures around Antarctica suggest that the mid-Holocene was a time of generally reduced sea ice (e.g., Crosta et al., 2022 and references therein). In the Ross Sea, other evidence of past sea-ice variations comes from marine diatoms (e.g., Leventer et al., 1993; Cunningham et al., 1999; Mezgec et al., 2017). High percentages of *Fragiliaria curta* are thought to reflect extensive sea ice and *Thalassiosira antarctica* to indicate long and/or warm summer ocean-water temperatures, possibly induced by intrusion of modified Circumpolar Deep Water (mCDW; Smith et al., 2012, 2014). However, incorporation of old carbon (in addition to the standard marine reservoir effect) into bulk sediment samples used for dating has limited the accuracy of the marine records. Nevertheless, diatom data do show variations, which have been linked to sea-ice changes. For example, Mezgec et al. (2017) inferred substantial late-Holocene sea ice from a core at Wood Bay, just north of Edmonson Point, as well as two periods of elevated sea ice from ~3400-1800 yr BP. In general, there is little similarity between the SES record and Ross Sea diatom records except in the last 1500 yrs at Wood Bay. There, inferred decreased sea ice and longer, warmer summers at ~1500-1000 yr BP correspond to greater SES presence; an increase in sea-ice diatoms after 1000 yr BP coincides with the decline of the SES. However, immediately before 1500 yrs BP, expansion of SES apparently occurred during a time of increased sea ice at Wood Bay. Differences in the two types of records may arise from chronological limitations discussed above, seasonal differences in the timing of sea-ice diatoms vs. SES haul out, the fact that summer landfast ice exerts a primary control on SES haul out rather than pack ice (which may influence the diatoms), and/or local differences at Wood Bay relative to other coastal sites.

Finally, there is strong similarity, particularly in the last 3000 years, between the SES reconstruction and Cd/P ratios in penguin guano at Inexpressible Island, thought to reflect incursion of mCDW and associated nutrients into Terra Nova Bay (Fig. 7; Xu et al., 2021). Although exact correspondence is complicated by the different resolution of the two records (and the plotting of the SES data as summed radiocarbon probabilities rather than as individual points), there is resemblance between the curves, particularly in the younger part of the record, which is less affected by taphonomic loss of remains. This similarity suggests that the reduced sea ice/warmer ocean temperatures indicated by the SES may have been due to greater penetration of this relatively warm (~4 °C) ocean water deep onto the Ross Sea continental shelf, perhaps even to the front of the Ross Ice Shelf (near our southern sites). Peak Cd/P ratios coincide with high levels of SES occupation at ~1500 and ~1000 yr BP. Low levels correspond to reduced SES remains between ~3000-2000 yr BP at Terra Nova Bay sites. The Cd/P record does not show significant change during an earlier period of reduced SES evidence (e.g., 5000-3800 yr BP) most pronounced at southern sites. Most likely, mCDW intruded into Terra Nova Bay at those times, but was unable to penetrate to the central and southern VLC, where the decline of SES extent was more noticeable (Fig. 5).

6.3 Comparison to glacial records and implications

The interpretation of the SES record is consistent with geomorphic evidence from raised beaches that indicates 1) a long period in the Holocene of ice-free conditions at the immediate shoreline based on landforms and sediments indicative of open water; and 2) expansion of VLC glaciers in the last millennium following a long period of restricted glacier extent (e.g., Baroni and Orombelli, 1994b; Hall and Denton, 2002). For example, the Wilson Piedmont Glacier, as well as the Nansen and Hell's Gate ice shelves, have advanced over Holocene raised beaches within the last few centuries (Stuiver et al., 1981; Hall and Denton, 2002; Baroni and Hall, 2004). In addition, at Cape Roberts, very recent recession of the Wilson Piedmont Glacier revealed a landscape covered with SES skin and hair, as well as a mummified adult male seal. The remains must have been covered almost immediately by snow to prevent removal by wind, and thus their ages suggest that growth of permanent snowbanks followed by glacier expansion occurred at or shortly after 1050 yr BP.

Expansion of coastal glaciers over the last 1000 years probably is linked directly to cooler ocean temperatures and increased sea ice. Air-temperature decrease is not expected to cause ice advance in this setting, because glaciers at this latitude do not have significant surface melting ablation zones. In fact, colder temperatures lead to reduced accumulation (Simpson, 1934). Rather, advance of coastal glaciers is favored by the presence of landfast ice, which protects marine margins (e.g., Massom et al., 2010; Stevens et al., 2013), suppresses calving (Greene et al., 2018; Gomez-Fell et al., 2022), and promotes growth of ice tongues (e.g., Wearing et al. 2020), which are common along the VLC today. Loss of fast ice, even seasonally, can result in increased ice velocities and thinning, as shown by recent measurements on the Parker Ice Tongue (Gomez-Fell et al., 2022). Thus, the short duration or even lack of landfast ice during much of the Holocene, as implied by the SES data, would have been detrimental to coastal glaciers. Moreover, greater southward penetration of warm water, such as mCDW, would have enhanced melt rates on the underside of floating ice (i.e., Pritchard et al., 2012) and contributed to negative mass balance. Thus, current ice cover on the VLC, with its iconic ice tongues, may not have come into existence until after 1000 years ago.

The implications of reduced landfast sea ice, a warmer ocean, and possible mCDW penetration as far south as the front of the Ross Ice Shelf go beyond affecting Holocene glacier extent on the VLC. This warm water may have caused recession of the grounded ice sheet that occupied the Ross Embayment during the last glaciation. Ice-sheet retreat in much of the embayment occurred primarily in the Holocene (Conway et al., 1999), and final recession from the Terra Nova Bay region did not occur until ~8000 yr BP (Baroni and Hall, 2004; Gao et al., 2022), mere centuries prior to the oldest known post-glacial SES sample. Thus, ice-sheet recession may have been driven by the same warm water that allowed the seals to occupy the Ross Sea and the VLC.

Recent studies, based primarily on the presence of radiocarbon in sediments beneath Siple Coast ice streams, have suggested significant mid-Holocene recession of the WAIS grounding line behind its present position, followed by late-Holocene readvance (e.g., Kingslake et al., 2018; Neuhaus et al., 2021). Neuhaus et al. (2021) further suggested that ice retreat likely occurred because warm ocean water reached the grounding lines and accelerated sub-surface melt rates. Although these data remain controversial and unreconciled with ice-thinning histories of nearby outlet glaciers (which permit only the narrowest of windows for such a large ice-sheet fluctuation, e.g., Todd et al., 2010; Spector et al., 2017), our relative ocean temperature reconstructions are consistent with the mid-to-late Holocene timeline of proposed retreat and readvance. Based on the geographic extent of the SES occupation of the southern coast and on the inferred farthest southward penetration of warm water, mCDW, we suggest that the times most likely to contribute to any such ice recession were at ~5200 and ~2300-1800 yr BP (Fig. 8). However, whether the warm water that reached as far south as Ross Island could have extended ~600-1000 km under the Ross Ice Shelf to the WAIS grounding line to cause substantial melting remains uncertain.

Despite evidence for warm ocean temperatures and possible expansion of mCDW to its front, the Ross Ice Shelf does not appear to have undergone any significant ice retreat since it first anchored on Ross Island/Minna Bluff in the early to mid-Holocene (Conway et al., 1999; Hall et al., 2015). There are no known coastal deposits or mummified seals of any kind along the Ross Sea coast south of McMurdo Sound, both of which would be expected to exist had the ice shelf retreated from its present position. Pinning points in both the western (Ross Island, Minna Bluff) and eastern (Roosevelt Island) Ross Embayment are probably the root cause of this long-term stability and are critical to the future of the ice shelf, as no similar pinning points exist farther south along the front of the Transantarctic Mountains (Hall et al., 2015).

Our limited data for the presence of pre-LGM SES along the VLC imply that similarly warm conditions may have persisted just prior to the onset of ice-sheet advance across the Ross Sea continental shelf during the LGM. Dates of pre-LGM marine organisms are complicated by measurement uncertainties close to the limit of radiocarbon dating, an unquantified marine reservoir effect, and the potential for modern contamination of "carbon-dead" samples. The youngest of these pre-LGM seal samples, dating to ~25,000 yr BP, indicates not only that the ice sheet had not yet inundated Cape Ross by that time but also that relatively warm ocean water existed in the Ross Sea right up until the time of ice advance. Samples dating to 42,000-32,000 yr BP at Dunlop Island are close to the limit of radiocarbon and thus could be significantly older than they appear at face value. However, dates of former penguin rookeries also suggest that the VLC may have had less sea ice at various times between 50,000-25,000 yr BP than it does at present (e.g., Hall et al., 2004; Gardner et al., 2006; Emslie et al., 2007; Parks et al., 2015). Additional research into this pre-LGM period is necessary to constrain the occupancy times better. However, one potential implication of these data is that ice-sheet advance leading up to the LGM configuration may have been accomplished in the face of relatively warm ocean conditions. If so, this would highlight the importance of other driving mechanisms, such as lowered global sea level, in causing ice-sheet advance in Antarctica.

7. Conclusions

SES existed on the VLC between ~7100-500 yr BP in areas where they do not live at present. We infer that their former presence reflects reduced summertime landfast ice and likely warmer ocean temperatures compared to today for much of the Holocene. Based on the greatest extent of seal remains, particularly in the colder southern regions, we infer that periods with the least landfast sea ice and warmest ocean temperatures were at ~5200 and 2300-1800 yr BP (Fig. 8). A population crash at ~1000 yr BP (de Bruyn et al., 2009) and eventual abandonment of the coast by SES a few centuries later suggest that the coldest, iciest coastal conditions in the postglacial period occurred in the last millennium, in agreement with coastal geomorphology. These sea-ice and ocean-temperature changes may reflect variations in the extent of mCDW on the Ross Sea continental shelf.

The warm ocean conditions in the mid-Holocene and subsequent late-Holocene cold period had a strong influence on VLC glaciers through variations in buttressing sea ice and melt rates on the underside of floating ice, both of which would have impacted mass balance and ice extent. These glaciers had restricted extent in the mid-Holocene and expanded within the last millennium, coincident with the disappearance of SES from the coast. Our relative sea-ice and ocean-temperature reconstruction also is consistent with the hypothesized retreat of the WAIS inland of its present position in the mid to late Holocene, although the distance between our sites and the WAIS grounding lines is large (600-1000 km) and mCPDW may have been unable to penetrate so far south under the ice shelf. Finally, limited pre-Holocene SES data support the existence of warm ocean temperatures immediately prior to and perhaps even during ice build-up to the LGM position. If this could be confirmed, it would suggest that factors other than ocean temperatures, such as lowered sea level, may have been critical in causing ice-sheet advance in the Ross Embayment at the LGM.

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Table 1. Distribution of median ages (in calendar years BP) of seal remains by site. Gray boxes indicate no recorded seal presence (italicized sample may be an outlier). Due to the intersection of topography and isostatic rebound, suitable beaches were not present at Edmonson Point and Adélie Cove prior to the age of their oldest samples.

Site		**0-500**	**501-1000**	**1001-1500**	**1501-2000**	**2001-2500**	**2501-3000**	**3001-3500**	**3501-4000**	**4001-4500**	**4501-5000**	**5001-5500**	**5500-6000**	**6001-6500**	**6501-7000**	**7001-7500**
Victoria Land Coast																
Northern	Edmonson Pt.	1	9	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨
	Campbell Gl.	▨	2	▨	2	▨	1	2	3	1	3	2	▨	▨	▨	▨
	Adélie Cove	▨	4	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨
	Seaview Bay	1	11	10	10	3	1	2	2	1	1	▨	▨	1	1	▨
	South Bay	1	15	14	10	7	7	8	2	3	4	6	1	▨	▨	1
	Whisker Cove	▨	▨	2	▨	▨	1	1	1	1	1	1	▨	▨	▨	▨
Central	Unnamed Cove	1	▨	▨	▨	▨	▨	1	▨	▨	▨	▨	▨	▨	▨	▨
	Depot Pen.	▨	▨	1	2	1	3	▨	▨	▨	▨	▨	▨	▨	▨	▨
	Cape Ross	▨	▨	▨	▨	▨	▨	4	7	▨	▨	▨	▨	▨	▨	▨
	Cape Roberts	▨	4	7	9	▨	2	2	1		3	▨	▨	▨	▨	▨
	Dunlop Island	▨	1	3	6	10	3	3	1	1	▨	7	▨	▨	▨	▨
Southern	Spike Cape	▨	1	4	▨	2	3	▨	▨	▨	▨	▨	▨	▨	▨	▨
	Kolich Point	▨	▨	▨	▨	4	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨
	Gneiss Point	▨	▨	▨	▨	3	▨	*1*	▨	▨	▨	4	▨	1	▨	▨
	Marble Point	▨	4	4	2	2	1	▨	1	▨	▨	2	▨	▨	▨	▨
	Bernacchi Bay	▨	▨	1	▨	2	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨
	Cape Bernacchi	▨	▨	▨	▨	1	1	▨	▨	▨	▨	▨	▨	▨	▨	▨
	Explorers Cove	1	▨	▨	▨	1	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨
	Total	5	49	46	41	36	23	24	18	7	12	22	1	2	1	1
Ross Island																
	Cape Bird	2	1	5	8	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨

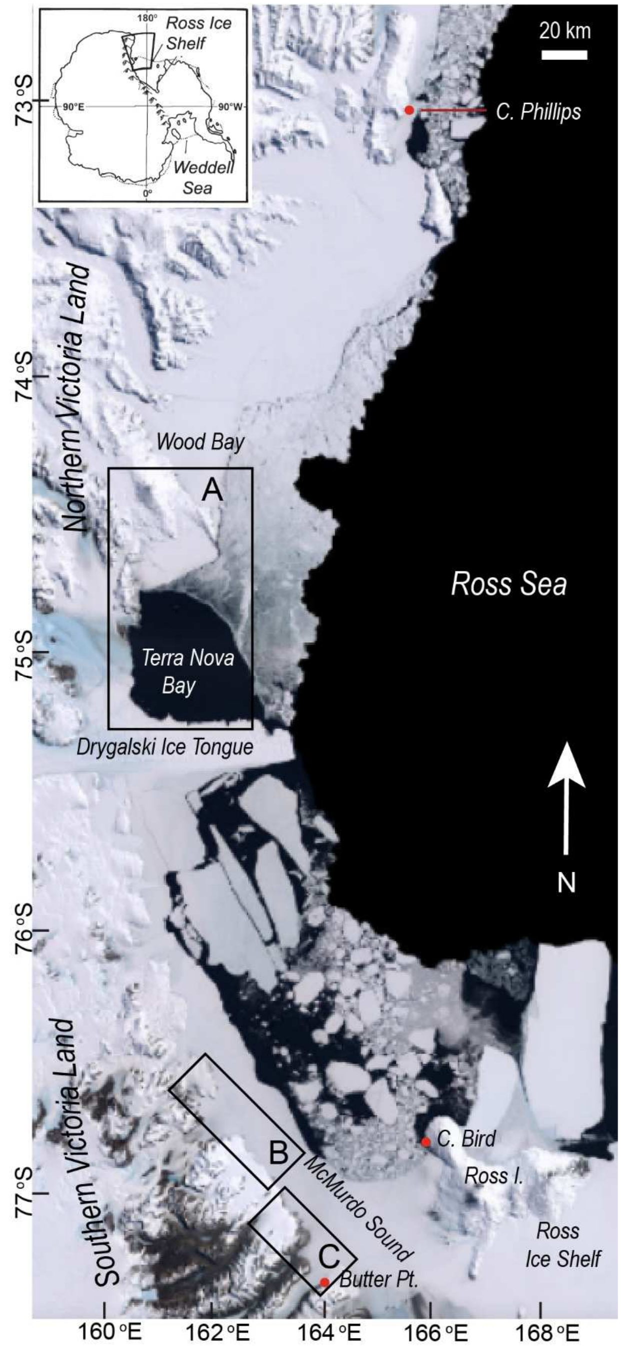

Fig. 1. Satellite image of summer sea ice along the Victoria Land coast of the western Ross Embayment. Base image is from the Landsat Image Mosaic of Antarctica (https://lima.usgs.gov). Labelled boxes show locations of Figs. 3A-3C.

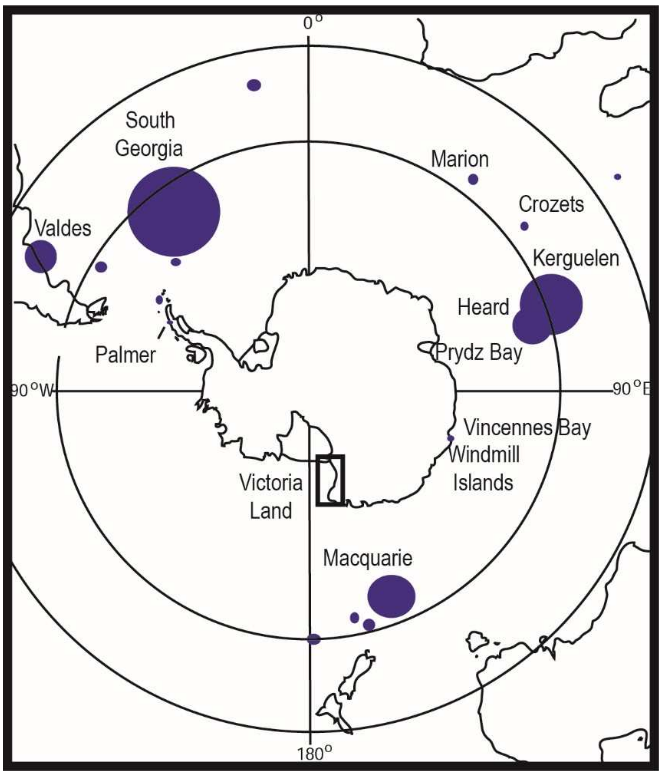

Fig. 2. Location of primary southern elephant seal colonies, with circles denoting relative size (after LeBoeuf and Laws, 1994). The black box marks the Victoria Land coast.

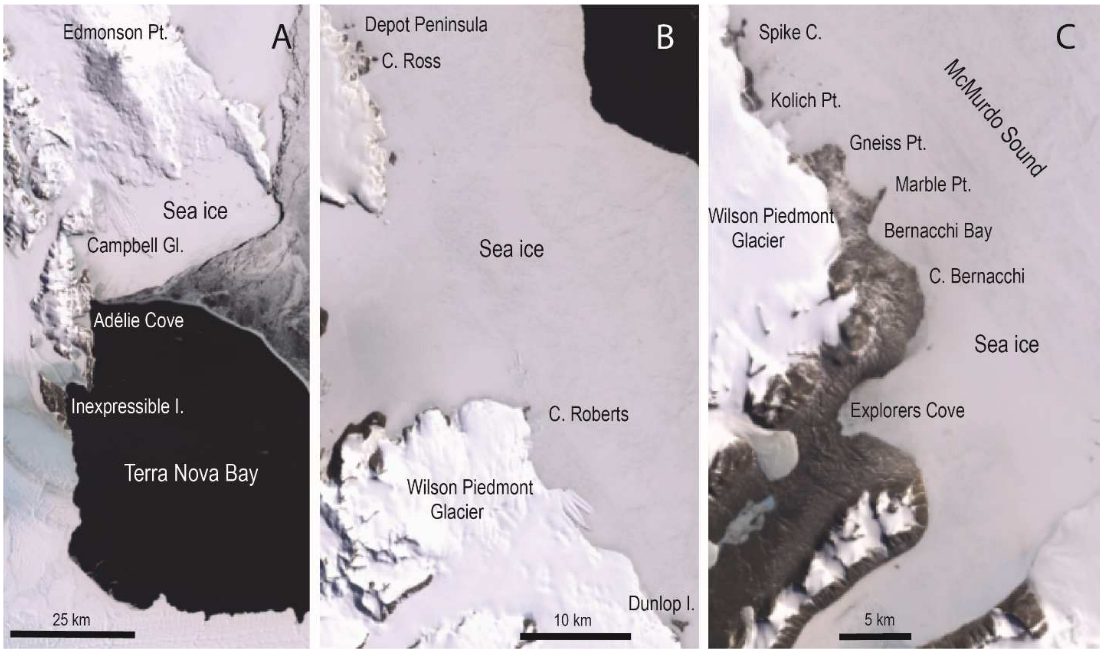

Fig. 3. Field locations along the Victoria Land coast, from north (A) to south (C), with locations corresponding to boxes in Fig. 1. Descriptions of each area are in the Supplemental Information. Base maps are from Google Earth imagery sourced from the US Geological Survey.

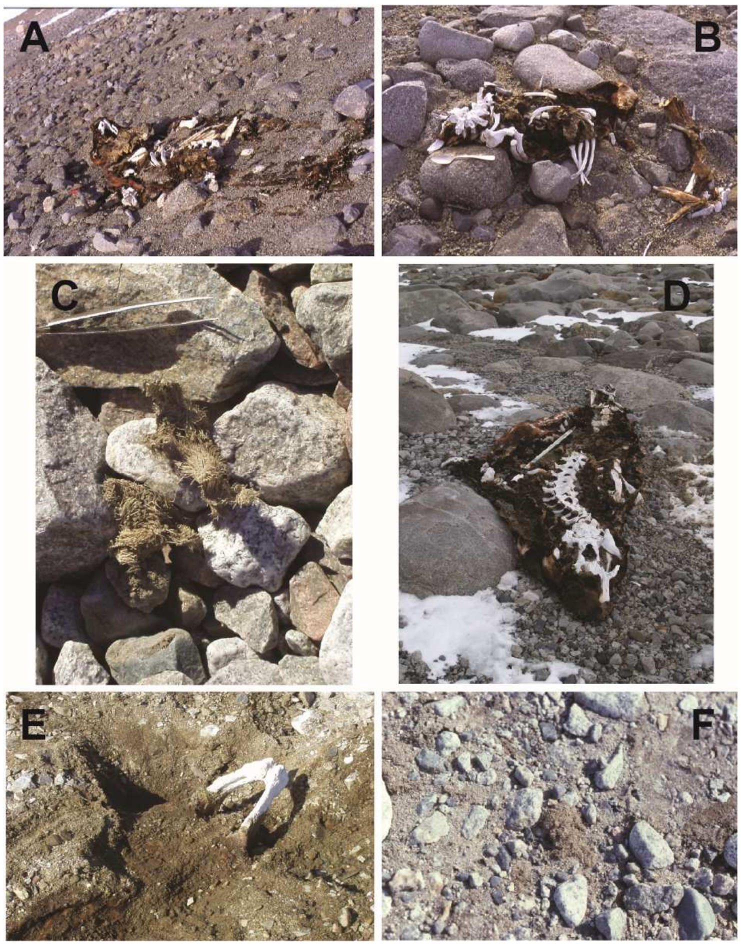

Fig. 4. Elephant seal remains. A. Large, incomplete adult male on a beach at South Bay, Inexpressible Island. See shovel (~1 m long) to the left of its shoulder for scale. B. Nearly complete, but heavily ablated small individual, South Bay, Inexpressible Island (spoon for scale). C. Recently exposed molted pelage, Cape Roberts. Tweezers provide scale. D. Mummified seal at Seaview Bay, Inexpressible Island, with ice axe for scale. E. Seal buried in a beach at Dunlop Island. Only the lower mandibles were exposed. F. Molted pelage on a beach at Cape Roberts.

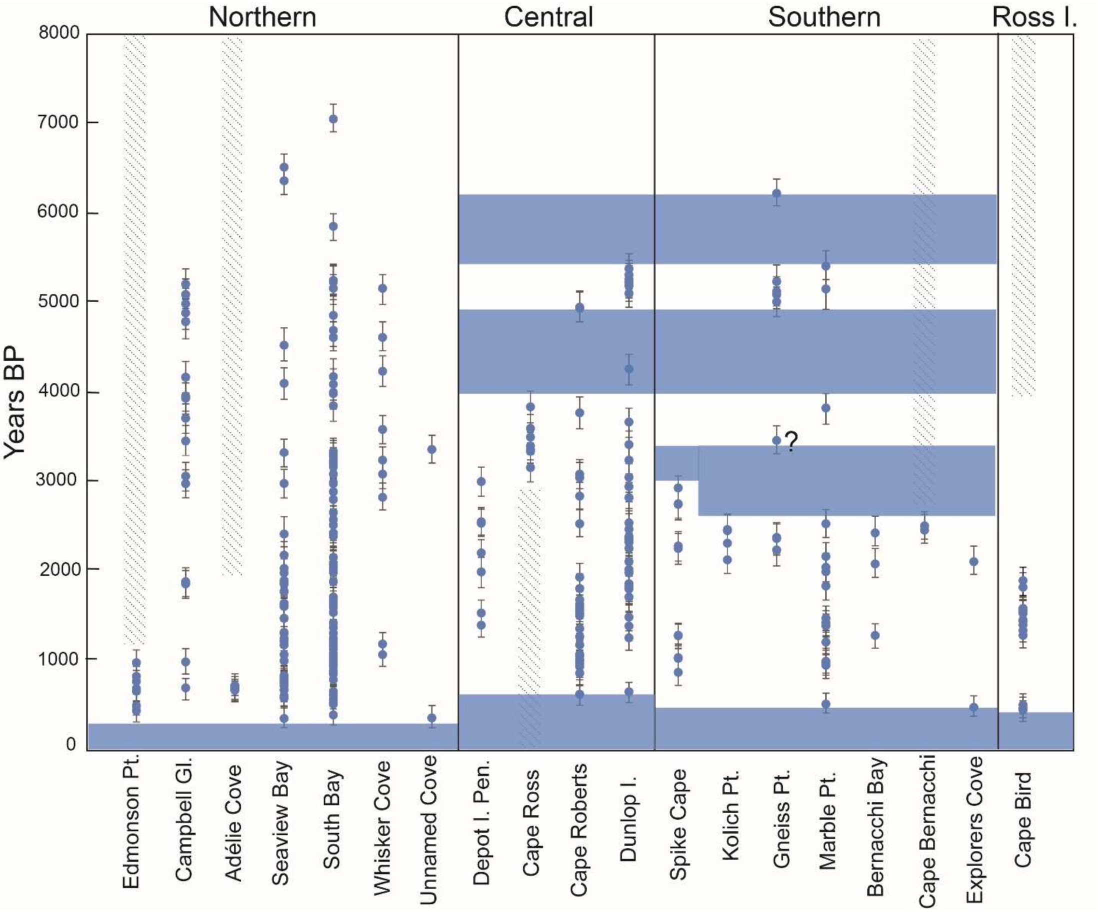

Fig. 5. Dated seal remains by site along the Victoria Land coast, arranged from north (left) to south (right) on the x-axis. Cape Bird is not on the Victoria Land coast, but on an offshore island and is not plotted by latitude. Blue bands indicate times when elephant seals likely were absent. Gray hash bars indicate times when elephant seals could not have accessed the site easily, due to the interaction of isostatic rebound and topographic features such as cliffs. Sample marked “?” may be an outlier.

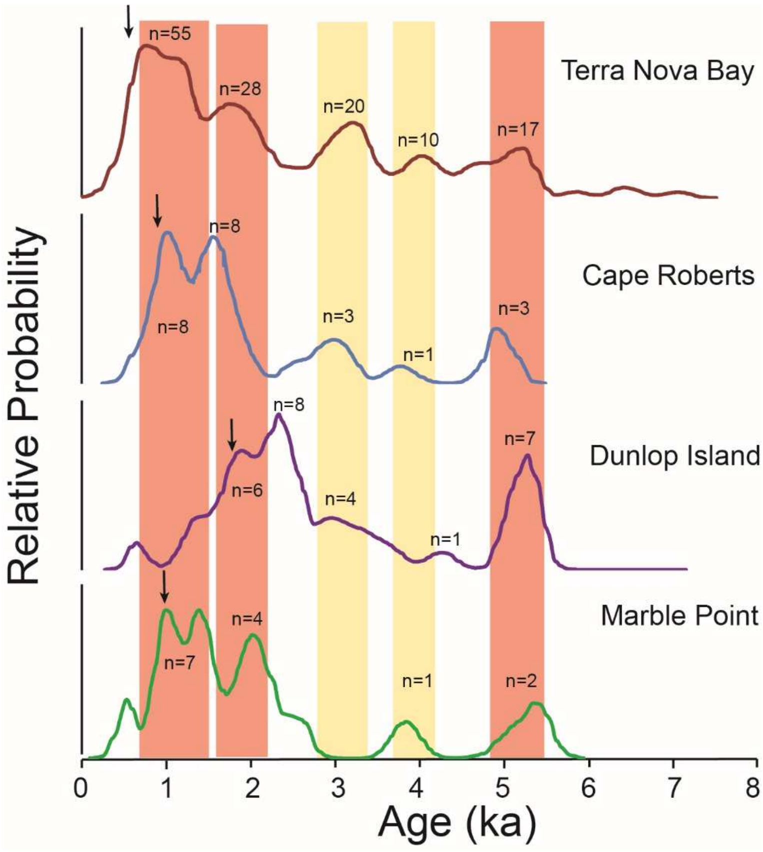

Fig. 6. Probability age distribution of seal remains at major occupation sites from north (top) to south (bottom), including Terra Nova Bay (Campbell Glacier, Adélie Cove, Seaview Bay, South Bay, Whisker Cove, Unnamed Cove), Cape Roberts, Dunlop Island, and Marble Point. Red bars show times of relatively high seal numbers and inferred reduced sea ice and warm ocean temperatures. Yellow bars denote times of lesser warmth, documented best at northern sites. Black arrows indicate possible times of final population collapse at each site.

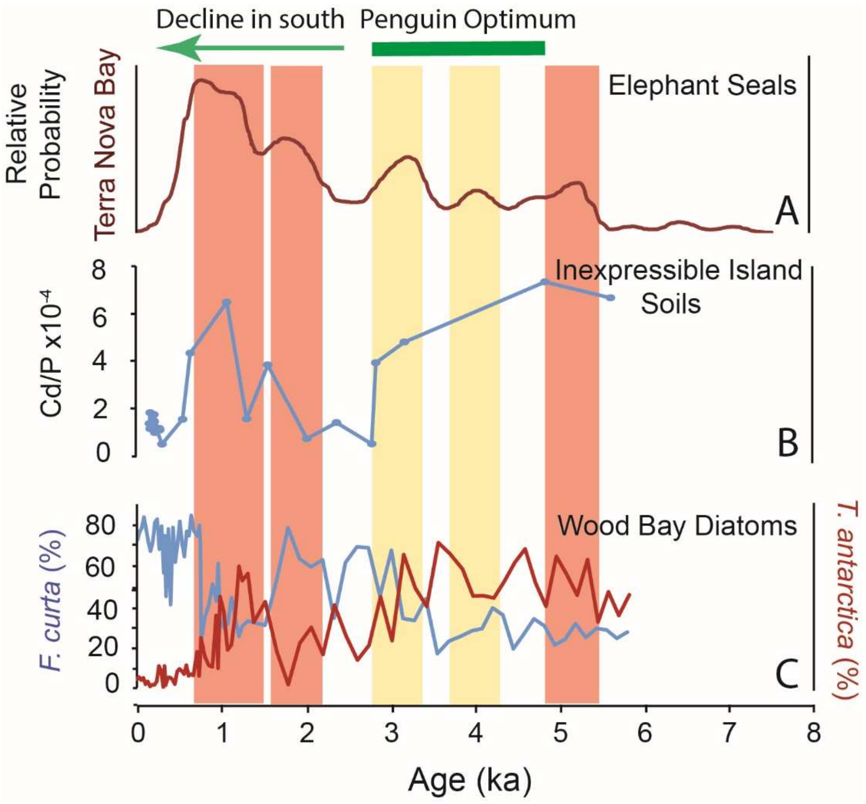

Fig. 7. Synthesis of Holocene climate records from the northern VLC discussed in the text. A. Age distribution of seal remains at Terra Nova Bay. B. Cadmium/phosphorus ratios of penguin guano at Inexpressible Island, inferred to be a proxy for the presence of modified circumpolar deepwater in Terra Nova Bay (Xie et al., 2021). C. Diatoms from a marine core at nearby Wood Bay (Fig. 1; Megzec et al., 2017), inferred to represent sea-ice extent (*F. curta* (blue) – high % = more sea ice) and summer temperature/duration (*T. antarctica* (red) – high % = warmer/longer summer). Green bar and arrow at the top of the figure denote the penguin optimum (Baroni and Orombelli, 1994) and decline of penguin rookeries at southern mainland locations. Red and yellow bands are from Fig. 6 and indicate times of relative warmth inferred from the elephant seals.

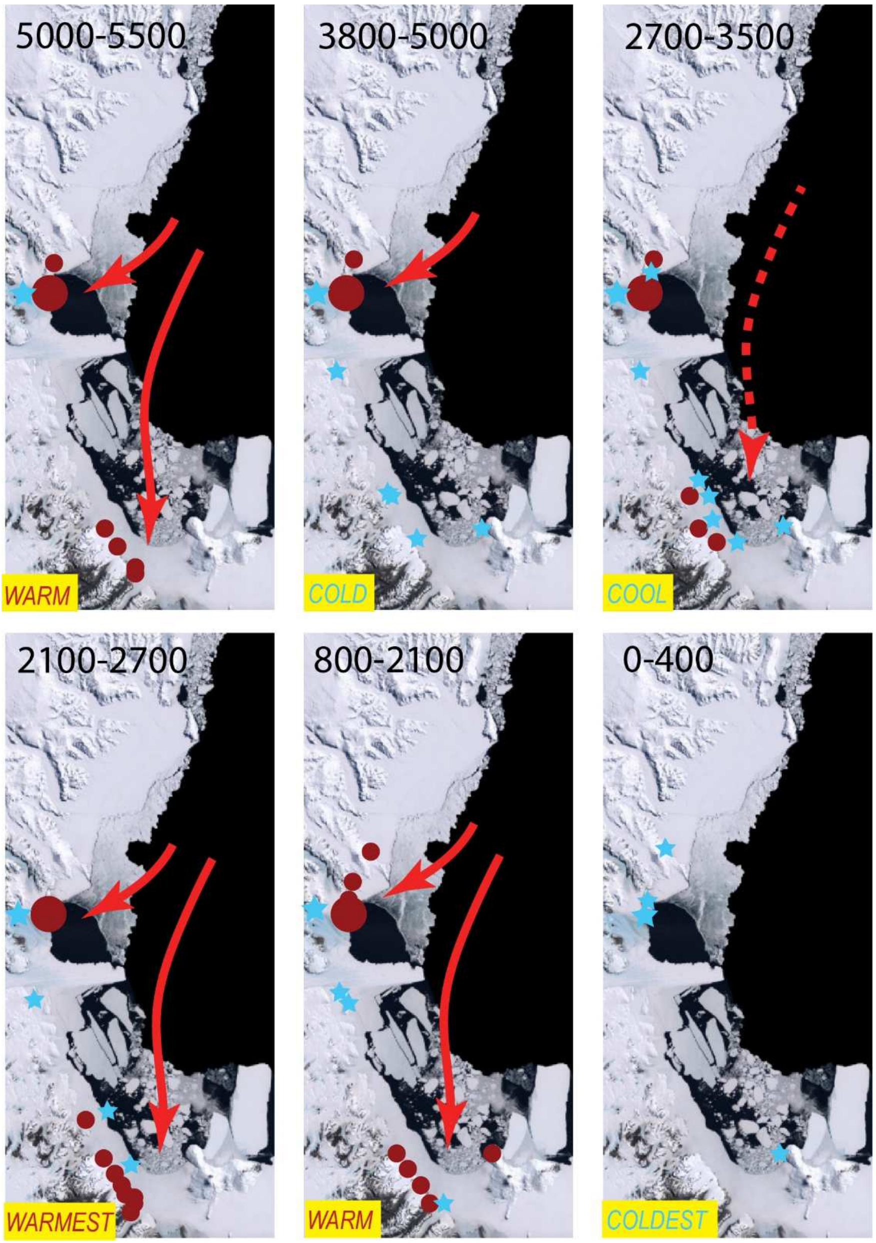

Fig. 8. Schematic of different time periods along the Victoria Land coast showing inferred relative ocean water temperature/sea ice. Red dots = elephant seals; blue stars = Adélie penguins (Baroni and Orombelli, 1994a; Dochat et al., 2000; Hall et al., 2004; Hu et al., 2019; Emslie, 2021; Gao et al., 2022). Red arrows indicate possible intrusion of modified circumpolar deepwater (dashed = weak). Times at top of panels are in years BP. Base image is from the Landsat Mosaic Image of Antarctica (https://lima.usgs.gov).