

Mummified and skeletal southern elephant seals (*Mirounga leonina*) from the Victoria Land Coast, Ross Sea, Antarctica

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ABSTRACT

We report on an accumulation of mummified southern elephant seals (*Mirounga leonina*) from Inexpressible Island on the Victoria Land Coast (VLC), western Ross Sea, Antarctica. This accumulation is unusual, as elephant seals typically breed and molt on sub-Antarctic islands further north and do not currently occupy the VLC. Prior ancient DNA analyses revealed that these seals were part of a large, Antarctic breeding population that crashed ~1,000 yr ago. Radiocarbon dates for Inexpressible Island mummies range from 380 to 3,270 yr before present, too old to have been created by Scott's Northern Party in 1912 and varying too widely in age to represent a catastrophic death assemblage. Skeletal measurements reveal that most Inexpressible Island mummies are adult or subadult males. The presence of male elephant seals on Inexpressible Island until several hundred years ago suggests that, at a minimum, it served as a haul-out site for the large Antarctic population and may have hosted a breeding colony. The conditions that allowed this Antarctic population to use the Ross Sea, the factors spurring its decline, and the implications for the adaptability and sensitivity of the species to environmental change all merit further study.

Key words: *Mirounga leonina*, mummy, paleoecology, Antarctica, Ross Sea, Holocene.

Fossil remains offer information on past geographic range, population biology, and ecology that can provide vital historical context for studies of extant species and conservation efforts (e.g., Newsome et al. 2007, Nichols et al. 2007, Rick et al. 2009). A frigid, dry climate and lack of large terrestrial scavengers enhance the preservation of animal remains in Antarctica, allowing development of multimillennial records of the distribution and ecology of its marine birds and mammals (Baroni and Orombelli 1994, Hall et al. 2006, Emslie and Patterson 2007). We report here on subfossil seals from the Victoria Land Coast (VLC) of the western Ross Sea (Fig. 1A). Although scattered seal carcasses occur along the entire VLC and at sites in the Dry Valleys (Dort 1981), an unusual accumulation of mummified carcasses (>30 individuals) occurs on Inexpressible Island (~75°S), adjacent to Terra Nova Bay (Fig. 1B).

Early field observations (Stuiver et al. 1981) and genetic evidence (Hall et al. 2006, de Bruyn et al. 2009) showed that many of the carcasses on Inexpressible Island are southern elephant seals (*Mirounga leonina*). In addition, elephant seal hair is common on ice-free beaches along the VLC from Inexpressible Island to Marble Point (77.4°S) (Hall et al. 2006). This wide distribution of elephant seal remains is

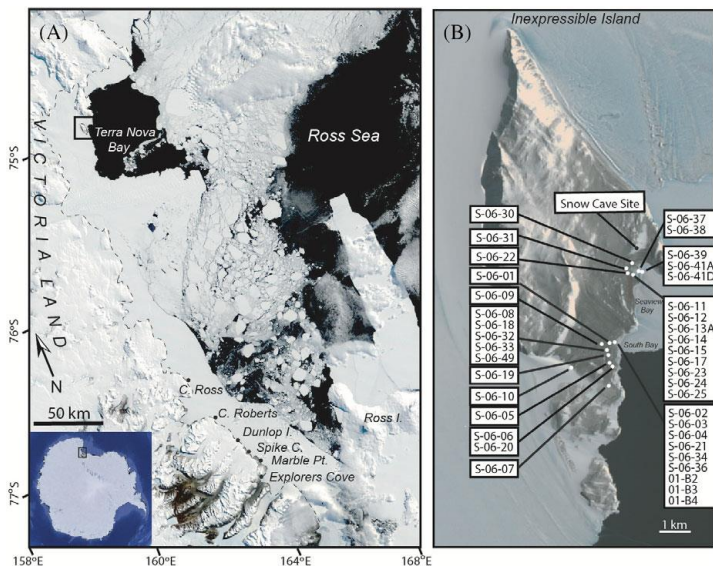


Figure 1. (A) Satellite image of the western Ross Sea and Victoria Land Coast (VLC). The dashed line indicates the land-sea border on the VLC. The black rectangle on panel A corresponds to the area presented in panel B. The inset map shows the location of panel A on the Antarctic continent. (B) Index map showing the location of seal remains on Inexpressible Island.

surprising, as the species typically breeds and molts on sub-Antarctic islands at lower latitudes (Fig. 2). The closest extant breeding colony to the VLC is on Macquarie Island (~54.5°S), ~2,400 km to the north. A small number of males from sub-Antarctic

rookeries molt on the northeastern Antarctic coast (~66°S) along Vincennes and Prydz Bays (Gales and Burton 1989, van den Hoff et al. 2003). Southern elephant seals forage in open areas and pack ice in the northernmost Ross Sea (Hindell et al. 2017), and a few dozen animals molted on Ross Island adjacent to the Ross Sea polynya in the early 1970s (Ainley 2010), but there are no regular molting or breeding sites on the VLC today. Unlike the Ross Island molting site, extensive land-fast and perennial sea ice adjacent to beaches north and south of Terra Nova Bay (Fig. 1A) make the distance to open water (which is only available in late summer) too great for elephant seals. Inexpressible Island and other sites on Terra Nova Bay are an exception, as strong winds open a polynya that persists through much of the year. We combed all published and many unpublished

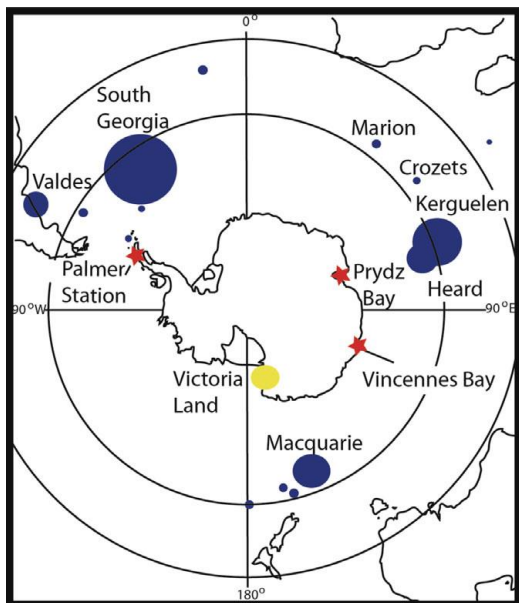


Figure 2. Modern distribution of sub-Antarctic southern elephant seal rookery sites (blue circles, size of the circle corresponds to the number of animals using the rookery), Antarctic haul out sites (red stars), and the location of the extinct Victoria Land Coast population (yellow ellipse). Modified after Laws (1994).

accounts of discovery and research on the VLC over the past 100+ yr and could find no mention of live elephant seals on these beaches.

Ross Sea beaches were freed of glacial ice about 8,000–7,500 yr before present (yr BP) (Conway et al. 1999), and elephant seals were present on Inexpressible Island by ~7,500 yr BP (de Bruyn et al. 2014). Analyses of ancient DNA (including both hair and Inexpressible Island mummies) reveal that the individuals on the VLC came from a large population with a female effective population size of >100,000 individuals (de Bruyn et al. 2009). The population was likely founded by Macquarie Island seals, but

it was a separate breeding colony that evolved independently from Macquarie (or any other known colony) until its collapse began about 1,000 yr ago (de Bruyn et al. 2014). Existing and new radiocarbon data (discussed here) also point to a crash starting 1,000 yr ago, with the last ancient specimen dating to ~380 yr BP. The presence of southern elephant seals, geomorphic evidence for wave-generated beaches, and diatom data from nearshore cores all indicate that, for much of the Holocene, open water was seasonally present on VLC beaches north and south of Terra Nova Bay (Hall et al. 2006, Mezgec et al. 2017). Together, these lines of evidence suggest that land-fast and multiyear sea ice has become much more pronounced in coastal settings over the last millennium.

Inexpressible Island also plays a role in historical exploration of the continent. It was first visited in 1912 by Scott's Northern Party, which was forced to overwinter in a snow cave. The party survived on seals and penguins, and debris from their activities is found near the cave site at Seaview Bay (Fig. 1B). Many mummified elephant seal remains are in the same area. The mixing of old and new materials has led to confusion about which seals were killed by the Northern Party and which died of natural causes. This distinction is important, because seals killed by the Northern Party form the basis for a marine radiocarbon reservoir correction for the Ross Sea (Stuiver et al. 1981, Mabin 1985, Whitehouse et al. 1989).

While much has been learned about this extinct population from studies of ancient DNA and radiocarbon (Hall et al. 2006; de Bruyn et al. 2009, 2014), the presence of elephant seal mummies and skeletons on the VLC lets us explore new questions. How do the carcasses on Inexpressible Island relate to the activity of Scott's Northern Party? What processes led to such a large grouping of seal remains (i.e., is this a catastrophic or an attritional assemblage)? Does the demography of the assemblage indicate that Inexpressible Island hosted an elephant seal breeding colony or merely a haul-out site? If environmental change drove the rise and fall of this population, what are the implications for the ecology and conservation biology of elephant seals?

METHODS

To address these questions, we studied 33 mummified and skeletal specimens found on Inexpressible Island (Fig. 1B). We include, for comparison, information on 14 other southern elephant seal remains at other sites on the VLC. Our work reflects the results of more than seven field seasons, during which we traversed all ice-free coastal areas from near Coulman Island (73.5°S) to Marshall Valley (78.1°S) on foot and recorded all seal remains present (Fig. 1A shows the portion of this expanse with elephant seal remains). In a few instances, snow cover may have prevented location of all individuals, but repeat visits in different years minimized this problem. Locations for all specimens are supplied in Table S1.

Physical Measurement of Specimens

Field identification of species was based on carcass size, tooth morphology (if available), and overall morphology. Morphological identification was not possible for isolated skin fragments, and given the scarcity of postcranial comparative materials, identification of isolated bones or fragments was difficult as well. In all cases, however, identification of remains as elephant seal was ultimately confirmed by mitochondrial DNA analysis.

We measured external, skeletal, and dental dimensions and noted the degree of fusion of epiphyses. We noted when measured length was an underestimate due to postmortem loss, but we could not quantify the reduction in body length due to shrinkage during mummification. Skeletal measurements were made with a flexible metal tape measure; dental measurements were taken with dial calipers. Body and skeletal measurements are as defined in Committee on Marine Mammals 1966–1967 (Scheffer 1967) or Table S2.

To estimate sex and age, we examined comparative materials and published data. For skeletal and dental comparisons, we studied specimens at the American Museum of Natural History, California Academy of Sciences, Museum of Comparative Zoology at Harvard University, Museum of New Zealand -Te Papa Tongerewa, and Smithsonian National Museum of Natural History. Measurements for these modern specimens are in Table S2; the criteria for distinguishing sex and age classes we developed from these materials are discussed in Appendix S1 and summarized in Table S3, and measurements on fossil specimens are in Table S4. Using measurements on fossils and the criteria in Table S3, we made a sex and/or age class determination for each measurement on each fossil, if possible.

Radiocarbon Analysis of Specimens

We obtained 50 radiocarbon dates on the seal remains (45 from elephant seals) and include one date from Nichols (1968). We removed sand from the samples by careful abrasion. Most samples were submitted to the National Ocean Sciences Accelerator Mass Spectrometry (NOSAMS) laboratory at Woods Hole Oceanographic Institution (OS sample numbers in Table 1). At NOSAMS, samples were pretreated with acid-base-acid leaches until solutions became clear, graphitized, and analyzed by accelerator mass spectrometry (see <http://www.whoi.edu/nosams/> for further details). A small set of samples was analyzed at the NSF-Arizona Accelerator Mass Spectrometry laboratory at the University of Arizona (AA sample numbers in Table 1). In all cases but one, these specimens were also analyzed at NOSAMS. Most samples were of skin or hair; if neither was available, we dated bone or dentin collagen. We converted the dates to calendar years using CALIB 7.0.1 with the

INTCAL Marine13 data set (Reimer et al. 2013) and a time-dependent reservoir correction (ΔR) for Holocene-aged material from the Ross Sea (Hall et al. 2010). ΔR averaged 791 \pm 121 yr over the Holocene, ranging from ~600–900 yr. All dates are in calendar years before present (yr BP) using the midpoint of the range with a 1-sigma error.

Table 1. All southern elephant seal carcasses from the VLC (with or without radiocarbon dates) and dated carcasses for other seals on Inexpressible Island. The probability of the calibrated ages is >95% unless otherwise stated. Latitude and longitude for specimens are provided in Table S1. For Lab Number, OS – National Ocean Sciences AMS laboratory; AA – NSF-Arizona AMS laboratory.

Genetic Analysis of Mummies

Most samples presented here were analysed in de Bruyn et al. (2009, 2014). For the six new samples (ECA-12-15, ECC-12-34, -52, -53, -56E, and MVC-13-24), the methodology for molecular analyses is as described in de Bruyn et al. (2009). Analysis of a 352 base-pair fragment of the mitochondrial control region hypervariable region 1 (HVR1) let us confirm species identification and place the seals in the context of our emerging VLC seal DNA database.

RESULTS

The seal remains on Inexpressible Island and at other sites on the VLC fall into three categories of preservation (Table 2). The first category is mummified seals, which occur in various states of breakdown (Fig. 3A–D). Most of these bodies have never been buried, except occasionally by snow. Most Inexpressible Island seals belong to this category. The second category includes the small number of frozen seals buried in beaches or being exposed by retreating ice (Fig. 3E). These specimens often have exceptional preservation not only of bones and skin, but also of internal organs and blubber. The third category comprises skeletal remains, most of which are disarticulated and highly incomplete (Fig. 3F, G). General observations about the taphonomy (processes of decay and fossilization) of VLC elephant seals remains are presented in Appendix S1.

Species Identification

The Inexpressible Island mummy accumulation consists largely of southern elephant seals (Table 1). Where relatively complete, they are easily identified by their large size, tooth and skull morphology, and, in some cases, a large proboscis. Elephant seal

carcasses or skeletal remains occur farther south at Explorers Cover, Marble Point, Spike Cape, Dunlop Island, Cape Roberts, and Cape Ross, but are rare in comparison to those at Inexpressible Island. In addition, with the exception of a mummified pup at Cape Roberts, remains from these other locations consist only of skeletal fragments or buried or recently exposed seals. There are no large surface accumulations of elephant seal mummies other than on Inexpressible Island, even though molted skin and hair attest to their former widespread presence all along the VLC (Hall et al. 2006).

Table 2. Measurements used to assess age and sex of elephant seal carcasses. Criteria for age and sex assignments are presented in Table S3. Measurements in bold are so large they must be adult or subadult males. Abbreviations: Loc, location; CRb, Cape Roberts; CRo, Cape Ross; DIs, Dunlop Island; ExC, Explorers Cove; IIs, Inexpressible Island; MPt, Marble Point; SpC, SpikeCape; M, male; F, female; ad, adult; sub, subadult; y, young; J-P, juvenile or pup; STL, straight-line snout-to-tail length; L, length; HW, half-width; Mand, mandible; Upr, upper; Lwr, lower; Can, canine; Me, mesiodistal; Bu, buccolingual; Hum, humerus; Rad, radius; Fem, femur; Tib, Tibia; PrS, preservation state; MR, mummied remains; FB, frozen or buried seals; IB, isolated bones; —, unavailable; ?, unknown.

Weddell seals (*Leptonychotes weddellii*), the other taxon reported in Table 1, are common in the Ross Sea today. They are the species most often found as decaying carcasses or mummies elsewhere on the VLC (CB, BLH, and PLK, personal observations). Crabeater (*Lobodon carcinophaga*) and leopard (*Hydrurga leptonyx*) seal carcasses occur in



Figure 3. Photographs showing different modes of preservation of southern elephant seals from the VLC. (A) A relatively complete elephant seal mummy lying on its stomach showing characteristic wind ablation (S-06-12). (B) The skull of a mummified adult male elephant seal with a proboscis (S-06-07). (C) A highly ablated seal carcass with the remaining bones retained by mummified skin (01-B4). (D) An isolated piece of elephant seal skin (S-06-06). (E) A buried elephant seal from Dunlop Island with its lower jaw and chest exposed (DIS-1). (F) Canine tooth of an elephant seal (CRoss). (G) Delicate mandible of a neonatal or fetal elephant seal (CRS-1).

lesser abundance on the VLC, although crabeater seals comprise the majority of mummies found at inland sites in the Dry Valleys (BLH and PLK, personal observations). Where well preserved and exposed, all four species could be distinguished morphologically. On Inexpressible Island, several of the Weddell seals were incomplete and so were identified genetically. Several other incomplete specimens were clearly not elephant seals but have not been identified further.

While many seal remains occur near the Snow Cave site on Inexpressible Island, those butchered by Scott's Northern Party in 1912 are easily identified. They consist of disarticulated or partially articulated bones with cut marks and green bone fractures, as well as folded piles of flensed skin. None of the elephant seal mummies bear such features and none of the isolated bones with cut marks are from elephant seals.

Radiocarbon Data

Table 1 presents radiocarbon data for all dated seal carcasses. We focus on southern elephant seals, which are unusual for this polar environment. These seals range from 380 110 to 5,090 220 yr BP. More complete mummies on Inexpressible Island date to the younger part of this age range, between ~530-1,680 yr BP, with a mode of ~800 yr BP (Fig. 4A). Fragments of mummies (i.e., isolated pieces of skin or bones) at Inexpressible Island have a bimodal distribution that covers a wider range (~380 to 3,270 yr BP) (Fig. 4B). In contrast, hair samples on Terra Nova Bay beaches span a greater range and are as old as ~7,500 yr BP (Fig. 4C), and hair elsewhere along the VLC shows the same wide range, with a precipitous decline after ~900 yr BP (Hall et al. 2006). The elephant seal carcasses and bones from further south tend to be older than those from Inexpressible Island (~500 to 5,090 yr BP, with a mean of ~2,500 yr BP) (Fig. 4D).

Sex and Age of Southern Elephant Seal Fossils

Elephant seals can be aged by counting growth bands in canines, but complete canines were not always present and, where present, their removal would harm the mummies. As a consequence, we used other osteometric and dental features to discriminate the following age-sex classes, based in part on the tremendous sexual dimorphism in the species: pups and juveniles of both sexes (birth to age 2); young-to-adult females (>2 yr old) and young males (2–4 yr old) (which are

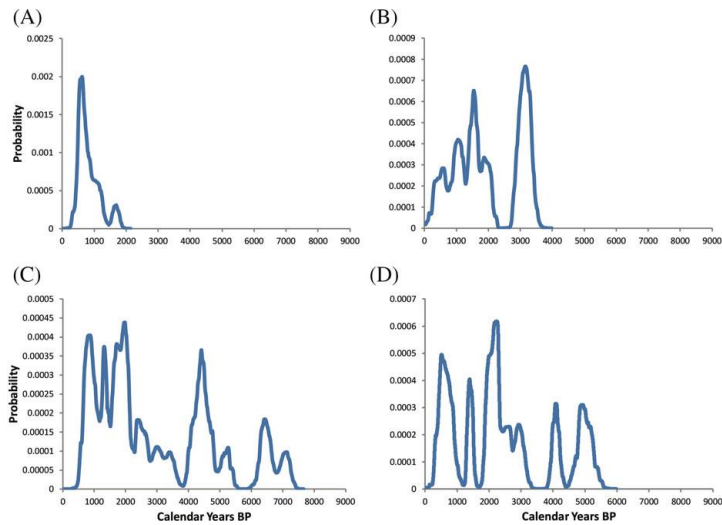


Figure 4. Probability density plots of radiocarbon-dated specimens.

(A) Inexpressible Island, mostly complete mummies; (B) Inexpressible Island, highly fragmented mummies or isolated pieces of skin or bone; (C) shed fur from the Inexpressible Island region (Inexpressible Island, Gondwana Station); and (D) carcasses and bones of elephant seals from sites on the VLC south of Inexpressible Island.

indistinguishable metrically); subadult males (4–6 yr old); and adult males (>6 yr old) (Appendix S1, Table S3). No individual fossil specimen retains all features, but in most cases, multiple features support our sex and age determinations.

Due to shrinkage and tissue loss, length measurements for mummies underestimate live length. Figure 5 shows body length data and/or best fit Gompertz equations of body length vs. age for modern elephant seal populations, as well as the lengths of VLC fossil elephant seals. Among the 14 larger specimens with snout-to-tail (STL) measurements (i.e., animals with some measurement so large they are unlikely to be juveniles), five are solidly in the size range for adult males (Table 2). Three individuals have STLs larger than Macquarie females, but near the asymptotic length of South Georgia females (S-06-03, -10, and -15, though the last carcass is incomplete). Another specimen, MVC-13-24, is 2.5 m long (near the asymptotic length for Macquarie females), but its head was buried in ice and could not be measured, so it is likely large enough to be a subadult male. Of the remaining animals, three (S-06-02, -30, and -36) have STLs near the asymptotic length for Macquarie females, and two are too incomplete to assess (S-06-09 and -31). Two specimens are small enough to be pups (01-B4 and CRS-5).

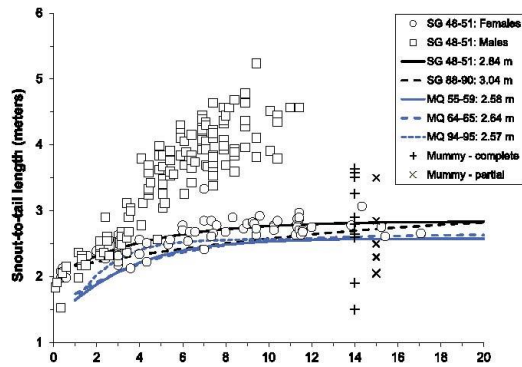


Figure 5. Elephant seal snout-to-tail length (STL) versus age. Crosses present STL for complete VLC mummies (placed at year 14 for visualization); X marks the STL for partial mummies (placed at year 15). Circles and squares are data for females and males, respectively, from the South Georgia (SG) population in 1948-51 from Laws (1953). As these data were measured as curvilinear length, they were reduced by 5% to convert to straight-line length (Bell et al. 2005). Different lines were fit to STL versus age data for females from SG in 1948–1951 and 1988–1990 and from Macquarie Island (MQ) in 1955–1959, 1964–1965, and 1994-95 using a Gompertz equation (Bell et al. 2005). The legend reports asymptotic length (in meters) for each cohort of females.

Skeletal measurements provide more reliable evidence as to sex and age, albeit one for which we lack a tight correlation to absolute age. Cranial and dental discrimination of sex and age classes is based on our measurements of comparative materials (Appendix S1, Tables S2, S3). For post-cranial elements, assessments are based on the ranges for males and females reported in Bryden (1972).

Among the 11 larger elephant seals for which we have measurements of skull length and/or width, eight fall in the size range of adult males and three are in the subadult male range, though two (S-06-02 and -30) are close to the lower limit of that range and one (S-06-03) is larger (Fig. 6, Tables 2, S3). Among the 11 larger elephant seal mummies for which we have mandible length, six fall in the size range for adult males and five fall in the subadult range (Fig. S1, Tables 2, S3). All 11 individuals that have at least one canine dimension on either uppers or lowers are classified as males (Fig. S2, Tables 2, S3).

For the 13 mummies with postcranial measurements so large that they are unlikely to be juveniles, 12 have lengths for one or more postcranial element that are greater than the range Bryden (1972) reports for Macquarie females (Tables 2, S3); one is in the adult female/young male range (S-06-20). Four specimens have a well-developed proboscis, which forms in males by about year 6 (Laws 1953). One specimen (S-06-13) has a baculum. Among the poorly preserved specimens, two (S-06-01 and -08)

have skeletal measurements greater than or equal to those of confirmed fossil males and one (S-06-24) has a value less than subadult males. We have little confidence in designating sex for these specimens given the lack of modern comparative samples.

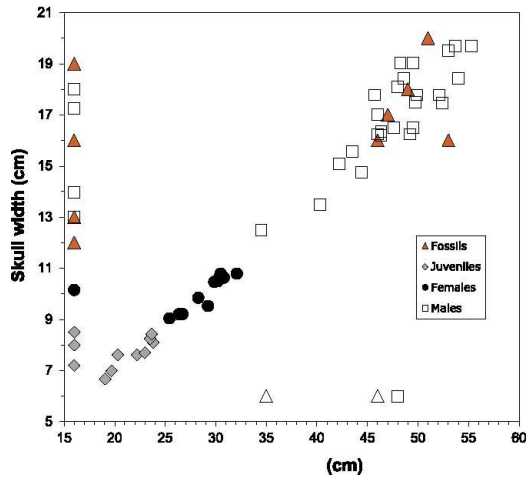


Figure 6. Skull measurements for fossil and modern southern elephant seals. Measurements of skull length and skull half-width are as described in Table S2. For visualization, modern specimens or mummies that lack skull length data are plotted at 16 cm; those that lack skull half-width data are plotted a 6 cm.

Table 2 also provides our summary assessments of sex and age class for each of the 24 larger, more complete carcasses using the criteria provided in Table S3 and giving skeletal measurements more emphasis in our assignments than body length. For these 24 carcasses, 14 are adult males (>6 yr old), three are either adult or subadult males, six are subadult males, and one has very few well-characterized measurements but is smaller than subadult males and could be a young male or an adult female.

Four specimens have dimensions so small that they are likely to be juveniles (<24 mo old), pups (new born or weaned animals that did not survive to migrate off the beach), or fetuses. CRS-1 (Fig. 3G) is a very small, fragile mandible with three tooth crowns in formation. It is smaller than any comparative sample and may be a fetus. CRS-5 and 01-B4 both have body lengths in the range of nursing or recently weaned pups, and the humerus length for 01-B4 is at the bottom of the size range reported by Bryden (1972), whose sample included nursing and weaned pups. Mandible length for CRS-3 is at the upper end of the range for juveniles (Fig. S1).

In summary, most carcasses that have sex and age determinations are adult or subadult males; only one skeleton is potentially attributable to an adult female. A few pups and perhaps a fetus are present, which may indicate the presence of breeding age females. The expected sex and age distributions at elephant seal breeding and haul-out sites,

and postmortem, processes that might bias those ratios among preserved specimens are explored in depth in Appendix S1.

Population Dynamics and Demography of Ancient DNA Analysis

Previous DNA analyses show that the southern elephant seal samples investigated here were part of an extremely large VLC population that was genetically distinct from all major extant breeding colonies (de Bruyn et al. 2009, 2014) (Fig. S3). The ancient population was characterized by a large number of shed fur samples collected along the entire VLC, as well as the carcasses studied here. We compared samples from Inexpressible Island with those from the rest of the Ross Sea and found no significant differentiation ($F_{ST} = 0.01$, $P = 0.15$; data from de Bruyn et al. 2009). We also tested for and found no significant differentiation among time periods (i.e., seals $>3,000$ yr BP, 3,000–1,500 yr BP, or $< 1,500$ yr BP; pairwise F_{ST} values all <0.01 ; P values all >0.10).

DISCUSSION

Prior ancient DNA work, which included Inexpressible Island mummies, concluded that the VLC population represented an independent breeding population because of its high diversity, preponderance of unique haplotypes, and significant differentiation from modern breeding populations (de Bruyn et al. 2009). Analyses that tested alternative scenarios strongly favored those with a single founder group from Macquarie Island establishing the VLC population (de Bruyn et al. 2014). Our comparison of ancient DNA from VLC mummies to the broader sample suite found no differentiation in space or time. Thus, the last remaining members of the VLC population that we find as mummies on Inexpressible Island were derived from the population that flourished in Antarctica earlier in the Holocene; they were not animals from Macquarie Island or any other modern sub-Antarctic breeding population that were hauling out on the VLC. These mummies let us address a number of questions about this extinct population.

Chronology of Seal Accumulations and Interactions with the Northern Party

The ages of the mummified and skeletal southern elephant seals suggest they abandoned Inexpressible Island ~ 400 yr ago, well before the arrival of the Northern Party in 1912. Butchered remains that can be identified are from Weddell seals and penguins, not southern elephant seals. The Northern Party's notes record that they saw or butchered "seals," without specifying species; we assume these were the commonly occurring Weddell seal. Crabeater or leopard seals must have been more unusual (as is the case on the coast today), because the notes referred to them specifically at certain points (Huxley 1913). Those notes do not mention the presence of live elephant seals

on Inexpressible Island, though they do report a “large number of old dead seals on the beach, the largest of which are more than 12 feet long” (Huxley 1913, pg. 125). Although the unusual accumulation was noted, rapidly deteriorating conditions did not permit the Northern Party to examine the remains. The presence of these mummies indicates that care should be taken when sampling historical materials for calculation of the marine reservoir effect. Significant variation in previous marine reservoir calculations from Inexpressible Island (e.g., Mabin 1985) suggests the possibility that some past workers may have inadvertently sampled seals that died well before the arrival of the Northern Party.

Do Carcasses Represent a Haul-out Site or a Breeding Colony?

The wide range of ages for the mummies on Inexpressible Island falsifies the hypothesis that the carcasses represent a catastrophic death assemblage. They must represent attritional mortality at a breeding or haul-out site. Given the great size of the VLC population, its sustained presence on continental Antarctica for much of the Holocene, and its eventual demise beginning 1,000 yr ago, it is important to understand whether the extensive ice-free beaches on the Holocene VLC were breeding or haul-out sites for elephant seals. While ancient DNA data indicate that the VLC fossils represent a large breeding colony independent from all extant colonies (de Bruyn et al. 2009, 2014), absent nuclear DNA with sex-specific markers (which would allow us to determine the sex ratio at a locality), genetic data are agnostic as to whether a particular fossil locality is a breeding site.

Along the entire VLC, the 24 large elephant seal remains complete enough for sex and age determination are strongly dominated by adult and subadult males; there is just one potential carcass from an adult female (Table 2). This result was found despite setting thresholds for sex determination biased towards identifying females. Statistical comparisons (Appendix S1) to demographic and mortality data from Macquarie Island (the only southern elephant seals data we are aware of) strongly suggest that this biased sex ratio is incompatible with deaths expected at a breeding colony. Intriguingly, pups are more common on the VLC than females, though only one occurs with the large accumulation of elephant seals on Inexpressible Island.

If the mummies from Inexpressible Island reflect mortality at a breeding site, then the overwhelming dominance of males would imply either that male, female, and pup carcasses have drastically different probabilities of preservation, and/or that mortality on land was much more strongly biased towards males than on Macquarie Island today. With respect to differential preservation, the rarity of pup skeletons is unsurprising; they are fragile and likely to be destroyed rapidly. The scarcity of female carcasses is more problematic, since they are as large as Weddell seals, which are preserved at sites along the VLC. If Inexpressible Island hosted a breeding colony

when most carcasses were deposited (i.e., near the end of the VLC occupation), the lack of female carcasses requires highly male-biased mortality, perhaps because molting males were more vulnerable to trapping by early fall sea ice. Such a bias in mode of death might be more likely at deep Antarctic sites than at the current sub-Antarctic breeding and molting sites.

If Inexpressible Island was chiefly a high-latitude male molting site at the end of the occupation period, the biased age and sex ratio of the carcasses is expected. Under this scenario, the population would need to be breeding further north at sites that have not yet been sampled for ancient DNA. Sites farther south are unlikely to have hosted the last remaining breeding colony, because they have few elephant seal bones or carcasses despite preserving remains of other seal species of this age (Hall and Koch, data not presented); most elephant seal remains that are preserved are older than the Inexpressible Island carcasses (Fig. 4). Possible breeding sites include Cape Adare, Cape Hallett, or the present-day haul-out site on Vincennes Bay, which receives males from Macquarie Island. Intriguingly, an elephant seal breeding colony on western Tasmania disappeared ~1,000 yr ago, likely due to over predation (Bryden et al. 1999), while a nearby rookery on King Island in Bass Strait disappeared with European hunting in the early 1800s (Ling et al. 1999). These rookeries are more than 4,100 km from the VLC beaches, a seemingly implausible migratory distance to be a source of VLC individuals.

The Rise and Fall of an Antarctic Population of Southern Elephant Seals

The most parsimonious interpretation is that the carcasses on Inexpressible Island represent mortality at a male haul-out site. The dates for these carcasses cluster in the latest Holocene (mode ~800 yr BP for relatively complete specimens, Fig. 4A) and include some of the last dated elephant seals on the VLC. Whatever role the VLC played in the earlier history of the population (haul-out site or breeding colony), a last stand male haul-out site on Inexpressible Island makes sense geographically, given the presence of open water even today along the Terra Nova Bay polynya. The Holocene elephant seal occupancy of the VLC prior to its last stand on Inexpressible Island is largely documented by fur and skin dating back to nearly 7,500 yr BP (Hall et al. 2006), yet the rare carcasses and bones found at sites south of Inexpressible Island are important. These rare specimens are older than modal age for mummies from Inexpressible Island (Fig. 4D). Five of the 14 specimens are too fragmentary to determine age or sex, but three of the nine remaining individuals are pups and the other six are adult or subadult males. This high ratio of pups-to-males might be viewed as evidence for breeding on the VLC earlier in the Holocene. Those beaches might have been part of a larger suite of sites that supported the large elephant seal population that flourished from 7,500 to 1,000 yr BP. Once it began to collapse, the southernmost breeding sites would have been abandoned first, with a male haul-out

persisting on Inexpressible Island supported by more northerly breeding sites, until the ultimate extinction of the entire population.

Our new radiocarbon dates, along with dates from molted skin and hair (Hall et al. 2006) and genetic analysis (de Bruyn et al. 2009, 2014), indicate that elephant seals had abandoned the VLC prior to sealing on Macquarie Island (main period, 1810–1830; Hindell and Burton 1988) or significant exploitation of Southern Ocean resources in recent decades (Ainley and Blight 2009, Ainley 2010). As a consequence, we must explore nonanthropogenic factors contributing to the demise of this large population.

Mezgec et al. (2017) use diatom data from marine cores and sea salt and isotopic data from ice cores to document the expansion and contraction of sea ice in the coastal zone (both land-fast ice and multiyear sea ice) versus the open ocean (pack ice) in the western Ross Sea. They note millennial cycles in sea ice since ~7,000 yr BP that are opposing between coastal and open ocean sites, with the iciest coastal conditions occurring over the last 1,000 yr, and relate changes in the abundance of elephant seals and other species to these climate cycles. In particular, the expansion of land-fast and multiyear sea ice in the latest Holocene likely contributed to the collapse of the VLC population, as argued previously (Hall et al. 2006; Mezgec et al. 2017; de Bruyn et al. 2009, 2014). The expansion of land-fast ice would eliminate most breeding sites along the VLC and perhaps further north.

This expansion of multiyear sea ice may also have caused oceanographic changes that were detrimental for elephant seals. The elephant seals molting and dying along the VLC were likely foraging on the large Ross Sea continental shelf, something that is uncommon today. While elephant seals from Macquarie Island do forage in the northernmost Ross Sea, very few penetrate dense sea ice to reach productive shelf sites, and an ongoing drop in the number of seals at Macquarie Island is associated with an increase in sea ice extent and concentration (Hindell et al. 2017). Loss of the Ross Sea shelf as prime foraging habitat due to increased sea ice and/or greater energy costs of traveling given the elimination of nearby haul-out sites may have led to a dramatic reduction in the number of elephant seals that could be supported in this sector of the Southern Ocean. Isotopic studies in progress on the diets of fossil VLC seals may shed light on the role of oceanographic or diet change in driving the collapse of this ancient population.

Conclusion

Dawson et al. (2011) emphasized that accurate prediction of the vulnerability and response of species to coming environmental change requires an assessment that merges mechanistic, experimental, and empirical understanding. They noted the

power of integrating paleoecological observations with study of modern and ancient DNA to reveal how populations have resisted extirpation and how species have avoided extinction during prior climate shifts. Using this approach, we are beginning to understand the sensitivity of elephant seals to large changes in environmental conditions in terms of population size and persistence.

For comparison, a recent study of the recovery of northern fur seals (*Callorhinus ursinus*) after the collapse of mid-latitude breeding colonies along the northeastern Pacific Rim 1,000–500 yr ago attributed their 20th century rebound to behavioral plasticity, a broad geographic range (with large individual migrations), a secure refuge, and panmixia (which preserved genetic diversity as breeding sites were lost) (Pinsky et al. 2010). Similar attributes, perhaps adaptations honed by flickering glacial climates of the past 2.6 million yr, may explain how southern elephant seals rapidly occupied the VLC as soon as it was ice-free in the early Holocene. Once conditions deteriorated 1,000 yr ago, the VLC population and much of its genetic diversity were lost. Possession of the attributes noted above may be useful in predicting how taxa will respond to future ecosystem changes and identifying the species most likely to benefit from management interventions.

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Table 1. All southern elephant seal carcasses from the VLC (with or without radiocarbon dates) and dated carcasses for other seals on Inexpressible Island. The probability of the calibrated ages is >90% unless otherwise stated. Latitude and longitude for specimens are provided in Table S2. For Lab Number, OS – National Ocean Sciences AMS laboratory; AA – NSF-Arizona AMS laboratory. *Pup; †From Nichols (1968); - indicates an undated specimen.

Sample	Location	Material Dated	Lab. Number	¹⁴ C age (±1σ) (¹⁴ C yr BP)	Calibrated age (±1σ) (calendar yr BP)	δ ¹³ C (‰)
<i>Southern Elephant Seals</i>						
S-06-01	Inexpressible I.	Skin/fur	OS-59683	2300 ± 30	968 ± 146	-25.2
S-06-02	Inexpressible I.	Skin/fur	OS-59759	2080 ± 30	767 ± 140	-23.7
S-06-03	Inexpressible I.	Skin/fur	OS-59577	1820 ± 25	521 ± 100	-21.8
S-06-04	Inexpressible I.	Skin/fur	OS-59704	2790 ± 30	1622 ± 92	-24.8
S-06-06	Inexpressible I.	Skin/fur	OS-59760	4010 ± 35	3035 ± 162	-25.3
S-06-07	Inexpressible I.	Skin/fur	OS-59761	1760 ± 30	479 ± 45	-26.7
"	Inexpressible I.	Skin/fur	AA-52683	1866 ± 36	562 ± 49	-22.4
S-06-08	Inexpressible I.	Skin/fur	OS-59686	4130 ± 35	3187 ± 160	-26.2
S-06-09	Inexpressible I.	Skin/fur	OS-59762	2390 ± 30	1070 ± 156	-27.4
S-06-10	Inexpressible I.	Skin/fur	OS-59673	1700 ± 30	436 ± 58	-22.9
"	Inexpressible I.	Skin/fur	AA-52676	1566 ± 37	396 ± 108	-19.2
S-06-11	Inexpressible I.	Skin/fur	OS-59764	2060 ± 25	756 ± 140	-31.0
S-06-12	Inexpressible I.	Skin/fur	OS-59765	1780 ± 35	493 ± 47	-28.3
S-06-13A	Inexpressible I.	Skin/fur	OS-59684	1810 ± 25	513 ± 44	-25.4
S-06-14	Inexpressible I.	Skin/fur	OS-59741	1800 ± 30	506 ± 45	-24.7
S-06-15	Inexpressible I.	Skin/fur	OS-59729	2030 ± 30	720 ± 130	-26.9
"	Inexpressible I.	Skin/fur	AA-52680	1884 ± 35	573 ± 48	-30.8
S-06-17	Inexpressible I.	Skin/fur	OS-59742	2800 ± 30	1632 ± 93	-29.2
S-06-18	Inexpressible I.	Skin/fur	OS-59766	3180 ± 25	2038 ± 93	-24.7
S-06-19	Inexpressible I.	Skin/fur	OS-66773	3920 ± 35	2997 ± 144	-23.6
S-06-20	Inexpressible I.	Skin/fur	OS-66774	2630 ± 25	1439 ± 81	-27.7
S-06-21	Inexpressible I.	Skin/fur	OS-66805	2410 ± 25	1082 ± 154	-19.4
S-06-22	Inexpressible I.	Skin/fur	OS-59767	2470 ± 35	1126 ± 155	-25.8
S-06-23	Inexpressible I.	Skin/fur	OS-59739	3020 ± 25	1854 ± 89	-26.4
S-06-24	Inexpressible I.	Skin/fur	OS-59792	1520 ± 30	245 ± 69	-20.8
S-06-25	Inexpressible I.	-	-	-	-	-
S-06-30	Inexpressible I.	Skin/fur	OS-59793	1970 ± 35	632 ± 42 (85%)	-23.0
S-06-31	Inexpressible I.	Skin/fur	OS-59794	2830 ± 40	1677 ± 100	-24.8
S-06-32	Inexpressible I.	Skin/fur	OS-66775	4200 ± 30	3274 ± 158	-26.0
S-06-33	Inexpressible I.	Skin/fur	OS-66748	4100 ± 30	3105 ± 110	-24.4
S-06-34	Inexpressible I.	-	-	-	-	-
S-06-36	Inexpressible I.	Skin/fur	OS-59735	2430 ± 30	1100 ± 154	-24.9
S-06-49	Inexpressible I.	Skin/fur	OS-66749	4170 ± 30	3227 ± 158	-25.1
01-B2	Inexpressible I.	Skin/fur	AA-52678	2469 ± 27	1126 ± 154	-27.8
01-B3	Inexpressible I.	Bone	OS-68027	2460 ± 25	1120 ± 153	-19.4
01-B4*	Inexpressible I.	-	-	-	-	-
CRoss	Cape Ross	Bone	OS-68028	4620 ± 45	4085 ± 95	-19.1
CRS-1*	Cape Roberts	Bone	OS-68026	2090 ± 25	773 ± 139	-20.7
CRS-3*	Cape Roberts	-	-	-	-	-
CRS-5*	Cape Roberts	Skin/fur	OS-66750	3550 ± 30	2568 ± 135	-26.3
CRS-7	Cape Roberts	Dentin	OS-68029	5460 ± 30	4945 ± 178	-17.0
MVC-13-24	Cape Roberts	Skin	OS-111998	1880 ± 160	3070 ± 25	-28.1
DIS-01	Dunlop I.	Tendon	AA-72484	3892 ± 36	2964 ± 143	-28.7
00-54	Marble Pt	Skin/fur	AA-42245	3258 ± 42	2162 ± 106	-28.1
MCZ 49641†	Marble Pt.	-	L-627†	5650 ± 150	5088 ± 217	-

Table 1. (Continued)

Sample	Location	Material Dated	Lab. Number	^{14}C age ($\pm 1\sigma$) (^{14}C yr BP)	Calibrated age ($\pm 1\sigma$) (calendar yr BP)	$\delta^{13}\text{C}$ (‰)
<i>Weddell</i>						
S-06-05	Inexpressible I.	Skin/fur	OS-74977	1870 ± 35	637 ± 107	-21.8
S-06-37*	Inexpressible I.	Skin/fur	OS-75009	1800 ± 35	589 ± 96	-25.4
<i>Unknown</i>						
S-06-39*	Inexpressible I.	Skin/fur	OS-75010	1820 ± 30	601 ± 97	-27.8
S-06-41A	Inexpressible I.	Skin/fur	OS-61688	1560 ± 25	319 ± 64	-25.5
S-06-41D	Inexpressible I.	Skin/fur	OS-75011	1320 ± 30	AD 1912	-30.9

Table 2. Criteria for assigning seals to age and sex classes. All measurements in cm. Can., canine; Mesiodist., mesiodistal; Buccoling., buccolingual

Body Length Criteria, based on Figure 5 ¹				
	Body Length			
Pup or Juvenile (< 24 months)	< 230			
Female (>24 months) or young male (24-48 months)	230-310			
Sub-adult and adult males (> 48 months)	> 310			

Skull and Mandible Criteria, based Figures 6A and 6B ²				
	Skull Length	Skull Half-Width	Mandible Length	
Juvenile and pup	< 25	< 9	< 15.5	
Adult female	25 - 33.5	9 - 12	15.5 - 23	
Sub-adult male	33.5 - 42	12 - 14	23 - 30	
Adult male	> 42	>14	> 30	

Dental Criteria, based on Table S3				
	Upper Can. Mesiodist.	Upper Can. Buccoling.	Lower Can. Mesiodist.	Lower Can. Buccoling.
Juvenile and pup	0.90-1.45	0.70-1.20	0.90-1.45	0.70-1.00
Adult female	0.95-1.95	0.80-1.65	1.05-1.20	0.85-1.50
Sub-adult and adult male	>2.10	>1.90	>2.20	>1.70

Post-cranial Element Criteria, based on Bryden (1972) ⁴			
	Female n = 45, total n = 19, >1 yr	Male n = 49, total n = 21, >1 yr	Criteria for ID as male
Body length	120 - 270 cm	125 - 470 cm	see above
Skull length	19.9 - 31.0 cm	20.3 - 43.4 cm	see above
Humerus length	9.2 - 19.7 cm	9.5 - 27 cm	> 21 cm
Radius length	10.2 - 20.6 cm	10.8 - 26.9 cm	> 22 cm
Ulna length	12.1 - 24.0 cm	12.4 - 29.6 cm	> 25 cm
Femur length	5.1 - 11.4 cm	5.2 - 16.4 cm	> 13 cm
Tibia length	12.9 - 29.5 cm	13.4 - 36.5 cm	> 31 cm

¹Criteria are based on the South Georgia population. The separation of young males/young-to-adult females from sub-adult/adult males was set using the asymptotic length for females in 1988-90, which is larger than that for all females but single outlier.

²For skull metrics, the separation of females from sub-adult males was placed at the mid-point between the largest female and the smallest sub-adult male. For mandible length, there is slight overlap between females and the smallest sub-adult male, so we set the separation slightly greater than the value for the largest female.

³Juveniles and females cannot be distinguished. The separation of females from males was placed at the smallest observed size for males

⁴Criteria are set by rounding up from the largest length observed for females by Bryden (1972) and adding 1 cm.

Table 3. Measurements used to assess age and sex of elephant seal carcasses. Criteria for age and sex assignments are presented in Table 3. Measurements in bold are so large they must be males. Measurements in italics may be males but we lack adequate comparative materials to confirm this assignment. L, length; W, width; HW, half-width; ad, adult; sub, sub-adult; y, young; J-P, juvenile or pup; M, male; F, female; STL, straight-line nose-to-tail length; Mand, mandible; Upr, upper; Lwr, lower; Can, canine; Hum, humerus; Rad, radius; Fem, femur.

Specimen	Sex	Age	Body STL	Skull L	Skull HW	Mand L	Upr Can M/B	Lwr Can M/B	Hum L	Ulna L	Rad L	Fem L	Tibia L	Comments
<i>Inexpressible Island</i>														
S-06-01	<i>M</i>	<i>ad</i>	-	-	-	-	-	-	-	-	-	-	-	Neck and part of skull, cervicals > any fossil adM
S-06-02	M	sub	260	-	12	-	-	2.3/1.8	25	-	-	-	39	Carcass
S-06-03	M	sub	290	-	13	27	-	3.3/2.1	30	-	29	-	39	Carcass
S-06-04	?	?	-	-	-	-	-	-	-	-	-	-	-	Neck and basicranium
S-06-06	?	?	-	-	-	-	-	-	-	-	-	-	-	Mummified skin fragment
S-06-07	M	ad	364	47	17	-	-	-	-	> 29	30	-	-	Carcass; proboscis
S-06-08	<i>M</i>	<i>ad</i>	-	-	-	-	-	-	-	-	-	-	-	Flipper; radius, ulna width ≥ fossil adM
S-06-09	M	sub	~230	-	-	> 26	-	-	-	-	-	-	-	Partial carcass
S-06-10	M	ad-sub	279	-	> 16	28	-	-	22	-	25	-	34.5	Carcass
S-06-11	M	ad	326	-	-	35	-	3.5/2.5	29	-	26	-	> 35	Carcass
S-06-12	M	ad	358	53	16	-	4.0/3.0	-	28.5	35	-	17.5	34	Carcass
S-06-13	M	ad	-	51	20	42	-	-	-	-	-	-	42	Head, neck, pelvis, flippers; baculum
S-06-14	M	ad	351	46	-	-	> 3/3.0	-	-	-	-	-	-	Carcass
S-06-15	M	ad	>280	46	16	-	-/ 3.0	-	-	-	-	-	-	Partial carcass
S-06-17	M	ad	-	-	-	-	-	-	-	-	-	-	-	Head skin; proboscis
S-06-18	M	ad	-	-	-	-	-	-	28	-	-	-	-	Flipper
S-06-19	?	?	-	-	-	-	-	-	-	-	-	-	-	Mummified skin with attached bone fragments
S-06-20	F-M yM-adF		-	-	-	-	-	-	-	-	-	-	>21	Partial carcass; measurements small relative to subM
S-06-21	?	?	-	-	-	-	-	-	-	-	-	-	-	Broken tibia
S-06-22	M	ad	-	-	-	36	-	4.0/3.0	-	-	-	-	-	Partial skull, mandible, and neck
S-06-23	?	?	-	-	-	-	-	-	-	-	-	-	-	Skull fragment
S-06-24	<i>F-M yM-adF</i>		-	-	-	-	-	-	-	-	-	-	-	Neck and part of skull; cervicals ≤ fossil subM
S-06-25	?		-	-	-	-	-	-	-	-	-	-	-	Mummified skin fragment
S-06-30	M	sub	265	35	-	-	-	-	-	-	-	-	-	Carcass
S-06-31	M	sub	>205	-	-	28	-	-/ 2.7	-	-	-	-	-	Partial carcass
S-06-32	?	?	-	-	-	-	-	-	-	-	-	-	-	Mummified skin fragment
S-06-33	?	?	-	-	-	-	-	-	-	-	-	-	-	Mummified skin fragment
S-06-34	?	?	-	-	-	-	-	-	-	-	-	-	-	Maxilla and neck
S-06-36	M	ad	264	-	19	34.5	-	3.3/2.8	30	-	-	-	40	Carcass
S-06-49	?	?	-	-	-	-	-	-	-	-	-	-	-	Mummified skin fragment
01-B2	M	ad	> 350	-	-	-	-	-	-	-	-	-	-	Head to pelvis only; proboscis present
01-B3	?	?	-	-	-	-	-	-	-	-	-	-	-	Carcass
01-B4	J-P		~190	-	-	-	-	-	~10	-	-	-	-	Pup carcass

Table 3. (Continued)

Specimen	Sex	Age	Body STL	Skull L	Skull HW	Mand L	Upr Can M/B	Lwr Can M/B	Hum L	Ulna L	Rad L	Fem L	Tibia L	Comments
<i>Cape Ross</i>														
CRoss	M	ad-sub	-	-	-	-	-	-	25.7	-	-	-	-	Disarticulated skeleton
<i>Cape Roberts</i>														
CRS-1	J-P		-	-	-	~7	-	-	-	-	-	-	-	Fragile incomplete mandible
CRS-3	J-P		-	-	-	15.2	-	-	-	-	-	-	-	Incomplete mandible
CRS-5	J-P		<150	-	-	-	-	-	-	-	-	5.8	14.4	Mostly complete carcass; skull broken
CRS-7	M	ad	-	-	-	-	-	3.4/2.7	-	-	-	-	-	2 canines
MVC-13-24	M	ad-sub	>250	-	-	-	-	-	20.5	-	-	13.5	35	Partial carcass, exposed by retreating glacier
<i>Dunlop Island</i>														
DIS-01	M	ad	-	49	19	33.9	-	3.4/2.6	32	30.4		15	38.4	Carcass; proboscis
<i>Marble Point</i>														
00-54	M	ad	-	-	-	34.3	-	-	-	-	-	-	-	Nearly complete buried carcass
MCZ 49641	M	sub	-	-	-	28.6	-	-	-	-	-	-	-	Skeletal parts

SUPPORTING INFORMATION

The following supporting information is available for this article online

at <http://onlinelibrary.wiley.com/doi/10.1111/mms.12581/supinfo>. Appendix S1. Table S1. Location data for seals in this study. Table S2. Modern elephant seal skeletal measurements. Table S3. Criteria for assigning seals to sex and age classes. Table S4. Fossil seal skeletal measurements. Figure S1. Mandible lengths for modern and fossil southern elephant seals. Measurement of mandible length is described in Table S2.

Figure S2. Canine size measurements for modern and fossil southern elephant seals. Measurements of mediobuccal and buccolingual length (proxies for tooth cross sectional area) were made with calipers at the widest available position on the canine. Dimension for upper and lower teeth are similar, and so are plotted on the same figure. Fossils lacking mesiodistal length are plotted at 0 cm.

Figure S3. Mid-point rooted Bayesian phylogenetic tree of all VLC (including mummified and skeletal remains) and extant breeding colony haplotypes (from de Bruyn et al. 2009). VLC and Macquarie samples are shaded in gray, with mummified/skeletal VLC remains illustrated in red, while all other extant breeding colonies are shown above (unshaded). The tree is consistent with a lack of genetic structuring in the ancient (VLC and mummies) samples. Scale bar is genetic distance.