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Postglacial Recolonization of the Southern Ocean by Elephant Seals Occurred From Multiple Glacial Refugia

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ABSTRACT

The Southern Ocean is warming more rapidly than other parts of our planet. How this region's endemic biodiversity will respond to such changes can be illuminated by studying past events through genetic analyses of time-series data sets, including historic and fossil remains. Archaeological and subfossil remains show that the southern elephant seal (*Mirounga leonina*) was common along the coasts of Australia and New Zealand in the recent past. This species is now mostly confined to sub-Antarctic islands and the southern tip of South America. We analyzed ancient seal samples from Australia (Tasmania), New Zealand and the Antarctic mainland to examine how southern elephant seals have responded to a changing climate and anthropogenic pressures during the Holocene. Our analyses show that these seals formed part of a broader Australasian lineage, comprising seals from all sampled locations from the south Pacific sector of the Southern Ocean. Our study demonstrates that southern elephant seal populations have dynamically altered both range and population sizes under climatic and human pressures over surprisingly short evolutionary timeframes for such a large, long-lived mammal.

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1 | Introduction

Polar and sub-polar species are particularly vulnerable to the impacts of global climate change because of their specialized habitats and the rapid warming experienced at high latitudes. The Arctic and Antarctic regions are warming at rates significantly higher than the global average, leading to drastic reductions in sea ice cover, altered food web dynamics and shifts in species distributions (Hoegh-Guldberg and Bruno 2010; Cole et al. 2019). Species such as polar bears (*Ursus maritimus*), Adélie penguins (*Pygoscelis adeliae*) and Antarctic krill (*Euphausia superba*) have shown variable responses to these environmental changes, including range shifts, changes in population size and altered breeding patterns (Fraser et al. 2012; Vianna et al. 2020). Characterizing the resilience and adaptability of these species is critical for understanding broader ecosystem responses to warming climates. Studying how polar and sub-polar fauna have historically responded to past climate change, through genetic and archaeological evidence, can provide valuable insights into their potential future responses and guide conservation efforts in rapidly changing environments (Fraser et al. 2009; Gonzalez-Wevar et al. 2018).

Top predators play a critical role in the Antarctic ecosystem, yet are highly vulnerable to the impacts of climate change on any or all parts of the food chain and the physical environment (e.g., Cole et al. 2019; Vianna et al. 2020). Southern elephant seals (*Mirounga leonina*) are a key species to test for the impacts of climate change and human impact due to the geographic and temporal range of individuals in the Late Quaternary. The southern elephant seal plays a key role in the Antarctic ecosystem. The largest pinniped and the largest non-cetacean marine mammal, southern elephant seals are apex predators that consume massive amounts of biomass to maintain their ~4000 kg bulk (males) during a nine-month foraging period (Gales et al. 1989; McMahon et al. 2005). This species inhabits a region that is undergoing rapid climate change—the sub-Antarctic and the Southern Ocean (Hoegh-Guldberg and Bruno 2010). The present-day population is split into four major breeding 'stocks' distributed in and around the Southern Ocean: the South Georgia and Península Valdés stocks, both located in the Atlantic Ocean sector; the Kerguelen and Heard Islands stock, in the Indian Ocean sector; and the Macquarie Island stock in the Pacific Ocean sector (Figure 1). About 98% of the global population of southern elephant seals breed in these locations (McMahon et al. 2005).

The population at Península Valdés may have been founded within the last 6000 years (Hoelzel et al. 2001) and has been steadily increasing over the last century (Ferrari et al. 2013),

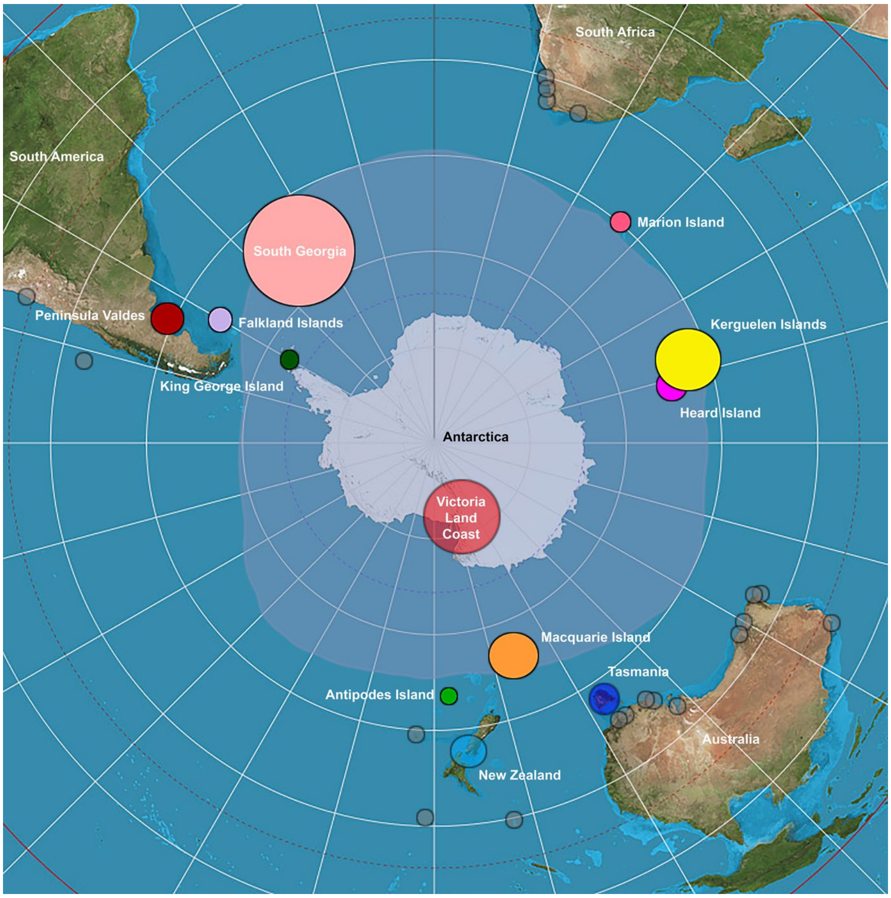

FIGURE 1 | Map of known extant and extinct southern elephant seal (*Mirounga leonina*) distribution. Marker size is representative of the relative number of seals at each location. The map shows extant breeding colonies (solid coloured circles), ancient extinct seal populations sampled for this study (opaque coloured circles: Victoria Land Coast; Tasmania; New Zealand), and ancient extinct seal populations not sampled in this study (opaque grey coloured circles). The opaque blue-grey colouring around Antarctica is the putative (see text) Last Glacial Maximum sea ice extent. Map lines delineate study areas and do not necessarily depict accepted national boundaries.

contrary to historical records that suggest it was founded circa the 1940s (van den Hoff et al. 2014). The South Georgia stock, and Kerguelen and Heard Island stock, have remained relatively stable since the end of industrial sealing (*circa* 1964). In contrast, the Macquarie Island stock has been decreasing for several decades (van den Hoff et al. 2014). The causes of this decline are not entirely clear. Tracking data show that Macquarie Island seals comprise three groups that utilize different foraging zones (Hindell et al. 2017), which appear to be stable through time (Bradshaw et al. 2004): the first group forages mostly in sub-Antarctic waters, the second group largely north of the Ross Sea, and the third group (40% of tracked seals) predominantly along the Wilkes, Oates and Victoria Land Coasts of Antarctica (Hindell et al. 2017). Increasing sea ice along these coastal regions (Hobbs et al. 2016; Hindell et al. 2017) is negatively correlated with population size at Macquarie Island and is a likely contributing factor for the overall population size decline in this breeding stock (Hindell et al. 2017).

Phenotypic differences persist among the four stocks of southern elephant seals, likely due to low levels of (mostly paternal) gene flow. Females from Macquarie Island are smaller than females from South Georgia (Koch et al. 2019) and reach reproductive age later than those in other colonies, and pup weaning weight varies between locations (Burton et al. 1997). This differentiation is thought to result from differences in food availability (McMahon et al. 2005; Fabiani et al. 2006), and the strong philopatry displayed by females (Fabiani et al. 2003). Sexually mature females return annually to the beach on which they were born, while subadult and mature 'bachelor' males may disperse, sometimes over huge distances, until they establish a harem of their own (Fabiani et al. 2003; Chua et al. 2022).

Although southern elephant seals display highly philopatric behaviour, the global population has changed dramatically several times during the late Holocene. In the southern Atlantic Ocean sector, the Península Valdés (Patagonia, Argentina) stock was likely founded during the Late Holocene and now births over 15,000 pups annually (Ferrari et al. 2013). In the Pacific sector of the Southern Ocean, Victoria Land Coast once hosted a southern elephant seal colony that was likely to have been founded around 8000 BP, then declined to extinction beginning approximately 1000 BP in response to a reduction in ice-free habitat (Figure 1) (de Bruyn et al. 2009, 2014). This population expansion and eventual disappearance was probably a direct result of Holocene climate change with southwards and northwards movement, respectively, of circumpolar westerly winds and oceanic fronts and associated temperature changes (Hall et al. 2006, 2023). This now-extinct population showed close genetic affinities with seals from Macquarie Island, the extant major breeding stock also located in the southern Pacific sector (de Bruyn et al. 2009, 2014).

Another putative independent population in the southern Pacific sector is more cryptic. Extensive southern elephant seal remains in Aboriginal middens date back to at least 8000 BP on Tasmania, Australia (Jones 1971). Prehistoric remains of some 300 seals were excavated from West Point Midden on the northwestern coast of Tasmania (Jones 1971) (Figure 2, Figure S1, Table S1), which was occupied between approximately 2000 and 1000 years ago (Jones 1971; Bryden et al. 1999). Extrapolation from the area excavated to the site as a whole suggests a minimum of 3000 individuals, and possibly as many as 6000 individual seals, were deposited at the West Point Midden over this time (Bryden et al. 1999). Analysis of 145 canine teeth (107 females, 38 males, 26% < 3 months old) determined age, sex, seasonal exploitation and reproductive patterns, suggesting that these seals had been procured from a nearby breeding colony (Bryden et al. 1999). There is no evidence of subsequent ongoing exploitation of elephant seals at the site after ~1000 BP, and Bryden et al. (1999) concluded that the nearby breeding colony became extinct at about this time. A breeding colony of southern elephant seals also existed on King Island, located between the Australian mainland and Tasmania, until the early 19th Century when they were exterminated by European sealers (Bryden et al. 1999). In the absence of paleogenetic studies; however, the links between these seals and those from other populations and the four major breeding stocks are unknown.

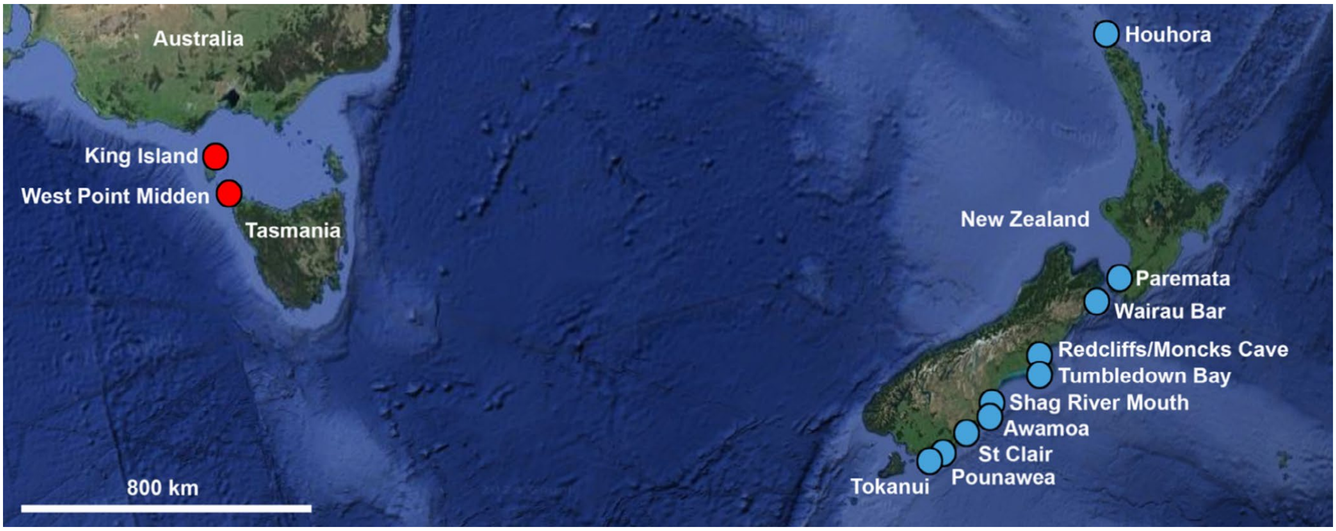

FIGURE 2 | Overview of all Australian (red) and New Zealand (blue) sites from which samples of southern elephant seal (*Mirounga leonina*) were obtained for ancient DNA analysis. Only sites with samples that yielded viable DNA are shown. Map lines delineate study areas and do not necessarily depict accepted national boundaries.

Remains of southern elephant seals have also been found in early Māori (~1250–1450 AD) coastal middens throughout Aotearoa New Zealand in the south Pacific sector (Figure 2, Figure S2, Table S2). This species was a consistent food resource throughout New Zealand (Smith 1985; Challis 1995). Like the seals from Tasmania (West Point and King Island), the remains are of unknown phylogenetic/population affinity. There are fewer remains than at West Point, and their early Māori association suggests that they are at least ~250 years younger than the youngest remains from the Tasmanian sites, that is, < 750 BP (Smith 1985; Challis 1995; Bryden et al. 1999). There is evidence for the exploitation of southern elephant seals in New Zealand as late as 600 BP (Smith 2013). The extant seal colony geographically closest to the New Zealand and Tasmanian mainland is located on the Campbell and Antipodes Islands, 600 and 860 km southeast of southern New Zealand, respectively (and 730 km from each other); again, little is known about these small rookeries. Macquarie Island, around 1500 km south of Tasmania and New Zealand, forms the major extant breeding stock in this south Pacific sector.

To understand how past climate change and more recent human pressures have affected population dynamics in southern elephant seals, we sequenced mitochondrial control regions and complete mitochondrial genomes (mitogenomes) from modern and ancient seals. Population genetic and phylogenetic analyses of these data sets show that extinct and extant seals from the south Pacific sector of the Southern Ocean form a distinct 'Australasian' lineage. Subfossil seal remains indicate that newly available habitat after the Last Glacial Maximum (LGM) allowed a major range expansion of seals. Our genetic results suggest this expansion occurred from multiple glacial refugia. However, much of this diversity was lost as climatic and human pressures have increased over the past millennium, leading to a major contraction in geographic range, population size, and genetic diversity of southern elephant seals.

2 | Materials and Methods

2.1 | Control Region Sequence Analysis

Partial control region (HVR1) sequences were successfully amplified from modern and ancient southern elephant seal samples. A data set with representative sequences from various southern elephant seal populations was constructed. Genetic diversity metrics were calculated, and F_{ST} values were used to measure genetic differentiation. AMOVAs were performed to infer geographic structure. A time-sensitive haplotype network was constructed (Supporting Information).

2.2 | Mitogenome Assembly

DNA extraction was performed on selected ancient southern elephant seal samples for mitochondrial genome assembly. Libraries were prepared, quantified, and enriched using hybridization-capture with bait from a closely related species. PCR amplification and pooling of samples were performed and sequenced using the Illumina MiSeq platform (Supporting Information).

2.3 | Mitogenome Data Processing

Sequence data, including previously unpublished raw sequence data from additional modern and ancient southern elephant seals, were processed using specific scripts to trim adapters, merge overlapping read pairs and filter low-quality reads. The processed reads were mapped to a reference mitochondrial genome using BWA and filtered for quality and duplicates. Consensus sequences were computed, and patterns of post-mortem DNA damage were assessed using MapDamage (Supporting Information).

2.4 | Phylogenetic Analysis of Mitogenome Sequences

Newly generated mitogenome sequences were aligned with the reference southern elephant seal mitogenome (GenBank accession no. NC_008422). We used Bayesian analysis in BEAST v1.8.2 (Suchard et al. 2018) to compare three models of post-mortem sequence damage: no damage, age-dependent damage, and age-independent damage (Ho et al. 2007; Rambaut et al. 2009). Models were compared using marginal likelihoods estimated by stepping-stone sampling (Xie et al. 2010). Posterior distributions of parameters were estimated using Markov Chain Monte Carlo sampling over 75 million steps, with samples drawn every 10^4 steps.

To infer a dated phylogenetic tree, we performed a Bayesian molecular dating analysis in BEAST. We used a skyride coalescent tree prior (for species with a dynamic population history) and a strict molecular clock, selected by comparison of marginal likelihoods calculated by stepping-stone sampling. Estimates of node times were calibrated using the sample dates for the ancient Tasmanian, New Zealand and Victoria Land Coast southern elephant seal sequences. We also fixed the mutation rate of HVR1 based on an estimate from a previous study of the southern elephant seal (de Bruyn et al. 2009). Posterior distributions of parameters were estimated using Markov Chain Monte Carlo sampling over 75 million steps, with samples drawn every 10^4 steps. We ran the analysis in duplicate to check for convergence and combined the samples after discarding the first 10% as burn-in. Sufficient sampling was confirmed by inspecting the samples in Tracer v1.7.1 (Rambaut et al. 2018).

3 | Results

3.1 | Global Population Genetic Structure in the Southern Elephant Seal

We first assessed the global population genetic structure of extant and ancient southern elephant seals using various summary statistics (Table 1), AMOVA, and temporally aware network analysis of mitochondrial control region sequences (Figure 3). These findings recapitulate previous results that split southern elephant seals into two major groups (AMOVA among groups: 35.9% variation, $p < 0.05$; among populations within groups: 14.4%, $p < 0.05$; within populations: 49.7%, $p < 0.05$): an 'Australasian' lineage that includes seals from Macquarie Island

TABLE 1 | Nucleotide diversity statistics for the mitochondrial control region (HVR1) from populations of the southern elephant seal (*Mirounga leonina*). n = sample size, S = number of segregating sites, k = average number of differences, Hd = haplotype diversity, πJC = Jukes-Cantor corrected nucleotide diversity, S/k = expansion coefficient.

	n	***S***	***k***	***Hd***	***πJC***	***S/k***
Elephant Island	32	15	3.815	0.921	0.0277	3.932
King George Island	25	18	3.833	0.980	0.0278	4.696
Antipodes Island	5	5	2.200	0.800	0.0159	2.273
Península Valdés	76	2	0.154	0.768	0.0011	13.014
Falkland Islands	70	18	3.888	0.882	0.0283	4.630
South Georgia	56	18	3.981	0.921	0.0289	4.522
Macquarie Island	64	40	5.141	0.843	0.0394	7.781
Heard Island	6	7	2.733	0.867	0.0198	2.561
Marion Island	47	18	3.587	0.942	0.0260	5.018
Victoria Land Coast	224	41	3.006	0.934	0.0217	13.639
Tasmania	5	3	1.200	0.400	0.0086	2.500
New Zealand	27	16	3.436	0.940	0.0244	4.657

and the now-extinct Victoria Land Coast population (both Pacific Ocean sector); and a lineage that includes the other extant populations (Falkland Islands, Elephant Island, Heard Island, Marion Island, South Georgia Island, King George Island and Península Valdés) (Hoelzel et al. 1993; Slade et al. 1998; Fabiani et al. 2003; Chauke 2008; de Bruyn et al. 2009; Bogdanowicz et al. 2013; Corrigan et al. 2016). Within the latter group, finer-scale subdivision, while limited, does reflect to some degree the currently described breeding stocks: the South Georgia and Península Valdés stocks (Atlantic Ocean sector) and the Kerguelen and Heard Islands stock (Indian Ocean sector) (Figure 3). The seals in our expanded data set, which includes modern samples from the Antipodes Islands and ancient samples from Tasmania (West Point Midden and King Island) and New Zealand, grouped with seals from Macquarie Island and Victoria Land Coast in the Australasian lineage in the Pacific Ocean sector, as expected based on geography (Figures 1–3).

3.2 | Genetic Diversity and Differentiation Among Australasian Seals

To examine relationships among seals from the Australasian lineage, we conducted further population genetic analyses. The Tasmanian (including King Island) and Victoria Land Coast seals were significantly differentiated from those of all other Australasian locations, and from each other, in pairwise comparisons of control region sequences. Non-significant pairwise comparisons of differentiation were found among Macquarie Island, Antipodes Island and New Zealand (Table S9). The Tasmanian samples appear to show extremely low genetic diversity (Table 1), with the caveat that this was the smallest sample in the data set (n = 5, alongside Antipodes Island). In comparison, the New Zealand samples (n = 27) showed the second-highest haplotype diversity (Hd) after Marion Island and were close to the median for all other diversity measures. The expansion coefficient (S/k) for the samples from Tasmania and Antipodes Island were the two lowest values found across populations. In contrast, values for the Victoria Land Coast (and Península Valdés, currently expanding) were an order of magnitude greater (Table 1). A caveat is that some of the populations included here are sampled across different time points, whereas others are sampled only at the present. In a population undergoing drift, sampling across a broad time range will yield a higher diversity measure in comparison to sampling at any single time point.

3.3 | Ancestry of Ancient Holocene Australasian Southern Elephant Seals

To further understand relationships among the Australasian seals, we sequenced whole mitogenomes from a subset of ancient samples from Victoria Land Coast (n = 3), Tasmania (n = 4) and New Zealand (n = 3), and modern samples from Macquarie Island (n = 12). These sequences were analysed in combination with one previously sequenced mitogenome (Accession no. NC_008422) (Figure 4). Ancient southern elephant seals from New Zealand were most closely related to the extant Macquarie Island and extinct Victoria Land Coast populations. A Victoria Land Coast sample (3530 BP) was the sister lineage to all other individuals in the tree, with the remaining seals forming two groups (Figure 4).

The temporally aware network of control region sequences showed sharing of haplotypes between ancient Victoria Land Coast seals and present-day seals from Macquarie Island and Antipodes Island, between ancient Victoria Land Coast and New Zealand seals, and a single shared haplotype between ancient New Zealand and Tasmanian seals. No haplotypes were shared between ancient Tasmanian and Victoria Land Coast seals, reflecting the significant pairwise comparisons of differentiation for these two locations. Mitogenomes further support the notion that Tasmanian seals were somewhat independent, although nested within the broader Australasian lineage, at least for the three females sampled here (Figure 4).

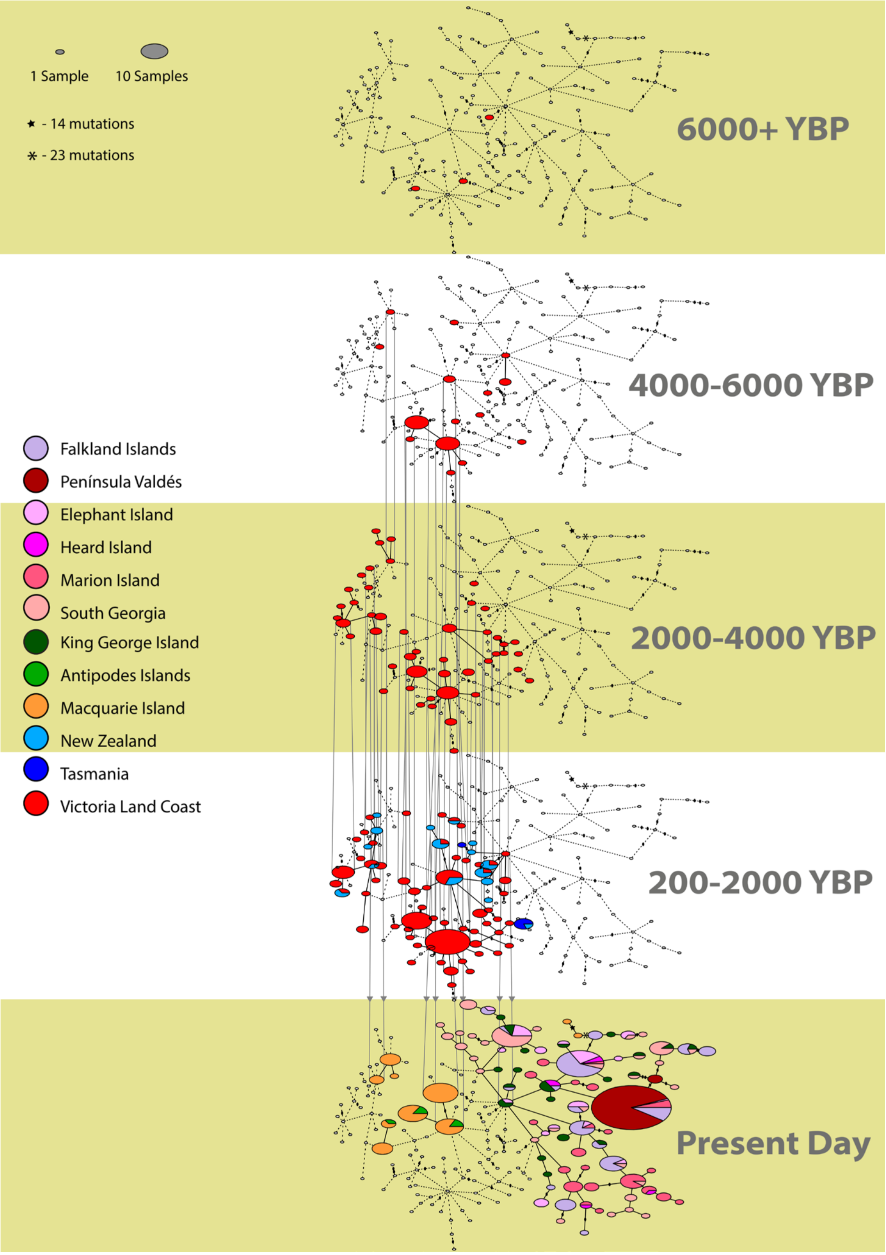

FIGURE 3 | Temporally aware haplotype network showing the relationships among haplotypes of southern elephant seal (*Mirounga leonina*) for five time periods. Haplotypes are represented as ellipses, coloured by location. Ellipse size represents haplotype frequency. Lines link haplotypes separated by one mutation; dots represent additional mutations. Haplotypes absent in any particular timeframe are shown as white ellipses on that layer.

4 | Discussion

4.1 | Archaeological and Genetic Insights Into Australasian Southern Elephant Seals

Confirmed southern elephant seal remains in an archaeological context have been found in coastal midden and occupation sites along the entire New Zealand archipelago, including the Chatham Islands, 800 km east of mainland New Zealand. These findings indicate direct human exploitation of the southern elephant seal for food and personal ornament manufacture by East Polynesian colonists to both New Zealand and the Chatham Islands (Figure S2, Table S2). Coastal archaeological sites along Tasmania (and its associated islands in the Bass Strait) and the western, southern and Victorian regions of the Australian mainland, and Norfolk Island (settled by Polynesians, not indigenous Australians), were also found to have southern elephant seal remains (Figure S1, Tables S1 and S3). Sparse seal remains are present in Africa and South America, as well as a historic population on St Helena, off the coast of West Africa (Table S3). All of these instances, excluding the Victoria Land Coast population that is presumed to have colonised and gone extinct between localised sea-ice retreat and expansion events, 8000–1000 BP (de Bruyn et al. 2009), occur north of the estimated Last Glacial Maximum winter sea-ice extent (from Gersonde et al. 2005; Fraser et al. 2009; Trucchi et al. 2014; Rawlence et al. 2022).

The majority of documented prehistoric remains of southern elephant seals are younger than the Last Glacial Maximum

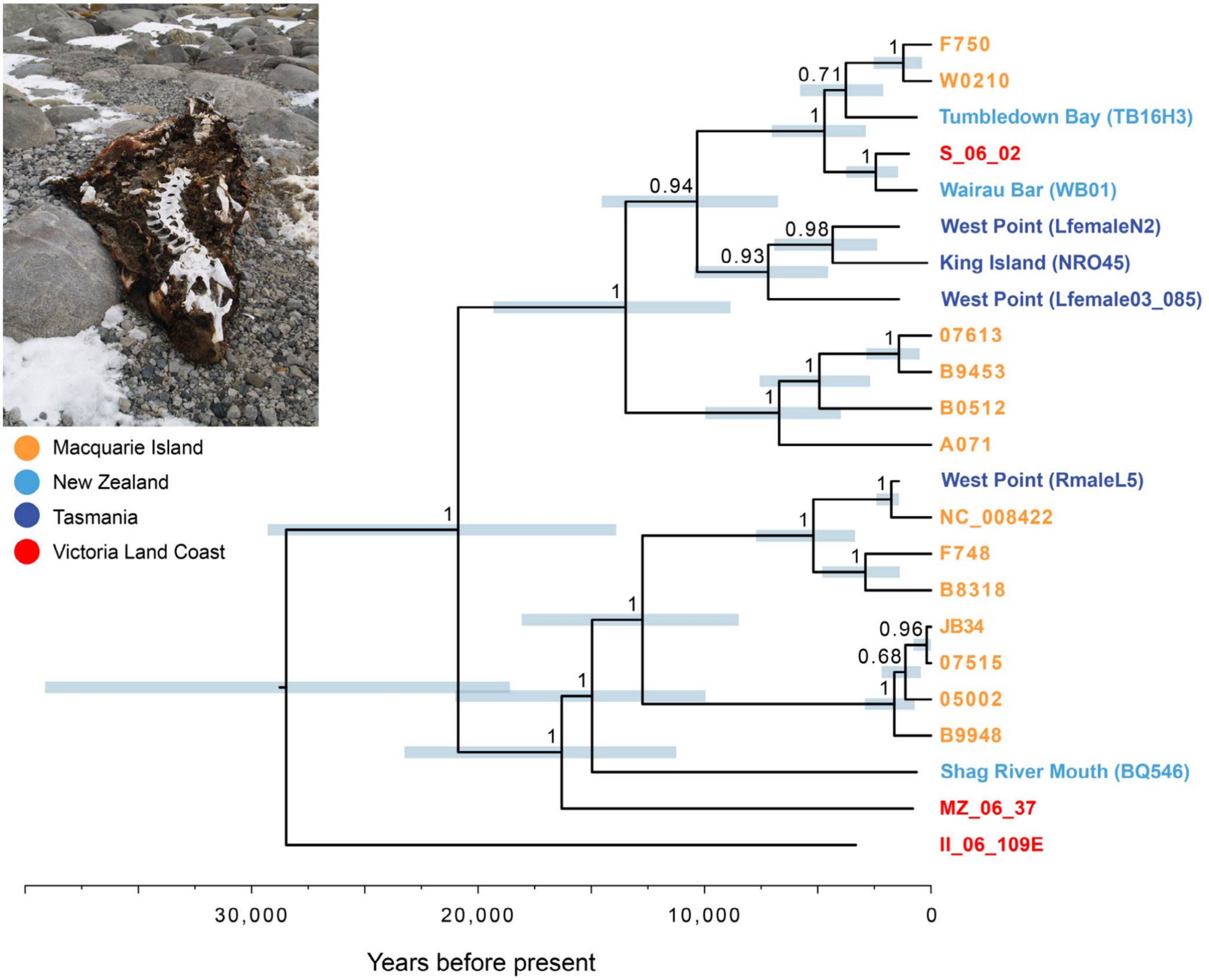

FIGURE 4 | Dated phylogenetic tree from Bayesian analysis of 23 mitochondrial genomes from southern elephant seals (*Mirounga leonina*; 10 ancient & 13 modern seals). Estimates of divergence times were calibrated using the radiocarbon dates of ancient mitochondrial genomes, along with a previous estimate of the mutation rate for the mitochondrial control region (HVR1) (de Bruyn et al. 2009). Light blue bars indicate 95% credibility intervals of age estimates. Nodes are labelled with posterior probabilities. Sex of the individual is shown where known. Inset shows a mummified southern elephant seal, which previously yielded ancient DNA, from the now extinct Victoria Land Coast population (de Bruyn et al. 2009).

(21,000–18,000 BP, Tables S1–S3), the only exceptions being rare moulted skin from the Victoria Land Coast of Antarctica immediately prior to the Last Glacial Maximum (Hall et al. 2023) and late Pleistocene fossils from South America (Valenzuela-Toro et al. 2015) and New Zealand (Boessenecker and Churchill 2016), supporting the hypothesis that these areas acted as glacial refugia. Fossils older than the Pleistocene–Holocene boundary ~10,000 BP and indeed the Last Glacial Maximum are comparatively rare and less likely to be found. The comparatively young age of many of the prehistoric specimens is likely to be a product of older coastal breeding sites being inundated at the end of the Last Glacial Maximum by rising sea levels until ~6000 BP (Lambeck and Nakada 1990). When Antarctic sea ice advanced during the Last Glacial Maximum, it displaced local pagophobic (ice-intolerant) species including the southern elephant seal, causing their ranges to shift northward. When the ice started to recede after the Last Glacial Maximum, new locations were open for exploitation. This is evidenced by the postglacial expansions inferred for many different taxa around Antarctica (Fraser et al. 2009, 2012; Nikula et al. 2010; Gonzalez-Wevar et al. 2018; Rawlence et al. 2022). At the end of the Last Glacial Maximum ~17,500 BP, there was rapid warming of southern mid- to high-latitudes facilitated by southward movement of circumpolar westerly winds and ocean fronts, which would have led to rapid southward range expansions into the sub-Antarctic of marine taxa up to the limit of the retreating sea ice, with Antarctica lagging behind (13,000 BP for the Ross Sea and 8000 BP for Victoria Land Coast).

Our analyses strongly suggest that, at the end of the Last Glacial Maximum, the southern elephant seal had a markedly different breeding range from what is seen today, reaching well into the current temperate zone before expanding deep into the sub-Antarctic and Antarctica during the Holocene, before contracting into the sub-Antarctic due to sealing pressures (Bryden et al. 1999; Thatje et al. 2008). New Zealand, Tasmania and some of the surrounding sub-Antarctic islands, such as Campbell Island, the Auckland Islands and potentially even the Chatham Islands, acted as important ice-free refugia for the Australasian southern elephant seal breeding stock when the current stronghold of Macquarie Island was likely impacted by sea ice during the Last Glacial Maximum (Gersonde et al. 2005; Fraser et al. 2009). The southern reaches of Africa and South America may also have acted as ice-free refugia for populations found now on islands that would have been displaced by encroaching sea ice, such as King George Island, Elephant Island and South Georgia (Hall 2004; Fraser et al. 2009; Rainsley et al. 2019; Rawlence et al. 2022; Rawlence et al. 2024; but see Gersonde et al. 2005; Scott and Turnbull 2019). This hypothesis is potentially supported by the presence of late Pleistocene southern elephant seal remains on these continents (Avery and Klein 2011; Valenzuela-Toro et al. 2015). However, the scarcity of southern elephant seal remains in these areas (see Valenzuela-Toro et al. 2015) is again likely due to sea level changes causing coastal sites to be lost, making their status as breeding populations impossible to verify at this stage.

Temporal comparisons revealed that many ancient samples of southern elephant seals across New Zealand had mitochondrial haplotypes identical to modern samples from Macquarie and Antipodes islands (Figure 3). These findings suggest that the prehistoric New Zealand population was genetically connected to other Australasian lineage populations (*cf. Phocarctos* sea lions; Collins et al. 2013; Collins et al. 2014; Rawlence et al. 2016). Although genetic evidence remains inconclusive about the status of New Zealand as a breeding site, archaeological evidence is somewhat contradictory. The ubiquity and sudden disappearance of elephant seals shortly after human settlement of New Zealand, and their lack of replacement (*cf.* Boessenkool et al. 2009; Collins et al. 2014; Rawlence et al. 2015; Waters et al. 2017) prior to European exploitation of sub-Antarctic populations in the late 18th Century, show a regionally consistent pattern of decline over the entire archipelago (Smith 1989, 1996, 2011; Nagaoka 2000).

All archaeological sites with southern elephant seals in New Zealand have been dated (either through radiocarbon dating or associated cultural assemblage) to ~1250–1450 AD (Table S2), indicating a sudden disappearance of southern elephant seals from the region coincident with the extinction (e.g., moa; Holdaway et al. 2014; Perry et al. 2014; *Phocarctos* sea lions; Collins et al. 2013; Rawlence et al. 2016; Waters et al. 2017; seabirds; Boessenkool et al. 2009; Rawlence et al. 2015b; Rawlence et al. 2017b) and severe range contractions and population bottlenecks (e.g., *Leucocarbo* shags; Rawlence et al. 2015a; *Arctocephalus* fur seals; Ling 1999b; Ling 2002; Salis et al. 2016) seen in terrestrial and marine megafauna. We do not see any evidence for recolonization events (e.g., Boessenkool et al. 2009; Collins et al. 2014). This rapid decline suggests a direct extirpation of mainland breeding populations. Similarly, there is compelling archaeological evidence of former southern elephant seal breeding populations, numbering hundreds or thousands of individuals, including females and pups, on the Tasmanian mainland and King Island (Bryden et al. 1999). On King Island, there is additional historical evidence of a small breeding colony that was exploited to the point of extinction by European sealers (Ling 1999a).

If the New Zealand mainland had been host only to occasional vagrants or moulting individuals from nearby populations (such as those on Campbell Island or Antipodes Islands), we would expect a reasonably constant presence/proportion of southern elephant seals throughout the pre-European and historic archaeological record. The consistent replacement from nearby, unexploited populations would have been similar to the pattern seen in leopard seals (*Hydrurga leptonyx*) (Anderson 1983; Smith 2011, 2013), *Phocarctos* sealions, *Megadyptes* and *Eudyptula* penguins, and *Cygnus* swans (Grosser et al. 2016; Rawlence et al. 2017a; Waters et al. 2017). The shared haplotypes among New Zealand, Antipodes Island, and Macquarie Island may be due to the former two (along with the Campbell Islands) being sea ice-free refuges during the Last Glacial Maximum when many of the sub-Antarctic islands south of the winter Last Glacial Maximum sea ice extent (Macquarie Island potentially included) were covered and/or surrounded in ice (Hall 2004; Fraser et al. 2009; Rainsley et al. 2019; Rawlence et al. 2022; Rawlence et al. 2024; but see Gersonde et al. 2005; Scott and Turnbull 2019). Population range expansion from the New Zealand region to Macquarie Island likely occurred shortly after the sea ice receded, similar to the colonisation of Victoria Land Coast from Macquarie Island inferred by de Bruyn et al. (2009).

When mitochondrial control region sequences for individuals from West Point Midden in Tasmania were compared with other sequences in the global network, they formed a distinct group; female mitogenomes form a similarly distinctive subclade (Figure 4). This inferred presence of a distinct Tasmanian breeding population is further supported by archaeological evidence, where multiple sites with abundant remains, including those of pups, are present along Tasmania's coastline for extended periods (Jones 1971; Bryden et al. 1999). Due to Tasmania's early colonisation by humans by at least 43,000 BP (Gillespie et al. 2012), any coastal geomorphological changes that may have occurred with changes in sea levels must also be taken into account. Rising sea levels since the Last Glacial Maximum may have contributed to many potential older archaeological southern elephant seal butchery sites now being submerged. Tasmanian sea levels began to stabilise ~6000 BP (Lambeck and Nakada 1990), which coincides with the dates of many of the elephant seal butcheries found on the Tasmanian mainland (Jones 1971; Bryden et al. 1999). The perseverance of elephant seal remains in the mainland Tasmanian archaeological record from the mid- to late Holocene (from at least 8000 BP; Jones 1971) might be attributable to, in part, recolonisation from refuge populations inhabiting offshore islands, such as King Island, which would have been isolated from the mainland by 6000 BP. The presence of elephant seal remains on three distinct islands in this region by the Late Holocene (Figure S1, Table S1), including the breeding population exploited by European sealers on King Island (Ling 1999a, 2002), lends credence to the hypothesis that there was at least one healthy offshore population acting as a reservoir for the exploited mainland population(s) during the mid- to late Holocene, ensuring the sustainability of Aboriginal subsistence hunting.

5 | Conclusions

The results of this study contribute to a growing body of evidence that demonstrates how polar and sub-polar species have historically responded to significant environmental changes.

For example, during the Last Glacial Maximum, many species adapted by shifting their ranges to available refugia, as evidenced by genetic data from kelp-dwelling crustaceans and other marine organisms (Fraser et al. 2009; Nikula et al. 2010). These adaptive responses, while showcasing resilience, also highlight the limits of such shifts when combined with anthropogenic pressures. Modern parallels can be drawn from current observations, such as declining populations of polar bears due to shrinking ice habitats and reduced hunting grounds, or changes in penguin breeding success as sea ice patterns alter access to feeding areas (Hindell et al. 2017; Vianna et al. 2020). By understanding the past resilience and vulnerabilities of polar and sub-polar species, conservationists can develop more targeted approaches to support species facing the dual challenges of warming temperatures and human-induced habitat disruption (Hoegh-Guldberg and Bruno 2010; Rawlence et al. 2022).

In conclusion, the Southern Ocean, a region currently undergoing rapid environmental change, prehistoric climate change (associated with the Last Glacial Maximum, Pleistocene–Holocene transition, and regional/local changes in sea ice extent), and human pressures over the past few thousand years in the Pacific sector, substantially altered the distribution of southern elephant seals over short evolutionary timescales. Genetic data, and historic, archaeological, and subfossil remains indicate that a post-Last Glacial Maximum expansion from middle latitude refuges on Australia, New Zealand and perhaps other locations, and sealing-induced contraction from multiple groups of humans have shaped Australasian populations of the southern elephant seal. Analyses of these diverse datasets illuminates the extent of 'dark intraspecific extinction' in a large, well-studied mammalian system; that is, a significant loss of within-species diversity (Figures 3 and 4), and a major reduction in geographic range (Figures 1 and 2), due to human and environmental pressures during the late Holocene.

Author Contributions

Andrew A. Berg: data curation, formal analysis, investigation, methodology, writing – original draft, writing – review and editing. **Megan Askew:** investigation, methodology, writing – original draft, writing – review and editing. **Frederik V. Seersholm:** formal analysis, investigation, writing – review and editing. **Alexander J. F. Verry:** formal analysis, investigation, writing – review and editing. **A. Rus Hoelzel:** conceptualization, formal analysis, methodology, writing – review and editing. **Andreanna Welch:** formal analysis, investigation, writing – review and editing. **Karen Greig:** formal analysis, investigation, writing – review and editing. **Richard Walter:** formal analysis, investigation, writing – review and editing. **Michael Knapp:** formal analysis, investigation, writing – review and editing. **Axel Barlow:** formal analysis, investigation, writing – review and editing. **Johanna L. A. Paijmans:** formal analysis, investigation, writing – review and editing. **Jonathan M. Waters:** conceptualization, formal analysis, funding acquisition, investigation, methodology, project administration, supervision, writing – original draft, writing – review and editing. **Michael Bunce:** formal analysis, investigation, supervision, writing – original draft, writing – review and editing. **Kate McDonald:** formal analysis, investigation, writing – review and editing. **Sue O'Connor:** formal analysis, investigation, resources, writing – review and editing. **Brenda Hall:** conceptualization, formal analysis, investigation, resources, writing – review and editing. **Paul L. Koch:** formal analysis, investigation, writing – review and editing. **Carlo Baroni:** formal analysis, investigation, writing – review and editing. **Maria Cristina Salvatore:** formal analysis, investigation, writing – review and editing. **Patrick Faulkner:** conceptualization, formal analysis, investigation, supervision, writing – review and editing. **Simon Y. W. Ho:** conceptualization, formal analysis, investigation, project administration, supervision, writing – original draft, writing – review and editing. **Nicolas J. Rawlence:** conceptualization, formal analysis, funding acquisition, investigation, methodology, project administration, supervision, writing – original draft, writing – review and editing. **Mark de Bruyn:** conceptualization, formal analysis, funding acquisition, investigation, methodology, project administration, supervision, writing – original draft, writing – review and editing.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

Consensus mitogenome (PQ776891–PQ776911) and control region (PQ773320–PQ773356) sequences have been deposited in GenBank. Sequence alignments have been deposited in DataDryad (https://doi.org/10.5061/dryad.xwdbrv1q9).

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Supporting Information

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