Population differentiation in the context of Holocene climate change for a migratory marine species, the southern elephant seal.

Laura J. Corrigan[1], Anna Fabiani[1,2,3], Lucas F. Chauke[1,4], Clive R. McMahon[5], Mark de Bruyn[1†], Marthán N. Bester[4], Armanda Bastos[4], Claudio Campagna[6], Monica M.C. Muelbert[7], A. Rus Hoelzel[1*]

1) School of Biological and Biomedical Sciences, Durham University, South Road, Durham, DH1 3LE, UK
2) Dipartimento di Biologia, Università degli Studi di Roma Tor Vergata, Roma, Italy
3) Elephant Seal Research Group, Sea Lion Island, Falkland Islands
4) Mammal Research Institute, Department of Zoology and Entomology, University of Pretoria, Private Bag X20, Hatfield, Pretoria 0028, South Africa
5) Sydney Institute of Marine Science, 19 Chowder Bay Road, Mosman NSW, 2088 Australia
6) Wildlife Conservation Soc, Marine Program, RA-1426 Buenos Aires, DF, Argentina
7) Instituto de Oceanografia, Universidade Federal do Rio Grande, Rio Grande - RS, CEP: 96203 – 270, Brasil

† Current address: School of Biological Sciences, Bangor University, Deiniol Road, Bangor, Gwynedd, LL57 2UW, UK

*Correspondence: A. Rus Hoelzel, School of Biological and Biomedical Sciences, Durham University, South Road, Durham DH1 3LE, UK, e-mail: a.r.hoelzel@durham.ac.uk, fax: +44 1913341201

Running head: elephant seal differentiation during Holocene
Key words: population genetics, evolution, Holocene, pinnipeds, molecular ecology

Abstract

Understanding observed patterns of connectivity requires an understanding of the evolutionary processes that determine genetic structure among populations, with the most common models being associated with isolation by distance, allopatry or vicariance. Pinnipeds are annual breeders with the capacity for extensive range overlap during seasonal migrations, establishing the potential for the evolution of isolation by distance. Here we assess the pattern of differentiation among six breeding colonies of the southern elephant seal, *Mirounga leonina,* based on mtDNA and 15 neutral microsatellite DNA markers, and consider measures of their demography and connectivity. We show that all breeding colonies are genetically divergent and that connectivity in this highly mobile pinniped is not strongly associated with geographic distance, but more likely linked to Holocene climate change and demographic processes. Estimates of divergence times between populations were all after the Last Glacial Maximum, and there was evidence for directional migration in a clockwise pattern (with the prevailing current) around the Antarctic. We discuss the mechanisms by which climate change may have contributed to the contemporary genetic structure of southern elephant seal populations and the broader implications.

Introduction

Patterns of population genetic structure generally reflect a combination of contemporary connectivity amongst populations, historical associations and demography. Contemporary connectivity is often correlated with geographic distance, and therefore natural discontinuous populations may show genetic structure that reflects a stepping stone model of isolation by distance (Kimura & Wiess 1964). Such a pattern may be expected in migratory species where different populations have overlapping migratory ranges, providing the opportunity for transfer among proximate populations. This is facilitated by habitats where there are few natural barriers to gene flow, such as in the open oceans. Patterns of genetic structure can also reflect past associations amongst populations, and be influenced by shared ancestry and population demography, such as during colonization events. Contemporary patterns of genetic structure can thereby reflect past demographic changes. Such knowledge is useful in predicting future population changes under scenarios of environmental change (e.g. de Bruyn et al. 2009, Prost et al. 2010).

We investigate these considerations for the southern elephant seal, a migratory marine species with extensive range overlap but high site fidelity to annual breeding sites in sub-Antarctic waters. Annual migrations involve travelling up to several thousand km to and from feeding grounds, often in Antarctic waters (e.g. Jonker & Bester 1998; Bornemann et al. 2000; Bailleul et al. 2007; Tosh et al. 2009), and satellite telemetry has revealed considerable foraging range overlap for seals from different breeding colonies (Biuw et al. 2007). Biuw et al. (2007) tracked foraging seals in the context of environmental variables, and found that improved body condition was associated with following deep water upwelling regions in open water and salinity/ temperature gradients under winter pack ice. Over time relevant oceanic conditions may change or shift location as the environment changes, and this may affect the distribution and dynamics of populations dependent on these conditions (including both predator and prey).

During the Milankovitch climatic cycles of the middle Pleistocene, interglacial periods occurred at a periodicity of approximately every 100,000 years (e.g. Lisiecki & Raymo 2005), associated with termination events that featured rapid climate warming, likely to have reduced the extent of marine ice. In terrestrial environments these cycles were often coupled with changes in the distribution and abundance of animal populations, contracting into refugia (often associated with reduced population size) during glacial periods followed by range expansion during the interglacials (e.g. Hewitt 2000, Hofreiter & Stewart 2009). This type of response to environmental change over the most recent glacial cycle has also been proposed for marine mammal species, such as harbor porpoise (*Phocoena phocoena*, Tolley & Rosel 2006), white-beaked dolphins (*Lagenorhynchus albirostris*, Banguera et al. 2010) and grey seals (*Halichoerus grypus*; Klimova et al. 2014) in the North Atlantic.

For the southern elephant seal (SES) in particular, de Bruyn et al. (2009) found evidence for population abundance and dynamics being impacted by climate cycles over a much shorter time frame, during the Holocene (since ~14K YBP). A now extinct breeding population on the Victoria Land Coast in the Ross Sea was apparently founded when retreating ice released breeding habitat about 8,000 YBP. The new population grew to approximately an order of magnitude greater abundance than the source population at Macquarie Island, and then declined to extinction when the ice returned approximately 1,000 YBP. These inferences were based on genetic data. Extant breeding populations of the SES have a circumpolar distribution among sub-Antarctic islands and one mainland population in Argentina (Figure 1). Results from de Bruyn et al. (2009) showing substantial demographic changes to the Antarctic population in the early to mid-Holocene, raise questions about how the sub-Antarctic breeding populations may have been impacted by these climatic transitions.

This study addresses questions about the influence of climate change by investigating the contemporary population genetic structure of SES using methods that estimate division times, effective population size (Ne) and directional gene flow. Earlier studies based on mark/ recapture and population trends have suggested four regionally distinct population stocks: the South Georgia (SG) stock in the South Atlantic Ocean, the Kerguelen stock in the south Indian Ocean, the Macquarie (MQ) stock in the South Pacific Ocean and the Peninsula Valdés (PV) stock from Argentina (e.g. McMahon et al. 2005). Breeding colonies are distributed non-uniformly due to the discontinuous availability of suitable breeding habitat leading to regionally fragmented population structuring. However, elephant seals are capable of long-range dispersal and therefore theoretically high levels of gene flow (Hindell & McMahon 2000, Fabiani et al. 2003, Reisinger & Bester 2010). At the same time, there is evidence for female philopatry (Fabiani et al. 2006; Hofmeyr et al. 2012), as for other pinnipeds such as Steller's sea lion (Bickham et al. 1996) and the Australian sea lion (Campbell et al 2008). Site fidelity has been recorded in both sexes from mark recapture studies of natural populations, however male and female Southern elephant seals are both capable of traveling long distances, and have been observed migrating distances of up to 6000km from breeding sites to feeding areas (e.g. Bornemann et al. 2000, Hindell & McMahon 2000, Biuw et al. 2007, Muelbert et al. 2013).

Genetic studies have suggested that female elephant seals are more philopatric than males, and provided evidence for male-mediated gene flow (Fabiani et al. 2003, 2006). This has been supported by a mark-recapture study on the Sea Lion Island colony (Fabiani et al. 2006, but see Oosthuizen et al. 2011 for an example of greater female dispersal). Male-biased gene flow is consistent with tagging studies of elephant seals, which have shown that during the non-breeding season males generally disperse further than females (Campagna et al. 1999; Hindell & McMahon 2010; Reisinger & Bester, 2010). Earlier population genetic studies demonstrated distinct mtDNA geographic structuring (e.g. Slade et al. 1998), with the MQ and PV populations representing monophyletic groups. SG and Heard Island (HI; part of the Kerguelen stock) also showed distinct geographic structure despite sharing of some haplotype lineages (Slade et al. 1998). Biparental markers (nDNA loci) displayed much less genetic structure than mtDNA (Slade et al. 1998; Hoelzel et al. 1993, 2001; Fabiani et al. 2003).

Understanding the determinants of population connectivity and how this affects the pattern and level of biodiversity is a core objective in evolutionary biology. In this study we can test hypotheses about biodiversity evolution in the context of good information on behaviour and life history, and with prior knowledge that historical climate change has impacted at least two of the study species' breeding populations. Specifically, we test the hypothesis that population dynamics in the sub-Antarctic as estimated using genetic methods will be correlated to the same climatic events associated with the founding, rapid expansion and subsequent decline of the Ross Sea population in the Antarctic Ocean (de Bruyn et al. 2009, 2014). Further, we test the hypothesis that factors other than isolation by distance (such as population dynamics and environmental change) are important in the evolution of population structure in this species.

Materials and Methods

Study area and sample collection

Adult individuals from six breeding colonies throughout the range of the southern elephant seal were included (Figure 1): South Georgia Island (SG, *n* = 48), Elephant Island (EI, *n* = 46), Sea Lion Island, Falkland Islands (SLI, *n* = 80) all from the putative 'South Georgia' stock (Fabiani et al. 2006), Argentina, representing the 'Peninsula Valdés' stock (PV, *n* = 48; Hoelzel et al. 1999), Marion Island (MI, *n* = 48) from the 'Kerguelen' stock and Macquarie Island (MQ, *n* = 48) from the 'Macquarie' stock. Samples comprised 50% males and females and were collected over one to a few seasons. The chance of including close kin among the adults was shown to be very low in previous studies on kinship at some of the same colonies (Hoelzel et al. 1999, Fabiani et al. 2006). Individuals were initially genotyped at 17 polymorphic microsatellite loci (for details see Table S1). Microsatellite loci were multiplex amplified in 10 µl reactions containing 1 µl of the DNA extract, 10mM Tris-HCl pH 9.0, 1.5 mM $MgCl_2$, 10ng $µl^{-1}$ labelled primer, 0.2 mM each dNTP, and 0.2 units of *Taq* DNA polymerase. Thermocycling conditions were as follows: denaturation at 95 $^{\circ}$C for 15 minutes, 35 cycles of 1.5 minutes at annealing temperature (T^a $^{\circ}$C, Table S1), extension at 72 $^{\circ}$C for 1.5 minutes, and 45 seconds at 94 $^{\circ}$C, and a final extension of 72 $^{\circ}$C for 10 minutes. Forward primers were fluorescent labeled with FAM, HEX or NED. PCR products were electrophoresed on an ABI 3730 Sequencer, and alleles sized using Peak Scanner software (Applied Biosystems).

Linkage, null alleles, and Hardy—Weinberg equilibrium

The presence of null alleles, large allele drop-out and scoring errors were examined using Microchecker v2.2.3 (Van Oosterhout et al. 2004). Deviation from Hardy-Weinburg equilibrium was tested using a method analogous to Fisher's exact test using a modified version of the Markov-chain method (Guo & Thompson 1992), implemented in ARLEQUIN 2.000 (Schneider et al. 2000). Allelic richness for each locus and each population was calculated using the program FSTAT 2.9.3. (Goudet 2001), and differences among populations were tested using a Kruskal-Wallis test. Tests for linkage disequilibrium were carried out for each pair of loci using GENEPOP 3.3 (Raymond & Rousset 2001). The neutrality of microsatellite loci was also confirmed using Lositan (Antau et al. 2008). Lositan was run using a stepwise mutation model for 10,000 iterations with a false discovery rate of 0.05 and confidence limits set to 99%. A first simulation run removed potential selected loci to compute the initial mean F_{ST}. A forced mean F_{ST} was calculated over repeat simulations.

Population structure

Population structure was investigated using Structure 2.3.4 (Pritchard et al. 2000). We conducted 4 independent runs for each *K* between 1 and 7 using the admixture model and correlated allele frequencies. Exploratory Structure runs demonstrated that a burn-in period of 10^5 steps, followed by 10^6 steps of data collection was sufficient to ensure convergence of the MCMC. The highest hierarchical level of structure was assessed using the calculations proposed by Evanno et al. (2005) for ΔK as implemented in Structure Harvester (Earl & vonHoldt 2012).

The levels of differentiation between pairs of populations were also quantified by estimates of pairwise F_{ST} (Weir & Cockerham 1984), in ARLEQUIN v. 3.01 (Excoffier et al. 2005). Statistical significance was calculated by permutation tests with bootstrapping to provide 95 % confidence levels with 1,000 iterations. We tested for correlation between $F_{ST}/(1 - F_{ST})$ and geographical distance using Mantel tests implemented in the isolde extension of GENEPOP (Rousset 2008). Geographic distances were calculated using web tools (http://www.doogal.co.uk/LatLong.php; http://www.geodatasource.com/distance-calculator). Connections measured represented the shortest straight line paths with the exception of the path from MQ, which was direct to Peter 1 Island, south of the Antarctic Peninsula, and then on to EI (since a straight line would have crossed the Antarctic mainland).

The pattern of population differentiation was further assessed by performing a factorial correspondence analysis (FCA) in the program Genetix 4.0 (Belkhir, 1999) using the option that calculates the centre of gravity for each identified population. The use of FCA to analyse genetic data has been described by She et al. (1987).

Detection of Migrants

Sex-biased dispersal was investigated in FSTAT 2.9.3. (Goudet 2001). This test assumes post reproductive sampling and compares results for assessments of female and male datasets separately. It is based on the assumption that the dispersing sex should show weaker assignment to its source population, greater variance in assignment, lower measures of diversity among populations and higher values of diversity within populations (see Favre et al. 1997, Goudet et al. 2002). The ratio of male to female migration rates was estimated after Hedrick et al. (2013) using control region sequence data from de Bruyn et al. (2009) to determine a global F_{ST} for mtDNA (representing the female component of gene flow). Male F_{ST} was estimated based on the global F_{ST} from the microsatellite DNA data, and these values were then incorporated into Hedrick et al.'s formula 7b to estimate the ratio of male to female gene flow. All six populations were included for both microsatellite DNA and mtDNA, and global F_{ST} values were estimated using AMOVA as implemented in Arlequin (Excoffier et al. 2005).

Geneclass 2.0 (Paetkau et al. 2004; Piry et al. 2004) was used to detect first generation migrants using the likelihood-based statistic *Lh/Lmax* where *Lh* is the likelihood of finding a given individual in the population in which it was sampled and *Lmax* is the greatest likelihood amongst all sampled populations. This method is conservative although it can miss true migrants if there are unsampled populations (as in our study). Critical values of *Lh/Lmax* (indicating migrants for values above that threshold) were determined using Bayesian inference (Rannala & Mountain 1997) and resampling (Paetkau et al. 2004). An alpha level of 0.01 was chosen as a compromise between type one and type two errors, as suggested by Paetkau et al. (2004).

Demographic History & directional gene flow

An Isolation-with-Migration model was implemented in IMa (Hey & Nielsen 2004) to investigate the demographic history of pairs of populations. We incorporated both microsatellite and mitochondrial sequence data; approximately 325bp of mitochondrial control region, sequenced as part of a previous study (de Bruyn et al. 2009) was combined with microsatellite data from the present study. The program simultaneously estimates effective population sizes of extant (N_1, N_2) and ancestral (N_A) populations, time of splitting (t) and rates of migration since divergence (m_1, m_2). Model parameter estimates were converted to demographic parameter estimates using a mutation rate of 9.8×10^{-7} substitutions/ site/ year for mtDNA (calculated for this species and locus in de Bruyn et al. 2009), a scalar factor of 0.25, and a generation time of 4 years (based on mean age of first reproduction, see Charlesworth 1994, McMahon et al. 2003, de Bruyn et al. 2009). The mutation rate prior for microsatellite loci was set to 5×10^{-4} mutations/ locus/ year (after Whittaker et al. 2003). For each pair of populations a burn-in of 10^{6} steps and Markov chains of 10^{7} steps were used. Metropolis coupling was implemented using 150 chains and a two-step geometric implement model. At least two initial runs per population pair, with different random seed values, were carried out to ensure consistency of distributions. A version of the program that permits the inclusion of multiple populations (IMa2; Hey 2010a) was not used because the data available did not provide sufficient power to support the analysis (e.g. 73 loci were only marginally adequate for 3 and 4 populations of chimpanzee; Hey 2010b). Instead inference was draw from comparing multiple pairwise comparisons. Although some runs did not reach satisfactory convergence, all those presented did, and a sufficient representation of key comparisons is provided.

Past reductions in population size were analysed using Garza's *M*, a ratio of the number of alleles to the range in allele size (Garza and Williamson 2001). Values of $M < 0.7$ are indicative of historical reductions in population size (Garza and Williamson 2001). The signal for a possible post-bottleneck expansion was investigated using mismatch distributions (Rogers and Harpending 1992) estimated using ARLEQUIN v. 3.01 (Excoffier et al 2005). Estimates of the time (years) of expansion from the mismatch distribution (after Rogers and Harpending 1992) were calculated using the mutation rate, 9.8×10^{-7} s.s.yr^{-1} for mtDNA and a generation time of 4 years. Tajima's *D*

(Tajima 1989) and Fu's *Fs* (Fu 1997) neutrality test statistics were also estimated. All analyses based on mtDNA used the published data from deBruyn et al. (2009).

Results

Genetic diversity

The level of diversity was similar among populations, although *He* and allelic richness were lowest for MQ and PV (Table 1). No evidence of significant linkage disequilibrium (LD) was found ($P<0.05$, after Bonferroni correction) but one locus, PV17, showed evidence of null alleles. Further tests for errors in the data showed no evidence of stuttering or large allele dropout. When individual locations were examined for HWE, PV17 showed significant deviation in every population after Bonferroni correction. This locus was therefore omitted from further analyses. Another locus, LC28, was found to be a strong candidate for positive selection (using LOSITAN). It was therefore removed from further analyses, leaving a dataset of 15 microsatellite loci (details in Table S2). No loci showed evidence for balancing selection.

Population Structure

Pairwise F_{ST} comparisons show significant divergence between all of the sampled breeding colonies (Table 2), though comparisons between SG and either EI or SLI had the lowest values. The signal from Structure was relatively weak with Ln P(X/K) values suggesting a division at K = 3, separating out MQ and PV as most clearly differentiated (Figure 2a). According to the Evanno method (Evanno et al. 2005), K=2 separating MQ from all other populations (Figure 2b). When MQ is omitted, Evanno's 'ΔK'=3, but only two groups are clearly resolved, PV and the rest (Figure 2c). All putative populations apart from MQ show a high proportion of admixed individuals. When the LOCPRIOR function in Structure was applied to the sample set excluding MQ, $\Delta K=3$ distinguishing MI and PV from the rest (Figure 2d). The FCA analysis was used to identify two clusters; PV and MQ, surrounding a third cluster of overlapping individuals from MI, SLI, EI and SG (Figure 3), though MI was also somewhat differentiated from the shared cluster.

Mantel tests were used to explore the relationship between genetic differentiation and geographic distance. In Figure 4 the correlation of ln geographic distance against $F_{ST}/(1-F_{ST})$ for all population pairs is shown, and this was marginally significant ($p = 0.043$). When the comparison between PV and MQ is omitted (outlier point in the upper right of the plot) significance is reduced to $p= 0.058$. When untransformed geographic distance is used instead of log-transformed, there is no difference in the outcome or significance (Figure S1a). In figure 4, the effect of PV is illustrated by showing that for similar geographic distances, comparisons with PV always have a higher F_{ST}. The correlation is no longer significant ($p=0.23$) when MQ is omitted from the comparisons (Figure S1b). The correlation is significant when PV is omitted ($p=0.035$), however the relationship is not linear, with comparisons against MI lower than expected by a linear relationship (Figure S1c). Significance is again lost when both PV and MQ are omitted ($p = 0.15$; Figure S1d).

Detection of Migrants

Multiple IMa runs produced consistent results with good evidence of convergence and high ESS values. Table 3 summarizes the directional migration comparisons among population pairs. While population pairs could not be compared inclusively (some runs did not reach convergence), all three main clusters as represented in the FCA and Structure analyses were well represented among the populations compared. The results reflect average migration rate estimates for the period since an estimated splitting time (Table 4). In each case these estimates were well supported from the posterior distribution data, though sometimes the confidence limits were broad. The pattern of migration indicated in IMa was broadly consistent with that indicated from the F_{ST} data (Table 2), though often highly directional. Directionality suggested greater migration out of rather than into the mainland colony (PV), and in every other case there was migration in a clockwise direction around the Antarctic continent (consistent with the direction of the Antarctic Circumpolar Current; see Figure 1).

Geneclass2 identified six individuals as first generation migrants ($P<0.01$) based on the *Lh*/*Lmax* ratio (Table 5). Of the putative migrants identified, five out of six were males. The estimated ratio of male to female gene flow using the method described by Hedrick et al. (2013) was 3.13 (based on a global F_{ST} from the microsatellite DNA data of 0.0296 and a global mtDNA F_{ST} of 0.1039), however the analysis of sex-biased dispersal using FSTAT found no significant differences, though the trend was in the direction of male biased dispersal, and the power of this analysis is low (data not shown).

Demographic History

Splitting time estimates from IMa (Table 4) all suggested divisions since the last glacial maximum (LGM, about 20Ka) and after a period of rapid global warming at Termination 1 (~14Ka, see Lisiecki & Raymo 2005). These estimates of divergence times were based on a mutation rate derived directly from the Holocene southern elephant seal fossil record using BEAST (incorporating ancient DNA; de Bruyn et al. 2009). Ne estimates were very consistent among runs for all populations with the exception of SG, for which the range was broader (Table 4). Garza's M was high (ranging from 0.89 to 0.93) for each putative population providing no evidence for population bottlenecks. None of the Tajima's D values were indicative of expansion, however Fu's Fs was large, negative and highly significant (suggesting expansion) for MI and SG (Table 6). Mismatch distributions were consistent with expansion for MI, SG and PV, but provided less clear support for expansion at the other colonies (though not significantly divergent from the expansion model; Figure S2). Estimates of the time since expansion (from tau) in those mismatch distributions that also showed evidence of expansion from Fu's Fs were again consistent with events occurring after the LGM (Table 6).

Discussion

The evolution of population structure is influenced by the degree of geographic isolation among populations, dispersal behaviour and the effective size of populations. However, each of these factors may vary over time as habitat resources and other environmental factors change. Understanding how past environmental change influenced current patterns of diversity and structure, provides an opportunity to better understand how ongoing changes may affect patterns of biodiversity in the future (e.g. Hoelzel 2010). We interpret our case study of the SES in the context of an earlier study showing changes in habitat use and population dynamics during the Holocene for a now extinct population from the Ross Sea (de Bruyn et al. 2009). Our assessments of structure together with some earlier studies (see Fabiani et al. 2003, de Bruyn et al. 2009) separated out PV and MQ (and to some extent MI), and grouped SG, SLI and EI (see Figures 2&3).

Structure for SES is distinct from that seen for Antarctic fur seals (*Arctocephalus gazella*), found in many of the same breeding habitats, which shows a clearer geographic pattern of differentiation between the Atlantic, Indian and Pacific oceans (Wynen et al. 2000). In the absence of geographic barriers to gene flow for SES, and given high dispersal capacity (e.g. Fabiani et al. 2003), a ‘stepping stone’ model of population structure could have been expected (Kimura & Wiess 1964) leading to a pattern of isolation by distance. However, the relationship among populations is evidently more complex than this. Comparisons with PV consistently showed higher genetic distances for a give geographic distance than for comparisons among other colonies. At the same time, genetic distance was lower than expected for a given geographic distance for comparisons with MI (5,000-7,500km from all neighbours; Figures 1,4 & S1).

A previous study by Slade et al. (1998) also found relatively low differentiation between MI and SG, and suggested this was due to their sharing a breeding colony on the South African mainland during the LGM (and MI seals sometimes travel to South Africa today; Oosthuizen et al. 2011). This would be consistent with the post-LGM estimates of population divergence times identified here (see discussion below). From the demographic data, there is a clear signal for a recent expansion in SG and MI, but less support in other locations (Table 6, Figure S2). This may suggest a demographic history shared by SG and MI.

Isolation between PV and nearby colonies has been established from earlier studies for both genetic and morphological markers (Hoelzel et al. 1993, 2001, Slade et al. 1998). Especially striking is the low mtDNA diversity at PV, and the fact that two haplotypes can be derived from the third by single mutations (Hoelzel et al. 1993). Assuming female isolation since a founder event and using the reasoning proposed in Hoelzel et al. (1993) together with the substitution rate estimated in de Bruyn et al. (2009), this would suggest a founder event approximately 7,000 YBP. At the same time, our study suggests ongoing gene flow mediated by males (based on identified migrants from the Geneclass analysis and directional migration estimated in IMa). Divergent morphology, potentially associated with foraging behaviour (Hoelzel et al. 2001), together with a distinct pattern of foraging range and strategy for PV compared to seals from the island colonies (based on tracking data; Campagna et al. 2006, Biuw et al. 2007) may help explain why PV should remain relatively isolated from the oceanic colonies nearby. The morphological differences were associated with greater proportional hind flipper size in SG where foraging excursions are over larger distances compared to PV (see Hoelzel et al. 2001).

MQ is relatively geographically isolated from other sampled colonies, though a stepping-stone link to MI may be possible through Heard Island or Isles Kerguelen (see Figure 1), consistent with tagging data for modern seals (Bester 1989, Oosthuizen et al. 2011). MQ shows the clearest link to a mainland population, the now extinct population in the Ross Sea, Antarctica (and MQ is apparently the older source population from which the Ross Sea population was founded; de Bruyn et al. 2009, 2014). MQ shows relatively recent signals for division from other colonies (Table 4), while the maximum estimate for other splitting times are all consistently at around the start of the Holocene. This may be related to the connection with the now extinct population in the Ross Sea. de Bruyn et al. (2009) found a signal for Ross Sea animals returning to MQ when the Ross Sea population collapsed at approximately 1000 YBP. It is possible that this influx generated a signal for division between MQ and the rest (though we have data for only two comparisons, against MI and SG).

EI is closer to the Antarctic mainland than the other breeding colonies included in the present study, and the only one within the Antarctic Convergence. Modeling has shown that the Western Antarctic ice sheet at the LGM extended to the continental shelf margin (Denton & Hughes 2002). EI would therefore have been under ice at the LGM and breeding beaches would not have been available until after this time. The retreat of the ice sheet from this part of the continental shelf has been dated to before 14,000 YBP (Banfield & Anderson 1995; Anderson et al. 2002). Therefore the founding of this site must have been after the LGM. The observed profiles from the mismatch distributions for SLI and EI both diverge somewhat from the expansion model (Figure S2), but both have similar tau estimates from that analysis, distinct from all other populations (EI tau = 9.48, CI = 5.07-12.54; SLI tau = 9.69, CI = 3.52-12.83). This may suggest that they share ancestry and demographic histories (as for SG and MI, see above).

De Bruyn et al. (2009, 2014) investigated the founding and extinction of an elephant seal colony in the Ross Sea, Antarctica, timing the founding of that colony to roughly 8 Ka. From a comparative analysis of elephant seal presence and penguin distributions, Hall et al. (2006) suggested a pattern of warming at around 8 Ka, and cooling at around 1 Ka (leading to the loss of elephant seal breeding habitat in the Ross Sea). From our current study, there is a pattern of population division always after the time of proposed climate warming (Table 4). During the LGM the extent of ice cover would have been greater, with summer sea ice extending beyond modern winter sea ice maximums, and winter sea ice likely extending to the Antarctic Polar Front (see CLIMAP 1981, Gersonde et al. 2005). Therefore both SG and MQ may have been surrounded by ice in winter and close to the edge in summer. This may have meant that foraging excursions followed the ice edge predominantly east and west as opposed to the present north, south component now required to reach the ice edge (see Biuw et al. 2007), leading to greater connectivity during the glacial period. It is also possible that some colonies relocated further north during this time, possibly explaining the similar demographic histories of SG and MI if they both retreated to colonies in southern Africa, as previously suggested by Slade et al. (1998). This scenario would fit the consistent signal for population divisions after the LGM when the ice was retreating and foraging trajectories may have become less overlapping.

Our interpretation depends on an accurate substitution rate estimate for the relevant time frame, supporting the divergence time estimates. In our case, this is based on an estimate generated for this species based on time series data using ancient DNA (de Bruyn et al. 2009). The rate we determined in that study was consistent with rates published for various species (see Ho et al. 2007, Lambert et al. 2002) and critically, led to temporal population dynamic and divergence estimates that were consistent with known geologic and climatic events (see discussion in de Bruyn et al. 2009). We infer that our consistent signal for a period of change during the Holocene supports our stated hypotheses, that sub-Antarctic colonies were impacted by the same warming periods as apparently led to the founding of a new population in the Ross Sea, and that the consequent shifts in population dynamics and patterns of connectivity help explain the current pattern of population structure. However, our best supported estimates (rather than the full posterior distribution range) suggest splitting times near the time when the climate was again cooling (around 1,000 YBP). One possible explanation could be a lag in the shift from horizontal (east-west) to more vertical (north-south) migration during the warming period, possibly promoted by a shift in prey distribution as the climate cooled. Another possibility is that analytical biases mean that the true dates are older than our estimates.

Sun et al. (2012) show that human microsatellite DNA mutations tend towards the centre of the allele size distribution, and that this bias may affect divergence time estimates by up to a factor of two compared to a strict stepwise mutation model, though it is not clear if this holds for all species (see Anmarkrud et al. 2008). It is also true that some SES generation time estimates are longer, for example 8 years (Slade et al. 1998), which would double our time divergence estimates per year. Theses biases would mean older dates that we've estimated, however, our division HPD time estimates would remain within a Holocene timeframe, after the period of warming at 8Ka.

The details are unknown, but throughout the period when temperature was warming there would have been the opportunity to exploit new habitat, possibly including the re-colonisation of sub-Antarctic islands from mainland refugia. This process would have likely been facilitated by long distance foraging excursions, enabling the discovery of emergent habitat (see discussion in de Bruyn et al. 2009). Climate change over this period may also have altered oceanographic features, such as currents, frontal systems, and thermal layers which are thought to affect the abundance and availability of prey (e.g. Bost et al. 2009; Biuw et al. 2007; McIntyre et al. 2011, 2014). Melting ice can also increase local oceanic productivity by the release of algal cells and iron trapped in the ice (which accelerates algal growth; Smetacek & Nicol 2005). An impact on population dynamics and connectivity during times of rapid environmental change has also been proposed for other Antarctic species, such as Adelie penguins (*Pygoscelis adeliae*) confined to a single refugium in the Ross Sea during the last glacial maximum (LGM;

Ritchie et al. 2004), and Antarctic fur seals isolated in refugia on the tips of South Africa and South America during the LGM, expanding to colonise areas further south during postglacial warming (Wynen et al. 2000).

Although oceanic current systems likely differed somewhat during the last glacial period (see Fraser et al. 2012), after the LGM there has been a consistent clockwise current associated with the west wind drift (the Antarctic Circumpolar Current) at the latitudes where SES breed (Figure 1). Closer to the continent (within the Antarctic Divergence at 60^o South) the current runs counter-clockwise (the Antarctic Coastal Current). While it may seem unlikely that a highly mobile animal like the elephant seal would be affected by the direction of an oceanic current (though recolonization routes are proposed to follow the direction of the circumpolar current for various other species; see Fraser et al. 2012, potentially including SES prey), all of our directional migration estimates (with the exception of that associated with the Argentine mainland population) indicated migration consistent with the direction of the modern Antarctic circumpolar current.

Taken together these data emphasize the need to consider extant patterns of connectivity in a temporal context, and show how climate change may have broad impact on the evolution of population genetic structure. The complexities of population structure in this study system show the potential for other highly mobile marine species to reveal cryptic population structure, and for climate change to impact that structure by altering patterns of connectivity, promoting founder events, releasing new habitat, and affecting population dynamics.

Acknowledgements:

This research was funded in part by the Office of Polar Programs of the National Science Foundation and the South African National Antarctic Programme (SANAP), through funding from the Department of Science and Technology and the National Research Foundation, supported research at Marion Island, and provided a grantholder-linked MSc bursary to Lucas Chauke. We thank Joanne Stamford and Oliver Pye for lab assistance and Mark Hindell and the Antarctic Wildlife Research Unit, University of Tasmania, for help with the provision of Macquarie Island samples. We thank Filippo Galimberti and Simona Sanvito for field logistics and data collection on Sea Lion Island and the Falkland Islands Development Corporations and Strachan Visick Ltd. for allowing the research on Sea Lion Island.

References

Anderson JB, Shipp SS, Lowe AL, Wellner JS, Mosola AB (2002) The Antarctic Ice Sheet during the Last Glacial Maximum and its subsequent retreat history: a review. *Quaternary Science Reviews* **21**, 49-70

Anmarkrud JA, Kleven O, Bachmann L, Lifjeld T (2008) Microsatellite evolution: mutations, sequence variation, and homoplasy in the hypervariable avian microsatellite locus HrU10. *BMC Evol. Biol.* **8**, 138

Antao TA, Lopes A, Lopes RJ, Beja-Pereira A, Luikart G (2008) LOSITAN: A workbench to detect molecular adaptation based on a Fst-outlier method. *BMC Bioinformatics*, **9**, 323.

Bailleul F, Charrassin JB, Ezraty R, Girard-Ardhuin F, McMahon CR, Field IC, Guinet C (2007) Southern elephant seals from Kerguelen Islands confronted by Antarctic sea ice. Changes in movements and in diving behaviour. *Deep-Sea Research Part II*, **54**, 343–355.

Banfield LA, Anderson JB (1995) Seismic facies investigation of late Quaternary glacial history of Bransfield Basin, Antarctica, American Geophysical Union. *Antarctic Research Series*, **68,** 123–140.

Banguera- Hinestroza E, Bjørge A, Reid RJ, Jepson P, Hoelzel AR (2010) The influence of glacial epochs and habitat dependence on the diversity and phylogeography of a coastal dolphin species: *Lagenorhynchus albirostris*. *Cons. Gen.* **5**, 1823-1836

Belkhir K (1999) Genetix, v. 4.0. Laboratoire Genome, Polpulations, Interactions, CNRS UPR, Montpellier, France.

Bester MN (1989) Movements of southern elephant seals and Subantarctic fur seals in relation to Marion Island. *Mar. Mamm. Sci*. **5**, 257 – 265

Bickham JW, Patton JC, Loughlin TR (1996) High variability for control region sequences in a marine mammal: implications for conservation and biogeography of steller sea lions (*Eumetopias jubatus*). J. Mammal. 77, 95-108

Biuw M, Boehme L, Guinet C, Hindell M, Costa M, Charrassin J-B, Roquet F, Bailleul F, Meredith M, Thorpe S, Tremblay Y, McDonald B, Park Y-H, Rintoul SR, Bindoff N, Goebel M, Crocker D, Lovell P, Nicholson J, Monks F, Fedak MA (2007) Variations in behavior and condition of a Southern Ocean top predator in relation to in situ oceanographic conditions. *PNAS*, **104**, 13705–13710.

Bost CA, Cotté C, Bailleul F, Cherel Y, Charrassin JB, Guinet C, Ainley DG, Weimerskirch H (2009) The importance of oceanographic fronts to marine birds and mammals of the southern oceans. *Journal of Marine Systems* **78**, 363-376

Bornemann H, Kreyscher M, Ramdhor S, Martin T, Carlini A, Sellmann L, Plötz J (2000) Southern elephant seal movements and Antarctic sea ice. *Antarctic Science* **12**, 3 – 15.

Cornuet J-M, Piry S, Luikart G, Estoup A, Solignac M (1999) New methods employing multilocus genotypes to select or exclude populations as origins of individuals. *Genetics,* **153,** 1989-2000.

Campagna C, Fedak MA, McConnell BJ (1999) Post-breeding distribution and diving behavior of adult male southern elephant seals from Patagonia. *Journal of Mammalogy,* **80**, 1341–1352

Campagna C, Piola AR, Marin MR, Lewis M, Fernandez T (2006) Southern elephant seal trajectories, fronts and eddies in the Brazil/ Malvinas confluence. *Deep-Sea Res.* **53**, 1907-1924.

Campbell RA, Gales NJ, Lento GM, Baker CS (2008) Islands in the sea: extreme female natal site fidelity in the Australian Sea Lion, *Neophoca cinerea*. *Biology Letters*, **4**, 139-142.

Charlesworth B (1994). *Evolution in Age-structured Populations*. Cambridge: University of Cambridge Press. pp. 28–30.

CLIMAP (1981) Seasonal reconstructions of the Earth's surface at the last glacial maximum in Map Series, Technical Report MC-36. Boulder, Colorado: Geological Society of America.

de Bruyn M, Hall BL, Chauke LF, Baroni C, Koch PL, Hoelzel AR (2009) Rapid response of a marine mammal species to Holocene climate and habitat change. PLoS Genetics, **5**, e1000554

De Bruyn M, Pinsky M, Hall B, Koch P, Baroni C, Hoelzel AR (2014) Rapid increase in southern elephant seal genetic variation after a founder event. *Proc. Royal Soc. B.* **281**, 1779

Denton DH, Hughes TJ (2002) Reconstructing the Antarctic Ice Sheet at the Last Glacial Maximum. *Quaternary Science Reviews* **21**, 193-202

Earl DA, vonHoldt BM (2012) STRUCTURE HARVESTER: a website and program for visualizing STRUCTURE output and implementing the Evanno method. *Conservation Genetics Resources* **4**, 359-361

Evanno G, Regnaut S, Goudet J (2005) Detecting the number of clusters of individuals using the software STRUCTURE: a simulation study. *Molecular Ecology*, **14**, 2611–2620.

Excoffier L, Laval G, Schneider S (2005) Arlequin ver. 3.0: An integrated software package for population genetics data analysis. *Evol Bioinf Online* **1**, 47–50.

Fabiani A, Hoelzel AR, Galimberti F, Muelbert MMC (2003) Long-range paternal gene flow in the southern elephant seal. *Science*, **31**, 676

Fabiani A, Galimberti F, Sanvito S, Hoelzel AR (2006) Relatedness and site fidelity at the southern elephant seal, *Mirounga leonina*, breeding colony in the Falkland Islands. *Animal Behaviour*, **72**, 617-626.

Favre L, Balloux F, Goudet J (1997) Female-biased dispersal in the monogamous mammal *Crocidura russula*: evidence from field data and microsatellite patterns. *Proc. Roy. Soc. Lond. B Biol. Sci.* **264**: 127-132.

Fraser CI, Nikula R, Ruzzante DE, Waters JM (2012) Poleward bound: biological impacts of Southern Hemisphere glaciation. *TREE* **27**, 462-471

Fu Y-X (1997) Statistical tests of neutrality of mutations against population growth, hitchhiking and background selection. *Genetics* **147**, 915–925

Garza JC, Williamson EG (2001) Detection of reduction in population size using data from microsatellite loci. *Mol. Ecol.* **10**: 305-318

Gersonde R, Abelmann A, Brathauer U, Becquey S, Bianchi C, Cortese G, Grobe H, Kuhn G, Niebler HS, Segl M, Sieger R, Zielinski U, Futterer DK (2003) Last glacial sea surface temperatures and sea-ice extent in the Southrn Ocean (Atlantic-Indian sector): a multiproxy approach. Paleoceonography 18, 1-18

Goudet J (2001) *FSTAT, A program to estimate and test gene diversities and fixation indices. Version 2.9.3.* . http://www.unil.ch/izea/softwares/fstat.html.

Goudet J, Perrin N, Waser P (2002) Tests for sex-biased dispersal using genetic markers. *Mol. Ecol,.* **11**, 1103-1114.

Guo SW, Thompson EA (1992) Performing the exact test of Hardy-Weinberg proportion for multiple alleles. *Biometrics*, **48**, 361-372.

Hall BL, Hoelzel AR, Baroni C, Denton GH, LeBoeuf BJ, Overturf B, Topf AL (2006) Holocene elephant seal distribution implies warmer-than-present climate in the Ross Sea. *PNAS* **103**, 10213-10217

Hedrick PW, Allendorf FW, Baker CS (2013) Estimation of male gene flow from measures of nuclear and female genetic differentiation. *J. Hered.* **104**, 713-717

Hewitt G (2000) The genetic legacy of Quaternary ice ages. Nature 405:907–913

Hey J, Nielsen R (2004) Multilocus methods for estimating population sizes, migration rates and divergence time, with applications to the divergence of *Drosophila pseudoobscura* and *D. persimilis*. *Genetics*, **167**, 747–760.

Hey J (2010a) Isolation with migration models for more than two populations. *Mol. Biol. Evol.* **27**, 905-920.

Hey J (2010b) The divergence of chimpanzee species and subspecies as revealed in multipopulation isolation-with-migration analyses. *Mol. Biol. Evol.* **27**, 921-933.

Hindell MA, McMahon CR (2000) Long distance movement of a southern elephant seal (*Mirounga leonina*) from Macquarie Island to Peter 1 Øy. *Marine Mammal Science*, **16**, 504-507.

Ho SYW, Kolokotronis SO, Allaby RG (2007) Elevated substitution rates estimated from anceint DNA sequences. Biol. Lett. 3, 702-705

Hoelzel AR (2010) Looking backwards to look forwards; Conservation genetics in a changing world. *Con. Gen.* **11**, 655-660

Hoelzel AR, Le Boeuf BJL, Reiter J, Campagna C (1999) Alpha-male paternity in elephant seals. *Behavioral Ecology and Sociobiology*, **46**, 298-306.

Hoelzel AR, Campagna C, Arnbom T (2001) Genetic and morphometric differentiation between island and mainland southern elephant seal populations. *Proc. Roy. Soc. Lond.* B, **268**, 325-332

Hoelzel AR, Halley J, Campagna C, Arnbom T, Le Boeuf BJ, O'Brien SJ, Ralls K, Dover GA (1993) Elephant seal genetic variation and the use of simulation models to investigate historical population bottlenecks. J. Hered, 84, 443-449.

Hofmeyr GJG, Kirkman SP, Pistorius PA, Bester MN (2012) Natal site fidelity by breeding female southern elephant seals in relation to their history of participation in the winter haulout. *African Journal of Marine Science* **34**, 373-382

Hofreiter M and Stewart J (2009) Ecological change, range fluctuations and population dynamics during the Pleistocene. Current Biology, 19, R584-R594

Jonker FC, Bester MN (1998) Seasonal movements and foraging areas of adult southern female elephant seals, *Mirounga leonina*, from Marion Island. *Antarct. Sci.* **10**, 21-30.

Kimura M, Weiss G (1964) The stepping stone model of population structure and the decrease of genetic correlation with distance. *Genetics* **49**, 561-576.

Klimova A, Phillips CD, Fietz K, Olsen MT, Harwood J, Amos W, Hoffman JI (2014) Global population structure and demographic history of the grey seal. *Mol. Ecol.* **23**, 3999-4017

Lambert DM, Ritchie PA, Millar CD, Holland B, Drummond AJ, Baroni C (2002) Rates of evolution in ancient DNA from adelie penguins. Science 295, 2270-2273

Lisiecki LE, Raymo ME (2005) A Pliocene-Pleistocene stack of 57 globally distributed benthic δ18O records. *Paleoceanography* **20**, PA1003.

McIntyre T, Ansorge IJ, Bornemann AH, Plötz J, Tosh CA, Bester MN (2011) Elephant seal dive behaviour is influenced by ocean temperature: implications for climate change impacts on an ocean predator. *Marine Ecology Progress Series* **441**, 257–272.

McIntyre T, Bornemann H, de Bruyn PJN, Reisinger RR, Steinhage D, Márquez MEI, Bester MN, Plötz J (2014) Environmental influences on the at-sea behaviour of a major consumer, *Mirounga leonina*, in a rapidly changing environment. *Polar Research* **33**, 23808

McMahon CR, Burton HR, Bester MN (2003) A demographic comparison of two southern elephant seals populations. *J. Anim. Ecol.* **72**, 61-74

McMahon CR, Bester MN, Burton HR, Hindell MA, Bradshaw CJA (2005) Population status, trends and a re-examination of hypotheses explaining the recent declines of the southern elephant seal *Mirounga leonina*. *Mammal Review*, **35**, 82-100.

Muelbert M MC, Souza RB, Lewis MN, Hindell MA (2013). Foraging habitats of southern elephant seals, Mirounga leonina, from the Northern Antarctic Peninsula. Deep-Sea Res.II 88–89, 47–60.

Oosthuizen WC, Bester MN, Tosh CA, Guinet C, Besson D, De Bruyn PJN (2011) Dispersal and dispersion of southern elephant seals in the Kerguelen Province, Southern Ocean. *Antarctic Science* **23**, 567-577

Paetkau D, Slade R, Burden M, and Estoup A (2004) Genetic assignment methods for the direct, real-time estimation of migration rate: a simulation based exploration of accuracy and power. *Mol. Ecol.*, **13**, 55–65.

Piry S, Alapetite A, Cornuet J-M, Paetkau D, Baudouin L, Estoup A (2004) GENECLASS2: A Software for Genetic Assignment and First-Generation Migrant Detection. *J. Hered*, **95**, 536-539.

Pritchard JK, Stephens M, Donnelly P (2000) Inference of population structure using multilocus genotype data. *Genetics*, **155**, 945-959

Prost S, Smirnov N, Federov VB, Sommer RS, Stiller M, Nagel D, Knapp M, Hofreiter M (2010) Influence of Climate Warming on Arctic Mammals? New Insights from Ancient DNA Studies of the Collared Lemming *Dicrostonyx torquatus. PLoS One* **5**, e10447

Rannala B, Mountain JL (1997) Detecting immigration by using multilocus genotypes. *Proc. Nat. Acad. Sci.*, **94**, 9197–9201.

Raymond M, Rousset F (2001) GENEPOP. Version 3.3: Population Genetics Software for exact tests and ecumenicism.

Reisinger RR, Bester MN (2010) Long distance breeding dispersal of a southern elephant seal. Polar Biology **33,** 1289-1291.

Ritchie PA, Millar CD, Gibb GC, Baroni C, Lambert DM (2004) Ancient DNA Enables Timing of the Pleistocene Origin and Holocene Expansion of Two Adélie Penguin Lineages in Antarctica**.** *Mol. Biol. Evol.*, **21**, 240-248.

Rogers AR, Harpending H (1992) Population growth makes waves in the distribution of pairwise genetic distances. *Mol. Bid. Evol,* **9**, 552-569.

Rousset F (2008) Genepop'007: a complete reimplementation of the Genepop software for Windows and Linux. *Mol. Ecol. Resources* **8**, 103-106.

Schneider S, Roessli D, Excoffier L (2000) Arlequin: a software for population genetics analysis. Vers. 2.000 Genetics and Biometry Lab., Department of Anthropology, University of Geneva.

She JX, Autem M, Kotulas G, Pasteur N, Bonhomme F (1987) Multivariate analysis of genetic exchanges between *Solea aegyptiaca* and *Solea senegalensis* (Teleosts, Soleidae). *Biol. J. Linn. Soc.*, **32**, 357-371.

Slade RW, Moritz C, Hoelzel AR, Burton HR (1998) Molecular population genetics of the southern elephant seal *Mirounga leonina. Genetics*, **149,** 1945-1957.

Smetacek V, Nicol S (2005) Polar ocean ecosystems in a changing world. *Nature* **437**, 362-368

Sun JX, Helgason A, Masson G, Ebenesersdottir SS, Li H, Mallick S, Gnerre S, Patterson N, Kong A, Reich D, Stefansson K (2012) A direct characterisation of human mutation based on microsatellites. *Nature Gen.* **44**, 1161-1165

Tajima F (1989) The effect of change in population size on DNA polymorphism. *Genetics* **123**, 597–601.

Tolley KA, Rosel PE (2006) Population structure and historical demography of eastern North Atlantic harbour porpoises inferred through mtDNA sequences. *Mar. Ecol. Prog. Series* **327**, 297-308.

Tosh C, Bornemann H, Ramdohr S, Schröder M, Martin T, Carlini A, Plötz J, Bester MN (2009) Adult male southern elephant seals from King George Island utilize the Weddell Sea. *Antarct. Sci.* **21**, 113-121.

Van Oosterhout C, Hutchinson WF, Wills DPM, Shipley P (2004) MICROCHECKER: software for identifying and correcting genotyping errors in microsatellite data. *Mol. Ecol. Notes,* **4**, 535-538.

Weir BS, Cockerham CC (1984) Estimating *F*-statistics for the analysis of population structure. *Evolution,* **38**, 1358-1370.

Whittaker JC, Harbord RM, Boxall N, Mackay I, Dawson, Silby RM (2003) Likelihood based estimation of microsatellite mutation rates. *Genetics*, **164**, 781-787.

Wynen LP, Goldsworthy SD, Guinet C, Bester MN, Boyd IL, Giertz I, Hofmeyr GJG, White RWG, Slade R (2000) Postsealing genetic variation and population structure of two species of fur seal (*Arctocephalus gazella* and *A. Tropicalis*). *Molecular Ecology*, **9**, 299-314.

Figure Captions

1) Southern elephant seal distribution in the Southern Ocean (after Fabiani et al.2003). Circles reflect colony size and island names have been abbreviated as follows: SG, South Georgia Island; GOU, Gough Island; BOU, Bouvet Island; MI, Marion Island; CRO, Crozet Islands; KER, Kerguelen Islands; CAM, Campbell Island; FI, Falkland Islands (note that Sea Lion Island, SLI, is associated with FI); PV, Peninsula Valdés; EI, Elephant Island; HD, Heard Island; MQ, Macquarie Island**.** Sampled sites are in black text, all others in grey. Among sampled sites, SG, EI and SLI are from the SG stock, MI is from the Kerguelen stock, PV from the PV stock and MQ from the MQ stock. Modern current systems are illustrated as approximations, with the circumpolar current driven by the west wind drift shown in blue (bold, curved arrows), and the coastal current driven by the west wind drift shown in black (thin straight arrows).

2) Structure results for: a) Ln P(X/K) values indicate a division at K = 3; b) ΔK=2; c) when MQ is omitted, ΔK=3; d) Locprior applied and MQ omitted, K=3.

3) Factorial Correspondence Analysis (FCA) of individual Southern elephant seals.

4) Isolation-by-distance (IBD) relationship between all population pairs. Comparisons with PV highlighted with PV in bold text.

Figure 1:

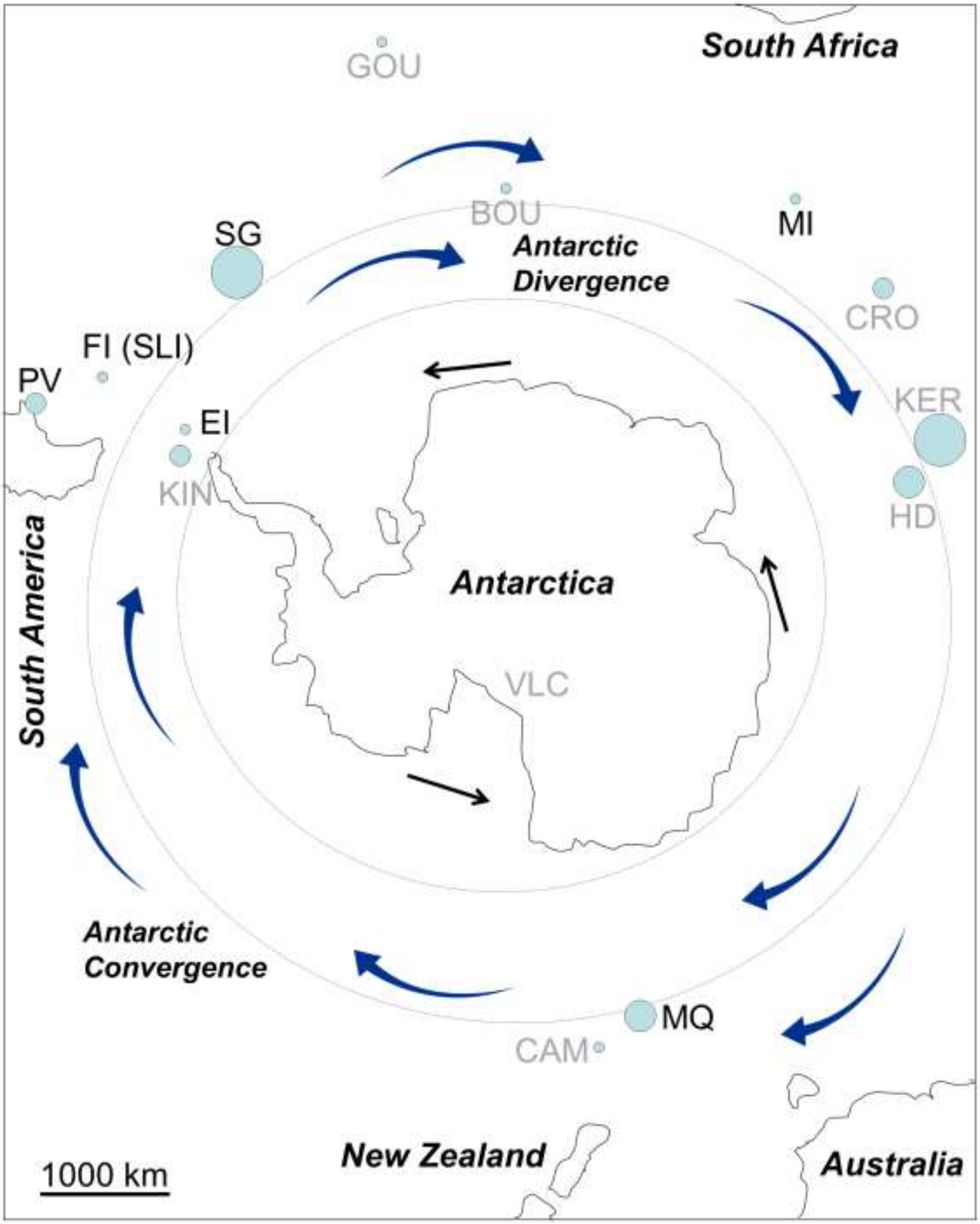
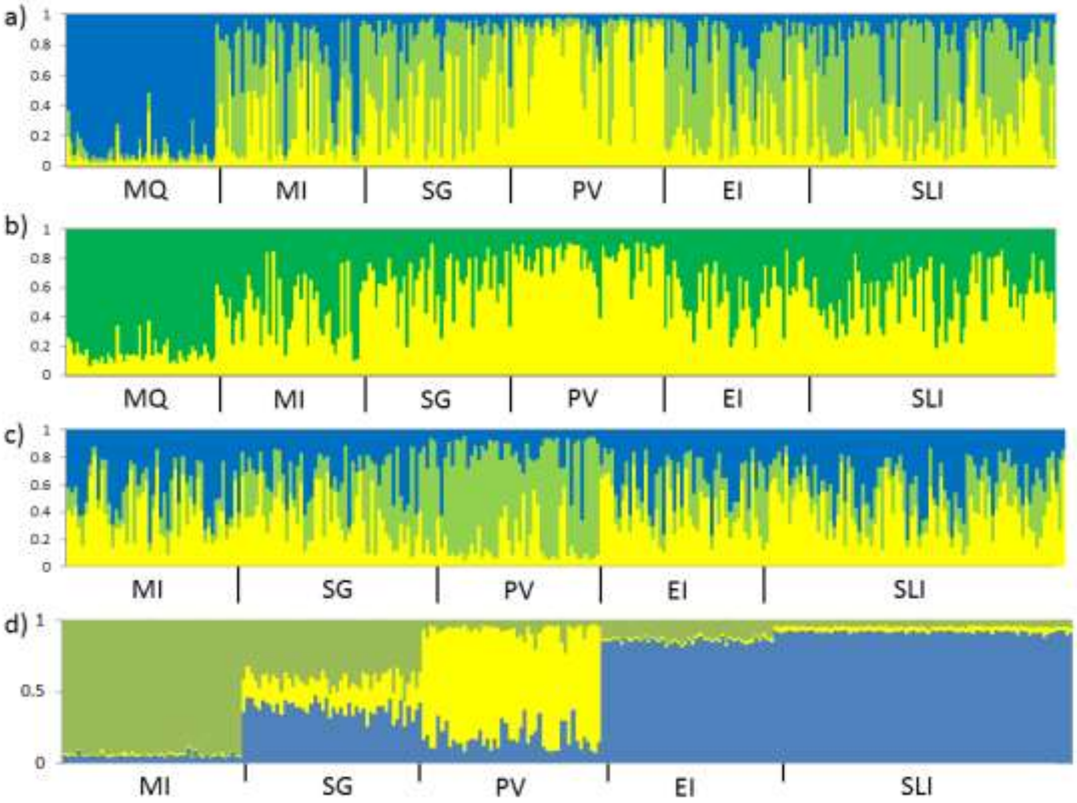

GOU
South Africa
BOU
MI
SG
Antarctic Divergence
CRO
FI (SLI)
PV
KER
EI
KIN
HD
Antarctica
South America
VLC
Antarctic Convergence
MQ
CAM
New Zealand
Australia
1000 km

Figure 2:



a)
1
0.8
0.6
0.4
0.2
0
MQ
MI
SG
PV
EI
SLI
b)
1
0.8
0.6
0.4
0.2
0
MQ
MI
SG
PV
EI
SLI
c)
1
0.8
0.6
0.4
0.2
0
MI
SG
PV
EI
SLI
d)
1
0.5
0
MI
SG
PV
EI
SLI

Figure 3:

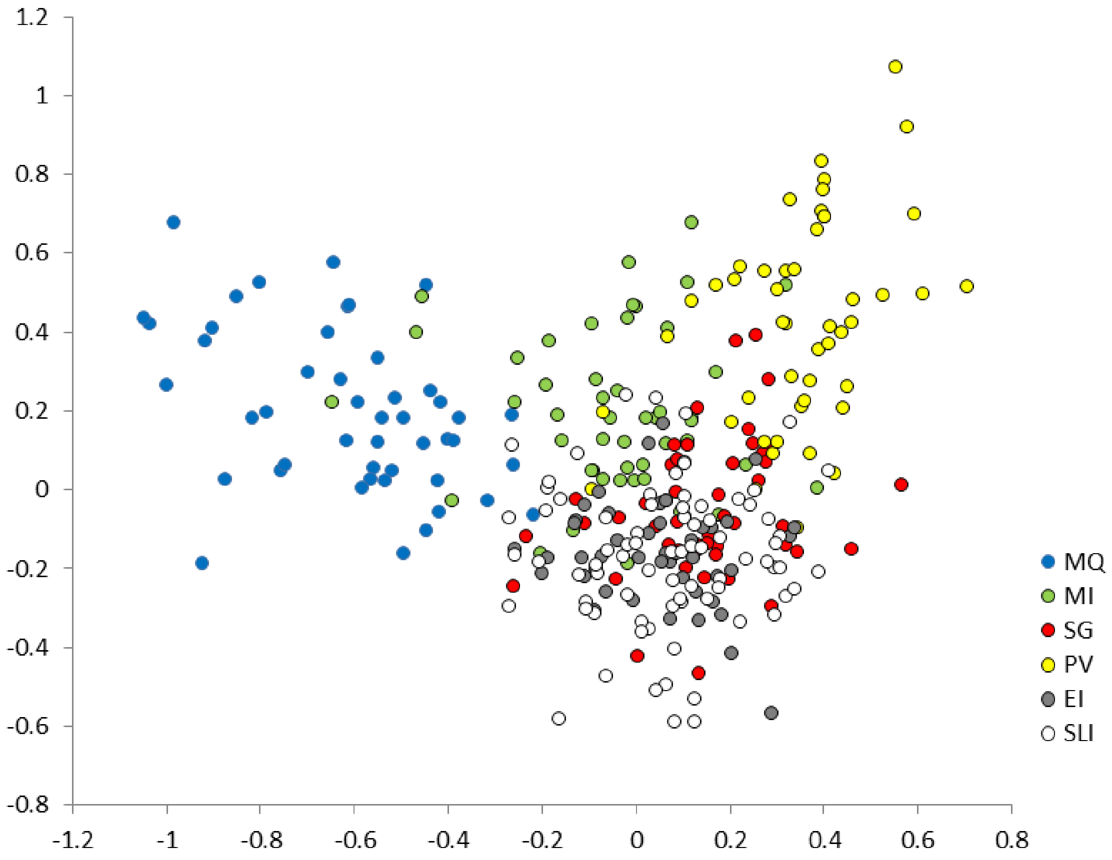

1.2
1
0.8
0.6
0.4
0.2
0
-0.2
-0.4
-0.6
-0.8
-1.2
-1
-0.8
-0.6
-0.4
-0.2
0
0.2
0.4
0.6
0.8
MQ
MI
SG
PV
EI
SLI

Figure 4:

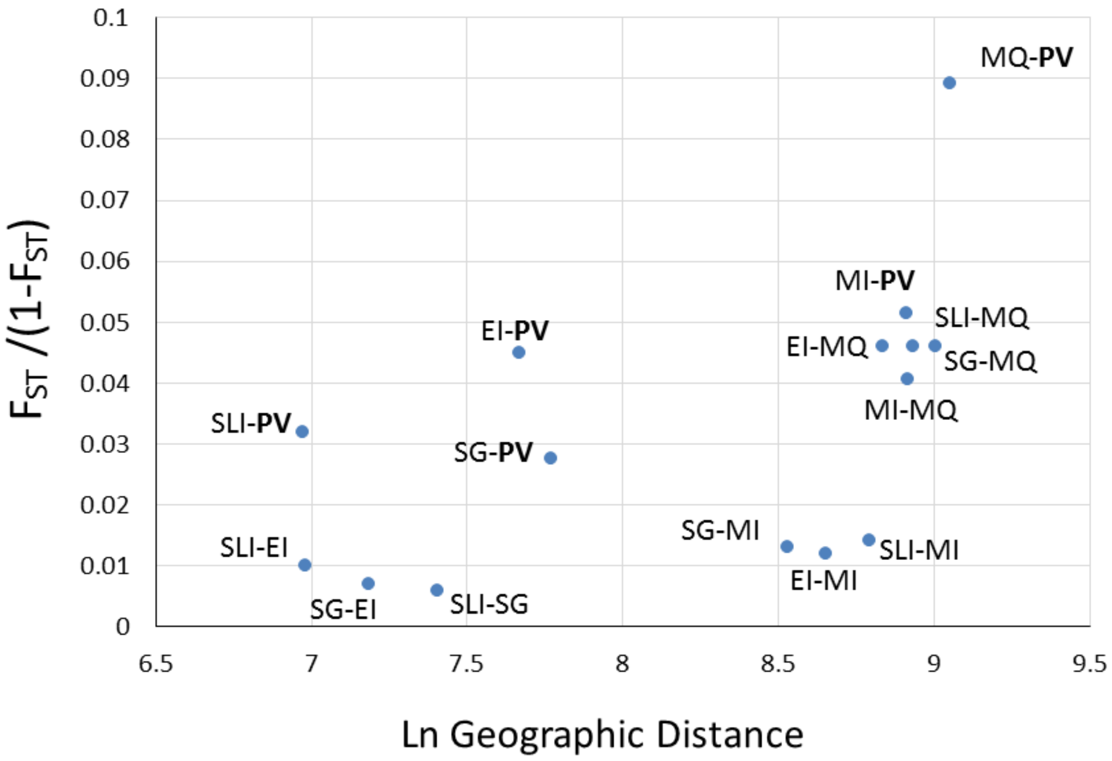

MQ-PV
MI-PV
SLI-MQ
EI-PV
EI-MQ
SG-MQ
MI-MQ
SLI-PV
SG-PV
SG-MI
SLI-EI
SLI-MI
EI-MI
SG-EI
SLI-SG
0.1
0.09
0.08
0.07
0.06
0.05
0.04
0.03
0.02
0.01
0
6.5
7
7.5
8
8.5
9
9.5
F_{ST} /(1-F_{ST})
Ln Geographic Distance

Table 1. Expected (H_e) and observed (H_o) heterozygosity, number of alleles per locus (A) and allelic richness (A_{rich}). Data are for means and (standard deviation) across all 15 loci.

	He	*Ho*	*A*	A_{rich}
MQ	0.611 (0.216)	0.606 (0.228)	5.40 (2.32)	5.20 (2.22)
MI	0.640 (0.184)	0.624 (0.193)	6.53 (2.90)	6.13 (2.63)
SG	0.639 (0.153)	0.647 (0.125)	6.40 (2.47)	6.10 (2.56)
PV	0.607 (0.144)	0.618 (0.148)	6.27 (2.31)	5.83 (2.04)
EI	0.632 (0.169)	0.616 (0.170)	6.33 (2.58)	5.97 (2.32)
SLI	0.639 (0.150)	0.624 (0.163)	7.13 (2.56)	6.34 (2.26)

Table 2. Pairwise Fst values between each SES population. P-values are given in the upper diagonal with $p < 0.000001$ marked by an *, and all other values given.

	MQ	MI	SG	PV	EI	SLI
MQ	-	*	*	*	*	*
MI	0.039	-	*	*	*	*
SG	0.044	0.013	-	*	0.021	0.010
PV	0.082	0.049	0.027	-	*	*
EI	0.044	0.012	0.007	0.043	-	*
SLI	0.044	0.014	0.006	0.031	0.010	-

Table 3. Range of values for the population migration rate (number of migrants per generation) between pairs of populations across IMa runs, showing the position of the peak of the posterior distribution together with the estimated 95% confidence intervals.

		Migrants from Population 1 to Population 2			Migrants from Population 2 to Population 1		
pop1/pop2	number of runs	Range of HiPt	Range 95Lo	Range 95Hi	Range of HiPt	Range 95Lo	Range 95Hi
PV/SLI	2	0.005-0.379	0.005-0.142	0.61-25.36	3.38-32.22	0.92-10.21	15.58-76.44
MI/SLI	2	0.33-0.37	0.05-0.068	33.94-41.11	8.52-14.42	0.49-1.88	34.96-36.0
MI/SG	1	0.88	0.16	23.98	8.1	1.42	42.32
MI/MQ	1	3.56	0.42	40.73	0.97	0.094	15.47
SG/EI	1	0.014	0.008	39.72	28.02	10.36	55.21
SG/MQ	3	0.017-0.43	0.009-0.019	2.49-5.45	6.12-9.88	0.76-1.34	15.86-43.6

Table 4. Range of values for current Ne (individuals) and divergence time (years) between pairs of populations across IMa runs, showing the position of the peak of the posterior distribution together with the estimated 95% confidence intervals.

		Current Ne (pop1; pop2)			Divergence time between populations		
pop1/pop2	# runs	range of HiPt	range 95Lo	range 95Hi	HiPt	range 95Lo	range95Hi
PV/SLI	2	70-349; 278-658	32-100; 176-414	176-728; 601-1022	478-593	383-488	7606-8519
MI/SLI	2	444-500; 398-462	94-124; 264-269	947-952; 773-798	1319-1392	662-683	7385-7990
MI/SG	1	305; 522	154; 313	603; 946	1013	499	6094
MI/MQ	1	298; 205	73; 63	590; 450	173	99	4409
SG/EI	1	2971; 2059	1948; 1202	11894; 2959	1037	837	10240
SG/MQ	3	41-157; 208-445	30-83; 129-235	177-279; 602-848	26-795	16-300	2294-4143

Table 5. Results of migrant detection analysis in Geneclass2. Results marked with an asterisk were close to the p = 0.01 threshold and were not always significant at $p < 0.01$ for repeat simulation runs (but always less than 0.012).

Sample	Sex	probability of assignment to source	Population	
			Home	Assigned
MQ1	M	0.001	MQ	MI
MI41	M	0.008*	MI	MQ
PV28	M	0.005	PV	SLI
PV39	M	0.008*	PV	MI
EI2	F	0.002	EI	SG
EI25	M	0.008*	EI	PV

Table 6. Fu's Fs, Tajima's D, Tau and calculated expansion times for each SES colony.

	Fs	*p for Fs*	Tajima's *D*	*Tau*	Expansion time (years)
MQ	-0.606	0.473	0.718	n/a	n/a
MI	-9.356	0.003	-0.24	7.58	16,962
SG	-15.194	0	0.249	7.63	17,073
PV	1.795	0.843	1.82	n/a	n/a
EI	1.88	0.775	0.723	n/a	n/a
SLI	8.912	0.978	0.475	n/a	n/a