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Bottom-up regulation of a pole-ward migratory predator population

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As the effects of regional climate change are most pronounced at polar latitudes, we might expect pole-ward migratory populations to respond as habitat suitability changes. The southern elephant seal (*Mirounga leonina* L.) is a pole-ward migratory species whose populations have mostly stabilized or increased in the past decade, the one exception being the Macquarie Island population which has decreased continuously over the past 50 years. To explore probable causes of this anomalous trend, we counted breeding female seals annually between 1988 and 2011 in order to relate annual rates of population change (r) to foraging habitat changes that have known connections with atmospheric variability. We found r (i) varied annually from -0.016 to 0.021 over the study period, (ii) was most effected by anomalous atmospheric variability after a 3 year time lag was introduced ($R = 0.51$) and (iii) was associated with sea-ice duration (SID) within the seals' foraging range at the same temporal lag. Negative r years may be extrapolated to explain, at least partially, the overall trend in seal abundance at Macquarie Island; specifically, increasing SID within the seals foraging range has a negative influence on their abundance at the island. Evidence is accruing that suggests southern elephant seal populations may respond positively to a reduced sea-ice field.

1. Introduction

Over one-third (36% or 43 species) of marine mammal species engage in a migratory life strategy that makes them dependent on a variety of environments that are responding to a range of human activities and pressures [1]. For example, pinnipeds (seals) use breeding habitats that, owing to global temperature increases, may be at risk from sea-level rise or sea-ice retreat and they search for food within the changing oceans during critical stages in their lives. Already some life-history parameters and vital rates of marine mammal predators have been correlated with recent Northern Hemisphere environmental changes [2].

The southern elephant seal (SES, *Mirounga leonina* L.) is the largest and perhaps best studied Southern Hemisphere (SH) pole-ward migratory pinniped species. Genetically distinct populations breed principally on mid-latitude islands close to the Antarctic Polar Front (APF), although they may also have occupied higher latitudes during periods of Holocene sea-ice retreat [3]. Following a mid-1800s period of commercial exploitation and subsequent recovery, some major elephant seal populations have exhibited substantial decreases, whereas others have increased or stabilized [4,5]. The drivers responsible for these differing population trajectories remain unresolved, but environmentally mediated food availability at the seals' foraging habitats stands out as the most likely explanation [4].

SH polar latitudes, where SES forage [6], have exhibited marked climatic (atmospheric and oceanographic) variability and change that, through associated changes in ice cover, affect biological productivity [7] and the quality and quantity of food available to upper trophic levels. In general, the Southern Ocean between 40° and 60° S has warmed appreciably, prevailing westerly

winds have strengthened and some Antarctic Circumpolar Current (ACC) oceanographic frontal positions (including the APF) have shifted pole-ward [8 and references therein]. Counter to expectation, mean circum-Antarctic sea-ice extent (SIE) has expanded at a significant rate over the past decades. This overall expansion is essentially the sum of larger opposing SIE trends in the Ross and Bellingshausen seas [9]. For example, the Amundsen–Bellingshausen seas are presently experiencing a three month shorter ice season, whereas the Ross Sea (RS) is experiencing a two month longer season [10–12]. In addition, inputs to the East Antarctic ice field currently exceed losses, ice concentrations are trending higher in the mid-pack, the width of the marginal ice zone is widening and there is evidence of multi-year ice cover in the RS [10–12].

These changes in Southern Ocean oceanography and the sea-ice field outlined above are taking place, as the principal mode of SH atmospheric variability, the southern annular mode (SAM), has trended towards a higher (positive) index state [13]. Briefly, the SAM describes monthly polarity anomalies in the strength of the Antarctic polar vortex (zonal winds) where a strengthened polar vortex is due to a stronger temperature gradient between the mid and high latitudes. Positive SAM anomalies are characteristic of a stronger polar vortex (i.e. stronger subpolar westerly winds) positioned farther south over the continental landmass, colder Antarctic temperatures and low atmospheric pressure over the icecap. The expected intensification of the colder westerly wind field during positive SAM conditions causes Ekman drift to strengthen northward and as a result sea-ice season and area can be extended [9,14,15]; however, the current literature is inconsistent in the degree to which sea-ice trends are associated with the SAM trend [16]. The SAM also exhibits a strong non-annular component, manifested as enhanced pressure anomalies over the Amundsen Sea. This non-annular component is known to induce significant climate variability over Antarctica via corresponding changes to meridional wind patterns [17]; specifically, warm (cold) air advection associated with northerly (southerly) winds promote decreased (increased) sea ice and higher (lower) surface air temperatures in the vicinity of the Antarctic Peninsula (RS) [10,13,17]. In this context, SESs are experiencing broad- and local-scale physical changes at their foraging habitats, changes that may be affecting food availability and ultimately their abundance.

Here, we test the hypothesis that changes in breeding female SES abundances at sub-Antarctic Macquarie Island is in response to climate-induced changes in food availability at the seal's foraging habitat [4]. To do this, we made regular annual censuses of females to determine the population trend and variability in abundances over a 24 year period (1988–2011). We then correlated the calculated inter-annual variability with variability in the SAM, and its known linkages with sea-ice fields and regional biological productivity at southern polar latitudes [16–23].

2. Methods

(a) Seal data collection and analyses

Harem-breeding female SESs were counted within a previously defined study area hereafter termed 'ISTHMUS', and for the whole island, hereafter termed 'ISLAND' [24]. ISTHMUS females were counted in all years from 1988 to 2011 ($n = 24$); ISLAND

females were counted on 18 occasions over the same study period. Counts were undertaken as near as practicable to the annually repeatable long-term peak haul-out date, if not counted on that day a correction factor was applied according to survey date and study area location [25]. On each occasion, all harem females were counted at least twice by two or more observers and, if observer estimates differed by $\pm 5\%$, further counts were undertaken until the estimates were within that margin of error. The mean of the two counts was then used as the maximum count estimate. This study was carried out with the necessary Animal Ethics Committee approvals and State Government Scientific Permits.

Numbers of ISTHMUS females were highly correlated to the ISLAND numbers ($F_{1,27} = 1008$, $r^2 = 0.97$, $p < 0.001$). The ISTHMUS was therefore considered a robust reflection of the ISLAND population trend and its variability for the study period, and thus we focus specifically on the continuous ISTHMUS time-series for subsequent analyses.

Annual rates of ISTHMUS population change (variability) were computed as the intrinsic rate of change (r_t) [26] as follows: $r_t = (\ln N_t - \ln N_0)/t$, where N_t is the number of reproductively active female seals present within the ISTHMUS study area in a particular year, N_0 is the number of reproductively active female seals present within the ISTHMUS study area in the preceding year and t is the time period between counts. Note N in any one census year consists of females in all age classes combined and that the assumptions underlying the model from which r is derived [25] are met.

(b) Climate data and analyses

Various observational and re-analyses datasets were used to investigate the possible causes of inter-annual variability in the ISTHMUS elephant seal population. Particular focus is given to determining associations with sea-ice, and the corresponding impact of the SAM owing to the well-established linkages between these variables and their subsequent impacts on ocean productivity (see above) and elephant seal foraging behaviours [27–30].

A monthly SAM index¹ is calculated by projecting monthly-mean 700-hPa geopotential height (Z_{700}) anomalies pole-ward of 20° S onto the leading empirical orthogonal function of monthly Z_{700} atmospheric pressure anomalies over 1979–2010. Monthly 500-hPa geopotential heights (Z_{500}) and 950-hPa wind fields [31] are available on a $2.5^\circ \times 2.5^\circ$ latitude–longitude grid.² Note that subsequent results are not sensitive to the choice of re-analysis product. These monthly data were converted to annual-means by averaging monthly values from December in year $x - 1$ to November in the year x . For example, year 1999 was calculated using the period December 1998 through November 1999. Each annual-mean period commences with the post-breeding foraging migration for female elephant seals from Macquarie Island (mid-end November) and ends with their return for pupping in mid-September [32].

To investigate associations with sea-ice, we use sea-ice duration (SID; also referred to as sea-ice season length [12]) as the primary metric of analysis. SID was chosen as it more closely captures the temporal variability in sea-ice; for instance, regions of high ice extent may be similar between years, whereas duration differs markedly [11]. In order to quantify SID, quasi-daily estimates of sea-ice concentration (SIC) processed using the Bootstrap algorithm [33] are used. The SIC data³ are gridded onto a 25×25 km mesh. Defining the sea-ice year to begin and end in November, SID is calculated at each grid point by determining the total number of days where the SIC is at least 15%, linearly scaled to 365 day a year [10,12,34]. As

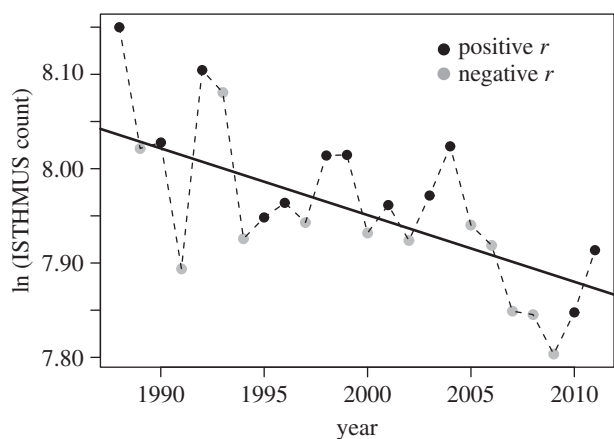


Figure 1. Lognormal transformation of the estimated numbers of female elephant seals breeding within the Macquarie Island ISTHMUS study area from 1988 to 2011. Seal numbers decreased at a rate of -0.8% per annum (black line; seal numbers = $24.96 - 0.008 \times \text{year}$) but varied between years such that there were 12 periods of increase (black circles) and 12 periods of decrease (grey circles).

shown by Parkinson [34], SID is largely insensitive to the ice concentration threshold used.

Prior to analysis, both the ISTHMUS population time-series and the SAM index were standardized by removing the long-term mean and dividing by the long-term standard deviation; as such, subsequent regression results relate to changes for a 1 s.d. positive event. Additionally, all data (SID, Z_{500} heights, and 950-hPa winds) were converted to anomalies by removing the climatological mean and detrended by removing the long-term linear trend.

Identifying drivers for population change in migratory species is complex, because there may be response time lags between observed demographic performance and the potential explanatory variables [35]. With this in mind, we incorporated a range of temporal lags (0–5 years) into our correlation analyses, so that seal counts in 1 year were related to SAM in that year (lag 0), in the previous year (–1) and so on.

Statistical significance of correlations was measured using a two-tailed Student t -test, with an uncorrected threshold of 95% set for all analyses. We applied a conservative post hoc Bonferroni correction for multiple comparisons and set the alpha cut-off value for significance to 0.008.

3. Results

(a) Inter-annual variability in seal numbers

Considerable inter-annual variation was detected in the intrinsic rate of ISTHMUS population change (r ; figure 1). The magnitude of this variability ranged between -0.16 and $+0.21$ with 12 years of positive change and 12 years of negative change within the time-series. The time-series also shows there were never more than 2 consecutive years of positive r -values, whereas there was a continuous period of 5 years (2005–2009 inc.) with negative r -values (figure 1).

We found variability in the ISTHMUS r was related to SH atmospheric variability (i.e. SAM). The largest effect was evident when a 3 year lag was introduced (table 1). This suggested the SAM itself or SAM-related environmental conditions 3 years prior to the seal census were driving seal abundances.

Figure 2*a,b* shows the SAM has large contemporary impacts on SID through corresponding effects on atmospheric circulation patterns (shown as wind vectors). In general,

Table 1. Correlation coefficients (R) and uncorrected statistical significance (p -value) between the annual rate of population change for female southern elephant seals (*Mirounga leonina*) breeding within the ISTHMUS study area at Macquarie Island and the annually averaged ($\text{Dec}_{(\text{year } x-1)} - \text{Nov}_{(\text{year } x)}$, 1988–2011) southern annular mode index lagged by 0–5 years. Italicized text has the largest effect size (R) and was marginally significant after a Bonferroni adjustment for multiple comparisons conservatively reset the p -value cut-off to 0.008.

time lag (years)	effect size (R)	uncorrected p -value
0	–0.15	0.47
–1	–0.18	0.40
–2	0.02	0.92
–3	<i>0.51</i>	<i>0.01</i>
–4	–0.19	0.37
–5	–0.01	0.96

warm northerly (cold southerly) air advection occurs in the regions of anomalously shorter (longer) SID. Within the seals foraging areas (compare figures 2 and 3) the northwesterly wind vectors highlight the red-shaded area of decreased SID which largely results from advection of warm maritime air over the region; the blue area of increased SID is consistent with colder offshore southwesterly continental air flow (see wind vectors). The RS region, a known feeding ground for adult female seals from Macquarie Island (figure 3), is experiencing among the greatest SAM associated SID anomalies for the SH (figure 2 and [10,11]).

Regressions based on a 3 year time lagged ISTHMUS r reveal very similar patterns in the Z_{500} anomalies, winds and the resulting SID, compared with those of the SAM (compare figure 2 left column with figure 2 right column). For example, the spatial correlations in Z_{500} and SID structures are 0.75 and 0.72, respectively. These similarities suggest that the SAM directly impacts SID through the corresponding impacts on the wind, but that these changes become most apparent upon elephant seal abundance 3 years later. Specifically, increased (decreased) SAM-induced SID within the seals Antarctic foraging grounds results in negative (positive) changes in their numbers on Macquarie Island 3 years later. We therefore conclude that the SAM, via changes to the SID, likely impacts the population dynamics (variability) of reproductively active female elephant seals from Macquarie Island.

(b) Multi-decadal trend in seal numbers

The long-term census data (figure 1) show an overall negative trend in numbers of ISTHMUS females (1988–2011); numbers decreased from an estimated 3463 in 1988 to a low of 2449 in 2011. The overall exponential rate of change (r_e) was -0.8% per annum ($F_{1,23} = 15.93$, $p < 0.01$, $r^2 = 0.38$, figure 1). By extrapolation from the ISTHMUS census data [25], we determined that there has been a considerable reduction of about 5400 breeding females for the whole ISLAND, including ISTHMUS, over the 24 year study period.

Our analysis does not explicitly test multi-decadal trends in SID and the SAM against seal abundance at Macquarie Island (see [16]). However, the results of our analyses for r (above) showed increased SID had a negative influence on seal abundance. From that association, we show evidence

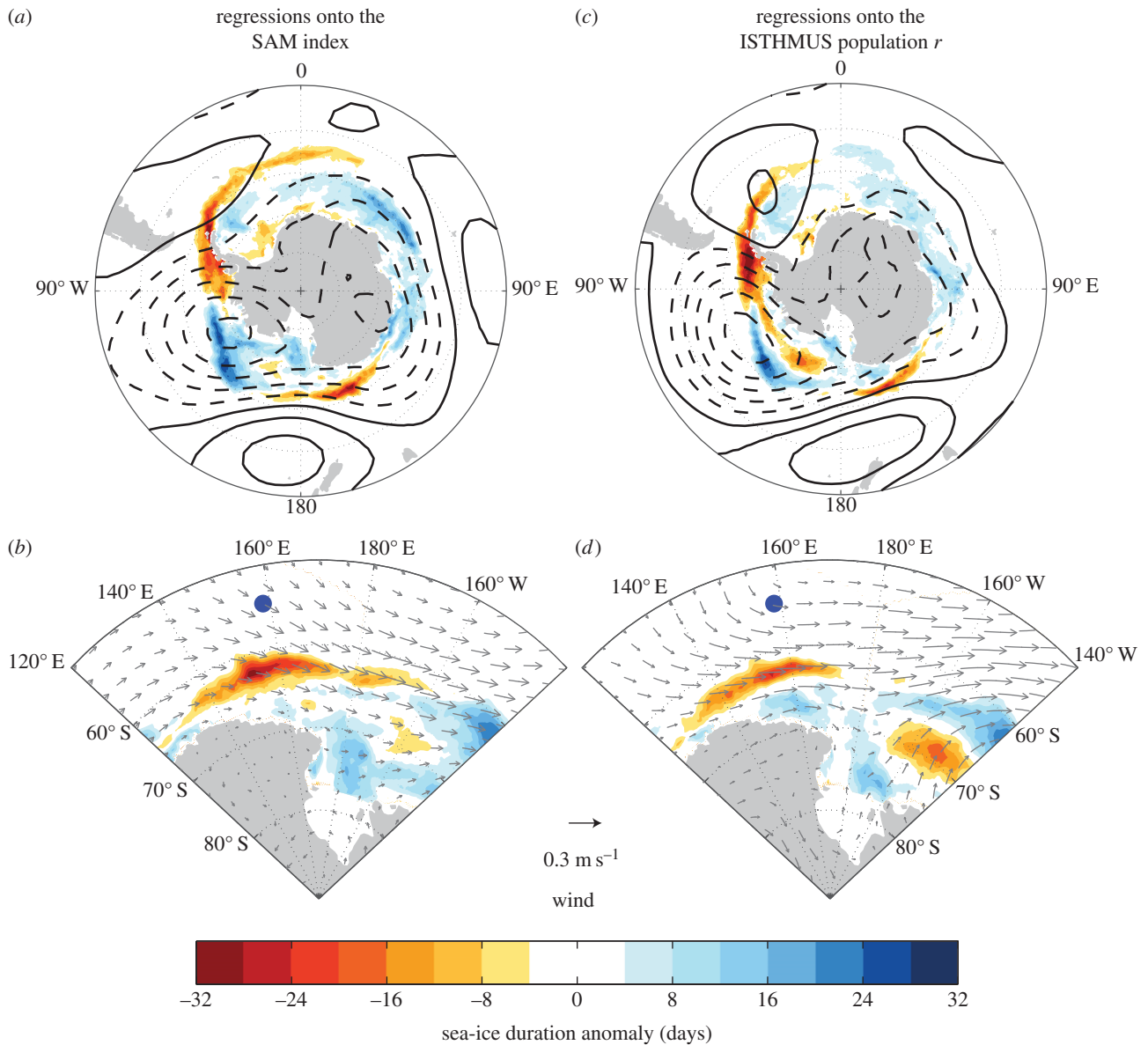


Figure 2. (a) Sea-ice duration (SID; shading) and annual-mean Z_{500} (contours) atmospheric pressure anomalies regressed onto the southern annular mode (SAM) index. Solid (dashed) contours denote positive (negative) pressure anomalies, and are drawn at 4 m intervals; the zero contour has been omitted. (b) SID (shading) and 925 hPa wind (vectors) anomalies similarly regressed onto the SAM index, displayed only for 120° E–140° W, the foraging habitat for female elephant seals from Macquarie Island (marked as a blue dot). (c,d) The equivalent figures for SID (shading), Z_{500} (contours) and 925 hPa wind (vectors) anomalies regressed onto southern elephant seal (*Mirounga leonina*) population variability (r) within the Macquarie Island ISTHMUS study area at a lag of 3 years. Note that all panels illustrate anomalies associated with a 1 s.d. unit change in the SAM and positive ISTHMUS population change. Negative SID anomalies (red shading) were strongest across the Ross Sea and toward the Dumont D’Urville Sea, East Antarctica directly to the south of Macquarie Island.

that attributes of the sea-ice field confronting female elephant seals during negative r years might also contribute to shaping the multi-decadal population trend.

The observed long-term decrease in seal abundance has coincidentally occurred at a time when SID, SIE, SIC and sea-ice motion (some of which may be linked) south of Macquarie Island have displayed positive time-series trends [9,12,14,16,38,39]. Generally, an expanding sea-ice field is confronting energy-depleted (owing to the costs of terrestrial fasting events) female elephant seals from Macquarie Island. Therefore, conceptually at least, the observed positive trends in the sea-ice field south of Macquarie Island could be an important overall driver of the population trend as well as inter-annual variability (above).

Changes in the sea-ice field south of Macquarie Island have been shown to be strongly associated, but not to be necessarily correlated, with large-scale climate variability

such as those attributed to the SAM [9,14,16,40]. However, significant change in RS SIC during the winter months (June–November) has been attributed to the SAM [16].

4. Discussion

This study illustrates the essential requirement in wildlife management practices to undertake and maintain less glamorous research tasks such as the basic monitoring of individuals. Having such long-term data revealed that numbers of female SESs at Macquarie Island continue to decrease despite an earlier, somewhat optimistic, suggestion of a population stabilization [25]. Within this downward trend, there is also considerable inter-annual variability in the numbers of females ashore (r). Over the 24 year study period, we identified an equivalent number of years showing positive and negative r ;

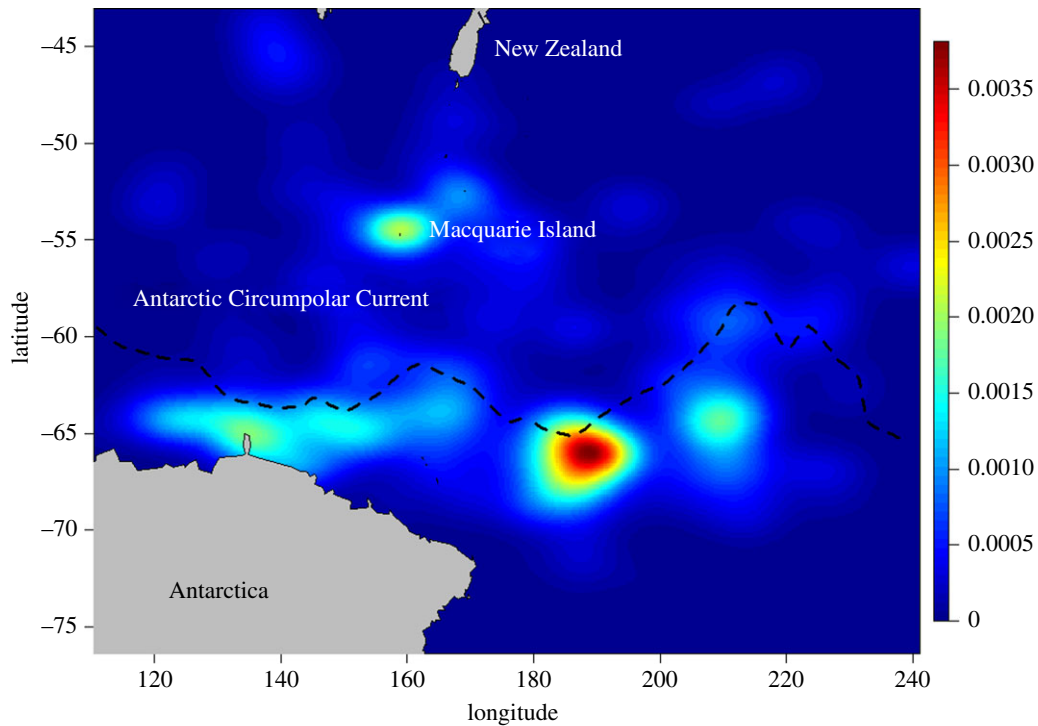


Figure 3. Favoured foraging areas for reproductively active female southern elephant seals (*Mirounga leonina*) migrating pole-ward from Macquarie Island. Displayed is a kernel density plot of area restricted search (ARS) locations (identified first-difference correlated random walk switching state-space models (DCRWS SSM) to the raw location data [36]) from 105 satellite tracked seals tracked from Macquarie Island between 1999 and 2005 [29]. The contours represent ARS densities expressed as 10% quantiles, red, greater proportion. Also shown is the long-term mean position of the Antarctic Circumpolar Current taken from [37].

the time-series also displayed lengthier continuous periods of negative r compared with positive r .

Having previously discounted emigration as a factor contributing to r at Macquarie Island [25], we conclude from the results of this study that female mortality exceeds recruitment and the conditions required to promote positive r (growth) occur equally as often as those that do not but conditions invoking negative r can operate over lengthier periods than positive periods (up to 5 years continuously versus 2 years). We found that inter-annual variability in r was best correlated (i.e. the largest effect size) with variability in a climate mode index, the SAM and also had associations with SID within the seals' high-quality foraging areas; positive (negative) r events were best correlated with positive (negative) SAM events and were in turn associated with reduced (increased) SID (figure 2). Most importantly, it was *not* current conditions that influenced annual population change; rather it was conditions at the foraging grounds 3 years previous. Another key outcome is that the environmental factors responsible for negative r years may be the same, or similar, to those contributing to the overall negative multi-decadal population trend at the island. Regional *per capita* food availability has been proposed as the most likely factor driving elephant seal trends [4]. We now examine that hypothesis using the Macquarie Island population as a test case, together with a climate index (SAM) and sea-ice as proxies for food availability.

We begin with some generally important and relevant life-history attributes for adult female SESs. Without exception, biologging studies have shown females undertake long-distance pole-ward foraging migrations from their terrestrial haul-out locations; the seals favoured foraging at ocean frontal systems and within the seasonal SIE over the Antarctic continental shelf south of the ACC [6,29]. The sea-ice zone influences both the foraging behaviour and success

of female elephant seals because it presents a physical barrier within which the seals are unable or unwilling to remain during winter when they accumulate the critical resources needed for breeding and rearing offspring [28–30,41]. In years when females were capable of foraging within the sea-ice as it seasonally extends over the Antarctic continental shelf they fed on higher-quality prey and exhibited six-times greater fat deposition rates compared with females that did not [27,29]. Like other capital breeding species, female elephant seals rely on energy acquired and stored as fat during their foraging migrations for self maintenance and the costs of reproduction. The amount of accumulated fat not only contributes to her size, and hence capacity to gestate, but also to the size of her offspring at weaning and its subsequent survival through at least the first 2 years of life [42,43]. A mother's foraging success and her offspring's survival have broader demographic consequences, because survival during the non-breeding phase is the most important determinant of elephant seal abundance [43]. Female elephant seals are also faithful to their individual feeding areas [27], so any variability or persistent change in foraging area quality could be an important determinant of future survival and breeding success [44].

While it is known that climate variability (e.g. the SAM) mediates regional biological productivity in polar ecosystems through changes in sea-ice conditions [16–23,45], the links between sea-ice conditions, seal foraging success and population change have not previously been quantified. At first glance, the negative annual population changes (r) and the overall declining population trend we observed run counter to expectation, because positive SAM and extended sea-ice conditions that dominate the region to the south of Macquarie Island are usually associated with elevated primary productivity [46,47] and a higher krill biomass [18,45]; and

krill are a keystone organism in the Antarctic pack ice food chain that sustains higher predators, including elephant seals [19,23,48]. Given this is not what we observed (i.e. positive SAM and SID anomalies were associated with negative r), we propose the following explanation for this apparent paradox.

As outlined above, the sea-ice field south of Macquarie Island has, over the past decades, trended towards increased duration (SID), extent (SIE) and concentration (SIC) and sea-ice affects female foraging behaviour and success. Most relevant to this study is that SID within the seals' feeding grounds (figure 3) has increased by up to 60 ± 10 days between 1979 and 2010 [11,15,16,20]. Our analyses of the seals relationship with SID indicated inter-annual decreases (increases) in seal numbers at Macquarie Island tend to be associated with a longer (shorter) SID 3 years previous to the census. Given that adult females avoid sea-ice, we think an earlier sea-ice advance (March–April) [11] could prevent pregnant females access onto the continental shelf and the higher-quality prey rewards available there during the critical first trimester when the seals are accruing the majority of their winter and lactation period blubber reserves [49]. A later ice retreat would simply extend the period of exclusion from the same shelf foraging areas. Increased SIC and SIE could have similar exclusionary effects on female foraging efforts. Thus, we propose female elephant seals cannot access high-quality feeding grounds in the extended presence of sea ice.

As a capital breeding species, that generally produce only one offspring per annum, poor foraging years will have far reaching consequences on female elephant seals, because poor maternal foraging success in high sea-ice years will translate directly into reduced juvenile survivorship and therefore female recruitment, which, in turn, reduces population growth rates [43]. A reduced survival of juvenile female seals accounts for the 3 year lag between poor foraging years with a long SID and the number of females counted in harems on the isthmus, because about 12% (authors unpublished data, 2014) of females begin to recruit into the breeding population at 3 years of age and give birth to their first pup at age 4 [50]. We conclude that breeding female abundance at Macquarie Island in any 1 year is to a large extent the consequence of environmentally mediated recruitment of 3 year old female seals into the population.

The mechanisms driving changes in the sea-ice fields are complex and difficult to diagnose. The substantial Arctic sea-ice decrease has been linked with global warming [51], and changes in the SH atmospheric circulation patterns are expected to have a strong influence on Antarctic sea-ice cover [39,52]. For example, the increased ice field in the RS region has been linked to the dipole (non-annular) component of the SAM such that there was more sea-ice in years with a high (positive) SAM index [17]. Results of direct correlation analyses of the sea-ice cover with Northern and SAM indices show relatively weak correlations [51], a finding supported by Simpkins *et al.* [12] that showed the trend in ice cover appears unrelated to the trend in the annular component of the SAM. Nonetheless, there is a general understanding that atmospheric forcing is the main driver of sea-ice presence, absence and variability [17,53], and SID has apparent influences on SES numbers at Macquarie Island (figure 2d).

Climate-associated oceanographic change will also have consequences for those individuals foraging pelagically outside the sea-ice zone within ocean frontal zones such as the

APFZ where they already encounter lower-quality prey [29]. Appreciable changes have occurred throughout the Southern Ocean [8,54][†] that either individually or cumulatively have the potential to spatially and temporally affect the distribution and abundance of elephant seal prey. A southward shift in ocean frontal positions alone may mean energy-depleted females along with weaned pups and juveniles departing Macquarie Island would expend more of their limited energy reserves on reaching frontal foraging grounds [55–57]. Additionally, these pelagic foraging grounds may have altered in their prey availability and quality, further compromising survival and breeding success.

The nature of high-latitude predator responses to environmental change can be complex, time lagged [35 and this study] and result in both top-down [58] and bottom-up regulation [58 and this study]. Nonetheless, as both a warming of the Southern Ocean and the positive SAM phase shift are predicted to continue as long as the ozone hole remains open and greenhouse gas emissions continue to increase [59–61], it can be reasonably expected that there will be ongoing changes in the structure and function of the Southern Ocean ecosystem. Such changes are likely to further affect productivity of the polar marine ecosystem [62] and mid- to high-order predator populations, some of whom will prosper while others struggle.

It is perhaps too early to label SESs climate change 'winners' or 'losers', but others have suggested the polar environment was changing in favour of elephant seals [6,63]. Some of the evidence supporting this notion comes from studies in the West Antarctic Peninsula (WAP) region, where the most rapid reductions in SH sea-ice have been observed [64]. WAP elephant seal abundances have increased [65,66] along with pup weaning mass (i.e. maternal energy reserves) and the quality of food available to the seals [67,68]. In the east Antarctic, a southward expansion in elephant seal breeding possibly occurred during the Holocene as the RS sea-ice field reduced [3], perhaps, because the highly productive RS continental shelf foraging grounds were more readily accessible to the seals during the same period of past ice retreat. This study has shown that a reduced sea-ice field south of Macquarie Island could, through improved food availability, maternal foraging and juvenile survival, promote elephant seal abundances at this island. Whether such a relationship holds for other SES populations could be explicitly tested where data exist.

Most importantly, our findings show that the effects of climate-driven variability on Antarctic sea-ice can be detected at the population level for a mid-latitude breeding but pole-ward migrating marine mammal predator, the SES. Such high-level responses make SESs potentially important sentinels of change, because they have the capacity to integrate and reflect conditions, such as ecosystem productivity, across a variety of changing habitat types [69] that are otherwise difficult to measure directly, especially during the Antarctic winter. The strategic geographical distribution of SES breeding sites throughout the Southern Ocean, their migratory behaviour and their individual capacity to carry scientific instruments gives this species the potential to become a significant contributor to measuring, identifying, understanding and explaining the impacts and physical responses of high-order Antarctic predators to SH climate variability and change.

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Data accessibility. Southern elephant seal census data are available from <http://data.aad.gov.au/aadc>.

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