

Running heading: Growth variability in fur seal pups

**Geographic variation in subantarctic fur seal pup growth: linkages with environmental variability and population density**

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Marine predator populations are sensitive to temporal variation in prey availability, but prey dynamics are often difficult to quantify. Long-term measures of offspring growth is a useful performance attribute to gauge the potential demographic direction for such predator populations, especially where other metrics (e.g., population size estimates) are lacking. Subantarctic fur seal (*Arctocephalus tropicalis*) females are central place foragers during a protracted lactation period, and their foraging success determines the growth and vitality of their offspring. Using data spanning over two decades, we assessed geographic and temporal variation in growth rates and weaning mass of subantarctic fur seal pups at two of the species' principal populations (Gough and Marion islands) and identified environmental conditions that may, through assumed bottom-up mechanisms, affect body mass at weaning. While Marion Island pups grew at an average rate of between 0.040 and 0.067 kg/day early in lactation (comparable to conspecific growth at Amsterdam Island), the mean growth rate at Gough Island (approximately 0.030 kg/day) was lower than the growth rate represented by the bottom 5% of the body mass distribution at Marion Island. Notwithstanding substantial inter-annual variability, we found support for a negative trend in weaning mass at both populations, suggesting a rise in limiting factors that is hypothesized to relate to concurrent local population size increases. Weaning mass tended to be higher when sea surface temperatures were warmer (with a stronger positive effect at Gough Island) and during positive phases of the Southern Oscillation Index (La Niña events), with a stronger positive effect in males. Given the low weaning mass of Gough Island fur seal pups, continued population growth here seems unlikely. While density-dependent regulation appears to have increased in

strength at Marion Island, terminating rapid population growth, current weaning weights remain above the physiological limits of growth in subantarctic fur seals.

*Keywords:* *Arctocephalus tropicalis*, body mass, Gough Island, growth rate, long-term, Marion Island, otariid, quantile regression, Southern Oscillation, weaning mass

Animal populations may naturally be regulated by intrinsic dynamics (e.g., density-dependent competitive exclusion), bottom-up processes, such as environmental variation affecting foraging success, and the top-down impacts of predation. Although these mechanisms often act in concert (e.g., Coulson et al. 2001; Schwarz et al. 2013; Horswill et al. 2014), their relative importance may temporally vary. Given the rapid changes of climate and substantial physical changes in marine ecosystems (Stenseth et al. 2002), great interest currently lies in how marine predator populations may respond to changes in their environment (e.g., Trites et al. 2007). Bottom-up effects, usually implying population regulation through climate driven changes (and limitation) in food availability, thus featured strongly as a paradigm in recent years. Physical forcing (short- to medium-term climatic fluctuations) may effect bottom-up regulation on predator populations by altering food availability, which impacts individuals' foraging success, energy assimilation, growth, survival, and fecundity, ultimately affecting their fitness. However, the ecosystem shifts induced by historic over-exploitation of predators such as fur seals and some penguin and large whale species in particular, may still play a

dominant role in shaping current population dynamics of these, and other marine predators.

Marine predators (including land breeding species) frequently range over vast areas of remote ocean habitat and it is challenging to observe directly how they interact with their environment. For long-range foragers, information on diet can be scant and detailed surveys of prey abundance and distribution in key foraging areas are often nonexistent. Consequently, inference about bottom-up regulation is frequently based on indirect evidence. The foraging success of predators, assumed to be related to food availability, can be quantified using indices such as transit rate (Robinson et al. 2010), foraging trip duration (Petersen et al. 2006), diving characteristics (Lea and Dubroca 2003; Lea et al. 2006; McIntyre et al. 2011) and measures of offspring growth (Bester and Van Jaarsveld 1997; Burton et al. 1997; Reid 2002; Le Boeuf and Crocker 2005). Although interpretation of these parameters involves assumptions or may include confounding effects (Williams and Croxall 1990), critical evaluation of long-term data of both physical and biological factors may improve our understanding of how predators interact with their environment. The Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR), for example, endorse such an Ecosystem Monitoring Programme (CEMP); its aim to detect ecosystem changes through the long-term monitoring of selected predator, prey and environmental indicators (Agnew 1997).

Otariid (fur seal and sea lion) mothers provision their offspring during lactation by augmenting stored resources through energy gained from foraging (“income breeders,” in

the capital-income typology that describes reproductive investment—Jönsson 1997). During this time, mothers are central place foragers (Orians et al. 1979) with the fasting constraints of their young (Verrier et al. 2011) restricting the foraging range of females. Consequently, environmental conditions that operate at specific spatial and temporal scales may influence the foraging success of mothers and affect subsequent transfer of energy to pups (e.g., Lea and Dubroca 2003; Lea et al. 2006). With females concentrating foraging effort around breeding sites, intra-specific competition for food is also most pronounced during lactation, especially for large populations. While subpolar otariids such as Antarctic fur seals (*Arctocephalus gazella*) wean their pups in approximately four months, liberating breeding females from a central place foraging strategy for most of the year, temperate-zone otariids often have a more protracted lactation period (up to over two years, Gentry and Kooyman 1986). Subantarctic fur seals (*A. tropicalis*) occur sympatrically with Antarctic fur seals on islands located north of the Antarctic Polar Front (the Subantarctic islands Marion, Prince Edward, Macquarie and Îles Crozet), but have a protracted 300-day lactation period (Bester 1987; Kerley 1987). Their range extends northwards to the temperate islands of Tristan da Cunha, Gough, Saint Paul and Amsterdam, near the Sub-tropical Front (Figure 1). During the austral winter, the foraging trips of lactating subantarctic fur seal females increase in distance and duration, interspersed by short periods ashore. Pups born at both Amsterdam- and Marion Island face some of the longest inter-suckling intervals of any mammalian infant and endure, on a mass-specific basis, of the longest fasts of any physically active mammal (Georges and Guinet 2000; de Bruyn et al. 2009; Verrier et al. 2011; Wege et al. 2015). Pup growth

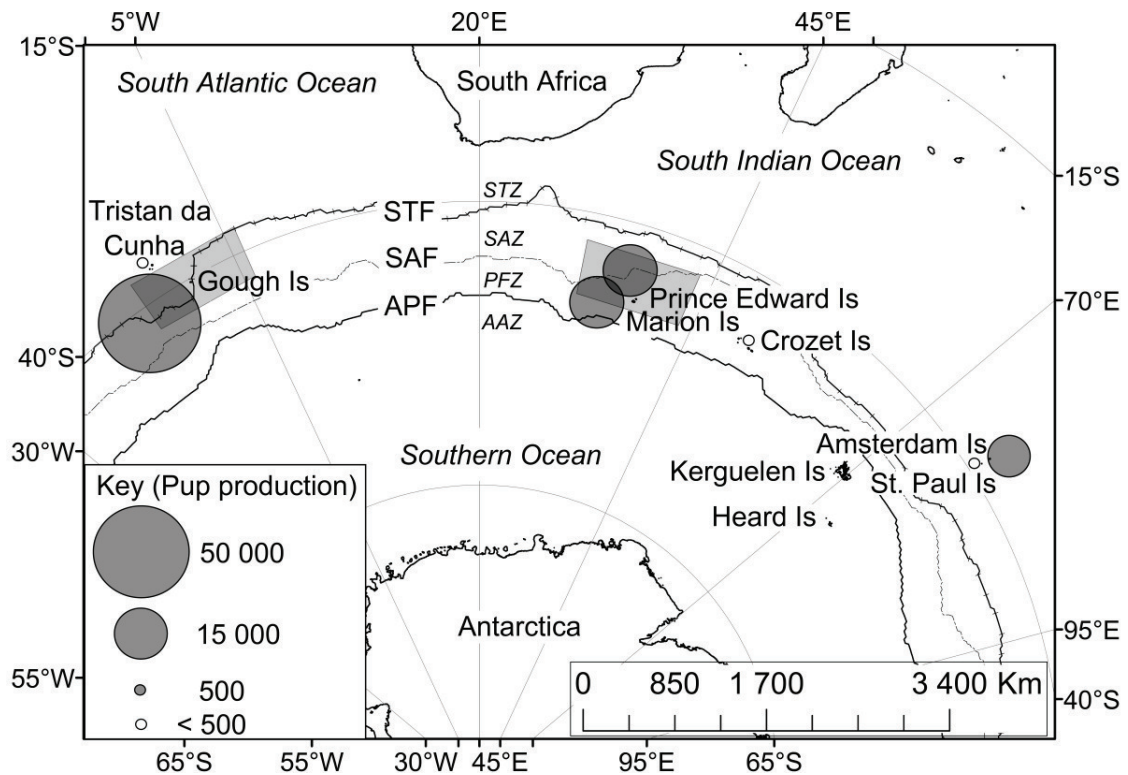


Figure 1. Present distribution of subantarctic fur seal *Arctocephalus tropicalis* breeding colonies. Approximate annual pup production is proportional to the size of the circles. Macquarie Island (< 200 pups born) is not indicated on the map. The average position of major fronts of the Antarctic Circumpolar Current (Subtropical Front, STF; Subantarctic Front, SAF; Antarctic Polar Front, APF) is indicated. Remotely sensed sea surface temperature data were extracted across the potential central foraging range of fur seals from Gough and Marion islands (shaded rectangles). *STZ*, Subtropical Zone; *SAZ*, Subantarctic Zone; *PFZ*, Polar Frontal Zone; *AAZ*, Antarctic Zone.

rates are, unsurprisingly, low on average (Kerley 1985; Guinet and Georges 2000; Kirkman et al. 2002; Chambellant et al. 2003).

Though the conditions that subantarctic fur seal pups born at Amsterdam and Marion islands face may appear extreme, they are likely to be even more severe at the world's largest, but poorly studied, subantarctic fur seal population: Gough Island. Previous comparisons between Gough, Amsterdam and Marion islands (the major breeding sites for subantarctic fur seals, Figure 1) indicated that pup growth rates were the lowest at Gough Island (Bester and Van Jaarsveld 1994, 1997; Kirkman et al. 2002). At the time, the recolonizing subantarctic fur seal population at Marion Island was increasing exponentially in numbers (from a single small rookery in the 1950's to some 16,000 pups born annually five decades later, Hofmeyr et al. 1997, 2006), implying overall favorable environmental conditions. Together with neighboring Prince Edward Island, the archipelago supports a population of approximately 150,000 subantarctic fur seals, roughly 30% of the global population (Hofmeyr et al. 2006). Recent population estimates at Marion Island suggest however that this population may now experience resource limitation, with pup production decreasing at the highest density rookeries (Mia Wege, University of Pretoria, Pretoria, South Africa, pers. comm., May 2015). Due to inaccessible terrain, a complete assessment of the Gough Island subantarctic fur seal population—estimated at over 50,000 pups in 1978 (Bester 1987) and comprising perhaps some 200,000 to 240,000 individuals representing over half the global population—has never been accomplished. Increased pup numbers on a few of the more recently colonized southeast coast breeding colony sites at Gough Island have been

interpreted as evidence for continued positive population growth (Bester et al. 2006), but population numbers and trend is subject to large uncertainty.

Long-term measures of offspring body mass (or equivalently growth rates) are useful performance attributes to monitor the well-being of populations, communities and ecosystems more generally, especially where other metrics (as fundamental as population size for subantarctic fur seals at Gough Island) are difficult to obtain. In this paper we compare pup growth and weaning mass, indices of the allocation and assimilation of maternal energy in offspring, at two of the principal populations of subantarctic fur seals globally: Marion Island in the South Indian Ocean and Gough Island in the South Atlantic Ocean. Our objectives were to 1) assess geographic and temporal variation in growth that may provide insight to the demographic state of each population, and 2) identify environmental conditions that may, through assumed bottom-up mechanisms, inhibit or enhance pup growth through lactation, an important determinant of juvenile survival in seal pups (e.g., McMahon et al. 2000; Beauplet et al. 2005). First, we derived a single, annual, sex-specific pre-weaning growth rate estimate of fur seal pups at Marion and Gough islands, in order to compare these to published growth rates from Amsterdam Island. But, instead of only focusing on the mean growth rate, we next use the entire body mass distribution to quantify intermediate and boundary responses (minimal to maximal growth rates) based on quantile regression. Lastly, we determine the form of the long-term trend in weaning mass (the measure for which we had the longest time series at both islands), and explore potential correlations between weaning mass and environmental covariates.



## MATERIALS AND METHODS

*Study sites.*— Gough Island, part of the United Kingdom Overseas Territory of Tristan da Cunha, is located in the central South Atlantic Ocean (Figure 1). It is a small (65 km<sup>2</sup>) volcanic island and the steep mountainous terrain mostly prevents access to the narrow coastline (~ 42 km). Gough Island lies at (or just poleward of) the southern limit of the general meridional band in which the Subtropical Front occurs (Andrew et al. 1995). Collectively, this frontal zone (the region between the northern and southern extent of the Subtropical Front) is referred to as the Subtropical Zone (STZ; Figure 1).

Marion Island, part of the Prince Edward Islands, is located in the South Indian Ocean (Figure 1). Marion Island (290 km<sup>2</sup>; coastline ~107 km) is situated within the Polar Frontal Zone (PFZ), a heterogeneous marine environment strongly influenced by the Antarctic Circumpolar Current (ACC). The PFZ is bounded by the Subantarctic Front (SAF) to the north and the Antarctic Polar Front (APF) to the south (Lutjeharms and Valentine 1984; Figure 1).

*Field protocol.*— Growth of pups was assessed using cross-sectional sampling, where a random sample of individuals in the population were weighed at predefined intervals, assuming little departure from the median birth dates of 11 December (Gough Island) and 17 December (Marion Island—Bester 1987; Hofmeyr et al. 2007). Standardization of weighing dates was strived for, but sampling effort nonetheless varied through time

owing to varying field capacity. At Cape Davis, Marion Island, approximately 50 pups of each sex were weighed at 35, 70, and 300 days of age (1993 - 1995), at 35, 70, 150, 200 (1996, 1997, 2001), and 300 days of age (1996 - 2001), and at age 0 (2002 - 2008), 30, 60, 90, 120, 150, 180, 200, and 300 days (2002 - 2014). Weighing at Gough Island (South Point and Tumbledown to Cave beaches) was less frequent; pups were mostly only weighed near weaning (at age 286 - 301 days; 1994 - 2000, 2008, 2009, 2011 - 2014), but pre-weaning mass measurements were also collected at 35, 70, 100, 150, 200 and 250 days of age in 2009 and 2012 - 2014. All ages are calculated from the appropriate island-specific median date of birth (age 0) up until weaning in mid-October (at age 300 days—Bester 1981; Kerley 1983, 1985). Therefore only weaning mass, collected annually at Marion Island (22 years) and intermittently at Gough Island (14 years), was comparable throughout the entire time series (1993 – 2014) and additionally to measurements made in the early 1980's. Sampling biases (e.g., behavioral segregation of pups of different ages or body mass) were minimized by sampling pups across the entire colony and being non-selective (e.g., weighing all individuals within a herded group—Trites 1993). Methods of capturing and weighing fur seal pups followed the guidelines for handling of marine mammals in field research (Gales et al. 2009) that are supported by the Society for Marine Mammalogy and that are consistent with the American Society of Mammalogists guidelines for research on wild mammals (Sikes et al. 2011).

*Mean annual growth rate.*— Pre-weaning growth in subantarctic fur seals is non-linear, with pups losing body mass towards the end of the lactation period (Figure 2). Growth is

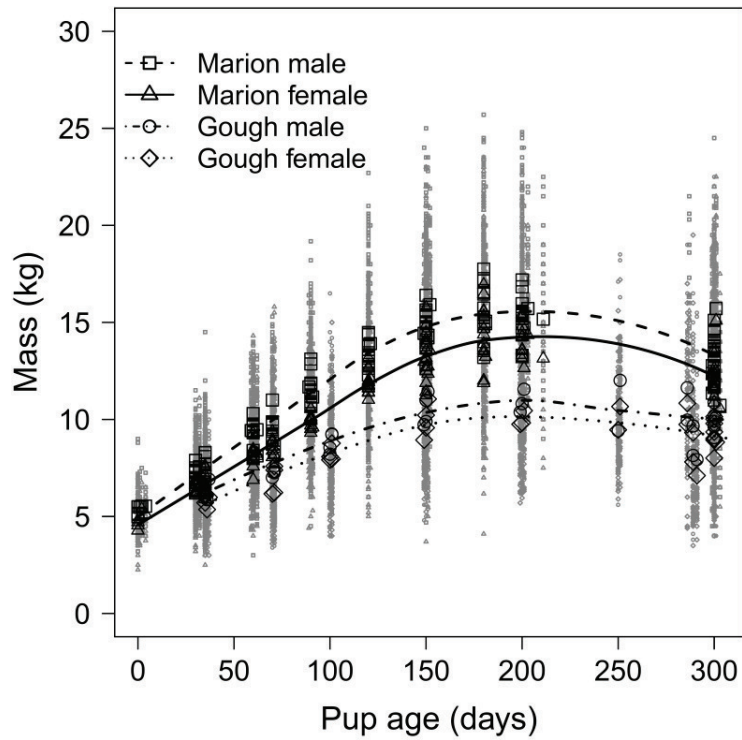


Figure 2. Change in mass for *Arctocephalus tropicalis* pups at Gough and Marion islands according to their age in days from 1993 to 2014. Open symbols represent the mean mass per weighing occasion ( $n \approx 50$  pups) per year. Individual measurements ( $n = 18107$ , plotted in grey), illustrate the increasing variance in body mass as pups grow older. For illustrative purposes, a loess smoothing curve traces the approximate average growth across all years for each group.

approximately linear between age 30 and 200 days (e.g., Kerley 1985; Chambellant et al. 2003) and we used linear regression to estimate a single slope coefficient (representing the mean growth rate) for this period so that our results can be compared to previous assessments of pre-weaning growth in otariids (Chambellant et al. 2003). Pups were weighed on five to seven occasions during all years considered (Marion Island, 2001 – 2014; Gough Island, 2009, 2012 - 2014). We recognize that several factors such as non-linearity, or the assumption that inter-annual variation in growth generates differences in the slope of the linear regression (rather than, for example the intercept), may bias growth rates derived from linear regression. Although growth rates based on linear regression should therefore be interpreted with some caution, comparative evaluations should be free of bias. As between-individual variance in body mass clearly increased with pup age, violating the homogeneity assumption of ordinary least squares regression, we fitted models using generalized least squares (GLS) using the nlme package (Pinheiro et al. 2013) implemented in R (R Core Team 2013). A fixed variance structure that ensured a variance proportional to age was effective to incorporate heterogeneity in modeling, and model validation (graphical plotting of standardized residuals) indicated no clear evidence of remaining heterogeneity. We tested for differences in growth (i.e., the regression of body mass against age) between males and females (sex), sites (Marion, Gough), and years, including the interactions between sex, site and age, using analysis of variance with Type III sum of squares for fixed effects (Zuur et al. 2009). Given that all terms included in the initial model were significant, we separately estimated the mean annual growth rate of male and female fur seal pups between 30 and 200 days of age for Marion Island (2001 - 2014) and Gough Island (2009, 2012 - 2014).

*Upper and lower limits of growth rate.*— An increasing number of factors that were not measured influence body mass as pups grow older, increasing the sampling variation with respect to the measured factors included in the regression model (Figure 2).

Heterogeneous variances implies that there are multiple slopes (growth rates) that characterize changes in the probability distributions, i.e., the relationship between body mass and age. Whereas the GLS regression focused on estimating rates of change in the *mean* of the response as a function of a set of predictor variables, quantile regression allows estimation of the functional relations between variables for all portions of a probability distribution, including the boundary (Cade and Noon 2003, Koenker 2005). By estimating multiple rates of change between the minimum and maximum response, quantile regression can provide a more holistic picture of the relationship between variables. We estimated regression parameters for the quantiles  $\tau = \{0.05, 0.1, 0.2, 0.3, \dots, \dots, 0.9, 0.95\}$ , where  $\tau = 0.9$  represents the line below which 90% of the data points are predicted to fall. Confidence intervals (95% *CI*) for quantile regression parameters were estimated using the rank inversion method (Koenker 2005) as implemented in package ‘quantreg’ (Koenker 2013), in R.

*Weaning mass trend.*— We fitted a suite of regression models to examine the long-term relationship between weaning mass and explanatory variables. The factors sex and site (Marion, Gough) explained part of the within-year variation in weaning mass.

Environmental covariates (SOI, SAM, SST – see below), year (fitted as a continuous variable “trend,” including quadratic functions), and interactions between these terms

were considered as explanatory effects of between-year variation in weaning mass. Density dependence in weaning mass can be estimated by fitting a regression model between density (equivalently population size) and weaning mass at time  $t$  in individual  $j$  (Lebreton and Gimenez 2013). However, although we suspect population changes to have occurred during the study period (Mia Wege, University of Pretoria, Pretoria, South Africa, pers. comm., May 2015), estimates of population size at Marion Island were based on few counts, whereas accurate population size estimates were unavailable for Gough Island. We approximated the annual population size at Marion Island by fitting a four-parameter logistic model to count data (see Supporting Information S1). However, the values obtained from this regression were 1) naïve, in that the regression ignored uncertainty in population size (Lebreton and Gimenez 2013) and 2) highly correlated with “trend” (i.e., time; Pearson’s correlation coefficient = 0.86). Consequently, population size was not included as a covariate to directly estimate the strength of density dependence and we limited ourselves to a qualitative interpretation of its influence on weaning mass.

A null (intercept) model, baseline models including sex and site, and models specifying temporal trends were evaluated first; environmental covariates were then added to the most parsimonious temporal model. Model selection was based on Akaike’s Information Criterion, adjusting for sample size ( $AIC_c$ ). Models with the lowest  $AIC_c$  are the most parsimonious; models with a difference of less than 2  $AIC_c$  units have similar support from the data. A difference of more than 7  $AIC_c$  units indicate strong support for the

model with the lower AIC<sub>c</sub> (Burnham and Anderson 2002). Graphical summary plots conformed with assumptions of normality and constant variance of residuals.

*Environmental parameters.*— Many environmental covariates potentially influence predator population parameters, but to reduce the probability of spurious correlations, we limited our investigation to three indices known to widely affect Southern Ocean predator populations. First we considered the El Niño Southern Oscillation (ENSO), a large scale climatic mode that results in near global perturbations in climate (“ENSO-events”— McPhaden et al. 2006; Trathan et al. 2007). Large scale climatic modes such as ENSO (and SAM – see below) may better predict ecological processes compared to local weather indices by incorporating several different weather components and reducing complex space and time variability characteristics of local weather variables (Hallett et al. 2004; Stenseth and Mysterud 2005). ENSO has its origins in the tropical Pacific, but propagates westward with oceanographic transport (Turner 2004) or through atmospheric teleconnections (Klein et al. 1999), also affecting top predator populations in the southern Atlantic and Indian Oceans (e.g., Barbraud et al. 2012 and references therein). Strong regional relationships exist and ENSO has a significant impact on the low to mid-latitudes of the South Atlantic Ocean (Colberg et al. 2004).

We quantified the strength of ENSO using the Southern Oscillation Index (SOI), measured as the standardized difference in sea-level pressure between Tahiti and Darwin (Australia). Monthly SOI values were obtained from the Australian Bureau of Meteorology (2015). For each year  $t$ , we calculated the annual SOI anomaly by

subtracting the 50 year mean (1965 - 2014) for the October ( $t - 1$ ) to June ( $t$ ) period from the mean October ( $t - 1$ ) to June ( $t$ ) values recorded in year  $t$  (see Supporting Information S2). These SOI anomalies are a representation of the environmental conditions immediately prior to and during the first six months of lactation when pup growth is positive. Anomalies calculated over different time periods (e.g., December [ $t - 1$ ] to October [ $t$ ]) were highly correlated with our index. Positive SOI anomalies correlate with cold anomalies in the tropical Pacific (La Niña events) whereas negative SOI anomalies are associated with global climate variability resulting from unusually warm conditions in the tropical Pacific (El Niño events—McPhaden et al. 2006).

The Southern Annular Mode (SAM) is the dominant mode of inter-annual extra-tropical atmospheric variability in the Southern Hemisphere (Thompson and Wallace 2000). Positive phases of SAM are characterized by a stronger than usual sea level pressure gradient between the mid- and high-latitudes; this leads to a poleward shift in surface westerly winds of increased zonal strength, especially during the austral summer (Hartman and Lo 1998). These westerly winds are highly influential in driving the circulation of the Southern Ocean, including the strong eastward flow of the Antarctic Circumpolar Current (ACC). Some of the upper ocean responses to SAM in the Subantarctic Zone (SAZ) and the Subtropical Zone (STZ; Figure 1) are potentially relevant to this study. During positive phases of SAM, poleward anomalies in Ekman transport cause warm sea surface temperature anomalies, increased convergence (downwelling), deepening of the mixed layer and decreased chlorophyll *a* concentration in the SAZ (Hall and Visbeck 2002, Lovenduski and Gruber 2005). In the STZ, warm



SST anomalies and increased stratification of the water column during positive SAM reduce macronutrient supply to the surface, leading to decreased surface chlorophyll *a* concentration (Lovenduski and Gruber 2005).

Monthly SAM index values were obtained from the United States National Oceanic and Atmospheric Administration (2015). For each year  $t$ , we calculated the annual SAM anomaly by subtracting the 35 year mean (1980 - 2014) for the October ( $t - 1$ ) to June ( $t$ ) period from the mean October ( $t - 1$ ) to June ( $t$ ) values recorded in year  $t$  (see Supporting Information S3).

Remotely sensed sea surface temperature (SST) data were used as a proxy of regional climatic conditions. Monthly SST data on a  $1^\circ$  scale (Reynolds et al. 2002; Integrated Global Ocean Services System 2015) were averaged over the period October ( $t - 1$ ) to June ( $t$ ) across the potential core foraging range of fur seals;  $42^\circ30' - 47^\circ30'S$ ,  $31^\circ30' - 43^\circ30'E$  (Marion Island) and  $37^\circ30' - 42^\circ30'S$ ,  $3^\circ30' - 15^\circ30'W$  (Gough Island; Figure 1). Annual SST anomalies were calculated by subtracting the 33 year mean (1982 - 2014) for the October ( $t - 1$ ) to June ( $t$ ) period from the mean October ( $t - 1$ ) to June ( $t$ ) values recorded in year  $t$  (see Supporting Information S4). All environmental covariates were standardized ( $\bar{X} = 0$ ,  $SD = 1$ ) prior to analysis.

## **RESULTS**

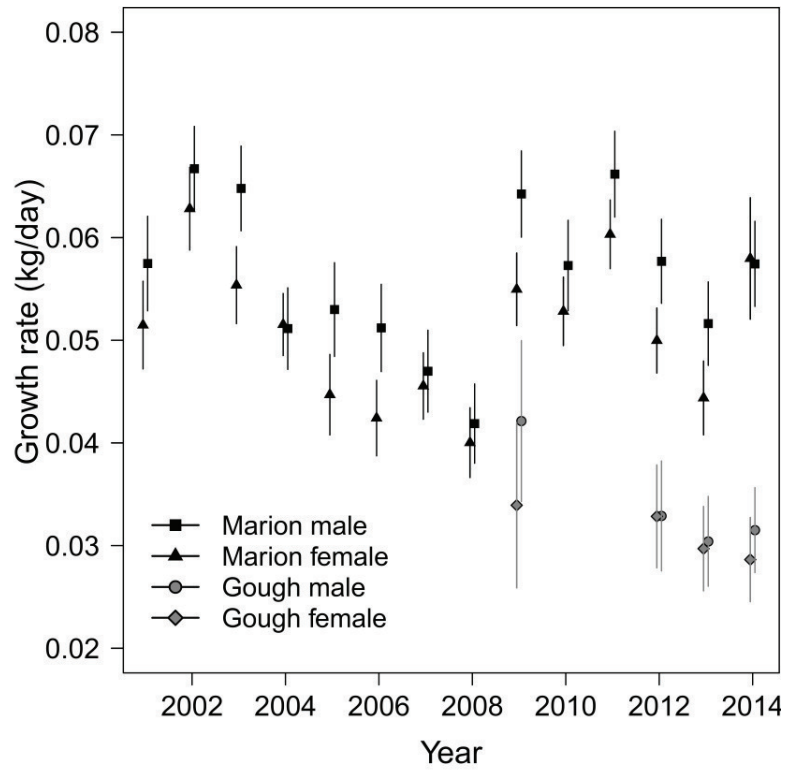


Figure 3. Mean growth rate of *Arctocephalus tropicalis* pups at Marion Island (2001 – 2014) and Gough Island (2009, 2012 - 2014) from 30 to 200 days of age. Points represent the estimated slope coefficient and 95% confidence interval of a least-squares regression of pup body mass against pup age.

*Mean, lower and upper limits of growth during early lactation.*— Between 30 and 200 days of age, Marion Island pups increased in body mass at an average rate of between 0.040 and 0.067 kg/day, depending on year ( $F_{(21)} = 23.32$ ,  $P < 0.01$ ; Figure 3). Growth rates at Marion Island tended to decrease from 2002 to 2008, but increased thereafter. Male pups tended to grow faster than female pups at Marion Island ( $\beta_{male} = 0.67 \pm 0.06$  SE;  $F_{(1)} = 122.11$ ,  $P < 0.01$ ) but at Gough Island, all pups grew considerably slower and often at more comparable rates of around 0.031 kg/day (female) and 0.034 kg/day (male) on average (sex\*site interaction;  $\beta_{male\ Gough} = -0.43 \pm 0.10$  SE;  $F_{(1)} = 19.14$ ,  $P < 0.01$ ). Quantile regression analysis revealed that the mean growth rate at Gough Island was lower than the growth rate represented by the bottom 5% of the body mass distribution at Marion Island. Growth rates derived from the 0.05th quantile (i.e., some of the lightest pups) at Marion Island were 0.032 kg/day (0.030 – 0.036 kg/day 95% CI) (female) and 0.037 kg/day (0.036 – 0.040 kg/day) (male). At Gough Island, growth rates were as low as 0.015 kg/day (0.014 – 0.018 kg/day) and 0.020 kg/day (0.016 – 0.023 kg/day) for female and male pups at the lower end of the distribution ( $\tau = 0.05$ ; Figure 4). Maximum growth rates ( $\tau = 0.95$ ) for Gough Island males were in the order of 0.043 kg/day (0.035 – 0.052 kg/day). Nearly 72% (female) and 85% (male) of pups born at Marion Island exceeded this rate of mass gain (Figure 4).

*Weaning mass trend.*— Among those models evaluated, model selection favored two related models that specified sex and site specific quadratic trends in weaning mass, together with SOI and SST (including interactions between SOI and sex and SST and site, respectively) as the most parsimonious representation of the data (Table 1). Weaning

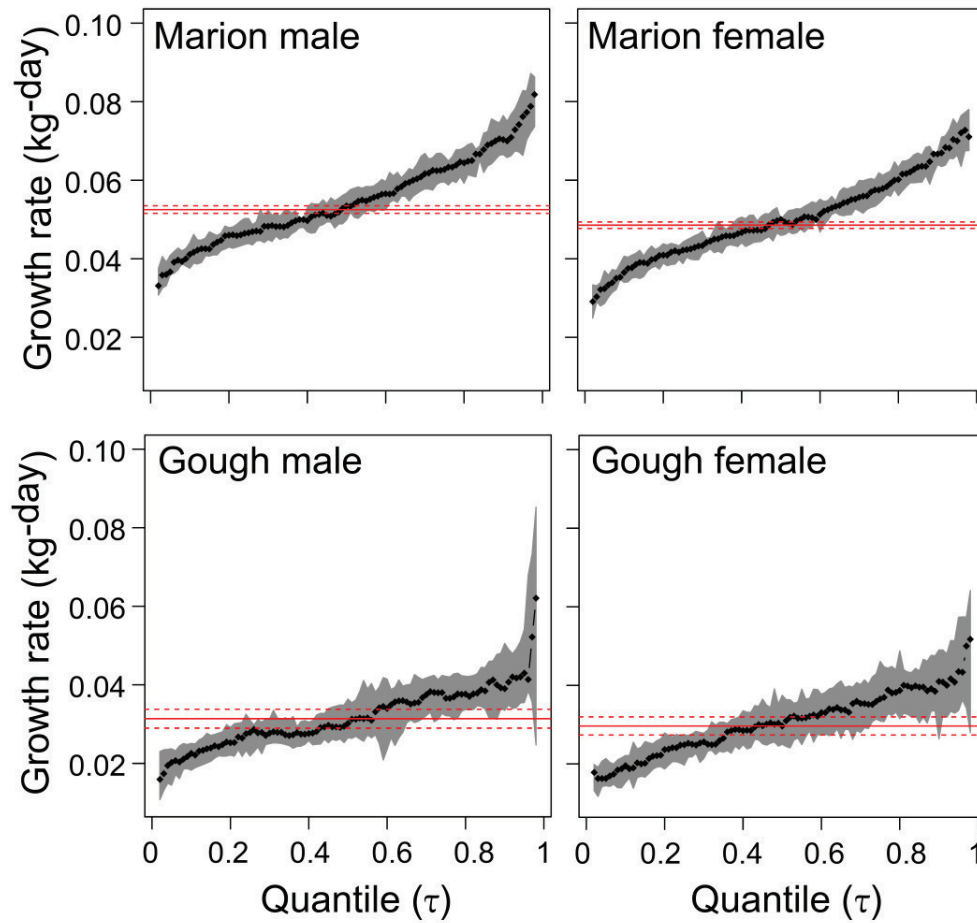


Figure 4. Linear quantile regression for *Arctocephalus tropicalis* pups weighed at Marion Island (2001 – 2014) and Gough Island (2009, 2012 - 2014). Horizontal axes depict the quantiles ( $\tau = 0.02, 0.03, \dots, \dots, 0.98$ ) of the dependent variable, body mass. Estimates of the slope coefficient (black dots) represent the growth rate (kg/day) from 30 to 200 days of age across the entire probability distribution. Uncertainty about predicted values is given by 95% confidence intervals (CI, grey shading). The comparable mean (constant) slope and 95% CI estimates from an ordinary least squares regression is indicated by the horizontal solid and dashed lines, respectively.

Table 1. Selection of models investigating *Arctocephalus tropicalis* weaning mass response to environmental covariates at Marion- and Gough Island. Additive effects (+) and interaction terms (\*) were considered. The number of parameters (k), model deviance,  $\Delta AIC_c$  (the  $AIC_c$  difference between the current model and the most parsimonious one), and Akaike weight ( $w_i$ , representing the relative support a model has from the data compared to the other models in the set) is given. Models with the strongest support are indicated in bold.

	Model	k	Deviance	$\Delta AIC_c$	$w_i$
1	Intercept	2	37429.65	1191.72	0.00
2	sex + site	4	28388.85	231.41	0.00
3	sex * site	5	28371.37	231.27	0.00
4	sex + site + trend <sub>(linear)</sub>	5	27478.69	119.75	0.00
5	sex + site * trend <sub>(linear)</sub>	6	27430.63	115.66	0.00
6	sex * trend <sub>(linear)</sub> + site	6	27476.35	121.46	0.00
7	sex + site * trend <sub>(quadratic)</sub>	8	27304.93	103.65	0.00
8	sex * trend <sub>(quadratic)</sub> + site	8	27389.18	114.40	0.00
9	sex * trend <sub>(quadratic)</sub> + site * trend <sub>(quadratic)</sub>	10	27247.09	100.28	0.00
10 <sup>a</sup>	sex + Gough * trend <sub>(linear)</sub> + Marion * trend <sub>(quadratic)</sub>	6	27527.36	127.94	0.00
11	sex * trend <sub>(quadratic)</sub> + site * trend <sub>(quadratic)</sub> + SOI	11	26587.70	16.84	0.00
12	sex * trend <sub>(quadratic)</sub> + site * trend <sub>(quadratic)</sub> + SAM	11	26782.94	42.36	0.00
13	sex * trend <sub>(quadratic)</sub> + site * trend <sub>(quadratic)</sub> + SST	11	26830.07	48.49	0.00
14	sex * trend <sub>(quadratic)</sub> + site * trend <sub>(quadratic)</sub> + SOI + SAM	12	26534.43	11.86	0.00
15	sex * trend <sub>(quadratic)</sub> + site * trend <sub>(quadratic)</sub> + SOI + SST	12	26487.63	5.70	0.03
16	sex * trend <sub>(quadratic)</sub> + site * trend <sub>(quadratic)</sub> + SAM + SST	12	26591.08	19.30	0.00
17	sex * trend <sub>(quadratic)</sub> + site * trend <sub>(quadratic)</sub> + SOI + SST + site*SOI	13	26487.61	7.71	0.01
18	sex * trend <sub>(quadratic)</sub> + site * trend <sub>(quadratic)</sub> + SAM + SST + site*SAM	13	26581.49	20.06	0.00
19	<b>sex * trend<sub>(quadratic)</sub> + site * trend<sub>(quadratic)</sub> + SOI + SST + site*SST</b>	<b>13</b>	<b>26429.08</b>	<b>0.00</b>	<b>0.53</b>
20	<b>sex * trend<sub>(quadratic)</sub> + site * trend<sub>(quadratic)</sub> + SOI + SST + sex*SOI</b>	<b>13</b>	<b>26432.52</b>	<b>0.45</b>	<b>0.42</b>
21	sex * trend <sub>(quadratic)</sub> + site * trend <sub>(quadratic)</sub> + SOI + SST + sex*SST	13	26487.41	7.69	0.01

<sup>a</sup> Gough and Marion refer to special cases of site, see text.

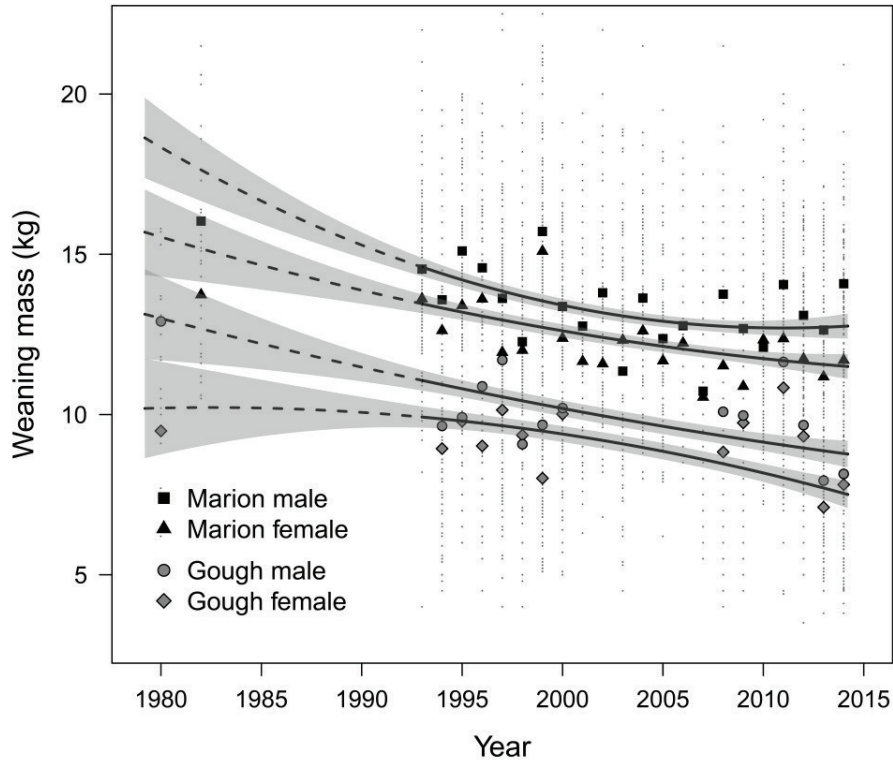


Figure 5. Long-term trend in weaning mass of *Arctocephalus tropicalis* pups at Gough and Marion islands. Filled points correspond to the observed average weaning mass per group; dots represent individual measurements ( $n = 3488$ ). The lines correspond to the trajectories of weaning mass between 1980 and 2014, based on parameter estimates from model 19 (Table 1). Prediction of the weaning mass trend prior to 1993 (dotted line) is based on very limited data and, as the trend line is mostly driven by observations made after 1993, trends prior to this date should be interpreted with care. The shaded areas represent 95% confidence intervals around the mean prediction.

mass of Marion Island pups were, on average, higher than Gough Island pups ( $\beta_{Gough} = -3.50 \pm 0.13 SE$ ; parameter estimate[s] averaged over models 19 and 20). Sex specific difference was somewhat more pronounced for Marion Island pups, although our model selection criteria favored the simpler interpretation that males were consistently heavier at weaning ( $\beta_{male} = 0.93 \pm 0.11 SE$ ), regardless of site. Weaning mass exhibited a decreasing trend at both populations with the rate of change dependent on sex and site (Figure 5). Environmental covariates reduced  $AIC_c$  values drastically compared to the most parsimonious model including only quadratic temporal trends (SOI,  $\Delta AIC_c = 83.44$ ; SAM,  $\Delta AIC_c = 57.92$ ; SST,  $\Delta AIC_c = 51.79$ ). Models including the additive effects of SOI and SST were best supported by the data. Weaning mass tended to be higher when sea surface temperatures were warmer ( $\beta_{SST} = 0.21 \pm 0.08 SE$ ), with a stronger positive effect at Gough Island ( $\beta_{SST\ Gough} = 0.43 \pm 0.15 SE$ , model 19) and during positive phases of SOI ( $\beta_{SOI} = 0.33 \pm 0.09 SE$ ), with a stronger positive effect in males ( $\beta_{SOI\ male} = 0.30 \pm 0.11 SE$ , model 20; Figure 6). The most parsimonious models accounted for roughly 30% of the variance in weaning mass.

## DISCUSSION

*Comparisons of growth across populations.*— Body mass is an easily obtained index of the allocation and assimilation of maternal energy in fur seal pups that is thought to relate to general food availability and adult female foraging success (Agnew 1997; Reid 2002; Hindell et al. 2003). The simplicity of the index makes it an ideal and essential part of basic population monitoring, especially for poorly studied populations. Gough Island, the

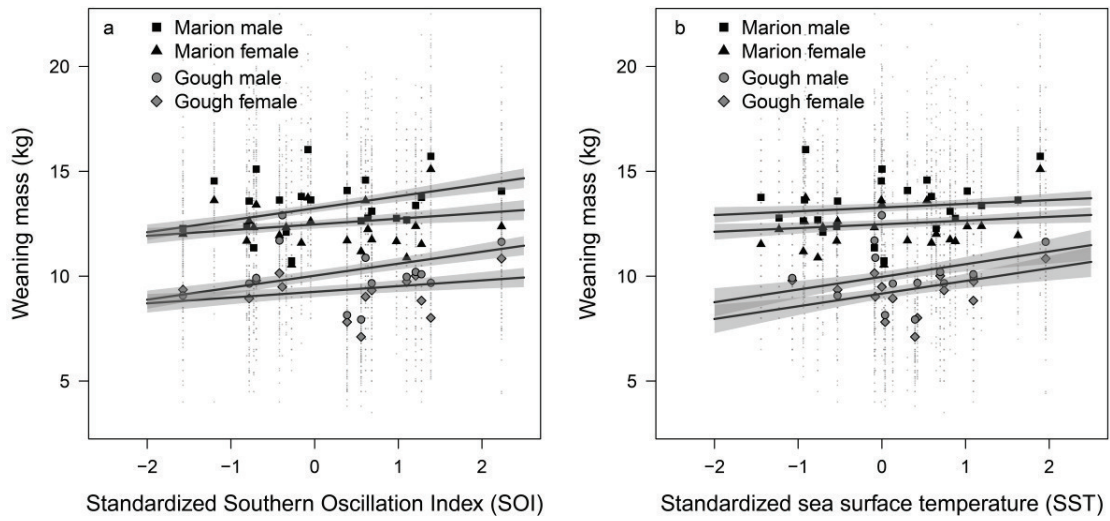


Figure 6. Positive relationship between weaning mass of *Arctocephalus tropicalis* pups at Gough and Marion islands and a) standardized Southern Oscillation Index (SOI); b) standardized sea surface temperature (SST). Predictions were derived from models 20 and 19, respectively (Table 1). Uncertainty about predicted values is given by 95% confidence intervals (grey shading). Filled points correspond to the observed average weaning mass per group; dots represent individual measurements ( $n = 3488$ ).



site of the largest subantarctic fur seal breeding population globally, provides a critical reference point for assessing the vigor of other populations of subantarctic fur seals, but scant information exists by which to gauge the health and demographic prospects of this population. Our long-term data on subantarctic fur seal pup growth clearly revealed a downward trend over the last two decades at both Gough and Marion islands, a trend that shorter-term studies failed to detect (e.g., Kirkman et al. 2002). Indications are that growth rates at Gough Island are perhaps some of the lowest growth rates among otariids (Chambellant et al. 2003), suggesting that adult females from this population were experiencing greater resource limitation compared to conspecifics at Amsterdam and Marion islands. Although body mass is not strictly equivalent to measurement of body condition (this requires variation in structural body size to be taken into account), there is likely a strong correlation between body mass and condition in fur seal pups (e.g., Osman et al. 2010 for Juan Fernández fur seal pups). It is unlikely that genotypic population differences (Wynen et al. 2000) predispose Gough Island pups to smaller structural body size or lower growth rates as adults here are of similar size (Kerley et al. 2000) or larger (Bester and Van Jaarsveld 1994) than at Marion Island. The growth rates of Marion Island pups were broadly similar to those previously recorded at Amsterdam Island (Guinet and Georges 2000; Chambellant et al. 2003), the only other major breeding site for subantarctic fur seals.

Quantile regression illustrated substantial heterogeneity in growth rates, both within and between island populations. The effects of sex and site were clearly important determinants of growth, but due to the relatively crude nature of cross-sectional sampling,

modeling still treated most individuals as alike. Some of the heterogeneity in growth rates arise from sampling variation. For example, because not all births occur exactly on the median pupping date, a distribution of ‘true’ ages is sampled at every weighing occasion that is based on intervals since the median pupping date. Furthermore, as pups age, an increasing number of factors that were not measured are likely to influence pup mass, thereby increasing the heterogeneity in the response variable relative to those factors included in the model. We expect that much of the site-specific heterogeneity in growth derived from maternal characteristics, for example maternal body size and age, as well as maternal attendance patterns (time since last suckling) in relation to weighing dates (e.g., Georges and Guinet 2000; Beauplet et al. 2004). While a case can be made for more intensive longitudinal pup growth studies including individual and maternal attributes (e.g., Forcada and Hoffman 2014), these studies are labor intensive and as a result, often short-term (e.g., one breeding season [Guinet et al. 1999, 2000; Guinet and Georges 2000]; two years [Goldsworthy 2006]; seven years [Chambellant et al. 2003]). For studies that aim to detect relationships between an explanatory variable and density- or environmental variation, temporal replication (i.e., sample size) is usually the number of study years and, for studies similar to ours, not the number of pups captured (Bradshaw et al. 2000). Intensive studies are often difficult to maintain longitudinally, and frequently hampered by a low number of statistical units (Grosbois et al. 2008). Our results illustrate the value of continuing population monitoring over longer periods that increase the number of statistical units and can incorporate population changes and a range of environmental conditions, despite the compromise of lower resolution data.

The prevailing local environmental conditions that govern prey availability are, together with density-dependent effects, probably key factors driving inter-island variation in growth. The physical features of the ocean habitat where fur seals from the different island populations forage will impact on the abundance and composition of prey, while the structure of the top-predator guild of each island may influence inter-specific competition. Adult female subantarctic fur seals from Marion Island typically forage in the Antarctic Polar Front Zone (PFZ), between the Antarctic Polar Front (APF) in the south and the Subantarctic Front (SAF) to the north, and in the Subantarctic Zone (SAZ), between the SAF and Subtropical Front (STF—de Bruyn et al. 2009). Mesopelagic fish, on which fur seals prey, occur at elevated densities at the APF and SAF (Pakhomov et al. 1996), but knowledge of prey distribution and especially their seasonal and inter-annual abundance in this region of the Southern Ocean is poor (McQuaid and Froneman 2008). Female fur seals from Amsterdam Island mainly forage within the Subtropical Zone (STZ; the meridional range of the STF) during lactation and, together with females from Marion Island, undertake some of the longest (distance traveled and duration) known maternal foraging trips of any fur seal (Beauplet et al. 2004; de Bruyn et al. 2009). Whether the low growth rates recorded at Gough Island are associated with similar, or perhaps even more extreme foraging behavior during lactation, is entirely unknown as no maternal attendance pattern or at-sea tracking data exists for this population. Gough and Amsterdam islands offer an interesting geographical comparison; whereas lactating females from Amsterdam Island often travel a few hundred kilometers southwards to the STF (Beauplet et al. 2004), this front is located in the vicinity of Gough Island in summer. Mixing of warm sub-tropical surface water across the STF may enhance prey

densities in this region (Lutjeharms et al. 1985), but it remains to be determined whether lactating Gough Island fur seals forage within the limits of this front.

Efficient energy consumption during lactation by subantarctic fur seals is not only affected by prey availability, but also the calorific value of prey species. Subantarctic fur seals at Marion Island predominantly prey on mesopelagic fish of the family Myctophidae (lanternfishes) (Makhado et al. 2013). Several myctophid species are particularly rich in lipids (e.g., *Gymnoscopelus* and *Electrona* spp., Tierney et al. 2002) leading to some of the highest energy densities of any fish species (9.3 kJ/g wet mass on average for myctophids caught in the South Indian Ocean, Lea et al. 2002). While energy rich myctophids constitute the major dietary component of Marion Island fur seals, analysis of stomach contents suggested that subantarctic fur seals at Gough Island prey predominantly on cephalopods, as only relatively small quantities of fish were recovered from stomach contents (Bester and Laycock 1985). Cephalopods have characteristically low energy content (2 to 4 kJ/g wet mass, Croxall and Prince 1982) and, based on calorific value alone, myctophids therefore appear to be more rewarding prey.

Differential prey digestion and retention lead, however, to underrepresentation of fish prey in stomach samples, and myctophids also feature strongly in scat samples collected more recently at Gough Island (Marthán Bester, University of Pretoria, Pretoria, South Africa, pers. comm., April 2015), as did cephalopods in the stomach contents of Marion Island animals (Ferreira and Bester 1999). The myctophid diet of female subantarctic fur seals breeding at Gough Island is expected to be more similar to those at Amsterdam Island (Beauplet et al. 2004), comprising a range of temperate to sub-tropical species, that

differ considerably to the species composition of prey taken by Marion Island seals (Makhado et al. 2013). Because the squid prey of fur seals at Marion Island may also be underestimated by scat analysis methodology (Ferreira and Bester 1999; Makhado et al. 2013), a reassessment of the diet of both island populations, in particular that of adult females, also using other methods (e.g., stable isotope, fatty acid or genetic analyses) that complement current knowledge will be a valuable contribution to comprehensively assess the preferred (or obtainable) prey types at each location.

*Resource limitation and potential competitive interactions.*— Inter-specific competition for prey seems most probable at Marion Island, where the myctophid diet of subantarctic fur seals overlaps substantially with that of the relatively small but increasing Antarctic fur seal population ( $n = \sim 4,000$  individuals, Hofmeyr et al. 2006, Makhado et al. 2008, Mia Wege, University of Pretoria, Pretoria, South Africa, pers. comm., May 2015) and large king penguin population (*Aptenodytes patagonicus*;  $\sim 165,000$  pairs—Crawford et al. 2009). However, ecological segregation based on different foraging behavior (dive depth, target prey size) and spatial segregation of preferred foraging areas effectively reduce resource competition between these predators (Klages and Bester 1998). Intra-specific competition, and specifically intra-sexual competition (i.e., between lactating adult females) is potentially a more significant regulating factor, especially for the large Gough Island population. Our study period was associated with increasing numbers of pups born on recently colonized southeast coast breeding sites at Gough Island (Bester et al. 2006), suggesting positive population growth. Such continued increases seem unlikely given the progressively poor body mass of pups at weaning.

Density dependence can be evaluated at the population level (e.g., time series population counts—McMahon et al. 2009) or by relating estimated population size to life history traits, whether demographic (e.g., survival, fecundity) or not (e.g., body mass—Gaillard et al. 1996, Mørbæk et al. 2013). Density dependence occurs through the depletion of key resources and population size is merely a proxy for the latent variable(s) that become limiting when population numbers increase (Lebreton and Gimenez 2013). Population size increases may, for example, initiate or intensify at-sea foraging competition among lactating females, or when space becomes limiting, aggravate negative effects onshore (e.g., Reid and Forcada 2005). Aggressive interactions, non-lethal infections and mother pup separation may, for instance, be more frequent at high densities. Reductions in individual growth rate and body mass is a typical response to increasing density (Bonenfant et al. 2009). We postulate that the difference in pup growth and weaning mass at Gough and Marion islands may partly be explained by differences in pup density at these islands, as observed for colonies of New Zealand fur seal (*Arctocephalus forsteri*) pups (Bradshaw et al. 2000). Temporal trends in population size at Marion Island (see Supporting Information S1) suggest that weaning mass may have decreased as population numbers increased—presumably a density-dependent effect. Admittedly, the high correlation between time (“trend”) and approximate population size do not allow us to unequivocally distinguish between the contribution of population size and any other, unidentified changes in the ecosystem that may have occurred co-linearly. But, the quadratic form of the weaning mass regression for Marion Island (decreasing rate of change) agrees with the apparent reduction in population growth at this site during the

latter part of the study period (Hofmeyr et al. 2006; Mia Wege, University of Pretoria, Pretoria, South Africa, pers. comm., May 2015). While the large disparity in weaning mass between subantarctic fur seal pups weaned at Gough Island (a high density population) and those living at Marion Island (a lower density population by comparison) furthermore submits population density as a major determinant of body mass, it is difficult to disentangle the regulating effects of density and regional environmental conditions when making such comparisons. As for New Zealand fur seal pups (Bradshaw et al. 2000), we expect distinct local environmental conditions (some to which we alluded earlier) and density to jointly influence body mass. Finally, commercially exploited fish do not comprise a major component of the diet of subantarctic fur seals (Makhado et al. 2013) and fisheries are not thought to have played a significant role in the decrease in growth of fur seal pups to date.

*Environmental correlations with weaning mass.*— Within the downward trend, there was also substantial inter-annual variability in the mean weaning mass. We found strong model support for higher (lower) weaning mass during years of positive (negative) SOI anomalies, i.e., during La Niña (El Niño) events. Several cycles of ENSO occurred during our study period, including by some measures, the strongest El Niño (1997/1998) and La Niña (2010 - 2012) events on instrumental record (McPhaden et al. 2006; Tobin and Skinner 2012). The correlation between weaning mass and ENSO was largely driven by higher than predicted weaning mass during 1999, 2008 (moderately positive SOI), and 2011 – 2012 (highly positive SOI and weaning mass anomalies), together with lower weaning mass recorded during the El Niño events of 1997/1998 and 2002/2003. These

results contrast earlier views based on a shorter time series (Kirkman et al. 2002), again highlighting the value of long-term monitoring. Males appear to realize significantly higher body mass than females only when conditions are good, with smaller gender differences observed at Gough Island and during El Niño events. This finding supports the view that male fur seal pups are not able to realize their growth potential under ‘poor’ conditions (Bester and Van Jaarsveld 1997; Vargas et al. 2009).

While substantial evidence of top predator responses to ENSO exists for other parts of the Southern Ocean (e.g., Testa et al. 1991; Trathan et al. 2007; Barbraud et al. 2012), it is unresolved how and if land-breeding predators from Marion Island are generally influenced by ENSO related environmental variation. Numerous seabird species breeding at Marion Island exhibited strong (and also contrasting) responses to the climatic perturbations associated with the strong 1997/1998 El Niño event. For example, while the demographic rates of several long-range foraging species (e.g., wandering albatross [*Diomedea exulans*], giant petrels [*Macronectes* spp.] and king penguins) were above average, 1997/1998 was a particularly poor breeding season for two species of inshore feeders (gentoo penguin [*Pygoscelis papua*] and Crozet shag [*Phalacrocorax [atriceps] melanogenis*])—Crawford et al. 2003). Whether these trends hold for less extreme El Niño events, and whether observed patterns are reversed during La Niña conditions, have not been investigated. At Îles Crozet, some 1000km due east of Marion Island, Antarctic- and subantarctic fur seal pup numbers tend to be lower in years following El Niño events, although only the former were statistically different to non-ENSO years (Guinet et al. 1994).



ENSO signals propagate to regions far removed from the tropical Pacific through both atmospheric and oceanic teleconnections (Klein et al. 1999); upper ocean temperature anomalies in the South Atlantic (to the north of Gough Island) associated with ENSO are, for example, primarily caused by atmospheric forcing (Colberg et al. 2004). There appears to be very weak relationships between SOI and SST in the regions we defined as the potential core foraging range for subantarctic fur seals. A cross-correlation analysis of SOI and SST using data from January 1982 to December 2014 ( $n = 396$  months), indicated that negative SOI anomalies (El Niño) preceded cooler sea surface temperatures by about three months, but the correlation was low for both Marion Island (0.128) and Gough Island (0.20; see Supporting Information S5). This cooling may be associated with a strengthening of the mid-latitude westerlies during the onset of El Niño events that enhance northward Ekman heat transport, favoring cooling in the mid-latitudes with a lag period of about three months (Colberg et al. 2004).

The linkage between weaning mass and ENSO was stronger than that of weaning mass and SAM. In the only other study attempting to correlate a life history trait of a marine predator breeding at Marion Island to variation in SAM, weaning mass of southern elephant seal (*Mirounga leonina*) pups born here exhibited no clear relationship with SAM (Oosthuizen et al. 2015). Although the foraging distribution of southern elephant seals extend much further west and southwards from Marion Island (McIntyre et al. 2011, Tosh et al. 2012, Oosthuizen et al. 2015) compared to that of subantarctic fur seals (de Bruyn et al. 2009), weaning mass in both species appears to fluctuate little in response to

variation in SAM. In other areas of the Southern Ocean, variation in SAM seems to have much more significant effects on marine predators. Positive SAM conditions are, for example, associated with poorer demographic performance of Antarctic fur seals at South Georgia (Forcada and Hoffman 2014). Negative annual rates of southern elephant seal population change at Macquarie Island are also associated with positive anomalies of SAM (Van den Hoff et al. 2014). However, regionally specific differences in the response of marine predators to SAM and other climatic indices are not entirely unexpected, and underline the need for studies from multiple geographic regions. The impact of SAM on SST, for example, is particularly strong along longitudes near the Ross Sea (Arrigo et al. 2008)—the principal foraging zone of southern elephant seals from Macquarie Island (Van den Hoff et al. 2014). In contrast, the influence of SAM on SST is much weaker in the South Indian Ocean (Arrigo et al. 2008), where marine predators from Marion Island forage pelagically.

While the regression coefficients described significant relationships between variables, these simple associations cannot strictly be interpreted as causal effects. Still, the inductive inference (cf. deductive inference that allows falsifying a hypothesis of interest) that observational studies offer, in our case the association between weaning mass and specific elements of the environment, is an important step towards identifying the processes that may impact populations (Grosbois et al. 2008). In many marine ecosystems, it is still uncertain how physical forcing propagates through the food web (Hindell et al. 2003) and little is known about the possible physical mechanisms that may link variability in SOI and SST and foraging conditions in the southern Indian and

Atlantic Oceans, including the ultimate impacts on predators. Identifying the mechanisms underlying the hypothesized relationships between climate and predator parameters remains an over-riding need (Hindell et al. 2003).

*Population and ecosystem monitoring.*— When reproduction competes with the amount of resources available for survival, individuals typically adopt risk sensitive regulation of their reproductive allocation (Bårdsen et al. 2011). This means that pup mass will be a more sensitive measure of environmental stress than parameters such as adult survival and population size, which are buffered against most limiting factors. Even so, female fur seals may modify their foraging behavior (e.g., increase intensity, shift foraging locations, switch prey) during years of low prey availability in order to maintain energy delivery to pups (Costa 2008). Pup mass, as an index of prey availability for females, may thus be safeguarded against short term reductions in prey availability through behavioral adjustments of foraging females. On the other hand, pup mass appears sensitive to regional scale abundance and longer-term changes in prey availability.

Because seal pup growth significantly influences juvenile survival (McMahon et al. 2000), and represents an objective measure of females' reproductive success (Beauplet et al. 2005), long-term trends in the growth rate of fur seal pups is a potentially informative indicator of future shifts in population status. Seeing that little information exists on the principal drivers of population growth such as adult survival and fecundity in subantarctic fur seals world-wide—but see Bester (1987, 1995) for Gough Island and Beauplet et al.

(2006) for Amsterdam Island,—pup growth rates provide essential information for detecting long-term changes in population status.

More generally—and perhaps optimistically—pup growth may be viewed as an ecosystem monitoring tool, providing insight into aspects such as the abundance, distribution and nutrient quality of lower trophic level prey (Hindell et al. 2003). Fur seals are clearly responsive to changes in the marine environment, but the challenge is to understand how these changes reflect variation in the physical environment and in primary and secondary production. Deciphering this message will demand a better understanding of the foraging ecology of fur seals and more critically, the factors influencing prey distribution and abundance.

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#### **SUPPORTING INFORMATION**

**Supporting Information S1.**—Subantarctic fur seal pup counts at Marion Island between 1952 and 2013.

**Supporting Information S2.**—Observed monthly Southern Oscillation Index (SOI) values and the trend component from 1982 to 2014.

**Supporting Information S3.**—Observed monthly Southern Annular Mode (SAM) values and the trend component from 1982 to 2014.

**Supporting Information S4.**—Remotely sensed monthly sea surface temperatures (SST) averaged across the potential foraging range of subantarctic fur seals from Marion- and Gough Island, respectively.

**Supporting Information S5.**—The sample cross correlation function (ccf) describing the relationship between the Southern Oscillation Index (SOI) and sea surface temperatures (SST) at Marion- and Gough Island, respectively.

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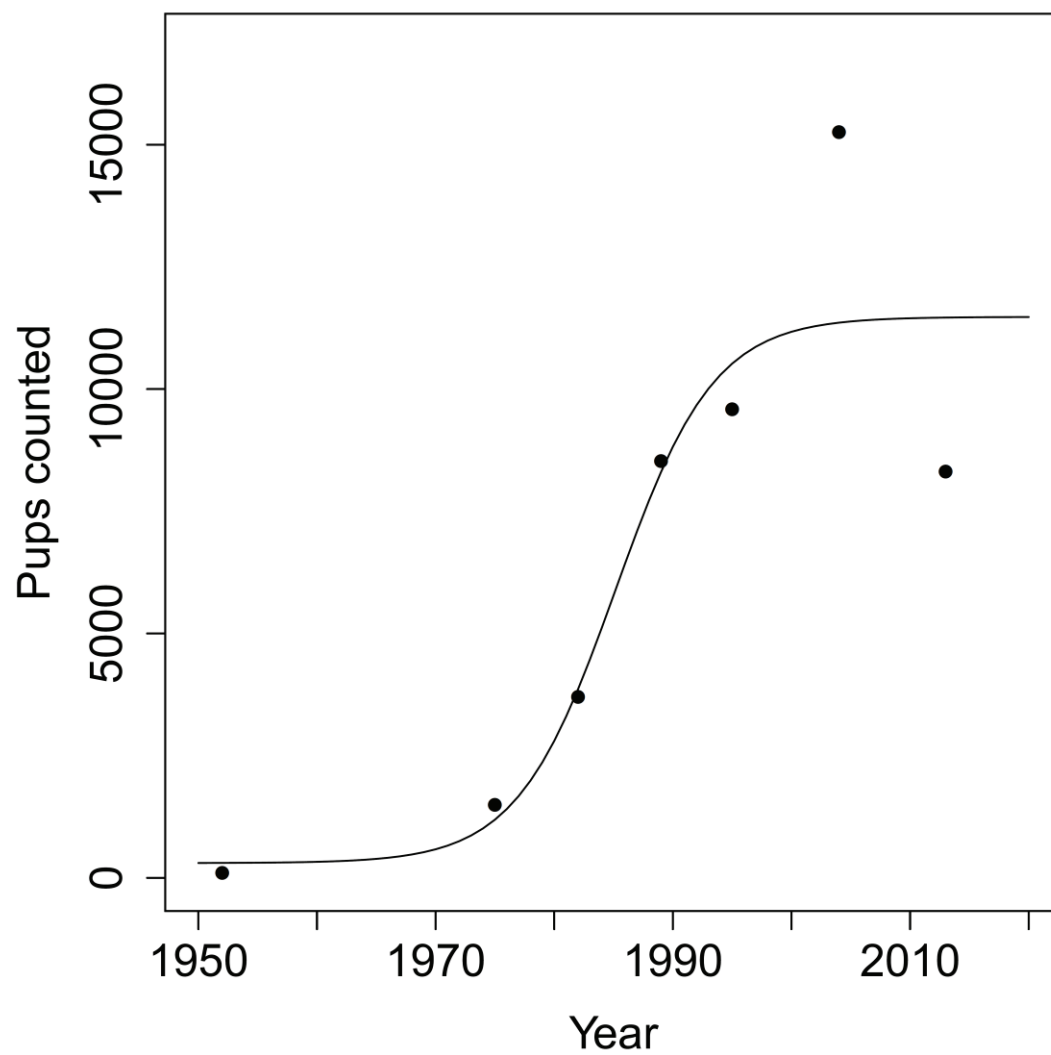
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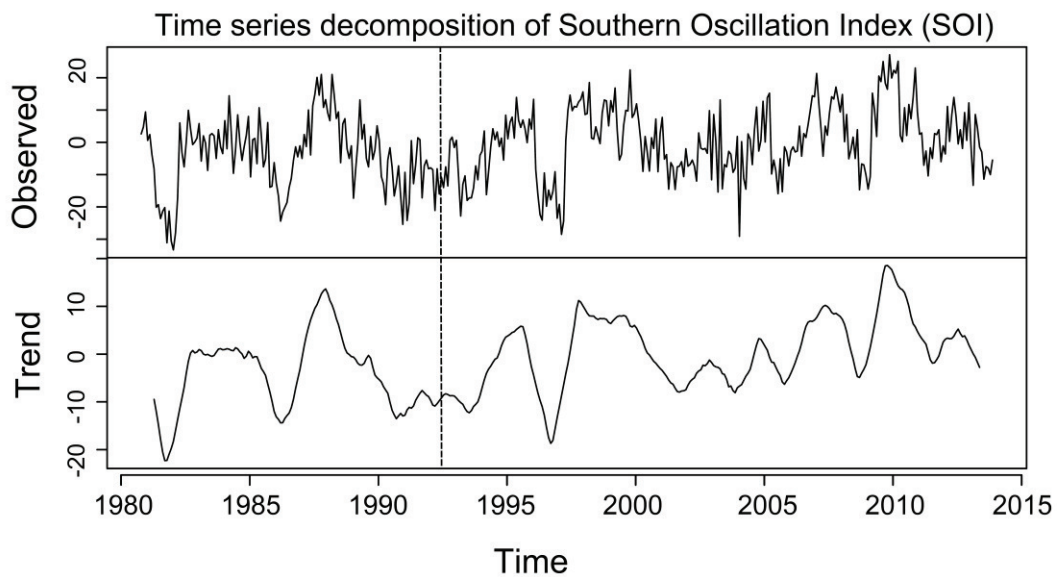
## SUPPORTING INFORMATION

Supporting Information S1. Four-parameter logistic model of *Arctocephalus tropicalis* population growth fitted to seven island-wide counts (filled circles) of pups made at Marion Island between 1952 and 2013. The model allows a lower as well as an upper asymptote.

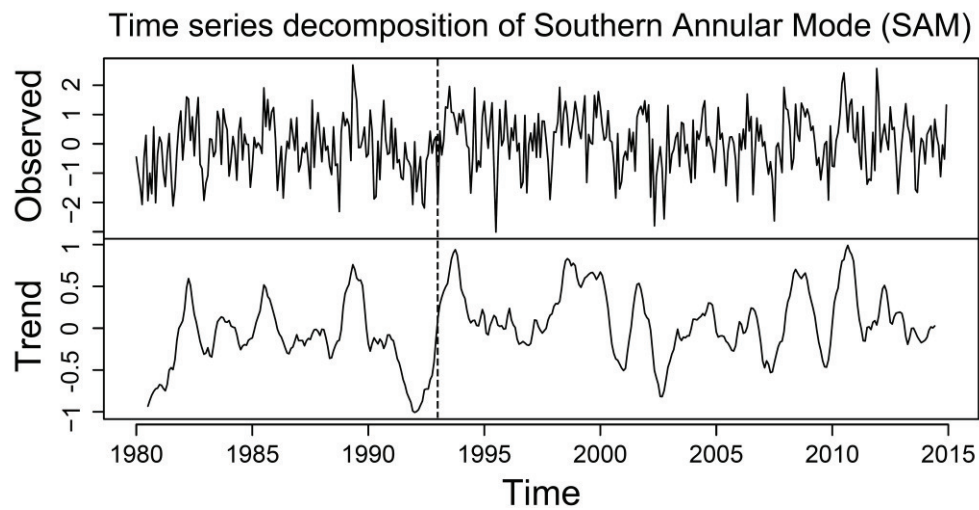




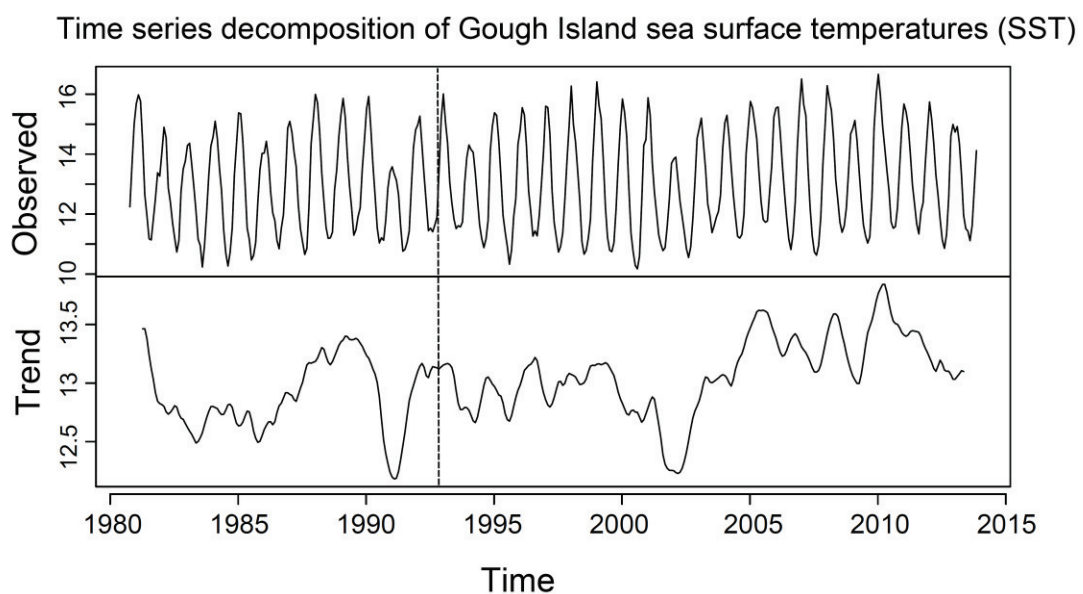
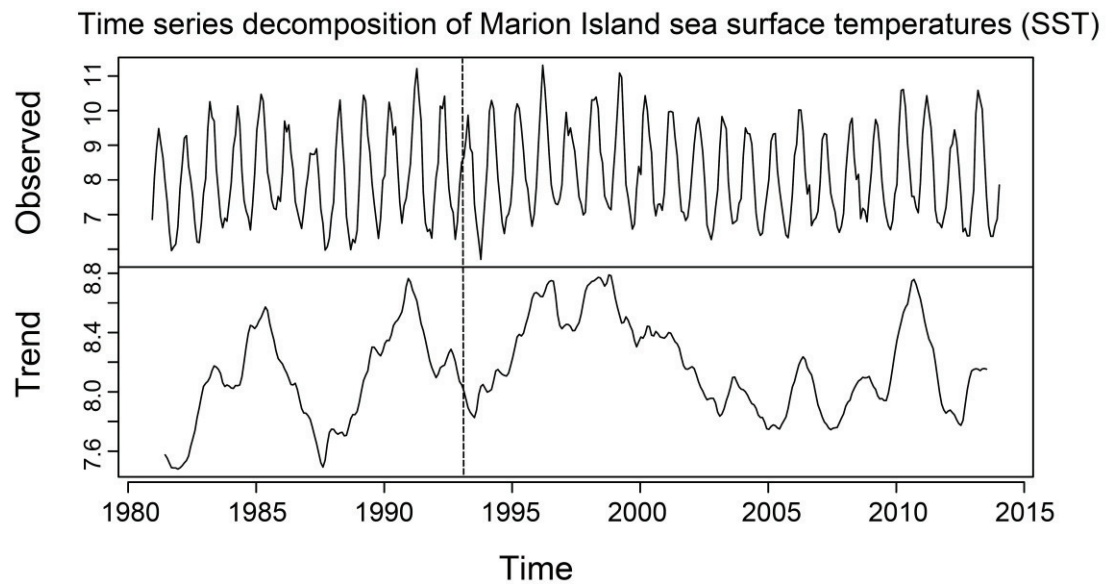
Supporting Information S2. Observed monthly Southern Oscillation Index (SOI) values (<http://www.bom.gov.au/climate/current/soihtm1.shtml>) and the trend component, obtained by using a moving average with a symmetric window and equal weights. The dotted line indicates the start of uninterrupted annual weaning mass measurements made at Marion Island. Covariates of environmental variation were standardized so that the mean and standard deviation over the long-term time series were set to 0 and 1, respectively.



Supporting Information S3. Observed monthly Southern Annular Mode (SAM) values (<http://www.cpc.ncep.noaa.gov/>) and the trend component, obtained by using a moving average with a symmetric window and equal weights. The dotted line indicates the start of uninterrupted annual weaning mass measurements made at Marion Island. Covariates of environmental variation were standardized so that the mean and standard deviation over the long-term time series were set to 0 and 1, respectively.



Supporting Information S4. Remotely sensed monthly sea surface temperatures (SST) (<http://ingrid.ldeo.columbia.edu/>) averaged across the potential foraging range of subantarctic fur seals *Arctocephalus tropicalis*; 42°30' – 47°30'S, 31°30'– 43°30'E (Marion Island) and 37°30' – 42°30'S, 3°30' – 15°30'W (Gough Island). The dotted lines indicate the start of continuous weaning mass collection at Marion Island. Monthly SST anomalies were standardized (mean = 0, standard deviation = 1) prior to analysis.



Supporting Information S5. Visualization of the sample cross correlation function (ccf) describing the relationship between the Southern Oscillation Index (SOI) and sea surface temperatures (SST) at Marion- and Gough Island, respectively. Negative lags indicate a correlation between SOI at a time before  $t$  and SST at time  $t$ . Positive correlations indicate that an above average value of SOI is likely to lead to an above average value of SST about three months later. Correlations that extend above or below the horizontal dotted lines are statistically significant at the 5 % level but here, all correlations are weak, especially for Marion Island.

