Decomposing the variance in southern elephant seal weaning mass: partitioning environmental signals and maternal effects

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Abstract. Predator populations are likely to respond to bottom-up processes, but there remains limited understanding of how wide-ranging marine predators respond to environmentally driven temporal variation in food availability. Widespread declines of several Southern Ocean predators, including southern elephant seals *Mirounga leonina*, have been attributed to decreases in food availability following environmental changes. We used linear mixed models to examine temporal process variance in weaning mass (a key fitness component) of southern elephant seals at Marion Island over a 27-year period (1986–2013). We quantified the contribution of within- and between-year covariates to the total phenotypic variance in weaning mass and determined whether the observed reversal of population decline was associated with a continued increase in weaning mass, suggesting improvement in per capita food availability to adult females. Weaning mass initially increased rapidly with maternal age, but reached an asymptote when females were nine years old. Longitudinal data examining between-individual maternal differences suggested latent, age-independent maternal influences on weaning mass. Between-year differences accounted for only 6% of the total phenotypic variance in weaning mass. We found no evidence for a systematic trend in weaning mass, but model predicted weaning mass was 8.70 kg (95% CI = 2.14–14.73) lower during the 1980s, suggesting that food limitation may have been most severe during these years when the population was declining. Model support for a population size effect was entirely driven by the low weaning mass and comparatively high (but declining) population size from 1986 to 1988; subsequent variation in population size had no detectable influence on weaning mass. Remotely sensed chlorophyll-*a* concentration within the seals' foraging distribution explained 45% of the between-year variation (1998–2013, $n = 9$) in weaning mass, with higher weaning mass in years of positive chlorophyll-*a* anomalies. Environmental variation associated with variability in the Southern Annular Mode poorly predicted temporal variation in weaning mass. Our long-term data on elephant seal weaning mass provides a perspective on variation in food availability in a pelagic environment which is poorly known. Examining the long-term regionally specific effects of environmental variability aids our understanding of how these predators interact with their environment.

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INTRODUCTION

The abundance of Southern Ocean marine predators fluctuated dramatically during the last two centuries, resulting in shifts in the structure and dynamics of the Southern Ocean ecosystem. During the latter half of the twentieth century, the trajectories of several marine predator populations (e.g., *Arctocephalus* fur seal species; Hofmeyr et al. 2006) were strongly positive, as low-density populations recovered from historic over-harvesting. But, consistent with global top predator trends (Heithaus et al. 2008), the population sizes of many other seabird and seal species breeding in the Southern Ocean decreased severely in recent decades, possibly due to changes in environmental conditions (Weimerskirch et al. 2003, Barbraud et al. 2011, Forcada and Hoffman 2014).

The southern elephant seal *Mirounga leonina* is one such predator species that has fluctuated considerably in abundance across its circumpolar range. Decimated by sealing in the 1700s and 1800s, populations initially recovered during the early 1900s, only to be followed by a sharp decline in all Indian and Pacific Ocean elephant seal populations between the 1950s and 1990s (McMahon et al. 2005*a*). Time-series data suggest continued decreases in some populations (Macquarie Island; van den Hoff et al. 2014), while others have remained relatively stable (îles Kerguelen; Authier et al. 2011) or increased slightly (Marion Island; Pistorius et al. 2011) recently. The most plausible hypothesis explaining these declines is a reduction in food resources and/or quality through environmental change (McMahon et al. 2005*a*). An alternative hypothesis based on historical fish extraction (Ainley and Blight 2008), again suggests that alteration in prey availability was key to population declines.

Although the underlying factors driving population changes are not fully understood (Hindell et al. 2003), analyses of southern elephant seal demographic rates give indirect support to food limitation as a principal driver of population declines (reviewed in Pistorius et al. 2011). Density dependence and increases in per capita food availability have subsequently been proposed as possible mechanisms leading to the termination of negative population trends at Marion- and other southern Indian Ocean islands (Pistorius et al. 2008, McMahon et al. 2009). The first objective of this paper is to evaluate if temporal trends in weaning mass at Marion Island substantiate these claims. Direct measurement of per capita resources for elephant seals is not feasible, but the body mass of recently weaned pups can be used as a broad-scale index representing prey availability to adult females during pre-breeding migrations (Fedak et al. 1996, Arnbom et al. 1997, Burton et al. 1997, Crocker et al. 2001, McMahon et al. 2003, Le Boeuf and Crocker 2005, McMahon and Burton 2005). Long-term monitoring of weaning mass therefore provides an opportunity to track temporal changes in prey availability for adult female elephant seals. We investigate variation in weaning mass in relation to temporal covariates, annual changes in population size, and variation in environmental conditions using 20 years of data collected over a 27-year period that included population decline and population growth. Given that weaning mass significantly influences juvenile survival and female recruitment (McMahon et al. 2000, 2003; W. C. Oosthuizen et al., *unpublished manuscript*), both key drivers of population growth (McMahon et al. 2005*b*), we expected an associated increase in weaning mass as population growth changed from negative to positive. Such an increase in weaning mass would provide support for the food limitation hypothesis and recent improvement in per capita resources to southern elephant seals.

Earlier studies indicated that most of the variation in weaning mass of elephant seals derives directly from variation in maternal body mass, with a positive correlation between maternal mass and age (Fedak et al. 1996, Arnbom et al. 1997, Burton et al. 1997, Crocker et al. 2001, Postma et al. 2013*a*). However, none of these studies contrasted the relative contributions of maternal effects and time-varying covariates to total phenotypic variance in weaning mass over periods (>4 years) incorporating a range of environmental conditions. Animal populations exist in inherently variable environments, and

the observed variance in biological time-series commonly increases with the length of the study. We may therefore expect more prominent fluctuations in environmental conditions over longer study periods, increasing the probability to detect important among-year variation in cohort specific traits, such as weaning mass. Quantifying temporal variance in such life history parameters is important, as inter-cohort variation may have significant consequences for population dynamics (Lindström and Kokko 2002). Using a subset of pups with known-aged mothers weighed during nine years of this study, we decompose the variance in weaning mass into components that specifically relate to maternal traits, residual within-year variation and annual environmental variation. Our objectives included (1) characterizing maternal age-related and maternal age-independent variability in weaning mass, (2) evaluating and contrasting the contribution of maternal and environmental covariates to total phenotypic variance in weaning mass, and (3) evaluate the explanatory power of environmental covariates that were hypothesized to contribute to annual variation in weaning mass.

METHODS

Study region and elephant seal foraging

Southern elephant seals are wide-ranging marine predators (Biuw et al. 2007). Marion Island's elephant seal population is part of the southern Indian Ocean or Kerguelen (super-) population (McMahon et al. 2005a). Although feeding ranges of the Marion- and significantly larger îles Kerguelen population overlap little (e.g., Bailleul et al. 2007, McIntyre et al. 2011a), resource availability within this geographical region is probably connected. Elephant seal females breeding at Marion Island forage pelagically within Subantarctic and Antarctic waters. Their latitudinal foraging distribution ranges from the Subtropical Front to high-latitude Antarctic waters south of the Antarctic Polar Front (APF; Fig. 1). Seals departing from Marion Island commence their extensive foraging migrations within the Polar Frontal Zone (PFZ), the region between the Subantarctic Front and APF. The Antarctic Circumpolar Current (ACC) dominates the physical structuring of the PFZ, but the physical oceanscape (e.g., temperature, biogeochemical parameters, sea-ice presence or absence) encountered by seals may vary markedly as seals traverse different frontal and oceanographic zones (Lutjeharms and Ansorge 2008). Elephant seals dive continuously and deeply (up to 2000 m but regularly to ~400 m) throughout their foraging trips (McIntyre et al. 2010), preying on fish (predominantly lanternfish, family Myctophidae) and cephalopods (squid; Cherel et al. 2008). Elephant seal females fast during lactation ("capital breeders", in the capital-income typology that describes reproductive investment; Jönsson 1997) and maternal investment is influenced by prey availability and female foraging success during the eight-month long (February–October) pre-breeding migration (Fedak et al. 1996).

Population monitoring and response variable

Elephant seal breeding sites were regularly surveyed throughout the breeding season as part of a long-term mark-recapture study (Bester et al. 2011). Between 1986 and 2013, a subset of the pups born was weighed at, or close to, their weaning date ($n = 20$ years, $n = 1617$ pups weighed, range = 39–118 pups weighed per annum; Appendix: Table A1). Pups were rolled into a net sling and weighed using a spring scale suspended from a pole resting on the shoulders of two researchers. Weighing took place along the east coast of Marion Island, between Sealer's Beach and Archway Bay. The median number of days between weaning and weighing was 1 day, but we considered all measurements made within 10 days of weaning. The weaning mass of pups not weighed on the day of weaning was reconstituted using a mass-loss correction factor of 9.2 g·kg·day^{-1} (Wilkinson and Bester 1990). Individuals of unknown sex ($n = 20$) as well as one outlying record (48 kg, 1986) were removed prior to analyses.

Within-year covariates

Sex.—Sex accounted for known influence of sex on weaning mass, with males (120.97 ± 22.79 kg, mean ± SD) weighing more than females (114.75 ± 22.11 kg) on average.

Site.—The sampling area included seven distinct sites (pebble beaches); however, weighing did not take place at all sites during all years.
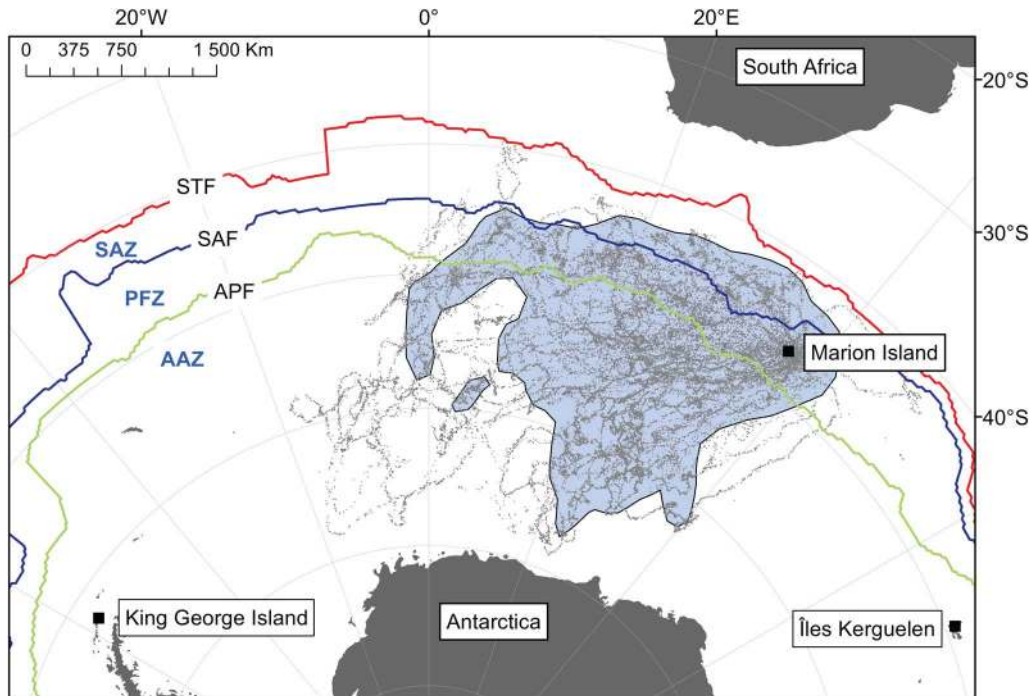
Fig. 1. At-sea distribution of adult southern elephant seal females from Marion Island. The 80% kernel density estimate (shaded area) derived from individual foraging tracks (points) were used to extract chlorophyll-*a* data. The mean position of the Subtropical Front (STF), Subantarctic Front (SAF), and Antarctic Polar Front (APF) is shown (Swart et al. 2010). SAZ is Subantarctic Zone, PFZ is Polar Frontal Zone, and AAZ is Antarctic Zone.

Sites vary in area and apparent suitability as breeding sites for elephant seals (Mulaudzi et al. 2008) and were subjectively characterized as "Good," "Medium," and "Poor" based on the physical characteristics of the site (Appendix: Fig. A1). Spatial variation is an important variable that was ignored in previous comparisons of weaning mass at Marion Island (Burton et al. 1997, McMahon et al. 2003). Due to unbalanced sampling, not accounting for differences between sites may bias or confound between-year variation in weaning mass.

Maternal age.—Maternal age at parturition was known for 226 pups born to nine cohorts (Appendix: Table A1, Fig. A2). Although the exact age of Marion Island tagged breeding females was known during all years, maternal relationships could only be established for pups marked with auxiliary tags during the pre-weaning period (de Bruyn et al. 2008). Maternal age-dependence in weaning mass was modeled as a factor, linear trend or cubic regression spline. Maternal age ranged from three (minimum age of first parturition) to 20 years; females aged ≥ 17 years ($n = 6$) were grouped.

Time-varying covariates

Temporal trend.—Long-term time-dependence in weaning mass (an increasing or decreasing trend) was modeled by fitting a linear trend or a penalized spline regression with two knots (Crainiceanu et al. 2005) as covariates. Models representing the hypotheses that weaning mass was different during the 1980s ($n = 3$ years) compared to the rest of the time-series ($n = 17$; McMahon et al. 2003) or alternatively that weaning mass was different during the period of population decline (1986–1994; $n = 6$) compared to population increase (1997–2013; $n = 14$) were also evaluated (McMahon et al. 2009).

Population size.—Population size was estimated annually on 15 October (the peak of the breeding season haulout) from an island-wide count of all adult female elephant seals. These counts contain minimal observation error (McMahon et al. 2009). We used the complete counts of the entire

adult female population as index of abundance (Appendix: Fig. A3).

Environmental variation—Southern Annular Mode (SAM).—While it would be particularly useful to relate prey abundance to weaning mass, no long-term measures of elephant seal prey species exist for our study region. Prey abundances are expected to vary spatially and temporally in relation to the biophysical characteristics of the oceanic environment, which is influenced by climatic conditions (Constable et al. 2003). The Southern Annular Mode (SAM) is the dominant mode of extra-tropical atmospheric variability in the Southern Hemisphere (Thompson and Wallace 2000). Positive phases of SAM indicate a stronger than usual sea level pressure gradient between the mid- and high-latitudes and are associated with a poleward shift in atmospheric westerly winds. These westerly winds are highly influential in driving the circulation of the Southern Ocean, including the strong eastward flow of the ACC. During positive phases of SAM, stronger westerlies between 50° S and 70° S enhance the northward Ekman transport of cold Antarctic water, leading to cold sea surface temperature anomalies at these latitudes. The Ekman drift generates anomalous divergence and upwelling near the APF (60° S), increasing diatom abundance south of the APF (Lovenduski and Gruber 2005, Hauck et al. 2013). In addition, as a consequence of greater wind stress, increased eddy activity follows positive SAM phases with a lag of 2–3 years (Meredith and Hogg 2006, Screen et al. 2009). Mesoscale processes such as eddies significantly enhance primary productivity within the PFZ (Lutjeharms and Ansorge 2008) and can induce prey aggregation. Several predator species, including elephant seals, appear to forage preferentially in association with these features (Bailleul et al. 2010, Dragon et al. 2010).

Monthly SAM index values (http://www.cpc.ncep.noaa.gov/) were converted to annual means by averaging monthly values from October in year $t - 1$ to September in year t (Appendix: Figs. A4 and A5). These annual-means allow a broad-scale perspective of the physical oceanographic changes induced by climate forcing and are at the coarsest of scales, a proxy of biological productivity that adult females encounter during their post-breeding ($t - 1$) and pre-breeding foraging

migrations. An alternative annual index that only considered climatic conditions during the pre-breeding foraging migration (over the period March$_{(t)}$ to September$_{(t)}$) was highly correlated with our index (Pearson's correlation coefficient = 0.79, $t_{(32)} = 6.79$, $p < 0.001$) and qualitatively yielded the same results. Productivity south of the APF appears to be elevated in years of positive SAM index; increased upwelling of cooler, deep waters rich in nutrients fuel the production of phytoplankton biomass (Lovenduski and Gruber 2005, Arrigo et al. 2008). We also considered temporal lags; a one year lag effect (SAM$_{lag1}$) allowed variability to be integrated into the food web, and a two year lag effect (SAM$_{lag2}$) permitted development of the intensified eddy field (Meredith and Hogg 2006) that may improve foraging conditions for elephant seals from Marion Island.

Environmental variation—chlorophyll-a concentration (chl-a).—Remotely sensed ocean color measurements provide a means of quantifying ocean productivity in terms of near-surface phytoplankton distribution and biomass. Several satellite derived productivity data sets exist, but none spanned the duration of our study period. The MODIS-Aqua satellite platform provides chl-a concentration (mg/m^{-3}) data from 2002 to present and allowed inclusion of chl-a as an index of primary production in our analysis that also included the influence of maternal age on weaning mass. Chlorophyll-a concentration maps with a ground resolution of 0.04° × 0.04° were obtained from the Giovanni Ocean Color portal (http://oceancolor.gsfc.nasa.gov/). We calculated the 80% kernel density estimate of the foraging distribution of adult female elephant seals from Marion Island, derived from satellite tracking ($n = 47$; Fig. 1) and extracted monthly chl-a concentrations from this area separately for all years. Extensive cloud cover causes a large percentage of missing pixels at southern latitudes, especially in winter. Following Authier et al. (2012), we calculated chl-a anomalies about the monthly mean for each pixel for every month between October ($t - 1$) and May, the primary period for chl-a production in Subantarctic waters. An index of the total surface chl-a production was derived for every year from cumulated anomalies (Appendix: Fig. A5).

temporal process variance. To quantify the amount of between-year variance attributable to covariates, we compared the variance of the random year effect (σ^2_α) between the null model and models where covariates were included. Covariates that explained part of the between-year variation in weaning mass reduced the variance of the random year effect. The proportion of the between-year variance explained by a particular covariate was calculated as the proportion change in variance: PCV (%) = 1 − ($\sigma^2_{\alpha(covariate)}/\sigma^2_\alpha$) × 100 (Nakagawa and Schielzeth 2013). For the year random effect, $PCV_{(year)}$ expressed the amount of temporal process variance in weaning mass accounted for by the relationship with the covariate(s) relative to the total temporal process variance only. Covariates likely to account for more than 20% of the temporal variation in weaning mass ($PCV_{(year)}$ ≥ 20%) were considered as potentially influential (Grosbois et al. 2008). As an absolute representation of model goodness-of-fit, we report the marginal R^2 ($R^2_{GLMM(m)}$; variance explained by fixed factors) and conditional R^2 ($R^2_{GLMM(c)}$; variance explained by both fixed and random factors) following Nakagawa and Schielzeth (2013). Mixed-effects models were fitted using the lme4 package (Bates et al. 2014) implemented in R 3.0.2 (R Development Core Team 2013). Graphical summary plots of residuals were used to confirm assumptions of normality and constant variance.

RESULTS

Long-term temporal variation in weaning mass

Between-year differences accounted for only 6% (95% CI = 2.2–10.6%) of the total phenotypic variance in weaning mass (Fig. 2). The preferred model (lowest AIC) among those models including only within-year covariates (models 1–4; Table 1), allowed for the additive effects of site and sex on weaning mass (model 3). Site explained more of the variation in weaning mass than sex, with pups born at 'poor' sites predicted to be nearly 23 kg lighter than pups born at 'good' sites. The fixed effects sex and site reduced the within-year variance component by 6.5% and, due to unbalanced sampling between years, also accounted for nearly 21% of the temporal variance in weaning mass.
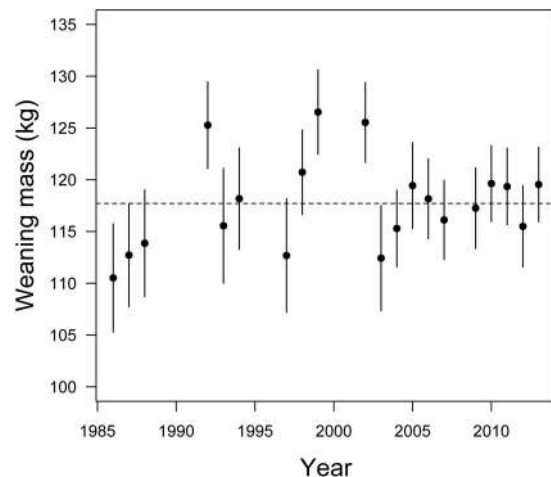
Fig. 2. Predicted mean (with 95% prediction interval) weaning mass of southern elephant seal pups from Marion Island from 1986 to 2013, based on a model that treated year as a random effect. The overall mean is given by the dotted line. Between-year differences accounted for 6% of the total phenotypic variance in weaning mass.

We found no evidence for a systematic trend in weaning mass during the study period (model 5). Time-dependence in weaning mass was best defined by separating the first three years of measurements (1986–1988) from those made in later years (model 7), with weaning mass in the 1980s on average 8.70 kg (95% CI = 2.14–14.73) lower than during subsequent years. Model 9 assumed that female population size had a linear effect on weaning mass and received similar support to model 7, with a predicted decrease in weaning mass as population size increased (β = −3.12 (−4.93 to −1.05)). However, further analysis showed that the effect of population size became negligible for the period 1992–2013; model support for a population size effect was thus entirely driven by comparatively high population size and low weaning mass from 1986 to 1988 and subsequent variation in population size (range 421–565 breeding females) had no detectable influence on weaning mass (β = −0.03 (−0.08 to 0.02)). Models including effects of environmental covariates were poorly supported by the data when they were the only predictors of between-year variation in weaning mass (models 11–13). A slight decrease in AIC suggested some improvement in model parsimony when the

Table 1. Model selection of long-term (1986–2013) variation in weaning mass of southern elephant seals at Marion Island.

Model	Fixed effects	np	Deviance	ΔAIC	w
Null	i	3	14636.14	116.08	0.00
Within-year variation					
m1	site	5	14562.30	46.24	0.00
m2	sex	4	14601.10	83.03	0.00
m3	site + sex	6	14521.30	7.24	0.01
m4	site × sex	8	14520.03	9.97	0.00
Temporal trend					
m5	site + sex + trend	7	14520.00	7.94	0.01
m6	site + sex + s(trend)	8	14515.79	5.73	0.02
m7	site + sex + [1986:1988–1992:2013]	7	14514.54	2.48	0.11
m8	site + sex + population.trend	7	14519.91	7.85	0.01
Population density					
m9	site + sex + population.size	7	14513.45	1.41	0.18
m10	site + sex + s(population.size)	8	14513.69	3.63	0.06
Environmental covariates					
m11	site + sex + SAM	7	14521.25	9.19	0.00
m12	site + sex + SAMlag1	7	14520.64	8.58	0.01
m13	site + sex + SAMlag2	7	14520.58	8.52	0.01
Population density and environmental covariates					
m14	site + sex + population.size + SAM	8	14512.66	2.60	0.10
m15	site + sex + population.size + SAMlag1	8	14512.19	2.12	0.13
m16	**site + sex + population.size + SAMlag2**	**8**	**14510.06**	**0.00**	**0.37**

Notes: Model selection was based on Akaike's information criterion (AIC). ΔAIC is the AIC difference between the current model and the model with the lowest AIC (in boldface); w is the Akaike weight, representing the relative support a model has from the data compared to the other models in the set; np is the number of estimated parameters; all models include a random year intercept. The fixed effect s(population.size) denotes a regression spline with two knots.

combined influence of population size and SAM_{lag2} on weaning mass was evaluated (model 16; Fig. 3). The SAM_{lag2} effect indicated that weaning mass was higher two years after more positive SAM indices. However, AIC evidence was inconclusive and equivocal for hypotheses represented by the simpler models of time-dependence or population size only, as described above. Residual variance remained the largest single component, accounting for 88% of the total phenotypic variance in models that minimized AIC.

Models comparing weaning mass from the 1980s to subsequent measurements or that related weaning mass to population size, explained 45 and 51% of the temporal process variance in weaning mass, respectively (Table 2). SAM_{lag2} had no explanatory power of between-year variance ($PCV_{(year)}$ did not change) when it was included as the only predictor of between-year variation in weaning mass (model 13). When population size was accounted for in the model, SAM_{lag2} contributed to only an approximate 8% reduction in the variance of the random year effect ($PCV_{(year)} = 59\%$ for model 16 and 51% for model 9), i.e., not accounting for enough of the temporal variation in weaning mass to be considered potentially influential ($PCV_{(year)} < 20\%$).

Modeling the effects of maternal age and chlorophyll-a concentration

Knowledge of mother-pup relationships had two important consequences for modeling weaning mass. First, a large part of the residual variance was transferred to the random intercept relating to maternal identity, indicating systematic between-individual differences in pup weaning mass for females with longitudinal records (Table 3). Secondly, maternal age, fitted as a cubic regression spline, drastically improved overall model fit (model 3 vs. model 6; ΔAIC = 156.18; Table 4). Weaning mass, initially increasing rapidly with maternal age, reached an asymptote when females were approximately 9 years old (Fig. 4). Female age explained 44% of the variation in the maternal identity random effect (Table 3); the variation that remained in this term indicates hidden heterogeneity and consistent between-individual differences in weaning mass for females of similar ages (Fig. 5). Chlorophyll-a concentration improved model fit (model 6 vs. model 8; ΔAIC = 3.02) and explained 45% of the between-year variation in weaning mass. Weaning mass was higher in years with positive chl-a anomalies (β = 4.51 (0.58–8.55); Fig. 6). Adding the linear effects of population size and SAM_{lag2} did not improve the AIC model fit relative to the basic age dependent model.

DISCUSSION

Our time-series of 20 years of sampling in a 27-year study period represents one of the longest
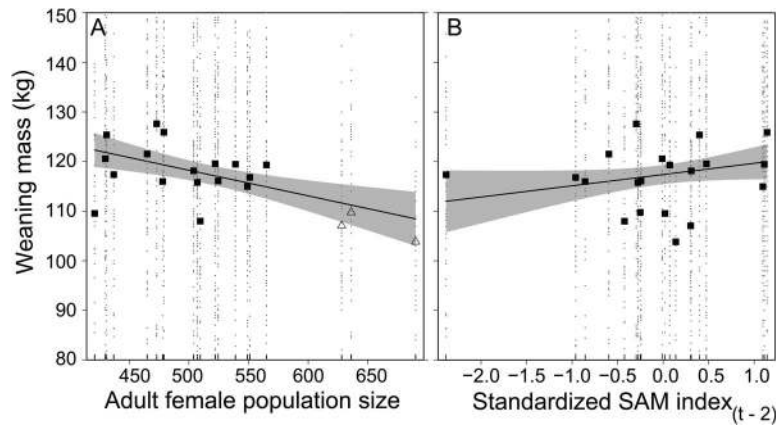
Fig. 3. Predicted change in weaning mass of southern elephant seal pups at Marion Island according to (A) variation in population size and (B) variation in the standardized Southern Annular Mode (SAM), with a two year lag period. Estimates are presented from model 16 (Table 1). Note that the relationship between population size and weaning mass was entirely driven by relatively large population sizes between 1986 and 1988 (open triangles), a period when the population was experiencing rapid long-term population declines.

Table 2. Model coefficients and variance partitioning of selected linear mixed-effects models of long-term (1986–2013) variation in southern elephant seal weaning mass at Marion Island.

Model	Null	Model 3 (site + sex)	Model 7 (1980s)	Model 9 (PopN)	Model 16 (PopN + SAM$_{lag2}$)
Model coefficients					
Fixed effects					
Intercept	116.91	117.71	110.08	118.08	118.22
	(113.9, 119.5)	(114.7, 121.0)	(104.2, 116.8)	(115.3, 120.3)	(115.6, 120.8)
Sex (male)	...	6.88	6.86	6.88	6.87
		(4.8, 9.0)	(5.0, 9.1)	(4.9, 9.0)	(4.9, 8.9)
Site (medium)	...	−7.44	−7.08	−7.23	−7.22
		(−9.7, −5.2)	(−9.3, −5.0)	(−9.4, −4.9)	(−9.6, −5.0)
Site (poor)	...	−22.97	−22.76	−22.74	−22.88
		(−28.9, −16.9)	(−29.0, −16.6)	(−29.3, −15.8)	(−28.8, −17.3)
Time (1992–2013)	...	...	8.70	...	...
			(2.1, 14.7)		
Population size	...	...	...	−3.12	−3.51
				(−4.9, −1.1)	(−5.5, −1.4)
SAM$_{lag2}$	...	...	...	...	2.26
					(−0.2, 4.8)
Variance components					
Random effects					
Year ($\sigma^2\alpha$)	31.79	25.14	17.51	15.62	13.00
Residuals ($\sigma^2\varepsilon$)	488.83	456.94	456.90	457.07	457.20
Fixed factors	...	35.10	44.37	44.59	47.31
PCV (year)	...	20.92%	44.92%	50.87%	59.11%
PCV (Residuals)	...	6.52%	6.53%	6.50%	6.46%
$R^2_{GLMM(m)}$	...	0.07	0.09	0.09	0.09
$R^2_{GLMM(c)}$	0.06	0.12	0.12	0.12	0.12
Deviance	14636.14	14521.30	14514.54	14513.45	14510.06
AIC	14642.14	14533.30	14528.54	14527.45	14526.06

Notes: Fixed effects are model specific parameter estimates (*β*) (with 95% confidence intervals [CI]; in parentheses) for covariates potentially underlying within-year and temporal variation in weaning mass; random effect variance components (VC) evaluate how much variance is explained at each level of the analysis (including fixed factors); PCV (proportion change in variance) monitors how the inclusion of additional predictor(s) modify each variance component relative to that of the null model. Inclusion of additional predictor(s) that reduce the variance component of a specific random effect, results in a positive PCV. For the year intercept, PCV is the percentage of the temporal variance in weaning mass explained by covariates; $R^2_{GLMM(m)}$ variance explained by fixed factors; $R^2_{GLMM(c)}$ variance explained by both fixed and random factors.

Table 3. Model coefficients and variance partitioning of selected linear mixed-effects models including the influence of maternal effects and chlorophyll-*a* concentration on weaning mass of southern elephant seals at Marion Island.

Model	Null	Model 3 (site + sex)	Model 6 (s(Age))	Model 8 (s(Age)+Chl)
Model coefficients				
Fixed effects				
Intercept	114.33	114.57	92.15	90.52
	(109.6, 118.8)	(108.9, 119.7)	(87.0, 97.8)	(85.2, 95.6)
Sex (male)	…	3.16	3.9	3.87
		(−1.6, 8.8)	(0.2, 7.6)	(0.6, 7.2)
Site (medium)	…	−2.92	−0.94	−0.99
		(−8.8, 2.9)	(−4.8, 2.9)	(−5.0, 3.2)
Site (poor)	…	−10.58	−2.4	−2.31
		(−23.4, 2.3)	(−11.6, 6.5)	(−11.1, 7.4)
s(Age1)	…	…	62.05	62.47
			(45.9, 76.0)	(48.6, 77.9)
s(Age2)	…	…	37.33	37.12
			(17.7, 58.5)	(20.0, 56.0)
s(Age3)	…	…	38.6	38.39
			(26.7, 49.7)	(25.8, 50.8)
Chl	…	…	…	4.51
				(0.6, 8.6)
Variance components				
Random effects				
Mother ($\sigma^2\gamma$)	294.50	276.01	164.57	160.12
Year ($\sigma^2\alpha$)	21.40	23.11	21.08	11.64
Residuals ($\sigma^2\varepsilon$)	165.70	174.27	66.94	69.22
Fixed factors	…	7.89	227.45	230.63
PCV (mother)	…	6.27%	44.12%	45.63%
PCV (year)	…	−7.99%	1.50%	45.61%
PCV (Residuals)	…	−5.17%	59.60%	58.23%
$R^2_{GLMM(m)}$	…	0.02	0.47	0.49
$R^2_{GLMM(c)}$	0.66	0.64	0.86	0.85
Deviance	2002.91	1998.43	1836.26	1831.23
AIC	2010.91	2012.43	1856.26	1853.23

Note: Model terms are as in Table 2. The fixed effects s(Age$_i$) denote a cubic regression spline.

published data sets of body condition available for a Southern Ocean marine mammal. By quantifying the annual variation in weaning mass, we provide a perspective on broad-scale prey availability to adult female elephant seals from a population that mainly forages in a pelagic environment that is poorly known, but which supports large populations of a diverse array of marine predators. Temporal variation in weaning mass provides support for an increase in per capita food availability early on during the study period, but no evidence for a long-term trend was found, with weaning mass fluctuating around a stable average during the last two decades. Most evidently, temporal process variance in weaning mass was small. Even though a positive correlation between chlorophyll-*a* concentration and weaning mass suggests that environmentally driven variation in productivity may induce cohort differences (e.g., Pistorius et al. 1999, Garrott et al. 2012), between-year

Table 4. Model selection of weaning mass of southern elephant seals at Marion Island for models including the influence of maternal effects and chlorophyll-*a* concentration.

Model	Fixed effects	np	Deviance	ΔAIC	w
Null	*i*	4	2002.91	157.68	0.00
Within-year variation					
m1	site	6	1999.98	158.75	0.00
m2	sex	5	2001.55	158.32	0.00
m3	site + sex	7	1998.43	159.20	0.00
Maternal age					
m4	site + sex + age	8	1903.52	66.28	0.00
m5	site + sex + factor(age)	21	1824.18	12.95	0.00
m6	site + sex + s(age)	10	1836.26	3.02	0.15
Population density and environmental covariates					
m7	site + sex + s(age) + population.size	11	1836.25	5.01	0.05
m8	**site + sex + s(age) + chl**	**11**	**1831.23**	**0.00**	**0.66**
m9	site + sex + s(age) + SAMlag2	11	1834.27	3.06	0.14

Notes: Model terms are as in Table 1. The fixed effect s(age) denotes a cubic regression spline. All models include random year and maternal identity intercepts.
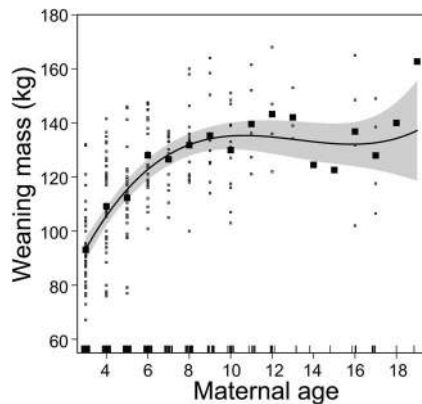
Fig. 4. Predicted change in weaning mass of southern elephant seal pups as a function of maternal age. The solid line is the LMM prediction from model 8 (Table 4); the grey shading represents 95% confidence limits. Individual data points (open squares) and age-specific average weaning mass estimates (solid squares) were derived from the observed data.

phocid seals that fast throughout lactation (Bowen et al. 2001). The strong evidence we found for a relationship between maternal age and pup weaning mass is driven by age-related variation in maternal body mass at parturition (Arnbom et al. 1997). At Macquarie Island, elephant seal females attain an asymptotic body length at 9 years of age (Bell et al. 2005), which corresponds well to the age-related plateau of relatively constant weaning mass that we observed. Maternal age ranged from first-time breeders to females approaching the life span of individuals observed in the wild, but a larger sample of very old females (>12 years; Péron et al. 2010) will be required to assess potential reductions in weaning mass at maternal ages where senescence may be expected. Although specific ages are not given, Fedak et al. (1996) noted that "some very large females (which were also the oldest animals in the sample...) used
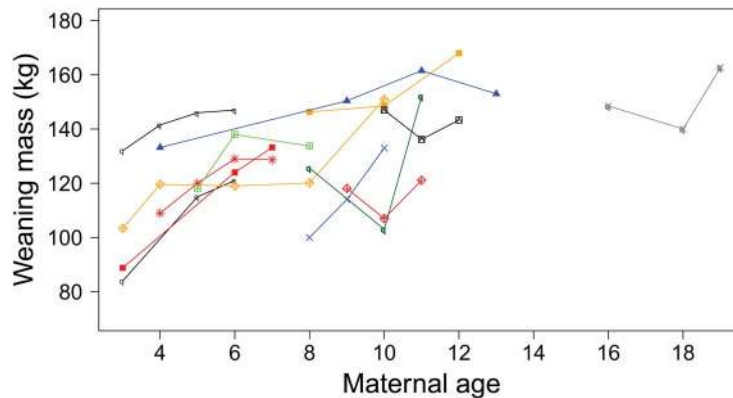
Fig. 5. Pup weaning mass as a function of female age for thirteen females with three to five observations each, illustrating individual variation between females.

differences accounted for only 6% of the total phenotypic variance in weaning mass. At weaning, a cohort of elephant seal pups is thus a highly heterogeneous aggregate of individuals (up to >100 kg or two-fold variations among individuals), suggesting the need to take individual differences into account when testing hypotheses about life histories.

Individual heterogeneity and age-related variation in weaning mass

Maternal effects are especially strong for

relatively little of their reserves and often produced relatively small pups." Although this observation should not be generalized, substantial evidence exists for senescent declines in various measures of reproductive performance in animal populations (Nussey et al. 2013). Senescent declines in either maternal body mass (e.g., Weddell seal *Leptonychotes weddellii* mothers; Proffitt et al. 2007) or physiological function (e.g., senescent reductions in body mass of grey seal *Halichoerus grypus* pups; Bowen et al. 2006), may potentially reduce the weaning mass of

Fig. 6. Predicted positive relationship between weaning mass of southern elephant seal pups and standardized chlorophyll-*a* concentration during adult female foraging cycles in the year preceding birth. The solid line is the LMM prediction from model 8; the grey shading represents 95% confidence limits. Individual data points and averaged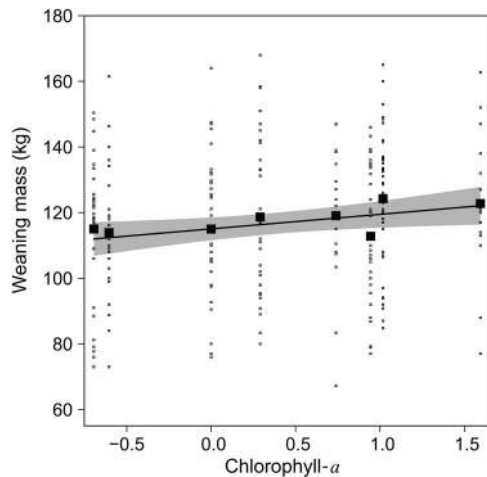 annual weaning mass estimates corresponding to every chlorophyll-*a* concentration were derived from the observed data.

pups born to the oldest females.

The Fedak et al. (1996) extract also draws attention to highly variable energy expenditure (allocation) between individual females. Female age explained nearly half of the variation in the maternal random intercept; the variation that remains in this component may suggest latent individual heterogeneity (Chambert et al. 2013). We found that some females repeatedly weaned heavier pups than others of similar age, perhaps suggesting difference in individual quality (here meaning important but unmeasured traits that contribute to among-individual fitness variation, Wilson and Nussey 2010). Such heterogeneity may arise from genetic makeup (Hunt et al. 2004), other phenotypic traits (e.g., physiology), behavior (e.g., diet; Authier et al. 2012), and variations in past or present environmental conditions experienced (Lindström and Kokko 2002, Chambert et al. 2013, Stauffer et al. 2013).

Although female elephant seals have high natal site fidelity (Hofmeyr et al. 2012), individuals do not always breed at the same site. If females choose larger harems in which to breed as they age (as at Macquarie Island; McMahon

and Bradshaw 2004), we can expect variation in weaning mass between sites as a function of maternal age. Indeed, females breeding in small harems on less suitable beaches were younger and weaned pups of lower mass than females breeding in large harems (Appendix: Figs. A1 and A2). Sampling constraints (predominantly associated with the early part of the study) and random variation in female breeding numbers per site, resulted in unbalanced sampling with regards to sites of different apparent quality. By including site and sex as fixed effects, we ensured that unbalanced sampling did not influence conclusions regarding inter-annual variation in weaning mass. Together, these two factors explained nearly 21% of the between-year variation in weaning mass, clearly indicating the potential dangers of ignoring site-specific differences when assessing temporal variation in weaning mass. Our results, which account for variable sampling per site, suggest that the difference in weaning mass between the 1980s and 1990s are probably somewhat smaller than previously suggested (Burton et al. 1997, McMahon et al. 2003). When maternal age was accounted for in models, site effects diminished.

Population decline, temporal variation in weaning mass and per capita food availability

Widespread population declines of southern elephant seals (e.g., 89% decline at Marion Island between 1951 and 1997) have been attributed to environmental change (McMahon et al. 2005*a*, 2009). More generally, Weimerskirch et al. (2003) suggested that various top predator declines in the southern Indian Ocean were associated with a climatically driven regime shift, affecting all levels of the trophic web. Climate change is a fundamental driver of current Southern Ocean ecosystem change (Trathan et al. 2007, Hoegh-Guldberg and Bruno 2010), but our understanding about the ecological outcomes of a changing environment remains critically limited for most regions and even for well-studied populations. Our results confirm that pup weaning mass was well below the long-term mean during the first three years of monitoring (1986–1988), when the population was still declining sharply. An increase in weaning mass during the early 1990s is likely to have contributed to the reversal in the population growth rate during the mid-1990s.

Notwithstanding large within-year variation, the increase in weaning mass that persisted through the 1990s and 2000s is thought to be biologically significant (McMahon et al. 2000, Authier et al. 2012). A potential pathway for population regulation may thus include improved adult female foraging success, a subsequent increase in weaning mass and associated improvement in juvenile survival. However, it remains uncertain whether juvenile survival, which appeared to have remained similar at the end of and immediately after the population decline, was proximately related to the decline of southern elephant seals at Marion Island (Pistorius and Bester 2002, Pistorius et al. 2011). An alternative, non-exclusive pathway may incorporate higher adult female survival and fecundity as a response to increases in per capita food availability (Pistorius et al. 2004).

Understanding the population-level effects of environmental variation

Data obtained from satellite tagging show that environmental variability, through hypothesized effects on prey distribution and abundance, affects the habitat selection, foraging success and mass gain of individual elephant seals (e.g., Bradshaw et al. 2004, Biuw et al. 2007, 2010). However, despite elegant modeling of individual foraging behavior in relation to physical and biological oceanographic properties (e.g., Bailleul et al. 2010, Dragon et al. 2010, McIntyre et al. 2011b, Jaud et al. 2012), much remains to be learned about the links between environmental variability and the species' demography (Hindell et al. 2003). We found that weaning mass, a strong predictor of juvenile survival (McMahon et al. 2000, 2003), tended to increase following periods where positive anomalies of chl-a concentration, a proxy of primary production, occurred in the main foraging region of adult female seals. Comparable results from îles Kerguelen (Authier et al. 2012) suggest that despite its limitations, chl-a concentration may be a reasonable predictor of general prey availability for elephant seals. The link between chl-a and elephant seal foraging is indirect, but surface chl-a concentration may be a bio-marker of local primary production and the secondary and tertiary consumers on which elephant seals prey (Dragon et al. 2010). Fine scale telemetry

observations revealed that the diving depths of elephant seals are reduced in areas of high surface chl-a concentration, perhaps due to the shallower distribution of prey species associated with greater attenuation of light (Dragon et al. 2010, Jaud et al. 2012). Elevated concentrations of chl-a may therefore not only increase prey availability, but also reduce energy expenditure, improving overall foraging efficiency.

In principle, studies from geographically separated populations may resemble experimental replications for investigating the effects of environmental variability on a particular species. Multi-population covariation (i.e., synchrony or lagged cross-correlation) of predator-parameters with the same climatic factor would strengthen evidence that the factor is impacting on the populations. However, habitat use by elephant seals differs substantially across ocean basins, and includes benthic shelf areas, the sea-ice zone and midwater pelagic water masses (Biuw et al. 2007). Trophodynamics also differ between individuals and regionally; e.g., myctophids constitute the main diet of adult females from îles Kerguelen (Cherel et al. 2008) whereas the diet of Macquarie Island adult females include more squid (Newland et al. 2009). Most importantly, climatic modes have strong regional effects (e.g., Trathan et al. 2007) and environmental variability may consequently have different effects on food availability for elephant seals depending upon their geographical foraging distribution and the regional food webs they reside within. Given this heterogeneity, comparisons of multiple, circumpolar elephant seal populations are perhaps more suited to assess the geographic variation in responses to environmental variability, rather than confirmation of the impact of particular factors. Comparative analyses across oceanic basins are needed to better understand how these predators interact with their environment, including potential responses of the global population to future changes in climate (McMahon et al. 2008, van den Hoff et al. 2014).

We found no clear relationship between weaning mass fluctuations and SAM, a large scale index of environmental variability in the Southern Ocean. In other areas of the Southern Ocean, variation in SAM significantly affects marine predators. Positive SAM conditions are, for example, associated with reduced krill avail-

ability and poorer demographic performance of Antarctic fur seals (*Arctocephalus gazella*) at South Georgia (Forcada and Hoffman 2014). Negative annual rates of elephant seal population change at Macquarie Island are also associated with positive anomalies of SAM. The association between SAM and Macquarie Island elephant seals is seemingly driven by SAM-induced modifications in sea-ice duration in the Ross Sea, the principal foraging zone of Macquarie Island elephant seals. Van den Hoff et al. (2014) suggested that a reduced sea-ice field (negative SAM) may improve foraging conditions for adult females by allowing earlier access to the continental shelf foraging habitat. However, for the same population, physical forcing related to increases in sea-ice extent during El Niño Southern Oscillation (ENSO) events tends to improve first-year survival (McMahon and Burton 2005, de Little et al. 2007), with the decay of larger areas of sea-ice in summer perhaps increasing regional prey availability (e.g., Antarctic krill *Euphausia superba*; Walters et al. 2014). Large climatic modes and sea-ice variation thus appear to have different consequences for the juvenile and adult components of this population, likely because of differences in the foraging distribution (Field et al. 2004) and diet (Walters et al. 2014) of juveniles and adults. Finally, physical forcing in the Bellingshausen Sea seems to follow a different set of rules: warm sea temperatures and reduced sea ice concentration during La Niña events correlate with heavier weaning mass of elephant seal pups on King George Island (Vergani et al. 2001, 2008). These examples of regionally specific repercussions of environmental variability underline the need for studies from across the distributional range of a wide-ranging species like the elephant seal (e.g., Postma et al. 2013*b*).

Refining population level studies to better understand environmental variation

Environmental data portraying average conditions experienced by an entire population are inevitably on a very coarse spatial scale compared to the fine scales over which individuals forage. Environmental conditions experienced by individual elephant seals will vary considerably depending on their specific foraging migrations and this heterogeneity may contribute to large inter-individual variance in weaning mass. Because local conditions may vary over small spatial scales, there is motivation to use large scale climatic modes (such as SAM) that incorporate several different weather components and reduce complex space and time variability of local weather variables (Hallett et al. 2004, Stenseth and Mysterud 2005). While these indices may sometimes better predict ecological processes compared to local weather indices (Hallett et al. 2004, Stenseth and Mysterud 2005), they remain extremely crude summaries of a complex environment. One of the strongest predictors of local conditions for Marion Island elephant seals are perhaps whether seals forage north of the Subantarctic Front, within the PFZ, or south of the APF. Stable isotope analysis affords an opportunity to assign more specific environmental drivers to a (relatively) large number of individuals within a population, based on the latitudinal $\delta^{13}C$ gradient in particulate organic matter (POM) in the Southern Ocean (Rau et al. 1989). This may improve insight into the foraging efficiency of individuals in relation to regional environmental conditions. Authier et al. (2012) used this approach to compare weaning mass of elephant seal pups at îles Kerguelen, distinguishing between mothers foraging in the PFZ and those foraging in Antarctic waters. The influence of sea-ice extent on pup mass could then be tested for only those females with a blood carbon isotope ratio suggestive of Antarctic foraging. Inadequate tissue sampling may negate the use of stable isotope analysis for most (if not all) existing long-term studies, but this approach may nonetheless help to reveal more detailed links between foraging strategies, a fluctuating environment and population traits over shorter time scales (e.g., four years; Authier et al. 2012).

The absence of information on weaning mass (and data in general) from the period before and during the greatest part of the general decline of elephant seals presents a challenge for the understanding of food limitation as a driver of population declines. Furthermore, generating estimates of per capita food availability is difficult. An alternative approach may be to ask questions about temporal changes in the dietary composition of top predators, rather than trying to estimate changes in the abundance of prey in general. Once more, stable isotope analysis has

the potential to offer insights into trophic relations that may improve our understanding of the consequences of broader environmental variability. The ratios of stable nitrogen and carbon isotopes may, at both short and longer time scales, provide a measure of temporal shifts in trophic relationships (e.g., Hanson et al. 2009). Analyzing dietary changes through time and reconstructing historical diet (where archival samples such as teeth may present an opportunity to do so) could advance our understanding of the important changes that have occurred in the Southern Ocean marine ecosystem over the last 60 years (Weimerskirch et al. 2003, Hanson et al. 2009).

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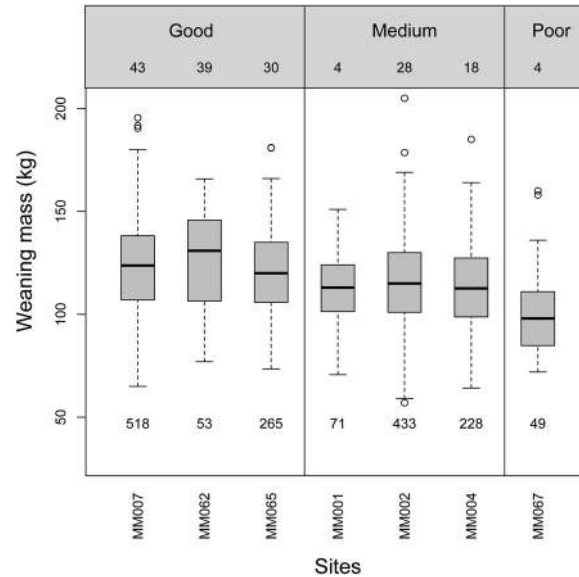SUPPLEMENTAL MATERIAL

APPENDIX

Fig. A1. Weaning mass of southern elephant seal *Mirounga leonina* pups weighed at seven distinct sites at Marion Island between 1986 and 2013. The number of pups weighed at every site throughout the study period is given at the bottom of each of the box-and-whisker plots. Weaning mass differed significantly between "Good," "Medium," and "Poor" sites (analysis of variance and Tukey's honest significant differences, all $p < 0.07$) but not between sites with the same assigned quality (all $p > 0.43$). Breeding harems within the sampling area differ in size, with larger harems typically occurring on more suitable breeding beaches. The average number of pups tagged annually at every site between 1983 and 2013 is given in the grey shaded area, as a proxy of a typical harem size for that site.
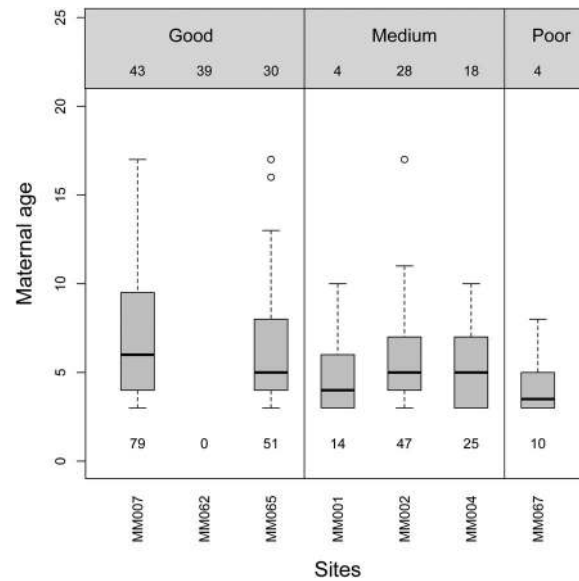
Fig. A2. Age distribution of southern elephant seal *Mirounga leonina* females breeding at seven distinct sites at Marion Island between 1986 and 2013. For every site, the number of known-aged females whose pups were weighed at weaning is given at the bottom of each of the box-and-whisker plots. The average number of pups tagged annually at every site between 1983 and 2013 is provided together with the site classification, as a proxy of a typical harem size for that site. Female elephant seals choose larger harems in which to breed as they age.
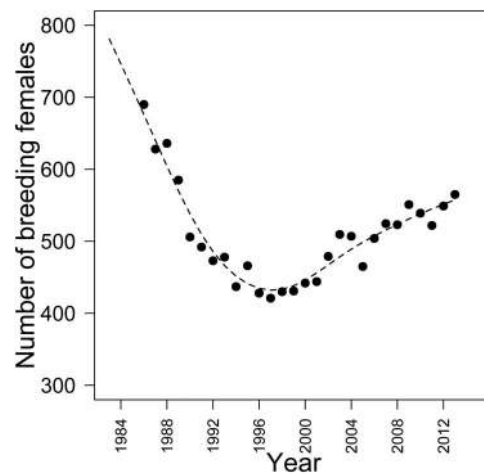

Fig. A3. Population trend of southern elephant seal *Mirounga leonina* females breeding at Marion Island between 1986 and 2013. The dotted line represents the prediction of the generalized additive model $N \sim s(year)$.
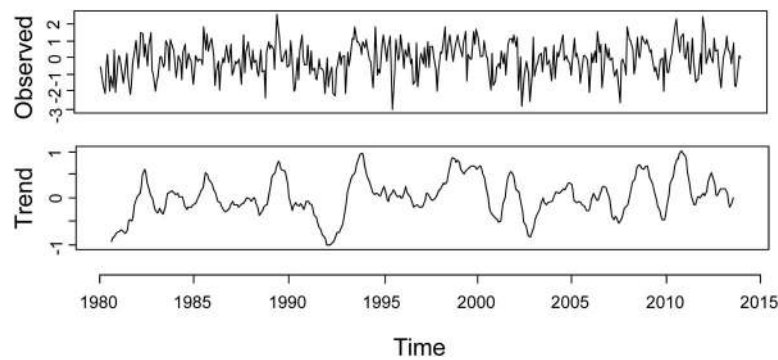
Fig. A4. Observed monthly Southern Annular Mode (SAM) index values (http://www.cpc.ncep.noaa.gov/), and the trend component, obtained by using a moving average with a symmetric window and equal weights.
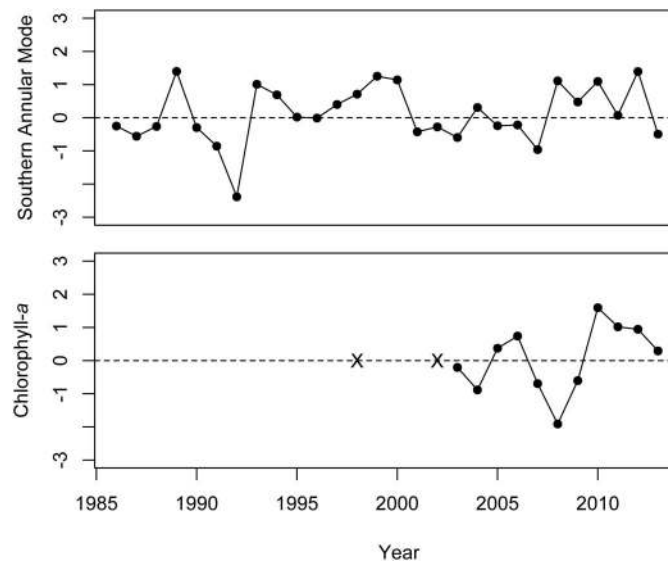

Fig. A5. Covariates of environmental variation were standardized so that the mean and standard deviation over the long-term time series were set to 0 and 1, respectively. Top panel: Southern Annular Mode time-series converted to annual-means by averaging monthly values from October in year $t - 1$ to September in year t. Bottom panel: Total surface chlorophyll-a concentration (mg/m^{-3}) derived from the MODIS-Aqua satellite platform (http://oceancolor.gsfc.nasa.gov/). Chlorophyll-a data were only available from 2002 to 2013; the standardized mean (0) were used as covariate values for 1998 and 2002 when modeling the effects of chlorophyll-a concentration on weaning mass.

Table A1. The number of southern elephant seal *Mirounga leonina* weaned pups weighed at Marion Island between 1986 and 2013. Maternal identity refers to the total number of pups weighed where maternal identity and age was known with certainty.

Year	Female	Male	Sex unknown	Total	Maternal identity known
1986	22	24		46	
1987	30	23		53	
1988	20	28		48	
1992	46	36		82	
1993	21	18		39	
1994	29	26		55	
1997	19	21		40	
1998	46	41	1	87	19
1999	46	41	1	87	
2002	57	43		100	14
2003	26	24		50	
2004	50	60	1	110	
2005	36	48		84	
2006	44	56	3	100	17
2007	53	49	1	102	30
2009	51	47	8	98	28
2010	49	63	1	112	14
2011	56	55		111	40
2012	44	51	1	95	31
2013	55	63	3	118	33
Total	745	754	17	1617	226

Note: Individuals with unknown sex were not included in analyses and do not contribute to row totals.