Effect of climate variability on weaning mass in a declining population of southern elephant seals *Mirounga leonina*

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ABSTRACT: With the global climate predicted to continue to change over the coming century, quantifying how animal populations respond to environmental variation is central for the prediction of future responses and consequences. To quantify how environmental change affects the foraging success of Macquarie Island female elephant seals *Mirounga leonina*, we related weaning mass — a function of maternal foraging success — to a series of intrinsic and extrinsic (environmental) covariates. We found that the weaning mass of elephant seals was positively related to the number of females ashore during the breeding season and negatively related to maximum sea ice extent in the Ross Sea region. Weaners weighed on average 3 kg more in years with more females ashore and 17 kg less in years of high ice extent. These relationships suggest that in years of poor female foraging conditions (i.e. high ice extent), Macquarie Island population growth is affected not only by a reduction in the number of females ashore for reproduction but also, given that weaning mass dictates first-year survival, by reduced pup survival rates. The decline in the Macquarie Island population over the past 60 yr has occurred concurrently with a positive trend in sea ice extent in the Ross Sea region. The negative relationship between weaning mass and sea ice extent suggests that the decline in the Macquarie Island population trajectory may, in part, be caused by increasing sea ice in the Ross Sea and mediated by a reduction in weaning mass, first-year survival and recruitment rates.

KEY WORDS: Life history · Survival · Maternal expenditure · Sea ice

INTRODUCTION

Over the last half century, regions of the Antarctic and Southern Ocean have experienced widespread environmental changes. These changes include warming of the upper layers of the Antarctic Circumpolar Current (Böning et al. 2008), intensification of westerly winds over the Southern Ocean (with consequent poleward shifts in the location of these winds and the major oceanic fronts; Sokolov & Rintoul 2009) and an overall growth in Antarctic ice extent, despite significant reductions in sea ice extent and duration over the western Antarctic Peninsula (Turner et al. 2014). For marine ecosystems, the implications of environmental changes can be profound and have the potential to generate cascading effects throughout the food web (Constable et al. 2014). Middle and top trophic level species, such as marine mammals and seabirds, are likely to be indirectly and gradually affected by environmen-

tal change through alterations in the abundance, quality, distribution and/or accessibility of their prey (Walther et al. 2002, Weimerskirch et al. 2003). Despite potential lags, the response of these animals to environmental change is likely to be significant and difficult to reverse (Sydeman et al. 2015). Indeed, this is increasingly being observed in predator populations across the Antarctic and Southern Ocean; for example, declines in Adélie and gentoo penguin populations on the northern tip of the Antarctic Peninsula have been attributed to reductions in ice-dependent krill stocks following years of reduced sea ice (Trivelpiece et al. 2011).

The southern elephant seal *Mirounga leonina*, a wide-ranging mesopredator in the Antarctic and Southern Ocean which has exhibited large population declines across much of its circumpolar distribution between the 1950s and 1990s, is another pertinent example (McMahon et al. 2005a, Pistorius et al. 2011). While the major stocks at Heard Island, Iles Kerguelen, South Georgia and Peninsula Valdes have since stabilized or increased recently (Hindell et al. 2016), the Macquarie Island population in the southern Pacific Ocean has continued to decrease by an average rate of 0.8 % per annum since the 1950s (van den Hoff et al. 2014). Although the cause of this decrease remains unknown, it is often attributed to reductions in the foraging success of the Macquarie Island seals, either as a result of the cascading ecological effects of changing oceanic conditions (Hindell et al. 1991, McMahon et al. 2005a) or as a consequence of the exclusion of breeding females from highly productive continental shelf waters in years of increased sea ice extent and duration (Hindell et al. 2016). Macquarie Island is the only population which is experiencing increasing sea ice extent within its maternal foraging areas (Hindell et al. 2016).

Southern elephant seals are capital breeders (Boyd 2000), and so the foraging success of females during their post-moult migrations is positively correlated with the mass of their pups at weaning (Arnbom et al. 1993, Carlini et al. 1997), which in turn determines first-year survival rates and recruitment into the breeding population (McMahon et al. 2000, Oosthuizen et al. 2015). Any long-term environmental variations that affect the foraging success of pregnant females and the mass of their offspring at weaning can therefore have long-term and potentially adverse implications for the growth of the population (McMahon et al. 2005b, 2017). Weaning mass has consequently been used in a number of studies to identify the nature of the links between environmen-

tal variability, female foraging success and offspring weaning mass and, ultimately, population dynamics (e.g. Vergani et al. 2001, 2008, Oosthuizen et al. 2015).

While studies have identified the effects of varying climatic conditions on maternal post-partum mass and first-year survival rates in the Macquarie Island population (McMahon & Burton 2005, de Little et al. 2007, McMahon et al. 2017), the links between global and local climate variability, maternal foraging success and the mass of elephant seal pups at weaning remain poorly understood, despite this being the proximate determinant of juvenile survival (McMahon et al. 2000). Further, the response of these seals to environmental conditions is likely to differ between populations due to distinct differences in the preferred foraging grounds of each elephant seal stock and the highly regionalized nature of environmental change in the Southern Ocean. For example, adult females from Marion Island predominantly forage in pelagic waters within the Frontal Zone and the Antarctic Circumpolar Current Zone, rarely entering into truly Antarctic waters (McIntyre et al. 2011), while Macquarie Island females forage in the pelagic waters of the sub-Antarctic or along the continental shelf and ice edge in the Ross Sea and adjacent to the coast of Victoria Land (Hindell et al. 2016). It is therefore important to understand how each distinct population is affected by environmental change.

This study aims to quantify and resolve how short-term environmental variability affects resource availability and the foraging success of Macquarie Island breeding females by studying inter-annual variations in offspring weaning mass in relation to a variety of both intrinsic and extrinsic (environmental) covariates.

MATERIALS AND METHODS

Weaning mass (response variable)

The weaning mass data used in this study were collected from the Isthmus study area at Macquarie Island (54° 30′ S, 158° 50′ E; Carrick & Ingham 1962) over 7 consecutive breeding seasons (September–November) from 1994 to 2000. The Isthmus study area represents approximately 13 % of the breeding population of southern elephant seals on Macquarie Island (Hindell & Burton 1987).

Three weeks after the birth of the first pups, daily searches of the beach and tussock areas were con-

ducted to find pups weaned the previous day. Weaned pups were captured, sexed and weighed to the nearest 1 kg in a net sling attached to a 300 kg Salter spring balance suspended from an aluminum tripod (McMahon et al. 2000). Weaners were permanently marked on each flank using a hot-iron alphanumeric brand denoting the cohort and the individual for future identification (Hindell & Little 1988, McMahon et al. 2006, 2007).

The size of females at parturition, a function of maternal age, foraging success and energetic reserves, is closely related to the size of their pups at weaning, with larger females typically rearing larger weaners (Engelhard et al. 2002, Wheatley et al. 2006). Further, southern elephant seals at birth are sexually dimorphic, with male pups weighing on average 6 kg (5%) more than females at weaning (Arnbom et al. 1993, 1997), and thus sex is also a strong determinant of pup size at weaning (McMahon et al. 2016). Given the importance of both maternal size and sex in determining pup weaning mass, we used only pups of known sex for which information on the size of their mothers at parturition was available. A total of 7276 weaners across 7 cohorts were included in the analysis, with a mean sample size per year of 910 ± 157 and sample size ranging from 552 (1994) to 982 (2000).

Intrinsic and extrinsic covariates

To quantify and explain inter-annual variations in the mean weaning mass of Macquarie Island elephant seals, a suite of intrinsic and extrinsic covariates was included in the analysis. The details of these covariates are as follows.

Intrinsic covariates

Sex. The sex of the weaner was included as a covariate to account for the known effect of sex on the weaning mass of elephant seal pups (Fedak et al. 1996, Arnbom et al. 1997).

Maternal size (msize). To account for the known effect of maternal size on pup weaning mass, maternal size, categorized by eye at parturition as either small (approximately 2.10–2.45 m), medium (2.46–2.58 m) or large (2.59–2.90 m) (McMahon & Hindell 2003), was included as an intrinsic covariate. Maternal body length at parturition is strongly related to mass, so this visual estimate will divide the seal mothers into 3 broad mass groups as well.

Log number of females ashore (lnfem). Lnfem ashore during the breeding season was estimated from the peak count of females ashore in the Isthmus study area (Hindell & Burton 1987, 1988) in each year. Because of the high energetic cost of reproduction, female elephant seals face a trade-off between survival and lifetime reproductive success (Desprez 2015). To increase their chances of survival and maximize their long-term reproductive success, female elephant seals should come ashore to breed only when in good condition (Desprez 2015). Therefore, lnfem ashore during the breeding season in any year is dependent on the ability of females to acquire and store energy (van den Hoff et al. 2014).

Spatial and temporal context

Southern elephant seals from Macquarie Island do not forage uniformly across their Southern Ocean range (Hindell et al. 2016); some regions are preferred over others. We used tracking data from 67 Macquarie Island female seals tagged between 2000 and 2010 (for details on these deployments, see Bradshaw et al. 2004, Thums et al. 2013, Hindell et al. 2016) to define the core post-moult foraging areas for adult female seals (February–October). Using the trip package in R (https://github.com/Australian AntarcticDivision/raadtools), we first calculated the time (h) spent in 50 × 50 km grid cells across the full range of observations for each of the 67 seals. These values were then averaged and expressed as the mean time spent in each cell (hereafter termed residence time) for all seals. By using mean residence time for all seals, we minimized the likelihood of inflating the importance of a cell that is frequented by a large number of seals but for only a short period of time, e.g. the cells immediately surrounding Macquarie Island. The core foraging area of the Macquarie Island seals, and therefore the spatial domain from which to extract extrinsic (environmental) covariates, was defined as the grid cells with a mean residence time in the top 70th percentile of cell residence times. Several studies have documented that individual elephant seals exhibit high philopatry to foraging sites (Bradshaw et al. 2004, Authier et al. 2012, Robinson et al. 2012, Cotte et al. 2015) and that a sample of approximately 40 elephant seals will describe over 90% of the potential foraging areas for the Macquarie Island population (Hindell et al. 2003). Therefore, even though our sample spans multiple years, it will provide a reliable picture of the broadscale use of the region by the seals.

Extrinsic covariates

We used a range of environmental covariates to help explain the weaning mass of elephant seal pups at Macquarie Island. A full description of each variable and rational for its inclusion in the analysis are provided in the Supplement at www.int-res.com/articles/suppl/m568p249_supp.pdf. The covariates fell into 2 broad categories: (1) global climate modes, which describe large-scale, sub-decadal climatic variation as a result of a number of global modes of atmospheric circulation and include the Southern Annular Mode (SAM) and the El-Niño–Southern Oscillation (ENSO); and (2) regional environmental variations, which were derived from within the core foraging areas illustrated in Fig. 1 and were included based on an *a priori* understanding of the influence that these variables have on oceanic and biological features likely to be important to the foraging success of Macquarie Island breeding females (Supplement). For each parameter, there was a single value calculated each year for the entire post-moult foraging trip. For example, weekly sea surface temperature (SST) values were estimated for each 50×50 km grid cell within the core area, and this was averaged to provide the SST value for that year.

Statistical analyses

Linear models were fitted to the data using the stats package in the statistics program R (version 3.1.1; R Core Team 2016) to quantify how extrinsic and intrinsic covariates affect elephant seal weaning mass. After first fitting the null (intercept) model, we fitted a series of models of increasing complexity that related intrinsic covariates (i.e. sex, msize and lnfem) to weaning mass. Extrinsic covariates explaining between-year variations in weaning mass (e.g. SAM, Southern Oscillation Index [SOI], SST) were then added sequentially to the top model from the suite of models previously constructed using only the intrinsic covariates. We also minimized the use of interaction terms in the model, only including one if inspection of the model outputs suggested an interaction term might improve the model.

Given that the number of statistical units available to detect the influence of covariates on elephant seal weaning mass was the number of years of data available (i.e. 7; Grosbois et al. 2008), we restricted each model to the top model explaining intrinsic variation in weaning mass plus a single environmental (extrinsic) covariate. By keeping the ratio of covariates to statistical units low, we mini-
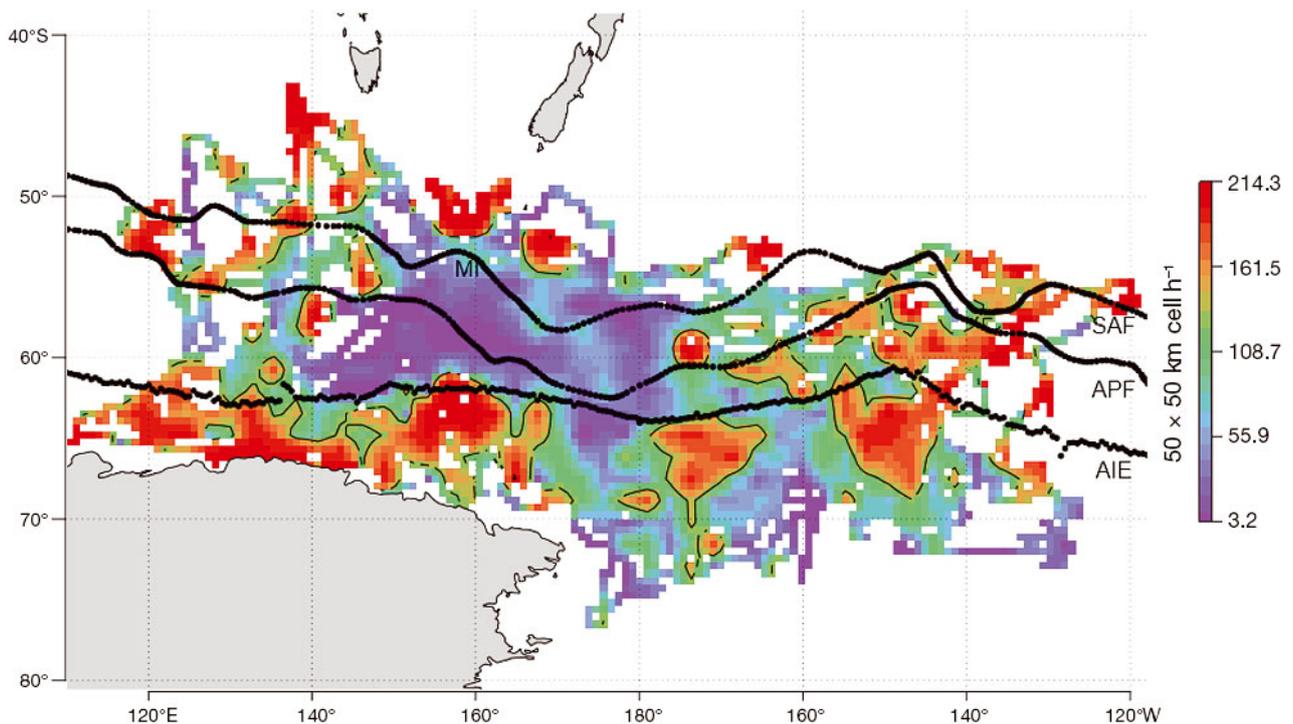

Fig. 1. Core foraging areas of female southern elephant seals from Macquarie Island (MI) over their post-moult migrations. Thin black lines represent the region where these seals spent at least 30% of their time. Black dotted lines indicate the mean position of the sub-Antarctic Front (SAF), the Antarctic Polar Front (APF) and the mean extent of the pack ice in August (AIE)

mized the likelihood of detecting spurious climatic effects (i.e. Type I error; Grosbois et al. 2008). All model parameters were fitted using maximum likelihood estimation. Model selection was based on Akaike's information criterion corrected for small samples (AICc; Burnham et al. 2011). Where required, explanatory variables were log transformed to ensure normality in their distributions.

RESULTS

Spatial context

Tracking data from 67 Macquarie Island adult females between 2000 and 2010 revealed that over the post-moult period, the seals have a geographic range from 42.54° to 76.73° S and 109.89° to 242.27° W (Fig. 1). The core foraging regions for these seals (defined here as 70th percentile of the mean residence in a 50 × 50 km grid cell) were located on and adjacent to the continental shelf adjacent to the Victoria Land coast, the region north of the Ross Sea, and in isolated patches between the Subtropical Front and the Polar Front south of southeastern Australia and New Zealand (Fig. 1).

The grid cells with the lowest residence times were immediately south, southwest and southeast of Macquarie Island (Fig. 1). These areas likely represent transit zones used by the breeding females as they disperse from Macquarie Island into high-latitude Antarctic waters and are therefore unlikely to be important foraging habitats.

Table 1. Mean, maximum and minimum values for global and regional extrinsic (environmental) covariates in the core foraging habitat of Macquarie Island adult females over the post-moult period between 1994 and 2000. SST: sea surface temperature; SSTg: SST gradient; SSHa: sea surface height anomaly; SSH-var: sea surface height variability; ice-c: sea ice concentration; ice-e: sea ice extent; SAM: Southern Annular Mode; SOI: Southern Oscillation Index

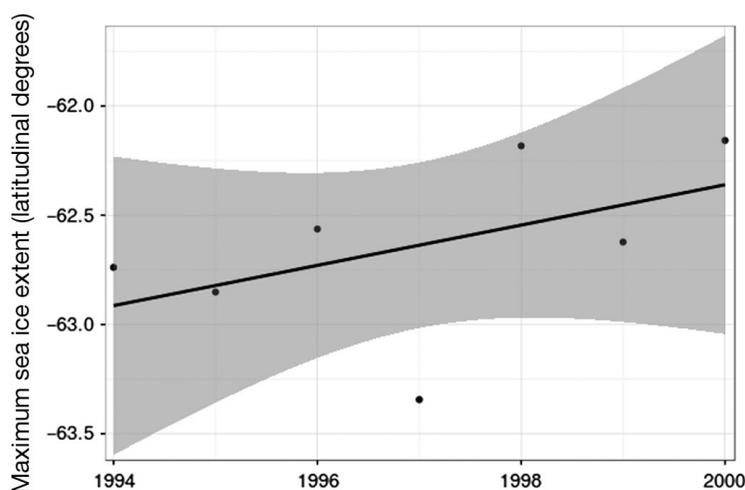| Environmental variable	Max.	Min.	Mean ± SD
SST (°C)	1.7	1.3	1.5 ± 0.2
SSTg (°C)	9.89×10^{-6}	7.13×10^{-6}	$8.42 \times 10^{-6} \pm 8.17 \times 10^{-6}$
SSHa (mm)	0.0154	−0.0008	0.0050 ± 0.0060
SSH-var (mm)	0.0044	0.0039	0.0040 ± 0.0002
Wind (m s^{-1})	11.3	10.5	10.8 ± 0.3
Current (m s^{-1})	0.15	0.13	0.14 ± 0.01
Ice-c (%)	42.6	36.0	39.6 ± 2.30
Ice-e (latitude °)	−62.1	−63.3	−62.6 ± 0.4
SAM	1.23	−0.35	0.37 ± 0.58
SOI	6.49	−13.63	−1.77 ± 8.76

Fig. 2. 1994 to 2000 trend in maximum sea ice extent in the Ross Sea region, including the linear regression line (solid black line) and standard error (gray shade)

Inter-annual environmental variability

All of the environmental parameters varied across the 7 yr (1994−2000) of the study (Table 1). During the study period, the SAM was predominantly in a positive phase, while the SOI was predominantly negative, with 4 out of the 7 yr showing positive SAM values (1997−2000) and negative SOI values (1994−1995 and 1997−1998). Similarly, the median August sea ice extent in the study region ranged from a minimum latitude of 62.157° S to a maximum of 63.343° S (Table 1, Fig. 2), a meridional difference in the median ice extent of approximately 132 km.

Inter- and intra-annual variations in weaning mass

There was considerable variation in the weaning mass of pups within each year, with mass varying by as much as 178 kg (1997) among male and female pups in a single cohort (Table 2). In all years, male weaners were, on average, 6 kg heavier than females, although this difference varied from a minimum of 5 kg (1996) to a maximum difference of 7 kg (1994; Table 2). Mean weaning mass also varied among years, with females ranging from a maximum mean weaning mass of 120 ± 27 kg in 1997 (n = 441) to a minimum of 112 ± 26 kg in

Table 2. Weaning mass (mean ± SD) of male, female and all (male and female seals combined) southern elephant seals at Macquarie Island between 1994 and 2000, including sample size (n) and maximum, minimum and range of weaning masses across all weaners in each year. Also shown is the percentage of mothers in each of the 3 size classes each year: small (approximately 2.10–2.45 m), medium (2.46–2.58 m) and large (2.59–2.90 m)

Year	Males at weaning		Females at weaning		All				Maternal size class (%)		
	n	Mean mass (kg)	n	Mean mass (kg)	n	Mean mass (kg)	Max. (kg)	Min. (kg)	Small	Medium	Large
1994	278	121 ± 27	274	114 ± 25	552	118 ± 26	199	42	6.0	80.4	13.6
1995	410	118 ± 27	426	113 ± 6	836	116 ± 26	215	41	29.7	42.2	28.1
1996	475	120 ± 28	497	115 ± 26	972	117 ± 27	204	47	18.3	50.8	30.9
1997	510	125 ± 28	441	120 ± 7	951	123 ± 28	222	44	14.0	58.4	27.4
1998	478	121 ± 28	480	115 ± 28	958	118 ± 28	208	38	5.4	68.6	26.0
1999	483	123 ± 27	479	118 ± 26	962	120 ± 27	204	40	19.4	60.0	20.6
2000	486	120 ± 29	496	115 ± 27	982	117 ± 28	202	40	7.1	50.4	42.5

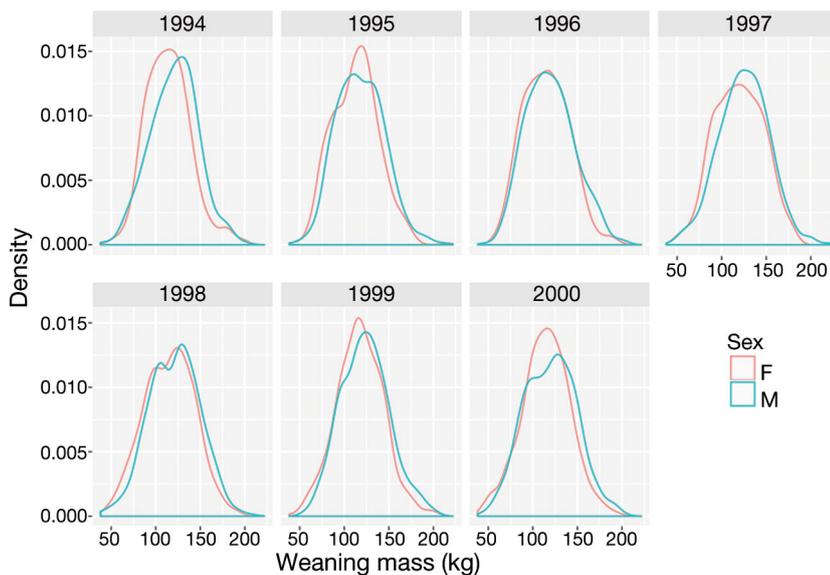

Fig. 3. Density plots of the mass (kg) of male (M; blue) and female (F; pink) Macquarie Island elephant seals at weaning from 1994 to 2000

Table 3. Model selection of weaning mass variation in southern elephant seals at Macquarie Island including intrinsic covariates (1994–2000), showing the model structure and the log likelihood of each model as well as the corrected Akaike's information criterion (AICc) and the delta AICc (difference between one model and the next). Msize: maternal size; lnfem: number of females ashore

Model	Log likelihood	AICc	ΔAICc
Sex + msize + lnfem	−28203.5	56419.0	0.0
Sex + msize	−28211.4	56432.8	13.8
Sex:msize	−28210.7	56435.4	16.4
Msize	−28245.1	56498.2	79.2
Sex	−29346.8	58699.5	2280.6
Null	−29378.7	58761.4	2342.5
Lnfem	−29377.9	58761.8	2342.9

1995 (n = 426), representing a difference of 6%. Similarly, the average mass of male pups at weaning varied from a maximum of 125 ± 28 kg in 1997 (n = 510) to a minimum of 118 ± 27 kg in 1995 (n = 410), representing a difference of 6%. The relative proportion of male and female pups did not vary among the years (Fig. 3). However, in some years (1995, 1998 and 2000), there is a suggestion of the males having a bimodal distribution of weaning mass. The proportion of mothers in 3 size classes also varied among the years (Table 2). Medium was the most common in all years but ranged from 50.4 to 80.4%. Small ranged from 7.1 to 29.7%, and large ranged from 13.6 to 42.5%.

Influence of intrinsic covariates on weaning mass

Intrinsic variation in weaning mass was best explained by the additive effects of sex, msize and lnfem; (Table 3). Male pups were always heavier than females at weaning, and weaning mass was positively related to the size of mothers at parturition, with larger females typically weaning heavier pups (Fig. 4). Additionally, weaning mass was positively related to infem, with pups weighing on average 3 kg more in years with greater infem to breed (Fig. 4), representing an increase in mass of 3.1, 2.5 and 2.1% for pups of small, medium and large mothers, respectively.
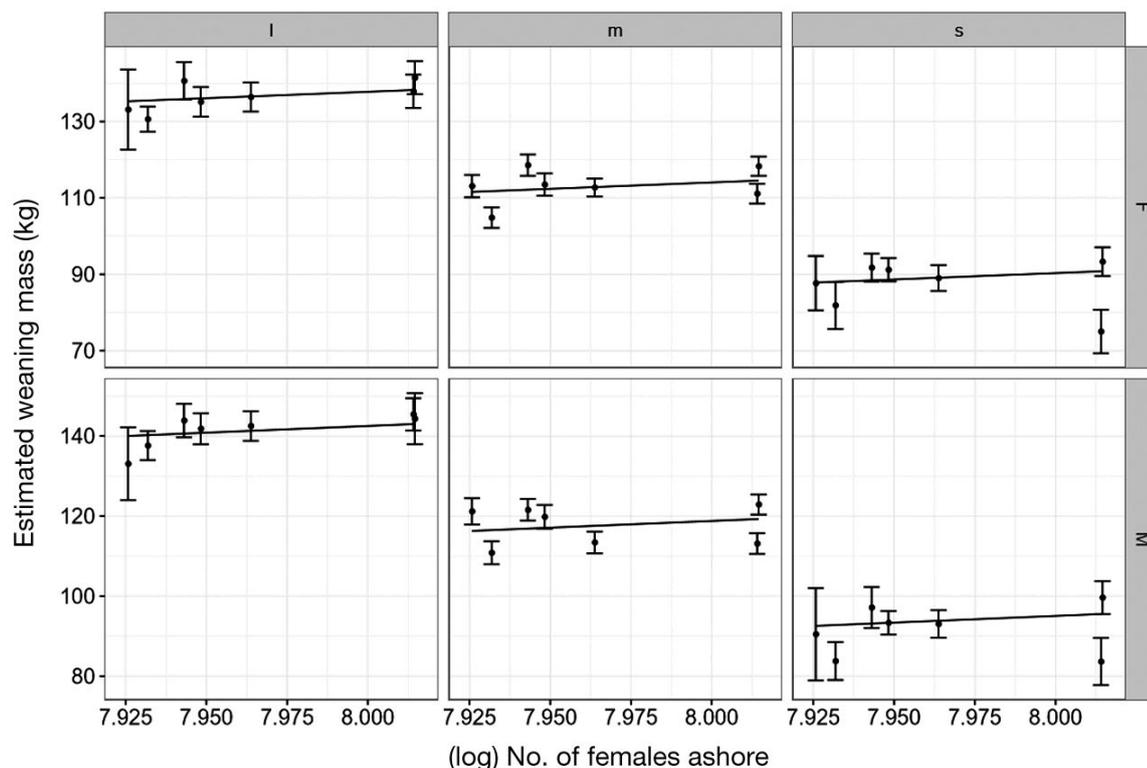
Fig. 4. Relationship between mean weaning mass of male (M) and female (F) Macquarie Island elephant seals and the (log) number of females ashore during the breeding season for small (s), medium (m) and large (l) mothers. Black dots and error bars represent the mean (±SE) mass of pups for each year. Black line represents the estimated weaning mass of pups relative to the number of females ashore each year predicted from the best-ranked model, wean mass = sex + msize + lnfem (Table 2), where msize: maternal size; lnfem: (log) number of females ashore

Environmental influences on weaning mass

The best overall model that described weaning mass included the additive effects of sex, msize, lnfem and median extent of sea ice (ice-e) in August; plus an interaction between ice-e and msize (msize:ice-e; Table 4). This model explained weaning mass better than the model that included only intrinsic covariates (i.e. sex + msize + lnfem; Table 4). August ice-e did not influence the weaning mass of pups of large mothers. For all others, however, median August ice-e negatively affected elephant seal wean mass, with pups weighing on average 17 kg less in years of high ice-e. This represents a relative decrease in mass of 16.8 and 13.5% for pups of small and medium

Table 4. Model selection of variation in weaning mass of southern elephant seals at Macquarie Island between 1994 and 2000 for models including the effect of extrinsic (environmental) covariates, showing the model structure and log likelihood of each model as well as the corrected Akaike's information criterion (AICc) and the delta AICc (difference between one model and the next). Msize: maternal size; lnfem: number of females ashore; ice-e: sea ice extent; SSH-var: sea surface height variability; SOI: Southern Oscillation Index; ice-c: sea ice concentration; SSTg: sea surface temperature gradient; SST: sea surface temperature; SSHa: sea surface height anomaly; SAM: Southern Annular Mode

| Model	Log likelihood	AICc	ΔAICc
Sex + msize + lnfem + ice-e + msize:ice-e	−28133.6	56271.3	0.0
Sex + msize + lnfem + ice-e	−28133.6	56281.3	10.0
Sex + msize + lnfem + SSH-var	−28147.8	56309.6	28.3
Sex + msize + lnfem + current	−28164.8	56343.5	62.2
Sex + msize + lnfem + SOI	−28178.6	56371.2	90.0
Sex + msize + lnfem + ice-c	−28181.4	56376.9	95.6
Sex + msize + lnfem + SSTg	−28188.5	56391	109.8
Sex + msize + lnfem + SST	−28188.8	56391.6	110.4
Sex + msize + lnfem + SSHa	−28191.1	56396.3	115
Sex + msize + lnfem	−28203.5	56419.0	137.7
Sex + msize + lnfem + wind	−28203.4	56420.8	139.5
Sex + msize + lnfem + SAM	−28203.5	56420.9	139.6
Null	−29378.71	58761.4	2480.1
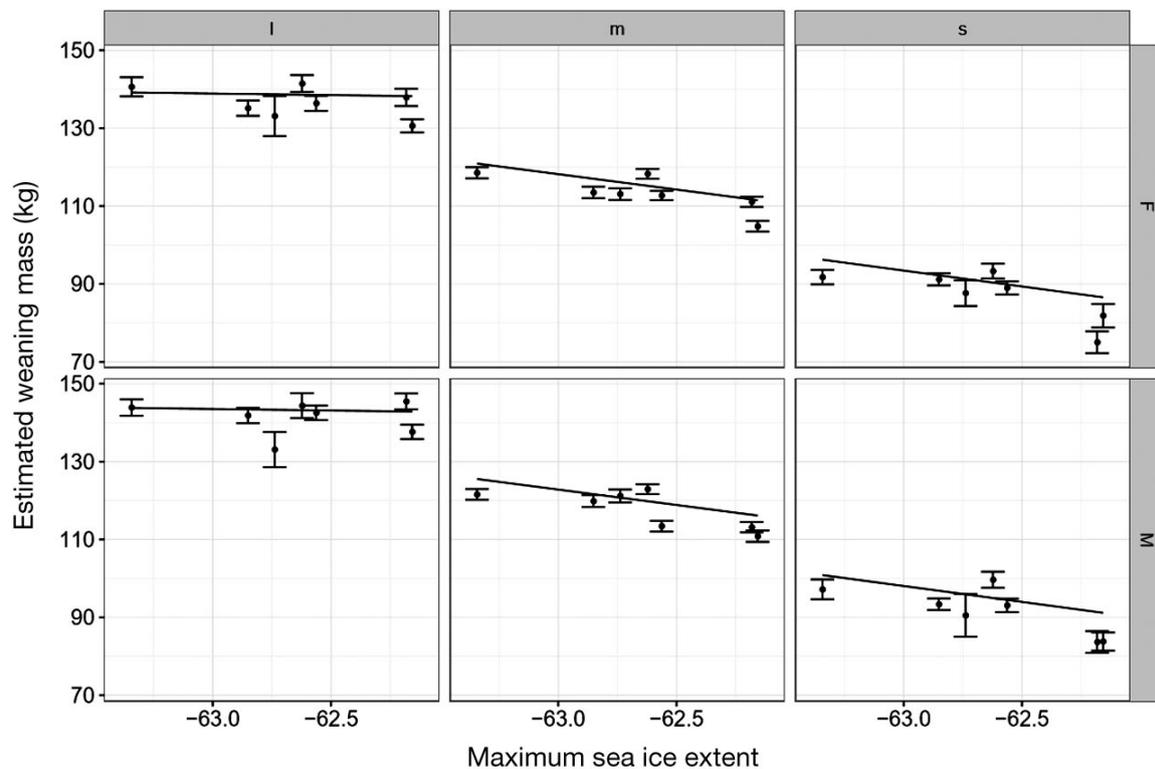
Fig. 5. Relationship between the estimated weaning mass of male (M) and female (F) Macquarie Island elephant seals at weaning and the (standardized) annual maximum extent of sea ice (degrees of latitude) for small (s), medium (m) and large (l) mothers. Larger latitude values represent higher sea ice extent (more northerly extent), while smaller values indicate years of low sea ice extent (more southerly extent). Black dots and error bars represent the mean weaning mass (±SE) observed for each maximum sea ice extent value. Black line represents the estimated weaning mass of pups relative to the number of females ashore each year predicted from the best-ranked model, wean mass = sex + msize + lnfem + ice-e + msize:ice-e (Table 3), where msize: maternal size; lnfem: (log) number of females ashore; ice-e: sea ice extent

mothers, respectively (Fig. 5). After ice-e, sea surface height variability, an index of long-term eddy activity, was the next best model, although it did not perform as well as the top-ranked model. Models including the SAM and SOI were not highly ranked, suggesting that regional covariates better explain maternal foraging success than global environmental covariates (Table 4). The small number of years in the study precluded testing of more complex models.

DISCUSSION

Intrinsic influences on weaning mass

In addition to sex and msize, the mass of Macquarie Island elephant seals at weaning was positively related to lnfem during the breeding season, as was also reported in the Marion population (Oosthuizen et al. 2015). At Macquarie Island, the mean mass of pups at weaning was on average 3 kg less in years

with the fewest females compared to years with the greatest number. Elephant seals are extreme capital breeders (Arnbom et al. 1997) and rely exclusively on stored energetic reserves acquired over the post-moult period both to maintain their own metabolism and to produce enough energy-rich milk to successfully wean their pups (Carlini et al. 2004). Consequently, reproduction in female elephant seals is energetically expensive, with females losing on average 35% of their post-partum mass over the 24 d lactation period (Fedak et al. 1996, Arnbom et al. 1997). Breeding may therefore come at a high cost to survival for both first-time and experienced breeders (Desprez 2015). Given this cost of reproduction on survival, female elephant seals may skip a breeding event when conditions during gestation are unfavorable, thereby increasing their chances of surviving and maximizing their long-term reproductive success (Pistorius et al. 2008, Desprez 2015). A major factor determining whether a female skips reproduction is the foraging conditions over the post-moult period,

i.e. the period when female elephant seals acquire and store the energetic reserves critical for reproduction and the post-partum survival of both the female and her pup (Arnbom et al. 1993, 1997). Therefore, when foraging conditions are favorable, greater numbers of females will be in good condition and able to reproduce, and the number of females ashore will also be higher than years when foraging conditions are relatively poor (van den Hoff et al. 2014). Years of poor foraging success would likely result in negative rates of population growth 3 to 4 yr later because pups born when conditions are below average will be smaller (McMahon et al. 2017), suffer greater mortality (McMahon et al. 2003) and therefore be less likely to recruit into the breeding population at age 4. The likely underlying mechanism for lower foraging success is reduced access to and time spent in the high-quality Antarctic continental shelf and shelf slope habitats (van den Hoff et al. 2014, Hindell et al. 2016).

Further, the positive relationship between weaning mass and infem indicates that when foraging conditions are poor, the growth of the population is negatively affected by both a reduction in the number of females that come ashore to breed (i.e. low pup production) and higher mortality among underyearlings, making the effect on the population 2-fold. Although the effect on weaning mass was relatively slight (approximately a 3% difference between good and bad years), this is sufficient to influence survival (McMahon et al. 2017). As suggested by van den Hoff et al. (2014), this reduction in pup production and pup survival would likely result in a substantial reduction in infem and would be reflected in negative population growth 3 to 4 yr later when pups begin to come ashore to breed.

Extrinsic influences on weaning mass

We found that the maximum ice-e negatively affected southern elephant seal weaning mass, with pups 17 kg heavier in years of relatively low ice-e compared to years with maximum extent. Interestingly, the pups of the large mothers were not affected by ice, but pups of mothers from other size classes were. This accords with previous studies from Macquarie Island which found that the effect of maximum ice-e on maternal post-partum mass was greater in smaller females than in larger females (McMahon et al. 2017). The negative relationship to ice extent is in contrast to greater rates of first-year survival reported in Macquarie Island seals following

El Niño events (McMahon & Burton 2005, de Little et al. 2007), when ice-e increases in the Ross Sea region (Stammerjohn et al. 2008). However, juvenile elephant seals do not forage in the Antarctic pack ice but rather remain in the vicinity of the Antarctic and sub-Antarctic fronts (Field et al. 2004) and so will not be directly affected by changes in ice-e.

The Macquarie Island population of southern elephant seals has been decreasing since the 1950s (van den Hoff et al. 2014). This decline has typically been attributed to a reduction in the foraging conditions encountered by breeding females and consequent reductions in the size and survival of their offspring (McMahon et al. 2005a). This hypothesis is supported by a decline in the size of Macquarie Island pups at weaning between the 1950s and the 1990s (Clausius et al. 2017). van den Hoff et al. (2014) suggested that the foraging performance of Macquarie Island females is declining as a result of increasing sea ice duration in the Ross Sea region, leading to the earlier and lengthier exclusion of females from preferred highly productive shelf waters. The negative relationship between weaning mass and maximum ice-e found in this study supports this hypothesis and, given the positive relationship between weaning mass and first year survival (McMahon et al. 2000), provides a critical link between sea ice conditions and population dynamics.

Lending further support to this hypothesis are the sea ice changes observed in the western Ross Sea over the satellite era. Since the late 1970s, ice-e in the western Ross Sea has increased at approximately 3.9% per decade, and the duration of the ice-free season has declined by roughly 2 mo (Stammerjohn et al. 2012, Turner et al. 2015, 2016). Given the negative relationship between maximum ice-e and weaning mass, and the importance of weaning mass on rates of first-year survival and therefore population dynamics, it appears that the decline in the Macquarie Island population since the 1950s is, at least in part, associated with the expansion of sea ice in the Ross Sea region over the same period.

While changes in ice conditions in the Ross Sea sector appear to be negatively affecting the Macquarie Island elephant seal population, environmental changes in the western Antarctic Peninsula and Bellingshausen Sea region may account for the increase in the South Georgia elephant seal population over the past 30 yr (Gil-Delgado et al. 2013). The western Antarctic Peninsula and Bellingshausen Sea region has seen substantial surface warming (approx. 2.9°C since 1951; Turner et al. 2016), a 3 mo longer ice-free season and a decrease in ice-e by roughly

3.4% per decade (Stammerjohn et al. 2012, Turner et al. 2015, 2016). These conditions may benefit the South Georgia and Antarctic Peninsula populations by allowing access to beach areas for moulting, breeding and pupping, as is the case on Anvers Island (Siniff et al. 2008), and by improving foraging conditions, for example, by enhancing growth of local prey species in years with warmer ocean temperatures (Hatfield 2000, Vergani et al. 2008). This is supported by a higher mean wean mass among Antarctic Peninsula seals following El Niño events (Vergani et al. 2001, 2008).

The contrasting trends in sea ice and temperatures in the Ross Sea region, the Amundsen–Bellingshausen seas and western Antarctic Peninsula are, in part, driven by the deepening of the Amundsen Sea Low (ASL) (Hosking et al. 2013, Raphael et al. 2016). Much of the inter- and intra-annual variability in ice-e, temperature and precipitation in West Antarctica is a result of the position and depth of the ASL and the influence that these parameters have on the meridional near-surface winds in the region (Hosking et al. 2013). Although much uncertainty remains regarding what drives the depth and position of the ASL (Raphael et al. 2016), deepening of the ASL has been linked to stratospheric ozone depletion (Turner et al. 2009, Fogt & Wovrosh 2015, England et al. 2016), anthropogenic greenhouse gas forcing (Hosking et al. 2016), the phase of ENSO and SAM (Turner et al. 2013) and tropical SST variability (Raphael et al. 2016). Given that greenhouse gas concentrations are projected to continue to rise over at least the coming century (IPCC 2013), it is therefore likely that the ASL will continue to deepen and will lead to (1) strengthening of the dipole, (2) increasing temperatures and (3) decreasing ice extent in the Amundsen–Bellingshausen seas (Stammerjohn et al. 2008b, 2012, Raphael et al. 2016). In the Ross Sea, temperatures will decrease and ice extent will increase. A deepening of the ASL will likely have adverse implications for the growth of the Macquarie Island population over the coming decades. Consequently, we may see Macquarie Island adult females shift their foraging efforts to predominantly sub-Antarctic waters as the Antarctic continental shelf foraging strategy is gradually selected against.

Our study highlights how short-term environmental variability affects the life-history traits of marine predator populations, including reproductive performance, first-year survival rates and recruitment into the breeding population, which allows for a more synthetic understanding of how future environmental changes might affect population viability.

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