Climate change and seal survival: evidence for environmentally mediated changes in elephant seal, *Mirounga leonina*, pup survival

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Maternal and physical factors play a significant role in animal life-history variability, which means that large scale climate change has the potential to affect the size and dynamics of animal populations indirectly through maternal investment and directly through conditions that animals are exposed to. However, little is known about the effects of large-scale oceanographic events such as the El-Niño southern oscillation (ENSO) that influence productivity in the Southern Ocean and the abundance, quality and distribution of prey. The possible mechanisms by which physical factors and primary productivity could influence life-history traits, such as survival of apex predators, includes direct influences such as food availability and foraging success and indirect influences such as stored maternal investment and resource transfer during lactation. Here, we quantify the relative contribution of maternal investment and climate conditions at remote foraging sites to survival in the first year of life for southern elephant seals. We present evidence linking climate (ENSO) and variations in a key demographic parameter—first-year survival—and demonstrate that survival was highest during ENSO events and that the ability of mothers to store and acquire resources, which is typically related to ocean productivity, is the most important determinant of survival in the first year. This functional link provides valuable insights that can be used to model the responses of the seal populations to climate change scenarios.

Keywords: environmental variability; survival; maternal investment

1. INTRODUCTION

An evaluation of the links between regular climatic variations, such as El Niño southern oscillation (ENSO), and predator demography allows us to assess, from relatively short-term datasets, the effects of long-term climate change on the life-history of animals. In the first instance, this requires the identification of the links between oceanic and atmospheric events in distant parts of the globe (Gloersen 1995; Kwok & Comiso 2002) because predators such as southern elephant seals (SESs) range widely across the world's ocean basins (Hindell & McMahon 2000). ENSO events affect the physical environment, including the sea-ice (Carleton & Carpenter 1990; Ledley & Huang 1997; Turner 2004) and the biological environment (Wilson *et al.* 2001; Atkinson *et al.* 2004) in Antarctica where elephant seals forage. In the case of elephant seals from Macquarie Island, whose foraging zones are located near the Ross Sea (Hindell *et al.* 1991; Slip *et al.* 1994), as much as 76% of the variation in sea-ice extent can be explained by ENSO (Arrigo & van Dijken 2004). The sea-ice environment is an important part of the southern ocean (SO) ecosystem because all biological activity is associated with the physical components of the sea-ice in the SO (Arrigo *et al.* 1997; Tynan

1998; Fraser & Hofmann 2003; Atkinson *et al.* 2004). In this general region, SES foraging zones are commonly concentrated around oceanic frontal zones and determined by the prey distribution within these zones (Hindell *et al.* 1999; Field *et al.* 2001, 2004), much of which is dictated by the thermal structure of the water column (Sokolov & Rintoul 2002) which in turn is influenced by ENSO through pressure and sea temperature changes (Carleton & Carpenter 1990; Ledley & Huang 1997; Turner 2004). The thermal structure and the long-term predictability of the relatively high productivity in these areas means that elephant seals have adopted a non-random foraging strategy so that they centre their foraging effort in areas to which they habitually return (Bradshaw *et al.* 2004), even though the position and the productivity around these frontal zones changes annually (Sokolov & Rintoul 2002; Constable *et al.* 2003). Such a strategy may have evolved because of the evolutionary advantage elephant seals gain from the (generally) higher productivity associated with these variable sites (Bradshaw *et al.* 2004), which enables female seals to, on average (i.e. over their lifetimes), produce and rear offspring that have the highest probability of surviving by producing offspring with higher than average weaning masses (McMahon *et al.* 2000, 2003; Bradshaw *et al.* 2004). We use the variability in the productivity of SESs foraging zones quantified as: (i) weaning mass (Fedak *et al.* 1996; Burton *et al.* 1997; Crocker *et al.* 2001) and (ii) ENSO as enumerated by the southern oscillation index (SOI) to assess the effect of

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varying climates on a key demographic parameter—survival—and to study the functional relationship between environmental conditions and animal demography. ENSO was selected because it is an accessible and, therefore, easily quantifiable environmental perturbation that is known to affect productivity in the SO through variations in, for example, ocean temperature and winter sea-ice extent. Variations (in particular, variations in sea-ice extent) mediated by ENSO are biologically significant because: (i) productivity in the SO is allied to sea-ice extent (Loeb *et al.* 1997; Atkinson *et al.* 2004) and (ii) the ecological influence of sea-ice extent has been demonstrated at all trophic levels (Ross *et al.* 1996; Fraser & Hofmann 2003). Thus, environmental perturbations such as ENSO events are likely to influence higher order predator life history traits such as survival.

The survival of naive seals (i.e. less than 1 year) was quantified because: (i) foraging success in the first year of life is not influenced by previous foraging experience, as has been demonstrated for adult elephant seals (Bradshaw *et al.* 2004) and (ii) recently weaned seals have finite stored resources (McMahon *et al.* 2000; McConnell *et al.* 2002) with which to successfully locate patchily distributed foraging areas and food (Constable *et al.* 2003) after which they will starve. Moreover, naive seals require more resources, at least in mass specific terms, for maintenance and growth (McLaren 1993) than adults and therefore environmental variability is more likely to affect juvenile survival than adult survival (Gaillard *et al.* 1998). Indeed, the consequences of such changes in survival, especially of young animals, are often far-reaching and have been associated with changes in population structure and size (Caughley 1977; Hindell 1991). Understanding the relationship between environmental conditions and the demography of an apex predator, such as the SES, is vital to our understanding and management of the SO ecosystem (Fraser & Hofmann 2003; Hindell *et al.* 2003), especially given the present predictions of dramatic global climate change in the next few decades (Levitus *et al.* 2000).

2. MATERIALS AND METHODS

At the Macquarie Island isthmus (54°30'S, 158°50'E) in the SO, 6504 recently weaned SES pups were branded and weighed from 1993 to 1999. Both rear flanks were branded with a four-character alphanumeric brand that uniquely identified individual seals (McMahon *et al.* 1999).

Daily searches of the isthmus beaches and tussock areas (main study area; McMahon *et al.* 1999, 2000) and once monthly searches of the entire island beaches and tussock areas were made to resight (recapture) these marked seals over 8 years (1993–2001). The recapture rates varied between years ($\chi^2_6 = 103.71$, $p < 0.001$) but this variation was taken into account (compensated for) when estimating seal survival by using the standard practise of including time-dependent recapture rates in the design matrices when estimating survival in the capture–mark–recapture programme—MARK (White & Burnham 1999). Capture-history matrices were constructed from the resight histories and used as input files for MARK (White & Burnham 1999). MARK provides survival (ϕ) and recapture (ρ) estimates under the Cormack–Jolly–Seber (CJS) model and under several models that appear as special cases of the CJS-model (White &

Burnham 1999). Likelihood ratio tests within MARK were used to test between nested models (White & Burnham 1999). In this case, the model ϕ (first-year survival constant for all cohorts) ρ (time-dependent) was nested/constrained within the general model; ϕ (cohort-specific 1st-year survival) ρ (time-dependent).

To quantify the direct affect of environmental variation (ENSO) on the response variable (first-year survival), we constrained the survival model (White & Burnham 1999) using the annual SOI values as a proxy measure for ENSO (Deser & Wallace 1987). In so doing, the fit of the constrained (i.e. including the direct measure of environmental variation) model can be compared with the fits of unconstrained models that included the indirect estimates of environmental variability (weaning mass) using the general rules of model selection (Burnham & Anderson 2002). The amount of variation accounted for by the covariates, i.e. the direct estimation and quantification of the relative effects of environmental variability on first-year survival, was determined using an analysis of deviance (Burnham & Anderson 2002).

The SOI values we used (January–October, i.e. when the seals were at sea during their first foraging trips) are available from the Australian Bureau of Meteorology at <http://www.bom.gov.au/climate/current/soihtm1.shtml>. These SOI values are, therefore, a direct representation of the environmental conditions when the naive seals are at sea for the first time, e.g. seals branded in 1993 were foraging in 1994 and the survival anomaly for the 1993 cohort is related to the SOI anomaly in 1994 (January–October). The annual SOI anomaly was calculated by subtracting the mean annual January–October values from the 50 year (1950–2000) mean value for the January–October period. Similarly, the survival anomaly was the annual survival value subtracted from the mean of all the annual values. Sustained negative values of the SOI indicate ENSO (El-Niño) episodes (Deser & Wallace 1987) which are manifested in the SO as lower sea-level air pressure, cooler air temperatures above the ocean surface, cooler sea-temperatures and greater sea-ice extent in the Ross Sea (Kwok & Comiso 2002).

3. RESULTS

The mean first-year survival estimate for each of the seven seal cohorts was 0.7461 ($\pm$ s.e. 0.0035, 95% CI 0.7393 and 0.7528), from this and the first-year survival estimates for each of the cohorts (1993–1999; table 1) we calculated the annual survival anomaly (figure 1a). First-year survival varied significantly ($\chi^2_7 = 206.9$, $p < 0.0001$) between cohorts and was highest for the 1993 and 1996 cohorts. There were two candidate models (i.e. $\Delta AIC < 2$; Burnham & Anderson 2002) that described the variability in first year survival. The best model excluded the direct measure of environmental variable to which naive seals were exposed—SOI—but included wean-mass, i.e. the indirect measure of environmental variability, while the next best model included environmental variability (SOI) and wean mass. From these two models, the generic model and following Burnham & Anderson's (2002) analysis of deviance, we were able to determine that wean mass explained 88% ($r^2 = 0.877$) of the variation in first-year survival and that SOI explained 12% ($r^2 = 0.123$) of the variation in first-year survival. Seal survival in the first year of life was primarily dependent on wean mass (87.7%) and therefore maternal foraging

Table 1. The mean ($\pm$ standard error, s.e.) first-year survival estimates and the lower and upper 95% confidence intervals (CI) for seven cohorts of southern elephant seals at Macquarie Island.

cohort	mean estimate	s.e.	lower 95% CI	upper 95% CI	mean wean mass (kg) $\pm$ s.d.	sample (<i>n</i>)
1993	0.8070	0.0101	0.7864	0.8260	118.17 $\pm$ 26.10	1061
1994	0.7517	0.0099	0.7317	0.7707	117.41 $\pm$ 26.43	585
1995	0.7622	0.0101	0.7419	0.7813	115.56 $\pm$ 26.37	816
1996	0.7993	0.0092	0.7808	0.8167	117.36 $\pm$ 26.75	962
1997	0.7627	0.0091	0.7444	0.7802	122.85 $\pm$ 28.09	953
1998	0.7456	0.0086	0.7284	0.7621	119.11 $\pm$ 28.78	1126
1999	0.7172	0.0089	0.6994	0.7343	120.03 $\pm$ 27.01	1001
all cohorts	0.7461	0.0034	0.7393	0.7528	118.79 $\pm$ 27.24	6504

success in the previous year is the fundamental determinant of survival (McMahon *et al.* 2000, 2003). However, while maternal investment was important for survival in the first year, environmental conditions to which naive seals were exposed were also important in determining survival (model $\Delta\text{AIC} < 2$), such that survival was highest during ENSO events (1993–1994 and 1996–1997) and lowest in between ENSO events (figure 1*a,b*), i.e. first-year survival of the 1993 and 1996 cohorts.

4. DISCUSSION

Here, for the first time, we have shown a correlation between a quasi-cyclic event (ENSO as measured by the SOI) and an important demographic parameter (first-year survival) of a large Antarctic predator. For the first time, we have also quantified the relative importance of pre-breeding foraging conditions (during which time females accumulate and store resources) and the post-breeding foraging conditions that offspring are exposed to, to survival in the first year of life of an apex, albeit naive, predator. We showed that the conditions to which pregnant female seals were exposed and typically enumerated as weaning mass (Fedak *et al.* 1996; Arnborn *et al.* 1997; Crocker *et al.* 2001) were more important to survival in the first year than the conditions to which pups were directly exposed during their first foraging trips (88% versus 12%). This is because weaning masses (maternal foraging conditions) are a true reflection of environmental conditions rather than a reflection of the age/experience or foraging zone in which females feed (Fedak *et al.* 1996; Arnborn *et al.* 1997; Crocker *et al.* 2001). Ours is a key finding because it describes a functional response of an apex predator in Antarctica to environmental conditions that can be used to predictively model population responses to climate changes, which is rarely achievable (Barbraud *et al.* 1999; Barbraud & Weimerskirch 2001; Wilson *et al.* 2001). The importance of our study lies in the quantification of the links between high order predators and environmental conditions, providing conservationists, ecologists and managers with the vital information, which in many instances is lacking (e.g. see Turner 2004 for a review), that they need to understand, conserve and manage ecosystems. Given that both the intensity and frequency of inter-annual sea-surface temperatures are expected to intensify with global warming (IPCC 2001), it follows that SES populations, in general, are likely to be negatively affected by the predicted warmer than average temperatures (Karl & Trenberth 2003).

ENSO can affect apex predators in several ways. Firstly, ENSO is an extreme Pacific Ocean climate state which is triggered from blocking weather systems in the west Pacific Region of the SO (Smith & Stearns 1993). These Antarctic blocking systems relate directly to sea-ice extent, which, in turn, results in the inter-annual variability of the position of ocean frontal zones and productivity (Sokolov & Rintoul 2002). Secondly, ENSO and its associated blocking systems may influence ocean stratification and the subsequent nutrient availability and therefore primary and secondary productivity which is available to apex predators (Richardson & Schoeman 2004; Sarmiento *et al.* 2004). Disruptions are therefore likely to alter nutrient balances and productivity in the SO between 45 and 60°S where elephant seals forage (e.g. Hindell *et al.* 2003; Field *et al.* 2004). Disruptions to the biological pump and the subsequent nutrient supply to the thermocline, where much biological productivity occurs (Sarmiento *et al.* 2004), will have further direct effects on elephant seals because elephant seals, concentrate their foraging effort at the thermocline (Boyd & Arnborn 1991; Slip 1997*a,b*). Variability in ocean productivity has been linked to variations in foraging performances in elephant seals by measuring mass gain in female elephant seals, which is highest when productivity is greatest and *vice versa* (Bradshaw *et al.* 2004). The positive relationship between ENSO events and mean first-year cohort survival has two possible explanations. First, weaning mass is an indirect cause because the resources that determine survival (McMahon *et al.* 2000, 2003) have been acquired and stored in the preceding year by the seal mothers and transferred to the pups during lactation (Fedak *et al.* 1996; Crocker *et al.* 2001). These resources are gathered on foraging trips to areas between the Antarctic Polar Front and the sub-Antarctic Front (Hindell *et al.* 1999; McConnell *et al.* 2002; Hindell *et al.* 2003), an area of high but variable productivity which is influenced by oceanographic phenomena such as the Antarctic Circumpolar Current and ENSO (Constable *et al.* 2003; Hosie *et al.* 2003). It is such variability that has been linked to variations in weaning masses (Vergani *et al.* 2001; McMahon *et al.* 2003) and first-year survival in elephant seals (McMahon *et al.* 2000). The difference in survival that results from weaning mass is probably owing to ontogeny differences, such that heavier pups are more precocious, make deeper and longer dives than lighter pups (Hindell *et al.* 1999) and are capable of spending longer periods (on average 10–11 days more) in search of

Figure 1. The general nature of the relationship between first-year survival (open squares) and the SOI (solid diamonds) recorded during January–October for each year of the first foraging trip for the seven cohorts (1993–1999) of southern elephant seals at Macquarie Island. The figure shows that survival is highest during ENSO events, i.e. when the SOI is lowest. However, we recognize that the time-series is relatively short, making rigorous time-series analysis difficult. Nevertheless, even when we take account of the temporal autocorrelation within the two time-series and calculate the effective degrees of freedom (Pyper & Peterman 1998), the strong correlation coefficient ($r = -0.868$) remains robust ($p = 0.05$). The data labels associated with the survival curve represent cohort membership for the seven seal cohorts we studied.

food (McMahon *et al.* 2000; McConnell *et al.* 2002). The second reason is more direct: survival of the pups will be higher if prey are more plentiful or of higher quality. We suggest that prey may be easier to acquire (greater abundance), or more nutritious, during ENSO events because sea-ice is more abundant, and because the subsequent decay of the sea-ice in summer releases particulate and dissolved organic matter to the water column, therefore enhancing biogeochemical cycling as well as the seeding of the water column with nutrients and phytoplankton (Brierley & Thomas 2002). The effects of such greater abundances or quality of prey will be easily observed in elephant seals because the principal prey of SESs is squid and squid have short annual life-cycles (Waluda *et al.* 1999), i.e. lag effects are unlikely to dilute the immediate effects of increased productivity. Recently, it has been shown that krill stocks in the South Atlantic sector of the SO have decreased in accordance with an increase in water temperature (Atkinson *et al.* 2004) and if these decreases and climate changes were to propagate westward it is conceivable that elephant seal populations would be negatively affected as the decreases in krill numbers cascade up through the food chain.

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