

CORRESPONDENCE



Guarding against oversimplifying the fundamental drivers of southern elephant seal population dynamics

Comments on Vergani, D.F., Labraga, J.C., Stanganelli, Z.B. & Dunn, M. (2008) The effects of El Niño–La Niña on reproductive parameters of elephant seals feeding in the Bellingshausen Sea. *Journal of Biogeography*, 35, 248–256.

ABSTRACT

Recently, Vergani *et al.* (2008) examined the climatic drivers of population dynamics (weaning mass) and foraging performance (diet variation) from southern elephant seals, *Mirounga leonina*, in the Atlantic sector of the Southern Ocean. The principal conclusion was that elephant seal weaning masses were greater in La Niña years, when higher ocean temperatures persisted in areas where most seals from the study population at King George Island forage. The authors infer that these conditions lead to improved prey quality and quantity; however, many of the questions and hypotheses they posed have already been addressed elsewhere in the Southern Ocean. We argue that substantial speculation and uncertainty could have been avoided by the authors had they consulted and examined this considerable available literature that confirms (and in some cases, fails to support) many of their conclusions. Such a spatially limited focus in biogeography increases the risk of making important errors of interpretation.

Keywords Antarctica, behaviour, climate change, *Mirounga leonina*, population dynamics.

Biogeographical studies that attempt to make inferences about species distributions, population dynamics, dispersal, behaviour and genetic isolation from regional samples must do so with the appropriate contextualization. Otherwise, researchers risk

overlooking global patterns that can hinder the general understanding of the long-term drivers of change to species distributions. Recently, Vergani *et al.* (2008) examined the climatic drivers of population performance of a southern elephant seal (*Mirounga leonina*) population in the Atlantic sector of the Southern Ocean (measured by pup weaning mass and an index of diet variation) and provided some interesting data in this regard; however, the study overlooked a large body of literature quantifying many of the questions and hypotheses posed in their paper. We argue that such a spatially limited focus increases the risk of making important errors of interpretation.

Southern elephant seals have a circumpolar distribution in the Southern Ocean, and although breeding colonies are generally restricted to widely dispersed oceanic islands, individuals forage throughout most of the Southern Ocean from north of the Antarctic Convergence to the Antarctic continent (Biuw *et al.*, 2007). Vergani *et al.* attempted to link weaning mass to variation in oceanic conditions as measured by the El Niño–Southern Oscillation (ENSO), suggesting that their ‘preliminary’ results ‘may explain geographical variations among Antarctic elephant seal populations’. Herein lies our concern – there was no mention of the work that has examined this very question for southern elephant seals at other locations in the Southern Ocean. We contend that this oversight may compromise the conclusions of the Vergani *et al.* study for this species that has a circumpolar distribution. A more cosmopolitan view would have been much more informative for addressing how different environments affect the life-history strategies used by this wide-ranging species.

Recent data from animal-borne sensors have demonstrated that the effect of oceanic conditions on elephant seal performance varies regionally. Biuw *et al.* (2007) demonstrated that the better body condition of seals in the Atlantic sector of the Southern Ocean was associated with regions of upwelling of circumpolar deep water within

the Antarctic Circumpolar Current, but that high-salinity shelf waters or temperature/salinity gradients under winter pack ice were more important in the Indian and Pacific sectors. Vergani *et al.* also omitted evidence that elephant seals demonstrate important regional fidelity to foraging areas despite annual variation in productivity (Bradshaw *et al.*, 2004), thus discounting a potentially important mechanism for variation in dietary composition. Bradshaw *et al.* (2004) also quantified many of the relationships speculated upon by Vergani *et al.* with respect to oceanic properties and foraging performance: for example, that fidelity to foraging regions in variable environments may confer ecological benefits to individuals, even when energy gain varies between years. Acknowledging these aspects within such a context would have allowed Vergani *et al.* to contextualize their observations within a greater body of work documenting elephant seal foraging behaviour, distribution, population dynamics and extinction risk.

On the subject of measuring foraging behaviour, diet variation and inferring shifts due to oceanic conditions, it is worth noting that the Vergani *et al.* sample size ($n = 3$) was too small to make any meaningful conclusion (although conceding this, they did not refrain from speculating). More importantly, however, dietary changes resulting from spatio-temporal shifts in foraging have been demonstrated for this species in recent years (Bradshaw *et al.*, 2003); discussing their small-sample results with these other findings would have allowed Vergani *et al.* to address with a little more confidence potential seasonal and regional differences in diet. As it stands, Vergani *et al.* could not account for such possible seasonal and regional differences in diet (Bradshaw *et al.*, 2003). Moreover, because the diet samples they collected were limited to prey ingested during the latter portion of the foraging trip (i.e. near breeding islands), they were unable to estimate the potentially important fish component of the diet already identified in other populations. Indeed, fish may constitute a

substantial component of the elephant seal diet, especially in high-latitude foraging areas (Bornemann *et al.*, 2000; Daneri & Carlini, 2002; Bradshaw *et al.*, 2003). This omission unfortunately undermines conclusions regarding the energetic implications of prey acquisition during pregnancy. Vergani *et al.* may be forgiven for not employing recent advances in the study of *in situ* diet composition (e.g. Bradshaw *et al.*, 2003); however, this does not negate at least discussing alternative findings and the complexities these imply.

One of the principal tenets of Vergani *et al.*'s study is that variation in weaning mass can be used as a proxy to predict first-year survival rates. However, the only known evidence for the link between weaning mass and survival in this species was not even cited (McMahon *et al.*, 2000, 2003). Further, there was no attempt to demonstrate how mass operates to modify survival: climatic conditions not only affect seal mass directly; it has been shown how they also modify demographic rates directly via changes in food availability (McMahon & Burton, 2005; de Little *et al.*, 2007). Recent work (Field *et al.*, 2005a,b, 2007a,b) has shown how the ontogeny of juveniles is important in determining strategies of energy acquisition that ultimately modify survival probability. Such changes in development can provide the mechanistic link between variation in juvenile survival, which is known to be one of the main drivers of population trends in this species (McMahon *et al.*, 2005b). Placing their results within the context of these previous findings is particularly important because Vergani *et al.* invoke the argument that the elephant seal populations in the Atlantic sector of the Southern Ocean are somehow unique, rather than looking for underlying commonalities between populations. Indeed, their conclusion has little support, given the clear evidence that weaning mass and juvenile survival drive the dynamics of most elephant seal populations studied to date (McMahon *et al.*, 2003, 2005b). Moreover, their arguments of uniqueness are not supported by a recent (uncited) review showing that the Atlantic populations do not necessarily demonstrate any more 'stability' than elsewhere (McMahon *et al.*, 2005b), or that generation time (a term confused by Vergani *et al.* as being synonymous with female 'recruitment') is shorter for populations in this region (McMahon *et al.*, 2005b). In support of their isolation hypothesis, Vergani *et al.* misquote recent genetic findings and erroneously conclude that the major

breeding populations in the Southern Oceans are 'genetically isolated' (Fabiani *et al.*, 2003). Although genetic differences do exist, there is good evidence demonstrating that there is some gene flow between populations (Slade *et al.*, 1998; Fabiani *et al.*, 2003).

Density regulation affects the strength and direction of environmentally induced variation in elephant seal demographic rates (de Little *et al.*, 2007); however, Vergani *et al.* did not account for this major modifier of population and individual performance. Recent and past work has established how the effect of environmental stochasticity on demographic rates is modified substantially by population density on land or at sea (Van Aarde, 1980; Bester & Lenghart, 1982; Pistorius *et al.*, 1999, 2001; Bradshaw *et al.*, 2002; McMahon & Bradshaw, 2004; de Little *et al.*, 2007). Failing to consider the regulatory effects of density can therefore lead to erroneous conclusions about the strength and even the direction of environmentally induced variation on demographic rates (de Little *et al.*, 2007).

Vergani *et al.* should be commended for their efforts to link climatic drivers to demographic parameters for a major Southern Ocean predator; however, it concerns us that their conclusions are oversimplified (at best) or incorrect (at worst) diminishing the value of their good data. Only by contextualizing one's scientific findings within the available literature can evidence be cross-referenced, overt speculation avoided and true progress made in understanding the relationships between biodiversity patterns and the biophysical environment.

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A reply to McMahon *et al.* (2008)

Recently, McMahon *et al.* (2008) criticized our article concerning the impacts of climate variability on the reproductive parameters of southern elephant seals (Vergani *et al.*, 2008). We characterized El Niño–Southern Oscillation (ENSO) climate anomalies in the periphery of Antarctica using reanalysed global atmospheric data from Kalnay *et al.* (1996) encompassing over 40 years of observations. We considered existing evidence for ENSO signals in delineated regions of Antarctica and the current understanding of propagation mechanisms from the source region in the tropical Pacific Ocean to high latitudes of the Southern Hemisphere. We then explored cause-and-effect relationships by comparing an index of El Niño and La Niña occurrences with a 10-year-long data set of weaning mass for elephant seal pups ($n = 1027$ individuals). McMahon *et al.* (2008) consider Biuw *et al.* (2007), but we argue that their results are not relevant to our research because it is not possible to draw conclusions about the impact of interannual climate variations on the basis of a single year of data. McMahon *et al.* (2008) also highlight the importance of fish in the diet of elephant seals based on Bornemann *et al.* (2000). However, those authors did not examine the diet and only speculate on the potential importance of fish in the elephant seal diet. Furthermore, McMahon *et al.* (2008) overlooked the conclusion of Kwok & Comiso (2002), who pointed out that the Bellingshausen Sea region is unique in its relationship with ENSO from a physical point of view. Overall, our results indicate that our proposed elephant

seal model could be related to physical ENSO-related properties.

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