

Population status, trends and a re-examination of the hypotheses explaining the recent declines of the southern elephant seal *Mirounga leonina*

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ABSTRACT

1. Between the 1950s and 1990s the southern elephant seal *Mirounga leonina* underwent large decreases in population size throughout most of its breeding range in the Southern Ocean. While current population estimates suggest a recent recovery, some breeding populations have continued to decrease in recent years (Macquarie and Marion Islands), others have either remained stable (South Georgia, Kerguelen and Heard Island) or have increased (Península Valdés, Argentina).

2. Intrinsic hypotheses for patterns of regional decline include factors that are affected by density-dependent mechanisms: (i) paucity of males, (ii) population ‘overshoot’ and (iii) pandemic disease. Extrinsic hypotheses include (iv) predation, (v) competition with fisheries concerns, (vi) interspecific competition, (vii) environmental change and (viii) human disturbance. Of the eight hypotheses proposed and examined here, we conclude that three can be discounted (i, v, viii), three are unlikely, but may require more testing (ii, iii, iv) and two are plausible (vi, vii).

3. The interspecific competition hypothesis is difficult to test because it requires the simultaneous monitoring of species that overlap directly with elephant seals, many of which have not been identified or little is known. However, an analysis of the relationship between log variance and log abundance (Taylor’s power law) for populations of southern and northern elephant seals suggests that interspecific competition is not a significant factor in the decline of the southern elephant seal.

4. The hypothesis that decreases in southern elephant seal populations between the 1950s and 1990s were caused by the environmental change is the easiest to test and most plausible of the hypotheses. We propose a framework by which to test this hypothesis to determine how food availability affects individual survival.

Keywords: environmental change, interspecific competition, marine mammals, Pinnipedia, population trends

INTRODUCTION

Understanding the causal factors responsible for rapid and marked changes in the status of long-lived, slow-reproducing species can be especially difficult because long time series are necessary to detect trends, this being particularly true for wide-ranging species that come into contact with a number of different ecosystems during the course of their life cycle. However, the detection of changes in population growth is important because such changes may indicate large-scale changes in ecosystem function or structure (Barbraud & Weimerskirch, 2001). In the Southern Ocean biome, one species of large, wide-ranging predator has demonstrated consistent, large decreases in population size through most of its breeding range between the 1950s and 1990s – the southern elephant seal *Mirounga leonina*. Although the patterns and magnitude of the decrease have varied among populations, some populations have declined by as much as 80% since the 1950s. Such pronounced decreases in the numbers of a large vertebrate predator cause concern because these changes potentially signal larger, unrecognized ecosystem changes (Caughley & Gunn, 1996).

The southern elephant seal is an abundant marine predator with a circumpolar distribution (Ling & Bryden, 1992). Four genetically distinct populations are recognized: the Peninsula Valdés population in Argentina, the South Georgia population in the south Atlantic Ocean, the Kerguelen population in the south Indian Ocean and the Macquarie population in the south Pacific Ocean (Slade *et al.*, 1998; Hoelzel, Campagna & Arnbom, 2001). The principal breeding colonies for these populations are located on: Peninsula Valdés, South Georgia Island, Heard and Kerguelen Islands, and Macquarie Island, respectively (Fig. 1).

There has been a considerable body of research since declines were first documented in the mid-1980s. Most major populations have had some regular censuses, and others have been the subject of more intensive demographic and foraging studies to investigate ele-

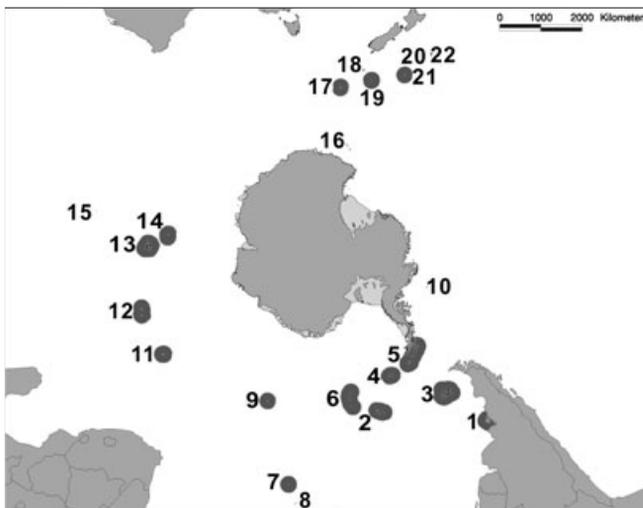


Fig. 1. The circumpolar breeding distribution of southern elephant seals *Mirounga leonina* in 2001. 1, Peninsula Valdés; 2, South Georgia; 3, Falkland Islands; 4, South Orkney Islands; 5, South Shetland Islands; 6, South Sandwich Islands; 7, Gough Island; 8, Tristan da Cunha; 9, Bouvetoya; 10, Peter 1 Øy; 11, Prince Edward Islands; 12, Îles Crozet; 13, Îles Kerguelen; 14, Heard Island; 15, Amsterdam & St. Paul Islands; 16, Balleny Islands; 17, Macquarie Island; 18, Auckland Island; 19, Campbell Island; 20, Bounty Island; 21, Antipodes; 22, Chatham Island.

ments of these declines (Condy, 1978, 1984; Burton, 1986; Hindell & Burton, 1987). Once these declines were accepted by the research community, there was a shift in the focus of research from fundamental biology to primary ecological research investigating elements such as survival and foraging ecology. The results of those studies (Hindell, 1991; Hindell, Burton & Slip, 1991) included the establishment of long-term demographic studies to quantify life-history parameters and the deployment of newly developed archival dive recorders and satellite telemetry systems to study foraging at sea. Much has been discovered and learnt about: (i) demography, (ii) foraging ranges, (iii) diet and (iv) disturbance since the last major review of southern elephant seal biology (Hindell, Slip & Burton, 1994).

With the recent advances in knowledge of this species and its role in the Southern Ocean ecosystem, it is now timely to re-examine trends in this species' status since the first attempt to do so in 1994 (Laws, 1994). In this paper we (i) reassess the worldwide status of southern elephant seals, (ii) compare the demography of the four subpopulations, (iii) re-examine previously postulated hypotheses on population decreases, and (iv) suggest directions for future research to account for the observed trends.

POPULATION SIZES AND TRENDS

Within the four main populations, the South Georgia population is the largest, followed by the Heard and Kerguelen islands populations, Macquarie Island and Peninsula Valdés populations (Table 1). Together, these five populations account for approximately 98% of the world population of the species. The remaining 2% is made up of small subpopulations scattered throughout the Sub-Antarctic and adjoining regions (Fig. 1). These subpopulations occur on the Prince Edward Islands, Gough Island, Îles Crozet, Campbell Island, Antipodes Islands, South Orkney Islands, South Shetland Islands, South Sandwich Islands, the Falkland Islands and Bouvet Island (Laws, 1994).

South Georgia population

This population includes subpopulations at South Georgia, the Falkland Islands, South Orkney Islands, King George Island, Nelson Island, Avian Island, the South Sandwich Islands, Gough Island and Bouvet Island. Of these, the South Georgia subpopulation is the largest (397 054) and constitutes >99% of the population. It also comprises approximately 54% of the global population (Boyd, Walker & Poncet, 1996). This subpopulation, and hence the regional population, has remained stable since 1951 and more generally, these subpopulations appear to have been stable since the 1990s (Table 1).

Îles Kerguelen population

The Kerguelen population consists of six island subpopulations: Îles Kerguelen, Heard Island, Marion Island and Prince Edward Island, Isles Crozet and Possession Island. All of these subpopulations declined since the 1950s, with rates of decline varying between 50% and 84%. The breeding subpopulations on Îles Kerguelen and Heard Island account for 97% of the total population. All of these subpopulations have decreased by approximately 50% since the 1950s (Barrat & Mougin, 1978; van Aarde, 1980; Bester & Lenghart, 1982; Burton, 1986; Bester, 1988; Bester & Wilkinson, 1994), but recently some of these subpopulations appear to have stabilized (Guinet, Jouventin & Weimerskirch, 1999; Slip & Burton, 1999; Pistorius *et al.*, 2001). Importantly, the two largest subpopulations, Îles Kerguelen and Heard Island, appear to have stabilized in recent years, although the Heard Island subpopulation is characterized by poor time-series data.

Table 1. The estimated population sizes of southern elephant seals in 2001. The pre-1970s estimates were those presented by McCann (1985) and the estimates for the 1990s were those presented by Laws (1994)

Population	Location	Subpopulation size – pre-1970s	Subpopulation size – 1990s	Subpopulation size – 2000s	Reference	Current status assessment
South Georgia	South Georgia	350 000	357 000	397 054	Boyd <i>et al.</i> (1996)	Stable
	South Orkney Is	350	20	20?	Laws (1994)	Unknown
	South Shetland Is	1 050	2 300	2 300?	Laws (1994)	Unknown
	Falkland Is	3500	3 500	1 827	Galimberti & Boitani (1999)	Stable
	Gough I	350	105	63	Bestier <i>et al.</i> (2001)	Decrease
	Bouvet I	Unknown	Unknown	308	Kirkman <i>et al.</i> (2001)	Increase?
Total population		355 250	362 925	401 572		
Kerguelen	Îles Kerguelen	157 500	143 500	153 237	Guinet <i>et al.</i> (1999)	Stable
	Heard I	80 500	40 355	61 933	Slip & Burton (1999)	Stable
	Marion I	3 850	2 009	2 131	Bradshaw <i>et al.</i> (2002b)	Decrease
	Prince Edward I	Unknown	782	Unknown		Unknown
	Isles Crozet & Possession I	10 500	2 023	1 995	Guinet <i>et al.</i> (1999)	Stable
Total population		252 350	188 669	219 296		
Macquarie	Macquarie I	136 500	77 791	76 000	H. Burton, personal communication	Decrease
	Antipodes I	Unknown	400	249	Anonymous (2001)	Decrease
	Campbell I	455	20	<10		Decrease
Total population		136 955	78 211	76 259		Decrease
Peninsula Valdés	Peninsula Valdés	13 800	33 726	42 371	Lewis <i>et al.</i> (1998) no. 2348	Increase
Total population		13 800	33 726	42 371		Increase
Total world population estimate		757 900	663 531	739 498		Increase?

I, island; Is, islands.

Macquarie Island population

Only three island subpopulations make up this population: Macquarie Island, Campbell Island and the Antipodes. However, 99% of the population is at Macquarie Island and as such the discussion of this population will centre on the status and change of the Macquarie Island subpopulation, which is one of the most continuously studied elephant seal populations (Carrick & Ingham, 1962; Hindell, 1991; McMahon, Burton & Bester, 2003). This population has decreased by 59% from approximately 183 000 in 1949 (Hindell & Burton, 1987) to approximately 76 000 in 2001 (Australian Antarctic Division, unpublished data). While the reasons for this precipitous decrease in numbers are not known it has been suggested that the low juvenile survival (Hindell, 1991) and food availability (McMahon *et al.*, 2003) are the most likely mechanisms driving the decrease in population size through lowered recruitment into the breeding population and lower survival of weaned pups (McMahon *et al.*, 2003).

Peninsula Valdés population

This population has only recently been recognized as a genetically distinct population (Slade *et al.*, 1998; Hoelzel *et al.*, 2001). Peninsula Valdés is the only continental breeding population; all the others are restricted to remote oceanic islands (although there are historical records of continental breeding colonies in South Africa (Ling & Bryden, 1992). This population has been increasing since 1975 (Campagna & Lewis, 1992) and continues to increase (Lewis *et al.*, 1998). Pup production at Peninsula Valdés increased by 41% between 1982 and 1997 from 7455 to 12 106 (Lewis *et al.*, 1998).

Current world population

Since the last review of southern elephant seal population status in 1994 (Laws, 1994), there appears to have been an increase in the world population of elephant seals by 11.4% between 1994 and 2002. From the evidence reviewed here the observed increase in southern elephant seal (SES) numbers can be best attributed to: (i) real increases in numbers at some populations such as at Peninsula Valdés or (ii) more precise population estimates (McCann, 1985) at populations such as South Georgia. Thus, caution is advised when interpreting the 11.4% increase for conservation and management purposes. It would seem more prudent, referring to the data from Table 1, to conclude that although some populations have clearly increased (Peninsula Valdés), it appears that the worldwide population may have been approximately stable since the last review (Laws, 1994) in 1994.

Given that it is not always easy to detect changes in population trend data (Fewster *et al.*, 2000) and the fact that population data are often highly variable (Hindell *et al.*, 1994), these conclusions need to be viewed with some caution. Many of the changes have not been tested by robust methods of trend analysis (Gerrodette, 1987); but it suggests that the factors responsible for the earlier decreases may have ameliorated in recent times (Guinet, Jouventin & Weimerskirch, 1992).

POSSIBLE REASONS FOR POPULATION CHANGE

The best way to diagnose the underlying cause of a population decline is to adopt a hypothetico-deductive approach, i.e. by deriving meaningful hypotheses and testing them experimentally (Caughley & Gunn, 1996). Manipulative experiment testing specific hypotheses in time-series data for population trends is difficult, if not impossible, so we have adopted a mensurative approach to examine each of the most plausible hypotheses forwarded and tested in the last 50 years. Our aims are to eliminate unrealistic hypotheses forwarded for the decline

and to understand the mechanisms of the more plausible ones posed. An advantage of the variability in population trends among populations within the Southern Ocean is that many of the hypotheses can be tested by comparing population and behavioural parameters from stable or increasing subpopulations vs. declining subpopulations.

Hypotheses for decline fall into two main categories: intrinsic and extrinsic. The intrinsic hypotheses include factors that are affected by density-dependent mechanisms: (i) the paucity-of-males hypothesis (Skinner & van Aarde, 1983), (ii) the 'overshoot' hypothesis (Hindell, 1991) and (iii) the pandemic disease hypothesis (Harwood & Hall, 1990). The extrinsic hypotheses include (i) predation (Condy, van Aarde & Bester, 1978; Guinet, 1992), (ii) competition with fisheries concerns (Pascal, 1986), (iii) interspecific competition (Hindell, 1991), (iv) environmental change (Burton, 1986) and (v) human disturbance (Wilkinson & Bester, 1988).

Paucity of males

Skinner & van Aarde (1983) suggested that there were fewer subordinate male elephant seals at Marion Island than at Kerguelen Island, and hypothesized that a significant number of female seals at Marion Island leaving the breeding harems (after weaning their pups) were not pregnant because there were not enough subordinate males to fertilize them. However, harem masters have been shown to be capable of high rates of sexual activity and mate with all the females present during the breeding season (Wilkinson & van Aarde, 1999). Dominant males have been shown to be fertile and have high rates of fertilization. The male-paucity hypothesis has therefore been rejected by Bester & Wilkinson (1994) and Wilkinson & van Aarde (1999), and it was concluded that other mechanisms should be sought to explain the decrease in the Marion Island population (Bester & Wilkinson, 1994; Wilkinson & van Aarde, 1999).

Population 'overshoot'

This hypothesis states that the decrease in SES populations was an indirect result of the eighteenth- and nineteenth-century exploitation of seals (Hindell, 1991) when populations were reduced well below pre-sealing numbers (Hindell & Burton, 1988a). This reduction then enabled prey species of elephant seal to increase (when elephant seal density was low), resulting in an abundant prey resource at the end of the sealing period. Elephant seal populations could then, in the presence of abundant per capita resources, increase in numbers sufficiently to 'overshoot' pre-sealing numbers. The subsequent decrease in seal populations is therefore a density-dependent equilibration process, whereby the seals over-exploit existing food resources and shift to a smaller and more sustainable population size. This hypothesis accounts for many of the characteristics of the observed population decreases such as the differences between the stability of the South Georgia population and the decrease of the Kerguelen and Macquarie populations because managed sealing (exploitation) continued at South Georgia for much of the twentieth century.

This hypothesis assumes (i) a simple and direct predator-prey relationship, and (ii) that elephant seal prey was not exploited by other non-harvested predators, such as the smaller toothed whales (e.g. Slip, 1995) and fish. Only under these conditions could the increase in the abundance of prey occur as proposed in the overshoot hypothesis (Hindell, 1991). However, the hypothesis has several problems. First, the existence of a simple predator-prey relationship is unlikely because elephant seals eat many different fish and squid prey species (Burton & van den Hoff, 2002; Bradshaw *et al.*, 2003) and complex relationships can exist for seals with even simple diets (Yodzis, 2000, 2001). Furthermore, the diet of the SES consists

of squid and fish of somewhat similar size and composition to those consumed by the southern bottlenose whale *Hyperoodon planifrons* (Slip, Moore & Green, 1995; MacLeod, Santos & Pierce, 2003). Recent studies have failed to reject this hypothesis outright. To test this hypothesis more completely, it will be necessary to develop appropriate tropho-dynamic models and to continue monitoring population trends and demographic composition.

Pandemic diseases

It has been suggested that disease may act in regulating pinniped populations (Harwood & Hall, 1990; Visser, Teppema & Osterhaus, 1991). Disease outbreaks have caused mass mortalities in many pinnipeds with dire consequences for small or endangered populations (Osterhaus *et al.*, 1997, 1998; Kennedy, 1998; van de Bildt *et al.*, 1999; Kennedy *et al.*, 2000). However, there is no evidence of widespread disease in southern elephant seals (Linn *et al.*, 2001). Also, there have been no reports of numbers of sick or dead seals occurring on island beaches. A zoonosis of similar severity to the recent North Sea seal distemper would have provided carcasses and visibly afflicted seals (Harding *et al.*, 2002). However, the effects of viral infections may not always be manifested in dramatic mass mortality events as observed in the Northern Hemisphere (Osterhaus *et al.*, 1997; Kennedy *et al.*, 2000), but may be subtle and difficult to detect. This is particularly relevant to elephant seals because they spend most of their lives as pelagic marine predators. Although this hypothesis has yet to be discounted, we conclude that it was unlikely to explain the observed trends, but it could be tested by a series of immunological assays on individuals from all populations.

Onshore human disturbance

The annual cycle of the southern elephant seal involves two pelagic periods at sea that are punctuated by two periods ashore, one for reproduction and the other for the annual moult (Hindell & Burton, 1988b). It is during these periods ashore that elephant seals are potentially vulnerable to disturbance. Human disturbance may affect a population by: (i) disrupting suckling and the transfer of resources between mother and offspring resulting in lighter weaning mass (Bryden, 1968) and increased mortality (McMahon, Burton & Bester, 2000); (ii) males trampling pups during charges at human intruders (Galimberti, Boitani & Marzetti, 2000b); and (iii) increasing the occurrence of mother–pup separations (Galimberti, Boitani & Marzetti, 2000a). However, no evidence exists for behavioural, physiological or morphometric differences between disturbed and undisturbed seals (Engelhard *et al.*, 2001, 2002a,b). Furthermore, there are similar levels of human disturbance (e.g. tourism, researchers) between populations that are declining and those that are stable or even increasing, which further negates the human disturbance hypothesis.

Predation on juveniles

A factor common to all four populations of elephant seals is the presence of killer whales *Orcinus orca* offshore from their breeding sites when weaned pups are first entering the sea. Predation by killer whales has been suggested as a major factor in the decrease of the southern elephant seal populations at Marion Island and at Îles Crozet (Condy *et al.*, 1978; Guinet, 1992). However, because these island subpopulations are small and constitute less than 1% of their respective populations it seems improbable that predation has played a significant role in the global decreases in elephant seal populations. Moreover, there is no evidence of differential predation rates between larger populations (e.g. South Georgia vs. Macquarie Island) where trends differ significantly. We conclude therefore that predation may become important only as populations decline to low numbers, e.g. Marion Island (McMahon *et al.*,

2003). However, some authorities (Estes *et al.*, 1998; Springer *et al.*, 2003) have suggested that predation on marine mammals such as seals and sea otters *Enhydra lutris* by small numbers of killer whales can alter population growth. The onset of increased predation on otters and seals by killer whales was believed to be a consequence of the reduction of the great whales – the preferred prey of killer whales – in the Northern Hemisphere (Springer *et al.*, 2003). A similar reduction of the great whales was observed in the Southern Hemisphere; thus, similar predation pressure by killer whales may have operated during the periods when southern elephant seal populations decreased most precipitously.

Competition with fisheries

Before discussing the potential dietary overlap with commercial fisheries, it is necessary to describe the diet of southern elephant seals. Diets determined from stomach contents collected at haul-out sites have identified fish and squid as the dominant prey items. Indeed, a suite of fish and squid taxa have been identified with notable differences in diet composition at the different island locations (Green & Burton, 1993; Slip *et al.*, 1995; Daneri, Carlini & Rodhouse, 2000; Daneri & Carlini, 2002; Piatkowski, Vergani & Stanganelli, 2002; van den Hoff, Burton & Davies, 2003). However, these observations need to be treated cautiously because they represent the diets of seals close to their haul-out sites. Indeed, elephant seals have highly efficient digestive systems (Krockenberger & Bryden, 1994), so comparisons of the diet at-sea are not yet available. Using the novel technique of blubber fatty acid analysis, it was possible to describe the temporal and spatial differences in the diet of seals at Macquarie Island (Bradshaw *et al.*, 2003). This is a major step forward in understanding the tropho-dynamics of a major Antarctic predator like SES and provides a vehicle for assessing spatial and temporal variation in diet structure.

It has been suggested that depletion of marine resources by commercial fisheries may have been responsible for the decrease of Indian Ocean elephant seal populations (Pascal, 1986). However, two observations discount this hypothesis. Elephant seals disperse widely from their breeding areas during single foraging trips thereby foraging collectively within most of the Southern Ocean (Hindell *et al.*, 2003b), but commercial fishing is restricted to specific areas within the south Atlantic and Indian Oceans. Therefore, there appears to be little overlap between the main foraging areas and these concentrations of fishing activity. Even where fisheries are more intensive (South Georgia, Kerguelen), seal populations nearby have been demonstrated longer-term or recent stability, whereas in the southern Pacific where seal populations have declined, commercial fishing activity is comparatively low (Hindell *et al.*, 2003b). Moreover Burton & van den Hoff (2002) have compared the dietary overlap between southern elephant seals and the active commercial fisheries in the Southern Ocean and concluded that competition between fisheries and seals was unlikely given the present level of fishing activity.

Interspecific competition

Competition between elephant seals and other animals in the Southern Ocean can take two forms: (i) direct or indirect competition for food resources and (ii) direct or indirect competition for haul-out (breeding and moulting) areas. Some Southern Ocean predators are known to consume some of the same prey species as southern elephant seals. These include odontocete whales, fur seals *Arctocephalus* spp. and king penguins *Aptenodytes patagonicus*. The southern bottlenose whale is a major consumer of cephalopods and, while in Antarctic waters, it may take the same squid species that have been found in some elephant seal stomachs such as the luminous squid *Histiotheuthis* spp. (Clarke & MacLeod, 1982;

MacLeod *et al.*, 2003; Sekiguchi *et al.*, 1993; Slip, 1995). The mean sizes of the prey species common to both were also similar (Slip, 1995; Slip *et al.*, 1995; MacLeod *et al.*, 2003). Concurrent diet studies of king penguins, a species that is increasing throughout its range, and elephant seals at Heard Island (Slip, 1995; Moore, Robertson & Weinecke, 1998) also showed some overlap in their prey items, particularly in some squid species. There is considerable overlap in the squid portion (especially the Ommastrephidae) of the diets of the larger odontocete whales *Orcinus orca*, *Pseudorca crassidens*, *Kogia breviceps*, *K. sima* and *Physeter macrocephalus*, fur seals *Arctocephalus gazella*, *A. tropicalis* and *A. australis* and elephant seals (dos Santos & Haimovici, 2001). However, dietary overlap does not necessarily imply competition (Lynnes *et al.*, 2002). To demonstrate competition, one needs to demonstrate spatial and temporal, and prey size overlap. To test this hypothesis appropriately, more data need to be collected on spatial and temporal variability in diet composition (Bradshaw *et al.*, 2003; Hindell *et al.*, 2003b), and there is a need to develop more comprehensive trophodynamic models that include the spatial and temporal assessments of diet but also the abundance of the prey species. Knowledge of the abundance of the prey species is important because if prey is abundant, competition is unlikely to occur or be a significant contributor to species interactions.

Although the hypothesis cannot yet be tested directly, there is one statistical approach that can be used to shed light on the possibility that interspecific competition is an important factor in the decline of this species. The species-specific relationship between the temporal (or spatial) variance of populations and their mean abundances (Taylor's power law – Taylor, 1961) predicts that the regression of log variances vs. log mean abundances (per population) gives a line with a slope of 2. This prediction is derived from the fact that any random variable X with finite mean μ and variance σ^2 scaled by some constant k results in the distribution kX with a mean $k\mu$ and variance $k^2\sigma^2$. Thus, $\log k^2\sigma^2$ vs. $\log k\mu$ produces a line with slope = 2 (Taylor, 1961; Kilpatrick & Ives, 2003). Despite this prediction, empirical data show that most species have slopes less than 2 (Taylor & Woiwood, 1982). Kilpatrick & Ives (2003) recently suggested that the ubiquity of Taylor's power-law slopes of between 1 and 2 indicates that the relationship provides fundamental information on ecological processes affecting species. They demonstrated that negative interactions among species in a community can produce slopes of Taylor's power law less than 2, thus providing a possible indication of the relative effects of interspecific competition. However, the relationship assumes that the primary source of variance in trends of abundance is temporal stochasticity rather than systematic sampling bias, and that environmental stochasticity in per capita growth rates overshadows the variance due to demographic stochasticity (Kilpatrick & Ives, 2003).

To examine the potential effect of interspecific competition on elephant seal population trends, we used published (Boyd *et al.*, 1996; Lewis *et al.*, 1998; Galimberti & Boitani, 1999; Guinet *et al.*, 1999; Slip & Burton, 1999; Bester *et al.*, 2001) and unpublished (McMahon *et al.*, in review) time-series data to examine the slope of log variance vs. log mean abundance for the SES subpopulations (Fig. 2). The slope of the line was 1.73 (S.E. = 0.284; $r^2 = 0.837$; $P = 0.001$; Fig. 2). We hypothesize that if the decline in SES populations is being driven by interspecific competition, the slope of the log variance vs. log abundance relationship should be lower than that for a similar species for which most populations were increasing. We therefore compared the slope for *M. leonina* to that derived from time-series data for northern elephant seal populations increasing in size (Stewart *et al.*, 1994), but removing data for small populations (Fig. 2). The removal of small populations is likely to account for the potential bias resulting from sampling error and demographic variation that certainly contribute to the relationship; indeed, sampling variance itself is unlikely to be important when the abundance

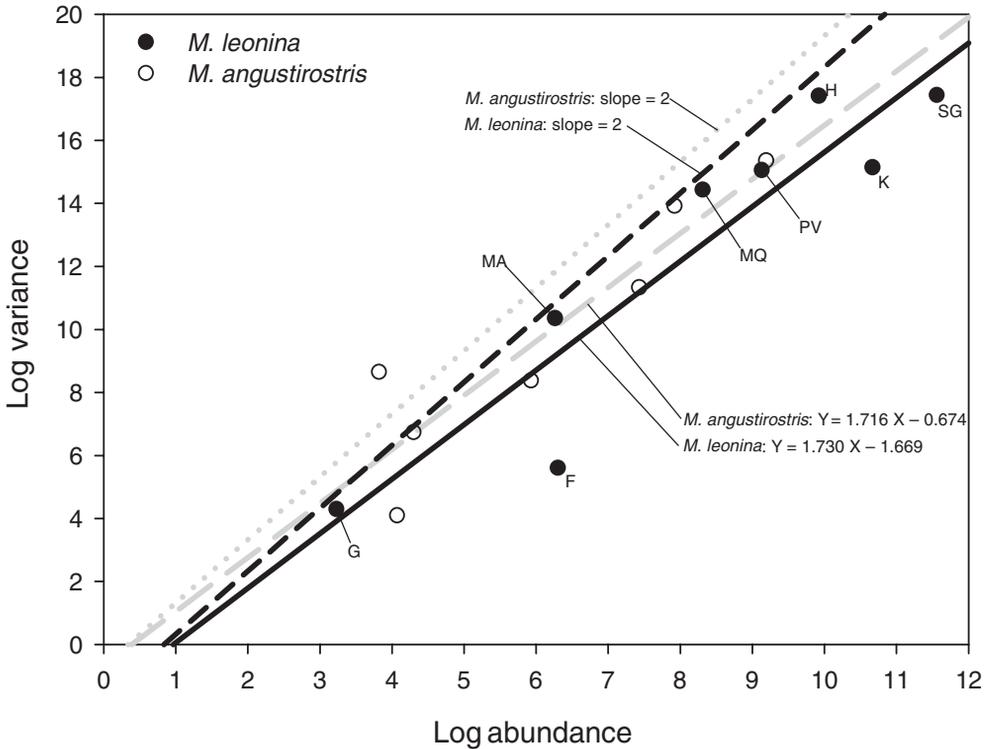


Fig. 2. Relationship between the temporal log variance and log mean abundance for populations of southern (*M. leonina*) and northern (*M. angustirostris*) elephant seals. Shown also are the abbreviations for the different populations of *M. leonina* used in the analysis (SG, South Georgia; H, Heard Island; K, Îles Kerguelen; PV, Peninsula Valdés; MQ, Macquarie Island; MA, Marion Island; F, Falkland Islands; G, Gough Island).

estimates are high (Kilpatrick & Ives, 2003). The relationship for northern elephant seal populations resulted in a slope = 1.716 (S.E. = 0.336; $r^2 = 0.807$; $P = 0.004$; Fig. 2). Because the slope for a species where most populations have been declining (*M. leonina*) was not significantly different (i.e. similar slopes; similar standard errors) to that for a species where most populations are increasing (*M. angustirostris*), we conclude that there is little indirect evidence for interspecific competition being a significant factor in the decline of the southern elephant seal population.

The beaches used by elephant seals are also used by other Southern Ocean predators including Antarctic fur seals, subantarctic fur seals, king penguins, macaroni penguins *Eudyptes chrysolophus* and royal penguins *E. schlegeli*. Competition for this limited haul-out space can be high, especially in those situations where large increases in the populations of fur seals and king penguins have occurred (Boyd *et al.*, 1995; Hofmeyr, Bester & Jonker, 1997; Woehler & Croxall, 1997; Shaughnessy, Erb & Green, 1998; Chamaille-Jammes *et al.*, 2000). The mechanism by which this competition could affect elephant seal populations is not known because elephant seals are large and not easily disturbed (Burton & van den Hoff, 2002). This suggests that it is unlikely that competition for space is an explanation for the observed widespread decreases in elephant seal numbers. Further, the temporal distance in breeding and moulting times of these taxa and the slightly different habitats used during the breeding season haul-out in particular (Kerley, 1983; Hindell & Burton, 1988b) provide additional information refuting the hypothesis of space competition.

Environmental change

Another explanation is that the decreases in seal numbers are due to changes in the ocean environment that have affected the abundance or availability of food of the southern elephant seal (Burton, 1986; McCann & Rothery, 1988; Hindell, 1991; Burton *et al.*, 1997). Because elephant seals from different populations forage within overlapping regions, any profound environmental change to broad areas of the Southern Ocean might at first be expected to affect all populations of SES that can range so widely. However, it seems that although individual seals may forage widely, most within each of the subpopulations share common foraging areas (Hindell *et al.*, 1991; McConnell & Fedak, 1996; Jonker & Bester, 1998; van den Hoff *et al.*, 2002; McConnell *et al.*, 2002) and that these areas are particular to each population.

The Southern Hemisphere climate is punctuated irregularly by two, semiregular fluctuations in climatic conditions: the Antarctic Circumpolar Wave (ACW), which is a 4-year cycle of anomalous atmospheric pressure (White & Peterson, 1996), and El Niño/Southern Oscillation (ENSO), which is an approximately 7- to 8-year pattern of anomalous sea temperatures (Allan, Lindsay & Parker, 1996). Both phenomena have been linked to changes in both environmental conditions such as sea ice extent (White, Chen & Peterson, 1998; Kwok & Comiso, 2002). ENSO and the ACW may affect marine predators in two ways: (i) directly, such as modifying the availability of a food source like krill (Priddle *et al.*, 1998; Murphy & Reid, 2001), or (ii) indirectly, by affecting sea ice production (Gloersen, 1995) and hence, primary production (Smith & Nelson, 1985a,b). There is a growing body of evidence that has documented the direct effects of ENSO events on a number of marine and land-based predators (Vergani, Stanganelli & Bilenca, 2001, 2004). However, our understanding of the links between physical processes such as the ACW and ENSO and biological processes still remains poor (Hindell *et al.*, 2003a).

DISCUSSION

Southern elephant seals have the capacity to travel long distances (Hindell & McMahon, 2000); however, the four elephant seal populations are considered genetically distinct (Slade *et al.*, 1998) despite evidence of some male-mediated gene flow between populations (Fabiani *et al.*, 2003). If individual populations are extirpated, the lack of immigration suggests that recolonization is rare or unlikely. It appears that each of the main southern elephant seal populations is a discrete ecological and management entity so that each population constitutes a unique case in the search for reasons for changes in status.

A fundamental component of managing these populations is to monitor changes in seal numbers in each population. However, given that it is not always easy to detect changes in population data (Fewster *et al.*, 2000) and the fact that population data such as those from Macquarie Island demonstrate much unexplained variation (Hindell *et al.*, 1994), observed trends need to be viewed with some caution. Although many of the declines have not been tested by robust methods of trend analysis (Bradshaw *et al.*, 2002b); it suggests that the factors responsible for the earlier decreases may have ameliorated in recent times. For example, it has been suggested that the subpopulation at Îles Kerguelen may have decreased on two occasions, the first between 1956 and 1960, and again between 1970 and 1977, although there are no data for the period between 1960 and 1970 (Pascal, 1986).

Our review has revealed that of the eight main hypotheses proposed and examined here to explain the population decrease of the southern elephant seal populations, three can be discounted, three we consider unlikely (but may require more testing), and two are plausible (Table 2). The plausible hypotheses include interspecific competition for food resources and

Table 2. A summary of our assessment of the eight main hypotheses that were proposed to explain the large-scale decreases in southern elephant seal populations. The most likely and easily testable hypothesis is the environmental change hypothesis, which suggests that the decreases (1950s–1990s) in SES populations were the result of large-scale environmental change

Hypothesis	Assessment	Testability	How?
Human disturbance	Discounted	N/A	N/A
Male paucity	Discounted	N/A	N/A
Fisheries interactions	Discounted	N/A	N/A
Juvenile predation	Unlikely, but may be important when populations are small	N/A	N/A
Overshoot	Unlikely, but failed to discount	Yes	Requires, interspecies studies
Pandemic diseases	Unlikely, but failed to discount	Yes	Requires antibody and viral studies
Interspecific competition	Unlikely	Yes	Requires, interspecies studies; see Fig. 2
Environmental change	Plausible	Yes	See Fig. 3

N/A, not available.

environmental change influencing absolute food supply or food quality, indeed; similar factors have been implicated as causes in the decrease of cetaceans in the Mediterranean (Bearzi *et al.*, 2003; Notarbartolo-di-Sciara *et al.*, 2003). However, interpreting the effects of climate change or regime shifts in the marine environment on apex marine predators is difficult (Benson & Trites, 2002) because of the response time lags that occur between changes in climate and the observed response in the marine predator in question (Weimerskirch *et al.*, 2003). The recent suggestion of a major regime shift in the Southern Ocean (Weimerskirch *et al.*, 2003) and the observations of similar regime shifts in the Northern Hemisphere provide an additional hypothesis to explain the population changes observed for southern elephant seals: exploring the relevance of the nutritional stress hypothesis, i.e. to assess the energetic content of seal diets and to evaluate whether there have been changes in the diets or indeed in energy content of prey (see Trites & Donnelly, 2003 for a review). The interspecific competition hypothesis is difficult to test directly because it requires the simultaneous monitoring of species that overlap directly with elephant seals, many of which have not been identified or of which little is known. Monitoring of candidate competitors such as beaked whales requires observing a concomitant increase in those populations during an elephant seal decline, and this is essentially impossible with the currently available technology. Nonetheless, the results of the Taylor's power-law analysis suggest that when compared with a similar species where most populations are increasing (*M. angustirostris*), interspecific competition does not appear to be an important factor in the decrease.

Alternatively, the environmental mediation of food supply hypothesis can be tested. Figure 3 provides a summary of how food availability – and indeed food quality, as has been shown for Steller sea lions (*Eumetopias jubatus* – Trites & Donnelly, 2003), can influence population trends in elephant seals. As with most species of large mammals, the status of an elephant seal population is determined by juvenile survival (step 8 – Caughley, 1977), and more specifically, the number of new animals recruited into the breeding population. If the number of new recruits is less than the number dying, the population decreases. In elephant seals there is a clear relationship between juvenile survival and the mass of individuals at weaning (McMahon *et al.*, 2000, 2003). The foraging success of juvenile seals (step 7) also plays a role in determining their survival, but exactly how this occurs is not known. The weaning mass and survival of pups is, in turn, dictated by the size of the mother (Fedak, Arnborn & Boyd, 1996; Arnborn, Fedak & Boyd, 1997) and her breeding experience (step 5

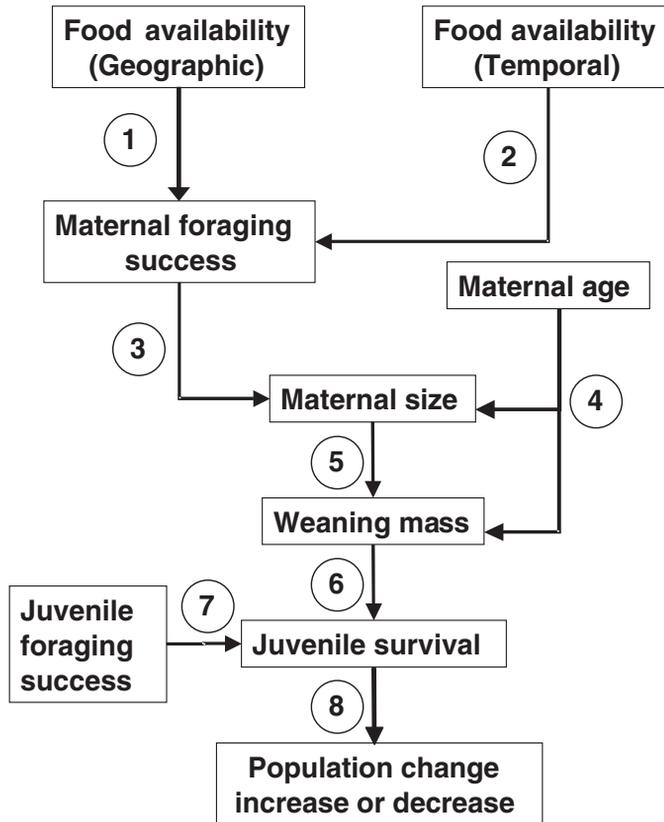


Fig. 3 A possible model for population regulation in the southern elephant seals highlighting the importance of juvenile survival on population growth and providing links that describe the factors which may affect juvenile survival.

– McMahon & Bradshaw, 2004), and this is a consequence of both the age of the mother (step 4), and her foraging success during the months at sea prior to the breeding season (step 3). Maternal foraging success is influenced by the availability of food, and this can vary in both space (step 1) and time (step 2). Therefore, a study is required that integrates and assesses both the maternal effects (steps 1–5) and the juvenile effects to examine the above hypothesis.

The most important aspect of the decrease in seal numbers at Macquarie Island was the decrease in first-year survival during the early 1960s to below 2% in 1965 (Hindell, 1991). During this time, however, survival probability for seals older than 1 years remained constant (Hindell, 1991). Consequently, it was suggested that changes in the Macquarie Island population since the 1960s were due to the subsequent low rates of recruitment into the population (Hindell, 1991). This leads to the hypothesis that first-year seals are different to seals older than 1 years with respect to diet and foraging. Therefore, examining the factors important in the survival of first-year seals should provide further evidence to test the hypothesis and explain the decrease in seal numbers (Hindell, 1991). There has been a growing body of information describing the behaviour and survival of first-year seals (Bell, Burton & Hindell, 1997; Hindell *et al.*, 1999; McMahon, Burton & Bester, 1999; Irvine *et al.*, 2000; McConnell *et al.*, 2002). Elephant seals in their first year of life exhibit different diving behaviour (Hindell *et al.*, 1999; Irvine *et al.*, 2000), use different foraging areas (Hindell *et al.*, 1999; McConnell *et al.*, 2002) and their survival is positively related to weaning mass (McMahon

et al., 2000, 2003). This latter point has accentuated the dependence of juvenile survival on maternal expenditure (McMahon *et al.*, 2000, 2003) and therefore, maternal foraging success (Fedak *et al.*, 1996; Arnborn *et al.*, 1997).

Another important requirement to test the proposed hypothesis is to establish a link between environmental variability and survival and fecundity. The conventional approach in conservation biology to test a food-shortage hypothesis is to manipulate the food supply (Rosen & Trites, 1999). This approach is not possible for southern elephant seals because mothers are at distant foraging areas prior to giving birth and consequently not available for capture in the months leading up to the birth (Laws, 1956). Therefore, the only approach is a 'natural', or mensurative, experiment – i.e. to use naturally occurring variation in food supply to test the hypothesis. Studies therefore need to run for sufficient time to encompass at least one of the climatic cycles described previously (i.e. ACW and ENSO). Comparing performance in high-resource vs. poor-resource years can be used to examine the influence of food availability on maternal foraging success and the effects of food availability on juvenile survival and adult fecundity.

Such a study would need to encompass several minima and maxima in environmental conditions to maximize the potential variation in food supply available. For each year, individual foraging areas would need to be assessed because there is a range of environmental conditions experienced by seals foraging in vastly different areas of the ocean (Bradshaw *et al.*, 2002a; Hindell *et al.*, 2003b). For example, the ACW travels easterly around the Southern Ocean during an average 8-year cycle (White & Peterson, 1996). Thus, seals foraging to the east of their natal area are likely to experience different environmental conditions to their conspecifics foraging to the west. Secondly, the foraging ranges and the associated foraging behaviour and variation in diet composition observed (Bradshaw *et al.*, 2003) must then be related to foraging success, measurable either as mass gain or changes in other physiological parameters (Fedak *et al.*, 1994; Carlini *et al.*, 1999). Finally, weaning mass needs to be examined in relation to these indices of maternal foraging success.

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REFERENCES

- van Aarde, R.J. (1980) Fluctuation in the population of southern elephant seal *Mirounga leonina* at Kerguelen Island. *South African Journal of Zoology*, **15**, 99–106.
- Allan, R., Lindsay, J. & Parker, D. (1996) *El Niño Southern Oscillation and Climate Variability*. CSIRO Publishing, Melbourne.
- Anonymous (2001) *Antipodes Island Report*. Department of Conservation, Wellington, New Zealand.
- Arnborn, T., Fedak, M.A. & Boyd, I.L. (1997) Factors affecting maternal expenditure in southern elephant seals during lactation. *Ecology*, **78**, 471–483.
- Barbraud, C. & Weimerskirch, H. (2001) Emperor penguins and climate change. *Nature*, **411**, 183–186.
- Barrat, A. & Mougou, J.L. (1978) L'Elephant de mer *Mirounga leonina* de L'île de la Possession, archipel Crozet (46°25'S, 51°45'E). *Mammalia*, **42**, 143–174.
- Bearzi, G., Reeves, R.R., Notarbartolo-Di-Sciara, G., Politi, E., Canadas, A., Frantzis, A. & Mussi, B. (2003) Ecology, status and conservation of short-beaked common dolphins *Delphinus delphis* in the Mediterranean Sea. *Mammal Review*, **33**, 224–252.
- Bell, C.M., Burton, H.R. & Hindell, M.A. (1997) Growth of the southern elephant seals, *Mirounga leonina*, during their first foraging trip. *Australian Journal of Zoology*, **45**, 447–458.
- Benson, A.J. & Trites, A.W. (2002) Ecological effects of regime shifts in the Bering Sea and eastern North Pacific Ocean. *Fish and Fisheries*, **3**, 95–113.

- Bester, M.N. (1988) Marking and monitoring studies of the Kerguelen stock of southern elephant seals *Mirounga leonina* and their bearing on biological research in the Vestfold Hills. *Hydrobiologia*, **165**, 269–277.
- Bester, M.N. & Lenglard, P.-Y. (1982) An analysis of the southern elephant seal, *Mirounga leonina*, breeding population at Kerguelen Island. *South African Journal of Antarctic Research*, **12**, 11–16.
- Bester, M.N., Möller, H., Wium, J. & Enslin, B. (2001) An update on the status of southern elephant seals on Gough Island. *South African Journal of Wildlife Research*, **31**, 68–71.
- Bester, M.N. & Wilkinson, I.S. (1994) Population ecology of southern elephant seals at Marion Island. In: *Elephant Seals: Population Ecology, Behaviour, and Physiology* (Ed. by B.J. LeBoeuf & R.M. Laws), pp. 85–97. University of California Press, Berkeley.
- van de Bildt, M.W.G., Vedder, E.J., Martina, B.E.E., Sidi, B.A., Jiddou, A.B., Barham, M.E.O., Androukaki, E., Kommenou, A., Niesters, H.G.M. & Osterhaus, A.D.M.E. (1999) Morbilliviruses in Mediterranean monk seals. *Veterinary Microbiology*, **69**, 19–21.
- Boyd, I.L., Croxall, J.P., Lunn, N.J. & Reid, K. (1995) Population demography of Antarctic fur seals: the costs of reproduction and implications for life-histories. *Journal of Animal Ecology*, **64**, 505–518.
- Boyd, I.L., Walker, T.R. & Poncet, J. (1996) Status of southern elephant seals at South Georgia. *Antarctic Science*, **8**, 237–244.
- Bradshaw, C.J.A., Hindell, M.A., Best, N.J., Phillips, K.L., Wilson, G. & Nichols, P.D. (2003) You are what you eat: describing the foraging ecology of southern elephant seals (*Mirounga leonina*) using blubber fatty acids. *Proceedings of the Royal Society London, B*, **270**, 1283–1292.
- Bradshaw, C.J.A., Hindell, M.A., Michael, K.J. & Sumner, M.D. (2002a) The optimal spatial scale for the analysis of elephant seal foraging as determined by geo-location in relation to sea surface temperatures. *ICES Journal of Marine Biology*, **59**, 770–781.
- Bradshaw, C.J.A., McMahon, C.R., Hindell, M.A., Pistorius, P.A. & Bester, M.N. (2002b) Do southern elephant seals show density dependence in fecundity? *Polar Biology*, **25**, 650–655.
- Bryden, M.M. (1968) Lactation and suckling in relation to early growth of the southern elephant seal, *Mirounga leonina* (L). *Australian Journal of Zoology*, **16**, 739–748.
- Burton, H. (1986) A substantial decline in numbers of the southern elephant seal at Heard Island. *Tasmanian Naturalist*, **86**, 4–8.
- Burton, H.R., Arnbohm, T.L.B.I., Bester, M.N., Vergani, D. & Wilkinson, I. (1997) Significant differences in the weaning mass of southern elephant seals from five sub-Antarctic islands in relation to population declines. In: *Antarctic Communities: Species Structure and Survival* (Ed. by B. Battaglia, J. Valencia & D.W.H. Watton), pp. 335–338. Cambridge University Press, Cambridge.
- Burton, H.R. & van den Hoff, J. (2002) Humans and the southern elephant seal (*Mirounga leonina*). *Australian Mammalogy*, **24**, 127–139.
- Campagna, C. & Lewis, M. (1992) Growth and distribution of a southern elephant seal colony. *Marine Mammal Science*, **8**, 387–396.
- Carlini, A.R., Marquez, M.E.I., Daneri, G.A. & Poljak, S. (1999) Mass changes during their annual cycle in females of southern elephant seals at King George Island. *Polar Biology*, **21**, 234–239.
- Carrick, R. & Ingham, S.E. (1962) Studies on the southern elephant seal *Mirounga leonina* (L) I Introduction to the series. *CSIRO Wildlife Research*, **7**, 89–101.
- Caughley, G. (1977) *Analysis of Vertebrate Populations*. John Wiley and Sons, London.
- Caughley, G. & Gunn, A. (1996) *Conservation Biology in Theory and Practice*. Blackwell Science, Cambridge, MA.
- Chamaille-Jammes, S., Guinet, C., Nicoleau, F. & Argentié, M. (2000) A method to assess population changes in king penguins: the use of a geographical information system to estimate area-population relationships. *Polar Biology*, **23**, 545–549.
- Clarke, M.R. & MacLeod, N. (1982) Cephalopods in the diet of southern elephant seals at Signy Island South Orkney Islands. *British Antarctic Survey Bulletin*, **57**, 22–31.
- Condy, P.R. (1978) The distribution and abundance of southern elephant seals *Mirounga leonina* (Linn) on the Prince Edward Islands. *South African Journal of Antarctic Research*, **8**, 42–48.
- Condy, P.R. (1984) The population of southern elephant seals, *Mirounga leonina*, at Marion Island, 1973–83. *South African Journal of Science*, **80**, 26–27.
- Condy, P.R., van Aarde, R.J. & Bester, M.N. (1978) The seasonal occurrence and behaviour of killer whales (*Orcinus orca*) at Marion Island. *Journal of Zoology, London*, **184**, 449–464.
- Daneri, G.A. & Carlini, A.R. (2002) Fish prey of the southern elephant seals, *Mirounga leonina*, at King George Island. *Polar Biology*, **25**, 739–743.
- Daneri, G.A., Carlini, A.R. & Rodhouse, P.G.K. (2000) Cephalopod diet of the southern elephant seal, *Mirounga leonina*, at King George Island, South Shetland Islands. *Antarctic Science*, **12**, 16–19.

- Engelhard, G.H., Brasseur, S., Hall, A.J., Burton, H.R. & Reijnders, P.J.H. (2002a) Adrenocortical responsiveness in southern elephant seal mothers and pups during lactation and the effect of scientific handling. *Journal of Comparative Physiology, B*, **172**, 315–328.
- Engelhard, G.H., Hall, A.J., Brasseur, S.M.J.M. & Reijnders, P. (2002b) Blood chemistry in southern elephant seal mothers and pups during lactation reveals no effects of handling. *Comparative Biochemistry and Physiology, A*, **133**, 367–378.
- Engelhard, G.H., van den Hoff, J., Broekman, M., Baarspul, A.N.J., Field, I., Burton, H.R. & Reijnders, P.J.H. (2001) Mass of weaned elephant seal pups in areas of low and high human presence. *Polar Biology*, **24**, 244–251.
- Estes, J.A., Tinker, M.T., Williams, T.M. & Doak, D.F. (1998) Killer whale predation on sea otters linking oceanic and nearshore ecosystems. *Science*, **282**, 473–476.
- Fabiani, A., Hoelzel, A.R., Galimberti, F. & Muelbert, M.M.C. (2003) Long-range paternal gene flow in the southern elephant seal. *Science*, **299**, 676.
- Fedak, M.A., Arnborn, T.A. & Boyd, I.L. (1996) The relation between the size of southern elephant seal mothers, the growth of their pups and the use of maternal energy, fat and protein during lactation. *Physiological Zoology*, **69**, 887–911.
- Fedak, M.A., Arnborn, T.A., McConnell, B.J., Chambers, C., Boyd, I.L., Harwood, J. & McCann, T.S. (1994) Expenditure, investment and acquisition of energy in southern elephant seals. In: *Elephant Seals: Population Ecology, Behaviour, and Physiology* (Ed. by B.J. LeBoeuf & R.M. Laws), pp. 354–373. University of California Press, Berkeley.
- Fewster, R.M., Buckland, S.T., Siriwardena, G.M., Baillie, S.R. & Wilson, J.D. (2000) Analysis of population trends from farmland birds using generalized additive models. *Ecology*, **81**, 1970–1984.
- Galimberti, F. & Boitani, L. (1999) Demography and breeding biology of a small, localized population of southern elephant seals (*Mirounga leonina*). *Marine Mammal Science*, **15**, 159–178.
- Galimberti, F., Boitani, L. & Marzetti, I. (2000a) Female strategies of harassment reduction in southern elephant seals. *Ethology Ecology and Evolution*, **12**, 367–388.
- Galimberti, F., Boitani, L. & Marzetti, I. (2000b) The frequency and costs of harassment in southern elephant seals. *Ethology Ecology and Evolution*, **12**, 345–365.
- Gerrodette, T. (1987) A power analysis for detecting trends. *Ecology*, **68**, 1364–1372.
- Gloersen, P. (1995) Modulation of hemispheric sea-ice cover by ENSO events. *Nature*, **373**, 503–506.
- Green, K. & Burton, H.R. (1993) Comparison of the stomach contents of the southern elephant seal, *Mirounga leonina*, at Macquarie and Heard Islands. *Marine Mammal Science*, **9**, 10–22.
- Guinet, C. (1992) Croissance des éléphants de mer de l'archipel Crozet (46°25'S, 51°45'E) pendant leur première année de vie. *Mammalia*, **56**, 459–468.
- Guinet, C., Jouventin, P. & Weimerskirch, H. (1992) Population changes, haulout pattern and movements of southern elephant seals on Crozet and Kerguelen Archipelago. *Polar Biology*, **12**, 349–356.
- Guinet, C., Jouventin, P. & Weimerskirch, H. (1999) Recent population change of the southern elephant seal at Iles Crozet and Iles Kerguelen: the end of the decrease. *Antarctic Science*, **11**, 193–197.
- Harding, K.C., Harkonen, T. & Caswell, H. (2002) The 2002 European seal plague: epidemiology and population consequences. *Ecology Letters*, **5**, 727–732.
- Harwood, J. & Hall, A. (1990) Mass mortality in marine mammals: its implications for population dynamics and genetics. *Evolution and Ecology*, **5**, 254–257.
- Hindell, M.A. (1991) Some life-history parameters of a declining population of southern elephant seals, *Mirounga leonina*. *Journal of Animal Ecology*, **60**, 119–134.
- Hindell, M.A., Bradshaw, C.J.A., Guinet, C. & Harcourt, R.G. (2003a) Ecosystem monitoring and modelling: can marine mammals signal or predict change? In *Marine mammals and humans. In: Towards a Sustainable Balance* (Ed. by N. Gales, M.A. Hindell & R. Kirkwood). CSIRO Publishing, Melbourne.
- Hindell, M.A., Bradshaw, C.J.A., Sumner, M.D., Michael, K. & Burton, H.R. (2003b) Dispersal of female southern elephant seals and their prey consumption during the austral summer: relevance to management and oceanographic zones. *Journal of Applied Ecology*, **40**, 703–715.
- Hindell, M.A. & Burton, H.R. (1987) Past and present status of the southern elephant seal (*Mirounga leonina*) at Macquarie Island. *Journal of Zoology, London*, **231**, 365–380.
- Hindell, M.A. & Burton, H.R. (1988a) The history of the elephant seal industry at Macquarie Island and an estimate of pre-sealing numbers. *Papers and Proceedings of the Royal Society of Tasmania*, **122**, 159–176.
- Hindell, M.A. & Burton, H.R. (1988b) Seasonal haul-out patterns of the southern elephant seal (*Mirounga leonina*) at Macquarie Island. *Journal of Mammalogy*, **69**, 81–88.
- Hindell, M.A., Burton, H.R. & Slip, D.J. (1991) Foraging areas of southern elephant seals, *Mirounga leonina*, as inferred from water temperature data. *Australian Journal of Marine and Freshwater Research*, **42**, 115–128.

- Hindell, M.A., McConnell, B.J., Fedak, M.A., Slip, D.J., Burton, H.R., Reijnders, P.J.H. & McMahon, C.R. (1999) Environmental and physiological determinants of successful foraging by naive southern elephant seal pups during their first trip to sea. *Canadian Journal of Zoology*, **77**, 1807–1821.
- Hindell, M.A. & McMahon, C.R. (2000) Long distance movement of a southern elephant seal (*Mirounga leonina*) from Macquarie Island to Peter I ØY. *Marine Mammal Science*, **16**, 504–507.
- Hindell, M.A., Slip, D.J. & Burton, H.R. (1994) Possible causes of the decline of southern elephant seal populations in the southern Pacific and southern Indian Oceans. In: *Elephant Seals: Population Ecology, Behaviour, and Physiology* (Ed. by B.J. LeBoeuf & R.M. Laws), pp. 66–84. University of California Press, Berkeley.
- Hoelzel, A.R., Campagna, C. & Arnbohm, T. (2001) Genetic and morphometric differentiation between island and mainland southern elephant seal populations. *Proceedings of the Royal Society of London, Biology Sciences*, **268**, 325–332.
- van den Hoff, J., Burton, H., R. & Davies, R. (2003) Diet of male southern elephant seals (*Mirounga leonina* L.) hauled out at Vincennes Bay, East Antarctica. *Polar Biology*, **26**, 27–31.
- van den Hoff, J., Burton, H.R., Hindell, M.A., Sumner, M.D. & McMahon, C.R. (2002) Migrations and foraging of juvenile southern elephant seals from Macquarie Island within CCAMLR managed areas. *Antarctic Science*, **14**, 134–145.
- Hofmeyr, G.J.G., Bester, M.N. & Jonker, F.C. (1997) Changes in population sizes and distribution of fur seals at Marion Island. *Polar Biology*, **17**, 150–158.
- Irvine, L.G., Hindell, M.A., van den Hoff, J. & Burton, H.R. (2000) The influence of body size on dive duration of underyearling southern elephant seals (*Mirounga leonina*). *Journal of Zoology, London*, **252**, 463–471.
- Jonker, F.C. & Bester, M.N. (1998) Seasonal movements and foraging areas of adult southern female elephant seals, *Mirounga leonina*, from Marion Island. *Antarctic Science*, **10**, 21–30.
- Kennedy, S. (1998) Morbillivirus infections in aquatic mammals. *Journal of Comparative Pathology*, **119**, 201–225.
- Kennedy, S., Kuiken, T., Jepson, P.D., Deaville, R., Forsyth, M., Barret, T., van de Bildt, M.W.G., Osterhaus, A.D.M.E., Eybatov, T., Duck, C., Kydyrmanov, A., Mitrofanov, I. & Wilson, S. (2000) Mass die-off of Caspian seals caused by canine distemper virus. *Emerging Infectious Diseases*, **6**, 637–639.
- Kerley, G.I.H. (1983) Comparison of seasonal haul-out patterns of fur seals *Arctocephalus tropicalis* and *A gazella* on sub-Antarctic Marion Island. *South African Journal of Wildlife Research*, **13**, 71–77.
- Kilpatrick, A.M. & Ives, A.R. (2003) Species interactions can explain Taylor's power law for ecological time series. *Nature*, **422**, 65–68.
- Kirkman, S.P., Hofmeyr, G.J.G., Bester, M.N. & Isaksen, K. (2001) Counts of southern elephant seals, *Mirounga leonina*, at Bouvet Island. *Polar Biology*, **24**, 62–65.
- Krockenberger, M.B. & Bryden, M.M. (1994) Rate of passage of digesta through the alimentary tract of southern elephant seals (*Mirounga leonina*) (Carnivora: Phocidae). *Journal of Zoology, London*, **234**, 229–237.
- Kwok, R. & Comiso, J.C. (2002) Spatial patterns of variability in Antarctic surface temperature: connections to the Southern Hemisphere Annular Mode and the Southern Oscillation. *Geophysical Research Letters*, **29**, 1029–1032.
- Laws, R.M. (1956) The elephant seal (*Mirounga leonina* Lin) II General, social and reproductive behaviour. *Falkland Islands Dependencies Survey Scientific Reports*, **13**, 1–88.
- Laws, R.M. (1994) History and present status of southern elephant seal populations. In: *Elephant Seals: Population Ecology, Behaviour, and Physiology* (Ed. by B.J. LeBoeuf & R.M. Laws), pp. 49–65. University of California Press, Berkeley.
- Lewis, M., Campagna, C., Quintana, F. & Falabella, V. (1998) Estado actual y distribución de la población elefante marino del sur en la Península Valdes, Argentina. *Mastozoología Neotropical*, **5**, 29–40.
- Ling, J.K. & Bryden, M.M. (1992) *Mirounga leonina*. *Mammalian Species*, **391**, 1–8.
- Linn, M.L., Joy Gardner, J., Warrilow, D., Darnell, G.A., McMahon, C.R., Field, I.C., Hyatt, A.D., Slade, R.W. & Suhrbier, A. (2001) Arbovirus of marine mammals: a new alphavirus isolated from the elephant seal louse, *Lepidophthirus macrorhini*. *Journal of Virology*, **75**, 4103–4109.
- Lynnes, A.S., Reid, K., Croxall, J.P. & Trathan, P.N. (2002) Conflict or co-existence? Foraging distribution and competition for prey between Adélie and chinstrap penguins. *Marine Biology*, **141**, 1165–1174.
- McCann, T.S. (1985) Size, status and demography of southern elephant seal (*Mirounga leonina*) populations. In: *Sea Mammals in South Latitudes: Proceedings of a Symposium of the 52nd ANZAAS Congress* (Ed. by J.K. Ling & M.M. Bryden), pp. 1–17. South Australian Museum, Adelaide.
- McCann, T.S. & Rothery, P. (1988) Population size and status of the southern elephant seal (*Mirounga leonina*) at South Georgia, 1951–85. *Polar Biology*, **8**, 305–309.

- McConnell, B.J. & Fedak, M.A. (1996) Foraging movements of southern elephant seals. *Canadian Journal of Zoology*, **74**, 1485–1496.
- McConnell, B.J., Fedak, M.A., Burton, H.R., Engelhard, G.H. & Reijnders, P.J.H. (2002) Movements and foraging areas of naive, recently weaned elephant seals pups. *Journal of Animal Ecology*, **71**, 65–78.
- MacLeod, C.D., Santos, M.B. & Pierce, G.J. (2003) Review of data on diets of beaked whales: evidence of niche separation and geographic segregation. *Journal of the Marine Biology Society Association of the United Kingdom*, **83**, 651–665.
- McMahon, C.R. & Bradshaw, C.J.A. (2004) Harem choice and breeding experience of female southern elephant seals influence offspring survival. *Behavioral Ecology and Sociobiology*, **55**, 349–362.
- McMahon, C.R., Burton, H.R. & Bester, M.N. (1999) First-year survival of southern elephant seals, *Mirounga leonina*, at sub-Antarctic Macquarie Island. *Polar Biology*, **21**, 279–284.
- McMahon, C.R., Burton, H.R. & Bester, M.N. (2000) Weaning mass and the future survival of juvenile southern elephant seals, *Mirounga leonina*, at Macquarie Island. *Antarctic Science*, **12**, 149–153.
- McMahon, C.R., Burton, H.R. & Bester, M.N. (2003) A demographic comparison of two southern elephant seal populations. *Journal of Animal Ecology*, **72**, 61–74.
- McMahon, C.R., Hindell, M.A., Burton, H.R. & Bester, M.N. (2005) Modelling southern elephant seal populations: a comparison of populations with varying rates of change and observations of a population on a demographic knife-edge. *Oikos* (in press)
- Moore, G.J., Robertson, G. & Weinecke, B. (1998) Food requirements of breeding king penguins at Heard Island and the potential overlap with fisheries. *Polar Biology*, **20**, 293–302.
- Murphy, E.J. & Reid, K. (2001) Modelling Southern Ocean krill population dynamics: biological processes generating fluctuations in the South Georgia ecosystem. *Marine Ecology Progress Series*, **217**, 175–189.
- Notarbartolo-di-Sciara, G., Zanardelli, M., Jahoda, M., Panigada, S. & Airoldi, S. (2003) The fin whale *Balaenoptera physalus* (L 1758) in the Mediterranean Sea. *Mammal Review*, **33**, 105–150.
- Osterhaus, A., Niesters, H., Groen, J., van den Bildt, M., Martina, B., Vedder, L., Vos, J., van Egmond, H., Abou Sidi, B. & Ely Ould Barham, M. (1997) Morbillivirus in monk seal mortality. *Nature*, **388**, 838–834.
- Osterhaus, A., van den Bildt, M., Vedder, L., Martina, B., Niesters, H., Vos, J., van Egmond, H., Liem, D., Baumann, R., Andriokakis, E., Kotomatas, S., Komnenous, A., Abou Sidi, B., Bent Jiddou, A. & Ely Ould Barham, M. (1998) Monk seal mortality: virus or toxin? *Vaccine*, **16**, 979–981.
- Pascal, M. (1986) Numerical changes in the population of elephant seals (*Mirounga leonina* L) in the Kerguelen Archipelago during the past 30 years. In: *Marine Mammal Fishery Interactions* (Ed. by J.R. Beddington, R.J.H. Beverton & D.M. Lavigne), pp. 170–186. George Allen & Unwin, London.
- Piatkowski, U., Vergani, D.F. & Stanganelli, Z.B. (2002) Changes in cephalopod diet of southern elephant seals at King George Island, during El Niño – La Niña events. *Journal of the Marine Biology Society Association of the United Kingdom*, **82**, 913–916.
- Pistorius, P.A., Bester, M.N., Kirkman, S.P. & Taylor, F.E. (2001) Temporal changes in fecundity and age at sexual maturity of southern elephant seals at Marion Island. *Polar Biology*, **24**, 343–348.
- Priddle, J., Boyd, I.L., Whitehouse, M.J., Murphy, E.J. & Croxall, J.P. (1998) Estimates of Southern Ocean primary production – constraints from predator carbon demand and nutrient drawdown. *Journal of Marine Systems*, **17**, 275–288.
- Rosen, D.A.S. & Trites, A.W. (1999) Metabolic effects of low-energy diet on Stellar sea lions, *Eumetpias jubatus*. *Physiological and Biochemical Zoology*, **76**, 723–731.
- dos Santos, R.A. & Haimovici, M. (2001) Cephalopods in the diet of marine mammals stranded or incidentally caught along south-eastern and southern Brazil (21–34°S). *Fisheries Research*, **52**, 99–112.
- Sekiguchi, K., Klages, N., Findlay, K. & Best, P.B. (1993) Feeding habits and possible movements of southern bottlenose whales (*Hyperoodon planifrons*). *Proceedings of the National Institute of Polar Research Symposium on Polar Biology*, **6**, 84–97.
- Shaughnessy, P.D., Erb, E. & Green, K. (1998) Continued increase in the population of Antarctic fur seals, *Arctocephalus gazella*, at Heard Island, Southern Ocean. *Marine Mammal Science*, **14**, 384–389.
- Skinner, J.D. & van Aarde, R.J. (1983) Observations on the trend of the breeding population of southern elephant seals, *Mirounga leonina*, at Marion Island. *Journal of Applied Ecology*, **20**, 707–712.
- Slade, R.W., Moritz, C., Hoelzel, A.R. & Burton, H.R. (1998) Molecular population genetics of the southern elephant seal *Mirounga leonina*. *Genetics*, **149**, 1945–1957.
- Slip, D.J. (1995) The diet of southern elephant seals (*Mirounga leonina*) at Heard Island. *Canadian Journal of Zoology*, **73**, 1519–1528.
- Slip, D.J. & Burton, H.R. (1999) Population status and seasonal haulout patterns of the southern elephant seal (*Mirounga leonina*) at Heard Island. *Antarctic Science*, **11**, 38–47.

- Slip, D.J., Moore, G.J. & Green, K. (1995) Stomach contents of a southern bottlenose whale, *Hyperoodon planifrons*, stranded at Heard Island. *Marine Mammal Science*, **11**, 575–584.
- Smith, W.O. & Nelson, D.M. (1985a) Phytoplankton bloom produced by a receding ice edge in the Ross Sea: spatial coherence with the density field. *Science*, **227**, 163–166.
- Smith, W.O.J. & Nelson, D.M. (1985b) Phytoplankton biomass near a receding ice-edge in the Ross Sea. In: *Antarctic Nutrient Cycles and Food Webs* (Ed. by W.R. Siegfried, P.R. Condy & R.M. Laws), pp. 70–77. Springer-Verlag, Berlin Heidelberg.
- Springer, A.M., Estes, J.A., van Vliet, G.B., Williams, T.M., Doak, D.F., Danner, E.M., Forney, K.A. & Pfister, B. (2003) Sequential megafaunal collapse in the North Pacific Ocean: An ongoing legacy of industrial whaling? *Proceedings of the National Academy of Sciences of the United States of America*, **100**, 12223–12228.
- Stewart, B.S., Yochem, P.K., Huber, H.R., deLong, R.L., Jameson, R.J., Sydeman, W.J., Allen, S.G. & LeBoeuf, B.J. (1994) History and present status of the northern elephant seal population. In: *Elephant Seals: Population Ecology, Behaviour and Physiology* (Ed. by B.J. LeBoeuf & R.M. Laws), pp. 29–48. University of California Press, Berkeley.
- Taylor, L.R. (1961) Aggregation, variance and the mean. *Nature*, **189**, 732–735.
- Taylor, L.R. & Woiwood, I.P. (1982) Comparative synoptic dynamic: 1. Relationships between interspecific and intraspecific spatial and temporal variance-mean population parameters. *Journal of Animal Ecology*, **51**, 879–906.
- Trites, A.W. & Donnelly, C.P. (2003) The decline of Steller sea lions *Eumetopias jubatus* in Alaska: a review of the nutritional stress hypothesis. *Mammal Review*, **33**, 3–28.
- Vergani, D.F., Stanganelli, Z.B. & Bilenca, D. (2001) Weaning mass variation of southern elephant seals at King George Island and its possible relationship with El Niño and La Niña events. *Antarctic Science*, **13**, 37–40.
- Vergani, D.F., Stanganelli, Z.B. & Bilenca, D. (2004) Effects of El Niño and La Niña events on the sex ratio of southern elephant seals at King George Island. *Marine Ecology Progress Series*, **268**, 293–300.
- Visser, I.K.G., Teppema, J.S. & Osterhaus, A.D.M.E. (1991) Virus infections of seals and other pinnipeds. *Reviews in Medical Microbiology*, **2**, 105–114.
- Weimerskirch, H., Inchausti, P., Guinet, C. & Barbraud, C. (2003) Trends in bird and seal populations as indicators of a system shift in the Southern Ocean. *Antarctic Science*, **15**, 249–256.
- White, W.B., Chen, S.-C. & Peterson, R.G. (1998) The Antarctic Circumpolar Wave: a beta effect in ocean–atmosphere coupling over the Southern Ocean. *Journal of Physical Oceanography*, **28**, 2345–2361.
- White, W.B. & Peterson, R.G. (1996) An Antarctic Circumpolar Wave in surface pressure, wind, temperature, and sea ice extent. *Nature*, **380**, 699–702.
- Wilkinson, I.S. & Bester, M.N. (1988) Is onshore human activity a factor in the decline of the southern elephant seal? *South African Journal of Antarctic Research*, **18**, 14–17.
- Wilkinson, I. & van Aarde, R.J. (1999) Marion Island elephant seals: the paucity – of – males hypothesis tested. *Canadian Journal of Zoology*, **77**, 1547–1554.
- Woehler, E.J. & Croxall, J.P. (1997) The status and trends of Antarctic and sub-Antarctic seabirds. *Marine Ornithology*, **25**, 43–66.
- Yodzis, P. (2000) Diffuse effects in food webs. *Ecology*, **81**, 261–266.
- Yodzis, P. (2001) Must top predators be culled for the sake of fisheries? *Trends in Ecology and Evolution*, **16**, 78–84.

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