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 (Peninsula 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-

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**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 & Lenglart, 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).

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

1. 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 7,455 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.,
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 $\mu$ and variance $\sigma^2$ 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
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 moultng 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, Lindesay & 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...
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, Arnbom & Boyd, 1996; Arnbom, Fedak & Boyd, 1997) and her breeding experience (step 5

### 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.

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

N/A, not available.
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

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**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.
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; Arnbom 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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