Viability of the southern elephant seal population of the Falkland Islands

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Abstract

Accurate long-term series of demographic data are available for most populations of southern elephant seals. However, research on the elephant seals of the Falkland Islands began only recently, and information for an accurate forecasting of the future of this population is lacking. In this paper we present data on the current status of the population and its trend in size during the last 11 years. We built an age-structured model of the population and analyzed the effect of variation in demographic parameters on population growth. Elasticity analysis demonstrated that variation in mortality has a more pronounced effect on instantaneous growth rate than an equivalent variation in fecundity. We examined the effects of environmental variability, inbreeding and catastrophes on population viability by a computer simulation using the VORTEX PVA programme. In the stochastic model, the most important factor affecting extinction risk was variability in mortality rates, in particular of the adult classes. We concluded that, although the population does not appear to be at immediate risk of extinction, its small size and isolation make it necessary to accurately monitor the population trends and to acquire additional information on life history and feeding strategies.

INTRODUCTION

The status of southern elephant seals (*Mirounga leonina*; SES hereafter) in the Falkland Islands is uncertain. While most populations of the circum-Antarctic distribution of SES have been studied for long periods (Laws, 1994), information about the Falkland Islands was almost completely lacking until very recently (Galimberti & Boitani, 1999).

In a recent survey of the Falklands coasts (M. Bingham, pers. comm.), very scarce signs of elephant seal breeding were observed, with the exception of the main breeding colony, Sea Lion Island (SLI hereafter). During the past 5 years, we have collected information from various sources that has led us to the conclusion that SLI is the only consistent breeding site. It is hence wise to consider the local population of Sea Lion Island as representative of the whole Falklands population (Galimberti & Boitani, 1999).

The SES population on SLI is small, with a net productivity during the 1999 breeding season of 513 pups

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and a total population size of about 1827 individuals that are 1 year old or older (Galimberti & Sanvito, 2000). It is also localized, with no other breeding site close to the island. The population is part of the South Georgia stock (Laws, 1994), but it is completely isolated during the breeding season (Lewis, Campagna & Quintana, 1996; Galimberti & Boitani, 1999). The isolation is reinforced by the phylopatry and breeding site fidelity of female elephant seals (Nicholls, 1970; Hindell & Little, 1988). Phylopatry and site fidelity are very high on SLI, both at population and breeding area level (F. Galimberti *et al.*, unpub. results). Therefore, the SLI population may be effectively modelled as a single isolated population.

Small and isolated populations present specific problems for conservation. Inter-annual variation in environmental quality may produce enough variance in demographic parameters to exceed their homeostatic capabilities (Berger, 1990), and they are prone to extinction due to catastrophic events (Miller & Lacy, 1999). Their viability may be severely reduced due to inbreeding depression (Lande, 1988; Lacy, 1997). Moreover, in small populations it is difficult to promptly detect a decline in abundance (Forcada, 2000).

Elephant seals of SLI are not only an important component of the biodiversity of the Falklands, but they are

also a notable economic asset, via nature-oriented tourism. Therefore, a full understanding of population dynamics will be valuable from both a scientific and practical point of view. Unfortunately, we are far from having enough information to achieve this goal. When complete data are not available, computer simulations may help in building alternative scenarios of the dynamics of the population, and suggest the areas where the collection of additional data is most needed (Boyce, 1992; but see Ludwig, 1999 and Fieberg & Ellner, 2000, for an alternative point of view). Simulation techniques, globally called population viability analysis (PVA), show a high predictive accuracy (Brook et al., 1999, 2000).

In this paper, we summarize data on the current status of SLI, we present an age-structured model of the population and the results of a population viability analysis, and we indicate the areas where collection of additional data is most needed.

METHODS

Modelling populations with overlapping generations and age-specific variation of mortality and fecundity requires the specification of many different parameters to be realistic. We gathered information from two sources: (1) a mark–recapture study conducted on SLI from 1995 to 1999 (for details, see Galimberti & Boitani, 1999; Galimberti, Sanvito & Boitani, 2000), (2) the literature

on SES demography, in particular for the South Georgia population, which is the only population of the stock for which a complete, sex-specific, life-table is available (McCann, 1985). The South Georgia population is a stable and undisturbed population (Hindell, Slip & Burton, 1994) and, hence, it is a realistic source of demographic parameters for SLI modelling. Demographic parameters are summarized in Table 1.

We examined the deterministic fate of the population with standard life-table analysis techniques (Caswell, 1989), including calculation of elasticities, i.e. the proportional change in λ (rate of growth per time unit) resulting from a proportional change in the corresponding entry of the projection matrix (de Kroon et al., 1986). We ran the population viability analysis using VORTEX (version 8.32; Miller & Lacy, 1999). Simulation parameters are summarized in Table 1. We modelled adult fecundity as age-independent because no senescence effects are evident in elephant seals (McCann, 1985; Le Boeuf & Laws, 1994). We modelled adult mortality as age-independent because mortality rates after maturity are almost constant in both sexes (McCann, 1985; Bester & Wilkinson, 1994). We assumed a stable age distribution because the population was stable in size during the last 11 years.

Stochastic modelling requires the specification of realistic values for environmental variability, i.e. the annual fluctuations of mortality and fecundity rates due to sto-

Table 1. Demographic and other input values used for the VORTEX PVA program

Parameter	Value	Source
A. DEMOGRAPHIC PARAMETERS		
Female breeding age (years)	4	Galimberti & Sanvito (2000)
Male breeding age (years)	7	Galimberti & Boitani (1999)
Maximum breeding age (years)	21	Arnbom et al. (1992) [SG]
Female mortality (%), EV in parenthesis from Pistorius et al. (1999) [MI]		
Age 0	40 (4.8)	Mark–recapture data; McCann (1985) [SG]
Age 1	15 (5.9)	McCann (1985): table 4–5 [SG]
Age 2	12 (7.1)	McCann (1985): table 4–5 [SG]
Age 3	12 (10.3)	McCann (1985): table 4–5 [SG]
Adults	16 (10.2)	Mark–recapture data
Male mortality (%), EV in parenthesis from Pistorius et al. (1999) [MI]		
Age 0	40 (6.3)	Mark–recapture data
Age 1	15 (6.8)	McCann (1985): table 4–5 [SG]
Age 2	17.3 (7.9)	McCann (1985): table 4–5 [SG]
Age 3	17.1 (11.4)	McCann (1985): table 4–5 [SG]
Age 4	17.1 (11.4)	McCann (1985): table 4–5 [SG]
Age 5	16.9 (10.0)	McCann (1985): table 4–5 [SG]
Age 6	19.9 (15.1)	McCann (1985): table 4–5 [SG]
Adults	29 (9.9)	Mark–recapture data
Fecundity (%), EV in parenthesis	88 (9.80)	Mark–recapture data
Maximum litter size	1	Galimberti & Boitani (1999)
Birth sex ratio, prop. of females	0.51	Census data
Mating system		Galimberti & Boitani (1999)
Type	Polygynous	
Males in the breeding pool (%)	28	
Inbreeding depression		
Lethal equivalents	3.14	Ralls et al. (1988)
Genetic load attrib. to lethals (%)	100	Miller & Lacy (1999)
B. SIMULATION PARAMETERS		
Initial population size	1827	Census data
Number of replications	500	Miller & Lacy (1999)
Number of years	100	Miller & Lacy (1999)
Extinction report interval	10	Miller & Lacy (1999)
Extinction criterion	0 females	Miller & Lacy (1999)

SG, South Georgia; MI, Marion Island.

chastic environmental fluctuations (EV, expressed as standard deviation in percentage rates: Miller & Lacy, 1999). We estimated the EV of fecundity and adult mortality from mark–recapture data. We calculated initial EV values from life-tables presented by Pistorius, Bester & Kirkman (1999) for the Marion Island population. To the best of our knowledge, this is the only SES population for which sex and age-specific life-tables of different cohorts have been published. The Marion Island population size is similar to the SLI size, but the population is currently decreasing at a rate of 1.9% (Bester & Wilkinson, 1994). Therefore, the estimates of EV are probably slightly conservative.

We excluded density-dependence from our models because density-dependence seems to have a secondary role in SES population dynamics (Hindell *et al.*, 1994). Two different density-dependent processes may affect the demography of elephant seals: an increase in pre-weaning mortality due to crowding of harems (Van Aarde, 1980; Reiter, Panken & Le Boeut, 1981) and density-dependent diffusion of epidemics (Harwood & Hall, 1990). In low-density populations of SES, pre-weaning mortality is low and is not affected by harem density (SLI: Galimberti & Boitani, 1999; Valdés Peninsula: Baldi *et al.*, 1996). Moreover, there is no indication of a higher diffusion of epidemics in the larger and more crowded SES populations (Hindell *et al.*, 1994).

RESULTS

Current status of the population

The population was almost stable during the 1995–1999 period, with a mean number of 522 breeding females, equivalent to a population of 1827 individuals aged 1 year old or older. Irregular counts carried out in the 1989–1994 period were kindly provided by local people (D. Gray, pers. comm.). These counts were standardized using a mathematical model of the haul out (i.e. arrival on land) process calibrated for SLI using daily census. The arrival on land and return to sea of female elephant seals is very regular, and it is almost perfectly approximated by a Gaussian curve having as parameters the mean and the standard deviation of the arrival day (Galimberti & Boitani, 1999; F. Galimberti & S. Sanvito, unpubl. results). Population size remained almost steady during the period 1989–1999. The slope of the linear trend showed a non-significant less than 1% increase per year.

In elephant seals, mortality of pups is related to population density and harem crowding (Macquarie Island: Carrick & Ingham, 1960; South Georgia: McCann, 1982; Peninsula Valdés: Baldi *et al.*, 1996). On SLI, pup mortality was very low during the past breeding seasons, from 1.93% in 1996 ($n = 517$) to 4.11% in 1999 ($n = 535$), at the bottom end of the typical range of the species. On SLI, the abundant breeding space maintained harem size at the bottom end of the typical range of the species (median = 30–35 females), and females' density was low (Galimberti & Boitani, 1999).

Weight at weaning is an approximate measure of habitat quality for elephant seals, because it is strongly correlated to the quantity and quality of resources available to the mother (Burton *et al.*, 1997). On SLI, mean weight at weaning ranged from 130.6–136.3 kg (Galimberti & Boitani, 1999; and unpubl. results), and it was on the high side of the range for SES populations. In particular, it is higher than the weight reported for South Georgia (126.5 kg: Burton *et al.*, 1997) and similar to values reported for the Valdés Peninsula (131.4 kg: Campagna *et al.*, 1992). It is also much higher than mean weight at weaning in three declining populations in the Indian Ocean (114.1–118.7 kg: Burton *et al.*, 1997).

Deterministic population dynamics

The population was almost steady, with a growth rate close to 0 (instantaneous rate of increase: $r = 0.0021$, net reproductive rate: $R_0 = 1.0181$). The calculation of elasticities demonstrated that a variation in survival entries of the projection matrix has a more pronounced effect on instantaneous growth rate than a proportional variation in fecundity entries.

To evaluate the effect of variation in age at maturity (α) on the dynamics of the SLI population, we calculated population growth indices increasing or decreasing age at maturity by 2 years from the base level. The variation had an exponential effect on net reproductive rate ($R_0 = 2.055 \; e^{-0.177 \, \alpha}$; $R^2 = 0.999$) and a steeper logarithmic effect on instantaneous rate of increase ($r = 0.117 - 0.0833 \ln \alpha$, $R^2 = 0.999$).

We examined the effect of four female life-table components on net reproductive rate: first year mortality, mortality of the three pre-breeding classes, adult mortality and fecundity. An increase in first year mortality produced a perfectly linear decline in net productivity rate (0.0170 variation in R_0 per 1% increase in mortality). An increase in mortality of the three pre-breeding classes again produced an almost linear decline in R_0 (linear fitting: $R^2 = 0.996$), but at a steeper rate than first year mortality (0.0352 decline in R_0 per 1% increase in mortality). Conversely, an increase in adult female mortality produced an exponential decline in net reproductive rate (exponential fitting: $R^2 = 0.992$), much steeper than the two previous linear processes, and with a rapid decrease in R_0 even for a small increase in mortality from the observed level ($R_0 = 1.053 \; e^{-5.334 \, \Delta q_x}$). Variation in fecundity had a small linear effect on net reproductive rate (0.0236 decrease in R_0 per 1% decrease in fecundity).
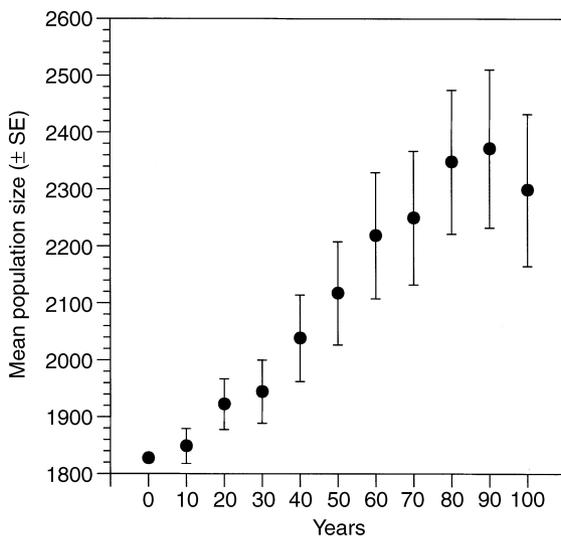
To confirm the relative role of survival and fecundity in determining population growth in our deterministic model, we calculated R_0 after systematically varying survival and fecundity in the ± 0.10 range in 0.01 steps. The surface fitted using distance-weighted least squares to the resulting R_0 values had a much lower slope on the fecundity axis than on the survival axis.

Population viability analysis

Environmental variability

The simulation with the initial EV values of mortality and fecundity rates produced no extinction in simulated populations, with a mean final population size of 2299 (± 2986) and a mean increase of 25.8% in 100 years (Fig. 1). Notwithstanding the increase in mean population size, the mean growth rate was slightly negative (r = –0.0042 (± 0.1245)). This was due to the non-symmetric distribution of the growth rates obtained in the simulations, with various strong negative outliers. EV alone was not enough to produce extinction, but greatly increased the variability of final population size (coefficient of variation (CV) = 129.9%).

To evaluate the effect of changes in EV, we ran several simulation series where age-specific standard deviation of each life-table value was changed by a variable amount (0–20%, in 1% steps). Firstly, we ran a series of simulations in which EV in mortality was changed, while maintaining the basal level for EV in fecundity. With large environmental variation, the probability of extinction (PE) had a large increase (from 0 with a 1% increase on base values to 0.996 with a 20% increase). The increment in probability of extinction with increase in EV of mortality had a sigmoid shape (logistic fitting, with asymptote at PE = 1: R^2 = 0.995; Fig. 2), initially increasing very slowly, and remaining under 10% for an increase up to 8%. Variation in EV of mortality greater than +12% led to extinction of a large proportion of populations. Mean final population size (FPS) decreased linearly with increase in EV (linear fitting: FPS = 2420 – 125.92 EV(q_x), R^2 = 0.969), at a rate of about 126 individuals per 1% increase of EV. Variability of final population size, expressed as the coefficient of variation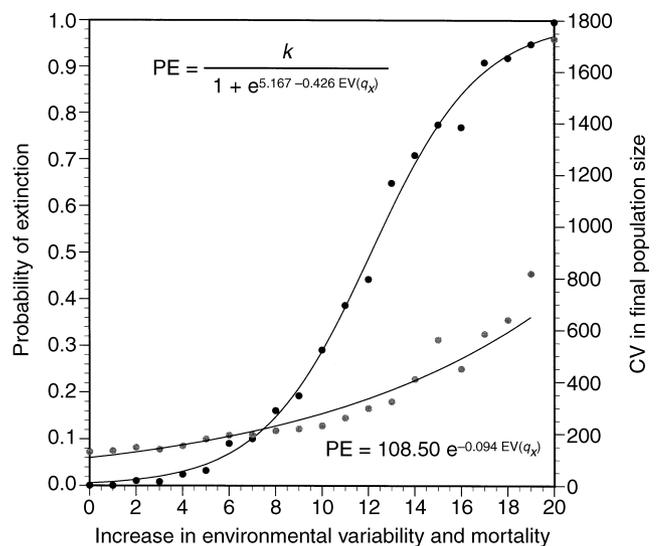, increased exponentially in the range 0–19%, and then more steeply to 20% (exponential fitting, 1–19%: R^2 = 0.949; Fig. 2).

We simulated variation from the initial standard deviation of fecundity by increasing variability from 1–20% in 1% steps. A very small likelihood of extinction resulted (0–0.008), with only a weak trend of increase with EV (linear fitting: PE = –0.0002 + 0.0002 EV(m_x); R^2 = 0.311). The variation in final size (CV = 120.1–153.5) was clearer, with about a 1% increase in CV with a 1% increase of standard deviation due to EV (linear fitting: CV(FPS) = 122.6 + 1.05 EV(m_x); R^2 = 0.591).

To evaluate the relative effect of EV in mortality and fecundity we first assumed that the same change in EV affected both mortality and fecundity. The increment in EV of both mortality and fecundity produced a sigmoid increase on the probability of extinction almost equal to the one obtained by a change in EV of mortality alone (logistic fitting: PE = $1/(1+ e^{5.143 - 0.432\ EV})$, R^2 = 0.992), with an increase in the curve's slope of about 1.4%. The variability of the final size for all populations (extant plus extinct) increased in a geometric fashion with increasing EV (geometric fitting: CV(FPS) = 128.01 EV$^{0.0326\ EV}$; R^2 = 0.968). Variability in the size of extant populations not only had, as expected, much lower CV values, but was also best fitted by a rational function with a maximum at about a 13% increase in EV, and then a stepped decrease corresponding to PE > 0.70 (rational function fitting: CV(FPS) = (134.59 – 6.33 EV)/(1 – 0.0860 EV + 0.00 21 EV^2); R^2 = 0.929). The final size of the population (including all populations, extant and extinct) ranged from 2158 with a 1% increase in EV to 143 with a 19% increase and 0 with a 20% (Fig. 3). The final size of the extant populations ranged from 2158 with a 1% increase (PE = 0), to 2160 with a 2% (PE > 0), to 876 with a 19% increase (PE < 1), and to 0 with a 20% (PE = 1).

Fig. 1. Mean population size (± standard error) at 10 year intervals resulting from a simulation of the basic model, with environmental variability values derived from the literature.
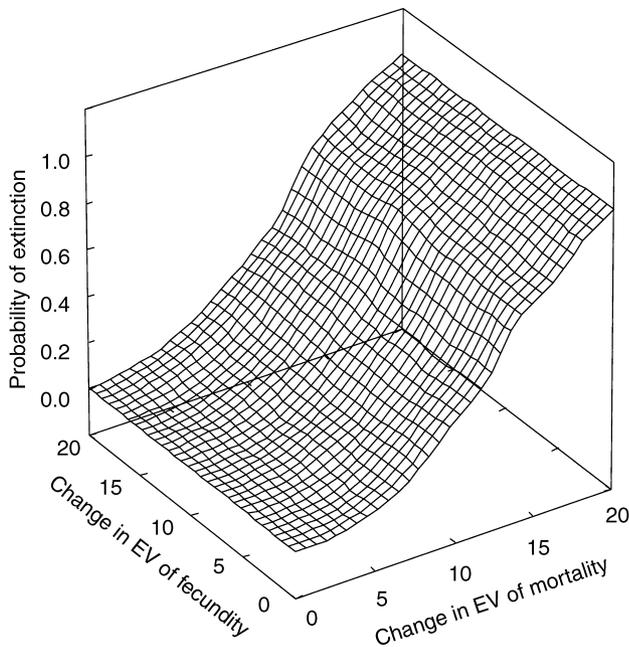

Fig. 2. Effect of increase in environmental variability of mortality on probability of extinction (sigmoid fitting) and variability of final population size after 100 years, expressed as coefficient of variation (exponential fitting).

Fig. 3. Effect of independent variation of environmental variability of mortality and fecundity on probability of extinction (surface fitted to the PE values on EV grid values by distance-weighted least squares).

We then relaxed the assumption, and repeated the simulation by independent variation of $EV(q_x)$ and $EV(m_x)$. These simulations confirmed that the probability of extinction depends almost entirely upon the change in $EV(q_x)$ and that the effect of $EV(m_x)$ is marginal. We fitted a surface to the scatterplot of PE versus $EV(q_x)$ and $EV(m_x)$ using distance-weighted least squares. We obtained a surface in which slope is almost completely determined by change in $EV(q_x)$, while change in $EV(m_x)$ produced only small perturbations of the surface (Fig. 3).

Inbreeding

In a model run without EV in age-specific mortality and fecundity schedules, extinction risk due to inbreeding alone was null (mean population size after 100 years = 2101 ($\pm$ 296); mean growth rate $r = 0.0013$ ($\pm$ 0.0116)), and variability in final population size was small (CV = 14.1%).

To evaluate interaction between EV and inbreeding, we modelled a population with basic or increased variability and various inbreeding levels, using 0.5–5 lethal equivalents in 0.5 steps. In the model with basic EVs, inbreeding had a modest effect on population growth, with a very low increase of extinction likelihood (from 0 to 0.002–0.006 depending on the number of lethal equivalents, with no definite trend). In models with EV of mortality augmented by 5–10–15 %, the probability of survival was affected almost only by EV and the inbreeding effect was small. For all three EV variation classes there was an almost linear increase in the prob-

ability of extinction with an increasing number of lethal equivalents, but the increase was modest and more than one order of magnitude lower than the increase produced by the increase in EV (slope of the linear model, EV + 5%: $b = 0.016$; + 10%: $b = 0.016$; + 15%: $b = 0.021$).

Catastrophes

We explored the effect of catastrophes by introducing in the base model a variable number of catastrophes (probability 1–5%, i.e. a mean of 1–5/100 years) with severity on survival and fecundity ranging from 0 (= 100% reduction in survival and/or reproduction) to 1 (no reduction). We first ran a series of simulations with equal severity for survival and reproduction (0–1 in 0.05 steps). The probability of extinction increased with increasing severity of the catastrophe, but the shape of the trend was quite different among simulations with a different probability of catastrophe. Simulations with 100% failure produced an exceptionally high mean probability of extinction, regardless of the probability of catastrophe. For 1% probability (a mean of 1 catastrophe/100 years) the extinction probability was low for severity in the range usually observed in pinnipeds, rising above 20% only when the catastrophe produced a 90% reduction in survival and reproduction. The variation of probability of extinction was best fitted by a family of logistic curves (logistic fitting: $R^2 = 0.996$–0.997). A common aspect of all curves was the behaviour of the 100% failure point, which represented a clear outlier in all cases. A 30% failure in fecundity and survival (the low extreme of the usual range for pinnipeds) increased the probability of extinction from 0 at 1% probability of catastrophe to 0.054 at 5%. At 70% failure the increase was from 0.062 to 0.722. The main increase in PE considering all catastrophe probabilities was in the 30–70% range. A series of simulations with independent variation of severity of survival and severity of reproduction showed that the impact on survival was much more important. The slope of the PE surface was almost completely determined by increased mortality, while a reduction in fecundity produced only marginal perturbations of the surface.

DISCUSSION

Population viability analysis techniques are rarely applied to pinniped species, due to the large population size typical of most species. They are, however, very appropriate for small and isolated populations, whose dynamics may strongly depend on stochastic factors (*Monachus schauinslandi*: Lombard, 1996; *Phoca vitulina*: Bjoerge, Steen & Stenseth, 1994; *Phoca hispida*: Kokko *et al.*, 1998). Our analysis showed that the SLI population of elephant seals appears to be in good shape, with no obvious indication of a decrease in abundance or immediate risk of extinction. However, this evidence should be considered with caution, because small variations in mortality and abundance are difficult to detect over short periods in small populations

(Forcada, 2000). Changes in environmental variability could greatly affect the likelihood of extinction of the SLI elephant seal population, due to its current small size. Modest variation of demographic parameters due to environmental fluctuations may lead to a reduction in population size, and an increase above 10% of environmental variability in life-table parameters significantly increases the risk of extinction.

Both the deterministic and the stochastic models revealed that some aspects of the life-table are more important than others. Environmental variability in mortality, in particular of adult mortality, had a much higher impact on the likelihood of extinction than did variability in fecundity. On the contrary, inbreeding seems to have a modest effect on SLI population viability. In northern elephant seals (*M. angustirostris*), a very high level of inbreeding that led to exceptionally low heterozygosity (Hoelzel *et al.*, 1993) had no effect on the population viability, which increased at a sustained rate (Stewart *et al.*, 1994). This result was not completely unexpected because, except in very small populations, demographic parameters and environmental stochasticity should have a bigger effect on likelihood of extinction than genetic population structure (Boyce, 1992).

Catastrophic events may have a significant impact on pinniped population dynamics. Mass mortality and exceptional reduction in productivity are associated with: epidemics due to viral diseases or parasites (e.g. morbillivirus: Kennedy, 1998); climatic changes due to the El Niño Southern Oscillation (ENSO) phenomena (Trillmich & Ono, 1991); oil spills (Loughlin, Ballachey & Wright, 1996); poisoning due to biological toxins (diatom bloom: Scholin *et al.*, 2000) or chemical compounds (Vidal & Gallo-Reynoso, 1996). The recorded effects of catastrophic events on mortality and fecundity of pinniped species are quite variable, both in quality and quantity. ENSO is a typical catastrophic event that affected various species of pinnipeds in the recent past, producing an increase in pre-weaning mortality (*Arctocephalus pusillus*, 95%: Roux, 1998), increase of sex and age specific mortality (*A. galapagoensis*, from 30% for adult females to 100% for territorial males: Trillmich & Limberger, 1985), reduction of productivity during the following breeding season (*M. angustirostris*: Huber *et al.*, 1991), and a drop in size of whole populations (*M. leonina*: Vergani & Stanganelli, 1980). Such severe effects are not limited to ENSO phenomena, and are common also in other catastrophic situations (e.g. oil spills, *Callorhinus ursinus*: Reed *et al.*, 1989). A careful evaluation of the environmental impact of the current rapid changes in the Falklands economy should also consider the potential effect of catastrophic events on the SLI elephant seals.

The most relevant operational conclusion that may be derived from our simulations is that not enough actual data are available. Any model or simulation is as good as its parameters are reliable, and many aspects of the life history and demography of SLI elephant seals are still poorly known. Southern elephant seals are not an endangered species, and the Falklands represent a very small, almost marginal, fraction of the South Georgia stock, which comprises about 397 000 individuals (Laws, 1994). However, the loss of the Falklands population should not be considered of secondary importance, not only for the reduction in local biodiversity, but also in relation to its possible role as a gene flow conduit between the South Georgia and the Valdés Peninsula populations (Hoelzel *et al.*, 1993). The potential increase in threats to population survival, due to the recent changes in lifestyle and economy of the Falklands (e.g. offshore oil exploration), makes the collection of more data on demography, life-history and feeding strategies a necessity.

From this conclusion, we derived three main operational suggestions. Firstly, more accurate age-specific schedules of mortality and fecundity are urgently needed. Adult females' mortality and fecundity may be effectively modelled as being constant, but detailed information on each age class are needed up to at least age 6. Therefore, the mark–recapture study should be continued in order to monitor some female cohorts for at least six consecutive breeding seasons. This will also allow the estimates of EV in adult mortality to be improved, the most important determinant of extinction risk. Secondly, the information collected on SLI should be complemented by a global assessment of the breeding status of the SES in the entire Falklands archipelago. This will allow modelling of the whole Falklands population as one meta-population, where most fragments may be near extinction. Lastly, long distance movement patterns should be urgently studied. Environmental variability of demographic parameters is ultimately related to food availability. Tracking seals at sea will permit the identification of foraging areas, which are at the moment completely unknown, a first necessary step towards the understanding of feeding strategies of the population.

Acknowledgements

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