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# Population viability of southern elephant seals of the Falkland Islands

Results and prospects

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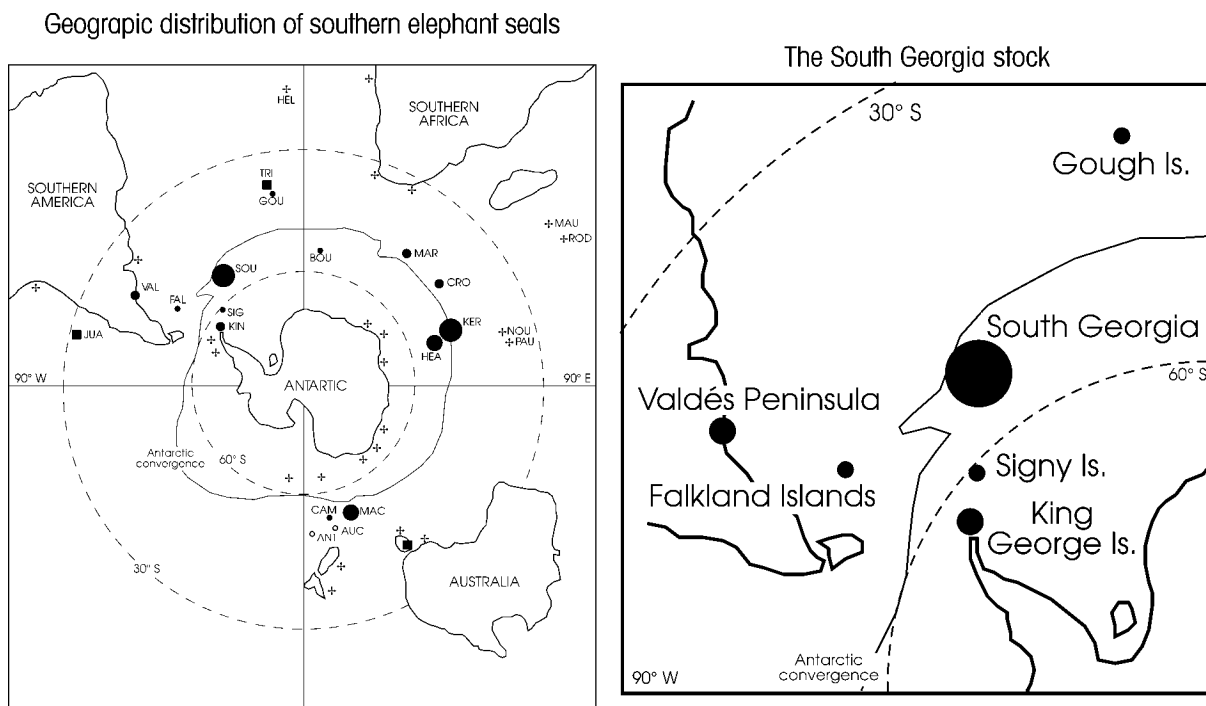
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## Introduction

The status of southern elephant seals (SES hereafter) of the Falkland Islands is uncertain. While most populations of the circum-antarctic distribution of SES (Figure 1; Table 1) were studied in detail for long periods of time (Laws, 1994), information about breeding of SES in the Falklands were lacking until very recently.

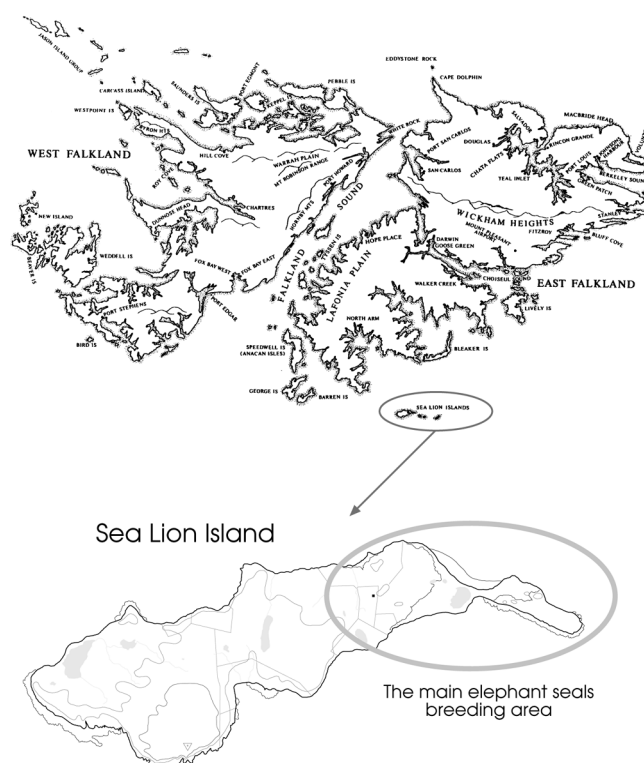


**Figure 1** - Left: world distribution of southern elephant seals. Right: the South Georgia stock

| Population       | Lat.      | Long.      | Dist. | Size   | Source                       |
|------------------|-----------|------------|-------|--------|------------------------------|
| Sea Lion Island  | 52° 26' S | 59° 05' W  |       | 1800   | Galimberti and Boitani, 1999 |
| Valdés Peninsula | 42°-43° S | 63°- 64° W | 1152  | 36400  | Falabella et al., 1993       |
| King George Is.  | 62° 16' S | 58° 37' W  | 1115  | 1960   | Laws, 1994                   |
| Nelson Island    | 62° 18' S | 59° 11' W  | 1114  | 370    | Vergani et al., 1987         |
| Signy Island     | 60° 43' S | 45° 36' W  | 1243  | 20     | Laws, 1994                   |
| South Georgia    | 54° 19' S | 36° 25' W  | 1553  | 357000 | McCann, 1985                 |
| Gough Island     | 40° 20' S | 9° 54' W   | 4006  | 105    | Bester, 1980                 |

**Table 1** - Position and size of populations of the South Georgia stock. Dist. = geodesic distance from Sea Lion Island, calculated with reference to IERS-92 ellipsoid ( distance of Valdés Peninsula was calculated using the coordinates for Punta Delgada, 42° 46' S 63° 38' W, the main breeding site of SES in the Peninsula).

In 1995 we begun a research project on behaviour and ecology of elephant seals of Sea Lion Island (Galimberti & Sanvito, 2000 a), a small island in the south of the Falklands (SLI hereafter, Figure 2).



**Figure 2** - Map of the Falkland Islands and of Sea Lion Island

In the past, elephant seals were probably quite common in the Falklands, although actual estimates of the size of the population are not available. They were severely exploited for oil from the end of 17th century, along with exploitation for skins of southern sea lions and fur seals. By 1871 the species disappeared from the island, to start reappearing as individual vagrants at the beginning of the 1900s (Strange, 1992). A survey carried out in the sixties reported a production of about one thousand pups, and more recently a guess-stimate of five thousands was suggested (Strange, 1992). This approximate estimate is somehow at variance with the results of a recent survey of the Falklands costs, during which very scarce signs of seals breeding were observed apart from SLI (Mike Bingham, pers. comm.). From our personal observations, and from the anecdotal information we were able to collect during the past five years, we concluded that Sea Lion Island is the only established and consistent breeding site of elephant seals in the Falklands, and that in the rest of the islands only few adult females breed, isolated or in small groups, with a very low net productivity (e.g., Elephant Point, Sounders Island: Poole-Evans, pers. com.). In absence of a proper census of seals on the whole cost of the Falklands, it is hence wise to consider the local population of Sea Lion Islands as equivalent to the whole population of the Falklands (Galimberti & Boitani, 1999).

The SES population of Sea Lion Island is small, with a net productivity during the 1999 breeding season of 513 pups survived to weaning (Galimberti & Sanvito, 2000 b), and

localized, with no other breeding site close to the island. The population is part of the South Georgia stock (Laws, 1994), but it's almost isolated from the other populations, and in particular from the big population of South Georgia, on the south, and from the midium-sized population of the Valdés Peninsula, on the north (Lewis et al., 1996). Our observations confirmed the isolation: during daily counts of the whole population during the 1995-1999 breeding seasons no marked immigrant was resighted on Sea Lion Island (while, on the contrary, there are frequent movements of marked males from/to the Valdés during the molt, unpublished data and Mirtha Lewis, pers. comm.).

Small and isolated populations present specific problems for conservation for three main reasons:

- inter-annual variation in environmental quality may produce enough variance in demographic parameters to outpace their homeostatic capabilities (Berger, 1990)
- they are prone to extinction due to catastrophic events that may produce non-recoverable reduction in number (Miller & Lacey, 1999)
- their viability may be severely reduced due to inbreeding depression (Lacy, 1997)

Moreover, they present also specific methodological problems, because in small populations it's difficult to promptly detect decline in abundance and survival rate, due to the intrinsic low power of analysis of small samples (Forcada, 2000).

Elephant seals of SLI are not only an important component of the biodiversity of the Falklands, but are also a notable economic asset, via nature-oriented tourism (D. Gray, pers. comm.). A full understanding of the dynamics of the population, and an accurate forecast of its likely future status, will be valuable from both a scientific and practical point of view: unfortunately, notwithstanding the significant amount of data collected by us during the past five years of field work on Sea Lion Island, we are yet far from having enough information to achieve these goals. When complete data is not available, computer simulations may help in building alternative scenarios, that may offer valuable insights on the dynamics of the population, and suggest the areas where the collection of additional data is more compelling (Miller & Lacy, 1999). Therefore, the targets of this report are:

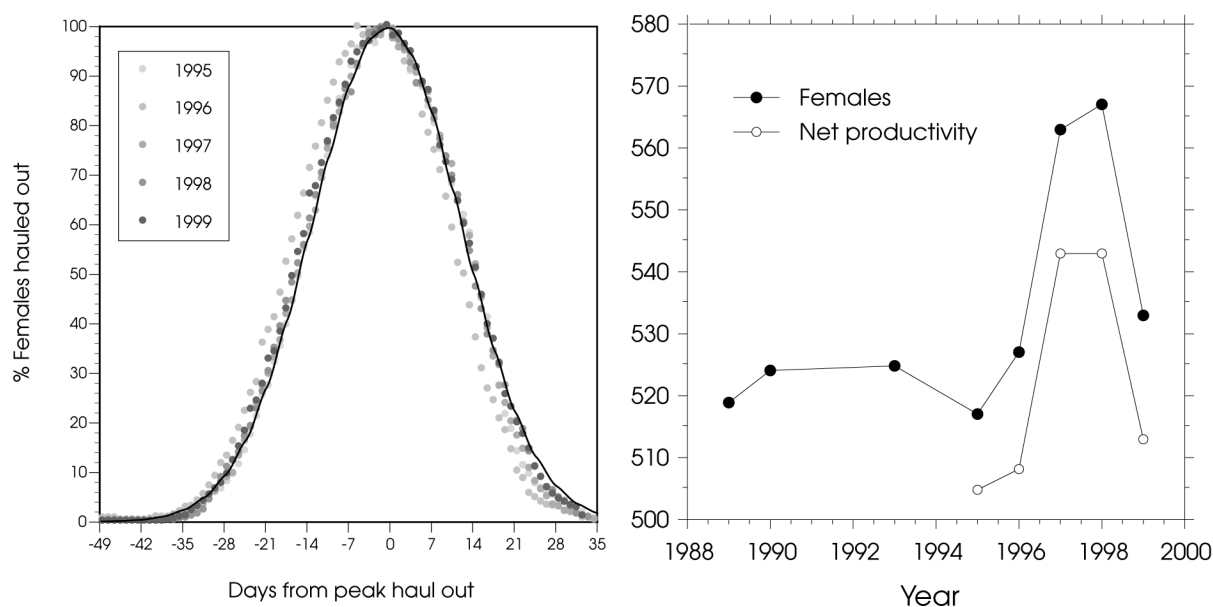
- to summarize data about the current status of Sea Lion Island population
- to build an age-structured model of the population, using the available information collected on Sea Lion Island, along with reasonable values for parameters non directly estimable from data, taken from the literature
- to carry out a population viability analysis, by simulation of stochastic and catastrophic variation in mortality and fecundity
- to recognize the areas where collection of additional data is more compelling

## Current status of the population

### *Variation in size of the population*

The population was almost steady in size during the past five years, with a mean number of breeding females of 522, equivalent to a population of 1827 individuals one year old or older (total population size = 3.5 times the number of breeding females: McCann, 1985). Scanty information was available for the period before 1995, but some counts were kindly provided by local people (David Gray, pers. comm.). These counts were made irregularly and not always close to the day of peak haulout of females, but, using a mathematical model of the haulout process, that works very well for SLI (Galimberti & Boitani, 1999; Figure 3 a), we corrected these counts to get estimates of size of the total female population. The resulting information (Figure 3 b), combined with the more accurate data available from 1995, demonstrate that the size of the population remained almost steady from 1989 to 1996 (slope of the trend 0.317 females per year); there was an increase in size of 6.95 % between 1996 and 1997, which was

maintained in 1998, but almost completely lost in 1999, when the number of females came down to the level of 1996 (and the net productivity to the level of 1995, due the slightly higher mortality). In all, the mean population increase in the period 1989-1999 was almost null (slope of the trend 0.958 females per year).



**Figure 3** - Left: Number of females hauled out during the breeding season in five consecutive years, fitted with a common gaussian model (day of the season expressed as  $\pm$  days from the day of peak haulout, 19-20 October in different years). Right: Number of breeding females (counts corrected using the gaussian model of haulout) and net productivity (estimated from records of marked pups).

### *Pup mortality*

In elephant seals, mortality of pups is related to density of the population and crowding of harems: this phenomenon is particularly evident in the northern species (Le Boeuf & Briggs, 1977), but also in the main breeding colonies of the southern (Macquarie Island: Carrick and Ingham, 1960; South Georgia: McCann, 1982). On the contrary, populations with low density of females and small harems have low preweaning mortality of pups (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 range typical for the species (see also Galimberti & Boitani, 1999). There was an increase in mortality in 1998 and 1999, but was related to a combination of bad weather and rough sea, and not to any variation in density of females. The relationship between pup mortality and density is mediated by behavioural phenomena: in crowded harems the likelihood of lose of contact between mothers and pups is higher, abandonment happens more frequently, and death from crushing/trampling by interacting males is more likely (Riedman & Le Boeuf, 1982). On SLI the abundant breeding space maintained harem size on the bottom end of range typical for the species (median harem size = 30-35 females), and the density of females was quite low (111 females per km of the coastline suitable for breeding) if compared to densities recorded in other sub-Antarctic populations (Galimberti & Boitani, 1999).

### *Parental investment and resource availability*

The mean weight at weaning is a good index of the capability of breeding females to invest in their pups, which should be related to the quality and quantity of resources they have available: hence, weight at weaning is an approximate measure of habitat quality for elephant seals (Burton et al., 1997). On SLI, mean weight at weaning ranged from 130.6 to 136.3 kg (Galimberti & Boitani, 1999; unpublished data), and hence is on the high side of the range of SES populations. In particular, it's higher than the one reported for South Georgia (Burton et al., 1997), which is a steady population (Boyd et al., 1996), and in line with values reported for the Valdés Peninsula (Campagna et al., 1992), which shelter an increasing population (Campagna & Lewis, 1992). It's also much higher than mean weight at weaning in three declining populations of the Indian Ocean, the small one of Marion Island, and the large ones of Heard Island and Macquarie Island (Burton et al., 1997).

In all, the SLI population of elephant seals appears to be in good shape, with no pressing indication of decrease in abundance or immediate risk of extinction, but evidences collected in the short term should be considered with suspicion, because small magnitude increase in mortality and decrease in abundance are difficult to be detected in due time in small population (Forcada, 2000). Moreover, the availability of breeding space, the high productivity and low mortality of pups, and the good availability of resources indicated by weanlings weight, are somehow at variance with the current lack of increase in the population: some undetected factor should limit the net reproductive rate. Therefore, more information about population dynamics is obviously needed.

### **Age-structured model of the population**

The modeling of populations of large mammals with overlapping generations, age-specific variation of mortality and fecundity, and complex mating systems requires the specification of many different parameters to be realistic. We put together information from two sources, a mark-recapture experiment started on SLI in 1995 (details in Galimberti & Boitani, 1999 and Galimberti & Sanvito, 2000 a), and the literature, in particular regarding the South Georgia population, which is the only population of the South Georgia stock for which a complete, sex-specific, life table is available (McCann, 1985); this population is also almost steady (Boyd et al., 1996), like SLI.

#### *Breeding age*

We fixed female breeding age ( $\alpha$ ) at 4, because 3 years old females represent a very small proportion of the breeding population, while 4 years old females of the 1995 cohort were quite common between the breeders in 1999 (Galimberti & Sanvito, 2000 b). In SES age of first breeding is variable in SES, ranging from 2 to 7 years; populations of the South Georgia stock have earlier breeding than populations of the Macquarie Island Stock, but there's variation even among cohorts of the same population (Hindell, 1991) We fixed male breeding age at 7 because, although males are mature from a physiological point of view at 4-5 years of age, the first class of subadults well represented among breeding males on SLI is SAM2 (= 7 years old: Galimberti & Boitani, 1999). We fixed maximum breeding age at 21, which is the estimate for South Georgia population (Arnbom et al., 1992), although some older marked females were observed breeding on Macquarie Island (Hindell & Little, 1988).

### *Survival*

Mortality ( $q_x$ ) of pre-breeding classes was calculated from the life table proposed for South Georgia by McCann (1985), both for males and for females. The main characteristics of this life table are the equal mortality during the first two years of life for both males and females (40% during the first year and 15% during the second), and higher mortality for males from age 2. Mortality rates of adults was calculated from mark-recapture data, and fixed at 16% for females and 29% for males (unpublished data). Survival during the first year of life is a crucial parameter of elephant seals life-history (Hindell, 1991). Hence, we checked values of South Georgia life tables against our estimate. Although we are tagging all pups born every year on Sea Lion Island, our resighting effort is concentrated during the breeding season: therefore, resighting is adequate to track adult individuals, but not young ones, which haul out almost all year round, with a peak in mid-December (Hindell & Burton, 1988). We, hence, calculated a provisional estimate of first year survival by counting survivors in November, and then applying a correction factor calculated from the proportion of one year old individuals expected to be hauled out in November (McMahon et al., 1999: Figure 3). This estimate was in accordance with the 40% mortality for both sexes calculated for South Georgia.

### *Fecundity*

Maximum litter size was set at 1, twin births are very rare (6 during 5 breeding seasons on Sea Lion Island; see also McCann, 1985). Fecundity ( $m_x$ ) for adult females hauled out is close to 100% (94.7 to 98.2% in different years), but some females skip breeding every year (see also Huber, 1987). We estimated the total number of adult females alive by summing breeding females hauled out during the breeding season, adult females hauled out in the rest of the year, and adult females known to be alive because resighted in next seasons. The mean proportion of adult females actually giving birth was hence estimated at 88% (unpublished data), in accordance to the estimate for South Georgia (McCann, 1985). No senescence effects are evident in elephant seals (Le Boeuf & Laws, 1994; McCann, 1985), hence fecundity was modeled as constant from age 4 to death. Sex ratio at birth was fixed a 0.51, the mean value of the observed sex ratio of five years, 1995 to 1999 (unpublished data).

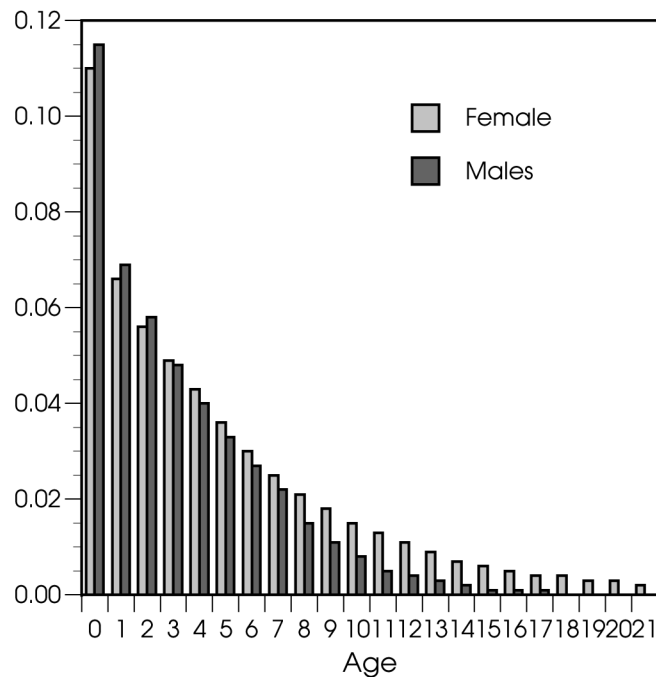
### *Mating system*

The mating system of elephant seals is strongly polygynous and based on harem defense (Le Boeuf & Laws, 1994); on SLI the sociometric sex ratio (= females per harem holder) ranged from 41.0 to 47.9 in different years. Hence, the population was modeled as polygynous, with 28% of males in the breeding pool, calculated as the mean proportion of males observed as resident breeders on the estimated size of male population.

## **Deterministic population dynamics**

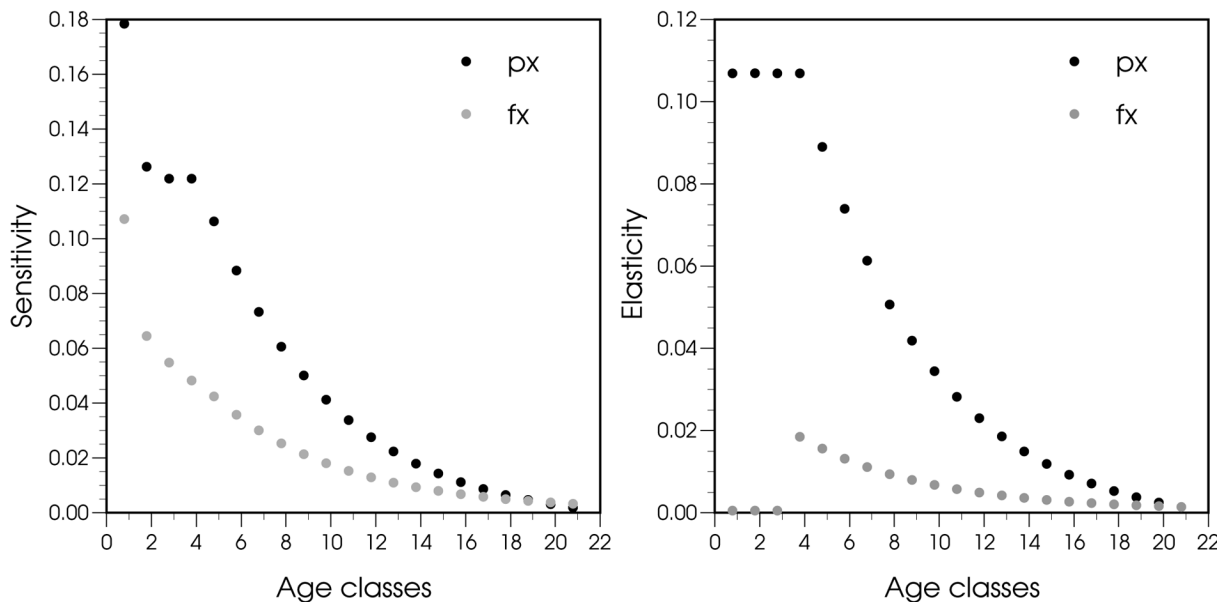
Before modeling the effect of stochastic variation, we examined the deterministic fate of the population with standard life table analysis techniques, that completely exclude the effect of stochastic factors, and assume demographic prevalence of females, no limitation of mates, no density dependence, and no inbreeding depression (Caswell, 1989). In the deterministic domain, the population was almost steady, with a growth rate close to 0 (instantaneous rate of increase:  $r = 0.0021$ , rate of growth per time unit:  $\lambda = 1.0021$ , net reproductive rate:  $R_0 = 1.0181$ , mean generation time:  $T_c = 8.43$  years), with the stable age distribution for females and males shown in Figure 4.





**Figure 4** - Stable age distribution for males and females

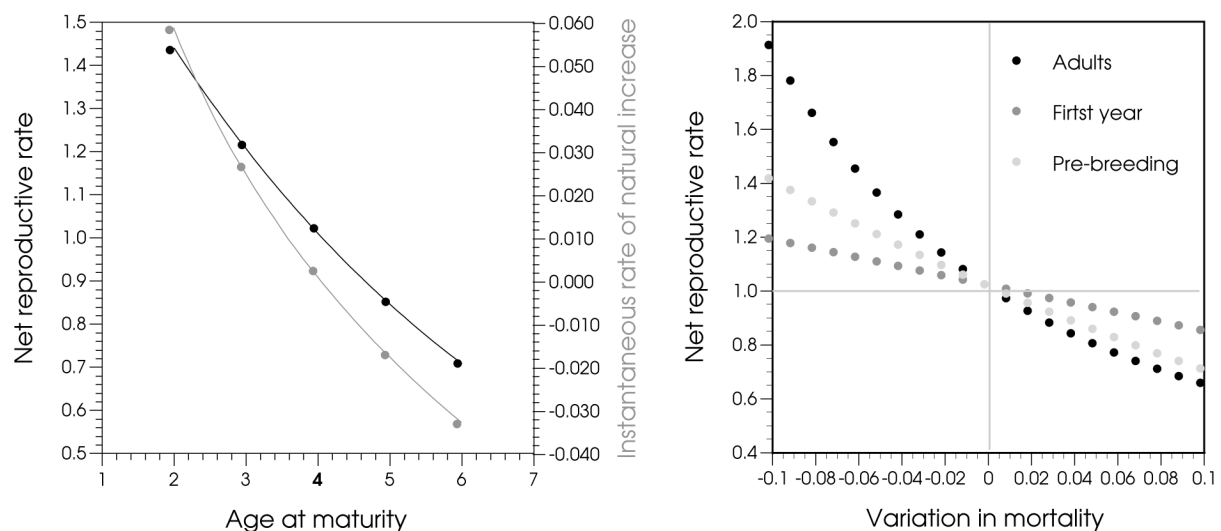
To evaluate the age-specific effects of mortality and fecundity parameters on population growth, we calculated sensitivities, i.e., the changes in  $\lambda$  (rate of growth per time unit) due to changes in age-specific mortality and fecundity.



**Figure 5** - Left: Sensitivity of growth rate to variation in age-specific mortality and fecundity. Right: Elasticity of growth rate to variation in age-specific mortality and fecundity.

Sensitivities are equivalent to the selection gradients on the entries of the age-specific survival and fecundity schedule (van Groenendael et al., 1988). Sensitivities were calculated from the left and right dominant eigenvectors of the Leslie matrix corresponding to the life table (Caswell, 1989). Sensitivities of survival rates were, as expected, higher in the first age classes, were almost homogeneous for pre-breeding classes, and decreased exponentially for adult ones. Sensitivity of effective fecundity had a similar exponential decrease, but at a slower rate and without homogeneity among pre-breeding classes (Figure 5/a). Direct comparisons of sensitivities between survival and fecundity is not possible because they are measured on different scales, although this effect is small in species where fecundity is low, like in elephant seals. Therefore, we standardized sensitivities and obtained elasticities, i.e., the proportional change in  $\lambda$  resulting from a proportional change in the corresponding entry of the projection matrix (de Kroon et al., 1986). 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 (Figure 5/b)

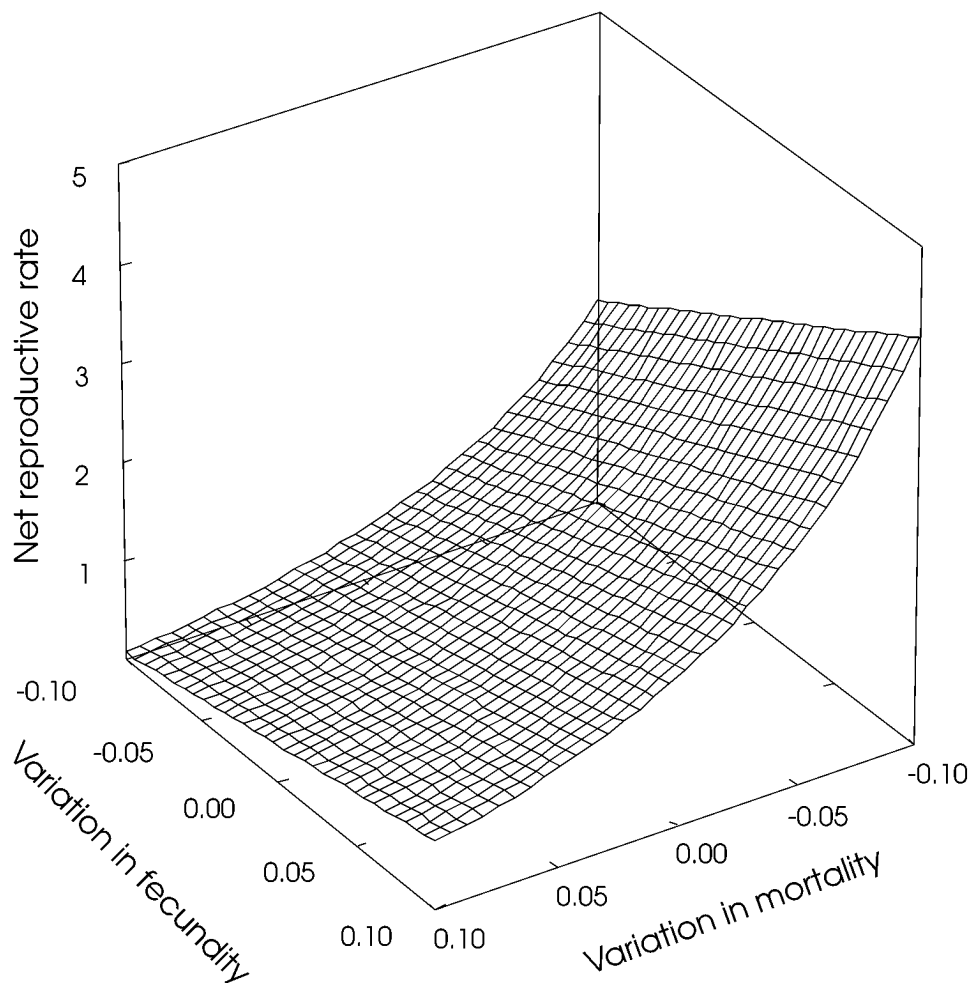
Age at maturity (i.e., the age at which the mean female give birth the first time,  $\alpha$ ) is a fundamental parameter of demographic processes. To evaluate the effect of variation in age at maturity on the dynamics of SLI population, we calculated growth indices increasing or decreasing age at maturity by 2 years from the base level. The variation had an exponential effect of net reproductive rate ( $R_0 = 2.055 e^{-0.177 \alpha}$ ;  $R^2 = 0.999$ ) and a steeper logarithmic effect of instantaneous rate of increase ( $r = 0.117 - 0.0833 \ln \alpha$ ,  $R^2 = 0.999$ ; Figure 6/a).



**Figure 6** - Left (a): Effect of variation in age at maturity on net reproductive rate (black; exponential fitting) and instantaneous rate of increase (grey; logarithmic fitting). Right (b): Effect of variation of mortality of different age groups on net reproductive rate.

We then examined in particular detail the effect of four component of the life table of net reproductive rate: mortality during the first year, mortality of the three pre-breeding classes, mortality of adults, and fecundity. Variation of mortality during the first year of birth produced a perfectly linear variation of in net productivity rate (0.0170 variation in  $R_0$  per 1% variation in mortality; Figure 6/b). Variation in mortality of the three pre-breeding classes produced an almost linear variation in  $R_0$  (linear fitting:  $R^2 = 0.996$ ), but at a steeper rate than first year mortality (0.0352 variation in  $R_0$  per 1% variation in mortality; Figure 6/b).

On the contrary, variation of adult female mortality produced an exponential variation 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 ( $R_0 = 1.053 e^{-5.334 \Delta q_x}$ ; Figure 6/b). Variation in fecundity had a small linear effect on net reproductive rate (0.0236 variation in  $R_0$  per 1% variation in fecundity).



**Figure 7** - Effect of independent variation of age-specific mortality and age-specific fecundity on net reproductive rate (surface was fitted using distance weighted last squares).

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  $\pm 0.10$  range at 0.01 steps. The surface fitted using distance weighted last squares (Wilkinson et al., 1992) to the resulting  $R_0$  values had a much lower slope on the fecundity axis than on the survival axis (Figure 7). This difference was evident also when perturbing values of adult classes only, instead of for the whole schedule.

## Population viability analysis

### *Simulation*

Population viability analysis is the application of techniques to estimate risk of extinction of populations and species, and related quantities, like variability in population size (Miller & Lacy, 1999). PVA is rarely applied to pinniped species, due to the large population size typical of most species, but it's very appropriate for small and isolated populations, which dynamics may strongly depend on stochastic factors (*Monachus*: Lombard, 1996; Seals, 1994; *Phoca vitulina*: Bjoerge, 1994). In principle, when demographic parameters and life tables are fully known, it is possible to develop analytical models of population growth and extinction processes. In real world, this rarely happens, because the knowledge of parameters is usually incomplete, and the importance of stochastic factors render analytical model intractable. When this is the case, the only way to proceed is to resort to computer simulations to project in the future a large set of populations with different initial parameters, and look at their destiny (Miller & Lacy, 1999). Even simple PVA models, build with a modest prior knowledge of population parameters, may highlight interesting trends, and point to the areas where the collection of new information is more compelling (Hamilton & Moller, 1995).

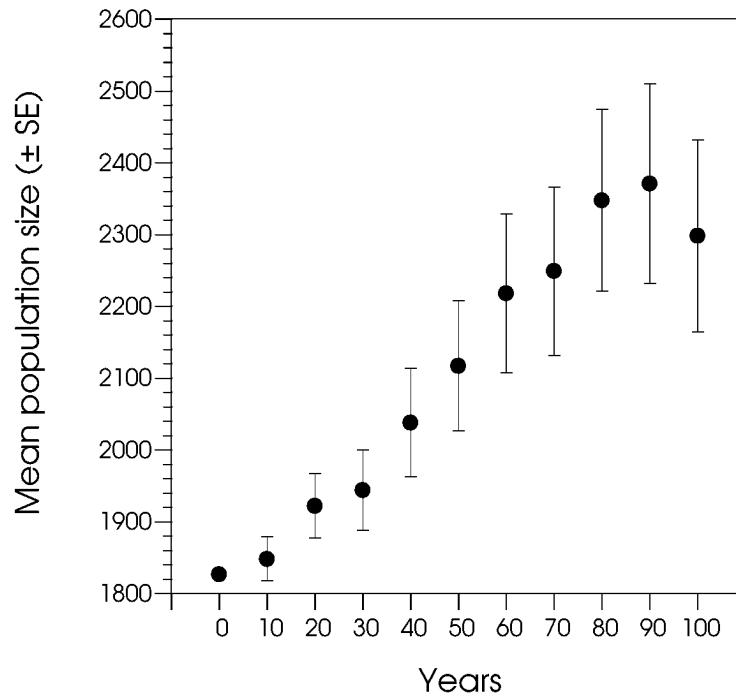
We ran simulations using VORTEX (version 8.32; Miller & Lacy, 1999; batch files used to run simulations are available upon request), a software for population viability analysis that permits the modeling of inbreeding, stochastic variance of population parameters and catastrophes, i.e. stochastic variation of age/fecundity schedules due to unpredictable environmental phenomena. We started with a population of 1827 individuals, our best estimate of population size in 1999. We ran simulations by replicating each population model 500 times to get accurate results (Miller & Lacy, 1999), and projecting each populations for 100 years, assuming an initial stable age distribution defined by the mortality and fecundity schedule of the deterministic model. We assumed absence of density dependence due to the very low density of the population and we fixed carrying capacity at ten times the current population size (with no trend in carrying capacity). Population model were ran in absence of management interventions (no harvesting and no supplementing). We present statistics as mean  $\pm$  standard deviations. To help interpretation of simulation results, we fitted linear and non-linear models to simulation statistics; although we preferred functional models (e.g., logistic models instead of polynomial ones) our choice was dictated only by an operational reason, i.e., to achieve a compact description of data, and no functional dependence of parameters was implied. We checked the validity of fitting by visual examination residual plots and test of normality of residuals.

### *Environmental variability*

Environmental variability (EV) of survival and fecundity parameters is difficult to estimate, because of the number of yearly values for component of the schedule needed to obtain accurate estimation (Miller & Lacy, 1999). We modeled the effects of environmental variability starting with standard deviation values in age-specific mortality calculated from life tables presented in Pistorius et al. (1999) for the Marion Island population. An important aspect of these tables, obtained in a accurate long-term mark-recapture study, is that inter-annual variability of demographic parameters is higher for males than for females, at least for all pre-breeding age classes, as expected from general patterns of life-history of elephant seals (Clinton & Le Boeuf, 1993). Environmental variation in mortality and fecundity were modeled as correlated, i.e., we assumed that environmental factors having a negative effect on survival also negatively affect reproduction. Environmental variability may be confounded by intrinsic demographic stochasticity due to sampling bias, but this should an important component of variability only in very small populations (Miller & Lacy, 1999), hence we ignored it.

The simulation with the initial values of EV of mortality and fecundity rates produced no

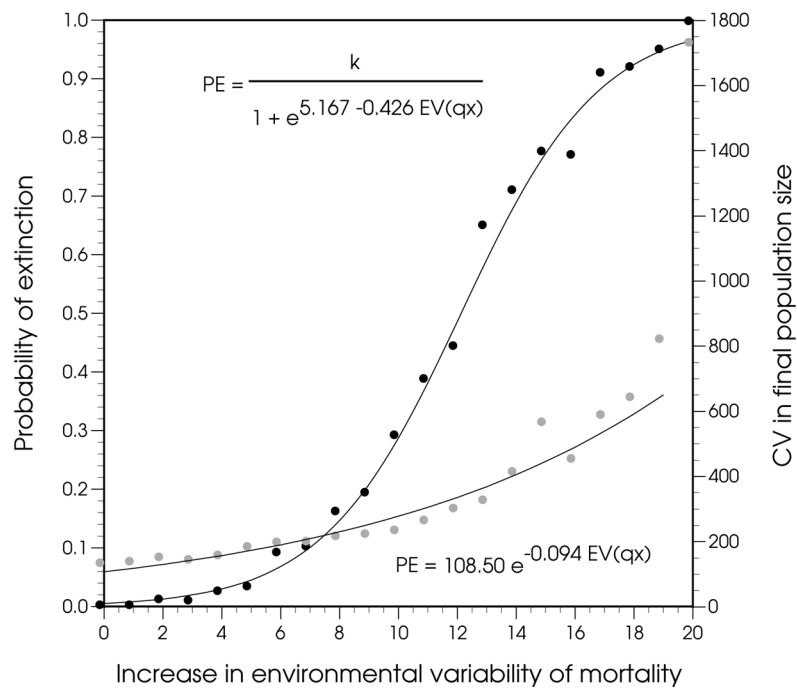
extinction in 500 simulated populations, with a mean final size of  $2299 \pm 2986$  (Figure 8) and a mean growth rate close to zero ( $r = -0.0042 \pm 0.1245$ ). Environmental variability alone in this case was not enough to produce extinction, but greatly increased the variability in final population size ( $CV = 129.9\%$ ). To evaluate the effect of changes in environmental variability, we ran various series of simulations in which age-specific standard deviation of each value of the life table was changed by a variable amount (in the range 1-20 %).



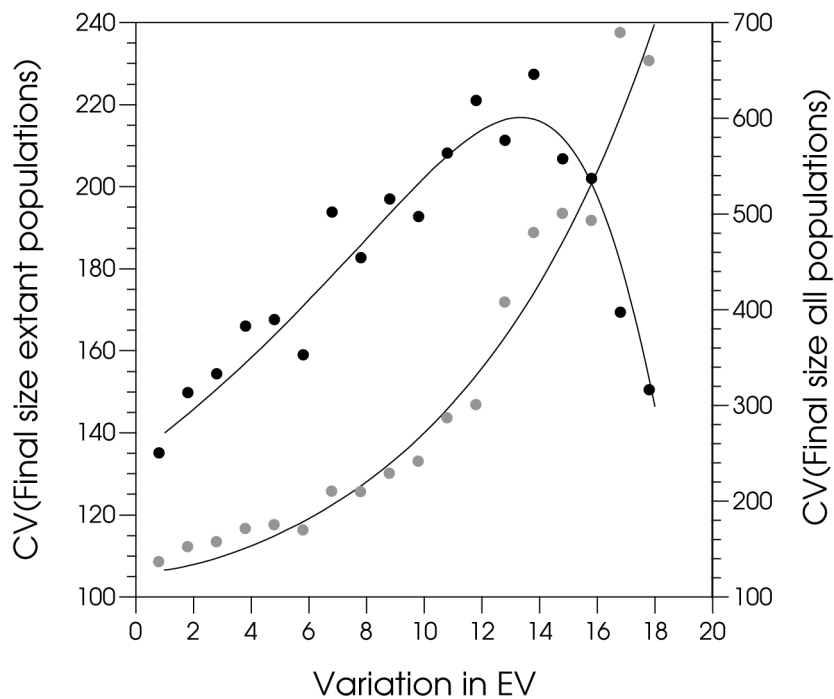
**Figure 8** - Mean population size of simulations of the base model, with environmental variability values derived from the literature

Firstly, we ran a series of simulations in which EV in mortality was increased from the base level by 1 to 20%, at 1 steps, while maintaining the basal level for EV in fecundity. With large environmental variation probability of extinction (PE) had a large increase (from 0 with 1% increase on base values to 0.996 with 20% increase). Increase in probability of extinction with increase in EV of mortality had a sigmoidal shape (logistic fitting, with asymptote at PE equal to 1:  $R^2 = 0.995$ ; Figure 9), initially increasing very slowly, and remaining under 10 percent for an increase up to 8%; variation in EV of mortality greater than +12% led to extinction 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, while variability of final population size, expressed as coefficient of variation, increased exponentially in the range 0-19%, and then more steeply to 20% (exponential fitting, 1-19%:  $R^2 = 0.949$ ; Figure 9).

Increase in environmental variance of fecundity had a modest effect on likelihood of survival of the population. We simulated variation from the initial standard deviation value increasing variability 1 to 20% at 1% steps. A very small likelihood of extinction resulted (0 to 0.008), with only a weak trend of increase with environmental variability (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 more clear, with about 1% increase in CV with 1% increase of standard deviation due to environmental variability (linear fitting:  $CV(FPS) = 122.6 + 1.05 EV(m_x)$ ;  $R^2 = 0.591$ ).



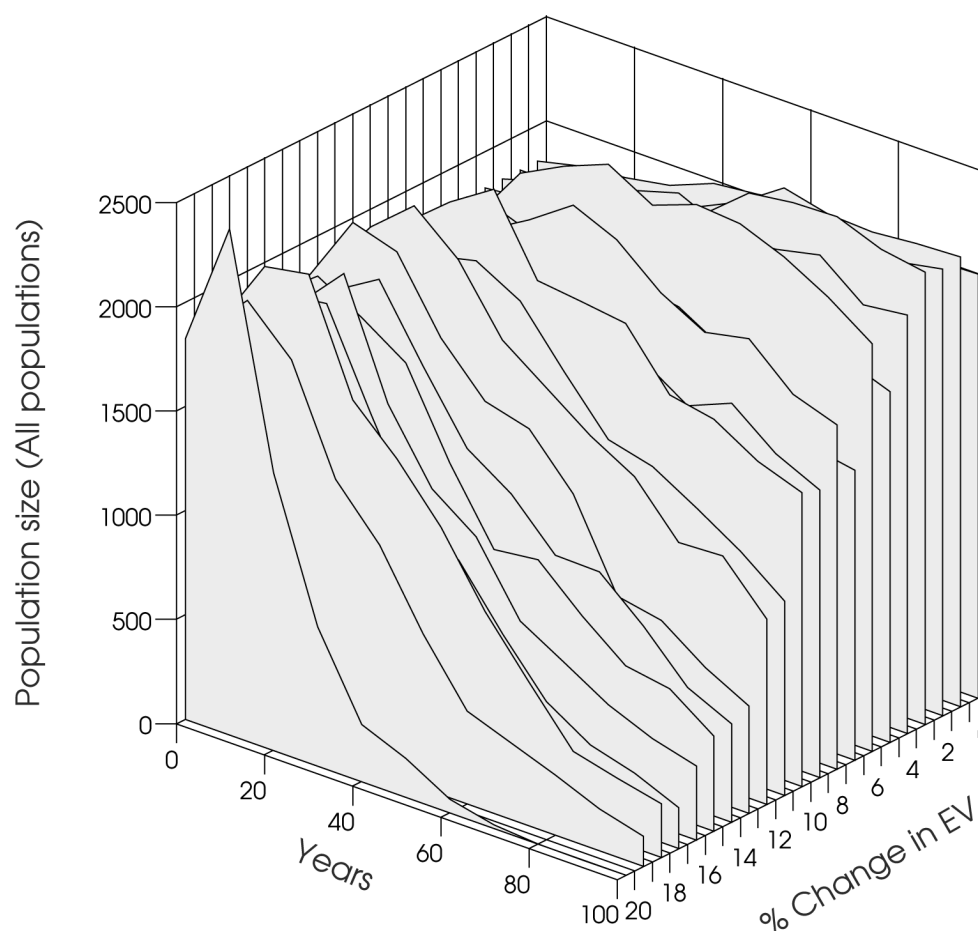
**Figure 9** - Effect of increase in environmental variability of mortality on probability of extinction (sigmoidal fitting) and variability of final population size after 100 years, expressed as coefficient of variation (exponential fitting).



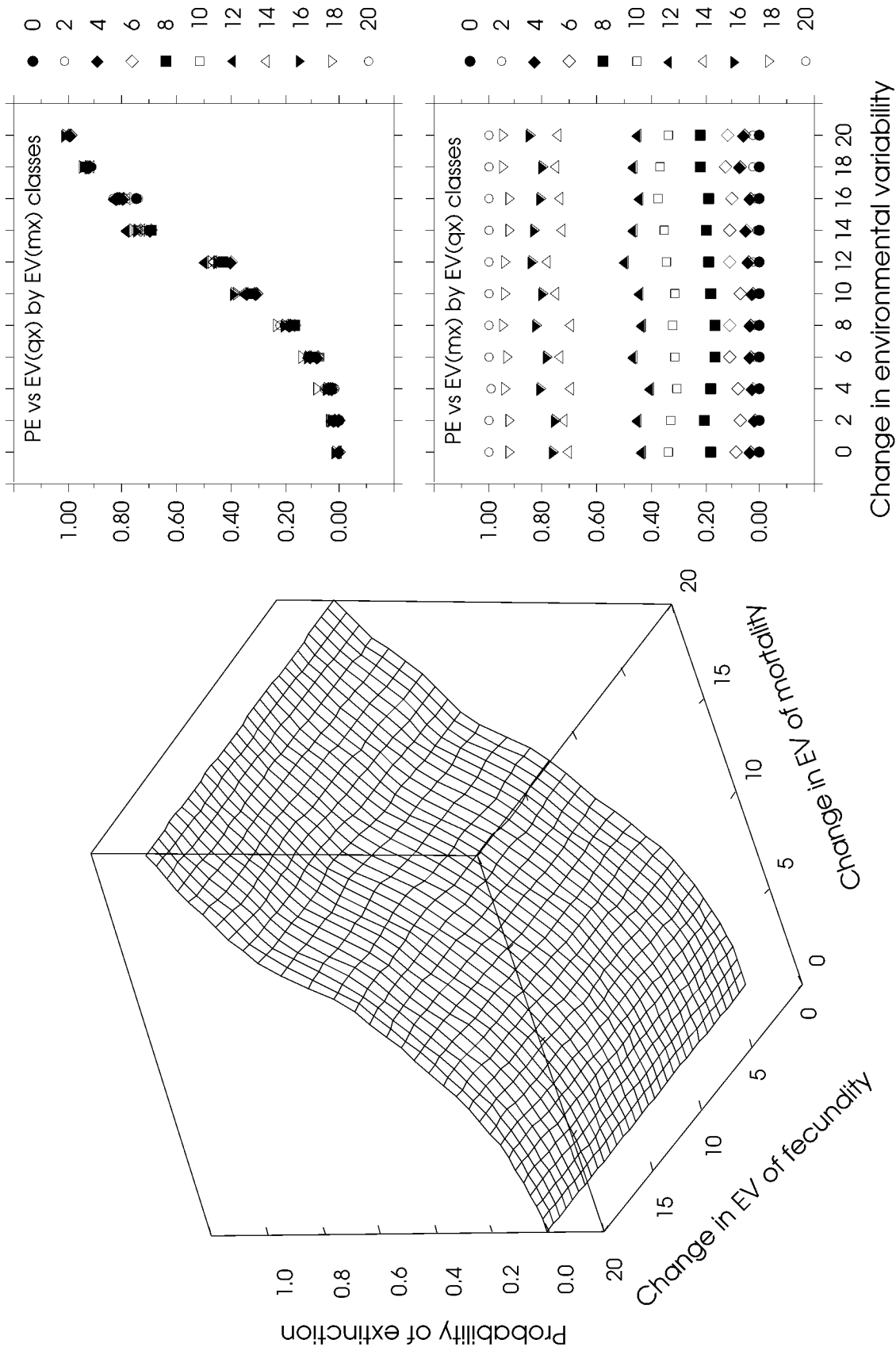
**Figure 10** - Effect of joint variation of environmental variability of mortality and fecundity on variability of final population size (geometric fitting on all populations; rational function fitting on extant population only)

To evaluate the relative effect of EV in mortality and fecundity we firstly assumed that the same change of in EV affected both mortality and fecundity, running simulations in which standard deviations for all parameters of the life table was changed by the same amount, in the range 1-20%, at 1% steps. The increment in environmental variability of both mortality and fecundity produced a sigmoidal increase on probability of extinction almost equal to the one obtained by 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 slope of the curve of about 1.4%. The variability of final size for all populations (extant plus extinct) increase, as expected, with increasing EV, in a geometric fashion (geometric fitting:  $CV(FPS) = 128.01 EV^{0.0326 EV}$ ;  $R^2 = 0.968$ ; Figure 10). Variability of 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 13% increase in EV, and then a step decrease corresponding to  $PE > 0.70$  (rational function fitting:  $CV(FPS) = (134.59 - 6.33 EV)/(1 - 0.0860 EV + 0.0021 EV^2)$ ;  $R^2 = 0.929$ ; Figure 10).

Final size of the population (including all populations, extant and extinct), ranged from 2158 with 1% increase in EV to 143 with 19% increase and 0 with 20% (Figure 11); final size of extant populations ranged from 2158 with 1% increase ( $PE = 0$ ), to 2160 with 2% ( $PE > 0$ ), to 876 with 19% increase ( $PE < 1$ ), and to 0 with 20% ( $PE = 1$ ).



**Figure 11** - Change in population size, at 10 years steps for 100 years, with different increments above the base level of environmental variability (joint variation of EV of mortality and fecundity in 0-20% range).



**Figure 12** - Effect of independent variation of environmental variability of mortality and fecundity on probability of extinction. Left (a): Surface fitted to the PE values on EV values grid by distance weighted last squares. Right Top (b): Bivariate plot of PE on EV (mortality) split by (EV fecundity) classes. Right Bottom (c): Bivariate plot of PE on EV (fecundity) split by (EV mortality) classes.

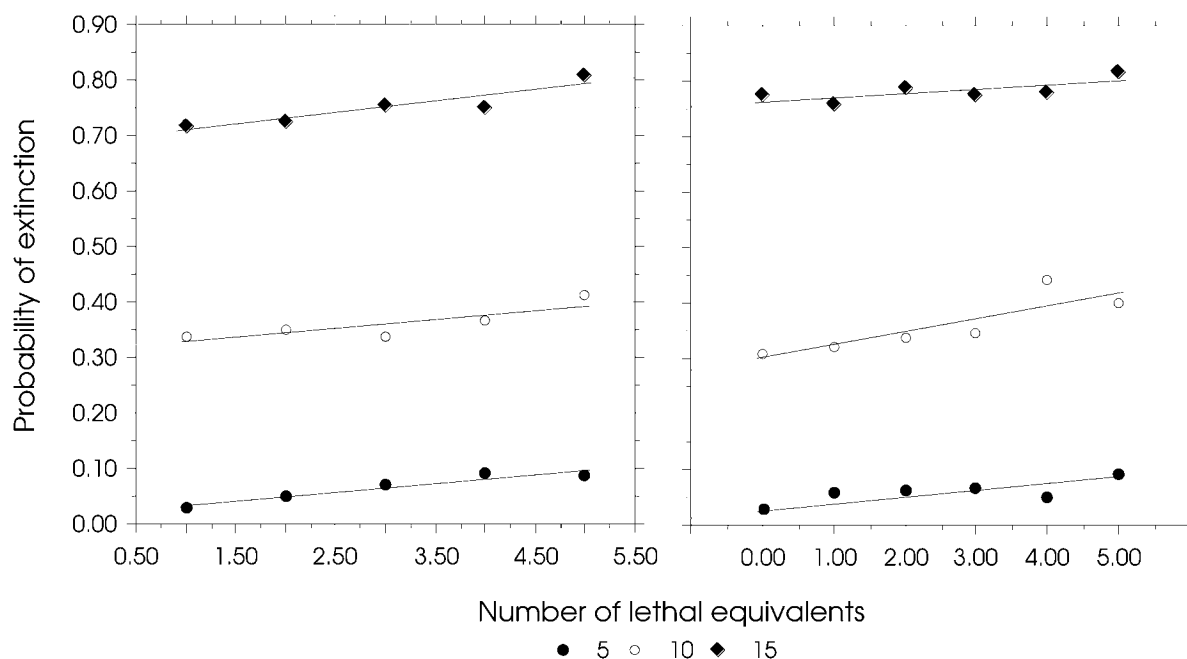


We then relaxed the assumption, and repeated simulation by independent variation of  $EV(q_x)$  and  $EV(m_x)$ . These simulations confirmed that probability of extinction depends almost only in change in  $EV$  of mortality, and that the effect of  $EV$  in fecundity is marginal. We fitted a surface to the scatterplot of  $PE$  versus  $EV(q_x)$  and  $EV(m_x)$  using distance weighted last squares, and 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 (Figure 12/a). We then plotted  $PE$  vs  $EV(q_x)$  split by  $EV(m_x)$  classes, and obtained the usual sigmoidal variation of  $PE$  (Logistic fitting:  $PE = 1/(1 + e^{4.641 - 0.387 EV(q_x)})$ ;  $R^2 = 0.991$ ), with very small intra-class variation in  $PE$  due to  $EV(m_x)$  (Figure 12/b); on the contrary, the plot of  $PE$  versus  $EV(m_x)$  split by  $EV(q_x)$  classes revealed an almost constant  $PE$  among each class (among class linear fitting:  $b = 0.0001-0.003$ ) and a large variation between classes (Figure 12/c). This was confirmed by examination of residuals from the logistic fitting, that ranged from  $-0.1037$  to  $0.0961$ , and were normally distributed.

Results of simulations demonstrated that changes in environmental variability may greatly affect the likelihood of extinction of the SLI population elephant seals, due to its small initial size. Moreover, environmental variability in mortality had a much more relevant impact on likelihood of extinction than  $EV$  in fecundity.

### Inbreeding

Firstly, we modeled inbreeding assuming 3.14 lethal equivalents per diploid genome (Ralls et al., 1988), and we attributed 100% of the genetic load to lethal alleles to speed up simulations, a reasonable assumption for population size equal or greater than 200 (Miller & Lacy, 1999).



**Figure 13** - Left (a): Effect of the number of lethal equivalents on probability of extinction, with environmental variability of mortality augmented by 5, 10 and 15%. Right (b): Effect of the number of lethal equivalents on probability of extinction, with environmental variability of fecundity augmented by 5, 10 and 15%.

In a model ran without environmental variability 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%). In northern elephant seals, a very high level of inbreeding that lead to exceptionally low heterozygosity (Bonnell & Selander, 1974; Hoelzel et al., 1993), had no effect on viability of the population, which increased at sustained rate, expanding outside its historical range (Stewart et al., 1994).

The effect of inbreeding depends on the size of the population, hence, inbreeding may have a marginal role if the population size remains relatively large, but may interact with environmental variability and affect likelihood of extinction during environmentally induced fluctuations. To evaluate interaction between environmental variability and inbreeding we modeled a population with basic or increased variabilities with various level of inbreeding, using 0.5 to 5 lethal equivalents at 0.5 steps, again attributing 100% of genetic load to lethal alleles. In the basic model, using calculated environmental variabilities inbreeding had a modest effect on the destiny of the population, with a very low increase in likelihood of extinction (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 %, probability of survival was affected almost only by EV and the effect of inbreeding was very small: for all three EV variation classes there was an almost linear increase in probability of extinction with 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%:  $b = 0.016$ , EV + 10%:  $b = 0.016$ , EV + 15%:  $b = 0.021$ ; Figure 13/a). Similar results were found in a model with symmetric variation of EV of mortality and fecundity: among each class of variation of EV (again + 5-10-15 % from basal level), variation in EV accounted for most variation in probability of extinction, and the slope of the linear dependence of probability of extinction on number of lethal equivalents in each EV variation class were small (+ 5%:  $b = 0.013$ , EV + 10%:  $b = 0.023$ , EV + 15%:  $b = 0.007$ ; Figure 13/b).

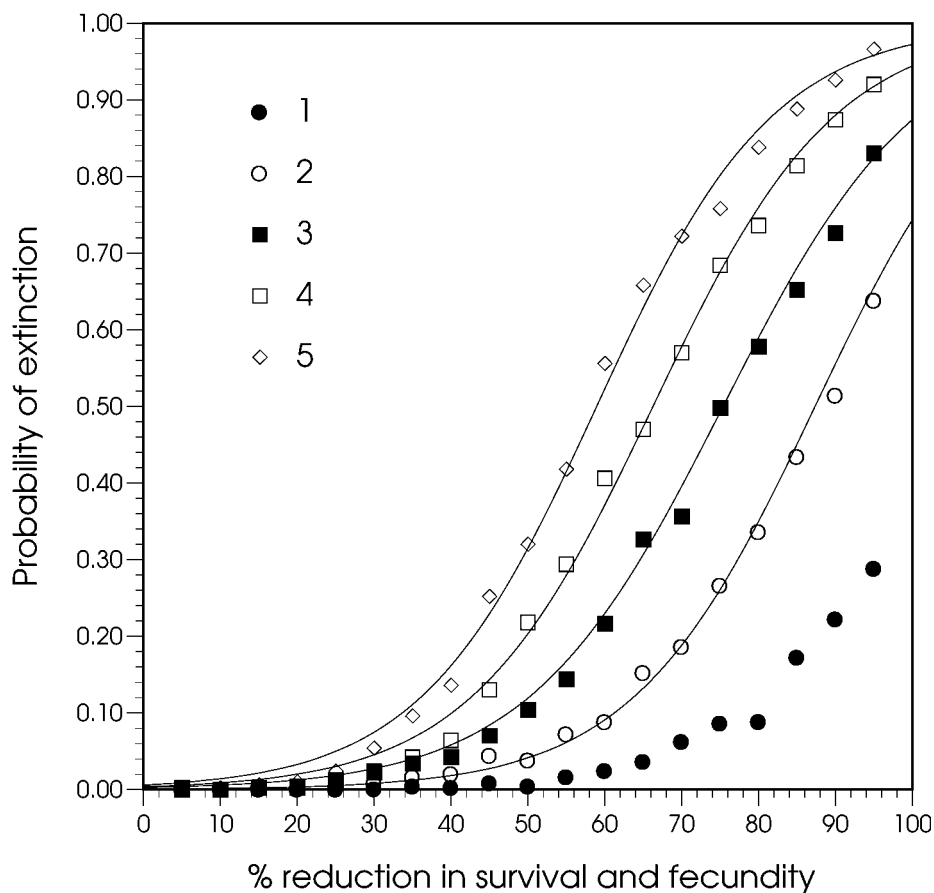
### *Catastrophes*

By catastrophe we mean occasional and unpredictable variations in environment that greatly exceed the usual inter-annual variability, and dramatically affect survival and/or fecundity schedules (Miller & Lacy, 1999). In pinnipeds, mass mortality and exceptional reduction in productivity are associated with epidemics due to viral diseases or parasites (herpesvirus: Stenvers et al., 1992; leptospirosis: Gulland et al., 1996; morbillivirus: Kennedy, 1998; phocid distemper virus: Osterhaus et al., 1990), climatic changes due to ENSO phenomena (Trillmich & Ono, 1991; *Arctocephalus*: Guinet & Jouventin, 1994), oil spills (Loughlin et al., 1996), poisoning due to biological toxins (diatom bloom: Hernandez et al., 1998; Scholin et al., 2000) or chemical compounds (Vidal & Gallo-Reynoso, 1996), or combinations of these factors (Thompson et al., 1993; Ross et al., 1996). Due to the social and grouping pattern of pinnipeds, die-off episodes may represent a significant threat of extinction for small populations and rare species (Raga et al., 1997), and may produce unpredictable variation in their genetic structure (Baker et al., 1994), that may increase extinction risk.

The effects on mortality and fecundity of catastrophic events are quite variable, both in quality and quantity. The El Nino Southern Oscillation (ENSO) is a typical catastrophic event that affected various species of pinnipeds in the recent past, producing increase of preweaning mortality (up to 100%, e.g., *A. 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 (*Zalophus californianus wollebaeki*: Trillmich & Limberger, 1985; *M. angustirostris*: Huber et al., 1991), and drop in size of whole populations (*A. pusillus*: Roux, 1998; *M. leonina*: Vergani & Staganelli, 1980). Long term modifications of life history traits and breeding

strategies have been related to ENSO, like delay of maturity and increase in number of skipped breeding seasons (Huber et al., 1991). Such severe effects are not limited to ENSO phenomena, and are common also in other situations (e.g., oil spills, *Callorhinus ursinus*: Reed et al., 1989).

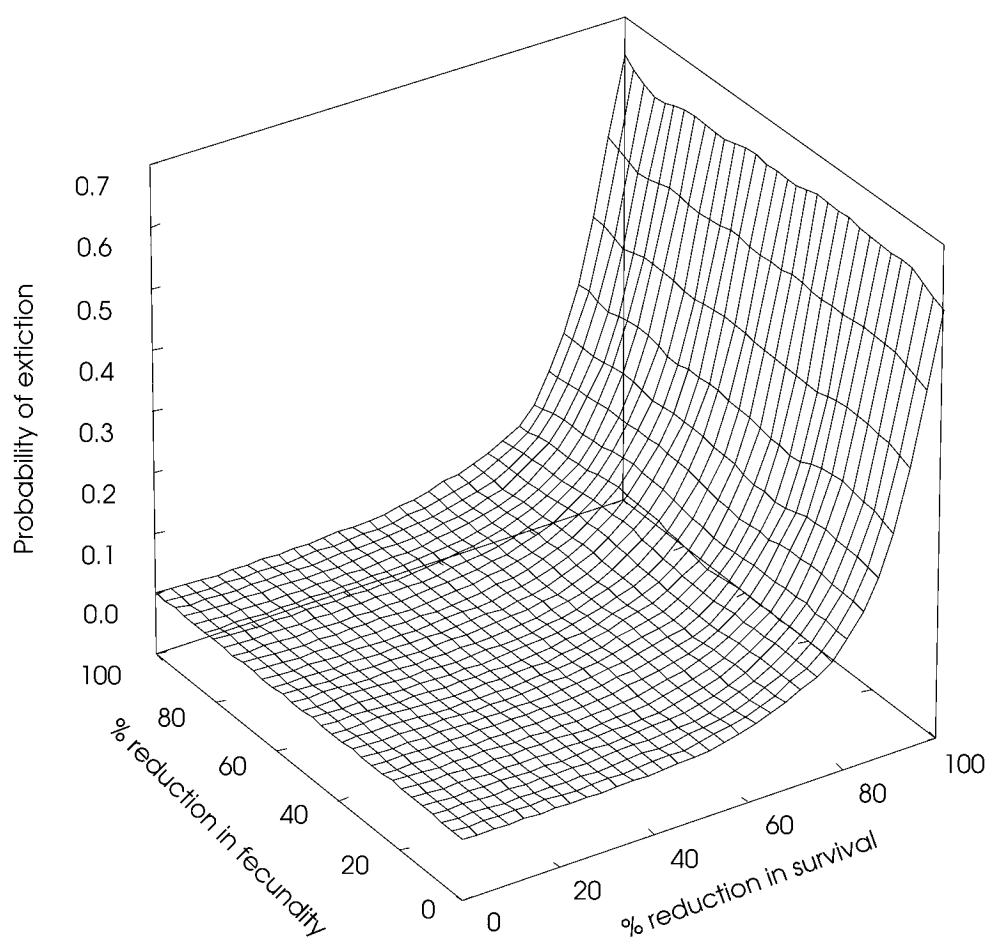
We explored the effect of catastrophes by introducing in the base model a variable number of catastrophes (probability 1-5%, i.e. 1 to 5 in mean per 100 years ran) with severity ranging from 0 (= 100% reduction in survival or/and reproduction) to 1 (no reduction). We first ran a series of simulations with equal severity for survival and reproduction, in the range 0-1 at 0.05 steps. Probability of extinction increased with increasing severity of the catastrophe, but the shape of the trend was quite different among simulations with different probability of catastrophe. Simulations with 100% failure produced an exceptionally high mean probability of extinction, regardless of the probability of catastrophe, and not in accordance with the trend apparent for other simulations with the same catastrophe probability. For 1% probability (a mean of 1 catastrophe per 100 years ran) 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.



**Figure 14** -Effect of joint reduction in survival and fecundity due to catastrophe with different likelihood to happen (1 to 5%) on probability of extinction (sigmoid logistic models fitted to catastrophe with probability in the 2-5% rang)

The variation of probability of extinction was best fitted by a family of logistic curves (Logistic

fitting:  $R^2 = 0.996-0.997$ ; Figure 14), except for the 1% likelihood of occurrence of the catastrophe, for which a good fitting by the sigmoidal model could be achieved only by excluding the 100% failure case (Logistic fitting, 100% point excluded:  $R^2 = 0.992$ ). A common aspects of all curves was the behaviour of the 100% failure point, that represented a clear outlier in all cases. Probability of extinction per 30% failure in survival and reproduction, the low extreme of the usual range recorded for catastrophic events in pinniped populations, increased 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 happened for all catastrophe probabilities in the 30-70% range.



**Figure 15** -Effect of independent reduction in survival and fecundity due to catastrophe with 1% likelihood to appen on probability of extinction (surface was fitted by distance weighted last squares).

To evaluate the relative impact of reduction of fecundity or survival during catastrophes, we ran simulations with independent variation of severity of survival and severity on reproduction. The surface fitted by distance weighted last squares on probabilities of extinction confirmed that impact on survival is much more important. The slope of the surface is almost completely determined by increased mortality, while reduction in fecundity produced only marginal perturbations of the surface (Figure 15).

## The way forward

Together, the examination of the available field data, the analysis of a deterministic model of the population, and the population viability analysis demonstrated three main points:

1) Currently, the population is steady at a level of about 1800 individuals, and nothing in the deterministic forecast indicates an immediate risk of significant reduction in size.

2) The equilibrium of the SLI population is particularly fragile due to its small size and isolation from other populations of the South Georgia stock. Modest variation of demographic parameters due to environmental fluctuations may lead to reduction in population size, and an increase above 10% of environmental variability in parameters of the life table significantly increase risk of extinction.

3) Both the deterministic and the stochastic models revealed that some aspects of the life table are much more important than others: in particular, variation in survival rates of adults had the largest effect of population size and probability of extinction.

Perhaps the most relevant operational conclusion that may be derived from simulation is that not enough actual data is available: any model or simulation is as much good as good its parameters, and many aspects of the life history and demography of SLI elephant seals are yet poorly known.

The available information, although scanty and mostly from anecdotal sources, indicate that only very small and scattered group of elephant seals breed outside Sea Lion Island in the rest of the Falklands, and that other breeding sites have been almost abandoned in recent years (e.g., Elephant Point of Sounders Island: Poole-Evans, pers. comm.). Southern elephant seals are not an endangered species, with at least 664000 individuals world-wide, and the Falklands represent a very small, almost marginal, fraction of the South Georgia stock, which comprises about 397000 individuals (Laws, 1994). So, why bother? We think that the loss of the Falklands population should not be considered of secondary importance, not only for the local loss of biodiversity, but also in relation to its possible role as gene flow conduit between the South Georgia and the Valdés Peninsula populations (Hoelzel et al., 1993; Anna Fabiani, pers. comm.). Although current information seems to exclude immigration and emigration of breeding individuals, the research on the genetic structure of the population is at the beginning, and only the collection of samples from different locations in the Falklands may definitively settle this issue. The lack of detailed information about population dynamics, and the potential increase in risk of threats to population survival, due to the recent changes in lifestyle and economy of the Falklands, make the collection of more data on demography, life-history, and feeding strategies, compelling.

The results of our analysis clearly demonstrate that the forecast of small population presents formidable problems, and that the current steady state of the population is far from granted in the long term. Various operational suggestions may be derived from this conclusion.

### *1) Accurate age-specific schedules of mortality and fecundity are badly needed.*

Life tables may be built using a cross-sectional design, which requires the knowledge of age of a large sample of individuals, or a longitudinal design, which requires the mark and resight of individuals from birth to death. Recently, it has been demonstrated that age may be determined in adult elephant seals by analysis of a tooth collected from restrained individuals (Arnbom et al., 1992), but this requires chemical anesthesia. Moreover, the calculation of life table parameters from age distribution in cross-sectional design requires a series of assumptions difficult to fulfill and verify (Krebs, 1989). Longitudinal design is the best way to go for both theoretical and practical reasons. The only obvious drawback is the time required to track lifetime long-living species. On SLI, a mark-recapture experiment was started in 1995, with tagging of the whole yearly net production of weanlings (Galimberti & Sanvito, 2000). For the most important part of the population, females, mortality and fecundity of adults may be effectively modeled as constant, but detailed information for each age class are needed for females up to at

least age 6. This means that a minimum number of female coorts should be monitored for at least six consecutive breeding season. This will permit an accurate estimation of survival to breeding, age at maturity, variation in fecundity during the first years of reproduction, all crucial aspects of the life history. Unfortunately, the status of the mark-recapture study is uncertain, because the long term prosecution of the project is not compatible with the current policy for granting of research permits.

*2) The information collected on SLI should be complemented by a global assessment of the breeding status of SES in the rest of the Falklands.*

A more accurate assessment of distribution and breeding in the rest of the Falklands should be accomplished through a global census of the islands at peak haulout of females, i.e. between the third and fourth week of October. This will permit a first assessment of distribution and the identification of the breeding sites. Due to the shape of the Falklands coast, and the necessity to carry out it in short time window to be able to standardize counts, a global census will probably require a series of aerial counts, but the current charter tariffs of the only local airline (FIGAS) make aerial surveys exceptionally expensive.

Along with the global count, the main breeding sites should be periodically visited to tag individuals and collect skin samples for genetic analysis. The extension of sampling and tagging should improve our knowledge of short-distance movements among the islands, and to study the fine genetic structure of the population, which may have a fundamental role in its long term survival.

*3) The PVA analysis could be profitably extended to model the whole Falklands population.*

Although SLI is the main breeding site of SES in the Falklands, small groups or isolated females should probably breed every year in other locations of the islands. Global censuses will permit the modeling of the whole Falklands population as a system of meta-populations, many of them very close to the risk of local extinction. The first requirement of meta-population modeling are good estimates of migration between populations, that should be achieved by an extension of the mark-recapture study to sites outside SLI.

*4) Long distance movement patterns should be studied by deployment of satellite tags.*

Environmental variability of demographic parameters, that strongly affect population growth and risk of extinction, are related to food availability. In elephant seals this relationship should be particularly strong because of the pattern of breeding effort in both females and males. Concentration of breeding effort in time and space, fasting while on land during both breeding and molting, exceptionally high loss of reserves during the breeding season for both lactating females and breeding males, put very high demands on the physiology and bioenergetics of this species. Elephant seals are somehow "extreme" animals, and hence environmental stress should have a significant effects on their likelihood of survival. Unfortunately, information on diet, foraging areas, competition with other species, and effects of human activities are completely lacking for the SLI population. From the detailed study of SES energy budgets in the South Georgia population (Boyd et al., 1994) two general conclusions were derived that should be valid also for SLI: males are more likely to be affected by short term environmental variation than females, and commercial fisheries represent a significant source of variation in quality of seals environment, and are therefore a significant potential threat to their survival. The tracking of seals at sea will permit a better understanding of the aquatic phase of the life cycle, and the identification of foraging areas, which are at the moment completely unknown. This will probably also led to the solution of the puzzling question of females molt (which has an important role in female energetic: Carlini et al., 1999). Almost none of the breeding females of SLI return there for molting (while about 70% of the breeding males are resighted on SLI during the molting season), and nobody knows where they go.

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