

Comparison of southern elephant seal populations, and observations of a population on a demographic knife-edge

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ABSTRACT: The dynamics of animal populations are determined by several key demographic parameters, which vary over time with resultant changes in the status of the population. When managing declining populations, the identification of the parameters that drive such change are a high priority, but are rarely achieved for large and long-lived species. Southern elephant seal populations in the South Indian and South Pacific oceans have decreased by as much as 50% during the past 50 yr. The reasons for these decreases remained unknown. This study used a projected stochastic Leslie-matrix model based on long-term demographic data to examine the potential role of several life-history parameters in contributing to the declines. The models simulated the observed population trends that were independently derived from annual abundance surveys. Small changes in survival and fecundity had dramatic effects on population growth rates. At Macquarie Island for example, a small change (ca. 5%) in survival and fecundity rates resulted in the population reverting from a decreasing one to a population that increased. The vital rates that had the greatest impact on fitness were, in order of importance: (1) juvenile survival, (2) adult survival, (3) adult fecundity and (4) juvenile fecundity. Population viability analysis (PVA) for each of the 2 decreasing populations revealed that there was a high probability of the Marion Island population becoming extinct within the next 150 yr, while the probability of extinction at Macquarie Island was low. The estimated mean times to extinction for each population was 134 yr (95% confidence intervals: 105 to 332 yr) at Marion Island and 564 yr at Macquarie Island (the earliest time to extinction was 307 yr).

KEY WORDS: Elasticity · Population fitness · Population trajectories · Vital rates

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INTRODUCTION

Identification of a population decrease operating over a decade or so may be the first indication that a species may be moving towards extinction. However, the management of decreasing populations requires more detailed information than simple population trends. One tool that is increasingly important, is pop-

ulation viability analyses (PVA), which can help researchers and managers predict, with clear assumptions, the fates of declining populations (Reed et al. 2002). There are several models for PVA, each with a suite of advantages and disadvantages (McCarthy et al. 2001b), but most rely on access to detailed life-history data (Ellner et al. 2002). Such data are often difficult to obtain, particularly for large, long-lived ani-

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mals. This makes assessment of population trajectories, and the development of hypotheses that address causal mechanisms, difficult. However, mathematical population models provide a means to test the relative contribution that each hypothesis makes at the population level (Cochran & Ellner 1992, Caswell 2001). Such models provide the link between the vital rates of survival and reproduction of individual animals and the population (Caswell 2001).

A stage-structured matrix model is a useful facility to study the population dynamics of animal populations (Cochran & Ellner 1992). Such a case exists where age-specific survival and fecundity are dependent on body size. From such matrix models, it is relatively straightforward to calculate the elasticities for each of the vital rates in the population matrix (Caswell 2001). 'Elasticity' is a measure of the relative sensitivity of a particular vital rate and can be defined as the effect on the population growth rate of a proportional change of a given fitness component (de Kroon et al. 2000). Analyses of elasticities thus provide the ideal medium for the estimation of the proportional change in the population growth rate for a proportional change in the vital rates (Benton & Grant 1999, Grant & Benton 2000, Caswell 2001). Such elasticity analysis can be used (1) to pinpoint the vital rates that contribute most to fitness and (2) to aid management decisions (Benton & Grant 1999).

Southern elephant seal *Mirounga leonina* populations at Marion Island and at Macquarie Island have continued to decrease (at annual rates of 3.4 and 0.8%, respectively) for at least the last 15 yr (Bradshaw et al. 2002), while the Îles Kerguelen and Heard Island populations are believed (Guinet et al. 1999, Slip & Burton 1999) to have stabilised after a period of decrease. The South Georgia population has remained stable (Boyd et al. 1996) and the Peninsula Valdes population has increased (Lewis et al. 1998). Although the reasons for these differences in population trends remain unknown, food (prey) availability is often hypothesised to be the ultimate factor determining population status (Hindell 1991, Hindell et al. 1994, Pistorius et al. 1999b). It has also been suggested that predation from killer whales *Orcinus orca* may be a confounding factor, especially in small populations (Guinet 1992, Trites et al. 1999, McMahon et al. 2003). The mechanism whereby food availability impacts on population status remains contentious and 2 principal schools of thought exist: (1) that adult (particularly female) survival is important (Pistorius et al. 1999a,b, Pistorius & Bester 2002) and (2) that survival of juvenile seals and their recruitment into the breeding population are the principal driving forces (Hindell 1991, McMahon et al. 2003). Such contention is not uncommon and has also been reported from studies on large herbivores (e.g. cervids and bovids), illustrating the importance and

difficulty in obtaining the necessary demographic data to make quantitative assessments of key demographic parameters, such as age-specific mortality and fecundity (Gaillard et al. 2000). Of course, these explanations need not be exclusive and indeed both contribute to the determination of population size.

Using 2 concurrent long-term (16 yr, 1986 to 2001) demographic data sets, this study had 4 primary aims: (1) to simulate/project the population growth rates for 3 populations of southern elephant seals (Marion Island, Macquarie Island and South Georgia Island) using life table information, (2) to discover and describe the critical components in determining fitness (population growth rate) for each population, (3) to assess the reliability of the model in predicting future population size and (4) to generate hypotheses of life-history agents driving population change.

MATERIALS AND METHODS

Population trends. Population trends for elephant seals from 3 island populations: South Georgia (see Boyd et al. 1996 for census details), Macquarie and Marion islands, were calculated from previously published population counts (Hindell et al. 1994, Bradshaw et al. 2002) and unpublished recent counts. At Macquarie and Marion islands, entire island counts were made on October 15 each year. October 15 is recognised as the day on which the maximum number of female seals are hauled out and counts made on this day are used for the analyses of population status (see Hindell & Burton 1987 for an overview). At Macquarie Island, daily counts during the breeding season were made from 1993 of all females present in the isthmus study area at Macquarie Island. The study area represents approximately 13% of all the females that breed on the island each year (Hindell & Burton 1987). The counts from the isthmus sub-population were used to supplement and extend the time series for Macquarie Island. This was done for 3 reasons: (1) they represent a long series of surveys (between 1949 and 2001), (2) the surveys are representative of total island counts (Hindell & Burton 1987) and (3) they provide a context within which to discuss the population trend seen during the 16 yr covered by this study.

The rates of population change were calculated as the annual proportional rate of change (r) and estimated as $r = e^b - 1$ (Krebs 1999), where b is the slope of the fitted regression. These observed rates of population change were compared with the simulated rates of change derived from the projection of the age-specific fecundity and survival matrix.

Life tables, Leslie-Matrix and the stochastic model. An age-specific-survival and fecundity model was con-

structured. A separate life table was generated for each population from the annual survival estimates for each population (Caughley 1977). The input data were derived from longitudinal capture-mark-recapture studies at Marion Island and at Macquarie Island, and from a cross-sectional study from harvested seals at South Georgia. At Marion Island, 2000 seals were tagged at weaning with 2 plastic flipper tags (3 digit 'Jumbo' Rototags supplied by Dalton Supplies) in their hind flippers. The subsequent resights, in the main study area (56 km of coastline), from 5 seal cohorts (1993 to 1997) formed the basis from which the life-tables were calculated. The practical details of this demographic study were summarised in Pistorius et al. (1999b) and Pistorius et al. (2001). A contemporaneous group of seals was also marked and recaptured at Macquarie Island. At Macquarie Island, ~1000 seals yr^{-1} were marked at birth with 2 plastic flipper tags (4 digit 'Super Flexi' Rototags supplied by Dalton Supplies) when birth masses were measured. At weaning, these same seals were recaptured and their wean masses measured. Shortly after weaning (approximately 3 wk), these seals ($n = 5000$) were permanently marked by hot-iron branding as described in McMahon et al. (1997, 1999, 2000), conducted under the Australian Antarctic Animal Ethics Committee (AAS 2265) and the Tasmanian Parks and Wildlife Service ethics approval. Daily searches of all the isthmus beaches (3.6 km), fortnightly searches of the northern third of the island (36 km), where most of the marked seals return to (Carrick et al. 1962, McMahon et al. 1999), and monthly searches of all the island's beaches (96 km) were made to re-sight branded seals. Capture-history matrices were constructed from these resight histories of the individual seals. Multiple resights within a year were treated as a single sighting. These capture matrices were used as input files for the capture-mark-recapture (CMR) program MARK (White & Burnham 1999) to estimate survival and capture probabilities from the resight records of the marked individuals. MARK provides survival (ϕ) and recapture (p) estimates under the Cormack-Jolly-Seber (CJS) model (Cormack 1964, Jolly 1965, Seber 1965) and under several models that appear as special cases of the CJS-model (Lebreton et al. 1992). Reports of marked seals from sites other than Macquarie Island were rare (McMahon et al. 1999, Hindell & McMahon 2000, van den Hoff 2001).

The location-specific life tables were converted into 2-dimensional matrices that were used to project population change through time (Caswell 2001). The matrix has the form $X_{(t+1)} = L(n_t) X_{(t)}$ and determines the age distribution of the population at time $t + 1$ from the distribution at time t , where $L(n_t)$ is the constant Leslie-Matrix and $X_{(t)}$ is the age distribution for only

the female population at time t . We only studied the female proportion of each population because female seals are the units by which the status and behaviour of elephant seal populations are measured (see Laws 1994 for a review). The matrix $L(n_t)$, and vector $X_{(t)}$ are described below:

$$L(n_t) = \begin{bmatrix} f1 & f2 & . & . & . & fn \\ s1 & & & & & \\ & s2 & & & & \\ & & . & & & \\ & & & . & & \\ & & & & . & \\ & & & & & s(n-1) \end{bmatrix} \quad (1)$$

$X_{(t)} = (x_{(1t)}, x_{(2t)}, \dots, x_{(nt)})^T$, where $f1$ is the fecundity rate of females aged 1, $s1$ is the survival probability of females at age 1 and T is the time interval step (yr). Here, fecundity and survival increase in whole yearly increments. Fecundity (f) is defined as the number of female offspring produced per female in the interval t to $t + 1$ and n is the maximum age of female seals.

Concurrent known age-specific survival estimates and fecundity rates for Marion and Macquarie islands (McMahon et al. 2003) were used to describe the behaviour of the 2 island seal populations, while historic, cross-sectional data were used to describe the South Georgia population (McCann 1985). Survival and fecundity data for seals aged 7 yr were used in the life tables to extrapolate the life tables to age 20 yr by assuming constant female survival and fecundity after age 7 yr (Pistorius et al. 2001); i.e., survival decreased and fecundity remained at a constant rate (derived for females aged 7 to 20 yr).

We developed a stochastic model by assuming that the variance in the vital rates is due to fluctuating environmental conditions (Fieberg & Ellner 2001). Environmental and intrinsic stochasticity was built into the model by including a random iteration process as the measure of variation (standard deviation [SD] of the multiple cohort estimates of survival and fecundity) of the estimates observed between years. Survival and fecundity were adjusted at each iteration using a randomly-selected value within the ranges described by the SD. It was assumed that these data were normally distributed around the mean value. As there were no estimates of the variance of estimates for the South Georgia Island life-history data (McCann 1985), we made this the mean of the variation observed at Marion and Macquarie Islands. We used 1000 random iterations to calculate the mean projected population value using Monte-Carlo simulations (Caswell 2001). This procedure randomly selects a value within the given range of variability for each parameter (survival and fecundity) and recalculates the expected population number using this random variable.

Elasticity of parameters. One of the advantages of using projection matrices to describe life-history data is that they facilitate data interpretation by linking the vital rates to population growth, i.e. λ (Caswell 2001). There are 2 ways of describing the proportional impact that age-specific survival and fecundity have on λ : (1) to calculate the sensitivities of parameters and compare them, or (2) to calculate the elasticities of the parameters and compare them (Caswell 2001). However, because survival (which can only vary between 0 and 1) and fecundity (which may vary between 0 and >1) are measured on different scales, it is preferable to use the dimensionless elasticity values (Stearns 1992, Caswell 2001), especially for elephant seals where survival varies between 0 and 1, and fecundity varies between 0 and 0.5. The age-specific elasticities (e_{ij}) were calculated for each island population to determine the influence of the age-specific vital rates on population growth, and secondly, the elasticities were grouped into juvenile and adult age classes to determine the phase-specific contribution to population growth. Elasticities are easily calculated from the general formula:

$$e_{ij} = \frac{\partial \lambda}{\partial L_{ij}} \frac{\lambda}{L_{ij}} \quad (2)$$

where L_{ij} is the transition matrix. At each island (South Georgia, Macquarie and Marion), juveniles were defined as those individuals in the non-reproductive ages, which varied between sites. The mean age at first reproduction was used as the delimiter between non-reproductive (juvenile) and reproductive (adult) individuals. The mean age at first breeding was 4.68 ± 0.38 and 3.95 ± 1.03 yr at Macquarie and Marion islands, respectively (McMahon et al. 2003) and at South Georgia Island, it was 4 yr (McCann 1980). Thus, at Macquarie Island, juveniles included females in all age classes up to and including age 5; adults were seals aged older than 5 (i.e. in their sixth year of life). At Marion Island, juvenile females included seals up to age 4, i.e. all seals older than 4 were considered to be adults (seals in the fifth year of life). At South Georgia Island, juvenile females were classed as such up to age 4 and adult females were those seals older than that.

Validation of the modelled values. Stochastic models, such as the model used here, can provide estimates of future population sizes. However, because models are simplifications of complex systems, it is important to validate the predicted values. A standard deviates test (McCarthy & Broome 2000) was used to determine the validity of the predicted values. The predicted (modelled) values and the observed (annual counts) values can be compared by subtracting the observed population size. Standard deviates for each of the years were thus generated, so that when the model predicts

the mean population size accurately, the mean standard deviate is zero. A single t -test (with the value t) of all years was used to test whether these mean values were different (McCarthy & Broome 2000).

PVA (extinction times and the probability of extinction). To estimate the probability of extinction, a PVA was performed (Caughley 1994, Reed et al. 2002). Extinction was assumed to have occurred when the population fell below 20 individuals because the northern elephant seal population may have recovered to its present population levels from a remnant population of as few as 20 seals (Bonnell & Selander 1974). The PVA returns an estimate of the time to extinction of a population with given population parameters. We assumed that the Macquarie Island population was closed because immigration has never been observed there and emigration was limited (Nicholls 1970). However, some migration to and from Marion Island has been recorded (Bester 1988, Guinet et al. 1992). To test the effect of a small net positive rate of immigration to Marion Island from the larger elephant seal population of the Kerguelen Archipelago, the Marion Island breeding population was supplemented with 1 female seal in each of the age classes 1 to 4 (i.e. aged 1, 2, 3 and 4, i.e. 0.6, 0.8, 0.9 and 1.0% of the seals alive in each age class) annually, and the simulations were re-run to quantify the effect of immigration on population persistence at Marion Island. To test the effect of greater immigrations rates, the Marion Island population was supplemented further with another female in each of the 4 age classes, annually (i.e. 8 additional females each year).

RESULTS

Annual census data and population trends

An annual count of all the female seals, at Marion Island and at the isthmus at Macquarie Island, ashore during each breeding season (1986 to 2001) was conducted to determine the maximum number of females ashore. For the 16 concurrent years that each of the elephant seal populations was monitored, they decreased at mean rates of 3.41 ($p < 0.001$) and 0.81% ($p = 0.03$) yr^{-1} at Marion Island and Macquarie Island, respectively (Fig. 1a). In addition to the data for these 16 yr time series, a 51 yr data set was also analysed for the Macquarie Island population. These analyses revealed that the longer-term (1950 to 2001) mean rate of change was -1.68% ($p < 0.001$) yr^{-1} (Fig. 1b) and that this rate had not changed in recent times (Fig. 2b). There were no changes in the rates of population decrease at Marion and Macquarie islands (Fig. 2).

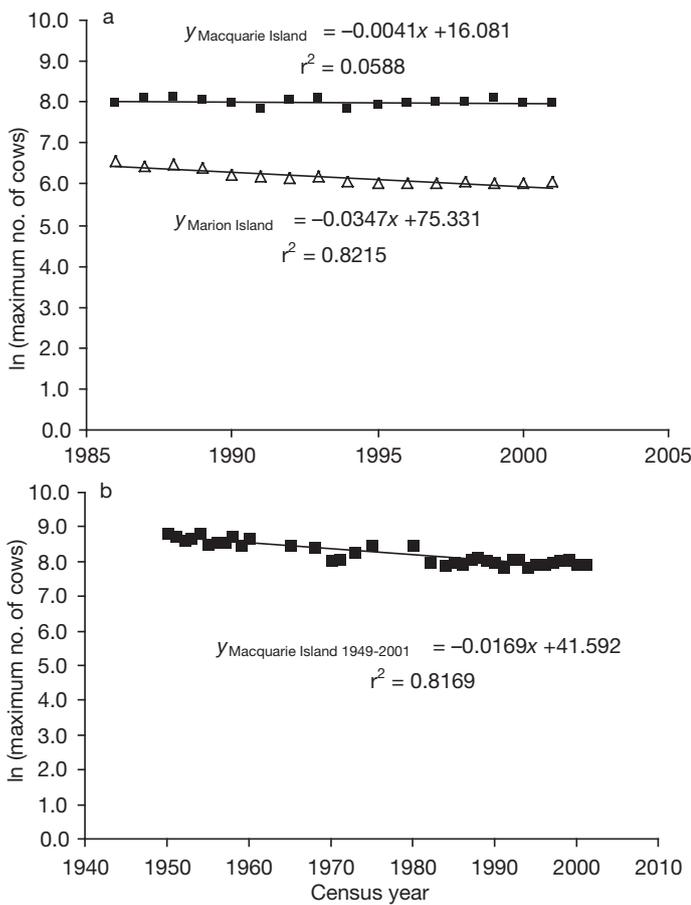


Fig. 1. *Mirounga leonina*. Elephant seal population decreases at Marion and Macquarie islands from 1986 to 2001 expressed as the natural logarithm (ln) of the observed maximum numbers of cows against time at (a) Marion and Macquarie islands, and (b) for the long-term (1949 to 2001) decrease at Macquarie Island

At Marion Island, the piece wise non-linear function that described population change in 2 stages (1986 to 1994 and 1994 to 1997) described 80% ($r^2 = 0.798$, here r refers to correlation coefficient) of the variation in population size. However, this fit was no better than a single stage function that also described 80% ($r^2 = 0.797$) of the variation. Thus, we could not determine any statistically significant evidence to suggest a change in the rate of decrease at Marion Island from 1986 to 1997. Indeed, when the same analyses are performed for the entire data set (1986 to 2001), there was little difference between the piecewise model ($r^2 = 0.828$) and the single-stage function ($r^2 = 0.809$). As the piecewise and single-stage models differed little, we concluded that there was insufficient evidence for any systematic changes in the rates of population change at Marion Island.

To test the reliability of the projected number of seals and the actual number of seals, we used the

first reliable counts of the maximum number of female seals as input values, which were made in 1949 at Macquarie Island on the isthmus when 6800 females were counted and in 1976 at Marion Island when 1173 females were counted. Using the present life tables as input values for the Leslie matrix model, and using 1949 and 1976 as starting dates and population numbers for each of the models, we predicted that there would be 474 (95% CI 275, 780) female seals at Marion Island and 3709 (95% CI 1684, 7108) females seals at Macquarie Island in 2001. The actual number of females seals counted at Marion Island in 2001 was 424 and at the isthmus at Macquarie Island it was 2825. These counts were within the 95% confidence intervals around the mean projected estimate (Fig. 3).

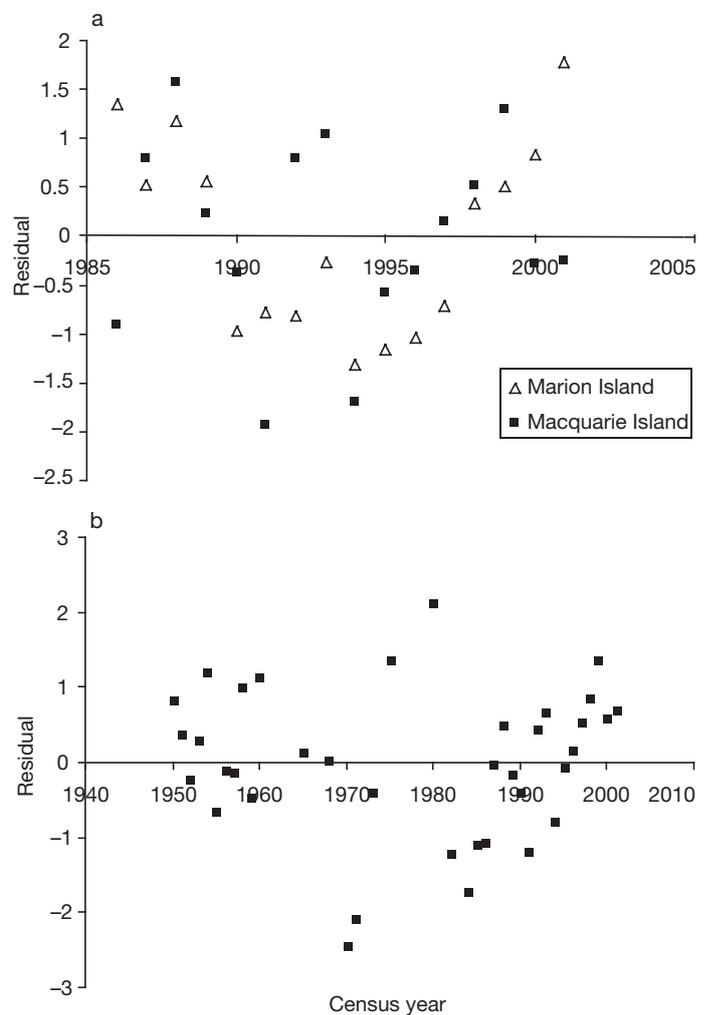


Fig. 2. Residual plots against the annual rates of change (a) from 1986 to 2001 at Marion ($p > 0.05$) and Macquarie islands ($p > 0.05$), and (b) the long-term (1950 to 2001) rate of change at Macquarie Island ($p > 0.05$), showing that the mean residuals values did not differ from zero

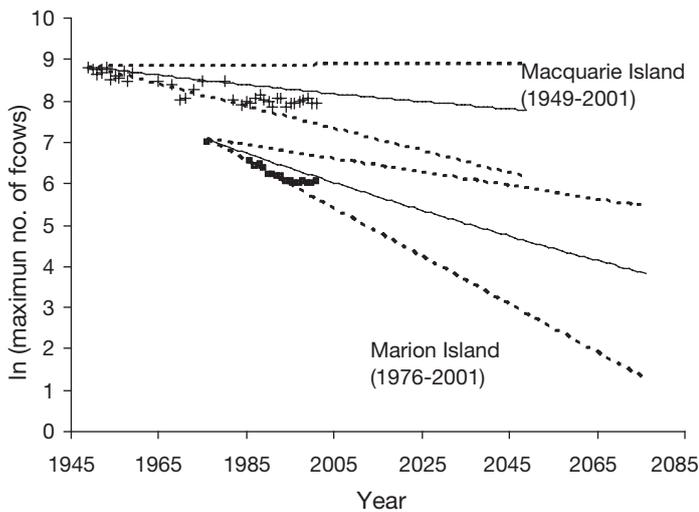


Fig. 3. *Mirounga leonina*. Empirical population counts of southern elephant seals at Marion Island and Macquarie Island with respect to the predicted population numbers derived from the stochastic model. The solid lines indicate the mean predicted values (with the upper and lower 95% confidence intervals indicated by the dotted lines)

Life tables and Leslie-Matrix models

Mean survival was higher at Macquarie Island than it was at Marion Island (Fig. 4). These differences were most pronounced in the first 10 yr of life when survival was greater at Marion and Macquarie islands, after which survival was greater at South Georgia. The survival curves for both islands were similar and showed a negative relationship between survival and age. At Macquarie Island, survival decreased at a constant ($r^2 = 0.997$) rate of 22.0%, while the mean annual rate of decrease was constant at Marion Island ($r^2 = 0.988$) at 22.5%. South Georgia Island was different to both Marion and Macquarie islands, in that the near constant ($r^2 = 0.842$) rate of decrease in survival was almost 3% greater (25.9%). There were no between-island differences in fecundity and all islands were remarkably similar, judging from the overlap in the 95% confidence intervals (Fig. 5). Seals breed at an earlier age at Marion Island than at Macquarie Island and there was an increase in fecundity with age. The maximum fecundity was reached after 6 yr at Marion and South Georgia islands, and after 8 yr at Macquarie Island.

Elasticities

Age-specific survival was an important parameter in the model of population growth for each of the 3 island populations (Table 1). The relative impact of age-specific survival on population growth at each island

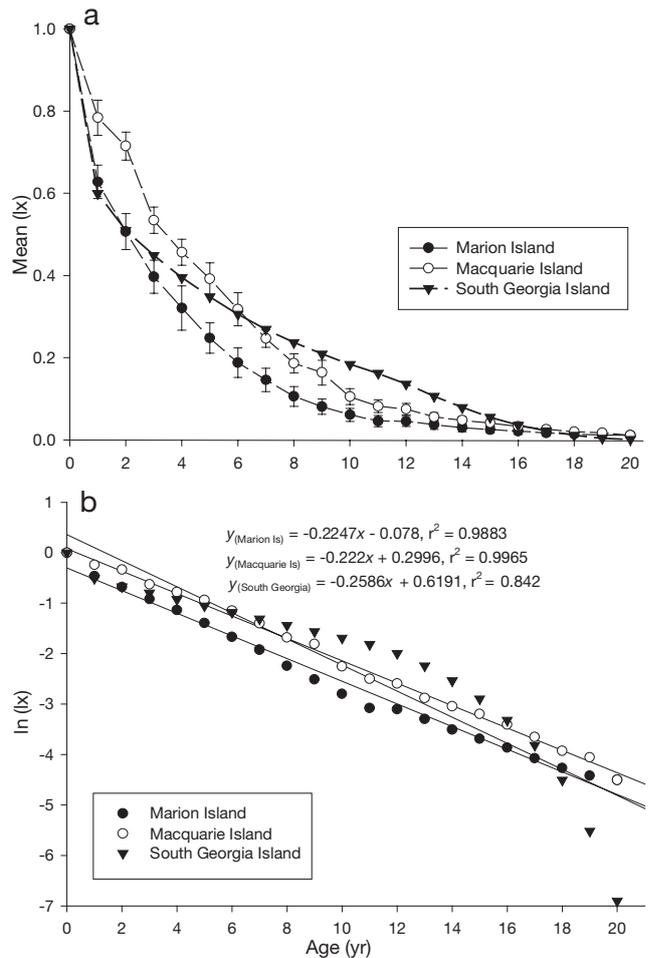


Fig. 4. *Mirounga leonina*. Mean survivorship curves (a) for 3 elephant seal populations at Marion, Macquarie and South Georgia islands, with 95% confidence intervals for the first 2 populations and (b) the log-transformed survivorship curves for the 3 island populations over the same period

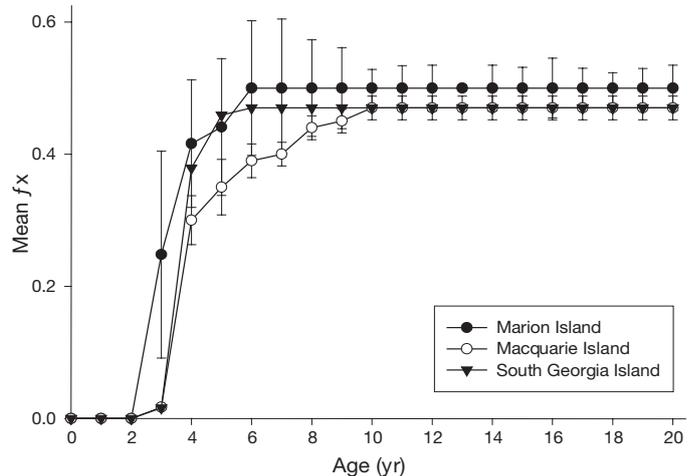


Fig. 5. *Mirounga leonina*. Mean fecundity curves for 3 elephant seal populations at Marion, Macquarie and South Georgia islands, with 95% confidence intervals for the first 2 populations

Table 1. *Mirounga leonina*. Age-specific (x) elasticities for survival (l_x) and fecundity (f_x) at each of the 3 island populations that were studied

Age	Marion Island		Macquarie Island		South Georgia Island	
	l_x	f_x	l_x	f_x	l_x	f_x
0	0.000	0.000	0.000	0.000	0.000	0.000
1	0.116	0.000	0.130	0.000	0.125	0.000
2	0.116	0.000	0.130	0.017	0.125	0.000
3	0.115	0.001	0.113	0.030	0.127	0.001
4	0.103	0.019	0.088	0.022	0.107	0.013
5	0.089	0.021	0.069	0.012	0.088	0.016
6	0.077	0.014	0.058	0.015	0.073	0.016
7	0.063	0.014	0.052	0.007	0.059	0.014
8	0.050	0.012	0.045	0.007	0.044	0.011
9	0.038	0.012	0.038	0.008	0.035	0.009
10	0.029	0.005	0.032	0.005	0.028	0.010
11	0.023	0.004	0.030	0.005	0.022	0.008
12	0.018	0.005	0.025	0.003	0.015	0.007
13	0.014	0.003	0.018	0.003	0.011	0.005
14	0.012	0.003	0.013	0.001	0.007	0.004
15	0.009	0.002	0.010	0.002	0.004	0.003
16	0.006	0.003	0.009	0.002	0.003	0.002
17	0.004	0.002	0.007	0.001	0.001	0.001
18	0.002	0.002	0.003	0.002	0.001	0.0002
19	0.001	0.001	0.002	0.0000	0.0003	0.0004
20	0.0000	0.001	0.0000	0.0000	0.0000	0.0001

was more than 86% (88.4, 87.0 and 87.5% at Macquarie, Marion and South Georgia islands, respectively). Fecundity had a relatively small impact on population growth (12.5, 14.3 and 12.0% at Macquarie, Marion and South Georgia islands, respectively). There were similar patterns in the relative sensitivities (elasticities) at each island, which showed that juvenile survival had primary dominance on population growth (Fig. 6). Fecundity did not play a major role in the growth of the populations, but it was interesting to note that the influence of juvenile and adult fecundi-

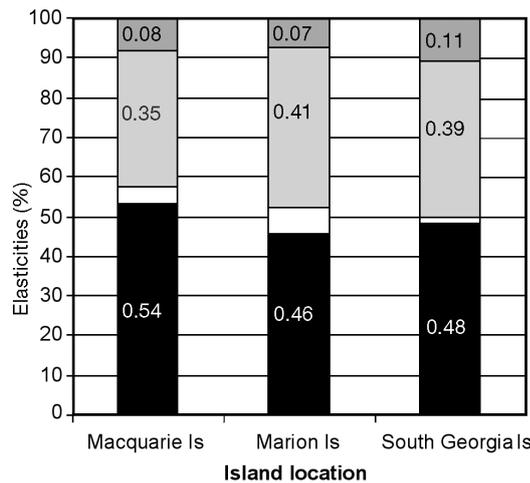


Fig. 6. Relative sensitivities (elasticities) of the vital life-history traits —■: juvenile survival; □: juvenile fecundity; ■: adult survival; ■: adult fecundity on population growth/fitness

ties were similar at Marion Island but not at Macquarie and South Georgia islands. At Macquarie and South Georgia islands, adult fecundity was greater than juvenile fecundity (Fig. 6).

Population trajectories

By incorporating some form of environmental variability into the model, in the form of the variation around the mean estimates of survival and fecundity, we were able not only to project the mean population trends, but also to project upper and lower confidence intervals for our estimated trend (Fig. 7). These projections suggested that: (1) it seems unlikely that the South Georgia population will change appreciably within the next proposed census period of 10 yr, (2) that the Marion Island population will continue to decrease given the present survival and fecundity estimates, and (3) that the Macquarie

Island population seems close to stability. The matrix projections for Macquarie Island show that the population may continue to decrease at near the present rate but that it could stabilise or even increase given small (ca. 5%, i.e. the upper estimates of variance) changes in the present survival and fecundity rates. The Macquarie Island seems close to stability, and had a 0.034 probability (after 5000 iterations) of having a finite rate of increase which was greater than 1. This means that there is a 1 in 29 chance of the population increasing if everything remains the same.

Validation of the predicted values

The predictions of the stochastic model used here are consistent with the measured seal population sizes from 1986 to 2001 (Table 2) at Marion Island ($t_{15} = 0.130$, $p = 0.260$) and at Macquarie Island ($t_{13} = -0.408$, $p = 0.690$). However, when applied to longer periods of prediction such as from 1976 to 2001 at Marion Island and from 1949 to 2001 at Macquarie Island, the model was unable to predict the population sizes ($t_{16} = -1.587$, $p = 0.06$ and $t_{26} = -7.838$, $p = 2.6 \times 10^{-8}$, respectively).

PVA (extinction times and the probability of extinction)

Calculation of the time to extinction for the 2 decreasing populations at Macquarie and Marion

Table 2. *Mirounga leonina*. Mean predicted and empirical life-history rates for Marion, Macquarie and South Georgia islands

		Modelled result	Empirical result
Overall rate of change (yr ⁻¹)	Marion Island (1986 to 2001)	-3.20 %	-3.41 %
	Macquarie Island (1949 to 2001)	-1.55 %	-1.69 %
	South Georgia Island	0.25 %	0.19 %
Total no. of female seals in 2001	Marion Island	477 (±68)	424
	Macquarie Island	28 792 (±10 740)	20 069
	South Georgia Island	128 172 (±16 777)	Unknown
Generation times (yr)	Marion Island	7.60	
	Macquarie Island	7.90	
	South Georgia Island	8.23	

islands (if all demographic parameters remain unchanged) showed that there was a ~71 % risk of extinction in the next 100 yr for the Marion Island population but a 0 % probability of extinction for the Macquarie Island population (Fig. 8). The mean time to extinction for the Marion Island population was 134 yr (105 to 332 yr). At Macquarie Island, the mean time to extinction was 564 yr and an earliest time to extinction of 307 yr (lower 95 % confidence limit). When each age group from 1 to 4 of the Marion Island population was supplemented with 1 female in order to test for the possible effects of immigration, the probabilities of extinction after 100 and 150 yr decreased to 0.355 (SE = 0.010) and 0.567 (SE = 0.016), respectively. When each of the above 4 age classes was supplemented annually with a further female, the extinction probabilities

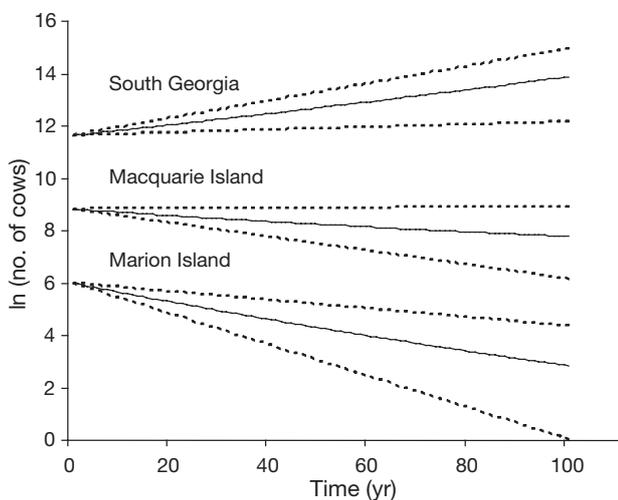


Fig. 7. *Mirounga leonina*. Projected population trajectories of the 3 southern elephant seal populations studied. These trajectories were calculated and projected from a matrix-model that randomly selected survival and fecundity values within a defined range around a mean. Dotted lines indicate the 95 % confidence intervals

decreased further to < 0.00001 (SE = 0.0001) and 0.003 (SE = 0.0012), respectively.

DISCUSSION

This study represents one of the few longitudinal studies of pinniped demographics and was initiated to identify the demographic mechanisms behind the observed decreases in elephant seal populations in the Indian and Pacific Oceans. One of the foremost findings here was that population growth in elephant seals was most sensitive to changes in juvenile survival, a

finding that was consistent for all 3 of the elephant seals populations that we studied. This was true even though each of these populations (Marion, Macquarie and South Georgia islands) behaved differently. Due to the universality of this finding, we conclude with some confidence that juvenile survival is the principal parameter determining population growth in elephant seals. This discovery makes a valuable contribution to understanding elephant seal population behaviour because it provides us with a focal point for concentrating future research efforts.

Key demographic parameters influencing the rates of change

Juvenile survival was identified as the most sensitive factor determining population growth at all 3 islands. In contrast, others (Pistorius & Bester 2002) have dis-

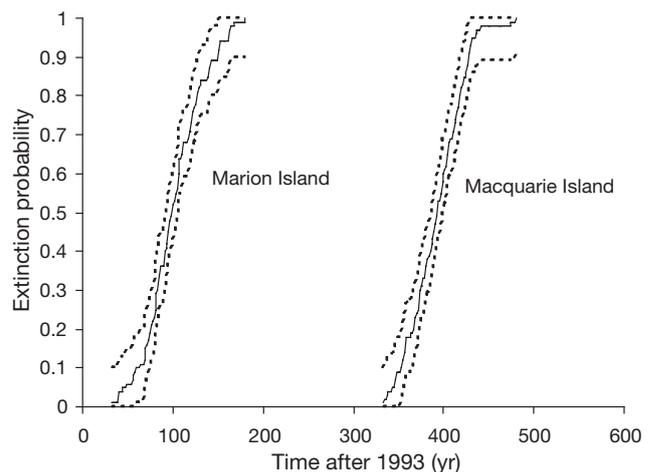


Fig. 8. *Mirounga leonina*. Extinction probabilities for 2 declining populations of elephant seals at Marion Island and Macquarie Island. Dotted lines indicate the 95 % confidence intervals

missed juvenile survival as an important population-regulating component for southern elephant seals. That interpretation is, however, contentious and needs to be treated cautiously because it relied on the pre-supposition that there had been a change in the status of Marion Island population, an observation that is not universally supported (Bradshaw et al. 2002 and this study). While neither we nor others (Bradshaw et al. 2002) preclude the possibility of a change in the Marion Island elephant seal population's status, we suggest that there were insufficient data in the Pistorius & Bester (2002) time series with which to detect a significant change and from which to draw conclusions about the effects that key demographic parameters such as juvenile survival have on population behaviour.

Juvenile survival in southern elephant seals is a composite of first, second and third year survival, and is subject to many different influences. We argue, focussing on first and third year survival, that food availability is probably the prime influence, considering that seals are naive in their first year of life and that many female seals attain reproductive maturity in the third year of life. First-year survival may be affected by predation and maternal investment as reflected by wean mass, and the relative importance of these may be different at different islands (McMahon et al. 2003). Wean masses have increased in recent times at Marion Island (McMahon et al. 2003), which suggests that either food is more available or that young adult female mortality is relatively high. Theoretically, high mortality amongst young females would influence wean mass by generating a female age structure biased to older animals; and because older females produce bigger and heavier pups (Fedak et al. 1996, Arnborg et al. 1997), weaning masses would be higher. However, because of a concurrent decrease in the age at first breeding (McMahon et al. 2003), which is only achieved through increased growth (Laws 1956), it seems unlikely that food is limiting. Juvenile survival may, therefore, be constrained by a number of intrinsic and extrinsic factors, as well as by factors such as climate variability, for instance, that may indirectly affect food availability and competition for resources with other predators. While a clear link has been established between wean mass (i.e. maternal foraging performance) and first year survival (McMahon et al. 2000), the mechanisms describing how the availability of food to juvenile age classes affects survival remains unclear. To be able to do this, the at-sea locations and behaviours of seals need to be determined. A limitation up to now on assessing the at-sea behaviour of predators such as seals, has been technology, most of which was based on archival data recorders that needed to be recovered to access the information stored within them. This was necessarily biased because the information that was gained from such studies was only represented by information from successful seals (surviving

and returning to natal islands), while information on seals that died thus remained unknown. However, with the advent of more recent sophisticated technology that allows at-sea behaviour to be recorded and transmitted via satellite, the behaviour of both successful and unsuccessful animals can be determined (McConnell et al. 2002). These data will allow an interpretation of the requirements that seals need to survive. Indeed, such data also provide information on the strategies used by seals to cope with environmental fluctuations such as those caused by the Antarctic Circumpolar Wave (ACW) (White & Peterson 1996, Loeb et al. 1997) and the effects these processes have on survival.

Fate of the populations

The Macquarie Island seal population appears to have an overall negative intrinsic capacity for increase, given that there were only a few years in which juvenile survival was maintained at the upper limit of the observed variation in survival. However, while the probability of such an increase is low (3.4%), it can be borne in mind that this prediction is based on present demographic values. It does not preclude a different outcome given a change in any of these demographic parameters. Given this, it would seem prudent that the demographic study at Macquarie Island be continued to provide the stochastic model with more recent life-history parameters calculated from a longer time period. This would comprise: (1) the continuation of the capture-mark-recapture program to determine variation in vital parameters (survival and fecundity) during large-scale environmental events such as the Antarctic Circumpolar Wave and (2) the inclusion of this variation in the stochastic model. However, the Marion Island population does not appear to have the demographic capacity for increase in the near future (several decades) unless there is a dramatic change in the fundamental life-history parameters, such as: (1) improved adult female survival (Pistorius et al. 1999b), (2) increased juvenile survival or (3) population supplementation.

Only integrated studies combining observational and experimental studies of life-history and ecology of a population can provide the more adequate information needed to interpret and manage populations. Models make assumptions about the ecology of a particular species and also assume that currently measured/assessed mean trends remain constant; this is unlikely. The evidence presented here suggests that the Marion Island population may become extinct in the next 100 to 150 yr. Marion Island experienced little immigration from proximate island colonies (Condy 1978, Bester 1989); however, neither the magnitude nor the effect of this migration has been quantified.

Indeed, immigration to a small population, like the one at Marion Island, may contribute to a considerable change in the rate of population change, similar to what was observed for northern elephant seals (Cooper & Stewart 1983) and has been illustrated with the aid of the simulation models here with the addition of migrants to the Marion Island population.

Another key finding from our analyses, was that the vital rates at Marion and Macquarie islands were broadly similar, but that small differences in these vital parameters between these islands had potentially large impacts on population growth rates. If small changes in population parameters are going to be used with any precision in estimating future population sizes, the errors associated with the estimates need to be small and thus long-time series are needed. Indeed, stochastic models such as the one used here are a valuable tool to manipulate populations under various theoretical conditions (Reed et al. 2002); and so doing, can provide useful insights for the management of endangered populations (Engen et al. 2001). Models, however, are not perfect representations of reality and should, therefore, be used cautiously and with some form of validation and confidence measure (McCarthy & Broome 2000, McCarthy et al. 2001a).

We concluded that while PVAs are valuable tools for predicting population trajectories (Brook et al. 2000), their value is limited by 2 assumptions: (1) that the distribution of the vital rates are constant between years and individuals, and (2) that changes in these rates may be readily detected (Coulson et al. 2001). This was the case for our estimates as the model was able to predict population sizes in the short-term when little variation in vital rates such as survival is known to occur (Pistorius et al. 1999b); however, predictions in the longer-term were unreliable where large variation in vital rates such as survival has been documented (Hindell 1991, McMahon et al. 1999).

Acknowledgements. This study was supported logistically by the Australian Antarctic Division, and financially by the University of Pretoria through a PhD scholarship to C.R.M. We are indebted to our colleagues of the all the Australian National Antarctic Research Expeditions (ANARE) to Macquarie Island and all the South African National Antarctic Program (SANAP) expeditions between 1993 and 2001 to Marion Island that so ably assisted us in the field by marking seals and collecting resights in often miserable conditions. The Australian Antarctic Animal Ethics Committee (AAS 2265) and the Tasmanian Parks and Wildlife Service approved and permitted this research at Macquarie Island. The Ethics Committee of the Faculty of Natural and Agricultural Sciences (etiek@scientia.up.ac.za) of the University of Pretoria endorsed the research at Marion Island (Reference number EC 990112-002) under a permit from the Director-General: Environmental Affairs and Tourism. We thank 3 anonymous reviewers for their constructive review of the paper.

LITERATURE CITED

- Arnbom T, Fedak MA, Boyd IL (1997) Factors affecting maternal expenditure in southern elephant seals during lactation. *Ecology* 78:471–483
- Benton TG, Grant A (1999) Elasticity analysis as an important tool in evolutionary and population ecology. *Trends Ecol Evol* 14:46–471
- Bester MN (1988) Marking and monitoring studies of the Kerguelen stock of southern elephant seals *Mirounga leonina* and their bearing on biological research in the Vestfold Hills. *Hydrobiologia* 165:269–277
- Bester MN (1989) Movements of southern elephant seals and sub-Antarctic fur seals in relation to Marion Island. *Mar Mamm Sci* 5:257–265
- Bonnell ML, Selander RK (1974) Elephant seals: genetic variation and near extinction. *Science* 184:908–909
- Boyd IL, Walker TR, Poncet J (1996) Status of southern elephant seals at South Georgia. *Antarct Sci* 8:237–244
- Bradshaw CJA, McMahon CR, Hindell MA, Pistorius PA, Bester MN (2002) Do southern elephant seals show density dependence in fecundity? *Polar Biol* 25:650–655
- Brook BW, O'Grady JJ, Chapman AP, Burgman MA, Akcakaya HR, Frankham R (2000) Predictive accuracy of population viability analysis in conservation biology. *Nature* 404:385–387
- Carrick R, Csordas SE, Ingham SE, Keith K (1962) Studies on the southern elephant seal *Mirounga leonina* (L) III The annual cycle in relation to age and sex. *CSIRO Wildl Res* 7:119–160
- Caswell H (2001) Matrix population models: construction analysis and interpretation. Sinauer Associates, Sunderland, MA
- Caughley G (1977) Analysis of vertebrate populations. John Wiley & Sons, London
- Caughley G (1994) Directions in conservation biology. *J Anim Ecol* 63:215–244
- Cochran ME, Ellner SP (1992) Simple methods for calculating age-based life history parameters for stage-structured populations. *Ecol Monogr* 62:345–364
- Condy PR (1978) The distribution and abundance of southern elephant seals *Mirounga leonina* (Linn) on the Prince Edward Islands. *S Afr J Antarct Res* 8:42–48
- Cooper CF, Stewart BS (1983) Demography of northern elephant seals, 1911–1982. *Science* 219:969–971
- Cormack RM (1964) Models for capture-recapture. *Biometrika* 51:429–438
- Coulson T, Mace GM, Hudson E, Possingham H (2001) The use and abuse of population viability analysis. *Trends Ecol Evol* 16:219–221
- de Kroon H, van Groenendael J, Ehrlén J (2000) Elasticities: a review of methods and model limitations. *Ecology* 81:607–618
- Ellner SP, Fieberg J, Ludwig D, Wilcox C (2002) Precision of population viability analysis. *Conserv Biol* 16:258–261
- Engen S, Sæther B-E, Møller AP (2001) Stochastic population dynamics and time to extinction of a declining population of barn swallows. *J Anim Ecol* 70:789–797
- Fedak MA, Arnbom TA, Boyd IL (1996) The relation between the size of southern elephant seal mothers, the growth of their pups and the use of maternal energy, fat and protein during lactation. *Physiol Zool* 69:887–911
- Fieberg J, Ellner SP (2001) Stochastic matrix models for conservation and management: a comparative review of methods. *Ecol Lett* 4:244–266
- Gaillard JM, Festa-Bianchet M, Yoccoz NG, Loison A, Toïgo C (2000) Temporal variation in fitness components and

- population dynamics of large herbivores. *Annu Rev Ecol Syst* 31:367–393
- Grant A, Benton TG (2000) Elasticity analysis for density-dependent populations in stochastic environments. *Ecology* 81:680–693
- Guinet C (1992) Le comportement de chasse des orques (*Orcinus orca*) dans l'archipel Crozet. *Can J Zool* 69:1656–1667
- Guinet C, Jouventin P, Weimerskirch H (1992) Population changes, haulout pattern and movements of southern elephant seals on Crozet and Kerguelen Archipelago. *Polar Biol* 12:349–356
- Guinet C, Jouventin P, Weimerskirch H (1999) Recent population change of the southern elephant seal at Iles Crozet and Iles Kerguelen: the end of the decrease. *Antarct Sci* 11:193–197
- Hindell MA (1991) Some life-history parameters of a declining population of southern elephant seals, *Mirounga leonina*. *J Anim Ecol* 60:119–134
- Hindell MA, Burton HR (1987) Past and present status of the southern elephant seal (*Mirounga leonina*) at Macquarie Island. *J Zool Lond* 231:365–380
- Hindell MA, McMahon CR (2000) Long distance movement of a southern elephant seal (*Mirounga leonina*) from Macquarie Island to Peter 1 ØY. *Mar Mamm Sci* 16:504–507
- Hindell MA, Slip DJ, Burton HR (1994) Possible causes of the decline of southern elephant seal populations in the southern Pacific and southern Indian Oceans. In: LeBoeuf BJ, Laws RM (eds) Elephant seals: population ecology, behaviour, and physiology. University of California Press, Berkeley, CA, p 66–84
- Jolly GM (1965) Explicit estimates from mark-recapture data with both death and immigration-stochastic models. *Biometrika* 52:225–247
- Krebs CJ (1999) Ecological methodology. Addison Wesley, Menlo Park
- Laws RM (1956) Growth and sexual maturity in aquatic mammals. *Nature* 178:193–194
- Laws RM (1994) History and present status of southern elephant seal populations. In: LeBoeuf BJ, Laws RM (eds) Elephant seals: population ecology, behaviour, and physiology. University of California Press, Berkeley, CA p 49–65
- Lebreton JD, Burnham KP, Clobert J, Anderson DR (1992) Modeling survival and testing biological hypotheses using marked animals: a unified approach with case studies. *Ecol Monogr* 62:67–118
- Lewis M, Campagna C, Quintana F, Falabella V (1998) Estado actual y distribución de la población elefante marino del sur en la Península Valdes, Argentina. *Mastozool Neotrop* 5:29–40
- Loeb V, Siegel V, Holm-Hanson O, Hewitt R, Fraser W, Trivelpiece W, Trivelpiece S (1997) Effects of sea-ice extent and krill or salp dominance on the Antarctic food web. *Nature* 387:897–900
- McCann TS (1980) Population structure and social organization of southern elephant seals *Mirounga leonina* (L). *Biol J Linn Soc* 14:133–150
- McCann TS (1985) Size, status and demography of southern elephant seal (*Mirounga leonina*) populations. In: Ling JK, Bryden MM (eds) Sea mammals in south latitudes: proceedings of a symposium of the 52nd ANZAAS Congress. South Australian Museum, Adelaide, p 1–17
- McCarthy MA, Broome LS (2000) A method for validating stochastic models of population viability: a case study of the mountain pygmy-possum (*Burramys parvus*). *J Anim Ecol* 69:599–607
- McCarthy MA, Lindenmayer DB, Possingham HP (2001a) Assessing spatial PVA models of arboreal marsupials using significance tests and Bayesian statistics. *Biol Conserv* 98:191–200
- McCarthy MA, Possingham HP, Day JR, Tyre AJ (2001b) Testing the accuracy of population viability analysis. *Conserv Biol* 15:1030–1038
- McConnell BJ, Fedak MA, Burton HR, Engelhard GH, Reijnders PJH (2002) Movements and foraging areas of naive, recently weaned elephant seals pups. *J Anim Ecol* 71:65–78
- McMahon CR, van den Hoff J, Burton HR, Davis PD (1997) Evidence for precocious development in female pups of the southern elephant seal, *Mirounga leonina*, at Macquarie Island. In: Hindell MA, Kemper C (eds) Marine mammal research in the southern hemisphere: status ecology and medicine, Vol 1. Surrey Beatty & Sons, Chipping Norton, p 92–96
- McMahon CR, Burton HR, Bester MN (1999) First-year survival of southern elephant seals, *Mirounga leonina*, at sub-Antarctic Macquarie Island. *Polar Biol* 21:279–284
- McMahon CR, Burton HR, Bester MN (2000) Weaning mass and the future survival of juvenile southern elephant seals, *Mirounga leonina*, at Macquarie Island. *Antarct Sci* 12:149–153
- McMahon CR, Burton HR, Bester MN (2003) A demographic comparison of two southern elephant seal populations. *J Anim Ecol* 72:61–74
- Nicholls DG (1970) Dispersal and dispersion in relation to the birth site of the southern elephant seal, *Mirounga leonina*, of Macquarie Island. *Mammalia* 43:147–159
- Pistorius PA, Bester MN (2002) Juvenile survival and population regulation in southern elephant seals at Marion Island. *Afr Zool* 37:35–41
- Pistorius PA, Bester MN, Kirkman SP (1999a) Dynamic age-distributions in a declining population of southern elephant seals. *Antarct Sci* 11:445–450
- Pistorius PA, Bester MN, Kirkman SP (1999b) Survivorship of a declining population of southern elephant seals, *Mirounga leonina*, in relation to age, sex and cohort. *Oecologia* 121:201–211
- Pistorius PA, Bester MN, Kirkman SP, Taylor FE (2001) Temporal changes in fecundity and age at sexual maturity of southern elephant seals at Marion Island. *Polar Biol* 24:343–348
- Reed JM, Mills LS, Dunning JB, Menges ES and 5 others (2002) Emerging issues in population viability analysis. *Conserv Biol* 16:7–19
- Seber GAF (1965) A note on the multiple recapture census. *Biometrika* 52:319–335
- Slip DJ, Burton HR (1999) Population status and seasonal haulout patterns of the southern elephant seal (*Mirounga leonina*) at Heard Island. *Antarct Sci* 11:38–47
- Stearns SC (1992) The evolution of life histories. Oxford University Press, Oxford
- Trites AW, Livingston PA, Vasconcellos MC, Mackintosh S, Springer AM, Pauly D (1999) Ecosystem change and the decline of marine mammals in the Eastern Bearing Sea: testing the ecosystem shift and whaling hypothesis. *Fisheries Centre Res Rep* 7:1–106
- van den Hoff J (2001) Dispersal of southern elephant seals (*Mirounga leonina*) marked at Macquarie Island. *Wildl Res* 28:41–418
- White GC, Burnham KP (1999) Program MARK: survival estimation from populations of marked animals. *Bird Study* 46:120–138
- White WB, Peterson RG (1996) An Antarctic Circumpolar Wave in surface pressure, wind, temperature, and sea ice extent. *Nature* 380:699–702