

# Expectations for population growth at new breeding locations for the vulnerable New Zealand sea lion (*Phocarctos hookeri*) using a simulation model

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## Abstract

Management plans for threatened or recovering large vertebrate species that are increasing in population size and range focus on the establishment of viable populations within set temporal limits. New Zealand (Hookers) sea lions (*Phocarctos hookeri*) were declared a threatened species in 1997, and New Zealand legislation requires that threatened species of marine mammals must be managed to reduce human-induced mortality and achieve a non-threatened status within 20 years. The present breeding distribution of *P. hookeri* is highly localised, with over 95% of total annual pup production located at Auckland Islands and almost all of the remainder at Campbell Island. Breeding elsewhere has been ephemeral or restricted to < 10 adult females. The only recorded sustainable breeding at a new location has been at Otago, South Island, New Zealand. This breeding population consisted of a total of four breeding females in 2002 and is derived from one immigrant female that gave birth to her first pup in the 1993/1994 breeding season. The New Zealand Department of Conservation management plan specifies that to achieve a non-threatened status *P. hookeri* (1) at Otago must increase in the number of breeding females to  $\geq 10$ , and (2) must establish  $\geq 2$  new breeding locations within the 20-year time frame, each with  $\geq 10$  breeding females. This study (1) projects the population growth trends at a new location (Otago) to see if it will achieve  $\geq 10$  breeding females within the legislated time frame, and (2) examines the likelihood that other breeding locations will establish elsewhere given the demographic information available for this species. We present 20 deterministic and three stochastic Leslie matrix model scenarios for female population growth for the initial years following the start of breeding at a new location. Our results indicate that (1) a new breeding population derived from one immigrant female is unlikely to reach 10 breeding females in 20 years; this duration is more likely to be 23–41 years (deterministic models) or 23–26 years (stochastic model), (2) the likelihood of two new sites establishing within 20 years is unquantifiable, but the probability is low, and (3) if the legislated outcome and time limit are not revised in the population management plan, the feasibility and effectiveness of re-locating young females could be investigated.

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## 1. Introduction

Some large species of carnivore that experienced considerable reductions in population size and range through anthropogenic causes are now recovering due to protective legislation, establishment of reserves, habitat improvement, and increases in food resources

(e.g. European wolves, *Canis lupus*—Boitani, 1992; Corsi et al., 1999; sea otters, *Enhydra lutris*—Dean et al., 2002). Management plans for such species focus on the establishment or recovery of viable populations within designated temporal limits (Tear et al., 1993), but the criteria set to achieve these goals are often arbitrary (Gerber and VanBlaricom, 2001) and there is rarely an attempt to test the likelihood of achieving management goals. For example, estimating the duration required for a species to achieve a viable breeding population at a new location is fundamental. Hence, numerical models

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are often effective methods to examine the feasibility of conservation management goals (e.g. Bessinger and Westphal, 1998; Corsi et al., 1999; Gerber and Hilborn, 2001; Gerber and VanBlaricom, 2001; Jones, 2002).

Many pinniped (seal) species have increased markedly since near extinction through anthropogenic causes. These increases are attributable mainly to the cessation of hunting and their intrinsic capacity for rapid population growth and expansion (Smith, 1988; Reijnders et al., 1995; Hofmeyr et al., 1997; Bradshaw et al., 2000; Gerber and Hilborn, 2001; Lalas and Bradshaw, 2001). In contrast, several pinniped species have not recovered, including New Zealand (Hookers) sea lions, *Phocarctos hookeri* (Gales and Fletcher, 1999; Powles et al., 2000; Gerber and VanBlaricom, 2001; Kretzmann et al., 2001; Pires and Neves, 2001). Pinnipeds tend to return repeatedly to breed at their natal site (i.e. demonstrate philopatry—Hindell and Little, 1988; Lunn and Boyd, 1991; Gentry, 1998; Bradshaw et al., 2000; Pomeroy et al., 2000; McConkey et al., 2002c) and this could limit the capacity of some species to colonise new areas.

The present breeding distribution of *P. hookeri* is highly localised, with over 95% of total annual pup production located at Auckland Islands (50°S, 166°E—Gales and Fletcher, 1999) and almost all of the remainder at Campbell Island (53°S, 169°E—McNally et al., 2001). Breeding elsewhere has been ephemeral or restricted to <10 adult females (Childerhouse and Gales, 1998; McConkey et al., 2002c). Their prehistoric breeding distribution extended northward to include the New Zealand mainland (North Island, South Island and Stewart Island) from where they were extirpated by hunting (Childerhouse and Gales, 1998; McConkey et al., 2002a). The most recent species population estimate is 11,100–14,000 (95% confidence interval), and the population is thought to be stable (Gales and Fletcher, 1999). Otago (46°S, 170–171°E), southeast South Island, New Zealand, is now the northern limit of a year-round presence of the *P. hookeri* population, with an immigrant population estimated at 108 males and three females in 1999 (McConkey et al., 2002a). Breeding at Otago began with one of these immigrant females giving birth to her first pup in the 1993/1994 breeding season (McConkey et al., 2002c).

*P. hookeri* was declared a threatened species in August 1997 under provisions in the New Zealand Marine Mammals Protection Act 1978. This legislation requires that threatened species of marine mammals must be managed to reduce human-induced mortality and achieve a non-threatened status within 20 years (Manly and Walshe, 1999; Maunder et al., 2000). This goal is facilitated through a species population management plan draft written by the New Zealand Department of Conservation (Department of Conservation, in litt., 1999). Reviews of the concepts and implications of this population management plan have

focussed only on the implications of fisheries and fisheries-related mortalities to the main population at Auckland Islands (Manly and Walshe, 1999; Maunder et al., 2000). However, the plan states “to achieve a non-threatened status, the New Zealand sea lion must establish breeding colonies in areas other than the Auckland Islands”, but it does not examine the likelihood of establishment of new breeding colonies.

Understanding the behaviour of immigrants (real and potential) is a key concept in the establishment of new breeding ranges (Maehr et al., 2002). Often the kin structure of pioneering populations is unknown (Lambin et al., 2001) and, in the case of pinnipeds, new colonies are typically well established before they are noticed (Baker, 1978). In contrast, the immigrant founder female and all *P. hookeri* born at Otago are identifiable individuals that have been monitored continually since 1991 (McConkey et al., 2002c).

Estimates of the values for key demographic parameters remain unknown for *P. hookeri* (Gales and Fletcher, 1999; Manly and Walshe, 1999). However, previous studies have applied ranges of estimates to each unknown parameter in an effort to simulate scenarios for population growth for the female component (Manly and Walshe, 1999) and for the demography of a stable total population (Gales and Fletcher, 1999). In this paper we apply the maximum, most-likely and minimum estimates for the parameters from Manly and Walshe (1999), Gales and Fletcher (1999) and Otago (based on McConkey et al., 2002c) in deterministic and stochastic versions of a Leslie matrix model (Leslie, 1945; Lebreton and Clobert, 1991; Stearns, 1992) for population growth. We present scenarios for female population growth for the initial years following the start of breeding at a new location, and consider the likelihood of viable breeding populations establishing in the legislated temporal requirement of 20 years. We discuss the implications of this population model to the New Zealand sea lion population management plan, and consider both passive and active management strategies as options for increasing the likelihood of new breeding locations establishing.

## 2. Methods

### 2.1. Threatened status of *Phocarctos hookeri*

Following IUCN criteria, *P. hookeri* is designated as vulnerable under code D2 “typically, area of occupancy < 100 km<sup>2</sup> or < five locations” (IUCN, 2000). The draft population management plan defined *P. hookeri* breeding locations as “sites where breeding produces at least 10 pups in each of at least three successive years, where the population is increasing, and where offspring return each year to the same site” (Department of Conservation, in

litt., 1999). The population management plan concluded that breeding was restricted to only two, possibly three, locations: northern Auckland Islands (Enderby and Dundas Islands), Campbell Island, and possibly Figure of Eight Island (southern Auckland Islands).

## 2.2. Females breeding at Otago

Breeding females at Otago were identified by tags applied during previous tagging programmes, or by distinctive features recorded photographically (McConkey, 1999). Females and pups at Otago were monitored to August 2002 following the methods described in McConkey et al. (2002c). A total of 9–10 pups were born at Otago up to and including the 2000/2001 breeding season, all in the lineage of the founder immigrant female (McConkey et al., 2002c). We updated these records to describe this population including the 2001/2002 breeding season.

## 2.3. Demographic parameters

Notation and definitions for demographic parameters are presented in Table 1. Because sea lions are polygynous, colonial breeders with pup production related to the abundance and demographic parameters of females, we followed the method used by Manly and Walshe (1999) and modelled only the female population.

Females at Auckland Islands give birth to a single pup from the first week in December to the third week in January, with a mean birth date of 24 December (Gales, 1995). McConkey et al. (2002b) designated 1 January (1 week later than the mean birth date in Gales, 1995) as the nominal birth date of New Zealand sea lions, so that the ages of individuals in integer years ( $x$ ) coincided with calendar years. Pups are suckled for up to 1 year, but suckling can extend to 2 years if mothers do not give birth in successive years (Cawthorn et al., 1985).

Females reach sexual maturity at 3 years of age, can give birth for the first time at 4 years of age, and can pup annually thereafter (Cawthorn et al., 1985; Gales, 1995). Gales and Fletcher (1999) and Manly and

Walshe (1999) designated females as adult once they reached 3 years—the age of sexual maturity. We changed this designation to 4 years, the age at which females can give birth to their first pup because the draft population management plan (Department of Conservation, in litt., 1999) defined breeding locations in terms of pup production, not by the number of adult females.

Manly and Walshe (1999) allocated two values for annual probability of survival of females: juvenile survival probability =  $S_J$  for the first 3 years of life ( $x=0, 1, 2$ ), and adult survival probability =  $S_A$  for older animals ( $x=3-17$ ). We replaced  $S_J$  with  $p_{0 \rightarrow 2}$  and  $S_A$  with  $p_{3 \rightarrow 17}$ . Gales and Fletcher (1999) used a different notation for annual survival probability, where their  $S_1$ ,  $S_2$  and  $S_3$  correspond respectively to  $p_0$ ,  $p_1$  and  $p_2$  in this paper.

Manly and Walshe (1999) set female maximum lifespan ( $L_{\max}$ ) at 18 years, following the maximum age deduced from growth layers in teeth from an unspecified sample size by Cawthorn et al. (1985). Under this designation, any females that survive to 18 years (probability =  $l_{18}$ ) die at the end of their 18th year. A sample of only eight adult females extended the maximum-recorded lifespan to 21 years (Dickie, 1999), and so additional samples are likely to further increase  $L_{\max}$ . We therefore designated  $L_{\max}=25$  years for all scenarios with the exception of those derived from values from Manly and Walshe (1999).

We defined annual fecundity ( $m_x$ ) as the annual average number of females born per adult female at  $x$  years of age. Both Manly and Walshe (1999) and (after adjustment for an even sex ratio at birth) Gales and Fletcher (1999) applied a range of 0.30–0.45 for  $m_x$  across all ages of adult females, but neither study designated a frequency of breeding (e.g. annual or biennial) with respect to their allocated values.

## 2.4. Deterministic Leslie matrix model

To test specific hypotheses of population change through time based on previous modelling attempts for this species (Gales and Fletcher, 1999; Manly and Walshe, 1999) and most-likely scenarios, we ran 20 deterministic Leslie matrix model scenarios (numbered M1–M20) for the number of females in the population through time. Matrices were projected with dimensions of 101 rows, where the sequence of rows represented consecutive calendar years ( $t=0-100$ ), and  $L_{\max}$  columns, where the sequence of columns represented consecutive year classes of female sea lions ( $x=0-L_{\max}$ ).

The first 21 rows of the model involved only small numbers of animals. This affected our presentation in two ways. First, in each year ( $t$ ) we calculated and presented the number of female pups:

$$N_{t,0} = \sum_{x=4}^{L_{\max}} m_x N_{t,x},$$

the number of females > 1 year of age:

Table 1

Notation and definitions for demographic parameters for female New Zealand sea lions

$x$	= age (integer years) of females
$t$	= time (integer years)
$p_x$	= probability of annual survival of females from age $x$ to age $x+1$
$l_x$	= survivorship: probability of a female surviving from birth to age $x = p_0 p_1 \dots p_{x-1}$
$L_{\max}$	= maximum lifespan: designated maximum age (integer years) of females
$m_x$	= annual fecundity: proportion of females at age $x$ that produce a female pup
$N_{t,x}$	= number (fractional number) of females at age $x$ in year $t = p_{x-1} N_{t-1,x-1}$
$N_{t,0}$	= pup production: number of female pups (age 0) in year $t = L_{\max} \sum_{x=4}^{L_{\max}} p_x N_{t,x}$
$\lambda$	= eigenvalue: annual rate of change in number for a population with stable demography

$$N_{t,1 \rightarrow L_{\max}} = \sum_{x=1}^{L_{\max}} S_{x-1} N_{t-1,x-1},$$

and the total number of females:

$$N_t = N_{t,0} + N_{t,1 \rightarrow L_{\max}}$$

as fractional numbers (a biological impossibility) rather than as integers. Average annual probabilities of survival are almost always  $< 1.0$ , and so presenting numbers as integers would reduce  $N_1$  (the sum of entries in row 2 of the matrix) to zero and therefore immediately terminate all simulations. Second, we targeted maximum, most-likely and minimum values for parameters so that our simulations generated absolute ranges in possible population size.

We applied a Leslie matrix model to simulate two series of scenarios for changes in female population size and demography following breeding derived from one adult female which gave birth to her first pup in year  $t=0$ . The first was for a hypothetical initiation of breeding at a new location. Here, entries for all cells in the first row were set to zero except for one 4-year-old female ( $N_{0,4} = 1$ ) and her female pup ( $N_{0,0} = 0.50$ ). The second was for extrapolations from females breeding at Otago in calendar year 2002. Here entries for cells were set to recorded numbers from year 0 (1994) to year 8 (2002).

The relationship between population sizes in consecutive years can be calculated as:

$$N_t = \lambda_t N_{t-1}$$

where  $\lambda_t$  = the annual rate of change of the population between years  $t-1$  and  $t$ . All our simulations assumed a constant annual rate of change in population size ( $\lambda$ ), and a concomitant stable demography within 30–50 years.

### 2.5. Stochastic Leslie matrix model

We applied values for the demographic parameters outlined in the deterministic model to create the three most-likely scenarios of growth in the Otago female breeding population incorporating a stochastic element. Stochastic projections of the Leslie matrix are based on estimates of standard deviation (S.D.) of the survival and fecundity parameters, and provide confidence intervals to numerical projections of population size and demography through time. The three scenarios (all using  $L_{\max} = 25$  years) modelled were:

1. The mean of the most-likely minimum and maximum values derived from Gales and Fletcher (1999). Estimates of standard deviation were calculated as half the difference between the

maximum and minimum values for each parameter value. Here,  $p_0 = 0.68$  (S.D. = 0.100),  $p_{1 \rightarrow 24} = 0.85$  (S.D. = 0.100) and  $m_{4 \rightarrow 25} = 0.375$  (S.D. = 0.075).

2. An assessment for Otago under a hypothetical scenario that one of the founder female's surviving daughters died before reaching reproductive age. Estimates of survival (and S.D.) were derived from the three scenarios where one of the founder female's surviving daughters died prior to reaching breeding age. Here,  $p_0 = 0.61$  (S.D. = 0.052),  $p_{1 \rightarrow 24} = 0.87$  (S.D. = 0.018) and  $m_{4 \rightarrow 25} = 0.375$  (S.D. = 0.025).
3. The mean of the most-likely minimum and maximum values for parameters derived from the Otago deterministic scenarios. In cases where the minima and maxima were identical, we assumed realistic values of standard deviation from other scenarios or previous modelling attempts (e.g. Manly and Walshe, 1999). Here,  $p_0 = 0.825$  (S.D. = 0.025),  $p_{1 \rightarrow 24} = 0.925$  (S.D. = 0.025) and  $m_{4 \rightarrow 25} = 0.375$  (S.D. = 0.025).

We designed a Monte Carlo simulation to project the Leslie matrix parameters as chosen randomly from a Normal distribution (i.e. assuming a Normal distribution around the mean and associated standard deviation for each parameter value—Manly, 1997). We ran 5000 iterations of the each scenario projecting the number of adult females (age  $\geq 4$  years) to 50 years from the first year a founding female gave birth to her first pup (i.e. 1 female age 4 years and 0.5 female pups in year 0).

## 3. Results

### 3.1. Records for females breeding at Otago

Records for breeding at Otago to the end of 2001 are described in detail in McConkey et al. (2002c). These values were updated to the end of 2002 (Table 2). The female population in 2001 included three breeders: the founder female ( $F_0$ ), her first ( $F_{0,1}$ ) and second daughter ( $F_{0,2}$ ). A total of 12–13 pups were born at Otago in the 8 years from the 1993/1994 to the 2001/2002 breeding seasons (Table 2). Through 2002 all four breeding females and their youngest offspring were based together at Victory Beach (45°50'S, 170°43' E), Otago Peninsula, Otago.

### 3.2. Estimates for values of parameters

The 10 of the 12–13 pups which survived their first 2 months of life were all alive in 2002, corresponding to values for  $p_0$  of 0.83 (from 12 pups) and 0.77 (from 13

Table 2  
Demography of the female breeding population of New Zealand sea lions at Otago

Female code	Female cohort	Female age (years) in 2002	Pup production by age of adult females (years)												
			4	5	6	7	8	9	10	11	12	13	14	15	
F <sub>0</sub>	1986/1987	15	0	0	Aborted foetus	Female F <sub>0,1</sub>	0	Female F <sub>0,2</sub>	0	Female F <sub>0,3</sub>	Male M <sub>0,1</sub>	Female F <sub>0,4</sub> <sup>a</sup>	Male M <sub>0,2</sub> <sup>a</sup>	Male M <sub>0,3</sub>	
F <sub>0,1</sub>	1993/1994	8	Male M <sub>0,1,1</sub>	0	<sup>b</sup>	Female F <sub>0,1,1</sub>	0								
F <sub>0,2</sub>	1995/1996	6	Aborted foetus	Male M <sub>0,2,1</sub>	Female F <sub>0,2,1</sub>										
F <sub>0,3</sub>	1997/1998	4	Female F <sub>0,3,1</sub>												

Records from McConkey et al. (2002c) from the initiation of breeding to 2001 updated to include the 2001–2002 breeding season, where 2002 records are the terminal entries in each row.

<sup>a</sup> Two pups were dead at <2 months old. All other animals were alive in 2002.

<sup>b</sup> Status unverified for one possible birth: F<sub>0,1</sub> appeared pregnant but no pup was found (McConkey et al., 2002c).

pups). One of the two verified pup deaths was attributable to anthropogenic causes (McConkey et al., 2002c). Because we were mainly focused on natural rates of population growth, we also considered omission of this pup from the total, which produced values for  $p_0 = 0.91$  (from 11 pups) and  $p_0 = 0.83$  (from 12 pups). A hypothetical addition of one extra death to total four deaths among 13 pups would have lowered  $p_0$  to 0.69. From this assessment we allocated a rounded maximum of 0.85 and minimum of 0.70 for values of  $p_0$  in our model scenarios.

None of the individuals in the study population (Table 2) died at the age of  $\geq 1$  year(s) through the 8 years following the initiation of breeding. Some indication of the values to use as the probability of survival was provided by the insertion of hypothetical deaths in 2002. Summing the ages of the females  $\geq 1$  year(s) (founder female, her three daughters and one of her granddaughters) produced a total of 34 sea lion-years with no deaths. If one of these females had died, then  $p_{1 \rightarrow L_{\max}} = 33/34 = 0.97$ . When this assessment was restricted to the total of 19 sea lion-years for the Otago-born females, one death would have  $p_{1 \rightarrow L_{\max}} = 18/19 = 0.95$  and two deaths would equate to  $17/19 = 0.90$ . We concluded that a maximum of 0.95 and minimum of 0.85 were realistic estimates for  $p_{1 \rightarrow 24}$ . We assumed an equal sex ratio at birth for all model scenarios as in Gales and Fletcher (1999) and Manly and Walshe (1999). The 12 pups of known sex born at Otago consisted of seven females and five males.

From the records of breeding females at Otago (Table 2), we allocated three values for annual age-specific fecundity ( $m_x$ ): a maximum of 0.50 female pups for  $m_{4 \rightarrow 25}$  to indicate that all females  $\geq 4$  years of age reproduced annually; a minimum of 0.375 for  $m_{5 \rightarrow 25}$  to indicate that half reproduced annually and half bien-

nially; and a minimum of 0.25 for  $m_4$  to indicate that half of adult females are primiparous at 4 years of age, and the other half at 5 years of age.

### 3.3. Scenarios for deterministic population growth in the 20 years following initiation of breeding

We ran 20 Leslie matrix model scenarios (M1–M20) for female population growth of New Zealand sea lions at a new location derived from one immigrant female which gave birth to her first pup in year 0 (Table 3). Corresponding survival–probability curves ( $l_{0 \rightarrow L_{\max}}$ ; Fig. 1) and population-growth curves ( $l_{0 \rightarrow 20}$ ,  $N_{4 \rightarrow 25}$ ; Fig. 2) are presented for the range of values for demographic parameters.

Application of minimum values for parameters from Manly and Walshe (1999) (M2 and M4) and from Gales and Fletcher (1999) (M7) generated negative growth in population size ( $\lambda < 1.00$ ). Under the Gales and Fletcher (1999) scenario (M8) presented as stable ( $p_0 = 0.68$ ,  $p_{1 \rightarrow 24} = 0.82$ ,  $m_{4 \rightarrow 25} = 0.375$ ), the population would decline at 2% per annum (Table 3). Our model using minimum values (M12) and Gales and Fletcher (1999) most-likely values (M6) generated zero growth in population size ( $\lambda = 1.00$ ). This discovery of two scenarios that generated long-term stability in population size (M6 and M12) prompted further investigation into the estimates of minimum annual probability of survival for females required to sustain a viable population. The obligatory dependence of pups <1 year of age on their lactating mothers implies that the survival rate of pups ( $p_0$ ) cannot exceed the annual survival rate of adult females ( $p_{4 \rightarrow L_{\max}}$ ). We generated new scenarios, therefore, by applying the same annual survival rates across all ages. Four scenarios were generated with annual survival rates set at 0.85 and 0.80 across the range of

Table 3  
Twenty scenarios (M1–M20) for population growth at a new location derived from one immigrant female that gives birth to her first pup in year 0

Scenario	Source	$L_{\max}$	$p_0$	$p_{1 \rightarrow 2}$	$p_{3 \rightarrow 17}$	$p_{18 \rightarrow 24}$	$l_{18}$	$l_{25}$	$m_4$	$m_{5 \rightarrow 25}$	$N_{20, 4 \rightarrow 25}$	$\lambda$
M1	M&W text maximum	18	0.85	0.85	0.95	0	0.32	0	0.45	0.45	7.3	1.12
M2	M&W text minimum	18	0.70	0.70	0.85	0	0.03	0	0.35	0.35	0.3	0.95
M3	M&W table maximum	18	0.85	0.85	0.95	0	0.32	0	0.40	0.40	5.8	1.11
M4	M&W table minimum	18	0.70	0.70	0.85	0	0.03	0	0.30	0.30	0.2	0.93
M5	G&F maximum	25	0.78	0.95	0.95	0.95	0.33	0.23	0.45	0.45	9.3	1.15
M6	G&F most likely	25	0.68	0.85	0.85	0.85	0.04	0.01	0.375	0.375	0.8	1.00
M7	G&F minimum	25	0.58	0.75	0.75	0.75	<0.01	<0.01	0.30	0.30	<0.1	0.86
M8	G&F $p_{1 \rightarrow 24} = 0.82$	25	0.68	0.82	0.82	0.82	0.02	<0.01	0.375	0.375	0.4	0.97
M9	Our model maximum	25	0.85	0.95	0.95	0.95	0.36	0.25	0.50	0.50	15.9	1.17
M10	Our model likely maximum	25	0.85	0.95	0.95	0.95	0.36	0.25	0.25	0.375	8.3	1.13
M11	Our model likely minimum	25	0.80	0.90	0.90	0.90	0.13	0.06	0.25	0.375	2.8	1.07
M12	Our model minimum	25	0.70	0.85	0.85	0.85	0.04	0.01	0.25	0.375	0.8	1.00
M13	$p_{0 \rightarrow 24} = 0.80$ ; $m_{4 \rightarrow 25} = 0.45$	25	0.80	0.80	0.80	0.80	0.02	<0.01	0.45	0.45	0.5	0.99
M14	$p_{0 \rightarrow 24} = 0.80$ ; $m_{4 \rightarrow 25} = 0.50$	25	0.80	0.80	0.80	0.80	0.02	<0.01	0.50	0.50	0.7	1.00
M15	$p_{0 \rightarrow 24} = 0.85$ ; $m_{4 \rightarrow 25} = 0.25$	25	0.85	0.85	0.85	0.85	0.05	0.02	0.25	0.25	0.6	0.98
M16	$p_{0 \rightarrow 24} = 0.85$ ; $m_{4 \rightarrow 25} = 0.375$	25	0.85	0.85	0.85	0.85	0.05	0.02	0.375	0.375	1.2	1.03
M17	Otago maximum	25	0.85	0.95	0.95	0.95	n.a.	n.a.	0.50	0.50	19.3	1.17
M18	Otago likely maximum	25	0.85	0.95	0.95	0.95	n.a.	n.a.	0.25	0.375	13.7	1.13
M19	Otago likely minimum	25	0.80	0.90	0.90	0.90	n.a.	n.a.	0.25	0.375	7.1	1.07
M20	Otago minimum	25	0.70	0.85	0.85	0.85	n.a.	n.a.	0.25	0.375	3.3	1.00

See Table 1 for notation. Source references for values for parameters: M&W = Manly and Walshe (1999); G&F = Gales and Fletcher (1999).

values for annual fecundity from 0.25 to 0.50 (Table 3: M13–M16).

The rate of increase in female population size accelerates if > 1 immigrant females begin breeding at a new location. Fig. 3 shows the relationship between the number of years required to achieve a breeding population of 10 adult females and the number of immigrant breeding females using the likely range in values for parameters derived from our model (Table 3: M10 and M11).

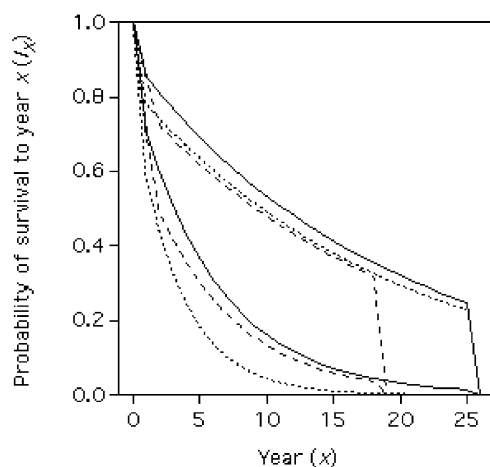


Fig. 1. Female survival curves for the range of scenarios (M) for annual survival probabilities in Table 3. Solid lines: values from this study with maximum lifespan  $L_{\max} = 25$  years (maximum = M9, M10 and minimum = M12). Dashed lines: values from Manly and Walshe (1999) with  $L_{\max} = 18$  years (M1, M3 and M2, M4). Dotted lines: values from Gales and Fletcher (1999) plotted to 25 years (M5 and M7).

Scenarios for growth of the Otago female breeding population (Table 3: M17–M20) were calculated from the range of values for parameters in our model (Table 3: M9–M12; Fig. 4). Population growth curves were extrapolated to 2018, the year that represents 20 years after the 1997 declaration of *P. hookeri* as a threatened species (Manly and Walshe, 1999). Year 20, designating 20 years after the instigation of breeding at Otago in 1994, is therefore 2014.

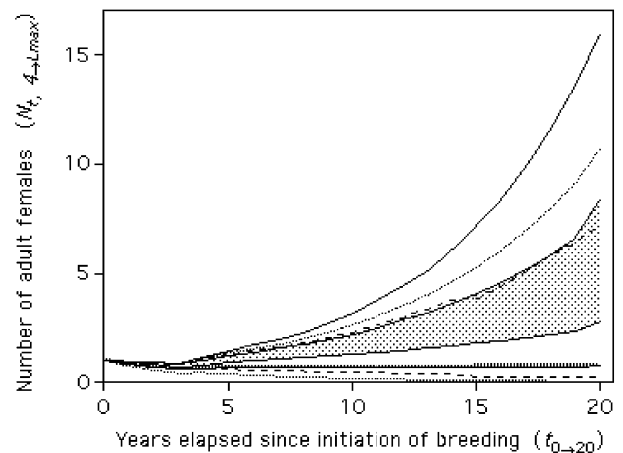


Fig. 2. Deterministic population growth curves for the 20 years following breeding derived from one immigrant female which gave birth to her first pup in year 0. The lines show the range of scenarios (M) from Leslie matrix model simulations of number of adults (females  $\geq 4$  years old) from values for demographic parameters in Table 3. Solid lines: our model—maximum (M9), likely range (M10 and M11) shaded, and minimum (M11). Dashed lines: values from Manly and Walshe (1999)—maximum (M1) and minimum (M4). Dotted lines: values from Gales and Fletcher (1999)—maximum (M5), most likely (M6) and minimum (M7).

### 3.4. Stochastic scenarios

Two of our three stochastic scenarios projected little or no increase in population size in the 20 years following the initiation of breeding at a new location (Fig. 5). The first of these scenarios (Fig. 5a) was derived from the most-likely values and ranges for parameters presented by Gales and Fletcher (1999), and the second scenario (Fig. 5b) was derived from the Otago data

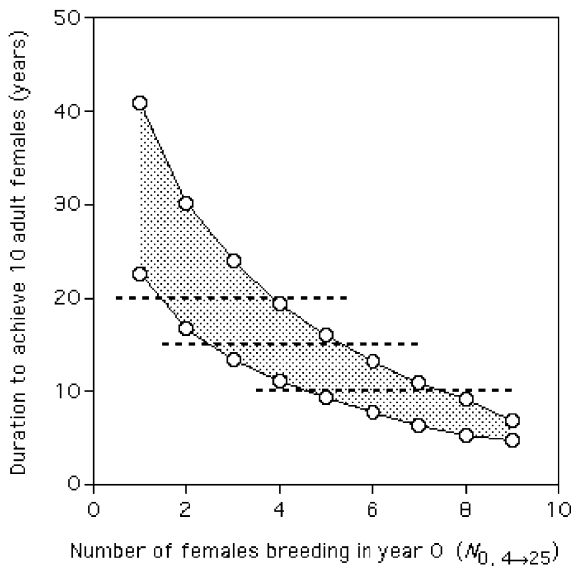


Fig. 3. Duration required to achieve 10 adult females ( $\geq 4$  years old) after the initiation of breeding at a new location. Presented range calculated from our model likely range scenarios (Table 3: M10 and M11). Horizontal dotted lines delineate numbers required for durations of 20, 15 and 10 years.

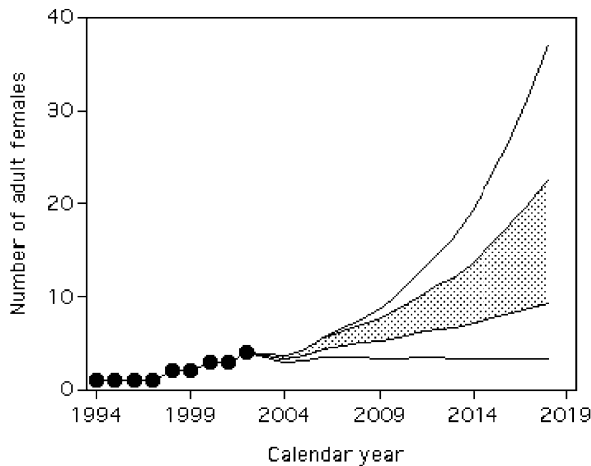


Fig. 4. Deterministic population growth curves for breeding females at Otago. Recorded numbers are plotted from the birth of the first pup in the 1993/1994 breeding season to 2002 and then extrapolated to include the 20 years following the declaration of threatened species status in 1997. The lines show the range of scenarios (M) from Leslie matrix model simulations of number of adults (females  $\geq 4$  years old) from values for demographic parameters in Table 3: maximum (M17), likely range (M18–M19) shaded, and minimum (M20).

modelled to account for the hypothetical death of one daughter of the founder female. Application of the most-likely Otago parameter values produced a tangible increase in the number of females ( $\lambda = 1.10$ ; Fig. 6), with a predicted adult female population of 5.7–7.5 individuals after 20 years. Under this scenario it would require 23–26 years to attain the target population of 10 adult females if the population were derived from one founder female.

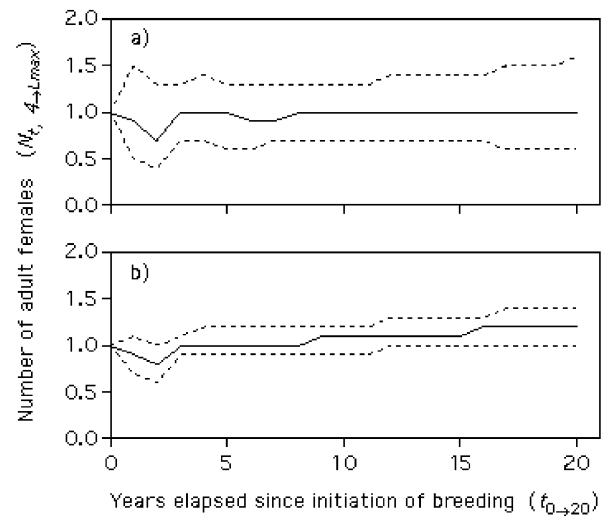


Fig. 5. Stochastic population growth curves and 95% confidence intervals for the 20 years following initiation of breeding for two scenarios with little or no increase in population size: (a) derived from deterministic scenarios M5–M7 (Table 3)—the most-likely scenario from Gales and Fletcher (1999) and (b) derived from deterministic scenarios M10–M12—the Otago scenarios assuming one of the founder female’s surviving daughters had died before reaching reproductive age.

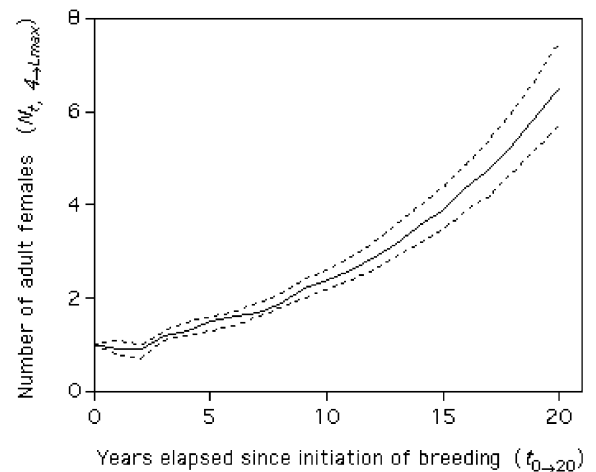


Fig. 6. Stochastic population growth curve and 95% confidence interval for the 20 years following initiation of breeding derived from deterministic scenarios M10 and M11 (Table 3)—the mean of the most-likely minimum and maximum parameters derived from the Otago scenarios.

## 4. Discussion

### 4.1. Reality of allocated values for demographic parameters

The depiction of survival-probability curves for female *P. hookeri* indicated a potentially important major disparity in the allocation of maximum lifespan ( $L_{\max}$ ). We regard the 18 years ( $L_{18}$ ) applied by Manly and Walshe (1999) as superseded by 21 years from the data presented by Dickie (1999). No rigorous definition exists for  $L_{\max}$  but three possible values have been used in population models: maximum recorded age, or the 99th or 98th percentile of age distribution in a sample (Slooten and Lad, 1991). Given that Dickie (1999) increased the maximum-recorded age of females by three years from a sample of only eight adult females, we regarded  $L_{25}$  as more realistic. However, survival from birth to 25 years ( $l_{25}$ ) appears realistic only when the minimum values of annual survival probability for females are used, and these minima do not generate increases in population size. Corresponding maximum values for  $l_{25}$  were approximately 0.25, a proportion too large to expect that all females 25 years of age would die within 1 year.

There are three possible explanations for this disparity between  $L_{25}$  and  $l_{25}$ . First, our value of 25 years for  $L_{\max}$  may still be too low. Steller sea lion (*Eumetopias jubatus*) females are known to live to 30 years, but data on reproductive longevity are generally lacking for pinnipeds (Wickens and York, 1997). Second, the average age-specific probability of survival may vary and, in particular, may decrease with age as for many ungulate species (Loison et al., 1999; Ericsson and Wallin, 2001). However, the values of survival used in our model are similar to those observed for other otariid seals (Wickens and York, 1997). Third, mass mortality events such as that recorded for the *P. hookeri* population at Auckland Islands in 1998 (Baker, in litt., 1999) may cause episodic depressions in the probability of survival (e.g. Trillmich and Ono, 1991).

To simulate both stable and increasing trends in population size, we estimated the minimum values for the annual probability of survival for pups ( $p_0$ ) and older females ( $p_{1 \rightarrow 24}$ ), and the annual fecundity of adult females ( $\geq 4$  years of age). For constant survival across all ages, an annual probability of 0.80 produced these trends only when all adult females reproduced annually. Although this represents a best-case scenario, it is unlikely. A corresponding annual survival rate of 0.85 did not produce the targeted population trends when all females reproduced biennially ( $m_{4 \rightarrow 25} = 0.25$ ), but generated a long-term increase of 3% per annum ( $\lambda = 1.03$ ) when half of the females reproduced annually and the other half biennially ( $m_{4 \rightarrow 25} = 0.375$ ). We conclude that two realistic series of values for demographic parameters

simulate stable female population sizes: the most-likely values from Gales and Fletcher (1999) ( $p_0 = 0.68$ ,  $p_{1 \rightarrow 24} = 0.85$ ,  $m_{4 \rightarrow 25} = 0.375$ ) and the minimum values from our model ( $p_0 = 0.70$ ,  $p_{1 \rightarrow 24} = 0.85$ ,  $m_4 = 0.25$ ,  $m_{5 \rightarrow 25} = 0.375$ ). Given that the Otago population is derived from a single mother and her progeny, and that the founder female has been a successful mother, the history of the Otago population should perhaps be considered as an extreme scenario. This further supports the use of the minimum values from our model as the most realistic. The intended scenario of stable population size modelled by Gales and Fletcher (1999) was not achieved using the parameter values that they concluded to be 'most likely'. Under their final scenario for a stable population ( $p_0 = 0.68$ ,  $p_{1 \rightarrow 24} = 0.82$ ,  $m_{4 \rightarrow 25} = 0.375$ ), sea lion numbers would decline at 2% per annum. To correct this scenario, Gales and Fletcher (1999) should have concluded that the scenario,  $p_0 = 0.68$ ,  $p_{1 \rightarrow 24} = 0.85$ ,  $m_{4 \rightarrow 25} = 0.375$ , was most likely. Indeed, regardless of the value used for  $L_{\max}$  (18 or 25), the above scenario produces a declining population size when  $p_{1 \rightarrow 24} < 0.85$ .

Values for the parameters applied in our model were within the range of estimates described for other species of otariid seals (fur seals and sea lions—Wickens and York, 1997). However, many parameters are still poorly understood not only for *P. hookeri* (Gales and Fletcher, 1999), but also for other species within the family (Wickens and York, 1997). Furthermore, it has been demonstrated that estimates of survival probability for pups and older females in the otariids can vary markedly among species, and intra-specifically with region, climate and population density (Wickens and York, 1997; Gales and Fletcher, 1999; Bradshaw et al., 2003). Thus, models for population growth probably produce representative scenarios over long periods (i.e. several generations) but may not be realistic through shorter durations (e.g. 10–20 years).

### 4.2. Breeding at Otago

The death of one pup attributable to anthropogenic causes and the unknown reproductive status of one female in 1 year precluded the calculation of an exact value for average natural survival rate of pups. Instead, the observed  $p_0$  should be considered as in the range 0.77–0.91 from 11–13 pups. No sea lions of either sex born at Otago have died at older than 2 months ( $p_{1 \rightarrow 8} = 1.00$  from four females and three males = 27 sea lion years).

Newly colonised locations can often present a different breeding environment to immigrants. Immigrants may demonstrate a decrease in adult survival that is attributable to a reduced capacity to find and acquire the necessary food and other resources at the new locations (Lambin et al., 2001); e.g. protection from intra-specific



aggression within breeding harems (Cassini, 1999). Alternatively, immigrants subject to density-dependent survival at their natal location may encounter reduced intra-specific competition for food resources and breeding space, thus experiencing improved breeding conditions at the new location. Otago represents a re-colonisation of part of the prehistoric distribution from which the species was extirpated by humans (Childerhouse and Gales, 1998; McConkey et al., 2002a). There is no evidence that the probability of survival for pups at Otago is lower than at the species' population base at Auckland Islands (McConkey et al., 2002c). Otago continues to satisfy the criteria suggested by McConkey et al. (2002c) for the creation of a new breeding location for *P. hookeri*. Locally born females have shown regional philopatry, high survival probability and high reproductive success. All four breeding females and their youngest offspring were based at the same site, a beach on Otago Peninsula, in 2002. Thus, this congregation may indicate the initiation of the colonial breeding typical of the species.

Future growth in the Otago breeding population was assessed from a range of values for demographic parameters. Using likely minimum and maximum values, the model predicted a population of 6–12 adult females at 20 years from the instigation of breeding, at a long-term rate of annual increase of 7–13% ( $\lambda = 1.07$ – $1.13$ ). Unlike the threatened species of New Zealand birds (e.g. Jones, 2002), sea lions appear to be unaffected by introduced mammals and loss of habitat. However, there are two potential impacts that could inhibit the predicted increase of the Otago breeding population: (1) a natural mass mortality event such as that which occurred at Auckland Islands in 1998 (Baker, in litt., 1999); (2) the congregation of all breeding females at one site accessible to the public leaves them vulnerable to deliberate killing by humans as has been recorded for sea lions elsewhere at Otago (McConkey et al., 2002c).

#### 4.3. Implications for conservation and management

New Zealand sea lions are restricted to two, perhaps three, breeding locations using the definition in the draft population management plan (Department of Conservation, in litt., 1999) that breeding locations are sites where the number of philopatric females is increasing and  $\geq 10$  pups are born in three successive years. The population management plan's goal is for this species to have  $\geq 5$  breeding locations within 20 years of the declaration of threatened species status in August 1997. Our projections indicate that Otago can attain the category of a breeding location within this time frame, with a most-likely range of 9–22 adult females by 2018 with the results from the deterministic model.

However, a new breeding population derived from one immigrant female is unlikely to reach 10 breeding

females in 20 years. Our model's most-likely range of demographic parameter values indicated that this duration is more likely to be 23–41 years (deterministic model) or 23–26 years (stochastic model). We suggest that managers should use the upper values of these ranges when planning management and recovery plans.

Recruitment of immigrant females may account for much of the population growth during the establishment of new breeding locations by seals (Stewart et al., 1994; Bradshaw et al., 2000; Lalas and Bradshaw, 2001), and this recruitment may be enhanced after the initiation of colonial breeding (Baker, 1978; Gentry, 1998). Although other immigrant females have been resident at Otago (McConkey et al., 2002c), none have been recruited into the breeding population through the 8 years (1994–2002) elapsed since breeding began. Consequently, the probability of recruitment of immigrant females into the breeding population cannot be modelled. However, estimates can be designated for the number of breeding females required to generate 10 adult females in a given duration. An initial breeding population of 2–4 would achieve this in 20 years, 3–5 in 15 years and 5–7 in 10 years. Here, 15 years marks the duration remaining from 2002 to achieve 10 adult females at a new location in 20 years from 1997.

We conclude that the goal of  $\geq 5$  breeding locations for New Zealand sea lions is unattainable by 2018 under the present definition of breeding location and under present management practices. The addition of Otago as a breeding location will raise the total number of breeding locations for the species from 3 to 4, but no other locations at this time appear to support sustained pup production (Childerhouse and Gales, 1998; McConkey et al., 2002c). Consequently, the probability for the initiation of breeding at a new location cannot yet be modelled. However, the rates of natural immigration and colony establishment appear to be extremely low.

The simple solution to achieving the 20-year goal is semantic; the definition of "breeding location" could be made less rigorous. Alternatively, management philosophy may need a radical revision to consider the possibility of re-introducing young females from the Auckland Islands to potential new locations. The IUCN definition of a re-introduction is an "attempt to establish a species in an area which was once part of its historical range, but from which it has been extirpated or become extinct" (IUCN, 1996). Translocation (an overarching descriptor for moving populations of animals, including re-introductions—Wanless et al., 2002) has been used or considered both for pinnipeds (Hindell and Pemberton, 1997; Fraker and Mate, 1999; Lavigne, 1999; Ragen and Lavigne, 1999) and other vertebrate taxa (Griffith et al., 1989; Short et al., 1992; Marsh and Trenham, 2001; O'Toole et al., 2002).

However, it may be difficult to promote colony establishment using this technique given the philopatric behaviour of adult females, the migratory capacity of this species, and the requirement of both suitable marine and terrestrial habitats. Indeed, Griffith et al. (1989) stated that successful translocations of threatened species are rare, especially for carnivores given their delayed maturity and relatively low reproductive rates. Management authorities must also consider other aspects related to translocation, such as the pathological, genetic and ethical implications of such an action. The possibility of introducing disease into a relatively small sub-population is a realistic scenario given that mass, disease-related mortality events have occurred in this and other marine mammal species in recent years (Osterhaus et al., 1997; Harwood, 1998; Baker, in litt., 1999; Harvell et al., 1999). The maintenance of genetic diversity in small seal populations should also be a management priority. Indeed, translocations have been proposed for species where inbreeding depression may further reduce already low genetic diversity (Kretzmann et al., 1997). Finally, management authorities must also consider the ethical implications of translocating individuals, especially in the light of public scrutiny of research and management interventions (Barry and Oelschlaeger, 1996; Meffe, 1999).

We suggest that management authorities should investigate the feasibility of translocating 1- or 2-year-old females screened for disease first to locations such as Otago where adult females are already breeding. If these translocated females remain and breed when mature, then more young females could be translocated to locations already occupied by male sea lions (e.g. The Catlins—McConkey et al., 2002a,c; Stewart Island—McConnell, 2001). This may be a realistic strategy because we have shown that the establishment of at least one breeding female is sufficient to engender a new breeding colony. Further, Gerber and Hilborn (2001) reported that many populations of otariid seal species have recovered from low numbers, suggesting an innate capacity for re-colonization. Re-introductions should initially target locations that can be monitored easily and regularly (O'Toole et al., 2002). If successful, more remote locations could be seeded with young females. Translocation of young females may be a realistic addition to the current management strategy to achieve the goal of removing the New Zealand sea lion from the status of a threatened species within the legislated time frame.

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