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Predicting Life-History Traits for Female New Zealand Sea Lions, *Phocarctos hookeri*: Integrating Short-Term Mark-Recapture Data and Population Modeling

B. Louise CHILVERS, Ian S. WILKINSON, and Darryl I. MACKENZIE

The trade-off between survival and reproduction by individuals is central to understanding life-history parameters of a species. Few mammal species have life-history information from long-term research. Instead, demographic models are commonly utilized to investigate an individual's life-history strategy, species dynamics, and population trends. This research investigates age-related survival and reproductive performance of adult female New Zealand (NZ) sea lions (*Phocarctos hookeri*), using multistate mark-recapture data from known-age branded individuals over five years. The mark-recapture analysis was integrated with a population model to predict the lifetime reproductive output of female NZ sea lions. The integration of an analysis of short-term datasets with population modeling allows for the prediction of life-history parameters of long lived animals when long-term information is not available. While such approaches involve some caveats, it provides a framework for investigating population dynamics and is preferential to unsubstantiated assumptions. This technique can lead to better design and implementation of conservation management for long lived species.

Base code is provided in the online supplement.

Key Words: Auckland Islands; Fisheries interactions; Multi-state mark-recapture model; Population dynamics.

1. INTRODUCTION

An organism's evolutionary success is defined by its lifetime reproductive ability, an energetic trade-off between reproductive costs and long-term survival. This trade-off is an important factor in shaping life-history strategy for a species (Stearns 1992). Age at first

B. Louise Chilvers (✉) is Scientist, Marine Conservation Group, Department of Conservation, P.O. Box 10-420, Wellington 6011, New Zealand (E-mail: *lchilvers@doc.govt.nz*). Ian S. Wilkinson was Scientist, Marine Conservation Group, Department of Conservation, P.O. Box 10-420, Wellington 6011, New Zealand and now works for Department of Environment and Conservation, Locked Bag 914, Coffs Harbour, NSW 2450, Australia. Darryl I. Mackenzie is Statistician, Proteus Wildlife Research Consultants, P.O. Box 5193, Dunedin 9058, New Zealand.

breeding, previous breeding experience, body condition, age, senescence, population density, habitat, and environmental conditions can all influence reproductive costs and, therefore, life-history strategy (Goodman 1981; Reiter and LeBoeuf 1991; Stearns 1992; Lunn, Boyd, and Croxall 1994; Arnould 1997; Dabin et al. 2004; Beauplet et al. 2006; Hadley, Rotella, and Garrott 2007). Long-term studies investigating individual strategies are essential for understanding species population dynamics, particularly the primary building blocks, reproduction, and survival rates. There are, however, few species for which these demographic factors are known from long-term research. Instead demographic models can be used (Goodman 1981; McCallum 2000). However, lack of data can result in considerable uncertainty and unsustainable decisions if used for management or conservation of a species. For long-lived species with low fecundity, e.g., large mammals, population change has been demonstrated to be sensitive to variation in adult survival and reproduction performance (Goodman 1981; Stearns 1992; Sinclair 1996; Gaillard, Festabianchet, and Yoccoz 2000; McCallum 2000). In particular, age-related variation in survival is assumed to influence the evolution of reproductive traits and output, and consequently affect the size and dynamics of a given population (Stearns 1992; McCallum 2000). Hence, precise estimates of age-specific survival and reproductive output are needed to improve the accuracy of demographic models in long-lived mammals (Eberhardt 1985).

This study investigates age-related survival and reproductive performance in female New Zealand sea lions (*Phocarctos hookeri*, previously known as Hooker sea lions). The NZ sea lion is one of the world's rarest and most highly localized pinnipeds; classified as "Vulnerable in slow decline" by the International Union for the Conservation of Nature (IUCN 2008) and "Threatened" under the New Zealand Threatened Classification System (Hitchmough, Bull, and Cromarty 2007) and protected by the New Zealand Marine Mammals Protection Act, 1978. Their population size is estimated at between 10,000 and 13,000 animals, comprising approximately 5,000 adult animals (Campbell et al. 2006). This is one of the smallest population sizes reported for an otariid. The species pup production has shown a decline of 30% in the last eight years (Chilvers, Wilkinson, and Childerhouse 2007).

Over the past decade, interaction between the NZ sea lion population and the arrow squid (*Nototodarus sloanii*) trawl fishery, which operates on the Auckland Island shelf, has been investigated (Gales 1995; Chilvers et al. 2005, 2006; Chilvers 2008a, 2008b). With both sea lions and trawlers seeking squid as prey, incidental captures of NZ sea lions in squid trawl nets are inevitable, and up to 140 NZ sea lion deaths have been reported to occur each fishing season (Wilkinson, Burgess, and Cawthorn 2003). The impact of fisheries related mortality on the NZ sea lion population is, as yet, not fully understood, with several models suggesting that this level of take may limit the capacity for NZ sea lions to increase in number and, under some scenarios, result in population decline (Doonan and Cawthorn 1984; Woodley and Lavigne 1993), while others (Breen and Kim 2006) suggested that there would be little impact. Current management of NZ sea lion/fisheries interactions is based on output controls set as the number of NZ sea lions the trawl fishery catches before the fishery is closed for the season. This is referred to as Fisheries-Related Mortality Limit (FRML) and is currently established using an "adaptive" rule modeled through a stochastic population model that incorporates all sources of information to estimate distributions for

demographic parameters using Bayesian methods of statistical inference (Breen and Kim 2006). Biological data available for this model were limited with two key parameters of the modeling, female reproductive rate (pups per year) and survival, based on limited datasets.

The objectives of this research were to estimate the reproductive life span, reproductive ability, and age-related survival of adult female NZ sea lions using multistate mark-recapture data from known-age branded individuals over five years. The mark-recapture analysis was integrated with a population model to predict the lifetime reproductive output of female NZ sea lions.

2. METHODS

2.1. PRESENCE AND BREEDING STATUS OF BRANDED FEMALE NZ SEA LIONS

In 2000, 135 lactating adult female New Zealand sea lions with pups of the season from Sandy Bay, Enderby Island, Auckland Islands (50°30′S, 166°17′E) were hot branded with four-digit numbers (Wilkinson unpublished). The ages of 126 of these females were known from being tagged as pups or estimated via teeth aging (Childerhouse, Dickie, and Hessel 2004). Ages of the 126 known aged females ranged between four and 19 years in 2000 and between eight and 23 by 2004 (Figure 1). The Sandy Bay NZ sea lion breeding area is the second largest for the NZ sea lion species and produces between 400 and 500 pups each year (Chilvers, Wilkinson, and Childerhouse 2007). The 126 branded females represent approximately 30% of all breeding females at this site. Daily resightings, including reproductive status, were collected for these females between December 1 and February 20 during the austral summers of 2000–2001 to 2004–2005. Branded females that were found dead or known to have died in fisheries interactions between breeding seasons were reported. From the observations from each season, females were classified according to their reproductive status being: (A) pupped and pup survived >8 weeks; (B) pupped and pup died within first 8 weeks; (C) suckling a pup from a previous year (hence no pup of the year); and (D) no pup of the year and not suckling a pup from a previous year. Of interest was how the reproductive status of females changed annually, and whether the probability of survival varied with reproductive state and age. A natural framework for addressing
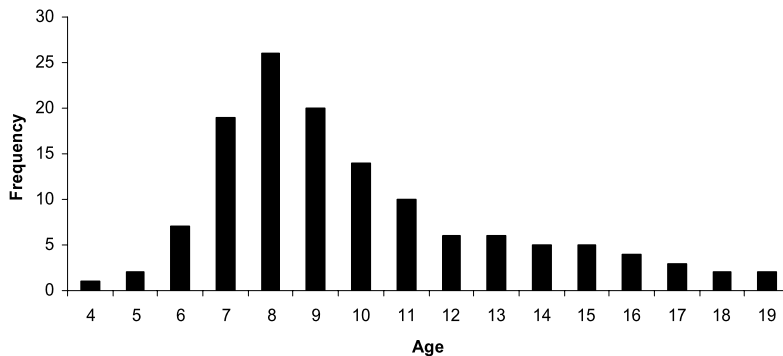

Figure 1.   Age distribution of female NZ sea lions at Sandy Bay when branded in 2000.

these questions is a multistate mark-recapture model (Williams, Nichols, and Conroy 2002) where "states" were defined by reproductive status.

2.2. ANALYSIS OF BRANDED FEMALE RESIGHTING DATA

In a multistate mark-recapture analysis, the probability of an animal being in a particular state at time $t + 1$, given its state at time t is defined by the transition probability matrix (TPM). The TPM thus provides a framework to estimate and model how the reproductive status of female NZ sea lions varies over time. Sea lion survival can also be incorporated in the TPM by considering death as a "state" with the obvious constraint that once dead, an animal remains dead. Technically this is known as an absorbing state. To define the TPM we incorporated four components;

1. Adult survival (S_a^k) is the probability a female of age a in state k in year t, is alive and in the population in year $t + 1$.

2. Pupping (P_a^k) is the probability a female of age a in state k in year t, produces a pup in year $t + 1$.

3. Pup survival (PS_a^k) is the probability a pup born in year $t + 1$ to a female of age a in state k in year t, survives the first 8 weeks.

4. Not suckling (NS_a^k) is the probability that a female of age a in state k in year t that does not pup in year $t + 1$, is not suckling a pup of a previous year in $t + 1$.

Through these four components we can fully specify the TPM (Figure 2). An important feature of the TPM is that each row must sum to 1, that is, regardless of which state an animal is in, in year t, it must be in one of the four reproductive states, or dead, in year $t + 1$. Also note that, as in many mark-recapture situations, it is not possible to distinguish between death and permanent emigration away from the Auckland Island study beaches, however, given the strong site fidelity seen for female NZ sea lions, permanent emigration is unlikely (Chilvers and Wilkinson 2008).

Age-specific rates for these four components were not estimated (due to relatively small sample sizes within each age group); hence a functional relationship for each component with age was assumed. A linear relationship with age was assumed for adult survival, pup survival (as a function of mother's age), and probability of not suckling a pup of a previous year. The relationship between age and probability of pupping was assumed to be quadratic (i.e., may initially increase before decreasing as females get older). Note that we did not assume a quadratic relationship between adult survival and age as no juvenile animals were included in the analysis. For each of these demographic parameters, the effect of age was assumed to be consistent regardless of the females' reproductive status, although reproductive status was included as an additive effect to the functional relationships (i.e., for any demographic parameter, females in different reproductive states would have different intercepts but a common slope with respect to age). As the probabilities must take values between 0 and 1, these functional relationships were defined on the logit scale (Equations (2.1)–(2.4)), hence the relationships are analogous to using logistic regression

		Reproductive status in year $t+1$			
		A: POY, pup alive	B: POY, pup dead	C: POPY, suckling	D: No POY, not suckling	E: Dead
Reproductive status in year t	POY, pup alive: A	$S_a^A P_a^A PS_a^A$	$S_a^A P_a^A (1 - PS_a^A)$	$S_a^A (1 - P_a^A)(1 - NS_a^A)$	$S_a^A (1 - P_a^A) NS_a^A$	$1 - S_a^A$
	POY, pup dead: B	$S_a^B P_a^B PS_a^B$	$S_a^B P_a^B (1 - PS_a^B)$	0	$S_a^B (1 - P_a^B)$	$1 - S_a^2$
	POPY, suckling: C	$S_a^C P_a^C PS_a^C$	$S_a^C P_a^C (1 - PS_a^C)$	$S_a^C (1 - P_a^C)(1 - NS_a^C)$	$S_a^C (1 - P_a^C) NS_a^C$	$1 - S_a^C$
	No POY, not suckling: D	$S_a^D P_a^D PS_a^D$	$S_a^D P_a^D (1 - PS_a^D)$	0	$S_a^D (1 - P_a^D)$	$1 - S_a^4$
	Dead: E	0	0	0	0	1

Figure 2. Transition probability matrix for a female moving between reproductive states in successive years. POY = Pup of Year. POPY = Pup of Previous Year. See text for parameter definitions.

to investigate the effect of age on each component. Age has been standardized according to Equation (2.5).

$$\text{logit}(S_a^k) = \beta_0^k + \beta_1 \tilde{a}, \tag{2.1}$$

$$\text{logit}(P_a^k) = \gamma_0^k + \gamma_1 \tilde{a} + \gamma_2 \tilde{a}^2, \tag{2.2}$$

$$\text{logit}(PS_a^k) = \eta_0^k + \eta_1 \tilde{a}, \tag{2.3}$$

$$\text{logit}(NS_a^k) = \delta_0 + \delta_1 \tilde{a}, \tag{2.4}$$

$$\tilde{a} = (a - 10)/10. \tag{2.5}$$

Note that due to small sample sizes, the probability of not suckling a pup of a previous year (given the female had not pupped in the current year) was constant for all reproductive states (i.e., no k superscript). Furthermore, the not suckling probability will be 1 if the pup died in the previous year or the female did not pup, hence rows 2 and 4 of the TPM are slightly different from rows 1 and 3 (Figure 2). Due to the higher energy expense of lactation relative to pregnancy (Oftedal 1985; Gittleman and Thompson 1988; Arnould 1997), the survival of females whose pups died within 8 weeks or were suckling in year t, was constrained to be equal (i.e., $\beta_0^B = \beta_0^C$).

An added feature of mark-recapture models is recognition of the fact that, generally, animals will not always be captured or resighted in any given year. As such there is ambiguity about the reproductive status of females not observed in any given year. Any method of analysis must account for the fact that an animal may have been in any of the four states (or possibly dead if never sighted again). Additional information about the death of a female is supplied by the recovery of dead animals (which is assumed to occur in the same year as death), but only a fraction of the animals that die in a year are ever recovered. As such there are additional "nuisance" parameters that also need to be accounted for within the mark-recapture model, namely resighting and the recovery probabilities. In this analysis resighting probabilities were estimated separately for each year and reproductive state to provide the greatest generality. Note that in order to resight an individual, it must be present on the beach and resighted by the researchers. As such, estimated resighting probabilities may be affected by temporary emigrants; female NZ sea lions with a particular reproductive status that year, but are absent from the breeding beaches. Because of the low number of recovered dead animals, the probability of recovering a female's carcass was assumed equal for all reproductive states and constant across time.

Following Dupuis (1995), we used Markov chain Monte Carlo (MCMC) methods to apply the multistate mark-recapture model to the data. The key is to consider the encounter history for any individual animal as the product of two processes; (1) the survival and change in reproductive status (the biological process); and (2) whether the individual is resighted or recovered each year given whether the animal is alive and its reproductive status that year (the sampling process). The true reproductive status of a female is unknown for years in which she was not observed, but it can be estimated as part of the MCMC analysis given the defined TPM, and a posterior distribution obtained. In particular we used the software WinBUGS (*http://www.mrc-bsu.cam.ac.uk/bugs*) and have provided the base code as supplemental material. It should be stressed that while the mechanics of conducting the

analysis is different from what is commonly performed for mark-recapture analyses (i.e., maximum likelihood estimation), the underlying philosophy of the models are identical.

A complication for this analysis was that the age of nine females was unknown. Rather than exclude these females from the analysis, their age was predicted as part of the modeling procedure. This was achieved relatively simply by incorporating the age distribution of the branded females as a separate facet of the available data and estimating the probability that a branded female was of age a, where a was between 4 and 25 years old and the only constraint on the shape of the age distribution being that the probabilities must sum to 1 (i.e., a branded female must be between 4 and 25 years old in 2000). The general approach used here is similar to that recently suggested by Schofield, Barker, and MacKenzie (2009).

The MCMC-based analysis was conducted using two chains with different starting values and was run for 45,000 iterations. Diagnostics (not presented here) suggested the chains converged quickly and the first 5,000 iterations were considered the "burn-in" period. The analysis is, therefore, based on 80,000 (2 chains × 40,000 iterations) samples from the approximate posterior distributions for the parameters. Relatively vague prior distributions where used for all regression coefficients to be estimated in Equations (2.1)–(2.4) (normal with $\mu = 0$, $\sigma^2 = 100$) and uniform (0, 1) prior distributions were used for resighting probabilities and recovery probability.

It should be stressed that all of our results are conditional upon this single model considered. We believe it is biologically reasonable and have not conducted any form of model selection. To ensure that the model is appropriate given the data, a Bayesian p-values was estimated to assess for lack of fit (Gelman et al. 2004), using the model deviance as the test statistic.

2.3. POPULATION MODELING

The main objective of this analysis is to estimate the reproductive output of a female over its lifetime. The TPM defined above also provides an age-stage structured population model with no density dependence, and with estimates of the associated components, we can simulate how the reproductive status of a female may change throughout her lifetime and hence predict her total reproductive output. Rather than take a two-step approach where parameters are first estimated, then applied to a separate series of simulations, here both the estimation and prediction phases of the modeling were performed simultaneously. One advantage of doing so is that all sources of uncertainty are correctly accounted for with respect to predicting reproductive output (Barker et al. 2009).

The youngest age at which a female has ever been observed with a pup in the Auckland Islands is four, therefore, we began the simulations with a three year old female that did not pup and was not suckling a pup of a previous year (reproductive state D), implying the minimum age of first reproduction is four. Given the females' reproductive status in year 1 (state D), her status in year 2 is a categorical random variable where the probability of each category is determined by the respective row of the TPM, i.e., the category in year 2 is predicted by rolling a five-sided dice where the probability of each face is determined by a row of the TPM. The females' reproductive status in subsequent years is predicted in a similar manner, and continues until the female dies. At this point the number of pups

produced by the female (and other life-history parameters, e.g., number of pups produced that survived >8 weeks, life span, reproductive life span) can be calculated. This one value is from a single iteration of the MCMC algorithm and hence at the completion of the MCMC run we obtain a posterior distribution for the life-history parameters that include both estimation and stochastic variation.

One important demographic parameter that the branded females do not provide any information on is the age of first breeding, as branded females had to have pupped in 2000. Age of first breeding is defined here in terms of an age-specific probability of first breeding, P_a^{First}. Given a female that has not bred previously that is of age a in year $t - 1$, P_a^{First} is the probability of breeding in year t. As this cannot be estimated directly from the available data, we assumed Equation (2.6) applied to females aged between three and six in year $t - 1$, based upon Chilvers (unpublished data). The probability of breeding for the first time for older females was assumed to be the same as the probability of rebreeding (as estimated above).

$$\text{logit}(P_a^{First}) = \gamma_0^{First} + \gamma_1^{First}\tilde{a}, \tag{2.6}$$

where, for each MCMC iteration, random values for γ_0^{First} and γ_1^{First} were selected from normal distributions with means of 0.94 and 6.37, and standard deviations of 0.10 and 1.00, respectively. The results in mean probabilities of 0.06, 0.11, 0.18, and 0.29 for females aged three through six. Within the TPM, P_a^{First} replaces P_a^D until the female becomes a breeder for the first time (i.e., transitions to states A or B).

3. RESULTS

The Bayesian p-value was 0.65 which does not indicate any lack of fit for the estimating model to the data.

3.1. RESIGHTING AND RECOVERY PROBABILITY

The median and central 95% credible interval for the posterior distributions of the resighting probabilities are presented in Figure 3. These are high for females that pupped in a given year and considerably lower (and estimated with much less precision) for the females that did not pup that year. This would be expected given that in this instance resighting probabilities consist of two components; (1) the probability of a female being present at the breeding beaches in that year; and (2) the probability of being sighted on the beach given it is present there. Females that have not pupped in a given year are less likely to be sighted at the breeding beach. The median of the posterior distribution for the recovery probability was 0.12 with a 95% credible interval of (0.05, 0.22). The mean and standard deviation for the posterior distributions of the regression coefficients are given in Table 1. Due to the standardization of age, the associated coefficients should be interpreted on the scale of a 10-year change.

3.2. ANNUAL SURVIVAL PROBABILITY

The estimated annual survival probabilities for each of the reproductive states (with survival for females whose pups did not survive and those suckling the previous years pup
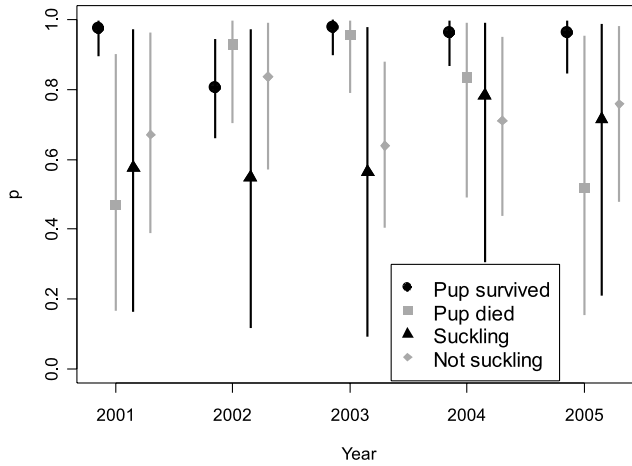
Figure 3. The median and central 95% credible interval for the posterior distributions of the resighting probabilities of female NZ sea lions dependant on whose pups survived >8 weeks in year t (Pup survived), did not survive to 8 weeks (Pup died), females that were suckling a pup of a previous year in year t (Suckling), and females who did not pup and were not suckling a pup of a previous year in year t (Not suckling).

assumed equal) as a function of age are presented in Figures 4(a)–(c). Survival between years t and $t + 1$ appear similar for all reproductive states, with survival decreasing with age from approximately 90%–95% up until 10 to 15 years of age, then dropping to below

Table 1. Mean and standard deviation (SD) of posterior distributions of regression coefficients used to define relationships between demographic parameters and age (see Equations (2.1)–(2.5)).

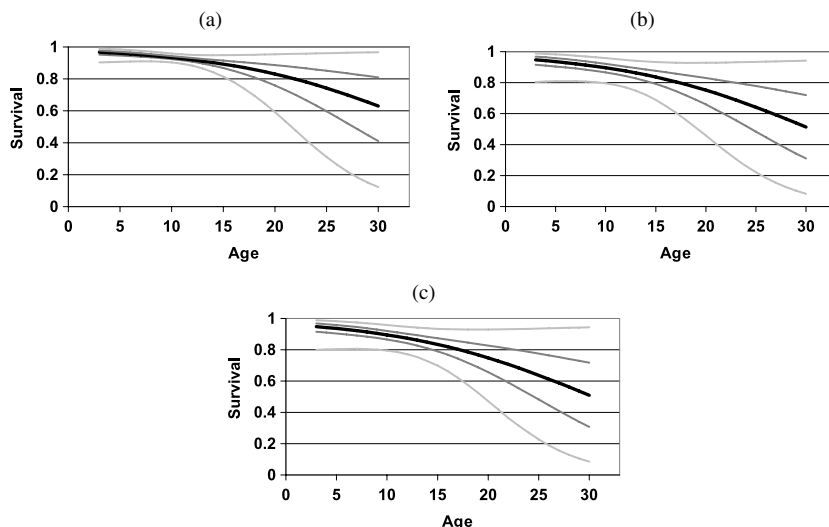| Demographic parameter	Coefficient	Mean	SD
Adult survival	β_0^A	2.66	0.23
	$\beta_0^{B=C}$	2.18	0.45
	β_0^D	2.17	0.46
	β_1	−1.05	0.70
Pupping	γ_0^A	1.57	0.17
	γ_0^B	3.48	0.88
	γ_0^C	0.60	0.97
	γ_0^D	0.52	0.38
	γ_1	−0.01	0.55
	γ_2	−2.70	1.23
Pup survival	η_0^A	1.84	0.20
	η_0^B	1.12	0.40
	η_0^C	0.80	0.94
	η_0^D	1.67	0.51
	η_1	0.03	0.71
Not suckling	δ_0	1.35	0.45
	δ_1	1.95	1.33

Figure 4.   Estimated probability of survival between years t and $t + 1$ for females whose pups (a) survived >8 weeks in year t, (b) did not survive to 8 weeks, and females that were suckling a pup of a previous year, in year t, and (c) females who did not pup and were not suckling a pup of a previous year in year t. Indicated is the median (black line), central 50% credible interval (dark gray), and central 95% credible interval (light gray).

80% by age 20. There is smaller variability in survival estimates for females whose pups survived >8 weeks than all other reproductive states. A notable feature of all figures is the increasing width of the credible intervals beyond age 15, which is simply a reflection of the fact that few older branded females were ever resighted (recall that most of the females were aged <17 by the end of the study, Figure 1). This highlights that care must be taken when extrapolating the results of this analysis to animals outside of the observed age band.

3.3. PUPPING PROBABILITY

The probability of pupping in year $t + 1$ as a function of the female's age and reproductive status in year t are presented in Figures 5(a)–(d). The quadratic relationship appears to be quite strong with the probability of pupping peaking at between 60% to 95% for females between the ages of 8 and 13-years and dropping sharply thereafter. The probability of pupping in the 8–13 age class was highest (~95%) for females who had pupped in the previous year but had lost their pups within the first 8 weeks after pupping. In the 8–13 year age classes, females who had pupped the previous year and their pup survived >8 weeks had a pupping probability of ~80%. However, the pupping probability dropped quickly after 13 years, being only 70% by 15 years, 30% by 18 years, and only 10% by 20 years. Those who had not pupped the previous year (either because they were suckling a yearling, or simply did not pup) had a maximum pupping probability of 65% and showed a more dramatic drop off with pupping probability dropping to 40% by 15 years and 5% by 20 years.
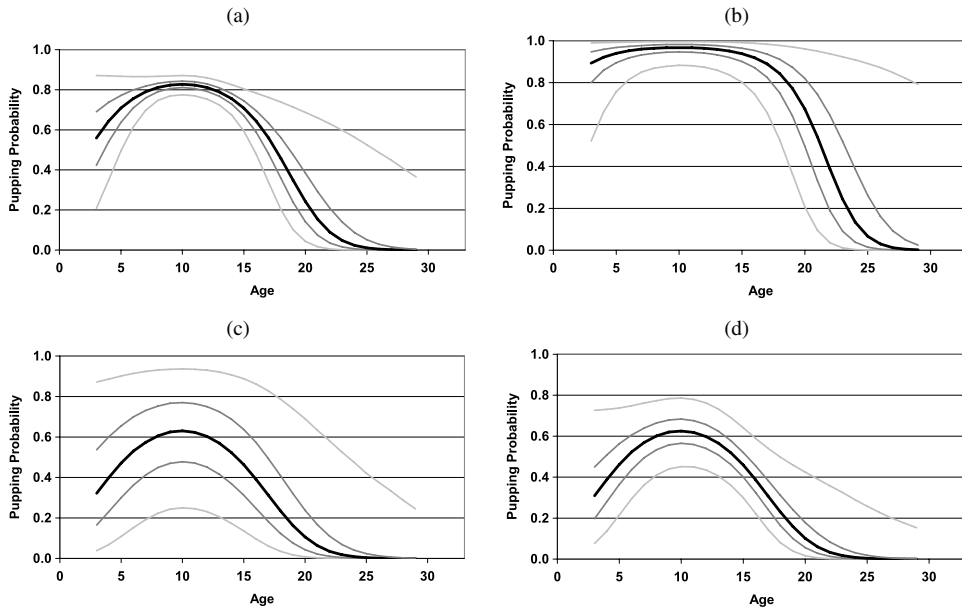
Figure 5. Estimated probability of female pupping in year $t + 1$ given her age and that (a) her pup survived >8 weeks in year t, (b) her pup did not survive 8 weeks in year t, (c) that she was suckling a pup of a previous year in year t, and (d) that she did not pup and was not suckling a pup of a previous year in year t. Indicated is the median (black line), central 50% credible interval (dark gray), and central 95% credible interval (light gray).

3.4. PUP SURVIVAL

Estimates of pup survival (Figures 6(a)–(d)) indicate that pups born to females whose pups also survived >8 weeks in the previous year or who had not pupped the previous year had higher survival than those whose mothers had lost a pup or had suckled a yearling. There is little indication that pup survival may be associated with the mother's age. The probability of a female not suckling a pup of a previous year in year $t + 1$ (Figure 7) appears to increase with the age of the female. This suggests that younger females may be more likely to suckle their young for a longer period.

3.5. LIFETIME REPRODUCTION

The predicted distribution for the number of pups a female NZ sea lion has during her lifetime based upon the model fitted to the data is given in Figure 8(a). According to the model, approximately 27% of females that survived to age three and had never pupped, will die before producing any offspring during their lifetime. The fraction of females producing 1, 2, 3, . . . to 9 pups is relatively consistent at approximately 7% each, and a decreasing fraction of females produce 10 or more pups during their lifetime (10 pups 6%, 12 pups 3%, dropping below 1% by 14 pups, Figure 8(a)). The predicted distribution for the number of pups produced that survived >8 weeks (Figure 8(b)) is similar to the above, although the distribution has shifted to the left slightly as would be expected (i.e., fewer pups survived >8 weeks than were born). Therefore, the predicted average (median) number of pups a female NZ sea lion will produce in her lifetime is 4.42 (4) with 95% of females predicted
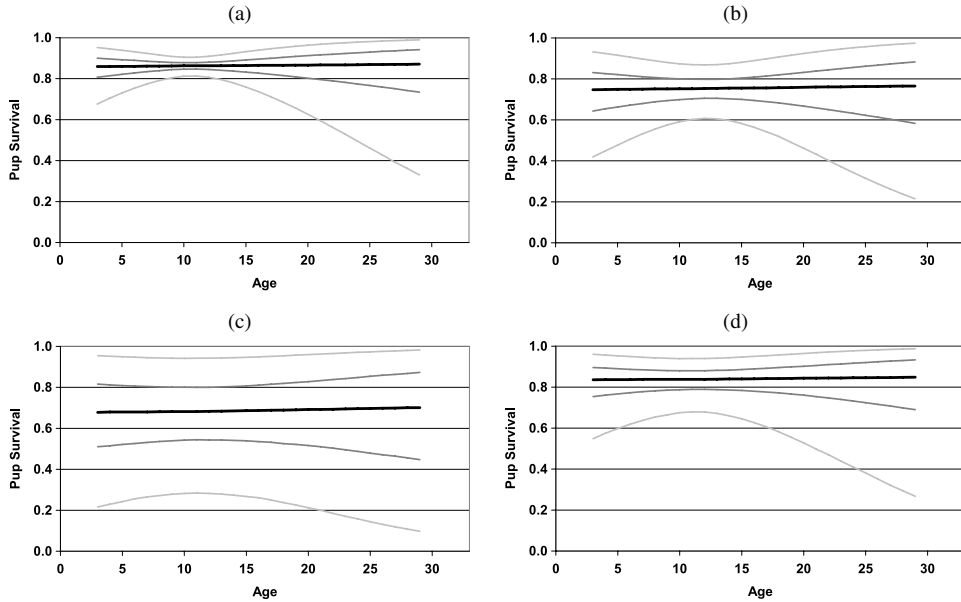
Figure 6.   Estimated probability of pup surviving the first 8 weeks in year $t + 1$ given the mothers age and that (a) her pup survived >8 weeks in year t, (b) that her pup did not survive the first 8 weeks in year t, (c) that she was suckling a pup of a previous year in year t, and (d) that she did not pup and was not suckling a pup of a previous year in year t. Indicated is the median (black line), central 50% credible interval (dark gray), and central 95% credible interval (light gray).

to produce between 0 and 12 pups, and 50% producing between 0 and 7 pups. The median (average) number of pups predicted to survive >8 weeks during a females' lifetime is 3.70 (3) with 95% of females producing between 0 and 11, and 50% producing between 0 and 6 pups.

The distribution for the age of first reproduction for females that survived to age three and had never reproduced is given in Figure 9(a) (where an age of zero represents females that never reproduced), which suggests females gradually recruit into the breeding popula-
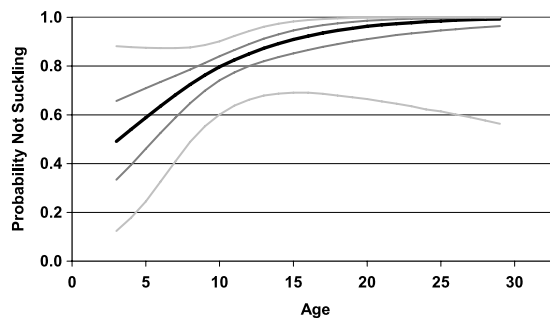

Figure 7.   Estimated probability of a female not suckling a pup of a previous year in year $t + 1$ given her age in year t. Indicated is the median (black line), central 50% credible interval (dark gray), and central 95% credible interval (light gray).
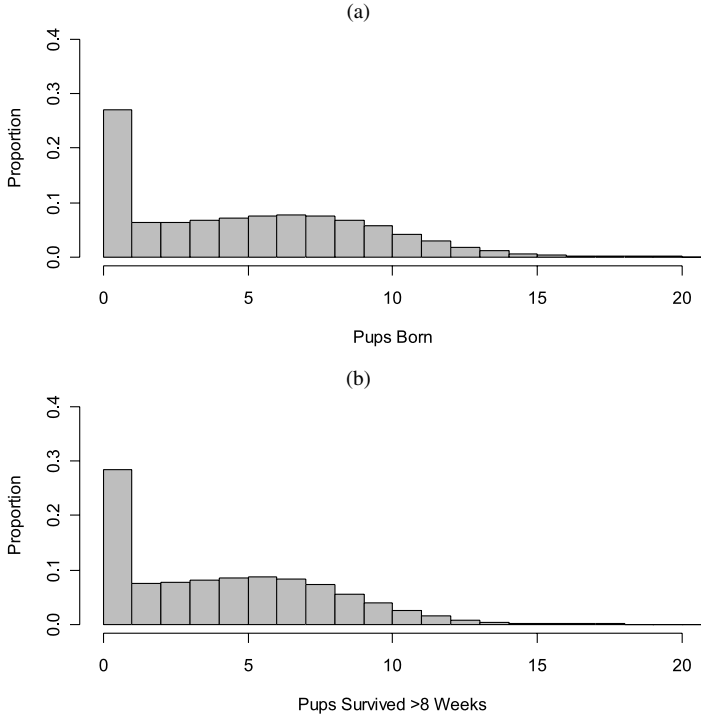
Figure 8.   Predicted distribution for the number of pups produced (panel (a)) and number of pups that survive >8 weeks (panel (b)) during the lifetime of a female NZ sea lion. Females were initially four-years-old and had never produced a pup.

tion between ages four and nine with approximately 50% of those females that are going to reproduce to have produced their first pup by age seven. The predicted distribution for the age of last reproduction is given in Figure 9(b) suggests that many females breed up to age 15–17, although some females may continue to reproduce beyond age 20.

4. DISCUSSION

Our results demonstrate that integrating the analysis of short-term multistate mark-recapture data with age-stage structured population modeling can be a useful tool for predicting reproductive, survival, and life-history parameters. This is important for a species that is long lived, threatened, declining, and logistically difficult to study due to their sub-antarctic location. Our results indicated that female survival appears more closely linked to age than reproductive status. Reproductive performance has a convex relationship starting at 4, peaking between 8 to 13 years, and dropping off sharply after the age of 15. 27% of all females that live to age three are predicted to never breed and 29% will not rear a pup that survives beyond 8 weeks. The average (median) predicted lifetime reproduction rate for a female NZ sea lion is estimated to be 4.42 (4) new born pups (95% CI 0–12) dropping to 3.70 (3) pups (95% CI 0–11) when pup survival to 8 weeks is accounted for. This lifetime reproductive ability may leave this species vulnerable to external influences such
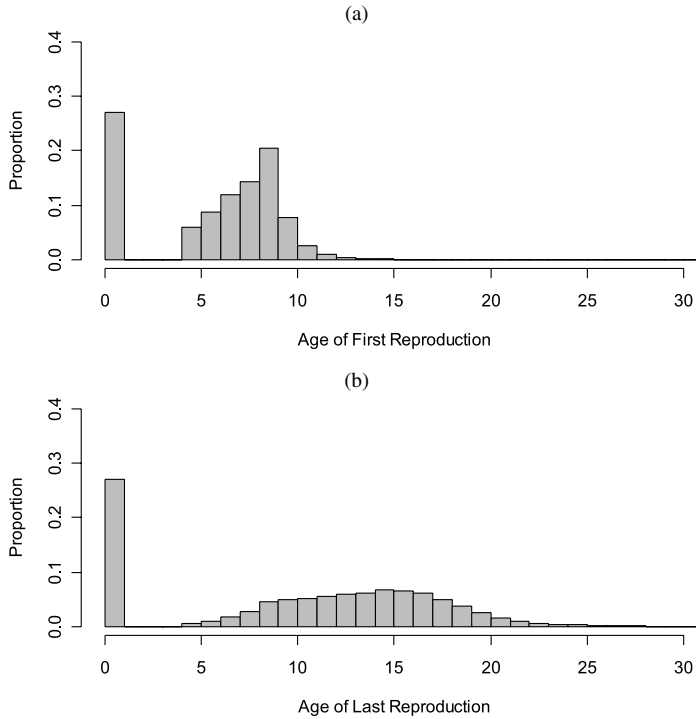
Figure 9.   Predicted distribution for the age of first (panel (a)) and last (panel (b)) reproduction of female NZ sea lions that had survived to age four and never reproduced. The zero age class indicates the proportion of females predicted to never reproduce.

as fishing pressure and bacterial mass mortality events. The species appears to be only just replacing itself and does not show the reproductive ability to compensate for additional external pressures, as seen in the pup production decline in recent years (Campbell et al. 2006; Chilvers, Wilkinson, and Childerhouse 2007; Chilvers 2008a).

Age of first reproduction is an important demographic parameter for predicting a female's lifetime reproductive output. As all females that were branded in 2000 had already bred, another source of information had to be used. Ideally we would incorporate all sources of information into a single analysis, to appropriately account for all sources of uncertainty, although insufficient resources were available when this work was conducted to do so. However, we did take some steps to assess the robustness of our conclusions to the validity of our assumptions on age of first reproduction. If it was assumed that all females less than eight that had not bred previously, had a probability of 0.15 of breeding for the first time next year, the predicted pup production numbers are virtually unchanged. With a more extreme case, where it is assumed the probability of first breeding is the same as the probability of rebreeding (as estimated directly from the branded females), the average number of pups produced increases by approximately 1. However, in both cases, the distribution for age at first reproduction is very different from Figure 9(a), with an unrealistically high number of first-time breeders aged four through six. Hence, we are confident that our predicted pup production estimates are appropriate. Reliable data, with sufficient sample

sizes, to estimate age of first reproduction within a fuller analysis is only now becoming available for females tagged as pups in the late 1990s and early 2000s. Incorporating these data into this analysis is a topic of future research.

Some caution must also be exercised when interpreting these results, as predictions about the reproductive output of female NZ sea lions requires extrapolation beyond the observed age range. As illustrated in the figures, there is a high level of uncertainty in the key components of the transition probability matrix (TPM) for animals >15 years old which would translate to the relatively long right-hand tail exhibited in some of the predicted distributions.

The range of adult female survival probabilities in this study were similar to the ranges to those previously reported for NZ sea lions at the Auckland islands (82% CI 76–86; Gales and Fletcher 1999; 87% ±0.018 (±1 SD); Lalas and Bradshaw 2003). Our results are similar to those observed among other female otariid species, Antarctic fur seals, *Arctocephalus gazella*, 92% (Boyd et al. 1990) 83% range 65%–93% (Boyd et al. 1995), 83%–92% (Wickens and York 1997), Subantarctic fur seals, *A. tropicalis*, range 68%–98% depending on age and reproductive status (Beauplet et al. 2006), Australian fur seal, *A. pusillus doriferus* 88% (Wickens and York 1997), Guadalupe fur seal, *A. townsendi*, 85% (Wickens and York 1997), Northern fur seals, *Callorhinus urinus*, 89% (Chapman 1964), 85%–89% (Wickens and York 1997), and Steller sea lions, *Eumetopias jubatus*, 84%–93% (York 1994), range 84%–93% (Boyd 1992) 82%–85% Marmot Island, 91%–93% Forrester Island (Pendleton et al. 2006). Individual age was found to influence annual survival and is considered more of an influence than reproductive status. Otariid species appear to vary in the importance of age versus reproductive status on survival and, therefore, life-history strategies. In contrast to NZ sea lions, Antarctic fur seal female survival is lowered by pregnancy and appears to be of greater influence than individual age, with the longest surviving females tending to have low fecundity (Boyd et al. 1995). For NZ sea lions this begs the question, if female survival is linked more closely to age than reproduction why are females not producing more pups in a lifetime as evolutionary theory would predict?

The quadratic age effect on P_a^k resulted in a convex relationship between breeding rate and age regardless of previous reproductive status. The relationship suggested that reproductive performance increases from age three, with an observed peak of maximum breeding rate for the 8 to 13 year olds and then declining with age (Figures 5(a)–(d)). There are two previous reproductive rate estimates based on observed data for NZ sea lions from the Auckland Islands both showing convex relationships with age (Breen and Kim 2006; Childerhouse 2007). Childerhouse (2007) used a dataset from 834 known age female NZ sea lions and reported estimates of 0.59 ± 0.10 for all breeding age females or 0.75 ± 0.02 for prime breeding age females (8 to 13 years) from modeled data and 0.64 ± 0.11 to 0.77 ± 0.08, respectively, for direct observed data.

Both our and Childerhouse's (2007) reproductive rate estimates are at the lower end of the range of reproductive rates observed for other otariid species. For example, a maximum breeding rate of between 63% and 84% has been recorded for subantarctic, Antarctic, and New Zealand fur seals (*A. forsteri*) between the ages of 7 to 13 years, with reproduction

dropping sharply after 13 years (Hes and Roux 1983; Boyd et al. 1990, 1995; Goldsworthy and Shaughnessy 1994; Lunn, Boyd, and Croxall 1994; Dabin et al. 2004; Beauplet et al. 2006). Steller sea lions have reported reproductive rates of between 60%–75% (Pitcher and Calkins 1981; Calkins and Pitcher 1982; Boyd 1992; York 1994), Californian sea lions, *Zalophus californianus*, 77% (Melin 2002), and Australian sea lions, *Neophoca cinerea*, 71% (Higgins and Gass 1993). Why NZ sea lions appear to have a low reproductive ability is unknown. There are many possibilities: genetic predisposition, low nutrient availability, direct or secondary low fertility due to bacterial outbreaks, habitat restrictions, or other unknown causes. Investigating the affects of these factors on fertility is an area for further research.

Pup survival of NZ sea lions on the Auckland Islands at two months of age varies appreciably from year to year from 42% to 91% (Chilvers, Wilkinson, and Childerhouse 2007). One of the most significant influences on pup survival in NZ sea lions over the last eight years has been bacterial epidemic mass mortality events which have been responsible for the deaths of up to 58% of pups before the age of two months at some breeding areas (mass mortality events occurred 1998–1999, 2001–2002, and 2002–2003; Wilkinson et al. 2006; Castinel et al. 2007; Chilvers, Wilkinson, and Childerhouse 2007). From data presented here, it appears that pup survival may be influenced by female age and previous reproductive performance, with the probability of pups surviving >8 weeks in year $t + 1$ higher for females whose pups in year t also survived >8 weeks, and older females. Female breeding behavior and the maternal care of their pup are likely to influence the possibility of starvation or trauma for their pups. Results that show pup survival may relate to previous female breeding performance support the hypothesis that, in female otariids, individuals may be poor breeders or nonbreeders as an alternative to an annual variation in reproductive success (Beauplet et al. 2006). In relation to female age, Figure 7 indicates that young females appear more likely to continue to suckle their pups as yearlings than older females.

The minimum observed age at first reproduction of female sea lions at the Auckland Islands is four years of age and the population modeling predicts that 50% of females that had survived to age three will have bred for the first time by age seven, if they are ever going to breed (27% never will; Figure 9(a)). There has never been a female younger than four-years-old observed to breed at the Auckland Islands and in 25% of years the youngest animals known to have bred for the first time are five year olds (Chilvers unpublished data). Age of first reproduction for other otariids is recorded as between three and six years with mean age of reproductive females between 7 and 13 and oldest reproductive 23 to 25 (Wickens and York 1997; Pitcher, Calkins, and Pendleton 1998; Dabin et al. 2004).

This age related reproduction data indicates a decline in survival and reproduction with age in NZ sea lions which supports the hypothesis of possible individual senescence in NZ sea lions, as has been suggested for other otariids including South American, Antarctic, Northern, and Cape fur seals, *Arctocephalus pusillus pusillus* (Arnould, Trinder, and McKinley 2003; Dabin et al. 2004; Beauplet et al. 2006).

The predicted average lifetime production of female NZ sea lions places them as the lowest and slowest reproducing otariids. Dabin et al. (2004) found similar results from their investigation of the lifetime reproductive rates of subantarctic fur seals in the In-

dian Ocean where low food availability appeared to restrict reproductive performance relative to more temperate living subantarctic fur seals. The average lifetime reproduction for the sub-antarctic fur seal females were estimated at 5.2 pups born per female, with 3.65 weaned pups per female life. Reproduction in female otariids is energetically expensive with long lactation periods relying on food resources adjacent to the breeding area where their offspring is located. This reproduction/near-to-breeding-area foraging strategy appears to make otariids particularly vulnerable to localized prey depletion which can lead to low population productivity.

In a management context, for a threatened species that has low population numbers, restricted breeding area where pup production is currently in decline and where breeding females are the predominant class being killed as by-catch in nearby fisheries (Chilvers 2008a), understanding lifetime reproductive productivity of breeding females and life-history strategies is essential for their management. Further research needs to investigate why NZ sea lions appear to have a low reproductive ability including investigating genetic predisposition, nutrient/prey availability, and fertility effects from bacterial epidemics. NZ sea lions life-history parameters and current pup production decline are not likely to be linked to any single natural or anthropogenic factor. However, understanding that reproductive ability in this population is low leaves the population vulnerable to extinction from the additional anthropogenic deaths caused by trawl fishing in the area.

SUPPLEMENTAL MATERIALS

Base code: Base code for fitting multi-state mark-recapture models in WinBUGS. (13253_2009_11_MOESM1_ESM.pdf)

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