Fisheries New Zealand
Tini a Tangaroa

An integrated biodemographic model for New Zealand sea lion (*Phocarctos hookeri*)

New Zealand Aquatic Environment and Biodiversity Report No. 256

C.T.T. Edwards
J.O. Roberts

ISSN 1179-6480 (online)
ISBN 978-1-99-100351-5 (online)

April 2021

New Zealand Government

Requests for further copies should be directed to:

Publications Logistics Officer
Ministry for Primary Industries
PO Box 2526
WELLINGTON 6140

Email: brand@mpi.govt.nz
Telephone: 0800 00 83 33
Facsimile: 04-894 0300

This publication is also available on the Ministry for Primary Industries websites at:
`http://www.mpi.govt.nz/news-resources/publications.aspx`
and `http://fs.fish.govt.nz` (go to Document library/Research reports)

Table of Contents

EXECUTIVE SUMMARY

Edwards, C.T.T.; Roberts, J.O. (2021) An integrated biodemographic model for New Zealand sea lion (*Phocarctos hookeri*).

New Zealand Aquatic Environment and Biodiversity Report No. 256. 39 p.

We present a new model for the New Zealand sea lion (*Phocarctos hookeri*), using the same data and similar partitions to the model used for the Threat Management Plan, but represented as a hidden state model, whereby the state transitions and observation processes are separated. This allows for more intuitive development of the model and likelihood components, easily incorporating uncertainty into the state observation process. The model is integrated, using census data on pup counts (from of all known breeding rookeries on Auckland Islands archipelago) alongside mark-recapture and mark-recovery data (from Sandy Bay, the best studied rookery). In addition it includes a standardised index of pup mass as a predictor of pup survivorship, and we show that this shrinks the uncertainty associated with estimation of pup survivorship for years where the tagging data are uninformative – notably in the most recent years of the assessment before individuals tagged as pups have first returned to the beach (around 4 years of age), making them available for recapture. We therefore expect that including pup mass as a covariate will improve predictive performance of the model. This has implications for effective monitoring of populations where it is not feasible to get consistent mark-recapture data (e.g., Dundas Island and Figure of Eight Island). An ability to include covariate data makes the model useful for understanding and predicting the effects of various factors that may affect the future status of these sea lion populations, e.g., fisheries, disease, prey availability, or climatic drivers of environmental change.

1 Introduction

The endemic New Zealand sea lion (*Phocarctos hookeri*) has a breeding distribution now centred on the Auckland Islands (Childerhouse & Gales 1998), in the Sub-Antarctic region of New Zealand's Exclusive Economic Zone, with smaller populations also found on Campbell Island, Stewart Island, and the Otago Peninsula. According to pup census counts and previous modelling work, the largest breeding population at the Auckland Islands has declined by about 40% since the late-1990s (Childerhouse et al. 2015, Roberts 2017) contributing to its designation as "Nationally Vulnerable," the second highest domestic threat rating (Baker et al. 2019). A low pup census count at the Auckland Islands in 2014 prompted a process leading to the adoption of a Threat Management Plan (TMP) for the species, a central component of which was development of a quantitative risk assessment based on a demographic model capable of simulating the population dynamics under alternate threat scenarios. This was initially conducted by Roberts & Doonan (2016), based on previous modelling work by Breen et al. (2012), MacKenzie (2012), and Roberts et al. (2014), and updated by Roberts (2017, 2019).

The demographic assessment model used by the TMP was created with the SeaBird assessment software (Francis & Sagar 2012) and fitted to a range of observational data. The most important data were individual mark-recapture observations, which allow estimation of the inter-annual survival, and pup census data, which provide information on the population size and trend over time. The SeaBird modelling software allows these different data types to be integrated in a statisitcally consistent manner. For the Auckland Islands assessment by Roberts & Doonan (2016), good fits were obtained to the data, and the model structure and parameter estimates appeared to be a reasonable representation of demographic processes that have affected population decline there (primarily low pup survival and low adult survival, but also delayed maturation and years of low annual pupping rate). The model was able to investigate the impact of a number of threats and potential threats, including disease-related pup mortality, nutritional stress, and commercial fishing. This work has been ongoing (Roberts 2017, 2019), but the modelling approach has some limitations. Specifically, there is no capacity within SeaBird to include continuous covariate data to provide better estimates of time-variant rate parameters.

The current SeaBird model (Roberts & Doonan 2016, Roberts 2017, 2019) uses a generalisation of the Cormack-Jolly-Seber (CJS; Cormack 1964, Jolly 1965, Seber 1965) approach for estimation of the annual survivorship and resight probabilities. This generalisation allows resights in a number of discrete states or partitions, so that transitions between states can also be estimated. Furthermore, the likelihood includes a novel component that allows for the classification of observations into different states to have some error associated with it (Francis & Sagar 2012). Because the CJS method treats observations as conditional on the first mark (i.e., only individuals that have been captured and marked are considered in the likelihood – the unmarked component of the population is ignored), it does not make any inference on the population size beyond the fact that it must be larger than the number of marked individuals alive at any one time. Information on the population size must be derived from additional data, which in this case were pup counts (or a pup "census"). Integration of census and mark-recapture data into a single model was an important advancement in the development of demographic population models (Besbeas et al. 2002). Finally, the model allowed for recapture of both live and dead individuals, the latter being clearly more informative for estimation of survivorship. However, despite its utility, SeaBird does not allow for continuous covariate data to be included.

The intention in the current project is to develop a new model, maintaining consistency by incorporating features of the current SeaBird model, but allowing covariate data to be included, illustrating the approach using data on the mass of pups and assuming it to be related to annual pup survivorship (Roberts et al. 2021). Variable pup mass has been demonstrated to be a good predictor of early-life survival across pinniped species (e.g., Harding et al. 2005), and should be responsive to changes in maternal resources and other external factors. Biometric measurements, including mass, standard length, and axial girth, have been collected from New Zealand sea lion pups at the Auckland Islands since the early 1980s (Roberts et al. 2021). At Sandy Bay, pup mass observations have been collected around the date of tagging according to a highly consistent approach since 1993/94 (DOC 2019). Roberts et al. (2021) used the Sandy Bay data to produce standardised annual indices of female pup mass, which showed strong temporal trends through time that had a similar pattern to first year pup survival estimated by Roberts (2017). By incorporating pup mass into the demographic assessment model, this project aims to investigate the extent to which the apparent relationship between pup mass and first year survival (as shown by Roberts et al. 2021) is reflected in subsequent mark-recapture data. Including this relationship could improve the precision of model estimates of first year survival, particularly for cohorts with missing or sparse recapture data (such as those marked in the most recent field seasons that have not yet been resighted). In so doing, it may also provide biological or ecological insight into the environmental drivers of population dynamics.

2 Description of model components

The new model is required to incorporate a number of features of the data:

1. Different data types: pup census and mark-recapture
2. Different mark-recapture data types: types of mark and the recapture of both alive and dead individuals
3. Categorical covariate data: the state in which an individual is observed
4. Continous covariate data: empirical measurements of an environmental covariate or proxy over time
5. Observation error: both categorical and continuous covariate data are observed with error

The model falls into a class known as Hidden Markov Models (HMMs; e.g., Gimenez et al. 2012), which describe the transition of individuals between discrete states over time, with each transition dependent only on the current state, and with the states themselves at least “hidden” (i.e., unobserved). An individual in each state has an associated probability of being recorded in one or more observation categories, with the probabilities of observation per category also unknown. Inclusion of a number of different data types means that the model can be referred to as *integrated* (e.g., Besbeas et al. 2002, Brooks et al. 2004), whereas through inclusion of categorical observation error it is known as a *multi-event* model (Pradel 2005). Here we describe the development of such a model for New Zealand sea lions, and illustrate its performance. The model is for females only and is similar to the “8+” model of Roberts & Doonan (2016) and Roberts (2019), including 9 age classes (with the last being a plus group) and an age-dependent probability of breeding.

2.1 Transition and observation probabilities

The possible states for an individual are listed in Table 1 as $\{x_{0,t}, x_{1,t}, \ldots, x_{16,t}\}$, defining ages 0 to 8+ for individuals that progress from being born as pups (age zero) to maturing at age four, subsequently

Table 1: Possible states per individual at the beginning of time t. Maturity is abbreviated and can be either Immature (*imm*) or Mature (*mat*). Status is one of Non-breeding (*nbr*), Breeding (*brd*), or Dead. The state category "Dead" is further partitioned into the recently dead ($x_{15,t}$), referring to those that have died during the previous state transition, and the subsequent category ($x_{16,t}$).

Notation	$x_{1,t}$	$x_{2,t}$	$x_{3,t}$	$x_{4,t}$	$x_{5,t}$	$x_{6,t}$	$x_{7,t}$	$x_{8,t}$
Age	0	1	2	3	4	4	5	5
Maturity	imm	imm	imm	imm	mat	mat	mat	mat
Status	–	–	–	–	nbr	brd	nbr	brd

Notation	$x_{9,t}$	$x_{10,t}$	$x_{11,t}$	$x_{12,t}$	$x_{13,t}$	$x_{14,t}$	$x_{15,t}$	$x_{16,t}$
Age	6	6	7	7	8+	8+	0+	0+
Maturity	mat	mat	mat	mat	mat	mat	–	–
Status	nbr	brd	nbr	brd	nbr	brd	dead	dead

breeding or not breeding per year, and ultimately dying. The temporal range is from 1990 ($t = 0$) to 2019 ($t = 30$) inclusive. The transitions between states are governed by a set of probabilities, notably the survivorship vector $\underline{\phi}$ and probabilities of breeding $\underline{\alpha}$ (see Table 3). The model is described assuming these rate parameters to be constant over time. For example:

$$p(x_{2,t}|x_{1,t-1}) = \phi_{imm}$$

is the probability of transition from $x_{1,t-1}$ to $x_{2,t}$, whereas:

$$p(x_{7,t}|x_{5,t-1}) = \phi_{mat} \cdot (1 - \alpha_{a(7)})$$

is the probability of transition from state $x_{5,t-1}$ to state $x_{7,t}$, encompassing survivorship from the beginning of timestep $t-1$ and instantaneous non-breeding $1 - \alpha_{a(7)}$ at the beginning of time t. The probability of breeding is age-dependent, using the subscript notation $a(k)$ to refer to the age at state k. States $x_{13,t}$ and $x_{14,t}$ (i.e. age 8+) are treated as a plus group. For states $x_{11,t}, \ldots, x_{14,t}$, which are referred to collectively as $x_{11:14,t}$, then:

$$p(x_{13,t}|x_{11:14,t-1}) = \phi_{mat} \cdot (1 - \alpha_{a(13)})$$
$$p(x_{14,t}|x_{11:14,t-1}) = \phi_{mat} \cdot \alpha_{a(14)}$$

noting that $a(13) = a(14) = 8+$. Individuals transition into $x_{15,t}$ (recently dead) when they die:

$$p(x_{15,t}|x_{11:14,t-1}) = 1 - \phi_{mat}$$

fulfilling the condition that transition probabilities out of a given state sum to one. In general, complete specification of the state transition probabilities implies that transition probabilities out of any state x_z sum to one:

$$\sum_k p(x_{k,t}|x_{z,t-1}) = 1$$

Finally, following death, individuals accumulate in $x_{16,t}$:

$$p(x_{16,t}|x_{15,t-1}) = 1$$

This distinction between the "recently dead" and "dead" allows us to accommodate different types of recapture data in the model. Specifically, for alive and dead individuals, the latter are referred

Table 2: Possible observations per individual during time t. Maturity is abbreviated and can be either Immature (*imm*) or Mature (*mat*). Status is one of Non-breeding (*nbr*), Breeding (*brd*), Unknown (*ukn*), Not seen (if the individual does not return to the beach), Unobservable (for when there was no recapture effort), or Dead.

Notation	$y_{1,t}$	$y_{2,t}$	$y_{3,t}$	$y_{4,t}$	$y_{5,t}$	$y_{6,t}$	$y_{7,t}$	$y_{8,t}$	$y_{9,t}$	$y_{10,t}$
Age	0	1	2	3	4	4	4	5	5	5
Maturity	imm	imm	imm	imm	mat	mat	mat	mat	mat	mat
Status	–	–	–	–	nbr	brd	ukn	nbr	brd	ukn

Notation	$y_{11,t}$	$y_{12,t}$	$y_{13,t}$	$y_{14,t}$	$y_{15,t}$	$y_{16,t}$	$y_{17,t}$	$y_{18,t}$	$y_{19,t}$
Age	6	6	6	7	7	7	8+	8+	8+
Maturity	mat	mat	mat	mat	mat	mat	mat	mat	mat
Status	nbr	brd	ukn	nbr	brd	ukn	nbr	brd	ukn

Notation	$y_{20,t}$	$y_{21,t}$	$y_{22,t}$
Age	0+	0+	0+
Maturity	–	–	–
Status	not seen	dead	unobservable

to in the literature as "recoveries" (e.g. Barker 2005). In the current setting, phantom tags are from individuals known and seen to be dead on the beach (i.e. "recently dead"), whereas for the other tag types death might have occured at any point since the last observation. The observation probabilities for these two states ($x_{15,t}$ vs. $x_{16,t}$) are different and conditional on the tag data type. They therefore need to be separated in the state partitions.

Observation probabilities are constructed differently for phantom tags and the other tag types. For phantom tags, using the subscript notation l to refer to the mark-recapture data type, we simply write:

$$p(y_{21,t,l=pha}|x_{15,t}) = 1$$

but zero otherwise, meaning that tags are only seen if the individual is recently dead. Individuals with phantom tags are always correctly identified as belonging to state $x_{15,t}$.

For the other mark-recapture data types (branded, chipped, and flipper tagged), observation probabilities for each state include the probabilities $\underline{r}$ of returning to the beach (and therefore being available for observation), whether an individual can be identified using a tag or other marking (described using a conditional resight probability $\underline{\upsilon}$), and an observation uncertainty $\underline{\delta}$ indicating whether the breeding status of an individual can be categorised or not (Table 3). For $l \neq phantom$, observations for $x_{5,t}$ are illustrative:

$$\begin{aligned}
p(y_{5,t,l}|x_{5,t}) &= \upsilon_{a(5),l} \cdot r_{nbr} \cdot \delta_{nbr} \\
p(y_{7,t,l}|x_{5,t}) &= \upsilon_{a(5),l} \cdot r_{nbr} \cdot (1 - \delta_{nbr}) \\
p(y_{20,t,l}|x_{5,t}) &= (1 - \upsilon_{a(5),l}) \cdot r_{nbr} + 1 - r_{nbr}
\end{aligned}$$

which refer respectively to the probabilities of an individual in state $x_{5,t}$ being recorded in observation categories $y_{5,t,l}$, $y_{7,t,l}$, or $y_{20,t,l}$, at time t for mark-recapture data type l.

Table 3: Table of notations used to construct transition and observation probabilities per year for reference case model with informed estimation of time variant pup survivorship.

Notation	Description
Subscripts and partitions	
$i = \{1, 2, \ldots\}$	individual
$t = \{0, 1, \ldots, 30\}$	time from 1990 to 2019 inclusive
$k = \{1, 2, \ldots, 16\}$	index for hidden state $x_{k,t}$
$m = \{1, 2, \ldots, 22\}$	index for observed state $y_{m,t}$
$a = \{0, 1, \ldots, 8+\}$	age
$a(k)$	age at state index k
$l = \{pha, bra, chp, tag\}$	mark-recapture data type, being one of phantom, branded, chipped, or flipper tagged.
Time invariant parameters	
$P_5(x_k)$	Simplex vector of proportions per state at time $t = 5$
N_5	Initial numbers scalar at time $t = 5$
$\underline{\phi}(0) = \{\phi_0, \phi_{imm}, \phi_{mat}\}$	probability of survivorship for pups (age 0), immature, and mature individuals
$\underline{\alpha}(0) = \{\alpha_a\}$	probability of pupping for age a
$\underline{r} = \{r_{imm}, r_{nbr}, r_{brd}\}$	probability of returning to beach for immature, non-breeding, and breeding individuals
$\underline{\upsilon} = \{\upsilon_{a,l}\}$	probability of observation for age a and mark data type l, conditional on return to the beach. For $l = tag$, this is as a function of the tag loss rate parameters u_0 and u (Equation 1)
$\underline{\delta} = \{\delta_{nbr}, \delta_{brd}\}$	probability of recording non-breeder or breeder as unknown
Time variant parameters	
$\underline{\phi}(t) = \{\phi_{0,t}\}$	probability of survivorship for pups (age 0) at time t
Error terms	
σ	dynamic regression variance term fixed at $\sigma = 1$ for reference model
τ	smoothing parameter with $0 < \tau < 1$

Similarly for an individual in state $x_{6,t}$:

$$\begin{aligned}
p(y_{6,t,l}|x_{6,t}) &= \upsilon_{a(6),l} \cdot r_{brd} \cdot \delta_{brd} \\
p(y_{7,t,l}|x_{6,t}) &= \upsilon_{a(6),l} \cdot r_{brd} \cdot (1 - \delta_{brd}) \\
p(y_{20,t,l}|x_{6,t}) &= (1 - \upsilon_{a(6),l}) \cdot r_{brd} + 1 - r_{brd}
\end{aligned}$$

The observation category $y_{20,t,l}$ records when an individual was not seen. If she is alive, this may be due to either not returning to the beach to breed or returning but not being identified (because of tag loss, for example). Alternatively, she may be dead (i.e. in state categories $x_{15,t}$ or $x_{16,t}$), in which case she is never seen:

$$p(y_{20,t,l}|x_{15:16,t}) = 1.0$$

Finally, for calculation of the mark-recapture likelihood using the forward algorithm (Section 4.1), observation probabilities for a state must sum to one and we therefore require an “unobservable” category for when no sampling effort took place. If there are data the unobservable observation category is always empty:

$$p(y_{22,t,l}|x_{k,t}) = 0.0$$

but conversely, if there was no sampling effort then for all k:

$$\begin{aligned} p(y_{1:21,t,l}|x_{k,t}) &= 0 \\ p(y_{22,t,l}|x_{k,t}) &= 1 \end{aligned}$$

This ensures that each state is always observed in one of the available observation categories:

$$\sum_k p(y_{k,t,l}|x_{z,t}) = 1$$

2.2 Conditional resight probabilities

We define $\upsilon_{a(k),l}$ as the probability of resighting an individual in state k, with tag type l, given that she has returned to the beach (Table 3). For the four types of mark-recapture data each has a resight probability that is considered differently. Individuals that are branded have a conditional resight probability of one: we assume that they are always seen if they return to the beach. Individuals that are observed dead (phantom tags) also have a conditional resight probability of one. Individuals that are chipped have an estimated resight probability that is constant across states. These are easily represented in the model. However, for individuals that have been tagged using flipper tags, we are required to model the tag-loss process so as to calculate the probability that an individual has lost both tags and therefore cannot be identified.

To model the loss of flipper tags, we assume a binomial process, but with a higher initial loss rate (loss in the first year of tagging) and with a plus group for ages 8+. Using the notation d, s, and m to represent double, single, and missing tags respectively, and $d \rightarrow s$, $s \rightarrow m$, and $d \rightarrow m$ to denote the various types of tag loss then:

$$\begin{aligned} \mathbb{P}[d \rightarrow d] &= 1 - \left(2 \cdot u \cdot (1-u) + u^2\right) \\ \mathbb{P}[d \rightarrow s] &= 2 \cdot u \cdot (1-u) \\ \mathbb{P}[d \rightarrow m] &= u^2 \\ \mathbb{P}[s \rightarrow s] &= 1 - u \\ \mathbb{P}[s \rightarrow m] &= u \\ \mathbb{P}[m \rightarrow m] &= 1 \end{aligned}$$

where u is the annual tag loss rate parameter. The intial tag loss is given the notation $\mathbb{P}_0[.]$ with parameter u_0. These can be used to calculate the probabilities at age of an individual having two, one, or no tags at age a. The age is initialised at $a = 1$, referring to the probability of tag loss between age 0 and age 1. Therefore, because tagged pups are all given double tags:

$$\begin{aligned} \mathbb{P}[d|a=1] &= \mathbb{P}_0[d \rightarrow d] \\ \mathbb{P}[s|a=1] &= \mathbb{P}_0[d \rightarrow s] \\ \mathbb{P}[m|a=1] &= \mathbb{P}_0[d \rightarrow m] \end{aligned}$$

and the conditional resight probability for age one individuals is:

$$\upsilon_{a(k)=1,l=\text{tag}} = 1 - \mathbb{P}[m|a=1]$$

which is strictly an upper bound, because even some individuals with single (or double) tags may not be identified.
Similarly for ages $a > 1$, we can calculate the probabilies of double, single, or missing tags:

$$\begin{aligned}
\mathbb{P}[d|a] &= \mathbb{P}_0[d \rightarrow d] \times (\mathbb{P}[d \rightarrow d])^{a-1} \\
\mathbb{P}[s|a] &= \mathbb{P}_0[d \rightarrow s] \times (\mathbb{P}[s \rightarrow s])^{a-1} + \\
&\qquad (\mathbb{P}_0[d \rightarrow d]) \times (a-1) \times (\mathbb{P}[d \rightarrow d])^{a-2} \times \mathbb{P}[d \rightarrow s] \\
\mathbb{P}[m|a] &= 1 - (\mathbb{P}[d|a] + \mathbb{P}[s|a])
\end{aligned}$$

$$\implies \upsilon_{a(k),l=\text{tag}} = \mathbb{P}[d|a] + \mathbb{P}[s|a] \qquad (1)$$

For the probability of d, s, or m tags for the 8+ age group, we calculate the above probabilities for ten additional age classes and take the average. The use of ten additional age classes to calculate the plus group probability was arbitrary and chosen through trial and error.

2.3 State dynamics

We describe transition between states as a deterministic process, governed by the probabilities outlined above, with reference to time t, which indicates the beginning of the time step. The numbers in state x_k at the beginning of year t is therefore:

$$N(x_{k,t}) = \sum_j N(x_{j,t-1}) \cdot p(x_{k,t}|x_{j,t-1}) \qquad (2)$$

which fulfills the condition that:

$$\sum_k N(x_{k,t}) = \sum_k N(x_{k,t-1}) \qquad (3)$$

meaning that the population is closed to emigration and immigration. Following transition of the numbers vector into time t, the number of pups born is then:

$$N(x_{0,t}) = \frac{1}{2} \cdot \sum_k N(x_{k,t}) \quad \text{for} \quad k = \{6, 8, 10, 12, 14\} \qquad (4)$$

since each breeding female is assumed to produce a single pup with a 50% probability of being female.

It should be noted that whereas transition probabilities are estimated over the full temporal range of mark-recapture data ($t = 0$ to $t = 30$), the abundance is estimated only for years containing pup census data (Table 5). The numbers are therefore initialised at $t = 5$, corresponding to 1995, and estimated through to $t = 30$. To initialise the model dynamics, the initial state proportions $P_{t=5}(x_k)$ were treated as estimated parameters and multiplied by a scalar:

$$N(x_{k,5}) = N_5 \cdot P_5(x_k) \quad \text{with} \quad \sum_k P_5(x_k) = 1 \qquad (5)$$

This parameterisation required a further constraint so that the number of pups in the first year was consistent with the number of breeding females (see Section 4).

2.4 Informed estimation of dynamic survivorship

To allow for covariate data to be included so as to inform the estimation of time-variant parameters, we need to introduce an observation model that relates an unobserved condition or state to an observed covariate value. Usually, this would be represented as a regression of the time-variant rate onto the observed covariate (e.g. Brooks et al. 2004, Gimenez et al. 2009, Schofield & Barker 2011). However, to do so assumes that the covariate is measured without error, which is not true. Instead, we require a model that allows for uncertainty in both the observation and the underlying state process. This is better represented as a state-space model, also known as a *dynamic linear regression* (Durbin & Koopman 2001). Not only does this approach better represent both the observation and process uncertainties, but it has a number of desirable features, including an ability to smooth responsiveness of the state, include a lag, account for missing observational data and allow the state to be correlated with more than one data time series.

In the current setting we are interested in the relationship between observed pup mass shortly after birth and the estimated (unobserved) pup survivorship in the first year of life, which we suspect to be positively correlated (Roberts et al. 2021). Including an index on pup mass follows naturally from our representation of time-variant pup survivorship, with an additional sub-model used to represent uncertainty in the relationship between $\phi_{0,t}$ and the normalised index of pup mass w_t:

$$\operatorname{logit}(\phi_{0,t}) = \operatorname{logit}(\phi_0) + \varepsilon_t \quad \text{with} \quad \varepsilon_t \sim N(0, \tau \cdot \sigma^2) \tag{6a}$$

$$w_t = \eta + \operatorname{logit}(\phi_{0,t}) \cdot \beta + \varepsilon_t \quad \text{with} \quad \varepsilon_t \sim N(0, (1-\tau) \cdot \sigma^2) \tag{6b}$$

This representation partitions the variance between temporal changes in the latent variable $\phi_{0,t}$ and the observation error, using the smoothing parameter τ. Smaller values of τ lead to a more damped response to variation in w_t under the assumption that the variation is attributable to observation error rather than true fluctuations in the survivorship. Either τ or σ can be estimated, but not both. In the currrent implementation, τ was estimated under a range of fixed values for σ. Alternative runs were attempted in which σ was estimated for fixed τ, but this failed to produce adequate fits to the pup mass index.

3 Data

Four sources of data were available to paramaterise the model. These data were identical to those used for the quantitative modelling conducted by Roberts (2019) with the exception of the standardised pup mass index, which was provided by Roberts et al. (2021) for the purposes of this project. Consistent with Roberts (2019), mark-recapture data was restricted to that collected at Sandy Bay, whereas pup census data was for the entire Auckland Islands archipelago. The data were:

- Mark-recapture: All pups were tagged on the beach and subsequent resightings recorded on their return. Individuals could be uniquely identified, substantially increasing the power of the data to resolve time variant life-history parameters. All resighted individuals were assigned to one of the observation categories listed in Table 2. Three different types of markings were used, beginning in 1990 and ending in 2019, and are listed in Table 4. Mark types were exclusive, meaning that each individual was assigned to only one mark type category. Precedence was given to branding, followed by passive integrated transponders (PIT tags or "chips"), and then flipper tags, which is the (descending) order in which they were most reliably resighted. For example, an individual that was both branded and chipped, was consider here as "branded", whereas an individual that was both chipped and flipper tagged was considered as belonging to the "chipped" mark data type. This assignment to a particular mark data type was based on how they were marked as pups and retained throughout their resight history regardless of how the resight was recorded.

- Counts of tag loss: Using data from all mark types, the number of flipper tags at age was calculated across all observed individuals (Table 6). Individuals with an unknown number of flipper tags were excluded. These data were used to directly estimate the tag loss rate at age.
- Dead pup counts: pups recorded as dead on the beach were considered to be an additional mark data type, referred to as "phantom" tags, because they were recorded as dead at the time of "tagging" (Table 4). For each dead pup recorded at time t a new observation time series was created, consisting of a mark at time t and a death at time $t+1$. This records the occurence of an individual known to have died during its first year. Inclusion of these data was necessary to ensure accurate estimation of pup mortality.
- Pup census counts: The number of pups on the beaches (live and dead) between 1995 and 2019 was counted and divided by two, giving important information on the annual pup production (Table 5).
- Pup mass data: a standardised index of female pup mass was provided for 1990 to 2019 (Table 5).

When considering the mark-recapture data, it is necessary to include the "observability," which is a binary variable indicating whether or not any resight effort had been expended in a particular year (this differs from the resight probability, which is conditional on there being positive sampling effort). The observability for brand, chip, and tag mark-recapture data types was one for all years except 1994 to 1997. For phantom tags, the observability is one for all years, because a "tag" automatically implies a resight and therefore resight effort.

4 Model fitting

The estimated parameters for the multi-event integrated HMM are listed in Table 3. Calculation of the likelihood for the mark-recapture data is described first, because this is the most important, followed by contributions of the tag-loss and pup census data. Finally, the likelihood for inclusion of the covariate data is described.

4.1 Mark-recapture data

Calculation of the mark-recapture likelihood is via the *forward algorithm* (Zucchini & MacDonald 2009), which calculates the joint marginal probability of both the current state and the preceding observations per individual. Dropping the i and l subscripts, for individual and data type respectively, we write this probability as $\gamma(x_{k,t}, y_{m,t}, \ldots, y_{m,1})$, which is the probability of state k at time t and all observations for the individual up until then. This is calculated recursively for each observed value $y_{m,t}$:

$$\gamma(x_{k,t}, y_{m,t}, \ldots, y_{m,1}) = p(y_{m,t}|x_{k,t}) \cdot \sum_j p(x_{k,t}|x_{j,t-1}) \cdot \gamma(x_{j,t-1}, y_{m,t-1}, \ldots, y_{m,1}) \tag{7}$$

The algorithm is initialised for each individual at $t = t_0$, which is the time of first observation (capture), and with initial conditions $\gamma(x_{k,t_0}, y_{m,t_0}) = 1$ and $\gamma(x_{j\neq k,t_0}, y_{m,t_0}) = 0$, corresponding to the fact that the initial capture state is known without error. The final individual likelihood contribution is calculated by marginalising $\gamma(x_{k,T}, y_{m,T}, \ldots, y_{m,1})$ across all possible states in the final time step $t = T$, to calculate the probability of the time series of observations, whilst accounting for uncertainty in the latent states:

$$\mathbb{L}\left[y_{m,T},\ldots,y_{m,1}\right]=\sum_{k}\gamma(x_{k,T},y_{m,T},\ldots,y_{m,1}) \tag{8}$$

4.2 Tag loss

The probabilities of double d, single s, or missing m flipper tags at age a are calcuated using Equation 1. The number observed ($n_{d,a},n_{s,a},n_{m,a}$; Table 6) is then modelled using a multinomial probability distribution:

$$\mathbb{L}\left[\mathbf{n}_d,\mathbf{n}_s,\mathbf{n}_m\right]=\prod_{a=1}^{8+}\frac{(n_{d,a}+n_{s,a}+n_{m,a})!}{n_{d,a}!\cdot n_{s,a}!\cdot n_{m,a}!}\cdot\left(\mathbb{P}\left[d|a\right]\right)^{n_{d,a}}\cdot\left(\mathbb{P}\left[s|a\right]\right)^{n_{s,a}}\cdot\left(\mathbb{P}\left[m|a\right]\right)^{n_{m,a}} \tag{9}$$

4.3 Pup census data

The pup count data is assumed to be Poisson distributed, with an expectation equal to the number of breeding females. For observed numbers n_t (Table 5), this was approximated using a Normal distribution:

$$\mathbb{L}\left[n_5,\ldots,n_T\right]=\prod_{t=5}^{T}\frac{1}{\sqrt{2\cdot\pi\cdot\mu_t}}\exp\left(-\frac{1}{2}\cdot\frac{(n_t-\mu_t)^2}{\mu_t}\right) \tag{10}$$

$$\mu_t=\frac{1}{2}\sum_{k}N\left(x_{k,t}\right)\quad\text{for}\quad k=\{6,8,10,12,14\}$$

4.4 Pup mass

The likelihood for the pup mass index has two components, both of which are dependent on τ, which is estimated, and a fixed input value for σ. First, for the dynamics of $\phi_{0,t}$ over time given the estimated expectation ϕ_0 (Equation 6a):

$$\mathbb{L}\left[\underline{\phi}\left(t\right)\right]=\prod_{t=1}^{T}\frac{1}{\sqrt{2\cdot\pi\cdot\tau\cdot\sigma^2}}\exp\left(-\frac{1}{2}\cdot\frac{(\phi_{0,t}-\phi_0)^2}{\tau\cdot\sigma^2}\right) \tag{11}$$

and then for the normalised pup mass index w_t given the expected value $\hat{w}_t=\eta+\phi_{0,t}\cdot\beta$ (Equation 6b):

$$\mathbb{L}\left[w_t\right]=\prod_{t=1}^{T}\frac{1}{\sqrt{2\cdot\pi\cdot(1-\tau)\cdot\sigma^2}}\exp\left(-\frac{1}{2}\cdot\frac{(w_t-\hat{w}_t)^2}{(1-\tau)\cdot\sigma^2}\right) \tag{12}$$

4.5 Priors and constraints

To invoke biological realism the survivorship is constrained to be higher in older age classes:

$$\phi_0\leq\phi_{imm}\leq\phi_{mat}$$

and similarly for the probability of breeding:

$$\alpha_{a-1}\leq\alpha_a$$

for $a=\{5,6,7,8+\}$. Finally, the return probability for breeding individuals is ordered such that:

$$r_{imm}\leq r_{nbr}\leq r_{brd}$$

The number of female pups born is deterministic (Equation 4), with the exception of the initial year ($t = 5$) for which the number of pups in the population is a component of the estimated vector $P_5(x_k)$ (Equation 5). Within a stochastic model the number of offspring produced by a cohort of females can be represented by a Poisson distribution (e.g. Brooks et al. 2004). Therefore, to ensure that the initial number of pups is consistent with the initial number of breeding females, a constraint is imposed in the form a Normal approximation to the Poisson:

$$N(x_{0,5}) \sim Normal(\mu_5, \mu_5)$$

$$\mu_5 = \frac{1}{2}\sum_k N(x_{k,5}) \quad \text{for} \quad k = \{6, 8, 10, 12, 14\}$$

All parameters contributing to the calculation of state transition and observation probabilities were given standard normal priors on the logit-scale:

$$\text{logit}\left(\underline{\phi}\right) \sim Normal(0,1)$$

$$\text{logit}\left(\underline{\alpha}\right) \sim Normal(0,1)$$

$$\text{logit}\left(\underline{r}\right) \sim Normal(0,1)$$

$$\text{logit}\left(\underline{\delta}\right) \sim Normal(0,1)$$

Tag loss rate parameters were:

$$\{u_0, u\} \sim Beta(1,1)$$

whilst $0 \leq \upsilon_{a,l=chp} \leq 1$ was estimated as a free parameter and $\upsilon_{a,l=bra}$ was fixed at one. Regression parameters were:

$$\eta \sim Normal(0,1)$$

$$\beta \sim Normal(0,1)$$

$$\tau \sim Beta(1,1)$$

Lastly, $P_5(x_k)$ and N_5 were each given improper uniform priors with a lower bound at zero.

5 Model development

The model was constructed using the **rstan** coding environment (Stan Development Team 2019, R Core Team 2019). A *base* model was first developed to assess essential validity of the code and estimation framework, assuming constant (time-invariant) rate parameters (and therefore no relationship between pup mass and survivorship). Validation was performed using simulated data to ensure that known parameter values could be recovered by the model (Section 6.1). Next, performance of the regression was investigated; specifically model fits to the pup mass index under differing error assumptions (Section 6.2). The selected model (the *reference* model) was taken through to estimation using Markov Chain Monte Carlo (MCMC), and model fits to the data are reported (Section 6.3). Finally, the model that includes a regression on pup mass was compared with a model with the same structure but no continuous covariate data (the *naive* model), so as to assess the benefits of including these data (Section 6.4). The different models and their utility are listed in Table 7.

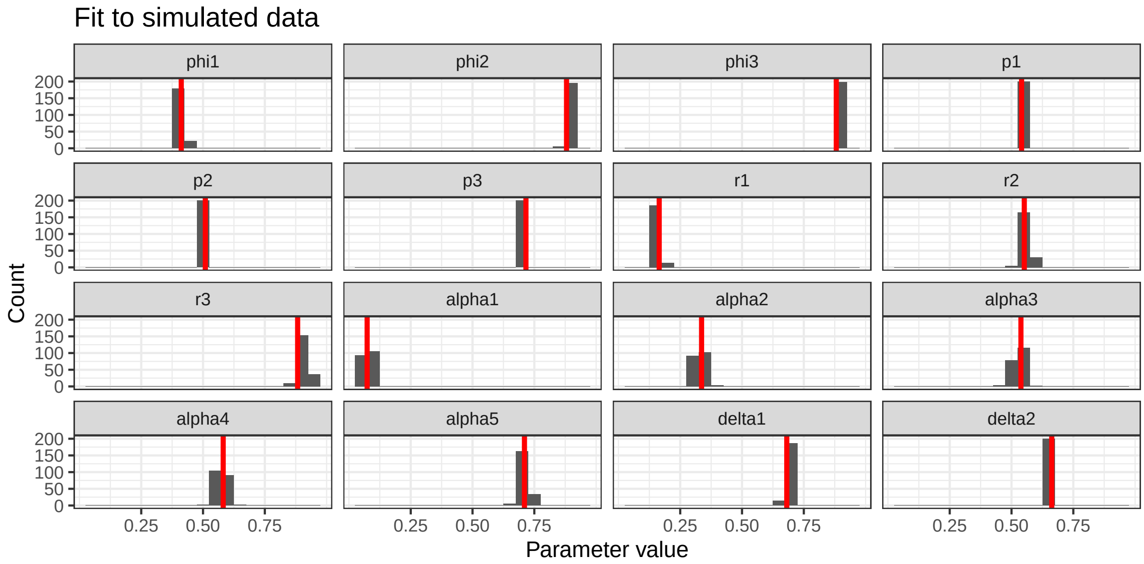


Figure 1: Simulation based validation of model structure. Data were simulated, and the model refitted to the simulated data using maximum posterior density estimation. Histograms show estimated values from the simulated data, relative to values used for the simulation (vertical red line).

6 Results

6.1 Model validation

The initial (base) model construct was first validated through simulation, which required the simulation of new mark-recapture data based on known parameter values, then re-fitting the model to assess whether the input values can be recovered:

1. Fit the model to the complete data using maximum penalised likelihood
2. Simulate 200 iterations of mark-recapture data using the fitted values
3. Re-fit the model to the simulated data

Results for the transition and observation probability parameters are shown in Figure 1. Typically, estimated parameter values are similar to those used to generate the data. Because similar parameter values are obtained from a fit to real or simulated data we can conclude that the model, as a statistical representation of the data, is a good approximation. If, for example, the model was a biased estimator of the survivorship, then simulated and observed data would be a poor match, and the input and estimated parameter values would be different.

6.2 Model selection

Performance of the regression (Equation 6) was explored by including the pup mass index and estimating the smoothing parameter τ under a range of fixed σ values. Fits of the model to the pup census and pup mass index, achieved through maximisation of the penalised likelihood, are shown in Figure 2.

Fits to the census data are good for all model runs. At smaller values of σ, the model predictions of the pup mass become increasingly accurate (up to a lower limit: for values of $\sigma \leq 0.5$ the minimisation

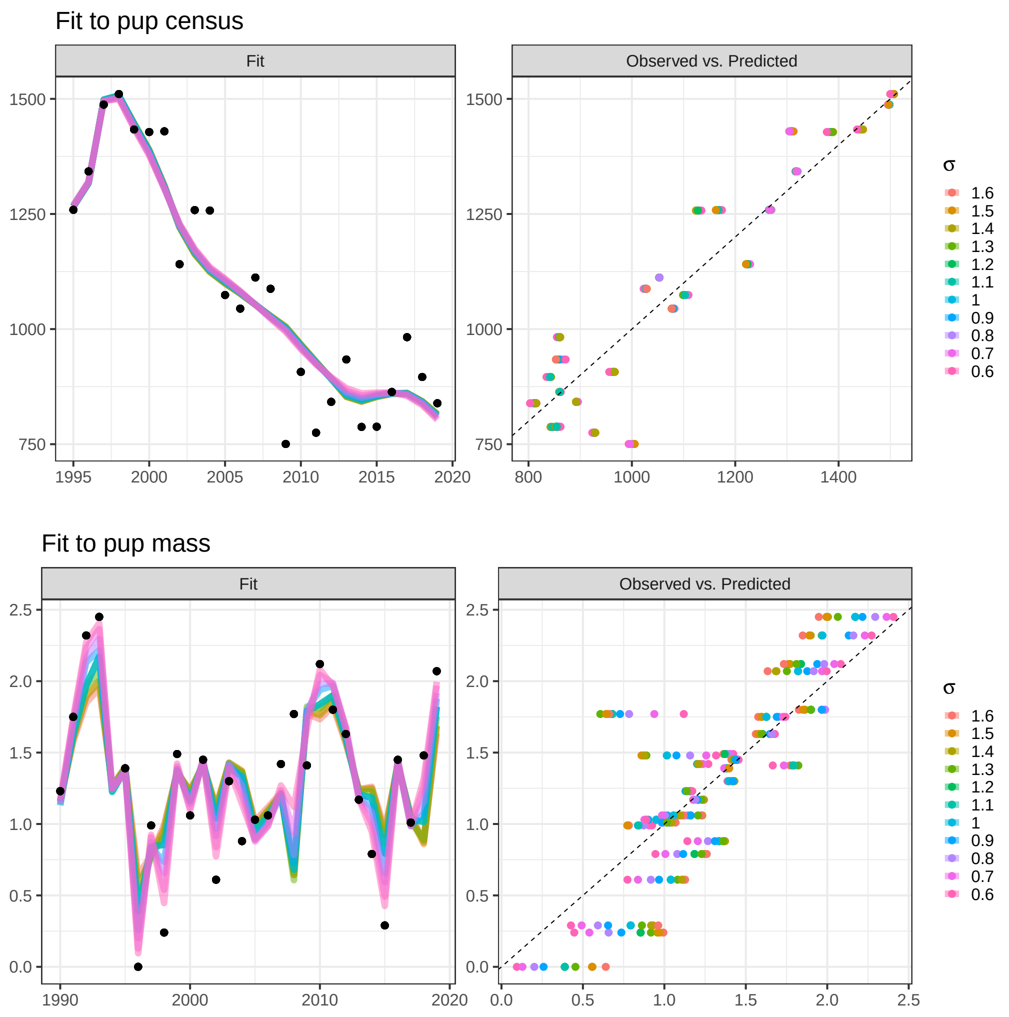


Figure 2: Fits of reference model to census and pup mass index under different assumed values of σ.

becomes unstable). Intuitively, smaller σ values place an increasing weight on the pup mass index at the expense of model flexibility to fit the other data types (because time-variant $\phi_{0,t}$ is more constrained). The mean prediction error was used to measure fits to the different data types. From Figure 3, it can be seen that improved fits to the pup mass impede the fit to the mark-recapture data, because at smaller values of σ there is an increase in the mean prediction error. Based on these results, a value of $\sigma = 1$ was adopted for the reference case model, because it allowed a good fit to the pup mass index without compromising fits to the mark-recpture observations.

6.3 Model fits

The reference model converges well, requiring fewer than 1000 iterations to reach stability of the MCMC chain (Figure 4). Fits to the pup census data are good (Figure 5), with the model reproducing the observed decline in pup numbers over time. Fits to the pup mass index (Figure 6) show that the model is responsive to the covariate data, with pup survivorship changing over time with pup mass. Fits to the tag loss data are shown in Figure 8. Although not included directly into the likelihood calculations, it is also reassuring to note that the model is able to accurately reproduce the proportion of breeding females (Figure 7).

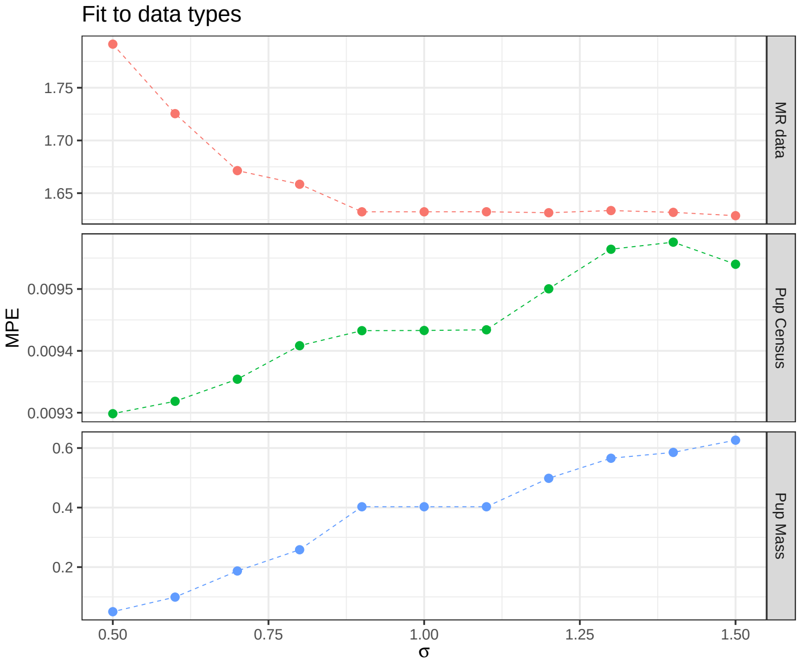


Figure 3: Mean prediction error for the three input data types under different assumed input values for σ (Equation 6)

Fits to the mark-recapture data are shown in Figure 9. For each individual in the mark-recapture data, posterior prediction was used to simulate a time series of states, from which observations could be simulated. Summing these simulated observations per tag data type, year, and observation class, these predicted values were compared to the observations. This is a form of posterior predictive checking (Gelman et al. 1996), based on the intuitive idea that if a model is a good fit to the data, then the replicated data ($y^*_{m,t}$) predicted from the model should look similar to the observed data ($y_{m,t}$). Parameter uncertainty is explicitly accounted for because the data realisations are generated from parameter values randomly drawn from the posterior distribution. To simplify the comparison, a summary statistic is used. In this case it is the multi-event m-array $M_{l,m,t}$ which is a summation of the numbers per tag data type, per observation class, per year. Comparisons of $M_{l,m,t}$ with $M^*_{l,m,t}$ are shown in Figure 9. As a further diagnostic, a discrepancy measure D was constructed so as to include both the simulated data and expected values (e.g. Chapter 7; Kéry & Schaub 2011). To achieve this, simulated tag observations $M^*_{l,m,t}$ were compared with the expected values from the model fit, and empircal tag observations $M_{l,m,t}$ were compared with the same expected values:

$$D_{l,m} = \sum_t \log\left(M_{l,m,t}\right) - \log\left(\mathbb{E}\left[M_{l,m,t}\right]\right)$$

$$D^*_{l,m} = \sum_t \log\left(M^*_{l,m,t}\right) - \log\left(\mathbb{E}\left[M_{l,m,t}\right]\right)$$

If the model is structured correctly, these two comparisons (summarised as $D_{l,t}$ and $D^*_{l,t}$) should generate a roughly equivalent residual. It can be seen from Figure 10 that the model in general provides a good match to the data, but that it underestimates the number of 8+ breeding (y_{18}) individuals in the branded data set, and the number of 8+ non-breeding and breeding individuals (y_{17} and y_{19} respectively) in the chipped data set.

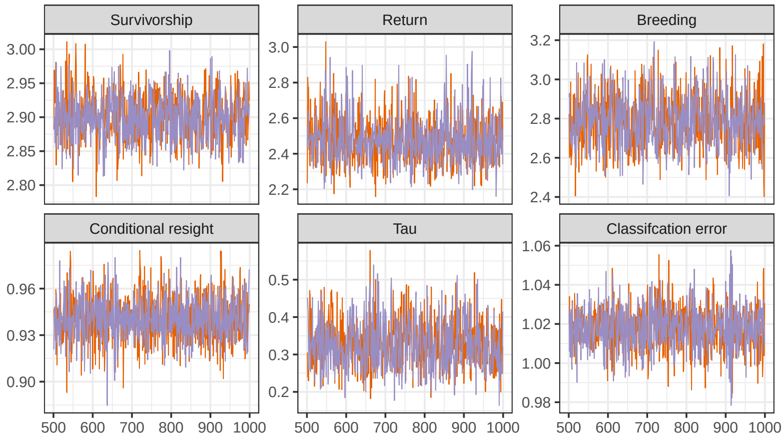


Figure 4: Trace diagnostics for estimated parameters (Table 3). The Euclidean norm ($||.||$) of parameter vectors is shown. Specifically: survivorship: $||\underline{\phi}||$; return: $||\underline{r}||$, breeding: $||\underline{\alpha}||$, resight: $||\underline{\upsilon}||$, Tau: τ, and Classification error: $||\underline{\delta}||$. Two overlapping chains are shown, each of 1000 iterations with the first half discarded.

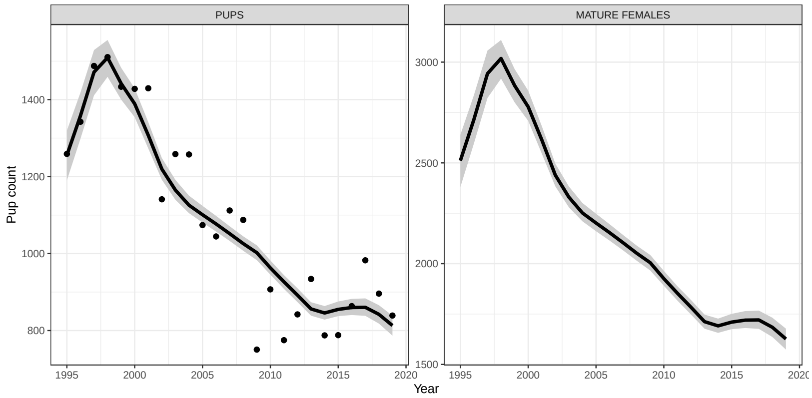
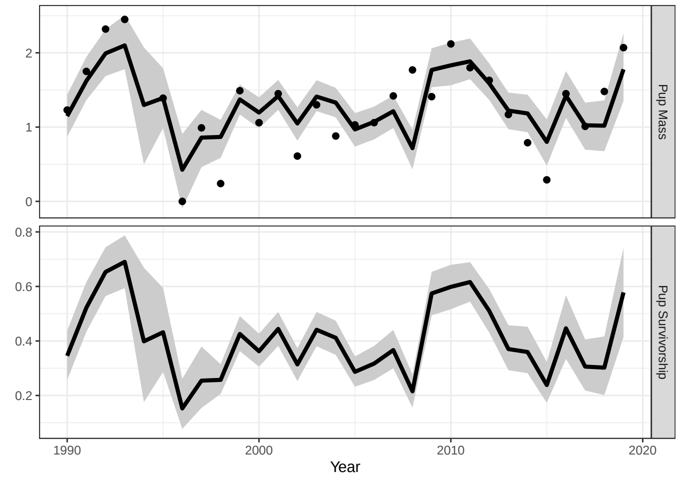
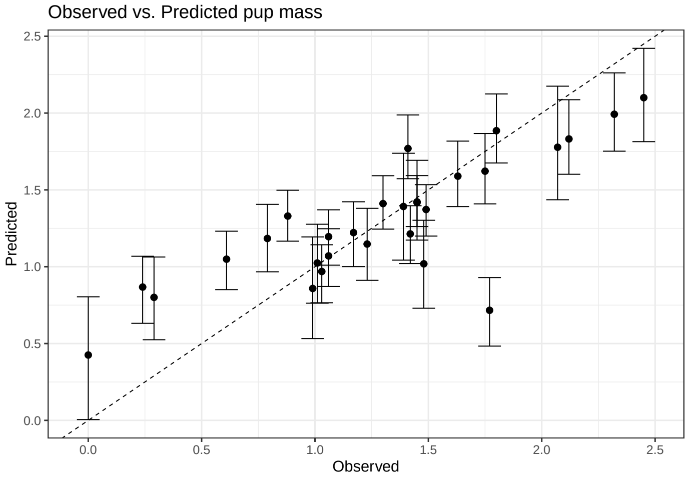


Figure 5: Time series of empirical pup counts for the Auckland Islands archipelago (points) and predicted values from the model fit. The associated number of breeding females is also shown. Predictions are shown as the median and 95th percentile of their respective posterior distributions.



(a) Time series of observed pup mass index values (points), predicted values from the model fit, and estimated pup survivorship ($\phi_{0,t}$) over time. Predictions are shown as the median and 95th percentile of their respective posterior distributions.



(b) Observed and predicted pup mass index values, with predictions shown as the median and 95th percentile of the posterior distribution.

Figure 6: Fit to pup mass data and estimated time series of pup survivorship.

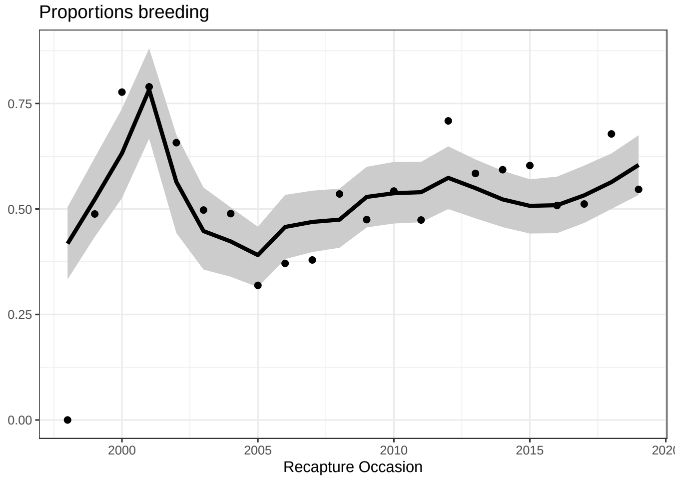


Figure 7: Observed and predicted proportions of the female population breeding per year. Proportions are calculated relative to the total number of mature individuals (breeding, non-breeding, and unknown).

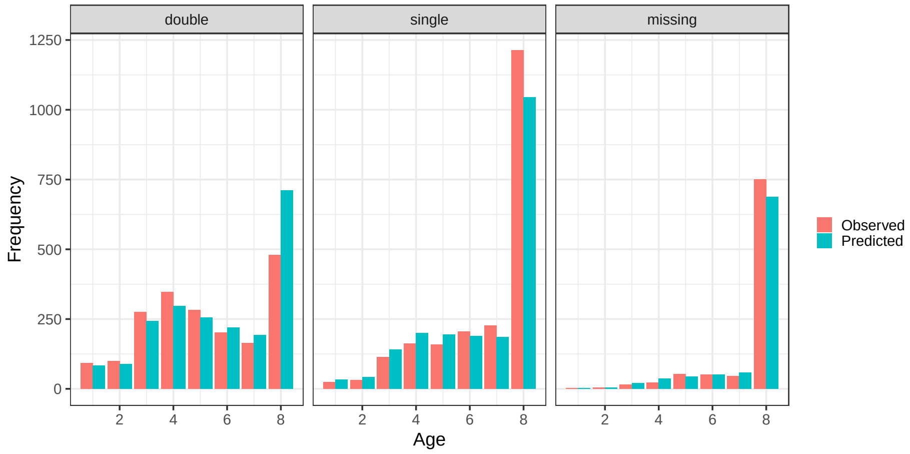


Figure 8: Fit to tag loss data. Observed and predicted frequencies of individuals with double, single, or missing flipper tags.

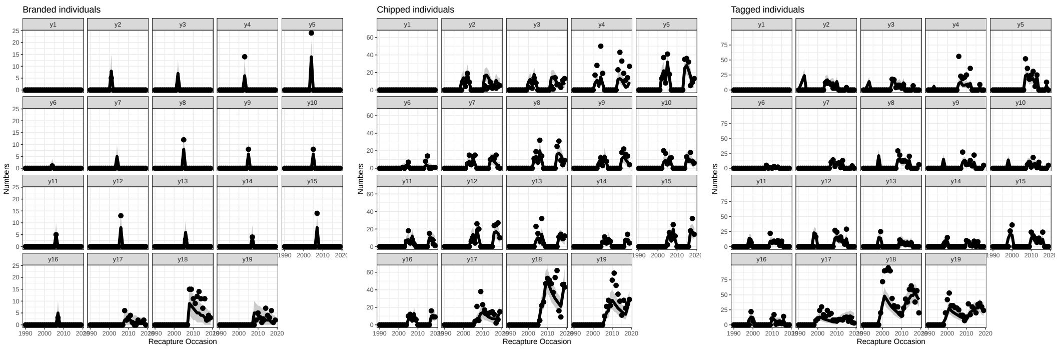


Figure 9: Fits to tag data. Observed numbers by mark-recapture data type (branded, chipped, or flipper tagged), class (Table 2), and year are shown as points. The median and 95th percentile of the posterior predicted values from the model fit are shown.

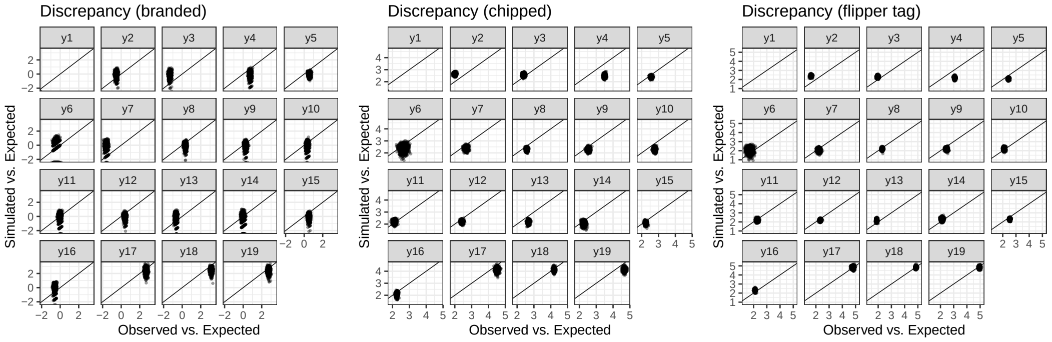


Figure 10: Discrepancy plots for each mark-recapture data type (branded, chipped, or flipper tagged), and class (Table 2) showing the relationships between $D^{*}_{m,l}$ (Simulated vs. Expected) and $D_{m,l}$ (Observed vs. Expected).

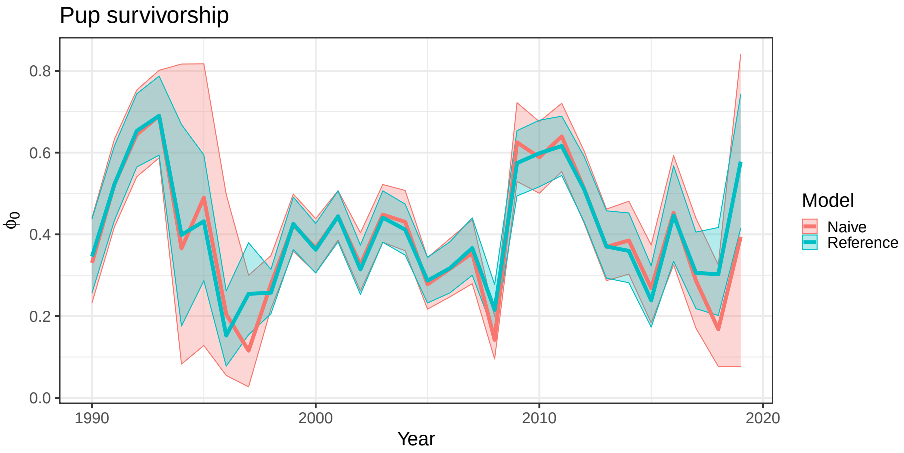


Figure 11: Estimated annual pup survivorships ($\phi_{0,t}$) over time for models with and without the pup mass covariate included (Table 7).

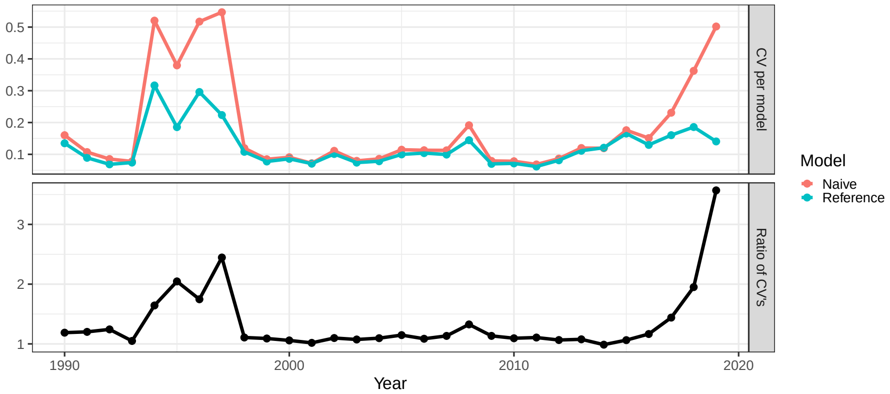


Figure 12: Uncertainty in estimates of the pup survivorship over time, $\phi_{0,t}$, measured using the $CV[\phi_{0,t}]$. The top panel shows the CVs for each model. The bottom panel shows the ratio of CVs from the naive to the reference case model, indicating that the CV for the naive model estimate is typically higher. Note the improvement in CV for cohorts that were not marked (1994–1997) or that had not been resighted by 2019 (2017–2019).

6.4 Utility of covariate data

The reference case model was fitted to the mark-recapture and pup census data, with and without the covariate data on pup mass. In the absence of this covariate data, the change in pup survivorship over time is a simple white noise process (i.e. stochastic with no correlated between years). Comparison of the pup survivorship estimates over time from the two models is given in Figure 11. It is interesting to note that both estimates are very close for much of the time series. This indicates that the mark-recapture data have a strong influence. However, it can also be seen that differences appear for periods of time when the mark-recapture data are either absent (1994–1997; Table 4) or uninformative (2017 onwards). The data are uninformative until individuals tagged as pups start to return to the beach approximately four years later. Hence there are few data with which to estimate pup survivorship in the last four years. Both of these features (the impact of missing and uninformative data) can be seen in Figure 12, which for the naive model shows an increase in the coefficient of variation for 1994–1997 and from 2017 onwards, compared with the model including the covariate data (the reference model; Table 7). We can therefore conclude that including the pup mass index provides information for the estimation of pup survivorship in years when the mark-recapture data are lacking, including the latest field seasons.

From Figure 6a, it can be seen that the predicted pup mass fits the data well. The fit is also good for recent years, this gives confidence that the estimated pup survivorship for 2017 onwards is at least consistent with the relationship between pup survivorship and pup mass, noting that this relationship was estimated in the context of informative mark-recapture data over most of the time series. This conclusion is particularly important if the model is to be used for projections, because if pup survivorship is better estimated in the current year, short term predictions of the population dynamics will be be better resolved. We note that previous SeaBird models, when conducting projections, have not used the most recent two years of pup survivorship as they are too poorly estimated.

7 Discussion and Conclusions

The reference case model integrates across disparate data types, namely mark-recapture (and "recovery") data, census (pup count) observations, and continuous covariate data (in the form of a standardised index of pup mass). It is able to provide good fits to all of these data series, showing predictions that match closely to the empirical values, and converges well when parameters are estimated using MCMC. Most importantly for the current project it is shown that the pup mass index can be used to inform estimation of the pup survivorship, which has important implications for years where the mark-recapture data are uninformative or missing. This includes the most recent cohorts, because resightings will be too sparse to obtain precise estimates of annual survival. An ability to predict survivorship from pup mass also has implications for the monitoring of sea lion colonies other than Sandy Bay (e.g. Dundas Island and Figure of Eight Island), where restricted access may mean that consistent collection of mark-recapture data is unfeasible, but occasional access to monitor pup mass may still be possible and provide some information indicative of first year survival.

The utility of pup mass for predicting pup survival suggests that pup nutritional status is a determinant of population productivity in New Zealand sea lions at the Auckland Islands. Since pups generally do not wean until around ten months post-partum (Gales 1995), it is likely that variation in pup mass relates in some way to the nutritional status of breeding females, which may in turn be driven by changes in the availability of key prey species (Roberts et al. 2018). In addition, bacterial disease (particularly *Klebsiella pneumoniae* infections, first detected in the early 2000s) and parasite burden (particularly hookworms) are thought to impact on pup survival (Michael et al. 2019, Roberts et al. 2014, Roe et al. 2015), and have an unknown effect on pup condition through time. We note that variable breeding rates (e.g., age at first breeding or annual breeding probability) of sea lions and other income breeders are also known to be responsive to changes in nutritional status (Gaillard et al. 2000), and future assessments could explore the potential for biological and environmental drivers of these demographic rates.

More generally, biodemographic models such as the one presented here could be used to develop a framework for assessing the population effects of nutritional stress and its environmental drivers, or other potential threats, to address a major shortcoming of previous multi-threat risk assessments, including those for New Zealand sea lions and Hector's and Māui dolphins (Roberts & Doonan 2016, Roberts 2019). We have not attempted this here. Conceptually, it would require formal comparisons between models that include different covariate inputs, each representing a potential threat, to assess which of these is both a strong determinant of the biological processes being modelled and of consequence for long term viability of the population.

7.1 Management implications

This project highlights the utility of pup mass measurements for monitoring the health of pups and predicting first-year survival. The standardised index of female pup mass used by this assessment was based on measurements from Sandy Bay. Given logistical difficulties with respect to the resighting of sea lions tagged as pups at the much larger rookery at Dundas Island, we recommend that future research considers the potential utility of using pup measurements to monitor both the Dundas Island population and the population at Figure of Eight Island.

Having identified an apparently strong relationship between pup mass and first year survival, we suggest that future research attempts to identify additional relationships, including the underlying drivers of these patterns. By including multiple threats, and assessing their impacts on the population's demographic rates, we could develop a framework capable of incorporating both top-down and bottom-up effects, useful for future iterations of the sea lion TMP, as well as for risk assessments of other threatened mega-fauna.

Table 4: Number of marks and resights per mark type and year. Mark types are exclusive, meaning that individuals are assigned to one only (see text).

	Phantom	Brand		Chip		Tag	
Year	Mark	Mark	Resight	Mark	Resight	Mark	Resight
1990						148	
1991						191	0
1992						226	0
1993						194	0
1994							
1995							
1996							
1997							
1998	5			255		0	1
1999	16			211	0	0	147
2000	11	139		105	11	0	181
2001	17	0	5	289	31	0	167
2002	33	0	2	174	68	0	153
2003	33	0	14	0	119	210	144
2004	16	0	26	0	155	252	145
2005	15	0	28	0	155	228	125
2006	19	0	21	0	161	211	159
2007	10	0	21	0	182	203	168
2008	11	0	21	0	124	208	193
2009	6	0	19	0	131	150	190
2010	9	0	19	171	127	0	201
2011	9	0	16	179	132	0	239
2012	9	0	14	181	110	0	186
2013	8	0	16	168	112	0	156
2014	3	0	18	81	214	76	185
2015	4	0	13	144	247	0	155
2016	7	0	15	167	240	0	151
2017	9	0	9	155	197	0	91
2018	11	0	7	166	236	0	108
2019			5		215		63

Table 5: Female pup counts (total pups, alive and dead, divided by two) for the Auckland Islands archipelago and standardised pup mass estimates

Year	Count	Pup mass index
1990		1.23
1991		1.75
1992		2.32
1993		2.45
1994		
1995	1 259.0	1.39
1996	1 342.5	0.00
1997	1 487.5	0.99
1998	1 510.5	0.24
1999	1 433.5	1.49
2000	1 428.0	1.06
2001	1 429.5	1.45
2002	1 141.0	0.61
2003	1 258.5	1.30
2004	1 257.5	0.88
2005	1 074.0	1.03
2006	1 044.5	1.06
2007	1 112.0	1.42
2008	1 087.5	1.77
2009	750.5	1.41
2010	907.0	2.12
2011	775.0	1.80
2012	842.0	1.63
2013	934.0	1.17
2014	787.5	0.79
2015	788.0	0.29
2016	863.5	1.45
2017	982.5	1.01
2018	896.0	1.48
2019	839.0	2.07

Table 6: Flipper tag counts at age, summed over all years and tag data types

Age	Frequency		
	Double	Single	Missing
1	92	25	3
2	100	32	4
3	275	114	16
4	347	163	23
5	282	159	53
6	202	206	51
7	164	227	45
8+	480	1 213	750

Table 7: Model descriptions

Model	Pup survivorship	Regression on pup mass	Notes
Base	Constant	False	Used for basic model validation through fit to simulated data (Section 6.1)
Naive	Time variant ($\sigma = 1$)	False	For comparison to *reference* model to evaluate benefit of including pup mass covariate data (Section 6.4)
Reference	Time variant ($\sigma = 1$, τ estimated)	True	Final model with σ selected following runs with alternate input values (Sections 6.2 and 6.3). Model code is provided in the Appendix (Listing A1).

8 Acknowledgments

This work was supported by NIWA core funding (project code FIFI1801) and Fisheries New Zealand (project code PRO2017-08C). Numerous individuals collected the raw data, including: Martin Cawthorn (Cawthorn & Associates), Simon Childerhouse (Blue Planet Marine), Louise Chilvers (Massey University), and field researchers contracted to the New Zealand Department of Conservation. The mark-recapture data are curated by Dragonfly Data Science were provided for this project in a suitable format. Samik Datta (NIWA, Wellington) provided a helpful review.

References

Baker, C.; Boren, L.; Childerhouse, S.; Constantine, R.; van Helden, A.; Lundquist, D.; Rayment, W.; Rolfe, J. (2019). Conservation status of New Zealand marine mammals, 2019. *New Zealand Threat Classification Series No. 29 held by the Department of Conservation* 18 p.

Barker, R.A. (2005). Handbook of Capture-Recapture Analysis. In: Modelling Demographic Processes in Marked Populations (Edited by S.C. Amstrup; T.L. McDonald; B.F.J. Manly), 142–163. Princeton University Press, Princeton, NJ.

Besbeas, P.; Feeman, S.N.; Morgan, B.J.T.; Catchpole, E.A. (2002). Integrating Mark-Recapture-Recovery and census data to estimate animal abundance and demographic parameters. *Biometrics* 58: 540–547.

Breen, P.A.; Fu, D.; Gilbert, D.J. (2012). Sea lion population modelling and Management Procedure Evaluations. *New Zealand Aquatic Environment and Biodiversity Report No. 175.* 89 p.

Brooks, S.P.; King, R.; Morgan, B.J.T. (2004). A Bayesian approach to combining animal abundance and demographic data. *Animal Biodiversity and Conservation* 27 (1): 515–529.

Childerhouse, S.; Gales, N. (1998). The historic distribution and abundance of the New Zealand sea lion *Phocarctos hookeri*. *New Zealand Journal of Zoology* 25: 1–16.

Childerhouse, S.; Michael, S.; Adams, L.; Burns, T.; Cockburn, S.; Hamer, D.; Maloney, A.; Pugsley, C. (2015). Final Report: New Zealand sea lion research at the Auckland Islands 2014/15. *Report produced by Blue Planet Marine for the NZ Department of Conservation* .

Cormack, R.M. (1964). Estimates of survival from the sighting of marked animals. *Biometrika* 51: 429–438.

Durbin, J.; Koopman, S.J. (2001). Time series analysis by state space methods. Oxford University Press, New York.

Francis, R.I.C.C.; Sagar, P.M. (2012). Modelling the effect of fishing on southern Buller's albatross using a 60-year dataset. *New Zealand Journal of Zoology* 39 (1): 3–17.

Gaillard, J.M.; Festa-Bianchet, M.; Yoccoz, N.G.; Loison, A.; Toïgo, C. (2000). Temporal Variation in Fitness Components and Population Dynamics of Large Herbivores. *Annual Review of Ecology and Systematics* 31 (1): 367–393.

Gales, N. (1995). Hooker's sea lion recovery plan (*Phocarctos hookeri*). *Threatened Species Recovery Plan Series No. 17 held by the Deparment of Conservation* .

Gelman, A.; Meng, X.L.; Stern, H. (1996). Posterior predictive assessment of model fitness via realized discrepancies. *Statistica Sinica* 6: 733–807.

Gimenez, O.; Bonner, S.J.; King, R.; Parker, R.A.; Brooks, S.P.; Jamieson, L.E.; Grosbois, V.; T, M.B.J.; Thomas, L. (2009). WinBUGS for Population Ecologists: Bayesian Modeling Using Markov Chain Monte Carlo Methods. In: Modelling Demographic Processes in Marked Populations (Edited by D.L. Thomson; E.G. Cooch; M.J. Conroy), 883–915. Springer US, Boston, MA.

Gimenez, O.; Lebreton, J.D.; Gaillard, J.M.; Choquet, R.; Pradel, R. (2012). Estimating demographic parameters using hidden process dynamic models. *Theoretical Population Biology* 82: 307–316.

Harding, K.C.; Fujiwara, M.; Axberg, Y.; Härkönen, T. (2005). Mass-Dependent Energetics and Survival in Harbour Seal Pups. *Functional Ecology* 19 (1): 129–135.

Jolly, G.M. (1965). Explicit estimates from capture-recapture data with both death and immigration-stochastic model. *Biometrika* 52: 225–247.

Kéry, M.; Schaub, M. (2011). Bayesian Population Analysis using WinBUGS – a hierarchical perspective. Academic Press.

MacKenzie, D.I. (2012). Estimation of Demographic Parameters for New Zealand Sea Lions Breeding on the Auckland Islands: 1997/98–2010/11. *Final Research Report for project POP2010-01 held by Department of Conservation* .

Michael, S.A.; Hayman, D.T.S.; Gray, R.; Zhang, J.; Rogers, L.; Roe, W.D. (2019). Pup mortality in New Zealand sea lions (*Phocarctos hookeri*) at Enderby Island, Auckland Islands, 2013–18. *PLoS ONE* 14 (11): 1–23.

Pradel, R. (2005). Multievent: An Extension of Multistate Capture–Recapture Models to Uncertain States. *Biometrics* 61: 442–447.

R Core Team (2019). R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.

Roberts, J.; Cawthorn, M.; Childerhouse, S.; Clemens-Seely, K. (2021). Biometric variability of New Zealand sea lion (*Phocarctos hookeri*) pups at the Auckland Islands and utility for predicting demographic rates. *New Zealand Aquatic Environment and Biodiversity Report No. 255.* 46 p.

Roberts, J.; O'Driscoll, R.; Hart, A.; Graham, B. (2018). Survey of New Zealand sea lion prey at the Auckland Islands and Stewart Snares Shelf. *New Zealand Aquatic Environment and Biodiversity Report No. 204.* 64 p.

Roberts, J.O. (2017). Supplemental sea lion population modelling to support an updated Squid Trawl Fishery Operational Plan. *Final Research Report for project SEA2016-24 held by Fisheries New Zealand* .

Roberts, J.O. (2019). Population effects of New Zealand sea lion mortality scenarios relating to the southern arrow squid fishery at the Auckland Islands. *New Zealand Aquatic Environment and Biodiversity Report No. 223.* 35 p.

Roberts, J.O.; Doonan, I. (2016). Quantitative Risk Assessment of Threats to New Zealand Sea Lions. *New Zealand Aquatic Environment and Biodiversity Report No. 166.* 111 p.

Roberts, J.O.; Fu, D.; Doonan, I.; Francis, R.I.C.C. (2014). New Zealand sea lion: demographic assessment of the causes of decline at the Auckland Islands. *Report prepared by NIWA for the Department of Conservation, Wellington, New Zealand* 142p.

Roe, W.; Rogers, L.; Pinpimai, K.; Dittmer, K.; Marshall, J.; Chilvers, B. (2015). Septicaemia and meningitis caused by infection of New Zealand sea lion pups with a hypermucoviscous strain of *Klebsiella pneumoniae*. *Veterinary Microbiology* 176 (3): 301–308.

Schofield, M.R.; Barker, R.J. (2011). Full Open Population Capture–Recapture Models With Individual Covariates. *Journal of Agricultural, Biological, and Environmental Statistics* 16 (2): 253–268.

Seber, G.A.F. (1965). A note on the multiple-recapture census. *Biometrika* 52: 249–259.

Stan Development Team (2019). RStan: the R interface to Stan. R package version 2.19.2.

Zucchini, W.; MacDonald, I. (2009). Hidden Markov models for time series: an introduction using R. Chapman & Hall/CRC.

Appendix: stan code

Code listing A1: Stan code for reference model

```
// -------------------------------------------------
// States (S):
// 1 I0
// 2 I1
// 3 I2
// 4 I3
// 5 M4N
// 6 M4B
// 7 M5N
// 8 M5B
// 9 M6N
// 10 M6B
// 11 M7N
// 12 M7B
// 13 M8N
// 14 M8B
// 15 JUST DEAD
// 16 DEAD
// Observations (O):
// 1 I0
// 2 I1
// 3 I2
// 4 I3
// 5 M4N
// 6 M4B
// 7 M4U
// 8 M5N
// 9 M5B
// 10 M5U
// 11 M6N
// 12 M6B
// 13 M6U
// 14 M7N
// 15 M7B
// 16 M7U
// 17 M8N
// 18 M8B
// 19 M8U
// 20 NOT SEEN
// 21 UNOBSERVABLE (NO SAMPLING EFFORT)
// 22 DEAD
// -------------------------------------------------

functions {

 /**
  ** Return an integer value denoting occasion of first capture.
  **
  ** @param y    Observed values
  ** @return Occasion of first capture
  **/
 int first_capture(int[] y_i, int[] input_zero) {
   for (k in 1:size(y_i)) {
            if (y_i[k] > 0) {
                  int zero = 0;
                  for (l in 1:size(input_zero)) {
                        if (y_i[k] == input_zero[l])
                              zero = 1;
                  }
                  if (!zero) {
                        return k;
                  }
            }
      }
   return 0;
 }

 /**
  ** Return a four dimensional integer m-array
  **
  **  Dimension 1: mark time
  **  Dimension 2: recapture time
  **  Dimension 3: mark-recapture data type
  **  Dimension 4: observation state
  **
  ** @param y integer matrix of observed states
  ** @param n_obs integer number of possible observed states
  ** @param zero integer values equal to the "not seen" and "unobservable" states
  **/
 int[,,,] calc_marray(int[,] input_y, int[] input_z, int n_data, int n_obs, int[] input_zero) {

      int n_time = size(input_y[1,]);
      int n_ind = size(input_y[,1]);

      int m[n_time, n_time, n_data, n_obs];
```

```
    // initialise
    for (i in 1:n_time)
          for (j in 1:n_time)
                for (k in 1:n_data)
                      for (l in 1:n_obs)
                            m[i, j, k, l] = 0;

    // loop over individuals
 for (i in 1:n_ind) {

          // loop over mark occations
    for (j in 1:n_time) {

                if (j == first_capture(input_y[i,], input_zero)) {

                      // record mark
                      // state "not seen" at time j
                      m[j, j, input_z[i], input_zero[1]] = m[j, j, input_z[i], input_zero[1]] + 1;

                      if (j == n_time) break;

                      // loop over recapture occasions
          for (k in (j + 1):n_time) {

                            // record recapture
                            // state input_y[i,k] at time k
                            m[j, k, input_z[i], input_y[i,k]] = m[j, k, input_z[i], input_y[i,k]] + 1;

          }
       }
    }
 }
 return m;
}

/**
 ** Return expected value for m-array
 **
 **/
    vector[,,] calc_mbar(vector[,] input_ps, vector[,] input_po, vector[,] input_pn, int[,] input_ov, int n_time, int
          n_states, int n_data, int n_obs, vector[,] input_marks) {

          vector[n_states] nbar[n_time, n_time, n_data];
          vector[n_obs] mbar[n_time, n_time, n_data];

          // initialise to zero
          for (i in 1:n_time) {
                for (j in 1:n_time) {
                      for (k in 1:n_data) {
                            for (l in 1:n_states)
                                  nbar[i, j, k, l] = 0;
                            for (l in 1:n_obs)
                                  mbar[i, j, k, l] = 0;
                            }
                }
          }

          // calculate expected numbers
          // per state
          for (l in 1:n_data) {
                for (i in 1:n_time) {

                      // all marks in observed state 1
                      nbar[i, i, l, 1] = input_marks[i, l, 1];

                      if (i == n_time) break;

                      // recapture occasion
                      for (j in (i + 1):n_time) {

                            for (k in 1:n_states)
                                  nbar[i, j, l, k] = sum(to_vector(input_ps[, j-1, k]) .* nbar[i, j-1, l]);
                      }
                }
          }

          // calculate expected numbers
          // per observation category
          for (i in 1:n_time) {
                for (j in 1:n_time) {
                      for (k in 1:n_data) {
                            for (l in 1:n_obs) {
                                  mbar[i, j, k, l] = (input_ov[k, j] == 1) ? sum(to_vector(input_po[, k, l]) .*
                                        nbar[i, j, k]) : sum(to_vector(input_pn[, k, l]) .* nbar[i, j, k]);
                            }
                      }
                }
          }

          return mbar;
    }
```

```
   /**
    ** Return the Euclidean norm of a vector
    **/
   real vector_norm(vector x) {

         real i = 0.0;

         for (j in 1:num_elements(x))
            i += pow(x[j], 2.0);

         return pow(i, 0.5);
      }
}
data {

      // DIMENSIONS
      int<lower=0> n_ind; // number of individuals
      int<lower=0> n_states; // number of states (including death)
      int<lower=0> n_obs; // number of observational categories (including not seen and unobservable)
      int<lower=0> n_time; // number of mark-recapture occassions
      int<lower=0> n_data; // number of mark-recapture data types (with different resight probabilities)
      int<lower=0> n_ages; // max age (i.e. number of age categories excluding zero)
      int<lower=0> n_plusgroup; // number of plus group ages considered for estimation of tag loss

      // DATA
      int<lower=0> x[n_time];                                // pup census per year
      int<lower=0,upper=n_obs> y[n_ind, n_time]; // mark-recapture history per individual
      int<lower=0> z[n_ind];                                 // mark-recapture data type
      int<lower=0,upper=1> observable[n_data, n_time]; // logical flag indicating whether mark-recapture data is
           observable (i.e. positive sampling effort)
      int<lower=0> loss[n_ages, 3];          // tag loss data
   vector[n_time] w;                    // observed pup mass data
   real<lower=0> sigma;                   // process error variance
}
transformed data {

      // specify "not seen" and "unobservable"
      // observation categories
      int zero[2] = {n_obs - 1, n_obs};

      // ages per state
      int<upper=n_ages> ages[n_states] = {0, 1, 2, 3, 4, 4, 5, 5, 6, 6, 7, 7, 8, 8, -1, -1};

      // sex ratio of pups
      real sex_ratio = 0.5;

      // observables
      int<lower=1,upper=2> ov[n_data, n_time];

      // census data
      // start time
      int start;

      // census data time
      // dimension (dynamics)
      int n_time_dyn;

   // standardised pup mass
   vector[n_time] w_std;

      // identify first observation that is not
      // equal to zero (no data) or the not seen and unobserved
      // observation categories
      int<lower=0,upper=n_time> first[n_ind];

      // count number of marks
      // per observed state
      vector[n_obs] marks[n_time, n_data];

      for (i in 1:n_time)
            for (j in 1:n_data)
                  for (k in 1:n_obs)
                        marks[i, j, k] = 0;

      for (i in 1:n_ind) {

            first[i] = first_capture(y[i], zero);

            marks[first[i], z[i], y[i, first[i]]] = marks[first[i], z[i], y[i, first[i]]] + 1;
      }

      // use vector to map observability
      // onto dimensions of observation array
      for (i in 1:n_data) {
            for (j in 1:n_time) {
                  ov[i, j] = 1;
                  if (!observable[i, j]) ov[i, j] += 1;
            }
      }

      // identify start of census
      // time series
```

```
      start = 1;
      for (t in 1:n_time) {
            if (x[t] > 0) {
                  break;
            } else {
                  start += 1;
            }
      }

      // record time dimension
      // for estimation of dynamics
      n_time_dyn = n_time - start + 1;

   // standardise pup mass
   {
      int n = 0;
      real mu = 0.0;
      real se = 0.0;

      for (i in 1:n_time) {
         if (w[i] >= 0) {
            mu += w[i];
            n += 1;
         }
      }
      mu /= n;

      for (i in 1:n_time) {
         if (w[i] >= 0) {
            se += pow(w[i] - mu, 2.0);
         }
      }
      se /= (n - 1);

      w_std = (w - mu) / se;
   }
}
parameters {

      // survivorship for pups, juveniles and
      // adults in ascending order
   vector[n_time] ph0_;
      ordered[3] phi_;

      // probability of pupping in ascending
      // order from ages M4 to M8 inclusive
      ordered[5] alpha_;

      // return probability in ascending
      // order for immature, non-puppers and
      // puppers
      ordered[3] r_;

      // resight and tag loss parameters
      vector<lower=0,upper=1>[3] p_;

      // probability of identifying pupper/non-pupper
      // as unknown (observation uncertainty)
      vector<lower=0,upper=1>[2] delta_;

      // initial number of pups
   real<lower=0> N0_initial;

   // initial numbers proportions
      simplex[n_states - 2] P0;

   // pup mass regression parameters
   real eta_;
   real beta_;

   // smoothing parameter
   real<lower=0,upper=1> tau;
}
transformed parameters {

      // sum to one probabilities
      simplex[n_states] ps[n_states, n_time];
      simplex[n_obs] po[n_states, n_data];
   simplex[n_obs] pn[n_states, n_data];

      vector[3] phi[n_time];  // survivorship
      vector[5] alpha[n_time]; // probability of breeding
      vector[3] r;            // probability of returning to beach (equal to one for breeders)
      vector[2] delta;        // probability of being unable to identify a breeder and non-breeder

      vector<lower=0,upper=1>[n_states] p[n_data]; // resight probability conditional on returning to beach
      vector<lower=0,upper=1>[3] theta[n_ages];   // multinomial probability of d/s/m flipper tags

      // number of breeders
      vector[n_time_dyn] NMB;

      // number of mature adults
```

```
    vector[n_time_dyn] NMA;

    // number of pups
    vector[n_time_dyn] NI0;

    // inverse transform of rate
    // parameters
 for (i in 1:n_time) {

    phi[i, 3] = inv_logit(phi_[3]);
    phi[i, 2] = inv_logit(phi_[2]);
    phi[i, 1] = inv_logit(phi_[1] - ph0_[i]);

          alpha[i, 5] = inv_logit(alpha_[5]);
          alpha[i, 4] = inv_logit(alpha_[4]);
          alpha[i, 3] = inv_logit(alpha_[3]);
          alpha[i, 2] = inv_logit(alpha_[2]);
          alpha[i, 1] = inv_logit(alpha_[1]);
    }

    r[3] = inv_logit(r_[3]);
    r[2] = inv_logit(r_[2]);
    r[1] = inv_logit(r_[1]);

    // observation error
    delta = delta_;

    // calculate tag loss probabilities
    {
          // binomial probabilities of
          // tag loss
          real pr_dd = 1 - (2 * p_[2] * (1 - p_[2]) + p_[2] * p_[2]);
          real pr_ds = 2 * p_[2] * (1 - p_[2]);
          real pr_dm = p_[2] * p_[2];

          real pr_ss = 1 - p_[2];
          real pr_sm = p_[2];

          real pr_mm = 1.0;

          // probabilities of initial loss
          // in year of tagging
          real pr_idd = 1 - (2 * p_[1] * (1 - p_[1]) + p_[1] * p_[1]);
          real pr_ids = 2 * p_[1] * (1 - p_[1]);
          real pr_idm = p_[1] * p_[1];

          // multinomial probabilities of
          // double/single/missing tags
          // at age
          // age at beginning
          // of time interval
          int age = 1;

          // initial tag loss during age = 0 to 1
          theta[age] = to_vector({ pr_idd, pr_ids, pr_idm });

          // subsequent tag loss in following years
          for (i in 2:(n_ages + n_plusgroup)) {

                age = i;

                if (age > n_ages) {

                      theta[n_ages,] += to_vector({ pr_idd * pr_dd^(age - 1), pr_ids * pr_ss^(age - 1) + pr_idd *
                            (age - 1) * pr_dd^(age - 2) * pr_ds, 0});

                } else {

                      theta[i,] = to_vector({ pr_idd * pr_dd^(age - 1), pr_ids * pr_ss^(age - 1) + pr_idd * (age - 1)
                            * pr_dd^(age - 2) * pr_ds, 0});
                }
          }

          theta[n_ages] = theta[n_ages] / (n_plusgroup + 1);

          for (i in 2:n_ages)
                theta[i, 3] = 1 - sum(theta[i]);
    }

    // Conditional resight probabilities
    for (i in 1:n_data)
          p[i] = rep_vector(0.0, n_states);

    // Branded mark-recapture data
    p[1, 1:(n_states - 2)] = rep_vector(1.0, n_states - 2);

    // Chipped mark-recapture data
    p[2, 1:(n_states - 2)] = rep_vector(p_[3], n_states - 2);

    // Tagged mark-recapture data
    p[3, 1] = 1.0;
    for (i in 2:(n_states - 2))
```

```
               p[3, i] = 1 - theta[ages[i], 3];

   // Phantom tags
   p[4, 1:(n_states - 2)] = rep_vector(1.0, n_states - 2);

// Define probabilities of state S(t+1) given S(t)

// Initialise
   for (i in 1:n_states)
      for (j in 1:n_time)
         for (k in 1:n_states)
            ps[i, j, k] = 0.0;

   for (t in 1:n_time) {

   // Immature transitions
   ps[ 1, t, 2] = phi[t, 1];
         ps[ 2, t, 3] = phi[t, 2];
   ps[ 3, t, 4] = phi[t, 2];

         // Mature transitions to
         // non-breeder or breeder

         // I3 to M4N/M4B
         ps[ 4, t, 5] = phi[t, 2] * (1 - alpha[t, 1]);
         ps[ 4, t, 6] = phi[t, 2] * alpha[t, 1];

         // M4N to M5N/M5B
         ps[ 5, t, 7] = phi[t, 3] * (1 - alpha[t, 2]);
         ps[ 5, t, 8] = phi[t, 3] * alpha[t, 2];

         // M4B to M5N/M5B
         ps[ 6, t, 7] = phi[t, 3] * (1 - alpha[t, 2]);
         ps[ 6, t, 8] = phi[t, 3] * alpha[t, 2];

         // M5N to M6N/M6B
         ps[ 7, t, 9] = phi[t, 3] * (1 - alpha[t, 3]);
         ps[ 7, t,10] = phi[t, 3] * alpha[t, 3];

         // M5B to M6N/M6B
         ps[ 8, t, 9] = phi[t, 3] * (1 - alpha[t, 3]);
         ps[ 8, t,10] = phi[t, 3] * alpha[t, 3];

         // M6N to M7N/M7B
         ps[ 9, t,11] = phi[t, 3] * (1 - alpha[t, 4]);
         ps[ 9, t,12] = phi[t, 3] * alpha[t, 4];

         // M6B to M7N/M7B
         ps[10, t,11] = phi[t, 3] * (1 - alpha[t, 4]);
         ps[10, t,12] = phi[t, 3] * alpha[t, 4];

         // M7N to M8N/M8B
         ps[11, t,13] = phi[t, 3] * (1 - alpha[t, 5]);
         ps[11, t,14] = phi[t, 3] * alpha[t, 5];

         // M7B to M8N/M8B
         ps[12, t,13] = phi[t, 3] * (1 - alpha[t, 5]);
         ps[12, t,14] = phi[t, 3] * alpha[t, 5];

         // M8N to M8N/M8B
         ps[13, t,13] = phi[t, 3] * (1 - alpha[t, 5]);
         ps[13, t,14] = phi[t, 3] * alpha[t, 5];

         // M8B to M8N/M8B
         ps[14, t,13] = phi[t, 3] * (1 - alpha[t, 5]);
         ps[14, t,14] = phi[t, 3]* alpha[t, 5];

         // Death
         ps[ 1, t,15] = 1.0 - phi[t, 1];
         ps[ 2, t,15] = 1.0 - phi[t, 2];
         ps[ 3, t,15] = 1.0 - phi[t, 2];
         ps[ 4, t,15] = 1.0 - phi[t, 2];
         ps[ 5, t,15] = 1.0 - phi[t, 3];
         ps[ 6, t,15] = 1.0 - phi[t, 3];
         ps[ 7, t,15] = 1.0 - phi[t, 3];
         ps[ 8, t,15] = 1.0 - phi[t, 3];
         ps[ 9, t,15] = 1.0 - phi[t, 3];
         ps[10, t,15] = 1.0 - phi[t, 3];
         ps[11, t,15] = 1.0 - phi[t, 3];
         ps[12, t,15] = 1.0 - phi[t, 3];
         ps[13, t,15] = 1.0 - phi[t, 3];
         ps[14, t,15] = 1.0 - phi[t, 3];
         ps[15, t,16] = 1.0;
         ps[16, t,16] = 1.0;
   }

   // Define probabilities of recapture O(t)
   // for marked individuals in state S(t)

   // Initialise
   for (i in 1:n_states)  // states
         for (j in 1:n_data) // tag data types
```

```
            for (k in 1:n_obs) { // observation categories
                  po[i, j, k] = 0.0;
      pn[i, j, k] = 0.0;
   }

// data types: branded, chipped, tagged
// observable observations
for (i in 1:3) {

      // Pups are not recaptured
      // using conventional tags
      po[ 1, i,20] = 1.0;

      // Immature
      po[ 2, i, 2] = p[i, 2] * r[1];
      po[ 2, i,20] = 1 - p[i, 2] * r[1];
      po[ 3, i, 3] = p[i, 3] * r[1];
      po[ 3, i,20] = 1 - p[i, 3] * r[1];
      po[ 4, i, 4] = p[i, 4] * r[1];
      po[ 4, i,20] = 1 - p[i, 4] * r[1];

      // M4N/M4B/M4U
      po[ 5, i, 5] = p[i, 5] * r[2] * delta[1];
      po[ 5, i, 7] = p[i, 5] * r[2] * (1 - delta[1]);
      po[ 5, i,20] = 1 - p[i, 5] * r[2];
      po[ 6, i, 6] = p[i, 6] * r[3] * delta[2];
      po[ 6, i, 7] = p[i, 6] * r[3] * (1 - delta[2]);
      po[ 6, i,20] = 1 - p[i, 6] * r[3];

      // M5N/M5B/M5U
      po[ 7, i, 8] = p[i, 7] * r[2] * delta[1];
      po[ 7, i,10] = p[i, 7] * r[2] * (1 - delta[1]);
      po[ 7, i,20] = 1 - p[i, 7] * r[2];
      po[ 8, i, 9] = p[i, 8] * r[3] * delta[2];
      po[ 8, i,10] = p[i, 8] * r[3] * (1 - delta[2]);
      po[ 8, i,20] = 1 - p[i, 8] * r[3];

      // M6N/M6B/M6U
      po[ 9, i,11] = p[i, 9] * r[2] * delta[1];
      po[ 9, i,13] = p[i, 9] * r[2] * (1 - delta[1]);
      po[ 9, i,20] = 1 - p[i, 9] * r[2];
      po[10, i,12] = p[i, 10] * r[3] * delta[2];
      po[10, i,13] = p[i, 10] * r[3] * (1 - delta[2]);
      po[10, i,20] = 1 - p[i, 10] * r[3];

      // M7N/M7B/M7U
      po[11, i,14] = p[i,11] * r[2] * delta[1];
      po[11, i,16] = p[i,11] * r[2] * (1 - delta[1]);
      po[11, i,20] = 1 - p[i,11] * r[2];
      po[12, i,15] = p[i,12] * r[3] * delta[2];
      po[12, i,16] = p[i,12] * r[3] * (1 - delta[2]);
      po[12, i,20] = 1 - p[i,12] * r[3];

      // M8N/M8B/M8U
      po[13, i,17] = p[i,13] * r[2] * delta[1];
      po[13, i,19] = p[i,13] * r[2] * (1 - delta[1]);
      po[13, i,20] = 1 - p[i,13] * r[2];
      po[14, i,18] = p[i,14] * r[3] * delta[2];
      po[14, i,19] = p[i,14] * r[3] * (1 - delta[2]);
      po[14, i,20] = 1 - p[i,14] * r[3];

      // Conventional tags
      // not seen if dead
      po[15, i,20] = 1.0;
      po[16, i,20] = 1.0;
}

// phantom tags
// observable
{
      // see them if just dead
      po[15, 4,22] = 1.0;

      // but not if they are really dead
      po[16, 4,20] = 1.0;

      // all other states not seen
      for (i in 1:14)
            po[i, 4, 20] = 1.0;
}

// when no sampling effort all states
// are in "unobservable" observation category
for (i in 1:n_data) {
      for (k in 1:n_states) {
            pn[k, i, 21] = 1.0;
      }
}

// Dynamics
{
      // numbers matrix
```

```
      vector[n_states] N0;
            vector[n_states] N[n_time];

            // initialise N matrix
            for (t in 1:n_time) {
                  for (k in 1:n_states)
                        N[t, k] = 0.0;
            }

      // initial state vector
      N0 = rep_vector(0.0, n_states);
      N0[1:(n_states - 2)] = N0_initial * P0;

            // iterate numbers forward
            for (t in 1:n_time_dyn) {
         if (t == 1) {
            for (k in 2:n_states) {
               N[t, k] = sum(to_vector(ps[, start - 2 + t, k]) .* N0);
            }
         } else {
            for (k in 2:n_states) {
               N[t, k] = sum(to_vector(ps[, start - 2 + t, k]) .* N[t - 1]);
            }
         }
                  // birth at beginning of time step
                  N[t,1] = sex_ratio * sum(N[t, {6,8,10,12,14}]);
            }

            // record number of pups
            // adults and breeders
            for (t in 1:n_time_dyn) {
                  NI0[t] = N[t, 1];
                  NMB[t] = sum(N[t, {6,8,10,12,14}]);
                  NMA[t] = sum(N[t, {5,6,7,8,9,10,11,12,13,14}]);
            }
      }
}
model {

      // census likelihood
      for (t in start:n_time)
            x[t] ~ normal(NI0[t - start + 1], sqrt(NI0[t - start + 1]));

      // Likelihood
      // Forward algorithm
   {
      real acc[n_states];
      vector[n_states] gamma[n_time];

      for (i in 1:n_ind) {

         gamma = rep_array(rep_vector(0.0, n_states), n_time);

         if (first[i] > 0) {
            for (k in 1:n_states)
               gamma[first[i], k] = (k == y[i, first[i]]);

            for (t in (first[i] + 1):n_time) {

               for (k in 1:n_states) {
                  for (j in 1:n_states) {
                     acc[j] = (ov[z[i], t] == 1) ? gamma[t - 1, j] * ps[j, t - 1, k] * po[k, z[i], y[i, t]] : gamma[t -
                           1, j] * ps[j, t - 1, k] * pn[k, z[i], y[i, t]];
                  }
                  gamma[t, k] = sum(acc);
               }
            }
            target += log(sum(gamma[n_time]));
         }
      }
   }

   // Poisson approximation for initial
   // number of pups
   NI0[1] ~ normal(sex_ratio * NMB[1], sqrt(sex_ratio * NMB[1]));

   // gaussian smoother for
   // survivorship
   {
      real ss[2];

      ss[1] = pow(tau * square(sigma), 0.5);
      ss[2] = pow((1 - tau) * square(sigma), 0.5);

      ph0_ ~ normal(0, ss[1]);

      // fit to pup mass data
      for (i in 1:n_time) {
         if (w[i] >= 0) {
            w_std[i] ~ normal(eta_ - beta_ * ph0_[i], ss[2]);
         }
      }
```

```
   }

      // tag loss data
      for (i in 1:n_ages)
            loss[i] ~ multinomial(theta[i]);

      // logistic parameters
      phi_ ~ std_normal();
      alpha_ ~ std_normal();
      r_    ~ std_normal();
   eta_ ~ std_normal();
   beta_ ~ std_normal();

   // smoother
   tau   ~ beta(1,1);
}
generated quantities {

   // m-arrays
      int marr[n_time, n_time, n_data, n_obs];
      int mhat[n_time, n_time, n_data, n_obs];
      vector[n_obs] mbar[n_time, n_time, n_data];

   // predicted census
   vector[n_time] xbar;
   vector[n_time] xhat;

   // predicted pup mass
   vector[n_time] wbar;
   vector[n_time] what;

      // discrepancy measures for
   // tag data
      real D[2, n_data, n_obs - 3];

      // mean prediction error
   // for each data type
      real MPE[3] = { 0.0, 0.0, 0.0 };

   // summary parameters for trace
   // diagnostics
   vector[6] trace_summary;

      /*
      ** SIMULATE MARK-RECAPTURE DATA
      */
   {
      int yhat[2, n_ind, n_time];

      for (i in 1:n_ind) {
         for (j in 1:n_time) {
            yhat[1, i, j] = 0; // TRUE
            yhat[2, i, j] = 0; // OBSERVED
         }
      }

      for (i in 1:n_ind) {

         if (first[i] > 0) {

            // mark simulated individuals using
            // empirical data
            yhat[1, i, first[i]] = y[i, first[i]];
            yhat[2, i, first[i]] = y[i, first[i]];

            if (first[i] == n_time) continue;

            // step through capture occasions
            // for each individual
            for (j in (first[i] + 1):n_time){

               // single sample from
               // multinomial state transition
               yhat[1, i, j] = categorical_rng(ps[yhat[1, i, j-1], j-1]);

               // single sample from
               // multinomial observation process
               yhat[2, i, j] = (ov[z[i], j] == 1) ? categorical_rng(po[yhat[1, i, j], z[i]]) :
                    categorical_rng(pn[yhat[1, i, j], z[i]]);
            }
         }
      }

      /*
      ** CALCULATE M-ARRAYS
      */

      marr = calc_marray(y, z, n_data, n_obs, zero);
      mhat = calc_marray(yhat[2,,], z, n_data, n_obs, zero);
      mbar = calc_mbar(ps, po, pn, ov, n_time, n_states, n_data, n_obs, marks);
   }
```

```
   /*
   ** CALCULATE DISCREPANCIES
   */

   for (k in 1:n_data) {
         for (l in 1:(n_obs - 3)) {
               D[1, k, l] = 0.0;
               D[2, k, l] = 0.0;
         }
   }

   for (i in 1:n_time) {
         for (j in 1:n_time) {
               for (k in 1:n_data) {
                     for (l in 1:(n_obs - 3)) {
            if (mbar[i, j, k, l] > 0.0 && marr[i, j, k, l] > 0.0 && mhat[i, j, k, l] > 0.0) {
               D[1, k, l] += log(marr[i, j, k, l] / mbar[i, j, k, l]);
               D[2, k, l] += log(mhat[i, j, k, l] / mbar[i, j, k, l]);
            }
                     }
               }
         }
   }

// predicted census
xbar = rep_vector(0.0, n_time);
xhat = rep_vector(0.0, n_time);

for (t in start:n_time) {
   xbar[t] = NI0[t - start + 1];
         xhat[t] = normal_rng(NI0[t - start + 1], sqrt(NI0[t - start + 1]));
}

// predicted pup mass
{
   int n = 0;
   real mu = 0.0;
   real se = 0.0;

   // mean
   for (i in 1:n_time) {
      if (w[i] >= 0) {
         mu += w[i];
         n += 1;
      }
   }
   mu /= n;

   // standard error
   for (i in 1:n_time) {
      if (w[i] >= 0) {
         se += pow(w[i] - mu, 2.0);
      }
   }
   se /= (n - 1);

   for (i in 1:n_time) {
      wbar[i] = (eta_ - beta_ * ph0_[i]) * se + mu;
      what[i] = normal_rng(eta_ - beta_ * ph0_[i], pow((1 - tau) * square(sigma), 0.5)) * se + mu;
   }
}

// MPE
{
   int n;

   // tag data
   n = 0;
   for (i in 1:n_time) {
      for (j in 1:n_time) {
         for (k in 1:n_data) {
            for (l in 1:(n_obs - 3)) {

               if (marr[i, j, k, l] > 0) {

                  n += 1;

                  MPE[1] += pow((marr[i, j, k, l] - mbar[i, j, k, l]) / marr[i, j, k, l], 2.0);
               }
            }
         }
      }
   }
   MPE[1] /= n;

   // census
   n = 0;
   for (i in start:n_time) {

      if (x[i] > 0) {
```

```
            n += 1;

            MPE[2] += pow((x[i] - xbar[i]) / x[i], 2.0);
         }
      }
      MPE[2] /= n;

      // pup mass
      n = 0;
      for (i in 1:n_time) {

         if (w[i] > 0) {

            n += 1;

            MPE[3] += pow((w[i] - wbar[i]) / w[i], 2.0);
         }
      }
      MPE[3] /= n;
   }

   // trace diagnostics
   trace_summary[1] = vector_norm(phi_);
   trace_summary[2] = vector_norm(r_);
   trace_summary[3] = vector_norm(p_);
   trace_summary[4] = vector_norm(alpha_);
   trace_summary[5] = vector_norm(delta_);
   trace_summary[6] = tau;

}
```