Department of Conservation Progress Report

Title of Report:	Demographic model options
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Project Code:	POP2012-02
Project Title:	4428 New Zealand sea lion – demographic assessment of the causes of decline at the Auckland Islands
Project leader:	Ian Doonan
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Objective:	1, identify which demographic parameters are the key drivers of the observed population decline of New Zealand sea lions at the Auckland Islands
Milestone:	2, Final model(s) developed

1 Abstract

State space demographic models were developed using NIWA's demographic modelling package, SeaBird in order to estimate time-varying survival, pupping rates, tag shedding, and age at first pupping of New Zealand sea lions at the Auckland Islands. The main data used were: mark-resighting data from animals tagged as pups at Sandy Bay, Enderby Island from 1990-2011, annual pup production at Sandy Bay from 1990-2012, and age-frequencies of breeding individuals by year were fitted to age distribution observations of lactating females at Sandy Bay from 1998-2001.

Preliminary model runs were used to find the best parameterisation based on Akaike information criterion (AIC) (model 7a). A Monte Carlo Markov Chain (MCMC) was run to assess variability of the parameter estimates. The model was expanded to estimate tag shedding, but no MCMC was performed on this model due to resource constraints. Model 7a was also used to estimate demographic rates for animals that were tagged and resighted at Dundas Island.

- **Candidate model 7a**
  - Survival estimates were aggregated within age categories 0, 1, 2-5, 6-14 and 15+.
  - Resighting probability was constant across ages 1 and 2 and was year-invariant. Other resighting groupings (3, 4-5, 6, 7, non-puppers) were year-varying. Resighting of puppers was fixed to 1.

- o Probability of pupping (for animals that did and did not pup in the previous year) and age at first pupping parameters were all year-varying.
- **Year effects on survival at Sandy Bay**
  - o Model estimates of survival at ages 0 and 1 indicate strong year effects on survival (e.g. years of high survivorship of pups born in 1990, 1991, 1992 and 1993; low survivorship of pups born in 1998, 2000, 2005 and 2008) and a long-term decline relative to the strong cohorts in 1990-1993.
  - o Estimates of survival at ages 0 and 1 were not very different when fitting to pup census observations (with good model fits) suggesting that the decline in juvenile survival since the early 1990s is a strong candidate for a proximate cause for the decline in pup production at Sandy Bay since the late 1990s.
  - o SeaBird cannot accurately partition mortality between these two ages due to low probability of resighting 1 and 2 your-old individuals. A proposed approach to using these data is to take the product of s0yr and s1yr+1 which had the effect of greatly reducing the size of prediction intervals around MCMC estimates of survival at these ages. Survival of pups born in 2008 may be the lowest of any year for which tagging has been undertaken.
  - o The retrospective analysis demonstrated a model bias towards underestimation of survival of juveniles in later years, though relatively low or high survival years are likely to remain as such with subsequent years of resighting effort.
  - o Low survival estimates at ages 6-14 in 2007, which appeared to affect a number of cohorts (born 2000, 2001 and 2002).
  - o The extent to survival at ages 0 and 1 is confounded with tag loss effects has not been explored in this assessment. Year-invariant annual tag loss rates were estimated for age 0 and all subsequent ages to be 0.085 and 0.049, respectively. Tag loss assumed independence between losing one tag and both tags. Non-independence was not investigated here.
  - o Including animals that had died previous to tagging as phantom tags mainly affected a decrease in survival at age 0 in 2002 and 2003, in years when disease mortality rates were high.
- **Year effects on pupping rates at Sandy Bay**
  - o There was no apparent long term trends in pupping rates through time, or strong cohort effects on reproductive output.
  - o There have been some years with low pupping rates, including 2000, 2002, 2005, 2006 and 2009. These one/two year reductions in pupping rate correspond with years for which low pup counts were estimated.
- **Year effects on age at first pupping at Sandy Bay**
  - o Age at first pupping was represented by a functional form with two parameters – the first of which estimates the proportion of 3 year olds that produce a pup at age 4; the second of which gives the rate at which this proportion increased at subsequent ages up to age 8 when all individuals were assumed to be mature.
  - o There appear to be year effects on the estimated proportion of individuals that had pupped at age 4, with an increased proportion in 1999-2001 and 2011-2012.
  - o Model estimates indicate that in a number of years (particularly 2001-2009) a large proportion of pups will not have pupped by age 8.
- **Year-effects on demographic rates at Dundas**
  - o There were too few observations with confirmed pupping status at Dundas to estimate pupping rates, owing to insufficient days of resighting effort (an individual must be seen

with or without pup on three different days before pupping status can be confirmed according to strict definition).

- o Age-specific survival estimates are very similar to those estimated for animals tagged at Sandy Bay. Strong year effects on survival with identical high (e.g. 1991 and 1992) and low survival years (e.g. 1998 and 2008) for pups born in different years, comparing Dundas and Sandy Bay.

Declines in survival of ages 0 and 1, as well as cohort effects on survival at age 6-14 may be sufficient to explain the long-term decline in annual pup census counts at Sandy Bay. Similarities in survival estimates at Dundas indicate that juvenile survival is a strong candidate for a proximate cause of the decline in pup production there also. Intermittent one and two-year declines in pup production (e.g. 2002 and 2009) are coincident with years where the probability of pupping was low. In addition, inter-annual variation in age at first pupping could also cause long term increases and decreases in pup production.

2   Introduction

New Zealand sea lions (*Phocarctos hookeri*) are listed as Nationally Critical (Baker *et al.*, 2009), they have a limited breeding range (almost all pupping at Auckland Islands and Campbell Island in the NZ Sub-Antarctic) and an approximate 40% decline in pup production has been observed at the Auckland Isles since the late-1990s (Chilvers, 2012). A number of sea lions die each year as a result of interactions with a squid trawl fishery which has operated at the Auckland Islands since the 1970s though the potential indirect effects of fishing remain poorly understood (MAF, 2012).

This project broadly aims to determine the key demographic factors driving the observed decline of New Zealand sea lions at the Auckland Islands with work divided into two project components:

- To identify which demographic parameters are the key drivers of the observed population decline at the Auckland Islands (e.g. do we see variation in survival or breeding rates and are there differences comparing rookeries?).
- To identify potential demographic mechanisms through which both direct and indirect effects of fishing can impact on sea lion population size at the Auckland Islands, or increase susceptibility of the population to such effects (e.g. if we see variation in juvenile survival then what are the probable biological mechanisms for this decline – with a focus on the potential direct/indirect effects of fishing?).

This report described demographic model options developed to address the first of these objectives: to identify time-varying demographic rates that may potentially have driven the observed decline in NZ sea lion pup production at the Auckland Islands (Project milestone 2, Table 1)

Table 1 Project milestones and outputs

Project milestone	Description of outputs
1 Data obtained	Relevant data sets obtained, groomed and exploratory analyses complete. Presentation of data summary and methodology to the CSP Technical Working Group.
2 Model options developed	**A report describing a number of candidate models for conducting the analyses.** **Presentation of modelling options to the CSP Technical Working Group.**
3 Final model(s) developed	One (or more) model options are further developed, with due consideration of feedback from technical review of model options. Presentation of the final model(s) to the CSP Technical Working Group.
4 Initial results	A report detailing initial results from the final model(s). Presentation of results to the CSP Technical Working Group.
5 DRAFT Final Report	A manuscript of a draft final report(s) describing all activities, data collected, results found and recommendations made under each specific objective. Presentation of results to the CSP Technical Working Group.
6 Final Report	Final Report suitable for DOC Publication

3 Methods

State space demographic models were developed using NIWA's demographic modelling package, SeaBird (Francis & Sagar, 2012) in order to estimate time-varying survival, pupping rates and age at first pupping of New Zealand sea lions at the Auckland Islands. Candidate models were fitted to mark-recapture observations, pup census estimates and age distribution observations.

SeaBird software has already been used to conduct demographic assessments of four NZ seabird species (e.g. Francis & Sagar 2012). SeaBird allows the analysis of individual (*i.e.*, non-aggregated) mark-resighting observations and integrated assessment modelling using different observation types, with Bayesian or likelihood based parameter estimation. Model partitioning (*e.g.* age, area, or breeding status), transitions and equations representing demographic processes are all user-defined.

3.1 Observations

3.1.1 Mark-resighting observations
Mark-resighting observations were extracted from the NZ sea lion demographics database maintained by Dragonfly Science (downloaded 18/12/2012).

- A subset of the data was taken including only observations of female individuals tagged as pups at Sandy Bay, Enderby Island (from 1990-1993 & 1998-2011) and resighted at Sandy Bay (from 1999-2012).
- Animals branded as pups in 2000 were initially omitted from the assessment as they are not affected by tag loss and the first models did not estimate lag loss rates of non-branded animals. In addition pups were branded in only one tagging year (2000).
- Also omitted were observations where a chip ID was recorded though the tag ID was not.
- Pupping state (and hence partition to which an observed individual was assigned in a particular year) is defined in Table 5.

A plot summarising aggregated mark-resighting observations by cohort, year of resighting and pupping status is given in Figure 1 and Figure 2.
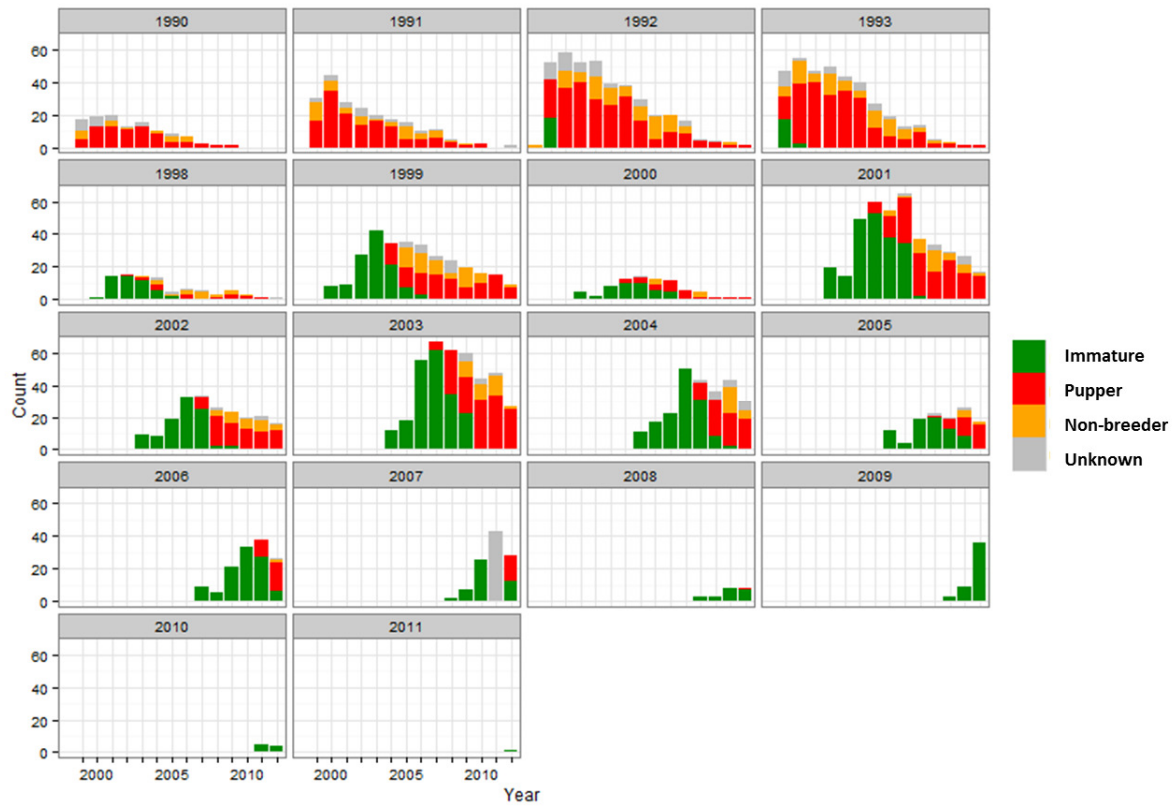

Figure 1 Summary of mark-resighting observations of animals tagged as pups and resighted at Sandy Bay with data subsets and pupping status described as above.
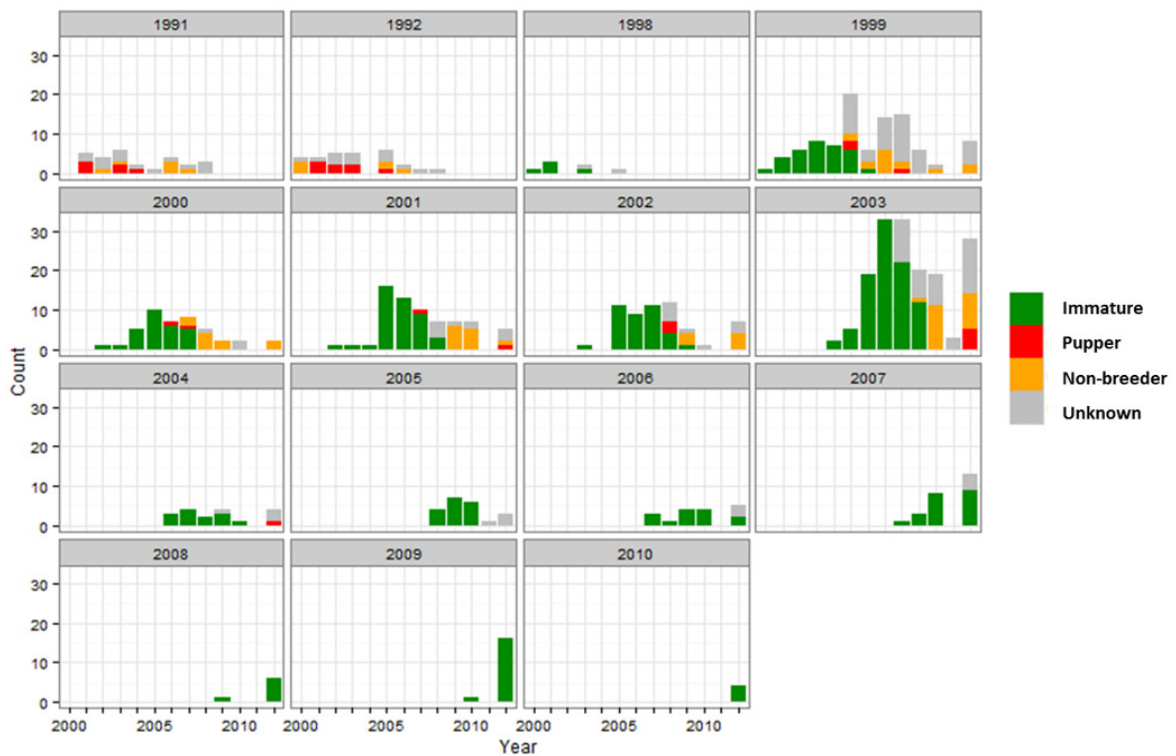
Figure 2 Summary of mark-resighting observations of animals tagged as pups and resighted at Dundas with data subsets and pupping status described as above.

A number of pups are reported as dead at the time of tagging. Not accounting for these would cause survival at age 0 to be overestimated. For each year a number of "phantom tags" were therefore assigned to these dead pups and included in the mark-recapture observations as not observed in all subsequent years of resighting effort. Because unobserved tags are indicative of mortality, this allowed observations of dead pups to be included in the model and used to inform estimation of survival. At Sandy Bay the annual frequency of phantom tags was equal to 50% of the number of pups reported dead at the time of tagging each season (Childerhouse et al., 2013), to give the female component of dead pups. At Dundas not all pups were tagged each year (typically less than half) and the annual frequency of phantom tags was taken to be 50% (female component) of the product of annual censes estimate of dead pups and the proportion of the annual censes estimate of pups that was tagged each year (Table 2).

Table 2 Estimated frequency of female pups that died prior to tagging by year at Sandy Bay and Dundas

| Tag year | Dundas | | | | Sandy Bay |
	Dead pups	Total pup count	Tagged pups	Phantom tags	
1998	313	1187	185	49	5
1999	115	1093	232	24	20
2000	62	1082	190	11	12
2001	173	1074	185	30	18
2002	181	878	200	41	42
2003	168	946	263	47	40
2004	60	935	50	3	17
2005	37	794	310	14	15
2006	116	791	317	47	20
2007	53	847	277	17	12
2008	62	818	310	23	12
2009	34	566	298	18	6
2010	76	685	315	35	11
2011	NA	NA	0	0	10

3.1.2   Pup census observations

In model runs where pup census data were used, the model estimated frequency of breeders in a year was fitted to census estimates of annual pup production at Sandy Bay, Enderby Islands, for all years from 1990-2012. These were the estimates of total pup production, i.e. inclusive of pups recorded as dead or alive. All observations over this time period have been attributed a high level of confidence (level "1" or "2", Table 1 of Breen *et al.*, 2012). The estimated number of female pups was assumed to be half the census estimate (i.e. 50:50 male-to-female sex ratio); see Table 3.

Table 3 Annual female pup count estimates at Sandy Bay, as used in this assessment

Year	Female pup count estimate
1990	217
1991	214.5
1992	244.5
1993	212
1995	233.5
1996	227.5
1997	254.5
1998	238.5
1999	256.5
2000	253
2001	281
2002	201.5
2003	244.5
2004	254
2005	220.5
2006	211
2007	218.5
2008	224
2009	150.5
2010	192.5
2011	189
2012	180.5

3.1.3 Age distribution observations

Model estimated age-frequencies of breeding individuals by year were fitted to age distribution observations of lactating females at Sandy Bay in 1998, 1999, 2000 and 2001 (Childerhouse et al., 2009). The raw data were supplied by Simon Childerhouse (05/02/2013); see Table 4.

Table 4 Age distribution of lactating females at Sandy Bay, as used in this assessment

Age	1998	1999	2000	2001
3	0	0.0069	0.0072	0
4	0	0.0138	0.0072	0.014
5	0	0.0414	0.0217	0.021
6	0.0667	0.131	0.0435	0.035
7	0.4667	0.1379	0.1232	0.042
8	0	0.1517	0.1812	0.1678
9	0	0.1034	0.1739	0.1748
10	0.0667	0.0621	0.1014	0.1678
11	0.0667	0.0828	0.0507	0.0769
12	0.1333	0.0414	0.029	0.028
13	0.1333	0.069	0.058	0.042
14	0	0.0345	0.0145	0.014
15	0	0.0552	0.0362	0.035
16	0	0.0276	0.029	0.035
17	0.0667	0.0069	0.0217	0.021
18	0	0.0069	0.0217	0.014

19	0	0.0138	0.029	0.028
20	0	0.0207	0.0507	0.0839

3.2 SeaBird demographic model

3.2.1 Partitions

The set of states that any sea lion can be in for a particular year is called the partition. The model partitioned the population into ages 1 to 20, with the last age class being a plus group. Each age class was further partitioned into a number states depending on whether the individual produced a pup in that year. The partition therefore accounted for numbers of sea lions by age and pupping status within an annual cycle, where movement between partition states were determined by the transition parameters. Sea lions entered the partition as pups and were removed by mortality.

Three partition schemes were used in the candidate models (the first two are shown in Figure 1):

- **Partitioning I** considers that sea lions between ages 0 to 7 are "immature" if they have never pupped (sea lions where assumed not to pup until age 4); a sea lion between age 4 and 20+ becomes a "pupper" if she produced a pup for that year. A sea lion that never produced a pup is considered as "immature" before age 7 but as "non-pupper" between age 8 and 20+. With this partition scheme, the model is able to estimate the probability of first-time pupping at age.
- **Partitioning II** considers that sea lions between age 0 and 3 are "immature" and sea lions between age 4 and 20 are either puppers or non-puppers depending on whether a pup was produced for that year. This partition scheme does not differentiate between sea lions that never pupped and those that were "resting" in-between breeding seasons. It is a slight simplification of Partitioning I as it consists of fewer partition cells (therefore fewer transitions), and was considered for models with more complex configurations.
- **Partitioning III** is an extension of Partitioning II, and incorporates the tagging status (number of tags) as a partition variable in addition to age and pupping status. Therefore each of the immature, pupper, and non-pupper state for each age class was further split into three sub-states indicating the number of tags associated with the animal. The tagging status considered were two (sea lions with both flipper tags), one (sea lions with either left or right flipper tag missing) and zero (sea lions with both tags missing). This partitioning scheme allows the rate of tag-loss to be estimated within the model.

    Accordingly each re-sighting observation in the mark-recapture dataset was assigned a state based on age and pupping status (as well as the number of remaining tags for the tag-loss model). The pupping status is based on the strict definition of puppers as described by Mackenzie & Chilvers (2012, see also Table 5).
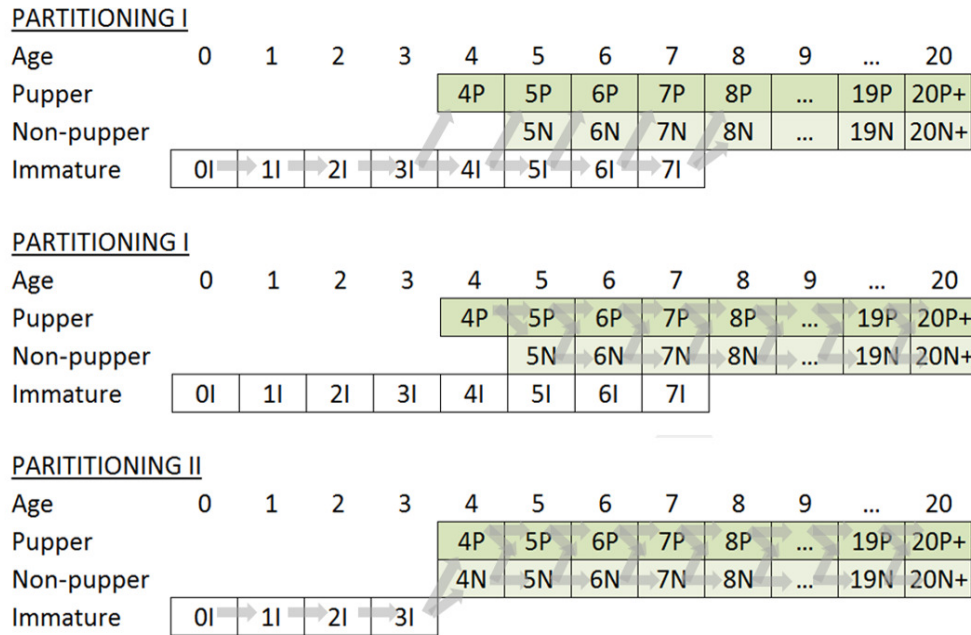
Figure 3 Partitioning and transitions used in candidate demographic models (Partitioning II used in model fit to pup census data with tag loss; Partitioning I used in all other models; possible transitions from immature partition at top; transition from "mature" partitions at middle).

Table 5 Pupping status definitions

Observed status	Model state
Female 3-5 YO, never pupped	immature
Yearling	immature
Yearling or 2 YO, suckling	immature
New born or pup	immature
Female, confirmed pupped	pupper
Female, probably pupped	pupper
Female, pup died	pupper
Adult female, confirmed no pup	non-pupper
Female, < 3 sightings, no pup	non-pupper
Pregnant female	pupper or non-pupper
Female, nursing yearling	pupper or non-pupper
Dead	pupper or non-pupper or immature
Idle	pupper or non-pupper or immature

3.2.2 Time steps

There can be one or more time steps within a year, with the observation of state at time step t_{trans}. This allows various process to occur before and after the time of observations, such as recruitment, transition processes, or fishing mortality.

The symbols, n_{ity} and n'_{ity} represent the number of sea lions in the ith class of the partition at time step t in year y before and after the partition process.

3.2.3 Transitions

Transitions move sea lions from one class of the partition to another as they develop or age (increase from age *n* to age *n*+1) or change behaviour (e.g., move from being a non-breeding adult to a breeding adult).

Transitions are achieved using simple matrix multiplication $n'_{ity} = Tn_{ity}$, where *T*, referred to as the *transition matrix*, is such that T_{ij} is the probability that an individual in partition class *i* will move to class *j*.

3.3 Parameter estimation

3.3.1 Survival

Survival s_{iy}, is the proportion of sea lions in the *i*th partition class that survive natural mortality to the end of year *y*. Potentially we can define f_t, the fraction of the annual natural mortality that occurs before time step *t* in each year, which gives $s_{iy}^{f_t}$. Because there can be fishing morality, SeaBird uses $s_{iy} = \prod_t s_{tiy}^{f_t}$ for annual survival in the likelihood. However the contributions from fishing have been ignored for this investigation.

Proportional mortality: the user can specify that an observation in time step *t* in year *y* occurred part-way through the mortality that occurred in that time step. Thus, if *p* is the proportion of that mortality had occurred before the observation we need to define $n_{ity;p}$, the number of individuals in the *i*th class at the time of the observation.

SeaBird offers two options for calculating $n_{ity;p}$:

weighted sum (default):
$$n_{ity;p} = (1-p)n_{ity} + pn'_{ity} = (1-p+pT_{ity})n_{ity} \text{ and}$$

weighted product:
$$n_{ity;p} = n_{ity}^{1-p}n_{ity}'^{p} = T_{ity}^{p}n_{ity}$$

where n_{ity} and n'_{ity} (= $s_{ity}n_{ity}$) are the numbers before and after the mortality in this time step.

3.3.2 Objective function

Parameter estimation was by maximum likelihood. The objective function is given by:

$$-\sum_i \log\left[L(\mathbf{p}|O_i)\right]$$

where **p** is a vector of the free parameters, *L* the likelihood function and O_i the *i*th observation.

For Bayesian fitting the objective functions is:

$$-\sum_i \log\left[L(\mathbf{p}|O_i)\right] - \log\left[\pi(\mathbf{p})\right]$$

where π is the joint prior density of the parameters **p**.

3.3.3 Likelihoods for mark-recapture observations

Symbols used in likelihood equations are presented in Table 6.

Table 6 Symbols used in likelihood equations.

Symbol	Comment
b	unique tag code
$y_{b,\text{tag}}$	The year the bth sea lion was tagged
$y_{b,\text{last}}$	last year that the bth sea lion was observed
O_{by}	observed state for the bth sea lion in year y
L_{by}	likelihood of the observation in year y given the observation in year y–1
t_{trans}	time within a year that the state of a sea lion is observed
X_{iyj}	the probability that a sea lion in stage i in year y will be alive and in stage j in the following year
$s_{\text{tot},ity}$,	survival of a sea lion during time step t in stage i in year y, includes fishery morality, if used.
p	the proportion of that mortality had occurred before an observation in a time step. Thus, we have subscripts like $n_{ity;p}$, to denote the number of individuals in the ith class at the time of the observation. For survival, we have $s_{\text{tot},ity;p} = 1 - p + ps_{\text{tot},ity}$.
$r_{j,y}$	resight probability, the probability of seeing a tagged individual in year y, given that it is alive and in the ith partition class
P_{biy}	the probability, given the observations on the sea lion with tag number b up to and including year y, that this sea lion is in non-composite stage i
$Nstage$	The number of stages

The data come from a series of observations on individual tagged sea lions, including, for each sea lion, the tag number b (a unique sea lion number), the year tagged $y_{b,\text{tag}}$, the last year of observation $y_{b,\text{last}}$, and the 'state' of the sea lion O_{by} in each year from $y_{b,\text{tag}}$ to $y_{b,\text{last}}$, where the 'state' indicates whether the sea lion was observed and, if so, which class of the partition the sea lion was in.

The negative log-likelihood for the sea lion with tag number b is given by -$\Sigma_y$log(L_{by}), where the summation is over $y_{b,tag} < y \le y_{b,last}$ and L_{by} is the likelihood of the observation in year y given the observation in year y–1. The likelihood calculation is a generalization of that used in the Cormack-Jolly-Seber model (Cormack 1964). Specifically, when the model partition is of size 1 (so the mark-recapture observations are simply presence/absence) the calculated likelihood is exactly the same as in the Cormack-Jolly-Seber model. SeaBird generalizes this likelihood by allowing multi-state observations (partition size greater than 1) and uncertainty about state (as expressed in composite observations).

Let X_{iyj} be the probability that a sea lion in stage i in year y will be alive and in stage j in the following year. This may be calculated by multiplying the overall survivals ($s_{\text{tot},ity}$) for each time step between the observations together with the transition probability. The equation for this depends on the relationship between the time step, t, for the mark-recapture observations, and that for the transition process, t_{trans}:

$$
X_{iyj} = \begin{cases}
\dfrac{s_{\text{tot},ity}}{s_{\text{tot},ity;p}} \left[\displaystyle\prod_{t'>t} s_{\text{tot},it'y} \right] \left[\displaystyle\prod_{t' \le t_{trans}} s_{\text{tot},it',y+1} \right] \left[\displaystyle\prod_{t_{trans} < t' < t} s_{\text{tot},jt',y+1} \right] s_{\text{tot},jt,y+1;p} T_{y+1,ij} & \text{if } t > t_{trans} \\[3ex]
\dfrac{s_{\text{tot},ity}}{s_{\text{tot},ity;p}} \left[\displaystyle\prod_{t<t' \le t_{trans}} s_{\text{tot},it'y} \right] \left[\displaystyle\prod_{t'>t_{trans}} s_{\text{tot},jt'y} \right] \left[\displaystyle\prod_{t'<t} s_{\text{tot},jt',y+1} \right] s_{\text{tot},jt,y+1;p} T_{yij} & \text{if } t \le t_{trans}
\end{cases}
$$

where we use the convention that 'empty' products are equal to 1 (e.g., the first product in the upper formula will be empty if t is the last time step).

To calculate the likelihoods L_{by}, we need to define P_{biy} to be the probability, given the observations on the sea lion with tag number b up to and including year y, that this sea lion is in non-composite stage i in that year. Obviously, if this sea lion is observed in non-composite stage j in year y, then

$$P_{biy} = \begin{cases} 1 & \text{if } i = j \\ 0 & \text{if } i \neq j \end{cases}$$

Otherwise, P_{biy} is calculated recursively as follows. If the observed stage at tagging (i.e., in year $y = y_{b,tag}$) is composite then

$$P_{biy} = \begin{cases} \dfrac{n_{ity;p}\, r_{iy}}{\sum_{i' \in O_{by}} n_{i'ty;p}\, r_{i'y}} & \text{if } i \in O_{by} \\ 0 & \text{if } i \notin O_{by} \end{cases}$$

where $n_{ity;p}$ are the numbers of sea lions at the time of the observations.

If the observed stage in year $y+1$ (i.e., $O_{b,y+1}$) is composite, or ≤ 0, then

$$P_{bj,y+1} = \begin{cases} \dfrac{\sum_{i \in O_{by}} P_{biy} X_{iyj}\, r_{j,y+1}}{\sum_{i \in O_{by}} P_{biy} \sum_{j' \in O_{b,y+1}} X_{iyj'}\, r_{j',y+1}} & \text{if } O_{b,y+1} > 0 \text{ and } j \in O_{b,y+1} \\ 0 & \text{if } O_{b,y+1} > 0 \text{ and } j \notin O_{b,y+1} \\ \dfrac{\sum_{i \in O_{by}} P_{biy} X_{iyj}\left(1 - r_{j,y+1}\right)}{1 - \sum_{i \in O_{by}} P_{biy} \sum_{j'} X_{iyj'}\, r_{j',y+1}} & \text{if } O_{b,y+1} = 0 \\ \sum_{i \in O_{by}} P_{biy} X_{iyj} & \text{if } O_{b,y+1} = -1 \end{cases}$$

where, for $O_{by} \leq 0$ the notation $\sum_{i \in O_{by}}$ implies a sum over all non-composite stages (i.e., from 1 to Nstage), as does $\sum_{j'}$.

The likelihoods are calculated as

$$L_{b,y+1} = \begin{cases} \sum_{i \in O_{by}} P_{biy} \sum_{j \in O_{b,y+1}} X_{iyj}\, r_{j,y+1} & \text{if } O_{b,y+1} > 0 \\ \left(1 - \sum_i P_{biy}\right) + \sum_{i \in O_{by}} P_{biy}\left[1 - \sum_j X_{iyj}\, r_{j,y+1}\right] & \text{if } O_{b,y+1} = 0 \\ 1 & \text{if } O_{b,y+1} = -1 \end{cases}$$

A point to notice is that the total log-likelihood associated with a tagged sea lion depends very little, if at all, on the numbers in the partition. These numbers enter the likelihood calculation for a tagged

sea lion only if the initial observation, $O_{by_b,band}$, is a composite stage, in which case $P_{biy_b,band}$ depends on partition numbers.

3.3.4 Likelihoods for absolute abundance, by-catch or parameter observations

For these observations, the likelihood is a formula involving the observation, O, and the population model's expected value, E, for the observation. The form of the formula depends on what error distribution is assumed for the observation (Table 7).

Table 7 Formulae for calculating negative-log likelihoods for different error distributions. C.v. is denoted by c*, standard deviation by* s*, and the robustification constant by* r*.*

Error distribution	Parameter(s)	Negative-log likelihood
normal	c	$\log(cE) + 0.5[(O–E)/(cE)]^2$
normal-by-stdev	s	$\log(s) + 0.5[(O–E)/s]^2$
lognormal	c^1	$\log(\sigma) + 0.5[0.5\sigma + \log(O/E)/\sigma]^2$
normal-log	c^1	$\log(\sigma) + 0.5[\log(O/E)/\sigma]^2$
robustified-lognormal	c^{1}, r	$\log(\sigma) - \log\left(\exp\left[-0.5\left(\dfrac{\log(O/E)}{\sigma} + \dfrac{\sigma}{2} \right)^2 \right] + r \right)$

^{1}In the likelihood, $\sigma = [\log(1+c^2)]^{0.5}$

3.3.5 Likelihoods for age distribution observations

Age distributions are fitted using a likelihood based on the multinomial distribution.

Let O be a vector of observations of proportions-at-age for a single year that sum to 1; let E be the corresponding fitted values; let N be the "effective sample size" parameter. Then the multinomial likelihood for that year, which are expressed on the objective-function scale of $-\log(L)$, is

$$-\log(L) = -\log(N!) + \sum_i \left[\log((NO_i)!) - NO_i \log(Z(E_i, r)) \right]$$

where $Z(x,r)$ is a robustifying function with parameter $r>0$ (to prevent division by zero errors), defined as

$$Z(x,r) = \begin{cases} x \text{ where } x \geq r \\ r/(2 - x/r) \text{ otherwise} \end{cases}$$

Here, r was set to 0 so $Z(x,r) = x$. N was set to 1000 for 1999-2001 data and to 200 for 1998.

3.4 Functional forms

3.4.1 Age at first pupping

We adopted the functional form for the probability of first pupping at age as used by Francis (2012). An animal that is a juvenile at age a-1 ($4 \leq a \leq 8$), and survives to age a, either breeds for the first time at age a, with probability $\Pr B1st_a$, or remains a juvenile where

$$\log it(\Pr B1st_a) = \log it(\Pr 1st_{a-1}) + (a-4)oddsmult \text{ where } \log it(\Pr B1st_a) = \log(\frac{\Pr B1st_a}{1 - \Pr B1st_a})$$

3.4.2 Survival

We investigated the functional form for mortality rate as suggested by Gilbert (2008). He defined mortality as a smooth, U-shaped function of age that gives the probability that a female will die in the year after achieving a given age, where μ_1 is the minimum function value (mortality rate), $0 < \mu_1 < 0.3$, μ_2 is the age at which the minimum is achieved, $0 < \mu_2 < 8$, μ_3 is the function value at age 0, $0 < \mu_3 < 0.8$, and μ_4 is the function value at age 20, $0 < \mu_4 < 0.8$. The mortality rate depends on parameter vector $\underset{\sim}{\mu}$,

$$
\mathrm{m}(a \mid \underset{\sim}{\mu}) =
\begin{cases}
\mu_1 \left(\dfrac{\mu_3}{\mu_1} \right)^{\left(\frac{a - \mu_2}{0 - \mu_2} \right)} & a \leq \mu_2 \\[2em]
\mu_1 \left(\dfrac{\mu_4}{\mu_1} \right)^{\left(\frac{a - \mu_2}{20 - \mu_2} \right)} & a > \mu_2
\end{cases}
$$

The function has a minimum value of μ_1 at age $a = \mu_2$, takes the value μ_3 at $a = 0$ and μ_4 at $a = 20$.

μ_2 is an integer and so cannot be estimated in the usual way, we investigated the model fit for a number of values between 0 and 8, and choose $\mu_2 = 3$ based on log-likelihood.

3.4.3 Pupping rate

Gilbert (2008) also proposed a functional form for pupping rate, which is a smooth, domed function of age that gives the probability that a high-fecundity cow will bear a pup in a given season. The function is determined by a vector of parameters, $\underset{\sim}{\beta}$, where β1 is the maximum value of the function, $0.4 < \beta1 < 0.95$, β2 is the age at which the maximum is achieved, $8 < \beta2 < 14$, β3 and β4 are the ages at which the left and right-hand limbs of the function fall to half the maximum, $4 < \beta3 < 8$ and $\beta4 > 14$.

$$
\mathrm{b}(a \mid \underset{\sim}{\beta}) =
\begin{cases}
\beta_1 2^{-\left(\frac{a - \beta_2}{\beta_3 - \beta_2} \right)^2} & a \leq \beta_2 \\[2em]
\beta_1 2^{-\left(\frac{a - \beta_2}{\beta_4 - \beta_2} \right)^2} & a > \beta_2
\end{cases}
$$

The function has a maximum value of β_1 at $a = \beta_2$, takes the value $0.5\beta_1$ at $a = \beta_3$ on the left and at $a = \beta_4$ on the right. We investigated a variation this functional form where we assumed the pupping rate is of a constant value (β_1) between age 4 and 14, then declines to half of this value at $a = \beta_4$. This simplified version involves only two parameters.

3.5 Model development and implementation

First we investigated age, cohort and year effects on demographic rates, using Partition 1 and assuming no tag loss, to describe the basic demographic biology of NZ sea lions at the Auckland Islands. This formed the basis for a model optimisation process in which an array of candidate models, including the different partitions, were fitted to empirical observations. This allowed us to

select a suitable model to describe time varying survival, pupping rates and age at first pupping, which could be responsible for the observed population decline. Candidate models differed in their parameterisation of survival, resighting probability, pupping probability and age at first pupping, for example:

- functional forms for age effects on survival, or pupping rate, or estimates for discrete age groups
- year-varying, year-invariant parameters or year-aggregated parameters
- aggregation of parameter estimates based on pupping status

Models were fitted to tag-recapture, annual pup count and age distribution observations and compared using the Akaike information criterion (AIC) which is a likelihood based measure of goodness-of-fit.

Following the model selection process, a Monte Carlo Markov Chain (MCMC) run was implemented with optimal model configurations (as determined in the previous section) to assess the level of uncertainty around estimated values of all free parameters. A chain length of 195,000 was generated, with samples taken every 500 iterations, giving a total of 390 samples (no burn-in).

4   Results: Initial model fits

4.1   Age effects at Sandy Bay

Model configuration and parameterisation:

- Partition Type I
- No estimation of tag loss parameters
- Phantom tags not included
- Year-invariant survival, resighting probability, pupping probability and age at first pupping
- Separate survival estimates for all ages 0-20+
- Separate pupping probability estimates for puppers in previous year (ages 4-20+) and non-puppers in previous year (ages 5-20+)
- Separate resighting probability for all partitions with immature pupping status, and constant across ages for puppers and non-puppers
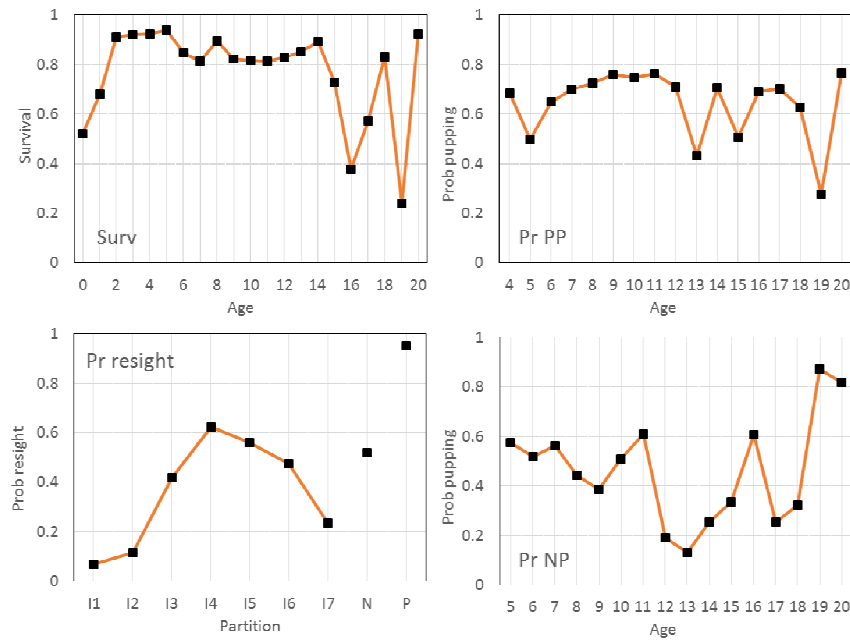
Figure 4 Estimated parameter values for model exploring age-effects on survival, resighting probability and probability of pupping

Key results (with reference to Figure 4):

- Estimated survival
  - Increase from ages 0, 1 and 2 (0.52, 0.68 and 0.91, respectively)
  - Peaks at ages 2-5 (ranging from 0.91-0.94)
  - Relatively constant across ages 6-14 (ranging from 0.81-0.90)
  - Variable at ages 15+ (ranging from 0.24-0.92).
- Resighting probability
  - Lowest annual probability of resighting for 1 and 2-year old individuals (0.07 & 0.12, respectively)
  - Of individuals not previously observed to have pupped, peak resighting probability is at age 4 (0.62), with a continuous decline to age 7 (0.23).
  - Probability of resighting non-puppers (0.52) similar to that of immature animals aged 3-6 (0.42-0.62).
  - Nearly all puppers resighted in each year on average (0.95)
- Pupping probability
  - Consistently high Pr PP at ages 7-12 (ranging from 0.70-0.76), with peak pupping rate between ages 9-11 (ranging from 0.75-0.76).
  - No obvious trend with increasing age in the probability of non-puppers pupping (Pr NP). Generally a reduced probability of pupping in comparison to individuals that pupped in the previous year (ranging from 0.19-0.61 across ages 7-12).

4.2　Cohort effects at Sandy Bay

Model configuration and parameterisation:

- Partition Type I (no tag loss)
- No estimation of tag loss parameters
- Phantom tags not included
- **Subsets of mark-recapture data to include only animals tagged as pups in a particular year**
- Year-invariant survival, resighting probability, pupping probability and age at first pupping parameters
- Cohort specific estimates of survival for age categories: 0, 1, 2-5, 6-14 and 15+
- Cohort specific estimates of pupping probability for age categories 4-14 and 15+
- Probability of pupping estimated separately for animals that pupped (Pr PP) or did not pup (Pr NP) in the previous year
- Separate resighting probability for all partitions with immature pupping status, and constant across ages for puppers and non-puppers
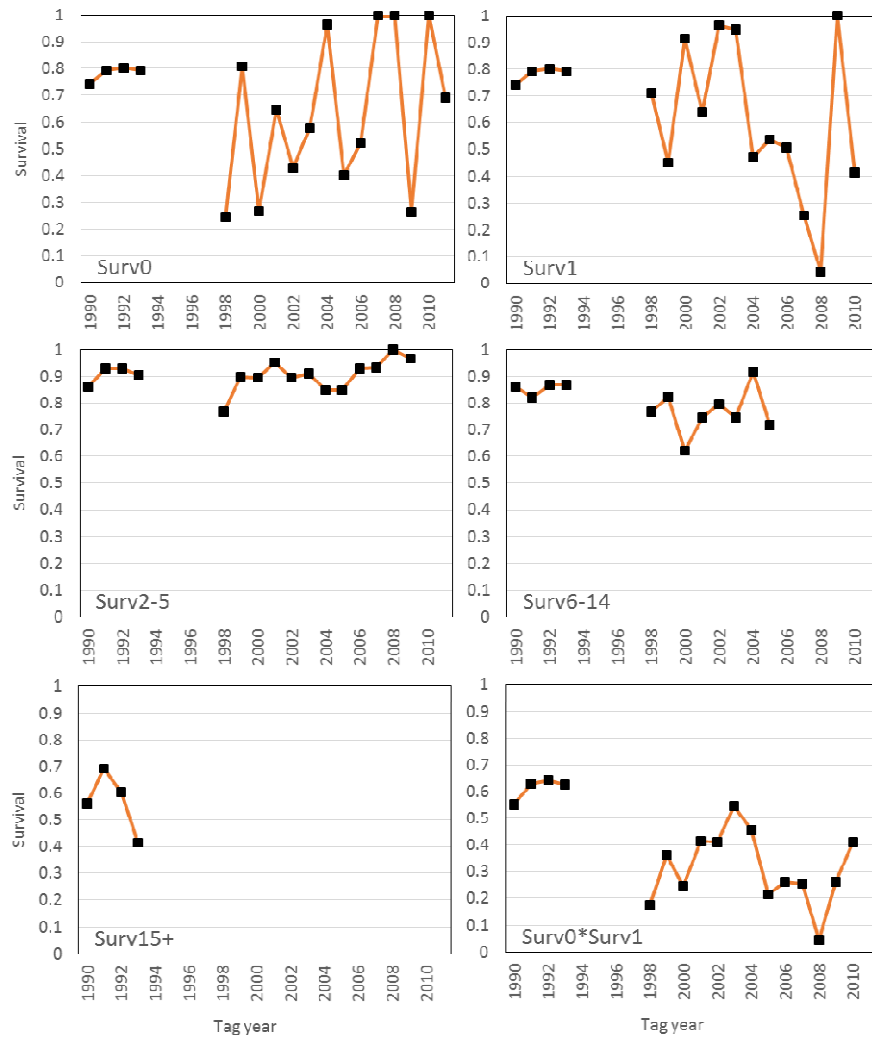
Figure 5 Model estimates of survival for model exploring cohort-effects on survival, resighting probability and probability of pupping. "Tag year" along y-axis relates to year of tagging as pup or "cohort". Bottom right panel plot gives product of survival across ages 0 and 1.
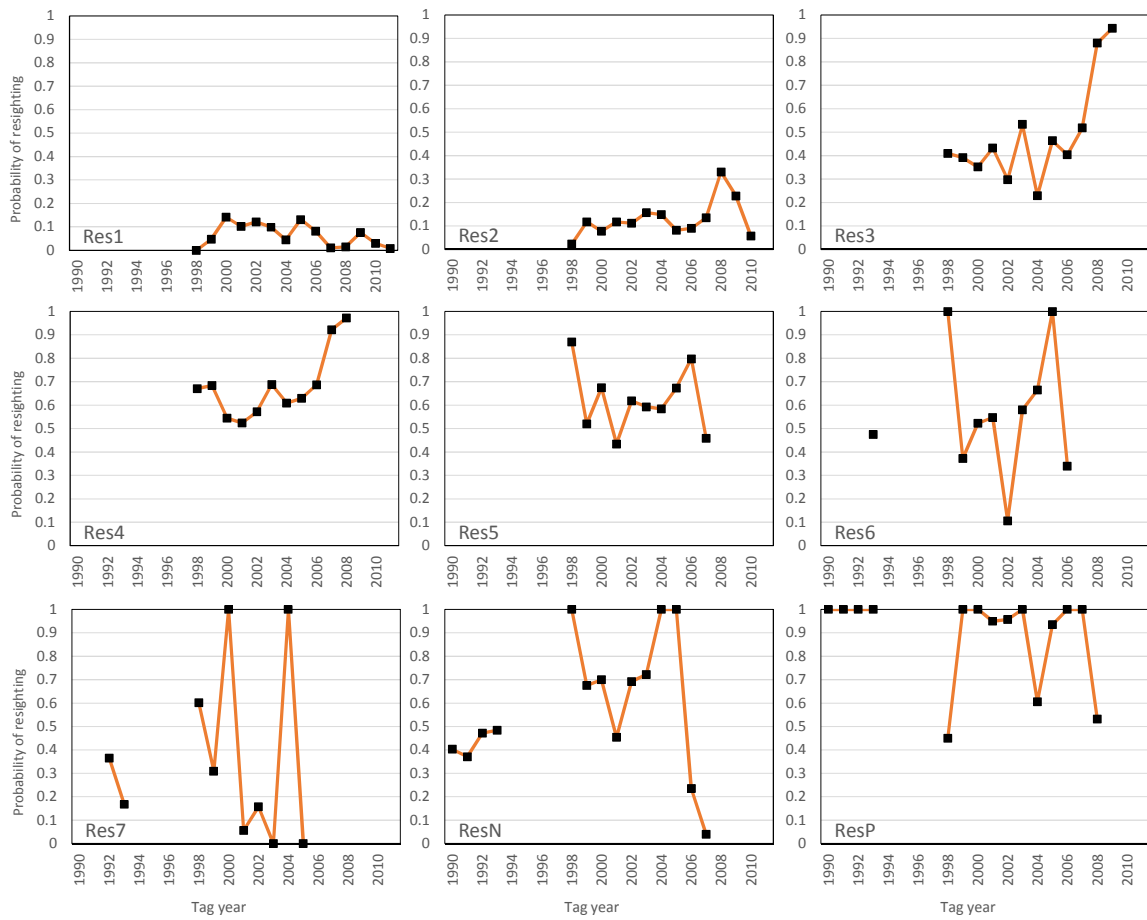
Figure 6 Model estimates of resighting probability for model exploring cohort-effects on survival, resighting probability and probability of pupping. "Tag year" along y-axis relates to year of tagging as pup or "cohort".
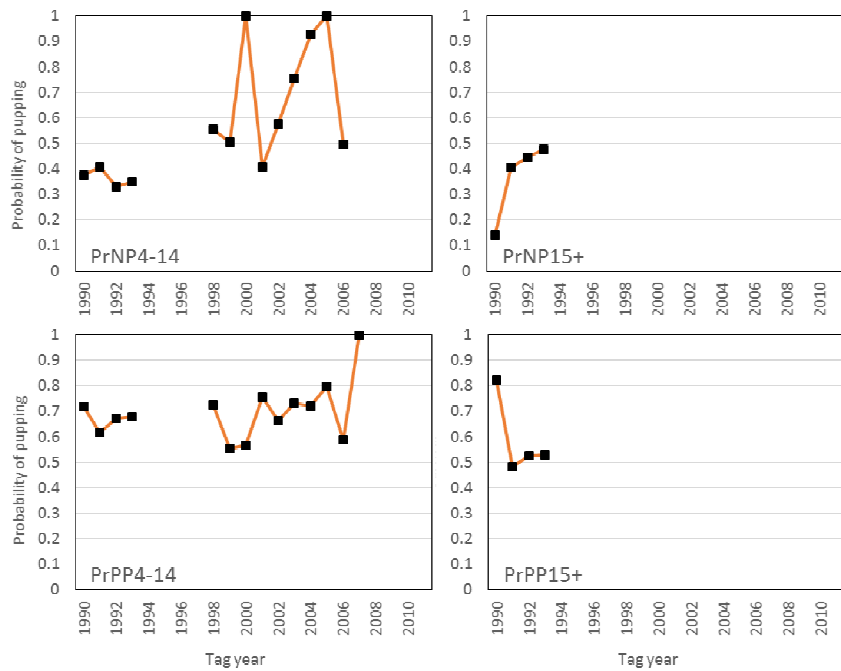
Figure 7 Model estimates of pupping probability for model exploring cohort-effects on survival, resighting probability and probability of pupping. "Tag year" along y-axis relates to year of tagging as pup or "cohort".

Key results:

- Estimated survival (with reference to Figure 5)
  - Relatively high survival rate of individuals tagged as pups in 1990-1993, across all age classes.
  - Negatively correlated survival at ages 0 and 1 for a given cohort (a consequence of low resighting probability at ages 1 and 2). Multiplying estimates reveals strong cohort effects on survival across ages 0 and 1 (cohorts 1990-1993 - ranging from 0.55-0.64; cohorts 1998-2010 - ranging from 0.04-0.55).
  - Minimal between-cohort variation in estimates of survival at ages 2-5 (ranging from 0.85-1.00, excluding 1998 cohort for which 0.77 was estimated).
  - Generally reduced survival at ages 6-14 of cohorts 1998-2005 (ranging from 0.62-0.92) relative to 1990-1993 cohorts (ranging from 0.82-0.87). Later cohorts do not inform estimation of survival at ages 15+
  - Only cohorts 1990-1993 inform estimation of survival at ages 15+
- Resighting probability (with reference to Figure 6)
  - No obvious cohort effect on resighting probability, except increased resighting probability of immature individuals aged 2-4 belonging to cohorts 2007, 2008 & 2009.
  - Generally increased resighting probability of non-puppers of cohorts born from 1998 and decreased probability of resighting puppers.
- Pupping probability (with reference to Figure 7)
  - Cohorts born from 1998 generally had an increased probability of non-puppers pupping in the next year.
  - There was not an obvious cohort effect on probability of puppers pupping in the next year, with lowest estimates for cohorts 1999 and 2000, 0.56 and 0.57 respectively, compared with 0.61-0.80 for all other tagged cohorts born between 1990-2005
  - Estimates likely to be highly uncertain for cohorts born later than 2005 owing to insufficient years of resighting effort at breeding ages.

4.3   Year effects at Sandy Bay

Model configuration and parameterisation:

- Partition Type I (no tag loss)
- Phantom tags not included
- **Year-varying survival, resighting probability, pupping probability. Year-invariant age at first pupping.**
- Age category specific estimates of survival for ages: 0, 1, 2-5, 6-14 and 15+
- Age category specific estimates of pupping probability for ages4-14 and 15+
- Probability of pupping estimated separately for animals that pupped (Pr PP) or did not pup (Pr NP) in the previous year
- Separate resighting probability for all partitions with immature pupping status, and constant across ages for puppers and non-puppers
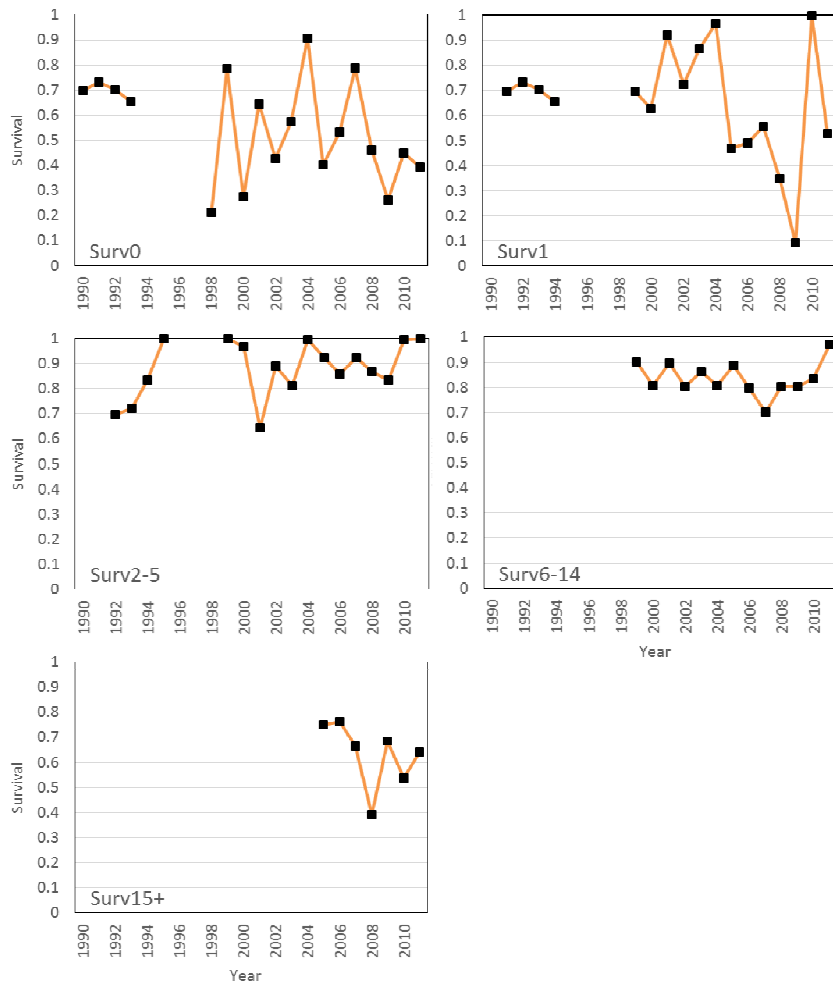
Figure 8 Model estimates of survival for model exploring year-effects on survival, resighting probability and probability of pupping. "Year" along y-axis relates to survival at year to year+1.
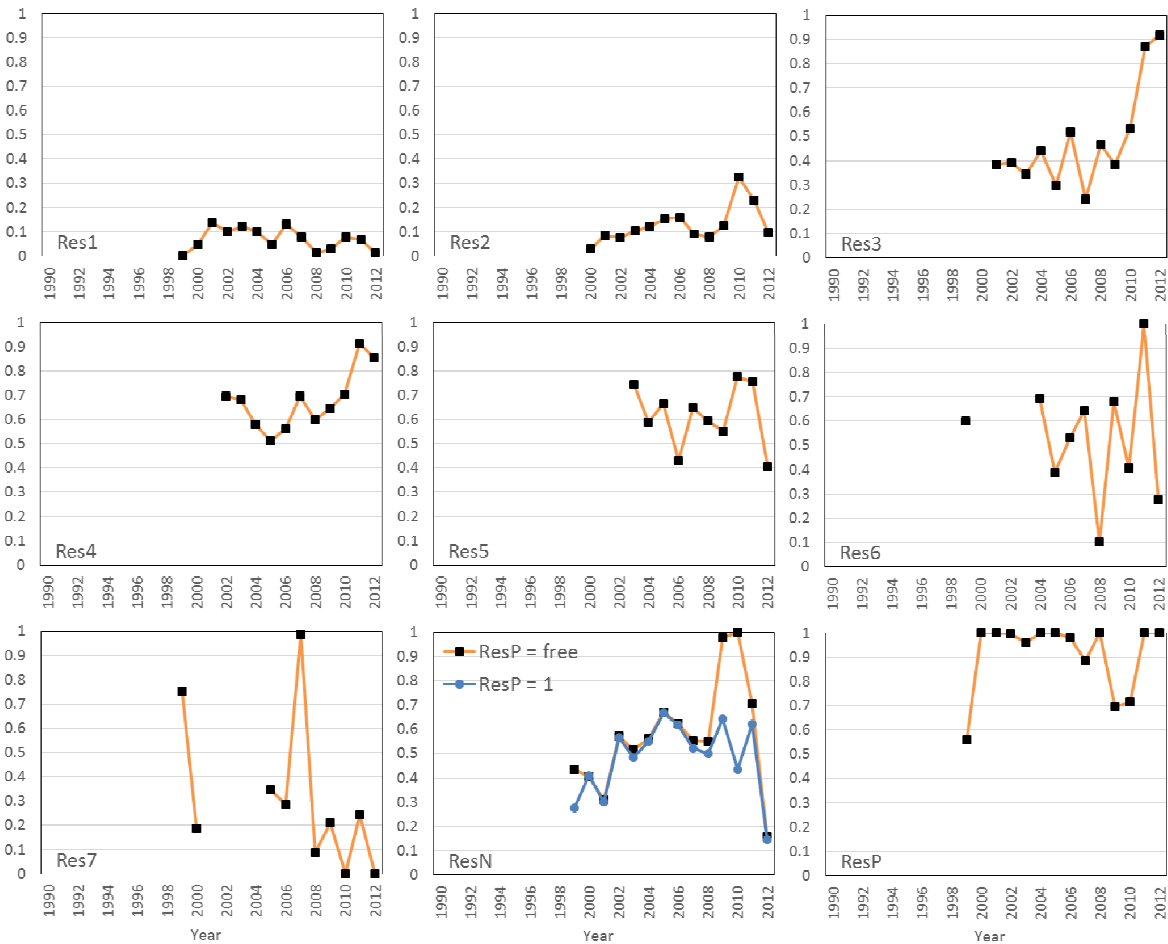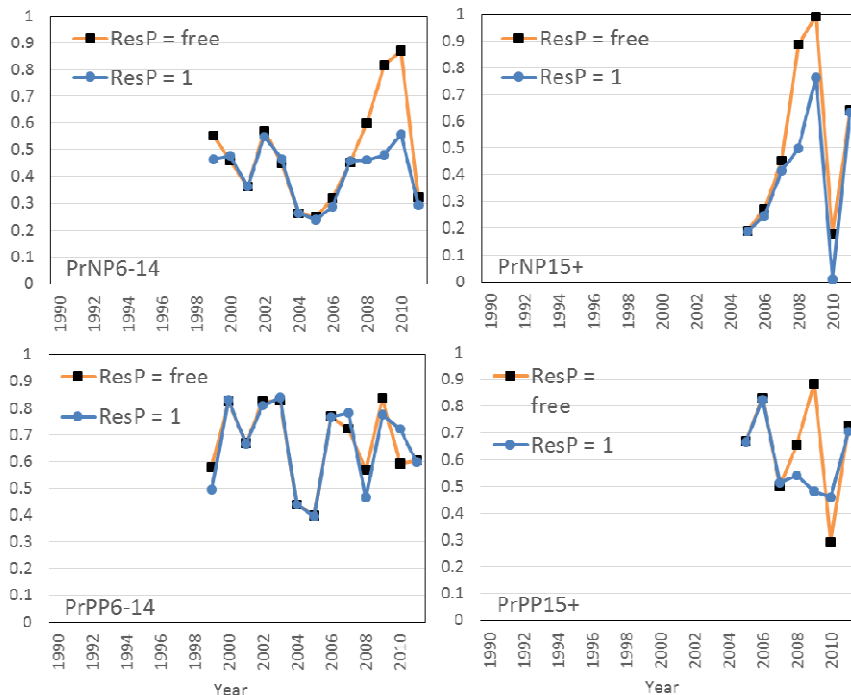
Figure 9 Model estimates of resighting probability for model exploring year-effects on survival, resighting probability and probability of pupping. "Year" along y-axis relates to survival at year to year+1; black points connected by orange lines are estimates with resighting probability of puppers free; purple points and lines are estimates with probability of puppers pupping constrained to 1.

Figure 10 Model estimates of pupping probability for model exploring year-effects on survival, resighting probability and probability of pupping. "Year" along y-axis relates to survival at year to year+1; black points connected by orange lines are estimates with resighting probability of puppers free; purple points and lines are estimates with probability of puppers pupping constrained to 1.

- Estimated survival (with reference to Figure 8)
  - Annual survival estimates for ages 0 and 1 are analogous to cohort effects in that they are each informed by resighting frequencies of single cohorts. As such, estimates for ages 0 in a year y and 1 in year y+1 will be confounded, given low resighting probability at ages 1 & 2.
  - Model estimates indicate a strong year/cohort effect on survival at ages 0 & 1, with reduced survival in cohorts born between1990-1993. (See MCMC results for more in-depth assessment of year effects on survival at ages 0 and 1)
  - Survival at ages 6-14 ranged from 0.80 to 0.90 in years 1999-2010, excluding 2007 - for which a value of 0.70 was estimated.
  - Reduced survival of individuals ages 15+ in 2008 (0.39) relative to all other years (ranging from 0.54-0.76)
- Resighting probability (with reference to Figure 9)
  - Increased resighting probability at ages 2-4 in years 2010 & 2011.
  - Low resighting probability of puppers in 2007, 2009 & 2010. Unlikely given high levels of resighting effort and given much higher estimates for all other years with similar resighting effort levels. Decision taken to fix resighting probability of puppers to 1 for all subsequent model runs. This effected a reduction in the resighting probability of non-puppers in 2009 and 2010.
- Pupping probability (with reference to Figure 10)
  - Fixing the resighting probability of puppers to 1 had a minimal effect on estimates of the probability of puppers pupping in the next year (Pr PP).
  - There are likely to be strong year effects on the probability of puppers pupping, with low estimates for 1998, 2001, 2004, 2005, 2008 and 2011. These estimates will correspond with pup count estimates in the following year.

o Model estimates also indicated year effects on the probability of non-puppers pupping (Pr NP) in the next year, with comparatively low estimates in 2001, 2004, 2005 and 2006. Estimates in 2008, 2009 and 2010 were reduced when the resighting probability of puppers was fixed to 1.

5 Results: Model optimisation and development

An array of candidate models using only tag resighting observations were developed, incorporating different parameterisations of demographic rates in the following order:

- survival (model runs 4a-m)
- resighting probability (model runs 5a-m)
- pupping probability (model runs 6a-d)
- age at first pupping (model run 7a)

Comparison of candidate models was by AIC, with the optimal model identified in each stage (lowest AIC) taken forward to the next stage Table 8). In addition model fits to tag resighting observations for each cohort were examined by eye (e.g. Figure 11).

For all models assessed in the optimisation process:

- Partition Type I (no tag loss)
- Phantom tags not included
- Resighting probability of puppers fixed to 1

Table 8 Candidate models ranked in ascending order of AIC

Model run	Survival estimates Age	Survival Yr groups	Breeding Prob estimates Age	Breeding Prob Yr groups	Resighting prob estimates Age	Resighting prob Yr groups	Maturation	LL	params	AIC
7a	0, 1, 2-5, 6-14, 15+	15+ year-invariant	4+ (P), 4+ (N)	Separate estimates all yrs	1-2,3,4-5,6,7,N	1-2 year-invariant	Year-varying	-7976.2	178	16,308
6b	0, 1, 2-5, 6-14, 15+	15+ year-invariant	4+ (P), 4+ (N)	Separate estimates all yrs	1-2,3,4-5,6,7,N	1-2 year-invariant	Year-invariant	-8023.6	152	16,351
6d	0, 1, 2-5, 6-14, 15+	15+ year-invariant	functional form	a4 & b4 year-invariant	1-2,3,4-5,6,7,N	1-2 year-invariant	Year-invariant	-8022.8	154	16,354
6a	0, 1, 2-5, 6-14, 15+	15+ year-invariant	4+ (P), 4-14 (N), 15+ (N)	Separate estimates all yrs	1-2,3,4-5,6,7,N	1-2 year-invariant	Year-invariant	-8020.5	159	16,359
5j	0, 1, 2-5, 6-14, 15+	15+ year-invariant	4-14 (P), 4-14 (N), 15+ (P), 15+ (N)	Separate estimates all yrs	1-2,3,4-5,6,7,N	1-2 year-invariant	Year-invariant	-8017.1	166	16,366
4m	0, 1, 2-5, 6-14, 15+	0 & 15+ year-invariant	4-14 (P), 4-14 (N), 15+ (P), 15+ (N)	Separate estimates all yrs	1,2,3,4,5,6,7,N	Separate estimates all yrs	Year-invariant	-7999.6	185	16,369
5m	0, 1, 2-5, 6-14, 15+	6+ year-invariant	4-14 (P), 4-14 (N), 15+ (P), 15+ (N)	Separate estimates all yrs	1-2,3,4-5,6,7,N	1-2 year-invariant	Year-invariant	-8032.2	153	16,370
6c	0, 1, 2-5, 6-14, 15+	15+ year-invariant	functional form	Separate estimates all yrs	1-2,3,4-5,6,7,N	1-2 year-invariant	Year-invariant	-8019.3	166	16,371
5l	0, 1, 2-5, 6-14, 15+	0 & 15+ year-invariant	4-14 (P), 4-14 (N), 15+ (P), 15+ (N)	Separate estimates all yrs	1-2,3,4-5,6,7,N	1-2 year-invariant	Year-invariant	-8036.4	149	16,371
5d	0, 1, 2-5, 6-14, 15+	15+ year-invariant	4-14 (P), 4-14 (N), 15+ (P), 15+ (N)	Separate estimates all yrs	1-2,3,4-5,6,7,N	Separate estimates all yrs	Year-invariant	-8008.5	179	16,375
5b	0, 1, 2-5, 6-14, 15+	15+ year-invariant	4-14 (P), 4-14 (N), 15+ (P), 15+ (N)	Separate estimates all yrs	1,2,3,4-5,6,7,N	Separate estimates all yrs	Year-invariant	-7999.3	192	16,383
5h	0, 1, 2-5, 6-14, 15+	15+ year-invariant	4-14 (P), 4-14 (N), 15+ (P), 15+ (N)	Separate estimates all yrs	1-2,3,4-5,6,7,N	4-5 year-invariant	Year-invariant	-8023.8	169	16,386
4i	0, 1, 2-5, 6-14, 15+	15+ year-invariant	4-14 (P), 4-14 (N), 15+ (P), 15+ (N)	Separate estimates all yrs	1,2,3,4,5,6,7,N	Separate estimates all yrs	Year-invariant	-7992.4	202	16,389
4k	0, 1, 2-5, 6-14, 15+	2-5 & 15+ year-invariant	4-14 (P), 4-14 (N), 15+ (P), 15+ (N)	Separate estimates all yrs	1,2,3,4,5,6,7,N	Separate estimates all yrs	Year-invariant	-8008	187	16,390
5f	0, 1, 2-5, 6-14, 15+	15+ year-invariant	4-14 (P), 4-14 (N), 15+ (P), 15+ (N)	Separate estimates all yrs	1-2,3,4-5,6,7,N	7 year-invariant	Year-invariant	-8025.2	170	16,390
5i	0, 1, 2-5, 6-14, 15+	15+ year-invariant	4-14 (P), 4-14 (N), 15+ (P), 15+ (N)	Separate estimates all yrs	1-2,3,4-5,6,7,N	3 year-invariant	Year-invariant	-8027.5	168	16,391
3	0, 1, 2-5, 6-14, 15+	Separate estimates all yrs	4-14 (P), 4-14 (N), 15+ (P), 15+ (N)	Separate estimates all yrs	1,2,3,4,5,6,7,N	Separate estimates all yrs	Year-invariant	-7987.6	208	16,391
4j	0, 1, 2-5, 6-14, 15+	6+ year-invariant	4-14 (P), 4-14 (N), 15+ (P), 15+ (N)	Separate estimates all yrs	1,2,3,4,5,6,7,N	Separate estimates all yrs	Year-invariant	-8007.2	189	16,392
5g	0, 1, 2-5, 6-14, 15+	15+ year-invariant	4-14 (P), 4-14 (N), 15+ (P), 15+ (N)	Separate estimates all yrs	1-2,3,4-5,6,7,N	6 year-invariant	Year-invariant	-8026.4	170	16,393
4h	0, 1, 2-5, 6+	Separate estimates all yrs	4-14 (P), 4-14 (N), 15+ (P), 15+ (N)	Separate estimates all yrs	1,2,3,4,5,6,7,N	Separate estimates all yrs	Year-invariant	-8001.7	201	16,405
4e	0, 1, 2-4, 5-14, 15+	Separate estimates all yrs	4-14 (P), 4-14 (N), 15+ (P), 15+ (N)	Separate estimates all yrs	1,2,3,4,5,6,7,N	Separate estimates all yrs	Year-invariant	-7995.1	208	16,406
4d	0, 1, 2, 3-5, 6-14, 15+	Separate estimates all yrs	4-14 (P), 4-14 (N), 15+ (P), 15+ (N)	Separate estimates all yrs	1,2,3,4,5,6,7,N	Separate estimates all yrs	Year-invariant	-7981.1	222	16,406
5e	0, 1, 2-5, 6-14, 15+	15+ year-invariant	4-14 (P), 4-14 (N), 15+ (P), 15+ (N)	Separate estimates all yrs	1-2,3,4-5,6,7,N	N year-invariant	Year-invariant	-8038.7	166	16,409
4g	0, 1, 2-14, 15+	Separate estimates all yrs	4-14 (P), 4-14 (N), 15+ (P), 15+ (N)	Separate estimates all yrs	1,2,3,4,5,6,7,N	Separate estimates all yrs	Year-invariant	-8010.7	194	16,409
5k	0, 1, 2-5, 6-14, 15+	15+ year-invariant	4-14 (P), 4-14 (N), 15+ (P), 15+ (N)	Separate estimates all yrs	1-2,3,4-5,6,7,N	0-7 year-invariant	Year-invariant	-8087.6	127	16,429
4c	0, 1, 2, 3, 4, 5, 6-14, 15+	Separate estimates all yrs	4-14 (P), 4-14 (N), 15+ (P), 15+ (N)	Separate estimates all yrs	1,2,3,4,5,6,7,N	Separate estimates all yrs	Year-invariant	-7977	243	16,440
5a	0, 1, 2-5, 6-14, 15+	15+ year-invariant	4-14 (P), 4-14 (N), 15+ (P), 15+ (N)	Separate estimates all yrs	1,2,3,4-7,N	Separate estimates all yrs	Year-invariant	-8053.7	175	16,457
4a	u1, u3, u4, max (u3) at age3	Separate estimates all yrs	4-14 (P), 4-14 (N), 15+ (P), 15+ (N)	Separate estimates all yrs	1,2,3,4,5,6,7,N	Separate estimates all yrs	Year-invariant	-8140	145	16,570
4b	u1, u3, u4, max (u3) at age2	Separate estimates all yrs	4-14 (P), 4-14 (N), 15+ (P), 15+ (N)	Separate estimates all yrs	1,2,3,4,5,6,7,N	Separate estimates all yrs	Year-invariant	-8141.1	144	16,570
5c	0, 1, 2-5, 6-14, 15+	15+ year-invariant	4-14 (P), 4-14 (N), 15+ (P), 15+ (N)	Separate estimates all yrs	1,2,3,4-6,7,N	Separate estimates all yrs	Year-invariant	-8411.4	182	17,187
4f	0-1, 2-5, 6-14, 15+	Separate estimates all yrs	4-14 (P), 4-14 (N), 15+ (P), 15+ (N)	Separate estimates all yrs	1,2,3,4,5,6,7,N	Separate estimates all yrs	Year-invariant	-8476.6	191	17,335
4l	0, 1, 2-5, 6-14, 15+	1 & 15+ year-invariant	4-14 (P), 4-14 (N), 15+ (P), 15+ (N)	Separate estimates all yrs	1,2,3,4,5,6,7,N	Separate estimates all yrs	Year-invariant	-8483.1	186	17,338

5.1.1 Model 7a parameterisation and fits to tagging data

Model run 7a had the lowest AIC of any model parameterisation (Table 8). Demographic rates and resighting probability were parameterised as follows:

- Survival
  - Separate age-aggregated estimates for different age categories: s_0, s_1, s_{2-5}, s_{6-14} and s_{15+}
  - Combined survival estimates of puppers and non-puppers
  - All parameters were year-varying except s_{15+} which was year-invariant across all years
- Resighting probability
  - Separate age-aggregated estimates for different partitions: r_{1-2}, r_3, r_{4-5}, r_6, r_7, r_N
  - All except r_{1-2} were year-varying
- Pupping rate
  - Constant across all ages (4-20+)
  - Separate estimates for individuals that pupped and did not pup in the previous year
  - All year-varying
- Age at first pupping
  - Both parameters – $\Pr B1st_a$ and *oddsmult* – year-varying.

With the exception of age at first pupping, none of the functional forms described in Section 3.4 were found to reduce AIC and were not carried forward to the next stage of model development.

Good fits to tag resighting observations were generally observed for all cohorts (pup tagging years) and across all resighting years, corresponding to the full range of ages from 1-20. Two exceptions to this include fits to the individuals tagged as pups in 1991 and 1998 for which survival appears to have been slightly overestimated (Figure 11).
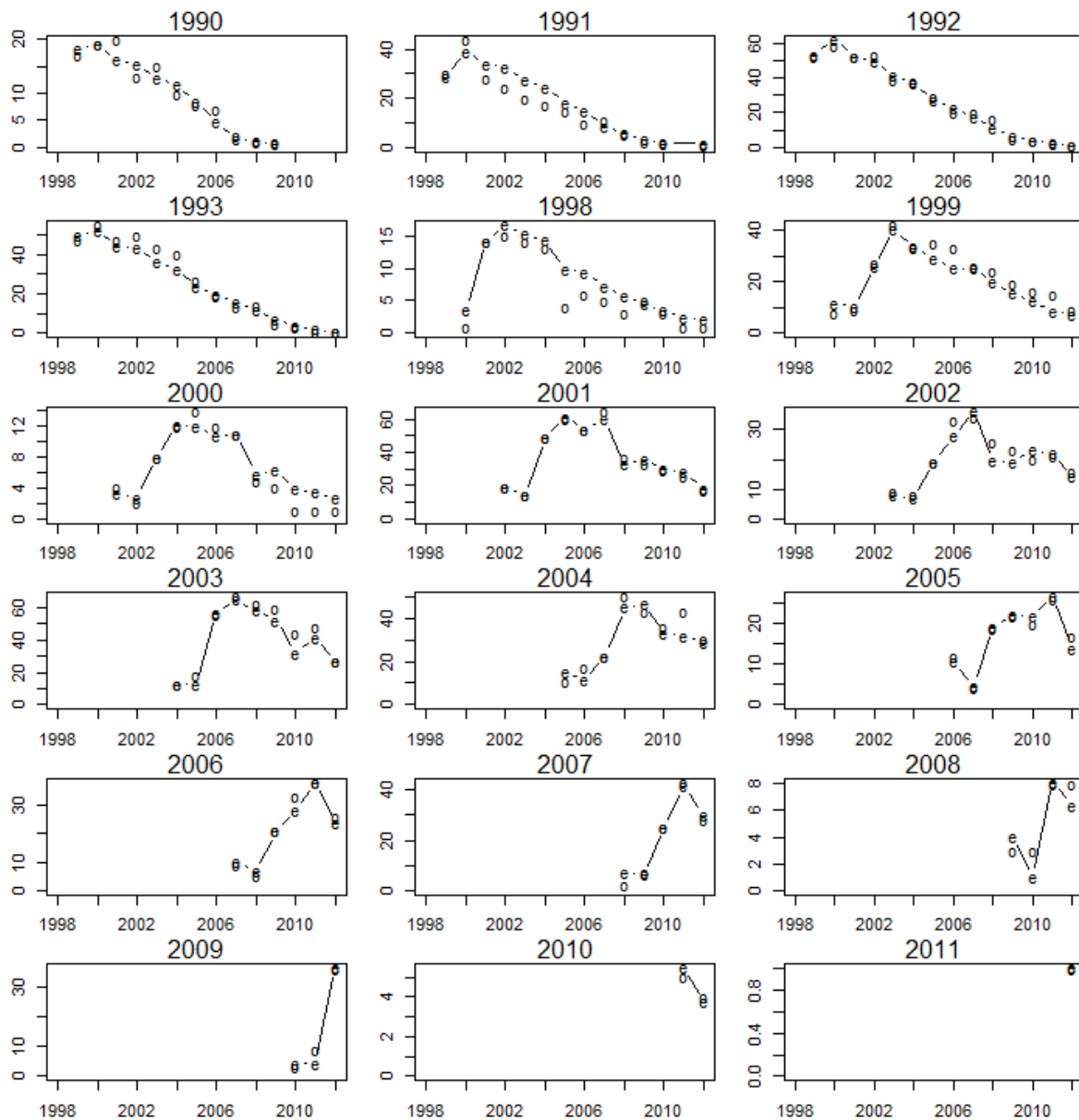
Figure 11 Fits of tag resighting frequency by cohort (one plot for each cohort) and year of resighting (y-axis), comparing model estimates ("e") and observed values ("o").

5.1.2   Age at first pupping estimates from model 7a

Parameter estimates from model run 7a are described in more detail in the MCMC output section. Here we describe year-varying age at first pupping, which was not explored prior to the model development/optimisation process. This indicated that the age at first pupping was relatively high from 2001-2008 and a large proportion of individuals may not have pupped by age 8 over this time period (Figure 12).
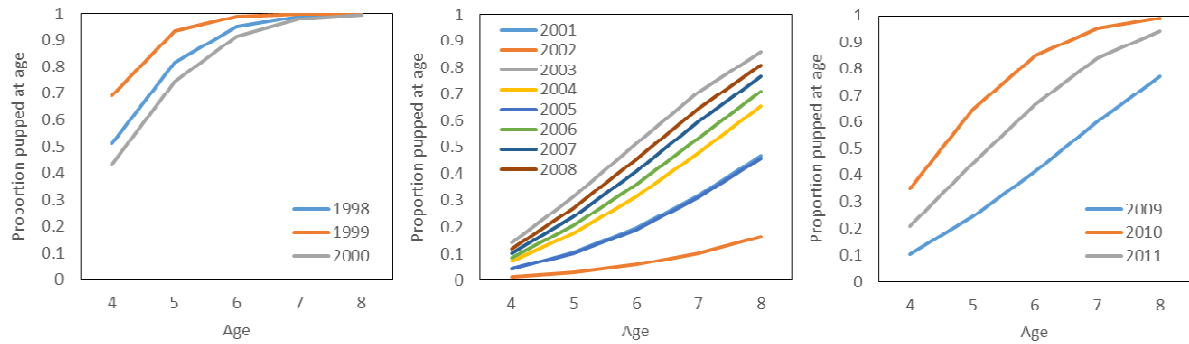
Figure 12 Cumulative proportion of individuals that will have pupped at age, derived from year-varying estimates of parameters from model run 7a. A separate plot is presented for relationships derived from 1998-2000, 2001-2008 and 2009-2011 estimates.

5.2   Pups dead at tagging Sandy Bay

The inclusion of "phantom tags" to account for pups that died prior to tagging primarily affected survival at age 0, with a very small effect on survival at age 1 in some years (model configuration and parameterisation as run 7a). As expected, phantom tags had the greatest effect on s_0 in years 2002 and 2003 when pup mortality rates prior to tagging were greatest (s_0 = 0.35 with phantom tags and 0.43 without in 2002, s_0 = 0.48 and 0.57, respectively in 2003; Figure 13; Table 2). Inclusion of phantom tags had almost no effect on the resighting probability of ages 1-2 (0.104 with phantom tags, 0.105 without).
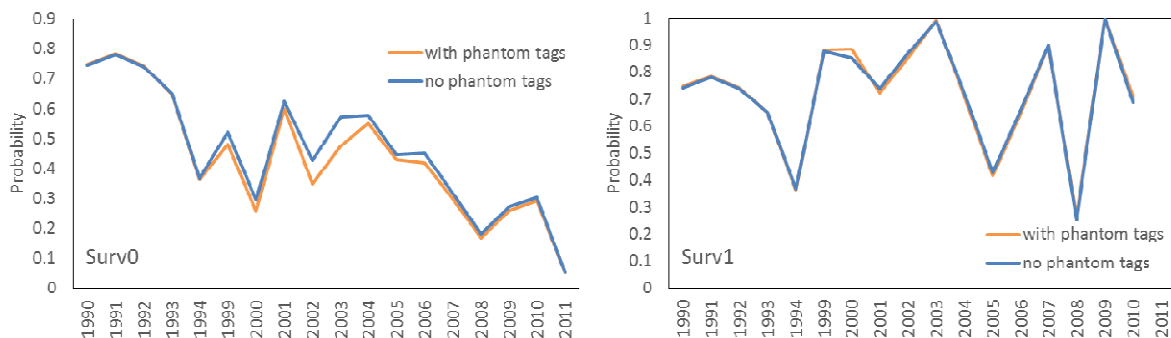
Figure 13 Effect of inclusion of phantom tags on model estimates of survival at ages 0 and 1.

5.3   MCMC Sandy Bay

The MCMC run was parameterised as run 7a (Section 5.1.1) and included phantom tags (Section 5.2).

Median estimates from the MCMC run were similar to those of the MPD run, with relatively high survival at ages 0 and 1 in the early 1990s and several years with very low estimates from 2006 onwards (Figure 14). A strong negative correlation was observed between survival at age 0 and at age 1 in the following year. Taking the product of these estimates affected a large reduction in the size of prediction intervals. Several very low survival cohorts were identified including pups born in 1998, 2005 and 2008 with relatively tight prediction intervals (Figure 15). Adult survival (age 6-14) did not vary much through time with the exception of a very low estimate in 2007 (Figure 14). A year-invariant value of survival rate was estimated for age 15+ at 0.58 (95% prediction intervals = 0.50-0.66).

Age-specific estimates of resighting probability were quite variable through time with increased estimates for age groupings 3 and 4-5 in 2011 and 2012. The prediction intervals around the estimates for age 7 were very large indicating that this parameter was not well estimated (Figure 16). Resighting probability estimate for age group 1-2 was 0.096 (prediction intervals 0.082-0.109; year-invariant).

Prediction intervals around probability of puppers pupping in years 2004, 2005 and 2008 (median estimates 0.40 – 0.46) did not overlap with those of estimates from all other years from 2000-2011 (median estimates 0.66 – 0.83), though were comparatively large around estimates of non-puppers pupping (Figure 17). There was also quite a high degree of variability around estimates of maturation at age parameters in years where relatively large median values were estimates (Figure 18).
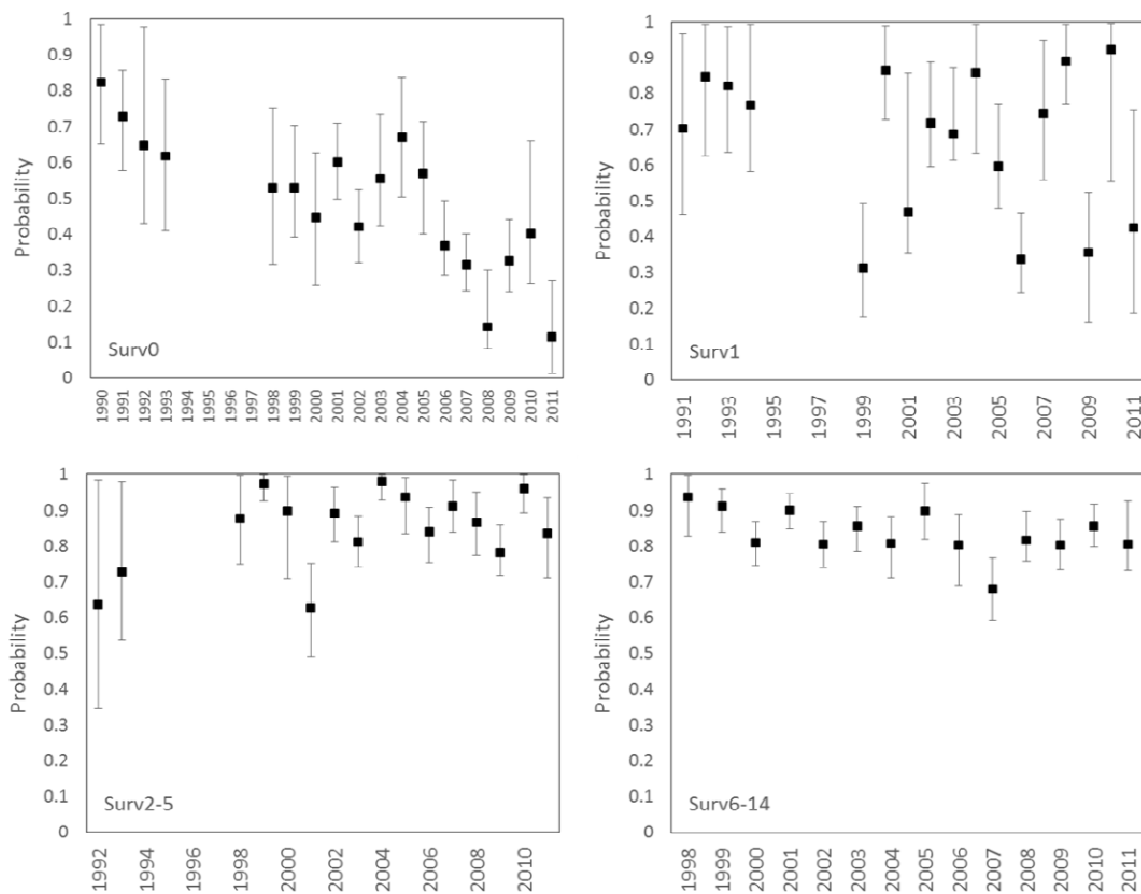
Figure 14 MCMC estimates of age-specific survival; bars are 95% prediction intervals
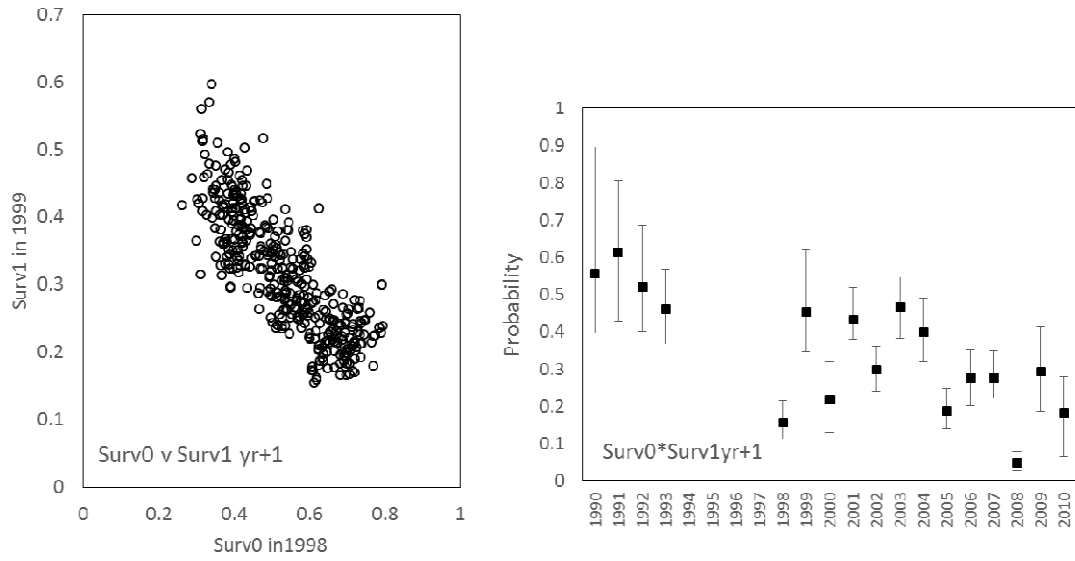
Figure 15 MCMC estimates of age-specific survival; negative correlation between survival estimates of at age 0 in yr and age 1 in yr+1 (left); the product of these MCMC survival estimates with 95% prediction intervals (right).
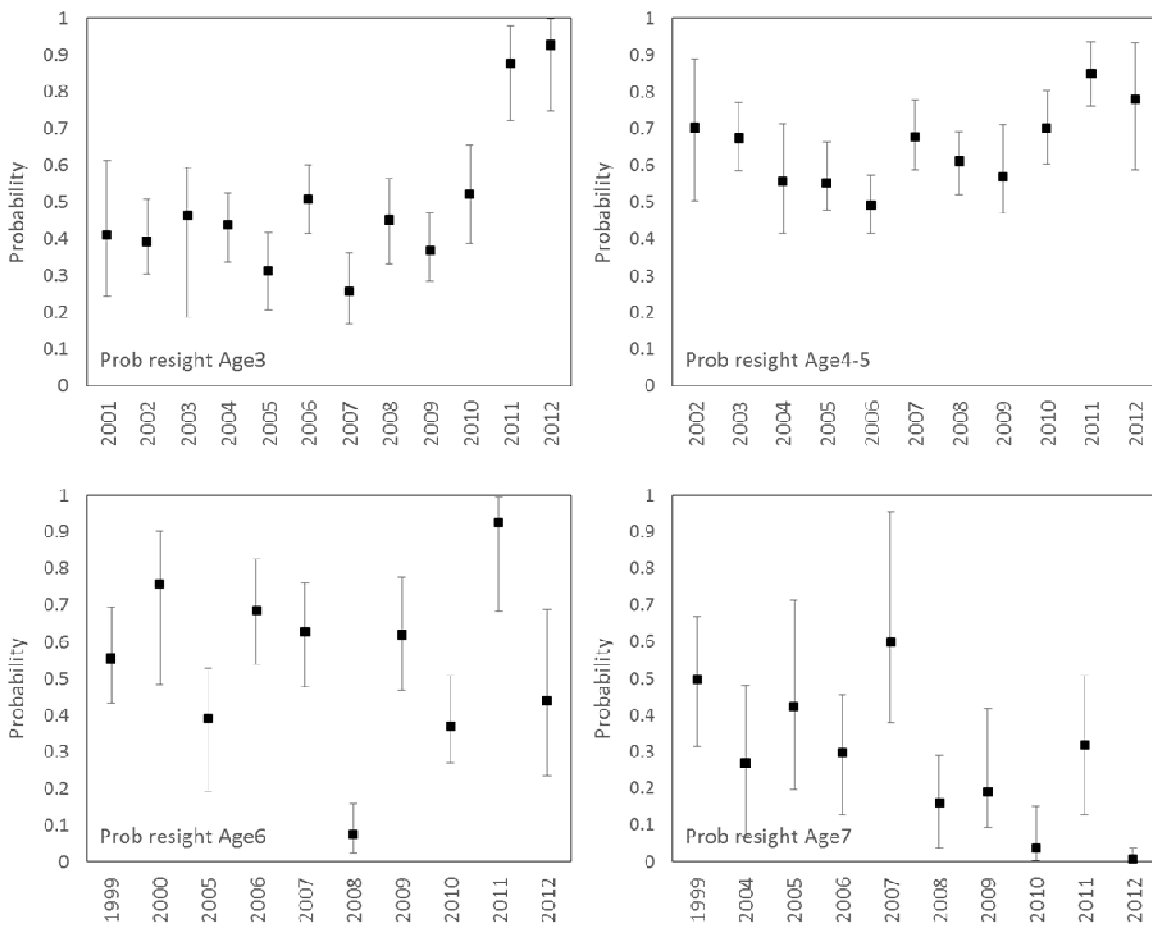
Figure 16 MCMC estimates of age/status-specific resighting probability; bars are 95% prediction intervals
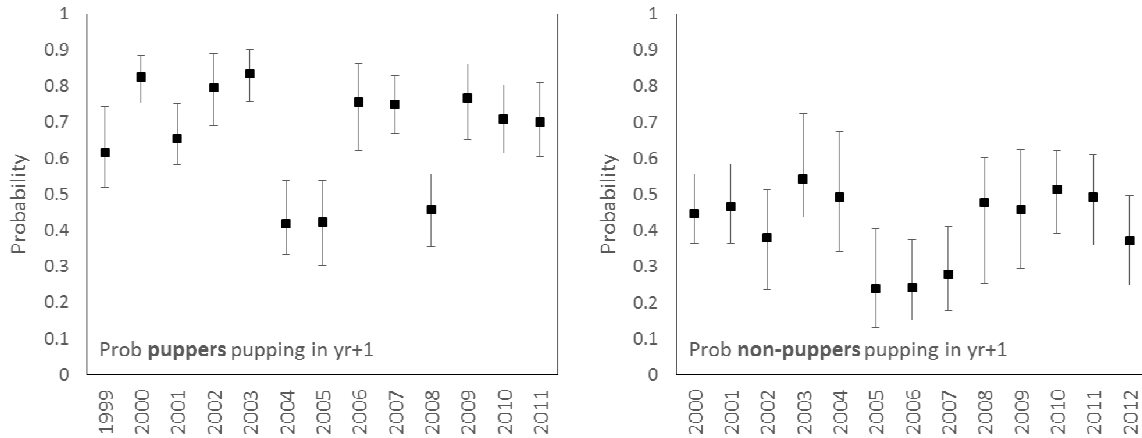
Figure 17 MCMC estimates of pupping probability; bars are 95% prediction intervals
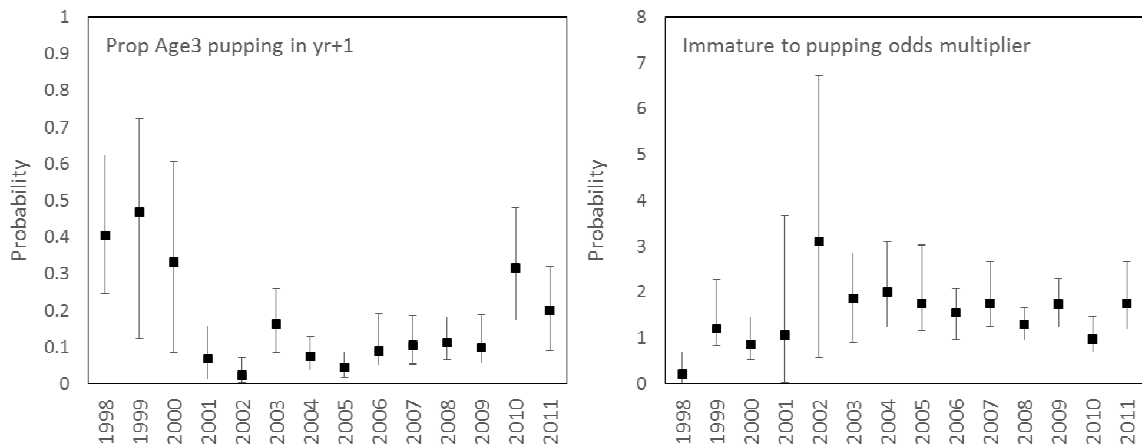

Figure 18 MCMC estimates of age at maturation parameters $\Pr B1st_a$ *(left) and **oddsmult** (right)*

6   Results: Further model validation

6.1   Retrospective analysis Sandy Bay

A retrospective analysis was conducted in which parameter values were estimated in the final year of tagging and tag resighting data were sequentially removed from the model input files. The model was parameterised as run 7a (Section 5.1.1) and included phantom tags (Section 5.2). This showed evidence of model bias in estimates of survival at age 0 (s_0) where this tended to increase with additional years of resighting. The rate of increase in survival estimates decreased after approximately 4-6 years of resighting data. Survival estimates for years that had relatively high (e.g. 2001) or low (e.g. 2008) estimates of survival after one year of resighting tended to remain so with additional years of resighting (Figure 19).
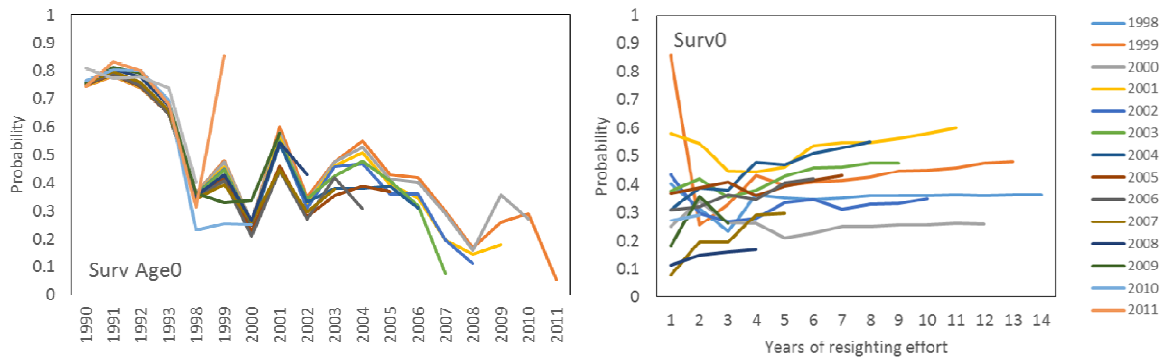
Figure 19 Retrospective analysis showing dataset time series and year effects on estimates of survival at age 0 (left); the same estimates presented as effect of number of years of resighting effort on estimates for a particular year (right).
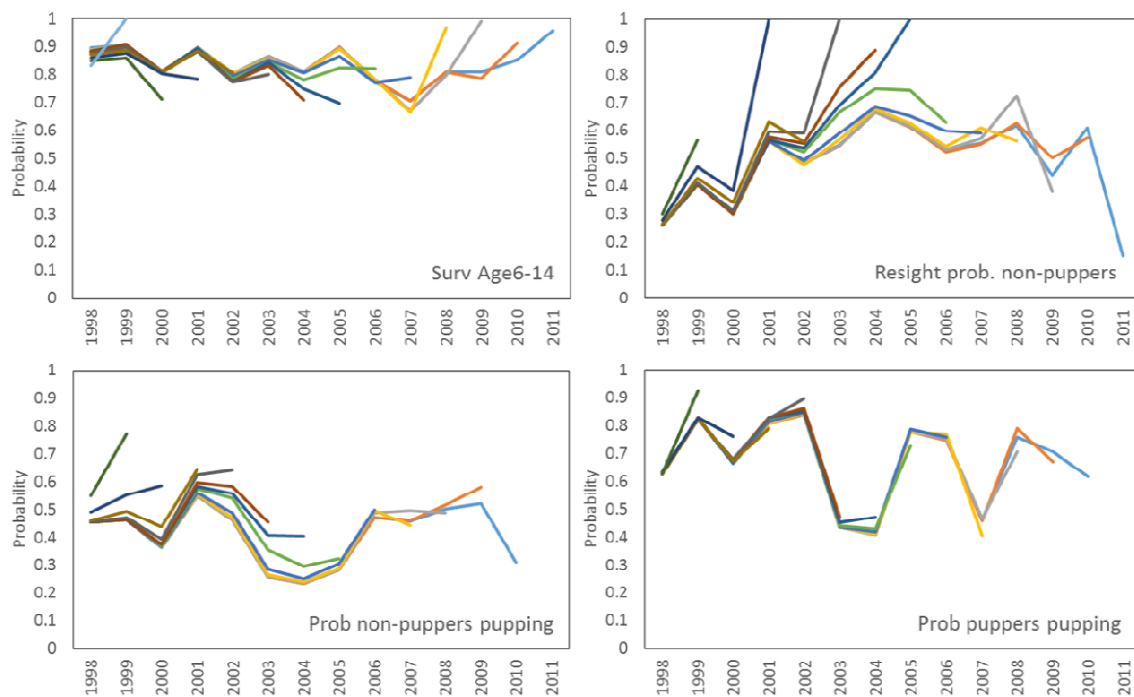

Figure 20 Retrospective analysis showing dataset time series and year effects on: estimates of survival at age 6-14 (top left); resighting probability of non-puppers (top-right); probability of non-puppers pupping (bottom-left); and probability of puppers pupping (bottom-right).

6.2 Tag loss model Sandy Bay

Model configuration and parameterisation:

- Partition Type III
- Phantom tags included
- As model run 7a, except:
  - No age at first pupping parameters
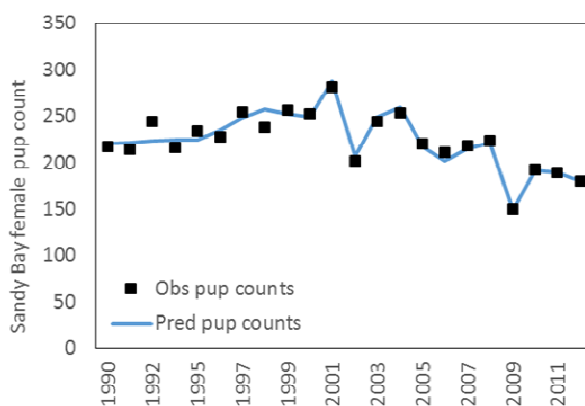 - Year-invariant tag loss parameters for age 0 and 1+

Figure 21 Estimates of survival at ages 0 and 6-14 for model run with tag loss parameters

- Tag loss
    - o Annual tag loss at age 0 estimated at (0.085)
    - o Annual tag loss at age 1+ estimated at (0.049)
- Survival (with reference to Figure 21)
    - o Incorporating tag loss affected a large increase in survival at age 0 (mean increase of 0.08) and in survival at ages 1+ (mean increase of 0.5)
    - o Increase in survival close to estimates of tag loss

6.3   Fitting to pup census and age distribution observations

6.3.1   Fit to pup census observations
Model configuration and parameterisation:

- Partition Type II
- Phantom tags included
- Fit to pup census observations (C.V. of 0.03 assumed)
- As model run 7a, except:
    - o No age at first pupping parameters
    - o Year-invariant tag loss parameters for age 0 and 1+

Figure 22 Model fits to pup census observations (points = observations; blue line = model estimates)

- Good model fits to pup census observations (Figure 22)
- Effect on parameter estimates (with reference to Figure 23)
    - o Minor effect on survival at age 0, the probability of puppers pupping

- General increase in survival of age 6-14, the resighting probability of non-puppers and decrease in the probability of non-puppers pupping
- Years with anomalously low estimates of survival and probability of puppers pupping remain as such when the model is fitted to pup census observations
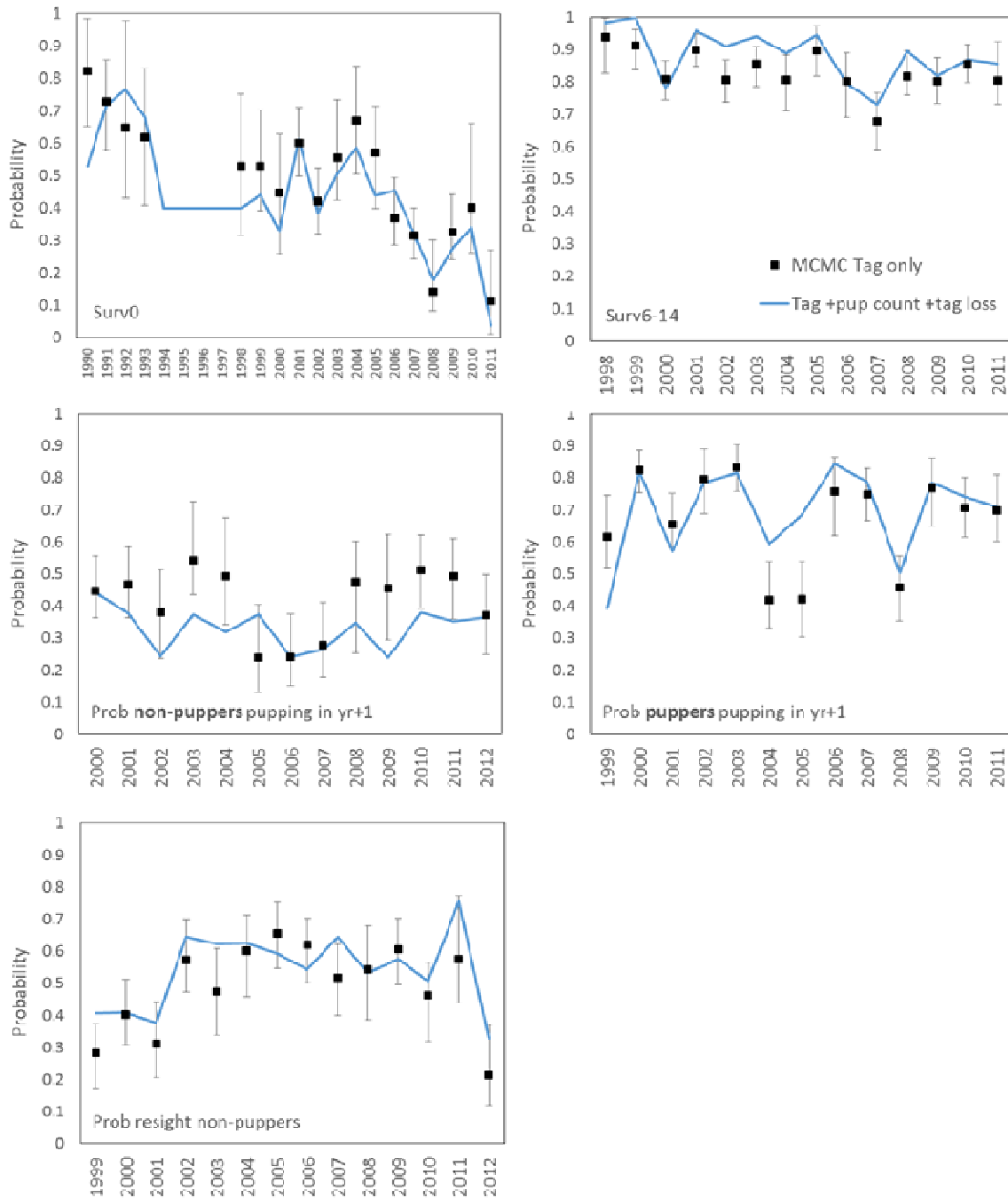- Increased tag loss rate compared with tag-resighting only model (0.103 for age 0 and 0.063 for age 1+

Figure 23 Model estimates of survival, pupping probablity and resighting probability from the model fit to pup census observations (blue line) compared with MCMC median estimates and prediction intervals (black points and bars; run described in Section 5.3).

6.3.2 Age distribution

Model configuration and parameterisation:

- Partition Type I
- Phantom tags included
- No tag loss parameters
- Fit to age distribution observations
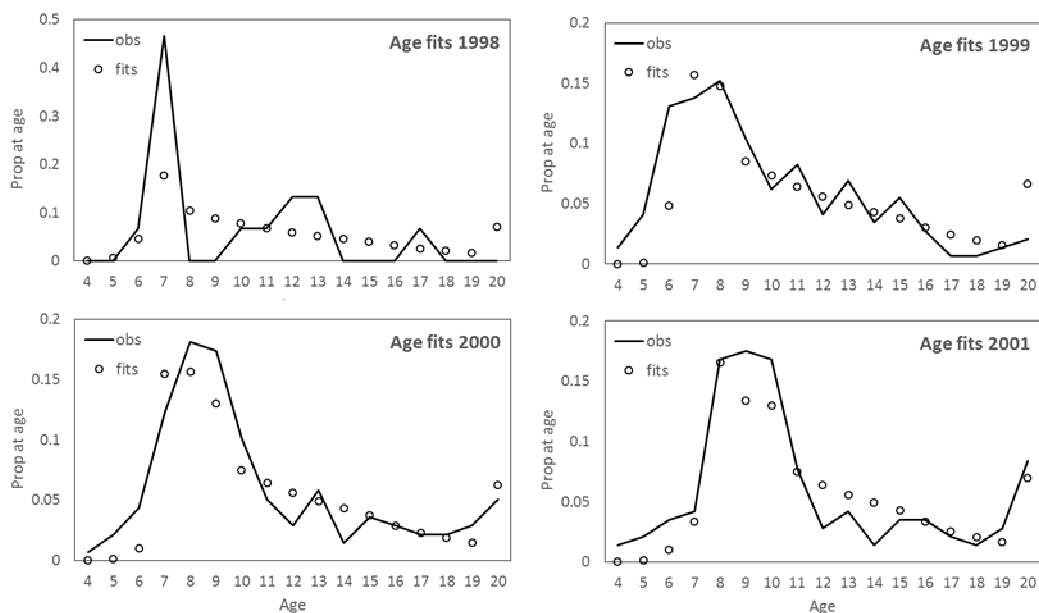- Parameterisation as model run 7a

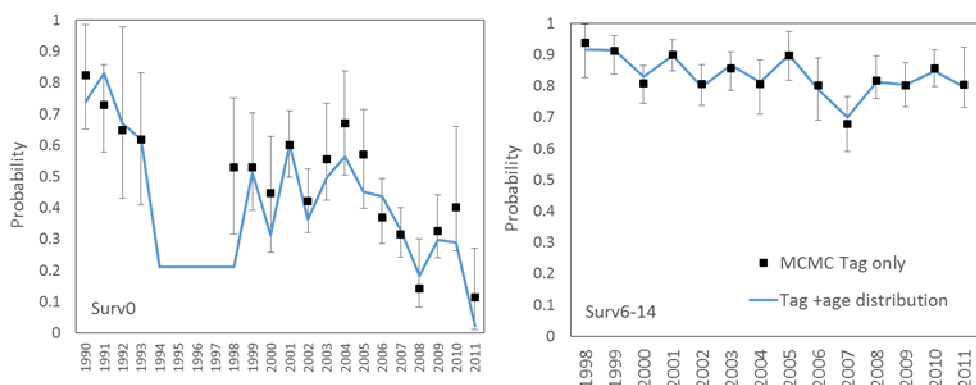*Figure 24 Model fits to age distribution observations*

Figure 25 Model estimates of survival at age 0 and 6-14 from the model fit to age distribution observations (blue line) compared with MCMC median estimates and prediction intervals (black points and bars; run described in Section 5.3).

- Good model fits to age distribution observations (Figure 24)
- Effect on parameter estimates (with reference to Figure 25)
  - Minor effect on survival at age 0, with high survival of pups born in 1990-93 and low estimate for pups born in 1994-1997 (no tagging program in these years)
  - Age distribution observations uninformative for all other parameters estimated in this model run

6.4   Dundas model

- Partition Type I
- Phantom tags included
- No tag loss parameters
- Dundas tag-recapture observations (tagged as pups at Dundas and resighting at Dundas only)
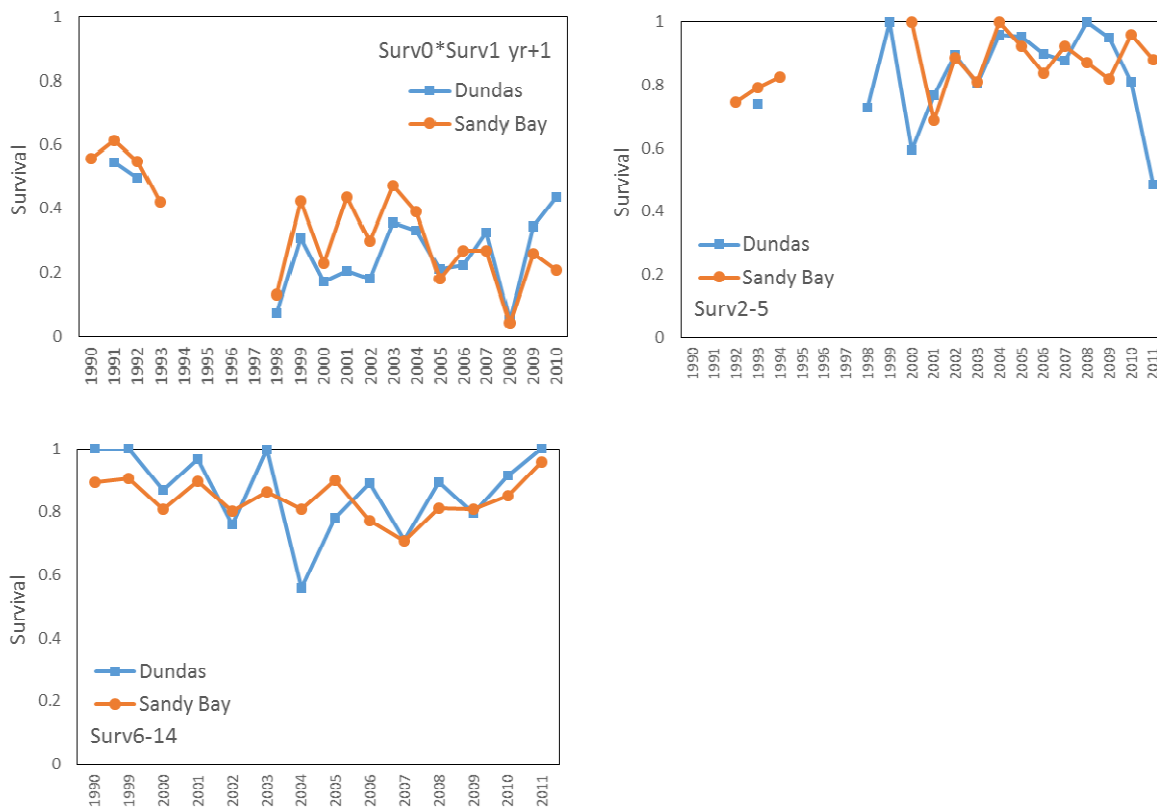- Parameterisation as model run 7a, except probability of resighting puppers unconstrained

Figure 26 Model estimates of survival of animals tagged as pups and resighted at Dundas compared animals tagged as pups and resighted at Sandy Bay

- Estimates of survival at ages 0 and 1 at Dundas very similar to that of Sandy Bay (presented as product of survival at age 0 and survival at age 1 in yr+1) (Figure 26)
- The same strong (1991 and 1992) and weak cohorts (1998 and 2008) comparing the two breeding rookeries
- Slightly lower estimates of survival at age 0 at Dundas in all years until 2005
- Similar rate of adult survival (age 6-14) comparing the two rookeries, though with a very low estimate at Dundas in 2004 not evident from model estimates using Sandy Bay observations
- Very few observations of animals confirmed to have pupped

6.5   Comparison of estimates from MARK and SeaBird programs

- MARK (White & Burnham, 1999) analysis by Clive McMahon and Mark Hindell at the University of Tasmania (McMahon & Hindell, 2013).
- MARK model

- o Cormack–Jolly–Seber (CJS) estimation of survival (as SeaBird)
- o Overdispersion factor
- o MARK model Fitted to Sandy Bay mark-resighting observations
- o No pupping status or estimation of pupping rates
- Parameterisation (MARK and comparable SeaBird model)
  - o Year-varying survival at ages 0, 2-4, 5-15, 16+
  - o Year-varying resighting probability (not age-specific)
  - o No tag loss estimation
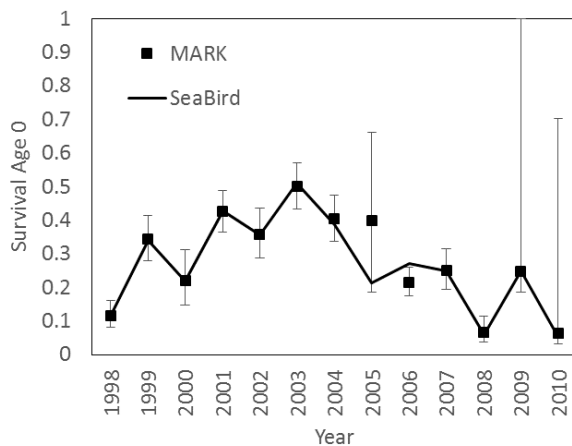 - o SeaBird partition type I

Figure 27 A comparison of MARK (points and confidence intervals) and SeaBird estimates (line) of survival at age 0 with the same parameterisations of survival and resighting probability.

- MARK and SeaBird gave near-identical estimates of survival at age 0 (identical to 4 significant figures) for all years except 2004, 2005 and 2006 (Figure 27).
- Wide 95% confidence intervals in 2009 and 2010, much larger than 95% prediction intervals MCMC run (Figure 14)

7 Summary of results and discussion

This report describes the process by which an array of candidate models were developed to estimate time-varying rates of demographic parameters, which might explain observed decline in NZ sea lion pup census estimates at the Auckland Islands breeding rookeries. We have also presented parameter estimates from selected candidate models. The principal findings of this assessment are presented below.

7.1 Age and cohort effects at Sandy Bay

- Age effects on survival, resighting probability and pupping rate were assessed with a model with year-invariant parameters. Survival estimates were greatest for ages 2-5 and declined at later ages. The apparent step-down in survival post age 5 may relate to the increased energetic costs and other constraints relating to the onset of reproduction. The peak in pupping rate occurred at ages 9-11, though was relatively high at all ages from 7-12. Individuals ages 1 and 2 had a very low probability of resighting <15% in a year. Also non-pupping animals had a much lower probability of being resighted relative to females confirmed to have pupped.

- There appear to be cohort effects on survival at ages 6-14, with greater estimates for animals born in 1990-1993. There are also likely to be strong cohort effects on survival at ages 0 and 1 and these are discussed in relation to year effects on survival, below.

7.2 Candidate model 7a

- An array of candidate models were developed during an optimisation process which trialled different parameterisations of survival, resighting probability, pupping rate and age at first pupping. Model run 7a had the lowest AIC and all subsequent models retained this parameterisation. For this model run:
  - o Survival estimates were aggregated within age categories 2-5, 6-14 and 15+ with separate estimates for ages 0 and 1.
  - o Resighting probability was constant across ages 1 and 2 and was year-invariant. Other resighting groupings (3, 4-5, 6, 7, non-puppers) were year-varying. Resighting of puppers was fixed to 1.
  - o Probability of pupping (for animals that did and did not pup in the previous year) and age at first pupping parameters were all year-varying

7.3 Year effects on survival at Sandy Bay

- Model estimates of survival at ages 0 and 1 indicated strong year effects on survival (e.g. years of high survivorship of pups born in 1990, 1991, 1992 and 1993; low survivorship of pups born in 1998, 2000, 2005 and 2008) and a long-term decline relative to strong cohorts in 1990-1993.
- Fitting to age distribution observations did not greatly affect estimates of survival at ages 0 and 1 of pups born in 1990-1993. Model estimates of survival for pups born in 1994-97 (for which there was no tagging effort) were relatively low when fit to age distribution observations.
- Estimates of survival at ages 0 and 1 were not very different when fitting to pup census observations (with good model fits to these data) suggesting that a decline in survival at ages 0-2 since the early 1990s is a strong candidate for a proximate cause for the decline in pup production at Sandy Bay since the late 1990s.
- SeaBird cannot accurately partition mortality between ages 0 and 1 due to the low probability of resighting 1 and 2 your-old individuals. A proposed approach is to take the product of s_{0yr} and s_{1yr+1}, which had the effect of greatly reducing the size of prediction intervals around MCMC estimates of survival at these ages. Survival of pups born in 2008 may be the lowest of any year for which tagging has been undertaken.
- The retrospective analysis demonstrated a model bias towards underestimation of survival at age 0 in later years, though relatively low or high survival years are likely to remain as such with subsequent years of resighting effort.
- Low survival estimate for ages 6-14 in 2007, which appeared to affect a number of cohorts (2000, 2001 and 2002; Figure 11).
- The extent to which cohort/year effects on survival at ages 0 and 1 are confounded with tag loss has not been explored in this assessment. Year-invariant annual tag loss rates were estimated for age 0 and all subsequent ages to be 0.085 and 0.049, respectively.
- Including animals that had died previous to tagging as phantom tags mainly affected a decrease in survival at age 0 in 2002 and 2003, in years when disease mortality rates were high.

7.4 Year effects on pupping rates at Sandy Bay

- There was no apparent long term trends in pupping rates through time, or strong cohort effects on reproductive output.
- There have been some years with low pupping rates, examples include 2000, 2002, 2005, 2006 and 2009. These one/two year reductions in pupping rate correspond with years for which low pup counts were estimated.
- There was evidence for very low survival of ages 6-14 in 2004, though no MCMC runs have been conducted to assess uncertainty around this estimate.

7.5 Year effects on age at first pupping at Sandy Bay

- Age at first pupping was represented by a functional form with two parameters – $\Pr B1st_a$ and *oddsmult* – the first of which estimates the proportion of 3 year olds that produce at pup at age 4; the second of which gives the estimated rate at which this proportion increased at subsequent ages up to age 8 when all individuals were assumed to be mature.
- There appear to be strong year effects on the estimated proportion of individuals that had pupped at age 4, with an increased proportion in 1999-2001 and 2011-2012. We have not explored the extent to which the parameters $\Pr B1st_a$ and *oddsmult* are correlated, i.e. how observations at ages 5-8 influence estimates of proportion of 3 year olds that pup at age 4 (Figure 18).
- Model estimates indicate that in a number of years (particularly 2001-2009) a large proportion of pups will not have pupped by age 8 (Figure 18).

7.6 Year-effects on demographic rates at Dundas

- There have been too few observations with confirmed pupping status to estimate pupping rates, owing to insufficient days of resighting effort (an individual must be seen with or without pup on three different days before pupping status can be confirmed according to strict definition).
- Age specific survival estimates are very similar to those estimates from Sandy Bay observations. Strong year effects with identical high (e.g. 1991 and 1992) and low survival years (e.g. 1998 and 2008) for pups born in different years, comparing Dundas and Sandy Bay.

7.7 Summary

An array of candidate models have been selected for the identification of demographic processes (proximate causes) which may be driving inter-annual variation and the longer-term decline in pup counts at the Auckland Islands breeding rookeries of NZ sea lions. In the next phase of the project final model structures will be specified that will generate estimates of time-varying rates for correlative analyses in the next phase of the project.

Declines in survival of ages 0 and 1, as well as cohort effects on survival at age 6-14 may be sufficient to explain the long-term declining trend in annual pup census counts at Sandy Bay. Similarities in survival estimates at Dundas indicate that juvenile survival is a strong candidate for a proximate cause of the decline in pup production there also. Intermittent one and two-year declines in pup production (e.g. 2002 and 2009) are coincident with years when the probability of pupping was low. In addition, inter-annual variation in the age at first pupping could also cause long term increases

and decreases in pup production, which do not instantaneously affect the number of animals at breeding age.

A correlative assessment in the next phase of the project aims to take these long term trends and to identify mechanisms that may ultimately be driving variation in key demographic rates, for example: the potential direct and indirect effects of fishing, disease, predation and variation in ocean climate. This assessment will be the primary focus of the project workshop planned for December 2013.

8   Acknowledgement

9   References

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