Pupping rate estimates for New Zealand sea lions

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Authors

D.J. Gilbert

B.L. Chilvers

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Reviewed and Approved for release by:

Dr John McKoy

General Manager, Fisheries Research

Executive summary

Here we report the final stage in this project. The mathematical formulae developed in the second stage to allow estimation of pupping rate involved mixture models. They proved unsatisfactory when attempts to fit the tag-re-sighting data were made. Therefore new and modified formulae are developed here. The formulae depend on stronger assumptions. We assume that we can determine categorically whether each observed cow has pupped each season and that all those that have, will be observed. As before the formulae include functions and their associated parameters that measure the likelihood of the behavioural observations. These functions are multiplied across all observations to produce total likelihood, which is maximised to produce the estimates. A pupping rate function is defined and estimated, based on several parameters. A mortality function must also be defined to allow the pupping rate to be estimated. For each age class the annual proportion that is alive but not sighted is estimated as well as its mortality rate so that a correct denominator for the pupping rate can be obtained. Our initial report (Gilbert 2007) modelled cows as being in two categories, high- and low-fecundity animals, but this failed to fit the data. It appears that a continuum of fecundities is more likely. We estimated a mean pupping rate function with a plateau between 9 and 13 years that is somewhat less than 50%. The function declines fairly steeply on both sides of this plateau to be below 10% at ages 4 and 20 years. This result suggests that sea lions may be less productive than previously thought. If our pupping rate estimate is used in a population model it should be done so that other parameters, especially population size, are estimated consistently with it.

1. Introduction

Our initial report (Gilbert 2007) discussed the viability of estimating pupping rate for New Zealand sea lions from the tag-resighting data collected during the summer breeding season on Enderby Island between 1999–2000 and 2006–07. Hereafter we refer to these seasons as 2000 and 2007 etc. Our second report described a mathematical model of pupping rate as a function of age defined by a set of parameters. It also described a model of mortality as a function of age. A model was described in which observations were made up of mixtures of breeders and non-breeders, high and low fecundity cows, and high and low visibility cows. We use the term breeder to refer to a cow that has a pup in a particular year, including a stillbirth or pup that dies. A cow may be a breeder one year and a non-breeder the next. Observations of birth definitively placed a cow into the breeder category. Many cows had seasonal sets of observations that were similar to those of the definite breeders and unambiguously identified them as breeders but some sets of observations were ambiguous. It was assumed that parameters could be estimated to determine the proportions in each category. In practice this proved not to be the case, even when the only mixture included in the model was a breeder – non-breeder mixture. It was therefore necessary to make somewhat stronger assumptions.

Here we describe an alternative, criterion-based model in which it is assumed that all breeding animals are seen and are positively identified as breeders during a season. The extensive experience of observers on the Enderby Island breeding colony is generally consistent with this assumption. The probability of observing non-breeders is estimated, and differs for 1-year-olds, 2-year-olds and cows of age 3 years or older. This allows the estimation of the pupping rate and mortality functions, the latter function including both mortality and tag loss. Tag loss was not separately estimated.

Estimation by maximum likelihood involves somewhat simpler formulae than for the previous mixture model. The formulae are developed that express the probabilities of making the observations that were actually made, conditional on the parameters. An important feature of the model is the treatment of animals whose last sighting was earlier than the 2007 season. For these animals it is uncertain whether they have died or whether they are still alive, have not pupped and have not been observed since their last resighting. The likelihood in these instances is the sum of mutually exclusive alternative scenarios. Our estimates gave plausible estimates of pupping rate and mortality (including tag loss).

Estimation by the modelling is a process in which the steps: hypothesis testing, diagnosis and hypothesis reformulation, are repeated until satisfactory diagnostics are obtained. The mixture model that was initially proposed failed to produce satisfactory diagnostics and was therefore rejected and replaced by a criterion-based model. This produced generally satisfactory diagnostics but small improvements were achieved by making minor enhancements to the pupping rate and mortality functions described in Gilbert (2008). Also a first-year mortality parameter was added for each tagged cohort to remove systematic deviations between the observed and predicted numbers. Our final diagnostics were satisfactory.

2. Model

To estimate pupping rate, we have developed a statistical model to explain the annual behavioural observation frequencies of the tagged sea lion cows. The model is governed by a set of parameters, which are estimated by maximum likelihood.

It is desirable to reduce the number of estimable parameters by expressing relationships in functional forms dependent on a few parameters. Over-parameterisation leads to estimates that lack robustness and tend to reflect random variations in the data rather than underlying relationships. The preliminary estimate of pupping rate in Gilbert (2007) has implausible spikes at ages 9, 12, 16 and 19 years. Here we express both mortality and pupping rate as smooth functions of age. The functions are parameterised so that the parameters are meaningful; for example, β_1 is the maximum pupping rate and it occurs for cows aged between β_2 and $\beta_2 + \beta_5$ years.

Because adequate behavioural observations commenced in 2000, the only data used prior to that season are the seasons of tagging. For the present purpose the breeding season behavioural observations are categorised into "Birth", "Nurse", "With pup" and "Unknown". This last includes any behaviour that gives no information as to whether the cow has pupped. These observations give a vector, the first element of which is binary (0 or 1) and the other elements are counts. This data vector may be all zeros for a given season if the cow is dead or if it is alive but not sighted. If a cow is sighted in a subsequent season the first alternative can be ruled out of the analysis. The time series of data for each cow must therefore be considered together, rather than as independent annual observations.

The resighting effort was similar amongst seasons because the field trips all ran from early December (pre-birth) to mid-February and were carried out according to a fixed routine. Gilbert (2008) described an estimable parameter $\underset{\sim}{\theta}$ to account for variability due to differences in effective resighting effort. This did not significantly explain variance and was not included in the final model.

The behavioural observations come from a mixture of breeders and non-breeders. The criterion-based model separates the cows into four groups each season: those that have a pup, all of which are assumed to be observed; those that do not have a pup and are observed; those that do not have a pup but are not observed; and those that are dead. These last two groups are not distinguishable in seasons after the last observation of an animal. The model must estimate parameters that predict and aggregate the numbers in these groups.

3. Data

2274 female pups were tagged between 1987 and 2003 but only 1374 of these were observed in the 2000 – 2007 seasons (Table 1). Most of the 1987 and 1990 cohorts had died, lost their tags or ceased breeding by 2000. Observations of the 2000 – 2003 cohorts include the tagging event to which the model is not fitted. We now describe the behavioural observations.

Let n, a, i, and y denote tag number, age, behaviour category and season. The data will be arranged in the following format:

1. The number of tagged cows, N

2. An $N \times 3$ matrix, each row containing: tag number n, tag season y_T and the last resight season, y_L. In season y the age of a particular cow would be $y - y_T$. y_L is required because in the seasons following y_L the possibilities of both death and survival without sighting must be included in the likelihood formulae. For cows where there have been no observations after 1999, y_L is null.

3. An array of N matrices each with four rows and 8 columns. There is one matrix for each tagged cow and a column for each of the seasons, 2000 to 2007. The rows contain the number of observations of each behaviour grouping: "Birth", "Nurse", "With pup" and "Unknown". The "Birth" behaviour grouping refers to the observations: birth, dead pup, pregnant and stillbirth. Mostly these behaviours are made once per season and indicate definite breeding. If at least one such behaviour is observed, the row will contain a one and otherwise a zero. The other groupings contain counts observations. The "Nurse" grouping refers only to the behaviour nursing a pup. The "With pup" grouping refers to the behaviours: calling a pup and with a pup. The "Unknown" grouping refers to all the other behaviours, which do not indicate breeding but do not necessarily exclude it. In reality the observation of nursing a yearling does exclude breeding but the frequency of this behaviour is so low that this fact has been ignored. For a given tag number in season y, the data in the corresponding row of the array is denoted by $\underline{x}_y = (x_{y1}, x_{y2}, x_{y3}, x_{y4})$.

The mixture model described by Gilbert (2008) failed to produce meaningful estimates so we have used a criterion-based approach. A criterion based on the observations is taken to indicate whether a cow has pupped in a given season. The experience of the field teams is that because of the necessity of a cow to return regularly to her pup, in a season that a cows breeds she will always be observed. The question is, will the observations of a breeding cow always identify her as such? Figure 1 shows the distribution of observation frequencies for cows known to have pupped (including those that have lost their pup) and the contrasting frequencies for juveniles, too young to breed. The great majority of known breeders have at least two probable-breeder observations ("Nurse" or "With pup"). 91% of known breeders had at least two probable-breeder observations. They also have at least 6 observations in total for the season. 98% of known breeders were seen at least 6 times. Even cows that had lost their pup were observed frequently. This suggests that adults with one or no probable-breeder observations are very largely, but not solely non-breeders. We can conclude that breeders are seen frequently and that animals with two probable-breeder observations are almost all breeders. Non-breeders are usually seen infrequently. 72% of observed juveniles were seen fewer than 6 times. 65% of adult cows observed with one or no probable-breeder observations were seen fewer than 6 times. This would be consistent with almost all these animals being non-breeders. Our criterion-based model will be based on the information in Figure 1.

4. Estimable parameters

The estimable parameters which determine the likelihoods of the behavioural observations are given here.

We define pupping rate as a smooth, domed function of age with a plateau, which gives the probability that a cow will bear a pup in a given season. The function is determined by a vector of parameters, $\underset{\sim}{\beta}$, where β_1 is the maximum value of the function, the plateau over which the maximum occurs lies between ages β_2 and $\beta_2 + \beta_5$ years, and β_3 and β_4 are the ages at which the left and right-hand limbs of the function fall to half the maximum. All the elements of $\underset{\sim}{\beta}$ may take non-integer values,

we define mortality as a smooth, U-shaped function of age determined by a vector of parameters, $\underset{\sim}{\mu}$ that gives the probability that a cow will die or lose its tags in the season after achieving a given age, where μ_1 is the minimum function value (mortality rate), μ_2 is the age in years at which the minimum is achieved, μ_3 is the function value at age 0 years, μ_4 is the function value at age 20 years, and μ_5 determines the curvature of the function,

let $\underset{\sim}{\chi}$ be a vector that determines visibility, where χ_1 is the probability that a surviving 1-year-old cow will be resighted in a season, χ_2 is the probability that a surviving 2-year-old cow will be resighted in a season, and χ_3 is the probability that a surviving non-breeding cow 3 years old or older will be resighted in a season,

let $\underset{\sim}{M}$ be a vector that determines the mortality (and tag loss) of each tagged cohort in its first season. Hence, for example, $1 - M_{1987}$ is the proportion of the tagged female pups that survive to age 1 year.

5. Pupping rate, natural mortality and visibility functions

The pupping rate function expresses the probability that a cow of a given age will bear a pup in a given season, and therefore implicitly includes maturation of cows. We therefore expect it to have a rising left hand limb, to reach a maximum between 8 and 14 years and then to decline gradually with age. This is the empirical shape found by Chilvers (2006) and Gilbert (2007). The function we define depends on parameter vector $\underset{\sim}{\beta}$ and gives the mean rate for the population,

$$b(a\,|\,\underset{\sim}{\beta}) = \begin{cases} 0 & a \le 3 \\ \beta_1 2^{-\left(\frac{a-\beta_2}{\beta_3-\beta_2}\right)^2} & a \le \beta_2 \\ \beta_1 & \beta_2 < a \le \beta_2 + \beta_5 \\ \beta_1 2^{-\left(\frac{a-\beta_2-\beta_5}{\beta_4-\beta_2-\beta_5}\right)^2} & a > \beta_2 + \beta_5 \end{cases}$$

The function has a maximum value of β_1 for a between β_2 and $\beta_2 + \beta_5$ and takes the value $0.5\beta_1$ at $a = \beta_3$ on the left and at $a = \beta_4$ on the right. In an alternative model of pupping rate $\underset{\sim}{\beta}$ was simply an arbitrary vector giving the pupping rate for each age.

Estimating $\underset{\sim}{\beta}$ gives the mean pupping rate for the population.

We require a mortality rate for each age class to determine how many cows were still alive in each season after they were last resighted. We will define mortality at age a as the probability that a cow of age a on 1 January dies between the preceding 1 December and the following 30 November. Mortality is expected to follow an asymmetric U-shape, typical of natural mortality in vertebrates, with high mortality for the youngest animals, declining steeply to a minimum and then increasing gradually (Begon et al. 2006, Goodman 1981). Mortality here includes incidental bycatches in fisheries (largely squid trawling) but also tag loss and loss of tag readability. A function for tag loss is included to give the overall function the right shape but the corresponding parameter is not expected to be well estimated. Tag loss could be estimated more satisfactorily using the numbers of animals that have retained one and two tags but tag loss was outside the scope of this project and its precise estimation was not essential to estimating pupping rate. The full mortality function depends on parameter vector $\underset{\sim}{\mu}$. The pure mortality part,

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

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 $a = 20$. We assume that tagged animals have two tags (not strictly true as some cows had only a single tag) and the probability of losing a tag is μ_5 each year and independent of the other tag. Then the proportion of survivors from a tagged cohort that has retained at least one tag at age a can be obtained from the binomial distribution,

$$
\left(1-\mu_5\right)^{2a} + 2a\mu_5\left(1-\mu_5\right)^{2a-1}
$$

Hence the mortality rate (including tag loss) from age a to $a+1$,

$$
\mathrm{m}(a) = 1 - \frac{\displaystyle\prod_{i=0}^{a}\left(1-\mathrm{m}'(i)\right) \times \left[\left(1-\mu_5\right)^{2a} + 2a\mu_5\left(1-\mu_5\right)^{2a-1} \right]}{\displaystyle\prod_{i=0}^{a-1}\left(1-\mathrm{m}'(i)\right) \times \left[\left(1-\mu_5\right)^{2a} + 2a\mu_5\left(1-\mu_5\right)^{2a-1} \right]}
$$

$$
= 1 - \left(1-\mathrm{m}'(a)\right)\left(1-\mu_5\right)^2 \frac{1+(2a+1)\mu_5}{1+(2a-1)\mu_5}
$$

Estimating $\underset{\sim}{\mu}$ gives the mean mortality rate for the population.

We also require a visibility function that expresses the probability that a non-breeding female of a given age will be observed at least once in a given season. The function we define depends on the parameter vector $\underset{\sim}{\chi}$,

$$
\mathrm{v}(a \mid \underset{\sim}{\chi}) = \begin{cases} \chi_1 & a = 1 \\ \chi_2 & a = 2 \\ \chi_3 & a = 3 \\ \chi_4 & a \ge 4 \end{cases}
$$

6. Likelihoods

The method of maximum likelihood obtains parameter estimates by finding the set of values that make the whole set of observations the most likely. To achieve this, the likelihood function must be expressed as an algebraic function of the parameters. It is built up by multiplying together the probabilities of the independent subsets of observations. The time series of observations of each cow make up each subset, dependence amongst seasons coming from the fact that the likelihoods of zero observations in a season depend on whether the any subsequent observations were made.

The mixture model described by Gilbert (2008) failed to produce meaningful estimates so we have used a criterion-based model instead. In this approach a criterion based on the observations is taken to categorically show whether a cow has pupped in a given season and all such cows are assumed to have been observed. The probabilities of observing non-breeders involve parameters that depend on age and that must be estimated. Our base case criterion was that a cow was a breeder if and only if either a "Birth" or at least two probable-breeder observations were made. This is expressed as a conditional probability function, dependent on χ,

$$f(\underset{\sim}{x}_y \mid \text{Breeder}, \underset{\sim}{\chi}) = \begin{cases} 1 & \text{if } x_{y1} = 1 \text{ or } x_{y2} + x_{y3} \geq 2 \\ 0 & \text{otherwise} \end{cases}$$

$$f(\underset{\sim}{x}_y \mid \text{Non-breeder}, \underset{\sim}{\chi}) = \begin{cases} 0 & \text{if } x_{y1} = 1 \text{ or } x_{y2} + x_{y3} \geq 2 \\ 1 - v\left(y - y_{\mathrm{T}} \mid \underset{\sim}{\chi}\right) & \text{if } \sum_{i=1}^{4} x_{yi} = 0 \\ v\left(y - y_{\mathrm{T}} \mid \underset{\sim}{\chi}\right) & \text{otherwise} \end{cases}$$

We fitted the model with two alternative criteria. The first included slightly more cows and took account of the evidence that frequent observation is indicative of breeding,

$$f(\underset{\sim}{x}_y \mid \text{B}, \underset{\sim}{\chi}) = \begin{cases} 1 & \text{if } x_{y1} = 1 \text{ or } x_{y2} + x_{y3} \geq 2 \text{ or} \\ & \left(x_{y2} + x_{y3} = 1 \text{ and } \sum_{i=1}^{4} x_{yi} \geq 5\right) \\ 0 & \text{otherwise} \end{cases}$$

$$f(\underset{\sim}{x}_y \mid \text{N}, \underset{\sim}{\chi}) = \begin{cases} 0 & \text{if } x_{y1} = 1 \text{ or } x_{y2} + x_{y3} \geq 2 \text{ or} \\ & \left(x_{y2} + x_{y3} = 1 \text{ and } \sum_{i=1}^{4} x_{yi} \geq 5\right) \\ 1 - v\left(y - y_{\mathrm{T}} \mid \underset{\sim}{\chi}\right) & \text{if } \sum_{i=1}^{4} x_{yi} = 0 \\ v\left(y - y_{\mathrm{T}} \mid \underset{\sim}{\chi}\right) & \text{otherwise} \end{cases}$$

where the conditions are abbreviated to "B" and "N" for convenience. The second included slightly fewer than the base case and assumed that "Nurse" observations were more strongly indicative of breeding than "With pup" observations,

$$f(\underline{x}_y \mid B, \underline{\chi}) = \begin{cases} 1 & \text{if } x_{y1} = 1 \text{ or } x_{y2} + x_{y3} \geq 2 \text{ or} \\ & \left(x_{y2} + x_{y3} = 1 \text{ and } \sum_{i=1}^{4} x_{yi} \geq 5 \right) \\ 0 & \text{otherwise} \end{cases}$$

$$f(\underline{x}_y \mid N, \underline{\chi}) = \begin{cases} 0 & \text{if } x_{y1} = 1 \text{ or } x_{y2} + x_{y3} \geq 2 \text{ or} \\ & \left(x_{y2} + x_{y3} = 1 \text{ and } \sum_{i=1}^{4} x_{yi} \geq 5 \right) \\ 1 - v\left(y - y_T \mid \underline{\chi} \right) & \text{if } \sum_{i=1}^{4} x_{yi} = 0 \\ v\left(y - y_T \mid \underline{\chi} \right) & \text{otherwise} \end{cases}$$

The total likelihood can now be obtained using the mortality and pupping rate functions as well as the visibility parameters. It is obtained by multiplying together the likelihoods from each season's observations. For a cow that was alive in 2000 but for which $y_T < 2000$, it is necessary to calculate the likelihood that it has survived to season 1999 using the mortality function,

$$L_{1999} = \prod_{y=y_T+1}^{1999} \left[1\text{-}m(y\text{ - }y_T\text{-}1 \mid \underline{\mu}) \right]$$

Our behavioural observations are only from the 2000 season onwards. The likelihood of observations up to season y_L, if $y_L \geq 2000$, must include the probabilities of survival. In what follows we will, for convenience, not include the parameters in the expressions for the functions, m(), b() and f(),

$$L_{y_L} = \prod_{y_1=y_T+1}^{1999} \left[1\text{-}m(y_1 \text{ - } y_T \text{-}1 \mid) \right] \times$$

$$\prod_{y_2=y_{2000}}^{y_L} \left[\left(1\text{-}m(y_2 \text{ - } y_T \text{-}1 \mid \underline{\mu}) \right) \left\{ b(y_2 - y_T) f(\underline{x}_{y_2} \mid B) + \left(1 - b(y_2 - y_T) \right) f(\underline{x}_{y_2} \mid N) \right\} \right]$$

The effect of the probability function is that only one term inside the braces is non-zero because only one of $f(\underline{x}_{y_2} \mid B)$ and $f(\underline{x}_{y_2} \mid N)$ can be non-zero. The total likelihood, i.e. of observations up to 2007,

$$L_{2007} = \prod_{y_1=y_T+1}^{1999} \left[1\text{-}m(y_1 \text{ - } y_T \text{-}1) \right] \times$$

$$\prod_{y_2=2000}^{y_L} \left[\left(1\text{-}m(y_2 \text{ - } y_T \text{-}1) \right) \left\{ b(y_2 - y_T) f(\underline{x}_{y_2} \mid B) + \left(1 - b(y_2 - y_T) \right) f(\underline{x}_{y_2} \mid N) \right\} \right] \times$$

$$\sum_{y_3=y_L+1}^{2007} \left\{ \prod_{y_4=y_L+1}^{y_3} \left[\left(1\text{-}m(y_4 \text{ - } y_T \text{-}1) \right) \left\{ \left(1 - b(y_4 - y_T) \right) f(\underline{0}_{y_4} \mid N) \right\} \right] \times m(y_3 \text{ - } y_T) \right\}$$

where $\underline{0}_y$ denotes the null observation vector of zeros in season y. Because all breeders are assumed to be observed there are no breeder terms in the braces. The first factor is the probability of survival to 1998, the second is that of the observations from 2000 to y_L and the last, involving the summation, includes the probabilities that the cow dies in each season from $y_L + 1$ to 2007 but is not observed in the seasons between y_L and the season it dies. The last factor is omitted if $y_L = 2007$.

If $y_L \ngeq 2000$, i.e. there are no behavioural observations 2000 - 2007, it is necessary to sum all the alternative seasons in which death may have occurred, i.e. y_T to 2007,

$$L_{2007} = m(0) + \sum_{y_1 = y_T + 1}^{1999} \left\{ \prod_{y_2 = y_T + 1}^{y_1} \left[1 - m(y_2 - y_T - 1) \right] \times m(y_1 - y_T) \right\} +$$

$$\prod_{y_2 = y_T + 1}^{1999} \left[1 - m(y_2 - y_T - 1) \right] \times$$

$$\sum_{y_3 = 2000}^{2007} \left\{ \prod_{y_4 = 2000}^{y_3} \left[(1 - m(y_4 - y_T - 1)) \left\{ (1 - b(y_4 - y_T)) f(\underline{0}_{y_4} \mid N) \right\} \right] \times m(y_3 - y_T) \right\}$$

If $y_T \geq 2000$ and $y_L \geq 2000$,

$$L_{2007} = \prod_{y_1 = y_T + 1}^{y_L} \left[(1 - m(y_1 - y_T - 1)) \left\{ b(y_1 - y_T) f(\underline{x}_{y_1} \mid B) + (1 - b(y_1 - y_T)) f(\underline{x}_{y_1} \mid N) \right\} \right] \times$$

$$\sum_{y_2 = y_L + 1}^{2007} \left\{ \prod_{y_3 = y_L + 1}^{y_2} \left[(1 - m(y_3 - y_T - 1)) \left\{ (1 - b(y_3 - y_T)) f(\underline{0}_{y_3} \mid N) \right\} \right] \times m(y_2 - y_T) \right\}$$

Where observations of the pup, which provide no relevant information, are not included. The expression for L_{2007} when $y_T \ngeq 2000$ is obtained similarly.

Estimation involves summing the negative logarithms of the likelihoods of the observations over tag numbers, n,

$$\Lambda = -\sum_{n=1}^{N} \ln \left(L_{n, 2007} \right)$$

and minimising Λ with respect to the estimable parameters. Estimation was carried out by coding the above functions using AD Model Builder© (Otter Research Ltd, Nanaimo, Canada) and minimising Λ. Starting values for the parameters were based on Gilbert (2007).

7. Results

Minimisation of the negative log-likelihood presented no problems and was fairly fast. The base case parameter estimates (Table 2) are plausible (negative log-likelihood 5751.50) and give satisfactory diagnostics. These differ little from the diagnostics when the model was fitted under the alternative criteria for identifying a breeder. We will therefore only present diagnostics for the base case. The discrete nature of the data (animals are observed as breeders, as non-breeders or not at all) means that diagnostics based on individuals are not informative. Instead we obtained diagnostics for each tagged cohort. The estimated parameters predict the numbers of breeders and non-breeders that will be observed, and the numbers that remain alive each season. These fit the data satisfactorily (Figure 2) but of course the validity of the interpretation of the observations depends on the validity of the breeder observation criteria. There is a small expected divergence between the fitted numbers that remain alive and the numbers known to be alive from the data, because the latter are necessarily underestimates, especially for the most recent few seasons of observations. Residuals for the numbers of breeders and observed non-breeders are generally satisfactory (Figures 3 – 5).

Our base case estimate of pupping rate as a function of age is a domed function with a maximum of 0.45 y^{-1} and declining left and right limbs (Figure 6). A flat plateau was added to the function that was originally proposed and the function was truncated so

that 3-year-olds had zero probability of breeding. These modifications significantly improved the fit (reduced the negative log-likelihood by 13.3).

The use of the alternative criteria for determining whether a cow had bred and of the different pupping rate function types did not change the effective pupping rate that was estimated a great deal. The criterion that included slightly more cows raised the maximum rate to 0.47 y^{-1} and that which included slightly fewer reduced it to 0.41 y^{-1} (Figure 6). The left and right limbs both declined to levels very similar to those of the base case. When the smooth, base case function was replaced by an arbitrary function (Figure 7) with a parameter for each age, the negative log-likelihood was reduced by 10.55 for the addition of 12 parameters. The Akaike Information Criterion would therefore suggest that the more parsimonious model should be preferred. The arbitrary function has a maximum at age 12 years, which is just to the right of the smooth function's plateau, and an unusually high value at age 19 years. These are more likely to be due to sampling variability than to represent true population means. A direct estimate of the pupping rate function can be obtained by using the base case criterion to get the number of breeders and using the number at age known to be alive each season as the denominator. This gives a function similar to the arbitrary function (Figure 7) except that it is systematically higher and tends to diverge upwards as age increases. This is because the direct approach does not estimate or allow for the animals that remain alive for some seasons after their last sighting. As fertility declines with age cows become more likely to be unobserved non-breeders that die some years after their last sighting. The base case estimate of pupping rate as a function of age avoids this problem and appears to be a good estimate the population mean rate.

An attempt to treat the cows as a mixture of high- and low-fecundity animals failed. Two extra parameters were required, one giving the proportion of high-fecundity animals and the other the multiplier for the maximum pupping rate. The negative log-likelihood was minimised with all animals placed in a single category, i.e. the model collapsed to the simpler base case and the two extra parameters gave no reduction in the negative log-likelihood. Gilbert (2008) showed that at all ages cows were more likely to breed in a season if they had borne a pup the previous season. It therefore appears that a simple mixture of high- and low-fecundity animals is not a good explanation of the data.

Early model fits showed systematic under- and over-estimation of individual cohorts. The simplest explanation for this was that there was a variation in first year mortality (including tag loss) amongst cohorts. Thus, the first-year mortality parameter vector $\underset{\sim}{M}$ was added to the model. This added 11 parameters and reduced the negative log-likelihood by 19.70 and therefore significantly improved the fit. Estimates ranged from 0.36 (1992 cohort) to 0.83 (1987 cohort). This range is quite plausible. The values do not correlate particularly well with the cohort pup mortalities (first two months) observed by Chilvers (2006) but are always higher than hers and are therefore not inconsistent. They suggest that considerable but variable mortality occurs after the pups leave the colony. The fact that no cohort was observed throughout its life-span means that there could be some confounding between these parameters and the mortality function parameters. When $\underset{\sim}{M}$ is not included in the model the mortality at age 20 years rises from 0.502 to 0.603 y^{-1}. The low numbers of observations of the 1987 and 1990 cohorts, seen only at relatively old ages, are fitted slightly better by high, first-year mortalities than by a high, old-age mortalities, but the data are insufficient to make a strong inference either way. The high value for M_{1987} may also be partly due to a higher rate of tag loss or loss of readability for this cohort (the tags used may not have been as good as those used later). Notwithstanding these

shortcomings the estimated first-year mortalities generally represent real differences amongst cohorts and for the more recent years these are reasonably well estimated. Fortunately, the pupping rate function is affected very little by whether or not $\underset{\sim}{M}$ is included in the model.

Breeders from the 1998 cohort are systematically over-estimated (Figures 2 & 3). Their lack of fit is likely to be a consequence of the epizootic that severely affected the 1998 pups (Baker 1999). We therefore conclude that the female pups that survived to reach maturity suffered impaired fertility. This would result in fewer breeders and more non-breeders being observed than the model predicted. The numbers of 1998 observed non-breeders are erratic but not systematically under- or over-estimated (Figures 2 & 4). This cohort may therefore have also suffered slightly above average annual mortality. The model could have been modified to include a "1998 cohort fertility" parameter which would have slightly improved the fit, but this was not done. The model supports the view that the 1998 cohort has suffered long-term impaired fertility as a result of the epizootic and possibly also a slightly lower annual survival rate.

The estimated first year mortality for the 1998 cohort, M_{1998}, is high (0.56), but not exceptionally so. Chilvers et al. (2007) estimated a mortality of 0.42 in the first two months alone and observations at that time suggested that mortalities would continue after the 1998 field trip ended. Our estimated M_{1998} is not inconsistent with Chilvers' figure although a higher estimate might have been expected.

The breeder number residuals do not show any trend over time (Figure 5). It appears that 2004 was an above average year for pupping. The large negative residual for the impaired 1998 cohort can be discounted, leaving the model under-estimating the number of breeders in 2004 in six of the seven remaining cohorts. Again, the model could have been modified to include a "2004 season fertility" parameter but this was not done. The seasons do not appear to be sufficiently different that failure to estimate individual season effects would have altered the estimated pupping rate function.

The estimated mortality rate function includes tag loss, which includes loss of readability. Tag loss varies between cohorts and individuals because different tags were used, some animals received only one tag, some animals were branded and some had microchip transponders implanted. The loss rates and the resightabilities therefore varied. These differences have not been taken into account in this analysis so that the estimated mortality rate function is an average across all the tag variations (and across cohorts that may suffer different mortality rates). The estimated function (Figure 8) has a minimum that occurs perhaps younger than expected and is surprisingly low (3.5% for 2-year-olds).

The tag loss parameter, μ_5, was added to the originally-proposed mortality function to improve the fit by adjusting the shape of the function in a manner consistent with the effects of tag loss. The single tag loss rate (4.0% per year) is unlikely to be a good estimate because it is not based on observations of animals that have lost one of two tags. Although the improvement was not significant (negative log-likelihood declined by 0.34) μ_5 was retained in the model as it produced an appropriately-shaped overall mortality function but minimal change in the pupping rate function. This lack of sensitivity encourages us that provided the criterion for determining whether a cow has bred is valid our estimated pupping rate function is robust to alternative assumptions regarding mortality.

8. Discussion

We have estimated a pupping rate function of age for female sea lions that properly accounts for non-breeding animals that are alive but unobserved each season. It is a smooth, domed function with a flat plateau and is determined by five estimated parameters. Estimation is based on the assumption that each season all cows seen are identified as breeders or non-breeders and that all breeders are seen. Our data contains females from Enderby Island; the cohorts 1987, 1990–1993, 1998, 1999, 2000–2003; and observation for the seasons 2000–2007. There are unusual cohorts (1998 is less fertile) and unusual seasons (2004 was more productive) and our estimate is a mean that includes these variations. There is no evidence of a trend in fertility between 2000 and 2007. It is reasonable to assume that the Enderby Island females are representative of all New Zealand sea lions and that our estimate of pupping rate is generally applicable.

The pupping rate function is one of the key pieces of information required to assess the resilience of the New Zealand sea lion population to withstand unusual or human-induced mortalities. The maximum rate (0.45 y^{-1}) is a good deal lower than values estimated by Chilvers (2006) and Breen & Kim (2006) whose analyses give values between 0.6 and 0.8 y^{-1}. The steepness in the decline of the right limb of the function is also greater than that implied by these authors. Our results show that New Zealand sea lions are considerably less productive than had been previously thought and would imply a lower maximum population growth rate, λ. When Breen & Kim (2006) estimated λ they applied a prior that ensured it did not fall too low. Their estimate of 3.3% (MPD) was based on a pupping rate function that reached 50% of its maximum at a similar age to ours but not only reached a substantially higher maximum but also declined more slowly with age. One of their datasets that probably biased their pupping rate upwards contained breeder observations of cows branded as adults. Gilbert (2007, 2008) showed that a pupping rate estimated from these data would be likely too high because high-fecundity females would be over-represented in the sample. Our result suggests that λ is likely to be less than that estimated by Breen & Kim (2006) and that the New Zealand sea lion population is likely to be less resilient than has been supposed.

If a population assessment were carried out using our estimate of pupping rate it would be important that other model parameters were estimated consistently with it. A probable consequence of a lower pupping rate would be a higher population size. Under a low pupping rate the number of mature adults per pup would be higher. The consequence of this is that although the population would be less resilient it would also be larger, so that the mortality rate incurred by a particular number of fishery by-catch deaths may be lower than previously estimated. We do not wish to speculate what the net effect of a lower pupping rate would be but stress the importance of estimating all population model parameters in a consistent manner.

The systematically lower fertility of the 1998 cohort appears to be a consequence of the epizootic that severely affected this cohort as pups. However the disease organism that is thought to have caused the mortalities, *Campylobacter* (Baker 1999) is not known to cause infertility.

Although the maximum of the estimated pupping rate function is near 50%, this is an average over the female population and does not mean that females can only breed every second year. The population of cows appears to be quite heterogeneous, with some cows breeding almost every year from 6 to 15 years of age and others breeding

only occasionally. An attempt to treat the population as a mixture of two types and to estimate the proportions in each failed. A more sophisticated approach using a random effects model that allows a cow's fecundity to be drawn from a distribution of fecundities may work better. This would provide a fuller description of the process of pupping in the population but would be unlikely to change the estimate of the (mean) pupping rate function.

Our criteria for identifying a breeder depend on being able to make an inference from the known breeders. Most breeders were seen frequently and had many probable-breeder observations (Figure 1). However we can also infer that a small proportion of breeders will not be seen frequently or will not have many probable-breeder observations. If we could positively identify some mature cows as non-breeders we could determine their distribution of observation frequencies and combined with that for identified breeders estimate the proportions of breeders in the unknown animals. Unfortunately mature animals cannot be positively identified as non-breeders. All 1- to 3-year-olds are non-breeders because they are immature, but their behaviour differs from that of mature animals. They tend to keep clear of the breeding areas until the dominant males have departed. We estimate that the probability of observing a 1- or 2-year-old at least once in a season is about half that of a non-breeding 4+-year-old cow. The sighting frequencies of juveniles that *are* seen are likely to be lower than those of mature non-breeders. Therefore we cannot determine very well what the distribution of observations of non-breeders is.

We have to make some assumptions that allow us to separate breeders and non-breeders. The criterion-based approach we have taken positively categorises each season's observations for a cow as a "breeder" or "non-breeder". A small proportion of animals will be mis-classified. A few cows will have two or three probable-breeder observations will not be breeders whereas a few seen frequently but with one or no probable-breeder observations will be breeders. We have assumed that these misclassifications will balance each other and the size of any overall effect on the pupping rate estimate will be small.

A mixture model to determine the proportions of breeders and non-breeders was described by Gilbert (2008). Our attempt at applying it failed, perhaps because of the lack of positively identified non-breeders. Mixture models work best when the mixed distributions do not overlap much. It is possible that a better description of the parts of the mixture might succeed. We suggest that further work should be carried out to try this approach. Ideally the method would work by extrapolating from the main body of a bivariate distribution of breeders' observations, so that the proportions in its tails that overlap with the body of the non-breeders' distribution could be estimated, and vice versa. The breeders' distribution should be able to be well estimated because we have animals that are categorically identified as breeders. The mixture model approach makes the assumption that proportions of animals in the relevant tails of the distributions can be well estimated by the fits to the bodies of the breeder and non-breeder distributions. Such an assumption would be somewhat less arbitrary than criterion-based assumptions. Further work should attempt to fit a mixture model to confirm that the method we have described to estimate pupping rate is not unduly biased.

Although further work could be carried out to refine our pupping rate function estimate, we believe the relatively low rates it predicts even at its maximum are well founded and that the function is a sound basis for assessing the New Zealand sea lion population.

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Table 1. Female sea lion tagged as pups.

Season of tagging	1987	1990	1991	1992	1993	1998	1999	2000	2001	2002	2003
Total tagged	99	154	192	233	195	261	218	248	285	174	215
Observed 2000 – 2007	5	31	62	88	78	66	95	248	285	174	215

Table 2. Base case parameter estimates.

| Process	Parameter	Parameter name	Estimated value
Pupping rate	Maximum (plateau) rate (y^{-1})	β_1	0.45
	Age maximum reached (y)	β_2	9.65
	Age at half maximum (left limb) (y)	β_3	6.35
	Age at half maximum (right limb) (y)	β_4	16.63
	Width of plateau (y)	β_5	1.55
Mortality rate	Minimum rate (y^{-1})	μ_1	0.022†
	Age at minimum (y)	μ_2	1.96
	Rate at age 0 years (y^{-1})	μ_3	0.73
	Rate at age 20 years (y^{-1})	μ_4	0.48
	Individual tag loss rate (y^{-1})	μ_5	0.040
Visibility	Probability of observing a 1-year-old	χ_1	0.23
	Probability of observing a 2-year-old	χ_2	0.25
	Probability of observing a 3-year-old	χ_3	0.49
	Probability of observing a non-breeder age 4+ years	χ_4	0.54
First year mortality	First year mortality of 1987 cohort	M_{1987}	0.83
	First year mortality of 1990 cohort	M_{1990}	0.58
	First year mortality of 1991 cohort	M_{1991}	0.40
	First year mortality of 1992 cohort	M_{1992}	0.36
	First year mortality of 1993 cohort	M_{1993}	0.38
	First year mortality of 1998 cohort	M_{1998}	0.56
	First year mortality of 1999 cohort	M_{1999}	0.53
	First year mortality of 2000 cohort	M_{2000}	0.63
	First year mortality of 2001 cohort	M_{2001}	0.53
	First year mortality of 2002 cohort	M_{2002}	0.52
	First year mortality of 2003 cohort	M_{2003}	0.49

† Applying the tag loss rate, the full mortality function has a minimum rate of 0.035 y^{-1} at age 2 years and reaches 0.502 y^{-1} at age 20 years
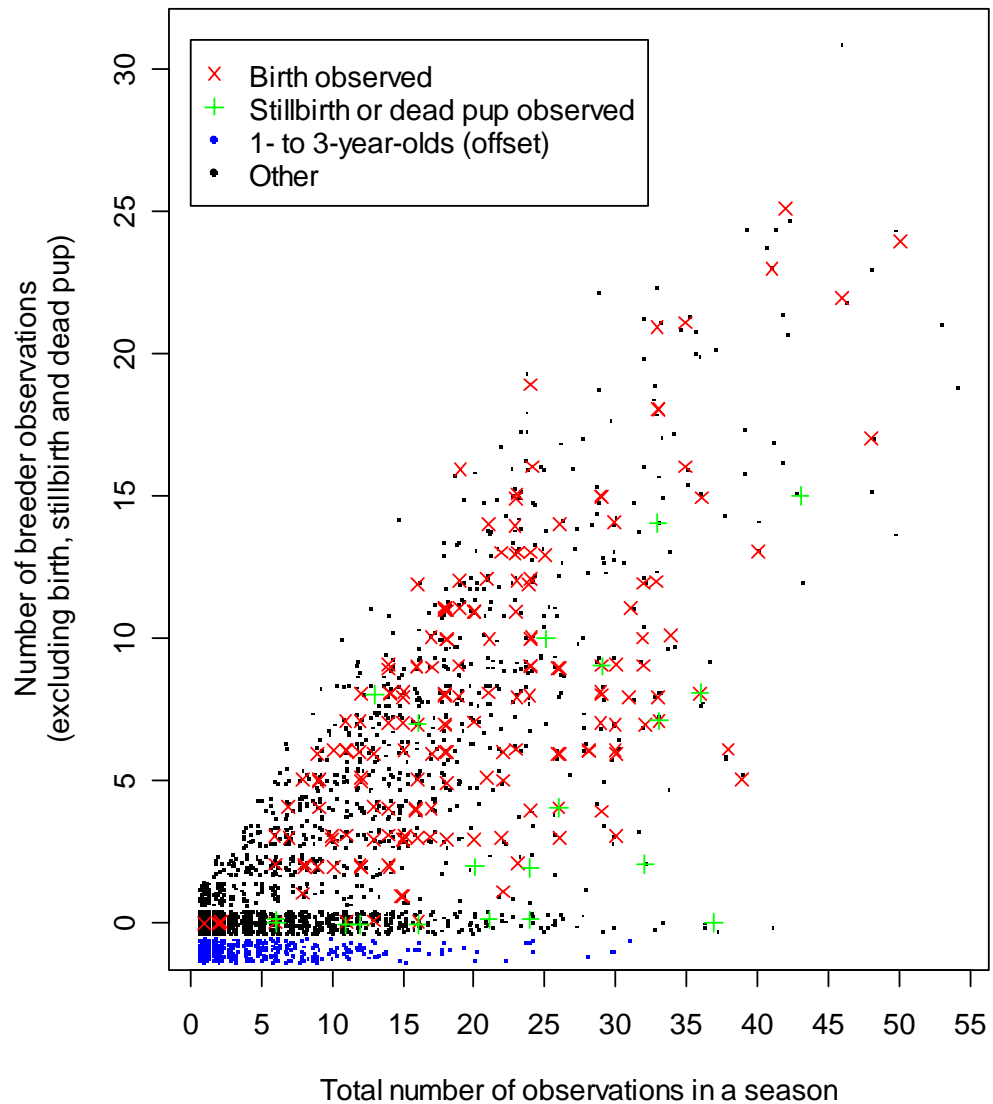
Figure 1. Seasonal observation frequencies of each tagged female excluding observations as pups. Probable-breeder observations (y-axis) are those that suggest breeding (nursing a pup, with a pup or calling). Certain breeders where a birth is observed are plotted ✕ (red) and where a stillbirth or dead pup is observed ✚ (green). Juveniles (1- to 3-year-olds) are plotted • (blue) and offset one unit below zero on the y-axis. All other observations, which may be breeders or non-breeders are plotted •. Plotted symbols are jittered.
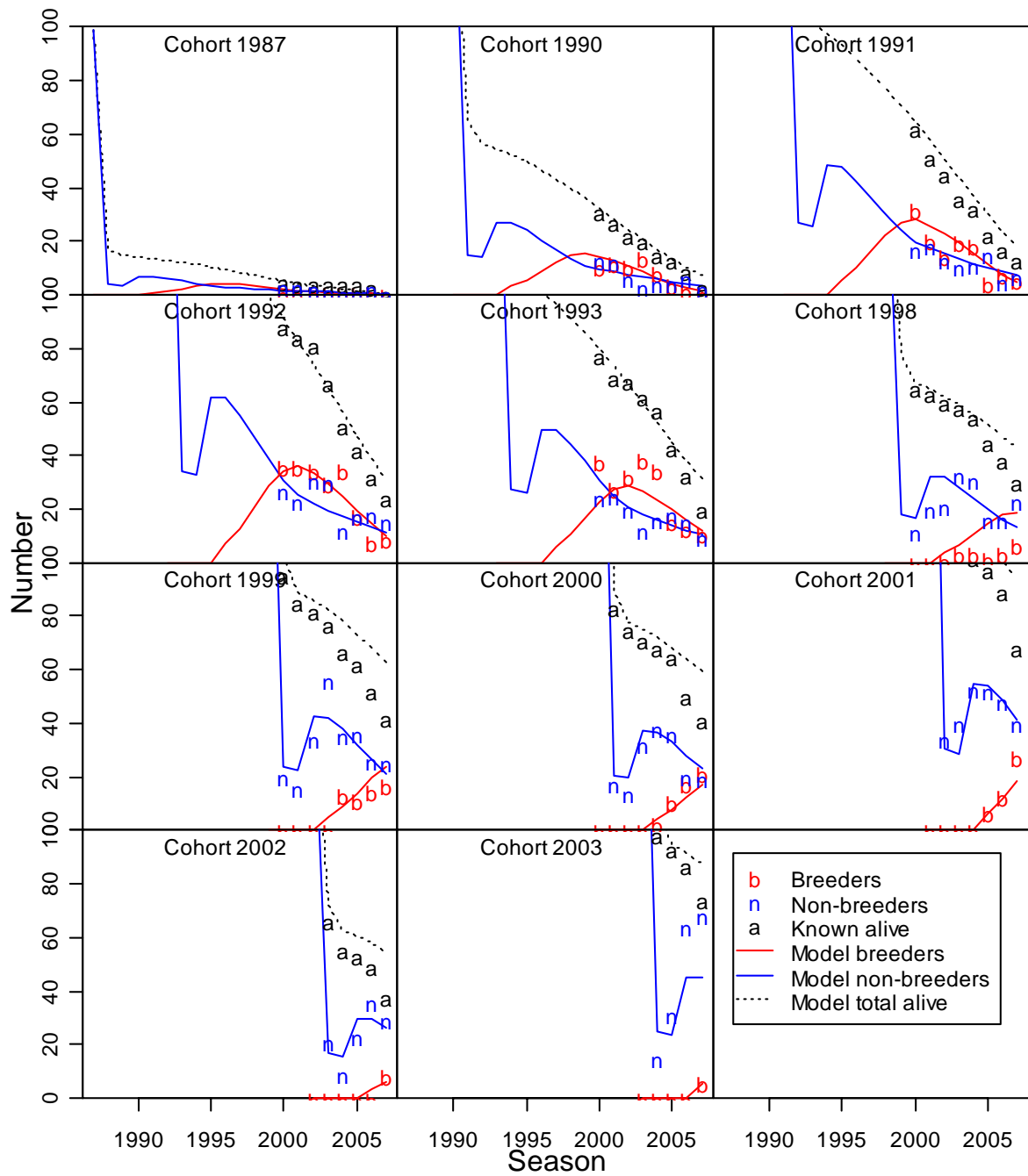
Figure 2. **Observed and predicted numbers of tagged female sea lions by cohort. The number of breeders each season are plotted b (red), the total number of observed non-breeders n (blue) and the number known to be alive (observed in the season or in a subsequent season) a. The fitted numbers of breeders and observed non-breeders are shown by red and blue lines and the number alive by a dashed line.**
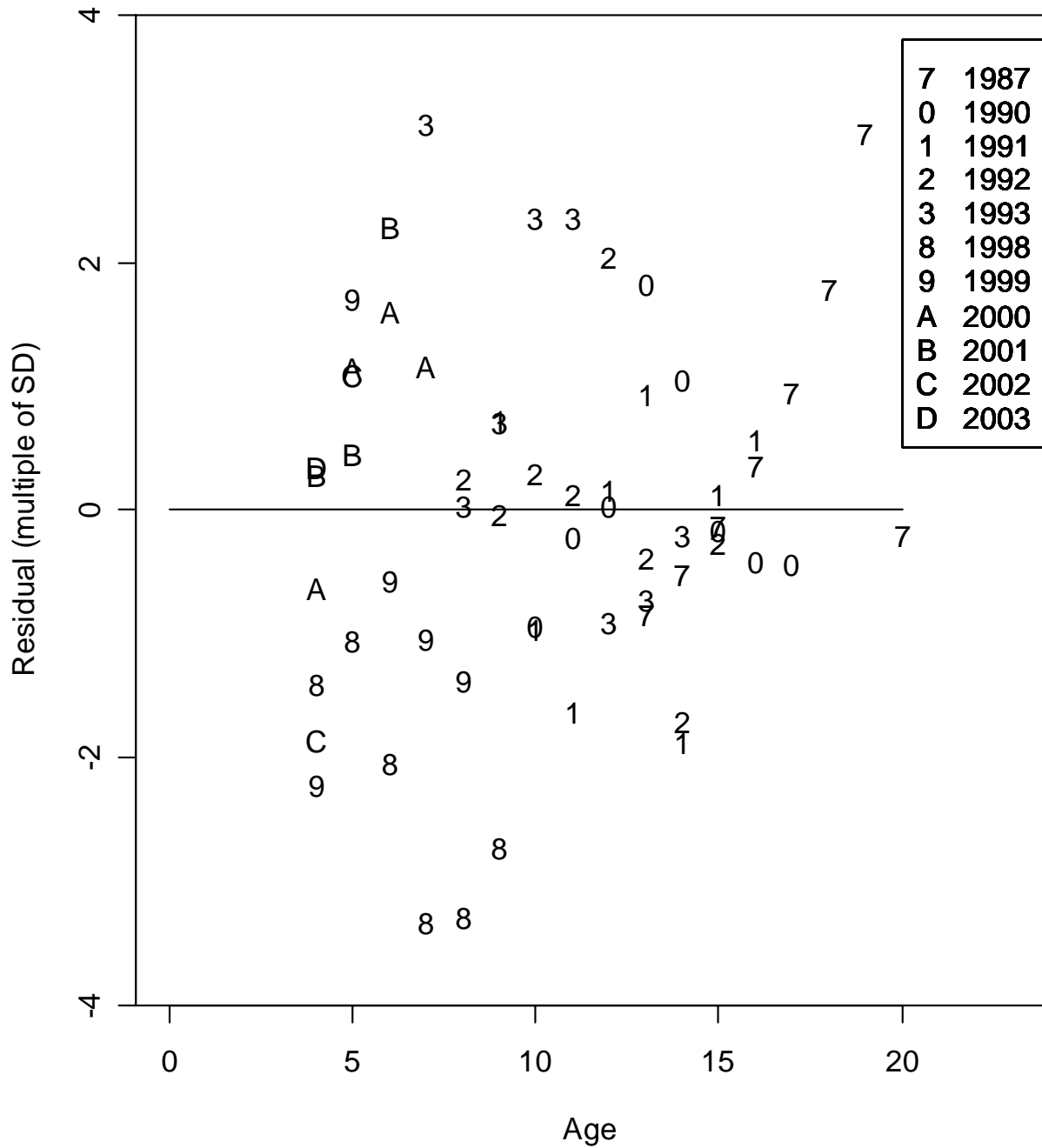
Figure 3. **Residuals of the fitted numbers of tagged female sea lions that pupped by age and cohort. Residuals are expressed as a multiple of the standard deviation, which is estimated as the square root of the fitted value.**
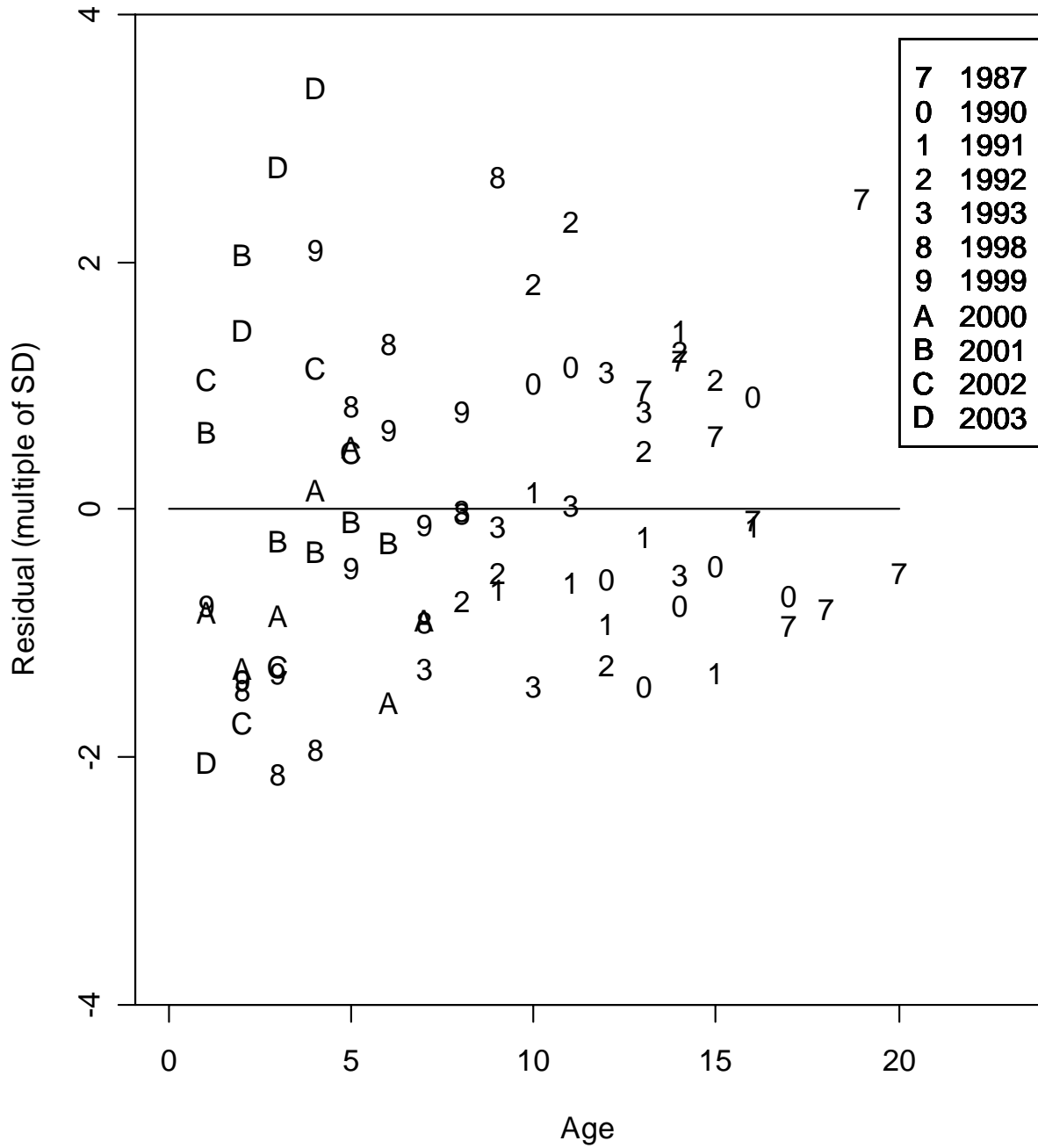
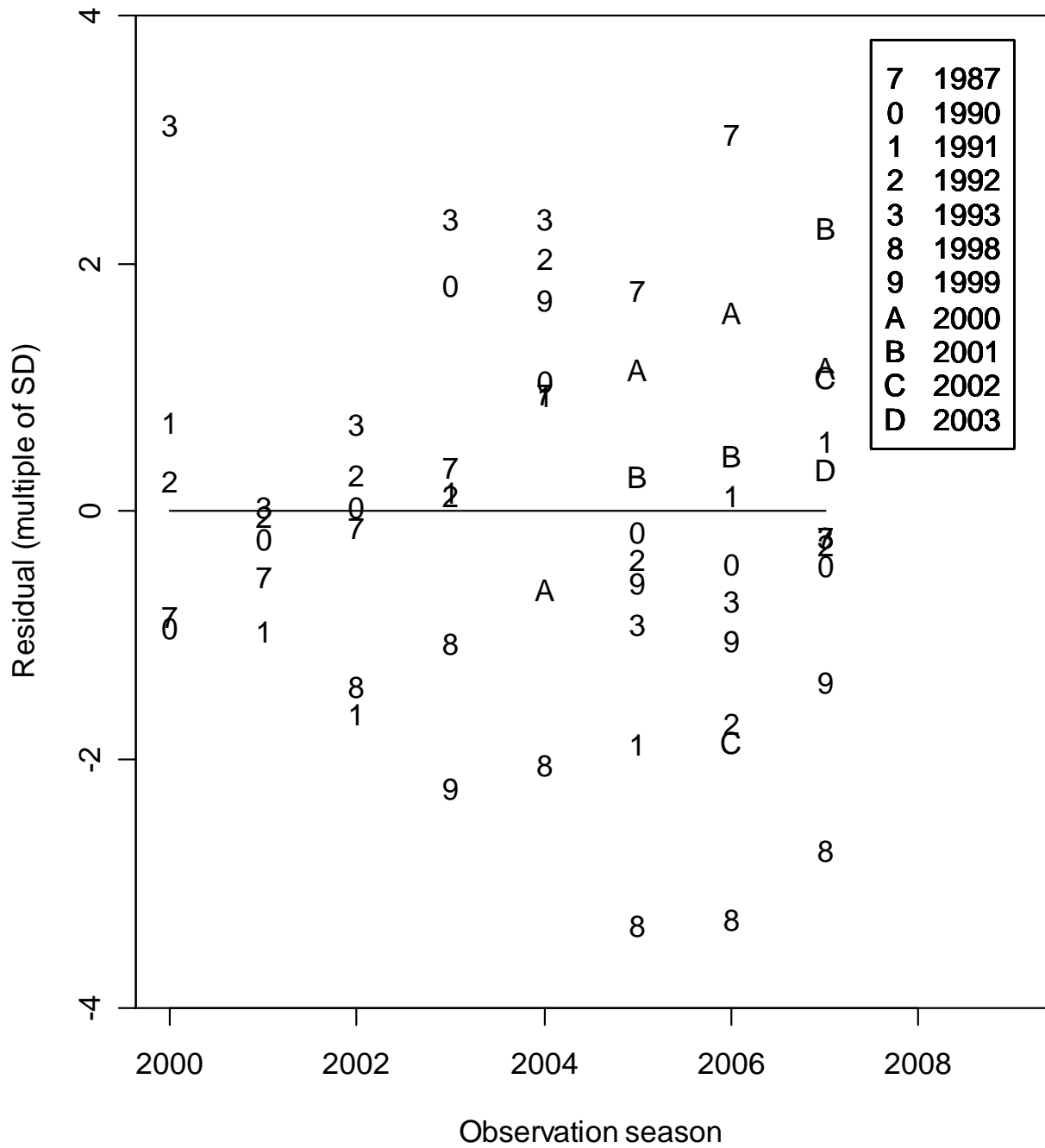**Figure 4.** **Residuals of the fitted numbers of tagged female sea lions observed as non-breeders by season and cohort. Residuals are expressed as a multiple of the standard deviation, which is estimated as the square root of the fitted value.**

Figure 5. **Residuals of the fitted numbers of tagged female sea lions that pupped by age and observation season. Residuals are expressed as a multiple of the standard deviation, which is estimated as the square root of the fitted value.**
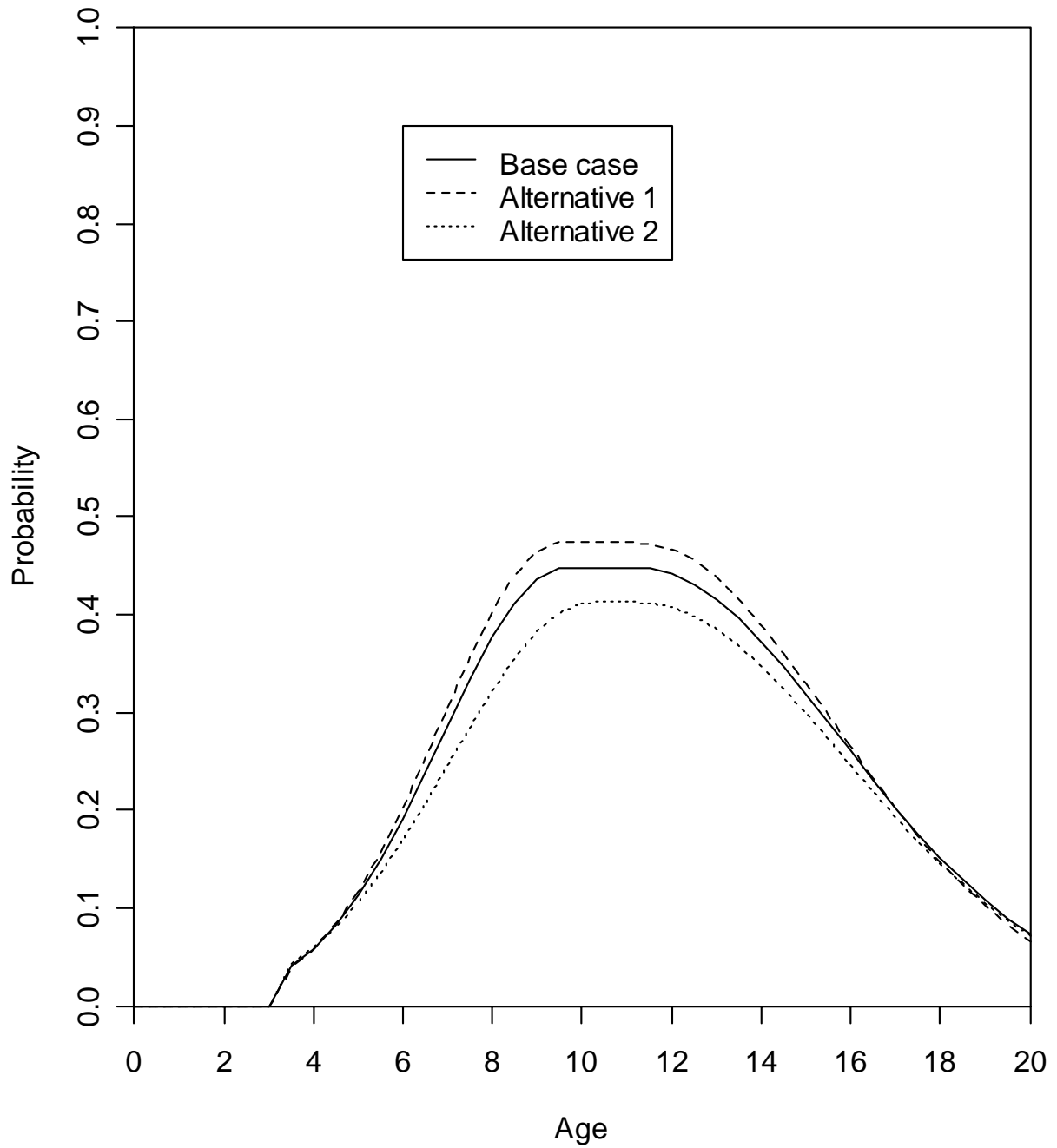
Figure 6. Estimated pupping rate as a function of age for three alternative criteria for deciding which animals have pupped. The base case is shown by a solid line. These functions of five parameters give the mean at each age for the population.
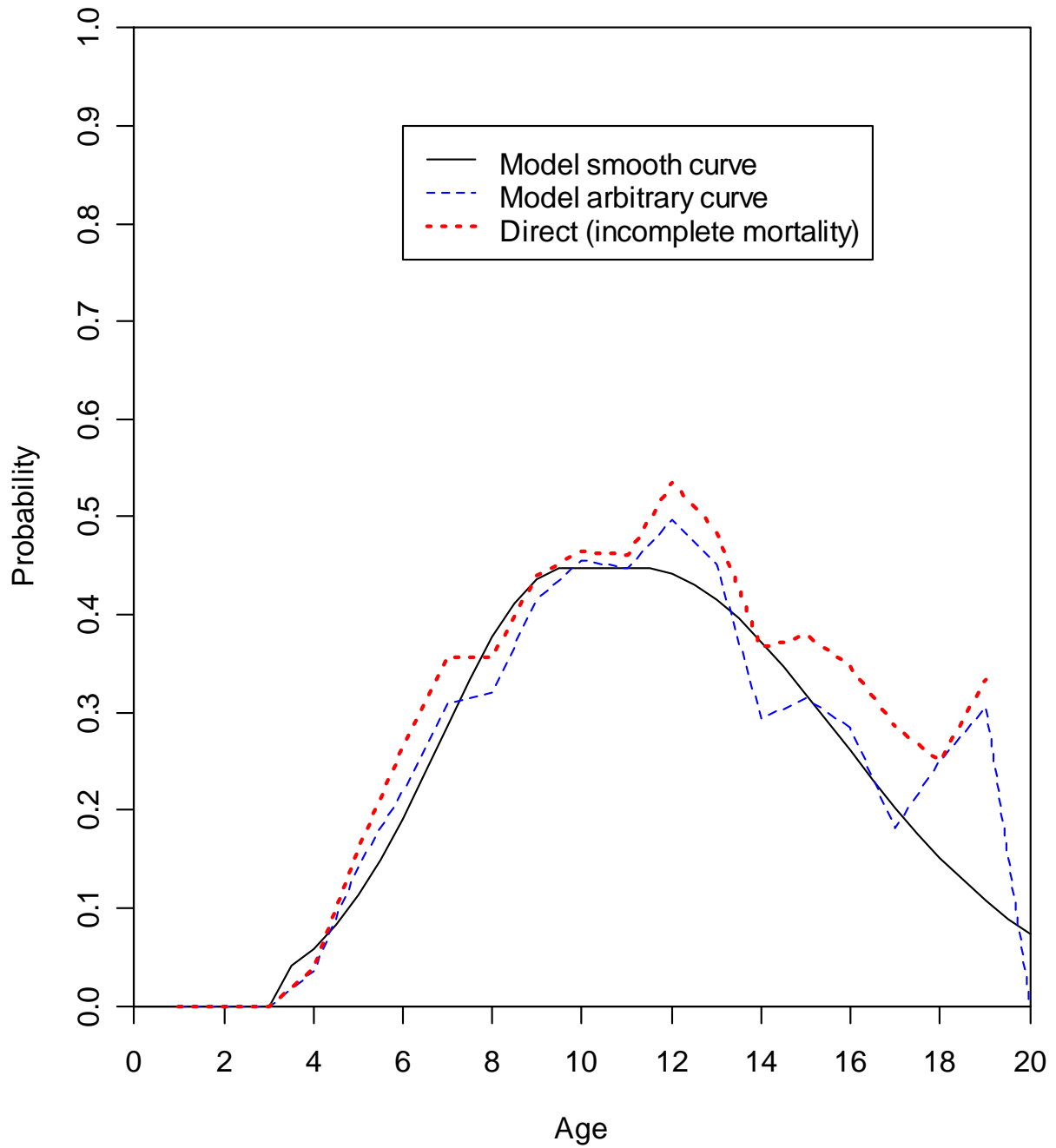
Figure 7. **Estimated pupping rate as a function of age. The base case function of five parameters is shown by the solid line; the fitted arbitrary function (one parameter for each age) under the base case criterion by the dashed line (blue); function estimated directly from the data using the base case criterion but assuming that the only animals alive in any season are those that have been observed in that or subsequent seasons by the dashed line (red).**
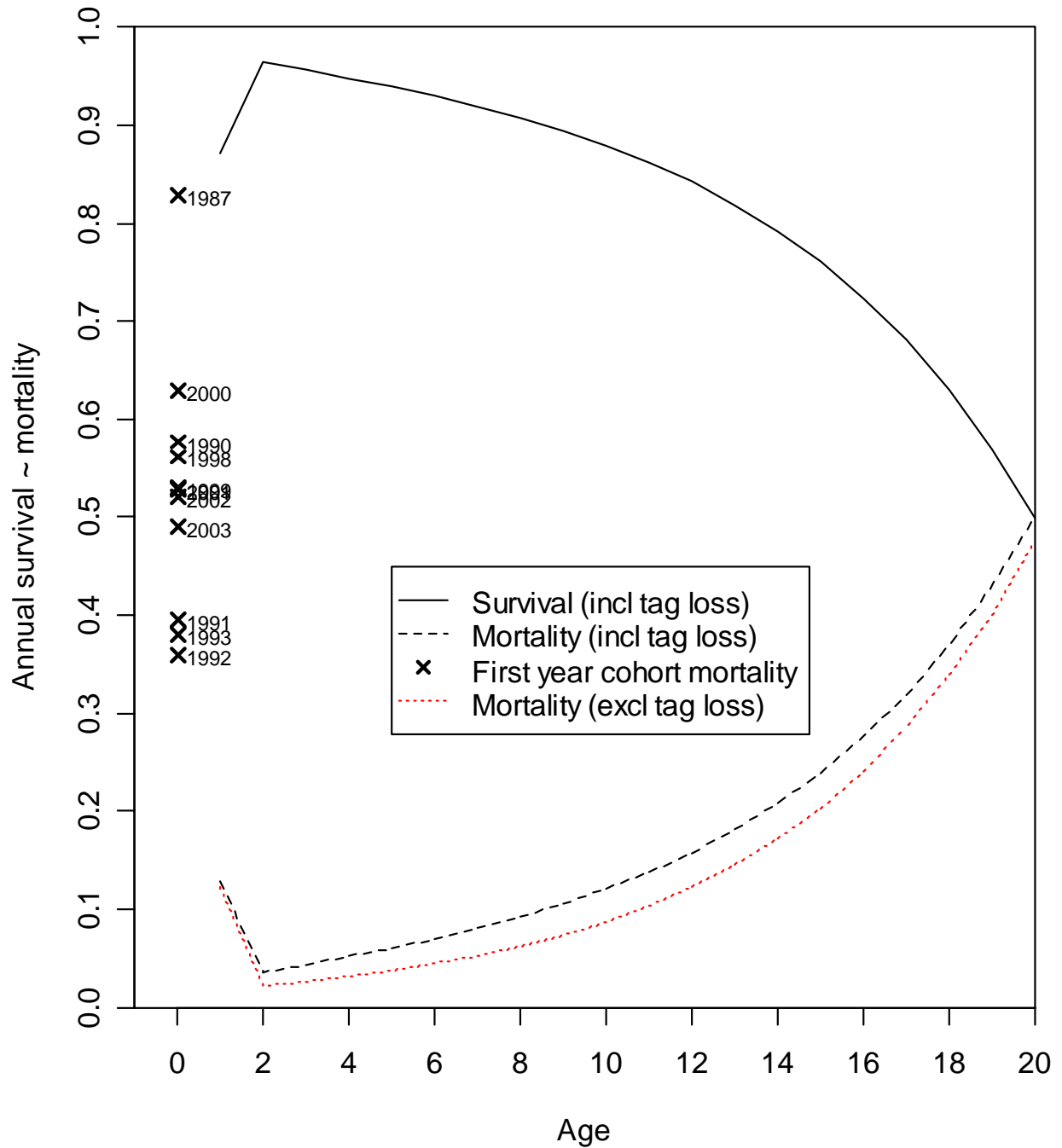
Figure 8. Estimated mortality and survival rates as functions of age. The base case mortality function that includes tag loss is shown by the dashed line; survival (one minus mortality) by the solid line; the first year mortality for each cohort is plotted ×; the mortality rate excluding the tag loss part is shown by the dotted line (red) but is unlikely to be well estimated.