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Long-term Changes in Grey Seal Vital Rates at Sable Island Estimated from POPAN Mark-resighting Analysis of Branded Seals

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Foreword

This series documents the scientific basis for the evaluation of aquatic resources and ecosystems in Canada. As such, it addresses the issues of the day in the time frames required and the documents it contains are not intended as definitive statements on the subjects addressed but rather as progress reports on ongoing investigations.

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ABSTRACT

Populations facing resource limitation are expected to exhibit changes in vital rates, such as reduced juvenile survival, delayed maturation and reduced adult survival. Population growth rate of grey seals at Sable Island, Nova Scotia, has been monitored from 1963 to 2010 by estimating pup production. Recently, the rate of increase in pup production has slowed to 4%/yr from 13%/yr prior to 1997. Periodically between 1969 and 2002, more than 7000 grey seals were uniquely branded at weaning. Sighting of branded grey seals has been conducted annually from 1983 to 2012 by means of 3-7 weekly censuses of the breeding colony. Here, we use the mark-resighting analysis of branded females to estimate i) juvenile survival (weaning to age 4), ii) adult survival and iii) age-specific pupping probabilities (ages 4 to 14) was used. Two groups of cohorts (1985-89 and 1998-2002) were analyzed separately to test for temporal changes in vital rates using the sightings of the previous group of cohorts to help estimate the probability of sighting. Sightings from 1987 to 1999 of the 1980s cohorts and from 2000 to 2012 of the recent cohorts provided estimates of juvenile survival and average age at first birth. The estimates of capture probability (p) from the POPAN model provide a lower bound for average reproductive rates at 53 to 78%. Estimated average apparent survival rates of adult females were 0.95 and 0.97 for the 1980s and the 1998-2002 cohorts, respectively. Estimated average age at first birth (over ages 4 to 14 years) has increased from 5.6 to 6.5 years between the 1980s and 1998-2002 cohorts. However, apparent juvenile survival decreased from 0.74 in the 1980s cohorts to 0.33 in the recent cohorts.

Changements à long terme des indices vitaux du phoque gris à l'île de Sable obtenus grâce aux analyses de POPAN faites à partir de phoques marqués et revus

RÉSUMÉ

Les populations qui font face à des ressources limitées devraient présenter des changements dans les indices vitaux comme la survie juvénile réduite, la maturation ralentie et la survie adulte réduite. Le taux de croissance de la population des phoques gris à l'île de Sable, en Nouvelle-Écosse, a été surveillé de 1963 à 2010 en estimant la production de petits. Récemment, le taux d'augmentation de la production de petits est passé de 13 % par année avant 1997 à 4 % par année. De 1969 à 2002, de façon périodique, plus de 7 000 phoques gris ont été marqués d'une valeur unique au sevrage. Des observations du phoque gris ont été conduites chaque année entre 1983 et 2012, à raison de 3 à 7 recensements hebdomadaires de la colonie de reproduction. Ici, nous nous sommes servi de l'analyse des phoques femelles marqués et revus afin d'estimer i) la survie des juvéniles (du sevrage à l'âge de 4 ans), ii) la survie des adultes, et iii) les probabilités de mise bas liées à l'âge (de 4 à 14 ans). Deux groupes de cohortes (de 1985 à 1989 et de 1998 à 2002) ont été analysés séparément afin de détecter les changements temporels des indices vitaux grâce aux observations du groupe de cohortes précédent pour estimer la probabilité d'observation. Les observations entre 1987 et 1999 des cohortes des années 1980 et celles réalisées entre 2000 et 2012 pour les cohortes plus récentes ont permis d'estimer la survie des juvéniles ainsi que l'âge moyen des primipares. Les estimations de la probabilité de capture (p) réalisées à partir du modèle de POPAN indiquent la limite inférieure du taux moyen de reproduction, soit entre 53 % et 78 %. Les taux de survie moyens apparents estimés des phoques femelles adultes atteignaient 0,95 et 0,97 respectivement pour les cohortes des années 1980 et celles comprises entre 1998 et 2002. L'estimation de l'âge moyen des primipares (entre l'âge de 4 et 14 ans) a augmenté, passant de 5,6 à 6,5 ans entre les cohortes des années 1980 et celles de 1998-2002. Cependant, les taux de survie apparents des juvéniles ont diminué de 0,74 pour les cohortes des années 1980 à 0,33 pour les cohortes récentes.

INTRODUCTION

Populations facing resource limitation are expected to exhibit changes in vital rates, such as reduced juvenile survival, delayed maturation and reduced adult survival (Eberhardt and Siniff 1977). The largest grey seal (*Halichoerus grypus*) breeding colony in the world is located on Sable Island, Nova Scotia, Canada. Population growth rate of this population has been monitored from 1963 to 2010 by estimating pup production (Bowen et al. 2011). Prior to the 1997 survey, the pup production increased at a rate of 13% a year, with a doubling time of about 6 years. Between 2007 and 2010, the rate of growth slowed to about 4% (Bowen et al. 2011) suggesting that the population may be facing resource limitation.

Large haul-out groups of grey seals can be found on Sable Island, Nova Scotia, Canada (43°57'0"N 59°54'57"W) year round, and breeding occurs between mid-December and early February. Grey seals are iteroparous, capital breeders, with indeterminate growth, and precocial young. Female grey seals mature at age 4 years or older, and continue to reproduce into their 30s (Bowen et al. 2006). During a brief lactation period of 17 days on average, pups feed on energy-rich milk containing 40-60% lipid and more than triple their birth mass (Iverson et al. 1993, Mellish et al. 2000). Females stay near their pup and use the same location in the breeding colony throughout the lactation period. Weaning is abrupt, with females quickly leaving the colony and returning to sea. The weaned pups undergo a post-weaning fast of several weeks before going to sea on their first foraging trip (Noren et al. 2008).

Here we estimate the survival probabilities of juveniles (weaning to first pupping) and adult females and age-specific birthing probabilities (ages 4 to 14). We did this using the POPAN mark-recapture analysis developed by Schwarz and Arnason (1996) and initially applied to sightings of individually branded female grey seals on Sable Island (Schwarz and Stobo 2000). We fit POPAN models to sighting histories for two groups of branded cohorts (1985-1989 and 1998-2002) during two time periods (1987-1999 and 2000-2012). Although pups have been branded from cohorts born in the 1960s and 1970s, the only cohorts branded since then are those in these two groups of cohorts identified above. These two groups of branded seals allowed comparison of female vital rates during periods of high and reduced population growth rate.

METHODS

Between 1963 and 2002, more than 7,000 grey seal pups were uniquely branded just after weaning. Weaned pups were either selected at random from the population or were pups of known-age mothers which had been previously branded. Individual brands contain 2 to 4 alpha-numeric elements with each element typically measuring 8-10 cm high and 6 cm wide on adults, making them easily read at a distance of 5-10 m. Each year since 1983, weekly censuses have been conducted of the entire colony over the course of the breeding season to resight branded seals. Censuses were conducted using all-terrain vehicles, which permitted the entire colony to be searched thoroughly in 2–3 days. The date and location (either verbal description or more recently, GPS position) were recorded as well as additional information to describe the quality of the brand and the lactation stage of the female's pup. From 1983 through 1990, the lactation stage of the female's pup was not always recorded. Because those older data do not allow us to identify breeders and non-breeders, we assumed that all females age 4 or older sighted during the breeding period were mature and breeding. Only a small fraction of sightings during the breeding season are of non-breeding females. During the breeding season, 96% of sightings of females branded between 1998 and 2002 were pregnant or lactating females. Thus, we expect the estimates of birthing probability to be unbiased.

All procedures used on study animals were in compliance with applicable animal care guidelines of the Canadian Council on Animal Care and were approved by The Department of Fisheries and Oceans Animal Care Committee.

STATISTICAL ANALYSIS

Schwarz and Arnason (1996) parameterized the Jolly-Seber (JS) mark-recapture model in terms of a super population (N) and the probability of entry ($pent$) to the population. The initial capture and marking is not included in the POPAN model, instead marked animals that are sighted for the first time since branding are treated as new entrants into the population, and the ratio of the total number of animals that returned to give birth (N) to the number marked provides an estimate of juvenile survival. In this way, the population of seals that have given birth for the first time is treated as an open population. The POPAN model was previously applied to sightings of female (Schwarz and Stobo 2000) and male (Manske et al. 2002) grey seals branded on Sable Island prior to 1990.

In the current analysis, we used resightings of females branded in two time periods – 1985 to 1989 and 1998 to 2002. We use only sightings of branded females age 4 or older. Comparable data on males is being collected, but as they recruit to the colony at an older age than females, several more years of resightings are needed. We have combined the sightings data from the multiple censuses within season, such that individuals are either seen or not seen during the breeding season. Because the estimates of age at first birth and juvenile survival are conditional upon seals having recruited to the breeding colony by the latest age in the sightings histories, we fit the POPAN model to the sightings histories for two time periods of the same length, 1987 to 1999 and 2000 to 2012, so that we can compare the age-specific probability of entry for the most recent cohorts (1998 to 2002) and the previously branded cohorts (1985, 1986, 1987, and 1989). Following Schwarz and Stobo (2000), we use the sightings of earlier branded cohorts (1980s and 1970s, respectively) to allow for the estimation of the probability of entry ($pent$) parameter for the first cohort in the first time period (i.e., 1985). This analysis updates the Schwarz and Stobo (2000) analysis of the 1985-1989 cohorts with five more breeding seasons and uses an edited data set which corrected for some erroneous assignments of sex by using adult sightings as opposed to the sex of seals recorded at branding.

Four parameter types are estimated phi (apparent survival), p (capture probability given the animal is alive and on the study area, i.e., available for capture), $pent$ (probability of entry into the population for this breeding season), and N (super-population size) (Fig. 1). For each cohort, for t breeding seasons, there are $t - 1$ phi estimates, t p estimates, $t - 1$ $pent$ estimates, and a single estimate of N . The $t - 1$ $pent$ estimates correspond to the probability of entry for occasions 2, 3, ..., t . The Logit link function is used for phi and p and the Log link is used for N . The MLogit link function provides a constraint that makes the sum of the $pent$ parameters equal to 1, such that the probability of entry into the population on the first occasion is $1 - \sum pent_t$. The parameter p has two components, the probability that a female will return to the breeding colony and the probability that having returned she will be sighted. Without additional information it is not possible to separately estimate these components.

The number of marked animals in the population on breeding season 1 is $N_1 = pent_0 \cdot N$. The number of new animals (births, B) entering the population prior to occasions $i = 2, 3, \dots, t$ is $B_i = pent_{(i-1)} \cdot N$. The population size on occasion $i = 2, 3, \dots, t$ is $N_i = (N_{(i-1)} - \text{losses on capture}) \cdot phi_{(i-1)} + B_i$. Estimates of the B_i and N_i are provided as derived parameters from models with the POPAN data type. Models were fit using the second partial matrix with Program MARK v. 6.2 (White and Burnham 1999).

Model Assumptions

The POPAN model makes the following assumptions in addition to those commonly made in Jolly-Seber (JS) recapture models, such as marks are not lost or overlooked:

- (i) All female seals have a zero probability of sighting prior to the year of their first pup,
- (ii) All females giving birth, whether they are primiparous or multiparous, have the same probability of sighting,
- (iii) All females, whether they are primiparous or multiparous, have the same probability of survival once they have recruited, and
- (iv) All females in each cohort that have survived have recruited by the end of the study. Otherwise, the age-specific estimates will be conditional upon seals having their first pup before the latest age in the sightings histories.

There are a large number of possible models that could be run. A suite of candidate models, with either constant, cohort- and/or time-specific estimates of ϕ , constant and time-specific estimates of p , cohort- and time-specific estimates of $pent$ and cohort-specific estimates of N , was developed from the full model. Evidence in favour of competing models was evaluated on the basis of lowest Akaike information criterion (AICc), smallest Delta AICc (Δ), and highest AICc weights (w) (Burnham and Anderson 2002).

Not all of the parameters can be estimated in the full time-dependent model. In the first and final year, the parameter estimates are confounded. Thus, in the full time-dependent models, we have fixed the first and last p as $p=1$, and we exclude the estimate of the final $pent$ parameter from the calculation of age-specific estimates of age at first birth for each cohort. In models where p or ϕ is constant ($p(\cdot)$, $\phi(\cdot)$), the parameters can be estimated in the final year, but we have fixed p in the first year to 1 in models where p varies with time ($p(t)$). For models where p varies with time, the first $pent$ for the previously branded group is also confounded with p at time 2, but neither of these parameters are of interest. The assumption that p is equivalent across groups allows us to estimate the $pent$ at age 4 for cohorts 1985 to 1989.

The average age at first birth (A_c) was estimated from probability of entry ($pent$):

$$A_c = \sum j * pent_{c,j}, \text{ where } j \text{ is ages 4 to 14.}$$

The estimated standard error (SE) is found by a Taylor series expansion (Schwarz and Stobo 2000).

Juvenile survival probability (S_{juv}) between weaning and the age at first birth (ages 4 to 14 years) is estimated as:

$$S_{juv} = N_c / Nrel_c$$

where N_c is the estimated size of the super-population and $Nrel_c$ is the number of female seals branded in that cohort. The juvenile survival rate is estimated by extrapolating the number of seals returning to give first birth at each age back to age 4 assuming that the survival rates from age 4 onwards are applicable to these seals. The proximate mean of the probability of sighting and survival was calculated as the arithmetic average of the model parameters.

RESULTS

In each of the 1985-1987 cohorts (groups), 400 females were uniquely branded, and in the 1989 cohort 500 females were branded (Table 1). The number of females that recruited to Sable Island (n_{ij}) and the number of those that were previously sighted (m_{ij}) increased rapidly at ages 4, 5, and 6 and more slowly thereafter (Table 1). There was no loss of marked females on recapture (i.e., $R_{ij} = n_{ij}$).

In each of the 1998-2002 cohorts (groups), between 156 and 267 female grey seals were uniquely branded (Table 2). Unlike the earlier cohorts, no females recruited to the breeding population at age 4 years in the 1998 and 1999 cohorts, but 4 year-olds were observed in 2000, 2001, and 2002. Although the numbers of females recruiting to the breeding colony increased with age, as expected, the magnitude of the increase was small compared to the 1980 cohorts.

MODEL FITS

We fit six models to the resighting data for the two groups of cohorts (Tables 3 and 4). Of those fitted, the model with annual adult survival rate, annual sighting probability, and cohort-specific probability of entry was best supported by the data for the 1980s cohorts (Table 3). Sighting probability averaged 0.66 but varied among years from 0.53 to 0.74 (Fig. 2). Adult survival rate averaged 0.949 ± 0.044 but varied from 0.91 to 0.98 (Fig. 3, Table 5). Juvenile survival rate (ages 0 -4 years) also was high averaging 0.735. However, juveniles in the 1985 and 1989 cohorts survived better than in 1986 and 1987 cohorts (Fig. 4, Table 5). Average age at first birth varied from 5.3 to 6.1 years, with an average of 5.6 years (Fig. 5, Table 6).

The best fitting model for the 1998 to 2002 cohorts differed from that of the 1980 cohorts, with adult survival differing among cohorts. Sighting probability was higher for the 1998-2002 cohorts than for those in the 1980s, averaging 0.745 (Fig. 6). Adult survival rate averaged 0.97 ± 0.027 (Table 7). Adult survival was uniformly high in the 1998-2001 cohorts, but was significantly lower in the 2002 cohort and 0.94 (Fig. 7). Juvenile survival rate declined significantly from the 1980s, averaging 0.331 (Table 7), but was higher in 1998 and 1999 than in the subsequent 3 years (Fig. 8). Average age at first birth varied little from 5.9 to 6.5 years, with an average of 6.5 years (Fig. 9, Table 8).

DISCUSSION

Estimates of pup production on Sable Island indicate that the population increased exponentially at a rate near the predicted R_{max} for grey seals. Over the past decade, however, the rate of increase in pup production has declined markedly (Bowen et al. 2011). The reduction in the rate of increase must be the result of changes in one or more vital rates. The results of our analysis indicate that, despite this slowing of population growth rate, adult survival rate and age at first birth have not changed greatly over time. Rather it seems clear that a marked decline in the survival rate of juveniles, ages 0 to 4 years, has been largely responsible for the slowing of the rate of increase in pup production. Changes in age-specific birth rate could also be contributing to the slowing of growth, but our estimates of sighting probabilities, which provide minimum estimates of average birth rate, suggest that birth rates have also remained high.

Over 30 years ago, Eberhardt (1977) and Eberhardt and Siniff (1977) proposed that there is an apparent sequence of changes in vital rates as population density increases toward maximal levels, with changes in juvenile survival being observed first followed by a reduction in birth rate and finally adult survival. Support for this sequence has been found in several taxa (e.g., Fowler 1981, 1987, Gaillard et al. 1998). Although there is support for this framework, it is often impossible or impractical to estimate temporal changes in vital rates in long-lived mammals. Our analysis of long-term sightings of known-age grey seal females adds further support to the Eberhardt (1977) theory of vital rate responses to population density of long-lived vertebrates.

Schwarz and Stobo (2000) used the same model to estimate female vital rates for the 1985-1987 cohorts based on resightings of branded seals from 1987 to 1994. Their estimates of adult and juvenile survival rates are similar to that those produced here with the addition of 5 more years or data. However, direct comparison is difficult as different models were fit in the previous analysis and the data have been further audited to remove errors. As the estimates of age at first birth are conditional upon seals having their first pup before the latest age in the study, it is

not surprising that the addition of more years and thus older ages did tend to increase estimates of adult survival and average age at first birth compared to those reported in Schwarz and Stobo (2000). Although cross-sectional data found no evidence of first pupping after age 9 years from samples taken in the Gulf of St. Lawrence (Hammil and Gosselin 1995), our longitudinal data from Sable Island indicate that small numbers of females recruit beyond the age of 9 years. As grey seals can give birth beyond the age of 25 years, a change of one year in the mean age of first reproduction will not have a large impact on individuals' contribution to population growth.

Violation in the assumptions of the JS model can bias point estimates of survival and capture (i.e., sighting) probability. The first assumption is that every marked female in the breeding colony has the same probability of being resighted. Age-specific changes in pregnancy rate could result in different sighting probabilities. This will be investigated in a robust analysis which uses information from multiple censuses within season to estimate the probability of sighting given that the females has returned to the colony. The second assumption of POPAN and the standard JS model is that every marked female has the same probability of survival to the next sampling period (i.e., breeding season). Again age-specific changes in survival probability could result in violation of this assumption although we expect the effect will be small over much of the reproductive life of females. The third assumption is that marks are neither lost or overlooked and are recorded correctly. Brands are permanent marks. Few brands in the population are difficult to read and as each female is generally observed multiple times within a season by different researchers, it seems unlikely that this assumption has been violated to any extent. The fourth assumption is that sampling periods are instantaneous and recaptured animals are released immediately. This assumption is upheld as resightings occur over a period of 4-6 weeks, which is a short period compared to the time period over which vital rates are estimated (i.e., annually). The fifth assumption is that all emigration of marked females from the sampling area is permanent. Small numbers of marked females do emigrate. Seven females branded between 1998 and 2002 that have not been sighted on Sable Island during the breeding season were sighted in other breeding colonies on the Eastern Shore of Nova Scotia or in haul out groups in the Gulf of Maine. The sixth assumption is that the fate of every marked female with respect to capture and survival is independent of the fate of other animals. This assumption could be violated to the extent that there may be heterogeneity among females in the breeding population. This will be investigated in future analyses.

With respect to POPAN assumptions, the assumption that females have a zero probability of sighting prior to recruitment, although not strictly true, is effectively true as only a handful of females have been sighted before recruiting to the breeding colony. There is no reason to expect that the second assumption is not true as females of different parity are not segregated within the breeding colony and therefore they can be expected to have the same sighting probability. Although, as noted above, age-specific changes in fertility could result in departures from this assumption. The final assumption is that all females in each cohort that have survived have recruited by the end of the study. Although a small proportion of females do recruit beyond the age of 10 years, this would only produce a small negative bias in age at first birth for the 1985 and 2002 cohorts. Overall, this assumption seems valid.

Models of grey seal population dynamics in Eastern Canada have been hampered by the lack of estimates of juvenile survival rate and other vital rates that may have changed as the population, particularly on Sable Island, has grown. The estimates of capture probability (p) from the POPAN model provide a lower bound for average reproductive rates at 53 to 78%. If the probability of resighting females that have returned to Sable to pup has not changed, the parameter estimates suggest that there may have been an increase in reproductive rates. Despite the slowing of the rate of increase in pup production in recent years, our results show that adult survival has remained high and there has been only a small increase in the age of first reproduction. However, there has been a large decline in juvenile survival rates between the

1980s and the late 1990s. Incorporation of these new estimates in population models should improve our understanding of dynamics.

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REFERENCES

- Bowen, D.W., C. den Heyer, J.I. McMillan, and M.O. Hammill. 2011. Pup production at Scotian Shelf grey seal (*Halichoerus grypus*) colonies in 2010. Fisheries and Oceans Canada. Canadian Science Advisory Secretariat. Research Document 2011/066.
- Bowen, W.D., S.J. Iverson, J.I. McMillan, and D.J. Boness. 2006. Reproductive performance in grey seals: Age-related improvement and senescence in a capital breeder. *Journal of Animal Ecology* 75:1340-1351.
- Burnham, K.P., and D.R. Anderson. 2002. Model selection and multimodel inference: A practical information-theoretic approach. 2nd edition. Springer-Verlag, New York, N.Y.
- Eberhardt, L.L. 1977. Optimal policies for conservation of large mammals, with special reference to marine ecosystems. *Environmental Conservation* 4:205-212.
- Eberhardt, L.L., and D.B. Siniff. 1977. Population dynamics and marine mammal management policies. *Journal of the Fisheries Research Board of Canada* 34:183-190.
- Fowler, C.W. 1981. Density dependence as related to life history strategy. *Ecology* 62:602-610.
- Fowler, C.W. 1987. A review of density dependence in populations of large mammals. *Current Mammalogy* 1:401-441.
- Gaillard, J.M., M. Festa-Bianchet, and N.G. Yoccoz. 1998. Population dynamics of wild herbivores: variable recruitment with constant adult survival. *Trends in Ecology and Evolution* 13:58-63.
- Hammill, M.O., and J. F. Gosselin. 1995. Grey seal (*Halichoerus grypus*) from the northwest Atlantic: female reproductive rates, age at first birth, and age of maturity in males. *Canadian Journal of Fisheries and Aquatic Sciences* 52:2757-2761.
- Iverson, S.J., W.D. Bowen, D.J. Boness, and O.T. Oftedal. 1993. The effect of maternal size and milk energy output on pup growth in grey seals (*Halichoerus grypus*). *Physiological Zoology* 66:61-88.
- Manske, M., W.T. Stobo, and C.J. Schwarz. 2002. Estimation of age specific probabilities of first return and annual survival rates for the male gray seal (*Halichoerus grypus*) on Sable Island from capture-recapture data. *Marine Mammal Science* 18:145-155.
- Mellish, J.E., S.J. Iverson, and W.D. Bowen. 1999. Variation in milk production and lactation performance in grey seals and consequences for pup growth and weaning characteristics. *Physiological and Biochemical Zoology* 72:677-690.
- Noren, S.R., D.J. Boness, S.J. Iverson, J. McMillan, and W.D. Bowen. 2008. Body condition at weaning affects the duration of the postweaning fast in gray seal pups (*Halichoerus grypus*). *Physiological and Biochemical Zoology* 81:269-277.
- Schwarz, C.J., and A.N. Arnason. 1996. A general methodology for the analysis of capture-recapture experiments in open populations. *Biometrics* 52:860-873.
- Schwarz, C.J., and W.T. Stobo. 2000. Estimation of juvenile survival, adult survival, and age-specific pupping probabilities for the female grey seal (*Halichoerus grypus*) on Sable Island from capture-recapture data. *Canadian Journal of Fisheries and Aquatic Sciences* 57:247-253.
- White, G.C., and K.P. Burnham. 1999. Program MARK: Survival estimation from populations of marked animals. *Bird Study* 46: Supplement (001) 120-138.

Table 1. JS summary statistics for the 1985-1989 cohorts and all previously uniquely branded female grey seals. n_{ij} = number of animals branded as young in cohort i , recruited to Sable Island, that are recaptured in calendar year j ; m_{ij} = number of animals in cohort i , recruited to Sable Island, that are captured in year j and were previously recaptured prior to year j ; R_{ij} = number of animals in cohort i , recruited to Sable Island, recaptured in year j and released in year j ; r_{ij} = number of animals in cohort i , recruited to Sable Island, from R_{ij} that are subsequently recaptured after release; z_{ij} = number of animals in cohort i , recruited to Sable Island, recaptured before year j , not recaptured in year j , and recaptured after year j .

Sighting year j	n_{ij}	m_{ij}	R_{ij}	r_{ij}	z_{ij}
Seals branded in $i = 1985$, total = 400					
1987	0	0	0	0	0
1988	0	0	0	0	0
1989	32	0	32	29	0
1990	104	15	104	100	14
1991	159	81	159	146	33
1992	157	123	157	146	56
1993	143	121	143	136	81
1994	115	109	115	108	108
1995	140	122	140	124	94
1996	184	167	184	164	51
1997	168	158	168	142	57
1998	142	139	142	107	60
1999	173	167	173	0	0
Seals branded in $i = 1986$, total = 400					
1987	0	0	0	0	0
1988	0	0	0	0	0
1989	0	0	0	0	0
1990	72	0	72	68	0
1991	140	41	140	130	27
1992	152	101	152	141	56
1993	153	134	153	147	63
1994	133	117	133	123	93
1995	135	123	135	126	93
1996	175	167	175	167	52
1997	182	175	182	163	44
1998	161	158	161	126	49
1999	180	175	180	0	0
Seals branded in $i = 1987$, total = 400					
1987	0	0	0	0	0
1988	0	0	0	0	0
1989	0	0	0	0	0
1990	0	0	0	0	0
1991	43	0	43	43	0
1992	121	29	121	112	14
1993	129	71	129	124	55
1994	116	91	116	112	88
1995	131	114	131	123	86
1996	194	167	194	181	42
1997	182	171	182	165	52
1998	171	164	171	132	53
1999	193	185	193	0	0

Table 1. Continued.

Sighting year j	n_{ij}	m_{ij}	R_{ij}	r_{ij}	Z_{ij}
Seals branded in $i = 1989$, total = 500					
1987	0	0	0	0	0
1988	0	0	0	0	0
1989	0	0	0	0	0
1990	0	0	0	0	0
1991	0	0	0	0	0
1992	0	0	0	0	0
1993	41	0	41	37	0
1994	105	16	105	101	21
1995	117	63	117	109	59
1996	191	120	191	173	48
1997	208	176	208	187	45
1998	198	180	198	139	52
1999	204	191	204	0	0
Seals branded in $i =$ all previous years					
1987	266	0	266	231	0
1988	236	157	236	215	74
1989	239	197	239	214	92
1990	247	221	247	231	85
1991	267	239	267	246	77
1992	221	217	221	208	106
1993	222	208	222	204	106
1994	199	193	199	184	117
1995	209	200	209	179	101
1996	223	210	223	187	70
1997	184	175	184	151	82
1998	177	172	177	124	61
1999	187	185	187	0	0

Table 2. JS summary statistics for the 1998-2002 cohorts and all previously uniquely branded female grey seals. Columns as per Table 1.

Sighting year j	n_{ij}	m_{ij}	R_{ij}	r_{ij}	z_{ij}
Seals branded in $i = 1998$, total = 156					
2000	0	0	0	0	0
2001	0	0	0	0	0
2002	0	0	0	0	0
2003	20	0	20	20	0
2004	26	13	26	24	7
2005	30	19	30	30	12
2006	32	26	32	30	16
2007	40	37	40	37	9
2008	36	35	36	36	11
2009	37	37	37	36	10
2010	40	38	40	34	8
2011	34	34	34	24	8
2012	34	32	34		
Seals branded in $i = 1999$, total = 258					
2000	0	0	0	0	0
2001	0	0	0	0	0
2002	0	0	0	0	0
2003	0	0	0	0	0
2004	41	0	41	39	0
2005	53	22	53	52	17
2006	60	47	60	60	22
2007	75	70	75	75	12
2008	77	73	77	75	14
2009	76	73	76	71	16
2010	73	72	73	69	15
2011	70	68	70	60	16
2012	77	76	77		
Seals branded in $i = 2000$, total = 249					
2000	0	0	0	0	0
2001	0	0	0	0	0
2002	0	0	0	0	0
2003	0	0	0	0	0
2004	3	0	3	2	0
2005	26	0	26	25	2
2006	35	14	35	30	13
2007	53	39	53	52	4
2008	49	43	49	47	13
2009	47	45	47	46	15
2010	48	44	48	42	17
2011	49	48	49	38	11
2012	50	49	50		

Table 2. Continued.

Sighting year j	n_{ij}	m_{ij}	R_{ij}	r_{ij}	Z_{ij}
Seals branded in $i = 2001$, total = 267					
2000	0	0	0	0	0
2001	0	0	0	0	0
2002	0	0	0	0	0
2003	0	0	0	0	0
2004	0	0	0	0	0
2005	2	0	2	2	0
2006	30	2	30	29	0
2007	34	18	34	33	11
2008	47	37	47	45	7
2009	40	35	40	39	17
2010	46	45	46	43	11
2011	51	49	51	37	5
2012	47	42	47		
Seals branded in $i = 2002$, total = 252					
2000	0	0	0	0	0
2001	0	0	0	0	0
2002	0	0	0	0	0
2003	0	0	0	0	0
2004	0	0	0	0	0
2005	0	0	0	0	0
2006	7	0	7	6	0
2007	17	1	17	16	5
2008	37	14	37	34	7
2009	38	28	38	35	13
2010	41	34	41	34	14
2011	50	41	50	32	7
2012	42	39	42		
Seals branded in $i = 1985$ to 1989					
2000	790	0	790	771	0
2001	714	576	714	687	195
2002	716	670	716	691	212
2003	745	697	745	716	206
2004	730	715	730	703	207
2005	702	692	702	675	218
2006	632	623	632	608	270
2007	695	686	695	651	192
2008	646	636	646	616	207
2009	662	650	662	607	173
2010	610	593	610	531	187
2011	603	590	603	415	128
2012	550	543	550		

Table 3. Model selection for the sightings histories of branded female grey seals in the 1985 to 1989 cohorts (groups, g) between 1987 and 1999.

Model	AIC _c	Δ AIC _c	AIC _c Weights	Model Likelihood	Number parameters
phi(t)p(t)pent(g*t)N(g)	15177.75	0	0.99985	1	77
phi(g)p(t)pent(g*t)N(g)	15196.17	18.41	0.0001	0.0001	72
phi(.)p(t)pent(g*t)N(g)	15197.41	19.66	0.00005	0.0001	68
phi(g*t)p(g*t)pent(g*t)N(g)	15271.85	94.09	0	0	169
phi(t)p(.)pent(g*t)N(g)	15352.22	174.47	0	0	69
phi(.)p(.)pent(g*t)N(g)	15555.66	377.91	0	0	56

Table 4. Model selection for the sightings histories branded female grey seals in the 1998 to 2002 cohorts (groups, g) between 2000 and 2012.

Model	AIC _c	Δ AIC _c	AIC _c Weights	Model Likelihood	Number parameters
phi(g)p(t)pent(g*t)N(g)	16714.94	0	0.99028	1	82
phi(t)p(t)pent(g*t)N(g)	16724.58	9.63	0.00802	0.0081	86
phi(t)p(.)pent(g*t)N(g)	16727.68	12.73	0.0017	0.0017	76
phi(.)p(t)pent(g*t)N(g)	16778.22	63.27	0	0	77
phi(.)p(.)pent(g*t)N(g)	16781.33	66.39	0	0	65
phi(g*t)p(g*t)pent(g*t)N(g)	16812.15	97.21	0	0	201

Table 5. Estimates of adult and juvenile (ages 0-4 years) survival rates for the 1980s cohorts from the preferred model (phi(t)p(t)pent(g*t)N(g)).

Age-class	Year	Survival rate	SE
Adult	1989	0.945	0.020
	1990	0.913	0.019
	1991	0.964	0.012
	1992	0.951	0.011
	1993	0.954	0.011
	1994	0.969	0.010
	1995	0.982	0.011
	1996	0.927	0.012
	1997	0.934	0.011
	1998	0.952	0.014
	mean	0.944	0.044
Age-class	Cohort	Survival rate	SE
Juvenile	1985	0.805	0.007
	1996	0.745	0.007
	1987	0.737	0.007
	1989	0.654	0.006
	mean	0.735	0.016

Table 6. Estimates age at first reproduction for the 1980s cohorts from the preferred model ($\phi(t)p(t)pent(g^*)N(g)$).

Cohort	Age (yr)	SE
1985	6.079	0.143
1986	5.263	0.126
1987	5.594	0.142
1989	5.444	0.132
mean	5.595	0.115

Table 7. Estimates of adult and juvenile (ages 0-4 years) survival rates for the 1998-2002 cohorts from the preferred model ($\phi(g)p(t)pent(g^*)N(g)$).

Age-class	Cohort	Survival rate	SE
Adult	1998	0.973	0.009
	1999	0.988	0.005
	2000	0.966	0.010
	2001	0.981	0.010
	2002	0.943	0.019
	mean	0.970	0.026
Juvenile	1998	0.376	0.008
	1999	0.392	0.004
	2000	0.316	0.005
	2001	0.265	0.007
	2002	0.305	0.007
	mean	0.331	0.024

Table 8. Estimates of age at first reproduction for the 1998-2002 cohorts from the preferred model ($\phi(g)p(t)pent(g^*)N(g)$).

Cohort	Age (yr)	SE
1998	6.504	0.315
1999	5.959	0.174
2000	5.874	0.201
2001	6.110	0.263
2002	6.189	0.203
mean	6.503	0.214

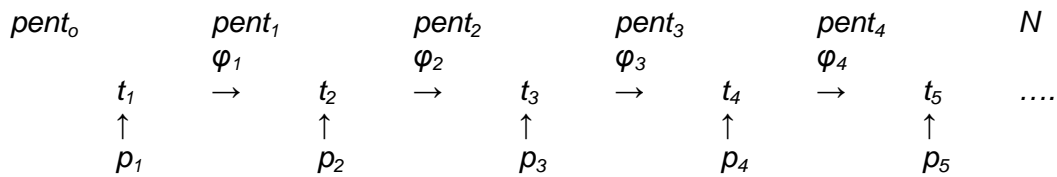


Fig. 1. POPAN process model. p_i is the probability of sighting at occasion i (t_i), ϕ_i is the probability of survival between occasion i and $i+1$; $pent_i$ is the probability of entry into the super-population (N) population between occasion i and $i+1$.

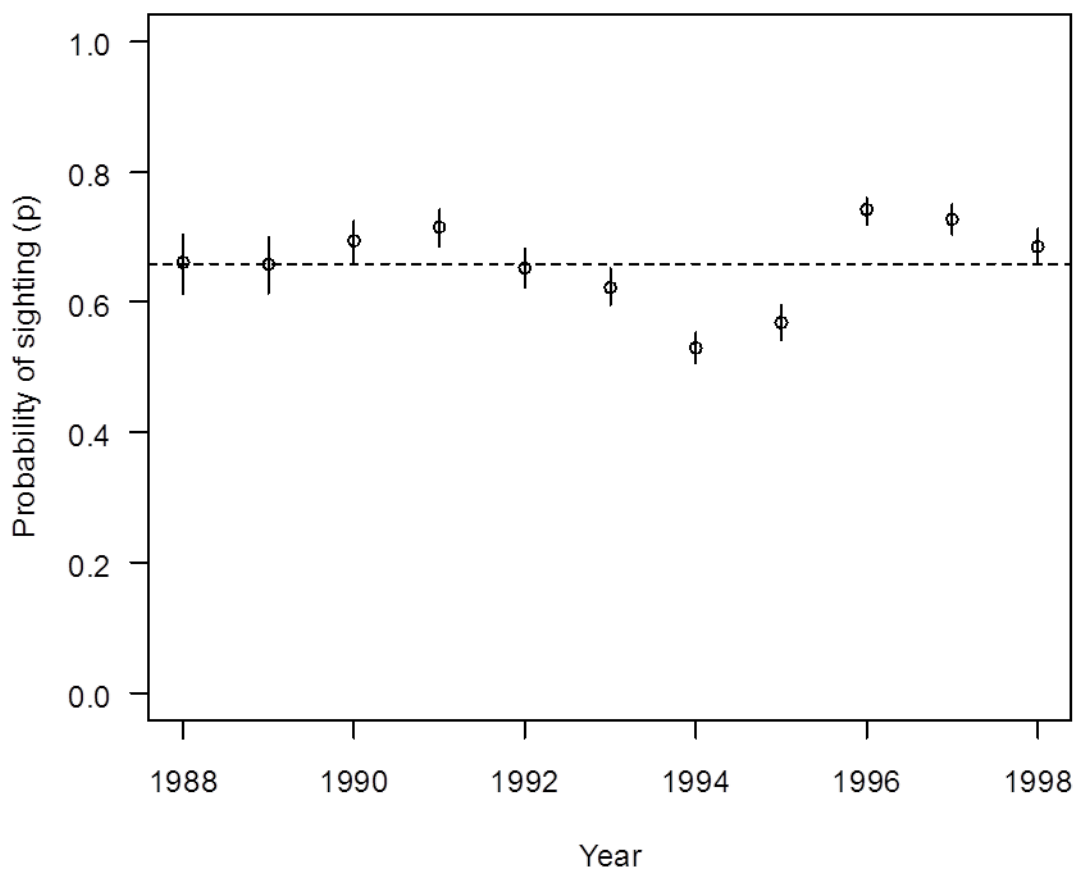


Fig. 2. Probability of sighting by year for the 1985 to 1989 cohorts and previously branded grey seals between 1988 and 1998 estimated from the preferred model ($\phi(t)p(t)pent(g^*t)N(g)$). Vertical bars indicate 95% confidence limits. The dashed line is the mean.

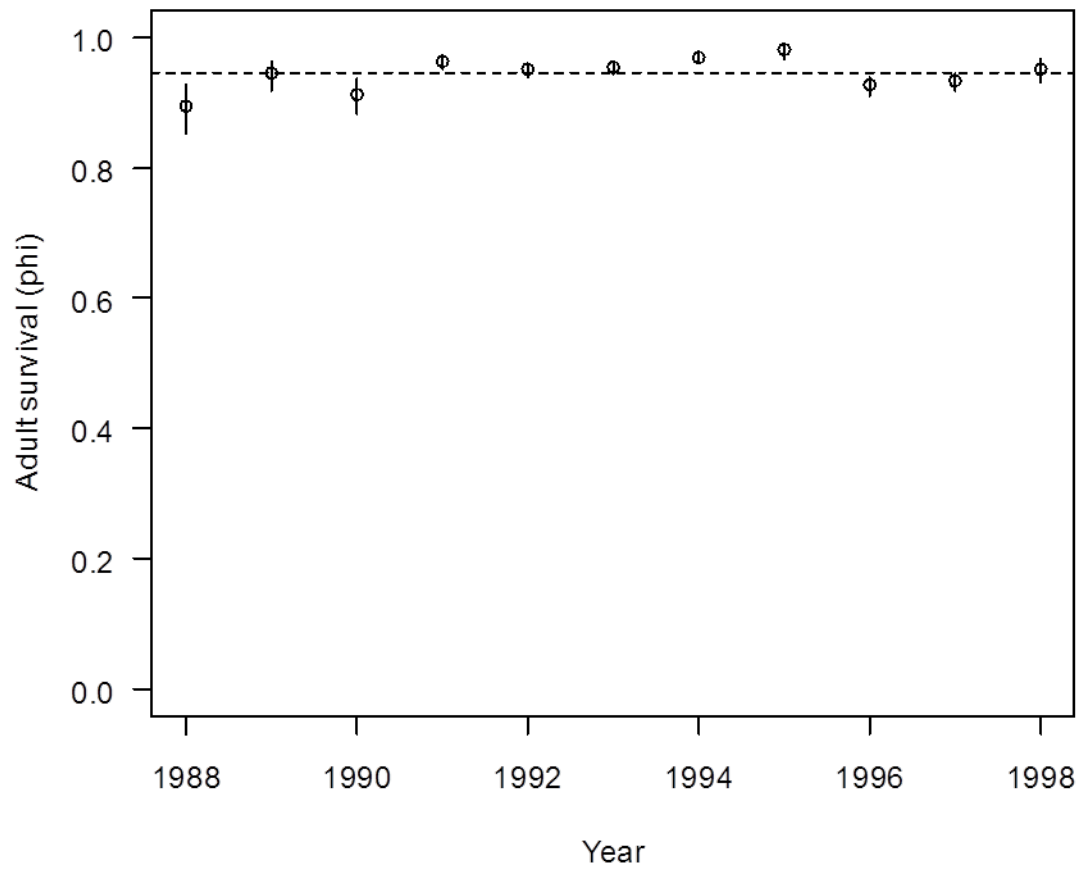


Fig. 3. Adult survival rate for 1985 to 1989 cohorts and previously branded grey seals between 1988 and 1998 estimated from the preferred model ($\phi(t)p(t)pent(g^*t)N(g)$). Vertical bars indicate 95% confidence limits. The dashed line is the mean.

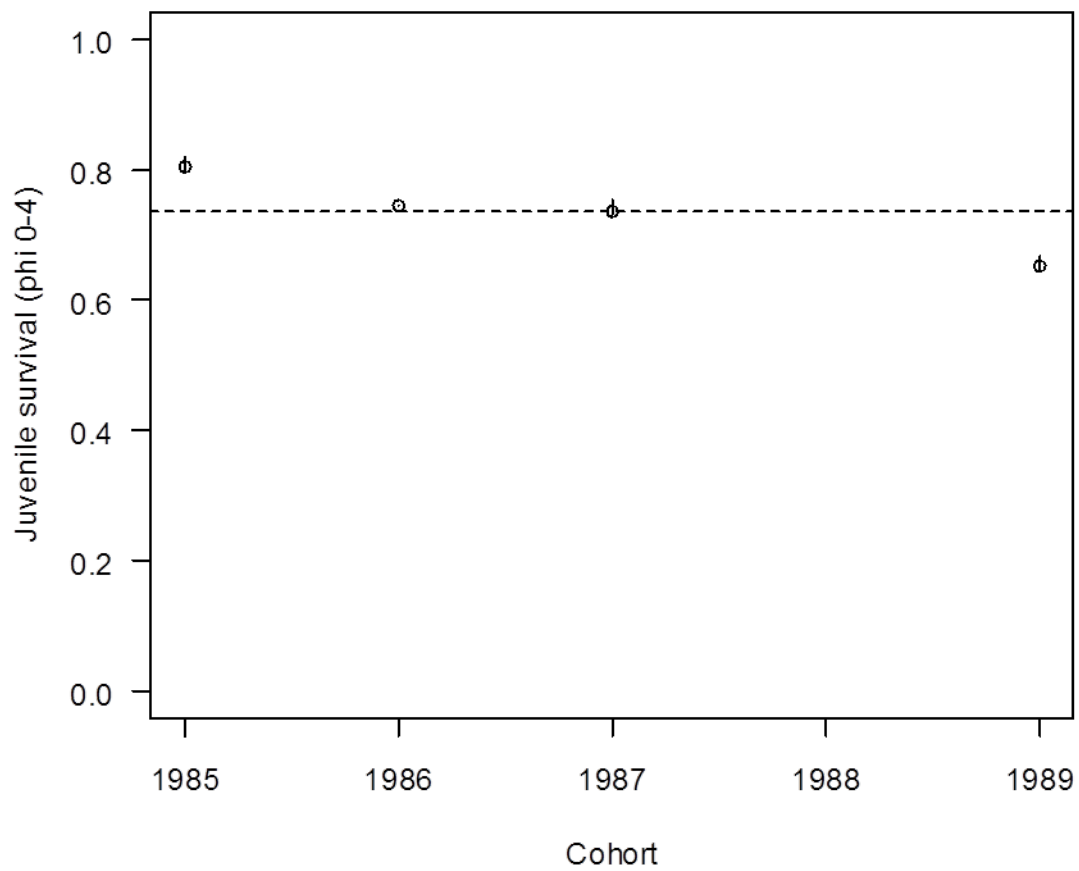


Fig. 4. Juvenile survival for 1985 to 1989 cohorts estimated from the preferred model ($\phi(t)p(t)pent(g^*t)N(g)$). Vertical bars indicate 95% confidence limits. The dashed line is the mean.

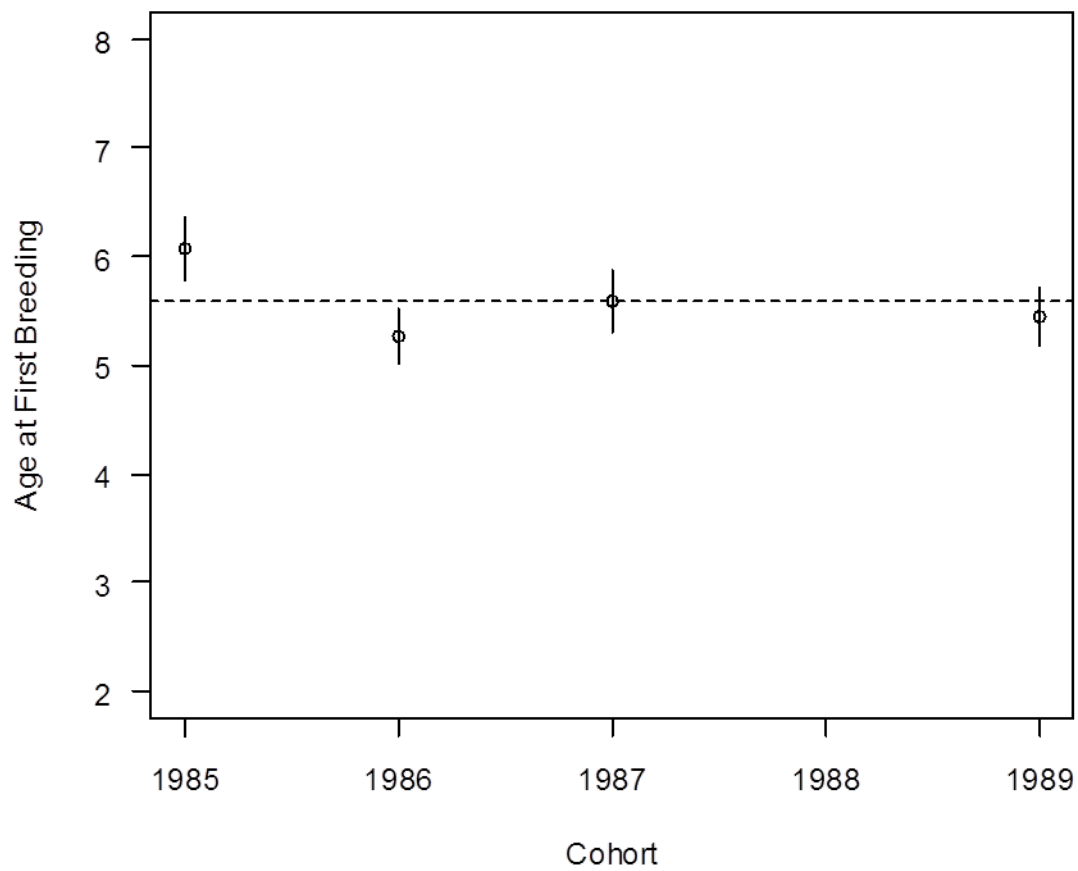


Fig. 5. Age at first breeding for 1985 to 1989 cohorts estimated from the preferred model ($\phi(t)p(t)pent(g^*t)N(g)$). Vertical bars indicate 95% confidence limits. The dashed line is the mean.

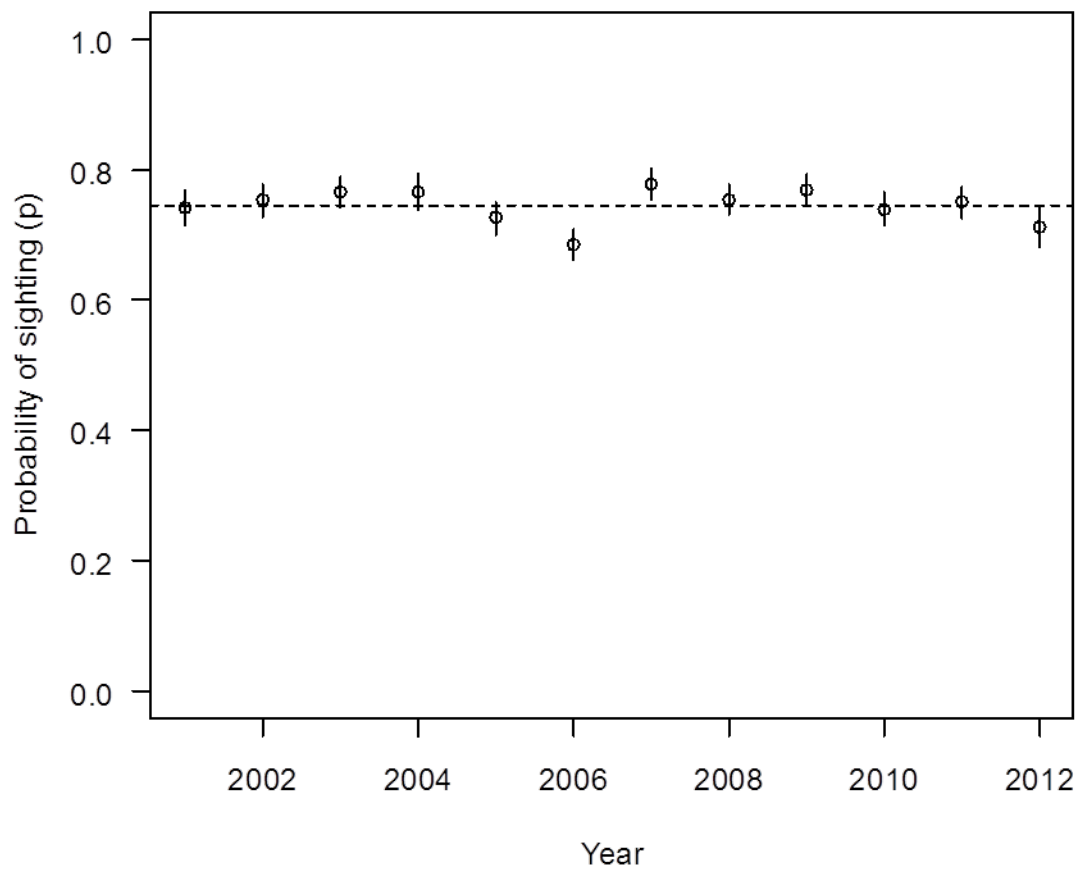


Fig. 6. Probability of sighting by year for 1998 to 2002 cohorts and previously branded grey seals between 2001 and 2012 estimated from the preferred model $(\phi(g)p(t)pent(g^*t)N(g))$. Vertical bars indicate 95% confidence limits. The dashed line is the mean.

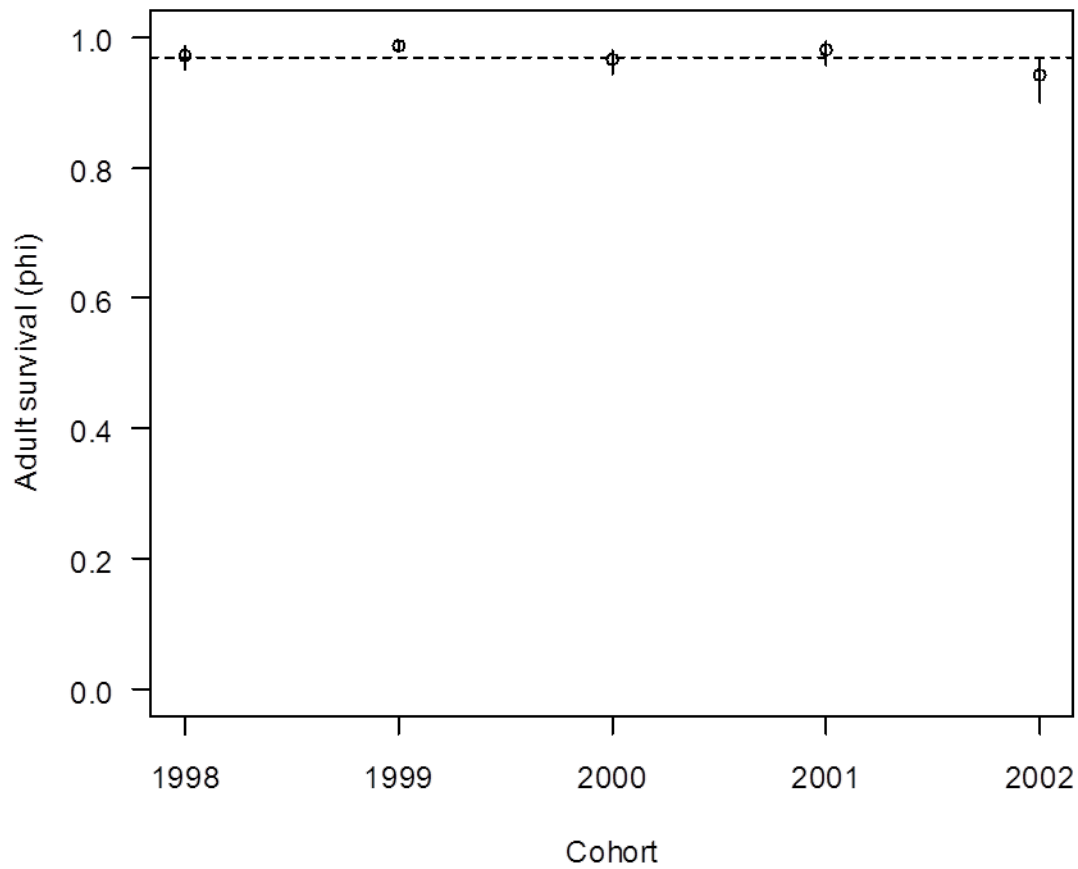


Fig. 7. Adult survival between 2001 and 2012 for the 1998 to 2002 cohorts estimated from the preferred model ($\phi_i(g)p(t)pent(g^*t)N(g)$). Vertical bars indicate 95% confidence limits. The dashed line is the mean.

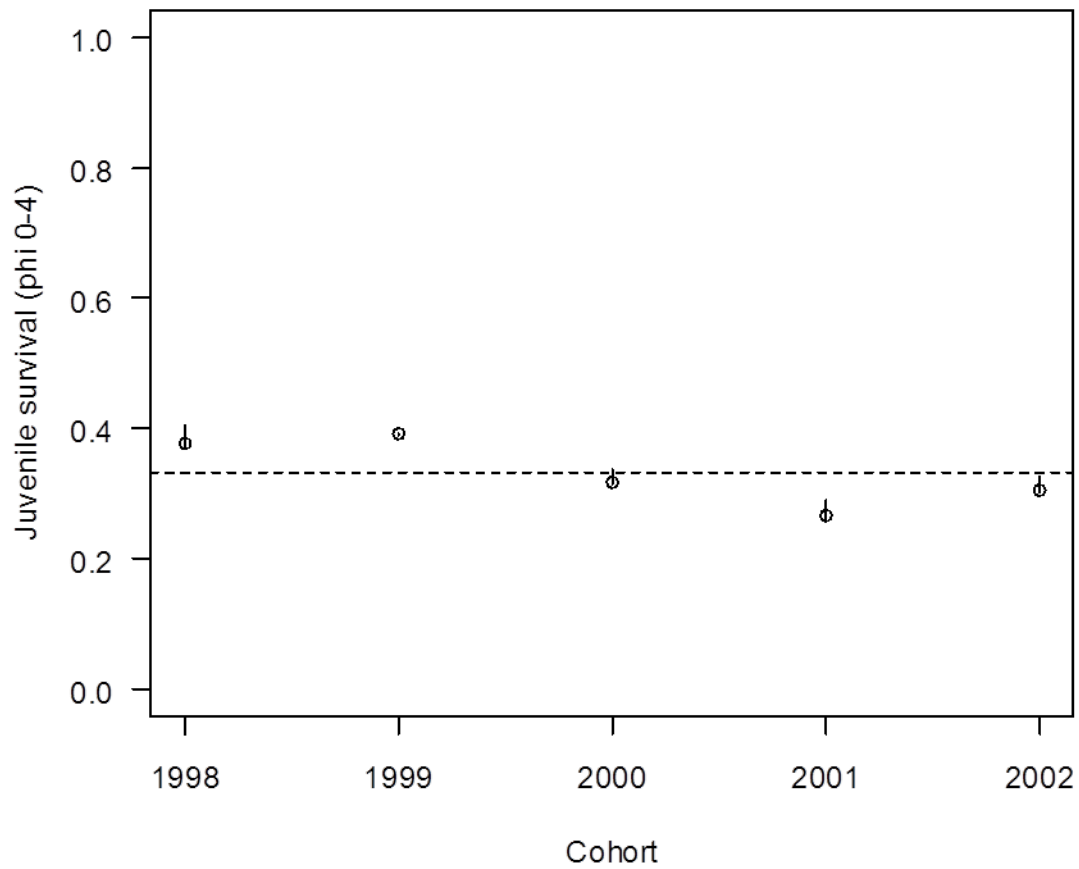


Fig. 8. Juvenile survival of the 1998 to 2002 cohorts estimated from the preferred model ($\phi(g)p(t)pent(g^*)N(g)$). Vertical bars indicate 95% confidence limits. The dashed line is the mean.

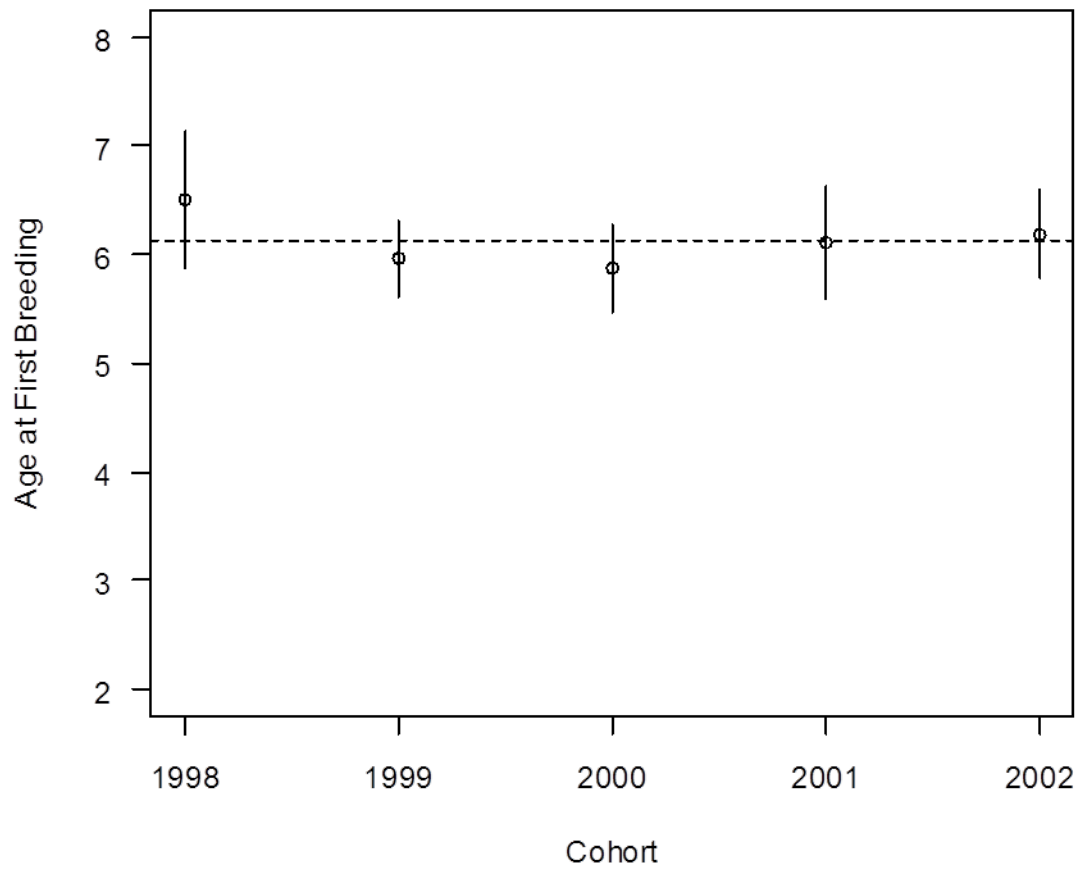


Fig. 9. Age at first breeding for 1998 to 2002 cohorts estimated from the preferred model ($\phi(g)p(t)pent(g^*)N(g)$). Vertical bars indicate 95% confidence limits. The dashed line is the mean.