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Estimating Changes in Vital Rates of Sable Island Grey Seals Using Mark-recapture Analysis

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Foreword

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ABSTRACT

After more than four decades of growth at 13%, the rate of pup production of Grey Seals (*Halichoerus grypus*) at Sable Island has declined to about 4% per year. As resource limitation becomes more acute, life history theory suggests that first juvenile survival, then adult fertility, and finally adult survival will change. Previously, mark-resight analysis of Grey Seals on Sable Island found that juvenile survival had been reduced by almost 50% between the early 1990s and early 2000s, suggesting that resources may have become limiting for this population. Here, we fit a Cormack-Jolly-Seber model to the resighting history of individually marked Grey Seals that have recruited to the Sable Island breeding colony since 1978 to estimate age- and sex-specific adult survival. Of those initially marked, 562 males and 1728 females were resighted in the breeding colony between 1978 and 2016. Average adult survival was high (male=0.943, Standard Error (SE)=0.003; female=0.976, SE=0.001), but male Grey Seals had lower survival at all ages. Resighting probability has remained between 60 and 80% since the late 1980s. Males are more likely to be sighted in a breeding season than females. Only female Grey Seals with pups are regularly sighted on the breeding colony; thus, those females that skip breeding are unobservable (temporary emigration). A multi-state open robust design model was used to estimate the transition probabilities between breeding (observable) and non-breeding (unobservable) states for individually marked females that were observed on the colony from 1992 to 2016. The first-order Markov state-dependent transition model was preferred over random transition probabilities. Females that gave birth had, on average, an 85% chance of pupping in the following year. However, females that did not give birth had a 56% chance of giving birth in the following year, suggesting that female quality plays a role in breeding probability. Although breeding probability varied among years, there was no trend over time suggesting the average natality rate has not changed and is not contributing to the slowing of the rate of growth in pup production.

Estimation des changements des indices vitaux des phoques gris de l'île de Sable au moyen d'une analyse par marquage-recapture

RÉSUMÉ

Après plus de quatre décennies de croissance à un taux de 13 %, le taux de production de petits de phoques gris (*Halichoerus grypus*) sur l'île de Sable a chuté à environ 4 % par année. Selon la théorie du cycle biologique, au fur et à mesure que les ressources se raréfient, on observe des changements d'abord dans les taux de survie des juvéniles, puis dans les taux de fertilité des adultes, et enfin dans les taux de survie des adultes. L'analyse des phoques gris marqués sur l'île de Sable a précédemment révélé que le taux de survie des juvéniles a diminué de près de 50 % entre le début des années 1990 et le début des années 2000, ce qui donne à penser que les ressources pourraient être devenues un facteur limitant pour cette population. Dans la présente étude, pour estimer les taux de survie des adultes en fonction de l'âge et du sexe, nous avons adapté un modèle de Cormack-Jolly-Seber à l'historique des observations répétées de phoques gris qui ont été marqués individuellement et recrutés dans la colonie reproductrice sur l'île de Sable depuis 1978. Parmi les phoques gris marqués au départ, 562 mâles et 1 728 femelles ont été observés une nouvelle fois dans la colonie reproductrice entre 1978 et 2016. On a constaté un taux moyen de survie des adultes élevé (mâles = 0,943, écart-type [ET] = 0,003; femelles = 0,976, ET = 0,001), et le taux de survie des phoques gris mâles s'est révélé être inférieur à tous les âges. La probabilité d'observation répétée oscille entre 60 % et 80 % depuis la fin des années 1980. Les mâles sont plus susceptibles d'être observés pendant la saison de reproduction que les femelles. Chez les phoques gris, seules les femelles accompagnées de leurs petits sont régulièrement observées dans la colonie de reproduction. Par conséquent, les femelles qui sautent une saison de reproduction ne sont pas observables (émigration temporaire). Un modèle multi-états ouvert à conception robuste a été utilisé pour estimer les probabilités de transition entre les états de reproduction (observables) et de non-reproduction (non observables) pour les femelles marquées individuellement qui ont été observées dans la colonie de 1992 à 2016. Un modèle de transition de Markov de premier ordre selon l'état a été préféré à des probabilités de transition aléatoires. Les femelles qui ont donné naissance avaient, en moyenne, une probabilité de 85 % de mettre bas l'année suivante. Toutefois, les femelles qui n'ont pas donné naissance avaient une probabilité de 56 % de mettre bas l'année suivante, ce qui donne à penser que la qualité reproductive des femelles joue un rôle dans la probabilité de reproduction. Bien que la probabilité de reproduction ait varié d'une année à l'autre, aucune tendance au fil du temps n'a été constatée, ce qui semble indiquer que le taux de natalité moyen est demeuré stable et qu'il ne contribue pas à la baisse du taux de production de nouveau-nés.

INTRODUCTION

The grey seal (*Halichoerus grypus*) breeding population at Sable Island grew exponentially from the time when monitoring of pup production began in the 1960s until the late 1990s (Bowen et al. 2007). As a result of this growth, Sable Island is home to the largest grey seal breeding colony in the world and currently accounts for more than 85% of the pup production in the Northwest Atlantic. The rate of increase in pup production slowed from 13% prior to 1997 to roughly 4% between 1997 and the present (Bowen et al. 2011, den Heyer et al. 2017). The reduced growth rate in this population suggests that the population is approaching carrying capacity. This conclusion is supported by a large reduction in the estimated juvenile survival of females from 65-80% in the late 1980s and early 1990s to 27-40% in the early and mid-2000s (den Heyer et al. 2014). Life history and population dynamics theory predicts that in long-lived vertebrate populations experiencing resource limitation density dependence in vital rates will be expressed first in juvenile survival, then in reduced natality and finally in reduced adult survival (Eberhardt 1985).

Grey seals are long-lived, size-dimorphic capital breeders (Bowen et al. 2006). Females are smaller than males and mature earlier. Longevity in males is about 35 years; females can live to 45 years (Mansfield and Beck 1977). On Sable Island, females begin to pup at age 4 years or older, and remain fertile for several decades (Bowen et al. 2006). Females are annual breeders giving birth to a single pup during the period December to February. They attend their pup for a 16-18 day lactation period during which they fast (Bowen et al. 2006, Iverson et al. 1993). Newly weaned pups fast for several weeks before going to sea for their initial foraging trip (Noren et al. 2008). Male grey seals recruit to the breeding colony at older ages than females, typically 7-9. Males are also considered capital breeders, although they may return to the sea to feed during the breeding season (Lidgard et al. 2005). As a result, their sighting probability at the breeding colony may be lower than that of females.

The Northwest Atlantic grey seal population is comprised of three breeding components – Sable Island, the southern Gulf of St. Lawrence, and the eastern shore of Nova Scotia (Thomas et al. 2007). The management plan for grey seals recognizes these three components to estimate the level and geographic distribution of sustainable removals. Population size of each of these components is estimated using an age-structured population model fitted to the time series of pup production estimates, estimates of female pregnancy rates and removals reported to Fisheries and Oceans Canada (DFO). During the period of exponential growth, the age structure, and average survival and fertility rates of the Sable population have been relatively constant. As the population growth rate has slowed, both vital rates and the age structure will have changed.

The annual sightings of uniquely branded animals allows for the estimation of changes in vital rates that are contributing to the reduction in the rate of increase in pup production. Here, we use a Cormack-Jolly-Seber (CJS) model to estimate the age-specific survival of adult male and female grey seals since 1988. We also fit a multi-state, open robust-design model to estimate the proportion of females that are unavailable for brand resighting on the breeding colony because they have skipped breeding (temporary emigration) between 1988 and 2016. The robust design allows for the estimation of the transition between the observed breeding state and the unobservable non-breeding state by estimating sighting probability from multiple brand resighting events during each breeding season. These vital rate data will improve our estimation of total population size from the number of pups produced at the breeding colonies throughout the Northwest Atlantic.

MATERIALS AND METHODS

DATA COLLECTION

Marking

We conducted our study on Sable Island (43°55′ N, 60°00′ W), a partially vegetated sandbar approximately 160 km off the east coast of Nova Scotia, Canada. Fisheries and Oceans Canada (DFO) has been monitoring the grey seal population of Sable Island for more than 40 years (Hammill et al. 2017). Between 1963 and 2002, more than 6,000 newly weaned pups were individually marked with permanent hot-iron brands (Table 1). Three selection criteria determined which pups were branded. First, pups had to appear healthy. Second, pups had to have moulted their lanugo. Third, pup's pelage had to be dry. Pups of branded mothers with known weaning mass which met the other criteria were preferentially selected. Pups were not selected on the basis of size. On an adult the characters are 8-10 cm high and 6 cm wide and easily read at a distance of 5-10 m.

Resighting Effort

Whole-island censuses to identify branded individuals have occurred annually during the 1978 to 2016 breeding seasons (Appendix 1). The objective throughout the time series was to census all branded adults during each brand resighting occasion. However, resighting methods and effort changed somewhat as the colony expanded to use more of the island and new technology became available. When the colony was small and confined to a small part of the island, resighting censuses were conducted on foot by 2-4 investigators. Since 1985, censuses have been conducted using all-terrain vehicles that permit the entire colony to be searched thoroughly for branded adults in 2–3 days. Resighting censuses prior to 1992 were completed every 5 to 7 days, and since 1992 resighting has occurred every 7 days. In the early 1990s, a sightings score (1 – good quality sighting or 2 –poor quality sighting) was added to the field protocol. Poor quality sightings occur when brands could not be determined because some of the characters were indistinct, or pelage pattern, colour, sand, or other debris obscured part of the brand. Only unscored (older data) and quality 1 sightings are retained for the analysis. Inevitably, some brands will have been misread. Thus, marked animals that were not sighted at least 3 times or whose sex was unknown were excluded. As the youngest females observed with pup are 4 years old, we also excluded sightings of animals age 3 or younger.

MARK-RECAPTURE MODELS

Cormack-Jolly-Seber (CJS)

Here we fit a CJS, survival only, model to sightings histories of male and female seals seen on the breeding colony between 1978 and 2016. For this analysis, the first year a seal is seen on the breeding colony it is considered marked. In subsequent years, if it is seen on one or more brand resightings within a breeding season it is considered resighted. The probability of sighting (p) is not estimated for the initial breeding season, but at each subsequent breeding season p is estimated. The first apparent survival (phi(1)), is from initial sighting to the first resighting and subsequent phi(i) is estimated between resighting events. Seals that emigrate are not available for resighting and so appear to have died. The survival rate between the last two encounter occasions is not estimable because only the product of survival and probability of sighting for this occasion is identifiable.

The assumptions of the CJS model are that:

- every marked animal present in the population at time (i) has the same probability of sighting;
- every marked animal in the population immediately after time (i) has the same probability of surviving to time (i+1);
- marks are not lost or misread;
- all samples are instantaneous relative to the interval between occasion (i) and (i+1); and
- independence of capture histories.

Using this model, we tested for differences in age-specific apparent survival of male and female grey seals (Table 2). Previous work has shown that adult females reach peak reproductive performance by age 8 to 10 and have high survival and reproductive performance until age 25 (Bowen et al. 2006). Males recruit to the breeding colony at older ages and have a shorter lifespan than females, thus we included the interaction of sex and age on apparent survival and probability of sighting. Because of low sightings of older animals, particularly males, we binned the oldest ages into a plus group (25+). We also fit models with 2 and 6 age bins (Table 2) to identify parsimonious models of age effects.

Multi-state Open Robust Design (ORDMS)

Adult female grey seals exhibit high colony site fidelity (Bowen et al. 2015). Sightings of branded females in breeding colonies other than Sable Island are rare. Although adult females that return to Sable Island to give birth are easily detected, pre-breeders and those that are not pregnant, rarely haulout in the breeding colony and are essentially unobservable. Here, we use a multi-state open robust design (ORDMS) mark-recapture model conditioned upon recruitment to the breeding colony to estimate the transition of females to and from the unobservable non-breeder state. The robust model uses the multiple resighting censuses (secondary sightings) within a breeding season (primary sightings) to estimate the probability of sighting in a breeding season (Figure 1). The open robust design model is a modification of Pollock's robust design (Pollock 1982, Kendall et al. 1997, 1995) that allows for both arrivals and departures within the primary sighting period (Schwarz and Stobo 1997, Kendall and Bjorkland 2001, Kendall and Nichols 2002).

As with the CJS model, the ORDMS assumes that there is homogeneity in sightings and capture probabilities, no tag loss, and independence of capture histories. The ORDMS with temporary emigration (unobservable state) also assumes:

- no mortality within a primary session;
- transition between states only occurs between primary sessions; and
- survival is the same for both the observed and unobserved state.

Secondary Sightings

There are three types of parameters associated with the secondary sightings in the open population model: probability of sighting (p), survival or emigration (Phi), and probability of entry (pent) (Schwarz and Stobo 1997). Here we use the Kendall and Bjorkland (2001) formulation that allows for the emigration term (Phi) to be a function of time since arrival (tsa).

The first step of our analysis was to identify appropriate models for the secondary sightings. To do this we fit a suite of multi-state open robust design models (Table 3) to each primary period. We included both time variable and time since arrival emigration (Phi) models as probability of female departure may vary with weather conditions and time since parturition. We know that grey seals arrive on the island between December and January with a peak in early January. Therefore, the probability of entry (pent) was modelled as time variable. Inclusion in this analysis is conditional upon being sighted within a primary period, so sum of all pent is equal to 1 and estimated with the mlogit link. We modelled the probability of sighting (p) on a secondary resighting census as constant or time variable. Complete resighting censuses were completed during each secondary sighting period, but variability in weather conditions and the resighting team may have resulted in temporal variability in the probability of resighting.

Based on the preliminary analysis, two secondary sightings models were included in the ORDMS models for the whole time series:

1. p(~session)Phi(~tsa)pent(~time), and
2. p(~session)Phi(~tsa)pent(~time:session).

For both models, the probability of sighting (p) for each secondary sighting occasion was modelled to be different for each primary period but constant within that breeding season. For both these models, emigration is a function of time since arrival. Again, the parameters are shared across all years, as we assume that parturition has not changed. The models differ in how the probability of entry is modelled. In the pent(time) model, it is assumed that the probability of entry is a function of the time within the primary session, with the parameters shared across years. In the pent(time:session) model, a separate set of pent parameters are fit for each primary session. The latter model was included to better describe variability in breeding colony phenology and the timing of arrival and departure of researchers.

Primary Sessions

The parameters in the open robust-design multi-state model are the probability of transition (Psi) between states and survival (S) between primary samples. Once recruited, females can be in one of two states during a breeding season – breeder (‘1’) or non-breeder (‘U’). The estimation of resighting probability for a primary period (p*) allows for the estimation of temporary emigration or transition to an unobservable state, in this case non-breeder. The mlogit link was used to constrain the total of Psi for each state, such that for any time between 2 primary sessions (t) the sum of Psi $_{\text{U to 1}}$, t and Psi $_{\text{U to U}}$, t is 1 and the sum of Psi$_{\text{1 to U}}$, t and Psi$_{\text{1 to 1}}$, t is 1.

We developed a small set of models (Table 7) to describe changes in reproductive rates over time. Because our earlier analysis indicated that survival varied with age, we included a model that estimated survival with 2 age bins (age 4 to 24 and 25 plus). We fit both random and first-order Markov transition probabilities. Random temporary emigration occurs when all individuals have the same probability of becoming a temporary emigrant (transitioning to the unobserved state). This is the transition processed fit by Schwarz and Stobo (1997), when they first developed open roust design mark-recapture analysis using the Sable Island grey seal mark-recapture program. First-order Markovian temporary emigration occurs when the probability of temporary emigration at time i is influenced by the state at time i-1, for example if a breeder in one year is more or less likely to breed in subsequent years. To address confounding of the terminal parameter in the Markov model, the transition probabilities in last 2 time periods are set to be equal. Future analysis will explore more biologically relevant age structures and test for variability between cohort groups in the transitions between juvenile and adult survival.

MODEL SELECTION

All models were fit using MARK (White and Burnham 1999) called through RMark (Laake 2013) in R 3.2.5 (R Core Team 2016). Evidence in favour of competing models was evaluated on the basis of lowest Akaike information criterion (AIC), with finite sample correction (AICc), smallest

Δ AICc, highest AICc weights (w) and evidence ratios (Burnham and Anderson 2002). A suite of candidate models was developed from the full model. All models having a Δ AICc < 2 were considered as having some support, but we preferred models with fewest parameters and the highest w, and, therefore, highest evidence ratio. Means are presented with standard errors (SE) throughout and results of hypothesis tests were judged significant at $p < 0{\cdot}05$. Goodness of Fit (GOF) was tested using RELEASE for the CJS analysis.

RESULTS

Between 1963 and 2002, 6213 grey seals were individually marked. Of these, 2290 were resighted on the Sable Island breeding colony between 1978 and 2016. The number of branded females sighted within any breeding season ranged from 62 in 1979 to 1155 in 2000 (Appendix 1). On average, individuals are seen twice in a breeding season. Prior to the mid-1980s the number of resightings was low and resighting effort varied from 1 to 6 whole island censuses per season. Since the mid-1990s, the resighting effort has stabilized with 4-7 weekly censuses.

In recent years, the number of branded seals seen during a breeding season has declined as cohorts marked in the 1980s are no longer alive. Schwarz and Stobo (1997) estimated a 4.6% misread of brands in the data collected from Sable Island grey seals between 1982 and 1995 based on the proportion of 1973 cohort brands sighted in 3 or fewer years (113 sightings of 2,438). Here we filtered any brands that were not sighted on 3 occasions in our entire sightings database from 1973 to present (1,324 sightings of 67,498 were dropped). The discovery curves for males and females show differences in recruitment to the breeding colony (Figure 2). Notably for both males and females, some seals first appear in the population older than age 16. It is possible that these are brand misreads. For the CJS model only those seals that were sighted for first time after age 20 were dropped (5 males and 5 females) to accommodate the later recruitment of males, and the low sighting probability in the early part of the time series. For the multi-state open robust analysis of female only sightings, seals that recruited after age 16 were filtered (n=15 females).

Ninety-eight models were fit to the resighting histories of male and female grey seals between 1978 and 2016. The models with the lowest AIC had probability of sighting (p) as a function of sex and time (Table 4, Appendix 2), with females having lower sighting probability than males (Figure 3, Appendix 3). A complete model selection table is presented in Appendix 2. The preferred model for apparent survival is an additive model indicating that apparent survival for females is higher at all ages (Figure 4). The Phi(ageb2+sex) model with just an adult (age 4-25) and senescent age bin (age 25+) provides estimates of survival that can be used in the assessment model: $\text{Phi}_{4\text{-}24,\text{male}}$=0.970 (SE=0.002); $\text{Phi}_{25\text{plus, male}}$=0.77 (SE=0.01); $\text{Phi}_{4\text{-}24,\text{female}}$=0.989 (SE=0.001); $\text{Phi}_{25\text{plus, female}}$=0.904 (SE=0.004). Adult survival estimated from the Phi(sex) model without age is Phi_{male}=0.943, SE=0.003; $\text{Phi}_{\text{female}}$=0.976, SE=0.001. Notably, the models with 6 age bins for survival had more weight than the fully age-specific models. Given that both sightings probability and survival differ for males and females, and that the data available with respect to range of age classes varies between the two sexes, further analysis explored separate models for each sex. However, here, in the context of a two sex model, we have shown a difference in survival of males and females.

The goodness of fit test (Table 5) suggested that the model did not adequately describe the heterogeneity in the survival.

ORDMS

Between 1992 and 2016, the Sable Island grey seal breeding colony has been growing and the brand resighting effort has been increased to cover a longer breeding season. In more recent years, the first brand resighting session has been done in mid to late December and brand resighting has continued until the third week of January. On average, there were 5 secondary periods per year. The probability of resighting (*p**) for each primary sampling period ranged from 0.80 to 0.95 (Table 6). The preferred model of emigration between secondary sightings (Phi) was time since arrival in all cases, except 2 years. In 2007 and 2016, emigration was constant in the preferred model. In all years except 2016, the probability of entry in the final brand resighting was less than 0.15, with only 4 years (1992, 1994, 2009 and 2016) above 0.10. Nonidentifiability of parameters near the end and start of secondary sampling chain does not lead to serious bias, as long as few animals arrive before the first secondary sample and the sampling process is continued until most animals have arrived (Schwarz and Arnason 1996; Schwarz and Stobo 1997). Thus, our estimates should not be biased as a result of missing a portion of the marked population.

All 8 multi-state open robust models converged. The top-ranked ORDMS models included the probability of entry as a function time and session (Table 7). Given the variation in breeding phenology as well as the variation in the extent and timing of our winter field programs, this is not surprising. Notably the probability of entry was not well estimated for the secondary sessions in nine primary sessions (Appendix 4). As there were data for these sessions, the number of parameters in the AIC calculations were not adjusted. The preferred model included age variable survival. These estimate $S_{4\text{-}24}$=0.988 (SE=0.001) and S_{25+}=0.904 (SE=0.004) are comparable to the CJS results fit to resightings histories of both males and females. The first-order Markov models of the transition parameters (Psi) had lower AIC and much higher weight than the models with random temporary emigration. The preferred model estimated a transition probability from breeder to breeder of 76% to 89% and the transition from unobserved to breeder to be 41% to 64% (Figure 5). The random temporary emigration model estimates probability of breeding at 80% with variation over time. There was no indication of a long-term trend in grey seal natality rate on Sable Island.

DISCUSSION

After more than four decades of growth at 13%, the rate of pup production of grey seals at Sable Island has declined to about 4% per year since the late 1990s. As resource limitation becomes more acute, life history theory suggests that first juvenile survival, then adult fertility, and finally adult survival will change. Here we use 40 years of mark-recapture data from uniquely marked seals on the Sable Island to estimate age and sex-specific adult survival. The results of our analysis indicate that despite this slowing of population growth rate, adult survival remains high and has not changed over four decades. The two-sex CJS model found that adult females have higher survival than males at all ages. We also fit a multi-state open robust design model to female resighting histories since 1992. The preferred model included a state-dependent probability of breeding that showed variation over time but no temporal trend over the past 2 decades. Breeding females had, on average, an 80% probability of breeding in subsequent years, while non-breeding mature females were less likely to breed in subsequent years, suggesting that there is heterogeneity in female quality.

Previous analysis of the mark-recapture data found a marked decline in the survival rate of juvenile grey seals at Sable Island (ages 0 to 4 years) from 76% to 33% (den Heyer et al. 2014). Eberhardt (1977) and Eberhardt and Siniff (1977) proposed that in marine mammals there should be a 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 theory has been reported in several marine mammal taxa (Brault and Caswell 1993, Caswell et al. 1999, Rotella et al. 2012), and in long-lived birds (Saether et al. 2002). 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 (1997) analysed the sightings between 1978 and 1994 of females born and branded in 1973. Throughout this period the estimated return rate, or proportion of females on the breeding colony, was high, ranging from of 0.804 to 1.09. Schwarz and Stobo (1997) also estimated sighting probabilities for female grey seals on the Sable breeding colony between 1978 and 1994. Probability of sighting varied between 0.110 and 0.868, with a marked improvement over time. Since that analysis, the sightings effort during the breeding season on Sable Island has become more standardized, and the CJS estimates of the probability of sighting during a breeding season for both males and females is just under 80%.

Both the CJS and the ORDMS models estimate apparent survival. While it is not uncommon to get reports of marked grey seals in haul out groups in US waters and elsewhere, we have received very few reports of seals marked on Sable at breeding colonies other than Sable (between 2010 and 2016, n=8, unpublished data). The one female marked on Sable Island and seen with a pup on a breeding colony in US waters (Seal Island, Maine, breeding season 2014), has not been seen on Sable since marking. Only those seals that recruited to the Sable breeding colony are included in the mark-resighting analysis presented here, and the high survival rates estimated for both adult male and female grey seals leave little latitude for emigration to confound our estimates of survival.

Violation in the assumptions of the mark-recapture models can bias point estimates of survival and capture (i.e., sighting) probability. The first assumption is that every marked animal has the same probability of being sighted. For the CJS model, temporary emigration to the unobservable non-breeding state is incorporated in the resighting probabilities for females. Individual variation, as well as age-specific pregnancy rates, could result in different sighting probabilities and introduce bias. Heterogeneity in resights typically results in small negative bias in survival estimates. Here we have such high survival rates and long encounter histories that the heterogeneity in resighting probability would have little impact on estimates of survival (Nichols and Pollock 1983). The second assumption of CJS and ORDMS models is that every marked female has the same probability of survival to the next sampling period (i.e. breeding season). Again, individual variation 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 because the survival rate is very high. The third assumption is that marks are neither lost or overlooked, and are recorded correctly. Brands are permanent marks that are easily read at a distance. While there are some poor quality brands in the population, our sightings data indicate that poor quality brands are rare. Misreads are probably not random, as some characters more likely than others to be confused, e.g. 3 and 8. If there are pairs of brands that are never seen in the same year, temporary emigration could be overestimated in the ORDMS model and sighting probability will be underestimated in CJS model. Given the ease with which individuals can be approached on the colony, and the rigorous and systematic nature of resighting censuses, it seems unlikely that this assumption has been violated to the extent that serious bias would result. 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 annual interval over which vital rates are estimated. The fifth 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.

There are additional assumptions for the multi-state open robust design model. First, it is assumed that an individual exists in only one state in a primary session. Here, all females seen on breeding colony pregnant or with pup are considered breeders in that year, and those animals not seen are either non-breeders or were missed during brand resighting censuses. We also assume that survival of both the breeders and unobservable non-breeders is the same. Again, as our apparent survival rates are high, there is little latitude for variation in survival. Finally, our model assumes no mortality in the secondary samples, which is justified as most females spend just under 3 weeks on the breeding colony (Bowen et al. 2006). Notably, the preferred ORDMS models included first-order Markov transition probabilities. Ignoring Markovian temporary emigration can produce bias in other parameters (Kendall et al. 1997, Kendall and Bjorkalnd 2001), and future mark-recapture analysis should include state-dependent transitions.

The long-term resightings data from the Sable Island grey seal breeding colony provides opportunity to better estimate demographic rates and understand the mechanisms that regulate the population. These estimates will help to improve our management of this commercial species and understand its role in the marine ecosystem. Here we present two analysis that estimate important demographic rates in the stock assessment model, adult survival and reproductive rates.

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TABLES

Table 1. Number of seals individually marked on Sable Island by cohort and resighted between 1978 and 2016. In some years the sex of the marked seals was not recorded, those years have a dash in the column for male and female.

Cohort	**Marked**			**Resighted**		
	Male	**Female**	**Total**	**Male**	**Female**	**Total**
1969	-	-	417	30	67	97
1970	-	-	575	48	102	150
1973*	300	300	600	74	112	186
1974	-	-	316	45	69	114
1985*	100	400	500	45	249	294
1986*	100	400	500	57	238	295
1987*	100	400	500	36	257	293
1989*	0	500	500	5	300	305
1998	145	155	300	34	51	85
1999	243	258	501	76	95	171
2000	252	248	500	41	63	104
2001	235	266	501	31	61	92
2002	252	251	503	40	64	104
Grand Total	**1727**	**3178**	**6213**	**562**	**1728**	**2290**

*prior to 1998 the sex of the pups at branding was not reliably recorded and the sex ratio of branded seals may vary.

Table 2. Models fit to the primary sightings (CJS model) between 1978 and 2016 where Phi equals apparent survival and p equals sighting probability. Age in years.

Phi	**p**
Sex Time age as factor: 4 to 24, and 25+ age as factor, with 2 bins: 4-24, and 25+ age as factor, with 6 bins: 4-9, 10-14, 15-19, 20-24, 25-29, 30+	Sex Time age as factor: 4 to 24, and 25+ age as factor, with 6 bins: 4-9, 10-14, 15-19, 20-24, 25-29, 30+

Table 3. Models fit to the secondary sightings between 1992 and 2016 where pent=probability of arrival, time=year, Phi = survival probability, tsa=time since arrival.

Secondary Sightings Models
pent(~time) Phi(tsa) p(~1)
pent(~time) Phi(tsa) p(~time)
pent(~time) Phi(~time) p(~1)
pent(~time) Phi(~time) p(~time)
pent(~time) Phi(~-1+tsa*time) p(~1)
pent(~time) Phi(~-1+tsa*time) p(~time)

Table 4. AIC for selected models fit to the resighting histories of male and females grey seals on Sable Island between 1978 and 2016. AICc= Akaike Information Criterion for small sample sizes, ∆AICc = relative change in AICc, w_i = AIC weights, K = number of parameter. The full model selection table is Appendix 2.

Model	**K**	**AICc**	**∆AICc**	**w_i**	**Deviance**
Phi(~ageb6 + sex)p(~time + sex)	46	52992.94	0	0.878687	39829.78
Phi(~-1 + ageb6:sex)p(~time + sex)	51	52996.9	3.960109	0.121313	39823.7
Phi(~ageb6 + sex)p(~time)	45	53039.78	46.84041	5.92E-11	39878.62
Phi(~-1 + ageb6:sex)p(~time)	50	53042.95	50.0058	1.22E-11	39871.75
Phi(~age + sex)p(~time + sex)	61	53124.19	131.2511	0	39930.91
Phi(~-1 + age:sex)p(~time + sex)	81	53146.77	153.8293	0	39913.28
Phi(~age + sex)p(~time)	60	53171.51	178.5704	0	39980.24
Phi(~-1 + age:sex)p(~time)	80	53194.61	201.6677	0	39963.13
Phi(~ageb6)p(~time + sex)	45	53213	220.0564	0	40051.84
Phi(~ageb2 + sex)p(~time + sex)	42	53220.13	227.1815	0	40064.98

Table 5. Goodness of Fit (GOF) test for CJS model with cohort of branding (birth year) and sex as the groups.

	Chi.square	**df**	**p**
TEST2	2801.7984	815	0.0000
TEST3	294.0963	321	0.8569
Total	3095.8948	1136	0.0000

Table 6. Summary of the open population (POPAN) models fit to secondary sightings in each year. For each year the preferred model, the number of brand resighting censuses (n sessions), the estimate of the probability of entry in the final resighting event (Final pent), the estimate probability of sighting for that primary sighting occasion or year (p) with upper and lower confidence intervals, and the estimate of the number of resighting events females available for sighting (Residence time, weeks). ll=lower 95% confidence limit, ul=upper 95% confidence limit.*

Year	Preferred Model	N sessions	N seals	Final pent	p*	p* ll	p* ul	Residence time
1992	pent(~time)Phi(~tsa)p(~1)	4	607	0.11	0.88	0.86	0.91	2.07
1993	pent(~time)Phi(~tsa)p(~1)	5	641	0.00	0.86	0.83	0.89	1.96
1994	pent(~time)Phi(~tsa)p(~1)	3	633	0.15	0.85	0.82	0.88	1.82
1995	pent(~time)Phi(~tsa)p(~1)	4	695	0.08	0.80	0.75	0.86	1.66
1996	pent(~time)Phi(~tsa)p(~1)	5	921	0.05	0.92	0.90	0.93	2.29
1997	pent(~time)Phi(~tsa)p(~1)	6	905	0.01	0.90	0.88	0.92	2.54
1998	pent(~time)Phi(~tsa)p(~1)	5	835	0.04	0.95	0.94	0.96	2.52
1999	pent(~time)Phi(~tsa)p(~1)	5	910	0.02	0.92	0.9	0.93	2.36
2000	pent(~time)Phi(~tsa)p(~1)	6	962	0.02	0.95	0.94	0.95	3.02
2001	pent(~time)Phi(~tsa)p(~1)	7	849	0.02	0.87	0.85	0.89	2.57
2002	pent(~time)Phi(~tsa)p(~1)	5	867	0.07	0.92	0.90	0.93	2.21
2003	pent(~time)Phi(~tsa)p(~1)	6	894	0.00	0.93	0.92	0.94	3.04
2004	pent(~time)Phi(~tsa)p(~1)	5	877	0.05	0.93	0.91	0.94	2.29
2005	pent(~time)Phi(~tsa)p(~1)	5	910	0.01	0.90	0.89	0.92	2.34
2006	pent(~time)Phi(~tsa)p(~1)	6	884	0.03	0.94	0.93	0.95	2.88
2007	pent(~1)Phi(~1)p(~1)	6	976	0.20	0.86	0.84	0.88	2.36
2008	pent(~time)Phi(~tsa)p(~1)	6	935	0.04	0.93	0.91	0.94	2.87
2009	pent(~time)Phi(~tsa)p(~1)	4	929	0.14	0.93	0.91	0.94	2.61
2010	pent(~time)Phi(~tsa)p(~1)	6	871	0.04	0.88	0.86	0.90	2.19
2011	pent(~time)Phi(~tsa)p(~1)	6	869	0.04	0.91	0.89	0.92	2.47
2012	pent(~time)Phi(~tsa)p(~1)	6	804	0.03	0.95	0.93	0.96	3.17
2013	pent(~time)Phi(~tsa)p(~1)	6	783	0.00	0.94	0.93	0.95	2.70
2014	pent(~time)Phi(~tsa)p(~1)	5	715	0.02	0.89	0.87	0.91	2.46
2015	pent(~time)Phi(~tsa)p(~1)	5	654	0.04	0.89	0.87	0.91	2.47
2016	pent(~1)Phi(~1)p(~1)	7	675	0.17	0.86	0.84	0.88	2.60

Table 7. Model section results for survival (S) and transition probability (Psi) between breeding seasons, and the probability of entry (pent), emigration (Phi) and sighting probability (p) within breeding seasons for female grey seals on Sable Island. AICc= Akaike Information Criterion for small sample sizes, ΔAICc = relative change in AICc, w_i = AIC weights, K = number of parameter.

Model	**K**	**AICc**	**ΔAICc**	**w_i**	**Deviance**
S(~agebin)Psi(~ctime+stratum) pent(~-1+time:session)Phi(~tsa)p(~session)	168	146367.1	0	1	146029.6
S(~1)Psi(~ctime+stratum) pent(~-1+time:session)Phi(~tsa)p(~session)	166	146994.0	626.8852	0	146660.5
S(~agebin)Psi(~time) pent(~-1+time:session)Phi(~tsa)p(~session)	167	147047.6	680.5325	0	146712.2
S(~1)Psi(~time) pent(~-1+time:session)Phi(~tsa)p(~session)	165	147679.4	1312.3279	0	147348.0
S(~agebin)Psi(~ctime+stratum) pent(~time)Phi(~tsa)p(~session)	65	154702.1	8334.9998	0	154571.9
S(~1)Psi(~ctime+stratum) pent(~time)Phi(~tsa)p(~session)	63	155261.6	8894.5165	0	155135.4
S(~agebin)Psi(~time) pent(~time)Phi(~tsa)p(~session)	64	155376.3	9009.1731	0	155248.0
S(~1)Psi(~time) pent(~time)Phi(~tsa)p(~session)	62	156004.4	9637.3500	0	155880.2

FIGURES

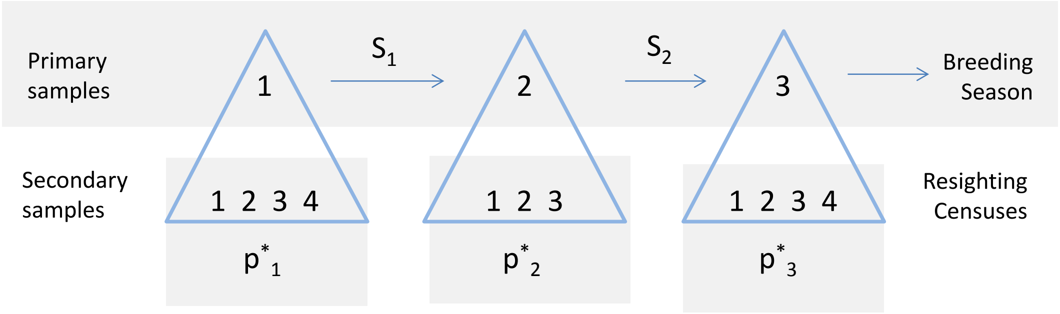
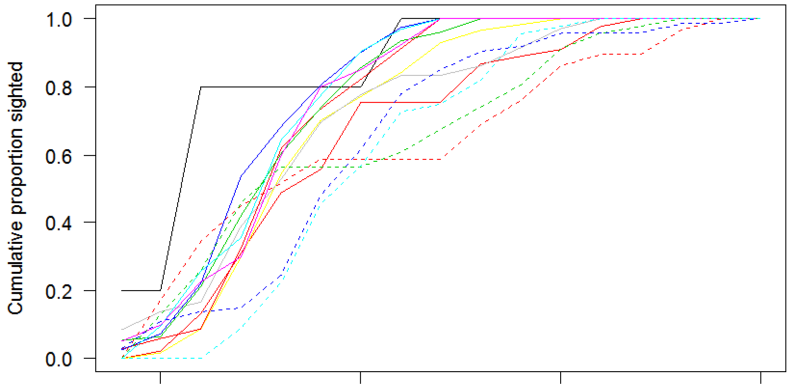


Figure 1. Basic structure of open robust design with probability of sighting (p^*_i) estimated from open mark resight model of secondary samples (weekly resighting censuses) and survival (S) estimated between the primary samples (breeding seasons).

a) Male



b) Female

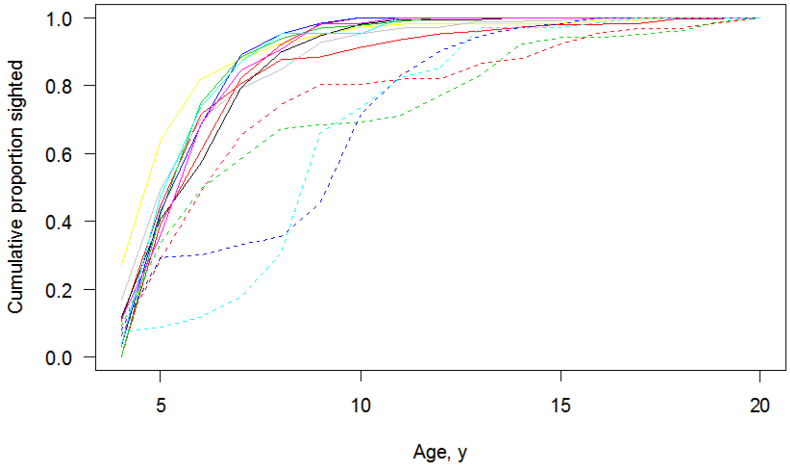


Figure 2. Male (a) and female (b) discovery curves for uniquely marked grey seals on Sable Island breeding colony. The dashed lines are the early cohorts (1969, 1970, 1973, and 1974) that began recruiting to the island when resighting effort was low and variable. The black solid line is the 2002 cohort which is the last cohort to have fully recruited to the breeding colony.

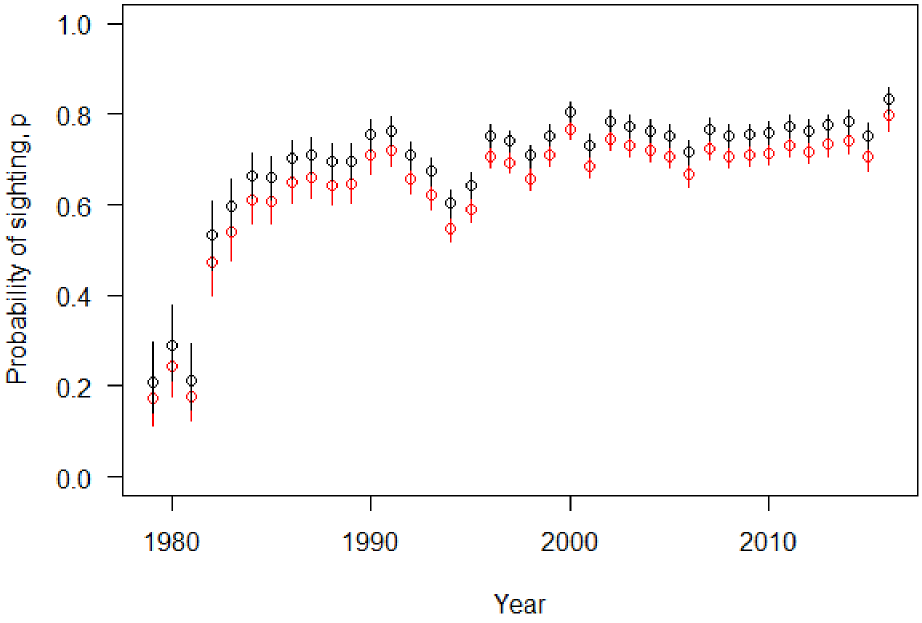


Figure 3. Plot of probability of sighting between 1979 and 2016 for males (black) and females (red) from preferred model: Phi(~ageb6 + sex)p(~time + sex). The horizontal bars represent the upper and lower 95% confidence intervals.

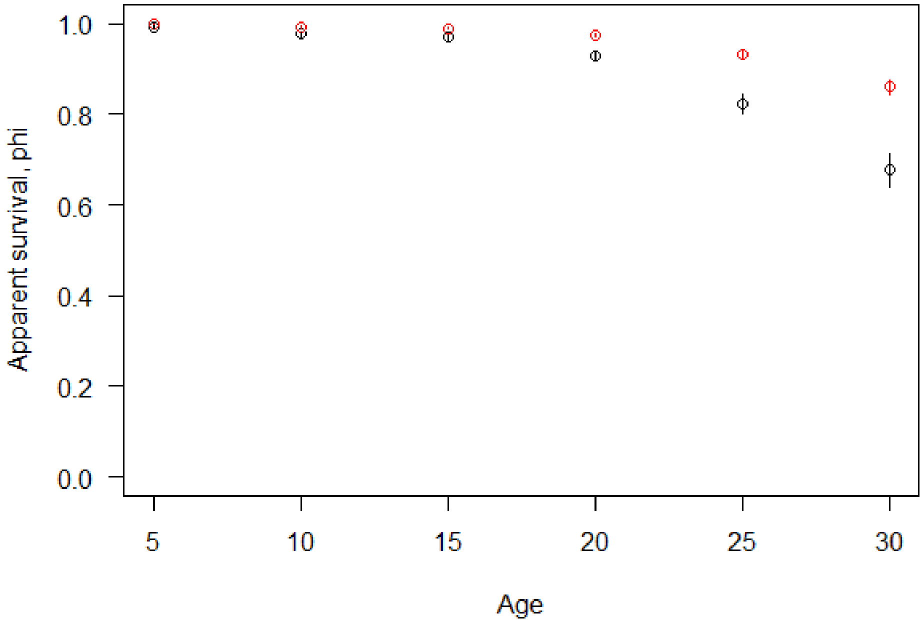


Figure 4. Plot of apparent survival by age for males (black) and females (red) fit for 6 age bins of the preferred model Phi(~ageb6 + sex)p(~time + sex). The horizontal bars represent the upper and lower confidence intervals.

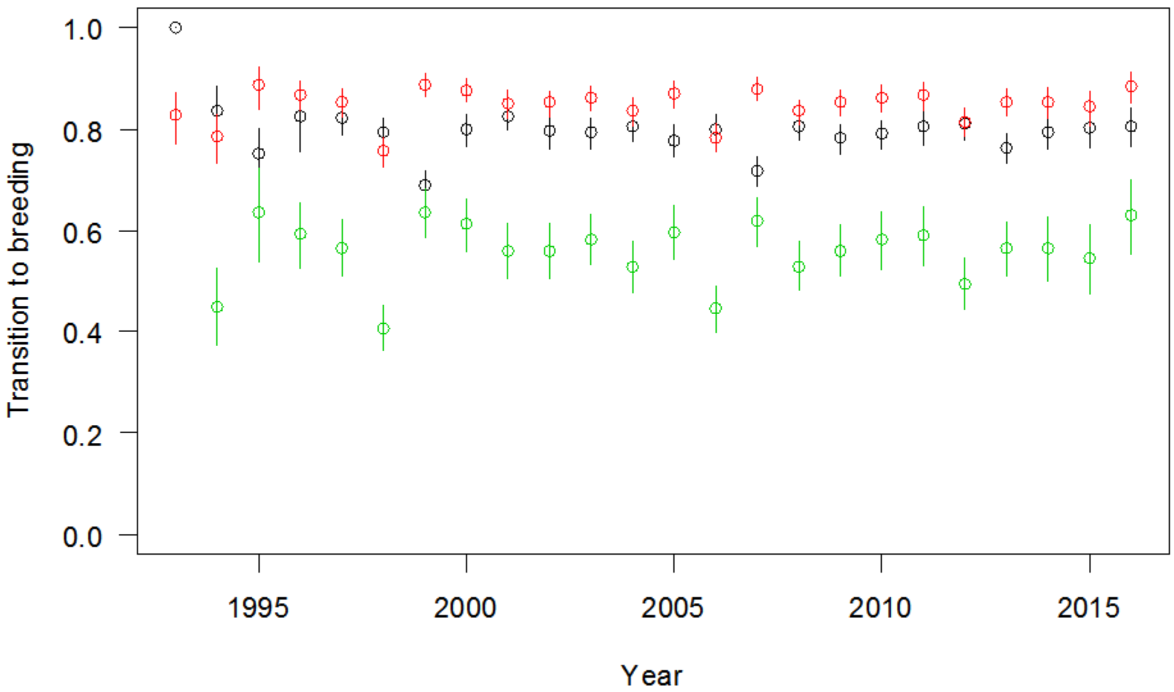


Figure 5. Plot of the probability of transitioning to breeder from breeder (red) and non-breeder (green) from preferred model: S(~agebin)Psi(~ctime+stratum)pent(~-1+time:session)Phi(~tsa)p(~session). Also plotted is the transition probability to non-breeder assuming random transition probabilities (black).

APPENDICES

Appendix 1. Summary of brand resighting effort on Sable Island between 1978 and 2016.

Year	Start First Brand Resighting, Date	End Last Brand Resighting, Date	Brand Resighting Events, N	Number of Brands Sighted	Number of Resightings
1978	1/1/1973	1/1/1973	1	195	227
1979	1/1/1974	2/10/1974	4	62	62
1980	1/1/1975	2/15/1975	6	82	82
1981	1/1/1976	1/28/1976	4	85	96
1982	1/1/1977	1/30/1977	2	254	303
1983	1/1/1978	2/4/1978	4	376	598
1984	1/1/1979	1/1/1979	1	431	1041
1985	1/1/1980	1/1/1980	1	472	1474
1986	1/1/1981	2/10/1981	3	494	1789
1987	1/20/1982	2/2/1982	3	493	1132
1988	1/1/1983	2/6/1983	6	481	1083
1989	1/1/1984	2/10/1984	5	516	1156
1990	1/1/1985	2/4/1985	5	681	1882
1991	1/1/1986	2/11/1986	6	836	2187
1992	1/1/1987	2/5/1987	5	856	1663
1993	1/1/1988	2/6/1988	4	887	1565
1994	1/1/1989	2/3/1989	5	867	1440
1995	1/7/1990	2/4/1990	6	918	1424
1996	12/29/1990	2/4/1991	6	1135	2232
1997	1/4/1992	1/26/1992	4	1115	2184
1998	1/6/1993	2/3/1993	5	1053	2384
1999	1/10/1994	1/30/1994	3	1092	2211
2000	1/8/1995	2/2/1995	4	1155	2563
2001	12/30/1995	1/31/1996	5	1008	1892
2002	12/29/1996	2/3/1997	6	1063	2352
2003	12/29/1997	1/28/1998	5	1037	2275
2004	12/30/1998	1/29/1999	5	1031	2271
2005	12/17/1999	1/26/2000	6	1049	2167
2006	12/17/2000	2/1/2001	7	1031	2343
2007	12/24/2001	1/27/2002	5	1131	2487
2008	12/22/2002	1/26/2003	6	1089	2373
2009	12/26/2003	1/23/2004	5	1090	2273
2010	12/26/2004	1/26/2005	5	1074	2329
2011	12/18/2005	1/24/2006	6	1058	2167
2012	12/15/2006	1/23/2007	6	978	2344
2013	12/14/2007	1/24/2008	6	934	2027
2014	12/24/2008	1/18/2009	4	885	1942
2015	12/13/2009	1/25/2010	6	788	1580
2016	12/12/2010	1/21/2011	6	830	2084

Appendix 2. AIC for selected models fit to the resighting histories of male and females grey seals on Sable Island between 1978 and 2016.

Model	**K**	**AICc**	**∆AICc**	**w_i**	**Deviance**
Phi(~ageb6 + sex)p(~time + sex)	46	52992.94	0	0.878687	39829.78
Phi(~-1 + ageb6:sex)p(~time + sex)	51	52996.9	3.960109	0.121313	39823.7
Phi(~ageb6 + sex)p(~time)	45	53039.78	46.84041	5.92E-11	39878.62
Phi(~-1 + ageb6:sex)p(~time)	50	53042.95	50.0058	1.22E-11	39871.75
Phi(~age + sex)p(~time + sex)	61	53124.19	131.2511	0	39930.91
Phi(~-1 + age:sex)p(~time + sex)	81	53146.77	153.8293	0	39913.28
Phi(~age + sex)p(~time)	60	53171.51	178.5704	0	39980.24
Phi(~-1 + age:sex)p(~time)	80	53194.61	201.6677	0	39963.13
Phi(~ageb6)p(~time + sex)	45	53213	220.0564	0	40051.84
Phi(~ageb2 + sex)p(~time + sex)	42	53220.13	227.1815	0	40064.98
Phi(~-1 + ageb2:sex)p(~time + sex)	43	53222.07	229.1217	0	40064.92
Phi(~ageb6)p(~time)	44	53248.86	255.917	0	40089.71
Phi(~ageb2 + sex)p(~time)	41	53264.67	271.7225	0	40111.53
Phi(~-1 + ageb2:sex)p(~time)	42	53266.29	273.3415	0	40111.14
Phi(~age)p(~time + sex)	60	53321.85	328.9034	0	40130.57
Phi(~age)p(~time)	59	53359.46	366.5138	0	40170.19
Phi(~ageb6 + sex)p(~-1 + sex:ageb6)	21	53376.58	383.6313	0	40263.53
Phi(~-1 + ageb6:sex)p(~-1 + sex:ageb6)	26	53378.4	385.4525	0	40255.33
Phi(~-1 + ageb6:sex)p(~sex + ageb6)	20	53419.45	426.5103	0	40308.41
Phi(~ageb6 + sex)p(~sex + ageb6)	15	53421.64	428.6994	0	40320.61
Phi(~-1 + ageb6:sex)p(~ageb6)	19	53422.7	429.7574	0	40313.66
Phi(~ageb6 + sex)p(~ageb6)	14	53425.11	432.1653	0	40326.08
Phi(~ageb2)p(~time + sex)	41	53429.51	436.5675	0	40276.38
Phi(~ageb2)p(~time)	40	53464.11	471.1656	0	40312.98
Phi(~age + sex)p(~-1 + sex:ageb6)	36	53529.48	536.5386	0	40386.37
Phi(~-1 + age:sex)p(~-1 + sex:ageb6)	56	53551.07	558.1278	0	40367.83
Phi(~age + sex)p(~sex + ageb6)	30	53571.14	578.2008	0	40440.07
Phi(~age + sex)p(~ageb6)	29	53574.91	581.9625	0	40445.83
Phi(~ageb6)p(~-1 + sex:ageb6)	20	53576.91	583.9623	0	40465.86
Phi(~-1 + age:sex)p(~sex + ageb6)	50	53592.13	599.1848	0	40420.93
Phi(~-1 + age:sex)p(~ageb6)	49	53595.98	603.0406	0	40426.8
Phi(~-1 + time:sex)p(~time + sex)	115	53598.83	605.8835	0	40296.86
Phi(~ageb2 + sex)p(~-1 + sex:ageb6)	17	53612.18	619.2391	0	40507.15
Phi(~-1 + ageb2:sex)p(~-1 + sex:ageb6)	18	53613.54	620.5987	0	40506.51
Phi(~time + sex)p(~time + sex)	78	53619.59	626.6478	0	40392.14
Phi(~-1 + time:sex)p(~time)	114	53644.34	651.395	0	40344.39
Phi(~ageb6)p(~ageb6)	13	53650.35	657.4013	0	40553.32
Phi(~ageb6)p(~sex + ageb6)	14	53650.94	657.9993	0	40551.92
Phi(~ageb2 + sex)p(~sex + ageb6)	11	53657.77	664.8267	0	40564.75
Phi(~-1 + ageb2:sex)p(~sex + ageb6)	12	53657.96	665.0134	0	40562.93

Model	K	AICc	ΔAICc	w_i	Deviance
Phi(~-1 + ageb2:sex)p(~ageb6)	11	53660.38	667.4347	0	40567.36
Phi(~ageb2 + sex)p(~ageb6)	10	53660.49	667.5501	0	40569.47
Phi(~time + sex)p(~time)	77	53676.9	683.9586	0	40451.46
Phi(~age)p(~-1 + sex:ageb6)	35	53717.01	724.0664	0	40575.91
Phi(~ageb6 + sex)p(~sex)	9	53776.18	783.2377	0	40687.16
Phi(~-1 + ageb6:sex)p(~sex)	14	53776.55	783.6063	0	40677.52
Phi(~age)p(~sex + ageb6)	29	53776.68	783.7365	0	40647.61
Phi(~age)p(~ageb6)	28	53776.73	783.7833	0	40649.66
Phi(~-1 + ageb6:sex)p(~1)	13	53793.94	801.0003	0	40696.92
Phi(~ageb6 + sex)p(~1)	8	53794.25	801.3104	0	40707.24
Phi(~ageb2)p(~-1 + sex:ageb6)	16	53809.49	816.5437	0	40706.46
Phi(~time)p(~time + sex)	77	53864.95	872.0096	0	40639.51
Phi(~ageb2)p(~ageb6)	9	53875.85	882.9087	0	40786.83
Phi(~ageb2)p(~sex + ageb6)	10	53876.58	883.6361	0	40785.56
Phi(~time + sex)p(~-1 + sex:ageb6)	53	53887.73	894.7862	0	40710.51
Phi(~-1 + time:sex)p(~-1 + sex:ageb6)	90	53897.18	904.2374	0	40645.58
Phi(~time)p(~time)	76	53914.8	921.8546	0	40691.37
Phi(~age + sex)p(~sex)	24	53920.43	927.4842	0	40801.37
Phi(~age + sex)p(~1)	23	53938.42	945.4777	0	40821.37
Phi(~-1 + age:sex)p(~sex)	44	53941.56	948.612	0	40782.4
Phi(~-1 + time:sex)p(~sex + ageb6)	84	53956.32	963.373	0	40716.79
Phi(~time + sex)p(~sex + ageb6)	47	53957.33	964.3837	0	40792.15
Phi(~-1 + age:sex)p(~1)	43	53959.78	966.8367	0	40802.63
Phi(~-1 + time:sex)p(~ageb6)	83	53961.06	968.119	0	40723.55
Phi(~time + sex)p(~ageb6)	46	53963.67	970.729	0	40800.51
Phi(~ageb6)p(~sex)	8	53998.95	1006.004	0	40911.93
Phi(~ageb6)p(~1)	7	54008.91	1015.97	0	40923.9
Phi(~ageb2 + sex)p(~sex)	5	54014.54	1021.597	0	40933.53
Phi(~-1 + ageb2:sex)p(~sex)	6	54015.55	1022.606	0	40932.54
Phi(~ageb2 + sex)p(~1)	4	54031.39	1038.447	0	40952.38
Phi(~-1 + ageb2:sex)p(~1)	5	54031.82	1038.872	0	40950.8
Phi(~time)p(~-1 + sex:ageb6)	52	54049.3	1056.356	0	40874.09
Phi(~age)p(~sex)	23	54119.23	1126.288	0	41002.18
Phi(~age)p(~1)	22	54129.98	1137.036	0	41014.93
Phi(~ageb2)p(~sex)	4	54226.43	1233.483	0	41147.41
Phi(~time)p(~sex + ageb6)	46	54228.48	1235.541	0	41065.32
Phi(~time)p(~ageb6)	45	54230.55	1237.603	0	41069.39
Phi(~ageb2)p(~1)	3	54236	1243.057	0	41158.99
Phi(~sex)p(~time + sex)	41	54313.51	1320.567	0	41160.38
Phi(~sex)p(~time)	40	54373.02	1380.075	0	41221.89
Phi(~-1 + time:sex)p(~sex)	78	54381.61	1388.665	0	41154.15
Phi(~time + sex)p(~sex)	41	54401.9	1408.956	0	41248.76

Model	**K**	**AICc**	**ΔAICc**	**w_i**	**Deviance**
Phi(~-1 + time:sex)p(~1)	77	54404.65	1411.704	0	41179.2
Phi(~time + sex)p(~1)	40	54427.59	1434.643	0	41276.46
Phi(~1)p(~time + sex)	40	54485.7	1492.758	0	41334.57
Phi(~sex)p(~-1 + sex:ageb6)	16	54507.88	1514.935	0	41404.85
Phi(~1)p(~time)	39	54536.65	1543.704	0	41387.52
Phi(~1)p(~-1 + sex:ageb6)	15	54582.52	1589.579	0	41481.49
Phi(~sex)p(~sex + ageb6)	10	54596.34	1603.397	0	41505.32
Phi(~sex)p(~ageb6)	9	54601.64	1608.697	0	41512.62
Phi(~time)p(~sex)	40	54654.69	1661.744	0	41503.56
Phi(~time)p(~1)	39	54674.69	1681.746	0	41525.57
Phi(~1)p(~sex + ageb6)	9	54787.29	1794.348	0	41698.27
Phi(~1)p(~ageb6)	8	54788.88	1795.935	0	41701.86
Phi(~sex)p(~sex)	4	55072.13	2079.191	0	41993.12
Phi(~sex)p(~1)	3	55098.92	2105.979	0	42021.91
Phi(~1)p(~sex)	3	55244.65	2251.709	0	42167.64
Phi(~1)p(~1)	2	55264.86	2271.912	0	42189.84

Appendix 3. Parameter estimates from the preferred CJS model (Phi(ageb6+sex)p(time+sex) of grey seal sightings between 1978 and 2016.

Parameter	**estimate**	**se**	**lcl**	**ucl**
Phi:(Intercept)	3.695253	0.112423	3.474905	3.915602
Phi:ageb6[4,10)	1.169518	0.293218	0.594811	1.744225
Phi:ageb6[15,20)	-0.25578	0.152155	-0.554	0.042447
Phi:ageb6[20,25)	-1.11385	0.128993	-1.36667	-0.86102
Phi:ageb6[25,30)	-2.15563	0.122038	-2.39483	-1.91644
Phi:ageb6[30,50)	-2.95614	0.125423	-3.20197	-2.71031
Phi:sex2	1.074222	0.068687	0.939595	1.208849
p:(Intercept)	-1.3427	0.242503	-1.81801	-0.86739
p:time1980	0.437335	0.314725	-0.17953	1.054195
p:time1981	0.027988	0.324899	-0.60881	0.664789
p:time1982	1.470088	0.28753	0.906528	2.033647
p:time1983	1.734596	0.274106	1.197348	2.271845
p:time1984	2.021213	0.265879	1.50009	2.542335
p:time1985	2.001239	0.262155	1.487414	2.515063
p:time1986	2.194202	0.261105	1.682435	2.705968
p:time1987	2.230871	0.260621	1.720053	2.741688
p:time1988	2.16355	0.259357	1.65521	2.67189
p:time1989	2.17142	0.258804	1.664165	2.678675
p:time1990	2.460324	0.259689	1.951332	2.969315
p:time1991	2.511592	0.255984	2.009863	3.013321
p:time1992	2.223032	0.251446	1.730198	2.715866
p:time1993	2.061007	0.249561	1.571867	2.550148
p:time1994	1.75431	0.24822	1.267799	2.240821
p:time1995	1.928028	0.247677	1.442582	2.413474
p:time1996	2.45377	0.248495	1.966719	2.940821
p:time1997	2.386709	0.247956	1.900715	2.872703
p:time1998	2.223899	0.24754	1.738721	2.709078
p:time1999	2.445428	0.248237	1.958885	2.931972
p:time2000	2.746617	0.24941	2.257773	3.235461
p:time2001	2.340022	0.248109	1.853728	2.826315
p:time2002	2.639884	0.249394	2.151071	3.128696
p:time2003	2.569819	0.249365	2.081063	3.058574
p:time2004	2.504862	0.249275	2.016284	2.993441
p:time2005	2.445221	0.24907	1.957043	2.933399
p:time2006	2.25954	0.248385	1.772706	2.746375
p:time2007	2.530132	0.24891	2.042268	3.017995
p:time2008	2.456221	0.248668	1.968831	2.94361
p:time2009	2.468289	0.248536	1.981158	2.95542
p:time2010	2.479316	0.248704	1.991856	2.966775
p:time2011	2.564226	0.249263	2.075671	3.052781
p:time2012	2.495131	0.249543	2.006027	2.984235

Parameter	estimate	se	lcl	ucl
p:time2013	2.577504	0.250403	2.086714	3.068295
p:time2014	2.611903	0.251413	2.119133	3.104672
p:time2015	2.42227	0.251876	1.928593	2.915947
p:time2016	2.893936	0.259767	2.384794	3.403079
p:sex2	-0.22634	0.032727	-0.29048	-0.1622

Appendix 4. Parameter estimates from the AIC-selected ORDMS model (S(~agebin)Psi(~ctime+stratum) pent(~-1+time:session)Phi(~tsa)p(~session)) of grey seal sightings between 1992 and 2016.

Parameter	estimate	se	lcl	ucl
S:(Intercept)	4.410701	0.069573	4.274338	4.547064
S:agebin[25,50)	-2.15966	0.088768	-2.33365	-1.98568
Psi:(Intercept)	-1.57191	0.179553	-1.92383	-1.21998
Psi:ctime2	0.274462	0.254318	-0.224	0.772925
Psi:ctime3	-0.49264	0.274765	-1.03118	0.045902
Psi:ctime4	-0.31094	0.222031	-0.74612	0.124245
Psi:ctime5	-0.19632	0.214105	-0.61596	0.223325
Psi:ctime6	0.439284	0.195337	0.056422	0.822145
Psi:ctime7	-0.49574	0.214029	-0.91523	-0.07624
Psi:ctime8	-0.39183	0.207745	-0.79901	0.015354
Psi:ctime9	-0.17518	0.214221	-0.59506	0.244692
Psi:ctime10	-0.17797	0.208474	-0.58658	0.230635
Psi:ctime11	-0.26721	0.207672	-0.67424	0.139831
Psi:ctime12	-0.0503	0.204955	-0.45201	0.351413
Psi:ctime13	-0.32991	0.215119	-0.75154	0.091724
Psi:ctime14	0.284042	0.198403	-0.10483	0.672912
Psi:ctime15	-0.41623	0.208402	-0.8247	-0.00776
Psi:ctime16	-0.05189	0.202361	-0.44851	0.344741
Psi:ctime17	-0.17758	0.20482	-0.57903	0.223863
Psi:ctime18	-0.26626	0.215466	-0.68857	0.156053
Psi:ctime19	-0.29895	0.215372	-0.72108	0.123178
Psi:ctime20	0.09091	0.202211	-0.30542	0.487243
Psi:ctime21	-0.19179	0.208878	-0.60119	0.217613
Psi:ctime22	-0.19305	0.219911	-0.62408	0.237971
Psi:ctime23	-0.11933	0.225784	-0.56187	0.323203
Psi:ctime24	-0.46748	0.237152	-0.9323	-0.00266
Psi:stratumU	1.507255	0.064063	1.38169	1.632819
pent:time1:session1	3.033983	0.430496	2.190211	3.877755
pent:time2:session1	1.177741	0.478402	0.240072	2.115409
pent:time3:session1	0.982439	0.555432	-0.10621	2.071086
pent:time1:session2	18.3318	0	18.3318	18.3318
pent:time2:session2	2.934777	0	2.934777	2.934777
pent:time3:session2	15.28756	0	15.28756	15.28756
pent:time4:session2	1.044606	0	1.044606	1.044606
pent:time1:session3	12.38513	38.79979	-63.6625	88.43272
pent:time2:session3	-0.79973	0	-0.79973	-0.79973
pent:time1:session4	4.749708	1.722904	1.372816	8.1266
pent:time2:session4	-14.2281	0	-14.2281	-14.2281
pent:time3:session4	1.636039	1.974271	-2.23353	5.505609
pent:time1:session5	3.386522	0.522981	2.36148	4.411564
pent:time2:session5	2.940597	0.523883	1.913786	3.967408

Parameter	estimate	se	lcl	ucl
pent:time3:session5	2.147697	0.53332	1.10239	3.193005
pent:time4:session5	1.008546	0.688721	-0.34135	2.358439
pent:time1:session6	14.76013	0	14.76013	14.76013
pent:time2:session6	13.72483	0	13.72483	13.72483
pent:time3:session6	13.19594	0	13.19594	13.19594
pent:time4:session6	9.678535	0	9.678535	9.678535
pent:time5:session6	10.29968	0	10.29968	10.29968
pent:time1:session7	2.648242	0.248696	2.160797	3.135687
pent:time2:session7	2.081572	0.255843	1.580121	2.583024
pent:time3:session7	1.563364	0.266575	1.040876	2.085851
pent:time4:session7	0.040371	0.428636	-0.79976	0.880497
pent:time1:session8	4.915028	1.049506	2.857997	6.97206
pent:time2:session8	3.276276	1.052759	1.212867	5.339684
pent:time3:session8	2.42393	1.063293	0.339876	4.507984
pent:time4:session8	1.3469	1.301541	-1.20412	3.89792
pent:time1:session9	3.336282	0.982875	1.409846	5.262717
pent:time2:session9	4.284124	0.980563	2.362221	6.206027
pent:time3:session9	4.14009	0.979489	2.220292	6.059888
pent:time4:session9	2.855986	0.98452	0.926327	4.785646
pent:time5:session9	1.545098	1.220877	-0.84782	3.938017
pent:time1:session10	1.275806	0.545997	0.205651	2.345961
pent:time2:session10	2.882691	0.520914	1.861699	3.903682
pent:time3:session10	3.77795	0.516761	2.765099	4.790802
pent:time4:session10	1.079933	0.692155	-0.27669	2.436557
pent:time5:session10	0.924823	0.604877	-0.26074	2.110381
pent:time6:session10	0.291731	0.796362	-1.26914	1.852601
pent:time1:session11	9.627262	71.00361	-129.54	148.7943
pent:time2:session11	12.13459	71.00326	-127.032	151.301
pent:time3:session11	8.766254	71.00631	-130.406	147.9386
pent:time4:session11	9.545485	71.00756	-129.629	148.7203
pent:time1:session12	12.91618	40.97465	-67.3941	93.2265
pent:time2:session12	13.22412	40.97299	-67.0829	93.53118
pent:time3:session12	12.6187	40.96786	-67.6783	92.91571
pent:time4:session12	10.85995	41.15502	-69.8039	91.52379
pent:time5:session12	3.713831	0	3.713831	3.713831
pent:time1:session13	2.947462	0.495812	1.97567	3.919253
pent:time2:session13	3.466064	0.4913	2.503117	4.429011
pent:time3:session13	1.748781	0.517381	0.734714	2.762847
pent:time4:session13	1.011681	0.639113	-0.24098	2.264342
pent:time1:session14	4.078719	0.492823	3.112786	5.044652
pent:time2:session14	2.160706	0.52358	1.134489	3.186924
pent:time3:session14	2.030438	0.513077	1.024807	3.036069
pent:time4:session14	-1.90527	4.523293	-10.7709	6.960381

Parameter	estimate	se	lcl	ucl
pent:time1:session15	1.374761	0.295823	0.794948	1.954574
pent:time2:session15	2.719824	0.281567	2.167952	3.271696
pent:time3:session15	1.945795	0.291732	1.374	2.51759
pent:time4:session15	1.612095	0.297115	1.02975	2.19444
pent:time5:session15	0.219158	0.454843	-0.67233	1.11065
pent:time1:session16	5.970471	0	5.970471	5.970471
pent:time2:session16	7.387294	0	7.387294	7.387294
pent:time3:session16	7.711775	0	7.711775	7.711775
pent:time4:session16	6.827417	0	6.827417	6.827417
pent:time5:session16	6.145686	0	6.145686	6.145686
pent:time1:session17	1.068996	0.548109	-0.0053	2.143291
pent:time2:session17	3.220387	0.523583	2.194165	4.246608
pent:time3:session17	3.241412	0.522721	2.216878	4.265946
pent:time4:session17	2.335274	0.529964	1.296546	3.374003
pent:time5:session17	1.185967	0.667823	-0.12297	2.494901
pent:time1:session18	3.77518	0.825895	2.156427	5.393934
pent:time2:session18	3.049746	0.823904	1.434894	4.664599
pent:time3:session18	2.419075	0.88356	0.687297	4.150853
pent:time1:session19	0.847885	0.349133	0.163585	1.532185
pent:time2:session19	0.949202	0.359651	0.244286	1.654119
pent:time3:session19	3.134534	0.317578	2.512082	3.756987
pent:time4:session19	0.811188	0.403064	0.021183	1.601193
pent:time5:session19	-0.12027	0.635624	-1.3661	1.125548
pent:time1:session20	0.646834	0.327146	0.005627	1.28804
pent:time2:session20	0.77549	0.332447	0.123894	1.427086
pent:time3:session20	2.958804	0.29424	2.382092	3.535515
pent:time4:session20	1.245226	0.338772	0.581233	1.909219
pent:time5:session20	0.061456	0.534281	-0.98573	1.108646
pent:time1:session21	1.161136	0.324801	0.524526	1.797746
pent:time2:session21	2.385953	0.308351	1.781585	2.990322
pent:time3:session21	2.404233	0.308631	1.799315	3.00915
pent:time4:session21	1.80442	0.317399	1.182318	2.426522
pent:time5:session21	0.413995	0.480371	-0.52753	1.355523
pent:time1:session22	2.138432	1.095541	-0.00883	4.285691
pent:time2:session22	3.422107	1.087365	1.290871	5.553343
pent:time3:session22	4.472488	1.083044	2.349722	6.595255
pent:time4:session22	2.956961	1.088459	0.823582	5.090341
pent:time5:session22	1.881899	1.228228	-0.52543	4.289225
pent:time1:session23	4.362351	0.72675	2.93792	5.786782
pent:time2:session23	2.189589	0.751472	0.716704	3.662474
pent:time3:session23	1.93922	0.748484	0.472191	3.406249
pent:time4:session23	0.614491	1.121712	-1.58406	2.813046
pent:time1:session24	4.400544	0.894881	2.646578	6.154511

Parameter	estimate	se	lcl	ucl
pent:time2:session24	3.309395	0.894577	1.556025	5.062765
pent:time3:session24	-1.40086	6.734374	-14.6002	11.79851
pent:time4:session24	1.400463	1.086542	-0.72916	3.530086
pent:time1:session25	11.75264	0	11.75264	11.75264
pent:time2:session25	12.90767	0	12.90767	12.90767
pent:time3:session25	13.36566	0	13.36566	13.36566
pent:time4:session25	13.2646	0	13.2646	13.2646
pent:time5:session25	12.39363	0	12.39363	12.39363
pent:time6:session25	11.3833	0	11.3833	11.3833
Phi:(Intercept)	2.053264	0.065857	1.924185	2.182343
Phi:tsa1	-1.48313	0.07831	-1.63662	-1.32965
Phi:tsa2	-3.35374	0.073105	-3.49703	-3.21046
Phi:tsa3	-3.35638	0.112943	-3.57775	-3.13501
Phi:tsa4	-3.35077	0.269371	-3.87874	-2.8228
Phi:tsa5	-2.65118	0.974215	-4.56064	-0.74172
p:(Intercept)	0.494134	0.085187	0.327168	0.661101
p:session2	-0.41542	0.110933	-0.63285	-0.19799
p:session3	-0.59014	0.111286	-0.80826	-0.37202
p:session4	-0.81133	0.109735	-1.02641	-0.59625
p:session5	0.203715	0.107951	-0.00787	0.415299
p:session6	0.068183	0.105306	-0.13822	0.274582
p:session7	0.84971	0.119463	0.615564	1.083857
p:session8	0.162509	0.106216	-0.04567	0.370692
p:session9	0.491951	0.105826	0.284531	0.69937
p:session10	-0.10751	0.103942	-0.31123	0.096221
p:session11	0.225549	0.108296	0.013289	0.437808
p:session12	0.283305	0.104079	0.079311	0.487299
p:session13	0.299743	0.109534	0.085057	0.514429
p:session14	0.055251	0.10499	-0.15053	0.261032
p:session15	0.636173	0.110166	0.420247	0.852099
p:session16	0.370087	0.103595	0.16704	0.573134
p:session17	0.430303	0.106559	0.221448	0.639159
p:session18	0.44204	0.109455	0.227508	0.656572
p:session19	0.016839	0.106729	-0.19235	0.226028
p:session20	0.211153	0.107566	0.000324	0.421981
p:session21	0.653152	0.109604	0.438328	0.867976
p:session22	0.47079	0.112507	0.250277	0.691303
p:session23	0.104797	0.11017	-0.11114	0.32073
p:session24	0.085086	0.112477	-0.13537	0.305542
p:session25	0.45976	0.108429	0.247239	0.672281