



Mark-recapture modeling accounting for state uncertainty provides concurrent estimates of survival and fecundity in a protected harbor seal population

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ABSTRACT

Harbor seal breeding behavior and habitats constrain opportunities for individual-based studies, and no current estimates of both survival and fecundity exist for any of the populations studied worldwide. As a result, the drivers underlying the variable trends in abundance exhibited by harbor seal populations around the world remain uncertain. We developed an individual-based study of harbor seals in northeast Scotland, whereby data were collected during daily photo-identification surveys throughout the pupping seasons between 2006 and 2011. However, a consequence of observing seals remotely meant that information on sex, maturity-stage, or breeding status was not always available. To provide unbiased estimates of survival rates we conditioned initial release of individuals on the first time sex was known to estimate sex-specific survival rates, while a robust design multistate model accounting for uncertainty in breeding status was used to estimate reproductive rate of multiparous and ≥ 3 -yr-old females. Survival rates were estimated at 0.95 (95% CI = 0.91–0.97) for females and 0.92 (0.83–0.96) for males, while reproductive rate was estimated at 0.89 (0.75–0.95) for multiparous and 0.69 (0.64–0.74) for ≥ 3 -yr-old females. Stage-based population modeling indicated that this population should be recovering, even under the current shooting quotas implemented by the recent management plan.

Key words: demography, *Phoca vitulina*, individual-based, vital rates, photo-identification, population dynamics.

Individual-based studies have greatly improved our understanding of the ecological factors that drive demographic change in many long-lived species, particularly where all individuals within discrete populations can be captured, marked, and detected regularly with a relatively high probability (Clutton-Brock and Sheldon 2010). Typically these studies have focused on terrestrial species, although some marine species, such as seabirds and pinnipeds that return regularly to terrestrial breeding sites, have proved amenable to study (Dunnet *et al.* 1979, Boyd *et al.* 1995, Hadley *et al.* 2007, Proffitt *et al.* 2007, Lee 2011). However, this has meant that

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individual-based research on pinnipeds has been biased towards the otariid and phocid species that haul out at accessible sites throughout the breeding season. In contrast, much less is known about phocids, such as harbor seals, which haul out on less accessible intertidal habitats or ice floes (Boness *et al.* 1994, Boness and Bowen 1996). Globally, harbor seals are one of the mostly widely distributed of pinnipeds (Bigg 1981), and high levels of interaction with fisheries and other human activities have resulted in a wide range of biological studies across the North Pacific and North Atlantic. Despite all this work the nature of their breeding strategy and habitats means that concurrent real-time estimates of harbor seal survival and fecundity do not exist for any of the populations studied. As a result, the drivers underlying the highly variable trends in abundance exhibited by harbor seal populations around the world (*e.g.*, Gilbert *et al.* 2005, Mathews and Pendleton 2006, Lonergan *et al.* 2007) remain uncertain.

Estimates of vital rates for harbor seals and many other phocids have typically been obtained from the analysis of dead animals that have been targeted either directly for scientific purposes (Bjørge 1992), harvested or culled (Harwood *et al.* 2000), or collected after disease outbreaks (Härkönen and Heide-Jørgensen 1990, Heide-Jørgensen and Härkönen 1992). This instantaneous and cross-sectional sampling is unlikely to capture temporal variation in survival and fecundity. Recent work has highlighted that unique pelage patterns of harbor seals can be used to remotely identify individuals and estimate vital rates within a mark-resight framework (Hastings *et al.* 2008, Mackey *et al.* 2008, Thompson and Wheeler 2008, Hastings *et al.* 2012, Cordes and Thompson 2013). The disadvantage of this approach in estimating survival is that, unless seals are first photographed as pups and unless observation sites or the methodology always allows sex determination while collecting photographs, there may be no information on an individual's sex or age. In such cases, where a significant proportion of sightings are of individuals whose sex is not identified at the time of data collection, careful treatment of data from individuals of unidentified sex is required to prevent positive bias in survival rates of known-sex individuals (Nichols *et al.* 2004). This is particularly problematic if the determination of sex is not random among individuals, for example when sex is determined by certain behaviors (*e.g.*, breeding; Nichols *et al.* 2004). Furthermore, when estimating reproductive rate, females might not always be sighted with their pup as the pup can be obscured by the female, or females sighted upon returning from foraging trips might not have located their pup, which can result in negative bias because too many females will be classified as being nonreproductive. Additionally, as groups of harbor seals typically contain both mature and immature individuals there may be no information on the age of individuals (Allen *et al.* 1988, Godsell 1988, Kovacs *et al.* 1990). Because harbor seals reach reproductive maturity at between 3 and 6 yr old (Boulva and McLaren 1979, Härkönen and Heide-Jørgensen 1990, Bowen *et al.* 1994), including sightings of immature individuals in the data for adults may cause underestimation of reproductive rate of breeding age females.

Given that harbor seal populations in both the North Pacific and North Atlantic have undergone severe declines in certain areas, it is crucial to obtain accurate estimates of vital rates to understand these differences in their population dynamics. For example, within the United Kingdom several major harbor seal populations have declined over the last 10–20 yr, but the causes still remain uncertain (Lonergan *et al.* 2007). The most intensively studied of these populations is in the Moray Firth, on the northeast coast of Scotland, but population-level studies carried out over two decades have failed to capture the underlying drivers of population dynamics. Nevertheless,

estimates of the numbers of seals shot due to perceived conflict with salmon fisheries suggest that shooting is likely to have played a significant role in the decline in this area (Thompson *et al.* 2007). In response to these findings, the Scottish Government developed the Moray Firth Seal Management Plan, which has introduced quotas for the number of seals that may be shot each year since 2005 (Butler *et al.* 2008).

Here, we use a Cormack-Jolly-Seber model conditioning release upon the identification of sex and robust design modeling approaches accounting for state uncertainty to reduce bias in estimates of survival caused by individuals of unknown sex as well as reducing potential bias in estimates of reproductive rate caused by uncertainty in breeding status. Our study aimed to obtain concurrent real-time estimates of survival and fecundity in a population of harbor seals using mark-recapture methods of naturally marked individuals over several years. These data were collected at a study site within the Moray Firth from 2006 to 2011, also allowing us to assess how vital rates have responded to recent protection under the Moray Firth Seal Management Plan, and investigate the impact of historic estimates of shooting on population rates of change.

MATERIALS AND METHODS

Study Site and Data Collection

The study was carried out in Loch Fleet National Nature Reserve in the Moray Firth on the northeast coast of Scotland (Cordes *et al.* 2011; Fig. 1). During low tide, seals haul out onto two sandbanks within the estuary. The main sandbank used by harbor seals was within 130 m of the on-shore observation point, allowing individual seals to be recognized using photo-identification (Thompson and Wheeler 2008). Photographic-identification survey data were collected over six consecutive years (2006–2011). During each pupping season (from the end of May to the end of July) the site was visited daily, resulting in a total of 321 surveys (2006 = 57, 2007 = 54, 2008 = 55, 2009 = 54, 2010 = 52, and 2011 = 49). The nature of the study site was such that individual seals would haul out on one side of the sandbank facing the water and also the observer. Seals are regularly vigilant when hauled out and so photographs were taken of the head and neck region using a digital camera (Nikon Coolpix 5100 camera [2006–2010]; Canon 60D [2011]) and a telescope (20–60 × 80 mm Swarovski HD-ATS 80) when seals raised their heads to look around. Depending on tidal state, seals moved between sandbanks with most or all seals located on the main sandbank. The same protocol for photographing seals on the sandbank was followed for each survey, whereby all seals hauled out on the sandbank were photographed starting from one end and working to the other. The quality of the photographs taken of an individual seal was checked on the camera at the study site to ensure that a good enough quality photograph had been obtained for identification. Prior knowledge of the seal or its breeding status did not influence how photographs were collected or which individuals were photographed. The same experienced observer (LSC) matched all photographs by eye against a catalogue of the best images (both left and right sides of the head) from all seals photographed during the study. Only photos of good quality (which meant that they were sharp enough and the angle of the seal's head permitted sufficient view of pelage patterns to identify poorly marked individuals) were evaluated for the assignment of individual ID.

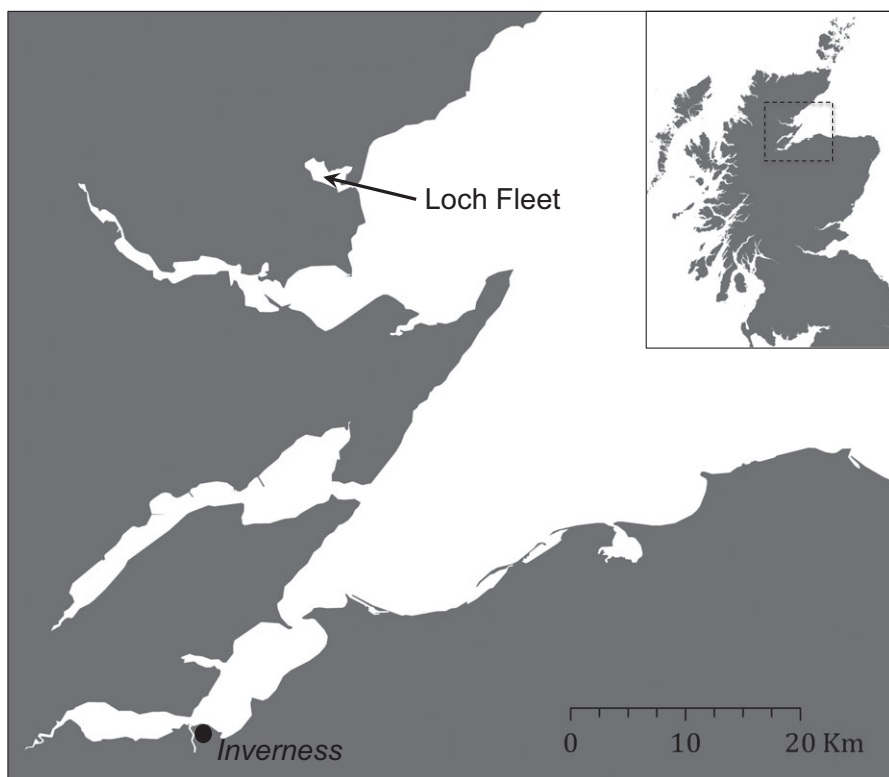


Figure 1. Map of Loch Fleet study area within the Moray Firth, northeast Scotland.

Photographs were also used to record whether individual females were with a pup on each survey day. Sex was determined from opportunistic photographs of seals lying on or rolling onto their sides while the head and neck photographs were being collected. Individuals were also identified as female if they were observed with a pup. Once sex of an individual was determined no systematic effort was put into identifying sex during future sightings. However, no additional observations ever led to a change in the sex determination of known individuals.

Estimating Apparent Sex-specific Survival When Sex Is Not Always Known

The Cormack-Jolly-Seber (CJS) model has commonly been used to estimate sex-specific survival of individually marked pinnipeds (*e.g.*, Croxall and Hiby 1983, Pistorius *et al.* 2004, Baker and Thompson 2007). However, if individuals of unknown sex are treated as a separate group in the CJS model, survival estimates of known sex individuals will likely be positively biased. This is because the probability of determining sex is higher for individuals that are seen in multiple years and the sample may therefore be biased towards individuals that survived (Nichols *et al.* 2004). We used the “*ad hoc* approach” described in Nichols *et al.* (2004) whereby sightings of individuals were not used for years prior to the year in which sex was determined. Once sex was observed for an individual, the individual remained in that state for all future years as

no systematic effort was subsequently made to identifying sex, and sex was treated as a group covariate in the model. Although discarding data before the sex of an individual was determined could result in a loss of precision, this approach yields unbiased results for known-sex individuals (Nichols *et al.* 2004). The model, which was essentially a CJS model, contained two parameters, apparent annual survival probability (S_T , the probability that an individual alive in year T survives to year $T + 1$) and recapture probability (p_T , the probability that an individual alive in year T is sighted in year T) (Cormack 1964, Jolly 1965, Seber 1965, Lebreton *et al.* 1992). Although survival rate is normally referred to as phi (Φ) in a CJS framework, for the sake of consistency between analyses we have chosen to use S in both cases. Furthermore, losses of animals from the population due to permanent emigration are treated as apparent mortality such that true survival is greater than apparent survival to the extent that permanent emigration occurred in the study. Capture histories were created for six annual occasions where multiple sightings of individuals in the same year were reduced to a single sighting per year (once sex had been determined). For S and p , we fit models with the parameters varying by *sex*, by *sex*year*, and constant across sexes and years, and for p we also fit models with the parameter varying by year alone.

Estimating Reproductive Rate While Accounting for State Uncertainty

To estimate reproductive rate, we used an open robust design multistate model with misclassification to allow uncertainty in breeding status (Kendall *et al.* 2003). We selected surveys encompassing the six weeks of the pupping and weaning season (1 June–12 July) (Cordes and Thompson 2013). In order to create the robust design, the six weeks were divided into six secondary occasions (t) and sightings histories of individual females were summarized within each week according to their state following the approach used by Kendall *et al.* (2003). Females could occupy one of two states, namely breeder (B), which was assigned with certainty when a female was seen with a pup, and nonbreeder (N), which could not be observed directly. We assume that no pup was assigned to a female that had not given birth in that year due to the strong mother-pup bond in harbor seals and the tendency for fostering to occur only when females have lost their pups (Boness *et al.* 1992). As a female could never be assigned to the state nonbreeder (N) with certainty, females that were seen but not observed with a pup were assigned to an uncertain state “ u ” (Kendall *et al.* 2003). The model included open primary occasions allowing female survival between breeding seasons to be less than one and allowing females to transition between N and B between years. However, within the open robust design multistate framework one of two assumptions must be fulfilled for secondary occasions: (1) there are no arrivals and departures, or (2) there is closure around female state. Since female harbor seals forage during lactation, may be absent at the start of the breeding season, and often depart on long foraging trips after weaning their pups, this violates the first assumption. Furthermore, as females are often not breeders from the start of the breeding season and may wean or lose the pup before the end of the breeding season there is a lack of closure regarding female state. There are currently no modeling approaches that deal with this special case of a brief seasonal event. To account for the lack of closure of female state we applied a quadratic function to δ_t^B (given a female has a pup, this is the probability that her pup was sighted with her).

In order to account for the potential bias in reproductive rate from younger females (3–5-yr-olds, PMT and LSC, unpublished data; see also Härkönen and Heide-Jørgensen 1990, Bowen *et al.* 1994) that cannot be visually distinguished from mature

females we ran two separate analyses. One analysis included only multiparous females by incorporating sightings of females following the year they were first seen with a pup (five primary occasions). The other included all sightings of ≥ 3 -yr-olds (six primary occasions). However, sightings of females as juvenile (< 3 yr old) were excluded based on pelage coloration and clarity of pelage patterns, as females at that age are unable to breed.

The model parameters of interest included the proportion of the population within the study area in year T that had a pup (ω_T , applies to primary occasions only), which is also the unconditional reproductive rate since it does not condition upon the females' state in the previous year (Kendall *et al.* 2003). The transition probability, ψ_T^{BB} was the probability that a female who pupped in year T also pupped in year $T + 1$. This parameter had to be obtained by subtraction ($1 - \psi_T^{BN}$), and since there were only two states in the model the variance was the same for both. The transition probability, ψ_T^{NB} , was the probability that a female who did not pup in year T pupped in year $T + 1$. These two transition probabilities are referred to as the conditional reproductive rates, as they are conditional upon the female's state in the previous year (applying to primary occasions only) (Kendall *et al.* 2003). Given that an adult female with a pup was detected, the probability that her pup was sighted with her (δ_T^B) was also estimated to account for misclassification of breeders as nonbreeders ($1 - \delta_T^B$). Although the nonbreeding state could not be observed directly, in principle a nonbreeder could never be wrongly assigned as a breeder and therefore δ_T^N was fixed to 0. Other model parameters included apparent annual survival (S_T) of breeders and nonbreeders, which is the probability that a breeder or nonbreeder alive in year T survive to year $T + 1$, and recapture probability (p_T), which is the probability that a breeder or nonbreeder alive in year T was sighted in year T . The model also included the probability a female was released in a certain state (π_T), the probability of entry to the study area (pent; e_T), and the probability of remaining on the study area (Φ_T) (see Kendall *et al.* 2003). For S , we fit only time constant models allowing variation by state or constant survival between states. For ψ , we fit models with variation between states, and with either variation between years or constant across years. For ω^B and π^B , we fit models with variation between years or constant across years. For p and Φ , we fit models with state effects, and either with variation between secondary surveys or constant across surveys. For e , we only fit models with state effects due to numerical convergence problems. Finally, for δ^B we only fit models with state effect, and variation across secondary surveys following a quadratic curve to account for the lack of closure of female state.

Sightings data were analyzed in the program MARK (White and Burnham 1999) and model selection was based on AIC_c scores according to the guidelines for dealing with small sample sizes (Lebreton *et al.* 1992, Bolker *et al.* 2009). The goodness-of-fit for the CJS model was tested in the program U-CARE. Currently there is no test for goodness-of-fit for the open robust design multistate model with state uncertainty. Instead we ran a goodness-of-fit test on the multistate version of the model, ignoring state uncertainty and the robust design, in U-CARE. This would give an upper bound variance adjustment factor. In all cases variance inflation factors (\hat{c}) were estimated to be < 1 ; we thus fixed \hat{c} to 1 as suggested by Burnham and Anderson (2002).

Population Modeling

A deterministic female-only stage-based population model (Caswell 1989) was used to explore potential population growth rates given the lower and upper bound

confidence intervals for the female survival rate estimated for the period 2006–2011, and to compare with likely growth rates under different estimated levels of shooting in the period prior to the implementation of the Moray Firth Management Plan (Thompson *et al.* 2007). The model contained three stages (pups, juveniles, and adults) and incorporated the adult female (≥ 3 -yr-olds) survival rate directly estimated from the mark-recapture analysis while conservative estimates of pup (< 1 -yr-olds: 0.70; Harding *et al.* 2005) and juvenile (1–3-yr-olds: 0.85; Härkönen and Heide-Jørgensen 1990, Heide-Jørgensen and Härkönen 1992) survival were included from other sources. A population projection matrix was produced incorporating the probability of survival in each stage ($P_i = \sigma_i (1 - \gamma_i)$), the probability of moving into the next stage ($G_i = \sigma_i \gamma_i$), where $\sigma_i = P$ (survival of an individual in stage i) and $\gamma_i = P$ (growth from i to $i + 1$ | survival). A density-dependent reproductive rate was then applied using Equation 1 (Taylor and Demaster 1993):

$$X_N = X_{N=K} + (X_{N=0} - X_{N=K}) \left[1 - \left(\frac{N}{K} \right)^z \right] \quad (1)$$

where X = reproductive rate, N = population size, K = carrying capacity and z = a parameter that shapes the form of the relationship between maximum and minimum reproductive rates (see Taylor and Demaster 1993 for further details). Here, we allowed the reproductive rate to vary between a maximum literature value for harbor seals of 0.95 (Boulva and McLaren 1979) and a minimum of 0.1 at carrying capacity (based upon observed change in northern fur seals) (Fowler 1990). Carrying capacity for the region was set at 1,000 females, which was slightly higher than when the population was at its maxima of 1,653 (95% CL 1,471–1,836) in 1993 (Thompson *et al.* 1997). We used a value of 3.5 for the shaping parameter z , as this provided reproductive values that approximated observed values at current population size relative to assumed values for carrying capacity. The model was based on an initial population size of 1,183 in 2010, which was estimated from the most recent Moray Firth count data (SCOS 2011) using the inflation factors described in Thompson *et al.* (1997). The female population was divided into the three stages by the following percentages, 26% (pups), 37% (juveniles), and 37% (adults), as estimated from the initial vital and transition rates given in the population matrix. Three different levels of shooting were used to explore the potential effects on population growth: (1) the quota set by the Moray Firth Seal Management Plan (30 female harbor seals per year; Butler *et al.* 2008), (2) the most probable level of culling estimated (76 female harbor seals per year; Thompson *et al.* 2007), and (3) the maximum estimated level of culling (86 female harbor seals per year; Thompson *et al.* 2007). This assumed no bias in the sex or age of seals shot and that animals were removed in each year in proportion to the size of the different stage classes. All matrix analyses were performed using Microsoft Excel and the Excel Add-In PopTools (Wittmer *et al.* 2007, Hood 2010).

RESULTS

Between 2006 and 2011, a total of 153 individuals were identified, 79 of which were female, 41 were male, and 33 individuals were not sexed. Of the 79 females, 71 were known to have produced at least one pup. The number of sightings per individual within each breeding season ranged from 1 to 42 (mean = 14, SD = 11).

Apart from the 108 individuals identified in 2006 an additional 15, 16, 7, 6, and 1 individuals were identified in each of the subsequent years of the study.

Estimating Apparent Sex-specific Survival When Sex Is Not Always Known

Five models were within three AIC_c scores of each other and together accounted for >0.95 of the AIC_c weight (Table 1). Due to the spread of weight between the top models, model averaging was used to estimate model parameters. Although model selection results did not provide strong support for sex differences in survival (the two top models in Table 1 were of similar weight), model averaged results suggested a lower survival probability for males (0.92, 95% CI: 0.83–0.96) compared to females (0.95, 0.91–0.97). Recapture rates (p) for both males and females were very high at 0.97 (0.92–0.99). Annual variation in S or p was not supported.

Estimating Reproductive Rate Accounting for State Uncertainty

For multiparous females two top models were within three AIC_c scores of each other and accounted for >0.95 of the AIC_c weight (Table 2a). Both supported a constant proportion of breeders across years. The first model suggested no variation in transition probabilities (ψ) over time, whereas the second suggested time variation in transition probabilities. However, the second model only accounted for 0.18 of the AIC_c weight and we therefore chose to present results from the first model (Table 3). The probability of pupping following a year of no pup (ψ^{NB}) was 0.56 (95% CI: 0.27–0.81). The probability of pupping in two consecutive years ($\psi^{BB} = 1 - \psi^{BN}$) was 0.88 (0.82–0.96). Finally, the unconditional reproductive rate (ω^B , proportion of females that pupped in each year) was estimated at 0.89 (0.75–0.95). Given that a multiparous female with a pup was sighted the probability that the pup was seen with her (δ^B) ranged from 0.28 (0.14–0.48) in the early season, to 0.94 (0.80–0.99) after most pups were born, to 0.87 (0.68–0.98) in the late season (not estimable for the first occasion).

For ≥ 3 -yr-old females, one model accounted for >0.99 of the AIC_c weight (Table 2b). Similar to the best model for multiparous females, this supported a constant proportion of females with pup across years as well as no time variation in transition probabilities (ψ) (Table 3). The probability of pupping following a year of no pup (ψ^{NB}) was 0.46 (95% CI: 0.33–0.59). The probability of pupping in two consecutive years ($\psi^{BB} = 1 - \psi^{BN}$) was 0.87 (0.81–0.96). Finally, the unconditional reproductive rate (ω^B , proportion of females that pupped in each year) was estimated at 0.69 (0.64–0.74). Given that a ≥ 3 -yr-old female with a pup was sighted the

Table 1. Comparison of fit of CJS models for estimating annual sex-specific survival rates. Only models with AIC_c scores <12 and AIC_c weight ≥ 0.001 are shown.

	ΔAIC_c	AIC_c weight	No. parameters
$S(\text{sex})p(\cdot)$	0.0	0.368	3
$S(\cdot)p(\cdot)$	0.5	0.292	2
$S(\text{sex})p(\text{sex})$	2.0	0.136	4
$S(\cdot)p(\text{sex})$	2.5	0.108	3
$S(\text{sex})p(T)$	2.8	0.092	7
$S(\text{sex}, T)p(\cdot)$	11.1	0.001	11
$S(\text{sex})p(\text{sex}, T)$	11.6	0.001	12

Table 2. Comparison of fit of robust design multistate models with state uncertainty (allowing variation between states (s), across years (T) or between secondary occasions (t)) for estimating reproductive rate of a) multiparous and b) ≥ 3 year-old harbor seal females in the Moray Firth, Scotland. Only models with AIC_c scores < 12 and AIC_c weight ≥ 0.001 are shown.

Model	ΔAIC_c	AIC_c weight	No. parameters
(a)			
$S(s)\psi(s,.)\pi^B(.)\omega^B(.)p(s,t)\delta(s,t^2)\epsilon(s)\Phi(s,.)$	0.0	0.792	28
$S(s)\psi(s,T)\pi^B(.)\omega^B(.)p(s,t)\delta(s,t^2)\epsilon(s)\Phi(s,.)$	3.0	0.178	34
$S(s)\psi(s,T)\pi^B(.)\omega^B(.)p(s,.)\delta(s,t^2)\epsilon(s)\Phi(s,.)$	7.1	0.022	20
$S(.)\psi(s,.)\pi^B(.)\omega^B(.)p(s,.)\delta(s,t^2)\epsilon(s)\Phi(s,.)$	10.9	0.003	17
$S(s)\psi(s,.)\pi^B(.)\omega^B(.)p(s,.)\delta(s,t^2)\epsilon(s)\Phi(s,.)$	11.4	0.003	18
(b)			
$S(s)\psi(s,.)\pi^B(.)\omega^B(.)p(s,t)\delta(s,t^2)\epsilon(s)\Phi(s,.)$	0.0	0.985	28
$S(.)\psi(s,.)\pi^B(.)\omega^B(T)p(s,.)\delta(s,t^2)\epsilon(s)\Phi(s,.)$	11.8	0.003	22
$S(s)\psi(s,.)\pi^B(.)\omega^B(T)p(s,.)\delta(s,t^2)\epsilon(s)\Phi(s,.)$	11.9	0.003	23

Table 3. Selected parameter estimates of interest from robust design multistate models with state uncertainty for estimating reproductive rate of multiparous and ≥ 3 year-old female harbor seals in the Moray Firth, Scotland, 2006–2011.

Parameter	Multiparous			≥ 3 -yr-olds		
	Estimate	SE	95% CI	Estimate	SE	95% CI
S^B	0.95	0.02	0.90–0.98	0.98	0.01	0.92–0.99
S^B	0.80	0.10	0.53–0.93	0.91	0.03	0.83–0.96
ψ^{BB}	0.88	0.03	0.82–0.96	0.87	0.04	0.81–0.96
ψ^{NB}	0.56	0.15	0.27–0.81	0.46	0.07	0.33–0.59
ω^B	0.89	0.05	0.75–0.95	0.69	0.03	0.64–0.74
δ_1^B	0.56	0.00	0.56–0.56	0.03	0.01	0.01–0.07
δ_2^B	0.28	0.09	0.14–0.48	0.33	0.03	0.27–0.40
δ_3^B	0.76	0.08	0.58–0.88	0.77	0.03	0.71–0.82
δ_4^B	0.93	0.05	0.75–0.98	0.92	0.02	0.88–0.95
δ_5^B	0.94	0.04	0.80–0.99	0.91	0.02	0.86–0.94
δ_6^B	0.87	0.07	0.68–0.96	0.70	0.03	0.63–0.76

probability that the pup was seen with her (δ^B) ranged from 0.03 (0.01–0.07) in the early season, to 0.92 (0.88–0.95) after most pups were born, to 0.70 (0.63–0.76) in the late season.

Population Modeling

Stage-based population modeling revealed that given the estimated lower (0.91) and upper (0.97) bound confidence intervals around female survival, the population would still be expected to grow at an average range of 4%–5% per year (over 10 yr) under the quota set by the Moray Firth Seal Management Plan. However, predicted growth slowed (1%–5% per year) when the number of seals shot was based upon the

most probable historical levels, and declines of 1%–11% per year were predicted when the number of seals shot was increased to the maximum historical levels.

DISCUSSION

These analyses provide the first concurrent estimates of sex-specific survival and reproductive rate from a wild population of harbor seals using mark-recapture models. Assuming these data are representative of seals using other haul-out sites within the region, this suggests that current protection through the Moray Firth Seal Management Plan has resulted in levels of survival (male = 0.92, 95% CI = 0.83–0.96; female = 0.95, 0.91–0.97) that should allow the population to recover after a period of sustained decline. In colony-based studies such as ours, estimates of apparent survival cannot account for emigration of individuals to other haul-out or breeding sites or in fact sex-specific differences in dispersal. Only in rare cases has this been possible (*e.g.*, Inchausti and Weimerskirch 2002). If this confounding occurred in our study, it would result in underestimates of survival and would therefore not alter our conclusion that this population is likely to be recovering.

If female harbor seals are seen without a pup, one cannot be certain that the female actually had no pup, therefore requiring a state misclassification model to estimate reproductive rate without bias. This is a similar situation to that of manatees, where females with calves were not always observed with the calf depending upon water clarity and other factors (Kendall *et al.* 2003, 2004). Furthermore, the mixture of all age-classes at breeding sites means that estimates of reproduction may be underestimated by including prebreeding age females. Consequently, we ran one analysis for multiparous females and one for ≥ 3 -yr-old females. Our results provided estimates of conditional (conditional on the female's state in the previous years) and unconditional (proportion of females with a pup in each year) reproductive rates for both multiparous and ≥ 3 -yr-olds. As predicted the unconditional reproductive rate of multiparous females (0.89, 95% CI: 0.75–0.95) was higher than that of ≥ 3 -yr-olds (0.69, 0.64–0.74). This was not the case for the conditional reproductive rates, ψ^{BB} and ψ^{NB} , where estimates were similar for multiparous and ≥ 3 -yr-olds, although there was a lot of variation around the estimate for multiparous females. It is important to note, however, that only individuals known to be females were included in the analysis, which may positively bias estimates of reproductive rate if most females were sexed when seen with pup, potentially excluding nonbreeding younger females or females in poorer condition. Nevertheless we believe that the individuals of unknown sex in our study were more likely to be transient animals (seen during 11% of weeks) and therefore not sexed as they were seen significantly less than individuals of known sex (males seen during 42% of weeks; females seen during 67% of weeks). In our study system there was a significant probability of misclassifying a breeder as a nonbreeder (particularly at the beginning and end of the breeding season) and supports the use of misclassification models for this as well as for other species where the breeding status of females can be uncertain. The open robust design model was also useful as it estimated the proportion of females that pup in each year as well as the conditional reproductive rates. Survival of nonbreeders was lower than that of breeders, and survival estimates of multiparous and ≥ 3 -yr-old females were similar to that estimated for females in the survival rate analysis (although the estimate for nonbreeding multiparous females was highly variable).

Comparative sex-specific survival rates and estimates of fecundity are sparse in the published literature and have mainly been obtained from dead animals. For example, analysis of seals collected in the Kattegat and Skagerak (a population that had previously shown healthy growth) after the northern European epizootic outbreak in 1988 revealed similar sex-specific survival rates to our study (male = 0.91, female = 0.95) (Härkönen and Heide-Jørgensen 1990, Heide-Jørgensen and Härkönen 1992). Only two other estimates of survival have been obtained from live harbor seals (Mackey *et al.* 2008, Hastings *et al.* 2012). Mackey *et al.*'s (2008) study was carried out in the Cromarty Firth (about 50 km south of Loch Fleet) from 1999 to 2002, but the sample of males was small and recapture rates low with just nine individuals seen in all four years. Adult survival for sexes pooled was estimated at 0.98 (95% CI = 0.94–1.00) using a CJS model. The estimate was slightly lower (0.97, 0.92–0.99) when an informative prior distribution was including using published survival data. Despite being obtained under different time periods and population trends this is similar to our female estimate. Hastings *et al.* (2012) published age- and sex-specific survival estimates with adult estimates of 0.93 and 0.88 for females and males (3–7-yr-olds), respectively, from Tugidak Island, Alaska. These estimates were slightly lower than ours, perhaps due to a younger age structure in their data, which included only known-age seals to age 7 yr.

The unconditional reproductive rate estimated in our study is slightly lower than those obtained from analysis of seals harvested in eastern Canada (0.95 for prime-aged females; Boulva and McLaren 1979) as well as those collected after the 1988 epizootic in the Kattegat and Skagerak (0.92; Härkönen and Heide-Jørgensen 1990). Similarly, seals sampled in Norway during a time of stable population growth revealed a reproductive rate for prime-aged females of 0.90 (Bjørge 1992). These previous estimates were obtained by counting placental scars, corpus luteum and corpus albicans, which develop in the ovaries after ovulation (Boyd 1984). However, the reliability of counting stained placental scars for estimating reproductive rates has only been tested in a few species (Strand *et al.* 1995, Elmeros and Hammershøj 2006). Furthermore, as corpus albicans may originate from sources other than corpus luteum of successful pregnancy, reproductive rates estimated using this method are likely to be overestimated (Boyd 1984). Another study from Norway, using live captures of females during the breeding season, estimated a reproductive rate of 0.93 (Lydersen and Kovacs 2005). However, the probability of capturing breeding females is likely to be higher than that of capturing nonbreeding females, which could have led to an inflated estimate of fecundity.

Our estimates of survival and fecundity were obtained during the period immediately after shooting had been restricted under the Scottish Government's seal management plan and may indicate that the decline of harbor seals in the Moray Firth could have been a result of lower fecundity and/or pup/juvenile survival. Although there remains some uncertainty surrounding the current population trend, the Moray Firth population appears to have stabilized over the last 5–7 yr, and there are signs of recovery (SCOS 2011). The long-term decline of harbor seals during the previous decade or so (Thompson *et al.* 2007) could have led to an increase in per capita food availability, resulting in adult vital rates that are similar to literature values reported from analyses of carcasses from increasing populations. However, these favorable conditions may not apply across age classes, particularly if age-specific competition is occurring either intra- or interspecifically. Imposing different levels of shooting on these baseline levels in our matrix model indicated that the proposed quota set under the Moray Firth Seal Management Plan (Butler *et al.*

2008) should allow the population to recover. Increasing the numbers shot to the most probable historic levels slowed, but did not impede, population growth. However, when culling levels were increased to the average maximum number estimated to have been shot in a single year the population declined rapidly. Although we used the lower and upper confidence intervals of female survival in our population model, it is important to note that our population model is deterministic and ignores temporal variation in vital rates. The population growth rates presented in this paper should therefore be considered as “potential” growth. Furthermore, the geometric mean lambda will be lower than arithmetic mean lambda and the size of this difference will be affected by the amount of temporal variation in various vital rates.

This study has highlighted how individual-based studies can underpin our understanding of the dynamics of harbor seal populations. At the same time, we recognize that such work will be possible at relatively few study sites, where conditions permit relatively close access to breeding groups. As with many other individual-based studies that are based upon single colonies (Dunnet *et al.* 1979, Boyd *et al.* 1995, Pendleton *et al.* 2006), this requires consideration of whether vital rates observed in these study colonies are representative of the regional population. In this case, our study site in Loch Fleet has only been used as a breeding site relatively recently, with the number of pups beginning to increase in the mid 1990s (Cordes *et al.* 2011). Nevertheless, parallel studies have shown that there is overlap in the foraging areas currently used by seals from Loch Fleet and those used historically by seals from other parts of the Moray Firth (Thompson *et al.* 1994, 1996; Cordes *et al.* 2011), suggesting that our study group is exposed to similar environmental conditions as the broader regional population. However, depending upon the contributing factors to its growth, the age-structure at Loch Fleet may be relatively young in comparison to other sites within the Moray Firth, and continued work should explore potential age-related changes in vital rates. The development of additional sentinel sites both within the regional population and in other populations would be a valuable addition to current efforts in understanding the factors that lead to widely different dynamics in harbor seal populations across their range.

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