

A Bayesian estimate of harbour seal survival using sparse photo-identification data

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Abstract

Survival rates have rarely been estimated for pinniped populations due to the constraints of obtaining unbiased sample data. In this paper, we present an approach for estimating survival probabilities from individual recognition data in the form of photographic documentation of pelage patterns. This method was applied to estimate adult (age 2+) survival for harbour seals in the Moray Firth, NE Scotland. An astronomical telescope was used to obtain digital images of individual seals, and high-quality images were used to document the annual presence or absence of individuals at a single haul-out site over a 4-year period. A total of 95 females, 10 males and 57 individuals of unknown sex were photographically documented during the study period. Survival and recapture probabilities were estimated using Jolly–Seber mark–recapture models in a Bayesian statistical framework. Computer-intensive Markov Chain Monte Carlo methods were used to estimate the probability distributions for the survival and recapture probabilities, conveying the full extent of the uncertainty resulting from unavoidably sparse observational data. The deviance information criterion was used to identify a best-fitting model that accounted for variation in the probability of capture between sexes, with constant survival. The model estimated adult survival as 0.98 (95% probability interval of 0.94–1.00) using our photo-identification data alone, and 0.97 (0.92–0.99) with the use of an informative prior distribution based on previously published estimates of harbour seal survival. This paper represents the first survival estimate for harbour seals in the UK, and the first survival estimate using photo-identification data in any species of pinniped.

Introduction

Estimation of survival and fecundity is central to understanding population dynamics (Caswell, 1989; McCallum, 2000). Typically, the rate of population change in species of long-lived birds and mammals has been demonstrated to be most sensitive to changes in adult survival (Brault & Caswell, 1993; Sinclair, 1996; Caswell, Fujiwara & Brault, 1999). Therefore, quantification of mortality levels has long been the focus of investigations aimed at understanding population change, and the development of management strategies (Hindell, 1991; Brault & Caswell, 1993; Festa-Bianchet & Gaboriko, 1997; Caswell *et al.*, 1999; Hårding, 2000).

Historically, estimates of survival in species of marine mammals have relied on retrospective analysis of age-frequency data, where individuals have been aged using teeth growth layer groups (e.g. Hewer, 1964; Harwood & Prime, 1978; Boulva & McLaren, 1979; York, 1983; Härkönen & Heide-Jørgensen, 1990; Barlow & Boveng,

1991; Hårding & Härkönen, 1995). However, using a sample of dead animals can introduce bias due to the nature of the harvest or collection (Hindell, 1991). Key problems in the analysis include the assumption of a stable population, and the assumption that the sample is representative of the population as a whole (Caughley, 1966; Hindell, 1991). Also, large numbers of dead animals are rarely available, and the use of specifically harvested animals for scientific research is currently not generally supported on ethical grounds. As an alternative to age-frequency data, survival can be estimated from the repeated captures or sightings of recognizable individuals over time, using mark–recapture models (Cormack, 1964; Jolly, 1965; Seber, 1965; Lebreton *et al.*, 1992; Buckland, Goudie & Borchers, 2000).

Mark–recapture studies investigating survival in species of birds, fish and mammals have typically relied on artificial tags or marks being added to a sample of animals from the study population to facilitate individual recognition (White *et al.*, 1987; Scott *et al.*, 1990; Hindell, 1991; Hastings, Testa & Rexstad, 1999; Hall, McConnell & Barker, 2001).

Similarly, studies investigating pinniped survival have often relied on the branding of individuals, as the annual moult results in tag loss between years (Hindell, 1991; Schwarz & Stobo, 2000). However, the logistical challenges of conducting tagging or branding studies of pinnipeds can constrain sample size, and result in the disturbance of both captured individuals and those individuals that are also hauled out at the time of capture. Here, we adopt an alternative approach for obtaining mark–recapture data for harbour seals through photographic identification techniques.

In many different species, individual recognition can be achieved through the photographic documentation of natural markings (Hammond, 1990; Bretagnolle, Thibault & Dominici, 1994; Karanth & Nichols, 1998; Langtimm *et al.*, 1998; Caswell *et al.*, 1999). Such ‘remote’ procedures allow the initial ‘capture’ to be non-invasive, with no physical capture or handling of animals. Aside from the welfare aspect of this approach, it also ensures that individuals do not exhibit a behavioural response that negatively affects their subsequent chance of being recaptured (Seber, 1982). In recent years, this photographic ‘mark’ and ‘recapture’ approach has also been extended to pinnipeds, with photo-identification used for abundance estimation in harbour seals (Yochem *et al.*, 1990; Crowley, Kelly & Daniel, 2001; Hastings, Small & Hiby, 2001; Middlemas, 2003), and other species of pinniped (Hiby & Lovell, 1990; McConkey, 1999; Forcada & Aguilar, 2000; Vincent, Meynier & Ridoux, 2001). Marks (pelage patterns) have been observed to be consistent between years in harbour seals (Yochem *et al.*, 1990), and several studies have also demonstrated that human observers can reliably recognize individual harbour seals based on these pelage patterns (Yochem *et al.*, 1990; Crowley *et al.*, 2001; Middlemas, 2003).

In this study, we use the photographic documentation of individual pelage patterns to estimate adult survival, specifically individuals aged two and above, for harbour seals within the Moray Firth, NE Scotland. This provides the first estimate of harbour seal survival specific to any UK population, and the first estimate of survival in any species of pinniped using photo-identification-based mark–recapture. We combine novel methods for the collection and analysis of photo-identification data, with modern Bayesian statistical approaches for analysing and communicating uncertainty when making inferences about survival and recapture probabilities. This allows imprecise, but useful, information about survival to be presented in the pragmatic form of ‘posterior probability distributions’ (Durban *et al.*, 2000; Wade, 2000). Knowledge of adult survival in this population provides useful information for management, specifically as a component of a population model for assessing and understanding population dynamics.

Methods

Study area

Shore-based surveys were made of the harbour seal population using an intertidal haul-out site in the Cromarty Firth, an estuary within the Moray Firth, NE Scotland (Fig. 1). Surveys were made in May, June and July, in each of 4 years (1999–2002), but also in April in 2000 and 2001. The field season was constrained to this time of the year because it encompasses the pupping season, when large numbers of individuals are hauled out (Thompson *et al.*, 1989, 1997). Surveys were not extended into late July and August, because animals cannot be reliably photo-identified during

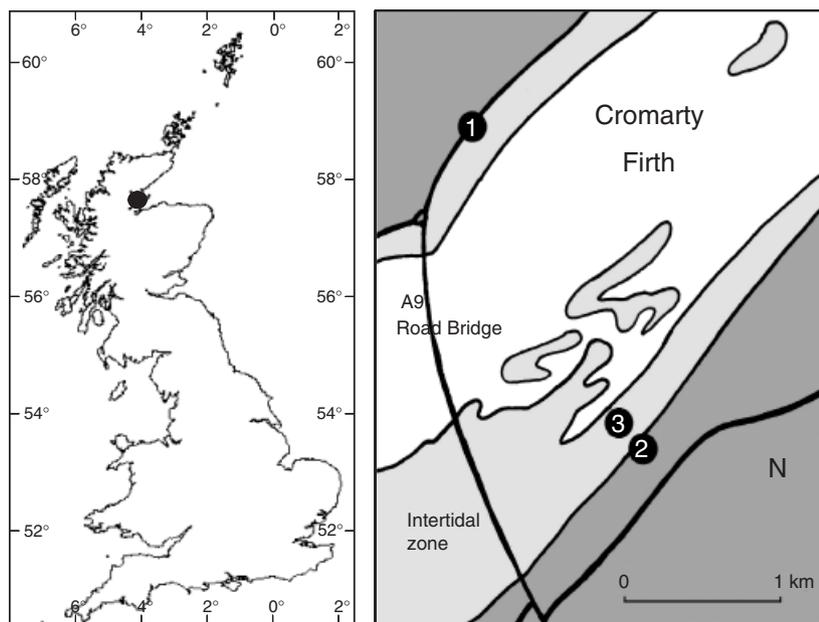


Figure 1 Location of the Cromarty Firth harbour seal haul-out site within the Moray Firth. The Cromarty Firth haul-out site; points 1, 2 and 3 represent locations where the telescope was set up for photographic capture of seals.

their moult. Animals were approached from one of three shore-based locations: a roadside on the north side of the firth (location 1, Fig. 1) a permanent hide on the south shore (location 2, Fig. 1), or a consistent location on the intertidal zone on the south shore (location 3, Fig. 1). On each survey, individuals within a maximum range of *c.* 300 m were observed. The total numbers of seals hauled out were counted within ± 2 h of low tide (Thompson *et al.*, 1997).

Photo-identification

Image capture was obtained by one of two methods. During all years, a Celestron Celstar 8 astronomical telescope (Celestron LLC, Torrance, CA, USA; 203 mm aperture, f/10, focal length 2032 mm) was connected to a low-light Hitachi KP-D581K colour digital CCTV camera (Hitachi Ltd., Tokyo, Japan), modified to run from a 12 V DC power supply. The output from the CCTV camera was recorded onto a Sony Digital Walkman (Sony Corporation, Tokyo, Japan; GVD900E). Each animal that was in a suitable position (side of their head facing the observer) was recorded for *c.* 2–5 min, or until suitable images were captured of at least one side of the head. While video recording, information was also noted on the sex, location of the seal and the presence of any pup in close association. Pups were identified by their small size and dark pelage. Sex was recorded by direct observation of the genitalia in males and females (Thompson, 1989), or the presence of a suckling pup. Still images were 'grabbed' from the video Walkman using Adaptec Hot Connect Ultra software. In addition to this method, in 2001 and 2002, the Celestron Celstar 8 telescope was connected to a Canon D30 digital SLR camera (Canon Inc., Tokyo, Japan). Images were taken, again of the side of the individual's head, and then cropped to a suitable size using Microsoft Photo Editor software. Images taken by either method were converted to greyscale and stored as TIF image documents before any analysis was carried out.

All the images were quality graded to reduce the chance of incorrect identification, which would lead to the creation of false positives or false negatives in the catalogue (Hammond, 1986; Friday *et al.*, 2000). Images were also classified according to four mark types, to ease the matching process: (1) well marked with distinctly contrasting light and dark pelage patterns; (2) predominantly dark pelage; (3) predominantly light pelage; (4) intermediate pelage pattern. Matches were based upon pelage patterns on the side of the head and neck region using only images of the two top-quality grades. Individuals with all mark types were used in the analysis. Images were first matched within each year, with the highest quality image of each animal then being used to construct a catalogue of identified individuals. This catalogue was then used to match photographs of the same individuals between years. Where images could not be matched to a previously identified animal, they were given new identification numbers. Photographs were taken of both the left and right side of the seals' head region, but it

was not always possible to match left- and right-side pictures to the same individual. Therefore, in order to maintain independence of samples, only pictures of the side of the head with the greatest sample size were used for survival analysis (Meekan *et al.*, 2006). An assessment of the error rates during manual matching was made by comparing the agreement rates of matches made by two independent observers using the Kappa statistic (Forcada & Aguilar, 2000; Viera & Garrett, 2005).

Model fitting and selection

Mark–recapture survival estimation depends on two key sets of parameters: recapture probabilities and survival probabilities. Recapture probabilities (p_{it}) relate to the probability of an animal that was first captured at time i , being recaptured at time t , given that it is alive. Survival probabilities (ϕ_{it}) give the probability of an individual that was first captured at time i , surviving over the period from t to $t+1$ (McCallum, 2000). There are several assumptions associated with any type of mark–recapture analysis. Homogeneity is assumed in both individual survival and capture probabilities. The sightings of individuals are also assumed to be independent, with every individual being identified correctly. These models also estimate apparent, rather than true, survival because an animal that permanently leaves the study area, or loses its marks, cannot be differentiated from one that has died (Lebreton *et al.*, 1992).

There is a wide array of mark–recapture models for recapture and survival probabilities. For a photo-identification data set, like the one used here, Jolly–Seber (JS) models are considered to be the most appropriate (Zeh *et al.*, 2002). However, JS models can be difficult to fit using conventional statistics, especially with sparse data. To overcome this problem, we follow Zeh *et al.* (2002) in fitting JS models using Bayesian statistical methods. Because of the sparse data available, from only 4 years of study, there is likely to be considerable uncertainty associated with parameter estimates. Bayesian methods have been repeatedly advocated and used for the analysis and communication of uncertainty in ecological data analysis (Ellison, 1996; Durban *et al.*, 2000; Wade, 2000; Link *et al.*, 2002; Wintle *et al.*, 2003), and have been shown to be well suited to mark–recapture survival analyses (Brooks, Catchpole & Morgan, 2000; Poole, 2002).

The Bayesian approach bases inference on full 'posterior' probability distributions for parameters of interest (Gelman *et al.*, 1995), rather than point estimates with associated standard errors. This approach first requires prior probability distributions to be assigned to each parameter; and these are then updated to posterior distributions by conditioning on the observed data. We initially adopted flat prior distributions that were uninformative, as we wished to obtain posterior probability distributions that were solely dependent on our photo-identification data. Survival and recapture probabilities were therefore initially assigned β prior distributions with probability mass equally spaced between 0 and 1:

Table 1 Parameter options and DIC values for the selection of alternative formulations of the Jolly–Seber model

Variation in probability of		DIC
Recapture (p)	Survival (φ)	
None	None	98.784
None	Temporal	100.566
None	Sex based	55.851 ^a
None	Sex based and temporal	60.384
Temporal	None	102.947
Temporal	Temporal	103.891
Temporal	Sex based	59.582
Temporal	Sex based and Temporal	63.526
Sex based	None	54.083
Sex based	Temporal	57.087
Sex based	Sex based	55.264 ^a
Sex based	Sex based and temporal	56.994
Sex based and temporal	None	54.554 ^a
Sex based and temporal	Temporal	56.201
Sex based and temporal	Sex based	54.367 ^a
Sex based and temporal	Sex based and temporal	57.334

The model with the lowest DIC, best-fitting model is highlighted in bold.

^aDenotes models with a DIC value within two points of the lowest model DIC.

DIC, deviance information criterion.

$$\varphi, p \sim \beta(1, 1)$$

where $\beta(a, b)$ indicates a β distribution with mean, $c = a/(a + b)$, and variance, $v = c(1 - c)/(a + b + 1)$.

The Jolly–Seber model also requires prior distributions to be set on the total number of identifiable seals alive just before time t that had not been previously ‘marked’, U_t . A discrete uniform prior distribution between 1 and 2000 was chosen for each U_t . The high upper limit provided a broad prior without excluding any plausible values, as this was an order of magnitude greater than our maximum count. The maximum counts of hauled-out adult harbour seals within the Cromarty Firth during the photo-identification surveys ranged between 137 and 145 (approximate population size of 225–238) after correction for haul-out behaviour (Thompson *et al.*, 1997)

Once these priors had been assigned, the model could be thought of as a full probability model, which described the joint distribution of both the unknown parameters and the observed data. We used the freely available WinBUGS software (Lunn *et al.*, 2000) to implement Markov Chain Monte Carlo (MCMC) sampling to simulate three separate sequences of values from the posterior distributions conditional on the observed data. For each model, a three-chain MCMC run was used to assess the convergence of the MCMC routine, and inference was based on 50 000 iterations after convergence was achieved. Convergence was assessed using the method of Gelman & Rubin (1992), as modified by Brooks & Gelman (1998), which is based on summary statistics comparing the variances within and between the three different simulated sequences. The

sampled values were then used to construct kernel density plots of the posterior distributions for parameters of interest, and also to estimate summary statistics for the posterior distributions.

We also examined whether there was temporal and/or sex-based variation in both capture probability and survival using a model-selection procedure. Alternative assumptions about temporal variability or sex differences in parameters were reflected in 16 alternative formulations of the JS model (Table 1). The most appropriate model was selected using the deviance information criterion (DIC) (Spiegelhalter *et al.*, 2002). The DIC has been specifically developed to select between Bayesian models and works on the same principle as the widely used Akaike’s information criterion (AIC) (Akaike, 1973; Lebreton *et al.*, 1992). The DIC consists of two terms: one representing goodness of fit, and the other a penalty for increasing model complexity. The DIC values have no intrinsic meaning, as with AIC, but the differences in DIC across the models are meaningful. The model with the smallest DIC is estimated to be the model that would best predict a replicate dataset of the same structure as that observed currently.

A useful feature of the Bayesian approach is the ability to incorporate relevant prior information directly into inference about quantities of interest (Box & Tiao, 1973). In this case, data on the survival probabilities of adult seals from other studies could be expressed through a possible mean value for φ and its likely spread about the mean, which in turn could be used to derive suitable values for a and b for incorporation into the prior $\beta(a, b)$. Using published estimates of adult harbour seal survival (Bigg, 1969; Härkönen & Heide-Jørgensen, 1990; Olesuik, Bigg & Ellis, 1990; Reijnders *et al.*, 1993, 1997; Ries, Hiby & Reijnders, 1998), we expected a mean survival $\mu(\varphi)$ of 0.90 and a likely variance $V(\varphi)$ of 0.003. In the β distribution $\beta(a, b)$, parameters a and b can be derived following Congdon (2001), with

$$a = \mu[\mu(1 - \mu)/V - 1]$$

$$b = a(1 - \mu)/\mu$$

Therefore, we constructed an informative prior for the adult survival of the form $\beta(25.67, 2.807)$. We then compared posterior inference in the best-fitting model when using this informative prior versus the non-informative $\beta(1, 1)$ prior that was used as a standard for the model-selection process.

In order to compare the Bayesian approach with the conventional approach to mark–recapture analysis, the program MARK was used to estimate adult survival through the basic Cormack–Jolly–Seber (CJS) model following Lebreton *et al.* (1992). This model provides an estimate of survival and probability of capture, both of which can vary over time. The model was run for all the sexes (female, male and unknown) separately as well as pooled. The goodness of fit of the capture histories to the CJS model was assessed, and then the best model was

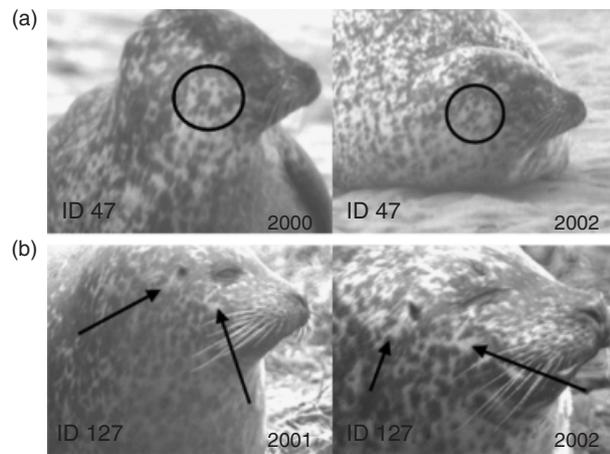


Figure 2 Examples of seals recaptured during the study: (a) female seal (ID 47) shown here on 18 July 2000 and 21 June 2002, (b) unknown sex seal (ID 127) shown here on 14 June 2001 and 10 June 2002.

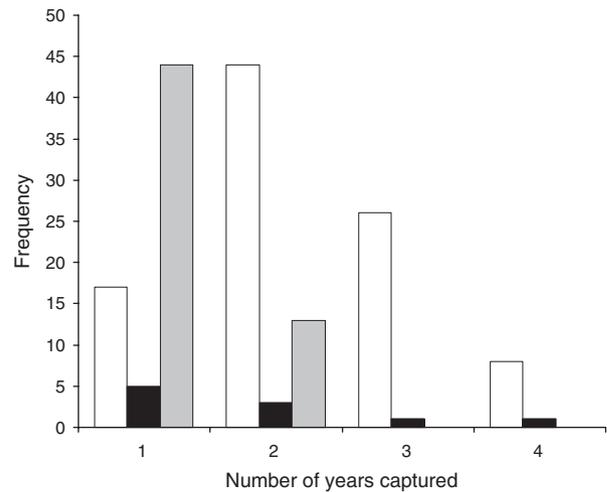


Figure 3 Frequency of recaptures of females (white), males (black) and unknown sex (grey) individuals throughout the study period.

Table 2 Estimates of survival (ϕ) resulting from the Jolly–Seber models with the top five DIC scores; 95% probability intervals are shown in brackets

Model	Parameter ϕ (female)	ϕ (male)	ϕ (unknown)
$\rho_s \phi$	0.9816 (0.938–0.9995)	0.9816 (0.9386–0.9995)	0.9816 (0.9386–0.9995)
$\rho_{s,t} \phi_s$	0.9781 (0.9279–0.9994)	0.862 (0.6006–0.9951)	0.6357 (0.3402–0.9651)
$\rho_{s,t} \phi$	0.9773 (0.925–0.9993)	0.9773 (0.925–0.9993)	0.9773 (0.925–0.9993)
$\rho_s \phi_s$	0.98 (0.9338–0.9994)	0.8821 (0.6378–0.9963)	0.7972 (0.4824–0.9915)
$\rho \phi_s$	0.9838 (0.944–0.9995)	0.8524 (0.5959–0.9931)	0.4426 (0.284–0.615)

DIC, deviance information criterion.

selected from a range of biologically feasible models using AIC.

Results

A total of 88 surveys were made during the study period: 18 in 1999, 28 in 2000, 24 in 2001 and 18 in 2002. A total of 162 individuals were identified from right-hand side photographs, and 146 from left-hand sides. Of these individuals, 108 had both left- and right-hand side images. Examples of recaptures of two different individuals are shown in Fig. 2. To avoid the statistical problem of non-independence of samples, only right-hand side captures are used in this analysis as they provided the largest sample size. There was no significant difference between the distributions of left- and right-hand side capture histories compared using a Mann–Whitney test ($U = 112$, $P = 0.98$).

There was a sex bias in the number of individuals photographed, with a total of 95 females, 10 males and 57 of unknown sex. The majority (77%) of unknown sex seals were identified only once throughout the study period; the remaining 23% were seen in a maximum of 2 years (Fig. 3). Half of the known males were seen only once. However, these re-sighting rates contrast to the known females; where

the majority of animals were seen on two or more occasions, 18% were seen in 1 year only. A total of eight females, and one male were recaptured in all 4 years of the study. Two observers B. L. M. and S. J. M. independently matched a subset of 85 pictures from the 2000 field season. They agreed matches in 91% of the cases, equivalent to a Kappa statistic of 0.903. This corresponds to an ‘almost perfect agreement’ (Viera & Garrett, 2005).

Model selection was carried out using all of the right-hand side capture histories. The parameter combinations that resulted in the lowest DIC were for the model incorporating sex-based variation in recapture probabilities, but no variation in survival (Table 1). Despite this model having the lowest DIC, and thus best fit to the data, four alternate models were within two DIC points of the best model and therefore deserve consideration (Spiegelhalter *et al.*, 2002). These alternative models incorporated temporal and sex-based variation in recapture with sex-based variation in survival, temporal and sex-based variation in recapture with no variation in survival, sex-based variation in recapture and survival and no variation in recapture and sex-based variation in survival.

The results of the survival parameter estimates for each of these five models are given in Table 2. The highest ranking model estimated a constant survival probability of 0.98

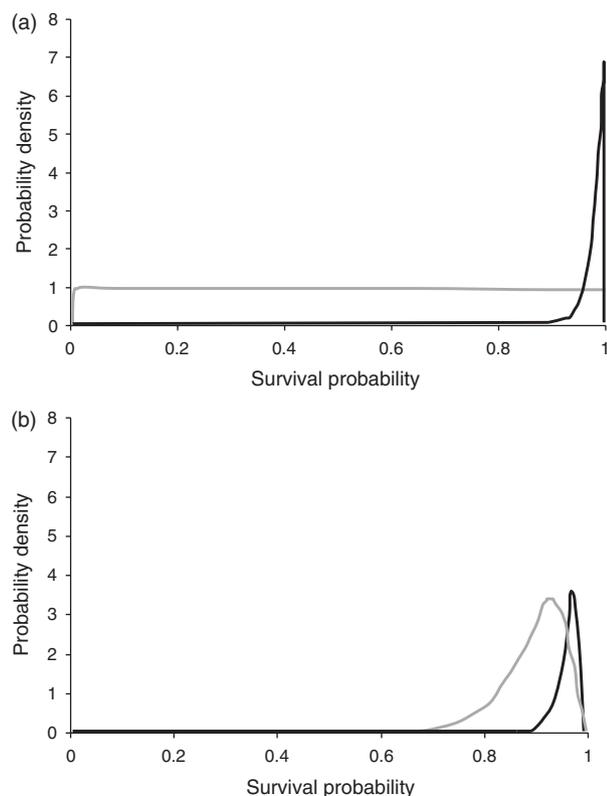


Figure 4 Prior (grey) and posterior (black) probability distributions for adult survival using the best-fitting model (sex-based variation in recapture and constant survival) with an (a) uninformative prior and (b) informative prior based on published data on harbour seal survival.

(95% probability interval of 0.94–1.00). Incorporating published survival data into an informative prior distribution for the constant survival term reduced the posterior estimate of survival to 0.97 (0.92–0.99). Although the posterior distribution was smoothed towards the prior mean of 0.90, our photo-identification data still resulted in a posterior estimate of survival that was notably higher than the prior expectation from other studies (Fig. 4). None of the lower ranking models (within two DIC points) incorporated temporal variation into survival probabilities. However, a sex-based variation was suggested by three of the five models, and in each case females had the highest and most precise estimates of survival. Unknown sex individuals had the lowest estimated survival probabilities in all cases; there was, however, a great deal of uncertainty around both the male and unknown sex individuals estimates (Table 2).

Estimates of recapture probabilities in the best-fitting models were constant, varied with sex or varied with sex and time. Where there was sex-based variation, unknown sex individuals always had the lowest recapture probability, and females had the highest recapture probability (Table 3). Where there was sex-based and temporal variation, again, female recapture probabilities were always the highest and unknown sex individuals were the lowest. However, the year of the highest recapture probabilities did vary between the

sexes: females were the highest in year 3 and the lowest in year 2, males the highest in year 4 and the lowest in year 3 and unknowns the highest in year 4 and the lowest in year 2. However, the size of the probability intervals around the male estimates reflects the large amount of uncertainty in this figure. Uncertainty was unsurprising due to the small number of males captured during the study.

Following Lebreton *et al.* (1992), adult survival was estimated using the general CJS model, for all sexes separately and pooled, within MARK. There were insufficient data to test for differences in survival or sighting probabilities between the sexes. Therefore, pooled data were used for further analysis. The goodness of fit of the CJS model was sufficient for the pooled data (Test2+Test3, $\chi^2 = 2.8727$, d.f. = 4, $P = 0.5794$). AIC values indicated that the best model was constant survival and capture probabilities between years with an adult survival probability of 0.94 (SE 0.04) and a recapture probability of 0.62 (SE 0.05).

Discussion

Information on adult survival is fundamental to the understanding of rates of population change (Caswell, 1989; McCallum, 2000). Estimates of harbour seal survival are relatively sparse in the published literature, and no published estimates of survival exist for UK harbour seals. Global estimates of adult harbour seal survival are variable but range from 0.8 (Bigg, 1969) to 0.96 (Härkönen & Heide-Jørgensen, 1990). To date, all the published examples of life-history data for harbour seals rely on the use of dead animals that have either been harvested (e.g. Harrison, 1960; Boulva & McClaren, 1979) or died under natural circumstances (e.g. Härkönen & Heide-Jørgensen, 1990). The study presented here represents the first use of photo-identification mark–recapture data to estimate survival in any species of pinniped. Despite only 4 years of data, the Bayesian approach allows an estimate of adult (age 2+) survival to be made, and the uncertainty around this estimate to be communicated. The best-fit JS model estimated adult survival to be 0.98 (95% probability interval of 0.94–1.00). This estimate is high compared with published estimates for other populations of harbour seals. The estimates of recapture probabilities for males and females are comparable with estimates of the haul-out frequency of adults radio-tagged in the Moray Firth in previous studies (Thompson *et al.*, 1997). In this earlier study, females were estimated to haul out on a greater proportion of low tides (0.698) than males (0.521) during the summer pupping period. Thus, females would be expected to have higher recapture probabilities during this time, and indeed our recapture probability estimates were higher in females than males (Table 3), although there is considerable uncertainty around the estimate for males. These similarities give us confidence in the mark–recapture estimates and model-selection procedure, despite the sample size constraints.

Traditionally, most mark–recapture estimates use CJS models, which were originally developed for bird banding studies (e.g. Cormack, 1964; Lebreton *et al.*, 1992). The

Table 3 Estimates of recapture probabilities (p) for years 2, 3 and 4 for female (f), males (m) and unknown sex individuals (u) resulting from the Jolly–Seber models with the top five DIC scores; 95% probability intervals are shown in brackets

Model	Parameter		
	$p(2,f)$	$p(2,m)$	$p(2,u)$
$\rho_s \varphi$	0.7144 (0.6402–0.7863)	0.4555 (0.2078–0.7176)	0.1745 (0.0923–0.2768)
$\rho_{s,t} \varphi_s$	0.6104 (0.4086–0.7936)	0.4728 (0.0285–0.9593)	0.1013 (0.0065–0.5723)
$\rho_{s,t} \varphi$	0.6081 (0.406–0.7936)	0.4623 (0.0251–0.9571)	0.0681 (0.0069–0.3233)
$\rho_s \varphi_s$	0.7157 (0.641–0.788)	0.4942 (0.2257–0.7783)	0.2432 (0.1089–0.4772)
$\rho \varphi_s$	0.6813 (0.6087–0.7519)	0.6813 (0.6087–0.7519)	0.6813 (0.6087–0.7519)
Model	Parameter		
	$p(3,f)$	$p(3,m)$	$p(3,u)$
$\rho_s \varphi$	0.7144 (0.6402–0.7863)	0.4555 (0.2078–0.7176)	0.1745 (0.0923–0.2768)
$\rho_{s,t} \varphi_s$	0.7484 (0.6311–0.8513)	0.3501 (0.0565–0.7413)	0.1119 (0.0839–0.3619)
$\rho_{s,t} \varphi$	0.7486 (0.6305–0.8524)	0.3335 (0.0524–0.7164)	0.0723 (0.0152–0.2171)
$\rho_s \varphi_s$	0.7157 (0.641–0.788)	0.4942 (0.2257–0.7783)	0.2432 (0.1089–0.4772)
$\rho \varphi_s$	0.6813 (0.6087–0.7519)	0.6813 (0.6087–0.7519)	0.6813 (0.6087–0.7519)
Model	Parameter		
	$p(4,f)$	$p(4,m)$	$p(4,u)$
$\rho_s \varphi$	0.7144 (0.6402–0.7863)	0.4555 (0.2078–0.7176)	0.1745 (0.0923–0.2768)
$\rho_{s,t} \varphi_s$	0.7155 (0.6094–0.8194)	0.6296 (0.2789–0.9546)	0.5142 (0.214–0.9201)
$\rho_{s,t} \varphi$	0.7162 (0.6086–0.8216)	0.56 (0.2472–0.8589)	0.2701 (0.1509–0.411)
$\rho_s \varphi_s$	0.7157 (0.641–0.788)	0.4942 (0.2257–0.7783)	0.2432 (0.1089–0.4772)
$\rho \varphi_s$	0.6813 (0.6087–0.7519)	0.6813 (0.6087–0.7519)	0.6813 (0.6087–0.7519)

DIC, deviance information criterion.

powerful software package MARK (White & Burnham, 1999) has been developed for fitting such models, and is now widely used as the standard tool for mark–recapture analyses. However, the CJS framework takes account of the different sampling process between initial captures and recaptures, as found in bird banding studies, by modelling recapture rates to be conditional on the number of birds already banded (Cormack, 1964; Zeh *et al.*, 2002). For a photo-identification dataset, like the one used here, JS models are more appropriate (Zeh *et al.*, 2002) because they assume that the probabilities of initial captures and recaptures on a given sampling occasion are the same (Seber, 1982). This assumption is met in photo-identification studies, as an attempt is made to photograph all animals regardless of whether or not they have been captured before. Unfortunately, MARK is not optimized to fit JS models, especially with sparse data, and can therefore perform poorly (Zeh *et al.*, 2002). In contrast, the process of fitting prior distributions on parameters in a Bayesian framework can greatly facilitate model fitting, simply by using prior distributions that constrain probabilities to lie within the correct 0–1 interval. Furthermore, the ability to use the DIC model-selection procedure (Spiegelhalter *et al.*, 2002) in the WinBUGS program allows the fitting of Bayesian JS mark–recapture models without sacrificing the AIC model-selection utility used in MARK (White & Burnham, 1999; Zeh *et al.*, 2002).

The Bayesian framework is also well suited for modelling sparse data, with the ability to analyse and communicate resulting uncertainty through probability distributions.

With sparse data, conventional methods for model fitting (such as the maximum likelihood approaches adopted in MARK) can become difficult, as shown with our data, where sex could not be included as a variable in the model. Problems with model fitting are particularly the case in relatively complex models with many parameters (Brooks, 1998; McAllister & Kirkwood, 1998; Durban *et al.*, 2000; Wade, 2000). The Bayesian approach also provided a formal framework for incorporating relevant prior information into inference in an attempt to provide more informative inference. A slightly lower estimate of adult survival (~ 0.97) was obtained when using prior distribution-based published information on harbour seal survival. The use of data in the construction of priors clearly involves assumptions about the relevance of related studies, and care should be taken to avoid incorporating data that may not be directly appropriate. However, in situations with relatively sparse data on the study population, information from related populations, or even different species, may be required for providing useful inference (e.g. Trenkel, Elston & Buckland, 2000). Furthermore, the comparison between priors and posterior distributions can facilitate inference. Despite some smoothing of the posterior distribution towards the mean of our informative prior, the photo-identification data from the study population still supported an estimate of harbour seal survival that was notably higher than the prior expectation from other studies (Fig. 4).

The model used here had several assumptions; each individual in the study had the same probability of survival between capture occasions, and every individual had an

equal probability of being captured at least once during the sampling period. The sightings of individuals were also assumed to be independent, with every individual being identified correctly. Equal probability of capture between individuals may be the hardest to justify in this study. Some seals in the population may be easier to photograph than others, and some seals may be easier to identify than others. Individuals that consistently used the haul-out sites that were within range of the photographic equipment, or were less likely to be disturbed by humans, would have had higher recapture probabilities than other individuals. Also, individuals that were 'well marked' may have been easier to recapture, by matching with the existing photograph catalogue than individuals that were not well marked. In addition, the probability of capture will depend on individual movements, and it has been shown that larger seals go on longer foraging trips (Thompson *et al.*, 1998). Some of this variation will be incorporated into the sex differences, but not all. The ability to determine the sex of an individual using the methods in this paper (the presence of a sucking pup, or direct viewing of genitals) was not uniform, and would increase with more capture occasions. Therefore, individuals of unknown sex were more likely to have been sighted only once during the study period, that is they have lower recapture rates (Fig. 3). Indeed, the estimated recapture probabilities for the individuals of unknown sex were always lower than the recapture probabilities for both males and the females (Table 3).

Although the best-fitting model had no sex-based variation in survival probability, models with only a slightly higher DIC values did suggest sex-based variation in this parameter (Table 1). Only 10 males, compared with 95 females, were captured at least once during the study period; if more data were available, sex differences between survival probabilities might become more apparent, and the inclusion of this variation could be justified. The larger number of females photographically captured is not unexpected due to the timing of the study; late May, June and early July encompass the breeding season in this region. During this time, greater numbers of females are known to haul out (Thompson *et al.*, 1989, 1997). The Cromarty Firth is also one of the main breeding sites within the Moray Firth, and female abundance is relatively high compared with males during the breeding season. The number of positively identified females is also likely to be biased upwards because individuals can be sexed using the presence of a pup. The probability of sexing individuals using solely their genitalia, as is the case for males, is much lower, as the seals must be lying with their ventral side facing the observer.

In addition to sex-based variation in survival probabilities, other models within two DIC points suggested temporal variation in recapture probabilities (Table 1). Time-dependent recapture probabilities are not unexpected from the data, as effort varied between years (18 surveys in year 1, 28 surveys in year 2, 24 surveys in year 3 and 18 surveys in year 4). The varying effort reflects the limitations of using the field equipment in certain weather conditions. It was not possible to use the equipment in wet conditions. Heat shimmer prevented use

during sunny weather, and the equipment was also sensitive to vibration, and so could not be used in windy weather.

Photo-identification has proved to be useful in this location, but it will only be suitable at sites where it is possible to get close enough to the seals to obtain sufficient numbers of high-quality images. Despite the limitations, it could also be used to estimate individual movement between haul-out locations and providing information on site faithfulness, which has rarely been studied at multi-annual time scales. The data presented here highlight that individuals are site faithful between years during the breeding season.

This study has used photo-identification to provide the first survival estimate of harbour seals in the UK. Estimation of such vital rates has been shown to be important for monitoring the status of populations (e.g. McCallum, 2000) and photo-identification is a potentially useful tool for monitoring the performance of Special Areas of Conservation, as designated under the European Union's Habitats Directive. Information on survival rates is also required by population models used to examine more general population and conservation questions (e.g. Caswell, 1989; Bjørge, Steen & Stenseth, 1994). Although the collection of the data required to estimate survival is often challenging, the Bayesian technique used here has proved to be useful at estimating survival from a sparse dataset.

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