

A Bayesian Capture–Recapture Population Model With Simultaneous Estimation of Heterogeneity

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We develop a Bayesian capture–recapture model that provides estimates of abundance as well as time-varying and heterogeneous survival and capture probability distributions. The model uses a state-space approach by incorporating an underlying population model and an observation model, and here is applied to photo-identification data to estimate trends in the abundance and survival of a population of bottlenose dolphins (*Tursiops truncatus*) in northeast Scotland. Novel features of the model include simultaneous estimation of time-varying survival and capture probability distributions, estimation of heterogeneity effects for survival and capture, use of separate data to inflate the number of identified animals to the total abundance, and integration of separate observations of the same animals from right and left side photographs. A Bayesian approach using Markov chain Monte Carlo methods allows for uncertainty in measurement and parameters, and simulations confirm the model's validity.

KEY WORDS: Abundance; Logits; Photo-identification; Survival; Trends.

1. INTRODUCTION

Estimates of changes in abundance are a fundamental requirement of most wildlife conservation and management programs (Williams, Nichols, and Conroy 2001). Capture–recapture methodology provides an important tool for estimating key demographic parameters such as survival, but it can also be used to obtain abundance. In traditional capture–recapture (Seber 2002), animals are initially captured, tagged, and then released. On subsequent capture occasions, individuals are recognized, and new animals are tagged, allowing construction of a capture history for each. Such parameters as survival and abundance are then derived from the capture histories. In the case of species with individually distinct natural markings, capture can correspond to photographing distinctive features (Würsig and Jefferson 1990). These photo-identification techniques are especially useful in situations where data must be collected nonintrusively to monitor the status of populations.

A difficulty with capture–recapture is that individuals may have differing catchabilities, manifesting as heterogeneous and time-varying capture probabilities (Chao 1987; Hammond 1986). The chance of observing an animal at a particular point in time and space also depends on the effort expended. But effort may be unimportant as long as each animal has an equal chance of capture at some point in its range during a sampling period. One effect of capture heterogeneity is to produce negatively biased estimates of abundance (Pollock, Nichols, Brownie, and Hines 1990; Cormack 1972), because an animal with a higher capture probability will be more likely to be caught on the first occasion, resulting in a decreased average capture probability on the second occasion and an underestimate of the total marked population. If the individual capture probabilities are uncorrelated between sampling periods, then

no bias is expected (Pollock et al. 1990), but it seems unlikely that the individual capture probabilities remain constant over time. Heterogeneity may also result in biased estimates of survival probability (Pollock et al. 1990).

Heterogeneous capture probability is usually considered a nuisance variable that must be estimated to obtain unbiased estimates of other parameters. However, the underlying causes of innate heterogeneous capture probabilities are not well understood and may be of interest, because they may provide insight into individual differences in range use, feeding strategies, or other behaviors. They may arise from variable responses to capture (Hammond 1990), social structuring within the population (Wilson 1995), nonoverlapping individual ranges (Wilson 1995), or temporary migration from the study area (Whitehead 2001a). Sampling methods themselves may introduce heterogeneity, and as such, the estimation of unequal capture probabilities may facilitate the development of improved sampling techniques. Estimates of survival probability may be biased by such unequal capture probabilities (Buckland 1982, 1990), although the effect may be small (Carothers 1979). Methods for dealing with heterogeneous capture include fitting specialized closed population models (Otis, Burnham, White, and Anderson 1978), jackknife (Burnham and Overton 1979) and coverage estimators (Chao, Lee, and Jeng 1992), modified trapping design (Pollock et al. 1990), stratification of estimates by covariates such as age or sex (Seber 2002), the use of covariates (Huggins 1989), selective analysis of capture histories (Hammond 1990), and the use of beta-binomial models (Dorazio and Royle 2003), logit models (Coull and Agresti 1999; Pledger 2000), and Rasch models (Fienberg, Johnson, and Junker 1999). Heterogeneity in survival also may occur. The biological factors underlying heterogeneity in survival probability are of interest, because they represent the response of different individuals to their environment.

Where natural marks are used to identify individuals, those animals lacking marks are by definition not identifiable (Pollock et al. 1990); for example, distinctive notches on dorsal fins of cetaceans may be present only on older animals in the population. This means that only part of the population is catchable. But this problem can be dealt with by inflation, using other data

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to estimate the proportion of the sampled population having distinctive marks (Seber 2002), or by double sampling (Pollock et al. 1990).

To address the aforementioned issues, we construct a model incorporating heterogeneity in capture and survival that makes use of the available data consisting of left-side and right-side photographic series. Individuals are regarded as captured after they have been identified by a specific type of dorsal fin marking, called “nicks,” that are visible in these photographs. Because these nicks appear on animals only as they mature, we include a nicking–recruitment process in the model. However, we lack knowledge of the probability of having nicks and the rate of acquiring nicks. Rather than adopt vague priors for these probabilities, we include separate data sources that provide these quantities. We also make use of the survival and capture information from the recapture model to obtain an estimate of the population size. Because some priors remain vague, we assess the effect of prior specification using simulated data. We apply the method to photo-identification data from a naturally marked bottlenose dolphin (*Tursiops truncatus*) population from the Moray Firth, Scotland. This is the only resident coastal population of bottlenose dolphins in the North Sea, and a Special Area of Conservation has been established to protect these animals in response to the 1992 EC Habitats Directive (Council Directive 92/43/EEC, Scottish Natural Heritage 1995). The U.K. government needs information on trends in the abundance of this population to report on the success of this conservation program to the European Union.

In this article we develop a general framework for estimating the total dolphin population size by embedding a standard capture–recapture model within a state-space model that describes the evolution of population size over time. We begin in Section 2 by describing the data available. In Section 3 we discuss implementation of the model. In Section 4 we discuss the Bayesian approach, including the use of Markov chain Monte Carlo (MCMC) techniques, the specification of priors, and a simulation study. In Section 5 we provide the results of our analysis and discuss the implications for the Moray Firth bottlenose dolphin (*Tursiops truncatus*) population. We conclude with discussion of the wider implications of our research and the utility of our approach for other wild animal populations.

2. DATA COLLECTION AND FORMAT

Between 1990 and 2002, boat-based surveys were conducted both in the inner Moray Firth and along adjacent coasts. Full details of survey protocols have been provided by (Wilson, Thompson, and Hammond 1997; Wilson, Hammond, and Thompson 1999). The number of trips made varied among years and areas. Most trips were made between May and September, with each trip encountering one or more groups of dolphins. Because the data collection effort in winter was low and available only for the early years of the study, these data are excluded from the analysis. Between 1990 and 1999, trips followed a fixed route (Wilson et al. 1997), but from 2000 onward, opportunistic surveys were conducted in an attempt to increase the number of dolphin groups sighted.

When bottlenose dolphins were encountered, photographs were taken of their dorsal fins using a single-lens reflex camera with a telephoto lens (Wilson et al. 1999). Both 35-mm

transparency and digital cameras were used during the study, with all photos subjected to the same strict grading of photographic quality (described in Wilson et al. 1999). Only high-quality pictures were used, to minimize errors in identification (Stevick, Palsbøll, Smith, Bravington, and Hammond 2001; Forcada and Aguilar 2000).

Individual bottlenose dolphins are identifiable by markings along the whole of the dorsal fin (see Fig. 1). Such fin marks have been shown to be of varying persistence and reliability (Wilson et al. 1999); therefore, we restricted our data set on those dolphins with nicks to the posterior edge of the dorsal fin, which have been shown to be relatively permanent and to accumulate over time. The accrual of individual nicks over time changes the dorsal edge profile, but reliable identification can still be obtained if the rest of the dorsal edge remains unaffected. Estimated nicked proportions are determined from a separate data set comprising the number of animals encountered in each trip and the number of those that were nicked.

On each occasion, animals could be photographed from the left side, the right side, or both sides. Individuals photographed from one side can be identified at later times from photographs of either side, because the dorsal trailing edge is visible from either side. This means that differences in left and right capture probability can be related to animal behavior and boat differences and left and right capture probabilities are of potential use in sampling programs. A total of 13 individuals are only known from the left side, and another 13 are only known from the right side. These individuals are included in the calculation since there is no evidence that they are not members of the population.

Each animal is assigned a unique identification code and a record made of the date and location it was observed. The observations of a single animal are represented as a capture history consisting of a series of 0's and 1's, where 1 indicates that the animal was observed in the corresponding time period and 0 indicates the animal was not observed. The entire data set consists of a matrix in which each row corresponds to a capture history for a single animal and each column represents one calendar year. Separate history matrices are constructed as described earlier for photoidentification series of the left and right sides. In addition, a bilateral history is constructed from both the left and right side series in which 0, 1, 2, and 3 indicate that the animal was unobserved or observed from the left side, right side, or both sides on each occasion. We denote the capture status for animal d at time j as h_{dj} , $h_{dj} \in [0, 1, 2, 3]$.

3. MODEL CONSTRUCTION

The overall model comprises a series of submodels that relate different elements of the observed (and indeed unobserved) data to common population parameters. We begin with a description of the component of the model that divides the population into two distinct classes: those animals that are nicked and thus identifiable and those that are not nicked. Using a standard capture–recapture model, the size of the nicked population can be determined and, from this, the total population size can be determined by estimating the proportion of nicked animals.



Figure 1. Example of dorsal fin showing nicks to the trailing edge. Insets show the changes in the dorsal fin for this animal over time with the earliest photograph on the left and the latest on the right. The background image corresponds to the third inset from the right. Apparent changes in shape of the inset images are the result of differences in camera perspective. The effect of these nicks is to produce a serrated edge, the whole of which is used to confirm the identity of the animal, rather than just a selected few nicks. Other markings, such as skin lesions, are not considered reliable enough to be used in this study. Minor changes in some nicks may occur over time, but as long as other nicks on the dorsal edge remain intact, identification can proceed.

3.1 Modeling the Nicked Population

We begin with the assumption that young animals are initially unnicked, but that as they mature they will accumulate nicks as they increasingly engage in social interactions. This is a reasonable assumption in light of the social development of juvenile bottlenose dolphins (Mann and Smuts 1999; Haase 2000). The animals can be considered as being recruited from the unnicked population to the nicked population. Once in the nicked population, individuals become observable and cannot return to the unmarked population.

We denote the number of dolphins recruited from the unnicked population to the nicked population at time $1 \leq j \leq J$ as B_j , and the number of nicked animals that survived between times $j - 1$ and j as S_j . Thus the nicked population size at time j is given by $S_j + B_j$; that is, the current population comprises new recruits and surviving former members. The nicked population is denoted by $N_j = S_j + B_j$.

We assume that previously nicked animals survive from time $j - 1$ to time j with probability $\theta_j = \exp(\alpha + \beta_j) / (1 + \exp(\alpha + \beta_j))$, where α denotes a global survival tendency and β_j denotes a time-varying survival component. Thus the number of surviving animals, S_j , is given a binomial distribution, so that $S_j \sim \text{Bin}(S_{j-1} + B_{j-1}, \theta_{j-1})$.

We also assume that unnicked animals acquire nicks with probability ω_j , so that the number of newly nicked animals has

a binomial distribution $B_j \sim \text{Bin}(W_{j-1} - N_{j-1}, \omega_j)$, where at time j , W_j denotes the total population and N_j denotes the nicked population. Given this definition, ω_j is the probability of acquiring nicks and also surviving. We believe that the number of newly nicked animals is relatively small, however.

We refer to this component of the model as the *population model*. It provides the probability distributions $P(S_j | S_{j-1}, B_{j-1}, \theta_{j-1})$ and $P(B_j | W_{j-1}, N_{j-1}, \omega_j)$.

3.2 Modeling the Total Population

In this case study, the total population size and its variation over time is the primary statistic of interest, but the total population comprises both nicked and unnicked animals. We can, however, estimate the size of the total population from the size of the nicked population using data on the proportion of animals in each group that have nicked dorsal fins. This is possible because, although unnicked individuals cannot be reliably identified over periods of months or years, they are recognizable over a period of days (see Wilson et al. 1999). This allows us to count the number of unnicked individuals captured on high-quality photographs in any one encounter and to estimate the proportion of nicked and unnicked animals in the group to provide an inflation factor.

Then the unnicked part of the total population is given by $W_j - N_j$. If the probability of an individual having nicks is

given by ν_j , then the size of the unnicked population at time j can be modeled as a negative binomial distribution conditional on the size of the nicked population, so that $W_j - N_j \sim \text{NegBin}(N_j, \nu_j)$. This approach allows the use of an independent data set to inform the ν_j , rather than relying on the recapture data to estimate this parameter. The negative binomial distribution is preferred over a binomial distribution, because the N_j 's already have been assigned a distribution in the population model.

In each time period j , suppose that there are T_j trips, each observing t_{ji}^w animals for $i = 1, \dots, T_j$, of which t_{ji}^n are nicked. Numerous trips are undertaken each year, and the number nicked is separately estimated on each encounter. A binomial distribution then can be used to describe the number of nicked animals seen per trip, so that $t_{ji}^n \sim \text{Bin}(t_{ji}^w, \nu_j)$. Thus the observations t_{ji}^n and t_{ji}^w allow us to estimate ν_j , and thus the total population size, given an estimate of the nicked population. We refer to this as the *inflation model*. It provides the probability distributions $P(W_j|S_j, B_j, \nu_j)$ and $P(t_{ji}^n|t_{ji}^w, \nu_j)$.

3.3 The Observation Model

In any time period, only a portion of the nicked population is seen. Examination of the data suggests that the left and right capture probabilities differ at the population level. The probability that an individual animal would be seen from the left or right side, $s \in [L, R]$, is given by $\rho_{js} = \exp(\delta_s + \epsilon_{js}) / (1 + \exp(\delta_s + \epsilon_{js}))$, where δ_s denotes a global capture tendency and ϵ_{js} denotes a time-varying capture component.

Then the number of nicked animals seen from side s , n_{js} , follows a binomial distribution, $n_{js} \sim \text{Bin}(N_j, \rho_{js})$, where $n_{jL} = \sum_d h_{dj} \in [1, 3]$ and $n_{jR} = \sum_d h_{dj} \in [2, 3]$. We refer to this model as the *observation model*. It provides the probability distributions $P(n_{jL}|N_j, \rho_{jL})$ and $P(n_{jR}|N_j, \rho_{jR})$.

We consider the n_{jL} and n_{jR} as independent counts. A dolphin seen in one year from one side contributes to the probability of observing that side, and one seen from both sides contributes to both probabilities. The introduction of capture probabilities for each side allows the combination of the two photographic series that otherwise would have been analyzed separately, because they would be correlated. It is also of interest to estimate these probabilities to assess the capture methods in use. We include the term ϵ_{js} to allow for observed differences between years in observing all dolphins from one side versus the other. These differences may have arisen from differences in boat work.

3.4 The Recapture Model

The population and observation models require estimates of the parameters α , β_j , δ_L , ϵ_{jL} , δ_R , and ϵ_{jR} , corresponding to the survival and capture probabilities. These probabilities can be obtained from the capture history data. To do this, we calculate the likelihood of the entire capture history matrix, which is the product of the probabilities associated with each animal's individual history, $\mathcal{L}(h_{dj})$.

To combine the photo-identification series from the left and right sides into a single bilateral analysis, the model allows different capture probabilities when animals are seen from each side. The number of animals seen also can differ between the

left and right sides. Other parameters do not depend on the side from which an animal is observed; for example, the population size and survival probability of an animal should not depend on which side is observed. However, the left-side capture probability for individual animals might be expected to differ from that of the right side; for example, the animal might be more likely to approach the boat from one side than from the other. Dolphins are also well known to have heterogeneous behavior (Wilson, Reid, Grellier, Thompson, and Hammond 2004).

Thus, to incorporate heterogeneity as well as observation from two sides, survival and capture probabilities are defined as $\text{logit}(\phi_{dj}) = \alpha + \beta_j + \gamma_d$ and $\text{logit}(\pi_{djs}) = \delta_s + \epsilon_{js} + \zeta_{ds}$, where γ_d denotes a survival effect, ζ_{ds} denotes a recapture effect for animal d , $s \in [L, R]$ for the left or right side, and $\text{logit}(x) = \log(x/(1-x))$. The logit function is the standard choice for binary data.

Note that the heterogeneity effects are not used in the population and observation models, because both of these are based on both the nicked and unnicked populations, and members of the latter will not have an individual effect parameter. Although we could adopt a random-effects model to ascribe individual effects to unnicked animals, this would imply that we believe the heterogeneity of survival and recapture to be the same in both the nicked and unnicked populations, which may not be the case.

The overall probability has components for animals in two situations. There are n_J animals observed at the final time, and some n_{J^*} animals last observed at some earlier time and that might have died or simply are not seen. Each individual history probability is conditional on the first time that the animal is seen, j_d^1 .

Thus the likelihood associated with the histories of $n = n_J + n_{J^*}$ dolphins is given by

$$\begin{aligned} & \prod_{s \in [L, R]} \prod_{d=1}^n \prod_{j=1}^J \mathcal{L}(h_{djs}) \\ &= \prod_{d=1}^{n_J} \prod_{j=j_d^1+1}^J \phi_{d,j-1} I(\pi_{djL}, \pi_{djR}, h_{djs}) \\ & \quad \times \prod_{d=n_J+1}^{n_J+n_{J^*}} \prod_{j=j_d^1+1}^{h_l} \phi_{d,j-1} I(\pi_{djL}, \pi_{djR}, h_{djs}) \left(1 - \phi_{dh_l}\right. \\ & \quad \left. + \sum_{j=h_l+1}^J \hat{\phi}_{dj} \prod_{k=h_l+1}^j \phi_{d,k-1} (1 - \pi_{dkL})(1 - \pi_{dkR})\right), \quad (1) \end{aligned}$$

in which ϕ_{dj} denotes the survival probability, $\hat{\phi}_{dj} = 1 - \phi_{dj}$ when $j < J$ and $\hat{\phi}_{dj} = 1$ when $j = J$, π_{djs} denotes the recapture probability from animal d observed in time j from side $s \in [L, R]$, j_d^1 and h_l denote the first and last times that individual d is seen; and $I(\pi_{djL}, \pi_{djR}, h_{djs}) = (1 - \pi_{djL})(1 - \pi_{djR})$ when $h_{djs} = 0$, $I(\pi_{djL}, \pi_{djR}, h_{djs}) = \pi_{djL}(1 - \pi_{djR})$ when $h_{djs} = 1$, and $I(\pi_{djL}, \pi_{djR}, h_{djs}) = (1 - \pi_{djL})\pi_{djR}$ when $h_{djs} = 2$, $I(\pi_{djL}, \pi_{djR}, h_{djs}) = \pi_{djL}\pi_{djR}$ when $h_{djs} = 3$. The ϕ_{dj} and π_{djs} parameters are defined only for $1 \leq j < J-1$ and $2 \leq j < J$. The values of n_J , j_d^1 , and h_l are determined from the capture histories.

We refer to this model as the *recapture model*. It yields the probability $P(h_{djs}|\phi_{dj}, \gamma_d, \pi_{djL}, \pi_{djR}, \zeta_{dL}, \zeta_{dR})$. This is a Cormack–Jolly–Seber model, which has been discussed elsewhere (Seber 2002; Lebreton, Burnham, Clobert, and Anderson 1992; Link and Barker 2005).

This completes the model specification. To summarize, we define a population model that describes the recruitment (ω_j) and survival (θ_j) of animals in the nicked population (N_j). The relative sizes of the nicked population (N_j) and total population (W_j) are described by the inflation model, which makes use of observed counts of nicked and unnicked animals. Using the capture probability (ρ_{js}) and the observed number of nicked animals, we estimate the nicked population. Finally, we estimate the heterogeneous capture (π_{djs}) and survival (ϕ_{dj}) probabilities from the capture histories. Because this is a Bayesian analysis, we also specify priors to the following parameters: S_0 , B_0 , ω_j , W_0 , N_0 , α , β_j , γ_d , δ_s , ϵ_{js} , and ζ_{ds} . We describe the priors in detail in the next section.

4. ANALYSIS

In this section we describe the statistical methodology required to analyze the model described in the previous section. We adopt a Bayesian approach and describe the prior specification and simulation techniques required here. In this modeling process, we use a Bayesian approach to allow for uncertainty in measurement and parameters used. The Bayesian approach allows for simultaneous consideration of all data and models, allowing for the proper propagation of uncertainty throughout the model. Identifiability is also less of a concern in a Bayesian analysis in which prior information is supplied (Gelfand and Sahu 1999). Moreover, the Bayesian approach has an advantage in that MCMC methods can be used, which greatly simplifies the computation compared with the corresponding classical tools. The remainder of this section discusses the process of prior specification and provides details of the implementation.

4.1 Priors

The first stage in the Bayesian analysis is to elicit priors for each of the model parameters. We do so here by grouping the parameters according to the component of the model in which they appear. The priors used and their associated parameters are summarized in what follows.

The Population Model. The model specifies the distribution of parameters S_j and B_j in terms of S_{j-1} and B_{j-1} for $j \geq 1$. Therefore, we need a prior for S_0 and B_0 . Because they only appear together, we set $N_0 = S_0 + B_0$ and assign a Poisson prior $N_0 \sim \text{Po}(\lambda_N)$. Its mean takes a gamma prior $\lambda_N \sim \text{Gam}(.76, .01)$, with parameters selected to obtain a mean for the nicked population of 76, as estimated by Wilson et al. (1999), and a large variance, so that it becomes uninformative compared with the range of reasonable population values.

Because the recruitment rates of nicked dolphins cannot be directly estimated from the photo-identification data set, the priors are parameterized with results from a separate analysis of randomly selected photographs with at least 2 years of data. Because it is thought that the rate of nicking might be greater for older animals due to increased social interactions, estimates are estimated from photographs of individuals that

are first identified as known-age calves. Identification is done using all attributes, such as fin shape and the presence of lesions. Photographs of seven of these animals are available for estimating the age at which these dolphins are first seen to have a nick in the dorsal fin. We consider these cases a random selection from the unnicked population, so that the mean number of nicks per year gives an approximate probability of nicking per year. We set the prior for ω_j to be reasonably vague: $\omega_j \sim \text{Beta}(.0238, 1)$. Although rough, these assumptions give a crude estimate for the parameter, which is then updated by the data.

The Inflation Model. The initial population size is assigned a negative-binomial prior, $W_0 - N_0 \sim \text{NegBin}(N_0, \nu_0)$. The initial inflation factor, ν_0 , is assigned a beta prior, $\nu_0 \sim \text{Beta}(1, 1)$, which is equivalent to a noninformative uniform prior.

The Recapture Model. The recapture model survival parameters have independent normal priors $N(0, 1.85)$, and the capture parameters have independent normal priors $N(0, 1.5)$. These priors span the range (0, 1) on the logit scale. Larger variances are not used, because these would obtain a U-shaped distribution on the logit scale.

4.2 Implementation

Once priors are assigned, the full joint distribution can be determined as the product of the likelihood with the associated prior distributions. The resulting posterior is complex and high-dimensional and so inference is obtained in the form of posterior means and variances obtained through MCMC simulation. We choose to use an implementation in which each parameter is updated in turn using either a Metropolis–Hastings or a Gibbs update, depending on the form of the associated posterior conditional distributions. The updating strategy is detailed in the Appendix. All simulation software is written in FORTRAN 77. The model was run for 500,000 iterations, and a 50% burn-in was used. Sensitivity studies and standard diagnostic techniques were used (Brooks and Roberts 1998) to assess model validity.

4.3 Simulation Study

To test the MCMC code and to demonstrate the utility of the framework developed earlier, we construct two artificial populations, one with homogeneous capture and survival probabilities and the other with heterogeneous capture and survival probabilities. These populations are constructed using the following procedure. An initial population of animals ($n = 130$) is sampled, and a proportion of this initial population is randomly marked as nicked. At each time period in the simulation, animals are randomly selected to die, some of the unnicked become nicked, and a proportion of the remaining animals are randomly selected to be observed. For each population, three simulations are run with differing priors for the ω_j and λ_N parameters. The priors are such that the three cases represent vague priors, precise priors, and very precise priors, but in each case the means differ from the actual population values. One possible outcome is that the precise prior simulations track the prior means more closely than the vague simulations.

The simulations are illustrated in Table 1, which shows the actual total abundances, the medians of the posteriors for W_j ,

Table 1. Actual and estimated median total abundances for two artificial populations with 95% HPDI and posterior p values from three simulations on each with differing priors

Population	Year	W_j	A		B		C	
			\hat{W}_j	p value	\hat{W}_j	p value	\hat{W}_j	p value
1	1990	124	119(99, 139)	.28	112(97, 130)	.07	107(90, 124)	.02
	1991	120	125(105, 146)	.67	118(95, 134)	.39	114(97, 135)	.25
	1992	114	116(96, 135)	.54	110(93, 127)	.30	106(92, 123)	.17
	1993	109	113(95, 134)	.63	108(92, 124)	.41	105(90, 121)	.26
	1994	103	111(93, 130)	.81	106(88, 124)	.63	103(86, 118)	.49
	1995	97	105(89, 125)	.86	102(87, 118)	.74	100(85, 114)	.62
	1996	95	98(84, 115)	.66	95(81, 110)	.48	93(81, 107)	.38
	1997	91	99(83, 114)	.85	96(80, 109)	.76	95(80, 108)	.65
	1998	89	94(79, 110)	.73	91(77, 105)	.56	90(77, 103)	.52
	1999	85	92(77, 108)	.78	89(75, 103)	.69	87(75, 103)	.63
	2000	76	82(65, 98)	.76	79(66, 96)	.65	79(65, 94)	.59
	2001	70	79(62, 99)	.84	77(58, 95)	.79	76(60, 95)	.75
2002	68	76(55, 93)	.78	75(56, 91)	.75	73(58, 92)	.70	
2	1990	124	135(100, 178)	.71	121(96, 159)	.42	116(90, 149)	.26
	1991	122	123(90, 158)	.51	112(87, 140)	.21	108(84, 134)	.12
	1992	119	114(87, 148)	.35	105(84, 130)	.10	101(78, 124)	.06
	1993	111	106(82, 138)	.34	99(75, 121)	.11	95(74, 117)	.06
	1994	106	102(76, 130)	.33	93(75, 118)	.12	91(68, 115)	.07
	1995	100	96(70, 122)	.38	91(74, 114)	.16	88(67, 108)	.08
	1996	93	93(66, 119)	.48	87(69, 109)	.26	85(65, 105)	.16
	1997	87	91(67, 115)	.60	85(68, 106)	.37	82(62, 102)	.28
	1998	77	79(59, 101)	.56	76(62, 95)	.39	72(57, 91)	.28
	1999	74	84(60, 108)	.80	80(62, 101)	.75	77(58, 97)	.62
	2000	72	78(57, 99)	.67	74(58, 94)	.58	72(55, 91)	.46
	2001	67	71(49, 92)	.62	69(48, 91)	.57	66(46, 88)	.43
2002	64	68(41, 91)	.59	65(44, 92)	.51	63(43, 88)	.44	

NOTE: Population 1 has homogeneous capture probability (.75) and survival probability (.95) while population 2 has heterogeneous capture probability (mean, .55; range, .05–.98) and survival probability (mean, .92; range, .68–.99). The simulations have different priors for ω_j and λ_N . Simulation run A has vague priors [$\omega \sim \text{Beta}(.0294, 1.2368)$, $\lambda_N \sim \text{Gam}(.76, .01)$], B has more precise priors [$\omega \sim \text{Beta}(.0237, 1.0)$, $\lambda_N \sim \text{Gam}(76, 1)$], and C has very precise priors [$\omega \sim \text{Beta}(.9299, 39.155)$, $\lambda_N \sim \text{Gam}(7,600, 100)$]. Their means are the same in each case (.023 and 76), but each differs from the actual population values (.06 and 106).

their 95% highest posterior density intervals (HPDI), and a p value. The p values are calculated by counting the proportion of iterations in which the W_j exceeded the true value. Examination of the results indicate that the median posterior estimates generally agree with the actual values. The agreement is satisfactory whether or not there is heterogeneity assumed. The p values are in the range .02–.88, suggesting that the model works correctly. The posterior p values for the recapture model coefficients are given in Table 2. The p values for α , δ_L , and δ_R are summarized, and those for the remaining parameters are summarized as the proportion of p values in each that lie inside the range .01–.99. Almost all p values are within the range .01–.99; the only exceptions are the capture coefficients for a small number of dolphins.

In general, the total population estimates for the homogeneous case are slightly greater and the 95% HPDI is narrower than the heterogeneous case, but all intervals contain the population values. The estimates also shrink slightly for the models with more precise priors. However, the p values in each case suggest an adequate fit, even though some priors are deliberately set to incorrect values. In the case of the recapture coefficients, there is no apparent difference between the homogeneous and heterogeneous models, or with any trend in the precision of the priors.

5. RESULTS

We obtain estimates of heterogeneous capture and survival coefficients, variation of capture and survival over time, overall survival and capture probabilities, the abundance, and the trend in abundance. The survival probabilities and capture coefficients from the left and right sides are shown in Figure 2 and Table 3. We can obtain an overall capture probability for the two sides by calculating $\exp(\delta)/(1 + \exp(\delta))$. The mean overall cap-

Table 2. Summary of posterior p values for survival and capture coefficients for two artificial populations from three simulations on each with differing priors

Population	α	β_j	γ_d	δ_L	ϵ_{jL}	ζ_{dL}	δ_R	ϵ_{jR}	ζ_{dR}
1	.16	1.00	1.00	.66	1.00	.98	.60	1.00	1.00
	.10	1.00	1.00	.59	1.00	.98	.53	1.00	1.00
	.08	1.00	1.00	.59	1.00	.98	.48	1.00	1.00
2	.34	1.00	1.00	.17	1.00	.97	.50	1.00	.98
	.22	1.00	1.00	.15	1.00	.97	.37	1.00	.99
	.23	1.00	1.00	.12	1.00	.97	.39	1.00	.99

NOTE: The populations and simulations are described in Table 1. The p values are calculated as the proportion of iterations greater than the actual population value. The p values for α , δ_L , and δ_R are shown. Because the remaining parameters are vectors of coefficients, those p values are summarized as the proportion of p values in each that are found inside the range .01–.99.

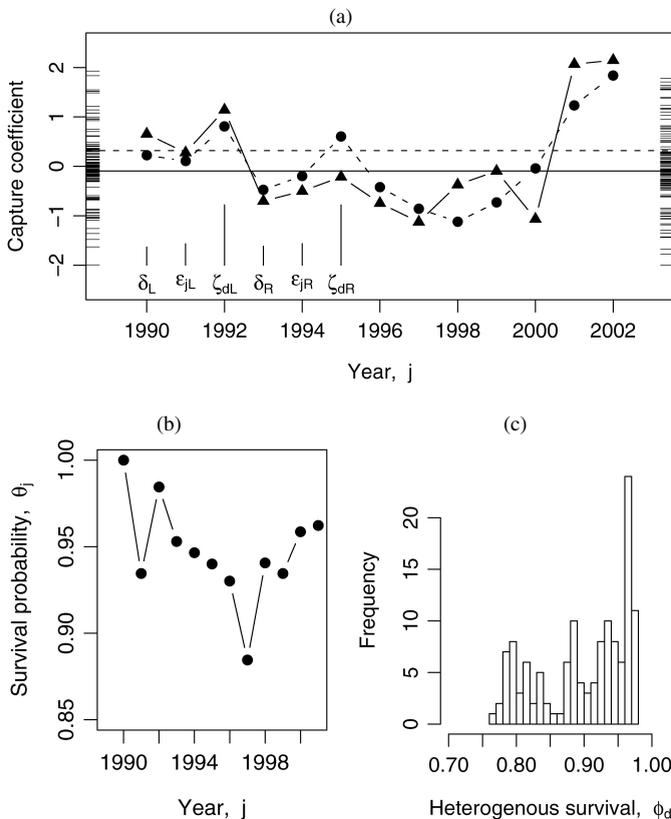


Figure 2. (a) Variation of mean capture coefficients over time for the left side, ϵ_L ($-\blacktriangle-$) and right side, ϵ_R ($- \bullet -$). The two horizontal lines indicate the global mean capture coefficients, δ_L (—) and δ_R (---). On the left vertical axis are the mean left-side heterogeneity capture coefficients, ζ_L and on the right vertical axis are the mean right-side heterogeneity capture coefficients, ζ_R . Standards errors for each coefficient are shown as vertical bars. (b) Variation of mean survival probability over time. (c) Histogram of mean heterogeneous survival probabilities.

ture probability for the left side is .48 (95% HPDI = .29, .68) and for the right side it is .58 (95% HPDI = .39, .77). Although this is a small difference, the probability of the right capture coefficient exceeding the left is .81. Examination of Figure 2(a) shows that the variation of capture coefficients over time is large compared with the overall coefficients, and that the left (ϵ_L) and right (ϵ_R) coefficients tend to track each other. The probability of the right capture coefficient exceeding the left varies over a wide range, .07–.96. This range results from some years in which the probability tends strongly to the left side (1995 and 2000; probability of observing the left side, .95) or right side (1998, 1999, 2001; probability of observing the right side, .91). Finally, the range of the heterogeneous coefficients is comparable to that of the time-varying coefficients.

The mean heterogeneous survival coefficient is not correlated with either of the mean capture heterogeneous coefficients (right, $r = .009$; left, $r = .022$). However, the mean left and right heterogeneous capture coefficients are correlated ($r = .714$), indicating that animals that are more likely to be seen from one side also are more likely to be seen from the other side. However, the heterogeneity capture coefficient of the right side (mean, .56) exceeded that of the left side (mean, .23), with 85% of animals having higher right coefficients than left

Table 3. Left-side and right-side capture probabilities and survival probabilities by year

Year	Left capture	Right capture	Survival
1990			1(.1, 1)
1991	.54(.40, .68)	.60(.47, .75)	.93(.84, .99)
1992	.74(.59, .86)	.75(.60, .86)	.98(.94, 1.00)
1993	.31(.20, .44)	.46(.33, .61)	.95(.88, 1.00)
1994	.36(.24, .47)	.53(.35, .66)	.95(.86, 1.00)
1995	.42(.27, .55)	.71(.56, .88)	.94(.86, 1.00)
1996	.30(.17, .42)	.48(.34, .63)	.93(.82, 1.00)
1997	.23(.14, .36)	.37(.23, .51)	.88(.75, .98)
1998	.39(.24, .53)	.31(.20, .45)	.94(.84, 1.00)
1999	.45(.31, .63)	.40(.25, .54)	.93(.82, 1.00)
2000	.24(.14, .36)	.57(.40, .72)	.96(.88, 1.00)
2001	.87(.78, .94)	.82(.73, .91)	.96(.89, 1.00)
2002	.88(.80, .96)	.89(.80, .96)	

NOTE: For each, the mean and the 95% HPDI limits are given. There is concordance between the left-side and right-side results. The capture probabilities are more variable and reach minimums in 1997 and 2000 for the left side and in 1998 for the right side, but both reach maximums in 2002. Survival reaches a maximum in 1992, declines to a minimum in 1997, and then rises again in later years.

coefficients. Because this is observed after adjustments for the overall and time-varying components, it suggests an effect due to behavior or sampling protocol.

The variation in the capture probability over time is likely to result from a combination of factors, including variation in dolphin ranging patterns (see Wilson et al. 2004), weather conditions, and other logistical factors that influence sampling in different areas. Most notably, sampling protocols were changed in 2000 specifically to increase the probability of capture. This change has proven to have been successful in the latter part of the study, while estimates of the survival probabilities and total population size remain unaffected. Second, another study (Wilson et al. 2004) has shown that the ranging pattern of the population changed in recent years, with some animals spending more time in the southern part of the population range along the east coast of Scotland, south of the Moray Firth to St. Andrews and the Firth of Forth. The effect of this would be to reduce the capture probability in the core study area in the inner Moray Firth and to potentially increase heterogeneity in capture probabilities. The more southerly areas also have been sampled, but the data are more sparse and cover only a small number of years. Once these histories have become more extensive, we expect that the capture probabilities will become less variable. Unlike other models, our estimates are also corrected for individual heterogeneity. Variation in capture probabilities also might have arisen from heterogeneous effort in space. Although this was not explicitly modeled, we could have stratified the capture histories by area by including separate capture coefficients for each area.

The overall mean survival estimate through the study period is .93 (standard deviation, .029; 95% HPDI = .861, .979). This is similar to an earlier maximum likelihood estimate of survival for the cohort of nicked individuals from this population first observed in 1990 (Saunders-Reed, Hammond, Grellier, and Thompson 1999). But our model estimate is slightly lower than survival estimates from other bottlenose populations of $96.2 \pm .76\%$ in Sarasota Bay, Florida (Wells and Scott 1990), $95.2 \pm$

1.50% in Doubtful Sound, New Zealand (Haase 2000), and 95–99% in the Sado estuary, Portugal (Gaspar 2003). However, this may be because our study included subadults while the other studies reported adult survival. Variation in survival probability occurs over time [Fig. 2(b); Table 3]. It is of interest that survival reached a minimum in 1997 but later returned to levels comparable to earlier years. The proportion of iterations in which the survival for 1997 are above the mean survival for the remaining years (mean $\phi = .95$; 95% HPDI = .85, 1.00) is only .08. The apparent low survival in 1997 may be due to migration, because this is not distinguishable from survival in the model. It is possible that an emigration event occurred in 1997 and that those individuals have not yet returned. Considerable heterogeneity in survival (range, .77–.97) is observed, as shown in Figure 2(c). The survival probabilities are not distributed smoothly, suggesting multimodality. The animals with a low survival coefficient may have died or migrated. In the case of migration, this result would indicate that some animals less consistently reside in the core areas compared with others.

Individuals with higher survival coefficients are frequently those seen earliest in the study. There is little information available on individuals seen only more recently, and consequently, their coefficients are close to 0. Some survival coefficients are more negative, and these correspond to animals that have not been seen for some time. As time goes on, and in the absence of a confirmed death or sighting, these coefficients can be expected to become more negative. However, some animals that are observed only on a few occasions have negative coefficients. The estimation of individual survival coefficients means that estimation of other coefficients in the model are adjusted for variable survival. The estimation of individual capture probabilities allows the results to be combined with other individual covariates, such as sex or body size, if these data become available. Similarly, where individuals differ in their home ranges, individual capture or survival probabilities could be related to local environmental conditions within their range, to prey availability, or to water quality.

Estimates of the total population size from bilateral analysis of the left and right photo-identification series and estimates from unilateral analyses of the left and right sides are shown in Figure 3(a). These are similar both to the maximum likelihood estimate of 129 (95% confidence interval = 110–174) for data collected in 1992 (Wilson et al. 1999) and to a Bayesian multisite mark recapture estimate of the nicked population of 85 (95% probability interval = 76–263) for data collected in 2001 (Durban et al. 2005). The credible intervals of the abundance estimates are generally narrower in the bilateral analysis (mean width, 88.6) than in left-side analysis (mean width, 137.3) and right-side analysis (mean width, 93.7). Figure 3(b) shows the prior and mean posterior recruitment probabilities, ω_j . It is interesting that higher probabilities occur in 1996 and 2001. This might be considered to variations in capture probability, but whereas the capture probability is high in 2001, it remains low in 1996 [see Fig. 2(a)]. Instead, calculating the probabilities of the posterior exceeding the prior recruitment probabilities, we find they are below .5 (range, .04–.44) for all years except 2001, in which it is .85. The higher recruitment probability in 2001 may be due to an improved protocol in that year that led to the

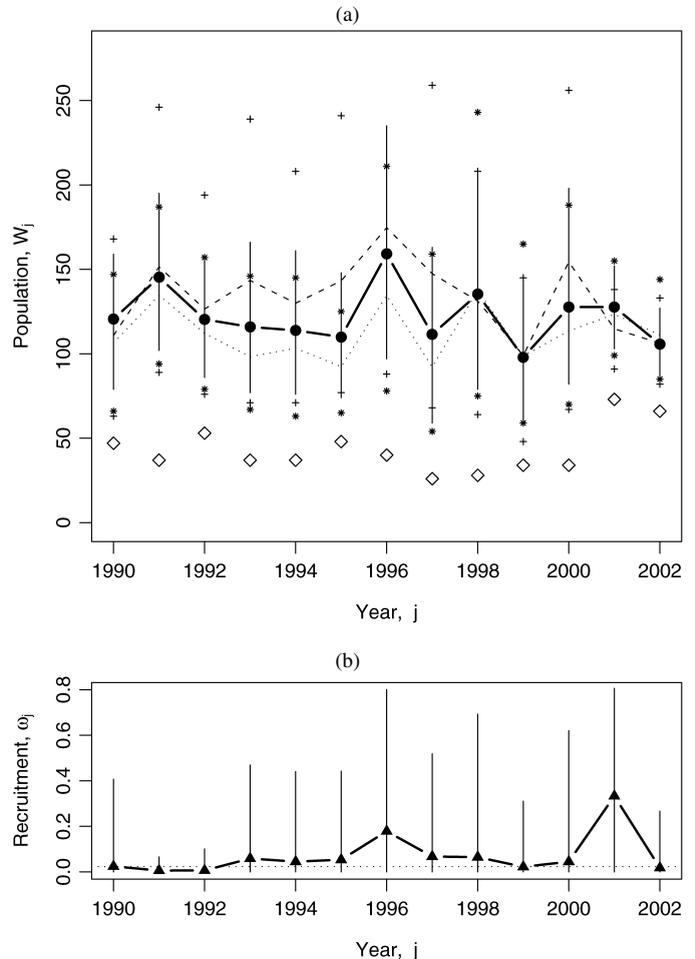


Figure 3. (a) Mean total abundance estimates from a bilateral analysis with 95% HPDI. Also shown are estimates from separate analyses of left (---) and right (···) sides along with associated 95% HPDI represented by symbols: left, +; right, *. Minimum numbers of animals known to be alive are indicated by diamonds. (b) Mean posterior recruitment probabilities, ω_j , with 95% HPDI. The prior value is represented as a dotted line.

identification of previously unrecognized nicked animals. We consider the rise in 1996 to have insufficient evidence to suggest an increase in recruitment in that year.

Earlier demographic modeling of this population has predicted that the population is in decline (Saunders-Reed et al. 1999). To examine this, we calculate the statistic $[\prod_{j=2}^J W_j / (W_{j-1})]^{1/(J-1)}$. Values of this statistic >1 indicate an increasing population, whereas values <1 indicates a decreasing population. The mean value is .989 (95% HPDI = .958, 1.02), and the probability of it being <1.0 is .77. This suggests that the population may be decreasing, but that the evidence for a decline is weak. By doing this, we are able to use the full time series of photo identification data to obtain simultaneous posterior estimates of the W_j to compare the probability of a population increase or decrease. In agreement with the earlier predictive modeling, these data indicate greater probability of a decline than of an increase. However, because it is likely that the population is expanding its range (Wilson et al. 2004), the decline may be confounded with temporary emigration.

6. DISCUSSION

Changes in the size of wildlife populations are often assessed by fitting trend models to independent abundance estimates, but the power of these techniques to detect trends often can be low (Gerrodette 1987; Taylor, Martinez, Gerrodette, Barlow, and Hrovat 2007). Here we use a capture–recapture model that incorporates an underlying population model and an observation model. We provide a probability that a population is in decline or increasing. Using photoidentification data from this bottlenose dolphin population, we generate the first empirical estimate of trends in abundance for any of the populations of small cetaceans inhabiting European waters. Because the methodological changes in sampling likely are absorbed by the time-varying capture coefficient, the remaining variation due to individual capture tendencies might reasonably be described by the individual capture coefficient. This then allows exploration of capture and survival relating to individuals rather than to populations. Information on individual survival could be important for addressing some management issues; for example, individuals differing in their spatial distribution.

By decomposing the capture probabilities into overall, time-varying, and heterogeneous terms, we find that the time-varying contribution and heterogeneous variation are comparable in magnitude, and their variation is greater than that of the overall term. This information can be used in the design of monitoring programs by suggesting how effort should be distributed. The difference in overall left and right capture probabilities might be interpretable as an artifact of the sampling techniques or of behavioral effects. However, after allowing for this, the probability of observing one side also varied over time, with some years strongly favoring one side or the other. This might be explained by variation in protocol between years, such as changes in personnel. The relative sizes of these effects may be of use in evaluating consistency of protocol over time. Finally, after allowing for the overall difference and time variation, the heterogeneous capture coefficients exhibit a bias to the one side, possibly due to behavior or protocol. These findings demonstrate that bilateral decomposition of capture probabilities can provide useful information.

We decompose the survival probability similarly and we find it to be unusually low in 1997, suggesting a possible multimodal heterogeneous survival probability that may be the result of migration or survival variation. This type of decomposition allows exploration of such effects in more detail. In particular, the multimodality of heterogeneous survival suggests that the population comprises individuals with different strategies, some visiting the core study area more or less often. Ongoing work is attempting to quantify individual heterogeneity, such as in exposure to sewage contaminated waters and boat-based tourism. Therefore, this technique could be used to determine whether exposure to different anthropogenic stressors is related to survival.

Our model also makes use of priors such as those on ω_j that are not informed by the recapture data set, but make use of information from other sources. An alternative approach might be to specify these as informative priors based on expert opinion or tuned to obtain satisfactory results. Our application illustrates how disparate data sources may be combined into a

single analysis. Although the data source for the prior recruitment probability is small and problematic, it is the only one available. Even when some priors are defined in the simulation study to incorrect values, the estimates of parameters of interest remain valid. The posterior probability also adds to the state of knowledge of this parameter.

Previous use of capture–recapture models with cetacean photoidentification data highlights the potential violation of model assumptions due to heterogeneity in capture and/or survival probabilities. This model explicitly accounts for heterogeneity and also provides simultaneous estimates of individual survival and capture probabilities. This can be used both to explore the biological basis of heterogeneity and to improve sampling programs. The individual survival coefficients also can be used to explore aspects of biology where correlates are available; for example, the relationship of survival to age, sex, or other variables may be of interest. Abundance under the assumption of heterogeneous survival has been estimated by Lee, Huang, and Ou (2004), whereas individual and time-varying survival estimates have been obtained using band-recovery models (Grosbois and Thompson 2005). Other studies have examined survival by group; for example, Franklin, Anderson, and Burnham (2002) obtained separate estimates of group-level survival for males and females using stratification in a banding study. Although we lack such variables as age and sex, theoretically it would be possible to examine individual survival by sex either as a post hoc comparison or through their integration into the model itself. For example, survival and capture could be modeled as $\text{logit}(\phi) = \alpha + \beta_j + \gamma_d + \tau$ and $\text{logit}(\pi) = \delta + \epsilon_j + \zeta_d + \chi$, where τ corresponds to stage-specific (e.g., young, immature, reproductive female, senescent) survival and χ corresponds to capture probabilities for various categories (e.g., young, reproductive adult).

Other cetacean studies have examined heterogeneity. Whitehead (2001b) obtained an estimate of the coefficient of variation (CV) for identification from a randomization test of successive identifications in whale track data. (The CV is also a measure of capture heterogeneity.) They found that the CV was significant in one of the two years and that probably depended on the sizes of the animals being observed. This is not comparable to the dolphin observations, in which heterogeneity is more likely to result from differences in animal behavior. In the present study, we use a likelihood in which heterogeneity of survival and capture has been incorporated by a logit function. This approach was described previously (Pledger, Pollock, and Norris 2003; Pledger and Schwarz 2002) within a non-Bayesian context. Pledger et al. (2003) classified animals into an unknown set of latent classes, each of which could have a separate survival and capture probability. A simplification allows for time-varying and animal-level heterogeneity. This approach is similar to ours, but we also integrate a dynamic population model and an observation model into the estimation process. Goodman (2004) also implemented a population model in a Bayesian context that combines capture–recapture data with carcass-recovery data, but assumes the absence of heterogeneity in capture probabilities. Durban et al. (2005) estimated abundance for the same population as us, but used a multisite Bayesian log-linear model and model averaging (King and Brooks 2001) across the possible models with varying combinations of interactions. Our

model could be extended to include multiple sites and years by using a capture–recapture history that includes site information and a year–site term in the capture probability expression. By doing this, we suggest that geographic areas with more data can be used to strengthen estimates from poorly sampled areas. This also may account for some individual variation currently identified as individual capture heterogeneity, because some individuals may be more closely associated with some areas than others, and may attenuate a possible confounding of migration with survival.

We use a separate data set and a negative-binomial model to inflate the estimate of the proportion of nicked animals in the samples. Another study (Da Silva, Rodrigues, Leite, and Milan 2003) obtained an abundance estimate for bowhead whales using an inflation factor derived from the numbers of good and bad photographs of marked and unmarked whales. Our analysis avoids the lack of independence between good photographs and distinctively marked animals in the photographs that might invalidate the estimate of variance in the inflation factor. Other studies avoid this issue by including only separately categorized good-quality photographs (e.g., Wilson et al. 1999; Read, Urian, Wilson, and Waples 2003). However, independent estimates of inflation, when available, such as in our study, are preferred.

We do not know of other cetacean studies that combine photo-identification series of the left and right sides, but an analogous approach is that of log-linear capture–recapture modeling (King and Brooks 2001), in which animals are identified from separate lists. Some photo-identification studies might use information from both sides in the process of identifying animals (Joyce and Dorsey 1990). A more robust approach is to perform the identification on each side separately. We have shown how these separate data can then be combined.

A major advantage to our modeling approach is its extensibility. Within the Bayesian framework, models can be compared by such methods as reversible-jump Markov chain Monte Carlo techniques (Green 1995). Model extensions include extending the population model considering an individual-level approach. This would allow incorporation of the heterogeneity into this part of the model and also modeling of the unobserved population. More detailed modeling of heterogeneity could be explored by including hyperpriors for the variances of the recapture model terms. For convenience, we analyze the data on an annual basis. Additional information would be available if the analyses were conducted on a finer time scale, such as months or by individual trip. This would allow the model to be extended to include seasonal effects. For example, dolphins are observed more frequently in summer months than in winter months, and this tendency could be included in an extended model by changing the capture probability to be $\text{logit}(\pi) = \delta_t + \epsilon_j + \zeta_d$, where $\delta_t, t \in [1, \dots, 12]$, is a monthly capture coefficient. This may be of use in modeling fine-scale movements. The response variable itself also can be generalized. Although we are careful to only include data from high-quality photographs and nicked animals, there is still the possibility of some identification errors, particularly for more subtly marked individuals. A possible extension of the model could allow identification to be assigned different levels of certainty, for example by incorporating an intermediate state between nonrecapture and recapture that we

term “possible recapture.” This could be done by replacing the logit function, $\text{logit}(v) = \log(v/(1 - v))$, where v corresponds to the probability of recapture, by a proportional odds function (McCullagh 1980). This technique has previously found application in a study of photo-identification used to model photographic quality scores and individual distinctiveness of humpback whale tail flukes (Friday, Smith, Stevick, and Allen 2000). In this approach, the probability of “possible recapture” is given by $v_1 = \pi_1$, the probability of certain recapture is given by $v_2 = \pi_1 + \pi_2$ and includes the possible recapture category, and the probability of no capture is given by $v_0 = 1 - \pi_1 + \pi_2$. There are two proportional odds functions corresponding to possible recapture and certain recapture, which are $\text{logit}(v_1) = \log(\pi_1/(\pi_2 + \pi_3))$ and $\text{logit}(v_2) = \log((\pi_1 + \pi_2)/\pi_3)$. We then could extend the recapture model using $\text{logit}(v_1) = \alpha + \beta_j + \gamma_{k1}$ and $\text{logit}(v_2) = \alpha + \beta_j + \gamma_{k2}$. This proportional odds approach may be particularly useful in situations where automatic matching algorithms (Sánchez-Marín 2000) provide an estimate of the likelihood of a match, which could then be incorporated into abundance estimate models.

APPENDIX: DERIVATION OF POSTERiors

Here we show how we derive the posterior conditional distributions for the model parameters and describe how each is updated within the MCMC algorithm. The full joint distribution has the form shown in (A.1). In (A.1), the first two lines correspond to the population model, the third line corresponds to the inflation model, the fourth line corresponds to the observation model, the fifth line corresponds to the recapture model, and the remaining lines correspond to priors:

$$\pi = P(B_1|\omega_1, N_0, W_0)P(S_1|\alpha, N_0)$$

(Sec. 3.1)

$$\times \prod_{j=2}^S P(B_j|S_{j-1}, B_{j-1}, W_{j-1}, \omega_j) \\ \times P(S_j|S_{j-1}, B_{j-1}, \alpha, \beta_{j-1})$$

(Sec. 3.1)

$$\times \prod_{j=1}^S P(W_j|S_j, B_j, v_j) \prod_{i=1}^{T_j} P(t_{ji}^n|v_j, t_{ji}^m)$$

(Sec. 3.2)

$$\times \prod_{j=1}^S P(n_{L_j}|\delta_L, \epsilon_{jL}, S_j, B_j)P(n_{R_j}|\delta_R, \epsilon_{jR}, S_j, B_j)$$

(Sec. 3.3)

$$\times \prod_{j=1}^S P(H_{dj}|\alpha, \beta_j, \gamma_d, \delta_L, \epsilon_{jL}, \zeta_{dL}, \delta_R, \epsilon_{jR}, \zeta_{dR})$$

(Sec. 3.4)

$$\times P(N_0|\lambda_N)P(W_0|N_0, v_0)P(\alpha, \delta_L, \delta_R, \lambda_N, v_0)$$

(Sec. 4.1)

$$\times \prod_{j=1}^S P(\beta_j, \epsilon_{jL}, \epsilon_{jR}, \omega_j, v_j) \prod_{d=1}^n P(\gamma_d)P(\zeta_{dL})P(\zeta_{dR}).$$

(Sec. 4.1)

(A.1)

For each parameter, we obtain the corresponding posterior conditional distribution by extracting all terms containing that parameter from the full joint distribution. When the conditional distributions have a standard form, we use the Gibbs sampler (Brooks 1998) to update the parameters; otherwise, we use Metropolis–Hastings updates (Chib and Greenberg 1995).

Within a Metropolis–Hastings update, we propose a new value for a parameter, x , and denote the proposed value by x' . To decide whether to accept the proposed value, we calculate an acceptance ratio, $\alpha = \min(1, A)$, where A is the acceptance ratio. The acceptance ratio is given by $A = \pi(x')q(x)/\pi(x)q(x')$, where $\pi(x)$ is the posterior probability of x and $q(x)$ is the probability of the proposed value. We accept the new value, x' , with probability α ; otherwise, we leave the value of x unchanged. (See Chib and Greenberg 1995 for an example.)

Normal proposal distributions are used for continuous parameters centered around the current parameter value. Discrete uniform proposals are used for discrete variables, each centered around the current parameter values. The discrete proposals also require constraints to ensure that the proposed values are valid. For example, a proposed value for N_0 must be less than the current value of W_0 . We provide a detailed description of each update next.

Population Model

The population model has parameters $\omega_j, \lambda, B_j, S_j$, and N_0 and are updated using Gibbs or Metropolis–Hastings samplers. The conditional posterior distributions for ω_j and λ_N can be derived as

$$\omega_j | B_j, S_{j-1}, B_{j-1} \sim \text{Beta}(B_j + .0238, W_{j-1} - S_{j-1} - B_{j-1} - B_j + 1)$$

$$\lambda_N | N_0 \sim \text{Gam}(.76 + N_0, 1.01).$$

These are individually updated using the Gibbs sampler during each iteration of the Markov chain.

The parameters B_j, S_j , and N_0 are updated by the Metropolis–Hastings algorithm using acceptance ratios calculated as described earlier. We use uniform proposals centered on the current parameter value and limited to the range of possible values.

For the S_j 's we use three alternative proposals:

$$S'_{j=1} \sim \text{Unif}(\max(0, S_1 - 5, S_2 - B_1, \max(n_{1L}, n_{1R}) - N_1, 2 - B_1), \min(S_1 + 5, N_0, W_1 - B_1, W_1 - B_1 - B_2, W_1 - B_1 - 1));$$

$$S'_{2 \leq j < J} \sim \text{Unif}(\max(0, S_j - 5, S_{j+1} - B_j, \max(n_{jL}, n_{jR}) - B_j, 2 - B_j), \min(S_j + 5, S_{j-1} + B_{j-1}, W_j - B_j, W_j - B_j - B_{j+1}, W_j - B_j - 1));$$

and

$$S'_{j=J} \sim \text{Unif}(\max(0, S_J - 5, \max(n_{JL}, n_{JR}) - B_J, 2 - N_J), \min(S_J - 5, S_{J-1} + B_{J-1}, W_J - B_J, W_J - B_J - 1)).$$

For B_j , we use three alternative proposals:

$$B'_1 \sim \text{Unif}(\max(0, B_1 - 15, S_2 - S_1, \max(n_{1L}, n_{1R}) - S_1, 2 - S_1), \min(B_1 + 15, W_0 - N_0, W_1 - S_1, W_1 - S_1 - B_2,$$

$$W_1 - S_1 - 1));$$

$$B'_{2 \leq j < J} \sim \text{Unif}(\max(0, B_j - 15, S_{j+1} - S_j, \max(n_{jL}, n_{jR}) - S_j, 2 - S_j), \min(B_j + 15, W_{j-1} - S_{j-1} - B_{j-1}, W_j - S_j, W_j - S_j - B_{j+1}, W_j - S_j - 1));$$

and

$$B'_J \sim \text{Unif}(\max(0, B_J - 15, \max(n_{JL}, n_{JR}) - S_J, 2 - S_J), \min(B_J + 15, W_{J-1} - S_{J-1} - B_{J-1}, W_J - S_J, W_J - S_J - 1)).$$

For N_0 , we use

$$N'_0 \sim \text{Unif}(\max(5, N_0 - 15, S_1), \min(N_0 + 15, W_0 - B_1, W_0 - 1)).$$

Inflation Model

The inflation model parameters, W_j and v_j , are updated using Metropolis–Hastings and Gibbs updates. The conditional posterior distributions for v_j can be derived as

$$v_0 | N_0, W_0 \sim \text{Beta}(N_0 + 1, W_0 - N_0 + 1)$$

and

$$v_{j>0} | S_j, B_j, W_j, t_{ji}^n, t_{ji}^w \sim \text{Beta}\left(S_j + B_j + \sum_{i=1}^{T(j)} t_{ji}^n + 1, W_j - S_j - B_j + \sum_{i=1}^{T(j)} t_{ji}^w - t_{ji}^n + 1\right).$$

These are updated separately using the Gibbs sampler on each iteration.

The remaining parameter, W_j , has a nonstandard conditional posterior distribution. We use larger updates than in the population model because the initial total population is expected to be larger in size:

$$W'_0 \sim \text{Unif}(\max(0, W_0 - 15, N_0 + 1, N_0 + B_1), W_0 + 15),$$

$$W'_{1 \leq j < J} \sim \text{Unif}(\max(0, W_j - 15, S_j + B_j + 1, S_j + B_j + B_{j+1}), W_j + 15),$$

and

$$W'_J \sim \text{Unif}(\max(0, W_J - 15, S_J + B_J + 1), W_J + 15).$$

Recapture Model

For the recapture model, we have parameters $\alpha, \beta_j, \gamma_d, \delta_L, \epsilon_{jL}, \zeta_{dL}, \delta_R, \epsilon_{jR}$, and ζ_{dR} . These all have nonstandard conditional posterior distributions, and we use the Metropolis–Hastings algorithm to update the parameters on each iteration. We use individual normal distribution proposals centered on the current parameter values and with variance equal to the prior variance, for example,

$$\alpha' \sim N(\alpha, 1.85).$$

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