Bayesian estimation of humpback whale (*Megaptera novaeangliae*) population abundance and movement patterns in southeastern Alaska

A.N. Hendrix, J. Straley, C.M. Gabriele, and S.M. Gende

Abstract: We used a mechanistic movement model within a Bayesian framework to estimate survival, abundance, and rate of increase for a population of humpback whales (*Megaptera novaeangliae*) subject to a long-term photographic capture–recapture effort in southeastern Alaska, USA (SEAK). Multiple competing models were fitted that differed in movement, recapture rates, and observation error using deviance information criterion. The median annual survival probability in the selected model was 0.996 (95% central probability interval (CrI): 0.984, 0.999), which is among the highest reported for this species. Movement among areas was temporally dynamic, although whales exhibited high area fidelity (probability of returning to same area of ≥ 0.75) throughout the study. Median abundance was 1585 whales in 2008 (95% CrI: 1455, 1644). Incorporating an abundance estimate of 393 (95% confidence interval: 331, 455) whales from 1986, the median rate of increase was 5.1% (95% CrI: 4.4%, 5.9%). Although applied here to cetaceans in SEAK, the framework provides a flexible approach for estimating mortality and movement in populations that move among sampling areas.

Résumé : Nous avons utilisé un modèle de déplacement mécanistique dans un cadre bayésien pour estimer la survie, l'abondance et le taux d'augmentation d'une population de rorquals à bosse (*Megaptera novaeangliae*) faisant l'objet d'un effort de capture–recapture photographique à long terme dans le sud-est de l'Alaska, aux États-Unis (SEAK). Plusieurs modèles concurrents ont été ajustés qui étaient caractérisés par des déplacements, taux de recapture et erreurs d'observation différents selon le critère d'information sur la somme des carrés des écarts. La probabilité de survie annuelle médiane dans le modèle retenu était de 0,996 (intervalle de probabilité centré (CrI) 95 % : 0,984, 0,999), soit une des valeurs signalées les plus élevées pour cette espèce. Les déplacements entre régions étaient dynamiques dans le temps, bien que les rorquals aient démontré une grande fidélité à la région (probabilité de retourner dans la même région $\geq 0,75$) tout au long de l'étude. L'abondance médiane était de 1585 rorquals en 2008 (CrI 95 % : 1455, 1644). En incorporant une abondance estimée à 393 (intervalle de confiance à 95 % : 331, 455) rorquals en 1986, le taux d'augmentation médian était de 5,1 % (CrI 95 % : 4,4 %, 5,9 %). Le cadre, appliqué dans la présente étude à des cétacés du SEAK, constitue une approche souple pour l'estimation de la mortalité et des déplacements dans des populations qui se déplacent d'une région d'échantillonnage à l'autre.

[Traduit par la Rédaction]

Introduction

Movement of animals among different areas creates difficulties for management. Management reference points, such as population abundance and population trend, are confounded with movement, and failure to account for movement can produce biased population estimates (Hammond 1986). For these reasons, models of population abundance and movement are used in populations where movement among areas is common (e.g., Mangel 2008; Maunder et al. 2000). Furthermore, estimates of movement rates are derived from statistical fitting of model predictions to observed data; therefore, estimates of movement rates are a function of the mechanistic model, the statistical fitting procedure, and the data. Data are typically from tag and recapture studies where animals are either tagged in batches (e.g., coded wire tags, disc tags, etc.) or individually (e.g., passive integrated transponder tags, acoustic tags, radio tags, natural markings, or genetic tags). While both maximum likelihood (e.g., Brownie et al. 1993; Schwarz et al. 1993; Hilborn 1990) and Bayesian approaches (King et al. 2009; Dupuis and Schwarz 2007) have been used to estimate movement rates among areas from the recaptures of tagged individuals, the Bayesian approach explicitly incorporates parameter uncertainty in the movement

A.N. Hendrix.[*] R2 Resource Consultants Inc., 15250 N 95th St., Redmond, WA 98052, USA.
J. Straley. University of Alaska Southeast, 1332 Seward Ave., Sitka, AK 99835, USA.
C.M. Gabriele. Glacier Bay National Park and Preserve, P.O. Box 140, Gustavus, Alaska 99826, USA.
S.M. Gende. Glacier Bay Field Station, 3100 National Park Road, Juneau, AK 99801, USA.

Corresponding author: A.N. Hendrix (e-mail: noblehendrix@gmail.com).

[*]Present address: QEDA Consulting, LLC, 4007 Densmore Ave. N, Seattle, WA, USA.

1784

Can. J. Fish. Aquat. Sci. Vol. 69, 2012

rate estimates through posterior probability distributions (Gelman et al. 2004). Furthermore, uncertainty in important management reference points, such as population abundance and population trend, can also be calculated as probability distributions from model parameters (Meyer and Millar 1999; Punt and Hilborn 1997).

The Hilborn (1990) model was developed to provide a biologically based modeling framework from which survival and movement parameters could be estimated in a maximum likelihood framework. In contrast with more statistical approaches of tag recaptures in multiple states (e.g., Brownie et al. 1993), the Hilborn (1990) approach uses relatively simple biological models of the movement and mortality processes to predict the counts of tagged individuals. Estimates of the model parameters are obtained by fitting the predicted counts to observed counts via a Poisson likelihood. The Hilborn (1990) model was initially applied to tagged fishes (Anganuzzi et al. 1994; Arrizabalaga et al. 2004) and elasmobranchs (Xiao 1996); however, applications more recently have been to humpback whales (*Megaptera novaeangliae*) in the North Atlantic (Stevick et al. 2006), sperm whales (*Physeter macrocephalus*) (Whitehead 2001), killer whales (*Orcinus orca*) (Foote et al. 2010), and tundra swans (*Cygnus columbianus*) (Wilkins et al. 2010). The advantage of the Hilborn (1990) approach is the flexibility with which the movement and mortality processes can be modeled for the tagged population, and consequently a number of extensions have been developed, including a framework for evaluating the precision and accuracy of movement estimators (Xiao 1996), the number of identifications as an estimate of effort (Whitehead 2001), and using the recapture rates to expand new captures to provide a population abundance estimate (Straley et al. 2009). Yet, nowhere has the statistical estimation of this framework been expanded to include uncertainty in the distributional assumptions of observations or in uncertainty in the estimation of movement and mortality rates.

The population of endangered North Pacific humpback whales spend the summer in discrete, high-latitude feeding aggregations and migrate to winter areas near Hawaii or Mexico (Straley et al. 2009). Photographic mark–recapture methods used on their summer feeding grounds are labor intensive, and thus only a few areas can be regularly monitored. Whales can move among areas or move to areas that are not monitored. Furthermore, detection probability may vary among dates within a sampling area owing to differences in effort, variation in factors that affect detection such as sea surface conditions, and individual diving behavior (Stevick et al. 2004; Nielson and Gabrielle 2008).

Glacier Bay National Park and adjacent waters represent a "hotspot" for humpback whales in Alaska (Nielson and Gabrielle 2008) owing to its high productivity and abundant forage fish (Robards et al. 2003). Understanding trend, abundance, and rates of mortality is important for park management because Glacier Bay is a summer destination for large cruise ships, with more than 220 ship entries into the park over the past several years (Gende et al. 2011). Ship routes overlap high-density areas used by whales resulting in frequent ship–whale encounters (Harris et al. 2012). Glacier Bay is the location of one of the world's longest and consistently monitored capture–recapture efforts for humpback

whales and is complemented by regular, but less frequent, monitoring of three other areas in southeastern Alaska (SEAK), including Frederick Sound, Lynn Canal, and Sitka Sound. Although basic mark–recapture models have been successfully used to derive abundance estimates from these data (Baker et al. 1992; Straley 1994), none have done so that explicitly accounts for uncertainty in model parameters.

Based on the Hilborn (1990) movement model, we developed a Bayesian estimation framework to generate biologically meaningful estimates of population abundance, survival, and movement rates for the population of humpback whales in SEAK. We considered alternative models to reflect different hypotheses regarding the temporal changes in movement rates, the mechanisms affecting recapture rates, and the error distribution in counts of recaptured whales. The Bayesian implementation of the movement model is not limited to whales, however, and provides a framework that can be applied to any study that marks and repeatedly recaptures marked individuals.

Materials and methods

Humpback whale data

Study areas

Our study site (SEAK) includes several areas that consistently support large aggregations of humpback whales and have been targeted for photographic capture–recapture efforts between June and September from 1994 to 2008. These feeding areas, which include Glacier Bay and Icy Straight (GBIS), Sitka Sound (SS), and Frederick Sound and Lynn Canal (FSLC) (Fig. 1), differ in the levels of sampling effort (number of days expended to identify whales) and spatial extent. Study areas were based on humpback feeding and movement patterns within SEAK (Straley et al. 2009).

Photo-identification

Humpback whales were individually identified by the black and white pattern on the ventral surface of the flukes. Photographs of the ventral flukes were taken with 35 mm film and digital cameras and compared with photographic catalogs (Straley and Gabriele 2000) to identify and establish a sighting history matrix for each individual. Photographic quality was graded as good, fair, or poor using standardized criteria. To eliminate or reduce bias, poor quality images were excluded from analysis. Furthermore, calves were excluded from analysis because the pattern on the flukes is subject to change during the first year, and calves are inconsistent in their ability to show their flukes upon diving. New whales were added to the monitored population (captured) each year when they could not be matched to existing photographs; such whales were assigned to a tag group *g* based on the year of capture. A whale is "recaptured" when resighted with photographic documentation. These terms are consistent with capture–recapture terminology; however, no whales were physically captured in this study.

Modeling framework

The movement model

The model predicts how many tagged individuals would be alive in tag group *g* coming from area *i* to area *j* in year *t*,

Fig. 1. Southeastern Alaska study area including Glacier Bay and Icy Strait (GBIS), Sitka Sound (SS), and Frederick Sound and Lynn Canal (FSLC).
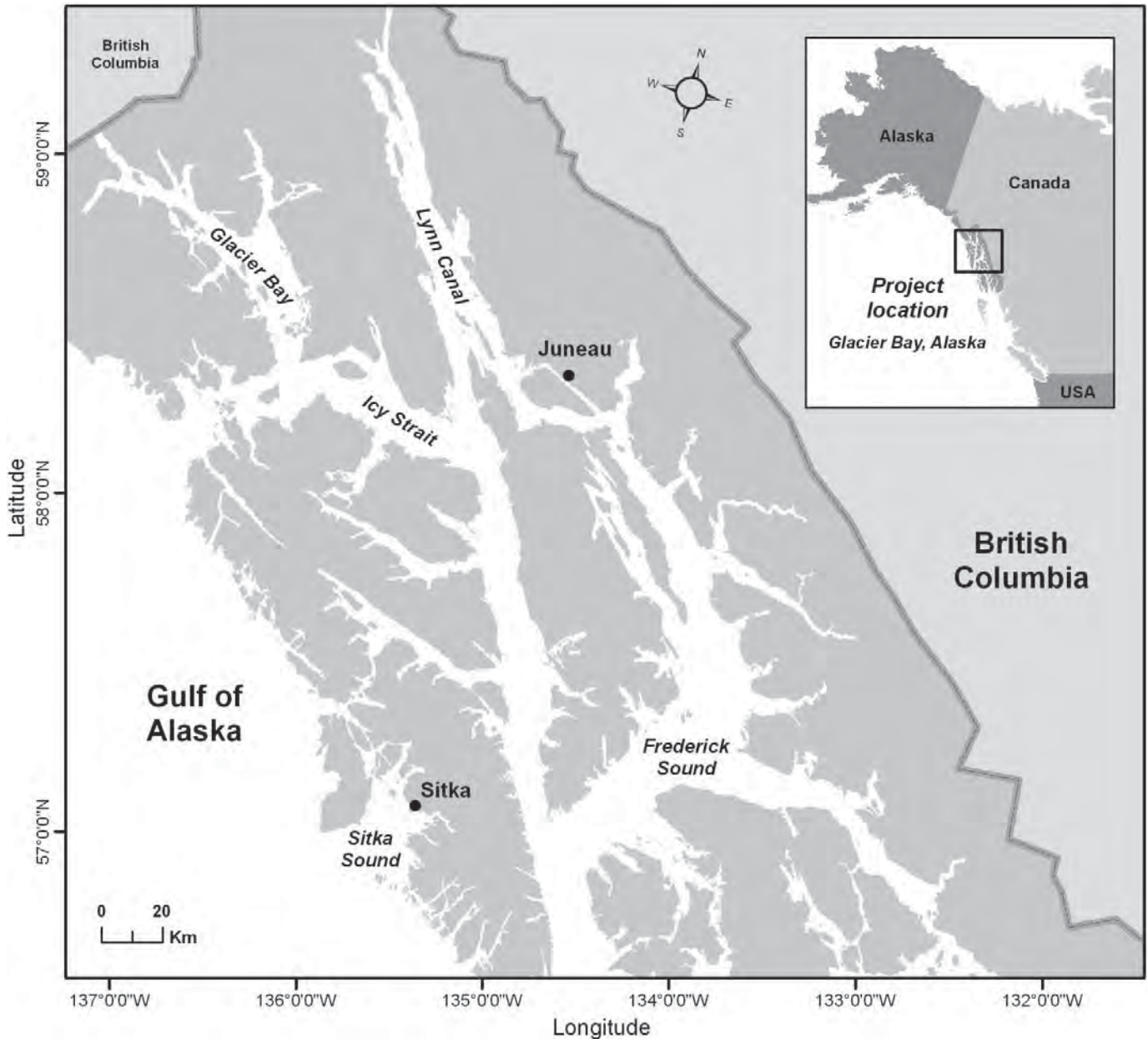
where t is after the year of capture. The model for the population dynamics of the tagged population is

$$(1) \qquad \widehat{N}_{g,i,j,t+1} = \widehat{N}_{g,i,t}(1 - \phi_t)\psi_{i,j,t}$$

where $\widehat{N}_{g,i,j,t}$ is the expected number of tagged animals in tag group g ($g = 1, \ldots, G$) from area i ($i = 1, \ldots, n$) in area j ($j = 1, \ldots, n$) in year t ($t = 1, \ldots, T$); ϕ_t is the mortality rate in year t, which we assume here is constant across years ($\phi_t = \phi$); $\psi_{i,j,t}$ is the probability of migrating from area i to area j during period t. The capture event for tag group g and area j is $T_{g,j,t}$. We set the initial number of whales for tag group g as being $\widehat{N}_{g,i,0} = T_{g,j,t}$, where $i = j$ is the first area the animals were captured. Thus, all values of i refer to the area where the animal was last recaptured. After year t, the (unobserved) number of tagged whales are summed over

their locations to create a vector of tagged abundances $\widehat{N}_{g,i,t+1} = \sum_{j=1}^{3} \widehat{N}_{g,i,j}$.

To model the observation process of tagged animals, a detection probability is applied to the predicted number of tagged animals

$$(2) \qquad \widehat{R}_{g,i,j,t} = \widehat{N}_{g,i,j,t} \times p_{j,t}$$

where $\widehat{R}_{g,i,j,t}$ are the expected number of recaptures, and $p_{j,t}$ are the recapture rates in area j at time t. Movement probabilities to the three areas (SS, GBIS, FSIS) were confined to sum to 1 (e.g., $\sum_{i=1}^{3} \psi_{i,j} = 1$). The original Hilborn (1990) application did not employ this constraint, which allowed the model to estimate the confounded parameter of mortality and movement to unsampled areas.

The model predicts $\widehat{R}_{g,i,j,t}$ to be the number of recaptures

for each tag group that came from area i to area j in each year t; therefore, the Poisson likelihood requires counts of individuals by group, previous area i, current area j, and year t. Individual capture histories were used to compute the cell values in the four-dimensional recapture array. The tag group g was defined as the year of initial capture. The initial area (i.e., the first "from" area) was the area of capture. We considered two alternatives for defining subsequent "from" areas i. The first option was to define i as the area of capture. This was the approach used in Hilborn (1990) and Straley et al. (2009). For short recapture histories or removals, this approach works well, but it will not be sensitive to dynamic patterns in movement (i.e., animals establishing patterns of returning to specific areas different from their capture area). Instead, we used a Markovian process where the "from" location i was updated based on the previous area of recapture. The area of current recapture was area j in year t. Note that there is the potential to introduce bias in estimates of movement probabilities if the probability of recapture and movement patterns are correlated (i.e., an individual habitually moves to a poorly sampled area where it is undetected and then moves to a well sampled area and recaptured). As an example of converting an individual recapture history, an individual captured in 2000 had the following capture–recapture history: 101103011, where 0 = not recaptured, 1 = GBIS, 2 = SS, and 3 = FSLC. The whale was initially captured in GBIS in 2000 and subsequently recaptured in GBIS in 2002 and 2003; therefore, all movements over this period were recorded as moving from GBIS to GBIS. In 2005 the whale was recaptured in FSLC and was recorded as having moved from GBIS in 2004 to FSLC in 2005. The whale was recaptured in GBIS in 2007 and subsequently recorded as having moved from FSLC in 2006 to GBIS in 2007 with a final recapture in GBIS in 2008. The data from this whale was combined with other whales captured in 2000 to produce a data array of 8 years by three "from" areas by three "to" areas.

To deal with identifying the same whale in multiple areas in a single year, a hierarchy of whale areas was established based on previous analyses of migration patterns of SEAK whales. Whales in SEAK typically stage in FSLC prior to moving either to SS or GBIS, and there has been little exchange observed between SS and GBIS in previous surveys (Straley et al. 2009). The hierarchy was GBIS > SS > FSLC as described in Straley et al. (2009). For example, a whale observed in SS in June 1999 and subsequently observed in GBIS in August 1999 would be recorded as "from" GBIS for that year.

Model structural uncertainty

To address alternative hypotheses about the movement and recapture rates, we composed several model structural forms with different rates of movement and several alternatives with variation in effort, areas, and time on recapture rates.

Movement rates

The movement among areas in year t was composed of a 3×3 matrix $\mathbf{\Psi}$ with each element of the matrix $\psi_{i,j}$ representing the rate at which whales moved from area i to area j between year t and year $t + 1$. Two alternatives were modeled for the movement rate matrix. The first approach assumed that movements remained constant over the period of

data analysis. The second approach assumed that movements shifted at 3-year intervals; thus, there were five movement matrices: $\mathbf{\Psi}_{1:5}$. The five movement rate matrices were estimated with the first one spanning the years 1994–1996 and the other four sequentially spaced in 3-year intervals among the 12 remaining years. The choice of 3-year intervals was somewhat arbitrary, but they provided a means of examining whether movement patterns changed over the course of the period of data analysis.

Recapture rates

The recapture rate was modeled using four forms of functions of effort (days). In the first two of these forms, the probability of sighting was modeled as a linear function of effort E in area j and year t.

$$(3) \qquad \text{logit}(p_{j,t}) = \alpha_j + \beta_j(E_{j,t} - \overline{E})$$

The logit() function was used to ensure that the probability of recapture would remain in the interval [0,1], and the effort covariate was standardized by its mean ($\overline{E}$). The probability of capture was modeled both as a single equation among all areas (i.e., $\alpha_j = \alpha$, $\beta_j = \beta$) and as area-specific equations. In the last two, the probability of sighting was modeled as an asymptotic function of effort in area j and year t.

$$(4) \qquad p_{j,t} = \gamma_j \left[1 - \exp\left(-\frac{E_{j,t}}{\delta_j}\right)\right]$$

where γ_j was defined on the interval [0,1] and $\delta_j > 0$. This functional form has an asymptotic recapture rate γ, which is approached quickly (low values of δ) or slowly (high values of δ). As in the linear case, the coefficients in the nonlinear form were modeled with area-specific coefficients or as a single equation among all areas.

Bayesian estimation

In Bayesian estimation, the posterior probability distribution is proportional to the prior times the likelihood (Gelman et al. 2004). Two likelihood functions were employed in the analyses: the Poisson and extra-Poisson. In the Poisson case, the observed tag recaptures for each group g from area i recaptured in area j in year t were modeled as

$$(5) \qquad R_{g,i,j,t}|\boldsymbol{\theta} \sim \text{Poison}(\lambda_{g,i,j,t})$$

where $\lambda_{g,i,j,t}$ is the expected number of recaptures, and $\boldsymbol{\theta}$ is the vector of model coefficients (e.g., $\boldsymbol{\theta} = (\alpha, \beta, \phi, \mathbf{\Psi}_{1:5})$ for a model with the recapture rate ($p_{i,j}$) as a linear function of effort across all sites and five movement matrices. From the equations in the Movement model section, the number of predicted recaptures for each group g from area i found in area j in year t can be calculated as the expected number of recaptures, thus $\lambda_{g,i,j,t} = \widehat{R}_{g,i,j,t}$. The probability mass function for a recapture from an individual group g from area i found in area j in year t under the Poisson likelihood is

$$(6) \qquad p(R_{g,i,j,t}|\widehat{R}_{g,i,j,t}) = \frac{\widehat{R}_{g,i,j,t}^{R_{g,i,j,t}}}{R_{g,i,j,t}!}\exp(-\widehat{R}_{g,i,j,t})$$

The extra-Poisson was also used because capture–recapture data may have additional variability beyond the Poisson distribution (i.e., both mean and variance = λ). Several items

may cause the variance in the observed recaptures to be greater than the mean: (*i*) recapture probabilities of individual whales may differ depending upon how the individual displays its fluke when making a dive (Straley et al. 2009); (*ii*) whales may emigrate from the study areas and thus not be available for capture in all years (Straley et al. 2009); (*iii*) movement among areas may be influenced by other members of the population; for example, movement to feeding areas may be maternally influenced (Baker et al. 1986); and (*iv*) heterogeneity in movement behavior. To incorporate such additional variability in the relationship between predicted and observed recapture data, the following relationship was constructed:

$$(7) \qquad R_{g,i,j,t} \sim \text{Poison}(\lambda_{g,i,j,t})$$
$$\lambda_{g,i,j,t}|\boldsymbol{\theta} \sim \log N(\mu_{g,i,j,t}, \tau)$$

The probability density function of the lognormal distribution is

$$(8) \qquad p(\lambda_{g,i,j,t}|\mu_{g,i,j,t}, \tau)$$
$$= \sqrt{\frac{\tau}{2\pi}}\frac{1}{\lambda_{g,i,j,t}}\exp\left\{-\frac{\tau}{2}[\log(\lambda_{g,i,j,t}) - \mu_{g,i,j,t}]^2\right\}$$

where the mean of the lognormal for group *g*, recovered in area *j*, coming from area *i* in year *t* is the predicted number of returns, $\mu_{g,i,j,t} = \widehat{R}_{g,i,j,t}$, and the precision τ is equal to the inverse of the variance ($1/\sigma^2$). The probability density function of the extra-Poisson distribution for an individual group *g* from area *i* found in area *j* in year *t* is

$$(9) \qquad p(R_{g,i,j,t}|\mu_{g,i,j,t}, \tau)$$
$$= \int_0^\infty \text{Poison}(R_{g,i,j,t}|\lambda_{g,i,j,t})p(\lambda_{g,i,j,t}|\mu_{g,i,j,t}, \tau)\,d\lambda$$

The likelihood was calculated for each observed recapture by multiplying across the individual probabilities of observing the recaptures $R_{g,i,j,t}$ given the parameter vector $\boldsymbol{\theta}$ (i.e., $f(\mathbf{R}|\boldsymbol{\theta}) = \prod_g \prod_t \prod_i \prod_j f(R_{g,t,i,j}|\boldsymbol{\theta})$).

Priors

All model parameters were given vague prior distributions (Gelman et al. 2004; Box and Tiao 1973) to reflect a lack of knowledge prior to analyzing the SEAK capture–recapture data. Priors on the mortality rate were given uniform priors ($\phi \sim U(0,1)$). Priors for the coefficients of the linear model relating effort to recapture rate were given normal distributions defined in terms of precision: $\alpha_j \sim N(0,0.001)$ and $\beta_j \sim N(0,0.001)$. Priors for the coefficients of the asymptotic model relating effort to recapture rate were given beta priors for the asymptotic capture rate (i.e., at high levels of effort) and noninformative uniform priors for the increase in capture rate as a function of effort (e.g., $\gamma_j \sim \text{Be}(1,1)$, $\delta_j \sim U(0,1000)$).

The joint posterior distribution of model parameters given the observed recaptures $p(\boldsymbol{\theta}|\mathbf{R})$ can be specified for each of the 16 models described above; for example, the joint posterior for the model in which the probability of capture was an area-specific, nonlinear function of effort and the measurement error was described by a extra-Poisson distribution.

$$(10) \qquad p(\boldsymbol{\theta}|\mathbf{R}) \propto G(\tau|0.001, 0.001)\text{Be}(\phi|1, 1)$$
$$\times \prod_{j=1}^{3}\text{Be}(\gamma_j|1, 1)U(\delta_j|0, 1000)$$
$$\times \prod_{k=1}^{5}\prod_{i=1}^{3}\prod_{j=2}^{3}\text{Be}(\psi_{k,i,j}|1, 1)$$
$$\times \prod_{g=1}^{G}\prod_{i=1}^{n}\prod_{j=1}^{n}\prod_{t=t_g}^{T}p(R_{g,i,j,t}|\mu_{g,i,j,t}, \tau)$$
$$\times p(\mu_{g,i,j,t}|\phi, \gamma_j, \delta_j, \psi_{i,j,t})$$

We constructed a directed acyclic graph of the model described in eq. 10 to provide a graphical depiction of the structure (Fig. 2).

Implementation of Bayesian estimation

The posterior distributions of the model parameters $\boldsymbol{\theta}$ were estimated by drawing samples from the full conditional distributions of each parameter given values of all other parameters. This was implemented by using a Metropolis within Gibbs Markov chain Monte Carlo (MCMC) approach (Gelman et al. 2004; Gilks and Spiegelhalter 1996). Several parameters did not have standard distributions, namely the mortality rate ϕ and the effort coefficient δ_j; thus, the posterior distributions for these parameters could not be updated using the Gibbs sampler (Roberts and Polson 1994) and were instead updated by using distribution-free adaptive rejection Metropolis steps (Gilks and Spiegelhalter 1996; Spiegelhalter et al. 2003). The Bayesian estimation was implemented in WinBUGS (Spiegelhalter et al. 2003), and WinBUGS code for the model described in eq. 10 is available as a supplement to this article (Supplemental Appendix S1[1]).

To evaluate if the posterior draws were arising from a stationary target distribution, multiple chains were run from dispersed initial values for each model, and the scale reduction factor (SRF; Gelman et al. 2004) was computed for all monitored quantities (model coefficients and tagged abundance estimates). The diagnostics were implemented using the R2WinBUGS package (Sturtz et al. 2005) in R (R Development Core Team 2009). Monitored parameters in all models had SRF values that indicated samples were being drawn from the target distribution (i.e., SRF $\approx$ 1) by 50 000 samples. The initial 30% of the samples were used to reach the stationary target distribution and were discarded with the subsequent samples thinned to produce approximately 1000 draws from the stationary target distributions. The 1000 draws were used to compute the posterior mean and symmetric 95% probability intervals or credible intervals (95% CrI).

We used deviance information criterion (DIC) to evaluate model predictive ability with a penalty for model complexity (Spiegelhalter et al. 2002). The DIC is a function of the deviance $D(\mathbf{R}|\boldsymbol{\theta})$ and the effective number of parameters p_D. In a hierarchical model, the effective number of parameters is typically less than the total number of estimated parameters, because information is being shared among random effects (e.g., the variability in the extra Poisson models being derived from a distribution with common precision τ). Model

---

[1]Supplementary data are available with the article through the journal Web site at http://nrcresearchpress.com/doi/suppl/10.1139/f2012-098.

1788

Can. J. Fish. Aquat. Sci. Vol. 69, 2012

Fig. 2. Directed acyclic graph of the model including a nonlinear effect of effort on the probability of recapture, time-varying movement matrices, and overdispersion in the Poisson counts of whale recaptures. Nodes (circles) are connected by dashed lines for logical (deterministic) relationships and solid lines for stochastic relationships; boxes indicate constants (data supplied to model and assumed known without error). See text for description of symbols.
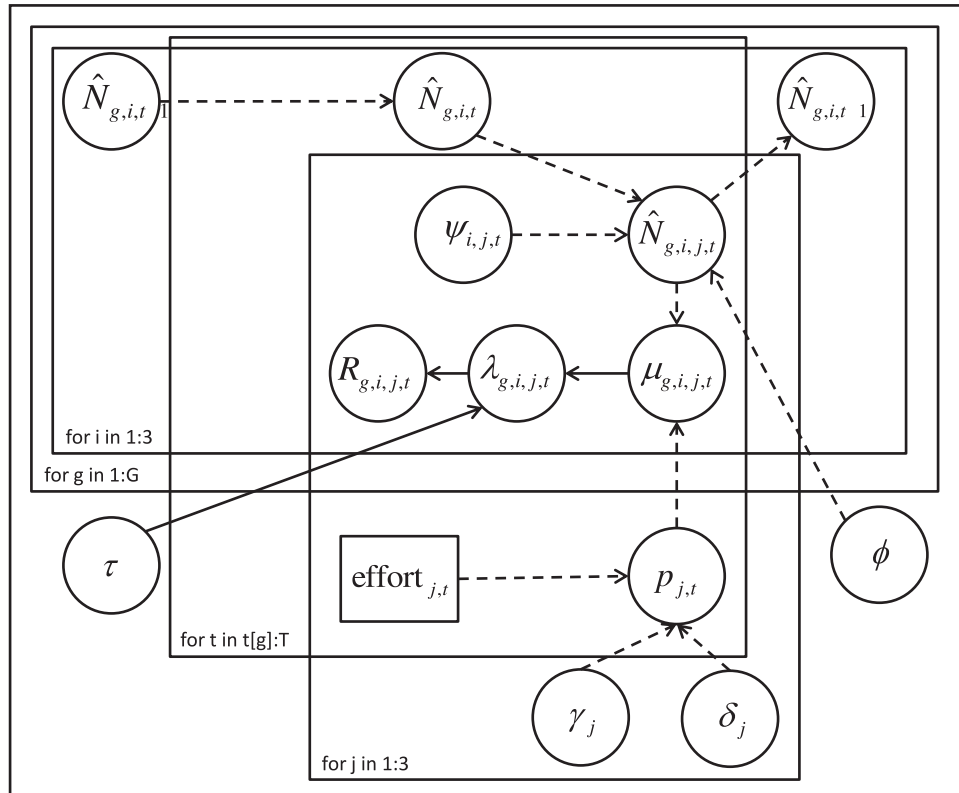
selection using DIC assumes that the posterior mean of the model parameters, which is used to calculate p_D, is a good point estimate for the posterior distribution (Spiegelhalter et al. 2002). In addition, recent work suggests that DIC may be biased toward selecting more complex models in some circumstances (Ward 2008). Each model was fitted several times to quantify the within-model simulation variability, and the average values were presented. The within-model simulation variability was on the order of three to four units of DIC; thus, differences among models of this magnitude were attributed to variability within the MCMC simulations.

Derived quantities: abundance and trend estimates

The population abundance estimate in area j and year t ($W_{j,t}$) was calculated as the sum of the estimated number of live tagged whales $\widehat{N}_{j,t}$ and untagged whales $U_{j,t}$ (Seber 1982):

(11)
$$W_{j,t} = \widehat{N}_{j,t} + U_{j,t}$$

$$W_{j,t} = \sum_{g=1}^{G}\widehat{N}_{g,j,t} + T_{g,j,t} \times \frac{1}{p_{j,t}}$$

Abundance estimates were calculated for each area j and year t with uncertainty by using samples from the posterior distribution of $p_{j,t}$ (e.g., $p_{j,t}^l$ for sample l, $l = 1, …, L$). Abundance estimates for the entire SEAK area were calculated with uncertainty by summing across the samples of $W_{j,t}^l$ (e.g., $W_t^l = \sum_{j=1}^{n} W_{j,t}^l$).

To evaluate the trend, a log-linear approach was used to estimate the average growth rate between 1995 and 2008 (e.g., $\log(W_t) = \log(W_{1995}) + \log(s) \times t$, where s is the growth rate (Quinn and Deriso 1999). The linear regression equation can be solved by using matrix algebra for each iteration l of the MCMC chain, thus producing posterior distributions for $\log(s)$ with the same convergence properties of the MCMC chain. We use the well-known equation (e.g., McCullagh and Nelder 1983) for linear regression coefficients in matrix form $\boldsymbol{b} = (\boldsymbol{X}^T\boldsymbol{X})^{-1} \boldsymbol{X}^T\boldsymbol{Y}$, where $\boldsymbol{b}$ is the vector of linear regression coefficients ($\boldsymbol{b} = [\log(W_{1995}), \log(s)]$, $\boldsymbol{X}$ is the vector of years, and $\boldsymbol{Y}$ is the vector of log abundance estimates, $\log(W_t)$. In addition, the population growth rate using an estimated abundance in 1986 of 393 (95% confidence interval (CI): 331, 455) (Straley 1994) was also computed by assuming log-linear growth between 1986 and 2008 (e.g., $\log(W_t) = \log(W_{1986}) + \log(s) \times t$). The vector of whale abundances in 1986 was generated by sampling randomly from a normal distribution with mean of 393 and standard deviation of 31 (1.5 × the standard deviation calculated from the Straley (1994) estimate).

Results

Model selection

Models were named according to how many movement matrices were used (P for a single matrix or P5 for multiple matrices), the recapture rate model employed (E for linear effort and NLE for nonlinear effort), whether the forms

Table 1. Deviance information criterion (DIC) for models assuming Poisson measurement error.

Movement matrices	Recapture rates	Deviance	p_D	DIC	Abbreviation
Single	Linear effort	3525.6	8.8	3544.4	PE
	Nonlinear effort	3474.2	8.3	3482.5	PNLE
	Area-specific linear effort	3498.9	12.8	3511.7	PE3
	Area-specific nonlinear effort	3416.8	10.6	3427.5	PNL3
Multiple	Linear effort	3398.6	30.4	3429.0	P5E
	Nonlinear effort	3351.3	30.4	3381.7	P5NLE
	Area-specific linear effort	3369.8	33.5	3403.3	P5E3
	Area-specific nonlinear effort	3294.5	32.4	3326.9	P5NLE3

Note: DIC is a sum of the deviance; p_D is the effective number of parameters in the model.

Table 2. Deviance information criterion (DIC) for models assuming extra-Poisson measurement error.

Movement matrices	Recapture rates	Deviance	p_D	DIC	Abbreviation
Single	Linear effort	2591.6	309.3	2900.8	PEXP
	Nonlinear effort	2571.1	298.5	2869.6	PNLEXP
	Area-specific linear effort	2578.8	306.1	2884.8	PE3XP
	Area-specific nonlinear effort	2561.4	293.3	2854.7	PNL3XP
Multiple	Linear effort	2557.0	308.3	2865.3	P5EXP
	Nonlinear effort	2538.9	297.7	2836.6	P5NLEXP
	Area-specific linear effort	2557.7	304.1	2861.8	P5E3XP
	Area-specific nonlinear effort	2538.3	293.1	2831.4	P5NLE3XP

Note: DIC is a sum of the deviance; p_D is the effective number of parameters in the model.

were area-specific (3), and whether they incorporated extra-Poisson (XP) variability in the whale count data (Tables 1 and 2). Overall, models that specified measurement error with a Poisson distribution had higher DIC values than models with extra-Poisson measurement error (Tables 1 and 2), owing to the lower deviance (on the order of 1000 units) relative to the number of additional effective parameters p_D (on the order of 200–300 units). The role of the extra-Poisson variability was to increase the dispersion in counts of recaptured whales relative to their expected value and suggested that some of the biological processes (e.g., variability in dive characteristics among individuals, emigration from the study area, and maternally influenced movement) were prevalent in the data.

For all models with the extra-Poisson variability, the model with the lowest DIC value was P5NLE3XP, whereas the next closest model was P5NLEXP, which had values of DIC that were within five to six units (Table 2). Models P5NLE3XP and P5NLEXP both had probabilities of recapture as a non-linear function of effort, but they differed in the number of parameters used to define the effort-to-recapture relationship. Model P5NLE3XP developed site-specific relationships, whereas P5NLEXP used a single relationship among sites. The reduction in DIC due to the additional recapture parameters was justified after taking the within-DIC variability into account. To facilitate discussion of the modeling results, subsequent reference to model P5NLE3XP will be the "SEAK model".

Model predictions of recaptures and dynamics of whale movement among areas from the SEAK model matched the observed recaptures well. Using the 1994 tag group, which was the tag group with the longest time series of recaptures, median predicted annual recaptures had similar annual pat-

terns as the observed recaptures (Fig. 3). In addition, the 95% credible intervals encompassed all observed recaptures, with the exception of a single observed recapture event in 2000 for whales heading from SS to FSLC.
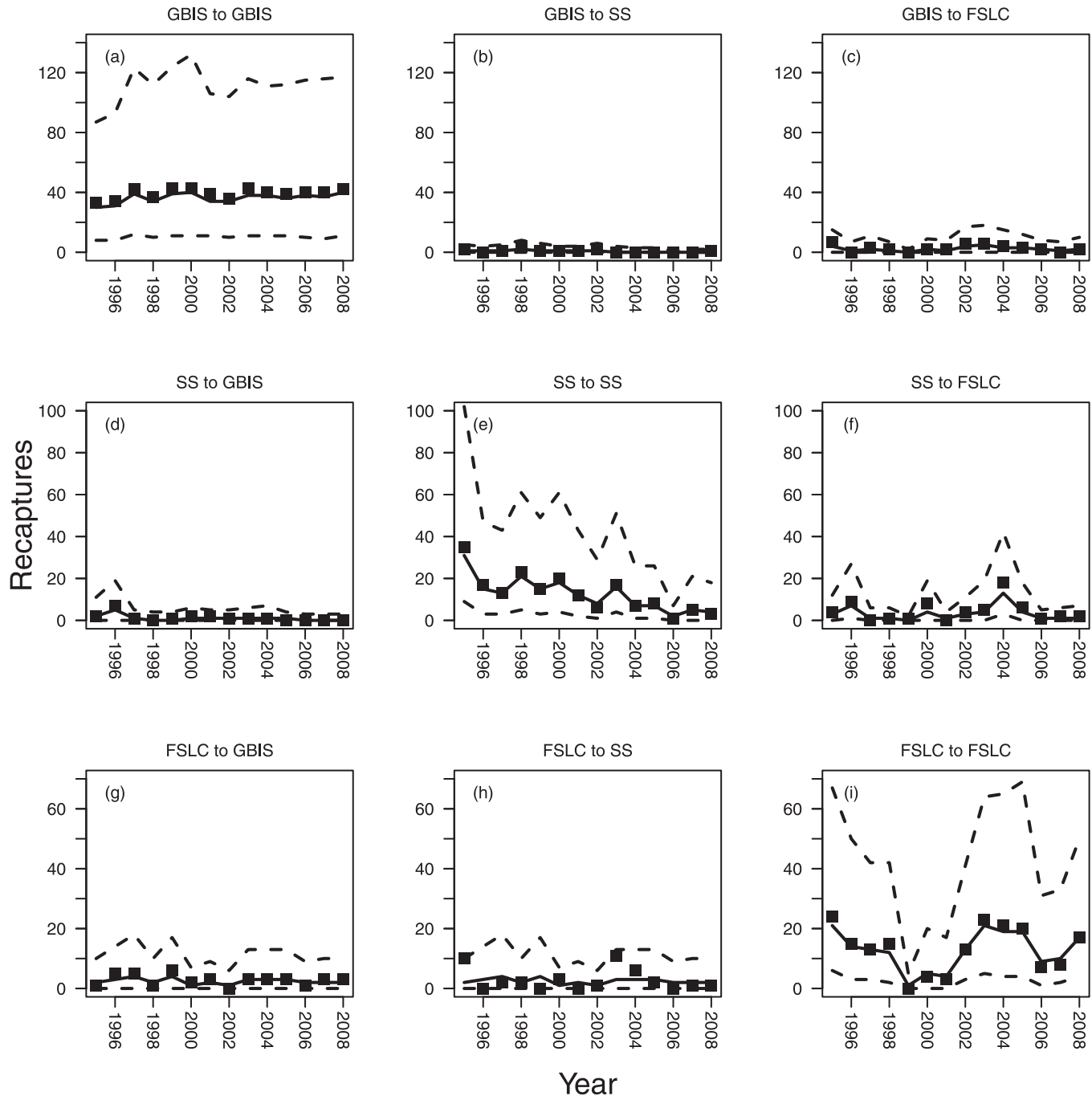
Movement rates

In general, whales tended to return to areas in which they had previously been recaptured. In the 1994 tag group, recaptured GBIS whales returned to GBIS with little movement to either SS or FSLC (Fig. 3), and this pattern was consistent among other tag groups (i.e., those whales captured in 1995, 1996, etc.). In contrast, there appeared to be some movement by whales from SS to FSLC over the study period (Fig. 3). In particular, in 2004 approximately 20 whales moved from SS to FSLC and then continued to return to FSLC from 2005 to 2008. Note that the observed number of whales recaptured in FSLC in 1999 were low because of limited study effort in that year (1 day).

To evaluate the major pathways of movement by whales among areas, movement rates were used to identify connectivity among areas (Fig. 4). Area fidelity was high among all areas, as whales were more likely to be recaptured (i.e., median probability of movement) in the area of previous recapture than any other area (Fig. 4). Although GBIS and SS had higher median area fidelity rates than FSLC over the entire study period, whales shifted among feeding areas toward FSLC in the later years. From 1994 to 2002, the movement patterns were characterized by high area fidelity on the order of 0.80 (Fig. 4). Notable movements among areas were exchanges of whales between FSLC and SS and between GBIS and FSLC, whereas there was little connectivity between GBIS and SS (Fig. 4). From 2003 to 2005, the SS to FSLC median movement rate was 0.232 (95% CrI: 0.163,

1790

Can. J. Fish. Aquat. Sci. Vol. 69, 2012

Fig. 3. Median predicted counts of whales (solid line), 95% credible intervals (dashed lines), and observed counts (points) for the group of humpback whales tagged in 1994. Predictions are from the lowest valued DIC model for GBIS to GBIS (*a*), GBIS to SS (*b*), GBIS to FSLC (*c*), SS to GBIS (*d*), SS to SS (*e*), SS to FSLC (*f*), FSLC to GBIS (*g*), FSLC to SS (*h*), and FSLC to FSLC (*i*). Note that the *y* axes differ in scale among the source locations.
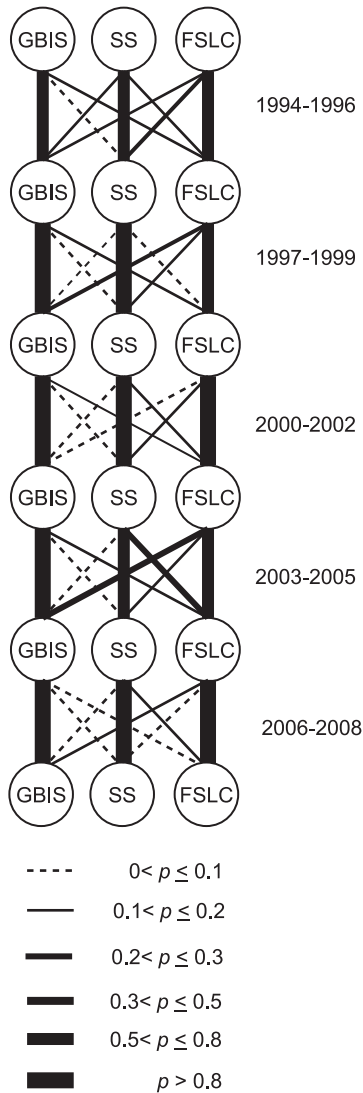

0.310); the SS to SS median movement rate was 0.681 (95% CrI: 0.597, 0.763), with little return of whales from FSLC to SS during this period (0.109; 95% CrI: 0.071, 0.166). In addition, during 2003–2005 the FSLC to GBIS movement rate was 0.205 (95% CrI: 0.141, 0.278), whereas movement between these two areas was approximately 0.15 or less during other periods.

Recapture rate and tagged abundance

The recapture rates were modeled as a nonlinear function of effort for each of the three areas. FSLC had the greatest range in the level of effort (1–54 days), which was similar to SS (7–52 days), whereas the range of effort in GBIS was higher and more consistent (52–87 days). The asymptotic levels of recapture rate were highest in GBIS with a median
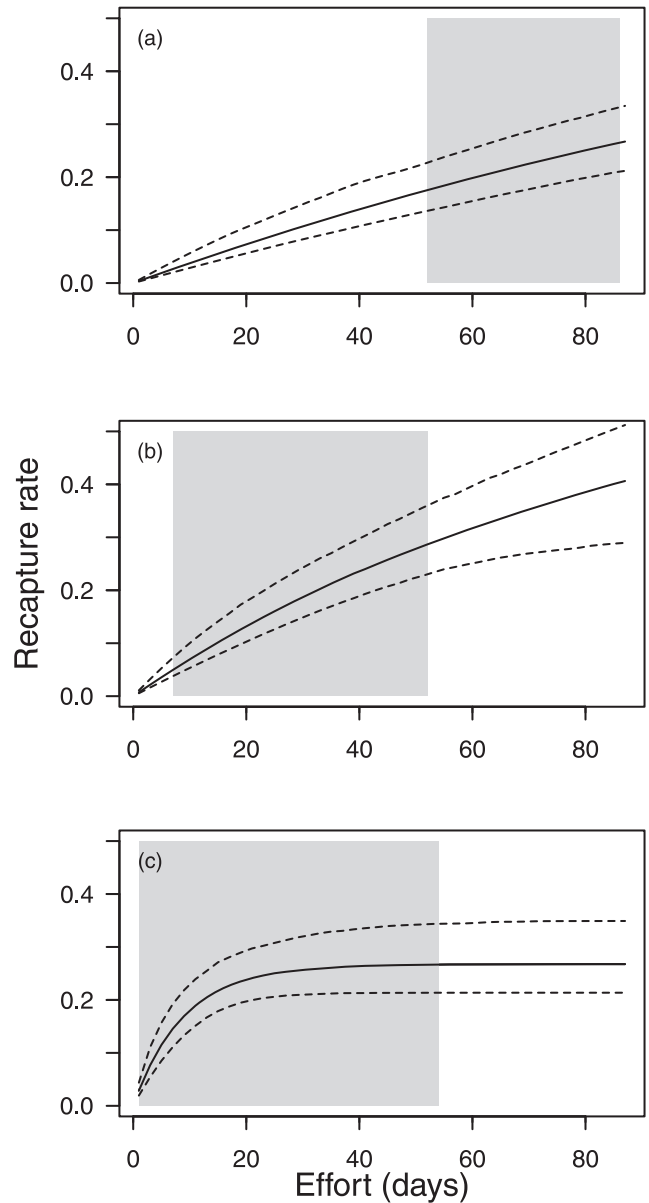
Fig. 4. Schematic indicating movement patterns among feeding areas in southeastern Alaska. Line width is proportional to median estimates of movement among areas.

Fig. 5. Modeled probability of recapture as a function of effort. Solid lines are median values, whereas dashed lines indicate 95% credible intervals. Grey boxes indicate the range of effort (days) in the study areas of Glacier Bay and Icy Straight (*a*), Sitka Sound (*b*), and Frederick Sound and Lynn Canal (*c*).

asymptotic rate 0.770 (95% CrI: 0.345, 0.991), whereas the median asymptotic rate was 0.718 (95% CrI: 0.305, 0.983) in SS and 0.268 (95% CrI: 0.210, 0.355) in FSLC. An asymptotic relationship between recapture rate and effort was only apparent in FSLC, whereas in the other two areas recapture rates were more linearly related to effort (Fig. 5).

Few tagged whales died during the study period, and the estimated median mortality rate was 0.00425 (95% CrI: 8.3×10^{-3}, 0.0164). Few tagged whales were lost, but new whales were added each year; therefore, the abundance of tagged whales increased over the study period (Fig. 6). The distribution of tagged whales remained relatively uniform across the study areas until 2003, when the number of tagged whales started to increase in FSLC and GBIS. Some of the increase in FSLC was due to capturing 75 whales there in 2004. In addition, the movement patterns described above from 2003 to 2005 (SS movement to FSLC) increased tagged abundance in FSLC (Fig. 6). Movement from FSLC to GBIS during 2003–2005 and captures in GBIS also increased the tagged abundance in GBIS. The uncertainty in the tagged abundance esti-

mates increased over the study period, which was due largely to the increased observation error associated with larger mean levels of tagged whales. In other words, as the number of whales increased in the study areas, the estimates became less precise. Such increases in variance at higher mean levels were a function of using the extra-Poisson error model.

Population abundance estimates and trends

Although the annual population abundance estimates (W_t) were somewhat variable, the SEAK stock abundance increased over the study period; the lowest median estimate of 696 (95% CrI: 672, 722) whales was found in 1997, whereas a median estimate of 1586 (95% CrI: 1455, 1644) occurred in 2008 (Fig. 7). The abundance estimates were relatively sta-

Fig. 6. Abundance estimates of tagged whales in each of the three study areas (Glacier Bay and Icy Straight, circles; Sitka Sound, squares; Frederick Sound and Lynn Canal, triangles) from 1995 to 2008. Median abundance estimate (points) and 95% credible intervals (lines) are plotted for each area.
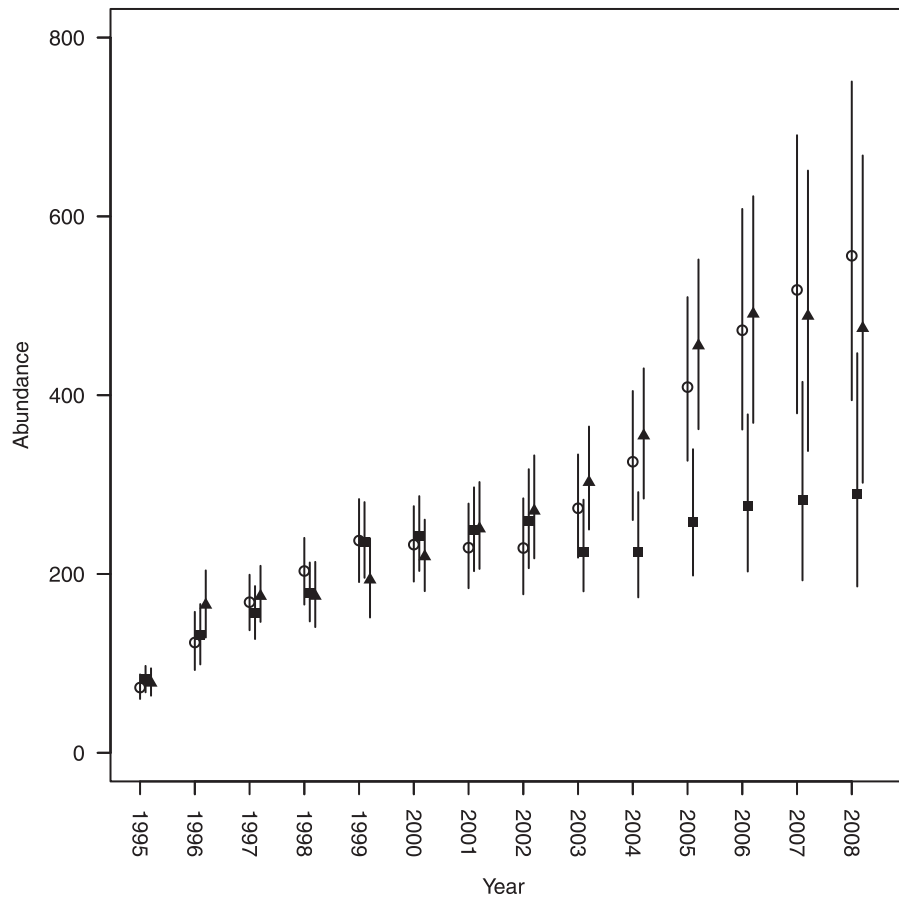
ble from 1995 to 2003 and from 2005 to 2008; however, abundance estimates increased sharply between 2003 and 2004. This jump in abundance was attributable, in part, to 128 newly tagged whales in 2004, which was markedly higher than in other years where the median rate was 54 newly tagged whales per year (not including 2004). W_t was sensitive to both the captures in year t ($T_{g,j,t}$) and the recapture rate $p_{j,t}$ (Seber 1982) (eq. 11). Recapture rates for all areas were typically less than 0.4, which increased the population abundance estimate by approximately 450 whales between 2003 and 2004. Median population abundance estimates corrected downward after 2004 because of fewer captures in those years. Uncertainty in the SEAK abundance estimates were a function of the uncertainty in tagged abundance (Fig. 7) and uncertainty in $p_{j,t}$. As a result, the uncertainty in W_t followed the general patterns in uncertainty from the tagged abundance estimates (i.e., greater uncertainty at higher abundances).

Quantification of the trends in abundance provided two estimates of the population growth rate for SEAK humpback whales. The median population growth rate over the study period was 5.84% (95% CrI: 4.98%, 6.52%), and the median growth rate by incorporating population abundance in 1986 (Straley 1994) was slightly lower at 5.13% (95% CrI: 4.43%, 5.86%). Because the growth rates were affected by the number and variability in annual abundance estimates, we utilized the growth rate obtained from the longest time series (5.13%;

95% CrI: 4.43%, 5.86%) to provide an estimate of population growth rate for SEAK humpback whales.

Effect of priors

Previous authors have found that the specification of the prior on the error variance term can have important implications for coefficient estimates (Su et al. 2004); however, we found that altering the prior distribution of the variance term did not appreciably affect the coefficient estimates of the SEAK model (Fig. 8). Alternative specifications of priors included using a Gamma $G(0.01, 0.01)$ rather than a Uniform $U(0,30)$ on the inverse of the variance (or precision equal to $1/\sigma^2$) of the lognormal distribution incorporated into the extra-Poisson error. The relative mean differences (difference in mean coefficient estimate divided by mean coefficient estimate under $U(0,30)$) of several parameter estimates changed by approximately 3.5%: both the coefficients defining the recapture rate in GBIS, a movement parameter from GBIS to SS in the last period, and the mortality rate. Thus, relative to the uncertainty in the model coefficients, the specification of prior had minimal impact on the coefficient estimates of the models and their 95% credible intervals (Fig. 8).

Discussion

Multiple structural models and a long-term photographic capture–recapture data set from three separate areas provided

Fig. 7. Estimates of abundance for southeastern Alaska stock of humpback whales from 1995 to 2008. Median estimates (squares) and central 95% probability interval (lines) are indicated.
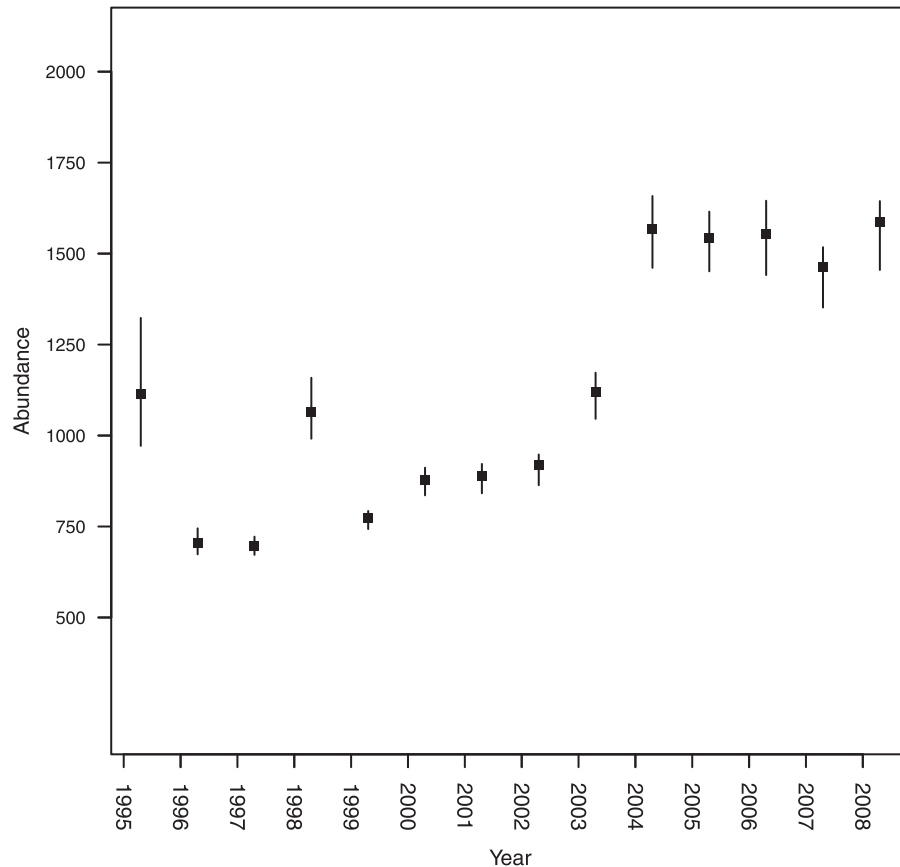
the opportunity to evaluate competing hypotheses regarding the movements, changes in abundance, and survival of humpback whales in SEAK. Our modeling effort indicated that the median population growth rate for humpback whales in SEAK was 5.1% per year since 1986, which is consistent with other estimates of SEAK humpback growth rates (e.g., 5.5%–6% in Calambokidis et al. (2008) and 6.5% in Barlow and Clapham 1997)).

In this study, few whales marked in any given year died during the study period, resulting in a very high estimate of annual survival probability (0.996; 95% CrI: 0.984, 0.999). We believe our survival estimates accurately reflect the true annual survival probability of whales in SEAK over the study period and are not a spurious model result. The annual survival probability estimated here is higher than humpback whales in the Gulf of St. Lawrence (survival = 0.93; Ramp et al. 2010) or the western Atlantic, which range from 0.950 (95% CI: 0.928, 0.972; Clapham et al. 2003) to 0.964 (95% CI: 0.946, 0.976; Rosenbaum et al. 2002); however, it is similar to estimated survival probabilities of other cetaceans located in the North Pacific such as bowhead whales (*Balaena mysticetus*) (survival = 0.99; Zeh et al. 2002) and gray whales (*Eschrichtius robustus*) (survival = 0.98; Punt and Hilborn 1997). Differences in survival between Pacific and Atlantic stocks of whales could be due to differences in mortality factors, such as entanglement, ship strikes, disease, and predation (Allen and Angliss 2011). Although the survival probability here is higher than SEAK humpback whales

from 1979 to 1996 (annual survival probability of 0.957, 95% CI: 0.943, 0.967; Mizroch et al. 2004), survival probability estimates may differ between the two studies because SEAK data were collected from two feeding areas in Mizroch et al. (2004), and only 3 years of overlap exist between the two data sets.

Our work indicates that there is little connectivity between the SS and GBIS study areas, whereas whales regularly moved to SS and GBIS from FSLC. Marine mammals have relatively small energetic costs to moving (Williams 1999), and humpbacks in particular can move vast distances (Rasmussen et al. 2007). During the summer months, humpbacks are primarily foraging on sand lance, capelin, herring, euphausiids, and krill (Witteveen et al. 2008), which can form dense concentrations in SEAK (Gende and Sigler 2006). Cetacean movement has been related to foraging opportunities in killer whales (e.g., Foote et al. 2010) and humpback whales (Stevick et al. 2006). Further, when humpback whales target prey resources (Stevick et al. 2006), abundances of humpbacks can increase dramatically owing to following their prey (Whitehead and Carscadden 1985). Such variability in prey resources may partially explain movement among areas in our study, which has important implications for management of the substock.

The dynamic nature of movements among areas and our model structure precludes calculating area-specific population growth rates. Thus, SEAK cannot be divided into constituent sample areas for management. This fact may complicate man-

1794

Can. J. Fish. Aquat. Sci. Vol. 69, 2012

Fig. 8. Evaluation of different priors for the precision (inverse of variance equal to $1/\sigma^2$). Mean coefficient estimates under a Uniform $U(0,30)$ and a Gamma $G(0.01, 0.01)$ for the inverse of the variance of the extra-Poisson error term (points) and 95% credible intervals (lines) indicate little difference in coefficient estimates between prior specifications.
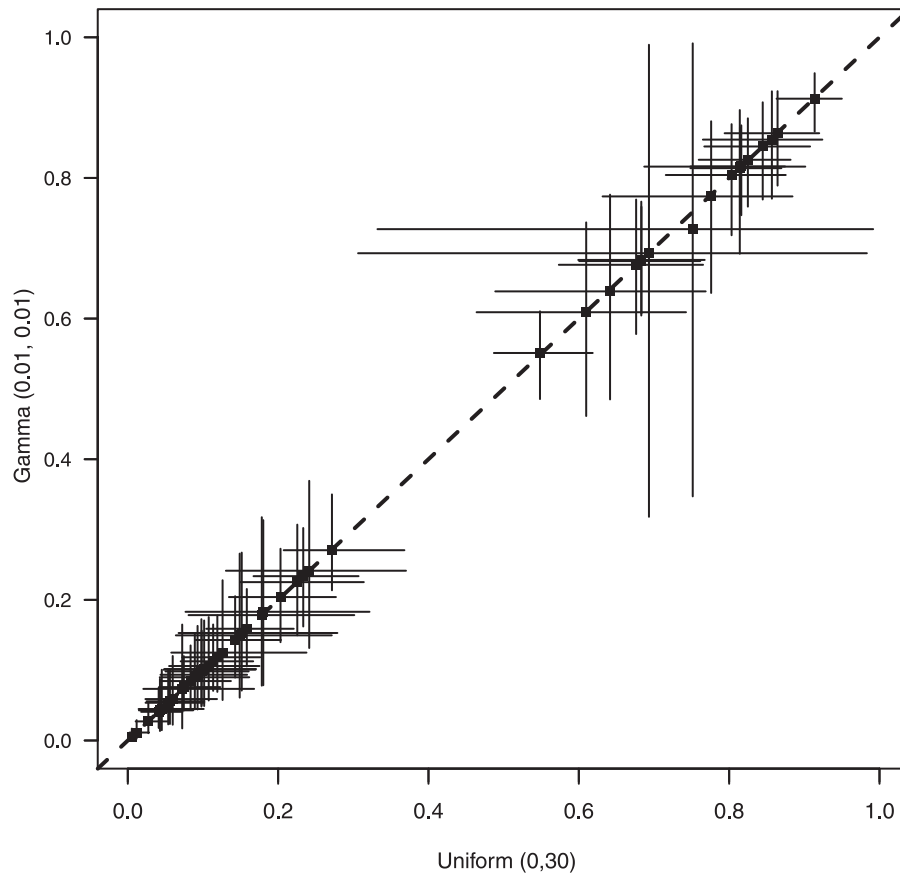
agement that must occur on smaller scales (e.g., Glacier Bay National Park), where government agencies have jurisdiction at a finer geographic level than the stock dynamics. The movement of whales among areas could mask increases in the mortality rate in one area because of high entanglement rates in fishing gear or high number of large vessels transiting; therefore, future monitoring and management will need to continue sampling efforts at the three areas to provide inference at the SEAK level.

In the present study, there were several instances where data were summed or discarded to meet the requirements of the Hilborn (1990) methodology, whereas using individual-level data may provide for a full treatment of all observations. For example, whales were summed by the year and area in which they were initially captured, the feeding area where they were previously recaptured, and the year and area in which they are currently recaptured. Thus, individual capture–recapture histories were lost. For individuals with relatively short capture histories, the summing across individuals may have little effect; however, for long-lived species with frequent recaptures, there is substantial value in the individual recapture histories.

Modeling the individual recapture histories provides opportunities for a richer set of modeling approaches (e.g., Zeh et al. 2002). For example, within-season observations of humpbacks among the three study areas could be utilized under the robust design of Pollock et al. (1990). Such robust

design models can be analyzed by methods similar to those employed here (e.g., log-linear models; Rivest and Daigle 2004). Further improvements to the robust modeling framework include incorporating individual-level covariate data to model the individual probability of recapture (Royle 2009) in addition to the probability of survival or movement. In the case of SEAK humpback whales, such covariates might include age, fishing gear entanglement, ship strikes, or maternal lineage. Furthermore, recent contributions in capture–recapture methods use data augmentation (Royle 2009) to estimate the tagged and untagged population size within the estimation framework, which is an improvement over previous methods (e.g., eq. 11).

Limitations to the Bayesian approach have been identified previously (Dennis 1996); however, there are multiple advantages to using a Bayesian estimation framework (Pollock 1991; Rivot and Prevost 2002; Smith 1991), such as incorporation of informative prior distributions based on simulations of upper bounds of population growth rates (e.g., Zerbini et al. 2010) or on previous analyses. For example, we could have used the annual survival probability estimates from Mizroch et al. (2004) as priors, but we were interested in an independent estimate of survival probability from this data set. The Bayesian framework also provides opportunities for developing a hierarchical model structure (Rivot and Prevost 2002; Su et al. 2004), which would improve the inference at the group, time, and area levels.

Although we did not include a hierarchical structure here (except in the case of overdispersion in the Poisson counts), adding such a structure would be a logical and important extension of the current modeling framework.

The Hilborn (1990) approach is valuable because biologically meaningful population dynamics models can be developed within a statistical estimation framework. Although the model was initially developed to use either Poisson or multinomial likelihoods (Hilborn 1990), most applications have opted to use the Poisson likelihood for inference (e.g., Anganuzzi et al. 1994; Deriso et al. 1991; Wilkins et al. 2010). In our application, models utilizing extra-Poisson likelihoods were strongly favored over their Poisson counterparts. Because the individual recapture histories are not being modeled, individual-level heterogeneity in recapture probability and dependent movement among individuals (e.g., group movement) are being incorporated into the extra-Poisson variability. Because many of the applications of the Hilborn (1990) model have been to fish or other species that move in groups (e.g., Foote et al. 2010; Stevick et al. 2006), future implementations of this framework should consider overdispersed likelihoods to deal with the statistical uncertainties appropriately. The negative binomial is a logical choice in addition to the log-Poisson that we used here.

The approach presented here differs in a few respects from other Bayesian multistrata capture–recapture models (e.g., Dupuis 1995; Dupuis and Schwarz 2007) by defining a population dynamics model and subsequently deriving an observation model for predicted captures of animals by tag group. Buckland et al. (2000) state that there is a growing desire among statisticians to embed biological processes in inference. This process can ostensibly occur from two sides: (i) statisticians can incorporate biological mechanisms into their stochastic empirical models (e.g., using state-space models; Meyer and Millar 1999); and (ii) process modelers can develop adequate models of stochastic uncertainty in the observation process. The modeling methodology presented here attempts to take the latter approach by augmenting a biologically based model with a more appropriate level of stochastic uncertainty.

Acknowledgements

References

Allen, B.M., and Angliss, R.P. 2011. Alaska marine mammal stock assessments, 2010. US Dept. Commer. NOAA Tech. Memo. NMFS-AFSC-223.

Anganuzzi, A., Hilborn, R., and Skalski, J.R. 1994. Estimation of size selectivity and movement rates from mark–recovery data. Can. J. Fish. Aquat. Sci. 51(3): 734–742. doi:10.1139/f94-073.

Arrizabalaga, H., Costas, E., Juste, J., Gonzalez-Garces, A., Nieto, B., and Lopez-Rodas, V. 2004. Population structure of albacore Thunnus alalunga inferred from blood groups and tag–recapture analyses. Mar. Ecol. Prog. Ser. 282: 245–252. doi:10.3354/meps282245.

Baker, C.S., Herman, L.M., Perry, A., Lawton, W.S., Straley, J.M., Wolman, A.A., Kaufman, G.D., Winn, H.E., Hall, J.D., Reinke, J.M., and Ostman, J. 1986. The migratory movement and population structure of humpback whales (Megaptera novaeangliae) in the central and eastern North Pacific. Mar. Ecol. Prog. Ser. 31: 105–119. doi:10.3354/meps031105.

Baker, C.S., Straley, J.M., and Perry, A. 1992. Population characteristics of individually identified humpback whales in southeastern Alaska: summer and fall 1986. Fish. Bull. 90: 429–437.

Barlow, J., and Clapham, P. 1997. A new birth-interval approach to estimating demographic parameters of humpback whales. Ecology, 78(2): 535–546. doi:10.1890/0012-9658(1997)078[0535:ANBIAT]2.0.CO;2.

Box, G.E.P., and Tiao, G.C. 1973. Bayesian inference in statistical analysis. Addison-Wesley, Reading, Mass.

Brownie, C., Hines, J.E., Nichols, J.D., Pollock, K.H., and Hestbeck, J.B. 1993. Capture–recapture studies for multiple strata including non-Markovian transitions. Biometrics 49(4): 1173–1187. Available from http://www.jstor.org/stable/2532259?cookieSet=1.

Buckland, S.T., Goudie, I.B.J., and Borchers, D.L. 2000. Wildlife population assessment: past developments and future directions. Biometrics 56(1): 1–12. Available from http://www.jstor.org/stable/2677097?cookieSet=1.

Calambokidis, J., Falcone, E.A., Quinn, T.J., Burdin, A.M., Clapham, P.J., Ford, J.K.B., Gabriele, C.M., LeDuc, R., Mattila, D., Rojas-Bracho, L., Straley, J.M., Taylor, B.L., Urbn, J., Weller, D., Witteveen, B.H., Yamaguchi, M., Bendlin, A., Camacho, D., Flynn, K., Havron, A., Huggins, J., and Maloney, N. 2008. SPLASH: structure of populations, levels of abundance and status of humpback whales in the North Pacific: Final report for Contract AB133F–03-RP-00078. Tech. Rep. No. AB133F–03-RP-00078. US Dept. of Commerce.

Clapham, P., Barlow, J., Bessinger, M., Cole, T., Mattila, D., Pace, R., Palka, D., Robbins, J., and Seton, R. 2003. Abundance and demographic parameters of humpback whales from the Gulf of Maine, and stock definition relative to the Scotian Shelf. J. Cetacean Res. Manag. 5(1): 13–22.

Dennis, B. 1996. Discussion: should ecologists become Bayesians? Ecol. Appl. 6(4): 1095–1103. doi:10.2307/2269594.

Deriso, R.B., Punsly, R.G., and Bayliff, W.H. 1991. A Markov movement model of yellow fin tuna in the Eastern Pacific Ocean and some analyses for international management. Fish. Res. 11(3–4): 375–394. doi:10.1016/0165-7836(91)90010-D.

Dupuis, J.A. 1995. Bayesian estimation of movement and survival probabilities from capture–recapture data. Biometrika, 82(4): 761–772. doi:10.1093/biomet/82.4.761.

Dupuis, J.A., and Schwarz, C.J. 2007. A Bayesian approach to the multistate Jolly–Seber capture–recapture model. Biometrics, 63(4): 1015–1022. doi:10.1111/j.1541-0420.2007.00815.x. PMID:17501941.

Foote, A.D., Similä, T., Vikingsson, G.A., and Stevick, P.T. 2010. Movement, site fidelity and connectivity in a top marine predator, the killer whale. Evol. Ecol. 24(4): 803–814. doi:10.1007/s10682-009-9337-x.

Gelman, A., Carlin, J., Stern, H.S., and Rubin, D.B. 2004. Bayesian data analysis. Chapman and Hall/CRC Press, Boca Raton, Fla.

Gende, S., and Sigler, M. 2006. Persistence of forage fish hot spots and its association with foraging steller sea lions (Eumetopias jubatus) in southeast Alaska. Deep Sea Res. Part II Top. Stud. Oceanogr. 53(3–4): 432–441. doi:10.1016/j.dsr2.2006.01.005.

Gende, S.M., Hendrix, A.N., Harris, K.R., Eichenlaub, B., Nielsen, J., and Pyare, S. 2011. A Bayesian appraoch for understanding the role of ship speed in whale–ship encounters. Ecol. Appl. **21**(6): 2232–2240. doi:10.1890/10-1965.1. PMID:21939057.

Gilks, W., and Spiegelhalter, D. 1996. Markov chain Monte Carlo in practice. Chapman and Hall/CRC, London UK.

Hammond, P. 1986. Estimating the size of naturally marked whale populations using capture–recapture techniques. Rep. Int. Whal. Comm. **8**: 252–282.

Harris, K., Gende, S.M., Logsdon, M.G., and Klinger, T. 2012. Spatial pattern analysis of cruise ship–humpback whale interactions in and near Glacier Bay National Park, Alaska. Environ. Manage. **49**(1): 44–54. doi:10.1007/s00267-011-9754-9. PMID: 21983996.

Hilborn, R. 1990. Determination of fish movement patterns from tag recoveries using maximum likelihood estimators. Can. J. Fish. Aquat. Sci. **47**(3): 635–643. doi:10.1139/f90-071.

King, R., Gimenez, O., Morgan, B., and Brooks, S. 2009. Bayesian analysis for population ecology. Chapman and Hall/CRC Press, UK.

Mangel, M. 2008. Uncertainty in ecology: a retrospective and prospective. Bull. Brit. Ecol. Soc. **39**(1): 25–28.

Maunder, M.N., Starr, P.J., and Hilborn, R. 2000. A Bayesian analysis to estimate loss in squid catch due to the implementation of a sea lion population management plan. Mar. Mamm. Sci. **16**(2): 413–426. doi:10.1111/j.1748-7692.2000.tb00933.x.

McCullagh, P., and Nelder, J. 1983. Generalized linear models. Chapman and Hall, New York.

Meyer, R., and Millar, R. 1999. BUGS in Bayesian stock assessments. Can. J. Fish. Aquat. Sci. **56**(6): 1078–1087. doi:10.1139/f99-043.

Mizroch, S.A., Herman, L.M., Straley, J.M., Glockner-Ferrari, D.A., Jurasz, C., Darling, J., Cerchio, S., Gabriele, C.M., Salden, D.R., and von Ziegesar, O. 2004. Estimating the adult survival rate of central North Pacific humpback whales (*Megaptera novaeangliae*). J. Mammal. **85**(5): 963–972. doi:10.1644/BOS-123.

Nielson, J.L., and Gabrielle, C.M. 2008. Results of humpback whale population monitoring in Glacier Bay and adjacent waters: 2008. Report to Glacier Bay National Park, National Park Service, Gustavus, Alaska.

Pollock, K. 1991. Modeling capture, recapture and removal statistics for estimation of demographic parameters for fish and wildlife populations: past, present and future. J. Am. Stat. Assoc. **86**(413): 225–238.

Pollock, K.H., Nichols, J.D., Brownie, C., and Hines, J.E. 1990. Statistical inference for capture–recapture experiments. Wildl. Monogr. **107**: 1–97.

Punt, A.E., and Hilborn, R. 1997. Fisheries stock assessment and decision analysis: the Bayesian approach. Rev. Fish Biol. Fish. **7**(1): 35–63. doi:10.1023/A:1018419207494.

Quinn, T.J., and Deriso, R.B. 1999. Quantitative fish dynamics. Oxford University Press, New York.

R Development Core Team. 2009. R: a language and environment for statistical computing [online]. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0. Available from http://www.R-project.org.

Ramp, C., Bérubé, M., Palsbøll, P., Hagen, W., and Sears, R. 2010. Sex-specific survival in the humpback whale *Megaptera novaeangliae* in the Gulf of St. Lawrence, Canada. Mar. Ecol. Prog. Ser. **400**: 267–276. doi:10.3354/meps08426.

Rasmussen, K., Palacios, D., Calambokidis, J., Saborio, M., Dalla Rosa, L., Secchi, E., Steiger, G., Allen, J., and Stone, G. 2007. Southern hemisphere humpback whales wintering off Central America: insights from water temperature into the longest mammalian migration. Biol. Lett. **3**(3): 302–305. doi:10.1098/rsbl.2007.0067. PMID:17412669.

Rivest, L.P., and Daigle, G. 2004. Loglinear models for the robust design in mark–recapture experiments. Biometrics, **60**(1): 100–107. doi:10.1111/j.0006-341X.2004.00157.x. PMID:15032779.

Rivot, E., and Prevost, E. 2002. Hierarchical Bayesian analysis of capture mark recapture data. Can. J. Fish. Aquat. Sci. **59**(11): 1768–1784. doi:10.1139/f02-145.

Robards, M., Abookire, A., Anson, J., Bodkin, J., Drew, G., Hooge, P., Piatt, J., and Speckman, S. 2003. Ecology of selected marine communities in Glacier Bay: zooplankton, forage fish, seabirds and marine mammals. USGS Alaska Science Center, Biological Science Office, Anchorage, Alaska.

Roberts, G., and Polson, N.G. 1994. On the geometric convergence of the Gibbs sampler. J. R. Stat. Soc. B, **56**: 377–384.

Rosenbaum, H.C., Weinrich, M.T., Stoleson, S.A., Gibbs, J.P., Baker, C.S., and DeSalle, R. 2002. The effect of differential reproductive success on population genetic structure: correlations of life history with matrilines in humpback whales of the Gulf of Maine. J. Hered. **93**(6): 389–399. doi:10.1093/jhered/93.6.389. PMID: 12642638.

Royle, J.A. 2009. Analysis of capture–recapture models with individual covariates using data augmentation. Biometrics, **65**(1): 267–274. doi:10.1111/j.1541-0420.2008.01038.x. PMID:18422793.

Schwarz, C.J., Schweigert, J.F., and Arnason, A.N. 1993. Estimating migration rates using tag-recovery data. Biometrics **49**(1): pp. 177–193. Available from http://www.jstor.org/stable/2532612?cookieSet=1

Seber, G.A.F. 1982. Capture–recapture methods. *In* Encyclopedia of statistical sciences (9 vols. plus Supplement). *Edited by* D.L. Banks, C.B. Read and S. Kotz. Volume 1, pp. 367–374. The Blackburn Press, Caldwell, N.J.

Smith, P. 1991. Bayesian analysis for a multiple capture–recapture model. Biometrika, **78**(2): 399–407. doi:10.1093/biomet/78.2.399.

Spiegelhalter, D.J., Best, N.G., Carlin, B.P., and van der Linde, A. 2002. Bayesian measures of model complexity and fit. J. R. Stat. Soc., B, **64**(4): 583–639. doi:10.1111/1467-9868.00353.

Spiegelhalter, D., Thomas, A., Best, N., and Lunn, D. 2003. WinBUGS version 1.4 user manual. Tech. Rep. MRC Biostatistics Unit, Cambridge, UK.

Stevick, P.T., Aguayo, A., Allen, J., and Avila, I.C. 2004. Migrations of individually identified humpback whales between the Antarctic Peninsula and South America. J. Cetacean Res. Manag. **6**(2): 109–114.

Stevick, P., Allen, J., Clapham, P., Katona, S., Larsen, F., Lien, J., Mattila, D., Palsboll, P., Sears, R., Sigurjonsson, J., Smith, T.D., Vikingsson, G., Øien, N., and Hammond, P.S. 2006. Population spatial structuring on the feeding grounds in North Atlantic humpback whales (*Megaptera novaeangliae*). J. Zool. (Lond.), **270**(2): 244–255. doi:10.1111/j.1469-7998.2006.00128.x.

Straley, J. 1994. Seasonal characteristics of humpback whales (*Megaptera novaeangliae*) in southeastern Alaska. Master's thesis, University of Alaska Fairbanks, Fairbanks, Alaska.

Straley, J.M., and Gabriele, C.M. 2000. Humpback whales of southeastern Alaska. Humpback whale fluke identification catalog. 3rd printing. National Park Service, Gustavus, Alaska.

Straley, J.M., Quinn, T.J., II, and Gabriele, C.M. 2009. Assessment of mark–recapture models to estimate the abundance of a humpback whale feeding aggregation in Southeast Alaska. J. Biogeogr. **36**(3): 427–438. doi:10.1111/j.1365-2699.2008.01906.x.

Sturtz, S., Ligges, U., and Gelman, A. 2005. R2WinBUGS: A package for running WinBUGS from R. J. Stat. Softw. **12**(3): 1–16.

Su, Z.M., Peterman, R.M., and Haeseker, S.L. 2004. Spatial hierarchical Bayesian models for stock–recruitment analysis of pink salmon (*Oncorhynchus gorbuscha*). Can. J. Fish. Aquat. Sci. **61**(12): 2471–2486. doi:10.1139/f04-168.

Ward, E. 2008. A review and comparison of four commonly used Bayesian and maximum likelihood model selection tools. Ecol. Model. **211**(1–2): 1–10. doi:10.1016/j.ecolmodel.2007.10.030.

Whitehead, H. 2001. Analysis of animal movement using opportunistic individual identifications: application to sperm whales. Ecology, **82**(5): 1417–1432. doi:10.1890/0012-9658(2001)082 [1417:AOAMUO]2.0.CO;2.

Whitehead, H., and Carscadden, J. 1985. Predicting inshore whale abundance — whales and capelin off the Newfoundland coast. Can. J. Fish. Aquat. Sci. **42**(5): 976–981. doi:10.1139/f85-122.

Wilkins, K., Malecki, R., Sullivan, P., Fuller, J., Dunn, J., Hindman, L., Costanzo, G., Petrie, S., and Luszcz, D. 2010. Population structure of tundra swans wintering in Eastern North America. J. Wildl. Manage. **74**(5): 1107–1111. doi:10.2193/2009-290.

Williams, T. 1999. The evolution of cost efficient swimming in marine mammals: limits to energetic optimization. Philos. Trans. R. Soc. B, **354**(1380): 193–201. doi:10.1098/rstb.1999.0371.

Witteveen, B.H., Foy, R.J., Wynne, K.M., and Yann, T. 2008. Investigation of foraging habits and prey selection by humpback whales (*Megaptera novaeangliae*) using acoustic tags and concurrent fish surveys. Mar. Mamm. Sci. **24**(3): 516–534. doi:10.1111/j.1748-7692.2008.00193.x.

Xiao, Y. 1996. A framework for evaluating experimental designs for estimating rates of fish movement from tag recoveries. Can. J. Fish. Aquat. Sci. **53**(6): 1272–1280. doi:10.1139/f96-050.

Zeh, J., Poole, D., Miller, G., Koski, W., Baraff, L., and Hugh, D. 2002. Survival of bowhead whales, *Balaena mysticetus*, estimated from 1981–1998 photoidentification data. Biometrics, **58**(4): 832–840. doi:10.1111/j.0006-341X.2002.00832.x. PMID:12495137.

Zerbini, A., Clapham, P., and Wade, P. 2010. Assessing plausible rates of population growth in humpback whales from life-history data. Mar. Biol. (Berl.), **157**(6): 1225–1236. doi:10.1007/s00227-010-1403-y.