



Bayesian implementation of a time stratified Lincoln–Petersen estimator for salmon abundance in the upper Matanuska River, Alaska, USA

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ABSTRACT

Time stratified Lincoln–Petersen mark–recapture models can generate estimates of salmon abundance that are robust to capture heterogeneity. Bayesian implementation of these estimators provides a flexible framework to formulate different model structures, including random effects structures and models with functional relationships between parameters and covariates, and can successfully generate estimates in the face of sparse data. In this article, we used a Bayesian time stratified Lincoln–Petersen model to provide first ever abundance estimates of chum, *Oncorhynchus keta*, coho, *O. kisutch*, and sockeye salmon, *O. nerka*, in the upper Matanuska River, Alaska, USA, using tagging data from 2009. For each species, we formulated a suite of twelve model structures and used deviance information criterion based multimodel inference and model averaging to estimate salmon abundance. Model averaged point estimates for upper river 2009 chum, coho, and sockeye salmon were 54,720, 11,430, and 13,750, fish respectively, supporting a growing body of ecological research which demonstrates that glacial river systems can sustain significant Pacific salmon runs. Results identified time varying probability of capture for chum and coho salmon, and population estimates were 17% and 8% higher, respectively, than estimates from a simple pooled Lincoln–Petersen model which has been demonstrated to be biased low in the face of capture heterogeneity. Capture heterogeneity was not found for sockeye salmon, and the model averaged time stratified and pooled Lincoln–Petersen estimates agreed closely. Time stratified models can potentially produce more accurate estimates, however, the additional model complexity results in less precise abundance estimates compared to the simple pooled Lincoln–Petersen estimator.

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1. Introduction

Abundance estimates for spawning salmon (escapement) in glacial river systems are difficult to obtain where turbid, fast flowing water precludes visual counts from towers or weirs. Mark–recapture techniques can provide a means to estimate escapement, however difficulties in sampling adult salmon can lead to violations of model assumptions and biased estimates. In this article, we present a Bayesian implementation of a time stratified Lincoln–Petersen estimator which can accommodate capture heterogeneity in order to assess the abundance of spawning adult salmon in the upper Matanuska River, Alaska, USA.

A workhorse of mark–recapture abundance estimation for salmon is the Lincoln–Petersen closed population estimator (e.g. [Seber, 2002](#)) which in its most basic form requires only two sample sessions: a tag release event and a recapture event. To be unbiased, the estimator requires several strong assumptions (e.g. [Otis et al.,](#)

1978, page 9) that can be difficult to satisfy when attempting to sample adult salmon returning to their natal streams. Of particular concern is that all animals in the population have equal probability of capture. Spawning salmon migrate along a directed route up river, and thus typical mark–recapture sampling designs require time stratified tag releases and recovery efforts such that all portions of the run are available for capture, tagging, and recovery. Due to a host of variables, it is likely that probability of capture is not constant throughout tagging and recovery efforts. Changes in water clarity, temperature, or flow can affect sampling gear effectiveness and thus capture probabilities. Salmon abundance at the tagging area changes through time and can result in differential tagging rates on components of the run unless tagging is conducted in direct proportion to abundance. Furthermore, sex-specific morphology and behavior can lead to capture heterogeneity, for example if males and females have different susceptibility to sampling gear and arrive at capture areas at different times. Capture probability heterogeneity typically results in negatively biased abundance estimates from traditional Lincoln–Petersen estimators ([Baker, 2004](#); [Otis et al., 1978](#)). To address capture heterogeneity, time (or space) stratified elaborations of the traditional Lincoln–Petersen

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abundance estimator were developed which allow for temporal (or spatial) variation in the probability of capture and which are naturally suited to the stratified tag release and recovery sampling design of many salmon abundance estimates (e.g. Darroch, 1961).

The basic idea of the stratified Lincoln–Petersen estimator is to divide up the population into homogenous groups of animals with respect to capture probability, overcoming any potential biases associated with a pooled model in the face of capture heterogeneity (Schwarz and Taylor, 1998; Seber, 2002). With immigrating adult salmon, stratification is in time, typically employing netting or a fishwheel to capture and tag fish at a downstream site with subsequent netting, fishwheel capture, or carcass surveys upstream for the recovery effort. Time stratified Lincoln–Petersen estimators were first formalized into a likelihood maximization framework by Darroch (1961) under the requirement of equivalent numbers of release and recovery temporal strata. Darroch's model was later generalized to accommodate differing numbers of release and recovery strata and improved by constraining some nuisance parameters associated with the probability of becoming available for detection as functions of covariates (i.e. days of travel time between release and recovery sites) by Schwarz and Dempson (1994), Banneheka et al. (1997), and Plante et al. (1998). While the generalized time stratified estimators take advantage of the efficiency of maximum likelihood estimation, sparse tag recovery data results in optimization problems. Several methods of pooling strata to avoid sparse data problems have been suggested (e.g. Bjorkstedt, 2005; Schwarz and Taylor, 1998), but the most recent wave of time stratified Lincoln–Petersen estimators have been implemented in a Bayesian framework and largely overcome sparse data issues by using Markov Chain Monte Carlo (MCMC) maximization routines (Bonner and Schwarz, 2011; Mäntyniemi and Romakkaniemi, 2002).

In this article, we follow the methods of Bonner and Schwarz (2011) and implement a Bayesian time stratified Lincoln–Petersen estimator using WinBUGS (Lunn et al., 2000) and the R statistical programming environment (R Development Core Team, 2011). Our methods depart from the modeling in Bonner and Schwarz (2011) by parameterizing the time stratified abundance estimator in terms of the number of animals available for capture at the tagging site as opposed to the number of animals available for capture at the recovery site. This parameterization was necessary to achieve unbiased abundance estimates when the study sampling design is such that not all animals that pass the tagging area have an opportunity to become available for detection and subsequent recovery (see below).

The Matanuska River is a glacial river with braided channels that empties into Upper Cook Inlet, Alaska, and is located in the Matanuska-Susitna Borough northeast of Anchorage. All five species of Pacific salmon have been documented in the Matanuska River, which contributes to Upper Cook Inlet set and drift gillnet mixed-stock commercial fisheries targeting sockeye, *Oncorhynchus nerka*, and coho, *O. kisutch*, salmon. A small in river sport fishery also occurs, however harvest is negligible (Sweet et al., 2003). Although the Matanuska River is a prominent feature in a relatively populated area of the state, little is known about salmon abundance in the river. The Alaska Department of Fish and Game conducted tagging and recovery efforts on mixed stocks in the Cook Inlet salmon fishing grounds in 2002 and estimated that coho salmon escapement into the Matanuska River was approximately 20,000 fish, a small component of approximately 2% of the overall Upper Cook Inlet coho escapement (Willette et al., 2003). However, prior to this study no direct in-river abundance estimate had been made for any salmon species in the Matanuska River.

We implemented the time stratified Lincoln–Petersen estimator, which can correct for time-varying capture probability heterogeneity, to provide abundance estimates of chum, *O. keta*,

coho, and sockeye salmon in the Matanuska River above river km 19 using data from 2009; estimates for chinook, *O. tshawytscha*, and pink salmon, *O. gorbuscha*, were not available because chinook populations run into the Matanuska River in the Spring before field crews can safely operate sampling gear and because pink salmon are rare in the system. These abundance estimates will contribute initial basic information necessary to inform harvest and land-use decisions regarding the Matanuska river salmon populations in the face of continued expected human population growth and development pressure in the drainage. Below we present detailed methodology on the construction of a suite of models with different structures to accommodate capture heterogeneity (e.g. hierarchical “random effects” models), example WinBUGS code, model validation, and finally deviance information criterion (DIC) based multimodel inference, presenting the primary management quantity of interest, total run size, as a model averaged estimate. Results suggest that capture heterogeneity was present for chum and coho salmon, resulting in abundance estimates that were higher than the traditional pooled Lincoln–Petersen estimator for these two species, whereas probability of capture was relatively constant in the sockeye salmon models and resulted in agreement between the time stratified and pooled estimators. The time stratified estimators can correct for capture heterogeneity and produce more accurate abundance estimates than the pooled model. However, estimates from the more heavily parameterized stratified estimators were less precise.

2. Methods

2.1. Study site

The Matanuska River is a turbid glacial river with headwaters in the Chugach mountains, flowing westward approximately 120 km to an outlet in the Knik Arm of Cook Inlet, and draining an area of approximately 5300 km². Further details on the study site are available in Anderson and Bromaghin (2009) and Curran et al. (2011).

2.2. Sampling design and data

Tagging of immigrating adult chum, coho, and sockeye salmon occurred at a fishwheel operated at river km 19 directly upstream of the Old Glenn Highway bridge and USGS gaging station 15284000 (fishwheel description provided in Anderson and Bromaghin, 2009; see Figure 4 in Curran et al., 2011 and Figure 7 in Anderson and Bromaghin, 2009 for detailed maps of the study area). The lower river below km 19 is dominated by a braided plain and is unsuitable for fishwheel sampling. Captured salmon were retained in a live well and healthy fish were marked with either a radio tag (as part of another research effort to identify spawning reaches in the study system; Anderson and Bromaghin, 2009) or marked with a series of operculum or fin punches corresponding to a specific release stratum. Tagging at the fishwheel occurred during daylight operable hours which varied from approximately 6–12 h a day depending on river conditions.

For the purposes of the time stratified Lincoln–Petersen abundance estimator, time was divided into release strata $i = 1, \dots, s$ and recovery strata $j = 1, \dots, t$. For a given release stratum, m_i tagged fish were released. Release strata were scheduled to cover the entire run for each respective species. Release strata were approximately one week long except for the terminal release stratum which was approximately two weeks long (complete data are presented in Table S1 of the Supplementary materials). The terminal release stratum was prolonged in order to ensure the tail end of the incoming run was captured for the radio tagging portion of the original study. However, due to an oversight, operculum/fin punches were

not changed to reflect different release weeks within the stratum. Consistent-length temporal release (or recovery) strata are not essential to implement the time stratified Lincoln–Petersen estimator as parameterized below because movement between release and recovery grounds is modeled as a function of calendar days between release and recovery strata (see below).

Tag recovery efforts involved opportunistic carcass surveys at a suite of eight known spawning locations in the middle and upper reaches of the Matanuska river that were accessible by foot and/or road (spawning areas B, C, E, F, G, J, T-1, and T-2 in Figure 7 of Anderson and Bromaghin, 2009). Each recovery site was sampled at least once in each recovery stratum by two or more observers and counts of unmarked and marked salmon were tallied by species. The caudal fins of examined carcasses were cut off to prevent double counting in subsequent surveys. Due to difficulties in accessing carcass grounds, recovery strata were two to three weeks in length (Table S1). The number of tags recovered during the j th recovery stratum that were released during the i th release stratum are denoted by r_{ij} , and tags never recovered are indicated by r_{it+1} , or in matrix form, \mathbf{R} , with s rows and $t+1$ columns. The number of unmarked fish recovered in the j th stratum is denoted by c_j whereas the (unobservable) total number of fish that become available for potential capture in recovery stratum j is u_j .

2.3. Statistical model

To estimate salmon abundance using mark–recapture data, we used a Bayesian implementation of a time stratified Lincoln–Petersen estimator. Primary features of the model detailed below include: (i) deconstruction of the probability of capture at recovery sites into availability for detection and probability of detection, (ii) time stratification of parameters, and (iii) specification of both “fixed” and “random” effects parameterizations of the model. The assumptions of the time stratified Lincoln–Petersen estimator as applied in this study are as follows: (1) there are no additions to the population between the release and recovery site, and any mortality or emigration between the release and recovery sites is randomly distributed throughout the marked and unmarked population, (2) tags are not shed or misidentified, (3) all animals (i.e. marked and unmarked) present in a given recovery stratum have the same probability of being detected, (4) all animals that pass the release site in a given release stratum have the same probabilities of arriving at the t different recovery strata, and finally (5) fish from the same release strata behave independently with respect to movement and fish in the same recovery strata are detected independently.

Assumption 1 specifies population closure, and note that if death or emigration to spawning areas that are not surveyed is randomly distributed throughout the population, valid estimates can still be made for abundance at the tagging site (e.g. Darroch, 1961; Krebs, 1999). In addition, under the time stratified model, some allowance can be made for systematic changes in death or emigration rates across strata by estimating stratum-specific probabilities of capture (see below). Assumption 2 is reasonable because fin clips/operculum punches cannot be shed and previous salmon telemetry studies found low to no radio tag shedding (e.g. Anderson and Bromaghin, 2009). Furthermore, survey teams were experienced in identifying salmon and multiple observers participated in each carcass survey. Assumptions 3 and 4 are necessary to assert that availability or detection parameters as estimated by sample data are representative of the true population of animals present in a given recovery stratum (Bonner and Schwarz, 2011). Reports from field crews indicated low scavenging rates on salmon carcasses and no obvious bias in size or sex in sampled carcasses within recovery strata, suggesting no systematic differences in probability of detection amongst salmon carcasses within recovery

strata as would be consistent with assumption 3. We maintain that assumption 4 is reasonable in the present study because tagging operations were carried out so as to minimize impacts on tagged adult salmon (Anderson and Bromaghin, 2009) and to prevent artificial differences in movement or spawning behavior between tagged and untagged groups. Assumption 5 implies that tag recoveries and unmarked animal captures can be described by a multinomial and binomial process, respectively (see Mäntyniemi and Romakkaniemi, 2002 for a time stratified Lincoln–Petersen model which relaxes the independent travel assumption and allows for overdispersion in tag recoveries).

In the time stratified Lincoln–Petersen model, the probability of capture of an animal on the recovery grounds is decomposed into the product of a process describing availability for detection and a detection process, where λ_{ij} is the probability of a fish released in stratum i becomes available for detection at the carcass survey grounds during recovery stratum j (i.e. moves on to the recovery area) and p_j is the probability an animal on the survey grounds during recovery stratum j is detected. Following the formulation of the time stratified Lincoln–Petersen model in Bonner and Schwarz (2011) and under the assumptions outlined above, the vectors of tag recoveries for marks released in stratum i , \mathbf{r}_i (i.e. $r_{i1}, \dots, r_{it}, r_{it+1}$), are multinomially distributed with a cell probability for marks never recaptured:

$$\mathbf{r}_i | m_i, \lambda_{i1} \dots \lambda_{it}, p_1 \dots p_t \sim$$

$$\text{Multinomial} \left(m_i, \left\{ \lambda_{i1} p_1, 1 - \sum_{j=1}^t \lambda_{ij} p_j \right\} \right) \quad (1)$$

An additional likelihood component is contributed by the observation of unmarked fish, which follows a binomial process conditional upon the (unobserved) total number of fish present during a given recovery stratum, u_j :

$$c_j | u_j, p_j \sim \text{Binomial}(u_j, p_j) \quad (2)$$

The full likelihood of the data is the product of the contributions from marked and unmarked fish, respectively, and total abundance, N , is the sum of the marked releases and of the vector of estimated u_j 's, \mathbf{u} .

Following methods outlined in Schwarz and Dempson (1994), Mäntyniemi and Romakkaniemi (2002), and Bonner and Schwarz (2011), we modeled travel times between the tagging site and recovery area as being lognormally distributed and used standardized travel times and the cumulative standard normal distribution, Φ , to estimate the probability of availability for detection, λ_{ij} , thereby constraining the number of parameters that need be estimated to populate the s release strata \times t recovery strata $\mathbf{\Lambda}$ parameter matrix. In the lognormal model, the probability a fish released in the i th stratum arrives at the recovery area in stratum j , λ_{ij} , is:

$$\lambda_{ij} = \begin{cases} \Phi \left(\frac{\log(x_{i1}) - \mu_{\lambda i}}{\sigma_{\lambda i}} \right) & \text{if } j = 1 \\ \Phi \left(\frac{\log(x_{ij}) - \mu_{\lambda i}}{\sigma_{\lambda i}} \right) - \Phi \left(\frac{\log(x_{i,j-1}) - \mu_{\lambda i}}{\sigma_{\lambda i}} \right) & \text{if } j > 1 \end{cases} \quad (3)$$

where x_{ij} is the number of days between the middle day of release stratum i and the middle day of recovery stratum j , and the mean and standard deviation of the underlying lognormal distribution are $\mu_{\lambda i}$ and $\sigma_{\lambda i}$, respectively. With this parameterization, estimates of $\mu_{\lambda i}$ and $\sigma_{\lambda i}$ are in units of $\log(\text{days})$ of travel. The information to estimate these parameters comes from the timings of release and recovery for recaptured tags. Eq. (3) presents a model with separate travel time parameters for each release stratum. However, below we also construct a model with a global travel time distribution common to all release strata (“pooled” $\mathbf{\Lambda}$ model). In our sampling

design, tag release efforts ceased before carcass surveys began such that release and recovery strata did not overlap. Because adult Pacific salmon perish after spawning, the first recovery stratum represents an accumulation of animals that arrived in the recovery area prior to the beginning of carcass surveys, which differs from travel models presented in earlier applications of the Schwarz and Dempson (1994) model (Mäntyniemi and Romakkaniemi, 2002; Bonner and Schwarz, 2011).

Given this travel model, the formulation of the likelihood for the observed unmarked animals, Eq. (2), is problematic if the goal is to estimate total abundance (the sum of marked animals and unobservable unmarked animals) and the movement parameters are such that a substantial portion of the fish passing the marking site never becomes available at the recovery site. This would be the case if recovery efforts stop before all fish that pass the marking site have the opportunity to become available for capture at the recovery site, or if fish spawn in areas not visited during carcass surveys. To account for this, we reparameterized the model for unmarks in terms of the number of (unmarked) fish that leave the release site during release stratum i , n_i , that become available for capture in recovery stratum j as follows:

$$C_j | p_j, \lambda_{1j}, \dots, \lambda_{sj}, n_1, \dots, n_s \sim \text{Binomial}(u_j = \lambda_{1j}n_1 + \lambda_{2j}n_2 + \dots + \lambda_{sj}n_s, p_j) \quad (4)$$

where the estimated parameters are the vector of n_i 's, \mathbf{n} , instead of \mathbf{u} . With this parameterization, abundance at the tagging site during a given release stratum, N_i , is the sum of marks released during the stratum and estimates of the unmarked fish population leaving the tagging site during the stratum, $N_i = m_i + n_i$, and total run-wide abundance is estimated as the sum of release-stratum specific run estimates, or $N = \sum_i (m_i + n_i)$. Note, that total abundance constructed by summing up the estimated \mathbf{u} vector from Eq. (2) only accounts for all animals in the population of interest (i.e. the total run passing the marking site) in the case where all animals become available for detection (though not necessarily detected) at some point through the recovery effort, whereas total abundance estimated by summing the \mathbf{n} vector under Eq. (4) accounts for all animals regardless of whether they have a chance to become available for capture at the recovery site, as long as \mathbf{A} can be estimated and provides an accurate description of fish availability for detection.

2.4. Model set

The time stratified Lincoln–Petersen models as outlined above was implemented in a Bayesian framework using WinBUGS as run from the R statistical programming environment using the R2WinBUGS package (Sturtz et al., 2005). This section outlines the suite of structures we formulated for the \mathbf{A} , \mathbf{p} , and \mathbf{n} component models, followed by discussion of prior specifications for estimated parameters.

We examined two different structures for the lognormal travel model: a “pooled” model which fits a single lognormal location and spread parameter for all release strata, and a “hierarchical” model with a different lognormal location and spread parameter for each release stratum with parameters drawn from hyperdistributions for mean travel time and for spread of travel time (Table 1), i.e. a random effect on release stratum for each of $\mu_{\lambda i}$ and $\sigma_{\lambda i}$.

We considered three models for probability of detection across recovery strata. The “constant” model constrained p_j to be constant across all recovery strata, $p_j = p$ for $j = 1, \dots, t$. Note, the effective probability of capture, the product of λ_{ij} and p_j , can still be heterogeneous across recovery strata under the constant $\lambda_{ij}p_j$ model if λ_{ij} varies across recovery strata. Detection heterogeneity was incorporated with a “hierarchical” model (i.e. random effects) which

Table 1
Prior distribution selections.

A	
Hierarchical	Hyperpriors: $\eta_{\lambda i} \sim \text{Normal}(\text{mean} = 0, \text{variance} = 5.0)$ $1/\varepsilon_{\lambda i}^2 \sim \text{Gamma}(\text{shape} = 1, \text{rate} = 0.1)$ $\eta_{\lambda \sigma} \sim \text{Normal}(\text{mean} = 0, \text{variance} = 5.0)$ $1/\varepsilon_{\lambda \sigma}^2 \sim \text{Gamma}(\text{shape} = 1, \text{rate} = 0.1)$ Lower level priors: $\mu_{\lambda i} \sim \text{Normal}(\text{mean} = \eta_{\lambda i}, \text{variance} = \varepsilon_{\lambda i}^2)$ $\log(\sigma_{\lambda i}) \sim \text{Normal}(\text{mean} = \eta_{\lambda \sigma}, \text{variance} = \varepsilon_{\lambda \sigma}^2)$ $\mu_{\lambda} \sim \text{Normal}(\text{mean} = 0.0, \text{variance} = 5.0)$ $1/\sigma_{\lambda} \sim \text{Gamma}(\text{shape} = 1.0, \text{rate} = 1.0)$
Pooled	
p	
Hierarchical	Hyperpriors: $\eta_p \sim \text{Normal}(\text{mean} = 0, \text{variance} = 3.0)$ $1/\varepsilon_p^2 \sim \text{Gamma}(\text{shape} = 1, \text{rate} = 0.1)$ Lower level priors: $\logit(p_j) \sim \text{Normal}(\text{mean} = \eta_p, \text{variance} = \varepsilon_p^2)$
Simple	t identical priors: $\logit(p_j) \sim \text{Normal}(\text{mean} = 0, \text{variance} = 3.0)$
Constant	$\logit(p) \sim \text{Normal}(\text{mean} = 0, \text{variance} = 3.0)$
n	
Hierarchical	Hyperpriors: $\eta_n \sim \text{Normal}(\text{mean} = 9.5, \text{variance} = 4)$ $1/\varepsilon_n^2 \sim \text{Gamma}(\text{shape} = 1, \text{rate} = 0.1)$ Lower level priors: $\log(n_i) \sim \text{Normal}(\text{mean} = \eta_n, \text{variance} = \varepsilon_n^2)$
Simple	s identical priors: $\log(n_i) \sim \text{Normal}(\text{mean} = 9.5, \text{variance} = 4)$

specifies a common hyperdistribution from which individual p_j for each release strata are drawn, and with a “simple” model (following Bonner and Schwarz, 2011) where a separate p_j was directly estimated for each recovery stratum with identical and separate priors for each p_j (Table 1).

Finally, we considered two statistical models for the estimated vector of n_i 's, following the parameterization of the likelihood for unmarked captures in Eq. (4). The “hierarchical” model for \mathbf{n} specified a common hyperdistribution from which individual n_i 's are drawn, and the “simple” model where a separate n_i was estimated for each release stratum with identical and separate priors for each n_i (Table 1).

The candidate model set included all combinations of the component models for \mathbf{A} , \mathbf{p} , and \mathbf{n} (Table 1). WinBUGS code for \mathbf{A} , \mathbf{p} , and \mathbf{n} component models is provided in the Supplementary materials section (Supplemental Text 1). From here on, specific models are referenced by three letter codes indicating a combination of component models for \mathbf{A} – \mathbf{p} – \mathbf{n} : C = constant, H = hierarchical, P = pooled, and S = simple. Due to a lack of available degrees of freedom resulting from a small number of strata used in this study, extensions of these models to include functional relationships between parameters and covariates were not possible, such as modeling p_j as a polynomial function of time or environmental conditions (e.g. Mäntyniemi and Romakkaniemi, 2002; Bonner and Schwarz, 2011); while not estimated here, the Supplementary materials provides example code to implement a model with probability of detection parameterized as a function of time (Supplemental Text 1). WinBUGS MCMC implementations for each of the candidate models were specified with multiple long chains to facilitate model convergence: number of chains = 5, number of iterations = 1×10^6 , burn in iterations = 9×10^5 , thin rate = 100. Under these specifications, a total of 5000 draws from the joint posterior parameter distribution are stored for subsequent inference.

Priors for estimated parameters in the component models applied to the Matanuska data are listed in Table 1. In all cases, vague priors were selected. However, for models with a hierarchical structure for p_j , we limited the variance of the hyperprior on the mean parameter of the hyperdistribution describing p_j (η_p) to

improve model convergence; the specified hyperprior for η_p still results in a diffuse distribution for p_j in the probability scale, with approximately 95% of the density falling between p_j and $p_j = 0.95$.

2.5. Model validation

Model validation included three phases: assessment of model convergence, testing for structural deficiencies, and assessment of parameter identifiability. Fitted models were checked for MCMC chain convergence by examining parameters' marginal posterior distributions for multiple peaks, which may indicate parallel chains had not reached a common stationary distribution, and by examining whether fitted parameters had Gelman–Brooks–Rubin \hat{R} statistics of less than 1.1 across parallel chains (Brooks and Gelman, 1998). To assess models for structural deficiencies, posterior predictive checks were implemented (Gelman et al., 1996, 2004) and Bayesian p -values were calculated for a suite of five discrepancy measures using code written in R to post process WinBUGS output. Let $T(y^{obs}|\theta, M)$ and $T(y^{rep}|\theta, M)$ represent a discrepancy statistic under observed data and data replicated from a posterior parameter draw, θ , from candidate model M . Replicated data include expected tag recoveries and unmarked fish recoveries given the observed tag releases, \mathbf{m} , and estimates of \mathbf{p} , $\mathbf{\Lambda}$, and \mathbf{n} . Discrepancy measures are as follows, with “ $\hat{\cdot}$ ” indicating a quantity replicated under M and θ : (i) total number of tags ever recaptured: $T_{r..} = (\sum_{i=1}^s \sum_{j=1}^t r_{ij} - \sum_{i=1}^s \sum_{j=1}^t \hat{r}_{ij})^2$, (ii) number of tags released in each respective release stratum that were recovered: $T_{ri.} = (\sum_{i=1}^s (\sum_{j=1}^t r_{ij} - \sum_{j=1}^t \hat{r}_{ij}))^2$, (iii) number of tags recaptured in each respective recovery stratum: $T_{r.j} = (\sum_{j=1}^t (\sum_{i=1}^s r_{ij} - \sum_{i=1}^s \hat{r}_{ij}))^2$, (iv) number of tags recaptured in recovery stratum j that were released in release stratum i (i.e. individual cells in a tag recovery matrix): $T_{rij} = (\sum_{i=1}^s \sum_{j=1}^t (r_{ij} - \hat{r}_{ij}))^2$, and finally (v) the number of unmarked fish captured in recovery stratum j : $T_{cj} = (\sum_{j=1}^t (c_j - \hat{c}_j))^2$. The Bayesian p -value for a given discrepancy measure is: $Pr(T(y^{rep}|\theta, M) \geq T(y^{obs}|\theta, M))$. An extreme Bayesian p -value measure indicates that it would be unlikely by chance alone to observe the discrepancy measure results if the candidate model were an adequate description of reality, i.e. the model is not consistent with the data. We chose to exclude models which resulted in p -values close to 0.0 or 1.0 across the discrepancy measures from multimodel inference (see below).

Bayesian implementation of complex wildlife models can be coded and fitted relatively easily in WinBUGS (Kery, 2010; Kery and Schaub, 2012; Ntzoufras, 2009). However, care needs to be taken to ensure that inference is not made on unidentifiable or weakly identifiable parameters. In a Bayesian framework, the fitted model output for a given parameter is a posterior distribution which is the prior distribution updated by the information in the observed data. If a parameter is unidentifiable, then it will pass through the model implementation and have a posterior that is unchanged or very similar to the prior. In this sense, the model can still be fit and potentially provide information regarding identified parameters; however, inference based upon poorly identified parameters would be akin to interpreting the prior as model output and fitted models still need to be checked for parameter identifiability.

Kery and Schaub (2012) distinguish between two types of parameter identifiability problems in model fitting. Intrinsic problems with parameter identifiability occur when a model contains redundant or inseparable parameters, and no amount of data will lead to identifiability of the parameters in question. In contrast, extrinsic identifiability issues occur when sparse data leads to parameter estimation problems, such as too few data for too many parameters. In the context of the candidate model set considered in this analysis, the most highly parameterized model scenario

would be one combining a “simple” model for \mathbf{p} and \mathbf{n} , and a hierarchical model for $\mathbf{\Lambda}$ (model H–S–S) in the case where the data are such that the estimated variance on the hyperdistributions for the mean and spread of the lognormal distributions which describe travel time between the marking and recovery sites were high. In this case, the hierarchical model for $\mathbf{\Lambda}$ would behave similarly to a “fixed effects” model, consuming a degree of freedom for each mean and variance parameter for s release strata as if they were independently estimated parameters (e.g. Hodges and Sargent, 2001; Askey et al., 2007). Under this scenario, the total number of fitted parameters would be equal to: t probabilities of detection (the p_j terms) + s means of travel time ($\mu'_{\lambda_i} s$) + s variances of travel time ($\sigma'_{\lambda_i} s$) + s release strata abundances ($n_i' s$) = $t + 3s$ parameters. The observed data contain t degrees of freedom from unmarked recaptures (c_j 's) and st degrees of freedom from recovered marks (r_{ij} 's), such that there are enough degrees of freedom to account for estimated parameters as long as $st - 3s \geq 0$ for the most parameterized candidate model scenario. In this study using data from the Matanuska River, $t = 3$ for all species' data, such that in the most highly parameterized model scenario the total number of parameters to be estimated is equal to the available degrees of freedom regardless of the value for s . Thus, in principle, the candidate models are not overparameterized with respect to the structure of the Matanuska River data. However, sparse data and unavoidable parameter confounding could still lead to identifiability issues. In light of this, we assessed parameter identifiability by visually inspecting the marginal posterior distributions of fitted parameters against their prior distributions. Parameters with substantial overlap between prior and marginal posterior distributions are weakly identified in a Bayesian sense and carry little or no information from the data (Gimenez et al., 2009; Kery and Schaub, 2012).

2.6. Multimodel inference

Relative support for models that passed the validation phase was assessed using the deviance information criterion (Spiegelhalter et al., 2002; Celeux et al., 2006). DIC is model performance metric similar to Akaike's information criterion in that it attempts to balance model fit and complexity:

$$DIC = \overline{D(\boldsymbol{\theta})} + pD \quad (5)$$

where deviance is defined as $D(\boldsymbol{\theta}) = -2 \log f(y|\boldsymbol{\theta})$, i.e. twice the negative log likelihood of the observed data y using the likelihoods from Eqs. (1) and (4), and $\overline{D(\boldsymbol{\theta})}$ is the mean of the deviances associated with the joint posterior draws of the parameters stored in the MCMC routine for a given model. Smaller DIC values indicate better model performance. The model complexity penalty, pD , estimates the effective degrees of freedom of a model and is defined as follows:

$$pD = \overline{D(\tilde{\boldsymbol{\theta}})} - D(\tilde{\boldsymbol{\theta}}) \quad (6)$$

with $D(\tilde{\boldsymbol{\theta}})$ representing the posterior deviance evaluated at the median of the marginal posterior distributions for each parameter in focus (see discussion in Spiegelhalter et al., 2002 regarding model focus), i.e. the median value for the marginal posterior distribution for each element of $\mathbf{\Lambda}$, \mathbf{p} , and \mathbf{n} . One difficulty with DIC is that the model complexity parameter, pD , is not straightforward with hierarchical models, and a variety of alternatives have been suggested (e.g. Gelman et al., 2004; Celeux et al., 2006). We chose to calculate pD using the median of marginal posterior draws for parameters because some posterior distributions were skewed (e.g. Askey et al., 2007). This implementation of pD gave sensible estimates of model complexity with models with fixed parameters (e.g. $\mathbf{\Lambda}$ “pooled” or \mathbf{p} “constant”) generally having lower complexity score than their more complex counterparts (Table 2). Finally, the focus of our analyses is on estimating total run size and thus

Table 2
Model results.^a

	Model (Λ – p – n)												Model averaged
	H–H–H	H–H–S	H–S–H	H–S–S	H–C–H	H–C–S	P–H–H	P–H–S	P–S–H	P–S–S	P–C–H	P–C–S	
Chum													
pD	6.35	6.21	6.90	6.56	6.83	6.62	5.00	4.35	6.04	5.71	–	–	
DIC	82.89	82.42	84.22	82.47	85.31	84.86	81.85	80.88	80.86	80.28	–	–	
Δ DIC	2.61	2.14	3.94	2.19	5.03	4.58	1.57	0.60	0.59	0.00	–	–	
w_{DIC}	0.064	0.081	0.033	0.079	0.019	0.024	0.108	0.176	0.177	0.237	–	–	
\hat{N} 95% CI low.	39,759	40,315	36,205	40,005	40,700	43,505	40,990	42,250	41,800	42,230	–	–	40,860
\hat{N}	57,193	57,610	53,760	57,134	58,976	60,886	53,600	54,711	57,711	59,748	–	–	54,720
\hat{N} 95% CI up.	80,491	79,856	78,406	79,675	87,643	87,111	70,420	72,835	80,306	82,905	–	–	79,073
Coho													
pD	7.56	7.68	6.19	6.49	7.92	7.74	5.17	5.94	5.07	5.10	3.55	3.32	
DIC	71.96	71.95	70.55	70.38	73.86	74.01	71.73	72.83	70.85	69.95	80.66	80.98	
Δ DIC	2.01	2.00	0.60	0.43	3.91	4.05	1.78	2.87	0.90	0.00	10.71	11.03	
w_{DIC}	0.076	0.076	0.153	0.167	0.029	0.027	0.085	0.049	0.132	0.206	0.001	0.001	
\hat{N} 95% CI low.	7460	8231	7667	8250	7567	8523	8651	8902	8562	8726	11,155	11,670	8170
\hat{N}	11,213	12,507	11,084	12,119	11,442	14,162	11,857	12,506	11,551	11,791	14,981	15,635	11,430
\hat{N} 95% CI up.	16,305	19,305	15,765	17,755	18,905	24,556	16,360	17,670	15,840	16,005	20,390	21,195	17,011
Sockeye													
pD	7.60	7.70	7.77	7.97	7.69	7.64	4.91	4.62	4.75	5.00	3.95	3.89	
DIC	91.29	92.52	93.25	94.03	92.10	92.99	92.03	90.56	93.30	90.97	92.43	89.73	
Δ DIC	1.56	2.79	3.51	4.29	2.37	3.26	2.29	0.82	3.57	1.23	2.70	0.00	
w_{DIC}	0.103	0.056	0.039	0.026	0.069	0.044	0.072	0.149	0.038	0.121	0.058	0.225	
\hat{N} 95% CI low.	9661	9940	9877	10,210	9453	10,360	10,990	11,490	11,110	11,570	11,120	11,630	10,470
\hat{N}	12,971	14,605	13,316	14,361	12,791	14,451	13,561	14,111	13,529	14,233	13,648	14,377	13,750
\hat{N} 95% CI up.	17,330	20,470	17,520	20,020	17,510	20,370	17,040	17,630	16,790	17,590	16,740	17,950	18,010

^aResults are shown only for models that passed the validation phase. \hat{N} estimates are posterior medians and 95% CI low. and up. indicate lower and upper 95% credibility interval limits.

deviance calculations were made using the lowest level parameters in any of the candidate models, i.e. using Eqs. (1) and (4).

Several models in the candidate set had similar DIC values when fit to observed data (see below). To account for model selection uncertainty, we computed DIC model weights and used these to construct a model averaged estimate of total run size, $\hat{N} = \sum_i^s \hat{n}_i + \sum_i^s m_i$. While there is no formal statistical theory behind the use of DIC weights, we employed it as an attempt to capture the relevant uncertainty in an estimate of total run size (e.g. Farnsworth et al., 2006; Thogmartin et al., 2006). Other methods of computing Bayesian model weights by directly sampling over parameter and model space are available, such as reversible jump MCMC estimation (Green, 1995; Lunn et al., 2009). However these can be difficult to implement and an advantage of DIC weights is ease of computation. A Bayesian model averaged posterior distribution for a quantity of interest is described as a mixture distribution with model weights represented by posterior model probabilities (Hoeting et al., 1999). Here, we use DIC weights, w_k , to represent relative model weights across candidate models, M_k for $k = 1, \dots, L$, and describe a model averaged posterior distribution for total run as:

$$P(\hat{N}|data) = \sum_{k=1}^L w_k P(\hat{N}|data, M_k) \quad (7)$$

DIC weights were calculated as:

$$w_k = \frac{e^{-0.5\Delta DIC_k}}{\sum_{k=1}^L e^{-0.5\Delta DIC_k}} \quad (8)$$

where ΔDIC_k is the difference between the DIC of model k and the lowest DIC model in the set of models considered (also see Supplemental Text 2).

2.7. Sensitivity analysis

We assessed the sensitivity of the Bayesian model averaged estimate of total run size, the primary model output of interest, to the

selection of priors by inflating variance parameters for Normal priors by 50% and by reducing the rate parameters for Gamma priors by 50% (see Table 1) in the models for Λ and n . In addition, we reduced the rate parameter for the Gamma hyperprior on $1/\varepsilon_p^2$ in the hierarchical model for p by 50% and changed priors for the pooled and constant p models to Uniform(0,1). To reduce computing time, we decreased the number of chains from five to three for sensitivity runs.

3. Results

3.1. Overall model results

In most cases, fitted models successfully converged, although we found it necessary to increase chain lengths for models fit to chum salmon data to 1.5×10^6 with a burn in length of 1.25×10^6 iterations to achieve Gelman–Brooks–Rubin \hat{R} statistics < 1.1 for tracked parameters. We suspect slow convergence resulted from confounding between probability of detection parameters, p , and those involved with the probability of becoming available for detection, Λ , as indicated by correlation plots between posterior draws for fitted models (not shown). In general, most parameters were identified, exhibiting substantial differences between marginal posterior distributions and their respective vague priors, with the exception of the variances on hyperdistributions: $\varepsilon_{\lambda\mu}^2$, $\varepsilon_{\lambda\sigma}^2$, ε_p^2 , and ε_n^2 . This result is not unexpected as these hyperdistribution (or “random effect”) variances were estimated with very few data points. For example, ε_p^2 , the variance for the distribution describing variation in probability of detection across recovery strata, was estimated from only three strata. We recommend that future sampling designs to implement a time stratified Lincoln–Petersen estimator employ shorter but more numerous tagging and recovery strata. Some estimates of run size within release strata exhibited posterior distributions with long right hand tails. Estimation problems with a few specific parameters appeared to have remained localized as we achieved successful estimates for other parameters of

interest, in particular the derived quantity total run size, \hat{N} , which in all cases exhibited a bell shaped posterior. Furthermore, posterior predictive checks suggested that all but two models fitted to chum salmon data adequately described the observed tag recovery data (Table S2). Model averaged total run size estimates were robust to the sensitivity analysis trials which modified prior specifications (Table S3).

Estimates of the parameters for the lognormal distributions describing travel time between release and recovery strata and subsequent availability for detection indicate long travel times. Most models estimated a mean travel time between the release site and the recovery grounds in the range of $e^{4.0} \pm 55$ to $e^{4.5} \pm 90$ days (Tables S4–S6), which is on the order of the same length of time as the entire mark–recapture study. These parameter estimates include consideration for animals that never become available for detection, for example if they died en route to recovery areas or spawned in areas not surveyed for carcasses, and manifest as low probabilities of availability for detection in any given recovery stratum. Thus, they are not directly meaningful for estimating actual travel times between release and recovery locations with this study design, rather these variables specify values for the nuisance parameters describing the probability animals become available for detection.

3.2. Chum salmon

Models fit to chum salmon data successfully converged. However, models P–C–H and P–C–S resulted in Bayesian posterior predictive p -values close to zero for two metrics, indicating these models could not adequately explain the tag recovery data (Table S2). As a result, these models were excluded from subsequent inference. DIC based multimodel inference suggests relative support for models with a “pooled” structure for the parameters describing lognormal distributions for travel times. Estimates of the probability of detection, p_j , are relatively stable over the recovery strata, fluctuating around approximately 0.3–0.6 (Table S4 and Fig. 1a). Estimates for the location and spread parameters of the lognormal distributions describing travel times between release and recovery strata indicated a slight increasing trend over release strata for μ_{λ_i} and a decreasing trend for σ_{λ_i} estimates (Table S4; Fig. 2a and d). Combining the probability animals become available for detection and the probability of detection in a recovery stratum, model estimates suggest the effective probability of capture ($\lambda_{ij}p_j$) declined through time (Fig. 3a). Estimates of run size within release strata do not suggest an obvious run curve and place many fish coming through in the last release stratum. Tag release data provide another index for run timing at the release site because tagging effort was approximately constant through time and in contrast to the run timing pattern estimated by the model, these data show a peak in release stratum three (Tables S1 and S4; Fig. 4a). It is possible that with a small number of release strata and sparse tag-release-recovery data, the time stratified Lincoln Petersen models as parameterized here do not have adequate power to resolve run timing curves; we conducted a brief trial of the time stratified estimator fit to simulated data with a larger number of recovery strata and higher tagging and recovery rates and found that the model can successfully describe a run timing curve (Supplemental Text 3). Furthermore, Bonner and Schwarz (2011) and Mäntyniemi and Romakkaniemi (2002) were able to successfully reconstruct run timing curves when using data on out-migrating smolts with a study design that had greater than 40 release and 40 recovery strata.

For the purposes of the present application, total run size is the primary quantity of interest. \hat{N} estimates were insensitive to model construction (Table 2). The model averaged estimate using DIC weights was 54,720 salmon in the upper river with a 95% credibility interval of 40,860–79,073. Model estimates indicate that effective

probability of capture declined through time, and in fact the traditional pooled Lincoln–Petersen estimate of total run size above river km 19 (Chapman variant; Seber, 2002) was 46,596 fish with a 95% confidence interval (parametric bootstrap method simulating the number of recaptured tags as hypergeometric; Buckland and Garthwaite, 1991) of 37,164–58,719, considerably lower than model averaged estimate from the Bayesian implementation of the time stratified estimator. The more complicated Bayesian model comes at a cost of precision with a 95% credibility interval that is approximately $\pm 35\%$ of the point estimate, whereas the traditional pooled estimator has a 95% confidence interval width of approximately $\pm 23\%$.

3.3. Coho salmon

All models fit to coho salmon data successfully converged and posterior predictive checks failed to identify lack of fit for any models (Table S2). Multimodel inference indicates support for a range of model structures, with relatively greater support for models with a “simple” structure for the probability of detection (Table 2) and relatively low support for models with the “constant” probability of detection model. Estimates of the probability of detection indicate an increasing detection trend through time (Table S5 and Fig. 1b). Estimates of the lognormal mean and spread parameters which determine probability of availability for detection are stable across release strata (Table S5 and Fig. 2b and e). Mean travel time estimates are higher than those for chum or sockeye, around $e^{4.5}$ or approximately 90 days, indicating that many coho that passed the tagging area never became available for recovery detection. Field observations of coho salmon spawning behavior in the Matanuska River (Anderson and Bromaghin, 2009) support this result and indicate that a substantial number of coho spawn in the far upper reaches of the watershed, bypassing spawning areas in the middle river where carcass surveys were conducted for the mark–recapture abundance study and where most chum and sockeye spawn. Estimates of the effective probability of capture (Fig. 3b) indicate an increasing trend across recovery strata. Similar to the chum results, estimates of run size by release strata were imprecise (Tables S1 and S5 and Fig. 4b). The model averaged total run size above river km 19 was estimated at 11,430 salmon with a 95% credibility interval of 8170 to 17,011 (Table 2), an approximate width of $\pm 39\%$. In contrast, in the face of capture probability heterogeneity, the traditional pooled Lincoln–Petersen estimate is lower at 10,591 salmon with a 95% confidence interval of 8049 to 14,021, an approximate width of $\pm 28\%$.

3.4. Sockeye salmon

Models fit to sockeye salmon data successfully converged, and posterior predictive checks failed to identify a lack of fit for any candidate model (Table S2). DIC weights suggest relative support for a range of models with no obvious preference identified for a particular structure for the component models for Λ , p , and n . Estimates of the probability of detection are high, on the order of 0.6–0.7, and stable across recovery strata (Table S6 and Fig. 1c). Similarly, most models estimated relatively constant parameters for the lognormal travel time distributions (Table S6 and Fig. 2c and f). In contrast to chum and coho, estimates of the effective probability of capture ($\lambda_{ij}p_j$) for sockeye are relatively stable across time (Fig. 3c), although capture probabilities in the first recovery stratum ranged widely. Estimates of release-stratum specific run sizes are imprecise but suggest a peak run in release stratum four, which is consistent with tag release data (Tables S1 and S6; Fig. 4c). The model averaged total run size above river km 19 was estimated at 13,750 salmon with a 95% credibility interval of 10,470–18,010, an approximate width of $\pm 27\%$ (Table 2). In this case, the traditional

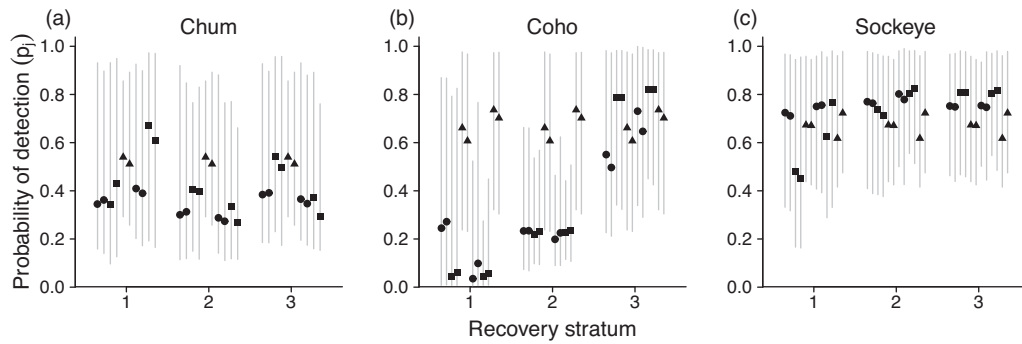


Fig. 1. Point estimates (posterior medians) and 95% credibility intervals for probability of detection, p_j , for a suite of models fitted to Matanuska River 2009 mark–recapture data for Pacific salmon. The order of points from left to right within each stratum correspond to the model structures outlined in the main text as follows: H–H–H, H–H–S, H–S–H, H–S–S, H–C–H, H–C–S, P–H–H, P–H–S, P–S–H, P–S–S, P–C–H, P–C–S. Models P–C–H and P–C–S did not pass the validation phase for chum salmon and are not shown. Circles indicate models with a “hierarchical” structure for p_j , squares indicate a “simple” model structure, and triangles, a “constant” model structure.

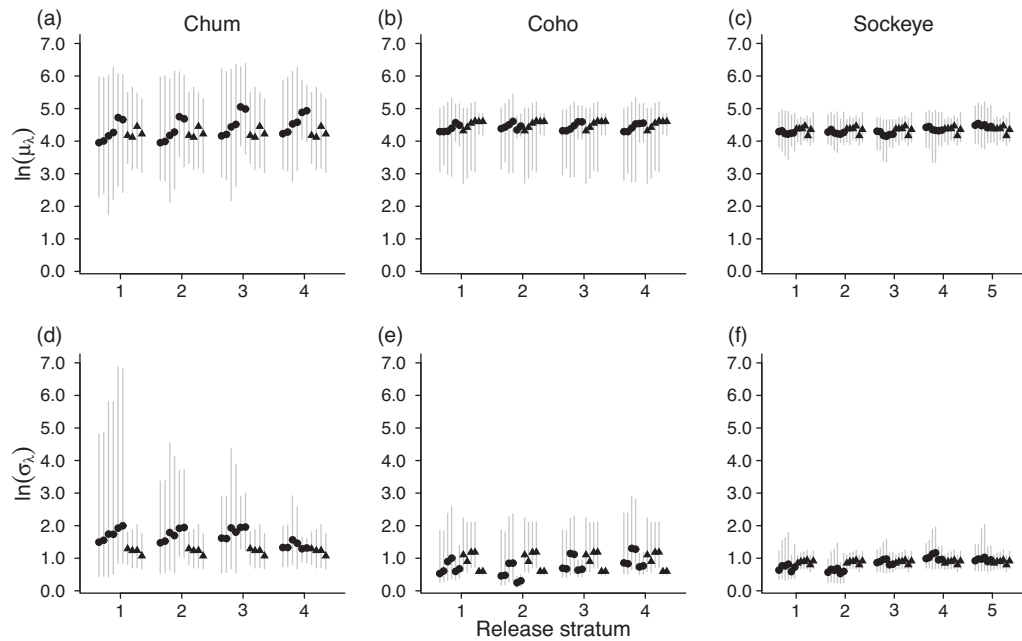


Fig. 2. Point estimates (posterior medians) and 95% credibility intervals for the mean, μ_λ , and spread, σ_λ , parameters for the lognormal distributions which describe travel times within release strata for a suite of models fitted to Matanuska River 2009 mark–recapture data for Pacific salmon (chum, a and d, coho, b and e, sockeye, c and f). The order of points from left to right within each stratum correspond to the model structures outlined in the main text as follows: H–H–H, H–H–S, H–S–H, H–S–S, H–C–H, H–C–S, P–H–H, P–H–S, P–S–H, P–S–S, P–C–H, P–C–S. Models P–C–H and P–C–S did not pass the validation phase for chum salmon and are not shown. Circles indicate models with a “hierarchical” structure for μ_λ and σ_λ , whereas triangles indicate a “pooled” model structure.

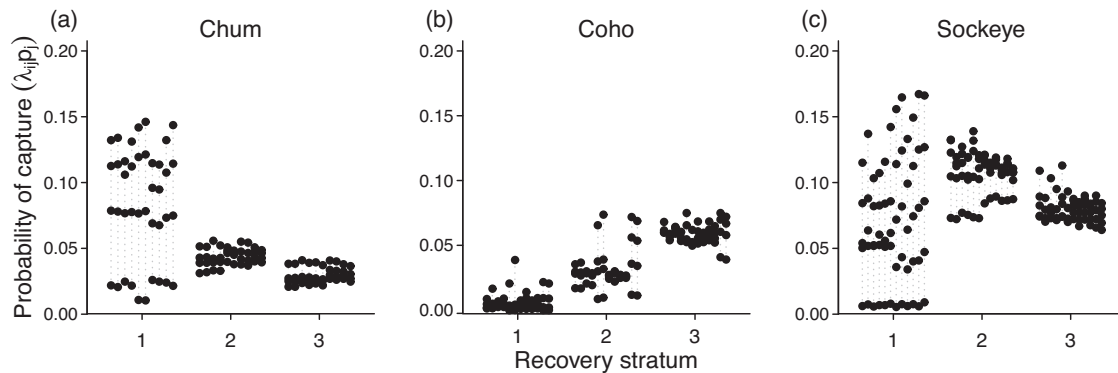


Fig. 3. Point estimates (posterior medians) of the effective probability of capture, $\lambda_{ij}p_j$, in recovery strata for a suite of models fitted to Matanuska River 2009 mark–recapture data for Pacific salmon. Each model estimates a set of s (number of release strata) effective probabilities of capture for each recovery stratum corresponding to $\lambda_{ij}p_j$ for $i = 1, \dots, s$ release strata; sets of capture probabilities are connected by dashed vertical lines. For example, each model fitted to chum data estimates $s = 4$ probabilities of capture for the first recovery stratum representing groups of fished released on one of four release strata that become available for capture during the first recovery stratum: $\lambda_{11}p_1$, $\lambda_{21}p_1$, $\lambda_{31}p_1$, and $\lambda_{41}p_1$. The order of sets of points from left to right within each stratum correspond to the model structures outlined in the main text as follows: H–H–H, H–H–S, H–S–H, H–S–S, H–C–H, H–C–S, P–H–H, P–H–S, P–S–H, P–S–S, P–C–H, P–C–S. Models P–C–H and P–C–S did not pass the validation phase for chum salmon and are not shown.

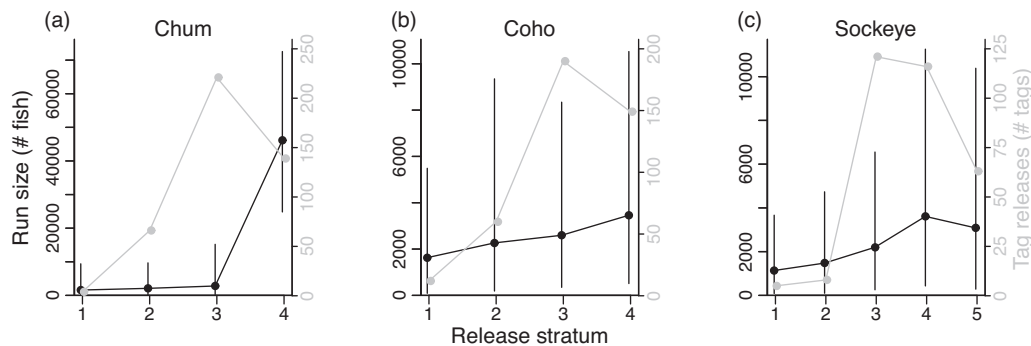


Fig. 4. Model averaged point estimates (posterior medians) and 95% credibility intervals of run size by release stratum (black points and lines, left axis) and tag releases (gray points and lines, right axis) for a suite of models fitted to upper Matanuska River 2009 mark–recapture data for Pacific salmon.

pooled Lincoln–Petersen estimate is quite similar with a point estimate of 13,530 salmon, only 1.6% lower than the time stratified model averaged estimate, and a 95% confidence interval of 11,231 to 16,495, an approximate width of $\pm 19\%$. The agreement between the pooled versus the time stratified Lincoln–Petersen point estimates is consistent with the estimates of stable effective probability of capture across time (Fig. 3c).

4. Discussion

Bayesian modeling in WinBUGS allows for a wide range of time stratified Lincoln–Petersen models to be formulated, including random effect structures, and models with parameters as functions of covariates. In the present application, Bayesian implementation of the time stratified Lincoln–Petersen estimators successfully generated abundance estimates of Pacific salmon populations that could accommodate (time-varying) capture heterogeneity in an application with few tag release and recovery strata and sparse data. In contrast, initial attempts to fit these data in a maximum likelihood frequentist framework using the DARR 2.0 software program (Bjorkstedt, 2005) resulted in pooling of tag release and recovery strata to overcome sparse data optimization issues that effectively reduced the time stratified estimator to a pooled Lincoln–Petersen estimator (results not shown).

The time stratified models highlighted capture heterogeneity for chum and coho salmon, resulting in abundance estimates that were 17% and 8% higher (median value of the model averaged estimate from the Bayesian time stratified model versus the Chapman pooled Lincoln–Petersen point estimate), respectively, than the potentially biased pooled Lincoln–Petersen estimates. The model complexity of the time stratified estimators, however, raises several disadvantages relative to the straightforward pooled Lincoln–Petersen estimator. First, Bayesian implementation of time stratified models requires knowledge of complex programs to implement MCMC algorithms, such as WinBUGS used here, and possibly knowledge of other programming languages to write custom MCMC routines or to digest MCMC output, such as R. Second, Bayesian model fitting is time consuming, requiring programming of model structures and validation procedures, as well as substantial computing time to run multiple parallel chains in an MCMC routine. Finally, the more complicated time stratified models result in less precise, albeit potentially more accurate, abundance estimates compared to the simple pooled estimator. The pooled estimator on the other hand is trivial to calculate and if statistically valid, more efficient than a stratified estimator (Darroch, 1961; additional performance testing of the time-stratified and pooled Lincoln–Petersen estimators are provided in Supplemental Text 4). For these reasons, design-based approaches to satisfy the pooled Lincoln–Petersen model assumptions and control for capture heterogeneity in the

field such as attempts to tag in proportion to abundance or conducting separate abundance estimates stratified by sex or some other demographic characteristic associated with tagging or recovery behavior will continue to be important tools to estimate salmon abundance. In cases where the sources of capture heterogeneity are unknown, when field-based controls of capture heterogeneity are not feasible, such as releasing a constant number of tags each release stratum (Supplemental Text 4), or when accuracy is of primary importance, for example when ground-truthing an abundance index such as sonar counts for salmon, the more complicated time stratified estimators may be a good choice.

These estimates of spawning abundance are applicable to the portion of the Matanuska River above river km 19. Salmon have been documented spawning in clear water side channels associated with the glacial braided plain that dominates the lower river habitat below km 19 (Curran et al., 2011; R. Hulbert unpublished documentation available at <http://conserveonline.org/workspaces/matsusalmonsymposium>, last accessed February 4, 2013), however, no abundance estimates are available for this portion of the river. Approximately one half of the river-wide cumulative length of clear water side channels occurs below the tagging site (Curran et al., 2011), suggesting that the lower river run may support salmon populations comparable to upper river runs sizes. However, upper river radio river radio telemetry results suggests that species display different preferences for spawning habitat locations (Anderson and Bromaghin, 2009) and we caution that a direct inflation of species-specific upper river run sizes based upon clear water side channel spawning habitat availability may not be appropriate.

By many accounts, the glacial Matanuska River is a harsh environment for spawning salmon with regular scouring events, high suspended sediment loads, and rapidly changing river morphology (Curran et al., 2011). In spite of this, the 2009 abundance estimates demonstrate that the glacial Matanuska River supports moderately sized chum and coho runs, and a smaller sockeye run. These observations corroborate recent studies of glacial rivers in high latitude systems which demonstrate that salmon are exceptional at finding suitable spawning habitat in glacial rivers, utilizing clearwater side channels as well as glacially silted locations in mainstem reaches (e.g. Anderson and Bromaghin, 2009; Curran et al., 2011; Young and Woody, 2007).

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.fishres.2013.02.004>.

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