

Juvenile Chinook Salmon Life History Variation: Improved Methods for Migration
Monitoring in a Wilderness Environment

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Authorization to Submit Thesis

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Abstract

Over the last century, wild populations of salmonids in the Columbia River basin have significantly declined. Several of these populations have been listed as “threatened” under the Endangered Species Act and collaborative multi-state, multi-agency efforts have been established to manage and restore at-risk populations. A thorough understanding of a species’ life history is necessary for effective conservation. A tool widely implemented to collect information during juvenile salmonid life stages is a rotary screw trap. Rotary screw traps sample juvenile salmonids as they migrate to the ocean but environmental conditions, low species abundances, and complex life histories can lead to sparse data. In this study I implemented a hierarchical Bayesian model to obtain abundance estimates from rotary screw traps with large periods of missing data and utilized this information to explore two predominant life history assemblages of juvenile Chinook salmon that have strong implications on survival and reproductive success.

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Dedication

I would like to dedicate this work to my two grandfathers, Donald Oldemeyer and Alden Homes. These men directly and indirectly helped instill the love and passion I have for the outdoors and largely shaped the person I have become today. Whether it was taking the time to teach a squirrely eight year old how to tie flies, supervising three brothers while they made bows and arrows from willows, or driving us grandkids into the sagebrush steppe to explore in the dust and shrubs; these men loved and appreciated the outdoors and passed that love and appreciation on to all of their children and grandchildren. Their vibrant personalities that brought countless hours of laughter, love, and life-lessons will not be forgotten.

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Chapter 1: Incorporating recurring juvenile salmonid migratory trends in a hierarchical Bayesian model to obtain abundance estimates from sparse and missing mark-recapture data.

1. INTRODUCTION

To effectively monitor or manage a species, information on survival rate, population growth rate, and recruitment are needed to understand mechanisms influencing a population (Fryxell et al 2014). To calculate this demographic information, it is often required to know abundances of individuals during various life stages but obtaining censuses of natural populations of fish and wildlife can be difficult (Seber 2002). Studies structured around sighting, capturing, or counting individuals and extrapolating these counts based on detection or sampling efficiencies are often implemented to estimate abundances when censuses are not feasible (Nichols 1992; Skalski and Robson 2012). These types of mark-recapture studies have been applied to estimate abundances of blue and humpback whales (Calambokidis and Barlow 2004), grizzly bear (Mowat and Strobeck 2000), herbivorous insects (Kareiva 1983), and numerous other species where marked individuals released into the population can be detected during later sampling periods.

In the most basic scenarios, mark-recapture studies require only two sampling events; one event to capture, mark, and release marked individuals into the population and a second event to recapture marked and unmarked individuals (Bailey 1951; Skalski and Robson 2012). By knowing the number of marked individuals released into the population and the number of marked and unmarked individuals captured during the proceeding sampling

period, the Lincoln-Petersen (L-P) estimator can be applied to calculate sampling efficiencies and population abundance estimates (Nichols 1992; Skalski and Robson 2012).

The L-P estimator is foundational for calculating abundances from mark-recapture data and has been widely implemented to calculate juvenile salmonid abundances from mark-recapture data collected at rotary screw traps (RSTs) (Zabel et al 2005; Venditti et al 2012; Copeland et al 2013). Rotary screw traps are passively operating traps that sample anadromous juvenile salmonids during their migration to the ocean (Johnson et al 2007). Since 1990, 153 RSTs have been deployed in the Columbia River basin with several RSTs operating for over 20 years (PSMFC 2015). Abundance estimates obtained from RST data are used to determine survival rates of juvenile salmonids, smolt-to-adult returns, and production of juvenile out-migrants (Venditti et al 2012; Copeland et al 2014). This demographic information is central for monitoring salmonid populations in the Columbia River basin and is often used to inform conservation actions (Venditti et al 2012; Copeland et al 2013).

Juvenile salmonid abundance estimates acquired using basic (e.g. pooled) L-P estimators from RST data can be inundated with violations of model assumptions, primarily the assumption of homogenous capture probabilities throughout the sampling period (Bonner and Schwarz 2012; Mäntyniemi and Romakkaniemi 2002). Juvenile salmonid migrations can span several weeks to several months (Groot and Margolis 1991) during which capture probabilities at the RST are likely to change due to environmental variables (e.g. discharge) or behavioral changes within a species (e.g. size of an individual affecting trap avoidance)

(Roper and Scarnecchia 2000; Tattam et al 2013). Because of this heterogeneity in capture probability during the migratory period, pooling data across the migratory period for L-P estimation can produce biased estimates (Nichols 1992). Sampling periods are often stratified temporally into smaller, more homogenous groups to minimize the violation of the capture probability assumption (Otis et al. 1978; Schwarz and Taylor 1998). Darroch (1961) was the first to implement this stratification approach in a maximum likelihood framework under the condition that equivalent numbers of mark and recapture strata occur. Darroch's (1961) time-stratified L-P estimator was later modified to accommodate varying amounts of mark and recapture strata and variations in the probability that an individual would be available for recapture during proceeding strata (Schwarz and Dempson 1994; Banneheka et al. 1997; Plante et al. 1998). These modifications broadened the application of the L-P estimator when sufficient data were available but stratifying sparse data frequently led to issues of division by zero when individuals were not recaptured and produced biased estimates when data were sparse (Seber 2002). To avoid issues associated with sparse data, several methods to pool adjacent strata with similar capture probabilities have been proposed (Bjorkstedt 2000) but tests of capture probability homogeneity between adjacent strata typically have low power due to small sample sizes. In addition, there are not standardized criteria for when pooling is appropriate (Bonner and Schwarz 2012).

Another approach to address missing data is to modify the stratified L-P estimator to eliminate issues of division by zero (Bailey 1951; Chapman 1951; Evans and Bonett 1994).

These modifications allow for point estimates to be obtained but the precision around these estimates are largely unknown. Combinations of manually pooling strata, pooling strata using specified algorithms, and modifying the L-P estimator to avoid division by zero are common strategies implemented by state, federal, and tribal agencies to obtain abundance estimates from RST data (Bjorkstedt 2000; Steinhorst et al 2004). Recent advances in computing power, Markov-chain Monte Carlo (MCMC) algorithms, and access to large data sets have made hierarchical Bayesian approaches an effective alternative for obtaining abundance estimates when data are poor, sparse, or contain variable capture efficiencies (Mackey et al 2008; Royle et al 2011; Sethi and Tanner 2013).

The Bayesian paradigm provides a flexible framework to incorporate prior biological knowledge of a species into models using hierarchal structures between parameters and by specifying informative prior distributions (Ellison 2004). When prior biological information is available, structuring models to incorporate this information can produce more accurate, and potentially more precise, estimates when data are sparse or missing (Royle and Dorazio 2008). Mäntyniemi and Romakkaniemi (2002) implemented a hierarchical Bayesian model to estimate Atlantic Salmon smolt abundances while accounting for overdispersion associated with the schooling behavior for this species in the Conne River, Canada, and the Tornionjoki, Scandinavia. Bonner and Schwarz (2011) increased the precision and accuracy of abundance estimates of Conne River Atlantic Salmon smolts by parameterizing the expected abundances of smolts as a smooth function of time using penalized Bayesian splines (p-splines). The p-spline smoothing function allowed information

between neighboring strata to be “shared” under the assumption there were temporal associations between adjacent strata. This approach increased the precision and accuracy of abundance estimates, particularly when data were sparse or missing, but had difficulty producing abundance estimates for our applications of several populations of “threatened” salmonids in Idaho that exhibited large periods of missing data (upwards of several weeks of missing data in some years).

To obtain estimates for populations missing large periods of data during the migratory period, I structured a hierarchical Bayesian model that utilized the recurring salmonid run characteristics expressed by juvenile Chinook salmon in Idaho. The number of unmarked fish passing the RST and their capture probabilities were parameterized using a stratified between year hierarchy, enabling strata with missing data to interpolate information from previous years of data during the same time period. This approach increased the accuracy and precision of estimates during large periods of missing data while incorporating the appropriate uncertainty about these estimates.

The goal of this study was to illustrate how four common hierarchical Bayesian models performed when calculating abundance estimates from mark-recapture data exhibiting varying degrees of sparse and missing data. I ran competing models on simulated data sets with known parameters representative of RST data found in Idaho and compared model parameter estimates to the known parameters used to create the simulated data. The models were then run on juvenile Chinook salmon data collected at Marsh Creek and Big Creek, Idaho to compare model estimates from real RST data.

2. METHODS

2.1 Sampling design and data

Mark-recapture protocol is fairly consistent between RSTs in Idaho. When a RST is in operation a trap tender removes captured fish from the holding box, salmonids are anesthetized, inspected for tags, and length and weights data are recorded (Johnson et al 2007). An allotted number of individuals are marked and released upstream of the RST (for a single trap design) or downstream (for a double trap design) to be recaptured during proceeding days. Rotary screw traps in Idaho typically operate from the beginning of the juvenile salmonid migratory season in early March to ice-up in November. The exact dates of RST installation and removal are dependent on yearly environmental conditions and trap sampling duration can vary by a week or two between years. In addition, unexpected ice, high water, and RST mechanical failures can hinder RST operations for several days to several weeks during a migration season.

Data collected at a RST consisted of the daily number of unmarked and marked fish captured, and the number of marked fish released the day prior. Bonner and Schwarz (2012) found that weekly stratification of RST mark-recapture data provided a sufficient balance between maintaining run characteristics while avoiding unnecessary data sparsity issues for their application in British Columbia under the assumption that capture probabilities were constant within the week. Because of this I opted to stratify year ($j = 1, \dots, t$) by ordinal week ($i = 1, \dots, s$). If capture probabilities were subject to high variability within weekly stratum, stratum size could be decreased to accommodate this. Weekly

stratification of the number of unmarked fish captured in the i th stratum in the j th year were denoted u_{ij} , the number of marked fish released in the i th stratum in the j th year n_{ij} , and the number of recaptured fish captured in the i th stratum in the j th year m_{ij} .

2.2 Statistical models

The likelihood function of the time-stratified L-P estimator implemented in the Bayesian framework consisted of two primary components: the probability an individual was captured at the RST and the estimated number of unmarked individuals passing the RST. The number of individuals recaptured in a stratum, m_{ij} , were binomially distributed by the number of marked individuals released upstream of the RST within the stratum, n_{ij} , and the probability that an individual passing the RST was captured, p_{ij} :

$$m_{ij} \sim \text{Binomial}(n_{ij}, p_{ij}) \quad (1)$$

Previous studies have modeled m_{ij} as a multinomial distribution incorporating an additional parameter describing the process of an individual's probability of being available for recapture during a later stratum (Mäntyniemi and Romakkaniemi 2002; Bonner and Schwarz 2011). To simplify our models and because most juvenile Chinook salmon (greater than 98%) recaptured at RSTs in our study did so within the proceeding day of upstream release, I chose to exclude this parameter. The likelihood of the model is complete when the number of unmarked individuals within a stratum, u_{ij} , is incorporated using the binomial distribution:

$$u_{ij} \sim \text{Binomial}(U_{ij}, p_{ij}) \quad (2)$$

where U_{ij} is the estimated number of fish passing the RST during the stratum. The assumptions of the time-stratified L-P estimator are as follows (Otis et al. 1978):

- 1) Individuals do not emigrate or die between marking and recapture,
- 2) Marks or tags are not shed,
- 3) Marks or tags are detected if present at recapture,
- 4) Marked and unmarked individuals within a stratum have the same probability of capture,
- 5) Individual movements within a stratum are independent,
- 6) Individuals passing or being released below the RST are emigrating downstream and remain below the RST.

2.3 Model set

I compared four models using the constructed likelihood components outlined above with different hierarchical parameter structures. The most basic model, M_{PS} , analyzed one year of data with a simple prior for U where $\log(U_i)$ shared identical normal priors with fixed mean and variance and p was pooled, $p_i = p$ for $i = 1, \dots, s$ across all strata. This model is closely related to the pooled frequentist L-P estimator in that capture probabilities, p_i , are structured to be pooled and constant across strata. The second model was composed of a hierarchical prior for both U and p that assigned $\log(U_i)$ and $\text{logit}(p_i)$ normal priors with common but unknown mean and variance. This hierarchical structure allowed information to be shared between strata within the year and the model is denoted M_{HW} . The third model is structured from Bonner and Schwarz (2011) but excludes the additional parameter

used to model the probability that an individual is available for recapture in proceeding strata. This model, M_{SPLINE} , uses the p-spline hierarchical prior for U to weight estimates using adjacent strata, effectively sharing information between adjacent strata within the year. A hierarchical prior for p assigned $\text{logit}(p_i)$ normal priors with common but unknown mean and variance was used for the M_{SPLINE} model. Our final model, M_{HB} , implements a hierarchical prior for U and p where $\log(U_{ij})$ and $\text{logit}(p_{ij})$ have a common and unknown mean within strata between years. By structuring the hierarchy between years, reoccurring run characteristics specific to each stratum (ordinal week for this study) were integrated into the model. Prior selection for the highest level of the model hierarchies were chosen to be vague and weakly informative in regards to their parameters and complete model structures can be found in table 1.1.

2.4 Simulated data

Eight data sets spanning ten years ($j = 10$) with thirty-five strata per year ($i = 35$) with known parameters U and p were constructed to represent various types of data collected from RSTs in Idaho (supplementary material S1.1). Parameters U_{ij} followed a smooth bimodal run with a small peak at strata 6 with the majority of the individuals centered around a peak at strata 29. This bimodal migratory pattern where the majority of a cohort begins emigration in the fall with the remainder of the cohort emigrating in the spring is a recurring process observed in most juvenile stream-type Chinook salmon populations in Idaho (Bjornn 1971).

Parameters p_{ij} were constant at 0.333 for strata 1 through 4 and 13 through 35, and 0.111 for strata 5 through 12. As discharge increases in the spring, RSTs are often relocated out of

the thalweg to slower portions of the river transect to avoid large debris and decrease mechanical stress on the sampling equipment. In addition, as discharge increases the relative amount of water sampled by RSTs decreases. These conditions often decrease trap efficiencies and are the justification for the decreased capture efficiencies for strata 4 through 12 in our simulated data. The number of marked individuals, n_{ij} , released in each stratum was equivalent to the number of unmarked individuals captured, u_{ij} , up to 50 individuals. The 50 individual restriction was implemented to mimic tag and handling permit constraints common when dealing with threatened or fragile species at RSTs.

The simulated data set constructed from the parameters listed above was denoted as “Full” due to the completeness across the migratory years and was used as the baseline data set for subsequent data sets. The second data set is identical to the Full data set with the exception of information from strata 5 through 8 in the first year being removed. This four stratum exclusion mimics RST conditions when spring flows cease RST operation for several weeks. The next data set had information from strata 5 through 8 removed from the first year. Also, the number of marked and recaptured individuals was reduced by 60% across all strata and years. The 60% reduction typifies data for several RSTs that have low capture efficiency due to RST site limitations and (or) low species abundances. The last data set removed information from eight strata, strata 12 through 19, from the first year of the data set and had a 60% reduction across all marked and recaptured individuals across all strata and years. This modification mimics several projects that did not operate the RST during summer months because it was thought that salmonid migration had ceased. It was later

realized that small, but significant, numbers of individuals did migrate throughout the summer and RSTs now operate throughout this time period.

Four additional data sets were constructed that retained the first year of each previous data set but added stochasticity for the proceeding nine years of data (supplementary material S1.2 and S1.3). Stochasticity was added to U_{ij} by incorporating an error term that was normally (0,100) distributed, p_{ij} values for strata 1 through 4 and 13 through 35 where sampled from a beta(20,40) distribution and p_{ij} values for strata 5 through 12 where sampled from a beta(2.5,20) distribution. Only model M_{HB} was run on the stochastic data set because it is the only model that utilized multiple years of information.

2.5 Model diagnostics

The statistical program JAGS run through the program R interface with the RJAGS package was used to compare the four time-stratified models (Plummer 2003; R Core Team 2015). The complexity of the models inhibited calculating an exact posterior distribution. As such, MCMC simulations were implemented in JAGS to create a representative posterior distribution where inference could be drawn. Three parallel chains initiated at random values were run for each model. Chains were run for a total of 500,000 iterations with the first 100,000 iterations discarded and the remaining iterations thinned by a factor of 100. The final sample size for each chain was 4,000 values. MCMC chain posterior distributions were visually inspected for multiple peaks and Gelman-Brooks test statistics were calculated to insure chain convergence. Multiple peaks in the posterior distribution or Gelman-Brooks

test statistics over 1.1 were subject to non-convergence and chains were run for additional iterations to try to achieve convergence.

2.6 Model performance

Model performance was evaluated on the parameter estimates produced for the first year of each data set compared to the known parameters used to simulate the data. Estimated median values and credible interval characteristics of posterior parameter distributions were examined to assess strata specific and yearly abundance estimates. Total yearly abundance estimates and corresponding credible intervals were calculated using a 50,000 iteration bootstrap of the posterior abundance distributions. Yearly model bias was measured by the difference of \hat{U}_{Tot} from the known U_{Tot} . Strata-specific accuracy was judged on the number of strata that included the known abundance parameter within the predicted 95% credible intervals.

2.7 Application

Abundance estimates were calculated for juvenile Chinook salmon during the 2014 migratory season at Marsh Creek and Big Creek, Idaho using the four competing models. Marsh Creek and Big Creek are tributaries to the Middle Fork of the Salmon River located in central Idaho that have varying degrees of data (figure 1.1). Marsh Creek is a third order tributary with a RST located at a river transect with morphology and hydrology conducive for the RST to operate through the majority of the migratory season with high capture efficiencies (Venditti et al. 2012). In addition, Marsh Creek RST was installed in 1993 and

has large populations of adult salmonids spawning upstream of the RST allowing for large samples of migrating juveniles to be captured (Venditti et al. 2012). The high capture efficiencies, abundant juvenile salmonids, and longevity of the study present a nearly ideal mark-recapture data set.

Big Creek is a fourth-order tributary located in the Frank Church River of No Return Wilderness. The RST was installed in 2007 and the restriction imposed by the wilderness designation limited RST site selection to wide stretches of river with widths varying from 30 to 40 meters resulting in low capture efficiencies (Copeland et al 2013). In addition, spring runoff regularly inhibited the RST from operating from 2-5 weeks in the spring while fish were presumed to be migrating out of the system. Big Creek RST data encompasses nearly all potential pit-falls present at traps operating in Idaho and obtaining accurate and precise population estimates for this RST has been difficult (Copeland et al 2013).

3. RESULTS

3.1 Simulated data results

All model scenarios had Gelman-Brooks test statistics < 1.1 and density plots that shared common distributions with the exception of the M_{PS} model estimating abundances with missing data. The M_{PS} model relied primarily on the vague prior U parameter distributions to construct posterior distributions when data were missing and MCMC algorithms required additional iterations (100,000) to find the highest density sample space and achieve Gelman-Brooks test statistics < 1.1 . The posterior U distributions obtained from missing

strata using the M_{PS} model were largely the product of the prior U distribution and added little relevant biological information to the study so these strata were removed from the analysis.

The pooled probability model, M_{PS} , produced the most accurate and precise estimates from the simulated data but these estimates can be misleading (table 1.2). When data were absent, posterior distributions from these strata were excluded from the analyses. This led to \hat{U}_{Tot} estimates for the simulated data sets missing four and eight strata to only incorporate information from 31 and 27 strata, respectively. Removing these strata should theoretically decrease \hat{U}_{Tot} estimates but the nature of the pooled capture probabilities overestimating \hat{U}_{Tot} coincidentally offset this bias. In addition, the extreme precision of the M_{PS} model relies on the assumption that capture probabilities are constant across all strata which was known not to be the case.

Model M_{HW} performed well with the Full data set with a \hat{U}_{Tot} median point estimate that was positively biased 516 with 95% CI that was 3,233 wide (Table 1.2). As strata were removed and data were reduced, \hat{U}_{Tot} estimates and uncertainty about these estimates greatly increased. This additional uncertainty can be attributed to the variability in the abundances and capture probabilities between strata within the year. The M_{SPLINE} model performed well with all simulated data sets with exception of the simulated data set missing eight consecutive strata. The hierarchical p-spline function failed to run when large periods of data were missing. The characteristics of the p-spline, primarily the interval of knot points, could have been altered to interpolate over additional U_i but would have led to a model

functionally similar to the pooled L-P estimator. The M_{HB} model had the most accurate \hat{U}_{Tot} median and was almost as precise as the M_{PS} model. As the quality of simulated data sets decreased, the within-year hierarchical structure was able to draw inference from previous years to supplement the missing and sparse data. When stochasticity was added to the additional nine years in the data sets, M_{HB} \hat{U}_{Tot} median estimates were largely unaffected but 95% CI widths increased. As between year variation increased, uncertainty of strata estimates from missing and sparse data increased as well.

All models with a hierarchical within-year p structure underestimated strata-specific true abundance parameters for strata 5 through 13. This phenomenon occurred for two reasons. The upper level p distributions were largely influenced by strata with more data (i.e. strata with a known p parameter of 0.333) and strata 5 through 13 were typically missing data or had such sparse data that the upper level hierarchical distributions of p outweighed strata-specific information.

3.2 Application results

Total population estimates for Marsh Creek were similar for all models (table 1.3). The M_{PS} model underestimated total population abundance relative to the other models and had the smallest 95% CI width. The total population abundance estimate for M_{PS} excluded potential fish migrating in ordinal weeks 11, 45, and 46 because strata with missing data were removed from the total population estimate. In addition, the M_{PS} model relies on the assumption that capture probabilities are constant across all weeks throughout the year and this condition is not likely satisfied due to fluctuating environmental conditions.

The M_{HW} model had the highest credible interval width with as nearly as much spread as the total population abundance estimate (table 1.3). Most of the uncertainty around the total population abundance estimate was acquired from strata with missing data. Posterior distributions for strata missing data using the M_{HW} model relied on capture probabilities and abundance characteristics from strata across the entire year to interpolate information. So as variability between strata within the year increased, uncertainty about these estimates for missing data increased as well. Models M_{HB} and M_{SPLINE} had nearly identical total population estimates with the M_{HB} model 95% CI width roughly 2,500 increments wider than the M_{SPLINE} model.

Big Creek total population estimates varied widely between models (table 1.3). The M_{PS} model estimated total population abundances using 28 out of the 37 strata due to missing data. Similar to Marsh Creek, the precision associated with the total population estimate for the M_{PS} model is dependent on the assumption of homogeneous capture probabilities throughout the year and is likely overstated in this application. The population estimate using the M_{HW} model was 216,291 with a credible width nearly double the point estimate. The uncertainty associated with estimates for missing data from the M_{HW} model were large and this was expressed in the total abundance 95% credible interval widths. The M_{SPLINE} model was not able to initiate due to the large number of consecutively missing data. As mentioned previously, p-spline characteristics could have been modified to pool across more strata but was out of the scope of this study. The M_{HB} model produced a \hat{U}_{Tot} of 148,110 with a 95% credible intervals width of 120,131. The Big Creek RST started operating

in 2007 so it was a relatively small data set compared to other RST data sets. In addition, the RST had low capture efficiencies and regularly did not operate from two to five weeks during spring high-water. This led several ordinal weeks in the spring to have only been sampled once or twice since the installation of the trap in 2007. Little is known about run characteristics during these periods and the M_{HB} model estimates reflect that uncertainty.

4. DISCUSSION

It was evident from the simulation study and Marsh Creek analysis that when data were “good”, abundance estimates were similar between competing models with the exception of the M_{PS} model. As missing strata were introduced to data sets, the inherent assumptions implemented from the model structures began to alter the accuracy and precision of the parameter estimates. By incorporating the prior biological knowledge of the recurring run characteristics of juvenile Chinook salmon into our model using the between year hierarchy, I was able to address large periods of missing data and produce estimates during these periods by pulling information from previous years. One could imagine several situations where the M_{HB} model may not be the most appropriate for obtaining abundance estimates. If a RST was newly installed and there were several weeks the trap did not operate during the migratory year, the M_{HB} model would have no prior years of data to draw inference from and posterior parameter distributions of the missing weeks would be constructed strictly from the prior distributions. Or, if there were time periods during the migratory year that the RST was never able to operate (e.g. spring high-water periods), the M_{HB} model posterior distributions for the missing strata would again be the product of the prior

distributions. For these situations, it may be advantageous to implement the M_{SPLINE} model and allow the p-spline structure to interpolate the missing data using within-year information rather than between-year information.

The M_{PS} model has niche application for estimating abundances of natural populations of fish and wildlife due to limitations of model assumptions. Environmental conditions and species behavior can be highly variable during a mark-recapture sampling period, and similar to the pooled L-P estimator, violations of the assumption of homogenous capture probabilities across a sampling period can lead to biased and overly precise estimates (Seber 2002). Where the assumption of this model can be satisfied, the simplicity of the M_{PS} model makes it an ideal candidate for obtaining abundance estimates.

Several estimators implemented by state, tribal, and federal agencies used to obtain abundance estimates of salmonids at RSTs do not provide an effective method for addressing missing data (e.g. Copeland et al 2013; Venditti et al 2012). Steinhorst et al (2004) stratified model implements a bootstrap approach to calculate confidence intervals and is effective at calculating abundance estimates when at least seven individuals are recaptured per stratum, sampling periods do not contain missing time periods, and stratified sampling periods have homogenous capture probabilities. Trying to satisfy all of these conditions at once can be difficult with sparse RST data and satisfying one condition often leads to issues with others. For example, to obtain homogenous capture probabilities within a stratum, sampling periods may need to be stratified into 2-day or 4-day periods. With sparse data, fine scale stratification can lead to stratum with low or no recaptures. To

avoid this, stratum are often aggregated together again under the untestable assumption that capture efficiencies are comparable between aggregated stratum. Software DARR (Darroch Analysis with Rank Reduction, Bjorkstedt 2002) uses a series of algorithms to aggregate strata without recaptures into adjacent strata tests the similarity of capture probabilities between adjacent strata, and pools adjacent strata with similar capture probabilities (Bjorkstedt 2000). This approach attempts to optimize the balance between satisfying model assumptions while maintaining fine resolution run characteristics but often results in a pooled estimator when data are sparse (Sethi and Tanner 2013). In addition, neither of these approaches account for periods when the RST is not able to operate but individuals are likely to be migrating, leading to negatively biased estimates.

The flexibility of hierarchical Bayesian models allow for additional covariates to be incorporated in the model. So long as there are biological foundations for these hierarchies and inclusions, covariates such as discharge, temperature, previous year redd counts, or previous year adult abundances, may help explain between year variability (example code for the M_{HB} model with the inclusion of two covariates is available in the supplementary material). An area of our on-going research is constructing a model that incorporates data from multiple species with different life history strategies into a single hierarchical model to obtain estimates when abundances of one species is extremely sparse. With appropriate assumptions, this multi-species model could be a powerful approach to obtain information for threatened and endangered species that have extremely low abundances and consequently low numbers of recaptures.

The use of hierarchical Bayesian models to calculate abundance estimates with sparse and missing data, while incorporating the appropriate uncertainty around estimates is a substantial advancement in population ecology (Royle and Dorazio 2008). However, these models have several disadvantages compared to maximum likelihood estimators. The complexity of hierarchical models do not allow for an exact posterior distribution to be calculated so advanced programs such as JAGS, BUGS, STAN, or knowledge on how to write custom MCMC algorithms, are required to create representative posterior distributions to draw inference (Mackey et al 2008; Royle et al 2011; Sethi and Tanner 2013). In addition, running complex hierarchical Bayesian models can be time consuming, computationally intensive, and validation procedures are not as straight forward as other statistical approaches. For these reasons, it is recommended that study designs strive to achieve the assumptions required for simpler estimator models and complex models be implemented when simpler model assumptions cannot be met.

The accuracy and precision of estimates will be conditional on the inherent assumptions associated with the structure of the model (Royle and Dorazio 2008). The simulation study in this paper belabored that point and it was apparent that dependent on the model, corresponding statistics produced from the same data could vary considerably. Because of this, it is recommended that the inherent assumptions associated with the selected models be consistent with expert biological knowledge of the species behavior.

The models in this paper have broad application to fish and wildlife studies that employ mark-recapture approaches to obtain population abundance estimates, particularly when

addressing issues of sparse or missing data. Others have implemented similar approaches to calculate adult salmonid abundance estimates in Alaska (Sethi and Tanner 2013), survival estimates of harbour seals in Scotland (Mackey et al 2008), and wolverine densities in Alaska (Royle et al 2011) using hierarchical Bayesian models to address data sparsity issues. In this study, I was able to produce abundance estimates for federally listed populations of threatened and endangered salmonids in Idaho that were previously inundated with issues of violations of model assumptions and sparse data by using a hierarchical model that incorporated the prior biological information about the species migratory characteristics.

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6. TABLES

Table 1.1. Model structures and prior distributions for the pooled p and simple U model (M_{PS}), hierarchical p and hierarchical U within year model (M_{HW}), hierarchical p and Bayesian penalized spline U model (M_{SPLINE}), and hierarchical p and hierarchical U between year model (M_{HB}).

Model	Structure
M_{PS}	Low level: $\log(U_i) \sim \text{Normal}(\text{mean} = 10, \text{variance} = 4)$ $\text{logit}(p) \sim \text{Normal}(\text{mean} = -2, \text{variance} = 1.5)$
M_{HW}	Low level: $\log(U_i) \sim \text{Normal}(\text{mean} = \eta_{iU}, \text{variance} = \varepsilon_{iU}^2)$ $\text{logit}(p_i) \sim \text{Normal}(\text{mean} = \eta_{ip}, \text{variance} = \varepsilon_{ip}^2)$ Hierarchical component: $1/\varepsilon_{iU}^2 \sim \text{Gamma}(\text{shape} = .001, \text{rate} = .001)$ $\eta_{iU} \sim \text{Normal}(\text{mean} = 10, \text{variance} = 4)$ $1/\varepsilon_{ip}^2 \sim \text{Gamma}(\text{shape} = .001, \text{rate} = .001)$ $\eta_{ip} \sim \text{Normal}(\text{mean} = -2, \text{variance} = 1.5)$
M_{SPLINE}	Low level: $\log(U_i) \sim \text{Normal}(\text{mean} = \sum_{k=1}^K b_k B_k(i), \text{variance} = \varepsilon_{iU}^2)$ $\text{logit}(p_i) \sim \text{Normal}(\text{mean} = \eta_{ip}, \text{variance} = \varepsilon_{ip}^2)$ Hierarchical component: $\varepsilon_{iU}^2 \sim \text{Normal}(\text{mean} = 0, \text{rate} = \varepsilon_U^2)$ $1/\varepsilon_U^2 \sim \text{Gamma}(\text{shape} = 1, \text{rate} = .05)$ $b[1] \sim \text{Uniform}(\text{alpha} = -\infty, \text{beta} = \infty)$ $b[2] \sim \text{Uniform}(\text{alpha} = -\infty, \text{beta} = \infty)$ $b[k] \sim \text{Normal}(\text{mean} = b_k + (b_k - b_{k-1}), \text{variance} = \varepsilon_b^2)$ $1/\varepsilon_b^2 \sim \text{Gamma}(\text{shape} = 1, \text{rate} = .05)$ $1/\varepsilon_{ip}^2 \sim \text{Gamma}(\text{shape} = .001, \text{rate} = .001)$ $\eta_p \sim \text{Normal}(\text{mean} = -2, \text{variance} = 1.5)$

Table 1.1 Continued

Model	Structure
M_{HB}	<p>Low level:</p> $\log(U_{ij}) \sim \text{Normal}(\text{mean} = \eta_{iU}, \text{variance} = \varepsilon_{iU}^2)$ $\text{logit}(p_{ij}) \sim \text{Normal}(\text{mean} = \eta_{ip}, \text{variance} = \varepsilon_{ip}^2)$ <p>Hierarchical component:</p> $\eta_{iU} \sim \text{Normal}(\text{mean} = \eta_U, \text{variance} = \varepsilon_U^2)$ $1/\varepsilon_{iU}^2 \sim \text{Gamma}(\text{shape} = .001, \text{rate} = .001)$ $\eta_U \sim \text{Normal}(\text{mean} = 10, \text{variance} = 4)$ $1/\varepsilon_U^2 \sim \text{Gamma}(\text{shape} = .001, \text{rate} = .001)$ $\eta_{ip} \sim \text{Normal}(\text{mean} = \eta_p, \text{variance} = \varepsilon_p^2)$ $1/\varepsilon_{ip}^2 \sim \text{Gamma}(\text{shape} = .001, \text{rate} = .001)$ $\eta_p \sim \text{Normal}(\text{mean} = -2, \text{variance} = 1.5)$ $1/\varepsilon_p^2 \sim \text{Gamma}(\text{shape} = .001, \text{rate} = .001)$

Table 1.2. Total yearly abundance estimate (\hat{U}_{Tot}), bias from true U_{Tot} parameter of 23477, standard deviation, 95% credible interval, absolute credible interval width, and the number of strata abundance 95% credible intervals ($U_i = 35$) that covered the true U_i parameter for the first year of each simulated data set produced by the four competing models. Data labeled “Full” had a complete 10 year, 35 strata per year, data set. Data “4 strata” were missing strata 5 through 8 from the first year. Data “4 strata 60% reduction” were missing strata 5 through 8 from the first year and had a 60% reduction in the number of marked and recaptured individuals across all years and strata. Data “8 strata 60% reduction” were missing strata 11 through 18 from the first year and had a 60% reduction in the number of marked and recaptured individuals across all years and strata. Stochastic data sets retained the first year from each of the prior data sets and added stochasticity to the proceeding nine years. Strata with missing data were excluded from the analysis for the M_{PS} model.

Models	Data	\hat{U}_{Tot}	Bias	SD	95% CI	CI width	% CI width	Strata coverage
M_{PS}	Full	25944	2467	339	(25214, 26685)	1561	6	12
	4 strata***	23059	-418	317	(22455, 23682)	1227	5	27
	4 strata 60% reduction***	24205	728	463	(23351, 25163)	1812	7	30
	8 strata 60% reduction***	26640	3163	588	(25528, 27841)	2313	9	11
M_{HW}	Full	24020	543	822	(22484, 25717)	3233	13	28
	4 strata	24492	1015	4178	(22412, 35035)	12623	52	31
	4 strata 60% reduction	23934	457	4725	(21771, 34895)	13124	55	31
	8 strata 60% reduction	30541	7064	5433	(25780, 45167)	19387	63	29
M_{SPLINE}	Full	23993	516	1107	(21939, 26298)	4359	18	29
	4 strata	22659	-818	924	(20955, 24586)	3591	16	27
	4 strata 60% reduction	22697	-780	1328	(20401, 25606)	5205	23	27
	8 strata 60% reduction	NA	NA	NA	NA	NA	NA	NA
M_{HB}	Full	23245	-232	370	(22538, 23976)	1438	6	35
	4 strata	23216	-261	365	(22517, 23968)	1451	6	35
	4 strata 60% reduction	22509	-968	533	(21536, 23594)	2058	9	35
	8 strata 60% reduction	22552	-925	548	(21534, 23698)	2164	10	35
M_{HB} (Stochastic data)	Full	23937	460	749	(22555, 25494)	2939	12	35
	4 strata	24083	606	836	(22530, 25826)	3296	14	35
	4 strata 60% reduction	23713	236	810	(22272, 25470)	3198	13	35
	8 strata 60% reduction	24503	1026	810	(23037, 26216)	3179	13	35

***Posterior parameter distributions for strata missing data were removed from the analysis

Table 1.3. Total abundance estimate (\hat{U}_{Tot}), 95% credible intervals, absolute credible width, and percent credible interval width for rotary screw trap mark-recapture data collected at Marsh Creek and Big Creek, Idaho, in 2014 using the pooled-simple (M_{PS}), hierarchical within year (M_{HW}), hierarchical penalized spline (M_{SPLINE}), and hierarchical between year (M_{HB}) models. The three posterior abundance distributions produced from missing information in the Marsh Creek data set and the ten strata missing information from the Big Creek data set were removed from the M_{PS} model analyses.

Model	Marsh Creek				Big Creek			
	\hat{U}_{Tot}	95% CI	CI width	% CI width	\hat{U}_{Tot}	95% CI	CI width	% CI width
M_{PS}^{***}	104594	(103149, 106064)	2915	3	106141	(101856, 104729)	2873	3
M_{HW}	121718	(110295, 208526)	98231	81	216292	(154931, 584029)	425498	197
M_{SPLINE}	112299	(105910, 120212)	14302	13	NA	NA	NA	NA
M_{HB}	114035	(106991, 123920)	16929	15	148110	(119758, 239889)	120131	81

*** Posterior parameter distributions for strata missing data were removed from the analysis

7. FIGURES

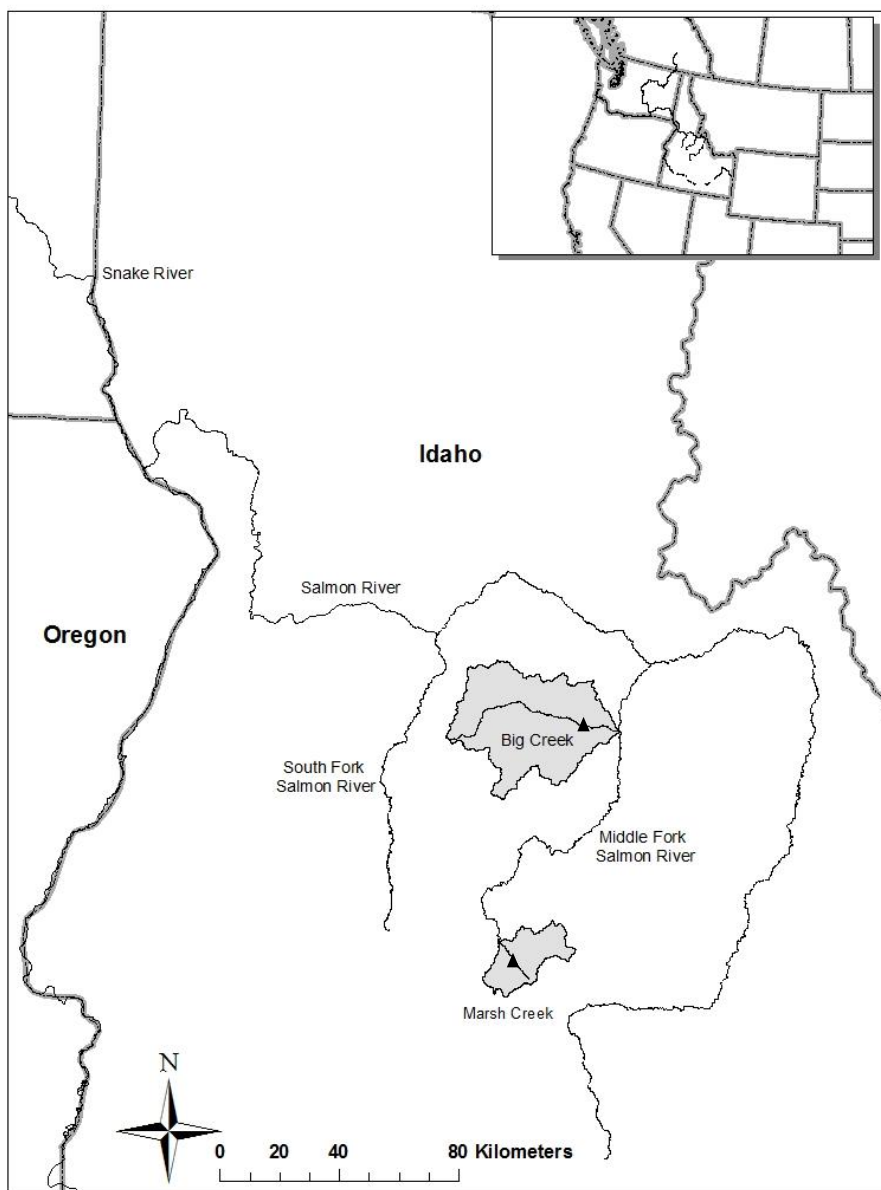


Figure 1.1 Big Creek and Marsh Creek watersheds located in Idaho, USA. Triangles represent rotary screw trap location within the watersheds.

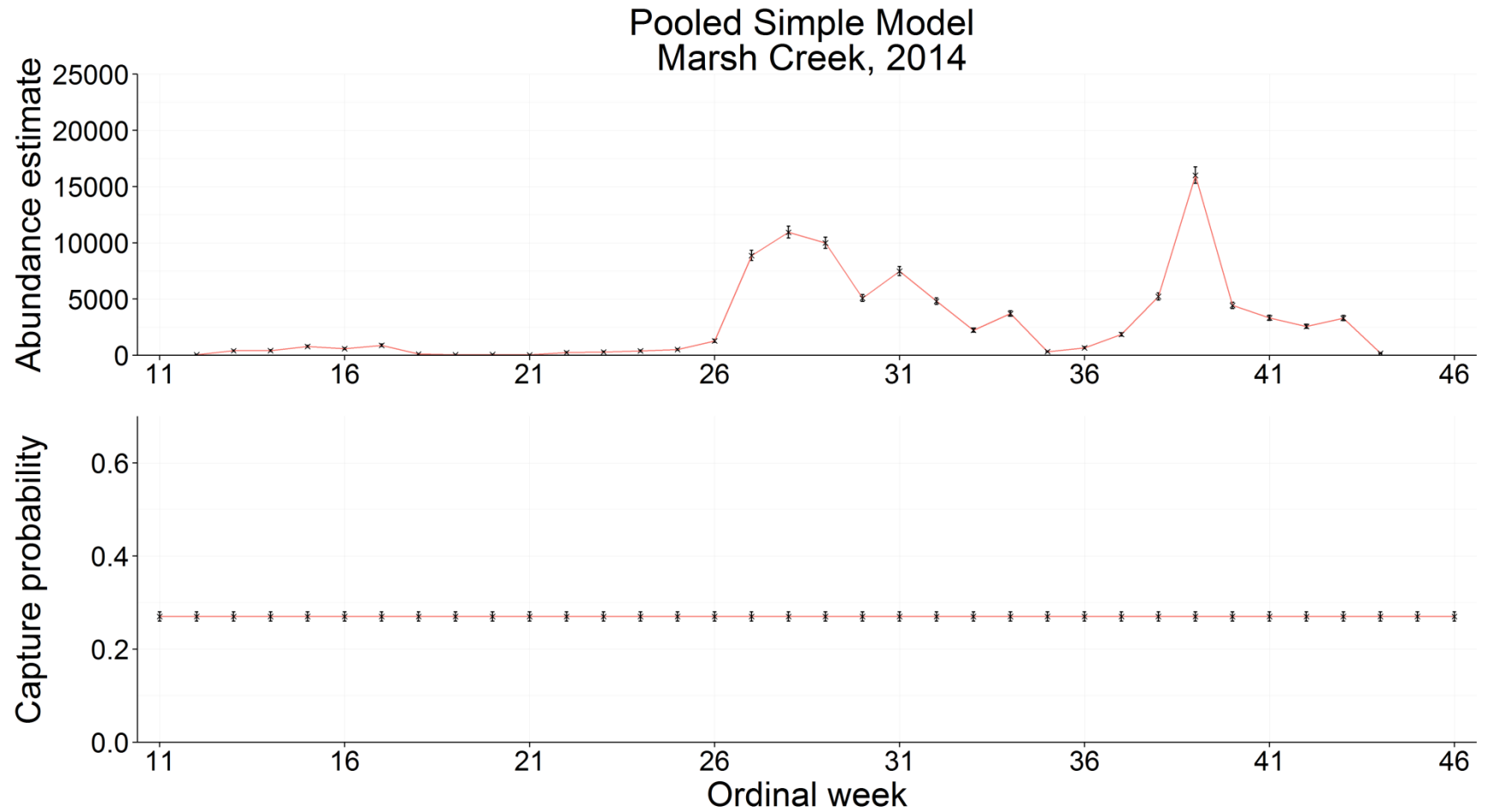


Figure 1.2. Weekly abundance estimates of juvenile Chinook salmon from data collected at a rotary screw trap from Marsh Creek, ID, 2014, using the M_{PS} model. Ordinal week 11, 45, and 46 were removed due to missing strata. Weekly abundance point estimates represent the posterior medians and the error bars represent the 95% credible intervals.

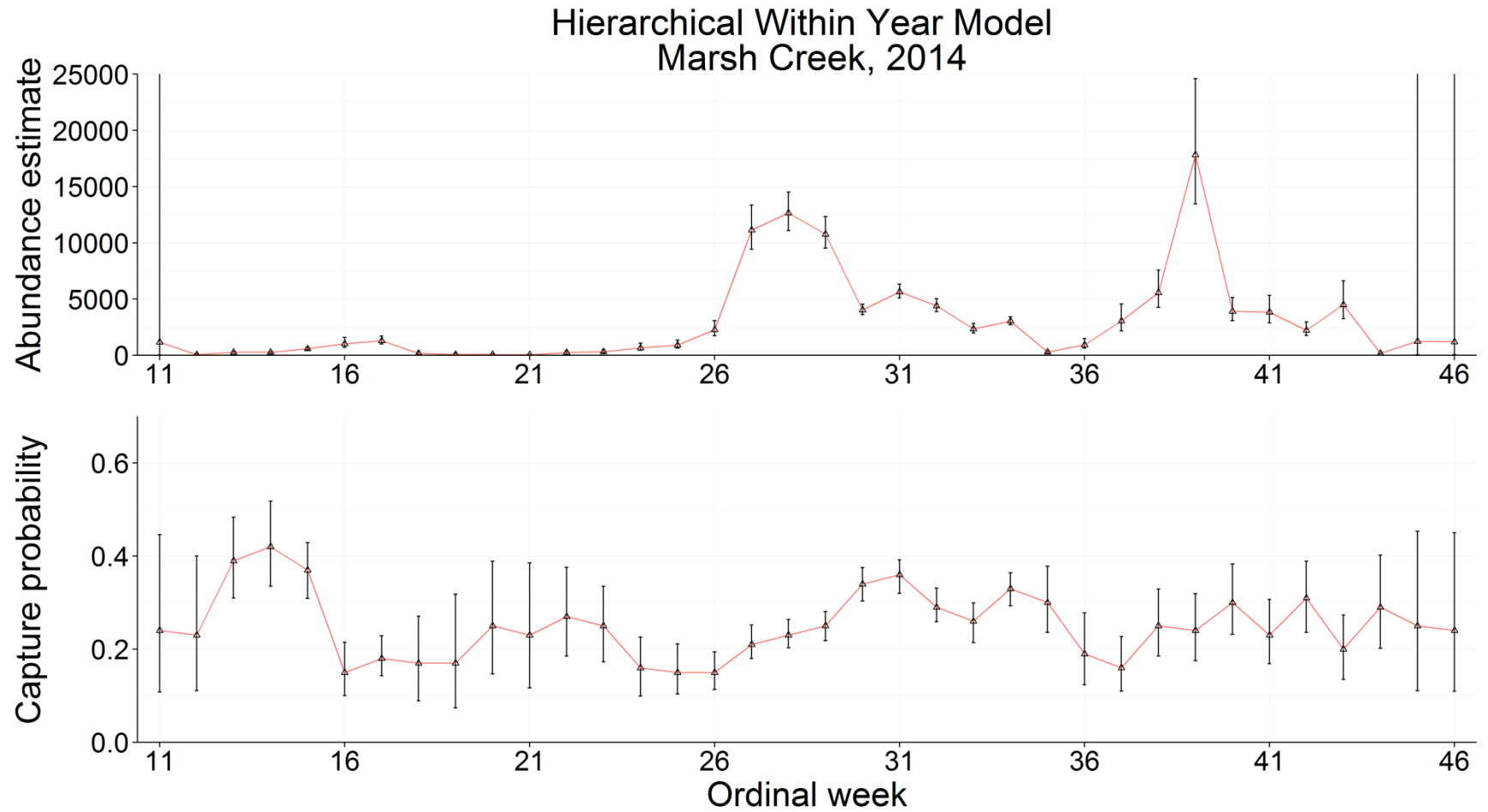


Figure 1.3. Weekly abundance estimates of juvenile Chinook salmon from data collected at a rotary screw trap from Marsh Creek, ID, 2014, using the M_{HW} model. Weekly abundance point estimates represent the posterior medians and the error bars represent the 95% credible intervals.

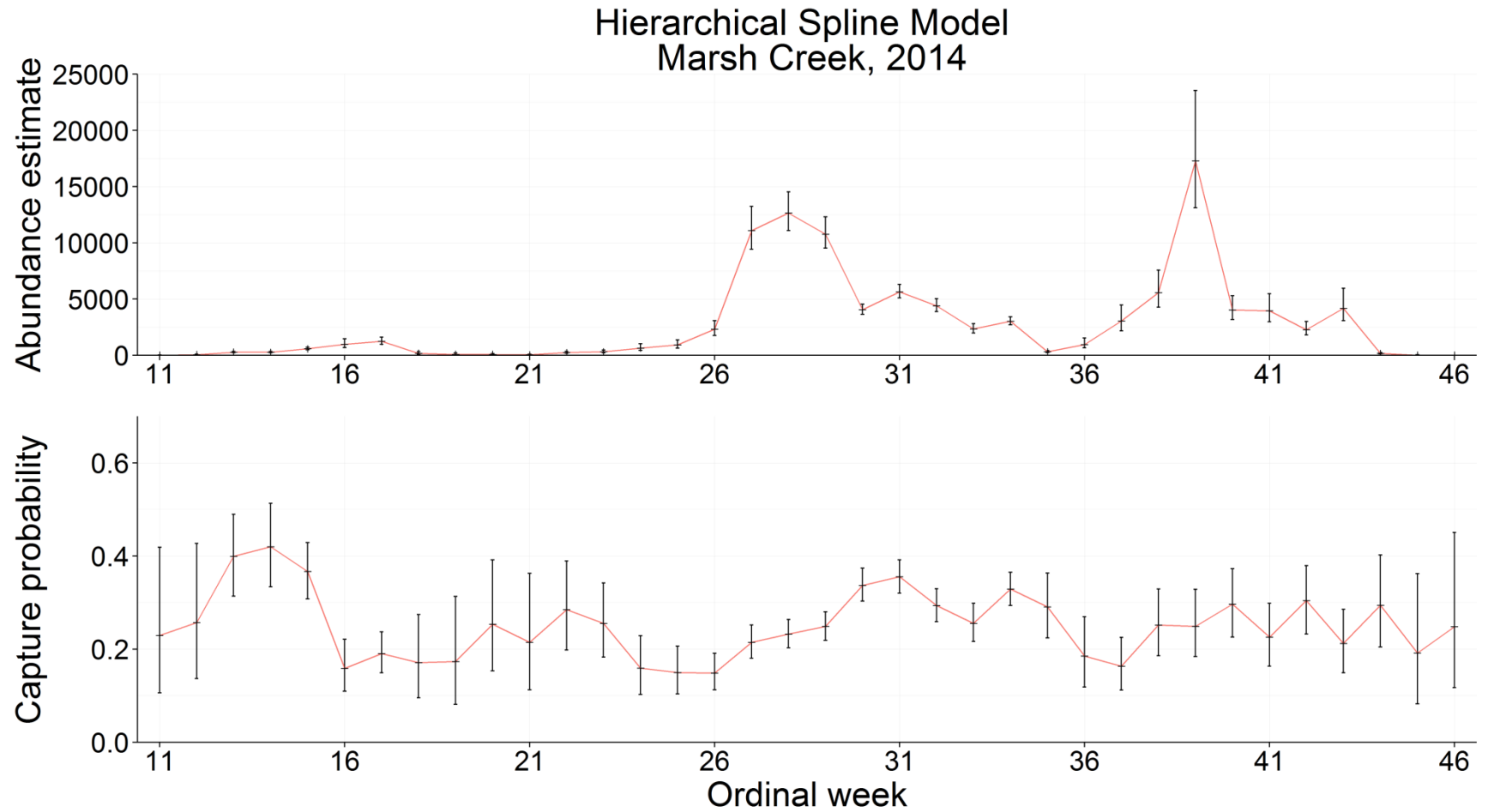


Figure 1.4. Weekly abundance estimates of juvenile Chinook salmon from data collected at a rotary screw trap from Marsh Creek, ID, 2014, using the M_{SPLINE} model. Weekly abundance point estimates represent the posterior medians and the error bars represent the 95% credible intervals.

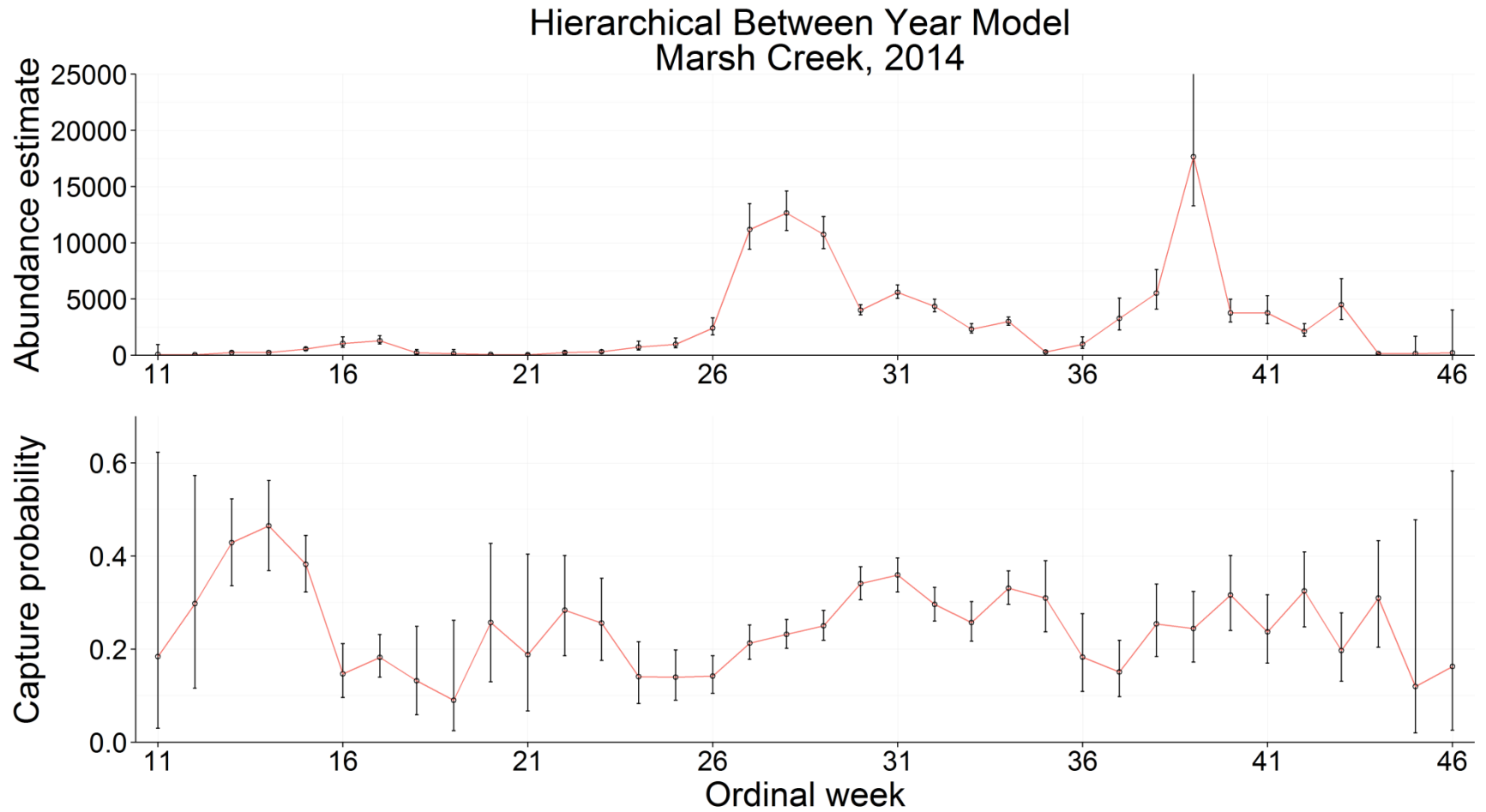


Figure 1.5. Weekly abundance estimates of juvenile Chinook salmon from data collected at a rotary screw trap from Marsh Creek, ID, 2014, using the M_{HB} model. Weekly abundance point estimates represent the posterior medians and the error bars represent the 95% credible intervals.

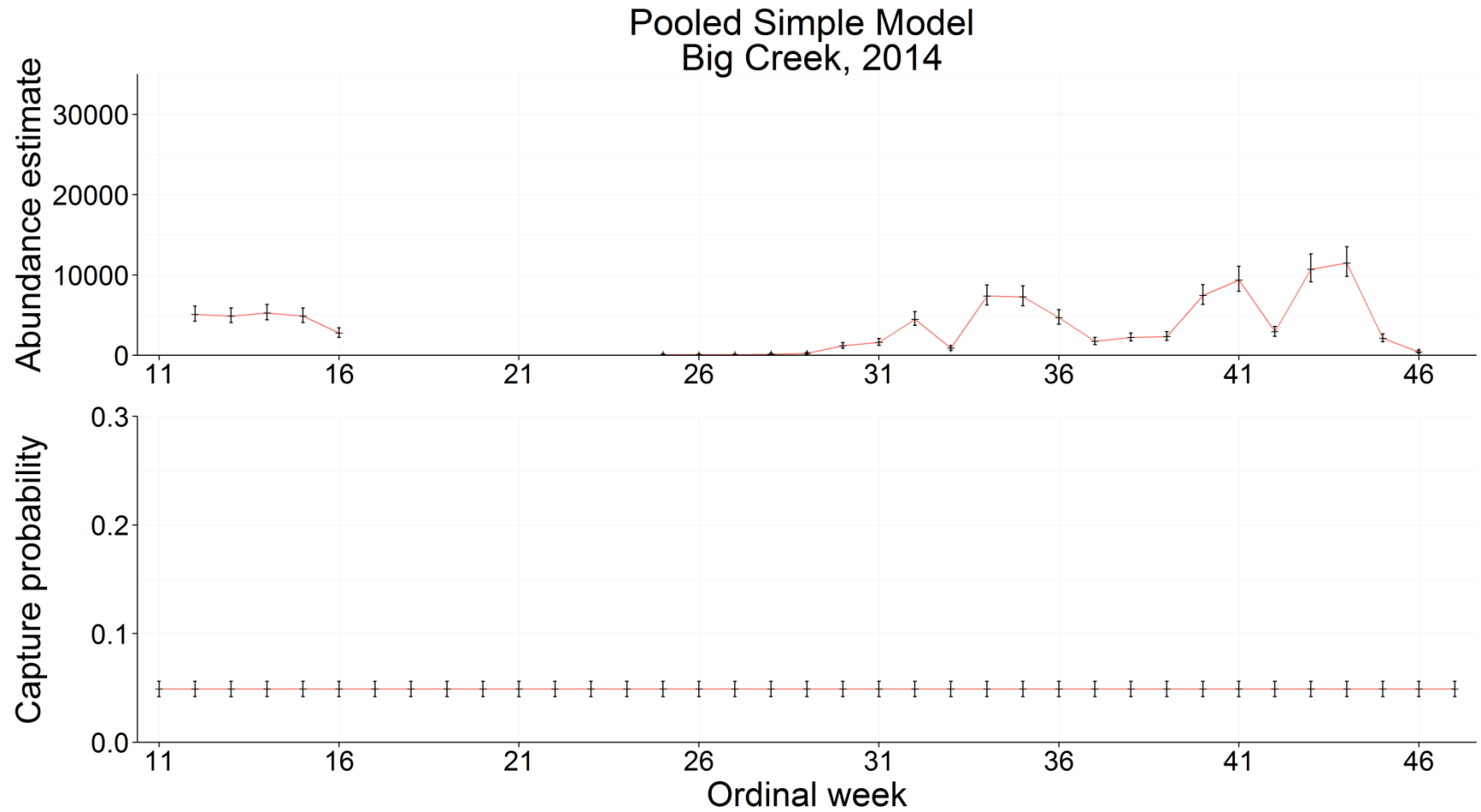


Figure 1.6. Weekly abundance estimates of juvenile Chinook salmon from data collected at a rotary screw trap from Big Creek, ID, 2014, using the M_{PS} model. Ordinal weeks missing data were removed from the study. Weekly abundance point estimates represent the posterior medians and the error bars represent the 95% credible intervals.

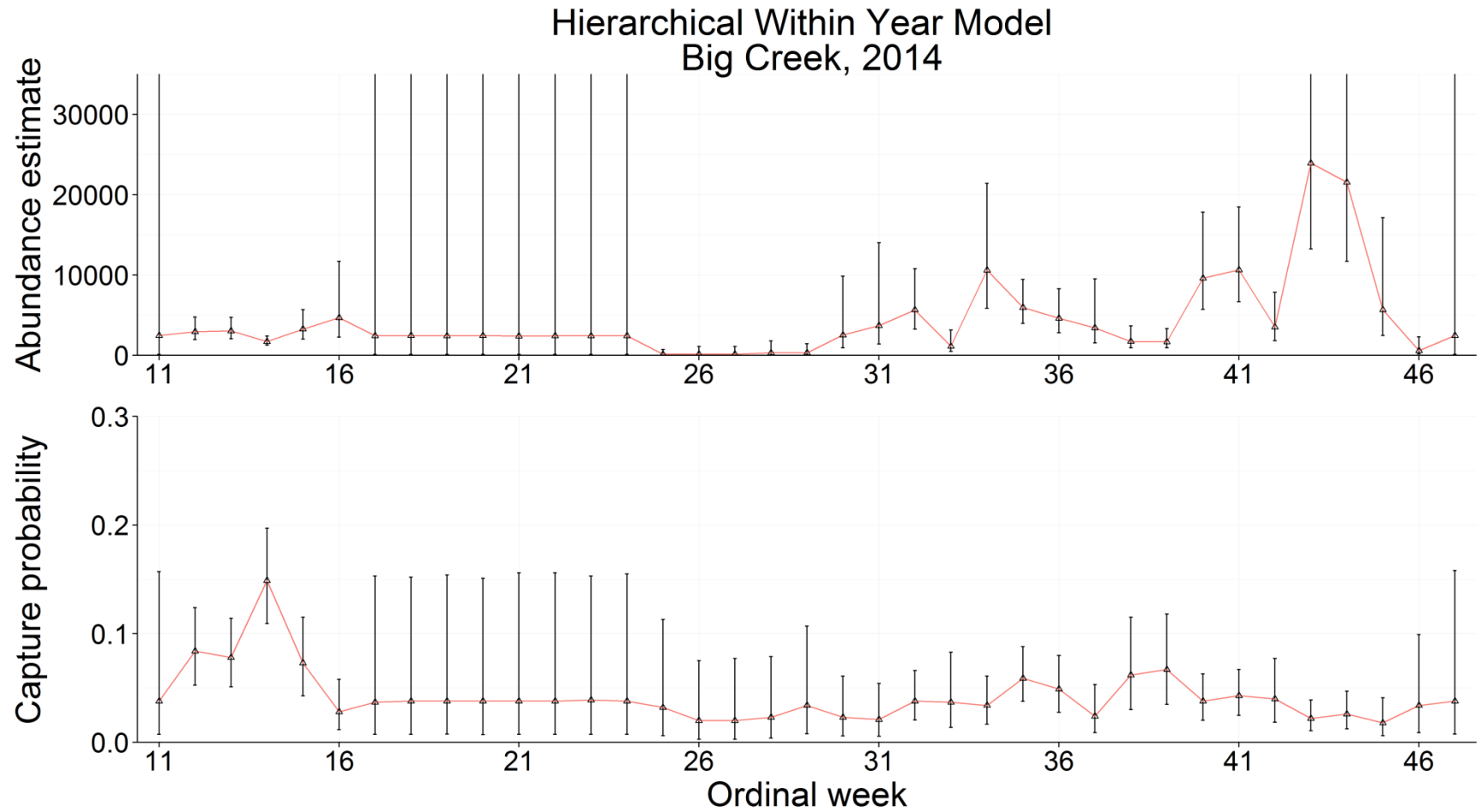


Figure 1.7. Weekly abundance estimates of juvenile Chinook salmon from data collected at a rotary screw trap from Big Creek, ID, 2014, using the M_{HW} model. Weekly abundance point estimates represent the posterior medians and the error bars represent the 95% credible intervals.

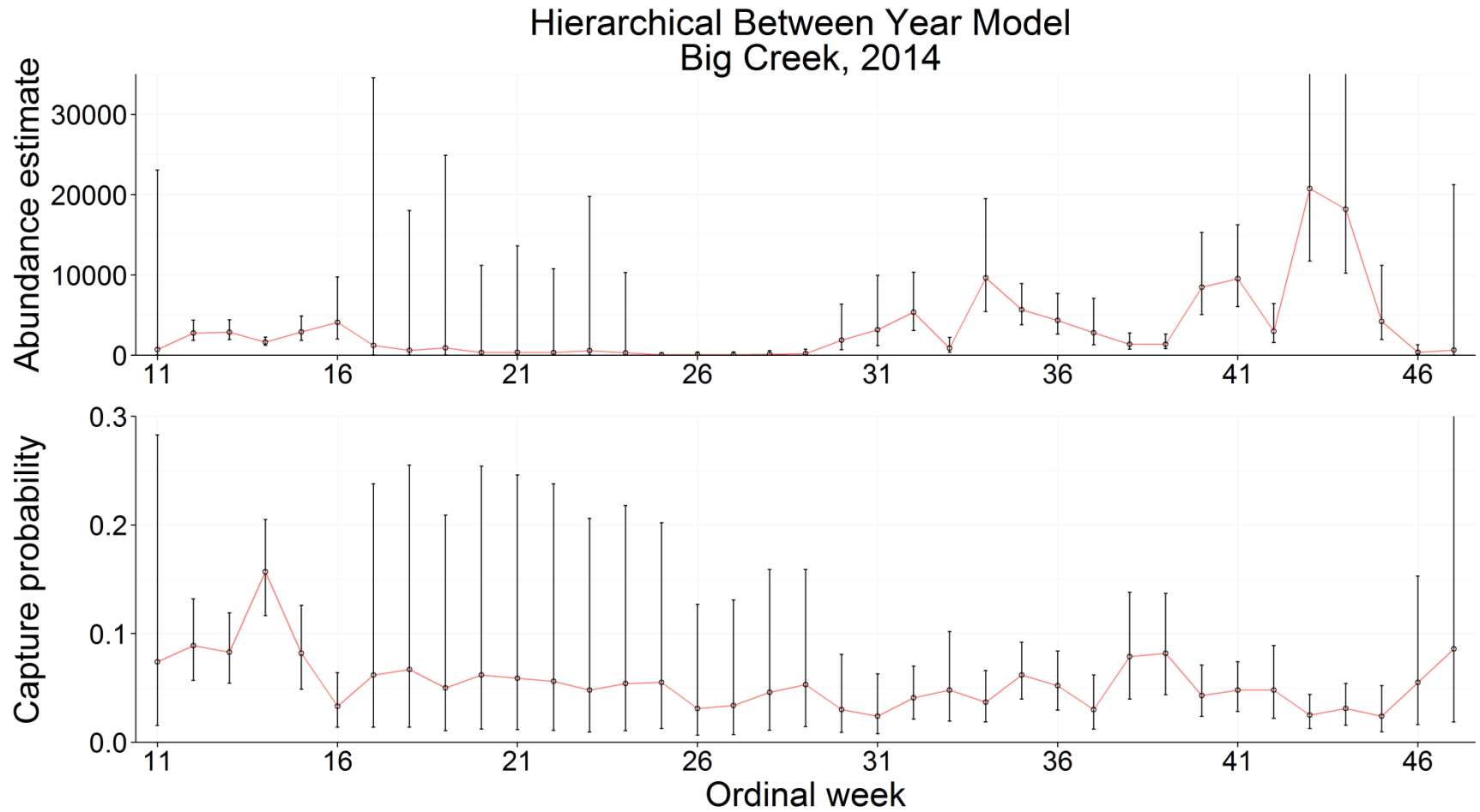


Figure 1.8. Weekly abundance estimates of juvenile Chinook salmon from data collected at a rotary screw trap on Big Creek, ID, 2014, using the M_{HB} model. Weekly abundance point estimates represent the posterior medians and the error bars represent the 95% credible intervals.

8. SUPPLEMENTARY MATERIALS

Table S1.1 The known parameters U and p used to produce the number of individuals caught, u , the number of individuals released upstream, n , and the number of individuals recaptured, m , for the first year of each simulated data set.

Strata	Known parameters		First year of data set											
			Full			4 strata			4 strata 60% reduction			8 strata 60% reduction		
	U	p	u	n	m	u	n	m	u	n	m	u	n	m
1	132	0.3333	44	44	15	44	44	15	44	18	6	44	18	6
2	157	0.3333	52	50	17	52	50	17	52	20	7	52	20	7
3	231	0.3333	77	50	17	77	50	17	77	20	7	77	20	7
4	376	0.3333	125	50	17	125	50	17	125	20	7	125	20	7
5	546	0.1111	61	50	6	NA	NA	NA	NA	NA	NA	61	20	2
6	625	0.1111	69	50	6	NA	NA	NA	NA	NA	NA	69	20	2
7	546	0.1111	61	50	6	NA	NA	NA	NA	NA	NA	61	20	2
8	376	0.1111	42	42	5	NA	NA	NA	NA	NA	NA	42	17	2
9	231	0.1111	26	26	3	26	26	3	26	10	1	26	10	1
10	157	0.1111	17	17	2	17	17	2	17	7	1	17	7	1
11	132	0.1111	15	15	2	15	15	2	15	6	1	NA	NA	NA
12	150	0.1111	17	17	2	17	17	2	17	7	1	NA	NA	NA
13	150	0.3333	50	50	17	50	50	17	50	20	7	NA	NA	NA
14	150	0.3333	50	50	17	50	50	17	50	20	7	NA	NA	NA
15	150	0.3333	50	50	17	50	50	17	50	20	7	NA	NA	NA
16	150	0.3333	50	50	17	50	50	17	50	20	7	NA	NA	NA
17	150	0.3333	50	50	17	50	50	17	50	20	7	NA	NA	NA
18	150	0.3333	50	50	17	50	50	17	50	20	7	NA	NA	NA
19	150	0.3333	50	50	17	50	50	17	50	20	7	50	20	7
20	150	0.3333	50	50	17	50	50	17	50	20	7	50	20	7
21	424	0.3333	141	50	17	141	50	17	141	20	7	141	20	7
22	620	0.3333	207	50	17	207	50	17	207	20	7	207	20	7
23	884	0.3333	295	50	17	295	50	17	295	20	7	295	20	7
24	1200	0.3333	400	50	17	400	50	17	400	20	7	400	20	7

Table S1.1 continued

Strata	Known parameters		First year of data set											
			Full			4 strata			4 strata 60% reduction			8 strata 60% reduction		
	U	p	u	n	m	u	n	m	u	n	m	u	n	m
25	1536	0.3333	512	50	17	512	50	17	512	20	7	512	20	7
26	1838	0.3333	613	50	17	613	50	17	613	20	7	613	20	7
27	2049	0.3333	683	50	17	683	50	17	683	20	7	683	20	7
28	2125	0.3333	708	50	17	708	50	17	708	20	7	708	20	7
29	2049	0.3333	683	50	17	683	50	17	683	20	7	683	20	7
30	1838	0.3333	613	50	17	613	50	17	613	20	7	613	20	7
31	1536	0.3333	512	50	17	512	50	17	512	20	7	512	20	7
32	1200	0.3333	400	50	17	400	50	17	400	20	7	400	20	7
33	884	0.3333	295	50	17	295	50	17	295	20	7	295	20	7
34	620	0.3333	207	50	17	207	50	17	207	20	7	207	20	7
35	424	0.3333	141	50	17	141	50	17	141	20	7	141	20	7

Table S1.2 The number of individuals caught, u , the number of individuals released upstream, n , and the number of individuals recaptured, m , for years 2 through 5 of each stochastic simulated data set.

Strata	Known parameters		Stochastic data											
	U	p	Year 2			Year 3			Year 4			Year 5		
			u	n	m	u	n	m	u	n	m	u	n	m
1	132	0.3333	53	50	16	75	50	17	52	50	15	59	50	23
2	157	0.3333	83	50	15	66	50	16	78	50	18	51	50	16
3	231	0.3333	63	50	16	73	50	22	51	50	20	75	50	19
4	376	0.3333	110	50	15	150	50	16	152	50	21	131	50	15
5	546	0.1111	145	50	13	64	50	5	38	38	3	40	40	4
6	625	0.1111	47	47	4	20	20	1	75	50	5	97	50	7
7	546	0.1111	53	50	5	203	50	16	109	50	9	102	50	7
8	376	0.1111	18	18	1	34	34	2	36	36	4	88	50	12
9	231	0.1111	13	13	2	19	19	1	24	24	2	49	49	8
10	157	0.1111	8	8	0	19	19	2	5	5	0	7	7	0
11	132	0.1111	32	32	9	30	30	3	29	29	6	18	18	2
12	150	0.1111	25	25	2	11	11	0	24	24	2	30	30	3
13	150	0.3333	69	50	16	72	50	19	51	50	14	114	50	21
14	150	0.3333	67	50	17	92	50	16	91	50	15	76	50	17
15	150	0.3333	211	50	21	60	50	15	108	50	19	94	50	20
16	150	0.3333	78	50	12	114	50	13	84	50	15	107	50	18
17	150	0.3333	64	50	16	143	50	19	89	50	21	90	50	15
18	150	0.3333	47	47	17	145	50	16	127	50	17	39	39	13
19	150	0.3333	146	50	19	47	47	12	69	50	11	70	50	16
20	150	0.3333	93	50	18	165	50	19	66	50	20	65	50	17
21	424	0.3333	242	50	23	141	50	17	217	50	17	265	50	24
22	620	0.3333	237	50	18	235	50	20	247	50	17	172	50	15
23	884	0.3333	263	50	20	399	50	18	341	50	21	368	50	19
24	1200	0.3333	511	50	19	541	50	23	282	50	16	690	50	18
25	1536	0.3333	404	50	16	861	50	21	345	50	10	438	50	20

Table S1.2 continued

Strata	Known parameters		Stochastic data											
			Year 2			Year 3			Year 4			Year 5		
	U	p	u	n	m	u	n	m	u	n	m	u	n	m
26	1838	0.3333	374	50	16	862	50	21	529	50	14	397	50	13
27	2049	0.3333	428	50	12	726	50	16	812	50	20	863	50	20
28	2125	0.3333	702	50	14	627	50	18	384	50	14	837	50	18
29	2049	0.3333	698	50	15	763	50	18	635	50	14	902	50	18
30	1838	0.3333	506	50	15	461	50	18	550	50	21	1042	50	19
31	1536	0.3333	617	50	20	705	50	16	363	50	21	357	50	15
32	1200	0.3333	413	50	18	300	50	14	438	50	19	640	50	21
33	884	0.3333	264	50	15	314	50	16	286	50	15	629	50	22
34	620	0.3333	191	50	15	227	50	19	223	50	19	124	50	14
35	424	0.3333	159	50	18	131	50	15	175	50	21	144	50	14

Table S1.3 The number of individuals caught, u , the number of individuals released upstream, n , and the number of individuals recaptured, m , for years 6 through 10 of each stochastic simulated data set.

Strata	Known parameters		Stochastic data														
			Year 6			Year 7			Year 8			Year 9			Year 10		
	U	p	u	n	m	u	n	m	u	n	m	u	n	m	u	n	m
1	132	0.3333	60	50	16	50	50	17	55	50	16	26	26	10	83	50	17
2	157	0.3333	140	50	23	8	8	2	45	45	17	0	0	0	86	50	18
3	231	0.3333	53	50	20	184	50	20	0	0	0	102	50	17	64	50	16
4	376	0.3333	133	50	20	90	50	14	163	50	19	123	50	13	119	50	18
5	546	0.1111	183	50	13	85	50	8	53	50	4	102	50	9	80	50	9
6	625	0.1111	131	50	9	30	30	1	46	46	5	34	34	2	126	50	8
7	546	0.1111	133	50	13	18	18	1	71	50	8	55	50	6	81	50	6
8	376	0.1111	37	37	4	56	50	6	24	24	1	48	48	5	76	50	7
9	231	0.1111	57	50	13	19	19	2	11	11	1	53	50	6	27	27	4
10	157	0.1111	0	0	0	13	13	1	22	22	2	31	31	6	10	10	0
11	132	0.1111	20	20	4	4	4	0	3	3	0	0	0	0	2	2	0
12	150	0.1111	34	34	3	16	16	1	22	22	1	47	47	6	13	13	1
13	150	0.3333	109	50	16	78	50	15	72	50	26	140	50	16	56	50	14
14	150	0.3333	89	50	17	116	50	20	68	50	11	73	50	15	51	50	14
15	150	0.3333	100	50	15	57	50	15	76	50	15	60	50	16	80	50	13
16	150	0.3333	66	50	16	70	50	19	124	50	21	107	50	16	156	50	18
17	150	0.3333	102	50	18	211	50	21	48	48	12	88	50	14	137	50	18
18	150	0.3333	66	50	17	53	50	11	62	50	16	106	50	14	28	28	8
19	150	0.3333	107	50	20	113	50	16	102	50	13	125	50	18	135	50	22
20	150	0.3333	103	50	14	226	50	23	61	50	18	107	50	19	109	50	19
21	424	0.3333	113	50	15	180	50	21	150	50	16	135	50	15	103	50	14
22	620	0.3333	286	50	21	214	50	17	166	50	16	251	50	18	226	50	18
23	884	0.3333	178	50	13	384	50	19	306	50	13	303	50	22	342	50	16
24	1200	0.3333	392	50	19	647	50	19	411	50	19	417	50	16	325	50	14
25	1536	0.3333	423	50	17	752	50	20	492	50	19	412	50	19	510	50	16

Table S1.4 Continued

Strata	Known parameters		Stochastic data														
			Year 6			Year 7			Year 8			Year 9			Year 10		
	U	p	u	n	m	u	n	m	u	n	m	u	n	m	u	n	m
26	1838	0.3333	712	50	15	877	50	24	752	50	21	824	50	21	441	50	15
27	2049	0.3333	553	50	16	1057	50	19	388	50	13	502	50	13	1110	50	19
28	2125	0.3333	538	50	14	936	50	19	570	50	18	722	50	15	459	50	12
29	2049	0.3333	568	50	17	507	50	14	419	50	11	636	50	14	534	50	15
30	1838	0.3333	437	50	15	699	50	15	716	50	17	614	50	17	682	50	20
31	1536	0.3333	686	50	20	380	50	12	573	50	22	556	50	18	443	50	14
32	1200	0.3333	340	50	12	396	50	16	294	50	13	451	50	19	223	50	15
33	884	0.3333	334	50	15	347	50	15	397	50	22	298	50	18	352	50	23
34	620	0.3333	180	50	15	85	50	8	204	50	17	210	50	15	139	50	12
35	424	0.3333	106	50	15	122	50	16	206	50	16	126	50	15	138	50	15

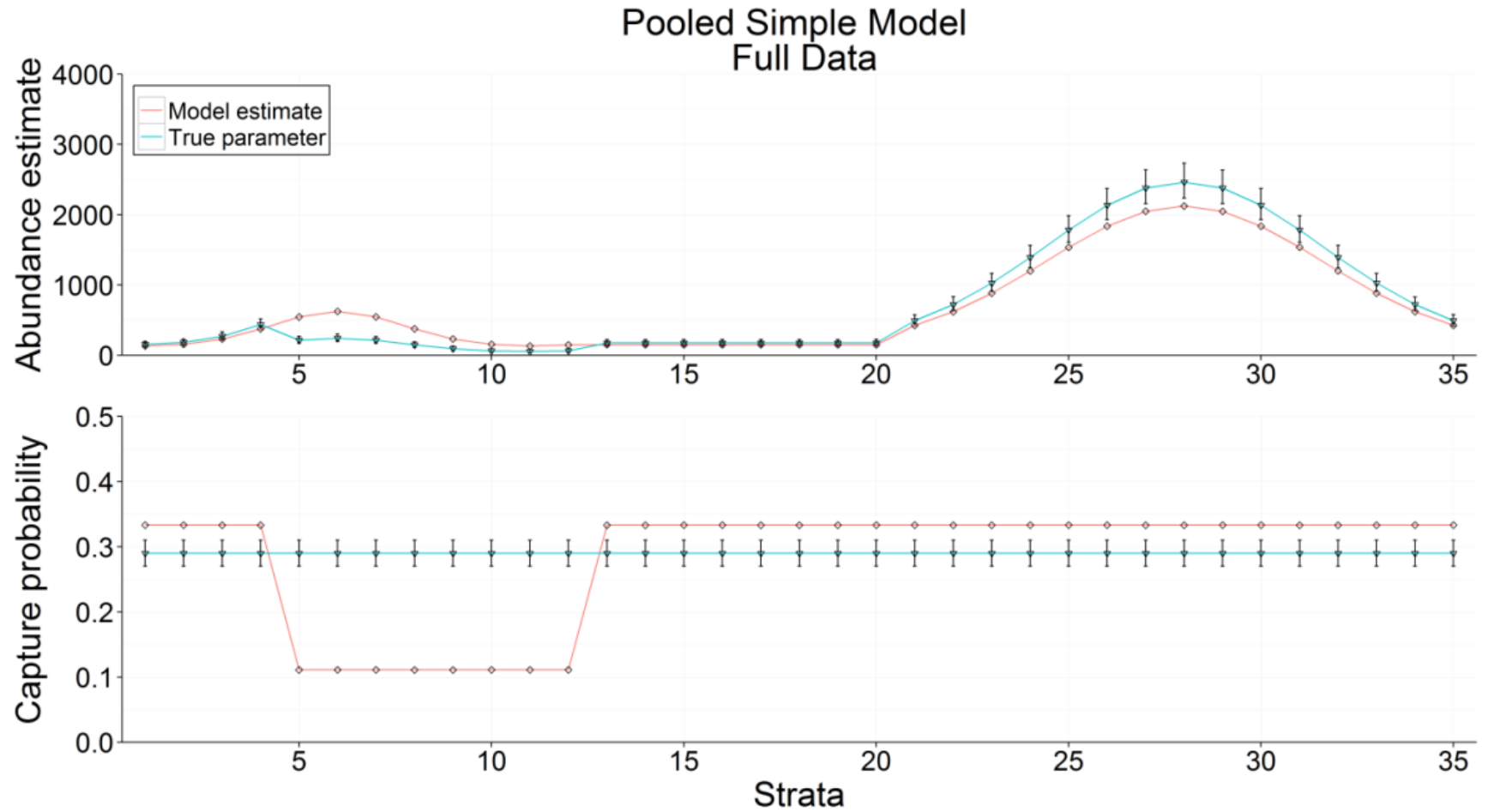


Figure S1.1. Strata abundance estimates, U_i , and capture probabilities, p_i , from model M_{PS} and the corresponding true parameters used to simulate data. Abundance point estimates represent the posterior medians and the error bars represent the 95% credible intervals.

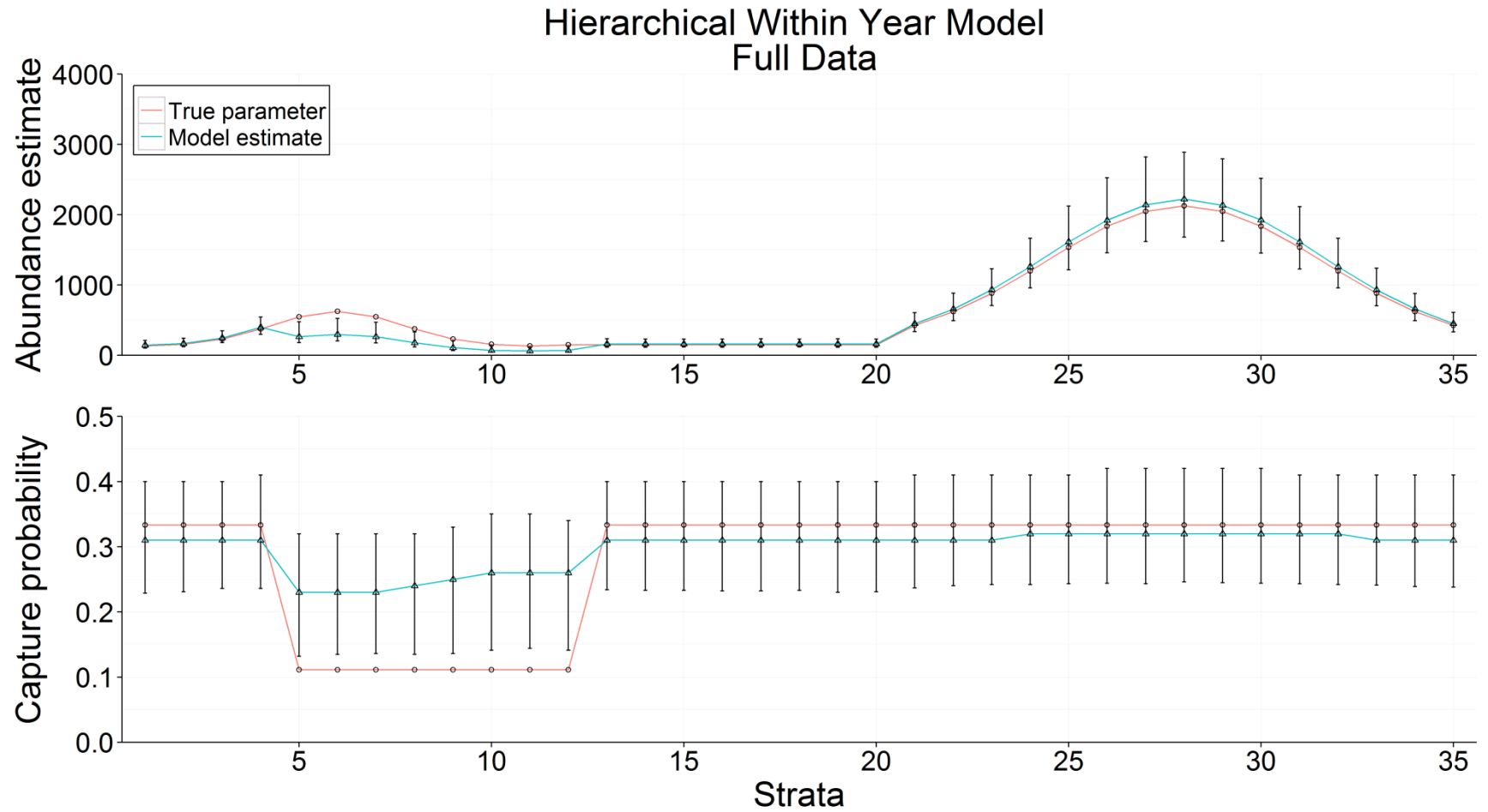


Figure S1.2. Strata abundance estimates, U_i , and capture probabilities, p_i , from model M_{HW} and the corresponding true parameters used to simulate the data. Abundance point estimates are represented as the posterior medians and the error bars represent the 95% credible intervals.

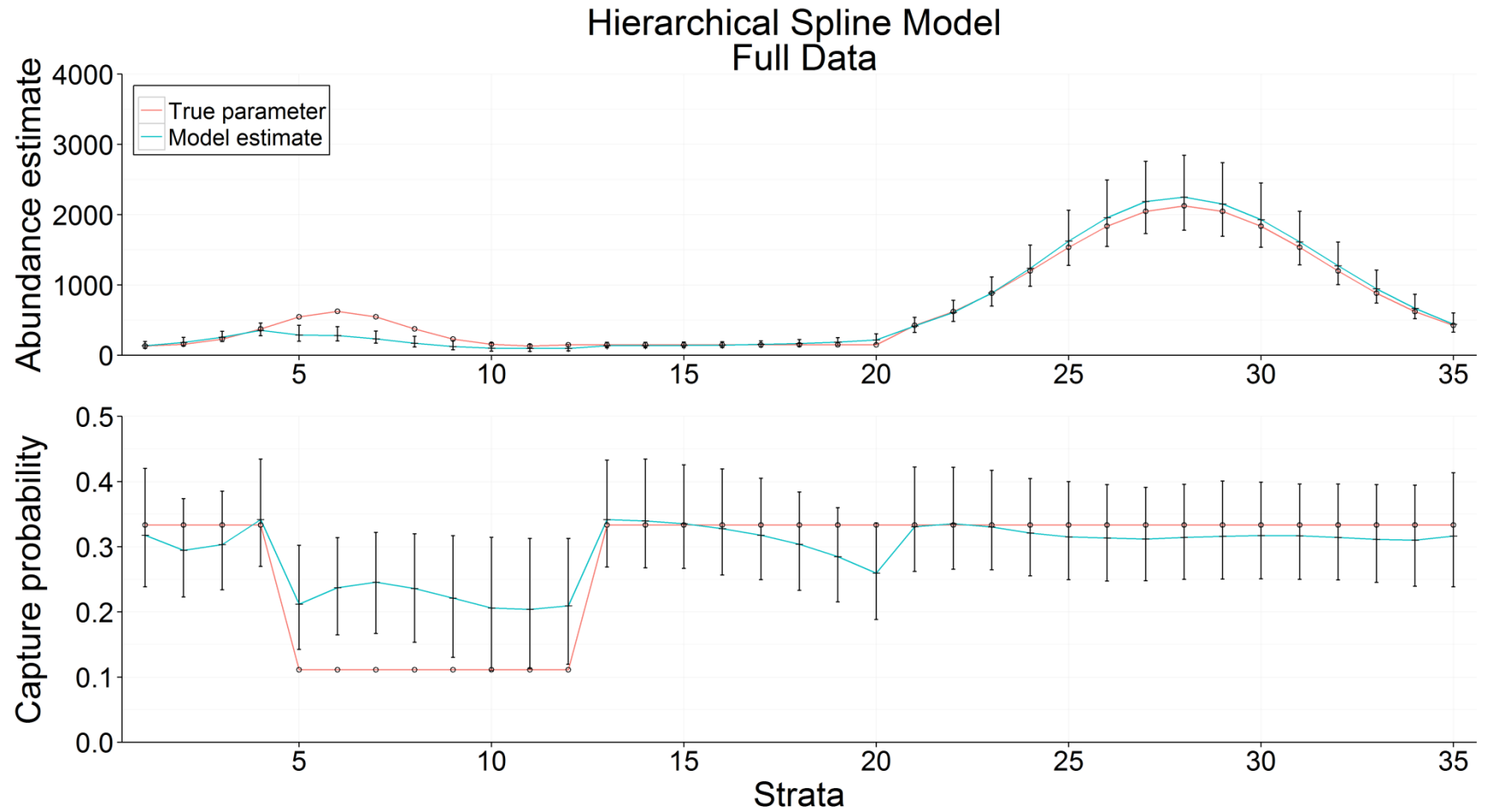


Figure S1.3. Strata abundance estimates, U_i , and capture probabilities, p_i , from model M_{SPLINE} and the corresponding true parameters used to simulate the data. Abundance point estimates are represented as the posterior medians and the error bars represent the 95% credible intervals.

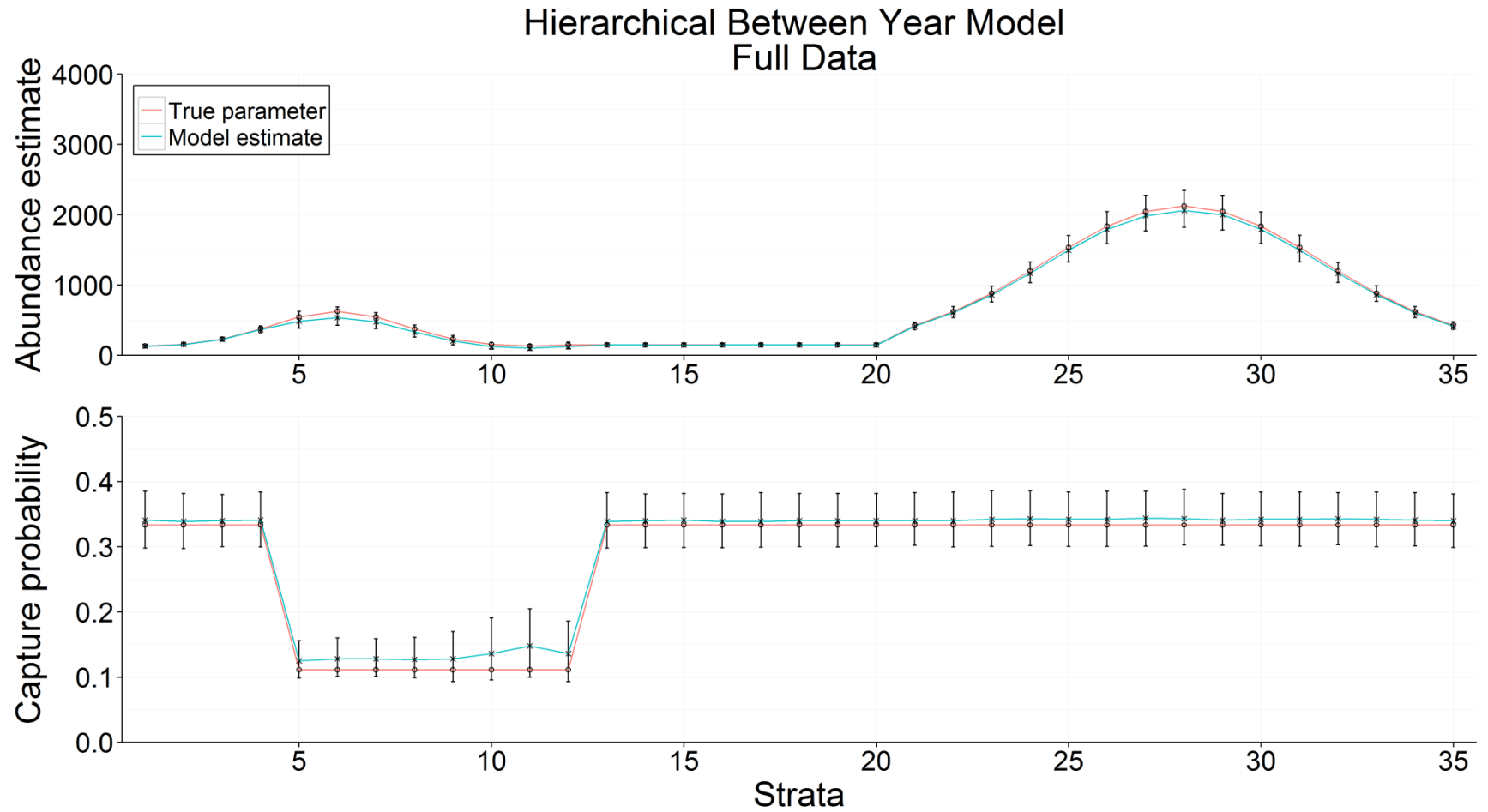


Figure S1.4. Strata abundance estimates, U_i , and capture probabilities, p_i , from model M_{HB} and the corresponding true parameters used to simulate the data. Abundance point estimates are represented as the posterior medians and the error bars represent the 95% credible intervals.

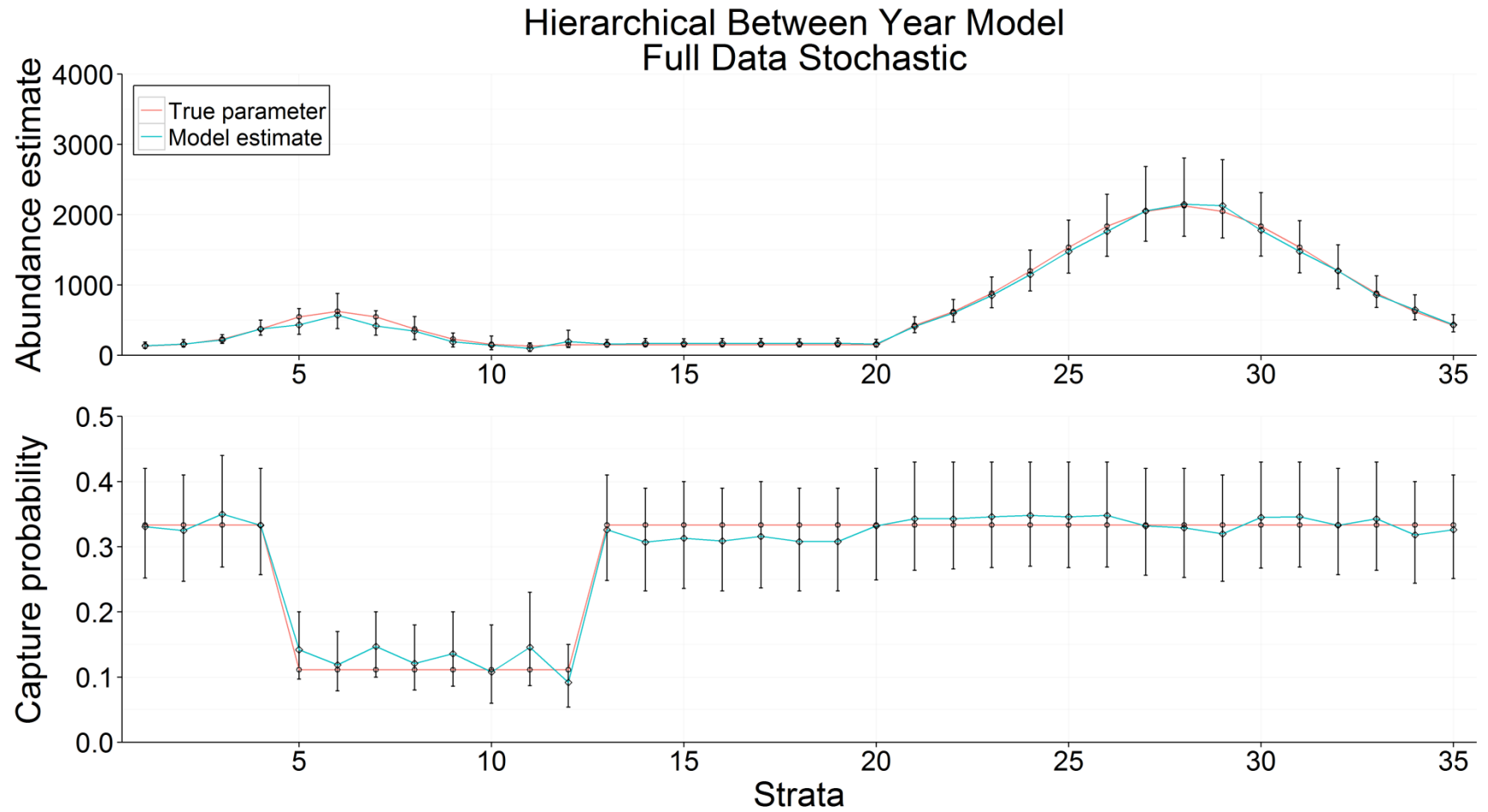


Figure S1.5. Strata abundance estimates, U_i , and capture probabilities, p_i , from model M_{HB} and the corresponding true parameters used to simulate the stochastic data. Abundance point estimates are represented as posterior medians and the error bars represent the 95% credible intervals.

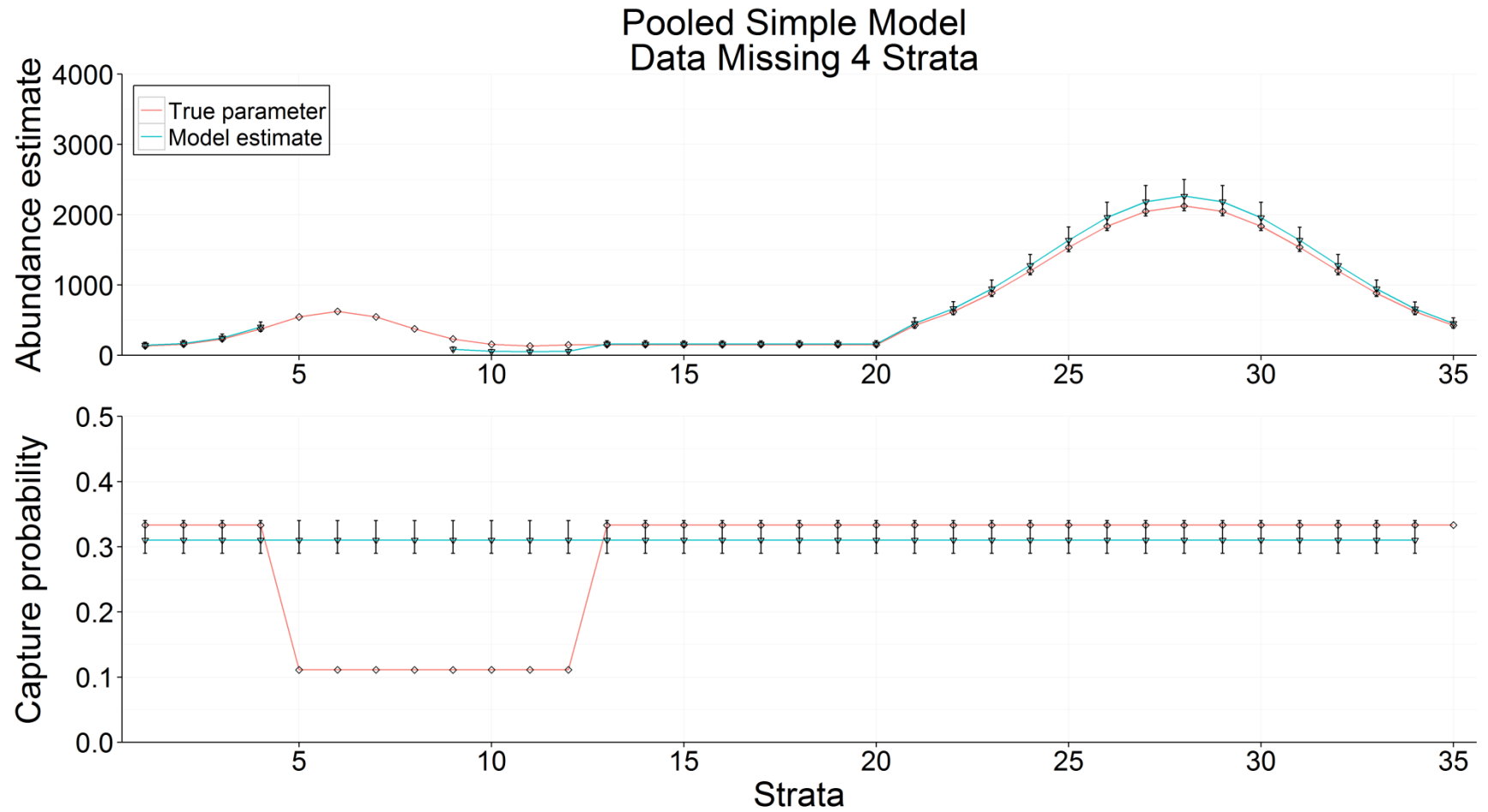


Figure S1.6. Strata abundance estimates, U_i , and capture probabilities, p_i , from model M_{PS} and the corresponding true parameters used to simulate the data set missing strata 5 through 8. Abundance point estimates are represented as the posterior medians and the error bars represent the 95% credible intervals. Posterior parameter estimates for strata 5 through 8 were removed due to missing data.

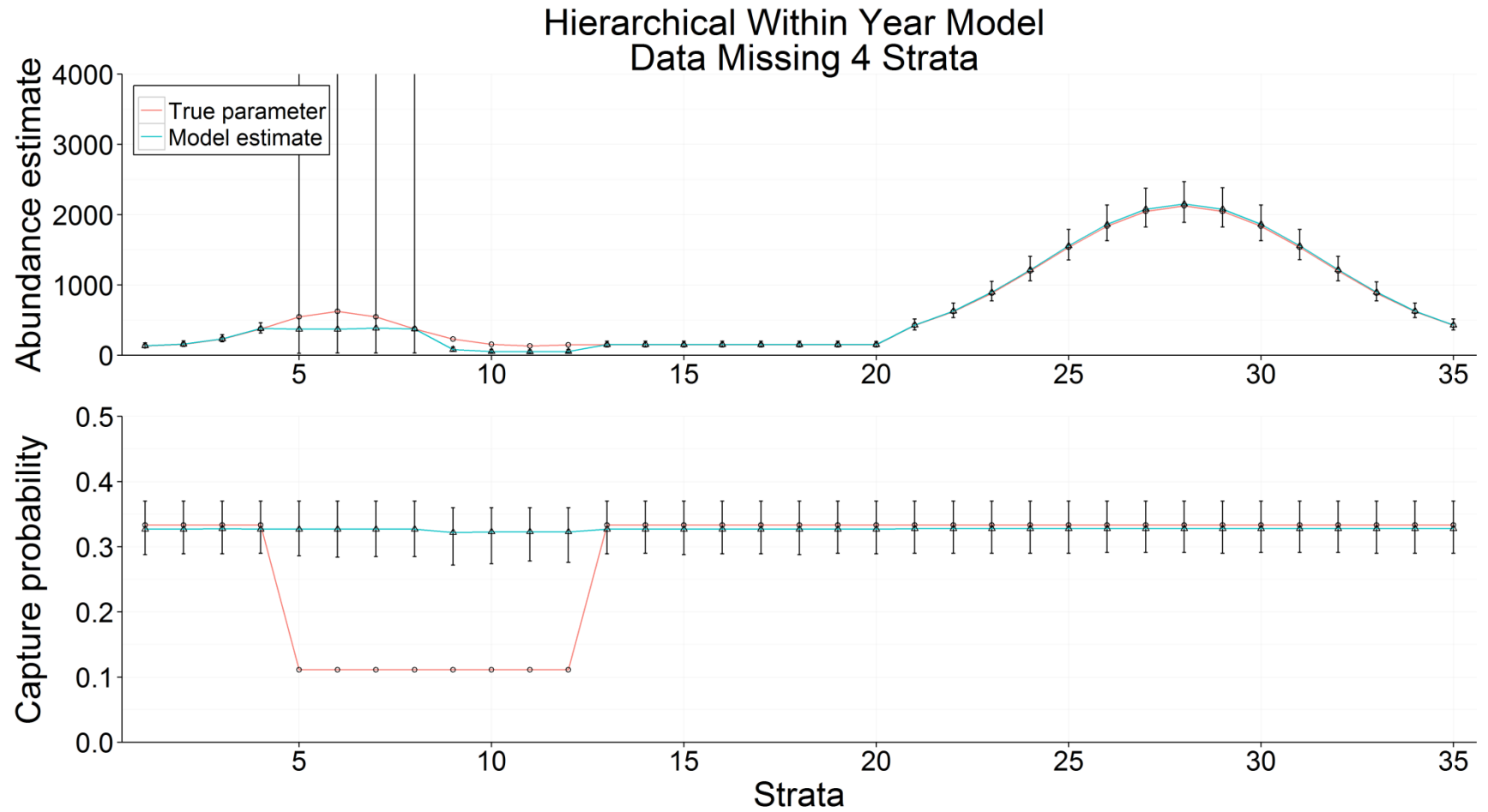


Figure S1.7. Strata abundance estimates, U_i , and capture probabilities, p_i , from model M_{HW} and the corresponding true parameters used to simulate the data set missing strata 5 through 8. Abundance point estimates are represented as the posterior medians and the error bars represent the 95% credible intervals.

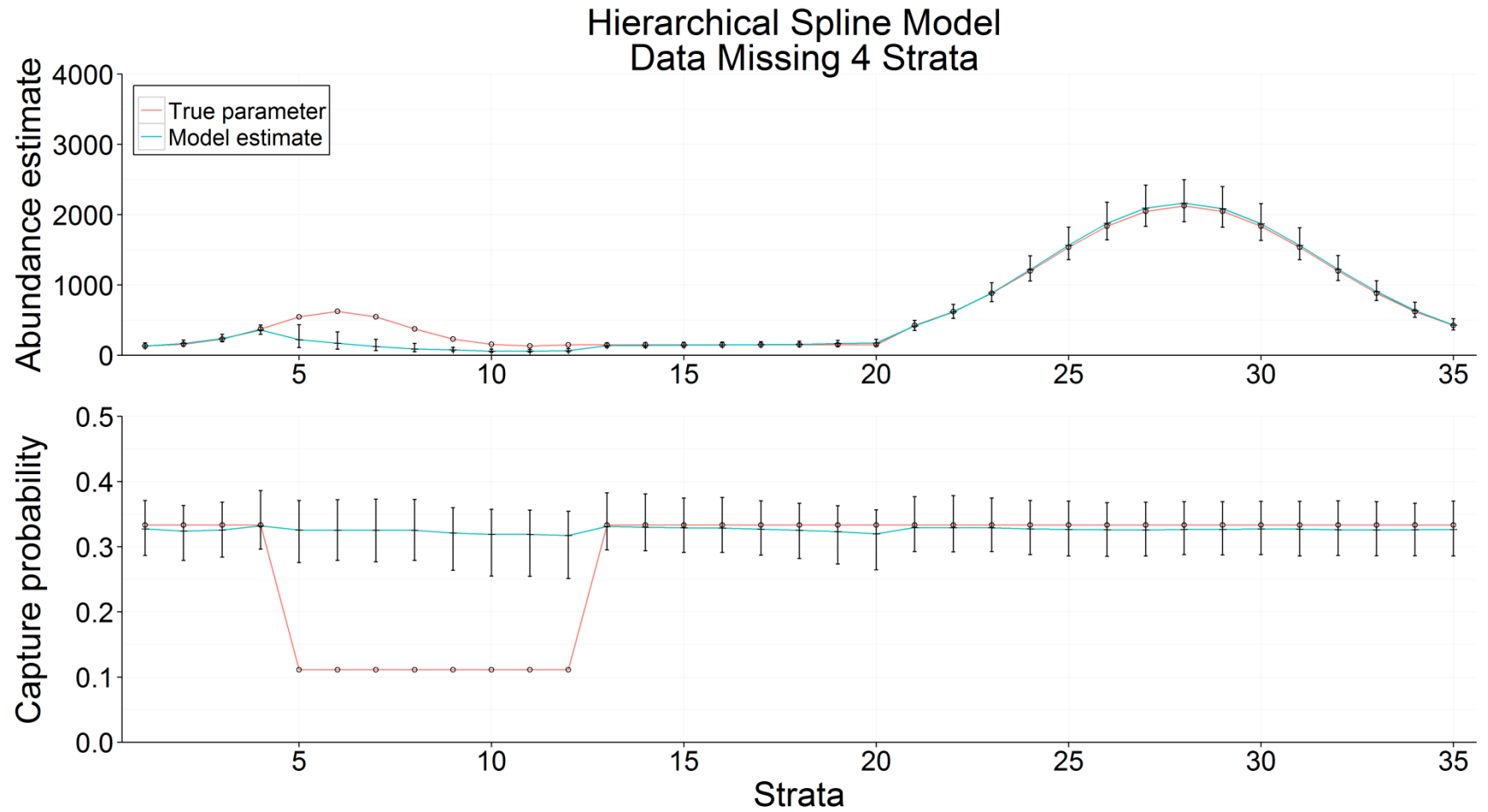


Figure S1.8. Strata abundance estimates, U_i , and capture probabilities, p_i , from model M_{SPLINE} and the corresponding true parameters used to simulate the data set missing strata 5 through 8. Abundance point estimates are represented as the posterior medians and the error bars represent the 95% credible intervals.

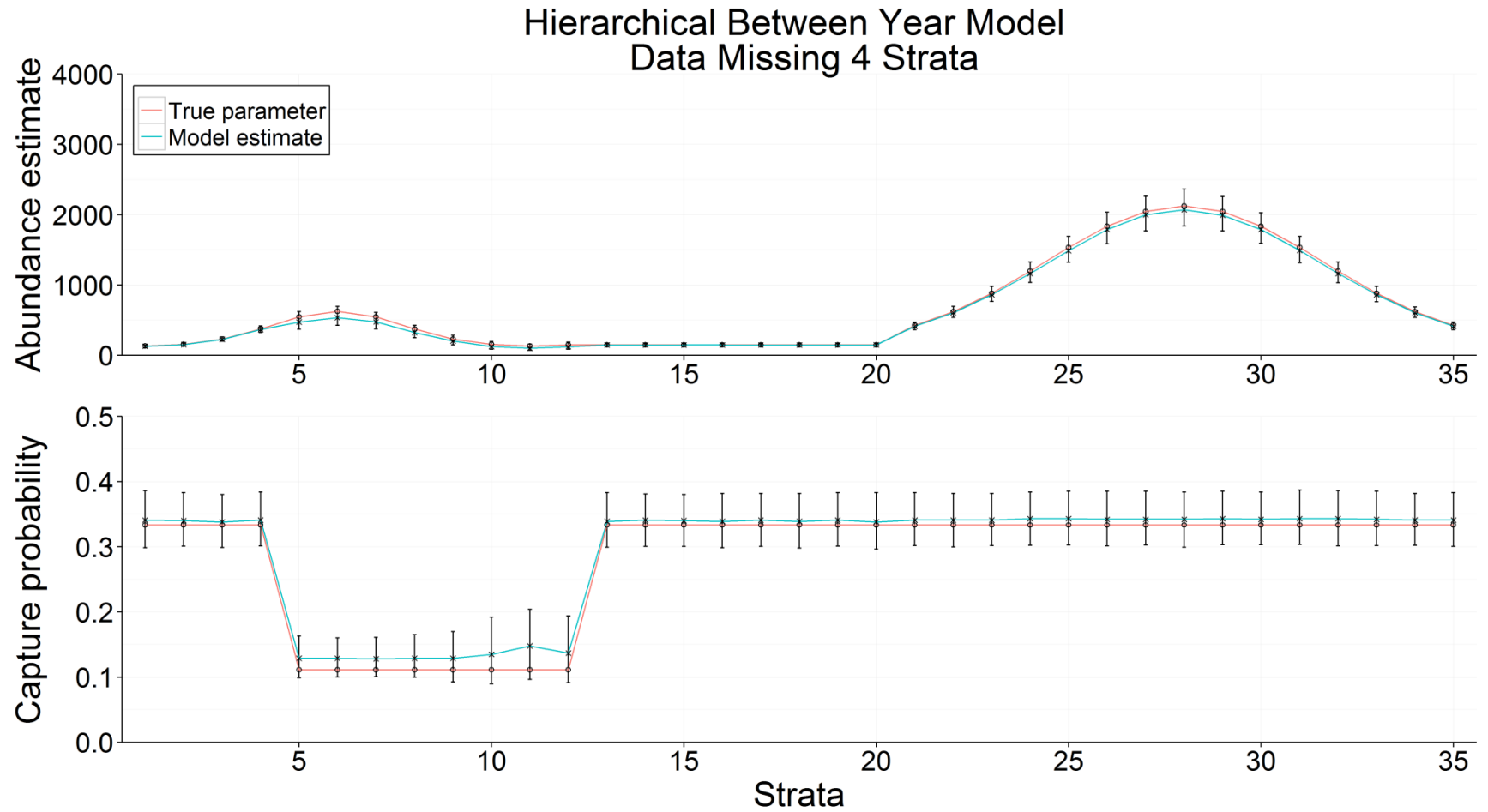


Figure S1.9. Strata abundance estimates, U_i , and capture probabilities, p_i , from model M_{HB} and the corresponding true parameters used to simulate the data set missing strata 5 through 8. Abundance point estimates are represented as the posterior medians and the error bars represent the 95% credible intervals.

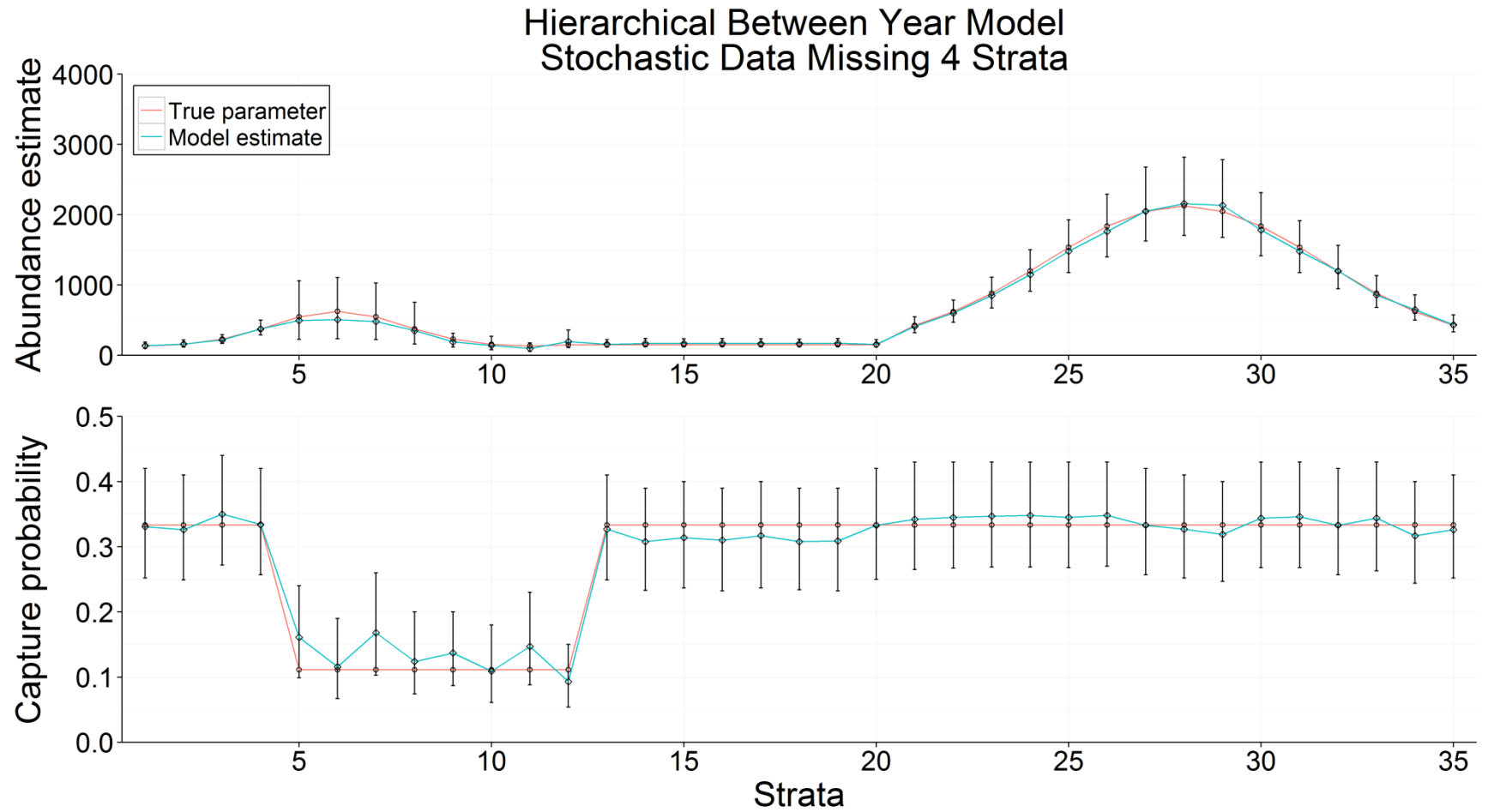


Figure S1.10. Strata abundance estimates, U_i , and capture probabilities, p_i , from model M_{HB} and the corresponding true parameters used to simulate the stochastic data set missing strata 5 through 8. Abundance point estimates are represented as the posterior medians and the error bars represent the 95% credible intervals.

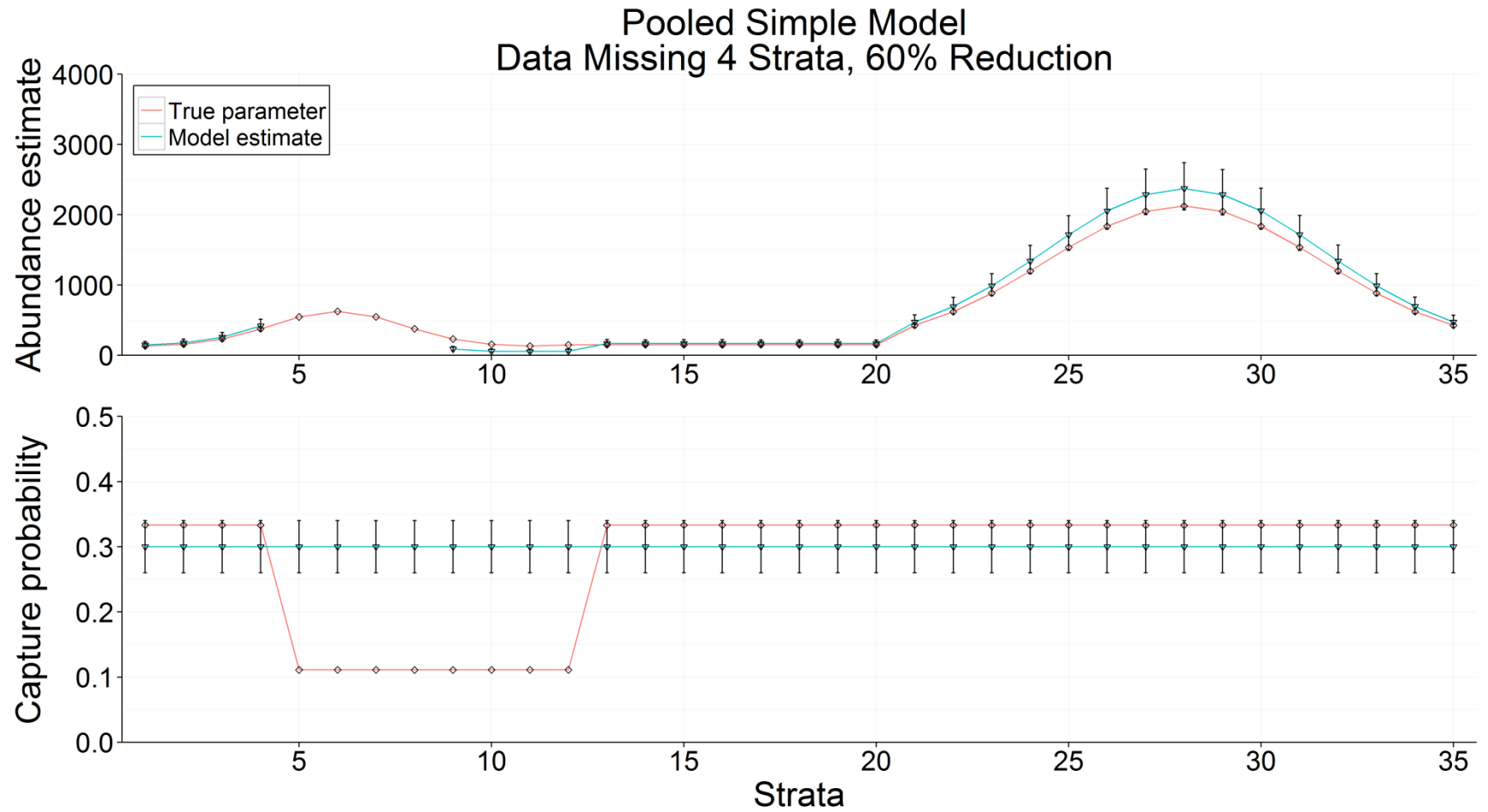


Figure S1.11. Strata abundance estimates, U_i , and capture probabilities, p_i , from model M_{PS} and the corresponding true parameters used to simulate the data set missing strata 5 through 8 with 60% reduction of marked and recaptured fish. Abundance point estimates are represented as the posterior medians and the error bars represent the 95% credible intervals. Posterior parameter estimates for strata 5 through 8 were removed due to missing data.

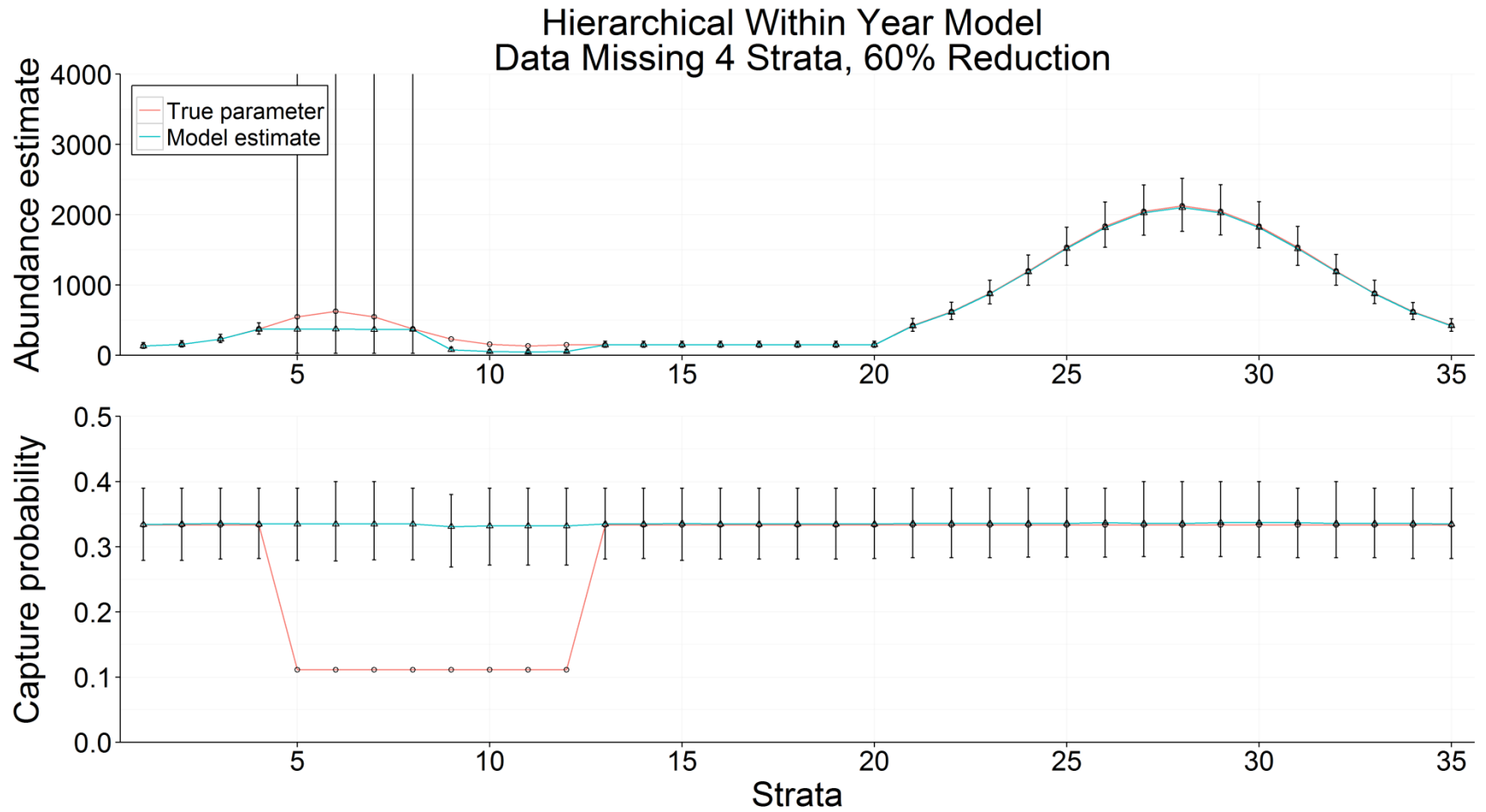


Figure S1.12. Strata abundance estimates, U_i , and capture probabilities, p_i , from model M_{HW} and the corresponding true parameters used to simulate the data set missing strata 5 through 8 with 60% reduction of marked and recaptured fish. Abundance point estimates are represented as the posterior medians and the error bars represent the 95% credible intervals.

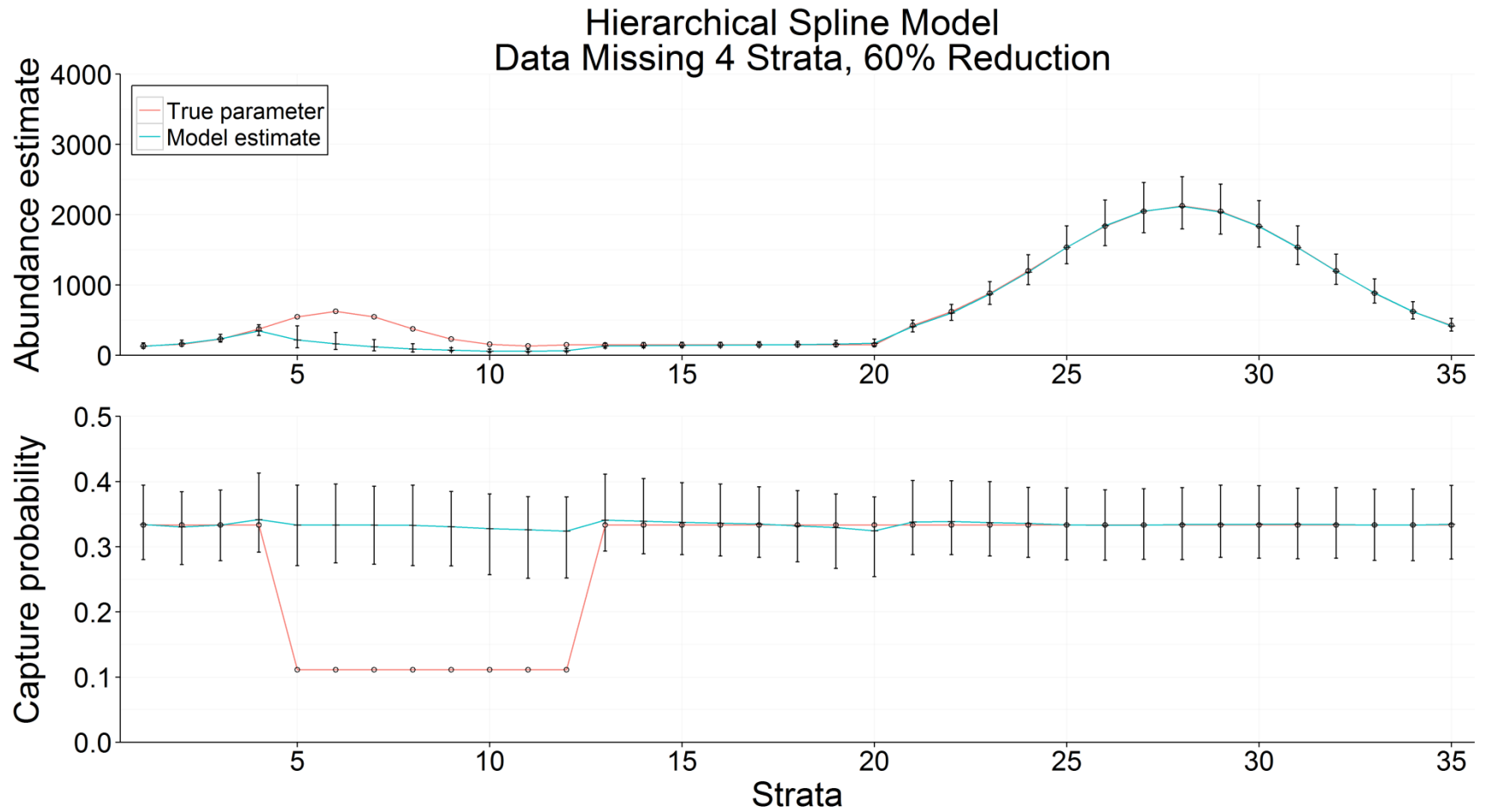


Figure S1.13. Strata abundance estimates, U_i , and capture probabilities, p_i , from model M_{SPLINE} and the corresponding true parameters used to simulate the data set missing strata 5 through 8 with 60% reduction of marked and recaptured fish. Abundance point estimates are represented as the posterior medians and the error bars represent the 95% credible intervals.

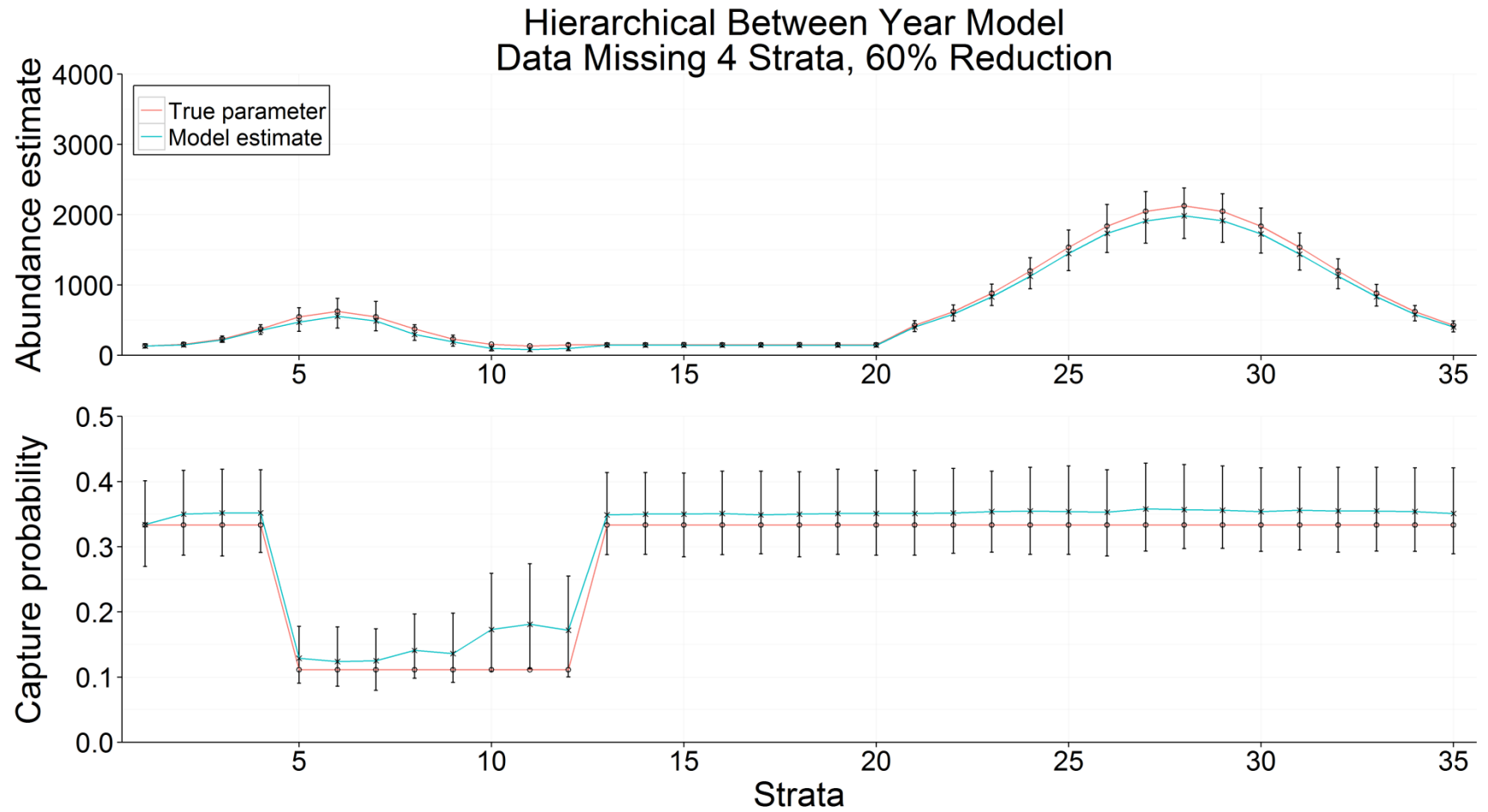


Figure S1.14. Strata abundance estimates, U_i , and capture probabilities, p_i , from model M_{HB} and the corresponding true parameters used to simulate the data set missing strata 5 through 8 with 60% reduction of marked and recaptured fish. Abundance point estimates are represented as the posterior medians and the error bars represent the 95% credible intervals.

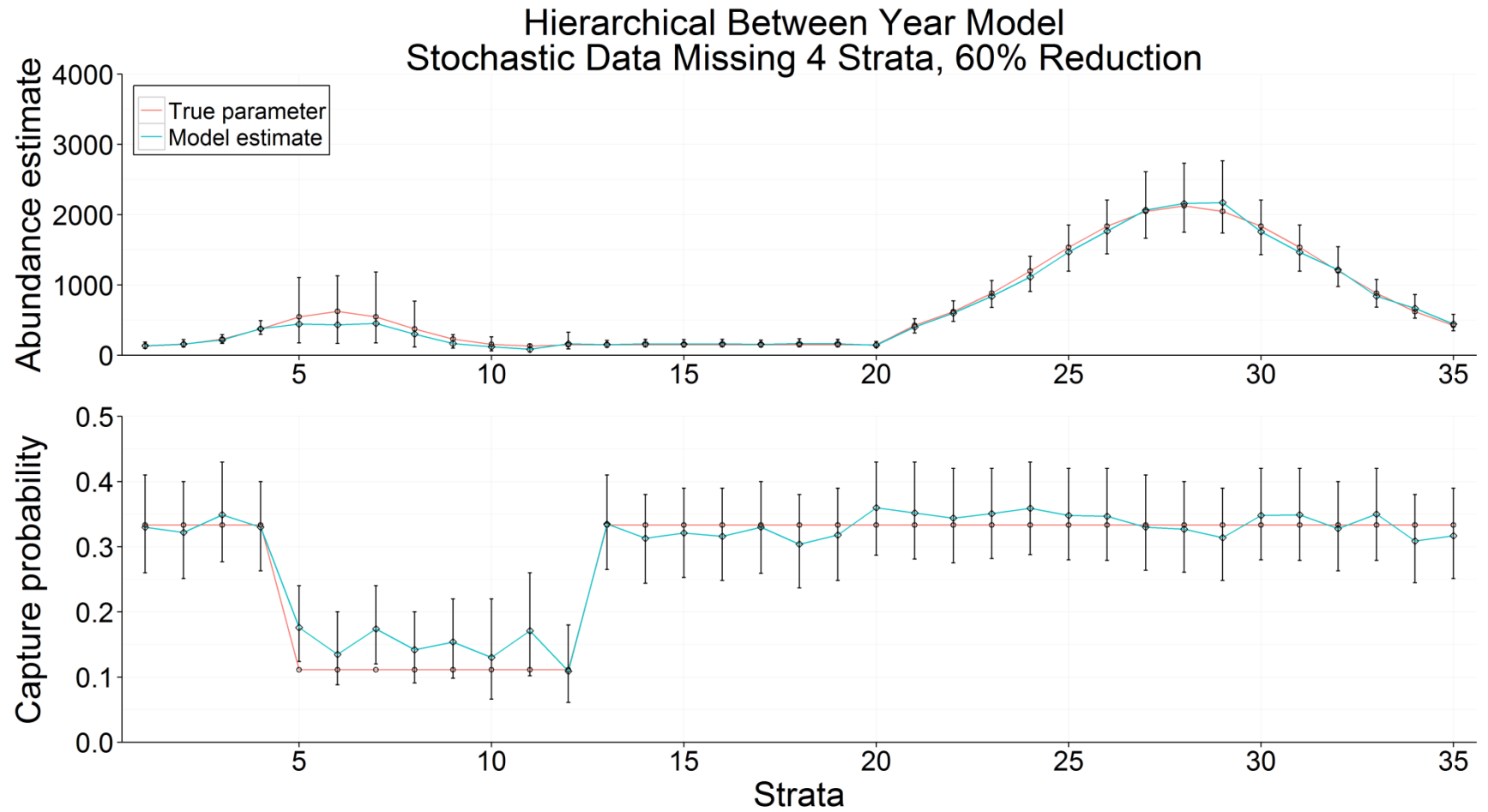


Figure S1.15. Strata abundance estimates, U_i , and capture probabilities, p_i , from model M_{HB} and the corresponding true parameters used to simulate the stochastic data set missing strata 5 through 8 with 60% reduction of marked and recaptured fish. Abundance point estimates are represented as the posterior medians and the error bars represent the 95% credible intervals.

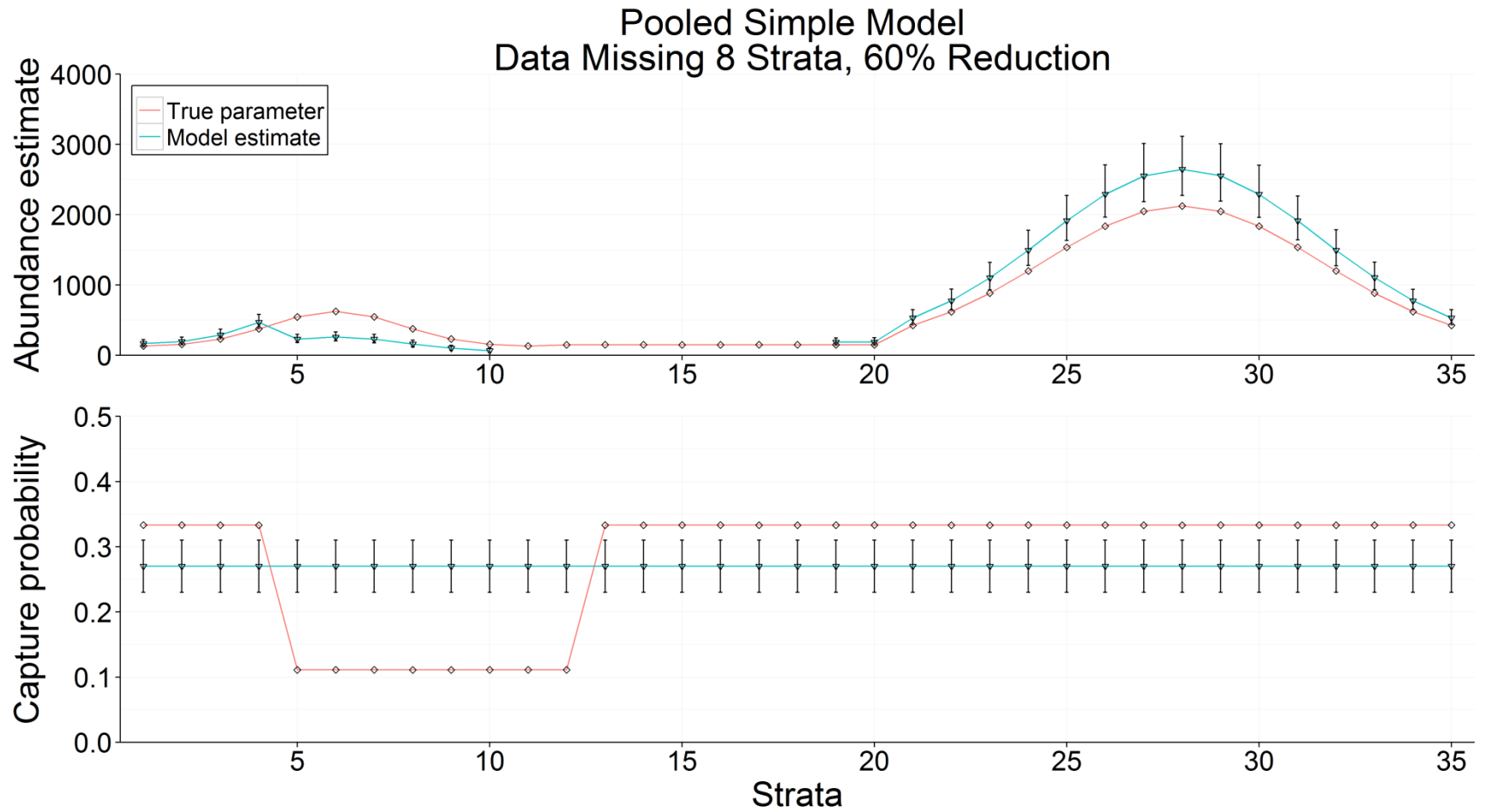


Figure S1.16. Strata abundance estimates, U_i , and capture probabilities, p_i , from model M_{PS} and the corresponding true parameters used to simulate the data set missing strata 11 through 18 with 60% reduction of marked and recaptured fish. Abundance point estimates are represented as the posterior medians and the error bars represent the 95% credible intervals. Posterior parameter estimates for strata 11 through 18 were removed due to missing data.

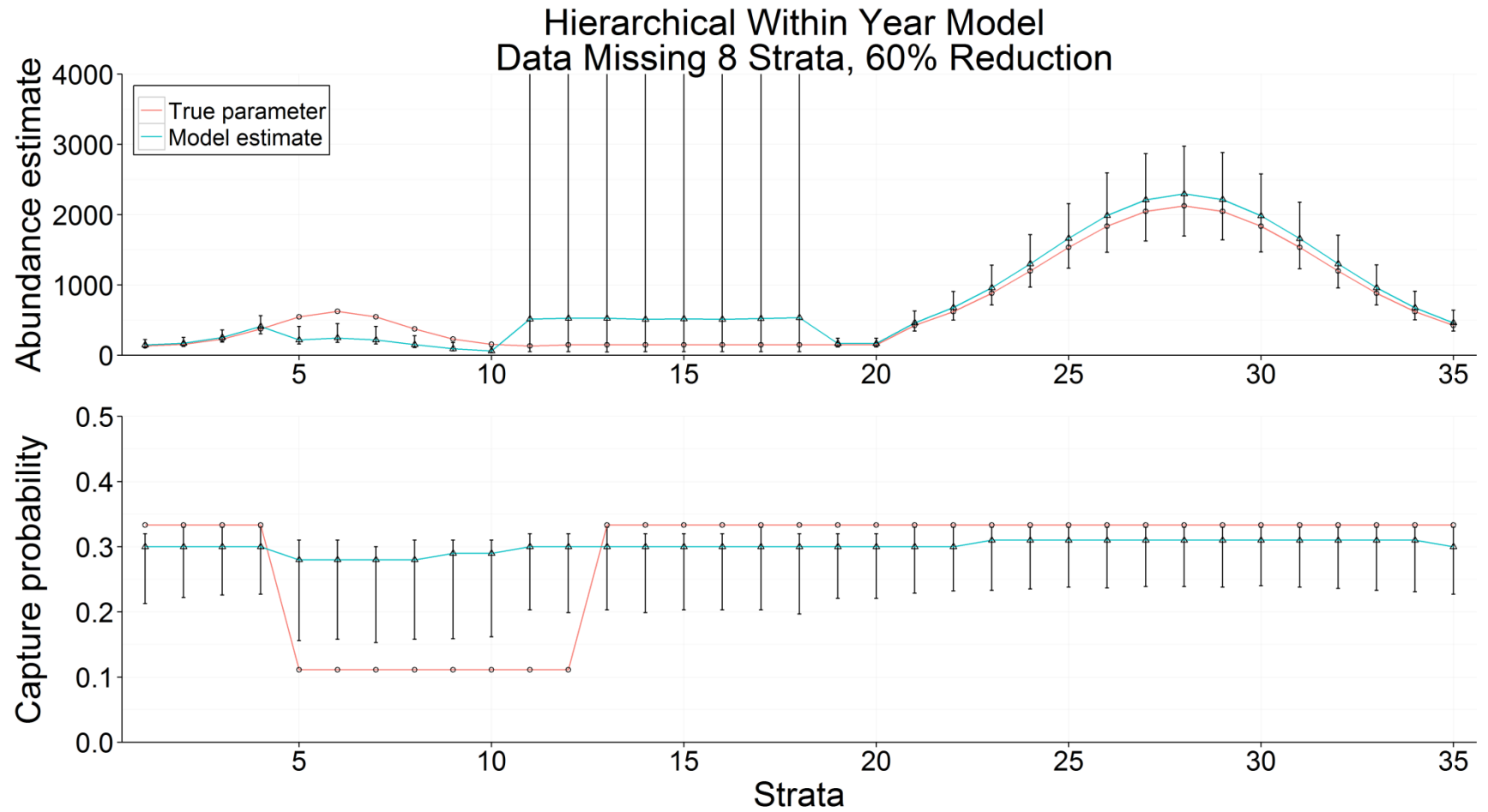


Figure S1.17. Strata abundance estimates, U_i , and capture probabilities, p_i , from model M_{HW} and the corresponding true parameters used to simulate the data set missing strata 11 through 18 with 60% reduction of marked and recaptured fish. Abundance point estimates are represented as the posterior medians and the error bars represent the 95% credible intervals.

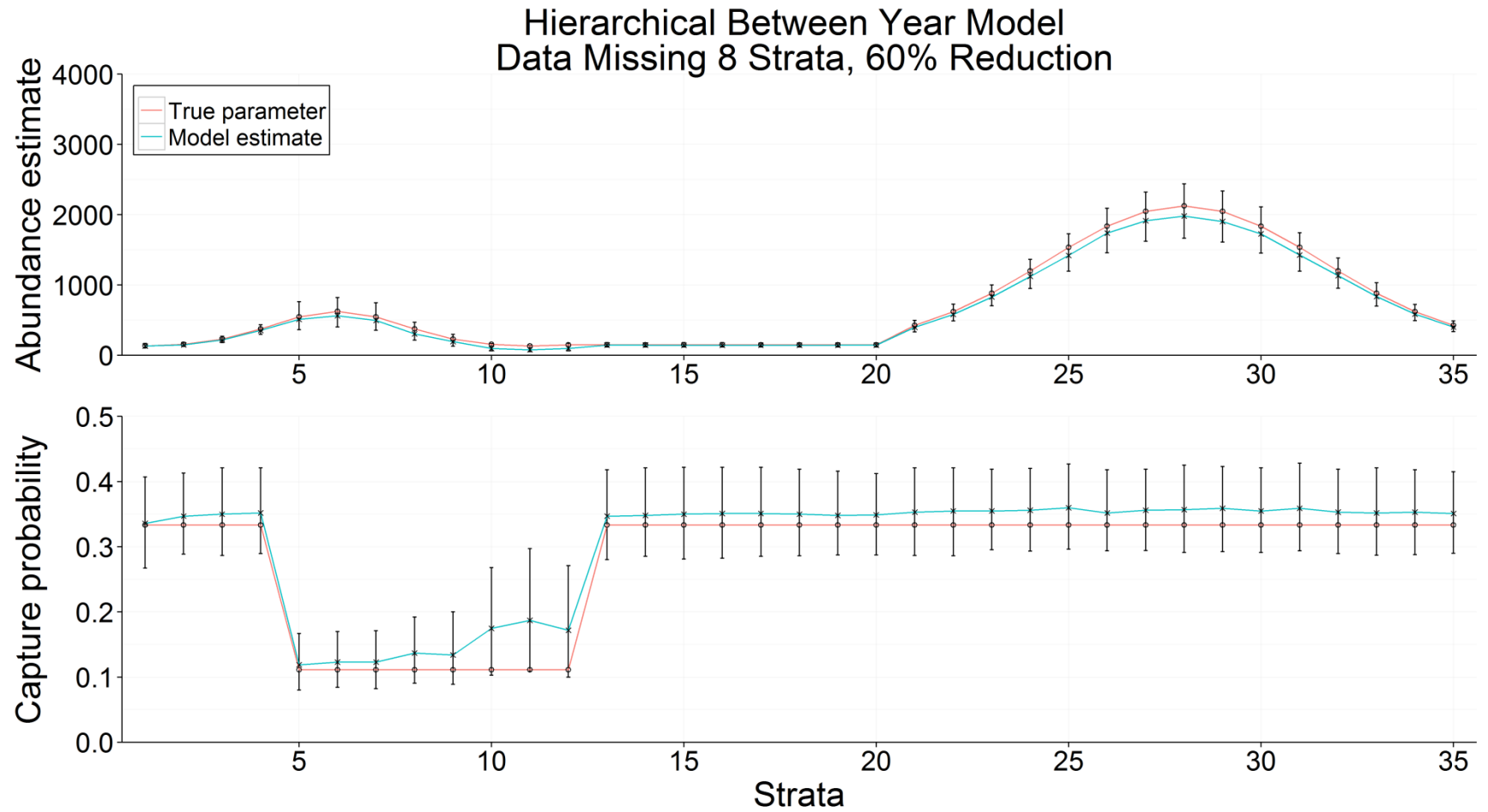


Figure S1.18. Strata abundance estimates, U_i , and capture probabilities, p_i , from model M_{HB} and the corresponding true parameters used to simulate the data set missing strata 11 through 18 with 60% reduction of marked and recaptured fish. Abundance point estimates are represented as the posterior medians and the error bars represent the 95% credible intervals.

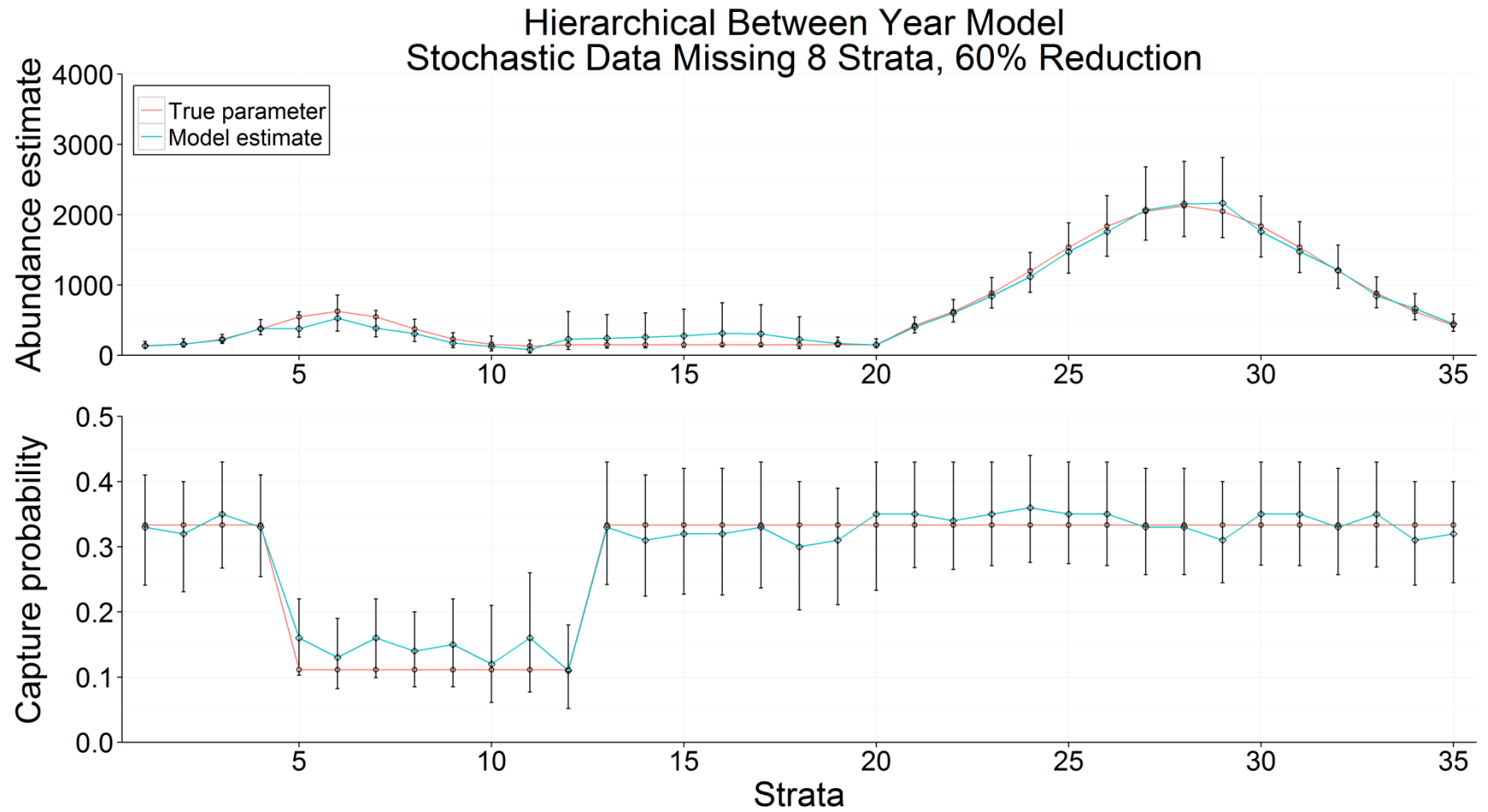


Figure S1.19. Strata abundance estimates, U_i , and capture probabilities, p_i , from model M_{HB} and the corresponding true parameters used to simulate the data set missing strata 11 through 18 with 60% reduction of marked and recaptured fish. Abundance point estimates are represented as the posterior medians and the error bars represent the 95% credible interval

Model Code S1.1. Model code for the hierarchical U , hierarchical p , between year model (M_{HB}) used for the analysis through the program R interface using RJAGS package and the JAGS program. Alternative example code incorporating covariates is specified.

```
##### Hierarchical Between Year Model #####

### Data sent to JAGS ###
## jweek <- number of strata
## year  <- number of years
## n     <- matrix of marked individuals released each week
## m     <- matrix of recaptured individuals
## u     <- matrix of unmarked individuals

model <- function() {
  ##### Likelihood #####
  for(i in 1:jweek){
    for(j in 1:year){

      ## Capture probability component ##
      m[i,j] ~ dbin(p[i,j],n[i,j])
      logit(p[i,j]) <- etaP[i,j]
      etaP[i,j] ~ dnorm(etaP1[i],tauP)

      ## Unmarked individual component ##
      u[i,j] ~ dbin(p[i,j],U[i,j])
      U[i,j] <- round(exp(etaU[i,j]))
      etaU[i,j] ~ dnorm(etaU1[i],tauU)
    }

    ##### Priors #####
    ##Capture probabilities and unmarked individuals ##
    etaP1[i] ~ dnorm(np,tp)
    etaU1[i] ~ dnorm(nu,tu)
  }

  ##### Hyper Parameters #####
  tauP ~ dgamma(.001,.001) #equal to 1/tauP
  sigmaP <- 1/sqrt(tauP) #variance

  tau ~ dgamma(.001,.001) #equal to 1/tauU
  sigmaU <- 1/sqrt(tauU) #variance

  np ~ dnorm(-2,.666) #variance is 1/.666
}
```

```

tp ~ dgamma(.001,.001) #equal to 1/tp
sigmatp <- 1/sqrt(tp) #variance

nu ~ dnorm(10,.25) #variance is 1/.25
tu ~ dgamma(.001,.001) #equal to 1/tu
sigmatu <- 1/sqrt(tu) #variance
}

#####
# Optional covariate inclusion example #
#####

### Covariate data sent to JAGS ###
## x1   <- matrix of covariate 1
## x2   <- matrix of covariate 2

## Likelihood covariate alternative ##
#for(i in 1:jweek){
# for(j in 1:year){
#etaP[i,j] <- etaP1[i] + beta1_p[i]*x1[i,j]
#etaU[i,j] <- etaU1[i] + beta1_U[i]*x1[i,j] + beta2_U[i]*x2[i,j] + beta3_U[i]*(x1[i,j]*x2[i,j])
# }

## Prior covariate alternative ##
#beta1_p[i] ~ dnorm(0,1E-6)
#beta1_U[i] ~ dnorm(0,1E-6)
#beta2_U[i] ~ dnorm(0,1E-6)
#beta3_U[i] ~ dnorm(0,1E-6)
#}

```

Chapter 2: The effects pre-smoltification life history strategies have on juvenile Chinook salmon in a wilderness environment

1. INTRODUCTION

The diversification of life history strategies, and the ensuing relative success or failure of these strategies, is dictated by a dynamic interplay between environmental and biological conditions (Crozier et al 2008; Knudsen and Michael 2009). The maintenance of diverse life history expressions within a population aids in the support of population resilience in a shifting environment (Kendall and Fox 2002; Schindler et al 2010), but not all strategies contribute equally or significantly to individual fitness or overall population production (e.g. Copeland and Venditti 2009). The degree to which different life history strategies contribute to successful individuals varies temporally and spatially within populations and results in difficulties when quantifying the relative impacts that differing strategies have on a population's viability (Kendall and Fox 2002; Iverson et al 2011). Understanding the relationship environmental conditions have on life history expressions and how life histories contribute back to the population is of fundamental interest to understanding populations and would aid greatly in their conservation.

Pacific Salmon (individuals from the genus *Oncorhynchus*) in the Pacific Northwestern United States play a central role in ecosystem functions (Gende et al 2002), provide recreational angling opportunities (Crutchfield and Pontecorvo 2013), and have cultural importance to the region (Lichatowich 2001). Over the last century, populations have declined due to a combination of overharvest, hatchery supplementation, habitat

degradation, introduction of invasive species, and modifications to their migratory corridors (Nehlsen et al 1991). These recent alterations have caused many salmonid life histories within populations to be eliminated or depressed, reducing overall abundances and leaving populations vulnerable to extinction (Gustafson et al 2007; Schindler et al 2010). Several populations have been listed as “threatened” or “endangered” under the Endangered Species Act (ESA) of 1973 and at-risk populations are under intensive monitoring and management by state, federal, and tribal agencies (NMFS 1992). These monitoring efforts have greatly increased the knowledge of basin-wide salmonid population characteristics but the complexity of life history strategies within populations require greater attention in order to implement effective conservation efforts.

Chinook salmon in Big Creek, Idaho, a fourth-order tributary of the Middle Fork of the Salmon River, comprise a significant population within the Snake River basin Evolutionary Significant Unit. Almost the entirety of salmon habitat within the 36,000 km² system lies within a roadless Wilderness environment and the salmon within the system, and the surrounding Frank Church River of No Return Wilderness as a whole, have experienced little to no hatchery influence or introgression (Hamann and Kennedy 2012; Thurow 2000). Extensive Chinook salmon monitoring efforts by many agencies and groups within the remote and habitat-rich portions of the Salmon River system have revealed unique attributes (Achord et al 2007; Copeland and Venditti 2009). The distribution of Chinook salmon fry throughout approximately 80 km of river length is strongly correlated to the clustered distribution of spawning habitat that is concentrated in braided alluvial segments

within an otherwise confined high gradient valley. In most years, the majority of utilized spawning habitat is concentrated in upper reaches of Big Creek with approximately 50% of redds (spawning nests) occurring in the roughly 8 km of upper Big Creek (Thurrow 2000; Hamann et al 2014).

The distribution of salmon rearing habitat in river ecosystems can be patchy and heterogeneous and must be considered at both large and hierarchical spatial scales to understand population responses (Fausch et al 2002, Kennedy et al. 2008). In Big Creek, both productivity and foraging behavior of juveniles has been shown to demonstrate spatial variation and longitudinal structuring related to temperature, habitat availability, density, and disturbance (Holecek et al 2009; Cromwell and Kennedy 2011; Mitchell et al. in prep). Achord et al (2007) found that juvenile Chinook salmon sampled in lower portions of the Big Creek watershed had one of the highest parr-to-smolt survival rates in the Salmon River basin while individuals residing in upper portions of the watershed had among the lowest. This suggests there is significant juvenile dispersal occurring in Big Creek that functionally links upper and lower portions of the basin and has important feedbacks to adult behavior (Hamann and Kennedy 2012). Data from otolith microchemistry (Kennedy in prep.) confirms that lower Big Creek individuals sampled during the fall originate from other regions of the basin.

Growth opportunity, and its variable distribution across the landscape, provides a mechanism for diversity of life history and migration timing diversity. Copeland et al (2014) investigated juvenile Chinook salmon dispersal exhibited by juvenile Chinook salmon in

seven streams in Idaho, one of which was Big Creek. For their study, they partitioned juvenile life histories into two general assemblages; individuals that resided in natal reach areas for their first winter before emigrating in the spring (natal reach rearing or NRR classification) and individuals that emigrated out of natal reaches and overwintered in lower portions of tributaries or main stem rivers for their first winter before spring migration (downstream rearing or DSR classification). They found that DSR individuals had, on average, higher juvenile abundances, higher smolt-to-adult rates, and comprised of the majority of adults returning to spawn.

Monitoring efforts within the Wilderness basin of Big Creek provides a rare opportunity to study the relationship between how size, growth, and environment are related to migration timing at spatially relevant scales within the Salmon River basin. The objectives of this study were to (i) understand the effects that disparate life histories in Big Creek have on juvenile Chinook salmon growth rate, size at migration, and migration timing, (ii) investigate potential biological and environmental factors influencing ratios of these two different life history strategies, and (iii) assess the contributions of these life histories into the adult population. This information will provide valuable insight into juvenile life history choices which have strong effects on fitness and that will inform life history models needed for effective conservation efforts.

2. METHODS

2.1 Study site

Big Creek is a fourth-order tributary to the Middle Fork of the Salmon River (MFSR) located in central Idaho, USA (figure 2.1). The main stem of Big Creek contains approximately 50 km of suitable Chinook salmon spawning and rearing habitat (Thurow 2000; Hamann et al 2014). The majority of the utilized spawning habitat is located in the upper 6 km of headwater reaches and at a braided alluvial valley located 20 km upstream of the confluence of Big Creek and the MFSR (Thurow 2000; Hamann et al 2014). The watershed encompasses 1543 km² of predominantly mountainous forest and grassland habitats located almost entirely within the Frank Church River of No Return Wilderness area (Hamann et al 2014). The 1980 designation of the wilderness, coupled with the region's limited access for Native American and European settlement, resulted in a landscape with minimal anthropogenic impacts and is one of the remaining pristine watersheds in the contiguous United States. This presented the opportunity to explore the two juvenile Chinook salmon life history assemblages in a relatively unaltered environment absent of confounding anthropogenic influences.

2.2 Study population

Big Creek Chinook salmon are a population of the ESA listed "threatened" Snake River basin Chinook Evolutionary Significant Unit (Matthews and Waples 1991). Overharvest and alterations to migratory corridors have negatively affected the Big Creek Chinook salmon

population (Nehlsen et al 1991) with various climate models predicting significant decreases in parr-to-smolt survival and overall abundances (Crozier et al. 2008). Adult Chinook salmon returning to Big Creek begin their migration up the MFSR in mid-summer and migrate to spawning reaches between late July through mid-September where they build redds to deposit eggs and decrease (Isaak and Thurow 2006). The eggs incubate in the substrate through the winter and fry emerge the following spring. After emergence, individuals remain in Big Creek or emigrate to the MFSR until the following spring when nearly all individuals migrate to the ocean as age-1 fish. After reaching maturation in 1-3 years, adults return from the marine environment to natal reaches to reproduce.

2.3 Sampling sites

Juvenile data used in this study were collected from 2007-2015 at four salmonid tagging and interrogation sites along Big Creek and the Snake River (figure 2.1). At each site, juvenile Chinook salmon were captured, passive integrated transponder (PIT) tags were detected or implanted into an individual, data were recorded, and fish were released. The four sites represent a longitudinal sequence over 598 river kilometers (rkm) extending from capture and tagging in the headwaters to recapture or resighting downstream at three potential locations. In close proximity to a magnetic field, PIT tags emit a unique ten digit code effectively assigning each tagged fish a personal identification that can be detected and recorded at interrogation sites throughout their lives. Tagging and detection data were uploaded to a database created to centralize data from all tagging activities within the Columbia basin (Passive Integrated Transponder Tag Information System, www.ptagis.org).

A brief description of the tagging and interrogation sites, along with corresponding procedures, are outlined below.

Upper Big Creek - Researchers from the National Marine Fisheries Service (NMFS) have monitored juvenile Chinook salmon survival since 1992 in Big Creek (Achord et al 2007; Zabel et al 2004). From 1989-2015, NMFS scientists captured and PIT tagged juvenile Chinook salmon yearly by electrofishing in headwater habitat between 1233-1236 rkm from the Pacific Ocean and lower Big Creek habitat 1184-1185 rkm from the Pacific Ocean. Sampling occurred for several days in mid-August to early September where roughly 600-1400 juvenile Chinook salmon were captured at each site yearly. Juvenile Chinook salmon 55 mm fork length or greater were anesthetized with Tricaine Methanesulfonate (MS-222), marked with 12 mm PIT tags, measured for fork length to the nearest 1 mm, and weighed to the nearest 0.1 g. Fork lengths were recorded for all tagged individuals while weight data were taken from a random sample. Individuals were held for 12 to 24 hours, monitored for recovery, and released back into Big Creek. PIT tag retention rates in juvenile salmonids are high and it was assumed that tags were not shed after being implanted into an individual (Dare 2003). For a complete synthesis of NMFS procedures see Achord et al (1996).

Lower Big Creek - The Idaho Department of Fish and Game (IDFG) operated a rotary screw trap (RST) in lower Big Creek at rkm 1184 from 2007-2015. Rotary screw traps are passively operating traps constructed of a partially submerged cone mounted to two pontoons (Johnson et al. 2007). The pontoons enable the RST to float while the cone funnels fish into a holding box located at the stern of the RST. Once fish are in the holding box, a helical twist

within the cone prevents individuals from swimming upstream and out of the trap. The RST operated throughout the migratory season beginning in spring ice-off (early March) continuing until the onset of ice in the fall (mid-November). Dependent on spring flows, the trap did not operate for several days to several weeks in May and June. The RST was monitored daily and captured individuals were anesthetized, scanned, and implanted with a PIT tag if one was not detected. Fork length to the nearest 1 mm, weight to the nearest 0.1 g, and physical condition were recorded and individuals were released back into Big Creek. Nearly all individuals captured from March through July 1, at which time the majority of age-1 smolts had emigrated past the RST, were implanted with a PIT tag and classified as NRR. From July 1 to the removal of the RST in November, up to 50 randomly captured individuals per day were implanted with a PIT tag and classified as DSR. Juvenile Chinook salmon released downstream of the RST were rarely recaptured at the RST and were assumed to reside in lower portions of Big Creek or the Salmon River drainage after being released. For a complete synthesis of RST procedures see Copeland et al (2014).

Lower Granite Dam - Lower Granite Dam is the first of eight hydroelectric facilities along the Snake River that Big Creek juveniles encounter during emigration to the ocean. Juvenile Chinook salmon pass Lower Granite Dam via spillways (when operational), turbine intakes, or a bypass system that directs juvenile salmonids away from the turbine intakes (Prentice et al 1990). The Lower Granite Dam bypass system is equipped with PIT tag monitors with nearly 100% detection rates and temporal data were recorded for each PIT tag detected (Prentice et al 1990). Beginning in 2011, emigrating juvenile Chinook salmon from upper Big

Creek were sampled and length and weight data were recorded at Lower Granite Dam. All data collected from the Lower Granite Dam bypass systems were uploaded to the central PTAGIS database.

Little Goose Dam - Little Goose Dam is the second hydroelectric facility along the Snake River that Big Creek smolts encounter during emigration to the ocean. Similar to Lower Granite Dam, smolts pass the dam via spillways, turbine intakes, or a juvenile bypass system. The Little Goose Dam juvenile bypass system has PIT tag actuated gates that redirected targeted individuals to a processing facility where length, weight, and physical data were recorded. Juvenile Chinook salmon tagged in Big Creek by NMFS fisheries detected at the Little Goose Dam juvenile bypass system were permitted for this additional data collection but RST tagged individuals were not.

Bonneville Dam - Bonneville Dam is the first hydroelectric facility along the Columbia River that returning adult salmonids pass as they exit the marine environment and travel to natal areas. Fish ladders installed at the facility allow for upstream passage and are equipped with PIT tag monitors with nearly 100% detection efficiency. Data collected from adults detected at Bonneville Dam were uploaded to the central PIT tag depository and were used for adult abundance estimates in this study.

2.4 Growth

Overwinter growth rates were calculated for juvenile Chinook salmon captured, tagged, and released in Big Creek from 2007-2015 using the standard growth equation:

$$G = (FL_1 - FL_0)/(D_1 - D_0) \quad (1)$$

FL_0 fork lengths used for NRR and DSR individuals were recorded in Big Creek in August or September by NMFS fisheries. NRR fork lengths, FL_1 , were recorded during recapture at the RST. Downstream rearing FL_1 , fork lengths were recorded during recapture at Lower Granite Dam or Little Goose Dam juvenile bypass systems. Growth rates were measured in fork length rather than weight due to insufficient recaptures of NMFS tagged fish with weight data recorded at initial tagging.

To be classified as NRR and used for the growth analysis, individuals had to be tagged and released in Big Creek in August or September by NMFS researchers and recaptured the following spring at the RST during emigration. DSR classified individuals needed to be tagged and released in Big Creek in August or September by NMFS researchers, recaptured the concurrent fall at the RST, and recaptured at the Little Goose or Lower Granite juvenile bypass systems the following spring. Chinook salmon tagged at the RST were not eligible for the analysis because length and weight data were not collected at the hydroelectric facilities for these individuals.

I ran 10,000 iteration non-parametric bootstraps to calculate means and corresponding confidence intervals for overwinter growth rates of DSR and NRR individuals. A two-way analysis of variance (ANOVA) was used to determine if rearing type, brood year, or an interaction between rearing type and brood year, had a significant effect on overwinter growth rates.

2.5 Fork length

Individuals classified as NRR and used for the fork length analysis consisted of Chinook salmon that were tagged and released in August or September by NMFS researchers and recaptured at the RST the proceeding spring. DSR individuals included in the fork length analysis were tagged and released by NMFS researchers in August or September, recaptured the concurrent fall at the RST, and recaptured at the juvenile bypass facilities the following spring. I ran 10,000 iteration non-parametric bootstraps to calculate means and corresponding confidence intervals for fork lengths of DSR and NRR individuals. A two-way analysis of variance (ANOVA) was used to determine if brood year, or an interaction between brood year and rearing type, had a significant effect on fork lengths.

2.6 Spring migration timing

All Chinook salmon tagged at the Big Creek RST and detected at the Lower Granite Dam juvenile bypass system were used for the spring migration timing analysis. Individuals captured between trap installation in March through July 1, when the majority of age-1 Chinook salmon were presumed to have emigrated out of Big Creek, were classified as NRR. Individuals captured from July 2 through trap removal in November were classified as DSR. Physical characteristics (e.g. size, parr marks, and silver coloration) were used to distinguish age-1 NRR and age-0 DSR individuals in early and mid-summer when the two life histories overlapped at the RST. I ran 10,000 iteration non-parametric bootstraps to calculate means and corresponding confidence intervals for Julian day detection at Lower Granite Dam for DSR and NRR individuals. A two-way analysis of variance (ANOVA) was used to determine if

brood year, or an interaction between brood year and rearing type, had a significant effect on Julian day detection at Lower Granite Dam.

2.7 Cohort Ratios

Ratios of NRR to DSR abundances within a cohort were hypothesized to be influenced by changes in seasonal discharge, seasonal temperature, and total cohort abundance. NRR and DSR abundance estimates used for ratios were calculated with a between year hierarchical time-stratified Bayesian estimator using mark-recapture data collected at the RST (Chapter 1). The between-year hierarchical model utilized recurring migratory patterns exhibited by salmonids in Big Creek to interpolate estimates from prior years when data were sparse or missing. This model enabled us to compare ratios without potential bias introduced by periods when the RST was not operable but fish were migrating. Abundance estimates for DSR individuals that were less than 60 mm at the RST during early summer migration and could not be tagged, were calculated by applying capture probabilities obtained from individuals that were large enough to be tagged and recaptured. Water depth and temperature data were collected every hour from 2008-2014 using an In-Situ Inc. Level Troll 300 sensors located roughly 60 km from the confluence of Big Creek and the MFSR. Seasons were partitioned as follows; winter was from January 1 through March 31, spring was from April 1 through June 30, summer was from July 1 through September 30, and fall was from October 1 through December 31.

Multi-model selection founded on Akaike's information criterion corrected for small sample size (AIC_c , Burnham and Anderson 2002) was used to compare the main effects of total

cohort abundance; spring, summer, and fall mean temperature; and spring, summer, and fall mean water depths to ratios of NRR to DSR abundances within cohorts. The best fit model was selected on the lowest AIC_c and residuals of the predicted to observed data were assessed to inspect model fit.

2.8 Adult recruitment

Adult abundance estimates for cohort and rearing type were calculated by expanding the number of adult Chinook salmon detected with PIT tags at Bonneville Dam by the proportion of tagged individuals within the cohort. Proportions of tagged individuals within cohorts were calculated by dividing the number of juveniles tagged at the RST by the estimated juvenile abundance. For consistency with previous studies (Copeland et al 2014) subtaggable DSR individuals were excluded from the adult analysis. Survival from tagging at the RST to adult return at Bonneville Dam (S_t) was calculated by dividing the estimated adult abundance at Bonneville Dam by the juvenile abundance estimate at the RST. To acquire estimates of the number of NRR and DSR adults returning each year, adults detected at Bonneville Dam were partitioned by their corresponding brood year and life history classifications and these counts were expanded by the ratio of tagged individuals within that cohort and life history type. I was able to obtain these estimates from 2009-2014 under the assumption that adults were fully recruited back into the population after three years in the marine environment. Redd data were collected by aerial and ground surveys conducted by state, federal, and tribal agencies throughout Big Creek from August through October.

3. RESULTS

NMFS fisheries crews tagged 8,313 juvenile Chinook salmon in Big Creek from 2007-2014. I was able to classify 32 NRR individuals and 59 DSR individuals for our fork length at migration and overwinter growth rate analyses. I was unable to classify DSR individuals from cohort 2006 due to a lack of sufficient numbers of recaptured individuals at the RST and hydroelectric facilities.

DSR overwinter growth rates were nearly double, 0.14 mm/day (0.13, 0.15 95% CI), that of NRR individuals, 0.08 mm/day (0.07, 0.09 95% CI) (figure 2.2). Results showed brood year or interactions between brood year and rearing type did not have significant effects on growth rates (P -value > 0.05). Mean DSR fork length during spring migration at Little Goose or Lower Granite dam was 106.9 mm (95% CI: 105.7, 109.1) and mean NRR fork length during spring migration at the RST was 84.8 mm (95% CI: 82.8, 86.8) (figure 2.3). Results showed brood year 2012 had a significant effect on fork length (P -values < 0.05) but this was likely an artifact from the imbalance between NRR and DSR individuals sampled during this brood year (nine out of the eleven individuals were classified as NRR for that brood year).

There were 38,182 Chinook salmon captured and PIT tagged at the Big Creek RST from 2007-2015 and 1,553 NRR and 3,342 DSR individuals were detected at the Lower Granite Dam juvenile bypass system. Mean Julian day arrival at the Lower Granite Dam was 125 (95% CI: 124, 126) for DSR individuals and 133 (95% CI: 132, 134) for NRR individuals (figure 2.4). Results showed both brood year, rearing type, and all interactions except brood year 2012 and rearing type interaction were statistically significant at the conventional 0.05

alpha value. Incorporating brood year and interaction effects, NRR individuals arrived four to fourteen days later than DSR individuals depending on the year.

The multi-model selection results showed the best fit model for predicting ratios of NRR to DSR abundances within cohorts included total cohort abundance as the sole explanatory variable with an AIC_c value -15.33, with the next competing model AIC_c value of -10.89 (table 2.1). Visual inspection of quantile-quantile plots and residual versus predicted plots showed model fit and distributional assumption for the AIC_c best fit model were satisfactory. The linear regression r^2 value of total cohort abundance to NRR/DSR ratios was 0.64 with a total cohort abundance coefficient P-value of 0.009 (figure 2.5).

Adult abundance estimates varied greatly between cohorts and years ranging from estimates of 43 NRR adults from the 2009 cohort, to 1044 DSR adults from the 2010 cohort (table 2.2). The disparity between NRR to DSR adult abundances within a cohort was greatest in 2010 where DSR individuals dominated recruitment by tenfold, and lowest in 2006 where NRR individuals composed of over one third of the total adult recruitment. With the exception of cohort 2007, NRR individuals had greater trap to adult survival. Linear regression comparing ratios of NRR to DSR adult abundance to corresponding NRR to DSR progeny had a negative correlation with an r^2 value of 0.3994 (figure 2.7).

4. DISCUSSION

Juvenile Chinook salmon that resided in natal reach rearing areas of Big Creek during their first winter had on average, slower winter growth rates, were smaller during spring

migration, and migrated later than individuals that overwintered in lower portions of Big Creek or the MFSR. During winter months, larger order streams typically have warmer temperatures, increased productivity, and more available habitat relative to their tributary counterparts (Vannote et al 1980), likely resulting in the observed differences in NRR and DSR growth rates and fork lengths at migration.

The increased overwinter growth rates resulted in DSR individuals achieving greater fork lengths during spring migration. Due to sampling limitations at the RST during spring high water periods in May, data collected for NRR individuals typically occurred in March and April, while data collected at Lower Granite Dam and Little Goose Dam typically occurred in early May. This created an average 29-day temporal discrepancy between NRR and DSR data collection and presented DSR individuals with additional opportunity for growth. For NRR individuals to achieve equivalent fork lengths at migration, it would require an average growth rate of 0.76 mm/day (nearly tenfold increase from their mean overwinter growth rates) during this 29 day period. For fork lengths to no longer be statistically different, it would require NRR individuals to grow at an average 0.68 mm/day. Due to increases in spring water temperature it is probable that growth rates increased for NRR individuals during this April and May time period. It is unlikely that NRR individuals were able to achieve the required growth rates to become comparable in size to DSR individuals during the April and May migration due to limitations in environmental conditions. For juvenile Chinook salmon in laboratory settings, optimal temperature for growth was found to be roughly 19°C (Brett et al 1982; Perry et al 2015). In natural environments, relationships

between growth and temperature become more complex when food availability becomes a limiting factor and can result in variable growth rates between and within populations of juvenile Chinook salmon of the same size and age (Carter 2005). Several extensive reports on juvenile Chinook salmon growth have been compiled (WDOE 2002; Carter 2005; Williams 2006) and maximum growth was typically found to occur between 15-18°C for natural populations of Chinook salmon. For studies that measured growth rates using fork lengths, maximum observed growth rates achieved in the optimal temperature range typically varied between 0.5 to 0.6 mm/day, with the exception of Connor and Burge (2003) that reported growth rates over 1.0 mm/day for fall-run Chinook salmon (Healey 1991; Weatherly and Gill 1995). Access to water temperature data on MFSR and the main Salmon River were not available until rkm 781 near Anatone, Washington. The site at near Anatone, WA, was installed and maintained by the National Oceanic Atmosphere Administration (NOAA) from 1959-2015. April and May mean temperatures recorded from 2007-2015 were between 9-14°C (<http://www.nwrhc.noaa.gov/>). Due to the sub-optimal growth temperatures recorded at the NOAA Anatone, WA data station on the Salmon River, it is unlikely that NRR growth rates increased enough for individuals to achieve the necessary growth to reach comparable sizes to DSR individuals during migration.

Emigrating from headwater habitat in the fall and overwintering in lower portions of the watershed led DSR individuals to arrive earlier to Lower Granite Dam than NRR individuals. Previous studies have found juvenile Chinook salmon that were larger during migration and that migrated earlier had a higher probability of returning as an adult (Zabel and Williams

2002; Williams et al 2005). Copeland et al (2014) found that DSR individuals had higher smolt-to-adult rates compared to NRR individuals. Results of this study showed that DSR individuals were larger during migration and migrated earlier than NRR individuals; providing a harmonious link between the physical characteristics of NRR and DSR expressions and the resulting survival and recruitment back into the population.

Migration characteristics are a heritable trait (Taylor 1990) so the negative correlation between adult to juvenile progeny ratios was somewhat surprising. This negative correlation suggests that density may effect influencing life history expressions within Big Creek. Increased juvenile abundances would increase competition for habitat in natal rearing areas making it advantageous for individuals, from both DSR and NRR parentage, to disperse downstream to less populated habitat. The correlation between NRR/DSR adult ratios and corresponding ratios of NRR/DSR juvenile progeny support this hypothesis. As ratios of adult NRR to DSR abundances increased, juvenile NRR to DSR ratios declined.

Trap to adult rates (S_t) were higher for NRR with the exception of cohort 2007. Downstream rearing individuals were smaller during emigration out of headwater habitat during fall periods, relative to NRR individuals that emigrated in the spring, and were likely subject to increased opportunities of predation by large populations of bull trout and cutthroat trout that inhabit the Big Creek and MFSR drainage. NRR individuals that remained in natal reach rearing areas were still subject to predation but did so during a period of increased flows, cooler water temperatures, increased water turbidity, and were larger in size, potentially resulting in the observed increase in NRR S_t . In addition, estimates of S_t for NRR individuals

do not include overwinter mortality since capture at the RST occurs during the spring period, biasing S_t estimates.

Due to the complexity and variability of life history strategies in populations of Chinook salmon within the Columbia River basin, partitioning the effects that life history decisions during critical life-stages have on survival and reproductive success is paramount in understanding a populations viability. This study provides a link between the physical and behavioral trade-offs of the two general life history assemblages of juvenile Chinook salmon in Big Creek that have significant implications on survival and reproductive success. This information, in addition to what environmental and biological forces may be acting upon life history variations, are a small, yet important, component needed to understand the Big Creek Chinook salmon population. With the array of Chinook salmon life history expressions and the diversity of environmental conditions within the Snake River basin, it is likely that trends found in Big Creek may not be apparent in other populations within the Snake River basin. In order to understand the dynamics of additional populations within the Snake River basin Chinook, similar analyses will be required and is an open avenue of research that I intend to explore.

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6. TABLES

Table 2.1. Akiake's information criterion corrected for small sample size (AIC_c), difference between AIC_i and best fit model (ΔAIC_c), and Akiake's weight (w_i) for the seven main effect models with lowest AIC_c for predicting natal reach rearing to downstream rearing juvenile Chinook Salmon cohort ratios in Big Creek, ID. The Null model only contained an intercept parameter. All other models contained an intercept parameter in addition to the parameters listed in the table. Explanatory variables included in model construction were as follows: cohort abundance; spring, summer, and fall mean water temperature; spring, summer, and fall mean water depth.

Model	AIC_c	ΔAIC_c	w_i
Abundance	-15.33	0.00	0.90
Null	-10.89	4.44	0.10
Spring mean depth	-3.17	12.16	0.00
Summer mean depth	-0.40	14.93	0.00
Summer mean temp	0.16	15.49	0.00
Abundance + summer mean temp	1.83	17.16	0.00
Abundance + summer mean depth	3.25	18.58	0.00

Table 2.2 Redd counts from Big Creek, Idaho, partitioned as the confluence of the Middle Fork Salmon River upstream 58 rkm to Logan Creek confluence (lower) and Logan Creek confluence to rkm 63 (upper). Brood year information on the number of juvenile Chinook Salmon tagged at the rotary screw trap (tags), juvenile abundance estimate (juvenile \hat{N}), the number of returning adults detected at Bonneville Dam (adult detected), estimated number of adults returning to Big Creek (adult \hat{N}), and trap to adult survival (S_t) for natal reach rearing and downstream life history assemblages from Big Creek, Idaho.

Cohort	Redds		Population statistics					
	Upper	Lower	Rearing	Tags	Juvenile \hat{N}	Adult tag	Adult \hat{N}	S_t
2006	9	14	NRR	725	17882	17	419	0.0234
			DSR	5454	39635	97	705	0.0178
2007	20	30	NRR	829	9939	7	84	0.0084
			DSR	3185	48950	37	569	0.0116
2008	42	22	NRR	1286	15815	20	246	0.0156
			DSR	4279	93247	37	806	0.0086
2009	92	32	NRR	1360	14753	4	43	0.0029
			DSR	5048	153649	6	183	0.0012
2010	46	46	NRR	551	8220	8	119	0.0145
			DSR	3253	212218	16	1044	0.0049
2011	61	35	NRR	1039	17212	6	99	0.0058
			DSR	2946	126737	15	645	0.0051

7. FIGURES

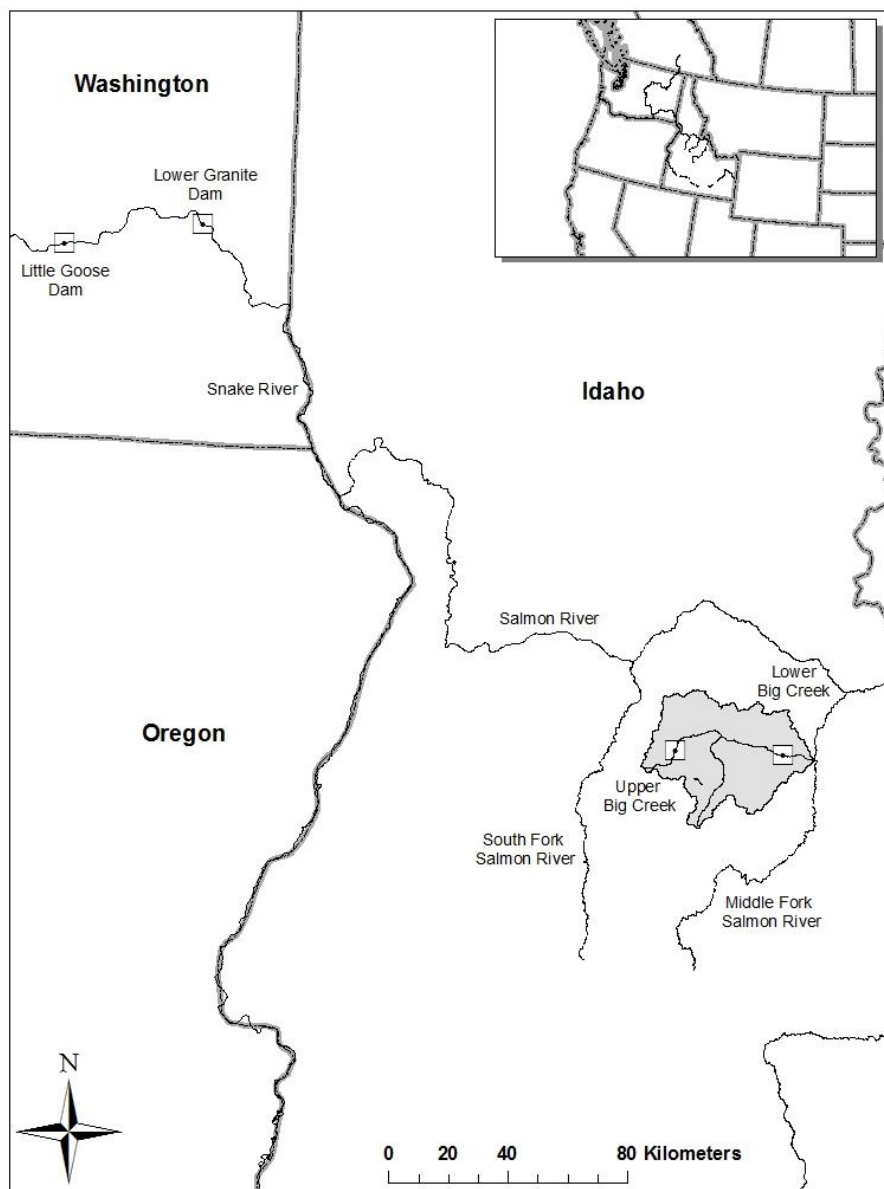


Figure 2.1 Big Creek watershed located in Idaho, USA. Squares with dots represent detection and interrogation sites. Upper Big Creek is the location of National Marine Fisheries Service electrofishing site, lower Big Creek is the location of the rotary screw trap operated by the Idaho Department of Fish and Game, Lower Granite Dam is the first hydroelectric dam juvenile Chinook Salmon from Big Creek encounter, and Little Goose Dam is the primary site used to collect physical data during spring migration for downstream rearing individuals from Big Creek.

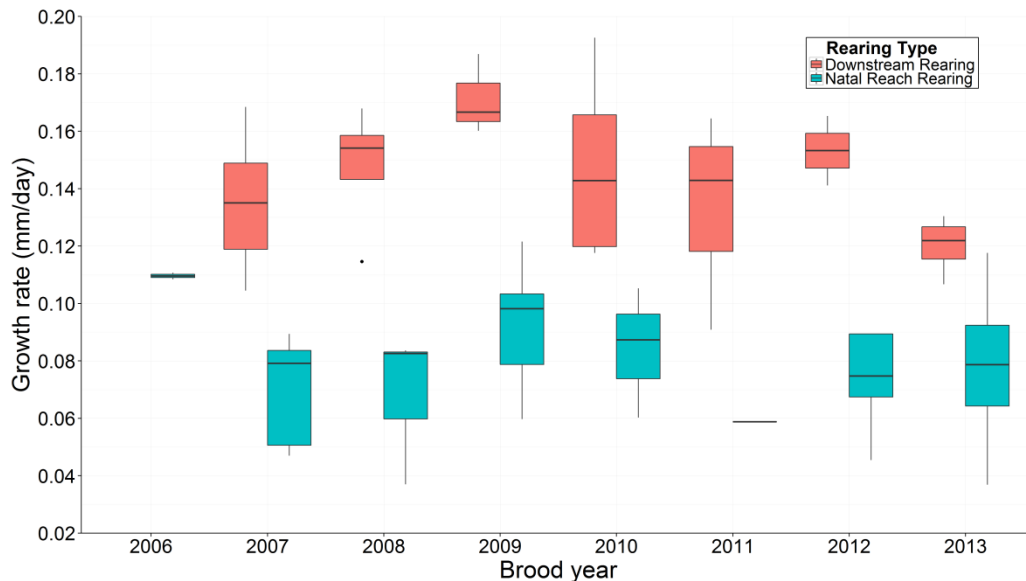


Figure 2.2 Overwinter growth rates for downstream rearing (n=59) and natal reach rearing (n=32) juvenile Chinook Salmon from brood years 2006-2013 from Big Creek, Idaho.

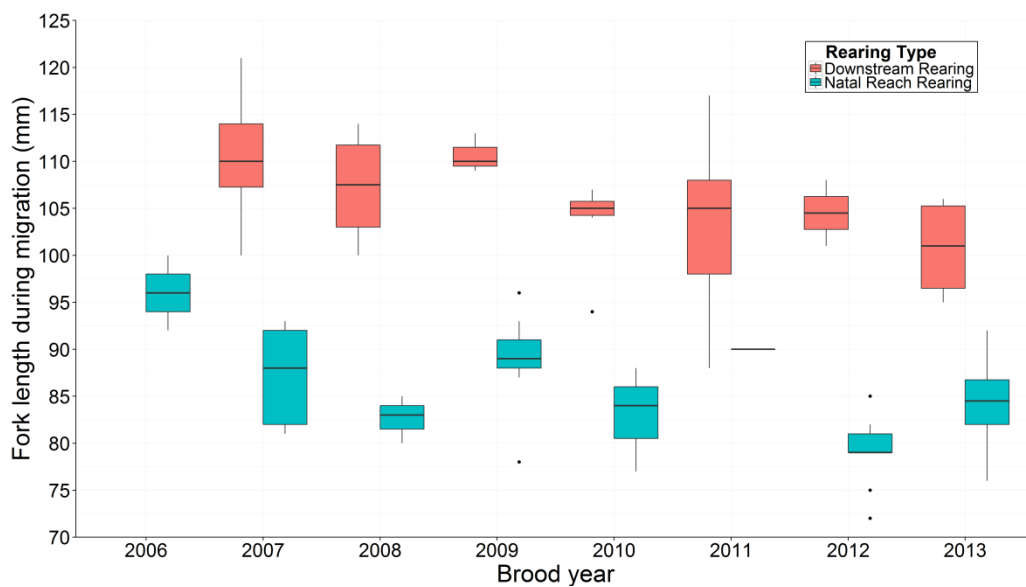


Figure 2.3 Fork Length at migration for downstream rearing juvenile Chinook Salmon at Lower Granite Dam or Little Goose Dam and natal reach rearing juvenile Chinook Salmon at the rotary screw trap from Big Creek, Idaho, for brood years 2006-2013.

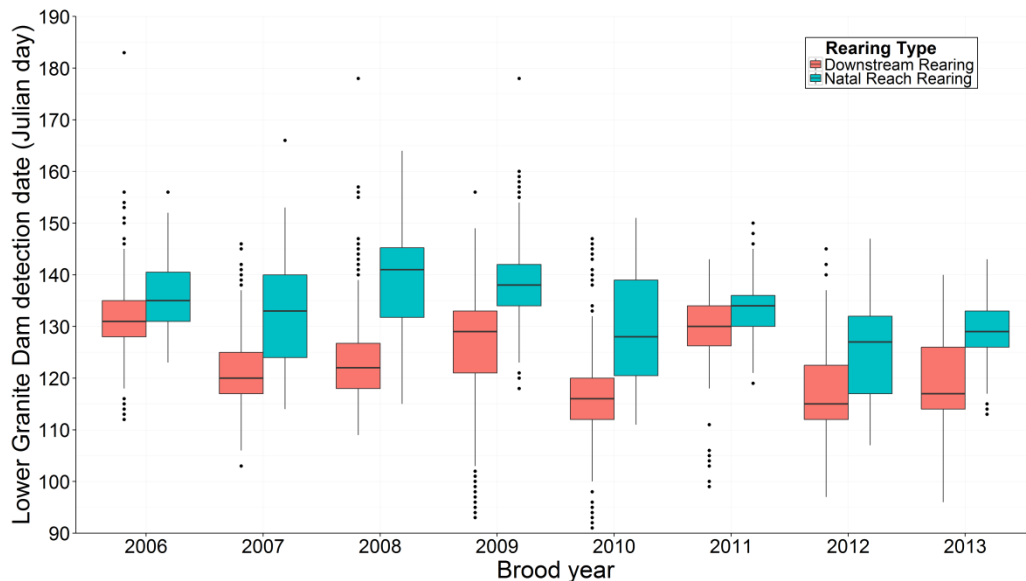


Figure 2.4 Julian day detection at Lower Granite Dam for downstream rearing (n=3,342) and natal reach rearing (n=1,553) juvenile Chinook Salmon from brood years 2007-2013 from Big Creek, Idaho.

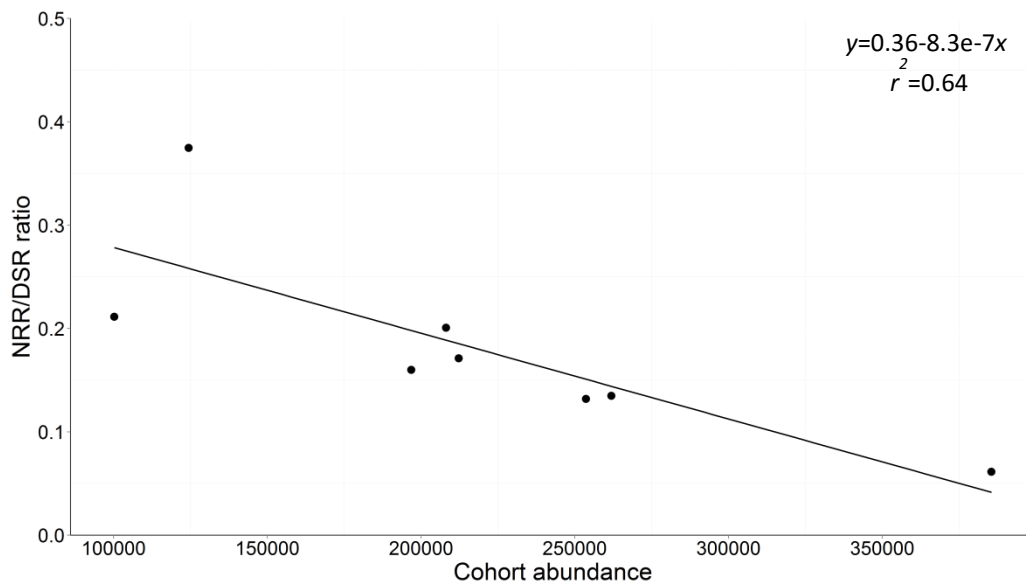


Figure 2.5 Correlation of yearly juvenile Chinook Salmon cohort abundance to natal reach rearing and downstream rearing cohort ratios for brood years 2006-2013 at Big Creek, Idaho.

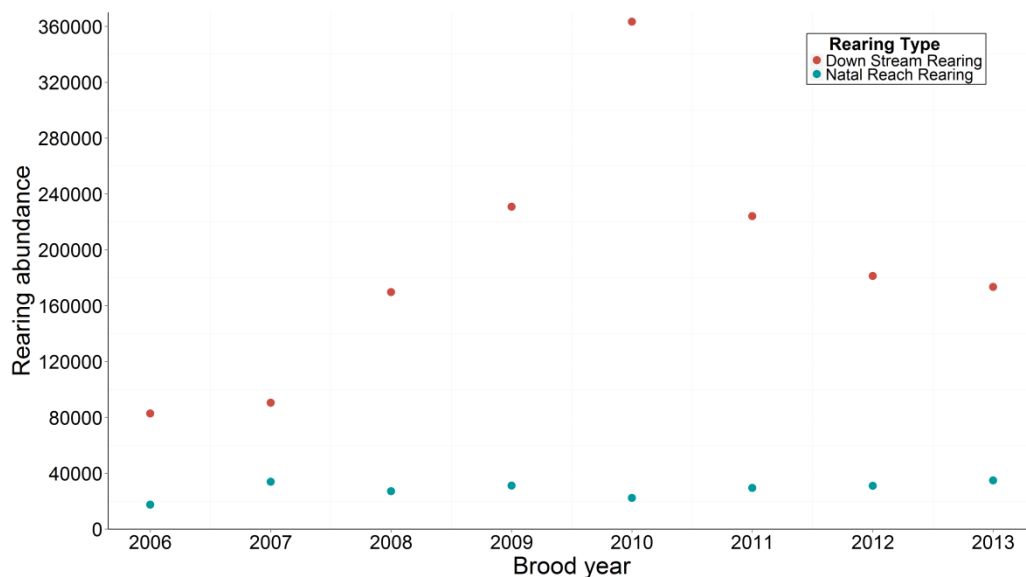


Figure 2.6 Juvenile Chinook Salmon natal reach rearing and downstream rearing abundance estimates for brood years 2006-2013 at Big Creek, Idaho.

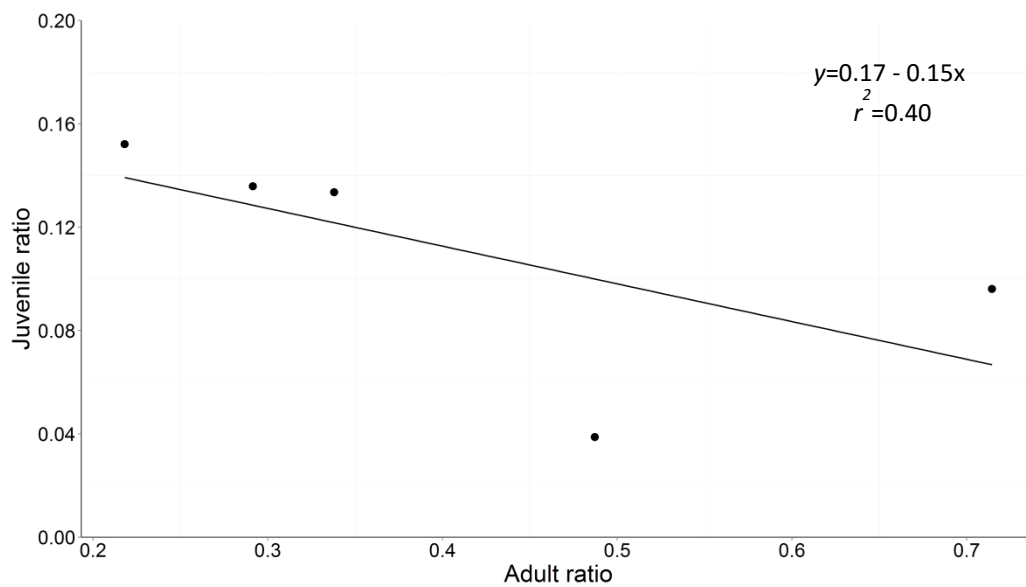


Figure 2.7 Natal reach rearing to downstream rearing adult Chinook Salmon ratios and corresponding ratios of natal reach rearing to downstream rearing progeny in Big Creek, Idaho, cohorts 2009-2013.