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A Bayesian hierarchical approach to integrating historical and in-season genetic data for real-time assessment of a mixed stock fishery

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Running head: In-season genetics for mixed stock fisheries
**Abstract:** With advances in molecular genetics it is becoming increasingly feasible to conduct genetic stock identification (GSI) to inform management actions that occur within a fishing season. While applications of in-season GSI are becoming widespread, such programs seldom integrate data from previous years, underutilizing the full breadth of information available for real-time inference. In this study, we developed a Bayesian hierarchical model that integrates historical and in-season GSI data to estimate temporal changes in the composition of a mixed stock of sockeye salmon returning to Alaska’s Chignik watershed across the fishing season. Simulations showed that even after accounting for time constraints of transporting and analyzing genetic samples, a hierarchical approach can rapidly achieve accurate in-season stock allocation, outperforming alternative methods that rely solely on historical or in-season data by themselves. As the distribution and phenology of fish populations becomes more variable and difficult to predict under climate change, in-season management tools will likely be increasingly relied upon to protect biocomplexity while maximizing harvest opportunity in mixed stock fisheries.

**Keywords:** Bayesian hierarchical, genetic stock identification (GSI), in-season fisheries management, mixed stock fishery, sockeye salmon
**Introduction:**

Managing harvest that simultaneously targets multiple populations is a classic and common challenge in fisheries. Failing to account for such demographic heterogeneity can lead to biased estimates of biological reference points, non-stationary stock-recruit relationships, overfishing of less productive stocks, and may have evolutionary consequences deleterious to long-term yield and sustainability (Cadrin, Goethel, Morse, Fay, & Kerr, 2018; Hard et al., 2008; Hilborn, 1985; Hilborn & Walters, 1992). Several methods of stock identification have been used to infer the composition of mixed stock fisheries, sometimes relying on morphological or meristic variation among populations (Cadrin, 2000; Cadrin, Kerr, & Mariani, 2013; Marshall et al., 1987). In particular, genetic stock identification (GSI) methods have become common, including the use of single nucleotide polymorphisms (SNPs) that are easily surveyed, powerful for discriminating stock structure, and amenable to high throughput and automation (Hauser & Seeb, 2008). With continuing advances in molecular genetics, it is becoming increasingly feasible to conduct GSI in near real-time to inform management decisions that occur within the fishing season (Bue, Borba, Cannon, & Krueger, 2009; Seeb et al., 2000; Shaklee, Beacham, Seeb, & White, 1999; Smith, Templin, Seeb, & Seeb, 2005). While in-season applications of GSI are becoming common, such programs seldom make use of all available data, ignoring information from previous years that may be leveraged to improve real-time inference on compositional dynamics.

Many Pacific salmon (*Oncorhynchus spp.*) populations in North America are managed under a fixed escapement policy wherein harvest is permitted only after sufficient individuals are projected to have escaped the fishery to achieve a certain target abundance, such as the number of spawners that produces maximum sustainable yield ($S_{MSY}$) (Hilborn & Walters, 1992).
Commercial fishing seasons for Pacific salmon are usually limited to the duration of the spawning migration, occurring over 1-3 months in most cases. To maintain life history variation in run timing and intra-population diversity, managers often decompose the total escapement goal into a schedule of interim targets across the season. The inferred escapement to a stock can then be compared to its interim escapement targets across the season to determine whether fishing should be allowed at a given point in time. However, during the marine and early freshwater portions of their spawning migration, salmon from multiple stocks may be present in the same location and an individual’s population of origin is not necessarily apparent. In these circumstances, reliable estimation of the escapement to each population can be crucial to regulating harvest on the stock mixture (but see Connors et al., 2020; Freshwater, Holt, Huang, & Holt, 2020).

Molecular genetics has played an increasingly important role in contemporary fisheries ecology and assessment, identifying cryptic stock structure and management units, informing stock-recruit dynamics, and improving estimates of population viability (Hauser & Seeb, 2008; Hauser & Carvalho 2008; Satterthwaite et al., 2014; Shaklee et al., 1999; Spies et al., 2018; Spies, Spencer, & Punt, 2015; Spies & Punt, 2015). In the management of Pacific salmon, genetic information from mixed stock fisheries is often used in run reconstruction and stock-recruit models that form the basis for forecasting future returns and establishing management reference points (Cunningham et al., 2017). Additionally, genetic tools are being used increasingly to inform management decisions that occur within the fishing season (Shaklee et al., 1999; Smith et al., 2005). For example, Dann et al. (2013) used in-season genetic data to detect migratory trends in the stock composition of Bristol Bay sockeye salmon (*O. nerka*) prior to arrival in the fishery, revealing spatial and temporal patterns that were unanticipated from
preseason forecasts. With this information, managers were able to re-allocate fishing effort in real time to avoid overfishing less abundant populations while maximizing harvest opportunity on robust stocks. Such successful applications of in-season GSI are encouraging, and reflect the broad utility of this approach for addressing the challenges of real-time fisheries management (Beacham, Lapointe, Candy, Miller, & Withler, 2004; Bednarski, Sogge, Miller, & Heinl, 2017; Bue et al., 2009; Seeb et al., 2000; Templin & DeCovich, 2009). However, as in-season GSI becomes more common, developing statistical frameworks to make the most efficient use of these data will be essential to maximizing their utility for managers.

Here, we explore a novel application of in-season GSI for sockeye salmon from Alaska’s Chignik watershed that incorporates information from other years to improve in-season inference on the stock composition. Fisheries in this region exploit two separate stocks of sockeye salmon that spawn in Black Lake and Chignik Lake. The two stocks differ in their run timing, with Black Lake fish arriving first, and the Chignik Lake run occurring later in the season (Dahlberg, 1968). However, there is sufficient temporal overlap between the two runs such that both stocks are typically present in appreciable portions for much of the fishing season. Because the two stocks are reproductively isolated (Creelman, Hauser, Simmons, Templin, & Seeb, 2011; Witteveen & Botz, 2003), they are managed with separate escapement goals, both of which are factored into real-time harvest control decisions (Wilburn, 2019; Wilburn & Stumpf, 2018). Throughout the fishing season, managers monitor the inferred escapement to each stock relative to its interim escapement target for that point in time and decide whether or not fishing should proceed. However, escaped fish are counted at a weir on the Chignik river, which both Black Lake and Chignik Lake fish pass through on their spawning migration. As such, methods to distinguish Black Lake fish from Chignik Lake fish in the aggregate escapement are needed in
order to track each stock’s escapement status and inform decision-making within the fishing
season. Within the past decade, the Alaska Department of Fish and Game (ADF&G) has
implemented a program for GSI of Chignik sockeye salmon to estimate the stock composition of
the escapement and explore the potential applications of this information for real-time
management (Stumpf, 2017). In this study, we develop a Bayesian hierarchical modelling
framework that integrates historical and in-season GSI data to efficiently estimate the stock
composition within the fishing season. An expectation for the timing and speed of the transition
between stocks is developed from historical data, and is modified sequentially as new data are
accumulated, thereby adjusting for annual deviations. Additionally, we conducted simulation
testing to examine the value of this approach for in-season assessment, and how its performance
varies with alternative implementation scenarios.

Methods:

Located on the south side of the Alaska Peninsula, the Chignik watershed is composed of
two lakes (Figure 1), each of which supports genetically distinct populations of sockeye salmon
with different migratory timings (Creelman et al., 2011). Black Lake produces sockeye salmon
that typically migrate into the watershed in June to July and spawn in late August and early
September. A second sockeye salmon run migrates into the watershed in late June through
September to spawn after early September in Chignik Lake and its tributaries. The Black and
Chignik lake stocks are reproductively isolated (but share rearing habitat) and managed as two
separate runs with their own escapement goals (Schaberg, Foster, & St. Saviour, 2019; Wilburn,
2019). Both Black Lake and Chignik Lake sockeye salmon are harvested together in the five
major fishing districts that target these populations (Dann et al., 2012a). Given the mixed stock
nature of the fisheries, reliable estimates of the proportion of early (Black Lake) versus late
(Chignik Lake) run fish present in the total escapement at any given point in time are needed to
determine if each stock’s interim escapement targets are being met, providing one of several
sources of information that can be used in harvest control decisions. Management is then
prosecuted through a system of fishery openings and closures which typically span 1-3 days at a
time.

To inform management objectives, the ADF&G operates a weir on the Chignik River
where enumeration and sampling of the escapement occurs. Fish passing through the weir are
counted daily, and up to 240 individuals are sampled for age, sex, and length (ASL) each week
(Wilburn & Stumpf, 2018). Prior to genetic sampling, several additional sampling programs
were implemented to infer the stock composition of sockeye salmon returning to the Chignik
watershed, the most recent of which was scale pattern analysis (SPA; Marshall et al., 1987)
which began in the 1970s. Since 2010, genetic samples have been collected from salmon passing
through the Chignik weir as a means to more accurately partition escaped fish among stock
components (Stumpf, 2017; Wilburn, 2019).

Genetic sampling and mixed stock analysis:

To fulfill the sampling requirements of GSI, each year tissue is collected from ~190
sockeye salmon passing through the Chignik weir during each of 5-11 sampling strata
throughout the transition period, concurrent with the routine ASL sampling (Wilburn & Stumpf,
2018). The sampling strata vary from year to year but are typically scheduled roughly four to six
days apart and timed to coincide with the period of the season during which the run is likely to
be transitioning from the Black Lake to the Chignik Lake stock (late June through late July).
Tissue samples are collected non-lethally from the axillary process and preserved in ethanol before being shipped via commercial air service to the ADF&G Gene Conservation Lab (GCL) in Anchorage, AK. Upon arrival at the GCL, DNA is extracted from the samples and genotyped for 24 sockeye salmon SNPs that have been shown to best distinguish the early and late runs (Dann, Barclay, & Habicht, 2012). A complete description of the sampling, extraction, genotyping and quality control and assurance protocols can be found in Dann et al. (2012). The stock composition for each sampling stratum is estimated using a Bayesian mixed stock analysis using the Pella-Masuda model as implemented in the program *BAYES* (Pella & Masuda, 2001). The Pella-Masuda model requires a baseline of allele frequencies for each population as well as prior information about the stock proportions in addition to the genotypes of fish sampled. The baseline allele frequencies for sockeye salmon populations and the groups into which the populations are combined are described in Dann et al (2012). Priors for each sampling event are Dirichlet distributed, with a mean and variance based on the posterior distribution from the previous stratum. For the first sample of each year, the prior is determined by the posterior from the first stratum of the previous year (Dann et al., 2012a; Pella & Masuda, 2001). From each sampling stratum, the Pella Masuda model generates a posterior distribution of the stock composition. Using the median estimate of the stock composition for each sampling event, we calculated the number of fish assigned to each stock, which serve as the data inputs for the hierarchical model described below. Importantly, this approach does not propagate uncertainty from the mixed stock analysis to the hierarchical model, representing a sequential rather than integrated modelling approach (Staton, Catalano, & Fleischman, 2017).

**Hierarchical logistic transition model:**
Genetic sampling and mixed stock analysis provide information on the composition of the escapement only for the days on which sampling occurs. To infer between and beyond these dates, the estimated stock composition data must be fitted to a model that describes the functional form of the transition between the early and late runs in the aggregate escapement. Historically, the transition has been assumed to follow a logistic curve, which the available data support (ADF&G unpublished data). However, fitting a model in-season for each year independently can be problematic, as the information available for parameter estimation is limited early in the season when few genetic samples have been processed and the escapement is typically still dominated by the early run. To overcome this challenge, the parameters of the logistic transition curve for a given year can be modelled hierarchically, as random variables originating from a common distribution shared among years:

\[
\phi_{i,y} = \frac{1}{1 + \exp \left( -\psi_y \left( i - \tau_y \right) \right)}
\]

(1)  \[ \phi_{i,y} = \frac{1}{1 + \exp \left( -\psi_y \left( i - \tau_y \right) \right)} \]

where \( \phi_{i,y} \) is the estimated proportion of late run (Chignik Lake) fish on day \( i \) of year \( y \), \( \psi_y \) is the steepness of the logistic transition curve for year \( y \) and \( \tau_y \) is a parameter specifying the midpoint of the curve at which the run is 50% early and 50% late run fish for year \( y \). To create more interpretable parameters, we used an alternative form of the logistic function:

\[
\phi_{i,y} = \frac{1}{1 + 19 \frac{\psi_y}{\psi_y}}
\]

(2)  \[ \phi_{i,y} = \frac{1}{1 + 19 \frac{\psi_y}{\psi_y}} \]
where \( \tau_y \) is interpreted as before, but the steepness term \( (\psi_y) \) now represents the additional number of days after \( \tau_y \) that are required for the escapement to reach 95% late run. To make use of other years’ data, we modelled the steepness \( (\psi_y) \) and midpoint \( (\tau_y) \) of a given season’s transition function hierarchically among years. Annual sets of parameter values \( (\theta_y) \) are assigned a bivariate normal prior distribution to allow for correlation between the steepness and midpoint terms.

\[
\theta_y = \begin{pmatrix} \psi_y \\ \tau_y \end{pmatrix} \sim MVN(\mu, \Sigma)
\]

Where \( \mu \) represents a vector of means for the model parameters and \( \Sigma \) is the covariance matrix of the distribution. To improve the stability of posterior sampling and avoid the bias that can occur when estimating hierarchical models using Monte Carlo methods (Betancourt, 2016; Monnahan, Thorson, & Branch, 2017; Stan Development Team, 2019), we implemented this distribution using a multivariate form of the non-centered parameterization, with the covariance matrix decomposed into the Cholesky factor of the correlation matrix \( (\Omega) \) and a vector of error terms \( (\xi, \eta) \), where \( \xi_{\tau} = \sqrt{\Sigma_{\tau,\tau}} \) and \( \xi_{\psi} = \sqrt{\Sigma_{\psi,\psi}} \):

\[
\theta_y = \mu + \text{diag}(\xi)\text{cholesky}(\Omega)z_y
\]

where:

\[
\Omega = \text{cholesky}(\Omega)\text{cholesky}(\Omega)^T
\]
and:

\[ \Sigma = \text{diag}(\xi) \Omega \text{diag}(\xi). \]  

In the non-centered parameterization, \( z_y \) is a vector of standard scaling factors for each parameter in each year \( (z_y^\psi, z_y^\tau) \) that are normally distributed with a mean of 0 and a standard deviation of 1 (Monnahan et al., 2017). The among-year means of the steepness \( (\mu_\psi) \) and midpoint \( (\mu_\tau) \) terms were each assigned uniform priors bounded between 1 and \( n \), where \( n \) is the total number of days in a season. These priors were selected to represent the full domain of feasible values for these parameters and were subject to sensitivity testing with alternative choices. The standard deviations of the among-year distributions of \( \tau \) and \( \psi \) \( (\xi_\tau \text{ and } \xi_\psi) \) were given vague half-normal priors, with means of 0 and standard deviations of \( n \). The Cholesky factor of the correlation matrix was given an LKJ prior (Lewandowski, Kurowicka, & Joe, 2009):

\[ \text{Cholesky}(\Omega) \sim \text{LKJCorr}(\eta) \]

where \( \eta \) is a shape parameter that controls the expected degree of correlation. We specified \( \eta \) equal to 2, which represents a weakly informative prior expectation of less correlation between parameters (Stan Development Team, 2019).
The number of fish within a genetic sample assigned to the late run ($x_{i,y}$) was assumed to follow a binomial distribution with a number of trials ($N_{i,y}$) equal to the total number of fish sampled for genotyping, and a probability of including a late run fish in the sample, $p_{i,y}$:

$$x_{i,y} \sim \text{Bin}(p_{i,y}, N_{i,y})$$

While the binomial distribution describes the error associated with sampling the escapement, there are additional potential sources of error in these data (e.g. the genotyping and genetic stock assignment procedures). As such, it is not surprising that model fits assuming binomial error displayed overdispersion (Figure S1). To account for extra-binomial variance, we specified a beta-binomial likelihood in which the probability of detecting a late run fish follows a beta distribution, implemented as a conjugate prior to the binomial:

$$p_{i,y} \sim \text{Beta}(\alpha_{i,y}, \beta_{i,y})$$

The shape parameters of the beta distribution where specified in terms of their mode ($\phi_{i,y}$) and concentration ($\kappa$).

$$\alpha_{i,y} = (\phi_{i,y})^{(\kappa - 2)} + 1$$

$$\beta_{i,y} = (1 - \phi_{i,y})^{(\kappa - 2)} + 1$$
where \( \omega_y \) is the set of dates on which sampling occurred for year \( y \). The concentration term (\( \kappa \)) was drawn from a uniform prior distribution bounded to be greater than 2 (Kruschke, 2014), and less than 200. Posterior sampling was achieved via Hamiltonian Monte Carlo (HMC) No-U-turn sampling (NUTS) through the stan model building software (Stan Development Team, 2015), implemented in R (R Core Team, 2015) using the Rstan package (Gelman, 2014). Sampling occurred over five chains of 5000 iterations each, with the first half of samples discarded as a “warmup” and each subsequent sample saved to develop the posterior distribution. Convergence was assessed using the Gelman-Rubin diagnostic (Gelman & Rubin, 1992) and effective number of samples, as well as trace-plots and autocorrelation plots of HMC chains. Posterior sampling was monitored for divergent transitions and low Bayesian Fraction of Missing Information (BFMI), neither of which were indicated in model fits to the complete data set. While divergences did occur when simulating the iterative re-fitting of the model (see ‘Scenario 2’, ‘Scenario 3’ below), any relevant bias was captured in the calculation of in-season assignment errors (\( \epsilon_{i,y} \); see 'performance metrics' below). Model goodness of fit was assessed by comparing predictive distributions to observed data (posterior predictive check, Figure S1-S2).

Simulation analysis:

We compared the performance of the hierarchical in-season GSI approach with two alternative information scenarios in a simulation framework. The first scenario (static hierarchical transition) assumes that genetic samples are collected within the fishing season but are not processed and analyzed until after the season has ended, such that in-season information on the current year’s stock composition is not available, but historical data are. As another alternative, we simulated a scenario in which GSI samples are collected and analyzed in-season,
but all historical data are ignored (in-season GSI only). Importantly while other forms of information are available to managers that may be considered in decision-making (e.g. total escapement, age composition, sex ratio, catch per unit effort, input from the fishing fleet, etc.) for the purposes of these simulations we assume that GSI is the sole data source informing the stock composition. All scenarios were evaluated for each year in which in-season GSI data were collected by the ADF&G (2010-2018). To evaluate the hierarchical in-season GSI and hierarchical static transition approaches for a given year, the hierarchical model was conditioned on the other eight years of data in a ‘leave-one-out’ design. In the case of the hierarchical in-season GSI scenario, the data for that year were then added sequentially and the model iteratively re-fitted after each new data point. This approach does not evaluate the change in model performance that might arise as more years of data are added to the hierarchical model, but only looks at performance across each season assuming a constant number of years’ historical data.

The performance of these three stock assignment procedures was compared using simulated beta-binomial compositional data for each of the dates on which sampling actually occurred for each year \((\omega_y)\) using the actual sample size for each stratum \((N_{i,y})\), and the median posterior estimate of the beta concentration parameter \((\kappa)\). These data were generated from the posterior medians of the estimated stock composition on the corresponding sampling dates \((\phi_{i \in \omega_{y,y}})\) from fits of the hierarchical model to all years’ data. Each stock assignment method was evaluated by comparing it’s estimates at any given point in time to the ‘true’ values from which the data were generated \((\phi_{i,y}^{true})\).

Scenario 1: hierarchical static transition:
In this scenario we assume that genetic samples would still be collected but not analyzed until after the season has ended, such that only GSI data from other years is available to infer the transition from early to late runs. To make use of all other years’ data in predicting the stock transition for a season without new information, we constructed a logistic transition curve using the posterior predictive distribution of the joint prior of the steepness ($\psi$) and midpoint ($\tau$) parameters (eq. 3), conditioned on all other years of data.

$$
\phi_{i,Y} = \frac{1}{1 + 19 \frac{(i - \tau^\text{pred}_Y)}{\psi^\text{pred}_Y}}
$$

Where if there are $Y = 9$ years of data in total, the posteriors of $\mu$ and $\Sigma$ are estimated using data from years $Y \neq y$. In this scenario, the transition curve is static within a year, and parameter values are only updated after a season has ended and the estimated stock proportions from that year’s run become available. For instance, in 2015, the preseason curve is constructed using the posterior predictive distributions of $\psi$ and $\tau$ conditioned on data from 2010-2014, and 2016-2018.

Scenario 2: hierarchical in-season GSI

In this scenario, we simulate the evolution of information of the stock composition within a season as genetic samples are collected and analyzed, and the hierarchical logistic model is re-fitted to the data after each GSI sample is analyzed. Prior to any genetic samples being processed for a given year $y$, stock apportionment is based on the model fit using $\tau^\text{pred}_Y$ and $\psi^\text{pred}_Y$ conditioned on all other years’ data ($Y \neq y$), as in the static transition approach (this is referred to as the ‘preseason curve’). However, after the first sample is processed, the model is re-fitted to
include the new data point, and the estimated transition curve is updated to reflect the new
information. This process is repeated after each sampling event, such that if there are \( N \) genetic
samples collected during year \( y \), there will be \( N + 1 \) sets of parameter estimates for that year
(including the initial preseason curve):

\[
\phi_{j,y}^{l} = \frac{1}{1 + 19 \dfrac{1}{\psi_{y}}}
\]

where \( j \) is the sample number on which a set of parameter estimates is based (with \( j = 0 \)
denoting the initial preseason curve, \( \tau_{y}^{j} = 0, \psi_{y}^{j} = 0 = \tau_{y}^{\text{pred}}, \psi_{y}^{\text{pred}} \)). To assess effects of the delay
imposed by shipping and processing genetic samples, we evaluated the performance of this
approach using a 0, 3, 5, and 20 day lag between when a sample is collected and when the
transition curve (and subsequent assignment of the escapement) is updated to include that sample

Scenario 3: in-season GSI only:

In this scenario, we assume that genetic samples are collected and analyzed in-season, but
historical data are ignored. With this approach, prior to any genetic samples being collected, the
preseason expectation is that the escapement is 100% early run fish. When the first GSI sample
is collected and analyzed, a non-hierarchical logistic model is fit to this data point, where the
steepness and midpoint are drawn from vague, independent priors (\( \text{uniform}(1,n) \)) rather than a
common distribution that is shared among years. Additionally, a binomial rather than beta-
binomial likelihood was used for the non-hierarchical implementation due to the difficulty of
estimating the concentration parameter \( (k) \) without the benefit of other years’ information. As
each subsequent data point is added, this model is re-fitted to include the new data such that the estimated stock transition curve evolves as more data become available during the season. We also evaluated the performance of this approach using a 0, 3, 5, and 20-day lag between when a sample is collected and when the transition curve and apportionment of the escapement are updated to include that sample.

Performance metrics:

The daily in-season stock assignments under all three scenarios were compared to the assignments based on the known transition curves for each year from which the simulated compositional data were generated. On any given day during the season, the number of escaped fish assigned to the late run was calculated as the cumulative sum from day 1 to \(i\) of the product of the estimated proportion late run fish (\(\phi_{i,y}\)) under the latest GSI sampling strata \(j\) (for scenarios 2, 3), and the total daily escapement count (\(E_i\)) up to day \(i\). The cumulative number of fish in the escapement assigned to the late run using the true transition curve from which the data were simulated (\(\lambda_{i,y}\)) is then subtracted from this estimate to calculate the cumulative assignment error (\(\varepsilon_{i,y}\)) for that point in time under each approach:

\[
\varepsilon_{i,y} = \begin{cases} 
\sum_{i=1}^{i} \phi_{i,y} E_i - \lambda_{i,y}, & \text{scenario 1} \\
\sum_{i=1}^{i} \phi_{i,y} E_i - \lambda_{i,y}, & \text{scenario 2, 3}
\end{cases}
\]

Where:


\[ \lambda_{i,y} = \sum_{1}^{i} \phi_{i,y}^{true} E_i \]

Positive values of \( \varepsilon_{i,y} \) represent the number of early run fish that were incorrectly assigned to the late run, while negative values reflect late run fish mis-assigned to the early run. For the purposes of these analyses, it is assumed that the total daily escapement counts \( (E_i) \) passing through the weir are observed without error. The \( \varepsilon_{i,y} \) metric reflects the quality of information available to a manager on each day of the fishing season about the status of each stock’s current escapement relative to its interim escapement target. If both stocks appear on track to meet their escapement goals at that point in the season, a manager is more likely to allow fishing, while if one or both stocks appear to be falling short of their escapement targets, a manager may decide to close harvest in order to allow additional fish to escape (depending on the estimated stock composition of the escapement at that point in time). As such, errors in stock assignment can create misleading inference on the escapement, and potentially interfere with in-season decision-making.

**Results**

*Model estimation and historical patterns:*

To estimate the variability among years in the transition between early and late runs, the hierarchical logistic model was first fit to all years (2010-2018) of data simultaneously. Estimates for both the steepness (\( \psi \)) and the midpoint (\( \tau \)) parameters of the logistic function varied substantially among years (Figure 2, 3). In particular, 2015, 2017, and 2018 showed late
transitions, while in 2012, and 2013, and 2014 the composition shifted earlier than expected (Figure 2, 3). Posteriors for the among-year distributions of the logistic function parameters indicated a mean for the midpoint term ($\mu_\tau$) of DOY 193 (July 11/12 depending on whether the year is a leap year), similar to the average calculated across the historical raw GSI and SPA data (July 9/10; Foster, Wilburn, Schaberg and Wadle, 2018). However, the estimated midpoint varied substantially among years from as early as July 4 in 2012 to as late as July 21 in 2018, with an estimated standard deviation among years of roughly 6 days (95% credible interval of ~4-11 days) (Figure 3). The steepness of the transition curves was also variable, with an estimated mean among years ($\mu_\psi$) of 15 days (95% credible interval of 11 to 19 days), and a standard deviation of 4 days (95% credible interval 2 to 9 days). The steepness of the transition curve was positively correlated with the midpoint (median $\Omega_{\psi,\tau} = 0.61$, 95% credible interval $= -0.16$ to 0.95) such that in years when the transition occurred early, the rate of switching was rapid while in years when the transition was later than average, the rate tended to be more gradual (Figure 3). For instance, in 2012 when the transition occurred early, the stock composition shifted from 50% to 95% late run in roughly 8 days, while in 2015, 2017 and 2018 — years in which the transition was late — this same conversion took over 18 days to complete.

In years with typical run transitions, in-season GSI did little to move the estimated transition function from the pre-season expectation (Figure 4). However, in years where there was a substantial departure from the pre-season curve, both of the GSI-updated (hierarchical and in-season only) models typically indicated so by mid-July (~July 10-20; Figure 4, Figure S3), before most of the late run had yet to arrive, but the opportunity to allow additional early run sockeye salmon to escape is limited. For example, in 2012 the run transition occurred earlier than the average, and the hierarchical GSI-updated transition model detected this, leading to near-
perfect assignment accuracy throughout the run (Figure 5, 6). While both of the GSI-updated models typically converged on similar estimates of the transition curve by the end of the season (see 2010, 2018 Figure 4, S3 for notable exceptions), the hierarchical model typically achieved accurate estimates earlier than the model conditioned on in-season data alone. This was due to the fact that without the benefit of information from other years, the in-season only model could not reasonably estimate the transition curve until after 2-6 samples had been analyzed (Figure S3). Conversely, in situations where the initial samples might otherwise have been misleading or uninformative (e.g. 2011) the benefit of information from other years prevented the hierarchical model from estimating nonsensical transition curves (compare Figure 4 to Figure S3).

To examine how use of the static, hierarchical, or in-season only transition curves influence the in-season assignment of escaped fish, we examined the apportionment of the cumulative escapement across the season under each information scenario from 2010-2018. In some years (e.g. 2010, 2011, 2013, 2016) the differences between the static and the GSI-updated transitions were relatively small, as indicated by the similar final cumulative seasonal escapement curves among the different approaches in those years (Figure 5). However, in the other five years of the study, there were larger differences in how escapement was allocated to the early and late runs depending on which method was used to model the run transition. For example, in 2012 the static approach estimated that escapement to the early run tracked the midpoint of the daily escapement targets almost perfectly throughout the season (Figure 5).

However, the GSI-updated approaches detected that the run transition had occurred early that year and the escapement to the early run did not gain appreciable numbers of fish after July 5, resulting in an end-of-season escapement close to the bottom of the escapement goal range. In 2014, another year when the transition occurred earlier than the pre-season expectation, both of
the GSI-updated approaches showed that the number of early run fish in the escapement was near the bottom end of the escapement goal range, whereas the static transition curve would have led to the conclusion that the early run escapement was well above the mid-point of the escapement goal range. In that year the static approach would have suggested that the late run was falling short of the escapement goal throughout most of the season, while the GSI-updated models would have shown that the late run escapement was actually tracking closely with the mid-point of the escapement goal range. While the in-season only GSI approach generally reached similar assignments to the hierarchical GSI model by mid-late July, its inability to reliably estimate the transition during the first 2-6 sampling strata resulted in larger early season assignment errors (Figure S3, Figure 5,6).

The results of the analyses described thus far assume that there is no delay between when genetics samples are collected and when the GSI data are available for updating the hierarchical or in-season only transition functions within the season. However, there are logistical challenges in collecting samples, transporting them to Anchorage for analysis in the GCL, and interpreting the data. Thus, we simulated a range of time lags between sample collection and when GSI data are available for updating the transition curve and assignment of the escapement. For comparison to the results presented above, we executed simulations with lags of 3, 5, and 20 days between sample collection and the application of the GSI-updated transition curve to the escapement data. A 3-day lag between sample collection and updating the transition curve had a negligible effect on the assignment of fish to the early or late runs over the season for both the hierarchical and in-season only models (Figure S4, S5). At a 5-day lag, there were moderate differences in the run allocations from those observed in the 0-day lag scenario (Figure S6, S7). Not surprisingly, a 20-
day lag generated substantial errors in stock assignments for both the hierarchical and in-season only models, effectively negating any benefit to the in-season GSI data (Figure S8, S9).

Across all years, the static approach resulted in a total of over 26.6 million cumulative in-season mis-assignments, compared to ~9.7 million for the in-season GSI only approach, and ~7.4 million for the hierarchical in-season GSI approach. While the in-season only and hierarchical in-season GSI approaches typically reached similar assignment accuracy by the end of the season, the in-season only model exhibited larger early season assignment errors, leading to the reduced performance of this method (Figure 6, Figure 7B). However, the hierarchical in-season GSI approach did not always outperform the other stock assignment methods. For instance, in 2013 assignments using only in-season GSI were more accurate than under the hierarchical GSI model, and the static approach exhibited noticeably better early season assignments in both 2010 and 2016. For the static approach, assignment accuracy for a given year depended on how different the run transition timing was from the among-year average, but this was not the case for the hierarchical or in-season only GSI-updated approaches (Figure 7A).

**Discussion:**

Analysis of all GSI data collected throughout the fishing seasons in 2010-2018 indicated substantial variation in the timing and abruptness of the transition from the early to the late run among years. In only 2 of 9 years did the estimated midpoint date of the run transition occur within 1 day of the among-year average, and the midpoint in any given year was as much as 9 days later, and 7 days earlier than the among-year average. Furthermore, during years when the midpoint of the transition was early, there was a tendency for the shift from the early to late run to be particularly abrupt. For instance, in 2012 the midpoint of the transition occurred one week...
earlier than the among-year average and reached 95% late run only 8 days afterwards. As a result, in simulations for 2012, by the time the static transition model indicated that the escapement had reached 50% late run, the actual stock composition was actually ~95% late run.

For in-season GSI to be useful for management, it must accurately identify the transition function for a given year early enough that there is still opportunity to alter management trajectories while a significant portion of the run remains subject to fishery management. Our analyses demonstrate that for the nine years included in this study, GSI would have provided little opportunity for altering in-season management on the early run compared to a static approach. In the case of the in-season only GSI model, early season assignment errors were often larger than under the static approach, suggesting that management of the early run could be impaired by relying solely on in-season GSI data. While the hierarchical model generally exhibited smaller early season assignment errors compared to the in-season only approach, it typically did not achieve substantially better accuracy than the static approach until much of the early run had arrived at the watershed (Figures 6). Conversely, by the time that the hierarchical model typically achieved improved performance over the static approach, the majority of late run fish had yet to arrive at the watershed, even with realistic analytical time lags (~3 days), thus informing the manager that the transition had occurred and allowing management to be adapted from the middle of the fishing season onwards (Figure S4, S5). Not only was the in-season only model slower to achieve accurate stock allocation than the hierarchical model, but in many years (e.g., 2010, 2012, 2014, 2018) it exhibited larger assignment errors through the end of the season as well. As such, the hierarchical model likely offers some advantages for post-season stock allocation and run reconstruction, in addition to in-season inference. However, it should be noted that in some years (e.g., 2010, 2016), the early season assignment errors produced by the
hierarchical GSI model exceeded those from the static transition model, which could potentially have negative consequences for management. Future analyses should explore explicit weighting schedules for treating the pre-season and in-season GSI data in the hierarchical model that minimize these errors and optimize overall assignment accuracy. Additionally, other types of data collected in-season that are informative to the stock composition (e.g., age composition) could be included alongside the GSI data in an integrated stock transition model that could improve real-time inference.

The results presented here can be viewed as the first step in a management strategy evaluation (MSE, Punt, Butterworth, de Moor, De Oliveira, & Haddon, 2016) that uses closed loop simulations to understand how alternative in-season stock assignment methods affect long-term production and yield given 1) uncertainties in the data and implementation of management procedures, 2) variation in the timing and relative strength of runs, and 3) feedbacks between population dynamics, management decision-making, and harvester behavior. Importantly, our simulation analysis did not model management actions in response to in-season stock assignments, nor did it consider key uncertainties in their implementation (Dorner, Peterman, & Su, 2009; Holt & Peterman, 2006, 2008), or model specification (Punt et al., 2016). A previous MSE for sockeye salmon has shown that when outcome error is considered, better information may not necessarily improve management performance (Dorner et al., 2009). Importantly, the realized effects of using any of the stock assignment approaches considered here will ultimately be determined by the decision-making process used by managers to update their in-season assessments and adjust harvest control, which we did not evaluate. Future analyses might also explore the performance of in-season GSI across a varying range of assignment accuracies.
associated with different SNP design protocols in a genetically-based MSE (Anderson, Waples, & Kalinowski, 2008; Waples, Punt, & Cope, 2008).

Despite marked potential for improving the assessment and conservation of living aquatic resources, genetic data can be challenging to integrate formally into fisheries assessment and management (reviewed in Waples et al., 2008). For Pacific salmon, the logistical constraints of real-time harvest control pose arguably one of the greatest challenges to full utilization of genetic information in management (Cunningham, Anderson, Wang, Link, & Hilborn, 2019; Dorner et al., 2009). However, our analysis shows that a hierarchical modelling approach can improve the performance of in-season GSI for inferring compositional dynamics in real time. As such, similar approaches may be useful in other scenarios to facilitate the incorporation of in-season data into real-time assessment and decision-making. Preseason forecast models to predict salmon returns remain highly uncertain, and MSE has shown that even if forecast accuracy can be improved, there may be no realized benefit to the management of the stock due to outcome error (Dorner et al., 2009). Conversely, in-season inference offers managers the opportunity to adaptively correct for pre-season uncertainties in real time, potentially reducing the magnitude of implementation errors (Dann, Habicht, Baker, & Seeb, 2013; Walters, 1989). As the timing and strength of salmon runs becomes more variable and difficult to predict due to climate change (Crozier et al., 2008; Crozier, Scheuerell, & Zabel, 2011), in-season stock identification methods may become increasingly important to ensuring the sustainable management of exploited populations. While future analyses that consider the full suite of relevant uncertainties are needed to comprehensively assess the value of alternative in-season stock assignment methods, our results indicate that a hierarchical approach may be a productive avenue for improving management outcomes. With growing recognition of the importance of population diversity for maintaining
the resilience of fish stocks to environmental change (Connors et al., 2020; Schindler et al., 2010), in-season management tools are likely to become increasingly relied upon to conserve biocomplexity while simultaneously maximizing harvest opportunities.

Data archiving statement: relevant data will be archived using Figshare.

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Figures and figure legends:

Figure 1. Map of the Chignik watershed located on the Alaska Peninsula with associated lakes, rivers, and other relevant locations indicated. Created in Esri ArcMap 10.6.1 using the Alaska Department of Natural Resources 2019 Simplified Alaska Coastline, and U.S. Geological Survey National Hydrography Dataset.
Figure 2. Fits of hierarchical logistic transition curves from 2010-2018. Each panel shows the estimated transition curve (blue lines) and associated uncertainty (95% credible intervals as shaded blue areas) for a given year. Gold circles and error bars are the medians and 90% credible intervals of the estimated stock composition from each GSI sampling event across the season. Orange vertical dashed lines in each panel show the estimated average midpoint date of the transition function across all years ($\mu_\tau$). Blue dashed lines show the transition date estimated for each individual year ($\tau_y$). The shaded orange area in each panel shows the difference between each year’s midpoint estimate ($\tau_y$) and the among-year average transition date ($\mu_\tau$).
Figure 3. Posterior distributions for hierarchical logistic transition model’s parameters. Individual transition midpoint (50:50) dates ($\tau_y$) for all 9 years of the study are shown in panel A. The among-year mean and standard deviation for this parameter are shown in panels B and C. Panel D shows the steepness parameter ($\psi_y$) estimates for each of the study years, with the among-year mean and standard deviation shown in panels E and F. In all plots the open circles show the median, the thick vertical bars show the 50% credible intervals, and the thin lines represent 95% credible intervals.
Figure 4. In-season evolution of the estimated logistic transition function under the hierarchical model for 2010-2018. Preseason curves (dashed) shown in each panel are conditioned on data collected from the other 8 years of the study, and each subsequent curve represents the addition of an in-season GSI sample to the model. Colored circles in each panel show the simulated compositional data points for each sampling date. The logistic curve matching the color of each
circle shows the updated stock transition function fit with all GSI data collected up to and including that point in the season, as well as the data from other years in the study. The light blue curve in each panel depicts the true transition curve for that year from which the simulated compositional data were generated. The horizontal dashed line denotes the 50:50 point in the run, and the vertical dashed line shows the expected preseason 50:50 transition date based on analyzing all other years of data ($\tau_{\text{pred}}^y$). Note that different numbers of GSI samples were taken and analyzed in each year of the study.
Figure 5. In-season allocation of sockeye salmon escapement to early and late runs compared to the escapement goal targets for the Chignik watershed in 2010 – 2018. The escapement goals shown here are those that were published by ADF&G in 2018. In each panel, the thin solid lines show the in-season escapement targets for the early (green) and late (dark blue) runs. The shaded area around each line shows the upper and lower limits of the escapement targets, which represent the range of values that constitute achievement of the escapement goal. The dashed black lines show how escapement would be allocated by the static logistic transition curve (scenario 1).
solid colored lines in each panel show how the escapement is allocated to the early and late runs using the hierarchical GSI model (scenario 2), and the brown lines with inlaid colored dots show the assignment using the non-hierarchical (in-season only) GSI model (scenario 3). For the hierarchical GSI and in-season only GSI assignments, the color of the solid lines (hierarchical GSI) or inlaid dots (in-season only) correspond to the number of in-season genetic samples that were used at that point in the run to inform the transition curve. In each panel, the solid light blue line shows the stock assignments under the true stock transition curve from which the compositional data were simulated for that year. These simulations assume there is no lag between when samples are collected and when the GSI data are available for updating the run transition curves.
Figure 6. Errors in allocation of sockeye salmon to the early and late runs over the course of the migration season into the Chignik River from 2010-2018 under different stock assignment methods. In each panel, the histograms represent the number of early run fish incorrectly assigned to the late run (left y axis). Negative values reflect late run fish mis-assigned to the early run. Grey histograms show mis-assignments under the static hierarchical approach (scenario 1), while the
solid, colored histograms show the number of mis-assigned fish using the hierarchical GSI model (scenario 2), and the bars with diagonal colored lines show the number of mis-assigned fish using the in-season GSI only model (scenario 3). For the colored histograms (solid or with diagonal lines), the different colors correspond to the number of in-season genetics samples that were used at that point in the run to inform the transition curve for both the hierarchical GSI (solid filled) and in-season GSI only (colored diagonal lines) models. The teal and dark blue lines in each panel show the number of fish belonging to the early run (teal) or late run (dark blue) that have yet to enter the fishery or escape to the across the season (right y axis). These curves were generated retrospectively using the true transition curve from which the data were generated, and the end of season catch and escapement counts. These simulations assume no lag between sampling and when data are available for updating the transition curve.
Figure 7. Transition timing and assignment accuracy under each stock assignment method. In panel A, the x axis shows the median posterior estimates of the midpoint date (\( \tau \)) for each year centered with respect to the among-year average (\( \mu \)). The y axis shows the maximum number of early run fish that were mis-assigned to the late run fish by the static (grey), hierarchical GSI (purple), and in-season only (orange) approaches for each year. Negative values reflect late run fish mis-assigned to the early run. In panel B, bars show the cumulative total number of fish that were mis-assigned across the duration of each year’s run under the static (grey), hierarchical GSI (purple), and in-season only (orange) approaches.