A General Model for Salmon Run Reconstruction That Accounts for Interception and Differences in Availability to Harvest

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A General Model for Salmon Run Reconstruction That Accounts for Interception and Differences in Availability to Harvest

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Abstract

Understanding population-specific spawner-recruit relationships is necessary for sustainable salmon management. Where multiple populations are harvested together, run reconstruction methods partition mixed-stock catches and allocate recruits back to their populations of origin. Traditional run reconstruction methods often use age composition data to inform catch partitioning. However age-only methods do not account for stock-specific differences in the availability of fish to harvest within fishing areas or the incidental harvest of non-target stocks in nearby fishing areas. Advances in molecular genetic techniques permit genetic stock identification (GSI) of both contemporary and historical catch samples. We present a statistical model for salmon run reconstruction that utilizes both age composition and GSI data to estimate differences in the availability of stocks within, and interception rates among, terminal fisheries. When applied to the commercial sockeye salmon (*Oncorhynchus nerka*) fishery in Bristol Bay, Alaska, new estimates of population productivity differed from those generated using previous age-only methods by 0.1-155.1%, with stock-specific mean absolute percent differences of 9.7-38.7% across years, underscoring the value of genetic data for run reconstruction. With more accurate run reconstruction methods, spawner-recruit relationships can be identified more precisely, thus providing more accurate management targets for salmon fisheries.

Introduction

Successful management of commercially-exploited species depends on an accurate understanding of how catch and harvest policy influences abundance over time.

Management of fish resources to achieve maximum sustainable yield (MSY) remains the principal goal, among other social and economic objectives, of fisheries regulation within the United States and in many other countries (Hilborn 2012). Defining MSY-based management targets for populations of Pacific salmon requires quantifying stock-specific spawner-recruit relationships, where “recruitment” is the number of individuals from a specific brood year that survive to return to freshwater or be caught in fisheries shortly before spawning. Estimating recruitment for salmon stocks exploited by terminal fisheries harvesting only a single stock is relatively straightforward, only requiring the collection of age composition data to assign recruits to their appropriate brood years. However, partitioning catches among component stocks is a more substantial challenge for fisheries that target a mixture of independently managed stocks with separate MSY reference points. Traditionally, some type of run reconstruction has been employed to partition catches in mixed-stock salmon fisheries using data available from coded wire tags (Johnson 1990), age-composition (Bernard 1983; Chasco et al. 2007) or information about migration path and timing of specific stocks (Starr and Hilborn 1988; Templin et al. 1996). Most recently Branch and Hilborn (2010) used age-composition estimates from commercial fishery catches and upriver escapements collected by the Alaska Department of Fish Game (ADF&G) to apportion terminal fishery catches of sockeye salmon from Bristol Bay, Alaska.

Bristol Bay sockeye salmon are a culturally and economically important resource within the state of Alaska, providing the basis for vibrant subsistence (Shaw 1998) and commercial fisheries. The several dozen sockeye salmon populations in Bristol Bay support the largest sockeye salmon fishery in the world (Steiner et al. 2011). In 2010, the

estimated wholesale value of the Bristol Bay commercial sockeye harvest was \$390 million, about one-sixth of the total value of all U.S. seafood exports (Knapp et al. 2013). Although management of the sockeye salmon fishery restricts effort to spatially-explicit terminal fishing areas or districts, these catches must still be partitioned to estimate annual stock-specific returns because several terminal fishing districts surround the mouths of multiple river systems where mixtures of stocks are harvested. In addition, some proportion of returning fish that are caught in specific districts may be bound for spawning grounds in other districts.

Branch and Hilborn (2010) describe a useful tool for partitioning catches in mixed-stock salmon fisheries based upon stock-specific differences in age composition (number of years spent in freshwater and the ocean), known as SYRAH (Salmon Yield Reconstruction Apportioning Harvest). This model estimates daily returns and arrival timing, but two difficulties limit its ability to accurately reconstruct age- and stock-specific run sizes. First, SYRAH does not account for the different availability of stocks to harvest within mixed-stock fisheries that arises from stock-specific differences in migratory pathways relative to where fishing takes place. Second, SYRAH incorrectly estimates the harvest rate for stocks by not accounting for incidental interception of returning salmon in other terminal fishing areas.

Interception of Bristol Bay sockeye salmon in non-natal districts has been well established by previous studies. Straty (1975) first demonstrated interception through the use of tagging studies. Menard and Miller (1997) further evidenced interception by analyzing the pattern of scale samples from Bristol Bay catches (1983-1995), estimating average interception rates of 10%–27%. More direct estimates come from genetic stock

identification (GSI, Habicht et al. 2007). For example, catch samples (2006–2008), using diagnostic single-nucleotide polymorphisms (SNPs), indicated that up to 30.2% of catches in some fishing districts were comprised of fish bound for neighboring river systems (Dann et al. 2009). Given these findings, it is clear that run reconstruction models must incorporate genetic data alongside age-composition data to accurately estimate interception rates, partition mixed stock catches, reconstruct true annual run sizes, and calculate the brood tables necessary to establish sustainable harvest policy. Without accurate run reconstruction, management of Bristol Bay sockeye stocks will be inconsistent with their underlying biology, resulting in foregone yield and possibly even jeopardizing the future sustainability of this fishery.

We developed the first run reconstruction model that partitions catches using both age and genetic composition information in order to address these issues and apply it to the commercial sockeye salmon fishery in Bristol Bay, Alaska. We also compare our results with those generated using traditional age-based methods employed by the Alaska Department of Fish and Game (ADF&G) (Bernard 1983) in order to understand how the new model improves estimates of historical stock productivity in Bristol Bay.

Methods

General model description

Our purpose was to create a generalized run reconstruction model capable of utilizing GSI data alongside catch, escapement, and age-composition data, to partition commercial fishery catches and reconstruct annual salmon returns. One key feature of this model is that it estimates interception of non-target stocks or incidental catches of

fish in one district that are bound for other river systems. The model described here reconstructs salmon runs at an annual time scale to generate brood tables, tables that describe age-specific recruitment by brood year and allow the relationship between spawning abundance and recruitment to be evaluated for setting management targets. This model is different from past salmon run reconstruction models that focused on identifying daily arrival distributions (Branch and Hilborn 2010; Chasco et al. 2007; Schnute and Sibert 1983; Starr and Hilborn 1988) or “preseason planning” (Cave and Gazey 1994). Age-classes are represented by the number of years in freshwater followed by the number of years in the ocean, thus 2.3 is a fish that spent two years in a river or lake, followed by three years in the ocean, before returning to spawn. This model is fit to age composition data for all 18 potential age-classes (0.1, 0.2, 0.3, 0.4, 0.5, 1.1, 1.2, 1.3, 1.4, 1.5, 2.1, 2.2, 2.3, 2.4, 3.1, 3.2, 3.3, 3.4), instead of focusing only on the four predominant Bristol Bay sockeye age-classes (1.2, 1.3, 2.2, 2.3) as commonly done in previous analyses (see Flynn et al. 2006; Branch and Hilborn 2010).

Bristol Bay sockeye salmon

Sockeye salmon returning to Bristol Bay are predominantly bound for eight major river systems: the Igushik, Wood, and Nushagak rivers on the western side, and the Kvichak, Alagnak, Naknek, Egegik, and Ugashik rivers on the eastern side (Fig. 1). Returning salmon are commercially harvested primarily in four terminal fishing districts (Nushagak, Naknek-Kvichak, Egegik, and Ugashik; Fig. 1) between June and August of each year, within which fishing effort is actively managed inseason by emergency order to achieve fixed seasonal escapement goals (Clark et al. 2006). The Nushagak District is a mixed-stock fishery located at the point where the Igushik, Wood, and Nushagak rivers

enter the northwest corner of Bristol Bay (Fig. 1). The Naknek-Kvichak District is also a mixed-stock fishery harvesting sockeye returning to the Kvichak, Naknek, and Alagnak rivers. The other two districts, Egegik and Ugashik are located at the mouths of those rivers and are operated as single-stock fisheries, although GSI data indicate a significant percentage (0.3–47.8%) of sockeye caught in select districts are bound for river systems in other fishing districts (Dann et al. 2009; Smith 2010).

Data

Four types of data are available to inform reconstruction of annual run sizes by stock and age-class: absolute counts in numbers of commercial fishery catches, upriver escapement counts, age composition of catches and escapements, and stock composition of commercial catches from GSI. Catch weights for each district are recorded on a daily basis throughout the fishing season. The weight of individual fish are sampled throughout the season by ADF&G biologists and used to translate the biomass of observed catches into numbers of fish. Escapement to the Igushik, Wood, Kvichak, Naknek, Egegik, and Ugashik river systems is enumerated on a daily basis with visual counts of upstream-migrating sockeye from elevated towers. Counts are conducted during 10-minute periods on each side of the river every hour, 24 hours per day between June and August, and scaled up to estimate daily escapement numbers. Visual escapement enumeration to the Nushagak River is impossible due to turbidity, so sockeye salmon are counted using horizontal-looking, bank-associated, sonar. The escapement counting tower on the Alagnak River has been operated sporadically throughout the period of reconstruction, so a combination of tower counts and end-of-season aerial survey estimates were used to estimate annual escapements. Given the current objective of reconstructing annual returns

by stock, daily catch ($c_{d,t,y}$) and escapement ($\varepsilon_{s,t,y}$) data are summed across days (t) to seasonal totals $C_{d,y}$ and $E_{s,y}$, for each district (d) and stock (s) in each year (y).

Age composition of both catch and escapement is available from scales sampled during multiple periods throughout the return migration in each year by ADF&G. Scale samples are collected for fishery catches through dock-side sampling programs and for escapements through beach seine at enumeration sites and subsequently aged by ADF&G staff. To calculate the seasonal age (a) composition of catches in each district, a proportion ($p_{d,a,y}^C$) weighted by the observed catch in each sampling period was calculated as

$$(1) \quad p_{d,a,y}^C = \frac{\sum_{i=1}^{I_{d,y}} P_{d,a,i,y}^C n_{d,i,y}^C}{\sum_{i=1}^{I_{d,y}} n_{d,i,y}^C}$$

$$n_{d,i,y}^C = \sum_{t \in \{D_{d,i,y}^C\}} c_{d,t,y}$$

where, $P_{d,a,i,y}^C$ is the observed proportion of age-class a , in catch samples from district d , during sampling period i of year y . $n_{d,i,y}^C$ is the observed catch by district, sampling period, and year, and represents the sum of daily catches $c_{d,t,y}$ across the set of days in each sampling period ($D_{d,i,y}^C$). $I_{d,y}$ is the number of catch age composition sampling events by district and year. Seasonal age compositions were calculated in a similar way for escapements

$$(2) \quad p_{d,a,y}^E = \frac{\sum_{i=1}^{I_{s,y}} P_{s,a,i,y}^E n_{s,i,y}^E}{\sum_{i=1}^{I_{s,y}} n_{s,i,y}^E}$$

$$n_{s,i,y}^E = \sum_{t \in \{D_{s,i,y}^E\}} \varepsilon_{s,t,y}$$

as the sum of age composition proportions observed for each sampling event $P_{s,a,i,y}^E$, weighted by the total of daily escapements $\varepsilon_{s,t,y}$ observed during that sampling period $n_{s,i,y}^E$.

Genetic stock identification data were available from two sources for different time periods in Bristol Bay. ADF&G's Gene Conservation Laboratory began GSI of commercial fishery catches in 2006 based upon samples collected from each of the commercial fishing districts during multiple sampling periods annually (Dann et al. 2013). In addition to GSI data for recent years (2006–2014), genetic estimates of stock composition of catches are also available from analysis of archived scale samples (Smith 2010). Evaluating the genetic stock composition from scale samples has often been hindered by low amounts of template DNA available for extraction from archived scales and the potential for contamination from preexisting DNA. These challenges resulted in low concentration DNA leading to high rates of PCR failure and errors in genotyping due to allelic dropout (Taberlet et al. 1996) and too many alleles from multiple individuals. Smith et al. (2011) utilized a novel combination of multiplex preamplification PCR to generate accurate genotypes with low failure and error rates, and amplification of microsatellite loci to detect DNA contamination of samples. Using this technique, Smith (2010) produced GSI estimates for Bristol Bay catch samples for a range of years in each commercial fishing district dating back to the early 1960's. GSI data are available for the

Nushagak District in 9 years between 1965 and 1999, the Naknek-Kvichak District in 14 years between 1964 and 2005, the Egegik District in 12 years between 1964 and 2002, and the Ugashik District in 8 years between 1964 and 2002 (Smith 2010). Observed genetic proportions by sampling period were translated into seasonal catch proportions using the same methods described for catch (Eq.1) and escapement (Eq. 2) age composition data.

Model structure

The core of the estimation process within the annual run reconstruction model is the continuous catch equation (Branch and Hilborn 2010; Megrey 1989)

$$(3) \quad \hat{C}_{s,a,d,y} = \hat{N}_{s,a,y} \left(1 - e^{-A_{s,d,y} S_{k_a,y} F_{d,y}} \right)$$

where $\hat{C}_{s,a,d,y}$ is the estimated catch of stock s , age-class a , in district d during year y .

$\hat{N}_{s,a,y}$ is the estimated number of returning fish in each year, by stock and age-class.

$A_{s,d,y}$ is the availability of stock s to harvest in district d , and describes the effect of differences in migration pathway for stocks relative to the spatial distribution of fishing effort in mixed-stock fisheries and the potential for non-target stock interception. $S_{k_a,y}$ is the selectivity of fishing gear by age group k_a in each year. $F_{d,y}$ is the instantaneous fishing mortality rate for each district in each year. This formulation differs from the traditional continuous catch equation by incorporating the $A_{s,d,y}$ term representing stock-specific availability to harvest within each fishing district, and assuming no natural mortality.

We borrowed two novel concepts from Branch and Hilborn (2010) that increased the generality of this model for application to other salmon fisheries and reduced the

number of estimated parameters. The first is representing fish as age and stock-specific groups, making the model easily generalizable for other systems with differing stock and age structures. The second is to use of a flexible system of indexing to link model groups to estimated gear selectivity and availability parameters. Therefore, despite modeling all stock-age-class combinations, gear selectivity $S_{k,a,y}$ is linked to the ocean age k of each age-class a . In this way the parameter representing the selectivity of fishing gear for the 2-ocean age-class is indexed to all 2-ocean individuals independent of the duration of their freshwater residency (i.e. 0.2, 1.2, 2.2, and 3.2 age-classes). This decision to estimate separate selectivity parameters only for distinct ocean age-classes was based on the observation that duration in the ocean is the primary determinant of size in maturing sockeye salmon (Quinn 2005) and findings by Kendall et al. (2009) indicating that size is a key determinant of selectivity in the gillnet gear used in Bristol Bay. To evaluate spatial and temporal differences in gear selectivity, separate selectivity parameters are estimated for every ocean age, in every year, and separately for the east and west sides of Bristol Bay. The decision to separate Bristol Bay districts into two regions (west and east) was predicated on the observed separation in return migration pathways (Dann et al. 2013; Straty 1975) and low interception rates between east and west side Bristol Bay stocks (Dann et al. 2009; Smith 2010).

Model-predicted escapement is calculated by subtracting the sum of predicted stock and age-class specific catches from the estimated number of returning individuals

$$(4) \quad \hat{E}_{s,a,y} = \hat{N}_{s,a,y} - \sum_{d=1}^{\omega_d} \hat{C}_{s,a,d,y}$$

where $\hat{E}_{s,a,y}$ is the estimated escapement of stock s and age-class a in year y , and ω_d is the number of fishing districts which intercept or harvest fish of that group.

The fishing mortality rate in each year and district $F_{d,y}$ is not directly calculated from equation 3 because no analytical solution exists, therefore repeat iterations of the Newton-Raphson method were used to approximate the solution, as suggested first by Sims (1982) and later evaluated by Restrepo and Legault (1995). This process begins by first determining an analytical solution for each district in each year

$$(5) \quad \begin{aligned} f_{d,y}^0 &= \ln \left(\frac{\frac{v_y}{v_y - \delta_{d,y}}}{\frac{\sum_{s=1}^{\omega_s} \sum_{a=1}^{\omega_a} A_{s,d,y} S_{k_a,y} \hat{N}_{s,a,y}}{v_y}} \right) \\ v_y &= \sum_{s=1}^{\omega_s} \sum_{a=1}^{\omega_a} \hat{N}_{s,a,y} \\ \delta_{d,y} &= \sum_{s=1}^{\omega_s} \sum_{a=1}^{\omega_a} \hat{C}_{s,a,d,y} \end{aligned}$$

where, v_y is the predicted total number of returning fish in year y , $\delta_{d,y}$ is the predicted total catch for each district and year. For $n = 20$ iterations the approximated fishing mortality rate $f_{d,y}$ is updated using the Newton-Raphson method (Eq. 6).

$$(6) \quad f_{d,y}^{n+1} = f_{d,y}^n + \frac{\delta_{d,y} - \sum_{s=1}^{\omega_s} \sum_{a=1}^{\omega_a} \hat{N}_{s,a,y} \left(1 - e^{-A_{s,d,y} S_{k_a,y} f_{d,y}^n} \right)}{2 \sum_{s=1}^{\omega_s} \sum_{a=1}^{\omega_a} A_{s,d,y} S_{k_a,y} \hat{N}_{s,a,y} e^{-A_{s,d,y} S_{k_a,y} f_{d,y}^n}}$$

After fewer than 20 iterations, $f_{d,y}$ converges to a stable estimate of the district-specific annual fishing mortality rate ($F_{d,y}$).

Likelihoods and penalties

Run reconstruction model parameters were estimated using maximum likelihood methods. The complete negative log-likelihood is the sum of the negative log-likelihoods of model predicted quantities given the observed data and penalties for scaling model parameters.

$$(7) \quad -\ln(L_{total,y}) = \sum_{l=1}^5 -\ln(L_{l,y}) - \sum_{p=1}^2 \tau_{p,y}$$

In equation 7, $L_{l,y}$ are observation error likelihoods for each of the five data types in each year, and $\tau_{p,y}$ are penalty values for scaling selectivity and availability parameters in each year. Maximum likelihood estimates for model and derived parameters were found by minimizing the total negative log-likelihood (Eq. 7) in each year.

The likelihood for catch data was assumed to represent a normally distributed observation process

$$(8) \quad -\ln(L_{1,y}) = \omega_d \ln \sigma_C + \frac{1}{2\sigma_C^2} \sum_{d=1}^{\omega_d} \left(\ln C_{d,y} - \sum_{s=1}^{\omega_s} \sum_{a=1}^{\omega_a} \hat{C}_{s,a,d,y} \right)^2$$

where $C_{d,y}$ is the catch observed in each district in each year, $\hat{C}_{s,a,d,y}$ is the model-predicted catch, and σ_C is the standard deviation of the observation error distribution.

This differed from methods by Branch and Hilborn (2010), which assumed that catch was observed without error. The likelihood for escapement data was also assumed to represent a normally distributed observation process

$$(9) \quad -\ln(L_{2,y}) = \omega_s \ln \sigma_E + \frac{1}{2\sigma_E^2} \sum_{s=1}^{\omega_s} \left(\ln E_{s,y} - \ln \sum_{a=1}^{\omega_a} \hat{E}_{s,a,y} \right)^2$$

where $\hat{E}_{s,a,y}$ is the model-predicted escapement for stock s and age-class a in return year y , $E_{s,y}$ is observed escapement by stock s and year y , and σ_E is the standard deviation of the observation error distribution. In practice, the variance parameters for the catch and escapement observation error distributions σ_C and σ_E tended toward zero during minimization when either estimated directly from the data or calculated using the analytical solution, so they were fixed at $\sigma_C = 0.5$ and $\sigma_E = 0.1$. Alternative fixed values for these parameters did not significantly alter the ability of the model to fit all data types, nor the value of estimated and derived parameters of interest.

The observation of age composition samples from both the catch and escapement was assumed to follow a multinomial process. The model-predicted age composition proportions of the catch ($\hat{p}_{d,a,y}^C$) and escapement ($\hat{p}_{s,a,y}^E$) were first calculated for each return year (Eq. 10).

$$(10) \quad \hat{p}_{d,a,y}^C = \frac{\sum_{s=1}^{\omega_s} \hat{C}_{s,a,d,y}}{\sum_{s=1}^{\omega_s} \sum_{a=1}^{\omega_a} \hat{C}_{s,a,d,y}}$$

$$\hat{p}_{s,a,y}^E = \frac{\hat{E}_{s,a,y}}{\sum_{a=1}^{\omega_a} \hat{E}_{s,a,y}}$$

Equation 11 describes the negative log likelihood of model-predicted seasonal age compositions for the catch $-\ln(L_{3,y})$ and escapement $-\ln(L_{4,y})$, given the observed seasonal total age composition samples (Eq. 1 and 2):

$$(11) \quad -\ln(L_{3,y}) = -\sum_{d=1}^{\omega_d} \left[\varepsilon \sum_{a=1}^{\omega_a} p_{d,a,y}^C * \ln(\hat{p}_{d,a,y}^C) \right]$$

$$-\ln(L_{4,y}) = -\sum_{s=1}^{\omega_s} \left[\varepsilon \sum_{a=1}^{\omega_a} p_{s,a,y}^E * \ln(\hat{p}_{s,a,y}^E) \right]$$

where ε is the effective sample size for age composition samples. While alternative likelihood functions for compositional data have been used effectively, including the logit-normal and Dirichlet (Schnute and Haigh 2007) and the robust normal (Fournier et al. 1990; Hilborn et al. 2003), these likelihood formulations are undefined for composition groups with zero proportions. Therefore the multinomial likelihood was selected given that when evaluating the full range of potential age-classes ($n=18$), some have very low or zero representation amongst samples.

The multinomial likelihood was also used to represent the observation process for GSI data from catch samples. The model-predicted proportional representation of stocks in catch samples $\hat{p}_{d,s,y}^G$ was calculated and the likelihood of this prediction given observed data was evaluated:

$$(12) \quad \hat{p}_{d,s,y}^G = \frac{\sum_{a=1}^{\omega_a} \hat{C}_{s,a,d,y}}{\sum_{s=1}^{\omega_s} \sum_{a=1}^{\omega_a} \hat{C}_{s,a,d,y}}$$

$$-\ln(L_{5,y}) = -\sum_{d=1}^{\omega_d} \left[\gamma \sum_{s=1}^{\omega_s} p_{d,s,y}^G * \ln(\hat{p}_{d,s,y}^G) \right]$$

where γ is the effective sample size for genetic stock composition of catch data. The effective sample size for both genetic γ and age ε compositions were fixed at 100 for all years. The decision to fix the effective sample size rather than estimate it iteratively as described by McAllister and Ianelli (1997) was predicated on: (i) the fact that compositional samples represent a weighted sum across multiple sampling events throughout each season, and (ii) trials with alternative effective sample sizes yielded similar fits to the compositional data, suggesting that estimation is insensitive to the fixed effective sample size.

In addition to the five likelihood functions, the total data likelihood (Eq. 7) also included two penalty functions for scaling model parameters. A penalty across all model-estimated gear selectivity parameters was added to the likelihood to standardize to a mean of one,

$$(13) \quad \tau_{1,y} = 1000 \left(\frac{1}{\omega_k} \sum_{k=1}^{\omega_k} S_{k_d,y} - 1 \right)^2$$

where ω_k is the number of selectivity age groups and is equal to the number of ocean age-classes. A similar penalty was added to the likelihood to ensure that availability parameters for stocks within a district also had a mean of one.

$$(14) \quad \tau_{2,y} = \sum_{d=1}^{\omega_d} 1000 \left(\frac{1}{\omega_s} \sum_{s=1}^{\omega_s} A_{s,d,y} - 1 \right)^2$$

where $\tau_{2,y}$ is the total availability penalty addition to the likelihood function. Both the selectivity parameter penalty $\tau_{1,y}$ and the availability parameter penalty $\tau_{2,y}$ will approach zero as the model converges, and therefore have no contribution to the total log likelihood.

Estimation procedure

Reconstruction of annual returns (1963 – 2016) was conducted in two sequential phases. First, the model was fit to data from years for which GSI data were available for all districts, to estimate availability parameters for stocks in each district ($A_{s,d,y}$). Subsequently, the model was fit to years for which partial or no GSI data were available. For districts in years without GSI data, the stock-specific availabilities were fixed at the mean of estimates from years with GSI data, as there was no consistent temporal trend in availability estimates. The model was implemented in AD Model Builder (ADMB)

(Fournier et al. 2012) separately for each year (1963 – 2016) to obtain estimates of model parameters including the reconstructed run size by stock and age-class $\hat{N}_{s,a,y}$. After fitting the model to available data, brood tables that describe the observed recruitment by brood year across age-classes were calculated by lagging age-specific returns back to their year of origin. Because of the low interception rates (average: 0.92%) between east and west side Bristol Bay stocks (Dann et al. 2009; Smith 2010), reconstructions were conducted separately for these two regions (Fig. 1). This assumed no interception of Igushik, Wood, and Nushagak stocks in the eastern Naknek-Kvichak, Egegik, and Ugashik districts and no interception of Kvichak, Alagnak, Naknek, Egegik and Ugashik stocks in the western Nushagak district.

Special harvest area, South Peninsula, and high seas catch allocation

There are several smaller sub-districts with known differences in stock composition within the Nushagak and Naknek-Kvichak commercial fishing districts (Fig. 1; Dann et al. 2009). To include catches from these areas with known stock composition differences in the formal run reconstructions would lead to biased run size estimates (L. Fair, Alaska Department of Fish and Game, Anchorage, Alaska, personal communication, 2012). For the Nushagak District these areas included the Wood River Special Harvest Area (WRSHA) and Igushik Section set net catches. The WRSHA is an in-river fishing zone opened periodically to allow for escapement to the neighboring Nushagak River while permitting exploitation of Wood River sockeye salmon. Catches in the WRSHA are almost completely comprised of the Wood stock as a result of its location upstream of the main commercial fishing district. Similarly, Igushik River set net catches are predominantly comprised of the Igushik stock (Dann et al. 2009) given the

location of fishing effort relative to the migration pathway for Wood and Nushagak stocks. Catches from these two areas were withheld from the formal run reconstruction in each year and allocated post hoc to Wood and Igushik Rivers in proportion to the observed age composition. Similarly, eastern Bristol Bay catches from the Kvichak Section set net fishery, Alagnak River Special Harvest Area (ARSHA), and Naknek River Special Harvest Area (NRSHA), were also withheld from the formal reconstruction and allocated post hoc to their respective rivers given minimal potential for interception. However, Kvichak Section set net catches include fish from other stocks and were therefore allocated in proportion to GSI data in that area, or the average of available GSI proportions for years in which data were not available.

Historically there have been two primary sources of fishing mortality for Bristol Bay sockeye in addition to the commercial fishing districts: interception in the South Peninsula commercial fishery and interception in the high seas salmon fishery. GSI data for the South Peninsula fishery on the Alaska Peninsula suggest a large proportion of sockeye catches are bound for Bristol Bay (Dann et al. 2012). A portion of South Peninsula fishery catches in each year were added into reconstructed run sizes, proportional to the observed distribution of sockeye across Bristol Bay and age composition. Similarly, the high seas salmon fishery that operated until 1987 intercepted sockeye bound for Bristol Bay tributaries, and therefore a portion of these catches were also added to reconstructed annual run sizes in the same manner as South Peninsula catches. The proportion of these non-Bristol Bay catches included in our reconstructions was determined by ADF&G staff.

Results

Model fits to data

Visual comparison of model-predicted catch, escapement, and genetic proportions of catch, with observed data indicated that model predictions capture interannual variation in these data with a high degree of accuracy and no significant bias. The ability of the run reconstruction model to explain observed interannual variation in age composition was slightly lower than its ability to explain the catch and escapement data, but still quite good. When the model-predicted age proportions of catch and escapement were compared with observed proportions (Fig. 2), we found that model accuracy depended primarily on whether compositional data were from catch or escapement and secondarily on the age-class in question. For all age-classes, the model-predicted age composition of the escapement more closely aligned with observed proportions across years and stocks, relative to the age composition of catches across districts and years (Fig. 2). With respect to age composition samples from the catch, the model had greater difficulty in fitting to the observed proportions of the 1-ocean age-classes (1.1 and 2.1) compared to others (Fig. 2). This is not unexpected, given the scarcity of 1-ocean fish in the catch. Biases in the relationship between predicted and observed age compositions were minimal, with a slight over-prediction of the 1.2 age-class in catches. No temporal trend in deviations between observed and predicted age compositions was identified.

Parameter estimates

Partitioning of mixed stock catches within the run reconstruction model is based in part on a comparison of the age composition of district catches, with that of stock-

specific escapements, and estimation of fishing gear selectivity by ocean age-class ($S_{k_{a,y}}$). Gear selectivity parameters estimated for each year, indicate similar patterns in relative exploitation of ocean age-classes for both sides of Bristol Bay. Selectivity was found to increase with the ocean age of fish, indicating older sockeye are more likely to be caught in the fishery, except for a slight reduction in estimated selectivity of the 4-ocean age-class (Fig. 3). High variability in predicted selectivity for the 4 and 5-ocean age-classes is not unexpected given their relatively small contribution to Bristol Bay returns as a whole.

Availability is the likelihood that a specific stock will be harvested in a particular fishing district, relative to other stocks. In the Nushagak District on the west side of Bristol Bay, the Igushik stock had the lowest availability (median: 0.50), followed by the Nushagak stock (1.01), with the Wood stock estimated to have the highest availability to harvest across years (1.38; Fig. 4). Model-predicted availability parameters for the east side of Bristol Bay indicated interesting patterns in the potential for interception and mixed-stock exploitation. The Naknek-Kvichak District is a mixed-stock fishery targeting the Kvichak, Alagnak, and Naknek stocks. Within this district, the Naknek stock was estimated to have the highest availability to harvest (2.03), with the Kvichak (1.41) and Alagnak (1.38) stocks having slightly lower availability (Fig. 4). The availability of the Egegik (0.09) and Ugashik (0.01) stocks to capture in this district was significantly lower than the three target stocks.

Within the Egegik and Ugashik Districts, the availability of the target stock was significantly higher than that estimated for other stocks (Fig. 4). However, the estimated availability of the non-target stocks was non-zero in some cases, indicating the important

influence of interception of non-target stocks on seasonal catches. Availability estimates for the Egegik District indicated that the Ugashik stock is more likely to be intercepted (0.34) than the Kvichak (0.20), Naknek (0.20), or Alagnak (0.09) stocks, but far less than the Egegik stock (3.99). Conversely, within the Ugashik District, the relative availability of stocks with the exception of Ugashik (4.69) and Egegik (0.23) are exceedingly close to zero (0.01 – 0.02), indicating that the Ugashik District is only a significant interceptor of the Egegik-bound sockeye (Fig. 4).

Apportioned catch

Harvest in the Nushagak District has predominantly been comprised of the Wood stock historically, representing 69.9% of catch on average (Table 1). The Nushagak stock was estimated to be the second largest component of Nushagak District catch (23.8%), representing a higher than average percentage during the 1975 – 1993 period (33.4%), while the Igushik stock was found to have represented a minimal share (6.3%) of catch between 1963 – 2016 (Fig. 5).

In the Naknek-Kvichak District, catch composition varied greatly over time, with large catches in 1965, 1970, 1983, and 1995, comprised predominantly (average: 84.6%) of the Kvichak stock (Fig. 5). However, averaged across the time series the Kvichak stock is estimated to have represented only 49.7% of catch, with the Naknek stock comprising only a slightly smaller percentage (33.6%) of catch (Table 1). The Alagnak stock was found to have represented only 10.8% of catch on average, but has represented a substantially higher percentage of total catch (18.1%) after 1995 (Fig. 5). The non-target Egegik and Ugashik stocks are estimated to have been significantly smaller contributors to Naknek-Kvichak District catches at 5.1% and 0.8% on average (Table 1).

Sockeye catches in Egegik and Ugashik, the two single-stock fishing districts, were mostly comprised of the target stocks, but with interception of sockeye bound for other river systems representing a non-zero percentage of catch historically. Catch in the Egegik District was primarily comprised of the Egegik stock (77.0%), but interception of Kvichak (10.8%), Ugashik (5.8%), Naknek (5.3%), and Alagnak (1.2%) was also observed (Table 1). Kvichak was found to represent a larger percentage of catches (15.0%) prior to the increase in Egegik production in the early 1980's (Fig. 5). The pattern in apportioned catch from the Ugashik District indicated the Ugashik stock (77.1%) to be the primary contributor, with Egegik (15.2%) second and Kvichak a minor contributor (5.7%), followed by the Naknek (1.3%) and Alagnak (0.7%) stocks.

Comparison of reconstruction methods

Brood tables reconstructed with the current method (Supplementary data) were compared with those reconstructed using previous age-only methods (Bernard 1983), by evaluating differences in estimated brood year productivity (recruits/spawner). For the west side of Bristol Bay, consistent and substantial differences between current model estimates and those generated using age-only methods were observed (Fig. 6, Table 2). Our model estimated the productivity of Igushik and Nushagak stocks to be 31.9% and 14.7% lower on average across brood years compared with estimates from the age-only method, while productivity of the Wood stock was estimated to be 12.3% higher.

Differences were less stark on the east side of Bristol Bay (Fig. 7, Table 2), and showed greater variability. The Egegik stock was consistently estimated to have lower productivity (average 9.4% lower) after accounting for interception (Table 2). Conversely, productivity for the Kvichak stock was 4.7% higher on average, although

this is largely driven by significantly lower estimates of productivity by age-only methods in a few brood years (1972, 1992, and 1996 – 1998) (Fig. 7). Our estimates of productivity for the Alagnak, Ugashik, and Naknek stocks were also 14.9%, 2.0%, and 0.9% higher on average respectively, relative to age-only methods, although with significant variation in this pattern over time (Table 2). Relative to average differences in productivity estimates between new and previous age-only reconstruction methods, differences observed for individual brood years were quite large in some cases. For the Alagnak stock, new productivity estimates ranged from 155.1% higher (1971) to 80.9% lower (1976) than estimates from previous age-only methods (Table 2). Similarly, while new productivity estimates for the Ugashik stock were only 2.0% higher on average (1963 – 2003), for individual brood years new estimates ranged from 42.5% lower (1978) to 25.3% higher (1967). Overall, the magnitude of the difference between productivity estimates, quantified as the mean absolute percent difference across years for each stock, ranged from 9.7% for the Ugashik stock to 38.7% for the Alagnak stock (Table 2).

Discussion

Management of salmon populations using maximum sustainable yield depends on being able to determine the relationship between spawning abundance and recruitment. In fisheries where a mixture of stocks are harvested in common fishing districts, estimates of recruitment depend on accurate methods for partitioning mixed-stock catches and allocating those catches to population of origin. While traditional run reconstruction methods have primarily relied on age composition data (Bernard 1983), the advent of modern, efficient, and low cost molecular genetic methods for stock identification of

current and historical catch samples means new data are available to inform run reconstruction models (Dann et al. 2013; Smith 2010). The statistical model described here draws inference from both genetic and age composition data to reconstruct annual run size and account for observed differences in stock-specific availability to harvest in specific fishing areas, while maintaining the flexibility to be applicable in other salmon fisheries with different stock and age structures. When applied to the Bristol Bay commercial sockeye salmon fishery, comparison of new estimates of stock-specific productivity with those generated using previous age-only run reconstruction methods indicated significant differences across time (Fig. 6 and 7). These comparisons showed that previous age-only methods had consistently overestimated the productivity of the Egegik, Igushik and Nushagak stocks, while consistently underestimating the productivity of the Wood stock (Table 2). However, substantial differences in productivity estimates between new and previous age-only reconstruction methods were observed for all stocks in some years, with these differences varying in magnitude and in some cases direction over time (Fig. 6 and 7). The magnitude of these differences highlights the informative nature of GSI data and the need to account for the interception of non-target stocks in run reconstruction. Furthermore, the observed lack of consistency in productivity differences between methods for the east side of Bristol Bay (Fig. 7) highlights the need for both greater GSI of historical catch samples and continued genetic sampling and analysis in the future. The resulting increase in the precision of spawner-recruit information should provide a better foundation for developing sustainable management targets by explicitly accounting for the differences in availability of sockeye

to harvest in mixed-stock fisheries and interception of non-target stocks during run reconstruction.

The run reconstruction model presented here also estimated differences in age-based selectivity by the commercial fishery. Fishing mortality rates increased with ocean age, except for a slight dip in selectivity for ocean age-4 fish. Our results concur with those in Kendall and Quinn (2009), who compared the length distributions of sockeye before and after the Nushagak District fishery and found that exploitation rates increase with size up to a certain point and then either plateau or decrease slightly. These results also suggest that the fishery has imposed strong selection on the age structure of Bristol Bay populations over time, reducing the survival and limiting the spawning potential of older individuals. Given the positive correlation between the size of female sockeye salmon and fecundity (Cunningham et al. 2013), this pattern of selection, paired with high fishing mortality rates, may have reduced population productivity over time. From an evolutionary perspective, the heritability of life history traits such as age-at-maturity ($h^2=0.21$; Carlson and Seamons 2008) combined with the observed strength of direction selection imposed by the Bristol Bay fishery, provide a viable evolutionary mechanism for changes in the age structure of populations over time with potential deleterious consequences to the stability of the sockeye salmon portfolio (Schindler et al. 2010). Changes in yield-determining traits in response to selective fishing have been cited as potential drivers of stock collapse (Olsen et al. 2004) and changes in population productivity (Law 2000) for some species, so concern is warranted about the potential implications of sustained selection on important life history traits imposed by the Bristol Bay commercial fishery. However, large-scale changes in age structure for Bristol Bay

sockeye populations have not been observed, potentially because fishery selection may be balanced by other forms of natural and sexual selection (Cunningham et al. 2013; Fleming and Gross 1994; Quinn and Foote 1994).

Natural mortality was assumed to be zero during migration between commercial fishing districts and the spawning grounds. Previous run reconstruction models have both included (Potter et al. 2004) and excluded (Branch and Hilborn 2010; Chasco et al. 2007; Flynn et al. 2006) natural mortality. Given that the commercial fishery operates through terminal fishing districts with short transit times (1-5 days) to escapement enumeration sites, natural mortality is likely to be negligible. However, gill net scarring is observed in up to 44% of sockeye escapement to some Bristol Bay river systems (Baker et al. 2014), and is associated with increased mortality on the spawning grounds and spawning failure (Baker and Schindler 2009). While the condition of escaping sockeye is not considered in current run reconstructions, it may have a substantial impact on the productivity of individual populations.

In conclusion, interception of sockeye in non-natal fishing districts during the return migration, and differences in the availability of stocks to harvest within fishing districts, have the potential to result in imprecise estimates of spawner-recruit dynamics and the potential for errors in establishing escapement goals for individual stocks. However, by including GSI data in run reconstruction models, catches can be more accurately allocated back to their stock of origin thus negating difficulties associated with imprecision in recruitment calculation. Given the magnitude of differences in reconstructed population productivity between traditional age-only methods and the model described here, it is clear that understanding recruitment dynamics and

establishing management targets for exploited salmon stocks will in part depend on the availability of both GSI data and run reconstruction models capable of incorporating multiple data types. The run reconstruction model described here was built as a generalizable framework that can easily be implemented to partition catches from any salmon fishery where sufficient data are available. While the commercial sockeye salmon fishery in Bristol Bay was the impetus for building this model, it has a direct application in other systems where a mixture of stocks are harvested in common fishing districts or salmon are intercepted while en route to the spawning grounds. The large differences in productivity we observed between traditional age-only methods and results from this model incorporating GSI data, demonstrate the usefulness of genetic data in improving run reconstructions.

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Figure 1. Map of Bristol Bay, Alaska. Crosshatched areas describe boundaries of terminal fishing districts, and gray labels indicate river systems of origin for reconstructed stocks. The Wood, Alagnak, and Naknek River Special Harvest Areas are located just upstream of each respective river mouth. Map created with shape files from the Alaska Department of Fish and Game Anadromous Waters Catalogue, and U.S. Geological Survey National Hydrography Dataset and National Elevation Dataset.

86x86mm (300 x 300 DPI)

Figure 2. Run reconstruction model fit to age composition data for Bristol Bay. Individual points describe the relationship between the observed and predicted age composition proportions for district catches and river escapements, across years for the six major age-classes.

177x146mm (600 x 600 DPI)

Figure 3. Distribution of estimated gear selectivity parameter values across years, for the West and East sides of Bristol Bay. The distributions of estimated values for ocean age specific selectivity parameters are illustrated as violin plots and boxplots describing the median, and 50th and 95th percentiles.

127x115mm (600 x 600 DPI)

Figure 4. Distribution of model estimated availability parameter values for stocks of Bristol Bay sockeye salmon in the four major fishing districts. Violin plots depict the distribution of parameter estimates, and boxplots the median, 50th and 95th percentiles of estimated values for the relative availability of each stock to harvest in each district.

1587x1852mm (72 x 72 DPI)

Figure 5. Reconstructed catch by stock for each commercial fishing district 1963 – 2016. Top panels are the estimated proportion of catch by stock in each year. Bottom panels are the estimated total annual catches by stock in each year.

177x103mm (300 x 300 DPI)

Figure 6. Comparison of productivity (recruits/spawner) estimates for western Bristol Bay stocks, between new (P_{new}) and previous age-only reconstruction methods (P_{old}), as the percent difference: $(P_{\text{new}} - P_{\text{old}}) / P_{\text{old}}$. The top row of panels displays differences in productivity estimates by brood year (1963 – 2003), while the bottom panels are histograms of the difference values. In all panels the dashed line indicates the mean difference in productivity estimates across brood years.

152x101mm (600 x 600 DPI)

Figure 7. Comparison of productivity (recruits/spawner) estimates for eastern Bristol Bay stocks, between new (P_{new}) and previous age-only reconstruction methods (P_{old}), as the percent difference: $(P_{new}-P_{old})/P_{old}$. The top row of panels displays differences in productivity estimates by brood year (1963 – 2003), while the bottom panels are histograms of the difference values. In all panels the dashed line indicates the mean difference in productivity estimates across brood years.

152x101mm (600 x 600 DPI)

Tables

Table 1 Summary of estimated fishing district catch composition for years 1963-2016. Listed is the mean, minimum, and maximum percent of catch in each district represented by each stock.

District	Stock	Mean	Min	Max
Nushagak	Igushik	6.3	0.9	25.0
	Wood	69.9	31.0	94.1
	Nushagak	23.8	2.3	67.9
Naknek-Kvichak	Kvichak	49.7	1.0	90.6
	Alagnak	10.8	0.1	47.2
	Naknek	33.6	1.8	77.6
	Egegik	5.1	0.3	16.5
	Ugashik	0.8	0.0	7.8
Egegik	Kvichak	10.8	0.2	46.6
	Alagnak	1.2	0.0	5.8
	Naknek	5.3	0.2	14.9
	Egegik	77.0	45.7	98.6
	Ugashik	5.8	0.0	15.8
Ugashik	Kvichak	5.7	0.0	47.0
	Alagnak	0.7	0.0	3.2
	Naknek	1.3	0.0	5.1
	Egegik	15.2	0.8	39.7
	Ugashik	77.1	25.6	98.1

Table 2 Summary of percent differences (1963 – 2003) in the reconstructed productivity (recruits/spawner) of Bristol Bay stocks, between new and previous age-only methods $(\hat{P}_{new} - \hat{P}_{old})/\hat{P}_{old}$. Values presented are the mean, minimum, maximum, and mean absolute percent difference between methods across the time series. Nushagak is highlighted in italics because comparisons are from 1978 – 2003, as available from ADF&G brood tables.

Stock	Mean	Min	Max	MAPD
Igushik	-31.9	-60.4	17.5	33.5
Wood	12.3	-11.4	45.3	14.3
<i>Nushagak</i>	<i>-14.7</i>	<i>-55.8</i>	<i>5.5</i>	<i>15.1</i>
Kvichak	4.7	-28.3	67.5	11.3
Alagnak	14.9	-80.9	155.1	38.7
Naknek	0.9	-28.6	36.4	11.2
Egegik	-9.4	-35.4	7.7	10.3
Ugashik	2.0	-42.5	25.3	9.7