Do smolt data improve adult sockeye salmon forecasting models in the Chignik Management Area?

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Abstract

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Preseason forecasts of adult returns for commercially-important Pacific salmon species provide initial guidance for fishery managers to meet escapement and harvest goals and serve to help the fishing industry plan appropriately for their fishing seasons. The goal of such forecasts is to reduce uncertainty in the management and harvesting processes, yet preseason forecasts often have limited predictive performance. This study compares predictive performance and forecast error of existing models – which use sibling relationships (returning adults of the same freshwater age and brood year) to forecast returns – to models with smolt and environmental predictor variables. I selected predictor variables related to the effects of smolt abundance, size, migration timing and water temperatures on subsequent adult returns and tested these in a nested set of model runs. In general, the simpler sibling models performed better in the most recent 5-year prediction periods than the more-complex smolt models. The two most common and

consistent predictor variables across smolt models were the length of the smolt outmigration season (number of days between 5% and 95% total smolt run) and the temperature of the river at the date of 95% of the total smolt outmigration. This prompted me to create a class of hybrid sibling models using sibling predictor variables and the mid-June average river temperature. Results from all model classes suggest that the standard sibling forecast model remains the simplest and best predictive model to use in the Chignik Management Area. The relatively high performance of sibling-return models probably derives from the fact that the biological information captured implicitly in sibling relationships are redundant to the types of information smolt data reflect.

Introduction

Due to the highly variable nature of interannual returns of Pacific salmon (*Oncorhynchus spp.*), there is a desire for fisheries agencies to generate preseason forecasts of adult returns for commercially-important salmon species (Noakes et al. 1990). These forecasts provide managers, fishermen, and processors with important information regarding the probable magnitude of the run before it begins, so they are better able to make management decisions to achieve adult escapement or harvest-related goals. These goals, in turn, are important for maintaining long-term sustainable fishery yields (Haeseker et al. 2007). Preseason forecasts provide fishery managers with an idea of the strength of the run and, depending on the fishery, can influence early decisions to open an area for harvest or to have it remain closed to protect spawning populations. Once fish begin to arrive to fishing districts or to the spawning grounds, more accurate measures of run strength and composition are available for managers to make more informed management decisions (Adkison 2002).

The fishing industry also uses preseason forecasts to make decisions regarding investments in fishing gear, fishing areas, and regional staffing and logistical decisions prior to the start of each season (Bocking and Peterman 1988). Accurate forecasts can help industry deal with actual returns that are slightly above or below the point estimate without increasing operational costs or losing profits (Mathews, 1971). However, the predictive performance of preseason forecast models is generally poor (Adkison and Peterman 2000) and, especially in fisheries with condensed seasons, can lead to missed escapement goals or lost profits in a fishery.

Salmon forecasting methods are prone to inaccuracies due to missing or incomplete datasets, errors involved in sampling and estimation methods, and variability and unknowns in natural systems. The number of salmon that survive and return to spawning rivers as adults is determined by complex interactions between biotic and abiotic variables (some well understood and others not) while common statistical and modeling approaches tend to use parsimonious models for describing what is clearly a complex system that controls survival and recruitment rates of salmon (Burke et al. 2013). In simplifying a complex set of relationships, crucial variables may be omitted in forecast models because their interactions or impacts on salmon returns are still unknown, are not well understood, are weak, or they are not included in models because the data do not exist for a time series long enough to produce functional forecasts.

The Chignik Management Area is unusual in that a weir that spans the entire width of the Chignik River has been in operation since 1922, allowing for highly accurate counting and sampling of returning adult salmon every year since then, with the exception of a period during World War II. The Alaska Department of Fish and Game (ADF&G) took over weir operations and management of the Chignik River fishery after Alaska statehood (i.e. early 1960's). These data contribute to an expansive and complete brood table, which are records of escapement counts and information on corresponding returns from those spawning adults, that can be used to inform forecasting models with historical data.

There are two distinct stocks of sockeye salmon (*Oncorhynchus nerka*) in the Chignik River watershed (Figure 1). The early run stock returns from early June through July and is comprised of fish that were spawned in the tributaries of Black Lake and typically spend one year rearing in freshwater as juveniles (Griffiths et al. 2012). The late run returns between mid-June through October and typically spawns along beaches and in tributaries of Chignik Lake and generally spend two years rearing in freshwater (Griffiths et al. 2012). ADF&G forecasts Chignik adult returns using sibling-return models – defined directly below – that are assessed with standard linear regressions (i.e., the overall relationship between predicted and observed returns). Particular age class returns that cannot be estimated using sibling relationships or statistical models are estimated using pooled medians (Brenner and Monroe 2017).

The sibling-return model (Peterman 1982) is often one of the best methods for calculating preseason forecasts of adult return abundance for populations of Pacific salmon. This model uses a simple linear regression to quantify relationships between fish of the same freshwater age that entered the ocean in the same year (hence 'siblings') but returned to spawn in different years. Age class composition is assumed to remain relatively constant within a sibling cohort, and each of these age classes are expected to experience similar environmental conditions when they enter the ocean, a time period during which survival to adulthood is thought to be established (Quinn 2005). The model forecasts abundance of a given age-class for a given year based on the abundance of the previous sibling age-class in the previous year (Haeseker et al. 2007). The age of sockeye salmon are designated X.Y where X is the number of winters spent in freshwater and Y is the number of winters spent in the ocean (Haeseker et al. 2007). Fish spend nearly an entire additional year incubating as embryos in the gravel, so the total age of a fish is one year more than the sum of X and Y. A sibling model forecasts the return of 2.3 fish in a given year from returns of 2.2 fish the year before (2.2 fish from 2.1 fish, etc.). The simplicity and relative accuracy of sibling models has lead ADF&G and the University of Washington (UW) to employ these models for official forecasting; however, ecological and environmental processes impacting the survival of Pacific salmon species at each stage in their life cycle are complex, and there is a desire to try to directly capture some of those biological and environmental factors in a model that forecasts adult returns.

Beginning in 1994, ADF&G monitored outmigration of sockeye salmon smolts in the Chignik River. These data represent the most robust smolt dataset in Alaska and have been used to assess the health and condition of smolt leaving the Chignik River and to estimate the age composition and marine survival of outmigrating populations (Loewen and Henslee *in press*). Data collected from outmigrating sockeye smolts include length, mass, age (from scale samples), along with environmental data (including air temperature, water temperature, absolute water depth, weather) collected at the trap site, and counts of all species captured in the smolt traps. This smolt dataset, combined with the complete adult brood tables for Black and Chignik Lakes, provide an excellent opportunity to explore the potential for improving upon sibling-return forecast models by including smolt and environmental predictor variables.

The purpose of this study is to test whether the inclusion of smolt and environmental data improve the predictive performance of forecast models for the Chignik River. I developed and evaluated forecast models that include smolt and environmental variables that were hypothesized to be related to adult returns to predict stock by age-class returns and compare model predictions to those from sibling-return models. This analysis focuses on the dominant age classes for the early and late runs destined for Black and Chignik lakes, respectively, which are 1.2, 1.3, 2.2, and 2.3. While other age classes are present in these stocks, they constitute less than 5% of the total returns, on average. When selecting predictor variables, I considered hypotheses regarding the impact of smolt abundance, body condition, length, outmigration timing, length of outmigration season, water temperature changes, and water temperature anomalies between the Chignik River and the Gulf of Alaska. Juvenile salmon phenology, and subsequent survival, is closely linked to prey availability and conditions in the marine environment upon entry (Crozier et al. 2008; Satterthwaite et al. 2014). I summarized these conditions by gathering data on annual river and ocean temperatures at different times during the smolt season and water temperature anomalies between the Chignik River and the ocean at critical periods for juvenile salmon.

I used a one-step ahead cross-validation method to determine the predictive ability of each models using only data that would have been available up to the prediction year. Finally, I calculated forecast error for all years using the predictions of the smolt-based and sibling-return models and the observed returns to compare the performance of smolt models to sibling-return models currently used for forecasting sockeye salmon returns to the Chignik watershed.

Methods

Data— I compiled data collected by the Alaska Department of Fish and Game (ADF&G) Chignik Smolt Enumeration Project on the Chignik River from 1994 through the conclusion of the project in 2016 (Loewen and Baechler 2016). ADF&G deployed two rotary screw traps off the bank of the Chignik River, upstream of the Chignik weir, where personnel counted and identified all fish species caught, collected biological data from sockeye smolts, and conducted mark-recapture events to calculate trap efficiency and estimate smolt abundance (Loewen and Baechler 2016). The screw traps were operated 24 hours per day (unless raised for repairs, cleaning, or emergencies), and live boxes were emptied and all species were identified and enumerated every 6-8 hours (more frequently during high outmigration periods). Species counts were summed across "smolt days", the 24-hours between high noon on subsequent days, because the majority of smolt migrate at night. ADF&G reports body condition of smolts using Fulton's condition factor (K) and estimates trap efficiency from mark-recapture experiments to estimate daily smolt outmigration and total smolt abundance (St. Saviour 2013). Mark-recapture experiments were performed weekly throughout the smolt season, or as soon as possible after a change in trap location or extreme change in outmigration magnitude in order to best estimate the smolt run.

In the instance when high numbers of smolts (> 1,000) were observed within the first days of the project, biologists estimated the outmigration for days prior to trap installation by using time-series analysis based on initial counts (Loewen and Baechler 2016). The peak date of the smolt outmigration is reported as the mode of the smolt counts. I used post-season abundance estimates for daily outmigration to calculate the calendar dates of, and the subsequent number of days between, 5% and 95% of total outmigration (considered to be the length of the outmigration season) (Table 1).

I also used stock by age-class data on adult sockeye salmon returns to the Chignik River (escapement plus harvest) complied by ADF&G from 1980-2017, focusing on the data relevant to the most prominent return age-classes for Black and Chignik Lakes (1.2, 1.3, 2.2, and 2.3). Return data are allocated to either Black or Chignik Lake stocks. Prior to 2009, managers used a cut-off date of July 4 to allocate returning spawners to either Black or Chignik Lakes, where fish returning before July 4 were considered Black Lake returns and those passing the weir after that date were allocated to Chignik Lake escapement. Beginning in 2009, ADF&G conducted in-season genetics sampling at the Chignik weir and post-season analysis of harvest and escapement data in order to more accurately allocate escapement to Black and Chignik Lakes and allow apportionment to continue during the period when stock returns overlap temporally (Wilburn 2017).

Due to the lack of project funding for genetic analysis of smolt samples collected at the study site, the biological smolt data included in this analysis are not stock-specific. Data for smolts of the same freshwater age are assumed to be similar across Black and Chignik Lake models; however, outmigrating smolt are assigned and apportioned by freshwater age based on post-season smolt scale aging conducted on samples taken in-season. I then merged adult stock by age-class escapement data with appropriate smolt data by matching adults with smolt data from the year in which they outmigrated as smolt of a particular freshwater age (i.e., 2.3 fish returning in 2005 outmigrated in 2002 as freshwater age-2 smolts). Environmental smolt data are also matched with adult returns based on the year in which the adults outmigrated as smolt.

Sea surface temperature (SST) often correlates with adult salmon returns (Adkison et al. 1996), so I obtained area-specific monthly mean temperatures from a 1° latitude and 1° longitude grid from the Royal Netherlands Meteorological Institute (KNMI) Climate Explorer web application (https://climexp.knmi.nl/) (Rayner et al. 2018). The two offshore locations are hypothesized to be used (or represent the actual area used) by sockeye in their crucial first year in the ocean. The data come from HadISST1 spatial scale reconstruction components. I selected one location offshore of Chignik Bay (56-57°N latitude, 156-157°W longitude), to represent a coastal area that may be occupied by juvenile sockeye salmon upon entering the ocean, an important life history period where water temperature differences between the freshwater and marine habitats can greatly impact marine survival of juvenile salmon (Burke et al. 2013; Crozier et al. 2008; Mantua et al. 1997). The second location is in the Gulf of Alaska (55-56°N, 149-150°W), an area chosen to represent the area likely used by juveniles shortly upon entering marine waters. Marine habitat use by particular stocks of salmon are not well-described, so these locations were selected as best estimates.

Using the SST data, I calculated the difference between the water temperature on the date of peak outmigration in the Chignik River and the June monthly average SST in Chignik Bay as a way to quantify the potential magnitude of a mismatch between environmental conditions in freshwater and marine habitats. The mean peak migration date falls between mid- to late-May, so to account for the time it takes smolts to travel from the smolt trap site, down the Chignik River, through the Chignik Lagoon and out into the Gulf of Alaska, I selected the month of June to represent the appropriate temporal scale. A second predictor variable created was the annual mean SST in the Gulf of Alaska grid cell for the month of August, which depicts a general ocean temperature a few months after salmon enter the ocean.

Sibling-return forecast modeling—First, I developed log-linear regression forecasting models fit with the data for 8 stock by age-class sibling relationships (models for predicting 1.2, 1.3, 2.2, and 2.3 adult returns separately for Black and Chignik Lakes). These stock-specific models use actual observed returns of sibling age classes in the previous year to predict the return of older siblings the next year. Some sibling-return models use either freshwater or ocean sibling relationships to predict returns; in the sibling-return model in this analysis, data from siblings from the same brood year and of the same freshwater age that returned to spawn at different ocean ages were used.

The sibling model used for forecasting is a linear model that forecasts returns of adults of ocean-age N in year t using the actual returns of their freshwater siblings of ocean-age N-1 in year t-1 (Haeseker et al. 2007; Peterman 1982), where c and d are model parameters (1).

$$(1)\ \log (\mathrm{N}_t) = c + d * (N - 1)_{t-1}$$

For age classes with data available for multiple sibling years (3-ocean fish can be predicted using either or both 1- or 2-ocean return data from the same freshwater cohort), sibling predictors were selected using AIC as described below in the smolt model selection process. These sibling models use only sibling age-class returns as predictors and include no additional co-variates. I used adult brood tables with data from 1980-2017 to retrospectively parameterize the linear model. The sibling model both assumes that both the age composition remains constant within a sibling cohort and the marine survival rates for siblings are approximately constant. By using data on siblings from the same brood year, this model accounts for covariation in responses to critical environmental influences they share during critical life stages in freshwater and the ocean, particularly the environmental conditions experienced in their first year at sea (Haeseker et al. 2007).

Smolt class forecast modeling – I then generated smolt-based forecast models using log-linear relationships between sibling and biological smolt and environmental predictors: smolt abundance, body condition, smolt length, peak outmigration date, length of outmigration season, Chignik River water temperature (on the date of 5%, peak, and 95% of total outmigration), water temperature difference between Chignik River and the ocean, and Gulf of Alaska sea surface temperature (Table 1).

Table 1. Name, category, and description of all predictor variables (not including sibling) included in smolt and hybrid smolt class model analysis

Predictor	**Description**
	Category 1 – Biological Smolt Variables
Abund	Estimated abundance of outmigrating smolt of a particular freshwater age
BC	Smolt body condition (Fulton K)
Length	Mean length of smolt by freshwater age
	Category 2 – Abiotic Smolt Variables
DOY.peak	Julian date of the peak of smolt outmigration (calculated as mode of outmigration)
OM.length	Length of the smolt outmigration season (calculated as number of days between 5% and 95% total smolt outmigration)
	Category 3 – Environmental (Temperature) Variables
Temp.early	Average 5-day river temperature (at smolt traps) around the date of 5% total outmigration
Temp.peak	Average 5-day river temperature (at smolt traps) around date of peak outmigration
Temp.tail	Average 5-day river temperature (at smolt traps) around the date of 95% total outmigration
Temp.anom	Difference in water temperatures between the Chignik River at the date of peak outmigration and the June monthly mean SST offshore in Chignik Bay
GOA.temp	August monthly mean SST in Gulf of Alaska

The structure of this model is, where N, t, and c are as in (1), and β are model parameters:

$$(2)\ \log(N_t) = c + \beta_1(N - 1)_{t-1} + \beta_2(\text{Abund}) + \beta_3(\text{BC}) + \beta_3(\text{Length}) + \beta_4(\text{DOY.peak}) + \beta_5(\text{OM.length}) + \beta_6(\text{Temp.early}) + \beta_7(\text{Temp.peak}) + \beta_8(\text{Temp.tail}) + \beta_9(\text{Temp.anom}) + \beta_{10}(\text{GOA.temp})$$

I used a multi-directional stepwise Akaike Information Criterion (AIC) method for variable selection for each of the 8 stock by age-class models and selected the smolt linear regression model with the lowest AIC score, those that explain the data with a minimum number of parameters, for each of the 8 stock by age-class models. To better reflect the distribution of salmon abundances and to avoid possible negative intercept values and predicted returns, I log-transformed the response variable; I then exponentiated the model result to report actual numbers of predicted adult returns.

I also created a class of hybrid smolt models using the same stepwise AIC method as described for the smolt class models; however, I selected models within a delta AIC score of two or less from the most parsimonious model that included less predictor variables. This process leads to a simpler model that is statistically indistinguishable from the model with the lowest AIC score (Yamashita et al. 2007). In cases where the next best (or nearly equivalent) stock by age-class models included more predictor variables, or when eliminating variables changes the AIC by more than 2, the hybrid smolt class models were considered identical to the smolt models.

One-step ahead cross-validation—To test the predictive ability for each of the model classes, I conducted a one-step ahead cross-validation for each stock by age-class in each of the sibling, smolt, and hybrid smolt class models. The cross-validation method attempts to simulate the historical implementation of the model by using only data that would have been available in a particular year to predict the next year's returns and does not inform the model of future data. The predictor variables remain constant in each of the linear models; however, the intercepts and variable coefficients change as more data are introduced to the model. Annual return predictions for each of the models were then compared to the observed returns for each age class, and the annual forecast error was calculated for each model using techniques described in Haeseker et al. (2008). Although models can over- or under-predict returns, forecast error summary statistics are reported in absolute value.

Predicted returns were calculated for each age-class model for all model classes and are also aggregated by stock to provide early- and late-run totals (e.g., early-run total would be the sum of returns for Black 1.2, 1.3, 2.2, and 2.3). In addition, the early- and late-run totals are summed to provide a prediction for the total run. I then calculated forecast error for early- and late-runs as well as the total run using observed age-class totals summed across stocks. I then compared the predictive capabilities and forecast error of the smolt and hybrid class models to the sibling class models to determine the model class with the best predictive ability from 2003-2017 for each of the individual stock by age-classes, aggregated early- and late runs, and the total run for the Chignik watershed.

Results

The average adjusted R-squared values across age-class models of the smolt and hybrid-smolt class models were more than twice those of the sibling models (Table 3); however, these models were nearly always more complex than the simple sibling models. The average R-squared values across all stock by age-classes for smolt models were 0.45 (smolt) and 0.42 (smolt hybrid), with a high of 0.71 for Chignik 2.2 and a low of 0.16 for Chignik 1.3. The adjusted R-squared values for the sibling model ranged from 0.03 (Black 1.2) to 0.37 (Black 2.3) and averaged 0.20 across all stock by age-class models. Adjusted R-squared values were similar across all model classes for Chignik 1.2 and 1.3 age classes. The high R-squared values for the retrospective linear smolt and hybrid class models demonstrate a strong correlation between smolt and environmental covariates and adult returns in model selection, meaning the variables are most likely capturing important biological and ecological relationships. However, models with the highest R-squared values also contain the most covariates, leading to potentially over-complicated models that do not perform well in a forecasting situation.

In 7 of the 8 sibling stock by age-class sibling models, adult returns were best predicted by the previous year's sibling age class of the same freshwater age (1.3 by 1.2, etc.); the only exception, Black 2.3, was a sibling model that included both 2.2 and 2.1 age classes. Among the smolt models, no single set of predictor variables yielded consistent effects (Table 2). Instead, the best individual models for different stocks (Black and Chignik) and age classes included different subsets of variables with the number of variables in each best-fit model ranging from 2 (Chignik 1.3) to 10 (Black 2.3). OM.length and Temp.tail were each present in 6 of the 8 stock by age-class models, both of them occurring as predictor variables in 5 of them. In general, OM.length and Temp.tail had respective negative and positive effects on total adult returns. In the AIC-selected smolt models, sibling relationship variables were only included in 4 of the most parsimonious models, 3 of which predicted Black Lake returns. These results indicate a strong retrospective relationship between adult returns and smolt and environmental covariates.

Forecast error was calculated for each stock by age-class, the total early- and late-runs, and the total run from 1981-2017 (sibling models) and 1997-2017 (smolt-based models). However, only calculated forecast errors between 2003-2017 were used for evaluating the predictive ability of each model due to the inherent drawbacks of using one-step ahead cross validation with only data that would have been historically available in the prediction year.

The range in forecast errors within and among model classes was large. Median forecast errors for the most recent 5-year period (2013-2017) for each stock by age-class for sibling, smolt, and hybrid smolt class models are summarized in Table 4. Between 2013 and 2017, the sibling class models presented the lowest forecast error for returns for Black 1.2, Black 1.3 and Chignik 1.3 age classes (average 39.8%) (Table 4). Over the same time period, the smolt hybrid class models had lower error than the smolt class models for Chignik 1.3, 2.2, and 2.3 age classes (hybrid smolt averaged 32.3% and smolt averaged 36.7%). However, the sibling class models display a much lower median error for the total early- and late-runs as well as the total run. The most recent 5-year median forecast error for sibling class models for the aggregated early-run is 12.1%, compared to 85.9% for the smolt class models, and the late- and total-run median errors are 4.0% and 4.7%, respectively, compared to 23.0% and 29.3% for the smolt class models over the same time period.

In general, all model types produce higher forecast error for the early Chignik Lake returns compared to the aggregated late- and total-run errors, where the mean of the median forecast errors for all three forecast model classes from 2013-2017 were 62.0%, 13.2%, and 21.5% for early, late, and total runs (Table 4). The smolt model drastically over-predicted returns for the early run in 2009, which is influenced by the extreme model over-prediction of a single age-class (Black 2.3) return for that year. The smolt class forecast models had lower absolute forecast error for the total run in 6 of the last 15 years, with the majority of those years falling between 2003 and 2012. The range in total run absolute forecast error from 2013-2017 for the sibling class models was 0.2% (2015) to 34.9% (2013), and the error ranged from 1.0% (2017) to

176.2% (2013) in the smolt class models (Figure 2; Table 5). Therefore, the annual variability in the total-run forecast error in the most recent 5 years is greater in the smolt class models compared to the sibling class models.

The median observed total run between 2003-2017 was 2.05 million fish; the sibling class model median prediction for the total run was 1.82 million over the same time period (Table 6). The smolt and hybrid smolt models predict a median return of 2.08 and 1.58 million fish, respectively. The smolt model median total run prediction is closest to the observed total run; however, in 2009, the smolt model predicts a total run of 182.46 million fish. This is due to an early-run model prediction of 181 million, when the observed early-run return was 0.85 million (Table 6; Figure 2). Therefore, the median values do not capture the variability and range in prediction errors in different models, especially the smolt class models.

Hybrid Sibling Model – Water temperature at the date of 95% smolt outmigration (Temp.tail) was a recurrent predictor variable in the smolt class models, and was, in general, positively correlated with adult returns. Due to this strong association across age classes, I created a hybrid sibling class model using the same sibling predictor variables as the sibling model and included another predictor variable (June.temp) that summarizes the relationship of water temperature at the end of the smolt outmigration season. For each year, I found the 5-day average water temperature at the smolt trap site around June 15 (representing the average date of 95% smolt outmigration across years). I selected and evaluated the model in the same manner as the smolt models. In order to allow for equal comparisons across sibling class models, I also calculated predictions for the standard sibling model using data from only 1997-2017 to inform the model; these predictions are identical to the original sibling class models and are therefore not presented separately as results.

In 6 of the 8 hybrid sibling models, the June temperature variable predicted a negative direction of influence on adult returns when included in the hybrid model with sibling relationships, which is the opposite influence demonstrated in the initial smolt class regression models. When comparing forecast error between the hybrid and standard sibling class models from 2003-2017, the hybrid sibling models had lower absolute forecast error for the early-, late-, and total runs in 6, 5, and 8 of the 15 years, respectively. However, between 2013 and 2017, the standard sibling models out-performed the hybrid sibling class models. Forecast errors for the early run ranged from 9.5% to 180.0% for the hybrid sibling class models and 6.2%-11.7% and 0.7%-82.6% for the late and total runs, respectively. There was very high variability in the hybrid sibling class model forecast error for the total run between 2013 and 2017, which is especially evident in the dramatic drop from 82.6% in 2015 to 0.7% error in 2016. Despite initial indication of a potentially strong predictive relationship between water temperature covariates and adult returns, the simple sibling-return regression model more consistently predicts returns with lower forecast error than the hybrid sibling model.

Discussion

Simple sibling-return models consistently outperformed the more complex models informed by smolt and environmental covariates for providing year-ahead forecasts of run strength of sockeye salmon to the Chignik River. No single model using smolt and environmental covariates provided a distinct combination of predictor variables that best predicted all of the adult age-class returns for Black and Chignik Lake stocks. No single smolt covariate was present in all 8 of the smolt class models, and those present varied in their direction of influence across age-class models. This could be due to the inter-annual variability in returns between age classes and across stocks, and the complex ecological interactions in the freshwater environments between years and smolt cohorts or the lack of strong ecological relationships that can be distinguished from the inherent variation in the data.

Sibling age-class variables were not present in the majority of smolt class models selected by the AIC method, which means that retrospectively, when combined with smolt and environmental data, the sibling relationships were less influential on the adult returns. The correlation between smolt biological variables and adult returns were inconsistent across models and present in very few models, whereas smolt abiotic and environmental predictor variables were much more frequently included and more consistent across stock by age-class models. A potential explanation for this pattern in prevalent predictor variables may be due to the inherent errors involved in enumerating smolts, including smolt trap avoidance that can impact results of mark-recapture events and subsequent smolt abundance estimates. However, measurements of river water temperature and duration of smolt outmigration are less prone to sampling error and are more consistent across years and models.

Many of the smolt biological predictor variables showed relationships to adult returns that were in direct conflict with biologically-based hypotheses. It is well known that smolt mortality rates are high immediately after smolts enter salt water (Beamish and Mahnken 2001), which can be partially attributed to smolt size (Pearcy 1992). The hypothesis presented in this analysis was that increased smolt body condition and length would positively influence adult returns; however, when included in models, body condition negatively influenced the returns in the model, and the length predictor variable was included in the smolt model, but was ultimately not statistically relevant in predicting adult returns (as evidenced by its removal in the smolt hybrid class models).

My initial hypothesis that smolt abundance would be positively correlated with adult returns was not supported by these results. The direction of influence of smolt abundance was inconsistent across models where it has a statistical correlation with adult returns. Smolt abundance is believed to be positively correlated to adult returns, as the probability for survival to adulthood should increase as the number of smolt entering the ocean increase; however, it is possible that competition for resources between smolt is positively correlated with abundance and leads to lower body condition and survival rates within the crucial first year of life in the marine environment (Irvine and Akenhead 2013) .

In this study, I selected models using a retrospective AIC method to select predictor variables for linear regression models, but model forecasting abilities were evaluated based on one-step ahead cross-validation using only data that would have been available in that year. Because of this, adjusted R-squared values for the smolt class models were much higher than the sibling class models; however, sibling class models out-performed the sibling models when predicting adult returns.

The inclusion of predictor variables beyond sibling relationships lowers forecast error in some age-class adult returns and aggregated stock and total returns between 2003 and 2017. Although ADF&G and the University of Washington forecast individual stock by age-classes, managers, fishermen, and industry rely more heavily on aggregated totals for Black and Chignik Lakes or the total return for the season. Therefore, I chose to focus my evaluation of model performance less on individual stock by age-class models and more on aggregated stock and run totals. When aggregated, forecast error and predictions were smaller than individual age-class model statistics. This effect was evident when comparing median forecast error between individual age-class models and the total stock and run returns.

Adult returns can be assigned with a high degree of accuracy to each stock due to the genetic analysis performed in-season at the Chignik weir, beginning in 2009. Although smolt samples are collected for genetic analysis, ADF&G budget constraints do not allow for genetic testing; therefore, smolt genetic data are aggregated for Black and Chignik Lakes. Using aggregated smolt abundance data as predictors for stock by age-class adult returns with distinct freshwater sibling cohorts could lead to incorrect inclusion or exclusion, and direction of influence in the smolt-based forecast models. This could partially explain the conflicting correlation and lack of inclusion of these variables across models. Smolt genetics data that distinguish outmigrating smolts by stock of origin would provide more information regarding the utility of the smolt abundance predictor variable in the model, and the relationships described in the current findings (or the lack thereof) could be misrepresentative at this time.

Environmental variables, such as the water temperature at 95% total smolt outmigration and length of the smolt outmigration season, were the most common predictors across all models. The average freshwater temperature at the beginning of smolt outmigration is about 4°C (ranging from 2.3°C to 5.2°C). Water temperature changes and thresholds are important biological triggers for smolt activity, and annual variation in water temperatures and seasonal timing of these variations can have a direct impact on smolt outmigration timing and the length of the outmigration season. The outmigration season length appears as a predictor variable in 6 of the 8 smolt models and has a negative direction of influence on adult returns in 5 of them. Years with longer outmigration seasons may be indicative of years with low smolt abundance or temperature mismatches between freshwater and saltwater conditions. Juvenile smolt survival depends crucially on the timing of transitions between life stages and habitats (Crozier et al. 2008). The temperature at the date of 95% total outmigration was included as a predictor in 6 of the 8 models and has positive direction of influence in 5 of them, which suggests that warmer temperatures during the tail of the outmigration season provide better conditions for the smolts to transition from freshwater to saltwater, leading to increased marine survival rates and adult returns. However, inclusion of water temperature in the hybrid sibling models did not improve their forecast performance, suggesting that temperature effects on smolt survival were already captured implicitly by the sibling-return relationships.

In general, all class models performed better for Chignik Lake age-classes and run predictions than models for Black Lake. Historically, the early-run adult returns were typically more variable across years –and therefore harder to predict– than the late-run returns, and this translated to higher annual forecast error in both sibling and smolt class models when compared to Chignik Lake. Between 2003 and 2017, the average observed total run was 2.17 million. Over this period, the lowest return was observed in 2014 at 1.2 million. All models predicted total run returns to be less than the 15-year average, but the sibling model provided a forecast of 1.5 million when the smolt and hybrid models predicted returns of 2.0 and 1.8 million, respectively.

Some drawbacks of using forecast error to evaluate model performance across years involve subjective judgment regarding what is or is not large forecast error, and the acceptable level of precision of error depends on the stakeholder. Another complication relates to the actual magnitude of the run in any given year. In years with total runs that are below the historical average, a forecast that over-predicts returns (even if forecast error is low) could be more detrimental to fishermen and industry, whereas years with returns that are well above the historical average, even high forecast errors could end up being inconsequential. In years where the total return is well below the historical average, a small error in the forecast prediction could have a larger impact than a similar forecast error in a year of average or above-average returns.

Therefore, analyzing how well different model classes predict returns that are well below or above average is important when evaluating model performance.

While the smolt and hybrid smolt models lower forecast error in some years, the sibling model performs better across all years of analysis. Because the sibling model is bounded by actual returns of fish in any given year (sibling relationships), the model did not produce predictions of aggregate runs that are unfeasible in the Chignik system, whereas, the smolt models are subject to unrealistic predictions (e.g. 2009 for a total run of 182 million) due to complex models and relationships between parameters. Due to the complexity of selected smolt and hybrid class models, the aggregated performances of each model can be greatly influenced by outlier predictions (Figure 3). The sibling model is the simplest and most parsimonious model, and the sibling-return relationships may already be capturing the biological and environmental relationships that I am trying to model with smolt data using variables that are most likely imperfect.

The Chignik River system is, in several ways, a compelling setting in which to evaluate the value of smolt data on adult forecasting, because the system is relatively small and the run is very well enumerated. The sibling relationship data are so strong, because we have the data to accurately apportion fish counts to stock and individual age classes. Compared to other large river systems, the Chignik River is also an ideal location for a smolt study, because the river is relatively small and allows for more accurate smolt enumeration and sampling. Smolt projects are expensive to start and operate, and decades of data are likely necessary to conduct a thorough statistical analysis of forecast performance. Salmon weirs are already used for in-season management purposes and incur no additional costs to use the adult data for forecasting methods. These results show that the sibling-return models produce forecasts with the lowest forecast error, are low-cost, and employ simple statistical techniques. Salmon returns are highly variable naturally, and this research shows that there is an inherent level of uncertainty in fisheries forecasting, and stakeholders must account for this uncertainty in fishing behaviors and their decisions made before the start of the season.

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Figures and Tables

Figure 1. Map of the Chignik River watershed, showing the Chignik River, Chignik weir, Chignik Lake, and Black Lake, and location relative to the state of Alaska.

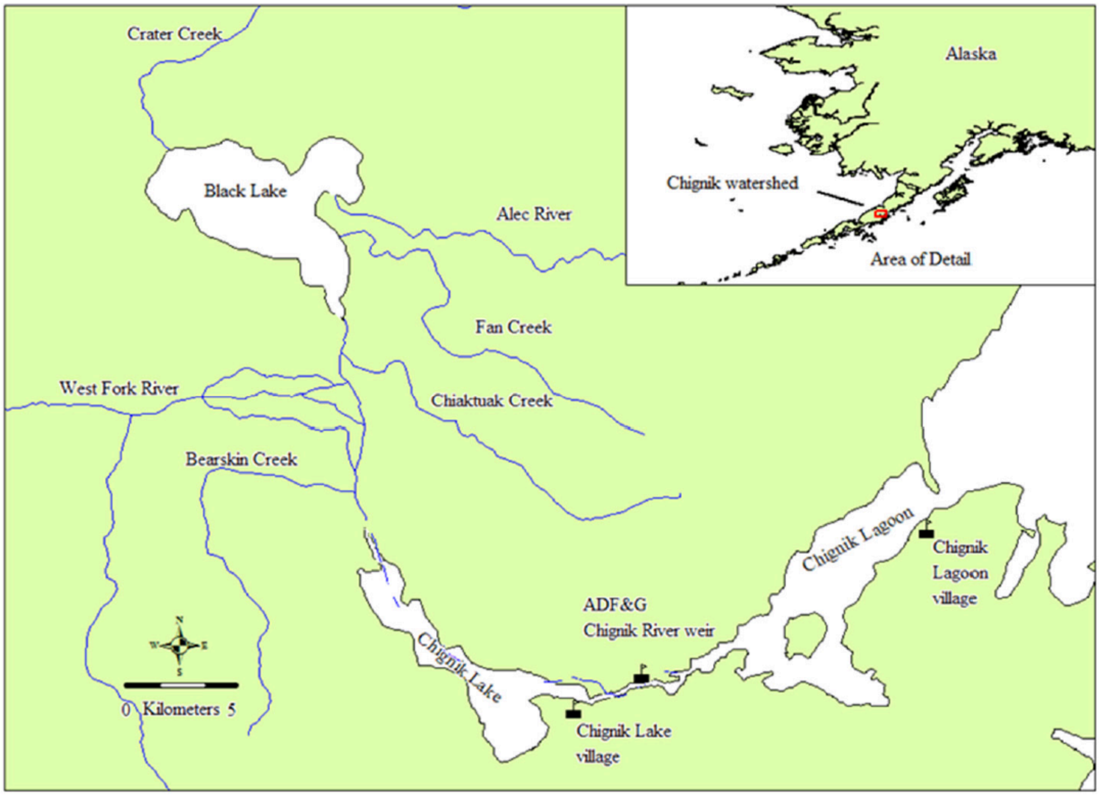


Figure 2. Plots of forecast error (%) for the early-, late-, and total-runs from 2003-2017 (excluding 2009 due to extreme outliers). The plot on the bottom right is observed returns as bars and the predicted returns for each of the three model types.

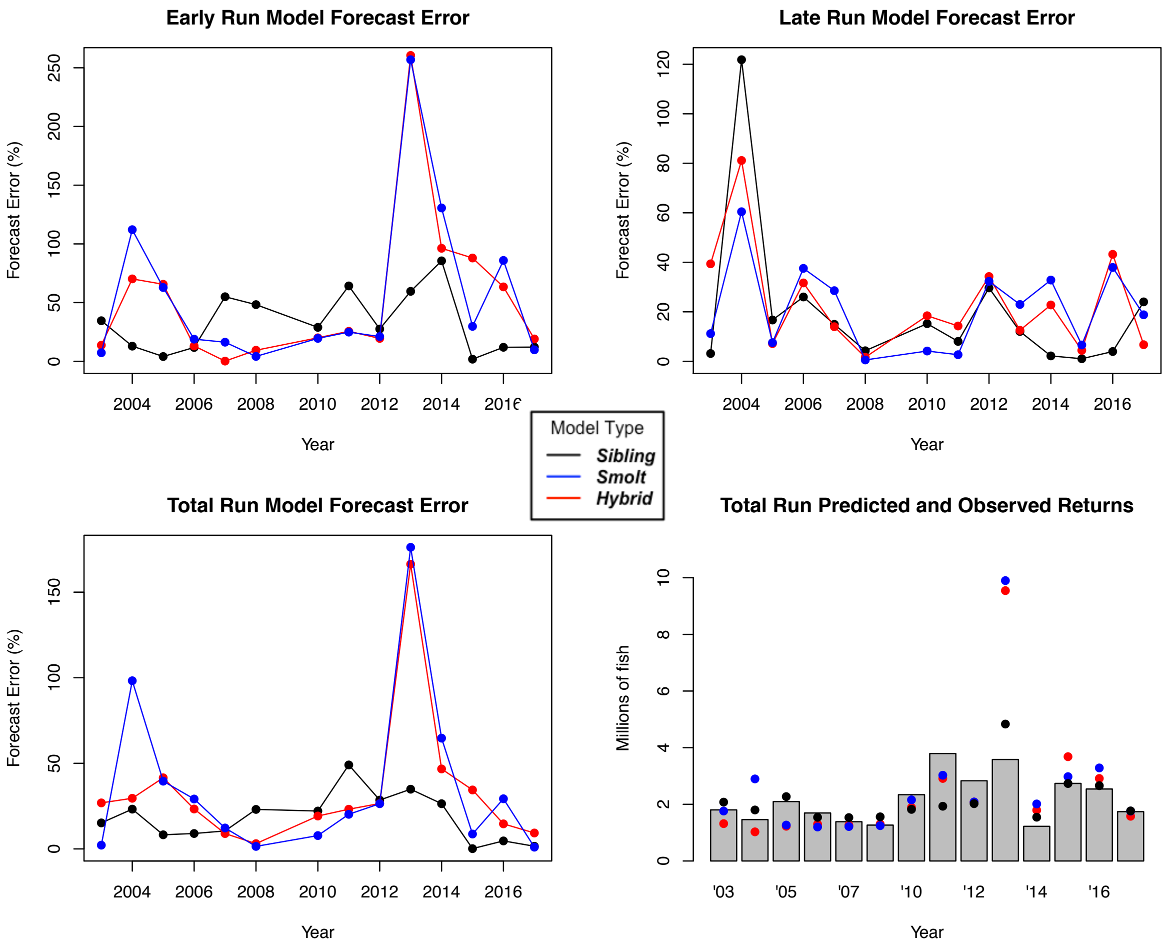


Figure 3. Plots of predicted returns (millions) to observed returns (millions) for different model classes (columns) for aggregated early-run (top), late-run (middle), and total run (bottom). Red lines are the linear regression trend lines and the black line is the one-to-one relationship.

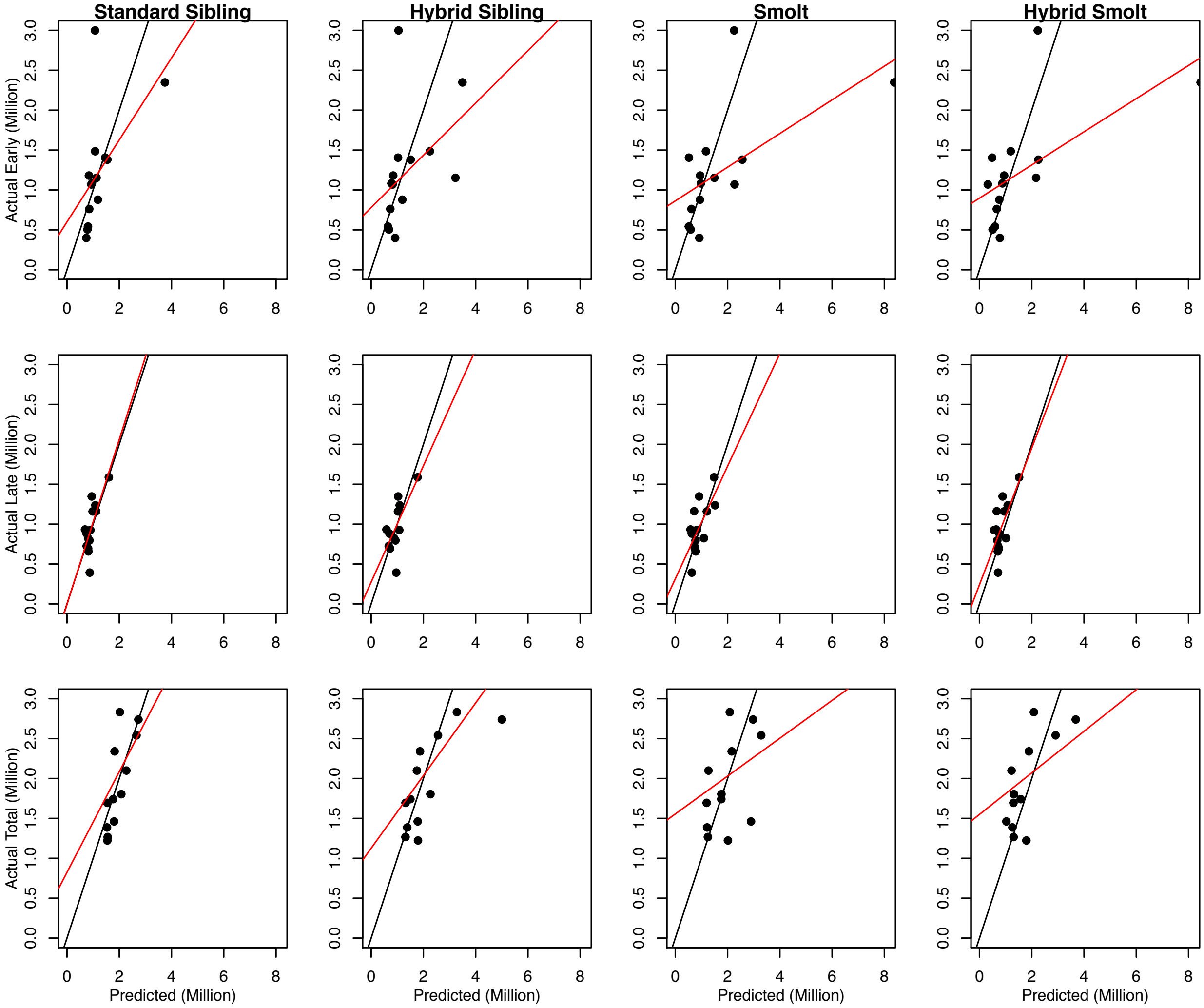
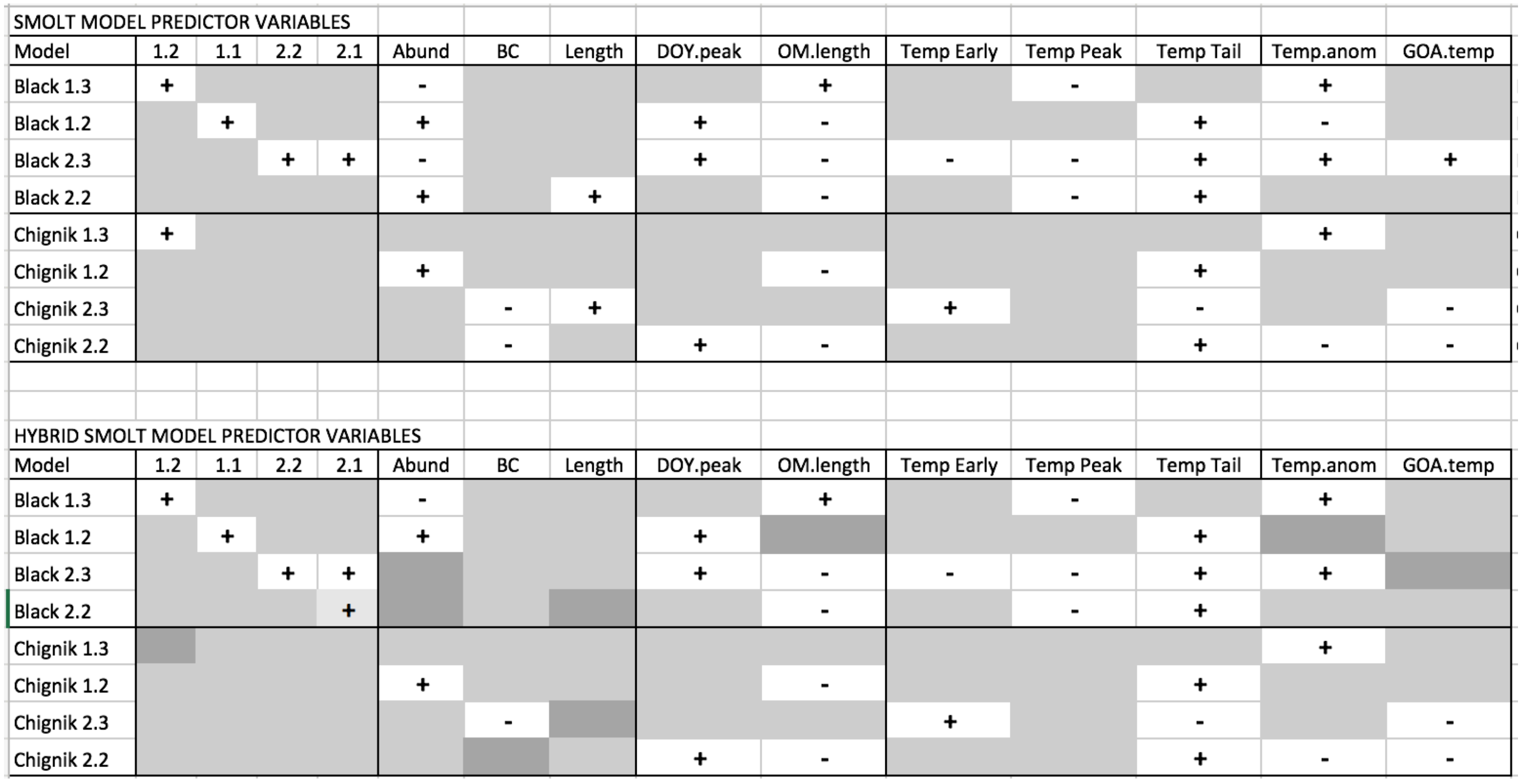


Table 2. Predictor variables present in smolt and hybrid smolt models. The sign in each box indicates the direction of influence of each variable on adult returns. Dark grey shaded boxes in the hybrid smolt model indicate the removal of variables from the smolt model, and the single lighter grey box indicates the addition (in Black 2.2 model).



SMOLT MODEL PREDICTOR VARIABLES

Model	1.2	1.1	2.2	2.1	Abund	BC	Length	DOY.peak	OM.length	Temp Early	Temp Peak	Temp Tail	Temp.anom	GOA.temp
Black 1.3	+				-				+		-		+	
Black 1.2		+			+			+	-			+	-	
Black 2.3			+	+	-			+	-	-	-	+	+	+
Black 2.2					+		+		-		-	+		
Chignik 1.3	+												+	
Chignik 1.2					+				-			+		
Chignik 2.3						-	+			+		-		-
Chignik 2.2						-		+	-			+	-	-

HYBRID SMOLT MODEL PREDICTOR VARIABLES

Model	1.2	1.1	2.2	2.1	Abund	BC	Length	DOY.peak	OM.length	Temp Early	Temp Peak	Temp Tail	Temp.anom	GOA.temp
Black 1.3	+				-				+		-		+	
Black 1.2		+			+			+	▨			+	▨	
Black 2.3			+	+	▨			+	-	-	-	+	+	▨
Black 2.2				+	▨		▨		-		-	+		
Chignik 1.3	▨												+	
Chignik 1.2					+				-			+		
Chignik 2.3						-	▨			+		-		-
Chignik 2.2						▨		+	-			+	-	-

Table 3. Adjusted R-squared values for each stock by age-class model for sibling, smolt, and hybrid smolt model classes (B = Black Lake, C = Chignik Lake).

Model	**Sibling**	**Smolt**	**Hybrid**
B1.3	0.34	0.44	0.44
B1.2	0.03	0.43	0.38
B2.3	0.37	0.66	0.63
B2.2	0.20	0.33	0.27
C1.3	0.14	0.16	0.10
C1.2	0.13	0.17	0.17
C2.3	0.14	0.67	0.66
C2.2	0.24	0.71	0.69

Table 4. 2013-2017 median* forecast error (%) for each stock by age-class model. (B = Black Lake, C = Chignik Lake). Mean of model medians reported for early, late, and total runs.

	B1.2	**B1.3**	**B2.2**	**B2.3**	**Early**	**C1.2**	**C1.3**	**C2.2**	**C2.3**	**Late**	**Total**
Sibling	47.40	27.42	47.15	33.02	**12.11**	56.20	44.73	103.40	25.15	**3.95**	*4.68*
Smolt	49.95	63.58	38.36	20.47	**85.93**	24.89	53.42	27.33	29.23	**22.97**	*29.30*
Hybrid	54.17	63.58	63.24	75.38	**87.99**	24.89	51.76	23.07	21.93	**12.54**	*30.57*
					62.0%					**13.2%**	*21.5%*

*The absolute value of the forecast error for each model was used to calculate the median.

Table 5. Summary table of forecast error* (%) by stock and total run for sibling, smolt, and hybrid smolt models

	Early Run			**Late Run**			**Total Run**		
Year	**Sibling**	**Smolt**	**Hybrid**	**Sibling**	**Smolt**	**Hybrid**	**Sibling**	**Smolt**	**Hybrid**
2003	34.56	7.30	-13.70	-3.15	-11.20	-39.39	15.20	-2.19	-26.89
2004	-12.92	112.12	-70.19	121.85	60.43	81.14	23.24	98.25	-29.58
2005	4.08	-62.86	-65.60	16.69	7.54	7.16	8.25	-39.57	-41.54
2006	11.80	-18.89	-13.11	-26.00	-37.55	-31.67	-9.00	-29.16	-23.32
2007	55.00	16.28	-0.18	-14.95	-28.55	-13.98	10.51	-12.23	-8.96
2008	48.28	-4.18	9.42	4.26	0.55	-1.65	23.09	-1.47	3.09
2009	-17.02	21283.90	-22.97	-36.38	-25.15	-27.02	-28.37	8790.83	-25.35
2010	-28.93	-19.53	-20.01	-15.21	4.16	-18.41	-22.13	-7.79	-19.22
2011	-64.21	-24.88	-25.56	8.04	-2.67	-14.28	-49.06	-20.22	-23.19
2012	-27.52	-21.07	-19.50	-29.66	-32.31	-34.26	-28.54	-26.42	-26.52
2013	59.60	256.88	260.52	-12.06	22.97	-12.54	34.88	176.19	166.32
2014	85.57	130.62	96.26	-2.18	32.83	22.77	26.42	64.70	46.72
2015	-1.82	29.77	87.99	1.04	-6.60	-4.42	-0.16	8.70	34.45
2016	11.95	85.93	63.40	-3.95	-37.92	-43.23	4.68	29.30	14.65
2017	-12.11	-9.78	-19.05	24.02	18.79	6.71	1.55	1.03	-9.30

*Positive values for forecast error represent over-predictions, and negative error values are under-predictions of actual returns.

Table 6. Model Predicted and Observed Returns (in millions) by stock and total run (Sib =Sibling, Smolt = Smolt, Hyb = Hybrid, Obs = Observed)

	Early Run				**Late Run**				**Total Run**			
Year	**Sib**	**Smolt**	**Hyb**	**Obs**	**Sib**	**Smolt**	**Hyb**	**Obs**	**Sib**	**Smolt**	**Hyb**	**Obs**
2003	1.18	0.94	0.76	0.88	0.90	0.82	0.56	0.93	2.08	1.76	1.32	1.80
2004	0.93	2.27	0.32	1.07	0.87	0.63	0.71	0.39	1.80	2.90	1.03	1.46
2005	1.46	0.52	0.48	1.40	0.81	0.75	0.74	0.69	2.27	1.27	1.23	2.10
2006	0.85	0.62	0.66	0.76	0.69	0.58	0.64	0.93	1.54	1.20	1.30	1.69
2007	0.78	0.59	0.50	0.50	0.75	0.63	0.76	0.88	1.53	1.22	1.26	1.39
2008	0.80	0.52	0.59	0.54	0.76	0.73	0.71	0.72	1.56	1.25	1.31	1.27
2009	0.70	181.56	0.65	0.85	0.77	0.90	0.88	1.20	1.47	182.46	1.53	2.05
2010	0.84	0.95	0.94	1.18	0.98	1.21	0.95	1.16	1.82	2.16	1.89	2.34
2011	1.07	2.25	2.23	3.00	0.86	0.77	0.68	0.80	1.93	3.03	2.91	3.79
2012	1.08	1.17	1.20	1.49	0.95	0.91	0.89	1.35	2.02	2.08	2.08	2.83
2013	3.75	8.38	8.46	2.35	1.09	1.52	1.08	1.24	4.83	9.90	9.55	3.58
2014	0.74	0.92	0.78	0.40	0.81	1.09	1.01	0.82	1.55	2.01	1.79	1.22
2015	1.13	1.50	2.17	1.15	1.60	1.48	1.52	1.59	2.73	2.98	3.68	2.74
2016	1.54	2.56	2.25	1.38	1.12	0.72	0.66	1.16	2.66	3.29	2.91	2.54
2017	0.95	0.98	0.88	1.08	0.82	0.78	0.70	0.66	1.77	1.76	1.58	1.74