Differential Fecundity among Yukon River Chinook Salmon Populations Revealed by a Generalized Genetic Mixture Model

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Abstract

Fecundity is a vital population characteristic directly linked to the productivity of fish populations. Historic data from Yukon River Chinook salmon suggest that fecundity differs either temporally or geographically, and may have declined by approximately 20% over 16 years in populations within the Tanana River tributary. Yukon River Chinook salmon have been harvested in large-mesh gill-net fisheries for decades, and a decline in fecundity was considered a potential evolutionary response to size-selective exploitation. The implications for fishery conservation and management led us to initiate a drainage-wide investigation of fecundity. Matched observations of fecundity, morphological traits, and genotypes were collected from a sample of adult females captured from the multi-population spawning migration near the mouth of the Yukon River in 2008. The conditional maximum likelihood mixture model, commonly used to estimate the composition of multi-population mixtures, was generalized to permit estimation of stock-specific fecundity parameters without assigning individuals to a putative population of origin. The suspected decline in the fecundity of Tanana River Chinook salmon was not verified, which implies that fecundity may have high inter-annual variability. However, length-adjusted fecundity estimates were found to decrease as migratory distance increased and fecundity was more strongly dependent on fish size for populations spawning in the middle and upper portions of the drainage. These findings provide insights into potential constraints on reproductive investment imposed by long migrations and warrant consideration in fisheries management and conservation. The generalized mixture model extends the utility of genetic markers to new applications and can be easily adapted to study a variety of population characteristics.

Introduction

Pacific salmon *Oncorhynchus spp*. exhibit a diversity of life-history strategies across their range, which undoubtedly influences fitness and population productivity. Run-timing, which is linked to productivity via competition for spawning habitat or mates (Morbey 2000, 2002), environmentally-driven survival (Crozier and Zabel 2006), timing of emergence (Beckman et al. 2007), etc., varies widely among species and populations within species. Chinook salmon *O. tshawytscha* display considerable diversity in their utilization of freshwater and marine habitats as juveniles (Unwin et al. 2000; Narum et al. 2007), which may influence productivity through resulting differences in the availability of prey and exposure to sources of mortality. Body size and morphology, maturation age, and sex composition of salmon populations also vary widely (Beacham and Murray 1987, Hard et al. 1999; Pyper et al. 1999; Hamon et al. 2000; Wertheimer et al. 2004; Scheuerell 2005; Tamate and Maekawa 2006). Divergence of multiple phenotypic and life-history traits in Chinook salmon populations from a common source population after introduction into, and subsequent colonization of, new habitats has been observed (Quinn et al. 2001).

Strategies for investing energy in the development of reproductive tissue and optimizing the trade-off between egg size and egg number (fecundity) are important life-history strategies that determine both individual fitness and population productivity in Pacific salmon (Smith and Fretwell 1974; Einum and Fleming 2000; Einum et al. 2004). Not surprisingly, the optimum strategy appears to vary among populations. Both fecundity and egg size vary latitudinally in Chinook, coho *O. kisutch*, sockeye *O. nerka*, and masu *O. masou* salmon, with northern populations tending to have less total ovarian mass, smaller eggs, and greater fecundity (Fleming and Gross 1990; Beacham and Murray 1993; Morita et al. 2009). Healey and Heard (1984)

found that fecundity varied both temporally and spatially among populations of Chinook salmon throughout the northeastern Pacific and the Bering Sea. Egg size and the proportion of total somatic energy allocated to egg development in Chinook salmon appear to be inversely related to the difficulty of migration (Beacham and Murray 1993; Kinnison et al. 2001). The apparent tendency for populations with more arduous migrations to invest less energy in ovaries may reflect an adaptation to maximize fitness under the constraint of increased energetic demands for migration (Roff 1988; Healey 2001). However, the influence of migratory costs on fecundity is less clear; Beacham and Murray (1993) found reduced fecundity in populations with long migrations, while Kinnison et al. (2001) hypothesized that fecundity should remain stable or perhaps increase as migratory costs increase.

Questions regarding spatial and temporal differences in fecundity for Yukon River Chinook salmon were raised by a recent investigation conducted by staff of the Alaska Department of Fish and Game (ADF&G). Jasper and Evenson (2006) found significant differences between the mean fecundity of Chinook salmon sampled in the Tanana River, a major tributary of the Yukon River, and in the Yukon River main stem above the terminus of the Tanana River; a significant proportion of the latter fish were likely bound for distant spawning locations in Canada. A comparison of the results reported by Jasper and Evenson (2006) and Skaugstad and McCracken (1991) suggests that the length-adjusted fecundity of Tanana River fish declined approximately 20% from 1989 to 2005, although Jasper and Evenson (2006) noted difficulties with tissue preservation and the disintegration of some individual eggs. In addition, the mean fecundity of both Tanana and upper Yukon groups of fish is approximately half of the reported fecundity of fish sampled from the lower Yukon River in 1965 and 1981 (Healey and Heard 1984). However, Healey and Heard (1984) pooled data from samples collected over many

years and the fecundity-length relationship was based on 15 pairs of average fecundity and average length rather than observations of individual fish, which may complicate comparisons with other data sources. Conversely, estimates of mean fecundity reported by Jasper and Evenson (2006) are similar to a single length-adjusted estimate based on data collected in Canada in 1987 and 1988 (Beacham and Murray 1993).

Whether the apparent differences among historic data on the fecundity of Yukon River Chinook salmon reflect a natural level of inter-annual variability, a downward trend in fecundity, or simply differences among populations sampled is unknown. Healey and Heard (1984) found fecundity to vary temporally and the most extreme inter-annual differences they reported approached the magnitude of the apparent decline in fecundity of Tanana River fish. If fecundity is trending downward, such a large and rapid decline would raise numerous concerns. Several fish populations, including Pacific salmon, appear to have adapted to high exploitation rates and size-selective harvests by altering reproductive strategies (e.g., Hamon et al. 2000; Law 2000; Quinn et al. 2002). Fishery-induced evolution via the preferential harvest of large individuals, which is receiving considerable attention worldwide (e.g., Hard et al. 2008; Dunlop et al. 2009) as well as on the Yukon River (Bromaghin et al. 2008), is one mechanism with the potential to reduce fecundity. If fecundity differs markedly among populations within the drainage, populations may respond differentially to local conditions, management practices, climate change, and similar selective pressures.

The differences in fecundity reported by the available sources of information led us to initiate the first comprehensive investigation of Chinook salmon fecundity within the Yukon River drainage. Our objectives were to investigate the degree to which fecundity differs among populations within the drainage, especially as a function of migratory distance, and verify

whether fecundity has decreased from historic levels. Chinook salmon were sampled from ADF&G test fishery catches in the lower Yukon River to avoid sacrificing additional individuals and ensure that populations from all regions of the watershed would be represented. Matched fecundity, length, and genotype data were incorporated into an extension of the conditional maximum likelihood model commonly used to estimate the composition of multi-population aggregations (Fournier et al. 1984; Millar 1987; Debevec et al. 2000; Koljonen et al. 2005). The Yukon River is an ideal system in which to conduct such an investigation; Chinook salmon populations spawn throughout the drainage, some spawning migrations are among the longest in the world, and populations display an isolation-by-distance pattern (Templin et al. 2005; Flannery et al. 2006).

The model we develop extends the utility of genetic markers to study non-genetic traits that differ among populations. The model shares similarities with the model of Fournier et al. (1984), but no information on non-genetic traits is obtained from the baseline, or learning, samples. The modeling framework can be modified in straightforward fashion to accommodate any trait for which a plausible probability distribution can be postulated.

Methods

Sampling and Sample Processing. —Chinook salmon were sampled from catches in test fisheries conducted by the ADF&G in the vicinity of Emmonak and Kotlik, Alaska, located near the terminus of the Yukon River in the eastern Bering Sea (Figure 1). Several morphological measurements, including fish length from mid-eye to fork-of-tail (MEF), were taken from each Chinook salmon included in the sample. Three scales per fish were collected for the estimation of age and a tissue sample (axillary process) was taken for subsequent determination of

genotype. Egg skeins were individually placed in sealable plastic bags, labeled, and refrigerated until they could be processed.

Many sampled females were expected to be hundreds to thousands of km from their spawning destination and most skeins were comprised of small, immature eggs that were difficult to separate. We developed, through trial and error, a method of processing immature skeins that produced acceptable results. Skeins were rinsed with water to remove blood and debris, placed in individual microwave steam bags, and covered with ethanol as a fixative. Skeins were kept in ethanol for three to four days and turned at least once to ensure all portions were exposed to ethanol. The ethanol was then poured off, skeins were rinsed with water, and the bags were filled with water and placed in a pot of boiling water for four or five minutes. Boiling loosened the skeins so that the eggs were easier to separate and also helped remove the ethanol odor. Water was then poured off and the skeins were allowed to air-dry, after which they were transferred to sealable plastic bags and frozen until fecundity was estimated.

Frozen egg skeins were allowed to slowly thaw in a cooler prior to processing. Upon removal from the cooler, skeins were patted dry with paper towels and total skein mass was measured to the nearest 0.1 g. Each skein was divided into 10 sections of approximately equal volume for sub-sampling and three sections were randomly selected without replacement using a previously-generated sequence of random integers. The mass of each of the three sub-sampled sections was determined to the nearest 0.1 g and the eggs in each were counted. A total count of all eggs in a skein was occasionally completed by each technician to allow the performance of the sub-sampling design to be assessed.

The number of eggs in a skein, E, was estimated using a ratio estimator (Cochran 1977). If E_i and M_i denote the number of eggs and the mass of the ith sub-sample from a skein, respectively, and M denotes the mass of the entire skein, then

$$\hat{R} = \frac{\sum_{i=1}^{3} E_i}{\sum_{i=1}^{3} M_i}, \quad (1)$$

$$\hat{E} = M\hat{R}, \quad (2)$$

and

$$\hat{V}\left(\hat{E}\right) = \frac{10^2\left(1-\frac{3}{10}\right)}{3(3-1)}\left\{\sum_{i=1}^{3} M_i^2\left[\frac{E_i}{M_i}-\hat{R}\right]^2\right\}. \quad (3)$$

The fecundity of an individual fish was estimated as the sum of the estimated number of eggs in its two skeins, and the variance of the estimated fecundity was estimated as the sum of the corresponding skein variances. Only fish for which the number of eggs in both skeins could be estimated were included in subsequent analyses.

Samples were genotyped using the following methods. Total genomic DNA was extracted from axillary process tissue (~25mg) using proteinase K with the Dneasy™ DNA isolation kit (Qiagen Inc. Valencia, CA). The amount of DNA was quantified by fluorometry and diluted to 30 ng/µl. The following 13 standardized microsatellite loci used for Chinook

salmon by the Genetic Analysis of Pacific Salmonids group (GAPS; Seeb et al. 2007) were typed for each sample: *Ots201b*, *Ots208b*, *Ots211*, *Ots212*, *Ots213*, (Grieg et al. 2003); *Ots3M*, *Ots9* (Banks et al. 1999); *OtsG474* (Williamson et al. 2002); *Ogo2*, *Ogo4* (Olsen et al. 1998); *Omm1080* (Rexroad et al. 2001); *Ssa408* (Cairney et al. 2000); and *Oki100* (Miller, unpublished data). Polymerase chain reaction (PCR) DNA amplification was done in 10 µl volumes; general conditions were: 2.5 mM $MgCl_2$, 1X PCR buffer (20 mM Tris-HCl pH 8.0, 50 mM KCl), 200 µM of each dNTP, 0.40µM fluorescently labeled forward primer, 0.40 µM unlabeled reverse primer, 0.008 units Taq polymerase, and 1 µl of DNA (30ng/µl). An MJResearch DNA Engine® thermal cycler was used to perform PCR. Standard thermal cycling conditions were: initial denaturation cycle of 94°C for 3 min, followed by 94°C for 1 min, 50-62°C for 1 min (locus-specific annealing temperature), 72°C for 1 min, with a final single cycle of 72°C for 10 min. One µl of PCR product was electrophoresed and visualized with the Applied Biosystems 3730 Genetic Analyzer utilizing a polymer denaturing capillary system. The sizes of bands were estimated and scored by the computer program GENEMAPPER® version 4.0. Applied Biosystems GeneScan™-600 LIZ® size standards, 20-600 bases, were loaded in all lanes to ensure consistency of allele scores. All scores were verified manually. Alleles were scored by two independent researchers, with any discrepancies being resolved by re-running the samples in question and repeating the double scoring process until scores matched.

Modeling Fecundity.—Daum and Flannery (2009) summarize the performance of a baseline, i.e., genotypic data collected from individual populations when segregated for reproduction, with data from 34 Chinook salmon populations located throughout the Yukon River drainage (Table 1, Figure 2). Given the large number of populations in the baseline, the density of samples per population was expected to be too low to support the estimation of

fecundity for a large number of individual populations. Therefore, we initially grouped the 34 populations into 12 stocks based on a combination of geographic proximity and genetic similarity (Table 1, Figure 2); we hereafter use the term "population" to refer to an aggregation of individuals sharing a spawning location and "stock" to refer to a group of one or more populations.

Preliminary analyses with the data of Skaugstad and McCracken (1991) and Jasper and Evenson (2006) suggested that fecundity (F) could be modeled as a normally (Gaussian) distributed variate (Johnson et al. 1994), with mean fecundity linearly related to length (L) and homogeneous variance across lengths. An allometric model, which has previously been used to model fecundity (e.g., Healey and Heard 1984; Beacham and Murray 1993), was also evaluated, but the error structure of that model did not fit the data as well and it was abandoned in favor of a linear model. Fecundity of a fish with length L from stock j was therefore modeled as a normal variate with mean $\beta_{0j} + \beta_{1j}L$ and standard deviation σ_j, i.e.,

$$g(F \mid L, j) = \frac{1}{\sigma_j \sqrt{2\pi}} e^{-\frac{1}{2\sigma_j^2}\left[F - (\beta_{0j} + \beta_{1j} L)\right]^2}. \quad (4)$$

Lengths were reduced by a constant so that the shortest fish in the sample had a length of 1 mm prior to modeling to increase the interpretability of the parameters β_{0j}, which therefore represent the mean fecundity of a fish 1mm shorter than the shortest fish observed in the sample, rather than the nonsensical fecundity of a fish with length 0 mm. Such a location transformation (i.e., centering) may also reduce the influence of round-off errors during parameter estimation (Seber 1977). The parameters β_{1j} represent the change in mean fecundity attributable to a 1 mm increase in length, and the parameters σ_j represent the variability of individual fecundity about

the mean fecundity. The parameters of the fecundity model (Eq. 4) for each stock were simultaneously estimated using maximum likelihood techniques (Stuart et al. 1999) and a generalized mixture model. Let

n_s = the number of stocks into which baseline populations are grouped,

$n_{p(j)}$ = the number of populations within stock j,

$\pi_{p(j)}$ = the relative abundance (mixture proportion) of population p in stock j, constrained to sum to 1.0 across all baseline populations,

$\theta_{i,p(j)}$ = the probability with which the genotype of the ith fish occurs in population p in stock j,

n = the number of fish sampled,

L_i = the length of the ith fish, and

F_i = the fecundity of the ith fish.

The likelihood of the observed data can then be expressed as

$$L = \prod_{i=1}^{n} \left\{ \sum_{j=1}^{n_s} \left[g(F_i \mid L_i, j) \sum_{k=1}^{n_{p(j)}} \theta_{i,k(j)} \pi_{k(j)} \right] \right\}. \quad (5)$$

The model does not assign individual fish to the populations to which they are most likely to belong, rather the population composition of the mixture is estimated (a mixture model). A primary characteristic of the model is that all data regarding fecundity is obtained from the mixture sample and the association of fecundity with baseline populations is achieved indirectly

via genotypes; we refer to this characteristic as a generalization of the mixture model. The θ parameters were estimated from allele proportions in the baseline data using a Bayesian estimator based on the Dirichlet distribution (Johnson et al. 1997; Rannala and Mountain 1997) prior to maximization of the likelihood function. The θ parameters were therefore treated as known constants and estimation of mixture parameters is conditioned on those constants, which is the defining characteristic of a conditional maximum likelihood mixture model (Fournier et al. 1984; Millar 1990; Koljonen et al. 2005). A computer program written in Fortran (Metcalf et al. 2004) was developed to maximize the likelihood function and obtain estimates of the parameters β_{0j}, β_{1j}, σ_j, and $\pi_{p(j)}$.

Our primary objective was to identify broad patterns of fecundity within the drainage, especially patterns associated with migratory distance, so we implemented a hierarchical, iterative algorithm to equate the fecundity parameters of geographically adjacent stocks if their fecundities did not differ statistically. Iterations began with an initial grouping of the 34 baseline populations into 12 stocks (Table 1). In each iteration, the parameters of an unconstrained model and a series of models constraining geographically adjacent pairs of stocks to have equal fecundity parameters were estimated. Likelihood ratio tests (Stuart et al. 1999) were used to test the equality of fecundity parameters as the comparisons made could not be planned a priori (Burnham and Anderson 2002). Among all tests conducted, the two stocks with the smallest value of the test statistic were combined if the significance of the test was greater than 0.01. This iterative process was then repeated with one fewer stock, and iterations continued until the significance of all pairwise tests were smaller than 0.01. The small threshold significance level of 0.01 was selected to protect against spurious results caused by low representation of some

287 stocks in the mixture sample and to facilitate the development of a parsimonious model
288 describing broad patterns of fecundity within the drainage.
289 An analysis was also conducted using classical individual assignment methods (e.g.,
290 Cornuet et al. 1999) for comparative purposes. As with the mixture analysis, the baseline data
291 were used to estimate the probability each fish came from each stock ($\theta_{i,p|j}$) using a Bayesian
292 estimator based on the Dirichlet distribution (Johnson et al. 1997; Rannala and Mountain 1997).
293 Individual fish were assigned to the population from which they were most likely to have
294 originated, i.e., the population having the highest baseline probability for that genotype.
295 Maximum likelihood estimates (Stuart et al. 1999) of the fecundity parameters were
296 independently computed using the data from the subset of fish assigned to each stock.
297 In both the mixture and assignment analyses, variances of the parameter estimates were
298 estimated by bootstrap re-sampling (Chernick 1999). For each of 1,000 bootstrap replications, a
299 new sample of n individuals was constructed by sampling with replacement from the data
300 observed in the mixture sample. Similarly, a bootstrap baseline was constructed by sampling
301 alleles with replacement from the baseline data, with the sample size per population being equal
302 to the actual sample sizes in the baseline. Parameter estimates were obtained with each replicate
303 bootstrap mixture sample and baseline. For each parameter, the standard deviation of the 1,000
304 bootstrap estimates was taken as an estimate of the standard error of the point estimate, and a
305 nonparametric 90% confidence interval was constructed from the 5th and 95th quantiles of the
306 bootstrap replicates.
307 Comparing Data Sources. —Estimates of fecundity based on genetic mixture modeling were
308 compared with estimates based on the four independent sources of information for which data
309 were available: 1988 Tanana River data (Skaugstad and McCracken 1991); 2005 Tanana River

310 data (Jasper and Evenson 2006); 2005 data from fish originating in the Yukon River main stem
311 upriver of the Tanana River terminus (Jasper and Evenson 2006); and unpublished data collected
312 in 2008 from the Yukon River main stem in the vicinity of Eagle, Alaska near the international
313 border with Canada (data on 49 females provided courtesy of Lara Dehn, University of Alaska,
314 Fairbanks, Alaska). All four independent data sets were obtained from an unknown mixture of
315 multiple spawning populations, which complicates making valid comparisons among them and
316 with our results.

317 Comparisons of fecundity estimates based on genetic mixture modeling and data
318 independently collected in 1988, 2005, and 2008 were facilitated by incorporating the
319 independent data into the genetic mixture modeling framework. This was accomplished by
320 augmenting the genetic baseline with an artificial population for each independent data source.
321 One artificial marker was added to the 12 markers in the original baseline for each independent
322 data source. Each artificial marker had none of the alleles observed in the original genetic
323 baseline (all of those allele frequencies were set to 0), but rather an allele that was unique, or
324 private, for a single independent data source, with a sample size of 100,000 alleles. In similar
325 fashion, the observed genetic mixture data were augmented with artificial records constructed
326 from each independent data source; artificial records contained the observed length and fecundity
327 data and identical genotypes containing only the private allele uniquely associated with the
328 appropriate independent data source. The effect was that the independent data sources were
329 added as new populations in the baseline, with no overlap in alleles so that each independent data
330 source was completely distinct from the original genetic baseline data and from the other
331 independent data sources. This approach established a common framework for modeling and
332 parameter estimation for two different types of information, and the fecundity parameters based

on the independent data sources were estimated using the same analytical methods and computer program as the genetic mixture estimates, eliminating a potential source of confounding.

Because of partial overlap in the populations likely contributing to independent data collected in 2005 (Yukon River main-stem above the Tanana River confluence) and 2008 (Yukon River main-stem near Eagle), two sets of artificial baseline and mixture files needed to be created as described above. To facilitate comparison of genetic mixture estimates based on 2008 data with the data collected in 1988 and 2005, a baseline of 37 populations was constructed by adding three populations, one for each of three independent data sets from 1988 and 2005, to the original baseline of 34 populations. A second artificial baseline was created to facilitate comparison of the genetic mixture estimates with the estimates for the independent data collected near Eagle, Alaska in 2008. In this case, only one artificial population was added to the original genetic baseline.

For the comparisons between genetic mixture estimates based on 2008 data with the data collected in 1988 and 2005, the 37 populations in the artificial baseline were grouped into a total of six stocks. The three independent data sets formed three stocks: Tanana 1988, Tanana 2005, and Above Tanana 2005. The 34 genetic baseline populations were grouped to form three additional stocks corresponding to the independent data sources: MM Below Tanana 2008, MM Tanana 2008, and MM Above Tanana 2008, where MM represents mixture modeling based on the original genetic baseline data. Fecundity parameters were first estimated without imposing any constraints, so that each of the six stocks had potentially unique estimates. Fecundity parameters were also estimated using four models imposing equality constraints between pairwise comparable data sources: MM Tanana 2008 = Tanana 1989, MM Tanana 2008 = Tanana 2005, Tanana 1989 = Tanana 2005, and MM Above Tanana 2008 = Above Tanana 2005.

Similarly, populations in the second artificial baseline were grouped to form a total of three stocks: MM Below Canada, MM Canada, and Canada (Eagle). In this case, only two models were compared, one unconstrained model with three sets of parameters and one model in which the fecundity parameters of the two Canada stocks were constrained to be equal. As these models were planned a priori, Akaike's Information Criterion (AIC) was used to evaluate the relative plausibility of the models (Burnham and Anderson 2002).

The only other published data of which we are aware are summarized by Healey and Heard (1984) and Beacham and Murray (1993). As the raw data underlying their summaries were not available to us, we are limited to making qualitative comparisons with their results. In addition, observations reported by Weidner (1972) were not utilized because of the extremely small sample size of 13 fish and uncertainty regarding locations sampled.

Results

Sampling and Sample Processing.—Chinook salmon were sampled from early June through mid-July 2008 and complete fecundity, length, and genotype data were obtained from 403 individuals. The smallest fish in the sample had length 585 mm, so lengths were reduced by 584 mm prior to mixture modeling. The methods used to sub-sample egg skeins and estimate fecundity were precise, with estimated coefficients of variation ranging from 0.0% to 4.2% and averaging 1.2% over all fish. As expected, the estimation variation was an order of magnitude smaller than the natural level of variation in fecundity for most fish, so we treated fecundity as a known constant in the likelihood function (Eq. 5) and let the natural variance parameters σ_j absorb the small estimation error. Complete counts were made of the eggs in 22 skeins, and estimated fecundities compared favorably with these known totals (Figure 3).

Modeling Fecundity.—Mixture modeling revealed broad regional patterns in fecundity, coarsely associated with migratory distance, within the drainage. The initial mixture model contained a unique set of fecundity parameters (Eq. 4) for each of the 12 stocks (Table 1). Hierarchical, stepwise likelihood ratio tests of the equality of fecundity for geographically adjacent stocks led to a model consisting of three stocks (Figure 4). The parameter estimates for these three stocks were significantly different ($P < 0.01$), so that additional stocks could not be combined. The three stocks into which populations clustered were coarsely correlated with migratory distance. The Lower stock consisted of the two populations lowest in the drainage, the Middle stock consisted of a broad range of stocks in the middle to upper reaches of the U. S. portion of the drainage and the two Canadian populations lowest in the drainage, and the Upper stock consisted of the remaining Canadian populations (Figure 1).

An inspection of the parameter estimates resulting from the three-stock model (not shown) revealed that the estimated slope (β_1) of the Lower stock did not appear to differ from zero and that the estimated slopes of the Middle and Upper stocks appeared similar. We therefore conducted four post-hoc hypothesis tests, that each slope parameter was equal to zero and that the slope parameters of the Middle and Upper stocks were equal. As these tests were unplanned, hypothesis tests were conducted using likelihood ratio tests. Our suspicions based on a casual inspection of the preliminary estimates were confirmed. The slope parameter of the Lower stock was not significantly different than zero, while the slope parameters of the Middle and Upper stock were significantly greater than zero but not significantly different from each other (Table 2).

Based on the results of hypothesis tests summarized above, our final model contained three stocks, with the slope parameter of the Lower stock constrained to equal zero and the slope

parameters of the Middle and Upper stocks constrained to be equal. The estimated model of fecundity for each stock is overlaid with the paired fecundity-length observations in Figure 5. Overall, both mean fecundity and the variation about the mean (σ_j) are inversely related to migratory distance. Measures of estimation precision, obtained via 1,000 bootstrap replicate samples, are presented in Table 3. Estimates were reasonably precise, with coefficients of variation ranging from 0.031 to 0.166. Estimates obtained via classical individual assignment (Cornuet et al. 1999) for each of the three stocks are also provided for comparative purposes in Table 3.

Comparing Data Sources.—Among the models comparing genetic mixture model estimates of fecundity with estimates based on data collected in 1989 and 2005, the model equating the fecundity of Tanana River populations based on 2008 mixture modeling and the 1989 data had the smallest AIC (Table 4). This model had an AIC relative weight of 0.786, while the weight for the unconstrained model was 0.214; both of these models can be viewed as reasonable representations of the structure in the data. The other three models all involved data collected in 2005 and had relative weights of 0.0, indicating substantial lack of fit. Both of the models involving only 2008 data provide reasonable representations of the data, with relative weights of 0.750 and 0.250, suggesting that estimates of fecundity for the composite of all Canadian populations based on mixture modeling and a sample taken when Canadian salmon were segregated from U. S. populations were similar. We interpret this result as a validation of the mixture modeling approach. In summary, all estimates of fecundity based on available data appear consistent, with the exception of data collected in 2005 (Jasper and Evenson 2006). The individual models based on these data sets, including the allometric model of Healey and Heard

(1984) and the length-standardized fecundity of Beacham and Murray (1993), are plotted in Figure 6.

Discussion

Our results reveal substantial differences in the relationship between fecundity and length among Chinook salmon populations within the Yukon River drainage. There is a general inverse relationship between fecundity and migratory distance, which was also reported by Beacham and Murray (1993). Perhaps the most significant finding is that fecundity appears to be nearly independent of length for populations spawning in the most downstream portions of the drainage, while the fecundity of populations spawning in the middle and upper portions of the drainage is significantly and positively dependent on fish length. As a consequence, small fish from the middle and upper portions of the drainage tend to have markedly fewer eggs than small fish from the lower portions of the drainage. Large fish display the same pattern, though the magnitude of differences between regions is reduced.

The pattern of mean fecundity we observed within the drainage is informative with respect to hypotheses regarding evolutionary optimization of reproductive fitness for migratory salmonids. The model of Smith and Fretwell (1974) suggests that there is an optimal investment of available energy into reproduction, which includes migratory costs, and an optimum balance between egg size and fecundity that maximizes maternal fitness. Kinnison et al. (2001) hypothesized that increased energetic costs of migration and reproduction would primarily be accommodated by reduced investment in ovarian mass and reduced egg size, and that fecundity would be maintained or perhaps even increase. That hypothesis is inconsistent with our findings, though that strategy may effectively optimize fitness for migrations less arduous than presented

447 by the Yukon River. As the energetic demand to migrate and successfully reproduce increases
448 beyond some threshold, that strategy may become ineffective and a reduction in fecundity may
449 be necessary to maximize fitness. A confounding factor is that compensatory fitness advantages
450 may be conferred by migrating to the upper portions of the drainage, attributable to localized
451 biotic or abiotic factors, which preserves long migrations in salmon populations (Jorgensen et al.
452 2008).

453 The optimum strategy for reproductive investment apparently depends on fish size as
454 well as migratory distance. Large individuals are likely more capable of storing adequate energy
455 reserves to both complete long migrations and maintain a comparatively high investment in non-
456 migratory reproduction. For small individuals, the energetic requirements of a long migration
457 may constrain the proportion of total reproductive investment that must be reserved as somatic
458 energy in order to successfully migrate and reproduce. For less rigorous migrations to the lower
459 portions of the drainage, smaller individuals appear able to allocate a greater proportion of their
460 total investment to reproductive tissue and maintain high fecundity. The inverse relationship we
461 observed between migratory distance and the variation in fecundity (Table 3, Figure 5) may
462 reflect a balance between individuals producing as many eggs of an adequate size as possible
463 under the constraints imposed by migratory costs.

464 Our investigation would have been strengthened by corresponding data on egg size and
465 total ovarian mass, but we were unable to investigate either characteristic. Sampled fish were
466 collected in the lower river over a period of several weeks. Fish sampled in the early portion of
467 the study tended to be ocean-bright and many were probably hundreds or thousands of km from
468 their spawning grounds, while some fish sampled late in the study period were beginning to
469 display secondary sexual characteristics. The variability in the state of maturation of sampled

fish precludes meaningful interpretation of either quantity. Information on egg size and ovary mass is obviously of limited value until the eggs are fully mature. However, the large size of the Yukon River drainage and the remoteness of most spawning locations necessitated data collection near the river terminous from individuals being sacrificed for other needs, which limited our investigation to fecundity alone.

Differences in fecundity-at-size of the magnitudes observed within the drainage likely have profound implications for both fisheries management and the health and productivity of Yukon River Chinook salmon populations, and perhaps similar populations in other large rivers. We envision two avenues for knowledge of differential fecundity to contribute to development of optimal management strategies. First, management of most North American populations of anadromous Pacific salmon is often based on the number of reproducing individuals necessary to sustain future yields. Our results suggest that a fish reproducing in the middle and upper reaches of the drainage may contribute less to subsequent generations than a similarly sized fish reproducing in the lower drainage. Management needs to be cognizant that populations from the middle and upper portions of the drainage may not have the same reproductive potential as lower-river populations, although the net result of reduced fecundity may be ameliorated by differential survival due to a number of other factors, such as habitat or gamete quality (e.g., Beacham and Murray 1986; Kinnison et al. 2001; Zabel and Achord 2004; Moffett et al. 2006). Second, the productivity of middle- and upper-river populations may be more dependent on the size of reproducing individuals than lower-river populations. Gill nets are known to be size-selective (e.g., Bromaghin 2005) and harvests in large-mesh gill net fisheries may reduce the productivity of middle- and upper-river populations to a greater extent than lower-river populations.

One of our primary objectives was to investigate the reduction in fecundity for Tanana River Chinook salmon implied by a comparison of the results of Skaugstad and McCracken (1981) and Jasper and Evenson (2006). Our estimates of fecundity for these populations were consistent with data from 1987 (Skaugstad and McCracken 1991) and significantly greater than Jasper and Evenson (2006) found in 2005 (Table 4, Figure 6). There are two plausible explanations for these results. One possibility is that the differences are attributable to natural inter-annual variation in fecundity. The observed level of variation is at the upper end of the temporal variability reported by Healey and Heard (1984), so this explanation is plausible. This possibility may be partially supported by the similarity between the results of Beacham and Murray (1993) and Jasper and Evenson (2006), though they sampled different populations, as well as by the small proportion of the variance in fecundity that is explained by fish size (Figure 5). Clearly, factors other than fish size, such as growth prior to maturation (e.g., Bromage et al. 1992; Campbell et al. 2006), are important determinants of fecundity and there is no reason to suppose such factors are temporally stable. In addition, a high level of inter-annual variability in fecundity may explain a sizeable proportion of the variation in return-per-spawner productivity observations (e.g., Dorner et al. 2008), which is usually attributed to variation in survival rates. A second possibility is that one or more of the estimates is biased, and Jasper and Evenson (2006) report experiencing difficulties with sample preservation and the physical integrity of individual eggs. These possibilities are not, of course, mutually exclusive.

The modeling approach we employed was successful given our objectives to describe broad patterns of fecundity within the drainage and compare available sources of data to determine whether fecundity has declined or is trending downward. The genetic baseline we employed does not contain a sample from every reproductively-isolated population within the

516 drainage. However, the baseline has drainage-wide coverage (Figure 1) and the populations
517 sampled are characterized by an isolation-by-distance pattern (Figure 2), so individuals from
518 populations not included in the baseline can be expected to have genetic characteristics most
519 similar to proximate populations that were included. Similarly, while populations included in the
520 same stock during mixture modeling undoubtedly do not have the exact same fecundity, we were
521 not interested in modeling fecundity at a fine population-specific scale, and any differences
522 might reasonably be expected to be small in comparison to the broad patterns within the
523 drainage. Even if that were not the case for a small number of populations locally adapted to
524 specific habitats, our findings would remain descriptive for the drainage as a whole.
525 A comparison of the mixture model and assignment estimates (Table 3) reveals important
526 differences in the two estimation techniques. For the Lower stock, the assignment estimate of the
527 intercept (β_0) is less, and the estimate of the slope (β_1) is greater, than the corresponding
528 maximum likelihood estimates. Because some of the populations from the middle portion of the
529 drainage appear most genetically similar to lower-river populations (Figure 2; Templin et al.
530 2005; Flannery et al. 2006), we suspect the assignment estimates are biased by the inclusion of
531 middle-river individuals, with middle-river fecundity traits, in the Lower stock. If so, this is
532 consistent with the general superiority of maximum likelihood estimation to assignment
533 estimation in mixture modeling (Millar 1990). We were surprised by the similarity in the
534 precision of mixture model and classification estimators (Table 3). Given that the mixture model
535 fully exploits all available information and avoids potential error in individual assignment, one
536 might expect the mixture model estimator to consistently display reduced variance. As
537 classification estimators tend to be biased in mixture applications (e.g., Millar 1990; Koljonen et
538 al. 2005), a complete evaluation of the statistical properties of the two estimators requires

knowledge of both bias and variance. We are unable to evaluate bias in this case because the fecundity-length relationships of the populations are estimated rather than known. Simulation studies under controlled conditions will be required to more fully explore the statistical properties of the maximum likelihood estimator for the generalized mixture model.

The probability model employed (Equation 5) represents a straightforward extension of a widely-used method to estimate the contribution of source populations to a mixture and expands the utility of genetic markers in the study and management of fish and wildlife resources. The model can easily be modified to accommodate any trait for which a plausible probability distribution can be hypothesized, through appropriate specification of the function g (Equation 4). Potential examples include a host of continuous morphological traits such as measures of size, as well as discrete parameters such as reproductive status or the presence of disease. Our general approach should be adaptable to the Bayesian mixture model (Pella and Masuda 2001), which we hope to accomplish in subsequent work. As in our specific application, this generalized model is likely to be most useful in situations in which large sample sizes are available and logistical constraints make it difficult to obtain independent samples from segregated populations.

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Table 1. Population-specific samples contained in the baseline, the stock each sample was initially assigned to, the number of individuals in each sample, and the stock in the final model in which each sample was placed. The numbers in parentheses after tributary names indicate sample locations in Figure 1.

Tributary sampled	Country	Initial stock	Sample size	Final stock
Andreafsky (1)	U. S.	Lower U. S.	208	Lower
Anvik (2)	U. S.	Lower U. S.	94	Lower
Gisasa (3)	U. S.	Gisasa	188	Middle
Tozitna (4)	U. S.	Tozitna	190	Middle
Henshaw (5)	U. S.	Upper Koyukuk	147	Middle
South Fork (6)	U. S.	Upper Koyukuk	56	Middle
Kantishna (7)	U. S.	Tanana	187	Middle
Chena (8)	U. S.	Tanana	189	Middle
Salcha (9)	U. S.	Tanana	133	Middle
Beaver (10)	U. S.	Border U. S.	100	Middle
Chandalar (11)	U. S.	Border U. S.	113	Middle
Sheenjek (12)	U. S.	Border U. S.	51	Middle
Chandindu (13)	Canada	Border Canada	566	Middle
Klondike (14)	Canada	Border Canada	102	Middle
Stewart (15)	Canada	Stewart	110	Upper
Mayo (16)	Canada	Stewart	195	Upper
Tincup (17)	Canada	White	32	Upper
Pelly (18)	Canada	Pelly	125	Upper
Little Kalzas (19)	Canada	Pelly	40	Upper
Big Kalzas (20)	Canada	Pelly	22	Upper
Earn (21)	Canada	Pelly	54	Upper
Glenlyon (22)	Canada	Pelly	23	Upper
Blind (23)	Canada	Pelly	160	Upper
Yukon Main. (24)	Canada	Mainstem	27	Upper
Tatchun (25)	Canada	Mainstem	366	Upper
Nordenskiold (26)	Canada	Mainstem	99	Upper
Little Salmon (27)	Canada	Mainstem	100	Upper
Big Salmon (28)	Canada	Mainstem	116	Upper
Whitehorse (29)	Canada	Upper	241	Upper
Michie (30)	Canada	Upper	47	Upper
Takhini (31)	Canada	Upper	167	Upper
Nisutlin (32)	Canada	Teslin	56	Upper
Wolf (33)	Canada	Upper	59	Upper
Morley (34)	Canada	Teslin	28	Upper

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Table 2. Results of post-hoc likelihood ratio tests involving the slopes (β_{1j}) of the mean fecundity of the three stocks in the final model.

Hypothesis	χ^2	df	P
$\beta_{1L} = 0$	2.4	1	0.121
$\beta_{1M} = 0$	18.4	1	0.000
$\beta_{1U} = 0$	43.8	1	0.000
$\beta_{1M} = \beta_{1U}$	2.0	1	0.157

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Table 3. Mixture model and assignment estimates of fecundity model parameters (intercept β_0, slope β_1, and standard deviation σ), by stock, in the final model, with measures of precision (standard error S. E., coefficient of variation C. V., and 90% confidence intervals C. I.) derived from 1,000 replicate bootstrap samples.

Stock	Statistic	β_0^*	β_1	σ
		Mixture Model Estimates		
Lower	Estimate	9853	0.00	1961
	S.E.	305	NA	291
	C.V.	0.031	NA	0.148
	90% C.I.	9212-10227	NA	1348-2328
Middle	Estimate	5796	11.23	1332
	S.E.	478	1.65	222
	C.V.	0.082	0.147	0.166
	90% C.I.	5065-6649	8.44-13.87	1155-1709
Upper	Estimate	4631	11.23	1020
	S.E.	443	1.65	68
	C.V.	0.096	0.147	0.066
	90% C.I.	3924-5391	8.44-13.87	912-1129
		Assignment Estimates		
Lower	Estimate	9590	0.00	1744
	S.E.	323	NA	273
	C.V.	0.034	NA	0.142
	90% C.I.	9008-10084	NA	1340-2249
Middle	Estimate	6556	8.81	1550
	S.E.	496	1.74	143
	C.V.	0.076	0.198	0.092
	90% C.I.	5629-7252	6.37-11.96	1358-1817
Upper	Estimate	5313	8.81	1098
	S.E.	469	1.74	84
	C.V.	0.088	0.198	0.077
	90% C.I.	4469-5969	6.37-11.96	992-1267

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Table 4. Summary statistics of models exploring the equality of mixture model (MM) estimates of fecundity with estimates obtained from independent data sources. Different stocks were defined for each of the two sets of models. Within each set of models, an unconstrained model is compared to models constraining the fecundity parameters of two data sources to be equal.

Comparison	AIC	ΔAIC	Akaike Weight
Comparisons with Historic Data			
Unconstrained	49711.8	2.6	0.214
MM Tanana 2008 = Tanana 1989	49709.2	0.00	0.786
MM Tanana 2008 = Tanana 2005	49761.4	52.2	0.000
MM Tanana 1989 = Tanana 2005	49765.4	56.2	0.000
MM Above Tanana 2008 = Above Tanana 2005	49895.0	185.8	0.000
Comparisons with 2008 Data			
Unconstrained	45117.8	0.00	0.750
MM Canada = Canada (Eagle)	45120.0	2.20	0.250

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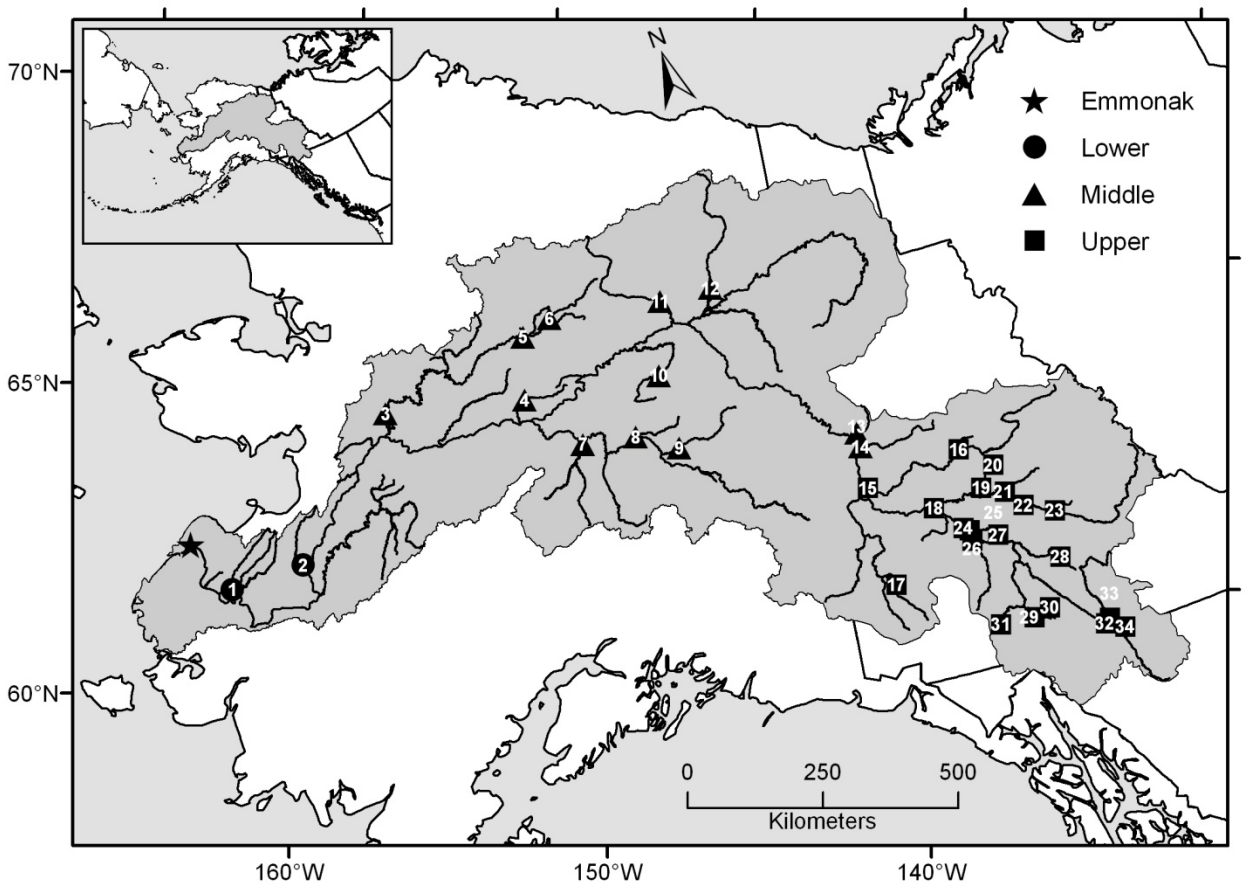

773

774 Figure 1. A map of the Yukon River drainage in Alaska and Canada, showing locations of
775 baseline sample collections and the base of mixture sampling in Emmonak, Alaska. Numeric
776 sample identifiers are provided in Table 1. Figure courtesy of Jeffrey Olsen, U. S. Fish and
777 Wildlife Service, Conservation Genetics Laboratory, Anchorage, Alaska.

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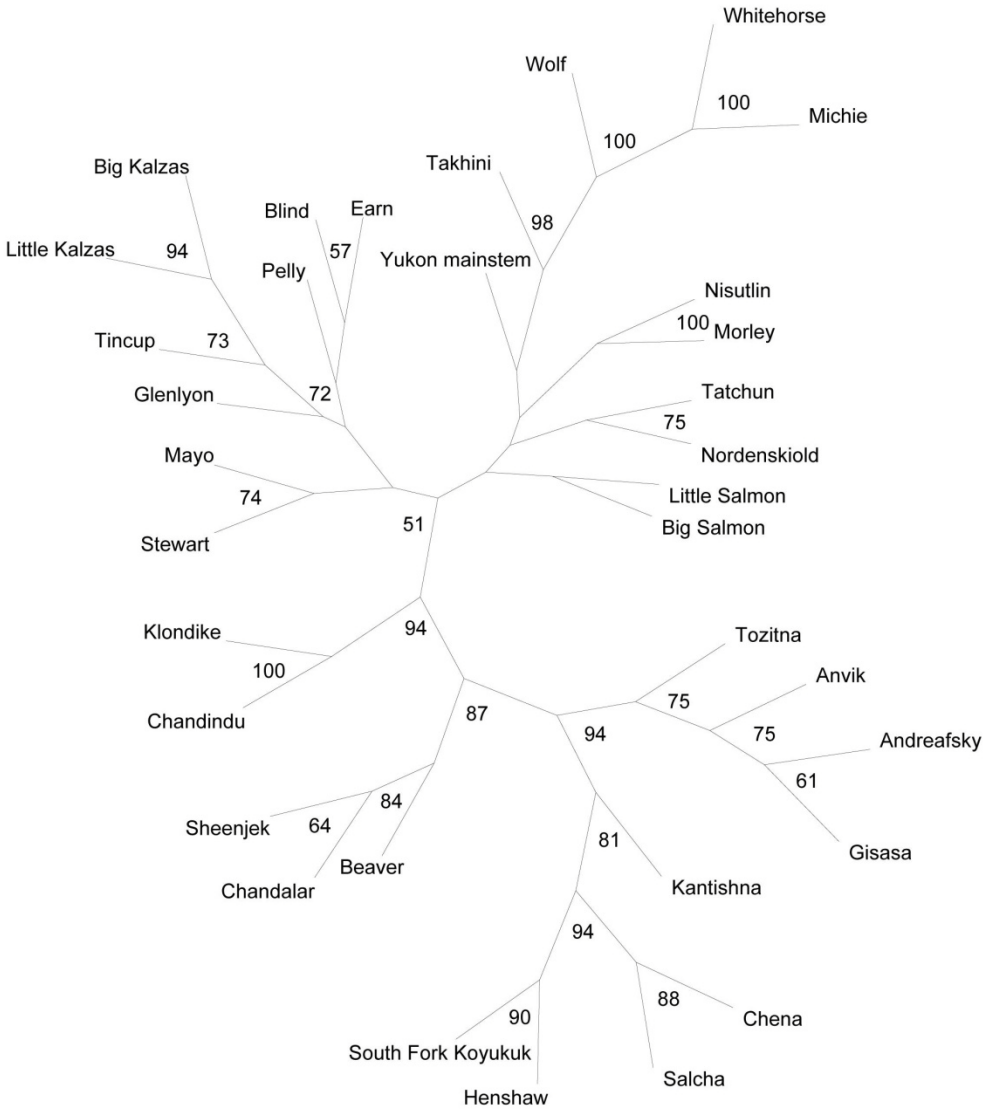

779

780 Figure 2. Consensus neighbor-joining dendogram of baseline samples based on Cavalli-Sforza

781 and Edwards (1967) chord distances calculated from allele frequencies at 13 microsatellite loci.

782 Bootstrap values are shown for nodes that clustered together at least 50% of the time.

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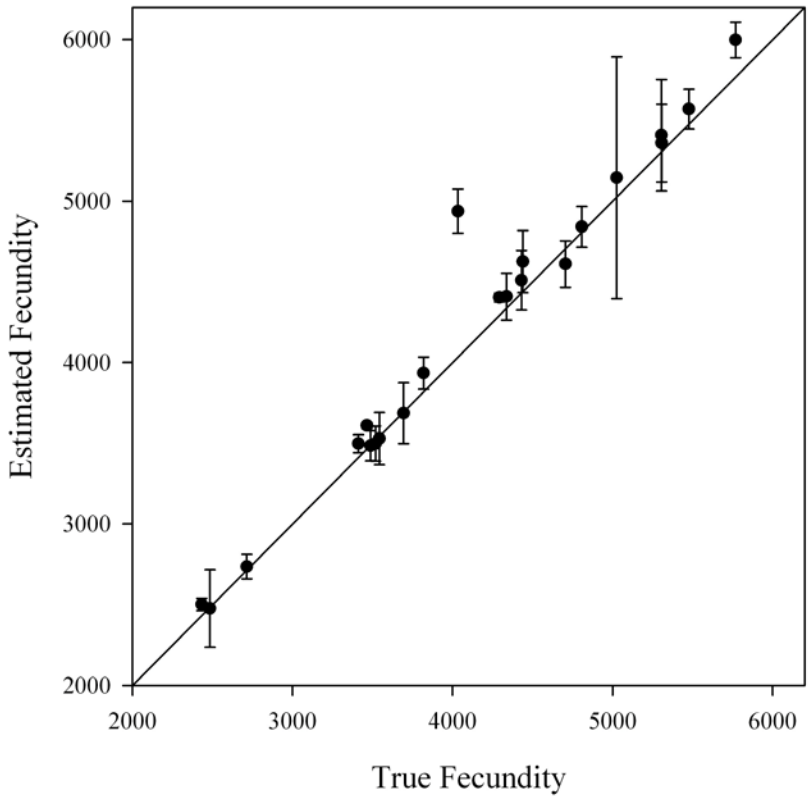

786

787 Figure 3. Estimated versus known fecundity for 22 Chinook salmon egg skeins for which a total

788 count of all eggs was made. Error bars represent 99% normal-approximation confidence

789 intervals.

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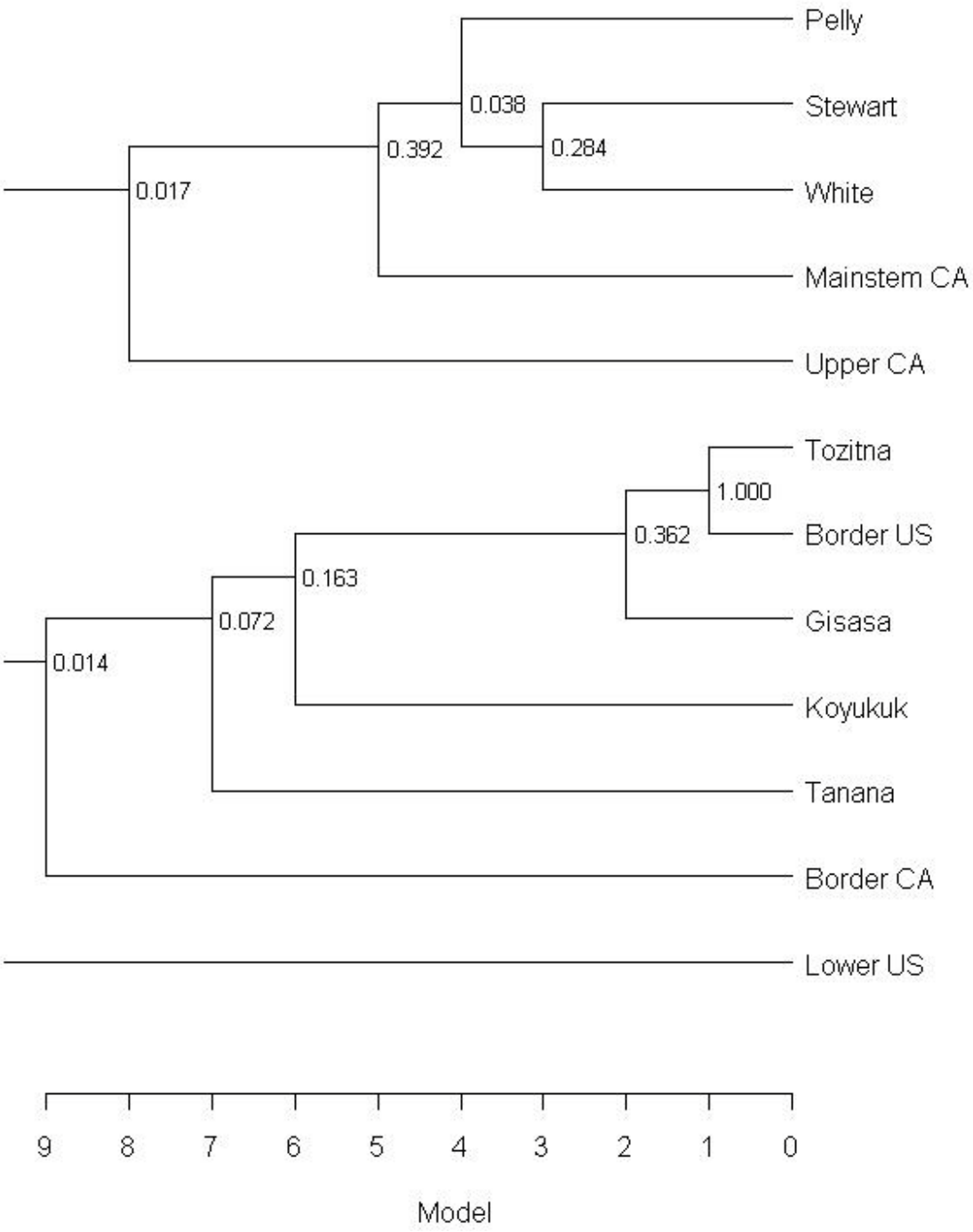

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792 Figure 4. Dendrogram showing the order in which the initial 12 stocks were pooled during

793 mixture modeling, with associated p-values of likelihood ratio tests of homogeneity.

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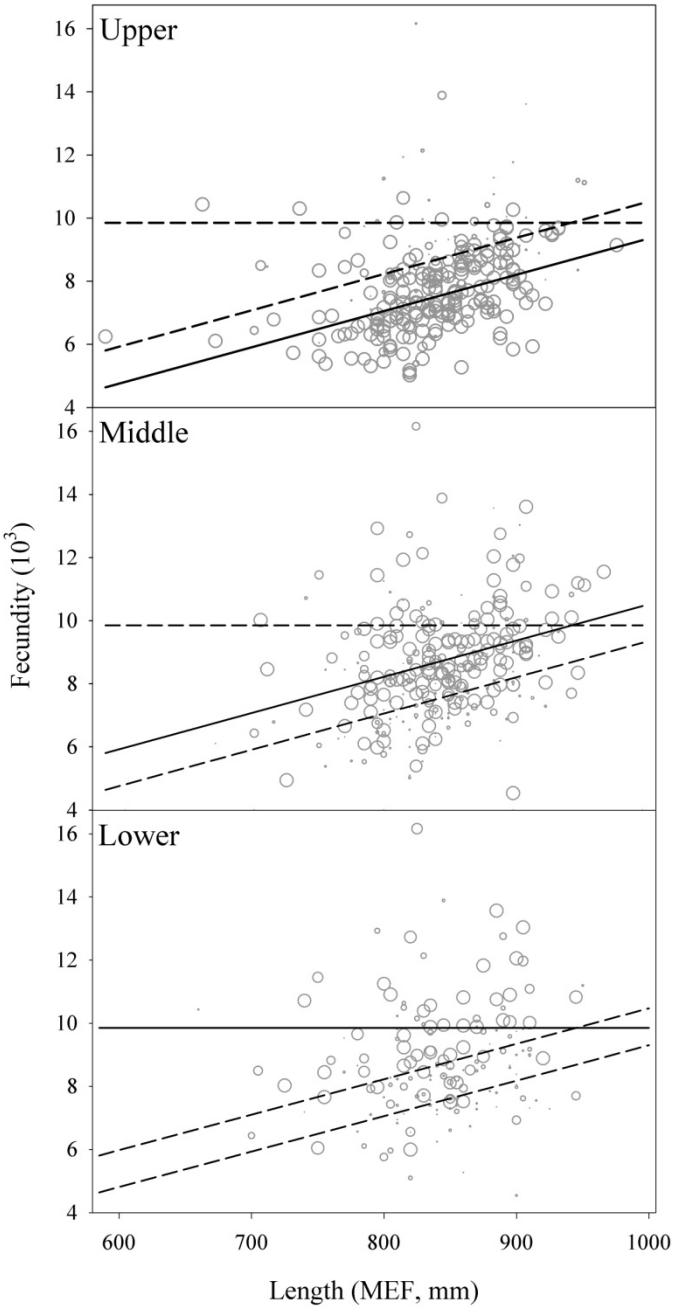

Figure 5. Mean fecundity as a linear function of length for each of the three stocks in the final model. Within each panel, the solid line represents the model for that stock, the other models are shown (dashed lines) to facilitate model comparison, and the areas of the symbols are proportional to the estimated probabilities individuals originated from that stock.

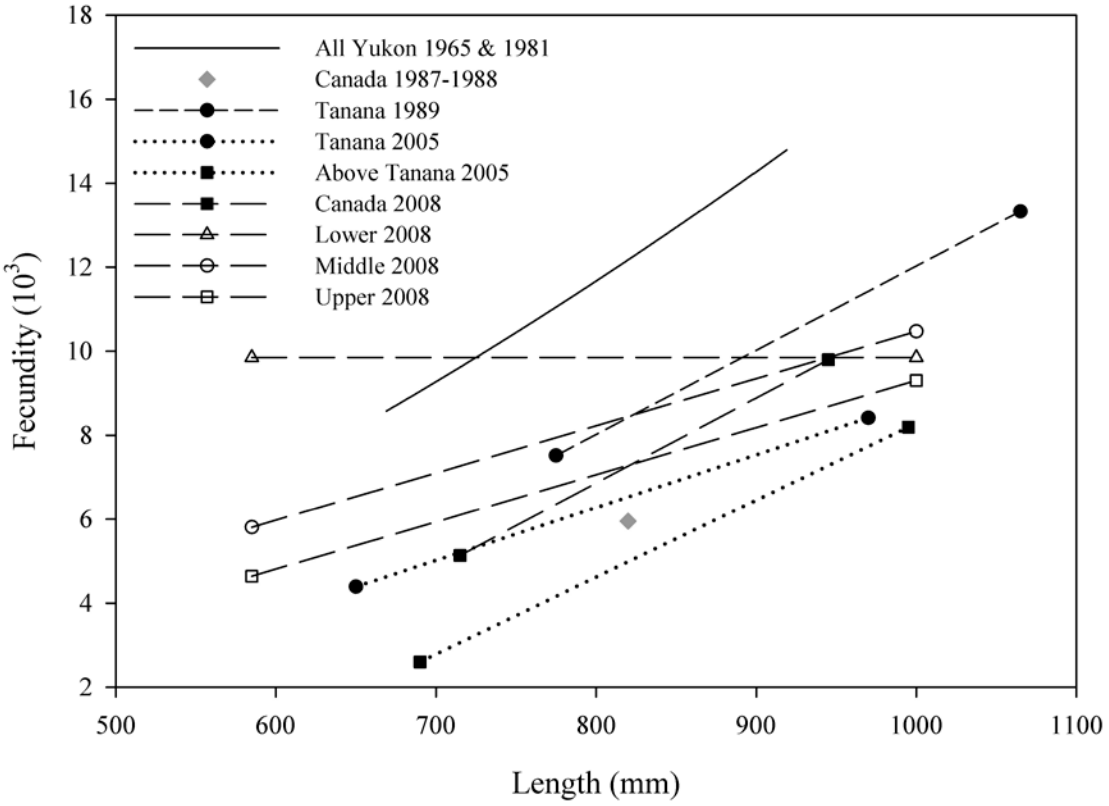

Figure 6. Individual models of fecundity as a function of length based on all available data sets of Yukon River Chinook salmon. All models are linear and historic models have been re-estimated from the original data, except the model based on 1965 and 1981 data (solid line), which is an allometric model taken from Table 1 of Healey and Heard (1984), and the single estimated (diamond) reported by Beacham and Murray (1993). The range of each model reflects the range of lengths observed in each collection.