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Heritability of traits in wild Chinook salmon

by:

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ABSTRACT:

Many Chinook salmon in the Kuskokwim River are harvested using "large mesh" (8 inches or larger) gillnets that preferentially capture older and larger fish. There is interest in determining if this selective fishery has a population-level impact on traits such as adult size and age. To evaluate this issue estimates of trait heritability are needed. Although heritability estimates are available from hatchery populations in the Pacific Northwest these estimates may not reflect the variety of environmental conditions that influence trait variation in wild Chinook salmon populations in western Alaska. In this study we used genetic markers to reconstruct a partial two-generation pedigree from a wild Chinook salmon population in the Tuluksak River. The inferred parent-offspring relationships, combined with phenotypic data on adult size (length) and age-at-maturity provide the first estimates of the heritability of these traits in western Alaska salmon. These estimates of heritability (0.240 and 0.238 for adult length and age-at-maturation, respectively) indicate both traits have detectable genetic variation in this population although the values are lower than those reported for a hatchery population of Chinook salmon in Puget Sound, Washington. While we could not conclude that these heritability estimates are significantly lower than those reported for the hatchery population, these new values do provide locally derived estimates from a wild population to use in future studies on the influence of gear selectivity. Because the reconstructed pedigree was smaller than expected, we were unable to estimate the genetic covariance among these traits or evaluate gender-specific heritability. The pedigree was also used to evaluate variation in family size however due to the small size of the pedigree the results were not conclusive. Given the value but very limited amount of information on heritability and family size variation in wild salmon populations, and the availability of weirs on some tributaries of the Kuskokwim River, we feel further work that builds on the results of this study should be pursued.

Key Words: heritability, pedigree, Chinook salmon, age-at-maturity, length, reproductive success, Kuskokwim River, Tuluksak River, western Alaska

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INTRODUCTION:

Chinook salmon (*Oncorhynchus tshawytscha*) returning to tributaries of the Kuskokwim River in western Alaska are intercepted by both commercial and subsistence gillnet fisheries. Most of the fish are harvested in the subsistence fishery using "large mesh" (8 inches or larger) gillnets (Molyneaux et al. 2005). The large mesh nets avoid unintentional harvest of smaller more abundant species (e.g. chum salmon, *O. keta*) but also preferentially capture older and larger Chinook salmon (Molyneaux et al. 2005). There is interest in determining if (and to what extent) selective fisheries such as that targeting Kuskokwim River Chinook salmon have a population-level impact on traits such as mean adult size, age structure and growth rate (Molyneaux et al. 2005; AYK SSI 2006). The selective harvest of large adults may also indirectly impact population abundance if, for example, family size (number of adult progeny) is not randomly distributed in the population and is correlated with the size of parents. In order to evaluate these issues estimates of trait heritability and family size for a sample of parents of known length are needed. Ideally, estimates of heritability and family size would come from wild populations in western Alaska and would be derived with minimal experimental intervention (i.e. without controlled mating, hatchery incubation, and rearing). Presently, no such estimates are available.

Empirical and modeling studies have shown that salmon fisheries have the potential to alter the genetic and phenotypic diversity of traits such as adult size (e.g. Hard 2004). Gillnet fisheries in particular may target fish of a certain size range which could result in directional or disruptive selection on size and traits often correlated with size (e.g. growth rate, age-at-maturity). Hamon et al. (2000) found that size selection in a gillnet fishery for sockeye salmon (*O. nerka*) likely caused directional selection on body size and shape within populations of a single age class but also caused disruptive selection on age structure in populations where age-at-maturity varied. Modeling studies have shown that a size-selective harvest could reduce size in Chinook salmon but that the level of influence would depend upon a number of factors including the heritability of size and correlated traits (Hard 2004; Bromaghin et al. 2011).

Heritability reflects the potential for a trait to evolve from selection. It also expresses the extent to which a given phenotype is determined by parental genes and thus will determine the degree of phenotypic similarity between related individuals. In a narrow sense, heritability (h^2) is the proportion of the total within population phenotypic variance (V_P) that is additive genetic (V_A) such that $h^2 = V_A/V_P$ and $0 \leq h^2 \geq 1$ (Falconer and Mackay 1996). Some estimates of heritability have been derived for adult size and associated traits in Pacific salmon. It is unclear, however, how broadly these estimates apply among species and populations that exhibit different size distributions and age structure and experience different environments that likely impart different selection regimes. For example, Smoker et al. (1994) and Funk et al. (2005) reported estimates of h^2 of 0.80 and 0.45, respectively, for adult length in male pink salmon (*O. gorbuscha*) from different regions in Alaska. Regarding Chinook salmon, Hard (2004) has derived estimates of h^2 for adult length, age, and growth rate of 0.34, 0.35, and 0.31 respectively. However, because these values were derived from a hatchery population in Puget Sound, Washington, they may not reflect heritability in natural Chinook salmon populations in Western Alaska. Indeed, most studies of heritability in salmon have used a controlled mating experiment requiring some artificial incubation and hatchery rearing (but see Dickerson et al. 2005). These studies probably do not reflect the variety of environmental conditions that could influence phenotypic variation in wild populations (e.g. Coyne and Beecham 1989).

Most studies of family size and reproductive success in salmon have also relied on controlled mating and hatchery incubation with some rearing (e.g. Geiger et al. 1997; Hedrick et al. 2000). Nevertheless, the results from these studies suggest that the variation in family size in Pacific salmon populations is probably not random (does not follow a Poisson distribution, Frankham et al. 2002) and that a few parents contribute a disproportional number of progeny to each generation. Non-random variance in family survival could result from non-genetic factors such as flooding but may also have a genetic basis. Geiger et al. (1997) inferred a genetic component to marine survival in pink salmon by comparing family size in full-sib and half-sib groups from a controlled mating experiment. They deduced that the favored phenotypes must vary across generations but did not explicitly examine this issue. In a study of Chinook salmon mortality resulting from a natural bloom of toxic marine algae, Hard et al. (2000) found that non-random mortality among half- and full-sib families (8.3% and 12.7%, respectively), was non-random and higher than that in the aggregate population (7.2%), indicating that the mortality of the fish associated with the bloom was influenced genetically. The non-random mortality reflected a modest estimate of heritability of mortality (0.15) based on a liability threshold model, and a corresponding reduction in effective population size of 9.4%. Mean half-sib family size declined from 52.0 to 48.2 fish as a result of the bloom, and mean full-sib family size declined from 16.3 to 15.1 fish. The coefficient of variation for half-sib family size increased from 0·33 to 0·34, and that for full-sib family size increased from 0·36 to 0·38. Seamons et al. (2004) and McLean et al. (2004) examined reproductive success in wild steelhead (*O. mykiss*) by reconstructing pedigrees of naturally spawning adults using molecular genetic markers. Seamons et al. (2004) found a positive but weak association between female size and reproductive success while McLean et al. (2004) found no association between adult size and progeny number.

In this study we will address three questions related to evaluating the impact of a size selective fishery on Chinook salmon in the Kuskokwim River. First, how heritable is adult size (length) and traits that may be correlated with adult size (growth rate, age-at-maturation) in males and females? Second, is variance in family size random? Third, if variance in family size is not random, is it related to size of the adult parent? We will study adult Chinook salmon from the Tuluksak River, a tributary of the lower Kuskokwim River (Figure 1). Molecular genetic markers (microsatellites) and recently developed statistical methods will be used to identify a pedigree consisting of adult progeny from the 2003 cohort (adults born in 2003) and their parents from the 2003 adult return. The reconstructed pedigree will be used to estimate heritability of adult size (length), growth rate, and age-at-maturation, and the level of genetic correlation among these traits in males and females. In addition, the pedigree will be used to evaluate family size. The 2003 cohort will be sampled over a three year period (2007-2009) because most adults mature in 4 to 6 years. By sampling the adults in the Tuluksak River, the heritability estimates will reflect lifetime selection just prior to spawning.

OBJECTIVES:

Objective 1. Estimate the heritability of adult size (length), growth rate, and age-at-maturation and the genetic covariance among these traits, in male and female Chinook salmon from the Tuluksak River.

We were able to identify for the first time and with a relatively high level of statistical certainty a partial two-generation pedigree for wild Chinook salmon from the Tuluksak River. Using the inferred pedigree combined with the phenotypic data we obtained for the first time estimates of heritability for adult length (0.240) and age-at-maturation (0.238) in wild Chinook salmon from a western Alaska population. However, because the reconstructed pedigree was smaller than expected we were unable to assess growth rate, the genetic covariance among traits, and gender differences in heritability. We attempted to improve the pedigree by rerunning samples that did not provide adequate genotype information and by attempting additional statistical analyses. However, the results did not change. We concluded that a larger pedigree will be needed to completely address objective one.

Objective 2. Determine if the variation in family size of Tuluksak River Chinook salmon is random, and if not, determine if family size is related to size of adult parent.

The results of the evaluation of variation in family size were equivocal and thus we concluded there was not sufficient evidence to suggest family size variation in Tuluksak Chinook salmon is non-random. These results did not support evaluating if family size is related to the size of the adult parent. As with the analysis of heritability, we feel the lack of clarity in the evaluation of family size is due to the limitations of the small pedigree.

METHODS:

Study Area

The Tuluksak River is one of several tributaries flowing into the lower Kuskokwim River and is located approximately 116 rkm northeast of Bethel, AK (Whitmore et al. 2005). The Tuluksak River is approximately 137 rkm in length and its watershed encompasses approximately 2,098 km^2, most of which is in the Yukon Delta National Wildlife Refuge (Harper 1997, Figure 1). It originates in the Kilbuck Mountains and flows to the northwest. The Fog River drains into the lower portion of the Tuluksak River and is the only major tributary. The Tuluksak River is a slow moving river for the majority of its length and is characterized by dense overhanging vegetation and cut banks. The lower portion of the river is characterized by low-gradient, silty substrate and turbid waters. A weir operated seasonally (June-August) by the USFWS is installed approximately 49 rkm from the mouth and is used to enumerate escapement of Chinook, chum, coho, pink, and sockeye salmon.

Sample collection

Tuluksak River adult Chinook salmon were sampled in the summer of 2003 (candidate parents) and in the summers of 2007-2009 (offspring) at and above the weir (Figure 1, Table 1) in order to reconstruct a pedigree and examine trait heritability and variation in family size. Most of the sample collection was performed by staff operating the weir including members of the Village Of Tuluksak. Weir operations were supervised by Darryl Sipary with oversight by Steve Miller of FWS, Kenai Field Office. Fin tissue samples for genetic analysis were collected from 108 Chinook in 2003 (55 males, 53 females). These samples represented 7.1% of the 776 male and 18.4% of the female Chinook that returned in 2003. Fin tissues samples were taken from 1,077 Chinook in the summers of 2007 (n=350), 2008 (n=422), and 2009 (n=305, Table 1). Individual fin tissue samples were stored in a 2 ml vial in 95% ethanol. Scales or otoliths for ageing were also collected from each fish sampled in 2007-2009. The 2007-2009 collections were taken from pre-spawn adults at the weir (n=765) and post-spawn adults above the weir (n=312). The project goal of sampling 1,000 individuals each year between 2007 and 2009 (3,000 individuals for the study) was not met because the average annual adult return for the three years of the study (2007-

2009) was 460 Chinook or 29.7% of the anticipated average annual return of 1,550 observed between 1991 and 2004.

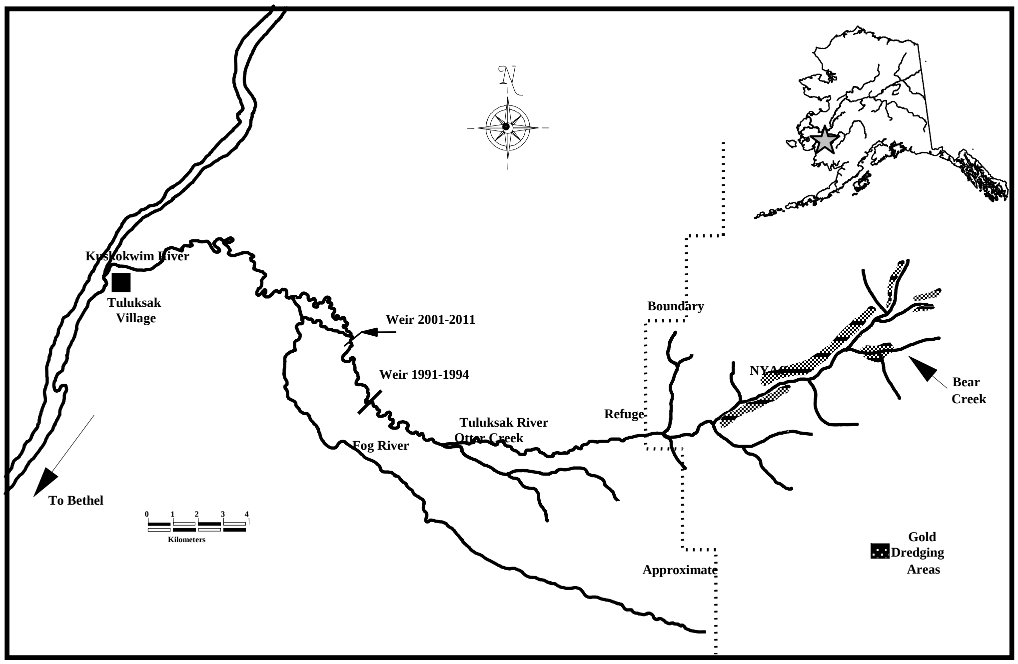

Figure 1. Map of the Tuluksak River showing the past and present weir sites.

Scales (pre-spawn adults) and otoliths (post-spawn adults) were used to age fish (see below) and identify the 2003 cohort from other cohorts in each of the three years. Because cohort ID was not possible until after the samples were collected, some samples taken each year (the other cohorts) were not used in this study. However, the information from these samples was used in other ways to complement ongoing monitoring and research. For example, the samples collected above the weir from post-spawn adults provided a rare opportunity to document the spatial distribution of spawners over a three year period.

Table 1. Sample summary for Tuluksak River Chinook salmon (2003, 2007-2009). Pre-spawn and post-spawn samples were taken at and above the weir, respectively. The column "2003 cohort analyzed" include only individuals from the 2003 cohort sample that were genotyped for 14 or more loci.

	Year	Estimated total run	Pre-spawn samples	Post-spawn samples	Total samples	% sampled	2003 cohort sampled	2003 cohort analyzed
Parent								
	2003	1,064	108	--	108	10.2	--	--
Offspring								
	2007	374	227	123	350	93.6	107	60
	2008	645	287	135	422	65.4	172	143
	2009	362	251	54	305	84.3	113	106
	2007-2009 total	1381	765	312	1077	78.0	392	309

Phenotypic data: Age, sex, and length

Age of adults was determined from scales and otoliths using standard methods (Koo 1962; Jearld Jr. 1983). The scales were processed by the Alaska Department of Fish and Game and the otoliths were processed by Dr. Chris Zimmerman, U.S. Geological Survey. Standardization of the two methods was performed by comparing scales and otoliths from fish sampled and tagged at the weir and recovered above the weir after spawning. Sex was determined by observation of external sex traits (Miller and Harper 2011). The length of all individuals was measured to the nearest 5 mm from the mid-eye to the fork of the caudal fin (MEF). The length of most individuals was measured to the nearest 5 mm from the mid-eye to hypural plate (MEH). Phenotypic data for the 392 samples from the 2003 cohort and the 108 samples from the 2003 adult return are included in Appendices 1 and 2, respectively.

Genetic data

Seventeen microsatellite loci (Table 2) were used to genotype 500 individuals including the 2003 cohort samples (n=392) identified by scale/otolith analysis (Table 1) and the candidate parent sample from the 2003 adult return (55 males, 53 females).

Total genomic DNA was extracted from the fin tissue (~25mg) using proteinase K with the Dneasy™ DNA isolation kit (Qiagen Inc. Valencia, CA), quantified with fluorometry and diluted to a standard concentration. An MJResearch DNA Engine® thermal cycler was used to perform polymerase chain reactions (PCR) 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). 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. Microsatellite allele sizes 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 as an internal lane standard. All scores were verified manually. Alleles were scored by two independent researchers, with any discrepancies being resolved by replicating the analysis for the samples in question and repeating the double scoring process until scores matched. The multi-locus microsatellite genotypes were stored in an Excel™ (Microsoft) spreadsheet prior to data analysis. The database software Access™ (Microsoft) was used for long term storage and archiving of the genetic data.

Objective 1

Pedigree reconstruction

To address objective 1 we first reconstructed a molecular pedigree from the Tuluksak River Chinook salmon genotypes (17 polymorphic loci) collected between 2003 and 2009. We compared a pedigree reconstructed with the program FRANz (Riester et al. 2009) with a pedigree reconstructed with the program Colony 2.0 (Wang 2004). Whereas Colony uses a likelihood algorithm to assign parentage based on the genotypes alone, FRANz uses a Bayesian framework and Metropolis-Hastings coupled Markov Chain Monte Carlo (MCMC) algorithm to assign parentage based on phenotypic data (age, lifespan) as well as genotypes. For this analysis, FRANz and Colony reconstructed nearly identical pedigrees, but FRANz assigned a few more parents than did Colony with high posterior probabilities of correct assignment. Consequently, we used the pedigree generated by FRANz for quantitative genetic analysis. Genotyping error was estimated at <1% for each locus; genotyping failure per locus ranged from 0 to 3.8%.

Heritability estimates

We used an animal model to estimate the heritabilities of length (length.mef) and total age at maturation (age.total) from the pedigree data (total age and SW age are equivalent in variation here because FW age is fixed for these Chinook salmon). The animal model explicitly incorporates the breeding value of each individual (i.e., an individual's contribution to the trait phenotype in a population, measured as the deviation of its progeny from the population mean) as a random factor to estimate genetic (co)variance and heritability for traits by regressing phenotypes on breeding values (Wilson et al. 2010). An individual's breeding value for a phenotype is estimated from its trait covariance with those of its relatives. We applied the Bayesian approach incorporated in the R package MCMCglmm ("Markov Chain Monte Carlo generalized linear mixed models"; Hadfield 2010) to evaluate the phenotypes in the pedigree. For length we used a proper, weakly informative prior based on half the phenotypic variance. For age we used a parameter-expanded Cauchy prior with scale = 25. Length was evaluated as a continuous trait, and total age (age-at-maturation) as an ordinal (multiple threshold) trait. The model incorporated adult sex as a fixed factor, so the estimates of heritability are conditioned on sex. Each analysis involved a single MCMC chain that was evaluated for convergence by inspection of the traces, posterior densities, and to ensure that the lag autocorrelation < 0.05. The 95% credible intervals for each estimate were obtained from the posterior densities.

The MCCglmm estimates obtained from the Colony pedigree were statistically indistinguishable from those obtained from the FRANz pedigree and are not reported here.

Objective 2

Family size evaluation

To address objective 2 we evaluated the number of adult progeny assigned to the 55 males and 53 females sampled in 2003. The distribution of family size (k) was evaluated by computing the index of variability $R_k = v(k)/(\bar{k})$ where $v(k)$ and $\bar{k}$ are the mean and variance of k. If survival is random, then $v(k) \cong \bar{k}$ and R_k is 1 (Crow and Morton 1955). We followed the protocol of Hedrick et al. (1995) and computed R_k for males and females. The resulting R_k estimates were compared to 1 (the expectation when family survival is random). In addition, the distribution of family size for each sex was tested for goodness-of-fit to a Poison distribution (Sokal and Rohlf 1995).

Because the run size and consequently sample size of the 2003 cohort was smaller than anticipated in the project proposal and because the evaluation of the distribution of family size did not indicate family survival deviated from random expectation, we did not test if family size was related to the size (length) of the parent.

RESULTS:

Genotyping, genetic diversity, and phenotypic data

Of the 392 samples from the 2003 cohort, 309 were genotyped for 14 or more loci and were used in the analysis (Table 1). Of the 83 samples that were not genotyped for at least 14 loci all were taken from post-spawn carcasses. All candidate parents (55 males and 53 females) from the 2003 adult return were genotyped for 14 or more loci.

The 17 loci exhibited relatively high levels of genetic diversity. The estimated number of alleles per locus ranged from five to 58 and averaged 24.2. The estimated heterozygosity ranged from 0.10 to 0.90 and averaged 0.80 (Table 2).

The average age-at-maturity for the 392 samples from the 2003 cohort was 5.0 y/o. The average age-at-maturity for the 108 samples from the 2003 adult return was 5.4 y/o. The average length of adults ranged from 508.1 mm (4 y/o females from the 2003 cohort) to 893.8 mm (7 y/o females from the candidate parents (2003 return, Table 3).

Table 2. Estimated number of alleles (A) and heterozygosity (He) for 17 microsatellite loci in Tuluksak River Chinook salmon. These estimates were derived using the 309 samples from the 2003 cohort and the 108 samples from the 2003 adult return.

Locus		A	He
Ogo2		13	0.74
Ogo4		12	0.73
Oke2		14	0.87
Oki100		37	0.95
Omm1080		43	0.96
Ots100		58	0.95
Ots101		35	0.91
Ots107		34	0.93
Ots201b		23	0.91
Ots208b		36	0.96
Ots211		24	0.94
Ots212		15	0.70
Ots213		28	0.93
Ots3M11		6	0.66
Ots9		6	0.55
OtsG474		5	0.10
Ssa408		22	0.87
	avg	24.2	0.80

Table 3. Average length (avgL, mid-eye to the fork of the caudal fin) in mm and standard deviation by age and sex for adult Chinook salmon from the Tuluksak River used in this study. The parent group returned in 2003 and the offspring group (progeny from the 2003 adults) returned in 2007-2009.

		4y/o			5y/o			6y/o			7y/o	
Return	n	avgL	SD	n	avgL	SD	n	avgL	SD	n	avg	SD
2003												
Females	n/a	n/a	n/a	9	770.0	42.0	33	864.1	47.5	8	893.8	52.7
Males	17	529.4	29.5	25	704.4	77.8	8	770.0	99.2	n/a	n/a	n/a
2007-09												
Females	8	508.1	34.0	54	762.0	72.8	85	858.9	49.1	n/a	n/a	n/a
Males	83	535.8	46.8	118	701.5	68.6	28	776.8	91.6	n/a	n/a	n/a

Objective 1

Pedigree reconstruction

Using the program FRANz, 49 of the 309 adult offspring (15.9%) were assigned at least one parent sampled from the 2003 return (Table 4).

Table 4. Reconstructed pedigree for adult Chinook salmon that returned to the Tuluksak River in 2003 and their adult offspring that returned in 2007, 2008, and 2009. The pedigree was generated using the computer program FRANz. Year of return for each sample is denoted by the first two numbers following “ktul”. The asterisk denotes the offspring for which both a male and female parent were identified. Phenotypic data for parents and offspring can be found in Appendices 1 and 2.

Parent 2003	Ofs 2007	Ofs 2008	Ofs 2009
Female			
ktul0310.001			ktul0902.028
ktul0310.004	ktul0704.045	ktul0803.118	
ktul0310.014		ktul0804.029	
ktul0310.016		ktul0804.082	ktul0901.241
ktul0310.031	ktul0705.029	ktul0803.075	ktul0901.210
ktul0310.032		ktul0803.147	
ktul0310.033		ktul0803.282	ktul0901.253
ktul0310.046			ktul0901.169
ktul0310.058			ktul0901.204
ktul0310.062		ktul0803.268	
ktul0310.068	ktul0705.032	ktul0803.171, ktul0803.210	ktul0901.220, ktul0901.238
ktul0310.070		ktul0803.019, ktul0803.164	
ktul0310.072		ktul0803.112	
ktul0310.078		ktul0803.240	ktul0901.182
ktul0310.082	ktul0704.093		
ktul0310.084		ktul0804.053	ktul0901.144
ktul0310.092		ktul0803.100, ktul0803.149	
ktul0310.097		ktul0803.030	
ktul0310.101	ktul0705.036, ktul0705.080	ktul0803.249	
ktul0310.102		ktul0803.224	
ktul0310.104	ktul0704.038		
ktul0310.108			ktul0901.222
ktul0310.109		ktul0804.009	
ktul0310.110	ktul0705.071	ktul0803.213, *ktul0803.229	
Male			
ktul0310.006		ktul0803.090, ktul0803.178	ktul0902.012
ktul0310.023		ktul0803.028	
ktul0310.056		ktul0803.024	
ktul0310.063			ktul0901.089
ktul0310.065		ktul0804.062	
ktul0310.073		ktul0803.038	
ktul0310.091		*ktul0803.229	

Forty eight offspring were assigned to a single parent: 40 offspring to a female parent and eight offspring to a male parent. One offspring was assigned both a male and female parent. Seven of the 55 males (12.7%) and 24 of the 53 females (45.3%) sampled in 2003 were assigned offspring. The sample of males and females from 2003 represent 7.1% and 18.4%, respectively, of the total 2003 return. The number of offspring assigned to a single parent ranged from 1 to 5.

Heritability estimates

The values and precision of the estimates of heritability derived from the R package MCMCglmm are summarized in Table 5 and in Figures 2-3. The heritability estimate for length (mid-eye to fork of caudal fin, MEF) was 0.240 (95% credible interval = 0.077-0.708, Figure 2). Sex had a significant ($P < 0.05$) effect on variation in length (males shorter than females), so the heritability estimate for length was conditioned on the fixed effect of sex. The heritability estimate for age-at-maturation was not greater than zero (Table 5). The plots in Figure 3 show the problems with the traces and posterior densities for heritability of this trait and indicate that heritability of age-at-maturation could not be reliably estimated as an ordinal trait with our pedigree data. Because of this problem, we adopted an alternative approach to estimate the heritability of total age as a dichotomous "threshold" trait (ages 4-5 vs. ages 6-7) by converting the threshold value to an underlying continuous liability value using the simple method described by Dempster and Lerner (1950). Using that method the estimate for heritability of "liability" of age at maturation was 0.238 (95% credible intervals 0.077-0.708, Figure 4). The effect of sex on variation in age at maturation was also significant ($P < 0.05$) with males younger than females, so the heritability estimate for age was conditioned on the fixed effect of sex.

Table 5. Heritability estimates for length (mid-eye to fork of caudal fin, MEF) and age-at-maturation for Tuluksak River Chinook salmon.

		95% Highest Posterior Density interval	
Trait	Posterior mode of heritability estimate	lower	upper
Length (MEF)	0.240	0.077	0.708
Age-at-maturation	<0.001	<0.001	0.001
"liability" of age-at-maturation	0.238	0.097	0.975

Estimated using a bivariate animal model, the phenotypic correlation between length and age was highly positive (+0.829, 95% confidence interval = 0.792-0.859). We could not estimate the genetic correlation between the traits reliably (the point estimate exceeded +0.995, which we do not consider to be reasonable). This may not be surprising, given the weak pedigree. The lag autocorrelation (-0.010) suggested that the model might have to be run longer, and the results suggest that a more suitable prior may be necessary. We attempted a variety of weakly informative priors, including parameter-expanded priors, in exploring these analyses to estimate the genetic correlation, but in the end we concluded that the analyses are limited primarily by the low power of the pedigree determined by the small sample size and the low frequency of parental assignments. The constraint imposed by the shallow pedigree cannot be overcome by simply extending chain length or choosing an appropriate prior.

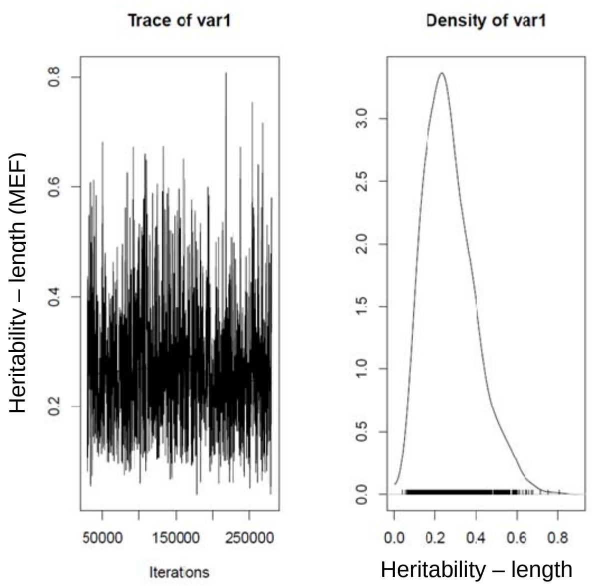

Figure 2. MCMC estimates of heritability of length (mid-eye to fork of caudal fin, MEF) for Tuluksak River Chinook salmon. The left panel shows the trace of the estimate of heritability for the fitted model plotted over the 2,300,000 iterations of the MCMC chain. The right panel shows the posterior density of the estimate of heritability for the fitted model.

Objective 2

Family size evaluation

The number of offspring ranged from 0 to 5 for the candidate females and 0 to 3 for the candidate males (Table 6). Most individuals were assigned one or no offspring. The estimate of mean family size $\bar{k}$ was 0.774 and 0.164 for females and males, respectively (Table 7). The variance in family size was 1.179 and 0.251 for females and males, respectively. Although the mean and variance estimates differed for females and males, the index of variability (R_k) was approximately 1.5 for both sexes (Table 7). However, the value for the males should be viewed with caution given the small sample size for individuals with one or more offspring.

The R_k estimates were larger than one (one is the expectation when family survival is random). Nonetheless, a chi-

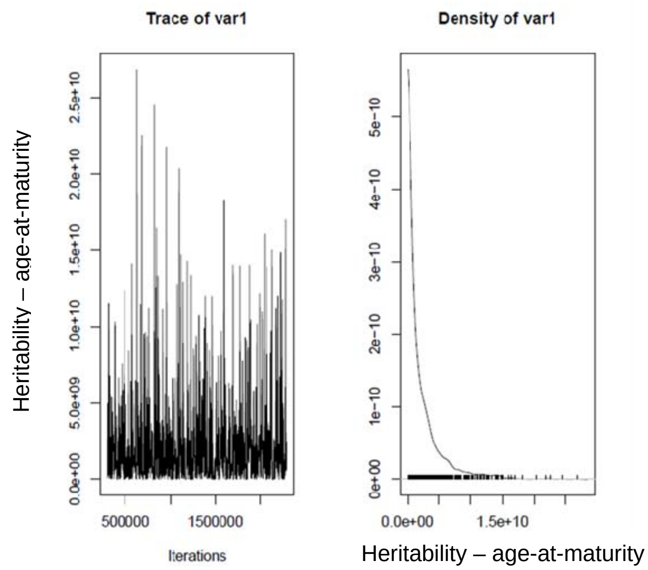

Figure 3. MCMC estimates of heritability of age-at-maturation for Tuluksak River Chinook salmon. The left panel shows the trace of the estimate of heritability for the fitted model plotted over the 2,300,000 iterations of the MCMC chain. The right panel shows the posterior density of the estimate of heritability for the fitted model.

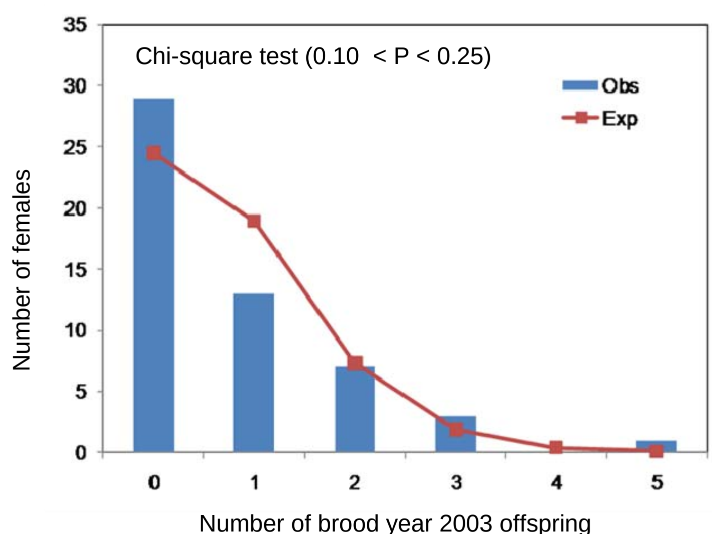

Figure 4. The observed and expected distribution of the number of adult offspring for 53 female Chinook salmon sampled from the Tuluksak River in 2003.

square test of goodness-of-fit did not indicate ($0.10 < P < 0.25$) that the distribution of family size for females exhibited a significant departure from a Poison distribution (Figure 4). The test was not performed for the males because the sample size was too small.

Table 6. The number of Tuluksak Chinook salmon offspring from the 2003 cohort assigned to a sample of candidate parents (53 females, 55 males) from the 2003 adult return.

Number offspring	female	male
0	29	48
1	13	6
2	7	0
3	3	1
4	0	0
5	1	0

Table 7. The index of variability $R_k = (v(k)/(\bar{k}))$ of family size for the sample of candidate parents from the 2003 adult return of Tuluksak River Chinook salmon. $\bar{k}$ and $v(k)$ are the mean and variance of family size.

	Females	Males
$\bar{k}$	0.774	0.164
$v(k)$	1.179	0.251
R_k	1.523	1.531

DISCUSSION:

Objective 1

Pedigree reconstruction

Pedigree information can provide valuable insight into the genetic basis of the variation observed in traits of interest to resource managers such as size, growth rate, and age-at-maturity. While there is a long history of evaluating pedigrees in of domestic plants and animals, reconstructing pedigrees for organisms in the wild is a challenging task (Pemberton 2008). Despite the difficulties, there is much interest in evaluating wild pedigrees for species of conservation and management concern because these pedigrees better reflect the variety of environmental conditions that, in addition to genetics, influence the observed variation in traits in wild populations (Coyne and Beecham 1987, Pemberton 2008). Developments in molecular genetics and the advent of more sophisticated statistical tools have made the task of pedigree reconstruction more feasible for wild populations. Nonetheless, many issues, such as the size of the wild pedigree often cannot be controlled and can limit the conclusions that can be drawn from the pedigree information. Thus, wild pedigrees, especially for Pacific salmon, are rare.

In this study, we were able to identify for the first time and with a relatively high level of statistical certainty a partial two-generation pedigree for wild Chinook salmon from a river in western Alaska. Two methods of parentage assignment, the likelihood and Bayesian approaches, each provided similar results with high probabilities for the individual parent-offspring assignments. The corroborative results are indicative of the robustness of the partial pedigree and demonstrate that molecular genetic methods can identify first order relatives in western Alaska Chinook salmon populations. More importantly, the inferred parent-offspring relationships, combined with the phenotypic data on length and age-at-maturity provide the first estimates of the heritability of these traits in western Alaska salmon. On the other hand, the small size of the reconstructed pedigree limited the extent of the heritability analysis and likely contributed to the relatively low precision (broad credible intervals) for each heritability estimate. These limitations are discussed further in the section on heritability estimates below. Here we discuss factors contributing to the small number and size of the families uncovered in the partial pedigree.

Three factors most likely contributed to the small size of the reconstructed pedigree. First, the number of families in the reconstructed pedigree was limited by the size of the sample from the parent population (the 2003 adult return). That sample included 55 males and 53 females and represented 7.1% and 18.4%, respectively, of the total number of each sex that returned in 2003. With that in mind, the fact that we only assigned parents for 15.9% (49 of 309) of the offspring from the 2003 brood year is not surprising. Many of the unassigned offspring are likely progeny of the unsampled portion of the 2003 adult return. Second, the fact that 29 of the 53 females (54.7%) and 48 of the 55 males (87.3%) were assigned no offspring despite the fact that close to 80% of the adult Chinook salmon were sampled during the years that the 2003 cohort returned suggests that many individuals from the 2003 return did not contribute adult offspring to the population. The size of each family in the reconstructed pedigree was limited by the fact that the total annual return during each of the sample years (2007, 08, 09) averaged just 460 fish, less than 30% of the annual average of 1,550 observed between 1991 and 2004. The small number of the Chinook salmon returning to the Tuluksak River continues to be a concern to the resource managers and is indicative of relatively poor survival of multiple cohorts including the 2003 broodyear sampled in this study. Finally, the size of each family was also limited by the fact that 83 of the 392 samples from the 2003 brood year were not included in the analysis because fewer than 14 of the 17 loci were identifiable. Most of these samples (78) were from carcass samples and it is believed that the failure to resolve most loci was due to poor tissue quality. Future studies should try, were possible, to acquire samples from mostly live samples. We were limited to sampling on a portion of live Chinook salmon at the Tulukak River weir in order to avoid excessive handling stress during the period when chum salmon (more numerous) are also present.

Heritability estimates

The first objective was to estimate the heritability of adult size (length), growth rate, and age-at-maturation and the genetic covariance among these traits, in male and female Chinook salmon from the Tuluksak River. Despite the small size of the reconstructed pedigree we were able to partially meet this objective and obtain the first estimates of heritability for adult length and age-at-maturation in wild Chinook salmon from western Alaska. These results also add to the limited information available on trait heritability in wild salmon in general. We detected modest estimates of heritability (0.240 and 0.238 for length and age-at-maturation, respectively) for wild Tuluksak River Chinook salmon using an animal model. In addition, the two traits showed high and positive phenotypic correlation, but the genetic correlation between them could not be reliably estimated from the molecular pedigree. These heritability results indicate both traits have detectable genetic variation in this population although the values are lower than those reported by Hard (2004) for a hatchery population of Chinook salmon (heritability of length = 0.34, heritability of age = 0.35) in Puget Sound, Washington. Given the relatively low precision (broad credible intervals) for each estimate in this study (Table 5) we cannot conclude that these heritability values are significantly lower than those reported by Hard (2004), however these new values do provide locally derived estimates from a wild population to use in future studies on issues such as the influence of gear selectivity on adult size (e.g., Bromaghin et al. 2011). In a broader context, the results here suggest efforts to estimate heritability in other western Alaska populations would be productive as even a small pedigree can provide some information.

Unfortunately, the small and incomplete pedigree limited the analysis and we were unable to assess growth rate, the genetic covariance among traits, and gender differences in heritability. While we demonstrated a phenotypic correlation between length and age-at-maturation, the test result for a genetic correlation was found to be unrealistically high (+0.995). We attempted to improve the pedigree by rerunning the 78 carcass samples that did not provide adequate genotype information. We did this at least three times before concluding that these individuals were not useable. We also attempted additional Bayesian analyses involving chains of different lengths and different types of uninformative priors to maximize the information content of the pedigree. However, the results did not change. We concluded that a larger pedigree will be needed to more completely address objective one and provide more precise estimates of the heritability of length and age-at-maturity. We feel this can be accomplished by sampling the parent year more thoroughly (preferably close to 100%) for a relatively small population in a river like the Tuluksak or the Tatlawiksuk in the Kukskokwim River drainage. Given the value but very limited amount of information on heritability and family size variation in wild salmon populations, and the availability of weirs on some tributaries of the Kuskokwim River, we feel further work that builds on the results of this study should be pursued

Objective 2

Family size evaluation

The second objective was to determine if the variation in family size of Tuluksak River Chinook salmon is random, and if not, determine if family size is related to size of adult parent. While previous studies have revealed a genetic basis for differences in family survival (Geiger et al. 1997; Hard et al. 2000) the evaluation of family size in the present study was equivocal. On one hand the estimates of the index of variation (R_k) were larger than one (one is the expectation when family survival is random) for both male and female parents. On the other hand the chi-square test of the distribution of family size for female parents indicated the variation in family size was not significantly different from random expectations (the test was not performed for males because the sample size was too small). These results did not support evaluating if family size is related to the size of the adult parent. As with the analysis of heritability, we feel the lack of clarity in the evaluation of family size is due to the limitations of the small pedigree. Nonetheless, some trends in the pedigree are worth noting with regard to family survival and may warrant further investigation. In particular, it is noteworthy that 54.7% and 87.3% of the females and males, respectively, in the candidate parent sample of 108 fish were assigned no offspring. This is unlikely to reflect inadequate sampling of the offspring escapement since close to 80% of the adult Chinook salmon were sampled during the years that the offspring (the 2003 cohort) returned. Thus, the reconstructed pedigree suggests that many adults (and more males than females) in the 2003 return did not produce offspring that contributed to the escapement in 2007-2009. This is not entirely surprising for the males given the fact that the estimated male escapement in 2003 was 776 fish while the estimated combined escapement of the 2003 cohort (2007-2009) was 535 fish (Zabkar and Harper 2004; Plumb and Harper 2008; Miller and Harper 2009; Miller and Harper 2010). On the other hand, the estimated female escapement in 2003 was 288 fish. So, despite the fact that on average 1.86 fish (535/288) from the 2003 broodyear returned for every female that returned to the river in 2003, many females (our sample suggests over 50%) did contribute to the next generation spawning population. For males, the fraction not contributing the next generation could be much greater (our results suggest over 80%) which may indicate that when the population is heavily weighted toward males (the ratio of males to females was 3.4:1 in the 2003 adult return) many males may not spawn or spawn unsuccessfully. It seems less likely that failure to spawn or unsuccessful spawning contributed to the lack of progeny for many of the females. However, little is known about Chinook salmon spawning in the Tuluksak River and subsequent survival of the progeny in freshwater and the marine environment. The results here support the need for more investigation to more fully examine reproductive success and variance in family size. Additional pedigree studies could provide valuable insight into reproductive success and help better establish if the offspring returns represent a relatively small number of the parental returns. As stated above for the heritability analysis, these studies should attempt to more fully sample the parent population.

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DELIVERABLES:

The following deliverables disseminate the findings from this study: 1) a final report and eight progress reports available through the AYKSSI program or from the authors, 2) two oral reports describing preliminary results presented at the annual Kuskokwim interagency meeting in 2010 and 2011, 3) genetic data (genotypes and allele frequencies) in Excel (Microsoft Office version 11) spreadsheets available from the authors, 4) phenotypic data (sex, age, and length) for each sample in an Excel (Microsoft Office version 11) spreadsheet available from the authors, 5), a manuscript in preparation for submission to a peer-reviewed journal.

PROJECT DATA:

Genetic and phenotypic data are archived in Excel (Microsoft Office version 11) spreadsheets available from the authors (Conservation Genetics Laboratory, U.S. Fish & Wildlife Service, 1011 East Tudor Road, Anchorage, Alaska, USA 99503. ph: (907) 786-3858, email: jeffrey_olsen@fws.gov).

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PRESS RELEASE:

Heritability expresses the extent to which a given trait is determined by parental genes. It also reflects the potential for a trait to evolve from selection. In the context of a gillnet fishery that captures fish a certain size and age, the potential for the fishery to, over time, alter these traits will depend in part on the heritability of size and age in the target population. Because many Chinook salmon in the Kuskokwim River are harvested using “large mesh” (8 inches or larger) gillnets that preferentially capture older and larger fish, there is interest in determining if this selective fishery has a population-level impact on traits such as adult size and age. Few heritability estimates exist for these traits in Chinook salmon and those that do exist are mostly from hatchery populations in the Pacific Northwest. The study “Heritability of traits in wild Chinook salmon” examined heritability of adult size (length) and age-at-maturity in wild Chinook salmon from the Tuluksak River in the Kuskokwim River watershed. Adult salmon returning to the Tuluksak River in 2003 and their offspring returning in 2007, 2008, 2009 were sampled at and above a weir located approximately eight miles from the river mouth. These samples were analyzed using genetic markers to identify parents and their offspring and reconstruct for the first time a partial two-generation pedigree from a wild Chinook salmon population in western Alaska. The inferred parent-offspring relationships, combined with data on adult length and age-at-maturity provide the first estimates of the heritability of these traits in western Alaska salmon. These estimates of heritability (0.240 and 0.238 for adult length and age-at-maturation, respectively) indicate both traits have detectable genetic variation in this population although the values are lower than those reported for a hatchery population of Chinook salmon in Puget Sound, Washington. While we could not conclude that these heritability estimates are significantly lower than those reported for the hatchery populations, these new values do provide locally derived estimates from a wild population to use in future studies on the influence of gear selectivity. The pedigree was also used to evaluate if offspring with large parents have higher survival than offspring with small parents. However due to the small size of the pedigree in this study the results of this evaluation were not conclusive. Given the value but very limited amount of information on heritability and family size variation in wild salmon populations, and the availability of weirs on some tributaries in the Kuskokwim River, we feel further work that builds on the results of this study should be pursued.

APPENDICES:

Appendix 1. Sample data for the 2003 cohort. MEF and MEH are the length estimates to nearest 5 mm from the mid-eye to the fork of the caudal fin (MEF) and from the mid-eye to hypural plate (MEH). Freshwater (FW) and saltwater (SW) age were derived from scales (live samples) or otoliths (carcasses).

Sample ID	Date	live_carcass	Sex	MEF	MEH	FW age	SW age	Total age
KTUL0702.002	08/15/07	carcass	m		445	1	2	4
KTUL0702.004	08/15/07	carcass	m		578	1	2	4
KTUL0702.006	08/15/07	carcass	m		505	1	2	4
KTUL0702.008	08/16/07	carcass	m		535	1	2	4
KTUL0702.009	08/16/07	carcass	m		595	1	2	4
KTUL0702.010	08/16/07	carcass	m		525	1	2	4
KTUL0702.014	08/17/07	carcass	m		575	1	2	4
KTUL0702.017	08/17/07	carcass	m		527	1	2	4
KTUL0702.018	08/17/07	carcass	m		471	1	2	4
KTUL0702.020	08/17/07	carcass	m		505	1	2	4
KTUL0702.021	08/18/07	carcass	m		470	1	2	4
KTUL0702.022	08/18/07	carcass	m		535	1	2	4
KTUL0702.023	08/18/07	carcass	m		440	1	2	4
KTUL0702.024	08/18/07	carcass	m		497	1	2	4
KTUL0702.025	08/18/07	carcass	m		455	1	2	4
KTUL0702.026	08/18/07	carcass	m		445	1	2	4
KTUL0704.012	07/04/07	live	m	700	640	1	2	4
KTUL0704.017	07/04/07	live	m	520	470	1	2	4
KTUL0704.022	07/04/07	live	m	630	560	1	2	4
KTUL0704.025	07/05/07	live	m	550	440	1	2	4
KTUL0704.035	07/05/07	live	m	440	380	1	2	4
KTUL0704.036	07/05/07	live	m	545	480	1	2	4
KTUL0704.038	07/05/07	live	m	480	415	1	2	4
KTUL0704.045	07/05/07	live	m	515	480	1	2	4
KTUL0704.075	07/13/07	live	m	510	450	1	2	4
KTUL0704.079	07/14/07	live	m	555	490	1	2	4
KTUL0704.093	07/18/07	live	f	500	460	1	2	4
KTUL0704.097	07/18/07	live	m	490	430	1	2	4
KTUL0704.104	07/19/07	live	f	480	445	1	2	4
KTUL0704.105	07/19/07	live	m	620	565	1	2	4
KTUL0704.130	07/20/07	live	m	595	520	1	2	4
KTUL0704.136	07/21/07	live	m	560	500	1	2	4
KTUL0704.161	07/23/07	live	m	490	460	1	2	4
KTUL0704.166	07/23/07	live	m	550	520	1	2	4
KTUL0704.169	07/23/07	live	m	460	430	1	2	4
KTUL0704.174	07/23/07	live	m	560	500	1	2	4
KTUL0704.195	07/25/07	live	m	485	450	1	2	4
KTUL0704.226	08/05/07	live	m	495	480	1	2	4
KTUL0705.006	08/04/07	carcass	m	515		1	2	4
KTUL0705.007	08/04/07	carcass	m	580		1	2	4
KTUL0705.008	08/04/07	carcass	m	600		1	2	4

Appendix 1. Sample data for the 2003 cohort. MEF and MEH are the length estimates to nearest 5 mm from the mid-eye to the fork of the caudal fin (MEF) and from the mid-eye to hypural plate (MEH). Freshwater (FW) and saltwater (SW) age were derived from scales (live samples) or otoliths (carcasses).

Sample ID	Date	live_carcass	Sex	MEF	MEH	FW age	SW age	Total age
KTUL0705.010	08/05/07	carcass	m	500		1	2	4
KTUL0705.012	08/06/07	carcass	m	550		1	2	4
KTUL0705.016	08/06/07	carcass	m	570		1	2	4
KTUL0705.018	08/09/07	carcass	m	500		1	2	4
KTUL0705.019	08/10/07	carcass	m	510		1	2	4
KTUL0705.020	08/10/07	carcass	m	460		1	2	4
KTUL0705.021	08/10/07	carcass	m	485		1	2	4
KTUL0705.025	08/10/07	carcass	m	600		1	2	4
KTUL0705.026	08/10/07	carcass	m	590		1	2	4
KTUL0705.028	08/11/07	carcass	m	575		1	2	4
KTUL0705.029	08/11/07	carcass	m	585		1	2	4
KTUL0705.032	08/12/07	carcass	m	475		1	2	4
KTUL0705.033	08/12/07	carcass	m	490		1	2	4
KTUL0705.034	08/12/07	carcass	m	530		1	2	4
KTUL0705.035	08/12/07	carcass	f	470		1	2	4
KTUL0705.036	08/12/07	carcass	m	590		1	2	4
KTUL0705.038	08/12/07	carcass	m	535		1	2	4
KTUL0705.040	08/13/07	carcass	f	510		1	2	4
KTUL0705.041	08/13/07	carcass	m	575		1	2	4
KTUL0705.042	08/14/07	carcass	m	560		1	2	4
KTUL0705.043	08/14/07	carcass	m	525		1	2	4
KTUL0705.044	08/14/07	carcass	m	580		1	2	4
KTUL0705.045	08/14/07	carcass	m	505		1	2	4
KTUL0705.046	08/14/07	carcass	f	550		1	2	4
KTUL0705.049	08/15/07	carcass	m	430		1	2	4
KTUL0705.050	08/15/07	carcass	m	500		1	2	4
KTUL0705.053	08/15/07	carcass	m	530		1	2	4
KTUL0705.055	08/16/07	carcass	m	560		1	2	4
KTUL0705.056	08/16/07	carcass	m	545		1	2	4
KTUL0705.057	08/16/07	carcass	m	495		1	2	4
KTUL0705.058	08/16/07	carcass	m	505		1	2	4
KTUL0705.059	08/16/07	carcass	m	540		1	2	4
KTUL0705.060	08/16/07	carcass	m	545		1	2	4
KTUL0705.061	08/16/07	carcass	m	510		1	2	4
KTUL0705.062	08/16/07	carcass	f	480		1	2	4
KTUL0705.065	08/16/07	carcass	m	510		1	2	4
KTUL0705.067	08/17/07	carcass	m	555		1	2	4
KTUL0705.068	08/17/07	carcass	m	570		1	2	4
KTUL0705.069	08/17/07	carcass	m	610		1	2	4
KTUL0705.071	08/17/07	carcass	m	510		1	2	4
KTUL0705.072	08/17/07	carcass	m	530		1	2	4
KTUL0705.073	08/17/07	carcass	m	480		1	2	4
KTUL0705.074	08/17/07	carcass	m	470		1	2	4
KTUL0705.075	08/18/07	carcass	m	540		1	2	4
KTUL0705.076	08/18/07	carcass	m	545		1	2	4
KTUL0705.077	08/18/07	carcass	m	595		1	2	4

Appendix 1. Sample data for the 2003 cohort. MEF and MEH are the length estimates to nearest 5 mm from the mid-eye to the fork of the caudal fin (MEF) and from the mid-eye to hypural plate (MEH). Freshwater (FW) and saltwater (SW) age were derived from scales (live samples) or otoliths (carcasses).

Sample ID	Date	live_carcass	Sex	MEF	MEH	FW age	SW age	Total age
KTUL0705.078	08/19/07	carcass	m	530		1	2	4
KTUL0705.079	08/19/07	carcass	m	490		1	2	4
KTUL0705.080	08/19/07	carcass	m	530		1	2	4
KTUL0705.081	08/19/07	carcass	m	585		1	2	4
KTUL0705.083	08/20/07	carcass	m	555		1	2	4
KTUL0705.084	08/20/07	carcass	m	460		1	2	4
KTUL0705.085	08/20/07	carcass	m	580		1	2	4
KTUL0705.087	08/20/07	carcass	m	510		1	2	4
KTUL0705.088	08/20/07	carcass	m	540		1	2	4
KTUL0705.089	08/21/07	carcass	m	580		1	2	4
KTUL0705.090	08/21/07	carcass	m	555		1	2	4
KTUL0705.091	08/21/07	carcass	m	555		1	2	4
KTUL0705.092	08/21/07	carcass	f	565		1	2	4
KTUL0705.094	08/22/07	carcass	f	510		1	2	4
KTUL0705.095	08/23/07	carcass	m	500		1	2	4
KTUL0705.096	08/23/07	carcass	m	510		1	2	4
KTUL0705.097	08/23/07	carcass	m	520		1	2	4
KTUL0705.098	08/24/07	carcass	m	595		1	2	4
KTUL0705.100	08/28/07	carcass	m	505		1	2	4
KTUL0705.101	08/29/07	carcass	m	560		1	2	4
KTUL0803.002	07/02/08	live	F	705	680	1	3	5
KTUL0803.006	07/06/08	live	M	730	665	1	3	5
KTUL0803.007	07/06/08	live	M	675	620	1	3	5
KTUL0803.011	07/07/08	live	M	610	565	1	3	5
KTUL0803.013	07/07/08	live	M	720	680	1	3	5
KTUL0803.014	07/07/08	live	M	610	560	1	3	5
KTUL0803.017	07/07/08	live	M	740	670	1	3	5
KTUL0803.018	07/07/08	live	M	750	670	1	3	5
KTUL0803.019	07/07/08	live	M	570	520	1	3	5
KTUL0803.021	07/07/08	live	M	750	700	1	3	5
KTUL0803.022	07/08/08	live	M	535	500	1	3	5
KTUL0803.024	07/14/08	live	M	890	815	1	3	5
KTUL0803.027	07/14/08	live	M	735	680	1	3	5
KTUL0803.028	07/14/08	live	M	710	665	1	3	5
KTUL0803.029	07/14/08	live	M	635	590	1	3	5
KTUL0803.030	07/14/08	live	M	680	630	1	3	5
KTUL0803.035	07/15/08	live	M	805	745	1	3	5
KTUL0803.037	07/15/08	live	M	680	625	1	3	5
KTUL0803.038	07/15/08	live	M	730	675	1	3	5
KTUL0803.041	07/16/08	live	M	680	625	1	3	5
KTUL0803.042	07/16/08	live	M	625	575	1	3	5
KTUL0803.051	07/17/08	live	M	660	615	1	3	5
KTUL0803.052	07/17/08	live	F	730	690	1	3	5
KTUL0803.054	07/17/08	live	M	755	685	1	3	5
KTUL0803.055	07/21/08	live	M	720	665	1	3	5
KTUL0803.057	07/21/08	live	F	660	615	1	3	5

Appendix 1. Sample data for the 2003 cohort. MEF and MEH are the length estimates to nearest 5 mm from the mid-eye to the fork of the caudal fin (MEF) and from the mid-eye to hypural plate (MEH). Freshwater (FW) and saltwater (SW) age were derived from scales (live samples) or otoliths (carcasses).

Sample ID	Date	live_carcass	Sex	MEF	MEH	FW age	SW age	Total age
KTUL0803.058	07/21/08	live	M	725	670	1	3	5
KTUL0803.059	07/21/08	live	M	695	645	1	3	5
KTUL0803.060	07/21/08	live	**F**	515	490	1	3	5
KTUL0803.061	07/22/08	live	F	740	730	1	3	5
KTUL0803.062	07/22/08	live	M	740	670	1	3	5
KTUL0803.063	07/22/08	live	**F**	660	610	1	3	5
KTUL0803.074	07/24/08	live	M	685	645	1	3	5
KTUL0803.075	07/24/08	live	M	690	630	1	3	5
KTUL0803.077	07/24/08	live	F	720	665	1	3	5
KTUL0803.078	07/24/08	live	F	785	735	1	3	5
KTUL0803.079	07/24/08	live	F	775	735	1	3	5
KTUL0803.083	07/24/08	live	M	680	625	1	3	5
KTUL0803.085	07/24/08	live	**F**	820	765	1	3	5
KTUL0803.086	07/24/08	live	M	750	690	1	3	5
KTUL0803.087	07/24/08	live	M	660	610	1	3	5
KTUL0803.088	07/24/08	live	F	715	669	1	3	5
KTUL0803.089	07/24/08	live	M	650	605	1	3	5
KTUL0803.090	07/24/08	live	F	695	630	1	3	5
KTUL0803.092	07/25/08	live	M	790	725	1	3	5
KTUL0803.093	07/25/08	live	F	770	705	1	3	5
KTUL0803.094	07/25/08	live	M	840	755	1	3	5
KTUL0803.095	07/25/08	live	F	840	780	1	3	5
KTUL0803.096	07/25/08	live	M	685	630	1	3	5
KTUL0803.098	07/25/08	live	F	825	750	1	3	5
KTUL0803.100	07/25/08	live	M	700	655	1	3	5
KTUL0803.101	07/25/08	live	F	820	760	1	3	5
KTUL0803.104	07/25/08	live	M	870	800	1	3	5
KTUL0803.107	07/25/08	live	F	780	710	1	3	5
KTUL0803.112	07/25/08	live	M	760	720	1	3	5
KTUL0803.116	07/25/08	live	F	715	660	1	3	5
KTUL0803.117	07/25/08	live	F	825	765	1	3	5
KTUL0803.118	07/26/08	live	M	650	615	1	3	5
KTUL0803.123	07/26/08	live	F	715	660	1	3	5
KTUL0803.126	07/26/08	live	F	765	700	1	3	5
KTUL0803.129	07/26/08	live	M	700	655	1	3	5
KTUL0803.131	07/26/08	live	F	825	760	1	3	5
KTUL0803.134	07/27/08	live	M	625	640	1	3	5
KTUL0803.140	07/27/08	live	M	725	670	1	3	5
KTUL0803.145	07/27/08	live	F	800	735	1	3	5
KTUL0803.146	07/27/08	live	M	790	735	1	3	5
KTUL0803.147	07/27/08	live	M	740	685	1	3	5
KTUL0803.149	07/27/08	live	M	755	700	1	3	5
KTUL0803.153	07/27/08	live	M	675	620	1	3	5
KTUL0803.156	07/27/08	live	M	765	710	1	3	5
KTUL0803.162	07/28/08	live	f	805	750	1	3	5
KTUL0803.164	07/28/08	live	f	835	770	1	3	5

Appendix 1. Sample data for the 2003 cohort. MEF and MEH are the length estimates to nearest 5 mm from the mid-eye to the fork of the caudal fin (MEF) and from the mid-eye to hypural plate (MEH). Freshwater (FW) and saltwater (SW) age were derived from scales (live samples) or otoliths (carcasses).

Sample ID	Date	live_carcass	Sex	MEF	MEH	FW age	SW age	Total age
KTUL0803.166	07/28/08	live	m	730	675	1	3	5
KTUL0803.168	07/28/08	live	**m**	775	705	1	3	5
KTUL0803.170	07/28/08	live	m	745	685	1	3	5
KTUL0803.171	07/28/08	live	m	775	720	1	3	5
KTUL0803.172	07/28/08	live	m	740	690	1	3	5
KTUL0803.173	07/28/08	live	f	770	725	1	3	5
KTUL0803.178	07/28/08	live	m	770	715	1	3	5
KTUL0803.180	07/28/08	live	f	830	770	1	3	5
KTUL0803.187	07/29/08	live	m	835	775	1	3	5
KTUL0803.188	07/29/08	live	m	860	800	1	3	5
KTUL0803.198	07/30/08	live	f	890	815	1	3	5
KTUL0803.199	07/30/08	live	f	790	750	1	3	5
KTUL0803.200	07/30/08	live	f	670	625	1	3	5
KTUL0803.201	07/30/08	live	f	790	725	1	3	5
KTUL0803.203	07/30/08	live	m	620	660	1	3	5
KTUL0803.204	07/30/08	live	m	660	610	1	3	5
KTUL0803.209	07/31/08	live	F	800	730	1	3	5
KTUL0803.210	07/31/08	live	M	670	625	1	3	5
KTUL0803.213	07/31/08	live	M	810	745	1	3	5
KTUL0803.214	07/31/08	live	F	815	760	1	3	5
KTUL0803.216	08/01/08	live	m	795	730	1	3	5
KTUL0803.217	08/01/08	live	f	815	755	1	3	5
KTUL0803.224	08/01/08	live	m	665	600	1	3	5
KTUL0803.229	08/02/08	live	f	845	790	1	3	5
KTUL0803.240	08/02/08	live	f	865	810	1	3	5
KTUL0803.242	08/02/08	live	f	800	735	1	3	5
KTUL0803.246	08/03/08	live	f	720	675	1	3	5
KTUL0803.249	08/03/08	live	f	785	720	1	3	5
KTUL0803.252	08/04/08	live	m	740	680	1	3	5
KTUL0803.254	08/05/08	live	f	690	625	1	3	5
KTUL0803.262	08/06/08	live	F	830	775	1	3	5
KTUL0803.263	08/06/08	live	F	775	715	1	3	5
KTUL0803.266	08/08/08	live	m	770	715	1	3	5
KTUL0803.268	08/09/08	live	M	800	740	1	3	5
KTUL0803.271	08/10/08	live	f	680	630	1	3	5
KTUL0803.274	08/11/08	live	m	805	740	1	3	5
KTUL0803.276	08/11/08	live	f	850	780	1	3	5
KTUL0803.277	08/12/08	live	m	905	830	1	3	5
KTUL0803.278	08/12/08	live	f	640	600	1	3	5
KTUL0803.279	08/12/08	live	m	760	700	1	3	5
KTUL0803.281	08/12/08	live	m	740	685	1	3	5
KTUL0803.282	08/12/08	live	m	745	685	1	3	5
KTUL0803.284	07/29/08	live	f	780	730	1	3	5
KTUL0804.001	07/29/08	carcass	M	600	560	1	3	5
KTUL0804.002	08/02/08	carcass	M	645	610	1	3	5

Appendix 1. Sample data for the 2003 cohort. MEF and MEH are the length estimates to nearest 5 mm from the mid-eye to the fork of the caudal fin (MEF) and from the mid-eye to hypural plate (MEH). Freshwater (FW) and saltwater (SW) age were derived from scales (live samples) or otoliths (carcasses).

Sample ID	Date	live_carcass	Sex	MEF	MEH	FW age	SW age	Total age
KTUL0804.005	08/06/08	carcass	F	670	610	1	3	5
KTUL0804.007	08/06/08	carcass	M	620	575	1	3	5
KTUL0804.008	08/06/08	carcass	M	690	740	1	3	5
KTUL0804.009	08/07/08	carcass	M	635	610	1	3	5
KTUL0804.010	08/07/08	carcass	M	695	637	1	3	5
KTUL0804.011	08/08/08	carcass	M	610	570	1	3	5
KTUL0804.012	08/08/08	carcass	M	615	575	1	3	5
KTUL0804.014	08/08/08	carcass	M	620	600	1	3	5
KTUL0804.020	08/09/08	carcass	M	630	610	1	3	5
KTUL0804.026	08/10/08	carcass	m	605	570	1	3	5
KTUL0804.029	08/10/08	carcass	m	750	720	1	3	5
KTUL0804.030	08/10/08	carcass	m	645	605	1	3	5
KTUL0804.031	08/10/08	carcass	m	620	575	1	3	5
KTUL0804.033	08/11/08	carcass	m	635	600	1	3	5
KTUL0804.034	08/11/08	carcass	m	660	620	1	3	5
KTUL0804.037	08/11/08	carcass	f	640	620	1	3	5
KTUL0804.039	08/11/08	carcass	m	635	590	1	3	5
KTUL0804.040	08/11/08	carcass	m	610	580	1	3	5
KTUL0804.043	08/12/08	carcass	m	690	640	1	3	5
KTUL0804.047	08/12/08	carcass	m	675	625	1	3	5
KTUL0804.049	08/12/08	carcass	m	740	665	1	3	5
KTUL0804.050	08/12/08	carcass	m	660	610	1	3	5
KTUL0804.053	08/12/08	carcass	m	720	680	1	3	5
KTUL0804.057	08/12/08	carcass	m	660	630	1	3	5
KTUL0804.058	08/12/08	carcass	m	640	600	1	3	5
KTUL0804.059	08/13/08	carcass	m	675	635	1	3	5
KTUL0804.062	08/13/08	carcass	m	650	620	1	3	5
KTUL0804.066	08/14/08	carcass	M	715	615	1	3	5
KTUL0804.067	08/14/08	carcass	F	850	790	1	3	5
KTUL0804.068	08/14/08	carcass	F	710	670	1	3	5
KTUL0804.070	08/14/08	carcass	M	670	615	1	3	5
KTUL0804.072	08/14/08	carcass	M	650	585	1	3	5
KTUL0804.073	08/14/08	carcass	M	730	695	1	3	5
KTUL0804.074	08/14/08	carcass	m	685	635	1	3	5
KTUL0804.079	08/15/08	carcass	m	670	625	1	3	5
KTUL0804.080	08/15/08	carcass	m	640	590	1	3	5
KTUL0804.081	08/15/08	carcass	m	630	585	1	3	5
KTUL0804.082	08/15/08	carcass	m	690	640	1	3	5
KTUL0804.083	08/15/08	carcass	m	630	595	1	3	5
KTUL0804.085	08/16/08	carcass	m	720	660	1	3	5
KTUL0804.090	08/17/08	carcass	m	775	725	1	3	5
KTUL0804.101	08/17/08	carcass	m	760	690	1	3	5
KTUL0804.102	08/18/08	carcass	m	705	635	1	3	5
KTUL0804.106	08/18/08	carcass	m	690	635	1	3	5

Appendix 1. Sample data for the 2003 cohort. MEF and MEH are the length estimates to nearest 5 mm from the mid-eye to the fork of the caudal fin (MEF) and from the mid-eye to hypural plate (MEH). Freshwater (FW) and saltwater (SW) age were derived from scales (live samples) or otoliths (carcasses).

Sample ID	Date	live_carcass	Sex	MEF	MEH	FW age	SW age	Total age
KTUL0804.108	08/18/08	carcass	f	750	705	1	3	5
KTUL0804.109	08/18/08	carcass	f	820	780	1	3	5
KTUL0804.112	08/19/08	carcass	m	760	705	1	3	5
KTUL0804.113	08/19/08	carcass	m	640	585	1	3	5
KTUL0804.116	08/19/08	carcass	f	660	605	1	3	5
KTUL0804.117	08/19/08	carcass	m	665	625	1	3	5
KTUL0804.124	08/21/08	carcass	m	720	685	1	3	5
KTUL0804.127	08/23/08	carcass	m	665	615	1	3	5
KTUL0804.129	08/23/08	carcass	m	650	585	1	3	5
KTUL0804.130	08/23/08	carcass	f	780	740	1	3	5
KTUL0804.134	08/24/08	carcass	m	630	580	1	3	5
KTUL0901.003	07/04/09	live	m	790	680	1	4	6
KTUL0901.005	07/05/09	live	m	955	860	1	4	6
KTUL0901.009	07/06/09	live	m	690	660	1	4	6
KTUL0901.013	07/06/09	live	m	790	720	1	4	6
KTUL0901.015	07/07/09	live	f	830	765	1	4	6
KTUL0901.016	07/07/09	live	m	755	692	1	4	6
KTUL0901.017	07/07/09	live	f	936	836	1	4	6
KTUL0901.018	07/07/09	live	m	734	686	1	4	6
KTUL0901.025	07/10/09	live	f	879	815	1	4	6
KTUL0901.026	07/10/09	live	f	830	780	1	4	6
KTUL0901.028	07/10/09	live	f	1010	970	1	4	6
KTUL0901.029	07/11/09	live	F	910	835	1	4	6
KTUL0901.036	07/12/09	live	f	850	788	1	4	6
KTUL0901.039	07/12/09	live	f	845	778	1	4	6
KTUL0901.045	07/12/09	live	f	865	800	1	4	6
KTUL0901.049	07/12/09	live	m	550	512	1	4	6
KTUL0901.055	07/12/09	live	f	830	769	1	4	6
KTUL0901.057	07/12/09	live	f	903	837	1	4	6
KTUL0901.061	07/15/09	live	f	828	768	1	4	6
KTUL0901.062	07/15/09	live	f	825	775	1	4	6
KTUL0901.065	07/16/09	live	f	877	810	1	4	6
KTUL0901.067	07/16/09	live	f	880	813	1	4	6
KTUL0901.069	07/17/09	live	f	880	833	1	4	6
KTUL0901.070	07/17/09	live	m	647	602	1	4	6
KTUL0901.071	07/17/09	live	m	835	774	1	4	6
KTUL0901.072	07/17/09	live	f	778	727	1	4	6
KTUL0901.073	07/17/09	live	f	784	720	1	4	6
KTUL0901.076	07/17/09	live	f	720	650	1	4	6
KTUL0901.081	07/17/09	live	m	892	827	1	4	6
KTUL0901.083	07/17/09	live	f	890	820	1	4	6
KTUL0901.084	07/17/09	live	f	875	811	1	4	6
KTUL0901.088	07/17/09	live	f	836	776	1	4	6
KTUL0901.089	07/17/09	live	f	875	815	1	4	6
KTUL0901.092	07/17/09	live	m	845	775	1	4	6

Appendix 1. Sample data for the 2003 cohort. MEF and MEH are the length estimates to nearest 5 mm from the mid-eye to the fork of the caudal fin (MEF) and from the mid-eye to hypural plate (MEH). Freshwater (FW) and saltwater (SW) age were derived from scales (live samples) or otoliths (carcasses).

Sample ID	Date	live_carcass	Sex	MEF	MEH	FW age	SW age	Total age
KTUL0901.093	07/17/09	live	f	830	770	1	4	6
KTUL0901.095	07/17/09	live	f	905	835	1	4	6
KTUL0901.096	07/17/09	live	f	916	846	1	4	6
KTUL0901.097	07/17/09	live	f	875	815	1	4	6
KTUL0901.098	07/17/09	live	m	756	696	1	4	6
KTUL0901.110	07/19/09	live	f	870	800	1	4	6
KTUL0901.112	07/19/09	live	m	825	755	1	4	6
KTUL0901.114	07/20/09	live	F	920	847	1	4	6
KTUL0901.115	07/20/09	live	f	860	796	1	4	6
KTUL0901.116	07/20/09	live	m	820	762	1	4	6
KTUL0901.118	07/20/09	live	f	910	842	1	4	6
KTUL0901.120	07/20/09	live	f	870	810	1	4	6
KTUL0901.123	07/20/09	live	f	835	780	1	4	6
KTUL0901.129	07/21/09	live	f	867	805	1	4	6
KTUL0901.130	07/21/09	live	f	920	852	1	4	6
KTUL0901.133	07/22/09	live	f	900	840	1	4	6
KTUL0901.138	07/23/09	live	f	870	810	1	4	6
KTUL0901.141	07/23/09	live	f	884	815	1	4	6
KTUL0901.144	07/23/09	live	m	708	702	1	4	6
KTUL0901.148	07/24/09	live	m	735	675	1	4	6
KTUL0901.151	07/24/09	live	f	874	805	1	4	6
KTUL0901.163	07/25/09	live	f	810	753	1	4	6
KTUL0901.164	07/25/09	live	f	875	810	1	4	6
KTUL0901.165	07/25/09	live	m	740	685	1	4	6
KTUL0901.166	07/25/09	live	f	815	760	1	4	6
KTUL0901.167	07/25/09	live	f	844	755	1	4	6
KTUL0901.169	07/25/09	live	f	900	825	1	4	6
KTUL0901.177	07/27/09	live	m	804	750	1	4	6
KTUL0901.178	07/27/09	live	f	800	740	1	4	6
KTUL0901.181	07/28/09	live	F	849	779	1	4	6
KTUL0901.182	07/28/09	live	F	817	763	1	4	6
KTUL0901.188	07/28/09	live	F	880	815	1	4	6
KTUL0901.191	07/29/09	live	f	920	855	1	4	6
KTUL0901.193	07/29/09	live	f	828	763	1	4	6
KTUL0901.194	07/29/09	live	f	720	680	1	4	6
KTUL0901.197	07/29/09	live	m	810	790	1	4	6
KTUL0901.199	07/29/09	live	f	753	693	1	4	6
KTUL0901.201	07/29/09	live	f	832	772	1	4	6
KTUL0901.204	07/29/09	live	m	863	800	1	4	6
KTUL0901.205	07/29/09	live	f	820	760	1	4	6
KTUL0901.207	07/30/09	live	m	710	660	1	4	6
KTUL0901.208	07/30/09	live	m	623	592	1	4	6
KTUL0901.209	07/30/09	live	f	916	835	1	4	6
KTUL0901.210	07/30/09	live	f	832	767	1	4	6
KTUL0901.213	08/01/09	live	f	852	794	1	4	6
KTUL0901.214	08/01/09	live	f	874	810	1	4	6

Appendix 1. Sample data for the 2003 cohort. MEF and MEH are the length estimates to nearest 5 mm from the mid-eye to the fork of the caudal fin (MEF) and from the mid-eye to hypural plate (MEH). Freshwater (FW) and saltwater (SW) age were derived from scales (live samples) or otoliths (carcasses).

Sample ID	Date	live_carcass	Sex	MEF	MEH	FW age	SW age	Total age
KTUL0901.217	08/01/09	live	f	870	800	1	4	6
KTUL0901.218	08/01/09	live	f	870	800	1	4	6
KTUL0901.219	08/01/09	live	m	760	700	1	4	6
KTUL0901.220	08/01/09	live	f	800	720	1	4	6
KTUL0901.222	08/01/09	live	f	800	750	1	4	6
KTUL0901.223	08/01/09	live	f	970	900	1	4	6
KTUL0901.230	08/02/09	live	f	870	800	1	4	6
KTUL0901.233	08/03/09	live	f	870	800	1	4	6
KTUL0901.234	08/03/09	live	m	769	709	1	4	6
KTUL0901.238	08/03/09	live	f	900	835	1	4	6
KTUL0901.240	08/03/09	live	f	835	782	1	4	6
KTUL0901.241	08/03/09	live	m	820	750	1	4	6
KTUL0901.242	08/03/09	live	f	790	720	1	4	6
KTUL0901.243	08/04/09	live	f	823	762	1	4	6
KTUL0901.244	08/04/09	live	f	850	772	1	4	6
KTUL0901.248	08/05/09	live	f	900	830	1	4	6
KTUL0901.251	08/05/09	live	f	860	792	1	4	6
KTUL0901.253	08/06/09	live	f	850	785	1	4	6
KTUL0902.001	08/04/09	carcass	f	890	830	1	4	6
KTUL0902.009	08/08/09	carcass	f	847	800	1	4	6
KTUL0902.010	08/08/09	carcass	f	905	850	1	4	6
KTUL0902.011	08/08/09	carcass	f	952	890	1	4	6
KTUL0902.012	08/08/09	carcass	f	914	850	1	4	6
KTUL0902.014	08/08/09	carcass	f	888	830	1	4	6
KTUL0902.015	08/08/09	carcass	m	850	800	1	4	6
KTUL0902.016	08/08/09	carcass	f	804	765	1	4	6
KTUL0902.021	08/10/09	carcass	m	960	895	1	4	6
KTUL0902.026	08/12/09	carcass	f	850	810	1	4	6
KTUL0902.028	08/12/09	carcass	f	865	825	1	4	6
KTUL0902.029	08/12/09	carcass	f	840	790	1	4	6
KTUL0902.044	08/15/09	carcass	m	715	653	1	4	6
KTUL0902.045	08/15/09	carcass	f	790	735	1	4	6
KTUL0902.047	08/15/09	carcass	f	825	775	1	4	6

Appendix 2. Sample data for the candidate parents from the 2003 adult return. MEF is the length estimate to nearest 5 mm from the mid-eye to the fork of the caudal fin. Freshwater (FW) and saltwater (SW) age were derived from scales.

Sample ID	Sex	MEF	FW age	SW age	Total age	BY
ktul0310.001	F	855	1	5	7	1996
ktul0310.003	M	495	1	2	4	1999
ktul0310.004	F	905	1	4	6	1997
ktul0310.005	F	960	1	5	7	1996

Appendix 2. Sample data for the candidate parents from the 2003 adult return. MEF is the length estimate to nearest 5 mm from the mid-eye to the fork of the caudal fin. Freshwater (FW) and saltwater (SW) age were derived from scales.

Sample ID	Sex	MEF	FW age	SW age	Total age	BY
ktul0310.006	M	850	1	4	6	1997
ktul0310.007	F	850	1	4	6	1997
ktul0310.008	M	500	1	2	4	1999
ktul0310.009	M	740				
ktul0310.010	F	960	1	5	7	1996
ktul0310.011	M	710	1	4	6	1997
ktul0310.012	M	525	1	2	4	1999
ktul0310.013	F	775	1	3	5	1998
ktul0310.014	F	760	1	4	6	1997
ktul0310.015	F	815	1	3	5	1998
ktul0310.016	F	740	1	3	5	1998
ktul0310.017	M	775	1	4	6	1997
ktul0310.018	M	585	1	3	5	1998
ktul0310.019	M	655	1	3	5	1998
ktul0310.020	M	685	1	3	5	1998
ktul0310.021	M	540	1	2	4	1999
ktul0310.022	M	555	1	3	5	1998
ktul0310.023	M	705	1	3	5	1998
ktul0310.024	F	850	1	4	6	1997
ktul0310.027	M	650	1	3	5	1998
ktul0310.028	M	780	1	4	6	1997
ktul0310.029	M	540	1	2	4	1999
ktul0310.030	M	505	1	2	4	1999
ktul0310.031	F	840	1	4	6	1997
ktul0310.032	F	940	1	4	6	1997
ktul0310.033	F	885	1	4	6	1997
ktul0310.034	M	720	1	3	5	1998
ktul0310.036	M	520	1	2	4	1999
ktul0310.037	F	845	1	4	6	1997
ktul0310.038	F	905	1	4	6	1997
ktul0310.039	F	820	1	5	7	1996
ktul0310.040	M	530	1	2	4	1999
ktul0310.041	M	595	1	3	5	1998
ktul0310.042	M	460				
ktul0310.043	M	730	1	3	5	1998
ktul0310.044	M	685	1	3	5	1998
ktul0310.045	M	510	1	2	4	1999
ktul0310.046	F	715	1	3	5	1998
ktul0310.047	F	735	1	3	5	1998
ktul0310.048	F	855				
ktul0310.049	M	745	1	4	6	1997
ktul0310.050	F	865	1	5	7	1996
ktul0310.051	F	765	1	3	5	1998
ktul0310.052	M	680	1	3	5	1998
ktul0310.053	F	795	1	3	5	1998
ktul0310.054	F	875	1	4	6	1997

Appendix 2. Sample data for the candidate parents from the 2003 adult return. MEF is the length estimate to nearest 5 mm from the mid-eye to the fork of the caudal fin. Freshwater (FW) and saltwater (SW) age were derived from scales.

Sample ID	Sex	MEF	FW age	SW age	Total age	BY
ktul0310.055	F	860	1	4	6	1997
ktul0310.056	M	890	1	3	5	1998
ktul0310.057	M	535	1	2	4	1999
ktul0310.058	F	830	1	4	6	1997
ktul0310.059	M	640	1	3	5	1998
ktul0310.060	F	890	1	4	6	1997
ktul0310.061	M	520	1	2	4	1999
ktul0310.062	F	860	1	4	6	1997
ktul0310.063	M	710	1	3	5	1998
ktul0310.064	F	880	1	4	6	1997
ktul0310.065	M	745	1	3	5	1998
ktul0310.066	F	865	1	4	6	1997
ktul0310.067	F	850	1	4	6	1997
ktul0310.068	F	875	1	4	6	1997
ktul0310.069	M	725	1	3	5	1998
ktul0310.070	F	880	1	4	6	1997
ktul0310.071	F	860	1	4	6	1997
ktul0310.072	F	870	1	4	6	1997
ktul0310.073	M	790	1	3	5	1998
ktul0310.074	F	775	1	4	6	1997
ktul0310.075	M	855	1	3	5	1998
ktul0310.076	F	840	1	4	6	1997
ktul0310.077	F	845	1	4	6	1997
ktul0310.078	F	920	1	4	6	1997
ktul0310.079	F	900				
ktul0310.080	M	670	1	3	5	1998
ktul0310.081	M	720	1	3	5	1998
ktul0310.082	F	895	1	4	6	1997
ktul0310.084	F	815	1	4	6	1997
ktul0310.085	M	810	1	3	5	1998
ktul0310.086	F	840	1	4	6	1997
ktul0310.087	F	745	1	3	5	1998
ktul0310.088	F	990	1	4	6	1997
ktul0310.089	M	780	1	4	6	1997
ktul0310.090	M	705	1	3	5	1998
ktul0310.091	M	590	1	2	4	1999
ktul0310.092	F	920	1	4	6	1997
ktul0310.093	M	505	1	2	4	1999
ktul0310.094	M	760	1	3	5	1998
ktul0310.095	M	630				
ktul0310.096	M	830				
ktul0310.097	F	905	1	4	6	1997
ktul0310.098	M	545	1	2	4	1999
ktul0310.099	M	930	1	4	6	1997
ktul0310.100	M	495	1	2	4	1999
ktul0310.101	F	880	1	5	7	1996

Appendix 2. Sample data for the candidate parents from the 2003 adult return. MEF is the length estimate to nearest 5 mm from the mid-eye to the fork of the caudal fin. Freshwater (FW) and saltwater (SW) age were derived from scales.

Sample ID	Sex	MEF	FW age	SW age	Total age	BY
ktul0310.102	F	845	1	3	5	1998
ktul0310.104	F	940	1	5	7	1996
ktul0310.105	M	735				
ktul0310.106	M	550	1	2	4	1999
ktul0310.107	M	590	1	4	6	1997
ktul0310.108	F	830	1	4	6	1997
ktul0310.109	F	765	1	4	6	1997
ktul0310.110	F	890				
ktul0310.111	F	870	1	5	7	1996
ktul0310.112	M	595	1	2	4	1999
ktul0310.113	M	690	1	3	5	1998
ktul0310.114	M	655	1	3	5	1998