Y-chromosome haplotypes drive variation in size and age at maturity in male Chinook salmon

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ABSTRACT

Variation in size and age at maturity is an important component of life history in salmon that is influenced both by environmental and genetic factors. Large size confers a direct reproductive advantage through increased fecundity and egg quality in females, while larger males gain a reproductive advantage by monopolizing access to females. In addition, variation in size and age at maturity in males can be associated with different reproductive strategies; younger smaller males may gain reproductive success by sneaking in among mating pairs. In both sexes there is a trade-off between older age and increased reproductive success and increased risk of mortality by delaying reproduction. We used RADseq data for 21 populations of Alaska Chinook salmon (*Oncorhynchus tshawytscha*) and identified four Y-chromosome haplotypes that showed regional and population-specific variation in frequency. These haplotypes exhibited associations with size at maturity in multiple populations suggesting that the lack of recombination between X and Y-chromosomes have allowed Y-chromosome haplotypes to capture different alleles that influence size at maturity. Ultimately, conservation of life history diversity in Chinook salmon may require conservation of Y-chromosome haplotype diversity.

Introduction

Variation in life history within populations is common across taxa and is often associated with alternative strategies for increasing fitness. This includes partial migration, where some individuals of a population migrate while others remain resident (Chapman et al. 2011), reproductive morphs that exhibit different mating strategies or sexually selected traits (Shuster 1989, Johnston et al. 2013, Küpper et al. 2015), age and size at maturity (Gibbons et al. 1981), and even length of life-span such as annual vs perennial plants (Hall et al. 2006). While life history variation is often assumed to be under the influence of many genes of small effect, examples of a simpler genetic basis of life history variation are increasingly being found, such as single genes that influence age at maturity and sexually selected traits (Johnston et al. 2013, Barson et al. 2015) and chromosome inversions contributing to annual versus perennial live history and variation in migration (Pearse et al. 2014, Twyford and Friedman 2015). The mechanism underlying variation in life history has important implications for how life history diversity is maintained under different selective regimes.

Variation in life history strategies is exhibited by many salmon species with size and age at maturity being an important component of this variation. In females, large body size confers a direct reproductive advantage through increased fecundity and egg quality (Healey and Heard 1984). In contrast, variation in size and age at maturity in males can be associated with different reproductive strategies that exhibit frequency dependent fitness. For example, older larger males gain reproductive success by monopolizing access to females while younger smaller males gain reproductive success by sneaking in among mating pairs (Healey and Heard 1984, Berejikian et al. 2010). For both sexes, there is a trade-off to delayed maturation where increased reproductive success is tempered by an increased risk of mortality before reproduction. The optimal age at maturity for a population should represent the balance between reproductive benefits and mortality costs of delayed maturation (Healey 1986), and forces that change these costs or benefits could result in shifts in age composition. Nonetheless, considerable diversity in age at maturation is maintained within many populations, presumably as a bet-hedging strategy to spread risks over the life-cycle of these fish.

Age at maturity in salmon is generally thought to be a threshold trait that is dependent either upon reaching a minimum size at age or upon growth rate at key periods (Healey 1991, Thorpe 2007). Environmental factors that influence growth rate have been shown to influence age at maturity in multiple salmon species. In the wild, studies show correlations between ocean conditions such as temperature and productivity and patterns of age at maturity (Otero et al. 2012, Siegel et al. 2017). In experimental

settings, age at maturity was manipulated through changing temperature (Heath et al. 1994, Harstad et al. 2018) or food ration (Rowe and Thorpe 1990, Larsen et al. 2006).

In addition to environmental effects, multiple lines of evidence show a genetic component to age at maturity. Age at maturity is highly heritable in multiple salmon species (Gjerde 1984, Gall et al. 1988, Hankin et al. 1993, Heath et al. 1994), and Quantitative Trait Locus (QTL) and Genome-Wide Association (GWAS) studies identified genomic regions associated with variation in age at maturity (Barson et al. 2015, Kodama et al. 2018, Micheletti and Narum 2018, Waters et al. 2018). Studies also demonstrated that offspring of alternative male phenotypes exhibit different growth rates (Garant et al. 2002, Berejikian et al. 2011). In Atlantic salmon (*Salmo salar*), individuals with different life histories exhibit differing maturation thresholds that are genetically based (Aubin Horth and Dodson 2004). Despite these findings, the genetic basis of maturation age in most salmonids remains poorly understood.

One complicating factor is that the genetic architecture underlying variation in age at maturity appears to vary among salmonid species and even among populations within a species. In Atlantic salmon, age at maturity is strongly influenced by a single gene (VGLL3) (Ayllon et al. 2015, Barson et al. 2015). This gene exhibits sex-dependent dominance which facilitates sexually antagonistic selection (Barson et al. 2015). While this gene explained 39% of the phenotypic variability in European Atlantic salmon, studies in North American Atlantic salmon and in Pacific salmon have not found a similar association (Micheletti and Narum 2018, Boulding et al. 2019).

Chinook salmon (*Oncorhynchus tshawytscha*) are the largest of the Pacific salmon and follow various life history strategies spending 0 to 2 years in fresh water and 1 to 4 or more years in the ocean (Riddell et al. 2018). Male Chinook salmon exhibit significant variation in size and age at maturity (Healey 1991) that is linked to differential reproductive tactics and is likely controlled by both environmental and genetic components (i.e. sneaker vs. dominant males, Berejikian et al. 2010, Young et al. 2013). Historically, males predominantly matured at age four or older; however, many populations throughout North America recently experienced marked declines in size and age at maturity (Lewis et al. 2015, Ohlberger et al. 2018). Explanations for decreased age at maturity have focused on the impacts of fisheries induced evolution or changing environmental conditions (Hard et al. 2008, Kendall et al. 2014, Siegel et al. 2017) though this explanation is not particularly consistent with the data (Ohlberger et al. 2018). While the genetic control of age at maturity in Chinook salmon is still poorly understood, past studies offer clues to genomic regions that may be associated with maturation age. In particular, Heath et al. (2002) identified a strong sex-linked component to age at maturity in Chinook salmon, suggesting the influence of genes on the Y-chromosome.

The X and Y chromosomes in most salmonid species are morphologically undifferentiated (Davidson et al. 2009), and available sequence data suggests that the primary difference between sex chromosomes is an insertion containing the sex-determining gene (SDY, Yano et al. 2013). Despite a lack of large-scale differentiation, the X- and Y-chromosomes could show sequence divergence due to sex-specific patterns of recombination. Recombination in females takes place along the full length of the chromosome while recombination in males is strongly localized to telomeric regions (Lien et al. 2011), restricting recombination between the X- and Y-chromosomes. Reduced recombination between sex chromosomes is supported by a 33Mb signal of sex association observed in Atlantic salmon (Kijas et al. 2018). In addition to facilitating divergence between sex chromosomes, sex-specific recombination could lead to the formation of different Y-chromosome haplotypes and the capture of adaptive genetic variants.

We identified four Y-chromosome haplotypes in Chinook salmon from Alaska that showed regional and population-specific variation in frequency. These haplotypes showed associations with size at maturity in multiple populations suggesting that the lack of recombination between X and Y-chromosomes has allowed Y-chromosome haplotypes to capture different genetic variants influencing size and age at maturity.

Materials and Methods

RAD Y-chromosome Haplotypes

We used existing RADseq data to examine patterns of genetic variation in the sex chromosome. RADseq data for 21 populations of Alaska Chinook salmon were obtained from previous studies (Larson et al. 2014, Dann et al. 2018, McKinney et al. 2018, McKinney et al. In Revision). RADseq data from Larson et al. (2014) and McKinney et al. (2018) are available in NCBI SRA accessions SRP034950 and SRP129894; raw data from Dann et al. (2018) and McKinney et al. (In Revision) are available from those authors upon request. Locations of populations ranged from Cook Inlet to the Upper Yukon River and include a total of 1,082 samples (Table 1). RADseq data were processed with Stacks V1.7 (Catchen et al. 2011, Catchen et al. 2013) using default settings with the following exceptions: process_radtags (-c -r -q -filter_illumina -t 94), ustacks (-m 2 -M 2, --model_type bounded --bound_high 0.05), cstacks (-n 2). The catalog of variation from McKinney et al. (In Revision) was used for consistent locus names among this and previous studies. A total of six individuals per population from Cook Inlet were added to this catalog to allow for additional allelic variation.

Paralogs are common in salmonid genomes due to an ancestral whole-genome duplication (Allendorf and Thorgaard 1984) but cannot be reliably genotyped in typical RADseq studies because of insufficient read depth (McKinney et al. 2018). Paralogs were identified using *HDplot* (McKinney et al. 2017) and removed from further analysis. Loci with more than 10% missing data and a minor allele frequency (MAF) < 0.05 were also removed from analysis. Finally, loci were aligned to the Chinook salmon genome (Christensen et al. 2018) using Bowtie2 (Langmead and Salzberg 2012) to determine genomic position; only loci that aligned to the sex chromosome (Ots17, Phillips et al. 2013) were retained for analysis.

Patterns of variation on the sex chromosome were visualized using principal component analysis (PCA). Clusters of samples on the PCA were identified visually; markers that differentiated clusters of samples were identified by estimating F_{ST} per marker between clusters using Genepop (Rousset 2008). Markers that differentiated clusters showed high linkage disequilibrium (LD) within clusters, suggesting inhibited recombination and exhibited genotype patterns consistent with Y-chromosome haplotypes. Full details are available in supplemental materials and methods (File S1).

Markers that differentiated clusters and appeared to be diagnostic for Y-chromosome haplotypes were made into an amplicon panel (GT-seq , Campbell et al. 2015) for expanded sampling. Markers that were unlikely to amplify single genomic regions were filtered prior to primer design following the methods of McKinney et al. (In Revision). Primers were designed using batch primer3 (You et al. 2008), and genome sequences were used to extend the original RAD sequence for primer design where necessary.

Expanded sampling

Additional samples ranging from Alaska to California were genotyped using the GT-seq panel to establish the geographic distribution of the haplotypes. In addition to the Y-haplotype markers, this panel included the sex identification marker Ots_sexy3-1 (Hess et al. 2016a) to confirm that Y-chromosome haplotypes were present only in male fish. A total of 1,341 samples from 27 populations were genotyped (Table 1). Samples were sequenced on a HiSeq 4000, and data were processed and genotyped using GT-score (McKinney et al. In Revision) available at https://github.com/gjmckinney/GTscore.

Y-chromosome haplotype analyses

Y-chromosome haplotype assignments were combined for GT-seq and RADseq samples to characterize the distribution and frequency of Y-chromosome haplotypes. Haplotypes were assigned to each sample based on multi-locus genotype patterns (File S1). Data for length and age at maturity were obtained from Alaska Department of Fish and Game (ADFG) for populations in Alaska and compared

with Y-chromosome haplotype data to determine if there were relationships between Y-chromosome haplotype and length and age at maturity. Significance of associations between Y-chromosome haplotypes and length were assessed using a Tukey test while significance of associations between Y-chromosome haplotypes and age at maturity were assessed using a chi-square test. There are multiple methods of reporting age in salmon (Koo 1962); we report freshwater and ocean age for each individual using European notation, so an individual with an age of 1.3 would have spent 1 year growing in freshwater after emergence followed by 3 years in the ocean for a total age of 5 years.

Results

RADseq Y-haplotype discovery

Analysis of the Y-chromosome showed multiple patterns consistent with Y-chromosome haplotype blocks. Individuals resolved into multiple distinct clusters when PCA was done on the sex chromosome (Figure S1-S3). Samples showed clustering by region (Cook Inlet vs Western Alaska) and also clustering by sex with multiple clusters of male samples (Figure S4). Some putative females were present in male clusters and vice versa; however, individuals had been visually sexed based on external features which is known to have variable accuracy (Lozorie and McIntosh 2014). Ranking loci by F_{ST} and examining genotype patterns revealed a set of 50 SNPs with $F_{ST} > 0.15$ that differentiated clusters (Table S2.1). A general pattern was observed for loci with high F_{ST} among clusters; within each region one cluster contained samples that were homozygous for a single allele for all high F_{ST} loci while the other clusters showed a pattern of high to fixed heterozygosity for different sets of high F_{ST} loci. In Cook Inlet, the homozygous cluster contained phenotypic females while heterozygous clusters contained phenotypic males (Figure S4). A total of four different patterns of fixed heterozygosity were observed throughout Yukon River, Western Alaska, and Cook Inlet populations suggesting the presence of conserved Y-chromosome haplotype blocks throughout western and southcentral Alaska (Figures 1, S5, S6). Within Alaska, Y-chromosome haplotypes showed regional variation in frequency with the AK Y1 haplotype being most frequent in Western Alaska and the AK Y3 haplotype the most frequent in Cook Inlet (Figure 2).

GT-seq Y-chromosome haplotype expanded sampling

A GT-seq panel was developed to genotype Y-chromosome haplotype markers for a set of samples representing the North American range of Chinook salmon. A total of 23 of the 50 RAD loci passed filtering criteria prior to primer design; of these 14 RAD loci were successfully converted to GT-seq assays (Table S1, Table S2.2). Genotyping of the expanded sample set confirmed that Y-chromosome haplotypes were sex-specific; 200 (81%) of the genetic males from Alaska were assigned a

Y-chromosome haplotype and no genetic females had genotype patterns consistent with the Y-chromosome haplotype blocks (Table S2.2). Males that were not assigned Y-chromosome haplotypes were concentrated in Southeast Alaska; 40 of the 46 unassigned males were from the Little Port Walter and Pullen Creek populations. Only 16% of males could be assigned a haplotype in Little Port Walter and a single male from Pullen Creek could be assigned a haplotype. Excluding these two populations results in 97% haplotype assignment of male Chinook salmon in Alaska. For the remaining six unassigned males, four were ambiguous for AK Y2 vs AK Y3 haplotypes and two were homozygous for all Y-chromosome haplotype markers. Distribution of Y-chromosome haplotypes varied regionally: Y-chromosome haplotype blocks identified in Alaska were not found in Chinook salmon outside of Western and Southcentral Alaska and had only a rare occurrence in Southeast Alaska.

Size and Age at Maturity

Size at maturity data were available for eight of the populations in this study; four populations were genotyped using RADseq data, three were genotyped using GT-seq data, and one was genotyped using both RADseq and GT-seq. Populations were grouped by region (Yukon River, Western Alaska, and Cook Inlet) for visualization. Boxplots of size at maturity for each Y-chromosome haplotype showed a consistent relationship throughout western and southcentral Alaska. The AK Y1 and AK Y2 haplotypes had the smallest individuals, the AK Y3 haplotype was associated with intermediate sized fish, and the AK Y4 haplotype was associated with the largest individuals in each region (Figure 3). In the Yukon River, individuals with the AK Y4 haplotype were significantly larger ($p<0.05$) than fish with the AK Y1 or AK Y2 haplotype, in Western Alaska, the fish with the AK Y3 haplotype were significantly larger fish than the AK Y1 haplotype, and in Cook Inlet, size differences between the AK Y1, AK Y3, and AK Y4 haplotypes were statistically significant ($p<0.05$) (Figure 3). Despite a tendency for differences in size distributions, the length of fish with the AK Y1 haplotype was not significantly different than the AK Y3 haplotype in the Yukon River, and the AK Y4 haplotype was not significantly different than other haplotypes in Western Alaska. This is likely due to low samples size for these haplotypes.

Age at maturity data were available for the Lower Yukon Test Fishery. Histograms of age at maturity for each Y-chromosome haplotype revealed that the AK Y3 haplotype had approximately three times as many 1.3 fish as 1.4 fish while the Y4 haplotype had nearly even proportions of 1.3 and 1.4 fish (Figure 4). While suggestive, this result was not significant, possibly due to the low samples size both of age 1.4 fish and of fish with the AK Y4 haplotype. Boxplots of size at age showed that fish with the AK Y4 haplotype were larger for age 1.3 and 1.4 than fish with the AK Y3 haplotype. Results were statistically significant for age 1.3 fish but not age 1.4, possibly due to low sample size. The smallest fish

had the AK Y1 and AK Y2 haplotypes; however, only a single fish had both size and age data for these haplotypes.

Discussion

Size and age at maturity are ecologically and evolutionarily important traits in Chinook salmon. Numerous studies have examined ongoing declines in age at maturity; however, it has been difficult to disentangle the interactions of environmental and genetic causes of this decline. Size and age associated markers and genes have previously been identified in genetic studies of Chinook salmon (Micheletti and Narum 2018, Waters et al. 2018); however, results were not consistent across populations, and no markers were located on the sex chromosome. We show that a conserved set of Y-chromosome haplotypes is associated with variation in size and age at maturity in Chinook salmon across Western and Southcentral Alaska. This observation opens a new line of research into the genetics of age at maturity in salmonids.

Range-wide distribution of haplotypes

Chinook salmon are represented by multiple genetically distinct lineages throughout the species range (Waples et al. 2004, Beacham et al. 2006, Moran et al. 2012). These lineages often show little gene flow among them due to differences in geographic range or spawn timing, and this isolation may result in different sets of Y-chromosome haplotypes and patterns of recombination across lineages. The Y-chromosome haplotypes we identified through extended linkage disequilibrium were consistently observed throughout Chinook salmon populations from the Upper Yukon River south to Little Port Walter in Southeast Alaska. The occurrences become rarer in Southeast Alaska, and no individuals south of Southeast Alaska could be assigned haplotypes suggesting that the haplotypes identified within Alaska are regionally restricted. This corresponds with observed breakpoints between Chinook salmon lineages near Cape Fairweather (Templin et al. 2011) which is approximately 200 miles northwest of Little Port Walter and 100 miles west of Pullen Creek. It is likely that other haplotype blocks and genomic regions of low recombination exist outside of Alaska; this could be determined by examining reduced-representation or whole-genome sequence data from additional populations.

Populations throughout Alaska showed variation in haplotype frequency which may be ecologically significant given the association between haplotypes and size and age at maturity. Populations from Western Alaska and the Lower Yukon River had a greater proportion of the AK Y1 and AK Y2 haplotypes which were associated with smaller fish. Populations in the Upper Yukon River and Cook Inlet were primarily composed of AK Y3 and AK Y4 haplotypes which were associated with larger fish. While we did not have enough samples with size data to characterize size distributions within region, this finding is consistent with a long-term analysis of Chinook salmon returns by Lewis et al.

(2015) who reported smaller fish on average in Kuskokwim and Nushagak river populations from Western Alaska relative to Yukon River and Cook Inlet populations. In addition, the Cook Inlet populations sampled in this study are adjacent to the Kenai River which has historically produced large Chinook salmon (Lewis et al. 2015, Schoen et al. 2017). The relationship between size and haplotype also varied by region, with the Yukon River having the smallest difference in sizes between haplotypes and Cook Inlet having the largest difference in sizes (Figure 3). Taken together, these results suggest that differing frequencies of Y-chromosome haplotypes may contribute to regional variation in size of Chinook salmon, and that the effect of haplotype on size can vary between regions, potentially due to other genetic influence or different environmental conditions.

Importance of Y-haplotypes for life history diversity

Male Chinook salmon exhibit life history diversity related to maturation age with dominant males successfully spawning by monopolizing access to females and jacks obtaining reproductive success by sneaking in among mating pairs. This diversity has been eroding as the proportion of dominant (age 4+) males declines and jacks (3 years or younger) increase in frequency (Ohlberger et al. 2018). The alternate life histories of male Chinook salmon exhibit frequency dependent fitness which in theory should exhibit stable proportions; however, this assumes populations are at equilibrium. Male sockeye salmon (*Oncorhynchus nerka*) exhibit similar frequency dependent life history variation but persistent demographic variation occurs as a result of strong selection events coupled with variation in recruitment (DeFilippo et al. 2019). If jacks are produced by specific Y-chromosome haplotypes, then fishing practices that increase the proportion of jacks may result in demographic shifts and loss of age diversity that are difficult to recover. The markers we developed can be used to characterize historic (i.e., from archived samples) and current Y-chromosome haplotype diversity in Alaska Chinook salmon to determine if demographic shifts correspond with shifts in frequencies of Y-chromosome haplotypes. Ultimately, conservation of life history diversity in Chinook salmon may require conservation of Y-chromosome haplotype diversity.

Hypotheses of population structure and delineation of management units using genetic data are typically based on genome-wide analyses consistent with the assumption that major life history traits are controlled by many genes with small effects. Waples and Lindley (2018) recently commented on the new challenges facing existing conservation frameworks when associations are identified between one or a very few genes and key life history traits. Their comment was prompted by the recent identification of SNPs from a GREB1L gene that explain a large proportion of the variation associated with adult migration time in steelhead (*O. mykiss*) and Chinook salmon (Hess et al. 2016b, Prince et al. 2017). Conservation of the Y-chromosome haplotype shares similar challenges to the GREB1L situation.

Waples and Lindley (2018) pose a series of key questions to help provide an informed basis for decisions or management actions. Among other key questions, they argue that a full understanding of the distribution of the variation in space and time is needed and that investigations into the genes and mechanisms responsible for the life history variation should be initiated. In the case of the Y-haplotypes, additional questions exist such as: whether the specific allelic variants at these SNP loci are important or is the strong linkage disequilibrium among loci a signal from other adaptive genes in these regions; do haplotype blocks exhibit consistent phenotypes in different environments and with different genetic backgrounds; and if haplotype blocks are found in other regions of the Chinook salmon range do they function in a similar manner to those suggested by the results of this study.

Conclusion

We identified Y-chromosome haplotypes that are associated with size, and likely age, at maturity in Chinook salmon throughout Alaska. These haplotypes were restricted to northern Alaska Chinook salmon where the most diversity in age-at-maturity exists, and likely represent a subset of the total diversity across the species range. Interestingly, this region holds the most stable populations of Chinook salmon in the Northeast Pacific (Griffiths et al. 2014), possibly due to the bet-hedging benefits of diversity in age at maturity. It is possible that each Chinook salmon lineage has a specific set of haplotypes and relationships between haplotypes and size/age at maturity may differ by lineage. The discovery of Y-chromosome haplotypes and their potential effect on life history variation in Chinook salmon may help understand the causes and consequences of the recent declines in size and age of adult Chinook salmon, trends that are most pronounced in the region with the highest haplotype diversity. Ongoing efforts to understand the causes of these declines point to a size-specific mortality filter on maturing fish, but also requires an unknown evolutionary basis (Ohlberger et al. In Review). The results presented here point to such a mechanism for the genetic control of changes in size-at-age and age-at-maturity in Chinook salmon, as future changes in environmental conditions and selective fishing will lead to further demographic responses in this economically and ecologically important species

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Data Accessibility

GT-seq data is available in NCBI SRA XXXXXXXXXX.

Supporting Information

File S1: Supplementary materials, methods, and results for identification and characterization of Y-chromosome haplotypes.

Table S1: Primer and probe sequence for GT-seq loci that were used for expanded genotyping of Y-chromosome haplotypes.

Table S2.1: F_{ST}, F_{IS}, and allele frequencies for RAD loci associated with differentiation between clusters in RADseq data.

Table S2.2: Genotypes for loci successfully developed into GT-seq. Genotypes are included for all samples, RADseq and GT-seq.

Tables and Figures

Table 1. Populations used for Y-chromosome haplotype identification. RADseq samples were used for haplotype discovery while GT-seq samples were used to confirm that haplotypes were male-specific and to examine the geographic distribution of haplotypes. For populations with both RADseq and GT-seq samples, samples sizes for RADseq are given first. Frequency of Y-chromosome haplotypes are given for populations in Alaska; Y-chromosome haplotypes could not be assigned outside of Alaska.

Map Number	Population	Data Type	Region	Lat	Lon	N	AK Y1	AK Y2	AK Y3	AK Y4
1	Big Salmon River	RADseq	Yukon River	61.87	-134.92	49	0.00	0.00	0.79	0.21
2	Kantishna River	GT-seq	Yukon River	64.76	-149.97	48	0.00	0.00	1.00	0.00
3	Lower Yukon Test Fishery	GT-seq	Yukon River	62.79	-164.81	95	0.04	0.02	0.75	0.19
4	Anvik River	RADseq	Yukon River	62.68	-160.21	56	0.40	0.08	0.48	0.04
5	Tubutulik River	RADseq	Western Alaska	64.74	-161.89	56	0.39	0.48	0.10	0.03
6	Necons River	RADseq	Western Alaska	61.10	-153.85	47	0.11	0.05	0.21	0.63
7	George River	RADseq/GT-seq	Western Alaska	61.90	-157.71	48/47	0.16	0.05	0.38	0.41
8	Kogrukluk River	RADseq	Western Alaska	60.84	-157.85	59	0.58	0.21	0.13	0.08
9	Aniak River	RADseq	Western Alaska	61.06	-159.18	47	0.15	0.54	0.23	0.08
10	Kisaralik River	RADseq	Western Alaska	60.86	-161.24	48	0.64	0.27	0.09	0.00
11	Kwethluk River	RADseq	Western Alaska	60.81	-161.45	47	0.26	0.41	0.30	0.04
12	Kanektok River	RADseq/GT-seq	Western Alaska	59.75	-161.93	48/47	0.29	0.25	0.45	0.00
13	Arolik River	RADseq	Western Alaska	59.69	-161.88	48	0.33	0.11	0.48	0.07
14	Goodnews River	RADseq	Western Alaska	59.25	-161.36	47	0.14	0.10	0.43	0.33
15	Togiak River	RADseq	Western Alaska	59.09	-160.37	48	0.21	0.05	0.63	0.11
16	Iowithla River	RADseq	Western Alaska	59.18	-158.06	48	0.19	0.06	0.65	0.10
17	Stuyahok River	RADseq	Western Alaska	59.68	-156.17	48	0.23	0.19	0.35	0.23
18	Koktuli River	RADseq	Western Alaska	59.94	-156.43	56	0.29	0.21	0.38	0.12
19	Karluk River	GT-seq	Western Alaska	57.57	-154.38	48	0.00	0.00	1.00	0.00
20	Montana Creek	GT-seq	Southcentral Alaska	62.18	-149.95	48	0.23	0.00	0.31	0.46
21	Chuitna River	RADseq	Southcentral Alaska	61.20	-151.66	57	0.10	0.03	0.76	0.10
22	Sucker Creek	RADseq	Southcentral Alaska	61.51	-150.83	57	0.06	0.00	0.88	0.06
23	Talachulitna River	RADseq	Southcentral Alaska	61.62	-151.15	57	0.09	0.04	0.65	0.22
24	Theodore Creek	RADseq	Southcentral Alaska	61.49	-151.09	56	0.10	0.03	0.84	0.03
25	Coal Creek	RADseq	Southcentral Alaska	61.62	-151.76	55	0.00	0.00	0.67	0.33
26	Pullen Creek*	GT-seq	Southeast Alaska	59.45	-135.32	48	0.00	0.00	1.00	0.00
27	Little Port Walter-Unuk River stock**	GT-seq	Southeast Alaska	56.09	-131.06	48	0.00	0.00	0.00	1.00
-	Harrison River	GT-seq	British Columbia	49.28	-121.92	48	NA	NA	NA	NA
-	Big Qualicum Hatchery	GT-seq	British Columbia	49.40	-124.62	48	NA	NA	NA	NA
-	Kitwanga River	GT-seq	British Columbia	55.10	-128.09	48	NA	NA	NA	NA
-	Kitsumkalum River	GT-seq	British Columbia	54.52	-128.66	48	NA	NA	NA	NA
-	Morice River	GT-seq	British Columbia	54.41	-126.75	48	NA	NA	NA	NA
-	Rapid River Hatchery	GT-seq	Idaho	45.35	-116.40	48	NA	NA	NA	NA
-	McCall Fish Hatchery South Fork Salmon River	GT-seq	Idaho	44.67	-115.71	48	NA	NA	NA	NA
-	Marblemount Fish Hatchery	GT-seq	Washington	48.52	-121.42	48	NA	NA	NA	NA
-	Soos Creek Hatchery	GT-seq	Washington	47.31	-122.16	48	NA	NA	NA	NA
-	Columbia River at Wells Hatchery	GT-seq	Washington	47.95	-119.87	48	NA	NA	NA	NA
-	Quinault Lake Pens	GT-seq	Washington	47.47	-123.89	48	NA	NA	NA	NA
-	Lyons Ferry Hatchery	GT-seq	Washington	46.59	-118.22	48	NA	NA	NA	NA
-	Wenatchee River at Tumwater Dam	GT-seq	Washington	47.61	-120.72	48	NA	NA	NA	NA
-	Spring Creek Hatchery	GT-seq	Washington	45.73	-121.55	48	NA	NA	NA	NA
-	Rock Creek, Umpqua River	GT-seq	Oregon	43.34	-123.00	48	NA	NA	NA	NA
-	Cole River Hatchery, Rogue River	GT-seq	Oregon	42.66	-122.69	48	NA	NA	NA	NA
-	Cedar Creek Hatchery	GT-seq	Oregon	45.22	-123.84	48	NA	NA	NA	NA
-	McKenzie Hatchery	GT-seq	Oregon	44.11	-122.68	48	NA	NA	NA	NA
-	Coleman National Fish Hatchery	GT-seq	California	40.40	-122.14	48	NA	NA	NA	NA

*Only one male from Pullen Creek was assigned a Y-chromosome haplotype. **Only four out of 20 males from Little Port Walter Unuk River Stock were assigned a Y-chromosome haplotype.

Figure 1. Plot of genotype patterns for loci successfully developed into GT-seq assays for Y-chromosome haplotype identification. The position of each marker along the Y-chromosome is shown by vertical lines. The heatmap shows individual genotypes color-coded for homozygous (0), heterozygous (1) and alternate homozygous (2). Samples are grouped by assigned haplotype on the Y-axis, with each row representing an individual fish. This plot includes samples genotyped with RADseq and with GT-seq. The AK Y1, AK Y2, and AK Y3 haplotypes share a common set of core markers up to ~6Mb but vary in markers with extended linkage. The AK Y4 haplotype is fixed for alternate alleles for a unique set of markers. Females exhibit two distinct genotype patterns for these SNPs, either nearly fixed homozygosity for most markers or the presence of all three possible genotypes.

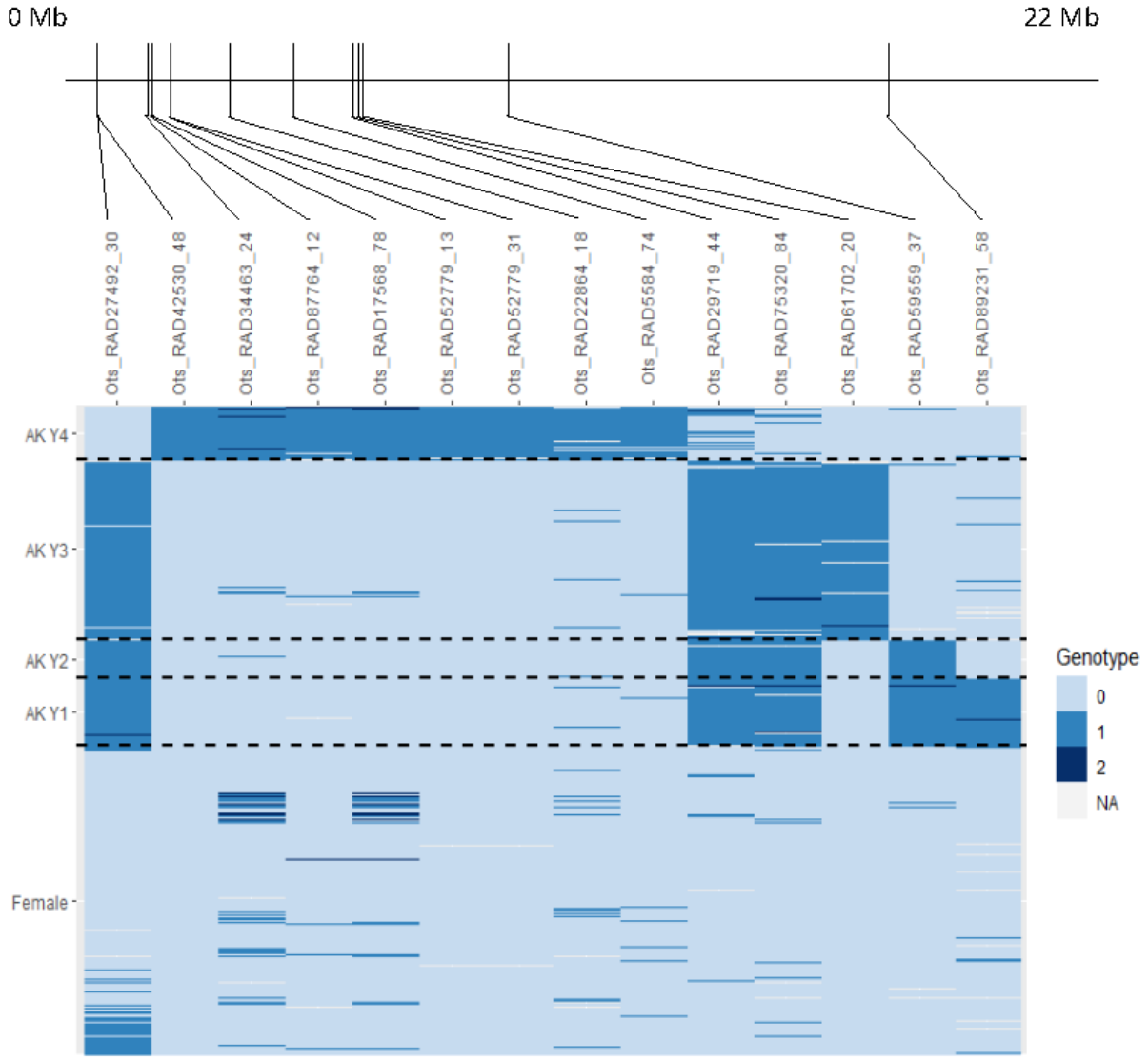


Figure 2. Frequency of Y-chromosome haplotypes throughout Alaska. Locations of populations are approximate to prevent overlap of pie charts. Population names are given in Table 1. Note that the location for the Lower Yukon Test Fishery (population 3) indicates where fish were caught on their return to the Yukon River and that these samples may represent fish from throughout the Yukon River.

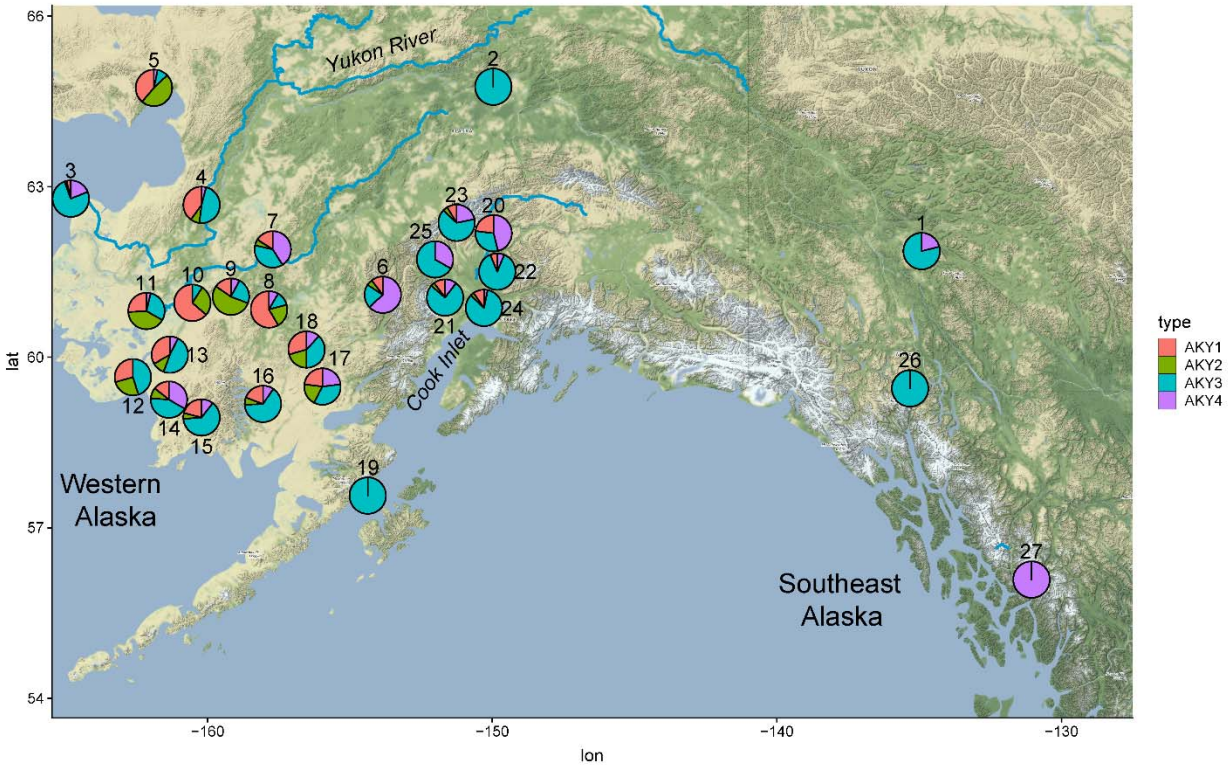
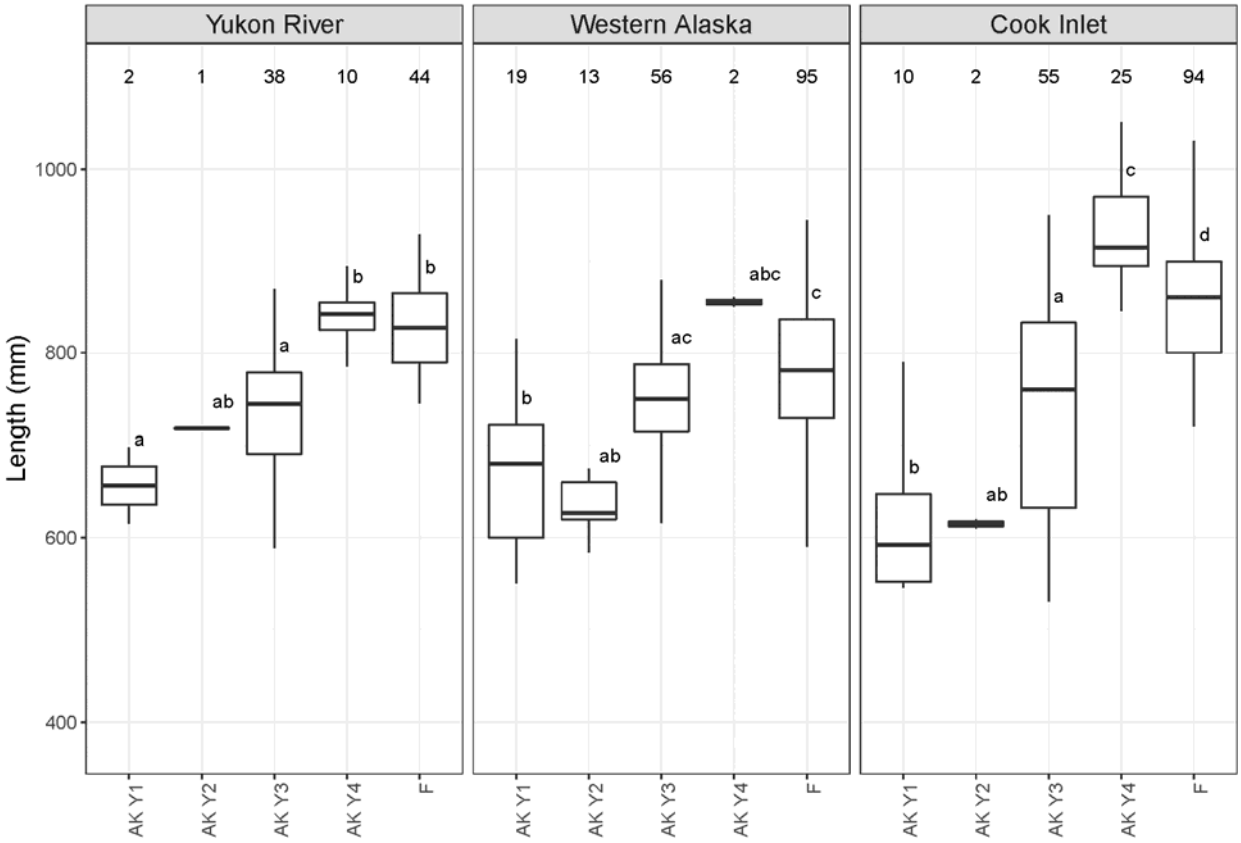


Figure 3. Distribution of size at maturity for each Y-chromosome haplotype for Alaska Chinook salmon. Female (F) size at maturity is included for comparison. Samples sizes for each haplotype are given above the boxplots. Within each region, Y-chromosome haplotypes with statistically different lengths are represented by different letters. Haplotypes with two letters (i.e., ab) do not have statistically different size distributions from haplotypes with a or b.



376 Figure 4. Distribution of A) age at maturity and B) size at age for each Y-chromosome haplotype in the
377 Yukon River. Within each age class, Y-chromosome haplotypes with statistically different lengths are
378 represented by different letters. Sample sizes for each haplotype are given above the boxplots.

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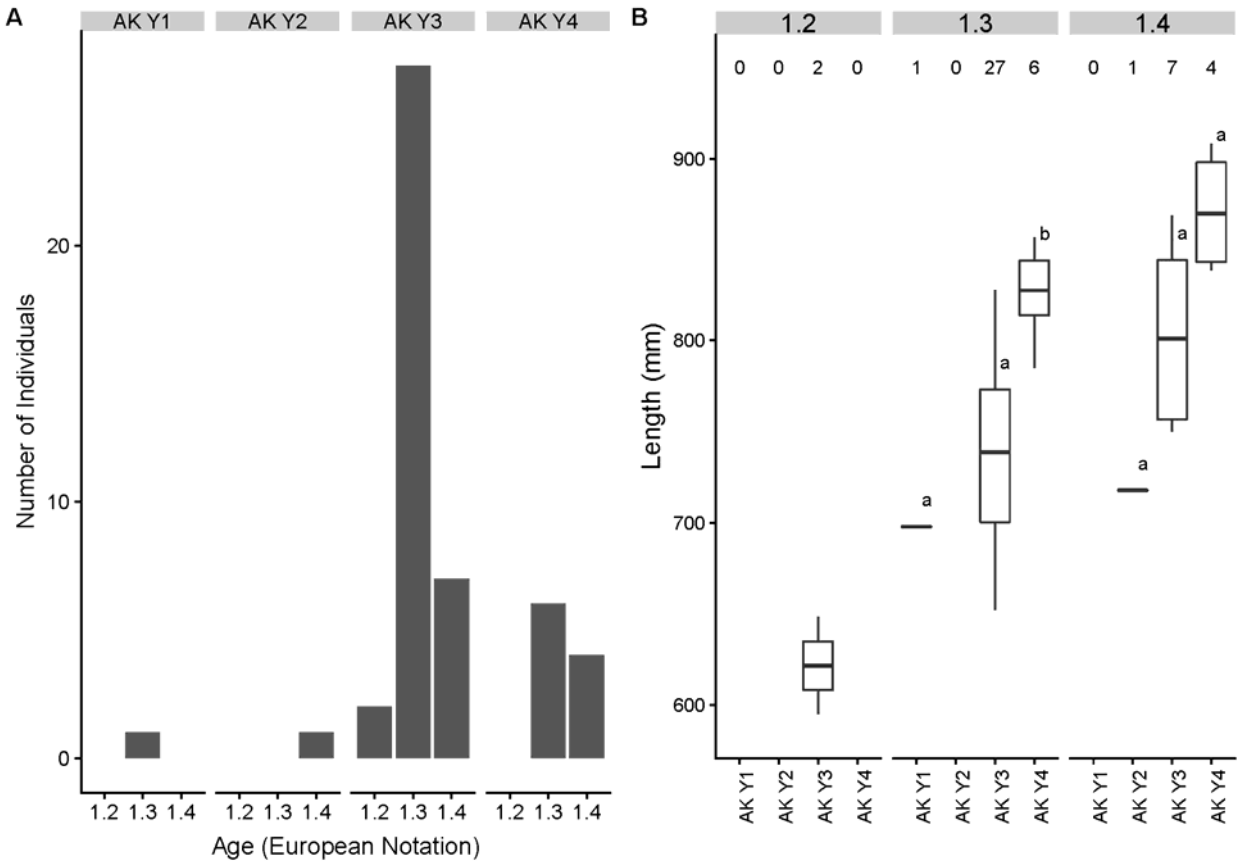

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