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GENETIC DIVERSITY OF WILLAMETTE RIVER SPRING CHINOOK SALMON POPULATIONS

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Summary

In this study, we used multilocus microsatellite genotype data from 813 spring Chinook salmon *Oncorhynchus tshawytscha* to investigate patterns of genetic diversity within and among wild and hatchery populations from the Willamette River and Catherine Creek (Grande Ronde River, Oregon). We found that hatchery populations from the Willamette River presented higher heterozygosities than local wild populations, though no pattern was found for allelic richness. An analysis of genetic divergence (θ) revealed little or no differentiation between hatchery and local wild populations within Willamette River subbasins. However, we observed weak but statistically significant structure among most Willamette River subbasins.

Phylogenetic analyses of Willamette River populations further indicated that hatchery populations are most similar to local wild populations, though no inference could be made for wild Middle Fork Willamette Chinook due to an inadequate sample size. Genetic population structure did not closely reflect geographic structure of the Willamette River, as North Santiam River populations clustered with McKenzie River populations and South Santiam River populations formed a clade with hatchery Chinook from the Middle Fork Willamette River. Structure was particularly weak among populations from the Middle Fork Willamette and South Santiam rivers.

We evaluated the accuracy of genetic stock identification for Willamette River spring Chinook, based on 13 GAPS (Genetic Analysis of Pacific Salmon) microsatellite markers. We found that with the GAPS baseline, individuals could be assigned to their population of origin (subbasin) with 43% - 64% accuracy. We estimated 100% assignment accuracy to the Catherine Creek Hatchery population, reflecting the distinctiveness of Willamette River Chinook relative to that population. We observed no measurable increase in assignment accuracy by adding four gene-linked markers to the GAPS baseline.

We tested for signals of positive selection on both GAPS microsatellites and four gene-linked markers by examining inter-locus patterns of genetic differentiation. Although we found no evidence for locus-specific selection among Willamette River populations, one GAPS microsatellite and an immune-relevant marker presented aberrantly large genetic diversity index (F_{ST}) values between Willamette River populations and the Catherine Creek population. This result suggests that these loci may be linked to genes under positive selection that has generated markedly different allele frequencies in Catherine Creek and Willamette River spring Chinook.

Lastly we used our empirical genotypic data from the McKenzie River hatchery and wild populations to perform forward-time simulations, modeling changes in θ, mean heterozygosity and total allele count over 30 generations. We use the term “migration” to describe the

interaction of hatchery and wild fish in these simulations; namely the proportion of natural-origin fish spawned in the hatchery as broodstock and the proportion of hatchery fish present on natural spawning grounds. Our findings indicated that migration rates of at least 5% resulted in <2% decline in heterozygosity and an asymptotic F_{ST} value of 0.005 or less. No migration from one or both populations resulted in markedly higher rates of population divergence, loss of heterozygosity and reduction in alleles present. The mean number of alleles present (per locus) in the hatchery and wild populations was more sensitive to differences in migration rate than heterozygosity, whereby low levels of hatchery straying and natural-origin broodstock integration best conserved genetic diversity.

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List of Acronyms and Terms

bp	Base pair
Clipped	Salmon without an adipose fin
DNA	Deoxyribonucleic acid
F_{ST}	Wright's fixation index, describes among-population genetic diversity
GAPS	Genetic Analysis of Pacific Salmon
GSI	Genetic stock identification
ODFW	Oregon Department of Fish and Wildlife
HGMP	Hatchery Genetic Management Plan
HWE	Hardy-Weinberg Equilibrium
LD	Linkage Disequilibrium
PCR	Polymerase Chain Reaction
pHOS	Proportion of hatchery origin fish on spawning grounds
pNOB	Proportion of natural origin fish in broodstock
RPA	Reasonable and Prudent Alternative
Theta	θ, an F_{ST} estimator for multiple loci and variable sample sizes
Unclipped	Salmon with an adipose fin
USACE	United States Army Corps of Engineers
UWR	Upper Willamette River
WDFW	Washington Department of Fish and Wildlife

Introduction

The Willamette Project Biological Opinion (NMFS 2008) identified the risk of genetic introgression between hatchery and natural origin spring Chinook salmon *Oncorhynchus tshawytscha* as a key limiting factor to species recovery in all major Willamette River subbasins. The Biological Opinion also recommended that Action Agencies "*preserve and rebuild genetic resources through conservation and supplementation objectives to reduce extinction risk and promote recovery*" (RPA 6.2) through implementation of Hatchery Genetic Management Plans (HGMPs) basin-wide (RPA 6.2.1), and the use of locally founded broodstocks, integrated with natural origin populations (RPA 6.2.2) (NMFS 2008). Accordingly, ODFW has periodically integrated locally collected, natural origin fish into (locally founded) UWR spring Chinook hatchery broodstocks. Draft HGMPs provide detailed plans for continued integration at an average pNOB of 5%, wherever possible, and in a manner that aims to provide maximum genetic benefit to hatchery broodstocks with the least risk to wild populations. However, an assessment of genetic benefit, risk and effectiveness of measures aimed to manage genetic characteristics of hatchery and wild populations requires empirical genetic information.

Some genetic information of Willamette River spring Chinook was provided by Myers et al. (2006), who examined microsatellite genotype data from several populations sampled in 1998, including wild Chinook from the Clackamas, North Santiam, and McKenzie rivers, and hatchery fish from Clackamas, McKenzie, Marion Forks (North Santiam River), and Dexter (Middle Fork Willamette River) hatcheries. The authors reported that genetic relationships among Willamette spring Chinook populations did not reflect geographic relationships. Instead, they found that hatchery fish appeared less similar to local wild fish than to wild fish from other subbasins. The authors acknowledged that this peculiar finding might be attributed to their use of juvenile samples (Myers et al. 2006), which can produce highly distorted and often exaggerated patterns of genetic divergence (Allendorf and Phelps 1981; Waples 1998).

However, microsatellite analyses of appropriate samples can provide reliable and informative population genetic information. Briefly, microsatellites are regions of the genome that consist of short nucleotide sequence repeats (typically 2 to 4 bp motifs), prone to relatively high mutation rates. Common polymerase slippage mutations increase or decrease the length of the microsatellite repeat region through additions or deletions of the repeat motif (Figure 1). Microsatellites typically occur in intergenic DNA and therefore are not translated into proteins. As such, they do not typically affect the phenotype and are not subject to the evolutionary force of selection. Instead, they are considered "neutral" elements of genetic variation. This selective neutrality and high mutation rate make microsatellites ideal markers for inferring demographic processes, such as migration or effective population size, since new variants can appear (through mutation or immigration) and accumulate within a population without fitness consequences or removal through selection.

On the other hand, because microsatellite variation does not translate into phenotypic variation, data from microsatellites cannot be used to infer the adaptive potential of individuals or populations. An exception occurs when a microsatellite is tightly linked to a gene that is actually or potentially subject to selection. Increasingly popular F_{ST} outlier detection approaches aim to identify gene-linked markers under selection, which exhibit unusual patterns of population divergence relative to those of ubiquitous neutral markers (reviewed by Luikart et al. 2003). Analyses of both marker types (neutral and non-neutral) can be used to infer the effects of selection and demography on the distribution of population genetic diversity.

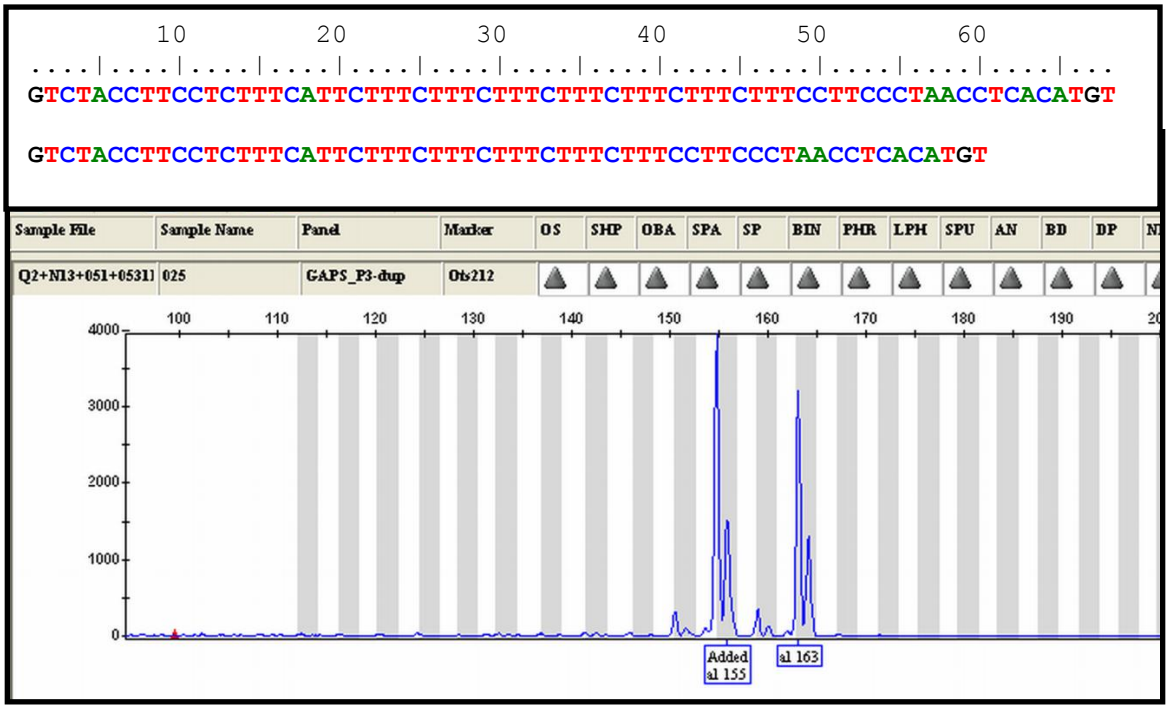


Figure 1. (Top) Excerpts of the *Ots212* microsatellite sequence (Greig et al. 2003) for two alleles of a hypothetical, heterozygous Chinook salmon. Scale indicates number of basepairs from an arbitrary sequence start point. Alleles for this locus vary through the number of 'CTTT' motif repeats. (Below) Electrophoretograms for the *Ots212* microsatellite from a heterozygous Willamette River spring Chinook salmon. The lengths of the PCR amplicons (155 and 163; *x*-axis) reflect the number of motif repeats for each allele. The *y*-axis indicates fluorescence intensity.

Given previously identified uncertainties related to the extent of genetic structure among Willamette River spring Chinook populations and the effects that alternate broodstock management practices could have over Chinook genetic diversity, our research carried the following objectives:

1. Collect tissue samples from natural and hatchery origin adult spring Chinook from major eastern subbasins of the Willamette River.

2. Genotype a representative sample of each hatchery and wild population using a suite of polymorphic microsatellite loci.

3. Estimate genetic diversity within and among sampled populations, using conventional population genetics measures.

4. Evaluate potential genetic effects of management actions, including integration of natural-origin broodstock.

More specifically, by using putatively neutral microsatellite markers from the GAPS baseline (Seeb et al. 2007) and four microsatellites thought to be linked to genes involved with immune response of Atlantic salmon *Salmo salar*, we genotyped hatchery and natural-origin spring Chinook from the Willamette River. We then used these genotypic data to:

- Estimate observed and expected heterozygosities, and allelic richness for hatchery and wild spring Chinook populations
- Describe patterns of genetic divergence among populations, as measured by the F_{ST} estimator θ (Weir and Cockerham 1984)
- Infer genetic relationships among hatchery and natural-origin populations
- Evaluate the accuracy of GSI methods for Willamette River spring Chinook
- Perform F_{ST} outlier tests to detect locus-specific signatures of selection
- Explore relationships between migration, heterozygosity and F_{ST}, as they relate to spring Chinook broodstock management

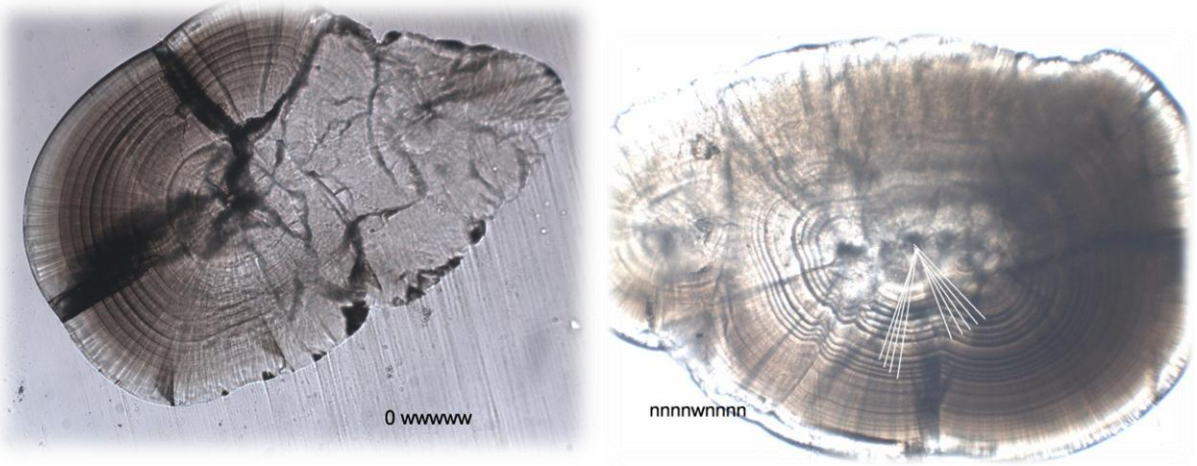


Figure 2. Polished otoliths from wild (left) and thermally marked hatchery (right) Willamette River spring Chinook. White lines overlayed on the otolith at right indicate thermal events (marks) and converge at the otolith core. Images are 200x magnification, provided courtesy of WDFW.

Methods

Study area and tissue sampling

For this study, we collected spring Chinook samples from major subbasins of the Willamette River, including the Calapooia and Molalla rivers. To allow comparisons with an out-of-basin spring Chinook population, we also obtained a small number of samples from Catherine Creek Hatchery (Grande Ronde River, Oregon; a tributary of the lower Snake River). With infrequent exceptions of experimental release groups, all spring Chinook produced by hatcheries in the Willamette River receive two marks. First, juvenile fish are intentionally exposed to thermal oscillations during incubation, which generate distinct otolith bands (Figure 2). Then, the adipose fin is removed (clipped) from juvenile hatchery Chinook prior to liberation, providing a permanent and readily visible "hatchery origin" mark. Redundant marking allows confident identification of Willamette River hatchery spring Chinook, despite imperfect adipose fin clip rates (Cannon et al. 2011).

Sampling was conducted from June-October, 2011. Field technicians collected fin tissue samples from adipose fin-clipped, adult hatchery spring Chinook at Clackamas Hatchery (Clackamas River), Bennett fishway (North Santiam River), Foster Dam (South Santiam River), McKenzie Hatchery (McKenzie River), Dexter Dam (Middle Fork Willamette River) and Catherine Creek Hatchery (Grande Ronde River). Samples were preserved in 95% ethanol and scales were collected from a subsample of fish. Otoliths, scales and tissue samples were collected from unclipped adult Chinook carcasses during spawning ground surveys of the Clackamas, Molalla, Calapooia, North Santiam, South Santiam, McKenzie and Middle Fork Willamette rivers (Figure 3). Otolith and fin tissue samples were stored in individually labeled vials containing 95% ethanol, and scales were placed in labeled envelopes. Biologists recorded the date, collection location, fork length, sex and mark status (clipped or unclipped) for each sample.

Sample processing and data collection

Determination of origin

We considered multiple approaches to infer the origin (hatchery or wild) of unclipped Chinook. Using scales from fish of known origin, we performed blind tests to assess the utility of scale analyses for hatchery-wild assignment. Albeit informal, these tests revealed that scale analyses failed to reliably discriminate between wild and hatchery origin spring Chinook from the Willamette River.

In contrast, Volk et al. (1999) demonstrated that otolith analyses provide a highly accurate means of identifying (thermally marked) hatchery spring Chinook. Accordingly, we sent otoliths from unclipped spring Chinook to the Washington Department of Fish and Wildlife

Otolith Lab, where the presence of thermal event bands was used to designate hatchery or wild origin status. Only unclipped fish without otolith thermal marks were classified as wild for our study. Only adipose fin-clipped fish were classified as hatchery origin Chinook. After we had determined the origins of our samples, we subsampled our tissue collection and initiated genetic analyses at Oregon State University's Marine Fisheries Genetics Laboratory in Newport, Oregon. For all analyses, samples were grouped *a priori* into putative populations, based on hatchery or wild origin and subbasin of sample collection.

DNA isolation and microsatellite genotyping

We used a glass fiber filtration-elution protocol (Ivanova et al. 2006) to isolate whole genomic DNA from spring Chinook tissue samples, and included a single negative control on each 96-well DNA plate.

We used touchdown PCR thermocycling profiles (Korbie and Mattick 2008) to amplify the following 13 GAPS microsatellite markers: *Ots208*, *Ots213*, *Ots9*, *Ots211*, *Ogo4*, *OtsG474*, *Ssa408*, *Ogo3*, *Ots3*, *Ots212*, *Oki100*, *Ots201*, *Oki100*, *Ots201* and *Omm1080*. Primer sequences for these markers are provided by references of Seeb et al. (2007). Individual reactions were performed in 6 μL volumes that contained 1 μL of template DNA and reagent volumes as provided in Appendix 1. PCR products were co-loaded with a 500-bp DNA standard, then separated and visualized by capillary gel electrophoresis on an ABI 3730XL DNA Analyzer. We used GeneMapper software to score and record microsatellite genotypes.

We then genotyped all samples at four microsatellite loci found to be immune-relevant in Atlantic salmon: *SsaIR003TKU*, *SsaIR010TKU*, *SsaIR013TKU*, and *SsaIR015TKU* (Tonteri et al. 2008). In this report, we abbreviate the names of these loci as *3TKU*, *10TKU*, *13TKU* and *15TKU*, respectively. For these loci we used PCR protocols similar to those of GAPS markers, though reactions were carried out in 5 μL volumes as detailed in Appendix 1. We visualized, scored and recorded genotype data as before.

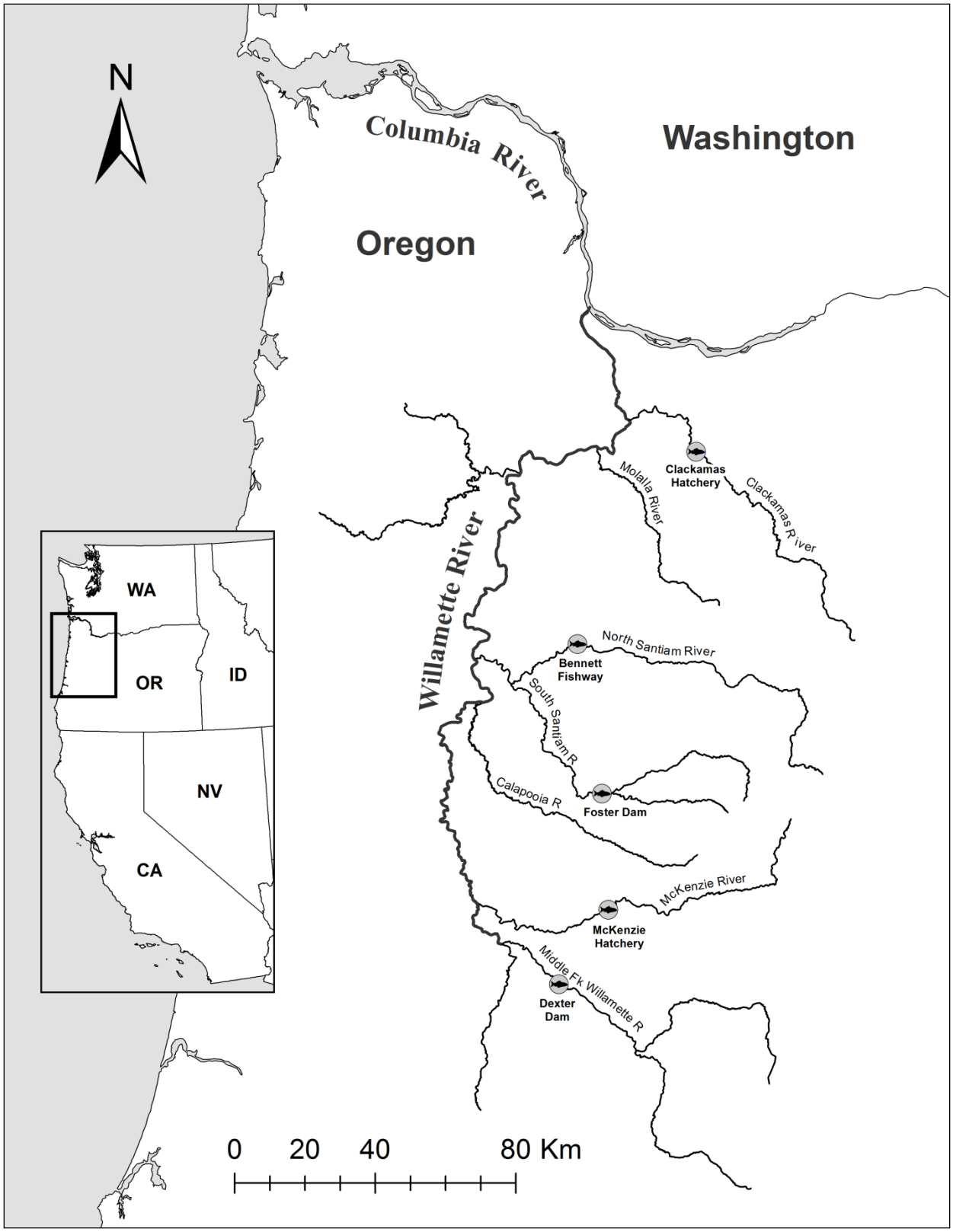


Figure 3. The Willamette River basin and collection sites for clipped (hatchery-origin) Chinook salmon tissue samples. Sampled from unclipped fish were collected from throughout the labeled tributaries.

Data analysis

Prior to analyses, we removed all samples that provided genotypic data for <65% of loci (minimum 11 of 17 loci scored) from our dataset. This step was performed to reduce bias from genotype errors that can occur from low quality DNA samples (Pompanon et al. 2005).

Heterozygosity, pairwise θ and allelic richness

We used genotypic data for all loci and the program GENETIX (Belkhir et al. 2004) to produce estimates of observed and expected heterozygosity for all spring Chinook populations. We used the program GENEPOP (Rousset 2008) to perform Hardy-Weinberg equilibrium exact tests (Haldane 1954) and *U* tests to detect locus-specific heterozygosity excesses and deficits (Rousset and Raymond 1995) within each population. We also used GENEPOP to perform exact tests for linkage disequilibrium between all locus pairs within populations. We assessed the statistical significance of results from these tests against a false discovery rate (FDR) adjusted critical value (Benjamini and Hochberg 1995) with unadjusted $\alpha = 0.05$.

We then used the GAPS loci data and GENETIX to calculate values for the F_{ST} estimator θ (Weir and Cockerham 1984) between all pairs of populations with $n \geq 30$. We performed permutation tests with 1,000 iterations on pairwise θ estimates, and assessed statistical significance against an FDR adjusted critical value (unadjusted $\alpha = 0.05$).

Briefly, heterozygosity provides a measure of genetic diversity for individuals of a population. Individual heterozygosities can be used to estimate mean population heterozygosity. Theta (θ) describes the proportion of total genetic variance attributable to among population differences (Weir and Cockerham 1984). For most analyses we applied a minimum population size criterion of $n = 30$ to avoid severe sampling bias on genetic distance estimates, which can arise from allele frequency data from small or under-represented populations (Kalinowski 2005).

Because sample sizes differed among populations, we used the program FSTAT (Goudet et al. 1995) to estimate allelic richness for all loci in each population. This approach uses rarefaction to account and correct for the effect of different sample sizes on the number of alleles observed within populations, and provides an index of diversity that can be directly compared among populations with different sample sizes.

Genetic structure among populations

We used allele frequency data from the GAPS microsatellite loci and the maximum likelihood program CONTML from the PHYLIP 3.69 software package (Felsenstein 2009) to infer the phylogeny of all spring Chinook populations with $n \geq 30$. We visualized the resulting dendrogram with the program TREEVIEW (Page 1996). To assess node confidence, we bootstrapped the GAPS microsatellite allele frequency data (1,000 resamples) with the program SEQBOOT, inferred phylogenies as before (for all 1,000 datasets), constructed a consensus tree with the program CONSENSE, then examined bootstrap values for each node.

The resulting bootstrapped phylogeny relates statistical support for a graphic representation of genetic relationships among hatchery and wild spring Chinook populations from the Willamette River. We then included the Catherine Creek Hatchery outgroup to this analysis to "root" the tree and provide a broader geographic scale to the phylogeny.

Evaluation of GSI

Genetic stock identification is a widely-used application of population genetics data, whereby baseline allele frequency data are used to assign individuals of unknown population origin to their most likely source population. If sufficient genetic structure currently exists among UWR Chinook populations to allow accurate GSI, juvenile or adult fish could be sampled at Willamette Falls or other locations and assigned to their most likely population of origin, providing a valuable tool for research and management.

The program ONCOR (Kalinowski 2007) can be used to perform genetics-based mixed stock analyses, individual population assignments and assignment accuracy tests. We used this program to implement the "leave-one-out test" (Anderson et al. 2008) to evaluate GSI accuracy for Willamette River spring Chinook. Briefly, this test removes an individual from the genotype baseline, performs a population assignment with that individual to the baseline, replaces that individual (more accurately, its multilocus genotype) to the baseline, then performs a series of repetitions of this sampling and assignment procedure. Ultimately, percent scores are generated that reflect the assignment accuracy of individuals back to their population of origin in the baseline. We performed this test with only GAPS microsatellite data, then repeated the test with baseline data for both GAPS and *TKU* markers. Only populations of $n \geq 30$ were included in the baseline file. We then used the GAPS genotype baseline to perform population assignments for individuals from populations of $n < 30$.

Evidence of loci under selection

We used F_{ST} outlier tests to investigate for signals of selection on GAPS and immune-relevant microsatellite markers. We first performed these tests using data from hatchery and wild UWR Chinook populations. In this case, the presence of an outlier could suggest that selection had markedly favored different alleles in hatchery and wild populations from UWR subbasins. We then performed F_{ST} outlier tests with data from UWR Chinook (hatchery and wild populations pooled) and the Catherine Creek population. This test aimed to detect locus-specific signals of selection between these geographically distant Chinook populations that could provide clues toward the molecular bases of local adaptation. We used the program LOSITAN (Antao et al. 2008) to execute the F_{ST} outlier detection methods described by Beaumont and Nichols (1996). We used the infinite alleles model and performed 50,000 simulations to construct F_{ST} distributions across the full range of possible heterozygosities. We used a highly conservative false discovery rate (0.05) and evaluated F_{ST} for each locus against a 99.5% confidence interval of F_{ST} values constructed from the simulated data. We chose to use the "neutral mean F_{ST}" and "force mean F_{ST}" options of LOSITAN, which iteratively identify and

remove F_{ST} outliers when calculating the global distribution of F_{ST}. These options are recommended by the program developers.

Genetic aspects of broodstock management

Natural origin fish spawned in the hatchery as broodstock and hatchery fish that spawn on natural spawning grounds contribute to "migration" between hatchery and wild spring Chinook populations. To investigate potential genetic effects from integration of natural-origin fish into the hatchery broodstock (Objective 4), we used our microsatellite genotype data and the program NEMO 2.2.0 (Guillaume and Rougemont 2006) to model changes in genetic diversity in context of various migration scenarios. These analyses predict how alternate pHOS and pNOB rates could influence heterozygosity, θ, and allele count of hatchery and wild Willamette River spring Chinook populations.

To perform these simulations, we first generated hatchery and wild "source populations" of size n = 3,000 by resampling our genotypic data (17 loci) with the software WHICHLOCI (Banks et al. 2003). We then used the forward-time simulation program NEMO 2.2.0 to fill two habitat "patches" of specified carrying capacity with individuals drawn at random (without replacement) from the source populations. This step constituted the "seeding" event. The simulations then proceeded as individuals within patches first mated and died, their offspring dispersed (migrated), aged to maturity and the cycle repeated. Adult statistics were recorded immediately after each generation's mating event. We specified these operations and parameter values through INIT files, as required by the software. An annotated INIT file example is provided in Appendix 2.

For all simulations, we used data from the McKenzie River hatchery and wild populations with patch sizes that allowed a maximum n = 650 and n = 800 for the hatchery and wild populations. We performed 5 replicate simulations for each of four migration rates (m; the proportion of offspring that emigrate to the neighboring patch) under three migration scenarios:

Scenario 1, symmetrical migration rates – Migration rate from the hatchery population equaled migration rate from the wild population. Effects of migration were evaluated at values m = 0.00, 0.05, 0.10 and 0.30.

Scenario 2, variable pNOB – migration from the hatchery population was constant at 0.05 and migration from the wild population was modeled at m = 0.00, 0.05, 0.10 and 0.30.

Scenario 3, variable pHOS – migration from the wild population was constant at 0.05 and migration from the hatchery population was modeled at m = 0.00, 0.05, 0.10 and 0.30.

For all simulations we used a stepping stone migration model and a monogamous mating system, reflecting the 1:1 mating protocol used in UWR spring Chinook hatcheries. Other parameter values are provided in Appendix 2. Simulations were run for 30 generations and at every third generation we recorded the mean values for θ, heterozygosity and total number of

alleles present in the combined hatchery-wild population complex and in the separate hatchery and wild populations (demic allele count). We then plotted mean values for these metrics against generation for all migration rates and scenarios.

Results

Characterization of samples and data quality

We collected 1,797 tissue samples from unclipped spring Chinook throughout the Willamette River Basin. Of these, 1,506 lacked otolith thermal marks and were classified as wild spring Chinook. No carcasses were recovered from the Calapooia River. We subjected 391 of these wild samples, from five UWR subbasins and the Clackamas River, to genetic analyses, together with 559 hatchery origin samples. Overall PCR success across all individuals and loci was 87.5%. We excluded 18 hatchery samples and 119 wild samples from statistical analyses due to insufficient genotype data (Table 1). Approximately 80% of the remaining 813 samples provided genotypic data for at least 16 of the 17 loci examined, and all loci were successfully amplified and scored for 530 samples (65% of samples included in statistical analyses). The PCR success rate was generally lower for wild samples than hatchery samples. This was likely a function of tissue quality, since wild samples were primarily collected from carcasses in various states of decomposition.

Table 1. Collection location and origin of spring Chinook subjected to genetic and statistical analyses. All samples were collected in 2011.

Collection Location	Origin	Number genotyped	Number used in statistical analyses (*n*)
Catherine Creek	Hatchery	34	33
Clackamas	Hatchery	95	80
North Santiam	Hatchery	95	95
South Santiam	Hatchery	95	94
McKenzie	Hatchery	95	95
Middle Fork Willamette	Hatchery	145	144
Clackamas	Wild	70	51
Molalla	Wild	11	8
South Santiam	Wild	95	62
North Santiam	Wild	95	72
McKenzie	Wild	95	67
Middle Fork Willamette	Wild	25	12
	Total	950	813

Genetic diversity

Heterozygosity

Within Willamette River subbasins, hatchery populations had higher observed heterozygosities than wild populations (Table 2). The four immune relevant loci included in our study presented fewer alleles and lower heterozygosities than most GAPS markers. Exact test results indicated that all populations except the Catherine Creek hatchery ($P = 0.0542$) and Molalla wild ($P = 0.8083$) populations were not in Hardy Weinberg equilibrium (all others $P < 0.0001$). Subsequent *U* tests revealed that this result was largely driven by lower than expected heterozygoties at three loci: *Omm1080, Ots213* and *10TKU*. That is, all populations except the Catherine Creek hatchery population and the small, putative wild populations from the Mollala and Middle Fork Willamette Rivers provided significant evidence for heterozygote deficiency at one or more of these loci. Only spurious departures from HWE were observed at other loci. For most hatchery-wild population pairs (within subbasins), fewer loci were out of HWE in the hatchery populations than in wild counterparts. We consistently found that more locus pairs were in linkage disequilibrium in hatchery populations than in wild populations (Table 2).

Pairwise θ values

Among populations from the Willamette River above Willamette Falls, pairwise θ values ranged from zero to 0.009 (Table 3). Pairwise θ values between the Catherine Creek hatchery population and upper Willamette River populations were at least an order of magnitude greater than observed between Clackamas and other upper Willamette River populations, where pairwise θ values ranged from 0.001 to 0.013 (Table 3). The Clackamas hatchery population appeared to be more diverged from UWR populations above Willamette Falls than the Clackamas wild population. Wild Chinook from the Molalla and Middle Fork Willamette rivers were not included in this analysis due to small sample sizes (Table 1).

We found that θ values for hatchery and wild population pairs within UWR subbasins above Willamette Falls were not significantly different from zero (North Santiam, $P = 0.047$; South Santiam, $P = 0.535$; McKenzie, $P = 0.317$). With a single exception, both hatchery and wild populations from all UWR subbasins were significantly diverged from hatchery and wild populations from other subbasins. Interestingly, we found no evidence that hatchery or wild Chinook from the South Santiam River were distinct from wild Clackamas River spring Chinook.

Allelic richness

Although per locus allele counts varied considerably among populations, we observed similar levels of allelic richness among populations when sample sizes were normalized through rarefaction to a minimum of 22 diploid individuals. Among Willamette River populations, wild fish from the Clackamas River presented the highest allelic richness and hatchery fish from the same subbasin presented the lowest allelic richness (Table 4). The Catherine Creek hatchery population presented the lowest allelic richness of any population examined. Overall, we

observed no clear pattern for differences in allelic richness between hatchery and wild spring Chinook populations from the Willamette River.

Table 2. Observed and expected heterozygosities (H_e and H_o) for hatchery and wild spring Chinook populations from Catherine Creek (Grande Ronde River) and major subbasins of the Willamette River, as estimated from GAPS microsatellite data and four immune relevant (IR) loci. Also, the number of loci not in Hardy-Weinberg equilibrium (HWE) and number of locus pairs in linkage disequilibrium (LD) in each population.

		GAPS Loci		IR Loci		HWE	LD
Collection Location	Origin	H_e	H_o	H_e	H_o		
Catherine Creek	Hatchery	0.744	0.735	0.494	0.405	0	0
Clackamas	Hatchery	0.806	0.815	0.550	0.558	3	35
North Santiam	Hatchery	0.819	0.820	0.564	0.470	4	9
South Santiam	Hatchery	0.814	0.813	0.572	0.520	3	5
McKenzie	Hatchery	0.821	0.805	0.557	0.550	3	12
Middle Fork Willamette	Hatchery	0.819	0.818	0.571	0.493	4	11
Clackamas	Wild	0.828	0.752	0.573	0.398	8	7
Molalla	Wild	0.753	0.823	0.532	0.310	0	0
North Santiam	Wild	0.796	0.777	0.556	0.454	4	1
South Santiam	Wild	0.808	0.746	0.553	0.347	8	3
McKenzie	Wild	0.824	0.788	0.560	0.459	7	1
Middle Fork Willamette	Wild	0.706	0.620	0.485	0.353	1	0

Table 3. Pairwise θ values (Weir and Cockerham 1984) among hatchery (H) and wild (W) origin spring Chinook populations from the Willamette River and Catherine Creek Hatchery (Grande Ronde River), estimated from genotypic data for 13 GAPS microsatellite loci. Values not significantly different from zero (FDR adjusted α = 0.001 – 0.050) are indicated in bold.

	Clackamas Hatchery	Clackamas Wild	Willamette Hatchery	McKenzie Hatchery	McKenzie Wild	N.Santiam Hatchery	N. Santiam Wild	S. Santiam Hatchery	S. Santiam Wild
Catherine Cr. H	0.111	0.106	0.106	0.107	0.102	0.100	0.110	0.099	0.104
Clackamas H		0.007	0.012	0.013	0.013	0.010	0.012	0.010	0.009
Clackamas W			0.004	0.003	0.003	0.004	0.005	**0.002**	**0.001**
Willamette H				0.007	0.006	0.008	0.009	0.003	0.004
McKenzie H					**0.000**	0.003	0.006	0.004	0.005
McKenzie W						0.004	0.006	0.004	0.003
N. Santiam H							**0.002**	0.005	0.005
N. Santiam W								0.005	0.005
S. Santiam H									**0.000**

Genetic structure among populations

Using genotypic data from the GAPS microsatellite loci, we inferred the phylogeny of Willamette River spring Chinook through a maximum likelihood approach (Figure 3). Results from this analysis suggested that within the Willamette River, hatchery populations are genetically most similar to wild Chinook from the same subbasin. In most cases, these subbasin level hatchery-wild pairings received bootstrap support approaching or exceeding 70%. An exception to this pattern involved the hatchery and wild populations from the South Santiam River, and hatchery fish collected from the Middle Fork Willamette River. These three groups formed a polytomy, with internal branch lengths that did not differ significantly from zero (95% CI) and with < 50% bootstrap node support.

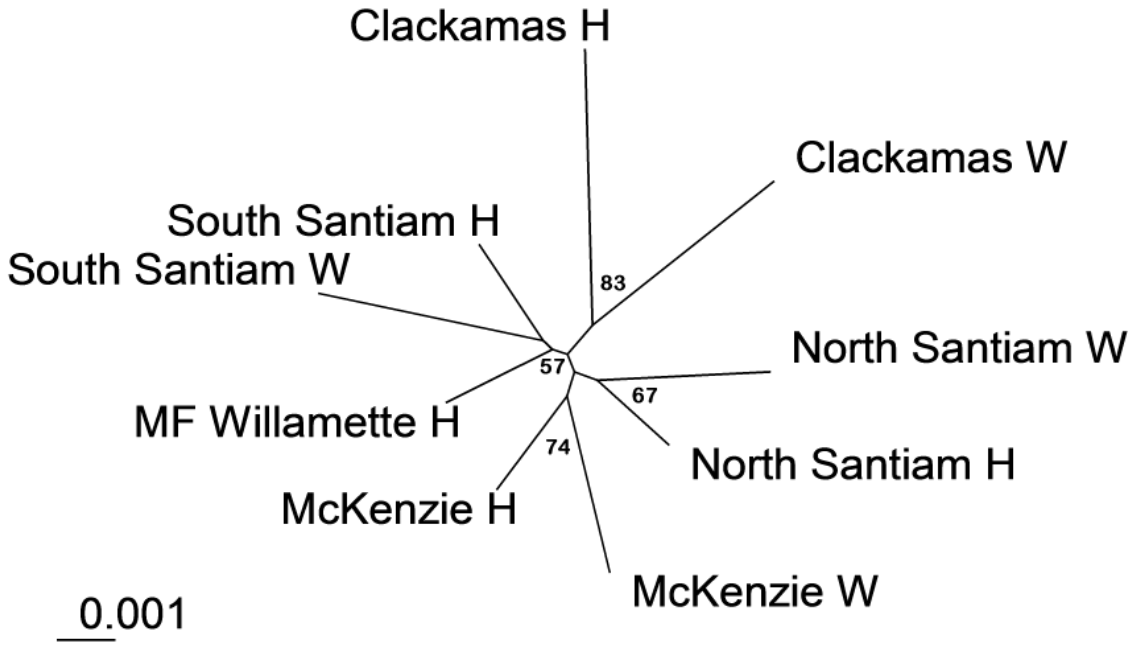


Figure 3. Unrooted maximum likelihood tree depicting genetic relationships among hatchery (H) and wild origin (W) spring Chinook populations from the Willamette River. Phylogeny inferred from genotypic data for 13 microsatellite loci. Branch lengths represent Cavalli-Sforza chord measures of genetic distances (Cavalli-Sforza and Edwards 1967). Bootstrap values are indicated for nodes with >50% support. Branch lengths of the South Santiam H-South Santiam W-MF Willamette H clade are not significantly different from zero (95% confidence interval).

To provide a broader sense of scale to the Willamette River spring Chinook population phylogeny, we repeated our analysis but included the out-of-basin Catherine Creek hatchery population. This phylogeny provided an illustrative example of the distinctiveness of Willamette River Chinook from other Columbia River Chinook populations (Figure 4). Bootstrap support for the bifurcation between Catherine Creek and Willamette River populations was 100%.

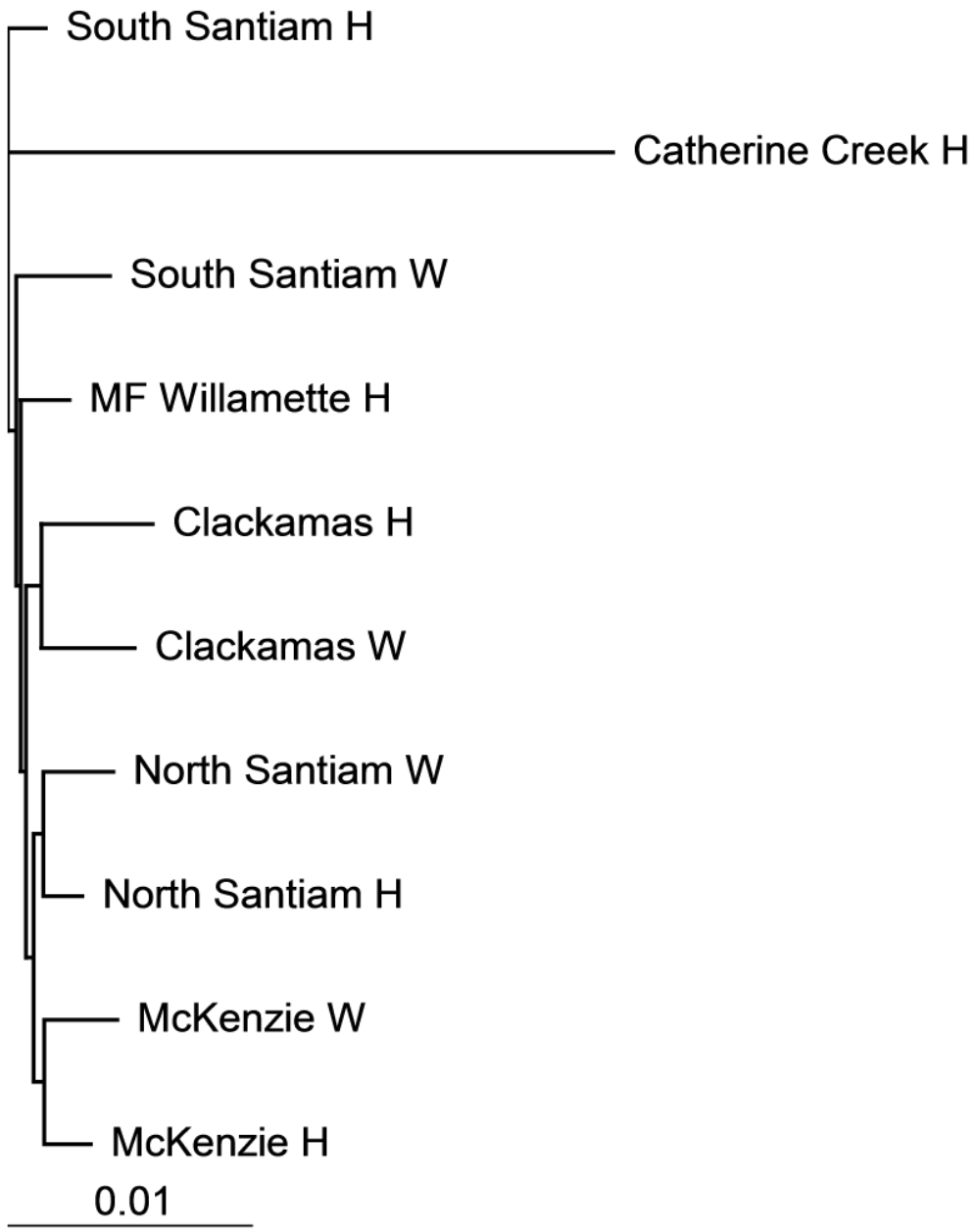


Figure 4. Maximum likelihood tree depicting genetic relationships among hatchery (H) and wild origin (W) spring Chinook populations from the Willamette River and the Catherine Creek hatchery population (Grande Ronde River). Phylogeny inferred from genotypic data for 13 microsatellite loci. Branch lengths represent Cavalli-Sforza chord measures of genetic distances (Cavalli-Sforza and Edwards 1967).

Table 4. Allele counts and allelic richness for GAPS and immune relevant (*TKU*) loci in spring Chinook populations from the Willamette River and Catherine Creek Hatchery, Grande Ronde River. Allelic richness normalized on a minimum of 22 diploid individuals.

	Locus	Catherine Cr. Hatchery	Clackamas Hatchery	N. Santiam Hatchery	S. Santiam Hatchery	McKenzie Hatchery	Middle Fork Willamette Hatchery	Clackamas Wild	N. Santiam Wild	S. Santiam Wild	McKenzie Wild
Allele Counts	*Ots208*	24	23	28	30	27	29	22	27	23	27
	Ots213	16	24	25	23	29	27	24	22	24	26
	Ots9	4	3	4	4	4	4	3	2	2	4
	Ots211	18	19	20	19	17	18	22	21	17	16
	Ogo4	7	8	8	10	8	9	9	9	8	7
	OtsG47	3	12	9	10	9	10	10	9	11	8
	Ssa408	12	18	18	21	23	25	21	19	15	16
	Ogo2	8	14	11	12	12	13	11	11	9	11
	Ots3	3	9	7	9	7	8	9	8	8	7
	Ots212	16	15	17	14	14	16	16	16	14	18
	Oki100	15	24	24	26	23	25	23	23	24	21
	Ots201	16	17	19	18	17	17	18	17	17	15
	Omm1080	24	24	35	35	35	35	26	26	22	28
	3TKU	2	2	2	2	2	2	2	2	2	2
	10TKU	4	3	5	4	6	4	4	5	4	4
	13TKU	4	5	5	5	5	5	5	5	4	5
	15TKU	2	3	3	4	3	3	6	3	3	5
Allelic Richness	*Ots208*	20	16	18	19	18	17	18	19	18	19
	Ots213	15	16	16	16	18	15	18	16	16	17
	Ots9	4	3	3	3	4	3	3	2	2	3
	Ots211	15	15	14	16	14	15	17	15	14	14
	Ogo4	7	6	6	7	7	6	7	7	7	6
	OtsG47	3	10	6	7	7	7	8	7	8	6
	Ssa408	11	15	15	16	16	17	16	14	14	14
	Ogo2	7	10	9	9	9	9	9	8	9	9
	Ots3	3	6	6	7	5	7	7	6	7	6
	Ots212	14	12	12	11	11	11	15	13	14	14
	Oki100	13	16	17	17	15	16	18	17	17	15
	Ots201	14	13	14	13	13	13	15	13	14	13
	Omm1080	21	17	23	20	22	21	21	19	18	21
	3TKU	2	2	2	2	2	2	2	2	2	2
	10TKU	4	3	4	4	4	4	4	4	4	4
	13TKU	4	4	5	5	5	5	5	5	4	5
	15TKU	2	3	2	3	3	3	5	2	2	4
Mean Richness		9	9	10	10	10	10	10	11	10	10

Accuracy of genetic stock identification

Because we found little or no evidence for genetic divergence between hatchery and wild populations within Willamette River subbasins (Table 3), we could not reasonably expect useful GSI power for hatchery and wild populations within subbasins. We therefore pooled hatchery and wild samples from each subbasin to generate a GAPS microsatellite genotype baseline for ONCOR analyses. We did not include wild Chinook from the Middle Fork Willamette or Molalla rivers in this baseline.

Using the "leave-one-out test" (Anderson et al. 2008), we found that accuracy of GSI to Willamette River subbasin populations ranged from 43-64% (Table 5). Discrimination between Catherine Creek hatchery and Willamette River spring Chinook was 100% accurate. Assignment accuracy was higher between populations from the Clackamas River and populations above Willamette Falls. Among populations above Willamette Falls, assignment accuracy was highest for the Middle Fork Willamette (hatchery) population. The addition of *TKU* marker data to the baseline did not provide consistent improvement to assignment accuracy, with only a minor increase in assignment accuracy for some populations (49.1% accuracy for McKenzie) offset by greater assignment error for other populations (61.5% accuracy for Clackamas).

Table 5. Percent assignment accuracy for Willamette River and Catherine Creek (Grande Ronde River) spring Chinook, using baseline data from 13 GAPS microsatellite loci.

Population	*n*	Percent Accuracy	Most Common Misidentification	Percent Error
Catherine Creek	31	100.0%		
Clackamas	44	63.6%	Middle Fork Willamette	18.2%
Middle Fork Willamette	124	58.1%	South Santiam	15.3%
South Santiam	94	42.6%	Middle Fork Willamette	22.3%
McKenzie	116	46.6%	North Santiam	20.7%
North Santiam	135	54.1%	McKenzie	17.8%

Despite low assignment accuracy, we performed an exploratory analysis of the composition of wild Chinook collected from the Molalla and Middle Fork Willamette rivers. We found that most wild fish collected from the Middle Fork Willamette assigned to either the Middle Fork Willamette or South Santiam populations, and that wild fish from the Molalla assigned at nearly equal ratios to the South Santiam, North Santiam and Middle Fork Willamette Rivers (Table 6). However, these results must be interpreted with caution, given our findings from the "leave-one-out" test and multiple low assignment probability scores for these wild fish (Table 6). Interestingly, though, one wild Chinook collected from the Middle Fork Willamette assigned with high probability (98%) to the Catherine Creek population. Although this fish may

be from a population not included in our baseline (i.e. not Catherine Creek), it is likely not from the Willamette River. We also performed individual assignments for wild Clackamas River Chinook, and found that over half (53%) assigned to either the North or South Santiam rivers. Again, these results should be interpreted with caution.

Table 6. Individual population assignments for wild spring Chinook sampled from the Molalla and Middle Fork Willamette rivers.

Individual	Best Estimate	Probability	Second Best Estimate	Probability
MFWILL_20	Catherine Creek	0.98	Middle Fork Willamette	0.02
MFWILL_18	McKenzie	0.97	Middle Fork Willamette	0.03
MFWILL_7	McKenzie	0.77	South Santiam	0.20
MFWILL_17	Middle Fork Willamette	0.62	South Santiam	0.35
MFWILL_21	Middle Fork Willamette	0.65	South Santiam	0.21
MFWILL_34	Middle Fork Willamette	0.98	McKenzie	0.02
MFWILL_5	North Santiam	0.62	South Santiam	0.37
MFWILL_2	South Santiam	0.82	Middle Fork Willamette	0.18
MFWILL_22	South Santiam	0.98	McKenzie	0.02
MFWILL_32	South Santiam	0.81	Middle Fork Willamette	0.13
MFWILL_66	South Santiam	0.39	McKenzie	0.23
MFWILL_8	South Santiam	0.83	Middle Fork Willamette	0.16
MOLALLA_W34	McKenzie	0.36	South Santiam	0.27
MOLALLA_W51	Middle Fork Willamette	0.71	South Santiam	0.22
MOLALLA_W61	Middle Fork Willamette	0.63	North Santiam	0.27
MOLALLA_W6	North Santiam	0.97	McKenzie	0.02
MOLALLA_W46	North Santiam	0.41	McKenzie	0.34
MOLALLA_W23	South Santiam	0.94	North Santiam	0.03
MOLALLA_W26	South Santiam	0.89	Middle Fork Willamette	0.08
MOLALLA_W40	South Santiam	0.51	McKenzie	0.21

Evidence of loci under selection

Among Willamette River spring Chinook populations, we found no evidence for selection having driven the F_{ST} value for any locus beyond what might be expected under a model of random genetic drift. That is, all loci provided evidence for similar levels of population divergence (F_{ST}), none appearing as outliers against a 99.5% confidence interval of F_{ST} values simulated from our data (Figure 5).

When we included the Catherine Creek hatchery population in a similar analysis (all analysis parameters held constant) we found that two loci, *10TKU* (*SsaIR010TKU*) and *OtsG474*, presented exceptionally high F_{ST} values, indicating locus-specific positive selection (Figure 6).

Our results also suggested that balancing selection might be elevating heterozygosity for *Ots212* and *Omm1080*, though this evidence was less compelling since F_{ST} values for these markers fell just outside the bounds of the 99.5% confidence interval. We did not include wild fish from the Middle Fork Willamette or Molalla rivers due to small sample sizes.

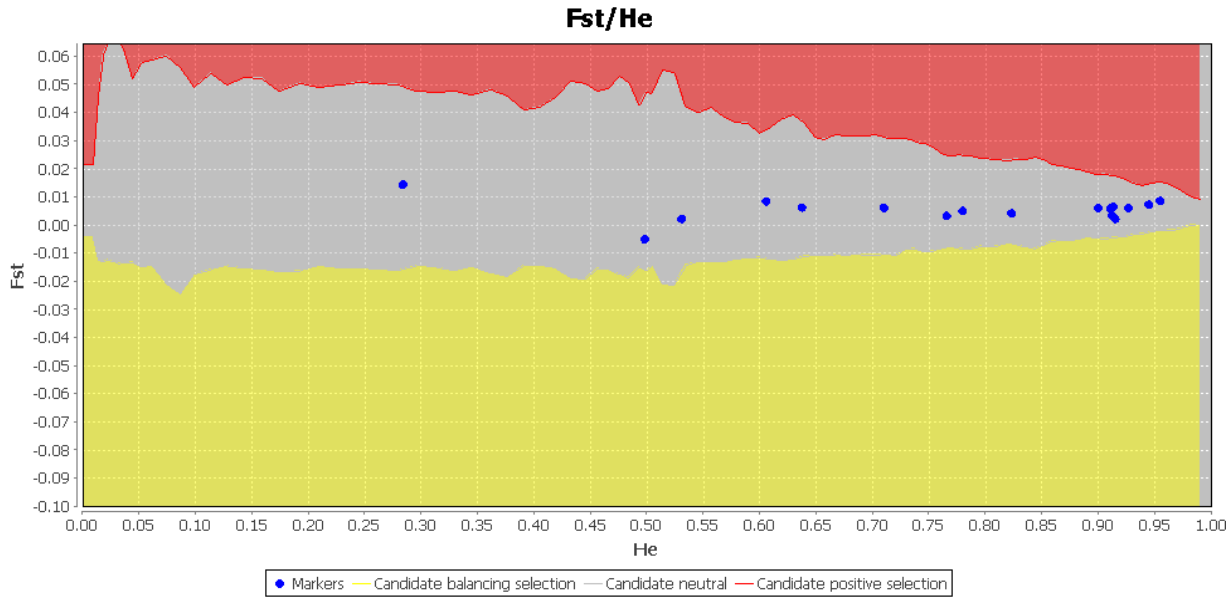


Figure 5. Overall F_{ST} values for 17 microsatellite loci (markers) plotted against heterozygosity, as characterized from nine Willamette River spring Chinook populations. Gray area defines the 99.5% CI of expected F_{ST} under neutrality. Other shaded areas indicate regions associated with positive (red) and balancing (yellow) selection.

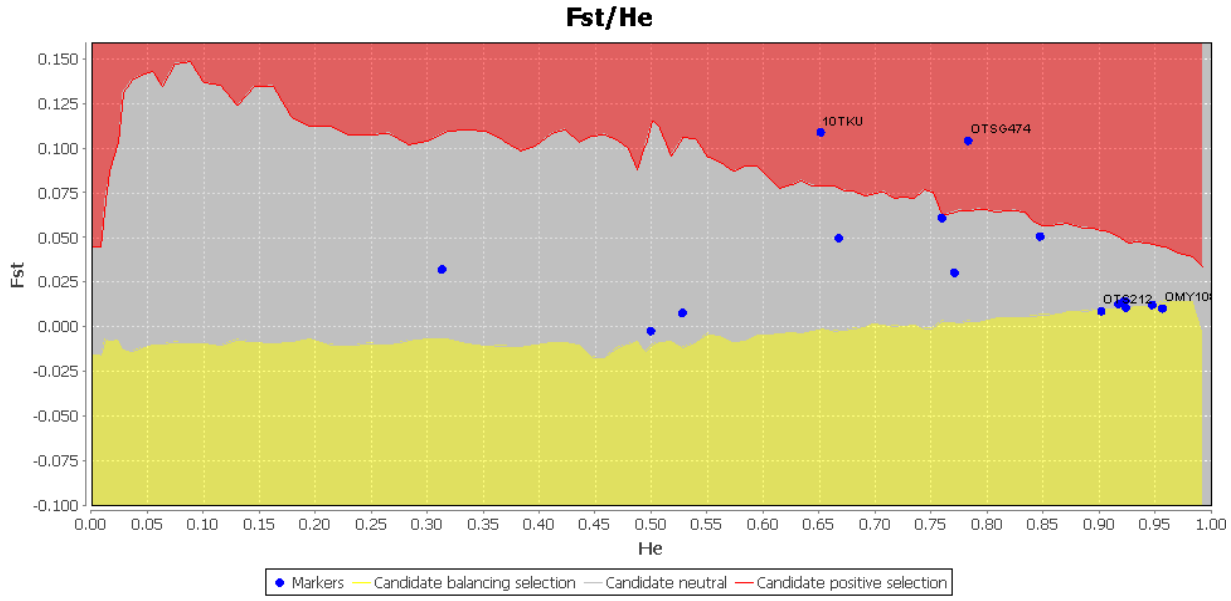


Figure 6. Overall F_{ST} values for 17 microsatellite loci (markers) plotted against heterozygosity, as characterized from the Catherine Creek hatchery and nine Willamette River spring Chinook populations. Gray area defines the 99.5% CI of expected F_{ST} under neutrality. Other shaded areas indicate regions associated with positive (red) and balancing (yellow) selection.

Migration and the genetic management of hatchery broodstocks

Using resampled genotypic data for 17 microsatellite loci (GAPS and *TKU* markers) from the McKenzie River hatchery and wild spring Chinook populations, we performed a series of forward time simulations to model the effects that various migration rates (m) had on mean heterozygosity, θ and the number of alleles present in the combined and separate hatchery and wild populations. Due to computational constraints, simulated population sizes were smaller than typically observed in the McKenzie River (hatchery n = 650; wild n = 800), though roughly equivalent to observed hatchery:wild population size ratios (see Appendix 4).

We found that under all scenarios and migration rates examined, there was some decline in mean heterozygosity. However, total decline after 30 generations was typically little more than 1% and migration rate did not appear to have a strong effect on the magnitude of heterozygosity loss, though m = 0 from one or both populations resulted in significantly greater decline under all migration scenarios (Figures 8a, 8b, 8c).

Under all migration scenarios, θ appeared to stabilize at a value less than 0.005 after nine generations whenever m was greater than zero from both populations. Theta stabilized at higher values under asymmetrical migration scenarios with no migration from either the wild (mean θ = 0.005 at generation 30; Figure 8b) or hatchery (mean θ = 0.007 at generation 30; Figure 8c) populations. Theta continued to increase steadily over 30 generations under a symmetrical, no migration scenario (Figure 8a).

We observed some interesting patterns for change in allele count in response to different migration scenarios. First, we found that allele loss was always greater within hatchery and wild populations (i.e. allele counts calculated separately for each population) than in the combined hatchery-wild population complex. Our results also suggested that even low levels of migration (5%) greatly mitigated within-population allele loss. Furthermore, when wild migration rates were held constant at 5%, optimal allele conservation was achieved with hatchery migration (stray) rates of 5-10% (Figure 8c). Under this scenario, a hatchery migration rate of 0% resulted in the greatest loss of alleles within populations and a 30% rate of hatchery migration produced the greatest loss of alleles in the combined hatchery-wild population complex.

We emphasize that these results reflect changes predicted for neutral microsatellite loci, and simulations did not incorporate potential effects from selection on allele frequencies and overall population genetic diversity.

Figure 8a. Simulated change in mean heterozygosity (upper left), theta (upper right) and mean per locus number of alleles present in the combined (lower left) and separate (lower right) hatchery and wild populations of McKenzie River spring Chinook. The percent of offspring that migrate from each population, *m*, is modeled at 0-30%. The model was seeded with genotypic data from 17 microsatellites. See text for additional model parameters.

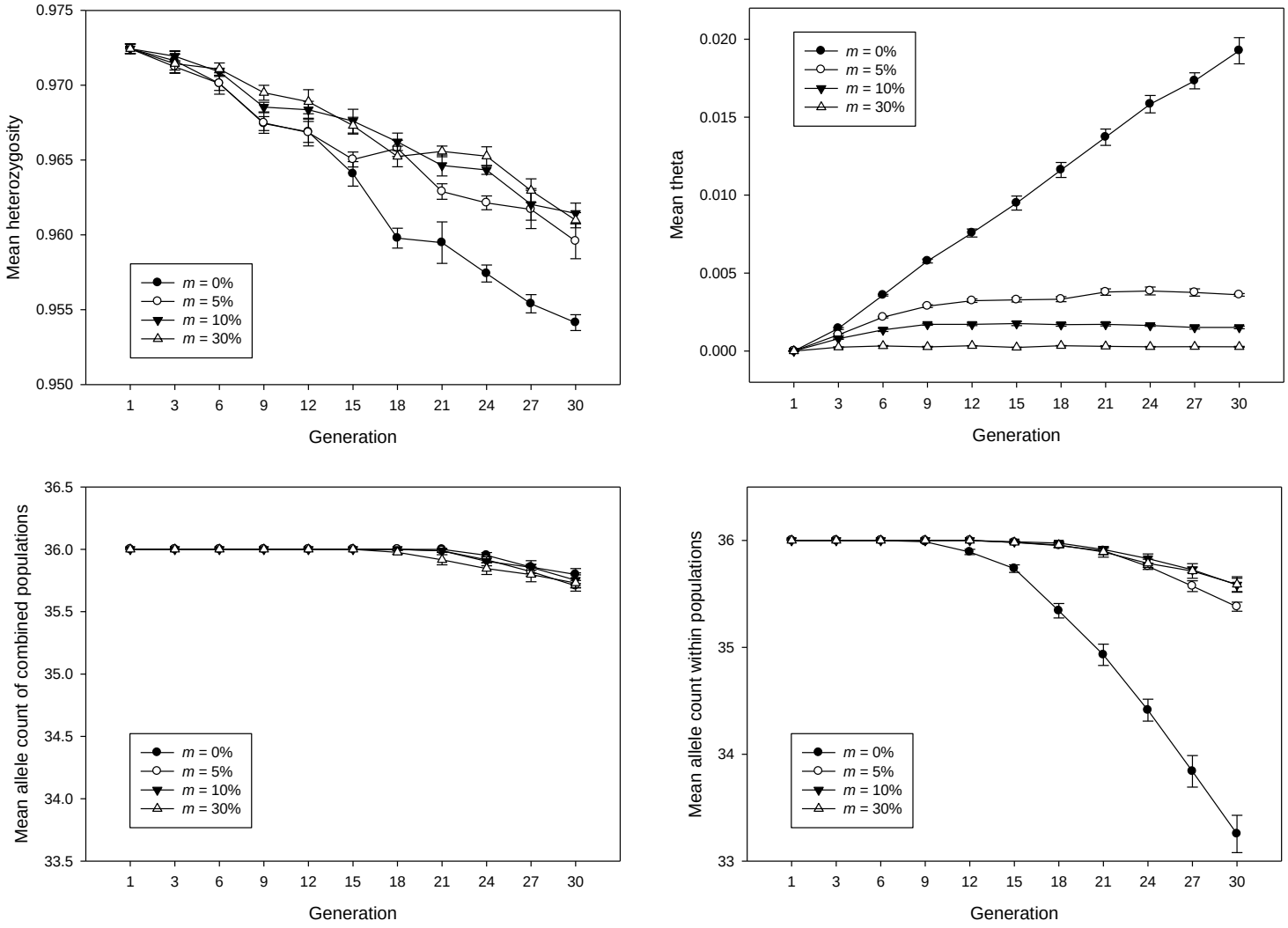


Figure 8b. Simulated change in mean heterozygosity (upper left), theta (upper right), and mean per locus number of alleles present in the combined (lower left) and separate (lower right) hatchery and wild populations of McKenzie River spring Chinook. The percent of offspring that migrate (*m*) is 5% for the hatchery population and 0- 30% for the wild population. The model was seeded with genotypic data from 17 microsatellites. See text for additional model parameters.

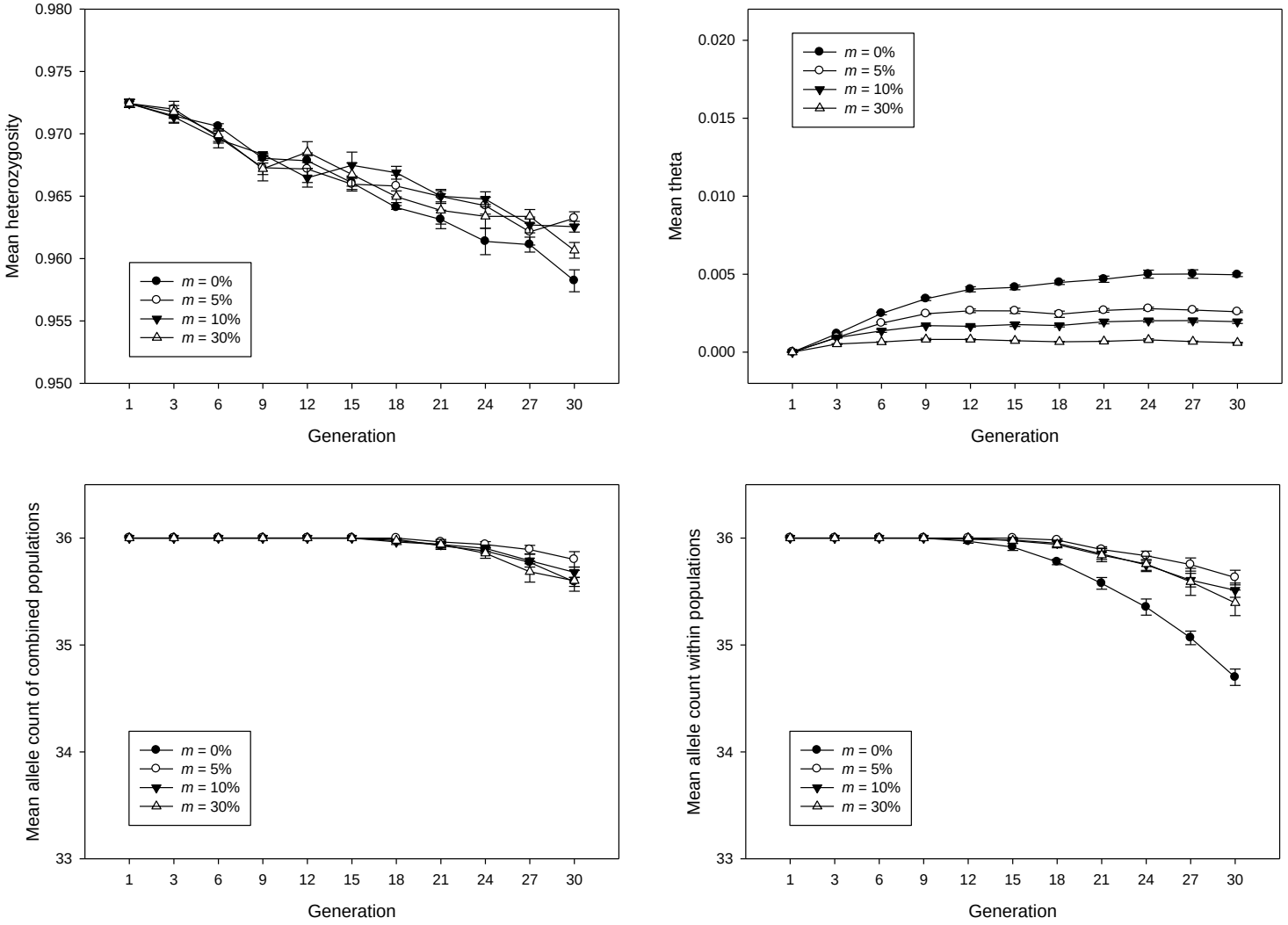
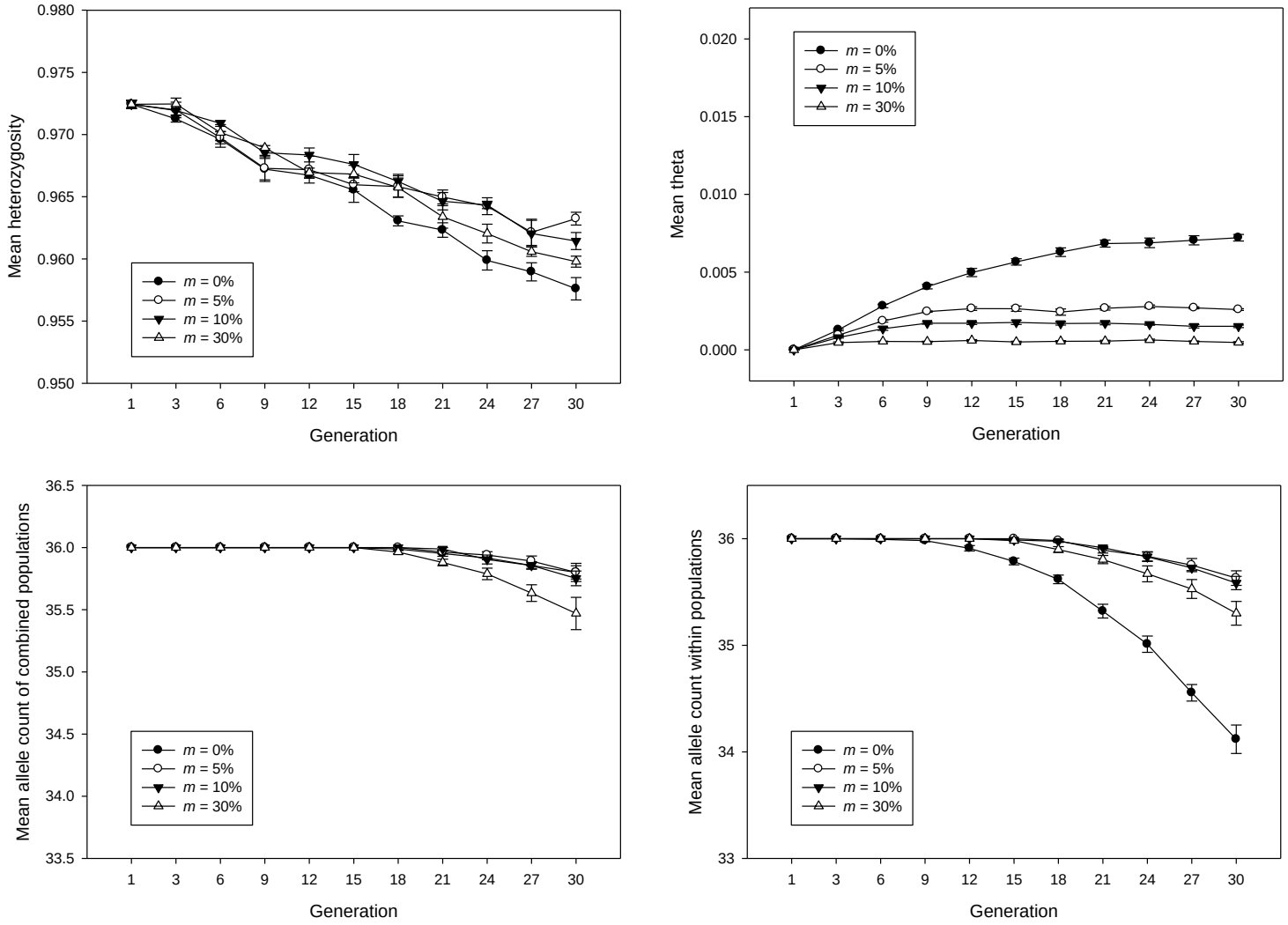


Figure 8c. Simulated change in mean heterozygosity (upper left), theta (upper right), and mean per locus number of alleles present in the combined (lower left) and separate (lower right) hatchery and wild populations of McKenzie River spring Chinook. The percent of offspring that migrate (*m*) is 0-30% for the hatchery population and 5% for the wild population. The model was seeded with genotypic data for 17 microsatellites. See text for additional model descriptions.



Discussion

Overview

Population genetic information can serve as a valuable resource to fisheries managers, providing a nexus between past processes and future directions. In this study, we have examined genetic diversity for 17 microsatellite loci in 813 spring Chinook from six Willamette River subbasins and the Catherine Creek hatchery population (Grande Ronde River). Using genotypic data from these loci, we have inferred mean population heterozygosities, allelic richness, levels of population genetic divergence and genetic relationships among populations. We have evaluated the accuracy of GSI for Willamette River spring Chinook and examined the stock structure of two small wild spring Chinook populations. In our final analyses, we used F_{ST} outlier tests to detect locus-specific signals of selection among spring Chinook populations, and modeled the effects that various levels of migration can have on hatchery-wild population genetic divergence, mean heterozygosity and allelic diversity through time.

Our analyses have provided the following results, which we discuss in detail in following sections:

1) Heterozygosity and allelic richness - Within subbasins of the Willamette River, heterozygosities are higher for hatchery populations than wild populations, though no clear pattern of difference was detected for allelic richness.

2) Genetic divergence (θ) - Genetic divergence between hatchery and wild populations within UWR subbasins was either insignificant or very low. We found evidence for weak but significant genetic divergence among all UWR subbasins, except for South Santiam populations, which were genetically similar to the Clackamas River wild population.

3) Genetic structure among hatchery and wild populations -
    a. Hatchery populations are most similar to wild (founder) populations from the same subbasin.
    b. The North Santiam and South Santiam river populations do not form a monophyletic group. Instead, the North Santiam River population appears to be more similar to the McKenzie River population than to the South Santiam River population.
    c. Genetic structure is very weak among Chinook populations from the South Santiam and Middle Fork Willamette rivers.
    d. Willamette River spring Chinook are very distinct from Catherine Creek hatchery spring Chinook.

4) Accuracy of GSI methods for Willamette River spring Chinook -
    a. Using GAPS microsatellite loci, we observed low population assignment accuracy to subbasins of the Willamette River
    b. We observed high GSI accuracy between Willamette River populations and the Catherine Creek hatchery population.
    c. A single out-of-basin, unmarked spring Chinook was detected with high probability among unmarked Chinook sampled in the Middle Fork Willamette River.

5) Locus-specific signatures of selection (F_{ST} outlier tests) -
    a. We found no evidence for locus-specific selection among hatchery and wild spring Chinook populations from the Willamette River.
    b. We found the Catherine Creek hatchery population to be exceptionally diverged from Willamette River spring Chinook populations at two microsatellite loci.

6) Relationships between migration and genetic diversity in the context of spring Chinook broodstock management -
    a. Absence of migration from either the hatchery, wild or both populations resulted in the highest rates of genetic divergence and erosion of diversity for most metrics.
    b. When migration from the wild population to the hatchery population was 5%, the rate of allele loss was highest in the hatchery-wild population complex under a high migration rate (30%) from the hatchery population.
    c. Greatest conservation of allelic diversity was achieved with low levels of reciprocal migration between the hatchery and wild populations at 5% or 10%. Minor changes in heterozygosity and allelic richness were similar under these migration rates, though θ reached a higher value with 5% migration than with 10% migration.

Heterozygosity and allelic richness

Genetic diversity is fundamental to both short-term population resilience and long-term adaptive potential (Allendorf 2005; Waples et al. 1990). Both heterozygosity and allelic richness are important components of genetic diversity that can be directly compared among populations.

We found that mean heterozygosities of Willamette River spring Chinook populations ranged from 62-82% for GAPS microsatellites and 31-56% for *TKU* loci. We observed the lowest mean heterozygosity in the small wild populations of the Middle Fork Willamette River. Within subbasins of the Willamette River, hatchery populations presented higher heterozygosities than local wild populations. The large census size (N) of hatchery populations and random, 1:1 spawning protocols used by Willamette River hatcheries may function to boost

population heterozygosities above levels found in smaller wild populations, in which the number of breeders (N_b) may be significantly less than N. Incidentally, our estimates of observed heterozygosity for hatchery populations from the North Santiam and McKenzie rivers (Table 2) differed by less than 1% from those reported by Narum et al. (2010), placing them among the top five of 37 Columbia River spring Chinook populations examined (Table 7). The lower heterozygosities observed for *TKU* loci, relative to GAPS markers, may be explained by the small number of alleles found at these immune relevant loci. With few alleles present, the number of possible allele combinations declines and the probability for homozygous pairings can be expected to increase.

Few Willamette River Chinook populations appeared to be in HWE at all loci examined (Table 2). Nearly all populations presented some evidence of heterozygote deficit at one or more of three loci, *Omm1080*, *Ots213* and *TKU10*. Moreover, all populations that showed departures from HWE also presented some evidence of LD (Table 2). This result could be interpreted as evidence of migration, which would disrupt HWE and generate LD. However, our data violate other key assumptions required for HWE, in addition to the no migration assumption. Specifically, the assumption of non-overlapping generations is violated by inclusion of multiple age classes among samples and some loci may be subject to the effects of selection. The cause for ubiquitous departures from HWE and LD is therefore unclear. The higher frequency of LD in hatchery populations may stem from differences between UWR hatchery spawning protocols (1:1 matings) and natural, polygamous Chinook mating systems (Bentzen et al. 2001).

Although hatchery populations presented higher heterozygosities than wild populations, we did not observe a similar pattern for allelic richness. Instead, we found that populations scored similarly for allelic richness, regardless of hatchery or wild origin. The Clackamas River wild population presented a slightly higher mean allelic richness than all other populations, perhaps as a result of admixture in this population; a hypothesis supported by the relatively high number of loci not in HWE for the Clackamas River wild population (Table 2).

Taken together, our findings suggest that wild and hatchery Willamette River spring Chinook populations harbor similar numbers of alleles *per capita*, but that in wild populations these alleles more often occur in homozygous states. Demic structure in wild populations, which would be disrupted by random mating practices in hatchery populations, could explain this result.

Table 7. Observed and expected heterozygosities (*He* and *Ho*) for 37 Columbia River spring Chinook populations examined by Narum et al. (2010). UWR populations appear in bold.

Rank	Population	*He*	*Ho*
1	Lewis Hatchery (spring)	0.866	0.870
2	Cowlitz Hatchery (spring)	0.861	0.853
3	Klickitat River (spring)	0.864	0.846
4	Kalama Hatchery (spring)	0.865	0.837
5	**McKenzie Hatchery (spring)**	0.817	0.812
6	**North Santiam Hatchery (spring)**	0.820	0.812
7	Winthrop Hatchery, Carson stock (spring)	0.792	0.809
8	Wenatchee River (spring)	0.795	0.803
9	Tucannon River (spring)a	0.791	0.803
10	Battle Creek (spring)	0.841	0.801
11	Cle Elum Hatchery (spring)	0.816	0.796
12	Red River (spring)a	0.795	0.795
13	Entiat Hatchery (spring)	0.782	0.793
14	Imnaha River (spring)a	0.783	0.793
15	Sawtooth Hatchery (spring)a	0.790	0.793
16	Dworshak Hatchery (spring)a	0.793	0.792
17	Pahsimeroi River (spring)a	0.780	0.790
18	Lochsa River–Powell Trap (spring)a	0.788	0.789
19	Methow River (spring)	0.793	0.788
20	Minam River (spring)a	0.790	0.788
21	South Fork Clearwater (spring)a	0.785	0.782
22	Big Creek-b (spring)a	0.760	0.782
23	West Fork Yankee Fork (spring)a	0.758	0.779
24	Marsh Creek (spring)	0.782	0.777
25	Catherine Creek (spring)a	0.775	0.776
26	Johnson Creek supplementation (spring)a	0.779	0.776
27	Johnson Creek (spring)a	0.776	0.775
28	Lolo Creek (spring)a	0.787	0.767
29	Rapid River Hatchery (spring)a	0.762	0.767
30	Big Creek-a (spring)a	0.754	0.764
31	Lostine River (spring)a	0.754	0.763
32	Secesh River (spring)a	0.773	0.763
33	Newsome Creek (spring)a	0.765	0.760
34	Shitike Creek (spring)	0.763	0.757
35	East Fork Salmon River (spring)a	0.769	0.757
36	John Day River (spring)	0.780	0.755
37	Warm Springs Hatchery (spring)	0.725	0.728

Genetic divergence (θ)

Contrasting with the findings of Myers et al. (2006), our analysis of pairwise θ values for Willamette River spring Chinook indicated that hatchery populations are most similar to local wild populations. In most cases, θ values between local hatchery-wild population pairs were not significantly different from zero, reflecting no measurable genetic differentiation. This finding was expected, because upper Willamette River hatchery populations were founded from local, wild broodstock in the 1990s (Johnson and Friesen 2010) and migration between hatchery and local wild populations has continued since that time through pHOS and wild broodstock integration (Appendix 4). The peculiar genetic relationships between hatchery and wild populations reported by Myers et al. (2006) were likely influenced by Allendorf-Phelps effects, as the authors acknowledged.

We found that Willamette River spring Chinook were weakly structured at the subbasin level. Although nearly all between-subbasin θ estimates were statistically significant (Table 3), they were lower than most pairwise values reported for spring Chinook populations from the Snake (θ = 0.017-0.045; Narum et al. 2007), Klamath (θ = 0.0111-0.0236; Kinziger et al. 2008) and California Central Valley rivers (θ = 0.005-0.026; Garza et al. 2008). Structure between Clackamas River populations and Chinook from above Willamette Falls was greater than among populations above the falls, with the exception of low divergence between the Clackamas wild population and South Santiam populations. This finding suggests that migration between the wild Clackamas population and South Santiam River populations is greater than between the Clackamas and all other UWR populations. Indeed, South Santiam strays into the Clackamas wild population could also explain the higher allelic richness, LD and HWE departures observed in the wild Clackamas population.

Genetic structure among populations

The maximum likelihood phylogeny of Willamette River spring Chinook provided further evidence that hatchery populations are most similar to local wild populations, as hatchery-wild populations within subbasins formed clades with compelling bootstrap support in all possible cases. This suggests that Willamette River spring Chinook populations are structured among subbasins, with little or no measurable neutral genetic structure between hatchery and wild populations within subbasins.

However, like Myers et al. (2006), we found that population genetic structure of Willamette River Chinook did not reflect geographic structure in several ways. Although the Catherine Creek Hatchery population and, to a much lesser degree, the Clackamas populations separated from UWR populations, North Santiam River populations clustered with McKenzie River populations and South Santiam River populations formed a weakly structured clade with hatchery Chinook from the Middle Fork Willamette River. Without analyses of archival samples, it is difficult to infer whether extant UWR Chinook population structure reflects historic

structure, or whether stock transfers and local extinctions entirely removed historic structure, only to be replaced in recent years through subbasin-level management actions. The weak population structure we found, along with its lack of geographic concordance and the long history of stock transfers in the UWR basin (Johnson and Friesen 2010; Myers et al. 2006) favor the latter hypothesis. Regardless, with continued management that limits stock transfers among subbasins, spring Chinook population structure in the Willamette River can be expected to strengthen and favor the accumulation of locally adapted traits.

GSI accuracy

Using the GAPS baseline data, we found that Catherine Creek Chinook could be discriminated from Willamette River stocks with 100% accuracy. This result is expected, since Willamette River spring Chinook have previously been described as genetically distinct from interior Columbia River populations (Waples et al. 2004) with high population assignment accuracy (98.3%) at a multiregional scale (Seeb et al. 2007). However, weak population genetic structure within the Willamette River afforded only low GSI power to the level of Willamette River subbasins. Although more accurate than random assignments, the 43% - 64% GSI accuracy that we observed will likely limit the utility of GAPS-based GSI as a research tool within the basin. However, our GAPS baseline data may be useful in other contexts, such as to detect out-of-basin strays (as we found in the Middle Fork Willamette River) and provide robust data for the UWR spring Chinook reporting group that is used coastwide.

Although the GAPS microsatellite baseline employs a standardized set of markers that are used by researchers throughout the region (Seeb et al. 2007), greater differentiation among some Chinook populations has been found with select gene-linked markers at regional scales (Heath et al. 2006; O'Malley et al. 2007). However, we found that no more than a 2.5% increase in assignment accuracy was achieved by adding four *TKU* markers to our GAPS baseline, and assignment error increased by up to 2% in some populations. Therefore, while other gene-linked markers might improve GSI power for Willamette spring Chinook, the *TKU* markers that we examined do not appear well suited for this purpose.

Evidence of loci under selection

Among Willamette River spring Chinook populations, we found no evidence for selection having influenced allele frequencies for GAPS or *TKU* microsatellite loci. Instead, all loci presented similar levels of differentiation once conditioned on heterozygosity, suggesting that demography and random genetic drift have driven the evolution of these loci among Willamette River spring Chinook populations. This result is interesting since we included potentially immune-relevant loci among our markers and examined both hatchery and wild populations. Conceivably, hatchery and wild populations have experienced rather different selective pressures, with respect to pathogen exposure and resultant fitness consequences. Yet, we found no genetic signal for selection among the loci examined.

A rather different pattern emerged when we included the Catherine Creek hatchery population in our analysis, as both *SsaIR010TKU* and *OtsG474* presented unusually large F_{ST} values, indicative of positive selection that has favored different alleles for these loci in the Catherine Creek hatchery population, relative to Willamette River populations.

Interestingly, Tonteri et al. (2010) also found the *SsaIR010TKU* marker to be an outlier locus for northern European Atlantic salmon, as it presented the highest F_{ST} value of 94 loci examined in eight populations. This marker is thought to be linked to the calmodulin-2 gene (Tonteri et al. 2010), whose protein product is involved in calcium modulated regulation of many downstream gene targets that affect viral penetration, inflammation, cell motility and immune response (among others; see O'Day et al. 2003). That this marker appears to be influenced by positive selection at the population level in both Chinook and Atlantic salmon suggests that variation at this locus may confer important local adaptation for diverse salmonid species.

Unlike most GAPS markers, phenotypic significance has also been described for the *OtsG474* locus, which is thought to discriminate between ocean and stream type Chinook from interior Columbia River populations (Narum et al. 2004). It is therefore somewhat surprising that we found such marked allele frequency differences between Willamette and Catherine Creek populations at this locus, since both have been described as stream type Chinook (Narum et al. 2007; Waples et al. 2004, but see Moran et al. 2013). Specifically, over 92% of the *OtsG474* alleles in the Catherine Creek population were of size 156 bp (designated as p:2 in Appendix 3), whereas the mean frequency of this allele in Willamette River populations was only 13%. Although multiple juvenile outmigration life histories have been described for wild Catherine Creek Chinook (Favrot et al. 2010), greater allelic diversity at *OtsG474* in Willamette River populations (Appendix 3) could reflect genetic potential for diverse juvenile life histories. Alternatively, absence of distinct ocean- and stream-type lineages in lower Columbia River stocks (Moran et al. 2013), such as Willamette River Chinook, would suggest that the high observed F_{ST} at this marker may not associate with juvenile life history variation, but instead reflect adaptive differences between interior and lower Columbia River Chinook.

Migration and the genetic management of hatchery broodstocks

Using genotypic data from the McKenzie wild and hatchery spring Chinook populations, we performed genetically explicit, forward-time simulations to evaluate the effects of various migration scenarios on genetic diversity. Some change in genetic diversity can be expected to occur in any finite population and in all simulations heterozygosity decreased, θ increased and allele counts decreased over a 30-generation period. However, the magnitude of genetic change under most migration rates and scenarios appeared to be minor. Simulated change for heterozygosity was less pronounced than change for total allele count, likely because heterozygosity is largely maintained by common alleles, whereas total allele count can decline quickly as rare alleles are lost through drift (Waples et al. 1990).

The most dramatic changes in genetic diversity occurred when migration was eliminated from one or both populations. With no migration between the hatchery and wild populations (scenario 1, $m = 0$), θ increased steadily and allele count declined precipitously within populations.

The mean number of alleles present in the combined hatchery-wild population complex varied little in response to differences in migration rate. Only when migration from the hatchery population was high (30%) and migration from the wild population was low (5%) did we observe a significantly greater decline in the mean allele count of the combined hatchery-wild population complex. It is noteworthy that these migration values (scenario 3, hatchery $m = 30\%$) most closely resembles current migration patterns (pNOB and pHOS) between the McKenzie hatchery and wild populations.

Greatest allele conservation appeared to occur with reciprocal migration between the hatchery and wild populations at rates of 5-10%. These low-migration scenarios may adequately prevent genetic "swamping" from the relatively smaller hatchery population, which would be more vulnerable to random drift, while allowing some geneflow from the hatchery population that could restore alleles lost from the wild population. We found little difference between the effects from 5% and 10% migration on genetic diversity, suggesting that wild brood integration at these rates provides a similar level of neutral genetic benefit (i.e. preventing drift).

We acknowledge that in some respects our models do not accurately reflect known characteristics of McKenzie River Chinook populations. Specifically, our model does not allow for overlapping generations. Also, population sizes were significantly smaller than observed in recent years, and monogamous mating systems were applied to both hatchery and wild populations. However, each of these discrepancies likely serves to decrease the effective population sizes used in our models below actual values, thereby inflating the effects of drift on genetic diversity. Therefore, our model results likely depict greater rates of neutral genetic change than can be expected to occur in real UWR Chinook populations.

We again emphasize that the models of genetic change we have presented represent dynamics that might be expected for neutral loci. Allele frequencies for genes subject to selection can be expected to respond not only to demographic variables such as migration and population size, but also to the direction and magnitude of selection. Integration recommendations that assume selection on loci have been provided by Paquet et al. (2011). Though we found no evidence for selection having influenced GAPS or *TKU* microsatellite allele frequencies among Willamette River spring Chinook populations, it is possible that other genetic loci, not considered in this study, could be subject to disruptive natural or artificial selection. Finally, our results suggest that allele count may be a more informative metric than heterozygosity for population genetic monitoring programs. Despite the limitations and assumptions of our genetic models, results from these simulations provide an empirical basis for informed discussion and management.

Conclusions

Taken together, our results provide evidence for weak but significant genetic structure among Chinook populations from different Willamette River subbasins and almost no evidence for genetic diverge between hatchery and wild populations within subbasins. We found Willamette River Chinook populations to be quite genetically diverse in terms of mean heterozygosity. We recommend that managers continue to restrict Chinook stock transfers among UWR subbasins to promote the evolution of locally adapted traits. We also suggest that a small proportion (5-10%) of wild fish be integrated into hatchery broodstocks to prevent loss of allelic richness and neutral divergence between hatchery and wild populations within subbasins. Our findings of strong divergence at two genetic loci suggest that Willamette River populations may be a particularly informative group for the study of adaptive evolution among Columbia River Chinook. Finally, we recommend that the genetic information provided in this report be applied in the context of other biological, social and scientific information to guide future management actions.

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Appendix 1. PCR reagent concentrations, volumes and thermocycling temperatures.

	Stock Reagent	Final concentration	µL/ Reaction	GAPS Loci
	ddH20		1.6530	*Ots208b+*
25	mM MgCl	1.8000	0.4320	*Ots213*
10	mM dNTPs	0.1750	0.1050	*201b*
20x	Addative		0.2500	*Ots9*
10	µM Primer F*	0.4500	0.5400	
10	µM Primer F*	0.4500	0.5400	Denaturation = 94 C
10	µM Primer F*	0.1750	0.2100	High Anneal = 58 C
10	µM Primer F*	0.2000	0.2400	Low Anneal = 54 C
	5x buffer	promega	1.0000	Extend = 72 C
5	U/µl Taq	0.0250	0.0300	
	Total reagents volume		5.0000	
1.0	µL DNA	Total volume	6.0000	

	Stock Reagent	Final concentration	µL/ Reaction	GAPS Loci
	ddH20		1.4250	*Ots211+*
25	mM MgCl	1.6250	0.3900	*Ogo4*
10	mM dNTPs	0.1750	0.1050	*OtsG474*
20x	Addative		0.2500	
10	µM Primer F*	0.6000	0.7200	Denaturation = 94 C
10	µM Primer F*	0.4000	0.4800	High Anneal = 58 C
10	µM Primer F*	0.2500	0.3000	Low Anneal = 54 C
10	µM Primer F*	0.2500	0.3000	Extend = 72 C
	5x buffer	promega	1.0000	
5	U/µl Taq	0.0250	0.0300	
	Total reagents volume		5.0000	
1.0	µL DNA	Total volume	6.0000	

Appendix 1 (continued)

	Stock Reagent	Final concentration	µL/ Reaction	GAPS Loci
	ddH20		0.0630	*SSA408*
25	mM MgCl	1.8000	0.4320	*Ogo2*
10	mM dNTPs	0.1750	0.1050	*Ots3*
20x	Addative		0.2500	*Ots212*
10	µM Primer F*	0.6000	0.7200	
10	µM Primer F*	0.6000	0.7200	Denaturation = 94 C
10	µM Primer F*	0.6000	0.7200	High Anneal = 58 C
10	µM Primer F*	0.8000	0.9600	Low Anneal = 54 C
	5x buffer	Promega	1.0000	Extend = 72 C
5	U/µl Taq	0.0250	0.0300	
	Total reagents volume		5.0000	
1.0	µL DNA	Total volume	6.0000	

6	µL Rxn Vol			
	Stock Reagent	Final concentration	µL/ Reaction	GAPS Loci
	ddH20		2.4150	*Oki100*
25	mM MgCl	1.6250	0.3900	*Omm1080*
10	mM dNTPs	0.1750	0.1050	
20x	Addative		0.2500	Denaturation = 94 C
10	µM Primer F*	0.5000	0.6000	High Anneal = 52 C
10	µM Primer F*	0.1750	0.2100	Low Anneal = 48 C
	5x buffer	Promega	1.0000	Extend = 72 C
5	U/µl Taq	0.0250	0.0300	
	Total reagents volume		5.0000	
1.0	µL DNA	Total volume	6.0000	

Appendix 1 (continued)

	Stock Reagent	Final conc	µL / Rxn	
	ddH20		2.0250	*10TKU*
25	mM MgCl	2.0000	0.4000	Denaturation = 94 C
10	mM dNTPs	0.2000	0.1000	High Anneal = 63 C
20x	Addative		0.2500	Low Anneal = 59 C
10	uM Primer F*	0.2000	0.1000	Extend = 72 C
10	uM Primer R*	0.2000	0.1000	
	5x buffer	promega	1.0000	
5	U/µl Taq	0.0250	0.0250	
	Total reagents volume		4.0000	
1.0	µL DNA	Total reaction volume = 5 µL		

	Stock Reagent	Final conc	µL / Rxn	
	ddH20		0.8250	*13TKU*
25	mM MgCl	2.0000	0.4000	Denaturation = 94 C
10	mM dNTPs	0.2000	0.1000	High Anneal = 63 C
20x	Addative		0.2500	Low Anneal = 59 C
10	uM Primer F*	0.4000	0.2000	Extend = 72 C
10	uM Primer R*	0.4000	0.2000	
	5x buffer	promega	1.0000	
5	U/µl Taq	0.0250	0.0250	
	Total reagents volume		3.0000	
2.0	µL DNA	Total reaction volume = 5 µL		

Appendix 1 (continued)

	Stock Reagent	Final conc	µL / Rxn	
	ddH20		1.8750	*15TKU*
25	mM MgCl	2.0000	0.4000	Denaturation = 94 C
10	mM dNTPs	0.2000	0.1000	High Anneal = 63 C
20x	Addative		0.2500	Low Anneal = 59 C
10	uM Primer F*	0.3500	0.1750	Extend = 72 C
10	uM Primer R*	0.3500	0.1750	
	5x buffer	promega	1.0000	
5	U/µl Taq	0.0250	0.0250	
	Total reagents volume		4.0000	
1.0	µL DNA	Total reaction volume = 5 µL		

	Stock Reagent	Final conc	µL / Rxn	
	ddH20		2.1250	*3TKU*
25	mM MgCl	1.5000	0.3000	Denaturation = 94 C
10	mM dNTPs	0.2000	0.1000	High Anneal = 63 C
20x	Addative		0.2500	Low Anneal = 59 C
10	uM Primer F*	0.2000	0.1000	Extend = 72 C
10	uM Primer R*	0.2000	0.1000	
	5x buffer	promega	1.0000	
5	U/µl Taq	0.0250	0.0250	
	Total reagents volume		4.0000	
1.0	µL DNA	Total reaction volume = 5 µL		

Appendix 2. Example NEMO 2.2.0 init file.

```
logfile logfile_MCKsim01.log                # INIT FOR MCKENZIE SOURCE_FILE 062012
run_mode overwrite
random_seed 678893
root_dir MCKENZIE_SIM_01
filename MCKsim01
replicates 10                               ## NUMBER OF REPLICATES TO RUN SIM
generations 30                              ## NUMBER OF GENERATIONS TO SIMULATE IS 30
#POPULATION#
patch_number 2                              ## TWO POPULATIONS
patch_capacity {{650, 800}}                 ## OF SIZES 650 AND 800
source_pop MCKSOURCE/MCK3000%01.dat         ## USING RESAMPLED GENOTYPE DATA
source_preserve                             ## SEEDING WITH EXISTING STRUCTURE
source_file_type .dat                       ## AT GENERATION 0
#LIFE CYCLE#
breed 1                                     ## THESE ARE THE ORDER
save_stats 2                                ## OF OPERATIONS DURING THE
disperse 3                                  ## SIMULATION
aging 4
save_files 5
store 6
#BREED AND SELECTION PARAMETERS#
mating_system 3                             ## MONOGAMY, AS IN 1:1 HATCHERY MATINGS
mating_proportion 0.95                      ## INCLUDE A 5% ERROR RATE IN MONOGAMY
mean_fecundity 1500                         ## EACH FEMALE PRODUCING 1500 EGGS
#extinction parameter#
extinction_rate 0.0001                      ## STOCHASTIC EXTINCTION
#disperse parameters#
dispersal_model 3                           ## STEPPING STONE, NO MATTER W/2 POPS
dispersal_rate 0.10                         ## 10% INTEGRATION AND STRAYING
#save stats parameters#
stat adlt.fstWC                             ## REQUESTING WEIR & COCKERHAM'S THETA
stat_log_time 3                             ## CALCULATE AND RECORD STATS EVERY 3 GENS
stat_dir MCKsim_data                        ## RECORD FILE
#store parameters#
store_dir MCKSIM_bin
store_generation 30                         ## SIMULATION GENOTYPE DATA STORAGE
#neutral markers#
ntrl_loci 17                                ## ALL 17 LOCI, GAPS AND TKU
ntrl_all 36                                 ## MAX ALLELES SET AT 36, FROM DATA
ntrl_mutation_rate 0.0001                   ## REASONABLE RATE FOR MICROSATS
ntrl_mutation_model 1                       ## SINGLE STEP MUTATIONS
#output#                                    ## INCREASE/DECREASE ALLELES BY 1 SIZE
ntrl_save_genotype
ntrl_output_dir MCKfstatntrl
ntrl_output_logtime 30
```

Appendix 3. Allele frequencies for GAPS and immune-relevant (TKU) microsatellite markers in spring Chinook populations (of n > 30 samples) from the Willamette River and Catherine Creek Hatchery (Grande Ronde River). The first column identifies loci and their alleles (arbitrarily numbered). N is the number of individuals per population that provided data per each locus.

	Catherine H	Clackamas H	Clackamas W	MF Willamette H	McKenzie H	McKenzie W	N. Santiam H	N. Santiam W	S. Santiam H	S. Santiam W
OTS208										
N	32	74	44	138	94	66	94	70	93	57
p: 1	0.016	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
p: 2	0.000	0.000	0.000	0.004	0.000	0.000	0.000	0.000	0.000	0.000
p: 3	0.016	0.000	0.000	0.004	0.000	0.045	0.000	0.000	0.000	0.000
p: 4	0.016	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
p: 5	0.031	0.000	0.000	0.000	0.000	0.008	0.000	0.007	0.000	0.000
p: 6	0.047	0.000	0.000	0.004	0.000	0.008	0.005	0.000	0.005	0.009
p: 7	0.016	0.014	0.034	0.051	0.016	0.008	0.011	0.007	0.027	0.061
p: 8	0.016	0.000	0.011	0.004	0.000	0.015	0.016	0.000	0.005	0.018
p: 9	0.000	0.020	0.023	0.022	0.021	0.015	0.016	0.029	0.016	0.018
p: 10	0.047	0.047	0.102	0.116	0.064	0.045	0.080	0.114	0.059	0.070
p: 11	0.047	0.135	0.114	0.080	0.080	0.159	0.085	0.057	0.081	0.184
p: 12	0.000	0.122	0.091	0.062	0.027	0.030	0.090	0.050	0.038	0.096
p: 13	0.047	0.041	0.091	0.098	0.080	0.106	0.112	0.100	0.032	0.061
p: 14	0.094	0.000	0.000	0.004	0.005	0.008	0.005	0.021	0.016	0.009
p: 15	0.016	0.000	0.023	0.000	0.011	0.015	0.011	0.043	0.005	0.018
p: 16	0.047	0.020	0.045	0.014	0.064	0.023	0.059	0.043	0.070	0.026
p: 17	0.016	0.007	0.000	0.043	0.016	0.045	0.027	0.029	0.011	0.026
p: 18	0.078	0.007	0.080	0.069	0.080	0.045	0.064	0.057	0.086	0.053
p: 19	0.250	0.000	0.023	0.062	0.021	0.076	0.048	0.043	0.086	0.035
p: 20	0.047	0.081	0.068	0.054	0.138	0.098	0.090	0.079	0.086	0.061
p: 21	0.031	0.027	0.045	0.072	0.074	0.015	0.053	0.071	0.048	0.061
p: 22	0.016	0.074	0.034	0.054	0.069	0.053	0.037	0.064	0.065	0.018
p: 23	0.031	0.014	0.011	0.043	0.032	0.045	0.053	0.057	0.043	0.061
p: 24	0.031	0.041	0.068	0.014	0.016	0.038	0.016	0.007	0.011	0.009
p: 25	0.016	0.189	0.045	0.040	0.037	0.008	0.037	0.036	0.043	0.061
p: 26	0.000	0.014	0.023	0.040	0.048	0.023	0.016	0.021	0.059	0.009
p: 27	0.016	0.034	0.034	0.011	0.021	0.008	0.016	0.014	0.032	0.018
p: 28	0.000	0.047	0.011	0.011	0.005	0.000	0.016	0.007	0.011	0.000
p: 29	0.016	0.007	0.000	0.004	0.005	0.000	0.000	0.000	0.000	0.000

Appendix 3 (continued)

p: 30	0.000	0.020	0.000	0.000	0.000	0.008	0.005	0.007	0.000	0.018
p: 31	0.000	0.000	0.000	0.004	0.027	0.030	0.016	0.007	0.022	0.000
p: 32	0.000	0.027	0.011	0.007	0.021	0.023	0.005	0.007	0.005	0.000
p: 33	0.000	0.000	0.000	0.004	0.011	0.000	0.005	0.000	0.005	0.000
p: 34	0.000	0.000	0.000	0.000	0.005	0.000	0.000	0.000	0.005	0.000
p: 35	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.007	0.005	0.000
p: 36	0.000	0.007	0.000	0.007	0.000	0.000	0.000	0.000	0.016	0.000
p: 37	0.000	0.007	0.011	0.000	0.000	0.000	0.000	0.000	0.000	0.000
p: 38	0.000	0.000	0.000	0.000	0.005	0.000	0.000	0.000	0.005	0.000
p: 39	0.000	0.000	0.000	0.000	0.000	0.000	0.005	0.014	0.000	0.000
OTS213										
N	32	79	47	142	95	67	92	69	90	60
p: 1	0.000	0.000	0.021	0.000	0.005	0.000	0.000	0.000	0.000	0.000
p: 2	0.000	0.006	0.000	0.000	0.000	0.015	0.000	0.000	0.000	0.008
p: 3	0.000	0.019	0.011	0.007	0.005	0.000	0.000	0.000	0.022	0.000
p: 4	0.000	0.000	0.032	0.007	0.026	0.037	0.011	0.014	0.039	0.058
p: 5	0.000	0.146	0.202	0.180	0.147	0.119	0.185	0.138	0.167	0.183
p: 6	0.016	0.006	0.011	0.025	0.000	0.007	0.000	0.014	0.006	0.008
p: 7	0.031	0.038	0.085	0.056	0.026	0.037	0.033	0.043	0.067	0.083
p: 8	0.000	0.013	0.011	0.039	0.026	0.082	0.087	0.043	0.067	0.025
p: 9	0.078	0.019	0.000	0.000	0.016	0.007	0.022	0.000	0.000	0.008
p: 10	0.078	0.038	0.032	0.000	0.005	0.007	0.005	0.000	0.000	0.000
p: 11	0.000	0.070	0.074	0.046	0.016	0.030	0.022	0.007	0.006	0.025
p: 12	0.000	0.013	0.032	0.021	0.011	0.030	0.022	0.058	0.039	0.025
p: 13	0.047	0.032	0.032	0.056	0.095	0.037	0.054	0.051	0.022	0.033
p: 14	0.000	0.006	0.000	0.000	0.011	0.007	0.011	0.000	0.006	0.008
p: 15	0.016	0.013	0.021	0.018	0.032	0.030	0.016	0.014	0.006	0.017
p: 16	0.125	0.006	0.000	0.018	0.042	0.000	0.000	0.007	0.028	0.008
p: 17	0.172	0.063	0.011	0.004	0.021	0.022	0.033	0.036	0.039	0.000
p: 18	0.016	0.082	0.043	0.056	0.084	0.104	0.114	0.065	0.061	0.033
p: 19	0.047	0.228	0.138	0.222	0.189	0.172	0.201	0.232	0.189	0.167
p: 20	0.078	0.095	0.064	0.060	0.053	0.082	0.054	0.109	0.100	0.092
p: 21	0.031	0.000	0.021	0.004	0.016	0.000	0.005	0.014	0.000	0.008
p: 22	0.063	0.019	0.032	0.007	0.032	0.015	0.016	0.036	0.006	0.000
p: 23	0.125	0.000	0.011	0.021	0.016	0.037	0.005	0.007	0.017	0.017
p: 24	0.016	0.006	0.000	0.004	0.011	0.007	0.005	0.000	0.000	0.000
p: 25	0.000	0.006	0.000	0.000	0.021	0.007	0.005	0.000	0.000	0.008
p: 26	0.000	0.019	0.053	0.092	0.032	0.052	0.022	0.036	0.017	0.025
p: 27	0.063	0.000	0.011	0.007	0.000	0.000	0.000	0.007	0.000	0.000
p: 28	0.000	0.000	0.000	0.000	0.005	0.000	0.000	0.000	0.000	0.008

Appendix 3 (continued)

p: 29	0.000	0.044	0.000	0.004	0.026	0.007	0.022	0.014	0.022	0.083
p: 30	0.000	0.000	0.011	0.007	0.011	0.000	0.011	0.000	0.000	0.000
p: 31	0.000	0.000	0.021	0.028	0.011	0.007	0.016	0.014	0.011	0.017
p: 32	0.000	0.000	0.000	0.007	0.000	0.007	0.000	0.000	0.017	0.000
p: 33	0.000	0.000	0.021	0.004	0.000	0.000	0.000	0.000	0.000	0.000
p: 34	0.000	0.013	0.000	0.000	0.011	0.030	0.022	0.036	0.050	0.050
p: 35	0.000	0.000	0.000	0.004	0.000	0.000	0.000	0.000	0.000	0.000
OTS9										
N	33	79	51	144	94	67	93	71	94	62
p: 1	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.011	0.000
p: 2	0.045	0.000	0.000	0.007	0.021	0.000	0.005	0.000	0.000	0.000
p: 3	0.667	0.854	0.765	0.816	0.782	0.776	0.823	0.937	0.872	0.887
p: 4	0.212	0.019	0.039	0.007	0.032	0.007	0.022	0.000	0.027	0.000
p: 5	0.076	0.127	0.196	0.170	0.165	0.209	0.151	0.063	0.090	0.113
p: 6	0.000	0.000	0.000	0.000	0.000	0.007	0.000	0.000	0.000	0.000
OTS211										
N	33	76	44	141	92	63	93	70	92	49
p: 1	0.000	0.020	0.011	0.046	0.043	0.040	0.027	0.007	0.038	0.020
p: 2	0.000	0.000	0.023	0.000	0.000	0.000	0.000	0.000	0.000	0.000
p: 3	0.000	0.000	0.034	0.007	0.000	0.000	0.005	0.000	0.000	0.000
p: 4	0.000	0.072	0.011	0.014	0.005	0.024	0.011	0.007	0.016	0.000
p: 5	0.000	0.020	0.023	0.000	0.000	0.000	0.005	0.014	0.000	0.000
p: 6	0.000	0.053	0.023	0.021	0.000	0.000	0.000	0.021	0.022	0.000
p: 7	0.030	0.007	0.023	0.000	0.000	0.000	0.000	0.000	0.000	0.000
p: 8	0.091	0.007	0.023	0.021	0.033	0.056	0.032	0.036	0.065	0.041
p: 9	0.091	0.066	0.068	0.078	0.065	0.063	0.075	0.043	0.060	0.041
p: 10	0.015	0.125	0.250	0.188	0.250	0.167	0.167	0.229	0.212	0.265
p: 11	0.000	0.000	0.023	0.032	0.054	0.016	0.016	0.007	0.043	0.031
p: 12	0.000	0.053	0.011	0.050	0.027	0.087	0.005	0.036	0.027	0.102
p: 13	0.000	0.046	0.023	0.043	0.038	0.048	0.038	0.021	0.022	0.020
p: 14	0.061	0.112	0.080	0.064	0.087	0.119	0.134	0.121	0.060	0.051
p: 15	0.030	0.020	0.034	0.124	0.049	0.048	0.075	0.121	0.065	0.051
p: 16	0.015	0.046	0.023	0.106	0.033	0.071	0.032	0.071	0.082	0.092
p: 17	0.106	0.105	0.114	0.085	0.136	0.056	0.167	0.114	0.087	0.082
p: 18	0.152	0.066	0.068	0.032	0.022	0.063	0.032	0.036	0.027	0.082
p: 19	0.076	0.099	0.034	0.032	0.098	0.079	0.118	0.043	0.076	0.020
p: 20	0.091	0.046	0.068	0.018	0.027	0.000	0.011	0.014	0.043	0.010
p: 21	0.015	0.020	0.023	0.039	0.005	0.048	0.016	0.036	0.033	0.041
p: 22	0.045	0.020	0.000	0.000	0.027	0.016	0.027	0.007	0.016	0.041
p: 23	0.015	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000

Appendix 3 (continued)

p: 24	0.000	0.000	0.000	0.000	0.000	0.000	0.005	0.007	0.000	0.010
p: 25	0.015	0.000	0.011	0.000	0.000	0.000	0.000	0.000	0.005	0.000
p: 26	0.121	0.000	0.000	0.000	0.000	0.000	0.000	0.007	0.000	0.000
p: 27	0.015	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
p: 28	0.015	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
OGO4										
N	32	66	51	143	95	67	94	72	94	61
p: 1	0.000	0.038	0.098	0.094	0.132	0.119	0.117	0.083	0.080	0.107
p: 2	0.000	0.008	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
p: 3	0.031	0.538	0.451	0.465	0.321	0.343	0.319	0.368	0.426	0.369
p: 4	0.000	0.000	0.010	0.000	0.000	0.000	0.000	0.000	0.000	0.000
p: 5	0.000	0.008	0.000	0.003	0.000	0.007	0.000	0.000	0.011	0.000
p: 6	0.000	0.000	0.000	0.007	0.000	0.000	0.000	0.000	0.000	0.000
p: 7	0.047	0.000	0.020	0.000	0.000	0.000	0.000	0.000	0.005	0.016
p: 8	0.000	0.295	0.294	0.297	0.342	0.358	0.356	0.368	0.346	0.402
p: 9	0.000	0.038	0.059	0.042	0.026	0.030	0.043	0.056	0.043	0.033
p: 10	0.172	0.000	0.010	0.021	0.021	0.000	0.005	0.021	0.005	0.016
p: 11	0.266	0.045	0.049	0.052	0.068	0.082	0.096	0.042	0.053	0.041
p: 12	0.344	0.030	0.000	0.017	0.079	0.060	0.059	0.035	0.027	0.016
p: 13	0.000	0.000	0.010	0.000	0.000	0.000	0.000	0.021	0.000	0.000
p: 14	0.063	0.000	0.000	0.000	0.011	0.000	0.005	0.007	0.005	0.000
p: 15	0.078	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
OTSG474										
N	33	67	50	142	94	66	94	70	93	58
p: 1	0.000	0.060	0.070	0.018	0.005	0.008	0.000	0.050	0.038	0.026
p: 2	0.924	0.134	0.150	0.162	0.080	0.106	0.117	0.086	0.194	0.172
p: 3	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.007	0.000	0.000
p: 4	0.045	0.328	0.390	0.338	0.426	0.371	0.394	0.393	0.387	0.345
p: 5	0.000	0.007	0.000	0.011	0.000	0.000	0.005	0.007	0.011	0.009
p: 6	0.000	0.022	0.010	0.000	0.005	0.008	0.000	0.000	0.000	0.017
p: 7	0.000	0.127	0.100	0.102	0.080	0.152	0.122	0.100	0.065	0.095
p: 8	0.030	0.157	0.210	0.299	0.282	0.295	0.213	0.264	0.237	0.276
p: 9	0.000	0.082	0.020	0.046	0.080	0.053	0.117	0.079	0.054	0.009
p: 10	0.000	0.007	0.010	0.014	0.000	0.000	0.005	0.000	0.005	0.017
p: 11	0.000	0.022	0.030	0.007	0.011	0.008	0.005	0.000	0.005	0.026
p: 12	0.000	0.022	0.010	0.004	0.032	0.000	0.021	0.014	0.005	0.009
p: 13	0.000	0.030	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
SSA408										
N	33	74	49	142	92	47	95	62	94	26
p: 1	0.030	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.005	0.000

Appendix 3 (continued)

p: 2	0.076	0.000	0.010	0.004	0.000	0.000	0.000	0.000	0.000	0.000
p: 3	0.000	0.034	0.000	0.004	0.022	0.011	0.000	0.008	0.000	0.019
p: 4	0.258	0.095	0.071	0.063	0.082	0.074	0.063	0.161	0.048	0.019
p: 5	0.061	0.034	0.041	0.049	0.043	0.032	0.063	0.024	0.032	0.096
p: 6	0.000	0.000	0.020	0.014	0.016	0.021	0.042	0.048	0.021	0.038
p: 7	0.045	0.149	0.173	0.099	0.201	0.223	0.184	0.202	0.154	0.115
p: 8	0.000	0.014	0.020	0.046	0.049	0.074	0.037	0.016	0.037	0.000
p: 9	0.015	0.007	0.031	0.067	0.038	0.021	0.047	0.016	0.032	0.038
p: 10	0.015	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
p: 11	0.121	0.068	0.020	0.046	0.049	0.074	0.058	0.016	0.032	0.019
p: 12	0.152	0.027	0.051	0.028	0.038	0.043	0.026	0.056	0.069	0.096
p: 13	0.000	0.088	0.082	0.060	0.092	0.085	0.079	0.056	0.122	0.115
p: 14	0.000	0.196	0.153	0.165	0.120	0.128	0.142	0.161	0.112	0.154
p: 15	0.061	0.061	0.133	0.070	0.103	0.074	0.100	0.097	0.128	0.135
p: 16	0.030	0.000	0.000	0.011	0.000	0.000	0.000	0.000	0.000	0.000
p: 17	0.136	0.014	0.000	0.032	0.005	0.000	0.000	0.000	0.011	0.000
p: 18	0.000	0.000	0.000	0.004	0.011	0.000	0.000	0.000	0.000	0.000
p: 19	0.000	0.047	0.010	0.000	0.000	0.000	0.000	0.024	0.000	0.000
p: 20	0.000	0.000	0.010	0.000	0.011	0.000	0.000	0.000	0.016	0.000
p: 21	0.000	0.000	0.010	0.004	0.005	0.000	0.016	0.024	0.000	0.000
p: 22	0.000	0.047	0.051	0.053	0.011	0.053	0.037	0.032	0.016	0.038
p: 23	0.000	0.047	0.020	0.028	0.011	0.000	0.032	0.000	0.016	0.000
p: 24	0.000	0.027	0.041	0.035	0.027	0.043	0.026	0.008	0.037	0.077
p: 25	0.000	0.027	0.031	0.035	0.022	0.021	0.021	0.016	0.048	0.019
p: 26	0.000	0.020	0.010	0.032	0.022	0.021	0.016	0.016	0.021	0.000
p: 27	0.000	0.000	0.000	0.018	0.011	0.000	0.011	0.016	0.005	0.019
p: 28	0.000	0.000	0.010	0.032	0.011	0.000	0.000	0.000	0.037	0.000
p: 29	0.000	0.000	0.000	0.004	0.000	0.000	0.000	0.000	0.000	0.000
OGO2										
N	33	78	50	136	90	47	89	64	93	31
p: 1	0.000	0.077	0.110	0.195	0.172	0.170	0.096	0.094	0.124	0.145
p: 2	0.000	0.026	0.030	0.022	0.017	0.011	0.017	0.008	0.000	0.016
p: 3	0.000	0.026	0.040	0.011	0.017	0.021	0.039	0.008	0.027	0.032
p: 4	0.227	0.083	0.020	0.011	0.022	0.032	0.017	0.008	0.005	0.000
p: 5	0.515	0.006	0.010	0.018	0.000	0.021	0.022	0.000	0.070	0.065
p: 6	0.015	0.051	0.000	0.063	0.044	0.021	0.034	0.031	0.032	0.065
p: 7	0.015	0.378	0.300	0.235	0.300	0.266	0.326	0.344	0.274	0.290
p: 8	0.152	0.135	0.170	0.265	0.167	0.149	0.253	0.258	0.199	0.177
p: 9	0.045	0.006	0.010	0.007	0.006	0.021	0.006	0.008	0.005	0.000
p: 10	0.000	0.006	0.000	0.007	0.011	0.000	0.000	0.016	0.011	0.000

Appendix 3 (continued)

p: 11	0.015	0.141	0.150	0.110	0.183	0.202	0.129	0.125	0.161	0.113
p: 12	0.000	0.000	0.010	0.000	0.000	0.000	0.000	0.000	0.000	0.000
p: 13	0.000	0.006	0.000	0.004	0.000	0.000	0.000	0.000	0.000	0.000
p: 14	0.015	0.051	0.150	0.051	0.056	0.085	0.062	0.102	0.081	0.097
p: 15	0.000	0.006	0.000	0.000	0.006	0.000	0.000	0.000	0.011	0.000
OTS3										
N	33	76	37	144	93	51	95	67	94	40
p: 1	0.000	0.007	0.014	0.000	0.000	0.000	0.000	0.000	0.000	0.000
p: 2	0.000	0.000	0.014	0.000	0.000	0.000	0.000	0.007	0.011	0.000
p: 3	0.000	0.007	0.000	0.028	0.005	0.000	0.005	0.000	0.005	0.013
p: 4	0.121	0.007	0.014	0.056	0.000	0.010	0.026	0.037	0.011	0.013
p: 5	0.197	0.309	0.270	0.313	0.285	0.225	0.237	0.194	0.293	0.263
p: 6	0.682	0.289	0.230	0.219	0.328	0.333	0.379	0.433	0.282	0.300
p: 7	0.000	0.184	0.230	0.149	0.140	0.147	0.168	0.187	0.197	0.138
p: 8	0.000	0.072	0.122	0.063	0.065	0.059	0.079	0.022	0.059	0.063
p: 9	0.000	0.000	0.000	0.000	0.000	0.020	0.000	0.000	0.000	0.000
p: 10	0.000	0.118	0.095	0.170	0.172	0.206	0.105	0.112	0.128	0.188
p: 11	0.000	0.007	0.014	0.003	0.005	0.000	0.000	0.007	0.016	0.025
OTS212										
N	32	76	27	137	91	46	91	57	91	22
p: 1	0.000	0.000	0.019	0.004	0.005	0.000	0.011	0.000	0.000	0.000
p: 2	0.031	0.059	0.074	0.066	0.077	0.120	0.049	0.088	0.055	0.023
p: 3	0.063	0.086	0.037	0.095	0.082	0.065	0.099	0.114	0.104	0.091
p: 4	0.109	0.178	0.148	0.204	0.148	0.054	0.203	0.158	0.203	0.205
p: 5	0.000	0.000	0.000	0.000	0.000	0.011	0.000	0.000	0.000	0.000
p: 6	0.156	0.125	0.111	0.157	0.121	0.163	0.049	0.035	0.176	0.136
p: 7	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.009	0.000	0.000
p: 8	0.031	0.204	0.111	0.106	0.143	0.120	0.115	0.114	0.093	0.205
p: 9	0.000	0.000	0.000	0.000	0.000	0.022	0.000	0.000	0.000	0.023
p: 10	0.125	0.000	0.019	0.033	0.033	0.033	0.011	0.026	0.022	0.000
p: 11	0.016	0.046	0.074	0.102	0.115	0.043	0.038	0.035	0.055	0.068
p: 12	0.000	0.000	0.000	0.000	0.000	0.011	0.000	0.000	0.000	0.000
p: 13	0.234	0.079	0.111	0.102	0.104	0.152	0.225	0.167	0.137	0.091
p: 14	0.000	0.000	0.019	0.000	0.000	0.000	0.000	0.000	0.000	0.000
p: 15	0.063	0.105	0.148	0.055	0.110	0.065	0.077	0.088	0.055	0.045
p: 16	0.016	0.020	0.037	0.055	0.033	0.000	0.011	0.061	0.011	0.023
p: 17	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.023
p: 18	0.000	0.000	0.000	0.000	0.011	0.043	0.027	0.009	0.011	0.000
p: 19	0.000	0.000	0.000	0.000	0.000	0.011	0.000	0.000	0.000	0.000
p: 20	0.000	0.020	0.000	0.004	0.000	0.000	0.016	0.018	0.000	0.023

Appendix 3 (continued)

p: 21	0.000	0.000	0.019	0.000	0.000	0.000	0.000	0.000	0.000	0.000
p: 22	0.063	0.013	0.000	0.000	0.000	0.000	0.038	0.061	0.027	0.023
p: 23	0.016	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
p: 24	0.016	0.000	0.000	0.000	0.000	0.011	0.000	0.000	0.000	0.000
p: 25	0.016	0.013	0.019	0.004	0.005	0.000	0.005	0.000	0.005	0.000
p: 26	0.016	0.020	0.000	0.004	0.000	0.000	0.011	0.000	0.000	0.000
p: 27	0.031	0.026	0.037	0.000	0.000	0.000	0.000	0.009	0.000	0.000
p: 28	0.000	0.000	0.000	0.007	0.011	0.054	0.011	0.009	0.044	0.000
p: 29	0.000	0.000	0.000	0.000	0.000	0.011	0.000	0.000	0.000	0.023
p: 30	0.000	0.000	0.019	0.000	0.000	0.000	0.000	0.000	0.000	0.000
p: 31	0.000	0.000	0.000	0.004	0.000	0.000	0.000	0.000	0.000	0.000
p: 32	0.000	0.000	0.000	0.000	0.000	0.011	0.000	0.000	0.000	0.000
p: 33	0.000	0.007	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
OKI100										
N	32	62	45	144	93	62	94	70	94	58
p: 1	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.017
p: 2	0.000	0.000	0.011	0.000	0.022	0.008	0.005	0.000	0.011	0.000
p: 3	0.000	0.040	0.000	0.003	0.000	0.000	0.011	0.014	0.005	0.009
p: 4	0.000	0.000	0.033	0.017	0.022	0.016	0.005	0.036	0.027	0.009
p: 5	0.000	0.016	0.033	0.007	0.000	0.000	0.027	0.043	0.021	0.009
p: 6	0.000	0.024	0.000	0.000	0.000	0.000	0.005	0.007	0.000	0.000
p: 7	0.000	0.016	0.022	0.028	0.097	0.097	0.011	0.050	0.043	0.078
p: 8	0.016	0.016	0.011	0.017	0.070	0.040	0.027	0.021	0.043	0.043
p: 9	0.000	0.008	0.000	0.014	0.011	0.008	0.032	0.086	0.005	0.009
p: 10	0.000	0.032	0.022	0.031	0.005	0.008	0.027	0.036	0.048	0.017
p: 11	0.000	0.185	0.044	0.021	0.011	0.016	0.011	0.021	0.032	0.069
p: 12	0.016	0.056	0.089	0.045	0.113	0.065	0.096	0.107	0.064	0.086
p: 13	0.188	0.145	0.211	0.181	0.151	0.177	0.128	0.136	0.149	0.129
p: 14	0.297	0.113	0.033	0.167	0.134	0.161	0.122	0.079	0.117	0.086
p: 15	0.172	0.097	0.100	0.104	0.113	0.105	0.112	0.093	0.080	0.138
p: 16	0.000	0.056	0.111	0.097	0.043	0.081	0.090	0.064	0.128	0.086
p: 17	0.016	0.040	0.067	0.038	0.054	0.024	0.048	0.021	0.037	0.026
p: 18	0.016	0.008	0.056	0.028	0.032	0.024	0.000	0.000	0.032	0.026
p: 19	0.047	0.008	0.022	0.007	0.005	0.032	0.016	0.000	0.000	0.000
p: 20	0.031	0.016	0.011	0.021	0.005	0.016	0.032	0.043	0.016	0.034
p: 21	0.078	0.056	0.033	0.049	0.048	0.032	0.032	0.029	0.027	0.034
p: 22	0.000	0.008	0.022	0.042	0.022	0.016	0.059	0.007	0.000	0.017
p: 23	0.031	0.008	0.011	0.003	0.016	0.000	0.016	0.014	0.016	0.000
p: 24	0.016	0.008	0.000	0.010	0.005	0.000	0.000	0.000	0.011	0.000
p: 25	0.016	0.008	0.011	0.035	0.011	0.008	0.021	0.014	0.027	0.017

Appendix 3 (continued)

p: 26	0.047	0.000	0.011	0.007	0.005	0.000	0.021	0.007	0.016	0.017
p: 27	0.016	0.024	0.022	0.024	0.005	0.056	0.048	0.064	0.032	0.026
p: 28	0.000	0.000	0.000	0.000	0.000	0.008	0.000	0.000	0.005	0.009
p: 29	0.000	0.008	0.011	0.003	0.000	0.000	0.000	0.007	0.005	0.000
p: 30	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.005	0.000
p: 31	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.009
OTS201										
N	33	72	48	143	94	65	94	71	93	60
p: 1	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.007	0.000	0.000
p: 2	0.000	0.000	0.000	0.007	0.005	0.000	0.000	0.000	0.005	0.000
p: 3	0.000	0.028	0.063	0.084	0.032	0.085	0.032	0.070	0.011	0.050
p: 4	0.045	0.007	0.010	0.000	0.000	0.000	0.016	0.021	0.005	0.025
p: 5	0.015	0.035	0.021	0.000	0.005	0.000	0.005	0.007	0.000	0.000
p: 6	0.061	0.097	0.021	0.059	0.032	0.062	0.037	0.028	0.059	0.042
p: 7	0.182	0.104	0.052	0.080	0.053	0.038	0.080	0.028	0.043	0.108
p: 8	0.091	0.069	0.042	0.091	0.048	0.077	0.080	0.106	0.097	0.058
p: 9	0.182	0.042	0.094	0.028	0.037	0.031	0.016	0.063	0.081	0.075
p: 10	0.015	0.076	0.073	0.031	0.080	0.069	0.117	0.092	0.022	0.067
p: 11	0.045	0.007	0.104	0.070	0.080	0.108	0.059	0.070	0.124	0.133
p: 12	0.030	0.000	0.010	0.007	0.016	0.023	0.011	0.007	0.011	0.008
p: 13	0.061	0.007	0.031	0.049	0.005	0.000	0.011	0.000	0.043	0.017
p: 14	0.030	0.014	0.042	0.007	0.027	0.000	0.032	0.000	0.005	0.008
p: 15	0.076	0.069	0.083	0.056	0.059	0.077	0.074	0.056	0.027	0.033
p: 16	0.121	0.215	0.052	0.115	0.138	0.092	0.101	0.134	0.129	0.117
p: 17	0.015	0.042	0.031	0.031	0.112	0.100	0.059	0.021	0.081	0.042
p: 18	0.000	0.146	0.188	0.220	0.223	0.208	0.165	0.232	0.204	0.142
p: 19	0.000	0.028	0.063	0.035	0.048	0.015	0.090	0.035	0.027	0.058
p: 20	0.000	0.014	0.021	0.028	0.000	0.008	0.011	0.021	0.027	0.017
p: 21	0.015	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
p: 22	0.000	0.000	0.000	0.000	0.000	0.008	0.000	0.000	0.000	0.000
p: 23	0.015	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
p: 24	0.000	0.000	0.000	0.000	0.000	0.000	0.005	0.000	0.000	0.000
OMM1080										
N	32	64	37	143	93	50	94	71	94	45
p: 1	0.000	0.000	0.027	0.017	0.000	0.000	0.011	0.000	0.032	0.000
p: 2	0.000	0.008	0.041	0.024	0.022	0.020	0.027	0.000	0.069	0.000
p: 3	0.000	0.000	0.000	0.007	0.011	0.020	0.000	0.000	0.011	0.000
p: 4	0.000	0.000	0.000	0.000	0.005	0.000	0.048	0.000	0.000	0.000
p: 5	0.000	0.023	0.000	0.021	0.011	0.020	0.016	0.000	0.011	0.000
p: 6	0.000	0.000	0.000	0.003	0.000	0.000	0.000	0.000	0.000	0.000

Appendix 3 (continued)

p: 7	0.016	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
p: 8	0.016	0.000	0.027	0.010	0.000	0.010	0.021	0.007	0.016	0.000
p: 9	0.016	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
p: 10	0.000	0.008	0.041	0.000	0.005	0.010	0.000	0.000	0.000	0.000
p: 11	0.016	0.000	0.014	0.031	0.032	0.010	0.005	0.000	0.016	0.022
p: 12	0.000	0.063	0.027	0.028	0.027	0.060	0.048	0.042	0.027	0.011
p: 13	0.016	0.008	0.095	0.035	0.043	0.060	0.032	0.014	0.064	0.078
p: 14	0.000	0.141	0.000	0.038	0.027	0.030	0.043	0.021	0.016	0.000
p: 15	0.000	0.000	0.014	0.003	0.000	0.000	0.000	0.000	0.005	0.000
p: 16	0.000	0.000	0.000	0.000	0.016	0.020	0.011	0.021	0.005	0.022
p: 17	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.007	0.005	0.056
p: 18	0.000	0.016	0.000	0.024	0.022	0.050	0.011	0.028	0.011	0.044
p: 19	0.016	0.000	0.000	0.010	0.000	0.000	0.000	0.007	0.000	0.000
p: 20	0.000	0.008	0.027	0.014	0.005	0.020	0.027	0.042	0.016	0.011
p: 21	0.031	0.008	0.000	0.007	0.011	0.040	0.011	0.049	0.000	0.000
p: 22	0.000	0.000	0.014	0.000	0.032	0.000	0.016	0.028	0.011	0.033
p: 23	0.094	0.000	0.014	0.000	0.027	0.010	0.011	0.007	0.011	0.000
p: 24	0.047	0.000	0.014	0.017	0.097	0.090	0.032	0.021	0.016	0.011
p: 25	0.047	0.109	0.081	0.021	0.032	0.020	0.032	0.077	0.037	0.044
p: 26	0.078	0.023	0.000	0.042	0.005	0.030	0.037	0.042	0.085	0.100
p: 27	0.031	0.086	0.054	0.063	0.027	0.050	0.101	0.063	0.074	0.100
p: 28	0.141	0.055	0.095	0.119	0.070	0.100	0.032	0.106	0.106	0.133
p: 29	0.047	0.109	0.054	0.098	0.032	0.090	0.080	0.106	0.090	0.144
p: 30	0.031	0.078	0.108	0.042	0.070	0.090	0.064	0.099	0.032	0.033
p: 31	0.031	0.047	0.068	0.115	0.134	0.060	0.069	0.070	0.069	0.033
p: 32	0.016	0.063	0.054	0.056	0.027	0.010	0.043	0.035	0.011	0.022
p: 33	0.000	0.000	0.027	0.028	0.022	0.030	0.016	0.021	0.016	0.000
p: 34	0.047	0.000	0.027	0.010	0.022	0.010	0.032	0.035	0.005	0.000
p: 35	0.109	0.039	0.014	0.003	0.005	0.000	0.011	0.000	0.005	0.011
p: 36	0.000	0.000	0.000	0.017	0.022	0.000	0.021	0.000	0.016	0.011
p: 37	0.000	0.023	0.000	0.007	0.054	0.010	0.021	0.000	0.005	0.022
p: 38	0.000	0.047	0.027	0.028	0.038	0.020	0.011	0.028	0.027	0.022
p: 39	0.016	0.008	0.000	0.024	0.005	0.000	0.027	0.014	0.005	0.000
p: 40	0.031	0.000	0.014	0.003	0.005	0.000	0.005	0.000	0.011	0.033
p: 41	0.063	0.008	0.014	0.003	0.011	0.000	0.016	0.000	0.005	0.000
p: 42	0.031	0.016	0.000	0.017	0.016	0.010	0.005	0.000	0.059	0.000
p: 43	0.016	0.000	0.000	0.007	0.011	0.000	0.011	0.007	0.000	0.000
p: 44	0.000	0.008	0.014	0.000	0.000	0.000	0.000	0.000	0.000	0.000

Appendix 3 (continued)

3TKU										
N	31	79	50	139	94	67	95	71	93	62
p: 1	0.565	0.468	0.430	0.439	0.484	0.470	0.489	0.479	0.468	0.468
p: 2	0.435	0.532	0.570	0.561	0.516	0.530	0.511	0.521	0.532	0.532
10TKU										
N	33	79	31	142	95	53	94	66	94	37
p: 1	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.008	0.000	0.000
p: 2	0.000	0.000	0.000	0.000	0.011	0.000	0.011	0.000	0.000	0.000
p: 3	0.758	0.114	0.194	0.123	0.058	0.085	0.090	0.098	0.069	0.081
p: 4	0.045	0.563	0.452	0.482	0.432	0.519	0.452	0.523	0.457	0.595
p: 5	0.182	0.323	0.306	0.380	0.468	0.377	0.426	0.348	0.452	0.257
p: 6	0.015	0.000	0.048	0.014	0.026	0.019	0.021	0.023	0.021	0.068
p: 7	0.000	0.000	0.000	0.000	0.005	0.000	0.000	0.000	0.000	0.000
13TKU										
N	30	80	42	137	95	66	95	63	94	57
p: 1	0.167	0.013	0.048	0.022	0.042	0.038	0.026	0.024	0.027	0.000
p: 2	0.033	0.500	0.607	0.453	0.495	0.492	0.458	0.421	0.426	0.465
p: 3	0.000	0.075	0.071	0.124	0.047	0.038	0.095	0.071	0.096	0.149
p: 4	0.500	0.344	0.238	0.314	0.368	0.394	0.368	0.437	0.335	0.351
p: 5	0.300	0.069	0.036	0.088	0.047	0.038	0.053	0.048	0.117	0.035
15TKU										
N	33	77	49	143	94	67	95	72	94	62
p: 1	0.000	0.000	0.000	0.000	0.000	0.007	0.000	0.000	0.000	0.000
p: 2	0.636	0.448	0.418	0.552	0.436	0.515	0.468	0.472	0.516	0.532
p: 3	0.364	0.532	0.500	0.430	0.532	0.410	0.521	0.521	0.457	0.460
p: 4	0.000	0.000	0.010	0.000	0.000	0.000	0.000	0.000	0.016	0.000
p: 5	0.000	0.019	0.041	0.017	0.032	0.052	0.011	0.007	0.011	0.000
p: 6	0.000	0.000	0.010	0.000	0.000	0.000	0.000	0.000	0.000	0.000
p: 7	0.000	0.000	0.020	0.000	0.000	0.015	0.000	0.000	0.000	0.008

Appendix 4. The number of natural origin (NOR) and hatchery origin (HOR) spring Chinook spawned at UWR hatcheries and the estimated number of spawners (HOR and NOR) on natural (in-river) spawning grounds of major UWR tribuaties, 2002-2010. The proportion of natural origin fish in the broodstock (pNOB) and proportion of hatchery origin fish on spawning grounds (pHOS) are also provided. Data are adapted from Cannon et al. 2011.

River, Year	Hatchery Broodstock			In-river Spawners		
	NOR[1]	HOR[1]	pNOB[1]	NOR[2]	HOR	pHOS[3]
McKenzie				(above Leaburg Dam)		
2002	13	1,034	0.01	3,222	1,516	0.32
2003	14	995	0.01	4,108	2,311	0.36
2004	24	985	0.02	3,950	2,035	0.34
2005	20	1,062	0.02	2,051	391	0.16
2006	100	891	0.10	1,948	291	0.13
2007	81	939	0.08	2,496	511	0.17
2008	90	1,176	0.07	1,289	210	0.14
2009	59	1,062	0.05	1,070	284	0.21
2010	21	1,575	0.01	1,214	683	0.36
North Santiam				(Bennett to Minto Dam)		
2002	4	678	0.01	103	633	0.86
2003	2	616	0.00	62	2,005	0.97
2004	12	554	0.02	146	897	0.86
2005	18	486	0.04	189	441	0.70
2006	197	347	0.36	195	396	0.67
2007	158	392	0.29	335	1,122	0.77
2008	154	348	0.31	403	149	0.27
2009	5	575	0.01	236	227	0.49
2010	27	467	0.06	238	754	0.76

[1] Adapted from Table 19 of Cannon et al. (2011)
[2] Adapted from Appendix 1 of Cannon et al. (2011)
[3] Adapted from Table 8 of Cannon et al. (2011)

Appendix 4. (continued)

River, Year	Hatchery Broodstock			In-river Spawners		
	NOR[1]	HOR[1]	pNOB[1]	NOR[2]	HOR	pHOS[3]
South Santiam				(below Foster Dam)		
2002	26	1,193	0.02	332	2,039	0.86
2003	25	1,071	0.02	200	1,338	0.87
2004	78	921	0.08	171	1,729	0.91
2005	71	1,018	0.07	279	1,050	0.79
2006	137	1,003	0.12	209	1,020	0.83
2007	89	796	0.10	232	1,057	0.82
2008	268	532	0.34	271	271	0.50
2009	2	738	0.00	775	475	0.38
2010	0	708	0.00	82	1,968	0.96
Middle Fork Willamette				(below Dexter)		
2002	5	1,655	0.00	7	133	0.95
2003	5	1,524	0.00	2	48	0.96
2004	16	1,835	0.01	4	27	0.87
2005	19	1,521	0.01	3	14	0.82
2006	45	1,663	0.03	251	-	-
2007	161	1,431	0.10	6	15	0.72
2008	105	1,395	0.07	126	57	0.31
2009	61	1,864	0.03	20	20	0.50
2010	15	1,494	0.01	5	11	0.68

[1] Adapted from Table 19 of Cannon et al. (2011)
[2] Adapted from Appendix 1 of Cannon et al. (2011)
[3] Adapted from Table 8 of Cannon et al. (2011)