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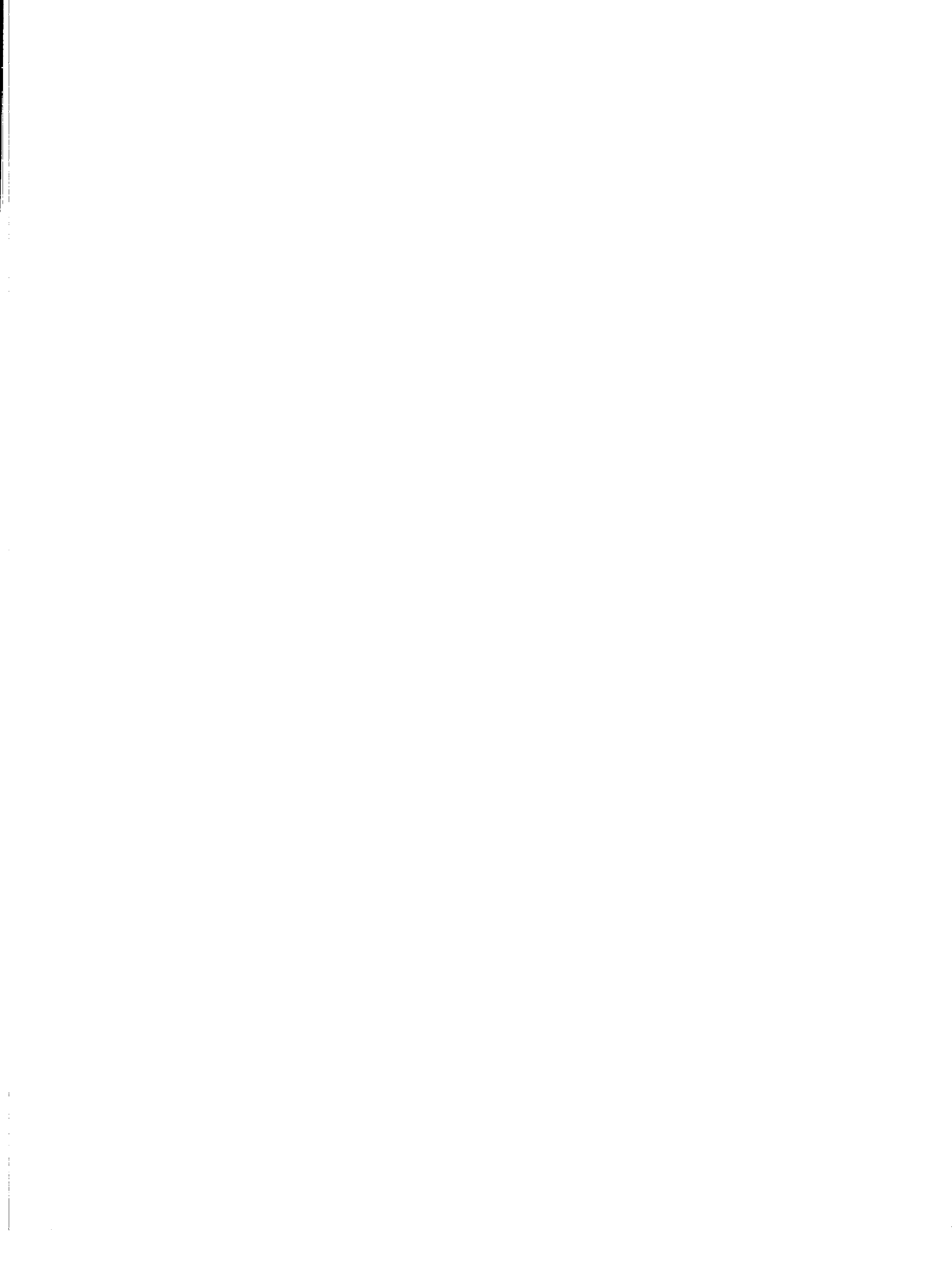
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**Molecular genetic markers and the conservation of anadromous fishes
at broad and local scales: coho salmon (*Oncorhynchus kisutch*) and
white sturgeon (*Acipenser transmontanus*) as case studies**

by

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B.Sc., University of Victoria, 1996**

**A dissertation submitted in partial fulfillment of the requirements for the degree of
DOCTOR OF PHILOSOPHY
in the Department of Biology**

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ABSTRACT

Nuclear microsatellite DNA and mitochondrial DNA variation were examined in coho salmon (*Oncorhynchus kisutch*) and white sturgeon (*Acipenser transmontanus*) populations in order to address conservation issues in each species. In coho the goal was to examine genetic structure on a broad scale, in order to facilitate the conservation of genetic resources within the species. Coho salmon were widely sampled across their North American range. In white sturgeon the goal was to characterize population structure within the Fraser River, in order to identify biologically meaningful management units within that system. White sturgeon sampling was restricted to two watersheds (the Fraser and Columbia rivers), allowing much more thorough sampling than was done for coho. For both species, the use of mitochondrial and nuclear markers proved advantageous over examining either marker alone. The coho data revealed two levels of intraspecific variation, and gave the best indication to date regarding how genetic resources might be distributed within this species. The data is useful for protecting this species' ability to evolve. In contrast, the sturgeon data identified four regions within the Fraser River between which migration is limited. The sturgeon data, therefore, facilitate prevention of extirpation of local populations within the Fraser River.

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In memory of Edith Aleen Chase

CHAPTER 1 - INTRODUCTION

Conservation biology

The Earth's biodiversity is thought to be increasingly threatened by the growth and behaviour of its human population. The field of conservation biology is the scientific community's response to elevated extinction rates and concerns over global climate change (Meffe & Carroll 1997). Mitigating anthropogenic effects on a region's biota requires knowledge of that biota. To this end conservation biologists study distributions of variation among taxa ranging from phyla to individuals (Mace *et al.* 1996). By understanding how biological diversity is distributed, it is reasoned, we can alter our behaviour so as to minimize our destructive influence. Presently this means altering the use of natural resources in order to minimize the loss of biological diversity. For example, scientific information may be used as a basis for deciding which taxa will be harvested or eliminated, and which will not (Dizon *et al.* 1992, Riddell 1993, Lesica & Allendorf 1995, Allendorf *et al.* 1997). The larger goal is that by understanding the biological world better we will value it more, and thus alter behaviours at the core of our destructive influence: reproduction and consumption (Ehrlich 1980, Avise 1996, Meffe & Carroll 1997).

Anthropogenic threats faced by endangered taxa are often divided into demographic and genetic categories. Immediate threats usually involve demographic factors (Lande 1988, Caughley 1994, Routledge & Irvine 1999). These include a wide range of influences which lead to reduction of recruitment or migration, and thus to reduced population size. Reduced population sizes then leave populations vulnerable to extinction via stochastic

events. Over evolutionary time, however, a species' ability to adapt to changing environments is based on its genetic variance (Fisher 1930). Genetic threats are based on human interference with the natural population structure of a species, and cause the quantity of intraspecific genetic variation to be reduced. Optimal species management requires consideration of both demographic and genetic factors.

A panmictic species is one in which mating is random among all individuals. Migration and gene flow are thus of no concern in managing a panmictic species and only the number of individuals need be maintained. Population structure is a concept that describes the departure of most extant species from panmixia. Migration, effective population size, mutation and natural selection act to define a species' population structure. Knowledge of population structure over a species' range provides insight regarding the distribution of that species' genetic resources and thus allows protection of those resources. The ability to estimate parameters, such as migration, on a local scale is useful for understanding demographic risks faced by populations of a species. Knowledge of population structure is thus potentially useful for minimizing both demographic and genetic risks.

The natural history of a species is often reflected in its population structure. A key concept linking species history with conservation interests is that of refugia. A refugium is a geographic region in which a species exists over long periods of time. Adjacent ephemeral populations are founded by and often share migrants with refugia. The periods of time over which refugia exist are relevant only relative to the ephemeral populations. The term "refugium" may thus be used to describe a region in which species survive for

millennia or for months while being eliminated from adjacent habitats. The relevance of refugia to conservation biology depends on the temporal and geographic scales of interest. On regional scales, refugia may act as source populations, providing adjacent regions with a continuous flow of migrants (Sedell *et al.* 1990). On an evolutionary scale refugia may define the major components of the species' genetic resources (e.g. Wood *et al.* 1994, Byun *et al.* 1997, Small *et al.* 1998b, Nesbo *et al.* 1999, Newton *et al.* 1999, McCusker *et al.* 2000).

Legislated protection of intraspecific diversity is complicated by questions regarding exactly what merits protection. Criteria for identifying targets of legislated protection need to be as unambiguous as possible. Inconsistencies in definitions of sub-species, as well as difficulties in identifying population structure within most species make generalizations troublesome. Distinct populations may be protected in the United States of America under the Endangered Species Act if they are designated Evolutionary Significant Units (ESUs). Adaptation of the ESU as a basic element of conservation management in Canada has also been suggested (McPhail & Carveth 1993). Several ideas regarding how ESUs should be defined have been put forward (Waples 1991, Dizon *et al.* 1992, Vogler & DeSalle 1994, Moritz 1996). Waples (1991) defined an ESU as a population that 1) is substantially reproductively isolated from conspecific populations and 2) represents an important component of the evolutionary legacy of the species. Substantial reproductive isolation should be strong enough to allow evolutionarily important differences to accrue in different population units. The second criterion is based on whether or not the unit makes a significant contribution to the ecological and / or genetic diversity of the species as a whole. This definition is appealing in that it

recognizes the importance of protecting a species ability to evolve, and is flexible enough to apply across a wide range of taxonomic and geographic scales. It is thus the definition commonly used in fisheries management and in this dissertation.

Molecular genetics

The field of molecular genetics has produced a large number of tools for assessing genetic variation (Li 1997, Strachan & Read 1999). Population structure is most commonly analyzed using markers which are neutral (not subject to natural selection), and for which the mutation rate is low relative to the topic of inquiry. Natural selection and mutation are both extremely complex parameters to estimate, so using markers for which they are ignored greatly simplifies analysis of population structure. Population structure is thus often described in terms of a balance between migration and effective population size using tools developed by Wright (1930, 1951) and others (summarized in Hartl & Clark 1989, Balding *et al.* 2001). DNA markers exhibit several attributes that make them the molecular tools of choice among conservation biologists. DNA markers generally require minute samples which can be drawn from a wide variety of tissues or materials, and thus do not necessitate destructive sampling (compared to protein markers). The small size of the individual samples, and the fact that they may be kept at ambient temperature, greatly simplify collection and storage. Following is a brief description of the two markers examined in this dissertation, although much more thorough reviews are available for both nuclear microsatellites (Jarne & Lagoda 1996, Ellegren 2000a, b) and mitochondrial DNA (Awise 1994, Kocher & Carleton 1997).

Satellite DNA or variable number of tandem repeats (VNTR) is a class of DNA sequence which includes microsatellites and minisatellites. It is composed of short tandemly repeated nucleotide sequences that are scattered throughout eukaryotic genomes.

Minisatellites are composed of repeated units between 10 and 75 base pairs (bp) in length, and commonly run from <500 bp to 50 kilobases (kb). Microsatellites are composed of relatively short repeat units (2-5 bp) and are often <200 bp in length. Polymorphisms at VNTR loci exist as sequence differences and as differences in the numbers of repeats. Differences in the number of repeats arise due to replication slippage, sister chromatid exchange, and unequal crossover. Although the evolutionary significance of VNTR loci is not well understood, they are assumed to be largely neutral (Chakraborty *et al.* 1991).

Microsatellite loci are subject to high strand-slippage mutation rates during DNA replication. This results in a high level of variability which makes microsatellites powerful tools for detecting recent divergences. Another result of the mutation process is that alleles often differ from one another by length and, therefore, may be distinguished by simple size-fractionation (although see Angers & Bernatchez 1997). The mutation process has also led to concern regarding the role of homoplasy and the applicability of existing analysis models to microsatellite data (Estoup *et al.* 1995, Garza & Freimer 1996). Recent studies indicate that microsatellites tend to change one or a few repeats at a time (Jones *et al.* 1999), supporting a modified stepwise mutation model (SMM). Assumptions required by existing SMMs, as well as a lack of evidence that these perform better than the more established infinite allele models (IAMs), however, have been used to argue in favor of IAM analysis (e.g. Banks *et al.* 2000).

Because the regions flanking microsatellites are generally less variable than the repeats themselves, there exists the potential to use polymerase chain reaction (PCR) primers developed from one species for characterization of another (Estoup *et al.* 1993, Olsen *et al.* 1996, Scribner *et al.* 1996, Wenburg *et al.* 1996). The likelihood of a set of primers working in two different species probably decreases with increasing phylogenetic distance (Angers *et al.* 1995). Differing success rates of such cross-species amplification among studies may result from the level of information required in each case (i.e. whether identifiable polymorphic alleles or just any PCR product is considered "success"). A microsatellite locus that is monomorphic within the groups being studied is of little use, as are loci for which PCR products are unscorable, non-Mendelian, or difficult to reproduce.

Mitochondria are the organelles in eukaryotic cells that serve as the sites for cellular respiration. Part of the legacy of their endosymbiotic origin is that mitochondria have their own genome. The mitochondrial genome is a circular molecule approximately 15 kb in length, although length varies both among and within some species. Mitochondrial haplotypes (haploid genotypes) are inherited uniparentally, generally from the maternal lineage. Mitochondrial DNA (mtDNA) is thus transmitted clonally from generation to generation. The lack of recombination greatly simplifies analysis of relationships among haplotypes relative to relationships among nuclear loci. This attribute has made mtDNA the marker of choice for phylogeographic analyses (e.g. Avise 1994).

Analysis of the mtDNA genome typically includes restriction fragment length polymorphism (RFLP) analysis or direct DNA sequencing. Since all of the genes on the

molecule are tightly linked, only a subset is usually analyzed. The control region, or D-loop, is thought to be the most variable region of the molecule and is thus commonly examined (Brown *et al.* 1986, Kocher *et al.* 1989). Limitations of mtDNA data for inferring population structure include that it only provides information about one locus in one sex. Extrapolation to the other sex and to the rest of the genome should be done cautiously, if at all.

Coho salmon and white sturgeon as conservation targets

The two species examined in this dissertation are both native to the Pacific coast of North America. The first species considered is coho salmon (*Oncorhynchus kisutch* Walbaum). The genus name "*Oncorhynchus*" means "hooked snout", and "*kisutch*" is the Kamchatkan vernacular name for this species. Members of the teleost family Salmonidae are found in rivers, lakes and oceans throughout the northern hemisphere. The Salmonidae descended from a tetraploid ancestor 50-100 million years ago (mya) (Allendorf & Thorgaard 1984). The earliest protosalmonid fossil (*Eosalmo driftwoodensis*) was found in middle Eocene deposits in western Canada (Wilson 1977). Phylogenies based on nuclear and mtDNA sequences suggest that *Oncorhynchus* diverged from a common ancestor with their Atlantic cousins, the genus *Salmo*, during the Miocene Epoch (McKay *et al.* 1996, Oohara *et al.* 1997, Phillips & Oakley 1997). Near the end of the Miocene, the genus *Oncorhynchus* underwent rapid diversification producing the four extant clades essentially instantaneously (McKay *et al.* 1996). Subsequent evolution of *Oncorhynchus* in the North Pacific has been punctuated by several glaciations, during which the species were forced into refugia. Studies of individual species of the genus *Oncorhynchus* have suggested that different species

persisted in different refugia (Wood *et al.* 1994, Small *et al.* 1998b, McCusker *et al.* 2000).

The second species considered in this dissertation is white sturgeon (*Acipenser transmontanus* Richardson). The genus name "*Acipenser*" is an old-world name for sturgeon, and "*transmontanus*" means "beyond the mountains", referring to the Pacific coast distribution of this species (Scott & Crossman 1973). Sturgeon belong to the order Acipenseriformes and are distributed throughout the northern hemisphere. Restriction of fossils and extant taxa to north of 22°N suggests that this group originated as part of the Laurasian ichthyofauna. Acipenserid fossils first appear in the Jurassic and are common and widely distributed in late Cretaceous deposits. *Acipenser* is the largest (17-18 species) and the most widely distributed genus in the order Acipenseriformes. Although sturgeon are ancient as a group, vicariance events of the Cretaceous, Tertiary and Quaternary are thought to have facilitated the divergence of extant species (Grande & Bemis 1996, Choudhury & Dick 1998).

Both coho salmon and white sturgeon were the bases of valuable fisheries to native North Americans and to early European colonists. Although coho populations are reduced compared to historical levels, commercial and sport fisheries have continued to operate to the present. A large body of research literature concerning coho and their congeners reflect their economic value over the past century. In contrast, all significant white sturgeon populations collapsed under fishing pressure in the early 20th century. Scientific literature on this species is correspondingly sparse. A recent resurgence of interest in the

white sturgeon sport fishery, as well as increasing belief in conserving this species for non-economic reasons, have lead to increased research. Even so, disparity in our knowledge of the two species is readily apparent. While anadromy, homing fidelity and reproductive structure are well documented in coho (summary in Sandercock 1991), these basic aspects of white sturgeon population biology are poorly understood.

The motivation for the present research is that habitat degradation and over-harvesting are threatening populations of many fish species throughout the Pacific coast of North America. Given our societal needs and limited conservation resources, not all populations of all species will be saved. Understanding the population structure of coho salmon and white sturgeon may guide management decisions to reduce the probability that we will drive either of these species to extinction. In coho, population structure was examined across this species' North American range. Insight regarding population structure at this geographic scale is useful for reconstructing the evolutionary history of the species and for understanding how intraspecific variation is distributed. This information is useful for protecting the ability of coho to respond to selection, and thus not go extinct. In white sturgeon, population structure was examined within the Fraser River. Knowledge of population structure at this geographic scale allows an understanding of localized patterns of migration and genetic drift. Using identified migration barriers as boundaries for management units should help reduce the probability that a species will be eliminated from a region over short temporal scales.

Coho salmon and white sturgeon are typical conservation targets in that they are large vertebrates upon which human society has placed economic and other values. It is hoped

that these two will act as “umbrella species”, in that measures taken to preserve them may also benefit less obvious species. Fishing restrictions, habitat protection and limitations on transplantation implemented to protect either of these charismatic species will potentially benefit several others.

CHAPTER 2 - COHO SALMON MICROSATELLITE DEVELOPMENT

Prior to the work described here, no microsatellite loci had been isolated from coho salmon. Three loci isolated from chinook salmon (*Oncorhynchus tshawytscha*) had successfully been used to examine coho populations (Small *et al.* 1998a, Small *et al.* 1998b). Examining a large number of independent loci is desirable in order to minimize sampling effects associated with marker choice. Therefore, characterization of additional loci was a prerequisite for the population analysis of coho. Options for identifying more loci included amplification of coho DNA using PCR primers developed in related taxa, and isolating novel loci from coho genomic DNA. This chapter is a technical description of efforts in each of these endeavors. Readers not interested in the technical details of microsatellite development may skip this chapter.

Characterization of microsatellite loci isolated in other salmonids

Amplification of coho DNA was attempted using primers isolated from other salmonids (Table 1). Genomic DNA from three individual coho was provided by Dr. John Nelson. One of the samples originated from Quinsam River, the second from Kitimat River, and the third from Whannock River.

PCRs were done in 25 μ L volume, which included 1 μ L template DNA (approx. 80ng). All PCRs described in this dissertation were done in a buffer developed by Dr. John Nelson (published in Small *et al.* 1998a): 100 pmol each primer, 80 μ M each nucleotide, 20 mM tris-pH 8.8, 2 mM MgSO₄, 10 mM KCl, 0.1% Triton X-100, 10 mM (NH₄)SO₄, 0.1

Table 1. Amplification of coho microsatellites using PCR primers isolated in other salmonid species. Ratings are as follows: - = no amplification, 1 = PCR product unscorable by methods used, 2 = clean PCR product with a single genotype observed, 3 = clean PCR product with multiple genotypes observed. T_a (°C) indicates optimal PCR annealing temperature observed.

Locus	Source	PCR primers (5'-3')	T_a	Gel conditions	Rating
<i>Ots104</i>	(Nelson & Beacham 1999)	GCACTGTATCCACCAGTA GTAGGAGTTTCATTTGAATC	58	6% 15 hours	3
<i>Ots107</i>	(Nelson & Beacham 1999)	TCAGACCAGACCTCAACA ATAGAGACCTGAATCGGTA	64	6% 15 hours	1
<i>1c</i>	(John Nelson pers comm.)	TGGAGTGATATAGTAGGC CTTTACCATTTCCCTTGC	56	10% 15 hours	2
<i>Ots100</i>	(Nelson et al. 1998)	CACCTTGCTCAATTTACC ATGAAGTGAACCTTTCAT	50	10% 18 hours	1
<i>3a</i>	(John Nelson pers comm.)	TACTCCAAAGTCAAAGACT TGTTACACCTGACGTAA	45	10% 15 hours	2
<i>Ots108 (R#1)</i>	(Nelson & Beacham 1999)	TTTCTATTAGTCTGTCACTAC TGGCAAGGAGAGACAGAG	-	-	-
<i>Ots108 (R#2)</i>	(John Nelson pers comm.)	TTTCTATTAGTCTGTCACTAC CTCGTCTCAAACACACTAAT	-	-	-
<i>Sfo 8</i>	(Angers et al. 1995)	CAAGCAGCACAGAACAGG CTTCCCCTGGAGAGGAAA	-	-	-
<i>Ssa171</i>	(O'Reilly et al. 1996)	TTATTATCCAAAGGGGTCAAAA GAGGTCGCTGGGGTTTACTAT	58	10% 15 hours	2
<i>RS1</i>	(LGL ltd. pers comm.)	AGGTTAACCCACAGGCATCAT GTGGTGCGTCCCTCTCTGAA	68	6% 14 hours	2
<i>RS2</i>	(LGL ltd. pers comm.)	CGGTTTCCGGGACACATATTA GTGCACGGCACTGCTCATACAG	60	10% 15 hours	2
<i>RS3</i>	(LGL ltd. pers comm.)	CCAATCAACCCAAATCATCCA GCAGACAGACCAGTTCCTTAC	62	10% 15 hours	2
<i>RS4</i>	(LGL ltd. pers comm.)	CCAATCAACCCAAATCATCCA GAGAACTCCTGATGGGGTCTTT	-	-	-
<i>SM60</i>	(Estoup et al. 1993)	CGGTGTGCTTGTGAGGTTTC GTCAAGTCAGCAAGCCTCAC	68	10% 15 hours	3
<i>Ots6</i>	(Banks et al. 1999)	TCTCTCCAGCACCACACA AGACAGTTTTTCCACATCC	57	10% 15 hours	2
<i>Omy 207</i>	(Olsen et al. 1996)	ACCCTAGTCATTGAGTCAGG GATCACTGTGATAGACATCG	60	10% 15 hours	3
<i>Ssa 197</i>	(O'Reilly et al. 1996)	GGGTTGAGTAGGGAGGCTTG TGGCAGGGATTTGACATAAC	56	10% 15 hours	2
<i>Oneμ11</i>	(Scribner et al. 1996)	GTTTGGATGACTCAGATGGGACT TCTATCTTTCCTGTCAACTTCCA	58	10% 12 hours	3
<i>Oneμ14</i>	(Scribner et al. 1996)	AGAAACATGAGAACAGTCTAGGT CCTTATGAGTTTGGTCTCCATGT	58	10% 15 hours	1
<i>Ssa 293</i>	(McConnell et al. 1995)	TGGTTATTTGTTTCCAGAG ATCAGATACACAGAGACGG	48	10% 15 hours	2

mg/mL bovine serum albumin. One Unit (U) of Ultratherm DNA polymerase (Eclipse) was added to each reaction. Reactions were carried out in a PTC200 thermal cycler (MJ Research) as follows: an initial denaturation of 3 min at 94°C, followed by 35 cycles of 94°C for 30 sec, 45°C for 1 min, and at 72°C for 30 sec. Once all of the cycles were completed, the reaction was cooled to 4°C.

PCR products were size-fractionated on 6% or 10% 19:1 acrylamide to bis-acrylamide gels, in 2X TAE buffer and stained with ethidium bromide. Photographs of the gels were taken digitally, and transferred to Bio Image Intelligent Quantifier 2.1.2a software (B. I. Systems Corp.).

Failed PCRs were repeated once before the primers were discarded. Where PCR product was observed, the reaction was repeated several times with the annealing temperature increasing by 2°C intervals, until an optimum was passed (Table 1). Of twenty primer sets examined, thirteen amplified a clearly resolvable product, and four of these exhibited more than a single genotype among the samples examined.

Isolation and characterization of coho salmon microsatellites

Genomic DNA was extracted (Stratagene DNA extraction kit) from the livers of 2 coho salmon and pooled in a partial *Sau3A1* digest. Fragments 300-500 base pairs long were purified from a 0.7% agarose gel using QIAEX II gel extraction kit (QIAGEN). These fragments were then ligated into the *Bam*H1 site of phosphatase treated pUC18. Plasmids were then used to transform DH5 α F'IQ *Escherichia coli* (Gibco BRL) cells.

Approximately 89×10^3 insert-bearing clones were plated and probed with the γ - ^{32}P labeled oligonucleotides (GTCT)₁₆, (CACG)₁₆, (GACA)₁₆, and (CAC)₁₆. One hundred and sixty positives were sequenced using the DYEnamic 21 M13 primer kit (Amersham) and analyzed on the ABI 377 sequencing instrument. Primers were designed for 60 of these loci with the aid of the program Primer3 (Rozen & Skaletsky 1997).

The novel PCR primers were then used to attempt to amplify loci in coho salmon, chum salmon (*Oncorhynchus keta*), sockeye salmon (*O. nerka*), rainbow trout (*O. mykiss*), cutthroat trout (*O. clarki*) and atlantic salmon (*Salmo salar*). Genomic DNA was extracted from opercular punches of 4-7 individuals of each species tested. This was done by incubating a 0.5 cm² piece of tissue in 0.2 mL of 5% Chelex (BioRad), 0.1% Tween-20, 0.1 mg/mL Proteinase K for 30 min at 50°C, followed by 15 min at 94°C. PCR was done in 25 μL volume in the buffer described on pages 11-13. Reactions were carried out in a PTC200 thermal cycler as follows: an initial denaturation of 3 min at 94°C, followed by 35 cycles of 94°C for 30 sec, 45°C for 1 min, and at 72°C for 30 sec. PCR products were fractionated on 10% 19:1 acrylamide to bis-acrylamide gel, in 2X TAE buffer and stained with ethidium bromide. Thirty primer sets (Table 2) amplified scorable products in at least one of the species (Table 3).

Table 2. Base repeats and PCR primer sequences for novel microsatellite loci.

Locus name	GenBank accession number	Base repeat	PCR primers (5'-3')
<i>Oki1</i>	AF055427	CTGT	AGGATGGCAGAGCACC CACCCATAATCACATATTCAGA
<i>Oki2</i>	AF055428	CTGT	TGACTTGAGTGCAATACTGATTCC TGAAGCATTAGGACCCTGCT
<i>Oki3</i>	AF055429	CAC	GGAGCCCCTTATTGGAAGG CTTCCAGCAGAGTGCCAG
<i>Oki4</i>	AF055430	CA	GCAACAAGATGCACAGTGTC CAACTGCACACAGGGTGA
<i>Oki5</i>	AF055907	CA	CCTTTAGCTCATGCATACGGA CCTGAGTTCGGGTAGACAA
<i>Oki6</i>	AF055431	GT	TCAACAGATAGACAGGTGACACA AACAGACAGCTAATGCAGAACG
<i>Oki7</i>	AF055432	CTGT	CTCAGCCCCTCAGCCCCTAC CCGTCAGGAAGTCCAGGAT
<i>Oki8</i>	AF055433	GT	AGCAGCTCTGTGATTGGA CCGTA AAA ACCGCAAGCAG
<i>Oki9</i>	AF055434	GT	GGGGTTTGTACCAGAGGGAG TACACACAAACACGCACGC
<i>Oki10</i>	AF055435	GTCT	GGAGTGCTGGACAGATTGG CAGCTTTTTACAAATCCTCCTG
<i>Oki11</i>	AF055436	GT	TCTGAGACAGGCAATGCAC GTTTTAAACCTCACCATTGAGT
<i>Oki13</i>	AF055438	GTGC/CA	AGTGTTGAATAAAAAAGTGCAGC CCTCTATCTGGTGCAGGTCA
<i>Oki14</i>	AF055439	GACA	GGATCCTCACAGGACAGAT CTAAAGATGAACAGCACGAA
<i>Oki15</i>	AF055439	GACA	TCTTTAGGGTCTCAGTAGATCCT ATGAACAGCACGAACCATGT
<i>Oki16</i>	AF055440	GACA	GATCGGGTAGGGGAGGAGT TGGGAGAACTACTCAGTGCAA
<i>Oki17</i>	AF055441	GT	AGGCAAAACACGGCTGTTC TCCCTGCTGCTCTGGACTAT
<i>Oki18</i>	AF055442	CCT	CTGTTGCTCGCAGGGCTA GCACCACAATATGACTGGG
<i>Oki19</i>	AF055443	CTGT	GCACAATTGGTGGCTGACTA AAATTTACGCCCTACAGTCC
<i>Oki20</i>	AF055444	CTGT	TGTCAGTTTCTGTTTCTGTTTCTG GACAGTAGAGAGGATAGAAGTTCA
<i>Oki21</i>	AF055445	CAGA	TCAGATGACACATTCCATT GCTGTCTCACACGTCACAGTC
<i>Oki22</i>	AF055446	CAGA	AGAGTCACACTCTGATGCATA CCATCTTGACCATCAAGCC
<i>Oki23</i>	AF055447	CTGT	CATCACACGCTTCTAGAGTGA CCTCATCCACGTTAGCATCA
<i>Oki24</i>	AF055448	GAG/GT	CCCAGAGAGAGGTAGAGAGGG CGTGGGCACTAGGCACTG
<i>Oki25</i>	AF055449	CTGT	AAGAGCATTGGACTGGGAAC TGGTATTGTGTTGTTGTTAAGTTG
<i>Oki26</i>	AF055450	GTCT	CACTAGGGAATAGCTGCAGAA TCTCAGATTGTCTAATGGAAGAG
<i>Oki27</i>	AF055451	GA/GACA	GGCTGGGTCTGTTACAAAT GGGCTCTCGCTGACAGACTA
<i>Oki28</i>	AF055452	CCT	TTGGAGGAGGCAGACGAG GCCCCACAGGACACAAC
<i>Oki29</i>	AF055453	CAGA	CAACTAGACCCAGCCTCACAG GGCCTTCCAGCAGAGATTA
<i>Oki30</i>	AF055454	GGT	TGACTGCTCACTCTAAAACCACA CCCCTATTCTGACCCATCC
<i>Oki31</i>	AF055455	CAGA	CCAGGACAGTCACACAGATAATG GTCCAGGGTATCGCCCTT

Table 3. Microsatellite primer assessment for loci isolated in coho salmon. Ratings (rat) are as follows: - = no amplification, 1 = PCR product unscorable by methods used, 2 = clean PCR product with a single genotype observed, 3 = clean PCR product with multiple genotypes observed. T_a ($^{\circ}$ C) indicates the PCR annealing temperature used to amplify products described.

Locus name	<i>O. kisutch</i>		<i>O. keta</i>		<i>O. mykiss</i>		<i>O. clarki</i>		<i>O. nerka</i>		<i>S. salar</i>	
	T_a	rat	T_a	rat	T_a	rat	T_a	rat	T_a	rat	T_a	rat
<i>Oki1</i>	58	3	53	3	49	2	60	1	60	3	50	2
<i>Oki2</i>	58	3	53	3	53	3	53	3	50	1	50	3
<i>Oki3</i>	58	3	49	3	60	2	50	2	60	2	50	1
<i>Oki4</i>	58	3	60	2	60	2	57	3	55	2	55	0
<i>Oki5</i>	58	3	45	2	60	2	60	1	45	2	45	2
<i>Oki6</i>	55	3	50	2	45	2	50	2	55	3	-	0
<i>Oki7</i>	55	2	55	2	55	2	60	2	60	2	60	3
<i>Oki8</i>	55	2	50	2	45	1	45	1	55	2	55	3
<i>Oki9</i>	55	2	60	2	55	2	50	3	55	2	45	1
<i>Oki10</i>	55	3	45	3	50	2	49	3	55	3	50	1
<i>Oki11</i>	55	3	50	2	45	2	45	2	50	2	55	1
<i>Oki13</i>	55	3	49	2	49	3	49	3	60	3	-	0
<i>Oki14</i>	55	3	45	2	55	2	45	2	55	3	-	0
<i>Oki15</i>	45	2	45	2	49	3	60	2	50	3	-	0
<i>Oki16</i>	55	3	45	2	60	3	53	3	55	3	55	1
<i>Oki17</i>	55	3	51	1	50	1	45	1	50	1	50	2
<i>Oki18</i>	54	3	49	3	45	2	49	3	50	2	55	1
<i>Oki19</i>	50	3	57	1	57	3	57	2	55	3	50	1
<i>Oki20</i>	50	3	45	2	45	2	45	2	-	0	50	1
<i>Oki21</i>	45	3	45	3	45	3	45	2	50	2	45	2
<i>Oki22</i>	45	2	45	2	49	3	49	3	50	3	45	2
<i>Oki23</i>	58	2	51	3	50	2	53	3	50	2	45	2
<i>Oki24</i>	45	3	55	2	57	3	55	2	55	2	60	1
<i>Oki25</i>	45	2	45	3	45	2	45	2	50	2	45	1
<i>Oki26</i>	45	1	49	3	50	2	45	2	50	1	-	0
<i>Oki27</i>	-	0	51	0	51	0	53	0	50	3	45	1
<i>Oki28</i>	60	2	49	2	49	2	49	3	50	2	55	1
<i>Oki29</i>	50	2	60	2	45	2	55	2	50	3	-	0
<i>Oki30</i>	60	2	60	2	55	2	60	2	60	3	55	1
<i>Oki31</i>	55	1	-	0	55	1	45	1	45	3	-	0

Discussion

The high mutation rate associated with microsatellite loci, the codominant segregation of alleles and the fact that alleles may be discriminated by relatively simple methods have made microsatellites the molecular tools of choice for several applications. In addition to population genetic studies, such as this dissertation, microsatellite loci have found broad application in forensic analyses, kinship studies, and in the construction of genetic maps. Such applications have presented insight into several aspects of population and evolutionary biology, including the inheritance of quantitative variation (for summaries, see Jarne & Lagoda 1996, Ellegren 2000b).

While amplification of microsatellite loci via the PCR is a relatively simple procedure, isolation and development of novel loci is an expensive and time-consuming process. Given that only three loci had been developed in coho prior to this work, the time spent finding additional markers was prerequisite to producing a strong data set for coho. It is expected that the thirty novel markers described here will provided a valuable contribution to the study of salmonids. This is especially true for coho salmon, in which the number of microsatellite loci available has been increased from three to twenty.

CHAPTER 3 – COHO SALMON POPULATION STRUCTURE ANALYSIS

Summary

To study the glacial biogeography of coho, 20 microsatellite loci and mitochondrial DNA D-loop sequence were examined in samples ranging from Alaska to California.

Microsatellite data divided samples into 5 biogeographic regions; 1) Alaska and northern coastal British Columbia, 2) the Queen Charlotte Islands, 3) the mainland coast of British Columbia and northern Washington State, 4) the Thompson River, and 5) Oregon and California. D-loop sequence data suggested 3 geographic regions; 1) Oregon and California, 2) the Thompson River, and 3) all other sites north of the southern ice margin. Microsatellite data revealed no difference in the number of alleles in different regions, but mtDNA data revealed a cline of decreasing diversity from south to north. The two signals presented by these different marker types illuminate two time frames in the history of this species. Endemic microsatellite diversity in Alaska and on the Queen Charlotte Islands provides evidence in favor of Fraser Glaciation refugia in these regions. The loss of mitochondrial variation from south to north suggests that one of the earlier, more extensive, Pleistocene glaciations eliminated coho from its northern range.

Introduction

Recent glacial history of the Pacific coast of North America

Large portions of northwestern North America were buried in ice during the 19 or 20 glaciations which characterized the Pleistocene Epoch (Pielou 1991). The ice, which consisted of several interconnected glaciers, is referred to as the Cordilleran Ice Sheet. During interglacial periods such as the present, the ice retreats, eventually being restricted to mountaintops and higher latitudes (Clague 1989a). The most recent advance of the Cordilleran Ice Sheet, known as the Fraser Glaciation in British Columbia (BC) and the McConnell / Macauley Glaciation in the Yukon and Alaska, began approximately 70-60 thousand years ago (ka). During the height of this glaciation, 23 to 18 ka, ice-free areas persisted both south and north of the ice (Fig. 1). There is also evidence of ice-free areas along the glaciated coast (Warner *et al.* 1982, Clague 1989b, Barrie *et al.* 1993, Barrie & Conway 1999, Cook *et al.* 2001).

The first major watershed encountered as one moves south of the glaciated region is the Columbia River. Thirteen ka, while the coast of southern BC was still largely blocked by ice, interior river systems including the Fraser River and perhaps the Skeena River drained southward into the Columbia River. Southern fauna was thus able to colonize interior BC thousands of years before adjacent coastal regions were available (McPhail & Lindsey 1986, McPhail & Carveth 1993, Wood *et al.* 1994, Beacham *et al.* 1996, Small *et al.* 1998a).

Low levels of precipitation at higher latitudes, as well as eustatic lowering of the sea level

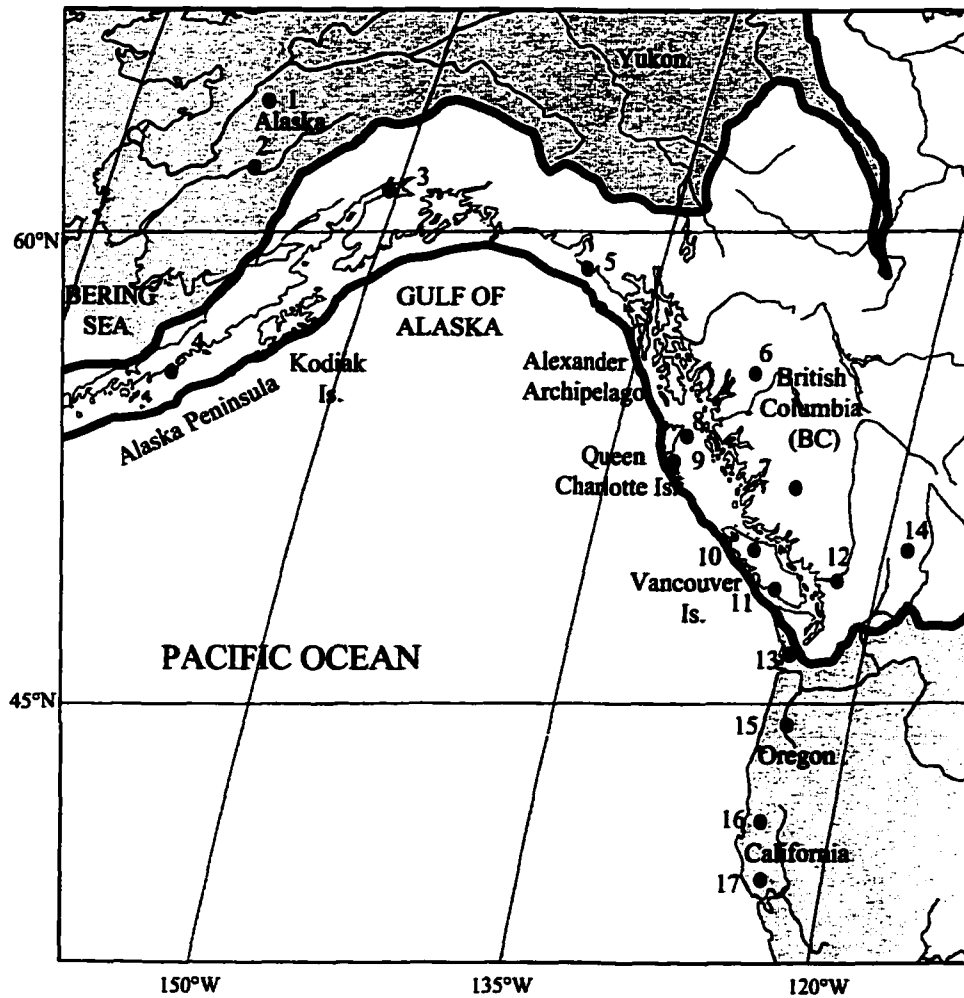


Figure 1. Pattern of land, sea and ice 23-18 ka, during the most recent glacial maximum (after Pielou 1991). Sample sites were 1 Yukon R., 2 Kuskokwim R., 3 Theodore R., 4 Kametolook R., 5 Ophir Ck., 6 Nass R., 7 Atnarko R., 8 Sangar R., 9 Yakoun R., 10 Quatse R., 11 Conuma R., 12 Capilano R., 13 Chehalis R., 14 Thompson R., 15 Alsea R., 16 Trinity R., 17 Noyo R.

created an ice-free region north of the Cordilleran Ice Sheet. Parts of Alaska, the Yukon, and the presently submerged continental shelf formed the refugium known as Beringia. Since ice in the south melted before ice in the north, the majority of fish populations in southern Alaska and northern BC are thought to be of Columbia River origin (McPhail & Lindsey 1986).

Several recent studies have supported the existence of a third refugium or series of refugia somewhere along the glaciated coast. In places where high mountains occur near the edge of the continental shelf, glaciers often cannot overtake segments of coastline in the mountain's "shadow". High mountains exist near the edge of the continental shelf in several places along the glaciated coast, including Kodiak Island, the Alexander Archipelago, the Queen Charlottes and Vancouver Island (Pielou 1991). Eustatic lowering of sea level along the glaciated coast was largely countered by isostatic fall of coastal land under the weight of ice. Glaciers are constantly broken up as they reach deep ocean, however, and thus cannot thicken near the edge of the continental shelf. Where proximity to the continental shelf kept ice thin, the sea level was much lower than at present (Clague 1989b). This lower sea level exposed tracts of continental shelf adjacent to Vancouver Island and the Queen Charlotte Islands, both of which exhibit evidence of serving as Fraser Glaciation botanical refugia (Warner *et al.* 1982, Clague 1989b, Mann & Peteet 1994, Ogilvie 1997). Several vertebrate taxa exhibit genetic and morphological disjunctions associated with the Queen Charlotte Islands, suggesting that these refugia may have supported diverse faunas (Wood *et al.* 1994, Deagle 1995, Byun *et al.* 1997, Byun 1999, McCusker *et al.* 2000, Cook *et al.* 2001, Cook & MacDonald 2001).

As the Cordilleran Ice Sheet retreated, habitat in present day BC and southern Alaska became available to populations in adjacent refugia. The presence of several distinct layers of glacial deposits indicates that glacial retreat was not uniform along the coast (Ryder & Clague 1989). Localized retreats and re-advances of ice, as well as the change in river paths as ice and glacial debris moved, created a complex and changing pattern of available habitat. As the ice retreated over thousands of years, many freshwater habitats opened, refroze, dried, or interconnected. Much opportunity for founding, extinction and merging of freshwater populations existed.

Coho salmon

Coho salmon are anadromous, homing to streams around the north Pacific Basin from Kamchatka in Asia to California in North America. On the basis of this species' to disperse via marine routes, and on their present distribution, McPhail and Lindsey (1970) suggested that coho persisted in both northern and southern refugia. Utter *et al.* (1980) summarized early genetic data supporting the division of several *Oncorhynchus* species into northern and southern groups. Recent genetic data has been used to suggest that both rainbow trout (*O. mykiss*) (McCusker *et al.* 2000) and sockeye salmon (*O. nerka*) (Wood *et al.* 1994) dispersed from refugia along the glaciated coast, as well as from northern and southern refugia, following the Fraser Glaciation.

Several studies have utilized genetic markers to examine population structure in coho (Reisenbichler & Phelps 1987, Wehrhahn & Powell 1987, Nielsen *et al.* 1994, Beacham *et al.* 1996, Van Doornik *et al.* 1996, Carney *et al.* 1997, Small *et al.* 1998a), often revealing divergence between adjacent rivers and among tributaries within drainages.

Most previous studies were designed for the purpose of identifying regional management units and / or for genetic stock identification. To this end, sample boundaries were often politically defined. Further, in the case of genetic stock identification, only those genetic markers most polymorphic in the region under consideration were examined. Both of these features made comparison of different study regions and examination of deep population structure difficult. Small *et al.* (1998b) examined population structure in coho within BC, and were able to identify three large groups within the province. Inference of origins for these groups was limited by the fact that northern and southern ice-free regions were outside the study limits. Based on allozyme and ecological data for coho throughout their southern US range, Weitkamp *et al.* (1995) identified six evolutionarily significant units (ESUs). As no comparable data exist for populations north of Washington State, the opportunity to analyze deep structure was again limited.

The goal of the present work was to determine whether coast-wide population structure in coho is concordant with any of the glacial refugia hypotheses mentioned above.

Specifically, did coho colonize their present range solely from southern refugia, or were there additional source populations in Beringia and / or along the glaciated coast? The division of present genetic variation into regions associated with potential refugia would be evidence for persistence of the species in those refugia. Also, the relative amount of variation in any region may be informative regarding the relative age of populations in that region.

Materials and methods

Sample collection

Operculum punches and fin clips were collected from adult coho in freshwater systems at 17 sites along the Pacific coast of North America (Table 4 and Fig. 1). Collections were made between 1993 and 1997 with each site being sampled in a single year. Samples were placed in 95% ethanol and stored at ambient temperature. Two chinook salmon (*O. tshawytscha*) from the Chena River (Alaska) were collected and included in the molecular and statistical analysis, in order to provide an outgroup for mtDNA analysis. Genomic DNA was extracted from each individual using Chelex as described on page 14.

Molecular analysis

Twenty PCR primer sets were used to amplify microsatellite loci (Table 5). PCR was done in 25 μ L volume in the buffer described on pages 11-13. One U of *Taq* DNA polymerase (QIAGEN) was added to each reaction. PCRs were carried out in a PTC200 thermal cycler. Initial denaturation of 3 min at 94°C was followed by an annealing temperature, which was lowered 1°C each round for the first 5 rounds, to that listed in Table 5. Thirty cycles of 94°C for 30 sec, annealing temperature for 30 sec, and 72°C for 30 sec were performed. PCR products were size-fractionated on either 8 or 10% 19:1 acrylamide to bis-acrylamide gels, in 2X TAE buffer and stained with ethidium bromide. Photographs of the gels were taken digitally, and transferred to Bio Image Intelligent Quantifier 2.1.2a software. Alleles were defined using standard fish and size-frequency histograms as described by Small *et al.* (1998a).

Table 4. Number of individuals examined for microsatellite and mtDNA variation from each sample site. Site numbers correspond to Fig. 1.

Location	Site number	Sample size	
		microsatellites	mtDNA
Yukon R.	(1)	19	19
Kuskokwim R.	(2)	26	20
Kametolook R.	(3)	30	19
Theodore R.	(4)	30	18
Ophir Ck.	(5)	20	16
Nass R.	(6)	45	19
Atnarko R.	(7)	32	17
Sangan R.	(8)	48	13
Yakoun R.	(9)	32	23
Quatse R.	(10)	32	18
Conuma R.	(11)	48	18
Capilano R.	(12)	32	18
Chehalis R.	(13)	42	18
Thompson R.	(14)	32	17
Alsea R.	(15)	33	20
Trinity R.	(16)	40	20
Noyo R.	(17)	18	18
total		559	311

Table 5. Primers and annealing temperatures used for PCR amplification of 20 microsatellite loci in coho. T_a ($^{\circ}\text{C}$) indicates the PCR annealing temperature used to amplify microsatellites.

Primer set	T_a	Source
<i>Oki1</i>	58	(Smith <i>et al.</i> 1998)
<i>Oki2</i>	58	(Smith <i>et al.</i> 1998)
<i>Oki3</i>	58	(Smith <i>et al.</i> 1998)
<i>Oki10</i>	55	(Smith <i>et al.</i> 1998)
<i>Oki11</i>	53	(Smith <i>et al.</i> 1998)
<i>Oki13</i>	56	(Smith <i>et al.</i> 1998)
<i>Oki16</i>	55	(Smith <i>et al.</i> 1998)
<i>Oki18</i>	54	(Smith <i>et al.</i> 1998)
<i>Oki20</i>	50	(Smith <i>et al.</i> 1998)
<i>Omy77</i>	47	(Morris <i>et al.</i> 1996)
<i>One11</i>	58	(Scribner <i>et al.</i> 1996)
<i>Ots3</i>	47	(Banks <i>et al.</i> 1999)
<i>Ots4</i>	51	(Banks <i>et al.</i> 1999)
<i>Ots9</i>	57	(Banks <i>et al.</i> 1999)
<i>Ots7.2</i>	57	(Banks <i>et al.</i> 1999)
<i>Ots101</i>	53	(Small <i>et al.</i> 1998a)
<i>Ots103</i>	58	(Small <i>et al.</i> 1998a)
<i>Ots105</i>	50	(Nelson & Beacham 1999)
$\mu 60$	62	(Estoup <i>et al.</i> 1993)
$\mu 73$	45	(Estoup <i>et al.</i> 1993)

The mtDNA D-loop was amplified using the PCR primers *M13/t-pro*:
TGTA AACGACGGCCAGTCCCAAAGCTAAGATTCTAAA (an *M13* universal forward primer followed by *t-pro* (Shedlock *et al.* 1992)), and *s-phe*:
GCTTTAGTTAAGCTACG (Nielsen *et al.* 1994). PCR reagent concentrations were identical to those described on pages 11-13; however, mtDNA was amplified in 100 μ L volume. The thermal profile was 3 min initial denaturation at 94°C, followed by 30 cycles of 94°C for 30 sec, 55°C for 30 sec and 72°C for 30 sec. PCR products were purified using QIAquick PCR purification kit (QIAGEN). The 5' end of the control region L-strand was cycle-sequenced using the DYEnamic 21 *M13* primer kit (Amersham). Cycle-sequencing reactions were electrophoresed on an ABI 377 DNA sequencer. Sequences were aligned using Lasergene99 (DNASTAR).

Statistical analysis

GENEPOP (Raymond & Rousset 1997) was used to test each locus in each site for departures from Hardy-Weinberg equilibrium (HWE) (using the method of Guo & Thompson 1992), and to test all pairs of loci for linkage disequilibrium. A correction for multiple comparisons (Rice 1989) was applied to both tests.

Northern (sites 1-2) and southern (sites 13, 15-17) ice-free regions were compared to the glaciated region to test for differences in numbers of alleles. The average number of alleles contributed per individual (number of alleles observed at site / n) was compared among regions using two-tailed t-tests. Variation in mtDNA data was quantified within

(haplotype and nucleotide diversity) and among (nucleotide divergence) sites (Nei 1987, pp. 179, 256, and 276, respectively) using REAP (McElroy *et al.* 1992).

Sites were grouped based on both mtDNA and microsatellite data using PHYLIP (Felsenstein 1995). Chord distance (D_{CSE}) (Cavalli-Sforza & Edwards 1967) was calculated based on both mtDNA data and on 2000 bootstrap replicates of the microsatellite data. Neighbor-joining (NJ) (Saitou & Nei 1987) was then used to group sites based on these distances. Correlation between pairwise D_{CSE} and geographic distance was calculated and tested using a permutation procedure (Mantel 1967) (10^6 permutations) implemented by Arlequin (Schneider *et al.* 1999). Relationships among mtDNA haplotypes were analyzed using a minimum-spanning tree (MST) (Rohlf 1973) based upon pairwise divergence (K) (Kimura 1980), as well as maximum likelihood (ML) estimates (Felsenstein 1981). Treeview (Page 1996) was used to display trees.

Analysis of molecular variance (AMOVA) (Excoffier *et al.* 1992) partitioned variance into three components. The “within sites” component quantified variation among individuals in the sites. The remaining variance, potentially informative regarding relationships among sites, was divided into “among sites within groups” and “among groups” components. A proposed structure that accurately describes observed data should result in the percent variance “among groups” being large relative to that “among sites within groups.” AMOVA was used to test groups identified by NJ analysis, as well as those predicted by published refugia hypotheses. Predictions of the one refugium and two refugia hypotheses were based on McPhail and Lindsey’s (1970) work. The three refugia hypothesis was based on phylogeographic groups identified in sockeye (Wood *et*

al. 1994). Structures examined included one group per refugium and an additional group of post-glacially colonized sites. Within each structure, the effects of 1) placing the Thompson River in each of the above groups as well as by itself (thus increasing the number of groups by one) 2) placing Conuma with the Queen Charlotte Islands and with the glaciated coast, 3) placing southern Alaska and northern BC sites with Northern Alaska and with the glaciated coast, and 4) including and excluding Noyo River were examined. This last variable was examined due to the complex transplantation history of Noyo (L. Weitkamp, personal communication) and evidence that introduced fish have altered local genetic structure (Nielsen *et al.* 1994). In total, 36 structures were tested. Distance matrices which take into account relationships among states (R_{ST} (Slatkin 1995) for microsatellites, K for mtDNA) as well as those based on identity / non-identity (F_{ST} estimates (Weir & Cockerham 1984, Michalakis & Excoffier 1996)) were subject to AMOVA. Significance of variance components was tested using ≥ 16000 permutations.

Results

Microsatellite variation

Gel photographs of PCR products amplified by each primer set are shown in Appendix 1. *Oki10* exhibited significant departures from HWE in all sites south of Alaska, except Thompson and Chehalis. Analysis of this locus in known crosses revealed a null allele, which could be distinguished from failed PCRs by the presence of bands from an isocus. The frequency of the null allele at each site was calculated as the square root of the frequency of null homozygotes. Similarly, a null allele at *Ots103* (Small *et al.* 1998a) likely contributed to the 5 (Capilano, Chehalis, Quatse, Thompson and Theodore) significant ($P < 0.05$) departures from HWE observed for that locus. Each of the remaining loci exhibited departures ($P \leq 0.05$) from HWE in two sites or less. No significant ($P \leq 0.05$) linkage disequilibrium was detected.

Average number of microsatellite alleles contributed per individual ranged from 2.0 (Conuma River) to 4.4 (Yukon River). No differences in numbers of alleles were found between either northern ($P = 0.20$) or southern ($P = 0.83$) ice-free regions and glaciated regions. Allelic composition was highly variable among sites (Appendix 2).

A positive correlation ($r^2 = 0.36$, $P < 0.01$) between microsatellite D_{CSE} and geographic distance was observed. Microsatellite NJ analysis placed most sites into one of four groups with $\geq 50\%$ bootstrap support (Fig. 2). Sites which did not fall into these groups were localized along the glaciated coast between central BC and northern Washington State.

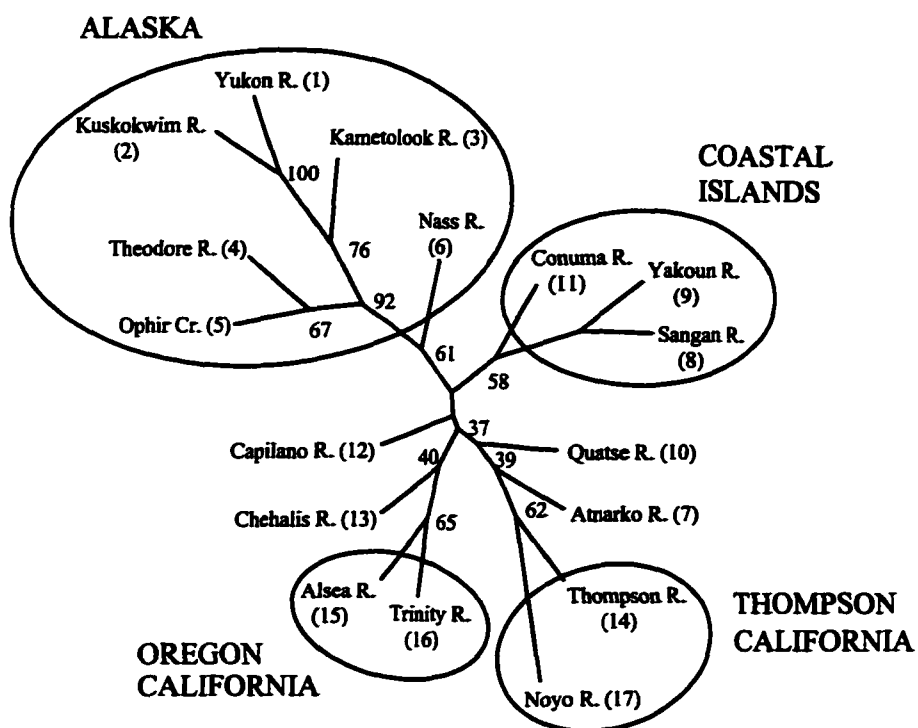


Figure. 2 Consensus NJ tree based on microsatellite D_{cse} . Numbers at the nodes indicate the percentage of 2000 bootstrap replicates that grouped sites distal to the nodes. Circles indicate groups that were supported more than 50% of the time. Site numbers (in parentheses) correspond to Fig. 1.

Mitochondrial variation

The 555 base pair (bp) region sequenced in coho mtDNA began on base 5 of the alignment of Shedlock *et al.* (1992). Twelve variable nucleotide positions distinguished 13 haplotypes (GenBank accession #s AF318025-AF318037) (Fig. 3). Haplotype diversity ranged from 0.00% in several northern sites to $0.68 \pm 0.07\%$ in Noyo. This later value is congruent with the estimate of $0.56 \pm 0.06\%$ for Noyo coho (Nielsen *et al.* 1994). The estimated range of nucleotide diversity (0.00 to 0.27%) was identical to that previously published for coho from Alaska to California (Moran & Bermingham 1994). Nucleotide divergence between sites ranged from 0.000 per kilobase (kb) to 1.136 per kb, with an average of 0.238 per kb.

The two chinook sequences differed by a single adenine – thymine transversion at position 132 (GenBank accession # AF318038). Published sequences for all *Oncorhynchus spp.* (Shedlock *et al.* 1992), as well as all coho in the present study reveal an adenine at this position. Previous estimates based on mtDNA place the divergence time between coho and chinook at 2.7 (Shedlock *et al.* 1992) and 3.8 mya (McKay *et al.* 1996). The data presented here indicate this split occurred 3.2 and 3.6 mya following calculation methods of the previous authors, respectively. Relationships among coho haplotypes inferred by MST and ML were congruent, consisting of four haplotype groups (Fig 4). Mean sequence divergence between haplotype groups ranged from 0.25% between *h1* and *h2* and 0.58% between *h3* and *h4*, with an average of 0.41%.

Haplotype	Base pair position												
	5	21	101	126	140	142	209	240	241	283	296	555	
h1a	G	T	-	T	T	G	C	T	-	A	G	T	
h2a	-	
h2b	
h2c	
h2d	
h2e	.	.	H	
h2f	.	C	C	.	.	.	
h3a	A	.	C	
h3b	A	.	C	
h3c	.	.	.	G	.	A	.	C	
h3d	A	.	C	.	.	A	.	
h4a	A	C	
h4b	T	A	C	
Chinook	A	.	T	C	.	A	.	

Figure. 3 Aligned sequences of the 13 variable sites observed in a 555 base pair region of the coho mtDNA control region. Sequences shown are for the L-strand, 5'-3'. Dots indicate identity and dashes indicate insertion / deletion.

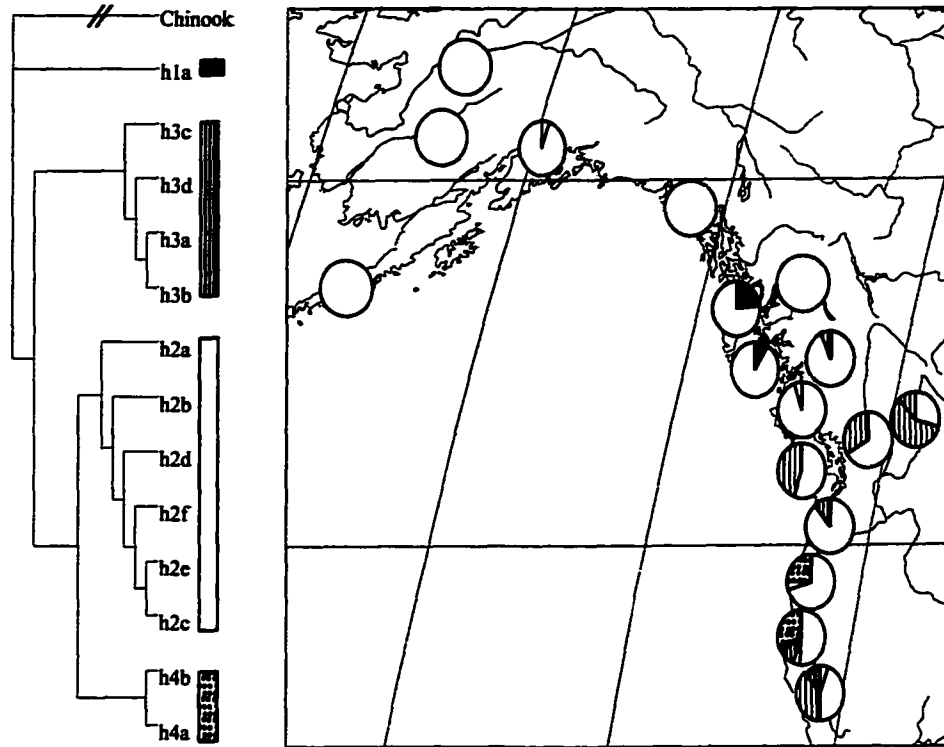


Figure. 4 Geographic distribution of coho salmon mtDNA haplotypes. Interhaplotypic relationships suggested by minimum-spanning and maximum likelihood analysis are indicated on the left.

Sites north of the ice margin (Yukon and Kuskokwim) were fixed for the most common mtDNA haplotype, *h2c*, while those south of the ice margin were polymorphic (Fig. 4 and Table 6). Glaciated coast sites had an average of 1.8 haplotypes each and those south of the ice had an average of 4.3 haplotypes each. Outliers were observed both north (Thompson, 3 haplotypes) and south (Chehalis, 2 haplotypes) of the southern ice margin. Nevertheless, average nucleotide diversity south of the southern ice margin (0.17%) was several times greater than north of it (0.04%).

In contrast to the microsatellite data, mtDNA D_{CSE} did not correlate significantly with geography ($r^2 = 0.02$, $P = 0.17$). However, with the exception of Conuma, mtDNA NJ analysis paired the same sites that were supported by microsatellite bootstrap data (Fig. 5).

Testing refugia hypotheses

Regardless of whether a model emphasized mutation (K) or drift (F_{ST}), mtDNA variation was best explained by dividing sites into 3 groups (southern refuge + Thompson + all other glaciated sites) (Table 7). Both infinite allele (F_{ST}) and stepwise mutation (R_{ST}) models for microsatellite data supported dividing sites among 5 groups (southern refuge + Bering group + Queen Charlotte Islands + Thompson + all other glaciated sites).

Including Thompson with the glaciated coast lowered among groups variance somewhat (1.07-1.27%) for microsatellite data, but severely (14.69-19.91%) for mtDNA data.

Optimal structure for both markers excluded the complex Noyo River. Including Noyo with the southern group under each scenario lowered the among groups variance slightly

Table 6. Observed mitochondrial haplotype counts, haplotype diversity and nucleotide diversity within coho sample sites.

Haplotype diversity (h) is the probability that two haplotypes drawn from a population are different. Nucleotide diversity (π) is the average number of nucleotide differences between two sequences. Site numbers correspond to Fig. 1.

Site (number)	h	π (x100)	Haplotype frequencies												
			$h1a$	$h2a$	$h2b$	$h2c$	$h2d$	$h2e$	$h2f$	$h3a$	$h3b$	$h3c$	$h3d$	$h4a$	$h4b$
Yukon R. (1)	0.000	0.000				19									
Kuskokwim R. (2)	0.000	0.000				20									
Kametolook R. (3)	0.000	0.000				19									
Theodore R. (4)	0.111	0.021		1		17									
Ophir Ck. (5)	0.000	0.000				16									
Nass R. (6)	0.000	0.000				19									
Atnarko R. (7)	0.118	0.022				16	1								
Sangan R. (8)	0.385	0.073	3			10									
Yakoun R. (9)	0.166	0.032	2			21									
Quatse R. (10)	0.111	0.021				17		1							
Conuma R. (11)	0.523	0.099				10			8						
Capilano R. (12)	0.471	0.089				12			6						
Chehalis R. (13)	0.209	0.040				16			2						
Thompson R. (14)	0.588	0.126				5			10		2				
Alea R. (15)	0.468	0.188				14		1							5
Trinity R. (16)	0.679	0.266			1	10						2	1		6
Noyo R. (17)	0.680	0.181			1	8			7	1					1

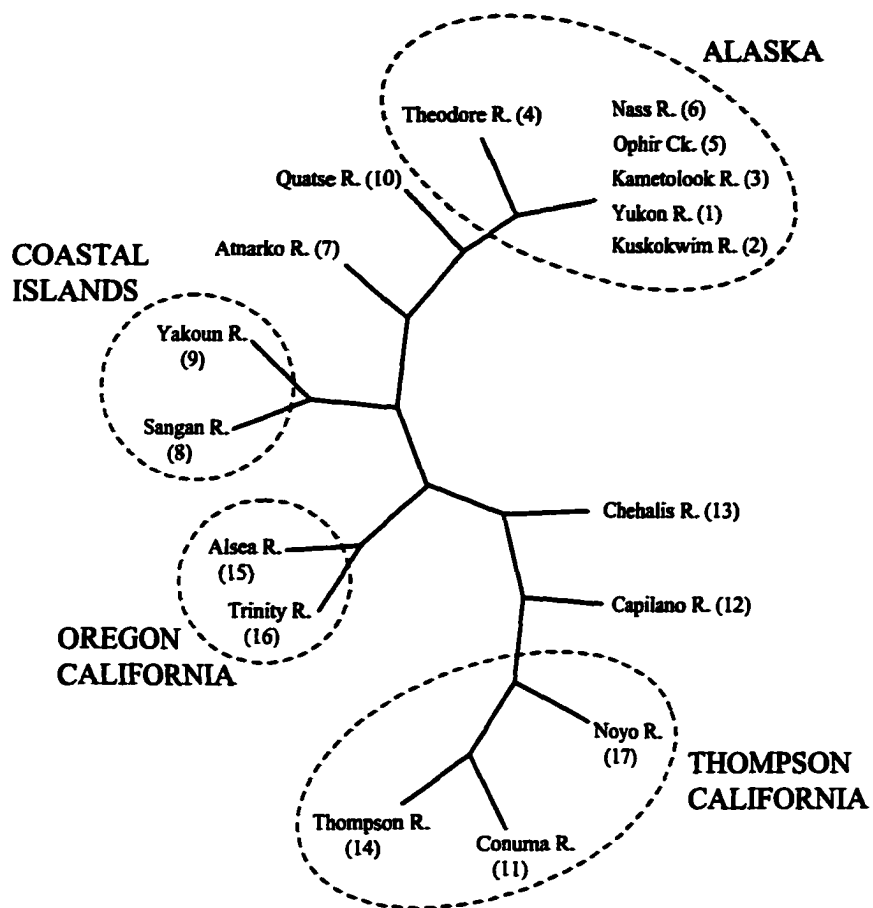


Figure. 5 Neighbor-joining tree based on mitochondrial D_{CSE} . Dashed circles indicate groups supported by microsatellite bootstrap data. With the exception of a single site, (Conuma) mtDNA NJ analysis paired the same sites that were supported by microsatellite bootstrap data (Fig. 2). Site numbers (in parentheses) correspond to Fig. 1.

Table 7. The 3 hypotheses of 36 examined which maximized among group variance in AMOVA. The first “3 refugia” hypothesis includes Conuma (11) with the glaciated coast, while the second “3 refugia” hypothesis places Conuma with the Queen Charlotte Islands. Variance component estimates and P values are given for matrices based on F_{ST} , R_{ST} and K. Site numbers correspond to Fig. 1.

Hypothesis (site numbers)	Variance component	Microsatellite				Mitochondria			
		R_{ST}	P	F_{ST}	P	K	P	F_{ST}	P
1 refugium south of ice (15-16) north of southern ice limit (1-13) Thompson (14)	Among groups	0.30	0.406	5.00	0.004	42.36	0.001	35.28	0.000
	Among sites within groups	13.64	0.000	8.52	0.000	5.72	0.000	7.62	0.000
	Within sites	86.06	0.000	86.49	0.000	51.92	0.000	57.10	0.000
3 refugia ¹ south of ice (15-16) north (1-5) coastal refuge (8-9) glaciated coast (6-7, 10-13) Thompson (14)	Among groups	5.69	0.005	4.71	0.000	27.55	0.000	22.5	0.003
	Among sites within groups	9.21	0.000	6.88	0.000	5.24	0.008	7.16	0.001
	Within sites	85.10	0.000	88.41	0.000	67.2	0.000	70.34	0.000
3 refugia ² south of ice (15-16) north (1-5) coastal refuge (8-9, 11) glaciated coast (6-7, 10, 12-13) Thompson (14)	Among groups	1.91	0.173	5.11	0.000	25.07	0.000	21.71	0.002
	Among sites within groups	12.18	0.000	6.39	0.000	6.90	0.002	7.43	0.000
	Within sites	85.91	0.000	88.50	0.000	68.03	0.000	70.85	0.000

(<1%). Microsatellite data grouped southern Alaska / Northern BC sites with the north rather than with the glaciated coast (0.91-2.52% higher among groups variance).

Discussion

Amount of variation

The number of microsatellite alleles did not differ between glaciated and non-glaciated regions, but the number of mtDNA haplotypes did. Estimates of mtDNA variability were generally concordant with published work, lending confidence to the novel finding of a south to north cline of decreasing genetic diversity in coho.

Testing refugia hypotheses

Microsatellite AMOVA divided sites into 5 groups, consistent with three source regions and two colonized regions. As R_{ST} incorporates relationships among alleles, as well as identity / non-identity, R_{ST} values were more extreme than F_{ST} and offered greater distinction among competing hypotheses. This greater distinction, however, came at the cost of the assumptions required for converting electromorph size to repeat number. The findings of this study did not depend on which estimator was used. Among groups variance based on both F_{ST} and R_{ST} was maximized under a three refugia hypothesis.

AMOVA of mtDNA data divided sites into 3 groups, consistent with a single source and two colonized regions. This structure maximized among groups variance regardless of which distance matrix was used. Partitioning of mtDNA data into a smaller number of groups was due to the smaller number of states observed for this locus, specifically the lack of polymorphism in the north. A similar reduction in mtDNA variation relative to nuclear, associated with post-glacial colonization, was documented in brown trout (*Salmo trutta*) (Bernatchez *et al.* 1992, Ferguson *et al.* 1995).

Interpretation of observed structures in terms of marker evolution

Differences in data from the two marker types may be explained by their respective mutation rates (μ) and variance effective population sizes (N_e). First, as mtDNA has a smaller N_e ($\approx 1/4$) than nuclear microsatellite loci, loss of states at the former will be relatively greater than loss of states at the later during founder events. This explains the stronger geographic correlation of microsatellite D_{CSE} than mtDNA D_{CSE} . Second, μ in the 5' end of the mtDNA D-loop (Shedlock *et al.* 1992) is low relative to microsatellite μ (reviewed in Jarne & Lagoda 1996, Ellegren 2000b). Following loss of genetic states during founder events, new variation would be generated 10-100 times faster at microsatellite loci than in the mtDNA D-loop (based on above rate estimates). The two levels of variation revealed by mtDNA data and microsatellite data illuminate relatively ancient and recent events, respectively.

Mitochondrial DNA data suggest that coho were eliminated north of Washington State or Oregon, perhaps during one of the earlier (more extensive) Pleistocene glaciations. Support for this hypothesis includes a greater number of haplotypes in the south, and greater genetic distance between those haplotypes. Comparable shifts in intraspecific mtDNA diversity associated with the glacial maxima have been documented for several other species (summary by Bernatchez & Wilson 1998). McLean *et al.* (1999) proposed that eulachon (*Thaleichthys pacificus*) radiated from a single refuge based on low sequence divergence between haplotype groups (0.4%) relative to that of a species which dispersed from multiple refugia (0.7% in rainbow smelt (*Osmerus mordax*) (Bernatchez

1997). Sequence divergence of 0.4% between haplotype groups in the present study is therefore interpreted as further evidence supporting dispersal of coho from a single refuge.

As this early glaciation subsided, coho would have colonized sequential rivers northward losing relatively more mtDNA haplotypes than microsatellite alleles to ensuing bottleneck events. Finally, during the subsequent interglacial(s), new variation evolved faster at microsatellite loci than in mtDNA. Microsatellite data in the present study suggest dispersal from three refugia, supporting claims that coho survived the Fraser Glaciation in Bering (Carney *et al.* 1997) and coastal island (Small *et al.* 1998b) refugia.

Both marker types revealed endemic diversity associated with the Queen Charlotte Islands, supporting the growing body of evidence for biological refugia in this region (Warner *et al.* 1982, Wood *et al.* 1994, Deagle 1995, Byun *et al.* 1997, Byun 1999, McCusker *et al.* 2000). AMOVA and NJ analysis of microsatellite data indicated a limited affinity of Conuma with the Queen Charlotte Islands. Sockeye (Taylor *et al.* 1996) and coho from Vancouver Island both seem to switch affinity for glacial biogeographic groups depending on the specific genetic loci examined. Genetic data may be unable to distinguish whether the west coast of Vancouver Island was part of a coastal refuge, or whether it was founded (likely from a coastal refuge) following glacial retreat. Persistence of coho in a coastal refuge somewhere near the Queen Charlotte Islands remains the best explanation for the data.

McCusker *et al.* (2000) proposed that rainbow trout colonized BC from southern, coastal, and possibly Bering refugia. The data presented here are analogous to theirs in at least 3 aspects: 1) endemic diversity associated with the Queen Charlotte Islands, 2) coast-wide genetic variance best explained by hypotheses involving a coastal refuge, and 3) more genetic diversity in California than in the proposed coastal (and potentially Bering) Fraser Glaciation refugia. Therefore, both of these members of the genus *Oncorhynchus* may have been eliminated from their northern ranges during some earlier event, but managed to survive in coastal and Bering refugia during the Fraser Glaciation.

Biological disjunction between the Thompson River and adjacent coastal regions has been documented for several species (summarized by McPhail & Carveth 1993). A combination of distinct founding events (Small *et al.* 1998a) and selective pressures (Taylor & McPhail 1985b, a) has been invoked to explain distinctiveness of Thompson coho relative to coastal conspecifics. The distinctiveness of both Thompson and Noyo, in terms of microsatellite allele frequencies, seems a more likely explanation for their NJ pairing than does a monophyletic origin. More extensive sampling would be required for further speculation regarding the Thompson and Noyo rivers.

Biological and distributional data for several fish species have provided evidence of a glacial refugium 20 km south of the ice margin, in the Chehalis River drainage (McPhail & Lindsey 1986, McPhail & Carveth 1993, McPhail & Taylor 1999, Taylor *et al.* 1999). The ice in this region reached its southernmost limit around 17 ka, when it is thought to have been 1 km thick in the vicinity of Seattle (Porter & Swanson 1998). The reduction in mtDNA diversity, characteristic of fish with ranges subject to Pleistocene glaciations,

often extends beyond the ice margins (Bernatchez & Wilson 1998). As haplotype and nucleotide diversity in the Chehalis were less than half the values observed in sites further south, the present data offer no support for coho in a Chehalis refugium.

The northern ice margin is believed to have followed the Alaska Peninsula (Fig. 1) (Mann & Peteet 1994). An associated phylogeographic disjunction between northern and southern Alaska has been described for several salmonids (Gharrett *et al.* 1987, Varnavskaya *et al.* 1994, Carney *et al.* 1997), and other marine species (O'Corry-Crowe *et al.* 1997, McLean *et al.* 1999). Microsatellite data identified this split among Alaskan coho (100% bootstrap), but D-loop sequence data did not. Further, when microsatellite data were examined on a coast-wide scale, all Alaskan sites were grouped as a single unit (92% bootstrap). Thus while an Alaska Peninsula disjunction was observed, it appeared relatively shallow.

Conservation of genetic resources

Divergences between the Thompson and the adjacent coast as well as between north and south of the Alaska Peninsula were initiated following the most recent glacial retreat. In the case of the Thompson, this has been long enough for adaptive variation to evolve (Taylor & McPhail 1985b, a). If microsatellite structure reveals groups that survived the Fraser Glaciation in separate refugia, these groups might have been isolated for 60-70 ka or more. It thus seems reasonable to suggest that each of these groups meet the "evolutionary legacy" criteria for Waples' (1991) ESU. While sampling in the present study precludes estimation of migration between sites, the data suggest that migration is limited among these biogeographic groups, relative to within them. Identifying these

groups as ESUs is conservative, as six such units have already been identified within the “southern group” used here (Weitkamp *et al.* 1995).

Mitochondrial data revealed that, as in the case of rainbow trout (McCusker *et al.* 2000), a large portion of coho’s genetic resources are concentrated in the southern quarter of its range. This finding emphasizes the importance of coho runs in Washington State, Oregon, and California to the evolutionary potential of the species, and provides additional rationale for the protection of stocks in this region. The microsatellite data concur with previous work (Small *et al.* 1998b) that variation within BC exists in at least 3 blocks (coastal islands, coastal mainland, and Thompson). Given that adaptive variation may evolve more rapidly than variation at neutral markers (Lynch 1996, Pamilo & Savolainen 1999), and that genetic variation has been directly correlated with fitness traits between at least one pair of these regions, it seems logical to use these regions as the minimum units for conserving genetic resources. Finally, within Alaska, the present data concur with earlier findings of two groups of coho separated by the Alaska Peninsula. While this split is relatively shallow on a coast wide scale, it identifies the two groups in Alaska between which migration is most limited. The goal of conserving genetic resources might thus best be served by dividing resources for conservation and further research among these regions.

CHAPTER 4

POPULATION STRUCTURE OF FRASER RIVER WHITE STURGEON

Summary

White sturgeon in the Fraser River are listed as imperiled (the second highest possible rating) by the British Columbia Conservation Data Centre. A difficulty in trying to protect this species in the Fraser River and elsewhere is the lack of knowledge regarding their population biology. Variation in the mitochondrial DNA control region and at four microsatellite loci was examined in order to characterize white sturgeon samples from throughout the Fraser River mainstem and from a major tributary, the Nechako River. Samples from the adjacent Columbia River were analyzed for comparison. In contrast to previous work, present data indicate that white sturgeon population structure in this region reflects post-glacial dispersal more than it does recent anthropogenic effects. The data divided the Fraser into four biogeographic regions: 1) the lower Fraser, below Hell's Gate, 2) the middle Fraser, between Hell's Gate and river km 553, 3) the upper Fraser, above the Nechako confluence, and 4) the Nechako River. These four groups are concordant with those suggested by tag and recapture and catch per unit effort data, and are separated by what have been identified as barriers to white sturgeon migration. Based on concordance between these different types of data, it is argued that the four groups identified here merit ESU status.

Introduction

Biogeography of the Fraser River

As mentioned in Chapter 3, a biological disjunction has been well documented between the lower Fraser River and the upper Fraser River, including the Thompson River. These two regions are separated by the Coast Mountains, and corresponding climatic differences likely contribute to the observed disjunctions. McPhail and Lindsey (1970) summarized species distribution data for this region and suggested that post-glacial dispersal routes offered another explanation for differences between the ichthyofauna of the lower Fraser River and that of the Thompson River.

The geographical region defined by inhabitants originating from the Columbia system and its smaller neighbors is often referred to as Cascadia. Cascadia includes all fresh-water bodies west of the Rocky Mountains between the Columbia system in the south and the Stikine River in the north (McPhail & Lindsey 1986). Thirteen ka, while the coast of southern BC was still largely blocked by ice, interior river systems including the Fraser River and perhaps the Skeena River are thought to have drained southward into the Columbia River. The Fraser watershed and Columbia watershed presently run in close geographic proximity at several points (Fig. 6). The melting glaciers caused massive flooding of adjacent lands, allowing the interconnection of these two systems at several times. Columbia River fish were thus able to colonize interior BC thousands of years before adjacent coastal habitat was available. When ice finally retreated from the Lower Fraser River, this region was colonized in a separate event from the Columbia and Chehalis rivers (McPhail & Carveth 1993).

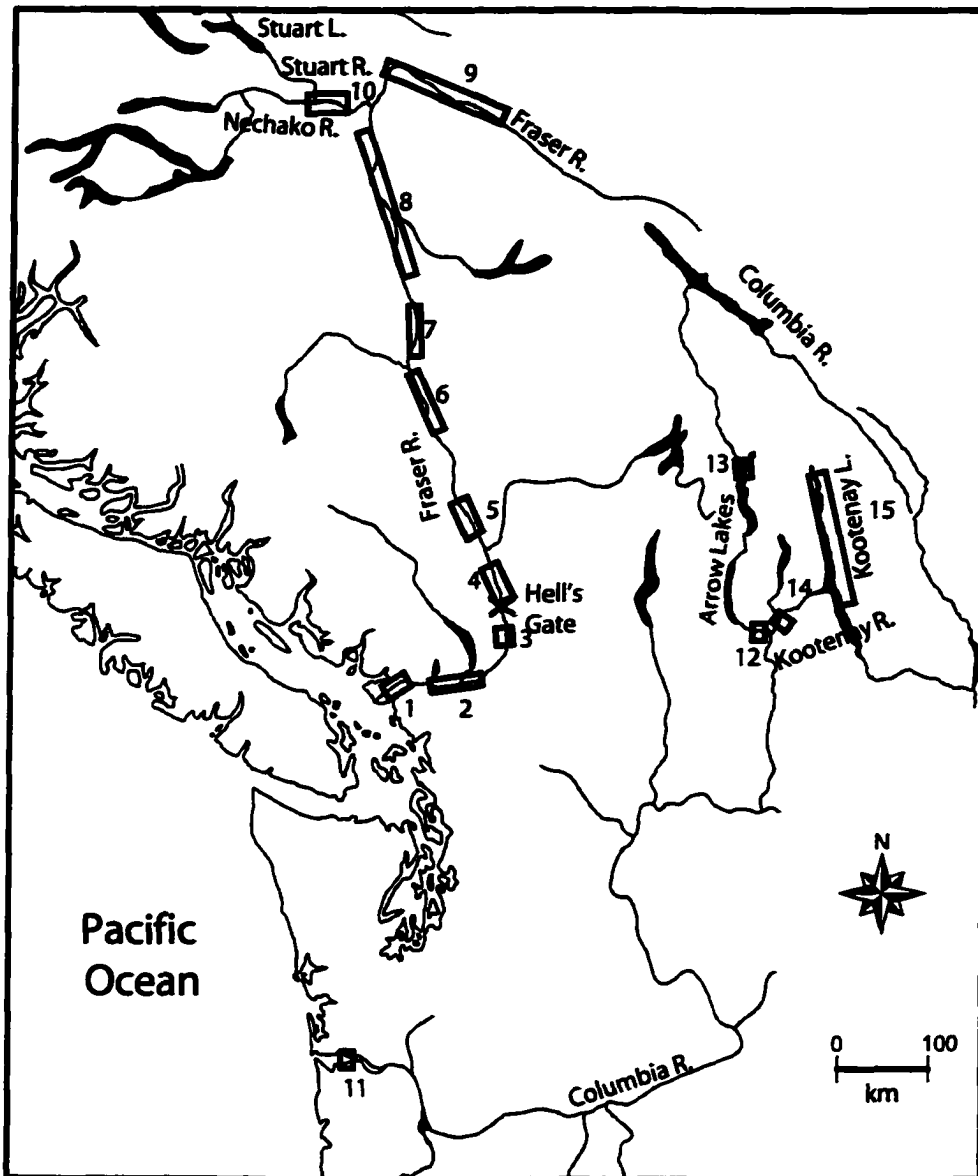


Figure 6. White sturgeon sample collection sites. 1) Fraser 1, 2) Fraser 2, 3) Fraser 3, 4) Fraser 4, 5) Fraser 5, 6) Fraser 6, 7) Fraser 7, 8) Fraser 8, 9) Fraser 9, 10) Nechako R., 11) lower Columbia, 12) upper Columbia, 13) Arrow L., 14) Kootenay R., 15) Kootenay L. Numbers of individuals examined for microsatellite and mtDNA variation are listed in Table 11 and Table 13, respectively.

Presently, the most significant physical barrier to migration on the Fraser River mainstem is at Hell's Gate rapids (Fig 6). Hell's Gate is a narrow passage in the Fraser Canyon where the flow rate is high enough to present a velocity barrier to many species.

Although this region was narrow historically, construction of the railway caused a rock-slide in 1913 which further narrowed the passage. McPhail and Carveth (1993) made the interesting observation that the canyon appears to be an effective barrier to downstream dispersal as well as upstream.

White sturgeon

White sturgeon have been reported from the Aleutian Islands in Alaska to southern California, but only three rivers are known to have historically supported spawning populations of this species: the Fraser River, the Columbia River and the Sacramento River. There is no evidence to suggest that white sturgeon might have survived recent glaciation events in Beringian or coastal island refugia. White sturgeon have been described as anadromous (Scott & Crossman 1973), diadromous and amphidromous (Echols 1995), reflecting uncertainty with regards the role of marine migrations in this species' life-history. Purely freshwater populations, such as that in Kootenay Lake, do exist within the species' natural range.

A commercial fishery for Fraser River white sturgeon was established in the late 1800's. By 1905, over-fishing had reduced annual harvests to less than 4% of what they had been previously (fishery and management history summarized in Echols 1995). Longevity of individuals (over 100 years in some instances) and their preference for deep turbid habitat have impeded our understanding of white sturgeon population biology. Management of

the current sport fishery, and decisions regarding habitat restoration are confounded by this lack of information. Knowledge of whether or not barriers to gene-flow exist within the Fraser, or between the Fraser and the Columbia, is prerequisite for conservation management of this species.

In assessing the utility of molecular genetic markers for characterizing white sturgeon populations, it is important to consider the relative complexity of this species' nuclear genome. The white sturgeon genome, and the genomes of sturgeon in general, are poorly understood compared to most vertebrates. Evolution of the family Acipenseridae has been characterized by several polyploidization events (summarized in Birstein *et al.* 1997). Genetic loci in individuals may exhibit either tetrasomic or disomic inheritance, depending on the locus examined (May *et al.* 1997). The white sturgeon genome is thought to be octoploid, but in an advanced stage of diploidization (Van Eenennaam *et al.* 1998b). Further, different individuals are known to have different chromosome numbers (Van Eenennaam *et al.* 1998a). Several authors have characterized (presumably nuclear) genetic markers in white sturgeon (Bartley 1987, May *et al.* 1997, Powell & Anders 1999, McQuown *et al.* 2000). While multiple attempts have been made to use these loci to characterize white sturgeon populations (Sheldon McKay, personal communication; Paul Anders, personal communication; Jeff Rodzen, personal communication; Bernie May, personal communication; Powell & Anders 1999) only one (Bartley *et al.* 1985) has ever appeared as a reviewed publication.

In contrast to nuclear inheritance, mtDNA inheritance in white sturgeon follows patterns typical of most vertebrates. Heteroplasmy, the occurrence of multiple haplotypes within a

single individual, has been observed only for a tandem repeat region in the D-loop (Brown *et al.* 1992b, Brown *et al.* 1996). Examination of DNA outside this repeat region has yielded population information on several sturgeon species (Stabile *et al.* 1996, Wirgin *et al.* 1997, Wirgin *et al.* 2000, Walsh *et al.* 2001) including white sturgeon (Brown *et al.* 1992a, Brown *et al.* 1993). The main limitation of using mtDNA to study white sturgeon is that it provides information on female population structure only. This is especially limiting in species such as white sturgeon, for which virtually nothing is known regarding natural male breeding behaviour.

The goal of the present study was to characterize population structure in Fraser River white sturgeon. Several rapidly evolving genetic markers were examined to test for gene-flow barriers within the Fraser and between the Fraser and the Columbia. Identification of such barriers would allow their use for partitioning management units within the Fraser River. Management of regions between which gene flow is limited as separate units will minimize the chances of each unit being eliminated. Moreover the grouping of regions between which migration is high will save valuable conservation resources. Knowledge of population structure within the Fraser River should thus benefit efforts to maintain white sturgeon throughout this basin. Mitochondrial DNA was examined because it is known to be informative in this species. Nuclear microsatellites were examined in order to address limitations posed by female inheritance of mtDNA.

Methods and Materials

Sample collection

White sturgeon were sampled along the length of the Fraser River mainstem and in the Nechako River, as well as in a few regions in the Columbia system (Fig. 6). The assumption was made that samples collected from a geographic site were, somehow genetically representative of that site. While this assumption may be unrealistic, it was necessary given the void of information on this species' population structure. The boundary between sites 1 and 2 was based on a management boundary between Federal (site 1) and provincial (site 2) jurisdiction. Boundaries for sites 2-15 were based on 1) the observed clustered distribution of white sturgeon within both watersheds, 2) potential migration barriers, and 3) the availability of samples. Collections were made by several groups, including RL&L Ltd., BC Regional Provincial biologists, First-Nations Groups, and the Fraser River Conservation Society between 1995 and 2000 (See appendix 3 for exact collection dates and locations). The vast majority of samples were caught using either set lines or angling (see Toth *et al.* 2000, McKenzie 2000, Yarmish & Toth 2001). Because so little is known of white sturgeon population biology (i.e. is there variability in population structure among sexes, cohorts, etc..?), and because this species was not equally abundant at all sites, the first 50 fish collected from each site were used regardless of sex or age composition, or the time over which the samples were caught. Pectoral fin clips were collected from each individual and stored in 95% EtOH at ambient temperature. Genomic DNA was extracted from each individual using Chelex as described on page 14.

Microsatellites

Dr Sheldon McKay (personal communication) identified thirteen microsatellite primer sets that produced PCR product in white sturgeon (Table 8). Eight of these loci had been isolated from other sturgeon species. The remaining five had been isolated from a white sturgeon library built and screened by Dr. McKay, following the protocol outlined on pages 13-14.

Each of these thirteen primer sets was examined in nineteen white sturgeon. PCR was done as described on pages 11-13, using the annealing temperatures listed in Table 9. Initial size-fractionation of PCR products was also done as described on page 13. Primers for which PCR products were too complex to analyze on the non-denaturing gels were subsequently fluorescent tagged (as indicated in Table 8). Labeled PCR products were run through 5% Long Ranger (FMC Bioproducts) gels on an ABI377 DNA sequencer. Data were collected for 1.5 hours per run by Genescan (ABI) software, and then converted to spreadsheet format by Genotyper (ABI) software. The size marker used was GS-2500 labeled with ROX dye (ABI). Dosage analysis of tetrasomic loci was done after May *et al.* (1997), using peak height in place of band intensity.

Pedigree analysis of loci which produced scorable PCR products (indicated in Table 8) was performed using 8 sets of known parents with 22-48 offspring each. Banding patterns produced by each primer set were compared to Mendelian expectations by means of a χ^2 test. Loci exhibiting one or two equally intense bands were tested against disomic expectations, while those exhibiting three to four polymorphic bands were tested against

Table 8. Microsatellite primers examined in white sturgeon. Primer sequences changed by Dr. Sheldon McKay from those published are indicated by *. T_a (?C) indicates optimal PCR annealing temperature observed.

Locus	PCR primers (5'-3')	T_a	Comments	Source
<i>LS19</i>	CATCTTAGCCGTCTGTGGTAC Fam- CAGGTCCTAATACAATGGC	60	Examined in pedigree	(May <i>et al.</i> 1997)
<i>LS34</i>	Hex- TACATACCTTCTGCAACG GATCCCTTCTGTTATCAAC	55	Examined in pedigree	(May <i>et al.</i> 1997)
<i>LS68B</i>	Fam- TTATTGCATGGTGTAGCTAAAC* AGCCCAACACAGACAATATC TATC*	52	3-10 poorly defined asymmetric bands per individual	(May <i>et al.</i> 1997)
<i>LS57B</i>	Tet- TTTGCTTGGTTGCTAGTTTGCTA* GTACAGATGAGACCAGAGGCGCATG*	54	Examined in pedigree	(May <i>et al.</i> 1997)
<i>Aox23</i>	Tet - CAGTGTGCTAGCTTCTCAATA GTTAGCTTAACCATGAATTGTG	58	Several poorly resolved bands. Banding pattern inconsistent among PCRs / gels	(Lubinski <i>et al.</i> 1998a)
<i>Aox27</i>	Fam-AATAACAATAACGGCAGAACCT TGTGTTGCTCAAGACAGTATGA	60	Examined in pedigree	(Lubinski <i>et al.</i> 1998b)
<i>Atr1</i>	GTACTTCCTTCTTTTAAGGTCCTGG CAACTAATGTCACAGTACGTCCC	56	Examined in pedigree	S. McKay (pers. comm.)
4-5	Hex-GATCCATTACAATTGATATATACCAA GGTTGTATGCCCAAGAAAAGCGT	54	1-5 asymmetric bands per individual	S. McKay (pers. comm.)
<i>Atr2</i>	TTCTATGTAACAACACTTGTATTACTAG TAGATAAACTATGCCGCTCATCC	56	Examined in pedigree	S. McKay (pers. comm.)
4-3F	TGAGACCATCAAAATTTCTGTGCGG CAATTCACAGAGACCATCATTACC	58	Examined in pedigree	S. McKay (pers. comm.)
<i>Atr3</i>	TTTTCATCATTAAGACCAGAGCC TTATTCTATAAGCAACATTTCAATTTCC	50	Examined in pedigree	S. McKay (pers. comm.)
5-1	CACTGGGGTTTATGTGCCCATGA AGTTCTGGATTTTATAATGAGAATC	50	Polymorphic bands very faint and inconsistent among PCRs / gels	S. McKay (pers. comm.)
5-7	CTGCAACACCCCGTAAACCAG TATGCACATTCTAAATCACTTAGGAC	50	Polymorphic bands very faint and inconsistent among PCRs / gels	S. McKay (pers. comm.)

tetrasomic expectations. Loci exhibiting two asymmetrically intense bands were tested against both disomic and tetrasomic expectations.

Based on the results of these tests (see below), the loci *Aox27*, *Atr1*, *Atr2*, and *Atr3* were examined in the white sturgeon population samples.

Mitochondria

A subset of the white sturgeon assayed for microsatellite variation were also examined for mtDNA control region restriction fragment length polymorphism (RFLP). Dr. Sheldon McKay sequenced 462 bp of the mtDNA D-loop in 78 white sturgeon from the Columbia and Fraser rivers. Seven novel haplotypes were observed and designated *cr20-cr26* (GenBank accession #s AF448426-AF448432). Based on these sequences plus the nineteen haplotypes identified by Brown *et al.* (1993), Dr John Nelson designed and executed the following RFLP strategy. The PCR primers L185 and H740 (Brown *et al.* 1993) were used to amplify 598 bp of the mtDNA D-loop. PCR was done in 50 μ l volume in the buffer described on pages 11-13. Reactions were cycled as follows: an initial denaturation of 3 min at 94° C, followed by 30 cycles of 94°C for 30 sec, 45°C for 30 sec and 72°C for 1 min. PCR products were purified using the QIAquick Purification Kit 96 (QIAGEN), and digested with *MseI*, *SfcI* (New England Biolabs) and *Hsp92II* (Promega). Digests were electrophoresed through either 7% (*SfcI*) or 10% (*MseI* and *Hsp92II*) 19:1 acrylamide: bis-acrylamide gels at 70 V for 8 hours. Gels were stained with ethidium bromide and photographed as described above.

Mitochondrial variation within sites was quantified as haplotype diversity (h) and nucleotide diversity (π) using Arlequin.

Relationships among sample sites

Because of the relatively small size of the Fraser 8 sample (Fig. 6), it was not included in analyses of population structure. PHYLIP was used to calculate D_{CSE} between all sample sites based on both microsatellite and on mtDNA data. In order to examine genetic variation among age-classes, sample sites represented by several adult (fork-length $\geq 150\text{cm}$) and sub-adult individuals were split in two samples. The data matrix containing these split sites (sites 2, 7, 10, 12), as well as the intact matrix and one containing only Fraser River sites were subject to unweighted pair-group method with arithmetic mean (UPGMA) (Sneath & Sokal 1963) analysis and NJ analysis. Concordance among microsatellite loci was examined using 10^3 bootstrap replicates. Correlation between microsatellites and mtDNA was calculated and tested using a permutation procedure (Mantel 1967) in Arlequin.

Statistical differences between sites were tested using nucleotide divergence (Nei 1987, pg. 276) for mtDNA data and F_{ST} (Weir & Cockerham 1984) for microsatellite data, each with a null distribution based on 10^5 replicates. The proportion of genetic variance explained by UPGMA and NJ structures (among groups), as well as the potential of the data to detect finer structure (among sites within groups) were assessed with AMOVA.

Results

Microsatellites

Complex banding patterns observed for several microsatellite loci prohibited their use in the present population analysis. Complications inherent in PCR-based techniques for population analysis of polysomic loci (Spruell *et al.* 1999) become magnified with increasing ploidy. Therefore, loci exhibiting more than 4 polymorphic bands were discarded. Pedigree analysis (Table 9) was not useful for 4-3, as this locus was fixed in all families. *LS57*, *LS19* and *LS34* exhibited multiple cases of F1 alleles which were not present in the P1 generation, and were thus not considered further. *Aox27*, *Atr1*, *Atr2*, and *Atr3* showed the least deviation from Mendelian expectations, and were thus used for population analysis. *Aox27* exhibited 1-4 bands per individual and ratios that matched tetrasomic Mendelian expectations. The 3 *Atr* loci exhibited asymmetric banding (May *et al.* 1997), with ratios which matched disomic Mendelian expectations. Even among these four loci, all except *Atr3* exhibited some departures from Mendelian rules as well as ratios (Table 9).

Gel photographs of PCR products amplified by *Aox27*, *Atr1*, *Atr2*, and *Atr3* are shown in Appendix 1. Microsatellite allele frequencies observed in all sites are listed in Table 10. UPGMA (Fig. 7) and NJ analysis (not shown) of microsatellite data divided the Fraser River sites among three groups with $\geq 50\%$ bootstrap support. These groups were: the lower Fraser (sites 1 & 2), the upper Fraser (all other sites on Fraser mainstem), and the Nechako R. Pairwise F_{ST} estimates within these groups were not significant ($P > 0.05$), while those among groups were significant ($P < 0.05$). Exceptions to this

Table 9. Pedigree analysis of microsatellite primers in white sturgeon. P values correspond to χ^2 tests for departures from Mendelian expectations (H_0 = no departure). The number of F1 successfully analyzed for each locus is listed. Some tests were non-applicable (n/a) because 1) both parents were homozygous, allowing only a single expected F1 genotype, 2) offspring were missing alleles from one parent, and / or 3) offspring exhibited alleles not present in either parent.

Locus		Cross								
		♀: ♂:	363 21	363 219	363 317	334 317	334 219	223 317	223 21	223 219
4-3	# of F1	26	25	28	26	25	24	22	25	
	P value (2N)	n/a ¹	n/a ¹	n/a ¹	n/a ¹	n/a ¹	n/a ¹	n/a ¹	n/a ¹	
	P value (4N)	n/a ¹	n/a ¹	n/a ¹	n/a ¹	n/a ¹	n/a ¹	n/a ¹	n/a ¹	
LS57	# of F1	22	23	28	26	25	22	18	25	
	P value (4N)	n/a ^{2,3}	0.002	0.000	0.408	n/a ^{2,3}	0.082	0.581	0.000	
LS19	# of F1	24	25	27	0	22	10	11	25	
	P value (2N)	n/a ^{2,3}	n/a ^{2,3}	n/a ^{2,3}	-	n/a ^{2,3}	1.000	1.000	n/a ^{2,3}	
LS34	# of F1	25	24	27	5	22	12	12	23	
	P value (2N)	n/a ^{2,3}	n/a ²	0.000	n/a ^{2,3}	n/a ²	N/a ^{2,3}	0.001	n/a ^{2,3}	
Aox27	# of F1	46	24	25	25	48	15	11	24	
	P value (4N)	n/a ²	0.043	n/a ¹	0.050	n/a ³	0.000	0.525	0.000	
Atr1	# of F1	39	25	28	25	45	24	19	24	
	P value (2N)	n/a ^{1,2}	n/a ^{1,2}	n/a ¹	n/a ¹	n/a ^{1,2}	n/a ¹	n/a ¹	n/a ¹	
Atr2	# of F1	44	21	23	25	25	19	17	18	
	P value (2N)	0.003	n/a ²	0.029	0.317	n/a ²	0.491	0.008	n/a ¹	
	P value (4N)	0.000	0.000	0.000	0.000	0.000	0.142	0.120	n/a ¹	
Atr3	# of F1	47	24	26	18	46	24	19	20	
	P value (2N)	0.255	0.160	0.000	0.121	0.054	n/a ¹	n/a ¹	0.078	
	P value (4N)	0.000	0.000	0.000	0.000	0.000	n/a ¹	n/a ¹	0.014	

Table 10. Observed allele frequencies at 4 microsatellite loci in white sturgeon from the Fraser and Columbia Rivers. Site numbers correspond to Fig. 6. Names of alleles correspond to the size of the PCR product in base pairs.

Site	N	<i>Atr1</i>		<i>Atr2</i>		<i>Atr3</i>		<i>Aox27</i>					
		130	134	184	193	128	132	126	130	134	138	142	146
1	56	0.581	0.419	0.580	0.420	0.955	0.045	0.012	0.054	0.381	0.345	0.161	0.048
2	55	0.372	0.628	0.548	0.452	0.877	0.123	0.014	0.027	0.373	0.386	0.136	0.064
3	46	0.349	0.651	0.535	0.465	0.977	0.023	0.033	0.006	0.250	0.328	0.322	0.061
4	50	0.245	0.755	0.480	0.520	1.000	-	0.021	-	0.201	0.325	0.433	0.021
5	50	0.510	0.490	0.449	0.551	1.000	-	0.050	-	0.160	0.340	0.435	0.015
6	50	0.418	0.582	0.552	0.448	1.000	-	0.015	-	0.165	0.410	0.405	0.005
7	56	0.381	0.619	0.510	0.490	1.000	-	0.022	-	0.179	0.304	0.446	0.049
8	10	0.400	0.600	0.500	0.500	1.000	-	-	-	0.313	0.188	0.500	-
9	43	0.465	0.535	0.593	0.407	1.000	-	0.032	-	0.129	0.427	0.411	-
10	50	0.420	0.580	0.615	0.385	1.000	-	-	-	0.214	0.541	0.245	-
11	50	0.333	0.667	0.542	0.458	0.949	0.051	0.006	0.017	0.344	0.450	0.156	0.028
12	50	0.296	0.704	0.460	0.540	0.970	0.030	0.027	0.016	0.282	0.564	0.064	0.048
13	20	0.400	0.600	0.531	0.469	0.975	0.025	-	0.038	0.200	0.675	0.050	0.038
14	50	0.367	0.633	0.418	0.582	1.000	-	-	0.011	0.223	0.670	0.069	0.027
15	50	0.270	0.730	0.071	0.929	0.930	0.070	-	-	0.203	0.622	0.174	-

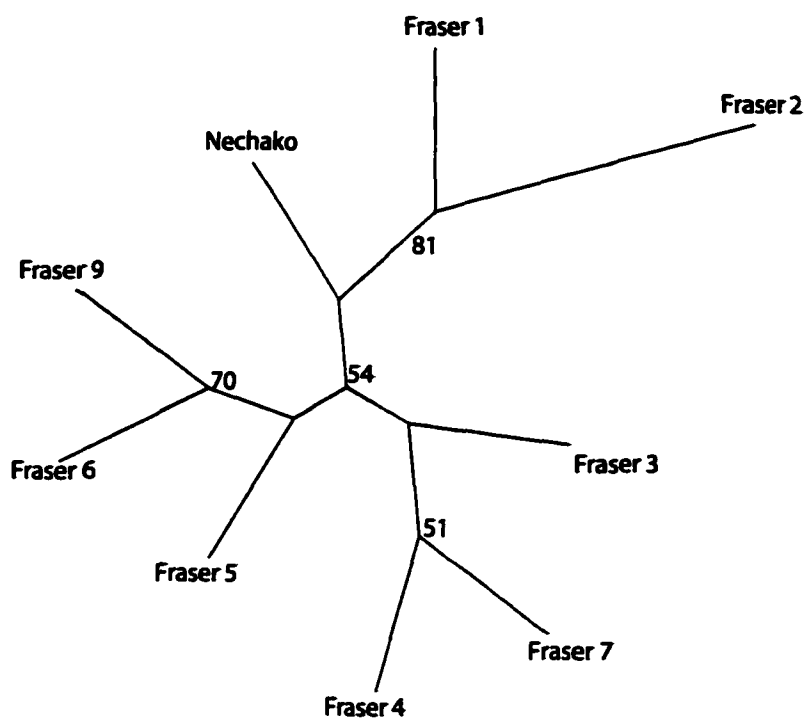


Figure 7. UPGMA dendrogram based on microsatellite D_{CSE} for Fraser River white sturgeon. Numbers on branches indicate the percentage of 1000 bootstrap replicates that support grouping the sites distal to that branch.

generalization were that the Nechako and uppermost Fraser site (9) were not significantly divergent ($P=0.189$), while Fraser 3 and Fraser 5 were significantly divergent ($P=0.007$). The same three Fraser River groups appeared when the Columbia sites were included in the analysis. The lower Fraser group joined the Columbia sites (58% bootstrap) while the other two Fraser groups were distinct from the Columbia.

Mitochondria

The mtDNA RFLP assay revealed 9 compound haplotypes (Table 11) (see Appendix 1 for gel images). No heteroplasmic individuals were observed. UPGMA (Fig. 8) and NJ analysis (not shown) of mtDNA data divided Fraser River sites among three major branches. Nucleotide divergence indicated that although the Nechako and uppermost Fraser were on the same UPGMA branch, the difference between them was highly significant ($P<0.000$). Variation among sites on each of the other two branches was not significant ($P\geq 0.05$), while pairwise comparisons between branches were significant ($P\leq 0.05$). There was a single exception in this case: sites 3 and 4 were not significantly different from each other ($P=0.063$). The same Fraser River groups appeared when the Columbia sites were included in the analysis.

Haplotype diversity ranged ten-fold from $h=0.07$ in Kootenay Lake to $h=0.79$ in the upper Columbia (Table 12). Relative diversity of the Columbia and Fraser rivers contrasted with predictions based on earlier work. Haplotype diversity within the Fraser ($h=0.71$) was similar to that based on RFLP of the entire molecule ($h=0.70$) (Brown *et al.* 1992a), but lower than that based on D-loop sequence ($h=0.97$) (Brown *et al.* 1993). Haplotype diversity in the Columbia ($h=0.63$) was also lower than that based on D-loop sequence

Table 11. Nomenclature for composite mtDNA haplotypes observed in white sturgeon.

Single restriction enzyme haplotype			Composite haplotype
<i>Hsp92II</i>	<i>MseI</i>	<i>SfcI</i>	
a	a	a	1
b	a	a	2
b	b	a	3
a	b	a	4
b	b	b	5
c	b	b	6
b	a	b	7
d	b	b	8
d	b	a	9

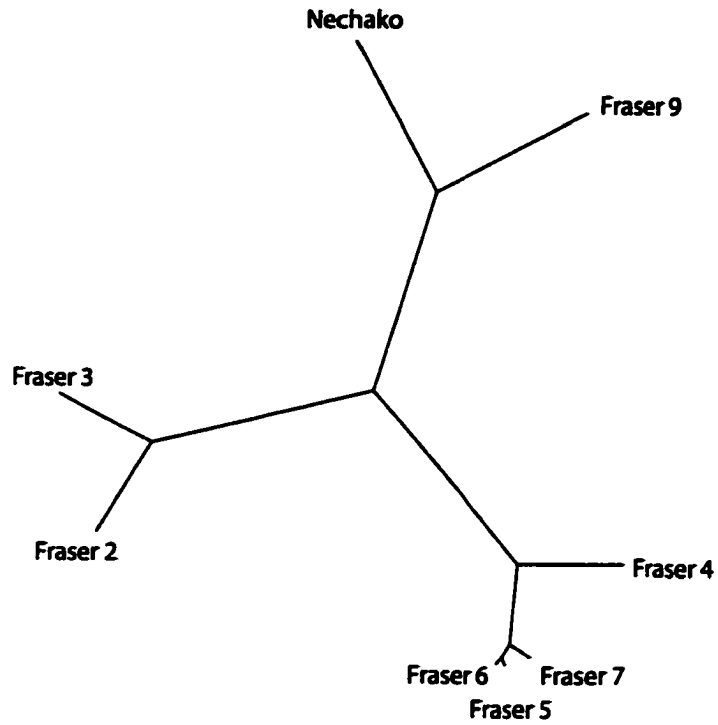


Figure 8. UPGMA dendrogram based on mitochondrial D_{CSE} for Fraser River white sturgeon.

Table 12. White sturgeon compound mtDNA RFLP haplotype frequencies observed at several sites in the Fraser and Columbia rivers. Site numbers correspond to Fig. 6.

Haplotype diversity (h) measures variation based on identity / non-identity in state, while nucleotide diversity (π) takes into account the distance between states.

Site	n	Composite haplotype									h	π
		1	2	3	4	5	6	7	8	9		
2	31	-	0.13	0.39	0.35	0.06	0.03	0.03	-	-	0.725	0.369
3	27	-	0.11	0.44	0.19	0.04	-	0.22	-	-	0.732	0.372
4	26	-	-	0.54	-	0.12	-	0.35	-	-	0.600	0.247
5	30	-	0.13	0.30	-	0.13	-	0.43	-	-	0.710	0.254
6	30	-	0.07	0.30	-	0.13	-	0.50	-	-	0.660	0.247
7	28	-	0.11	0.32	-	0.04	-	0.54	-	-	0.619	0.246
8	5	-	0.20	0.60	-	0.20	-	-	-	-	0.700	0.200
9	30	-	0.31	0.69	-	-	-	-	-	-	0.435	0.109
10	29	-	0.38	0.41	-	-	-	0.21	-	-	0.665	0.211
12	30	0.13	0.37	0.27	0.03	0.10	0.03	-	0.03	0.03	0.793	0.376
13	18	-	0.33	0.50	0.06	-	-	-	0.06	0.06	0.667	0.247
14	28	0.11	0.56	0.15	0.15	-	-	-	-	0.04	0.643	0.316
15	27	-	0.96	0.04	-	-	-	-	-	-	0.074	0.019

($h=0.93$) (Brown *et al.* 1993), but much higher than that based on RFLP of the entire molecule ($h=0.08$) (Brown *et al.* 1992a).

A positive correlation was observed between D_{CSE} based on microsatellite data and that based on mtDNA data ($r^2=0.34$, $P<0.000$).

When sites that were split based on fork length (sites 2, 7, 10 & 12) were subjected to the above analysis, microsatellite data paired small fish with large fish from the same sites in the Fraser (2 & 7) and Nechako (10), but not in the Columbia (12). In contrast, mtDNA only paired large and small fish from the Nechako. Mitochondria grouped small Columbia River fish on the Fraser branch, and small lower Fraser River fish on the Columbia branch. Adults from both rivers appeared on their "correct" respective branches.

AMOVA

Analysis of molecular variance revealed that 78.3% ($P=0.002$) of mtDNA variation and 95.5% ($P=0.004$) of microsatellite variation observed in the Fraser River was found among individuals within the sites, indicating the greater potential of mtDNA data for describing relationships among sites. The remaining variation was divided between "among groups" and "among sites within groups". Division of the Fraser into three groups (Fig. 19) best explained microsatellite variation, partitioning 5.0% ($P<0.001$) among groups and -0.5% ($P=0.933$) among sites within groups. Division of the Fraser into four groups (Fig. 22) best-explained mtDNA variation, partitioning 19.9% ($P<0.001$) among groups and 1.8% ($P=0.161$) among sites within groups. Small and non-significant

among sites within groups variance for data from both markers indicated that population structure on a finer scale would not be resolved with these data.

Discussion

Pyatskowitz *et al.* (2001) examined microsatellite inheritance in lake sturgeon (*Acipenser fulvescens*) and observed patterns that violated Mendelian expectations. Those authors invoked transmission of unreduced gametes and meiotic drive to explain these violations. Preliminary data from other researchers has further indicated that PCR products produced by microsatellite primers in sturgeon do not follow co-dominant Mendelian inheritance patterns (Radu Suci, personal communication; Lorenzo Zane, personal communication). Assumptions regarding the inheritance of individual loci need to be tested before inferences based on those loci are made. Pedigree analysis in the present study was successful in identifying limitations of the markers considered. As several loci were discarded based on an inability to interpret them, variability reported here seems likely to be only partially representative of that present in the white sturgeon genome.

Mitochondrial data in the present study provided more resolution than the microsatellites did (as indicated by AMOVA), and provided greater inferential power due to unambiguous inheritance. With all that is unknown regarding the basic biology of white sturgeon, however, extrapolation of mtDNA structure to species population structure must be viewed as speculative. Correlation and overall concordance between the two marker types lent an intuitive measure of confidence to doing so in this case.

In addition to assumptions about the markers being examined, the analysis assumed that samples collected from each site were genetically representative of that site, and therefore that the sites themselves had biological relevance. While these assumptions may not be

realistic, the lack of information available on white sturgeon population structure makes them necessary. The sites for which samples were split into juvenile and adult samples exhibited consistent allele frequencies. Although sample sizes and composition prevented rigorous statistical examination of this congruence, the observation lends an intuitive measure of confidence that at least some of the sites may have a biological basis. Significant variation among, and the lack of variation with groups identified here gives further confidence in a biological basis for those groups. Violations of the sampling assumptions might invalidate estimates of parameters, such as migration, between sites, but would not necessarily invalidate the groups described here.

Based on previous discussions (Brown *et al.* 1992a, Brown *et al.* 1993), relatively little genetic diversity was expected within the upper Columbia. During the last glacial retreat, Kootenay Lake was isolated from the remaining Columbia River sites by falls shortly after it was freed from ice (summarized by Northcote 1973). This allowed only a short founding period, and Kootenay Lake is known to be correspondingly less diverse than lower regions of the Columbia system (Bartley *et al.* 1985, Setter & Brannon 1992). When Kootenay Lake was removed from the present analysis, haplotype diversity was higher in the Columbia basin than in the Fraser. More mtDNA haplotypes and microsatellite alleles were seen in the upper Columbia than the upper Fraser. Bernatchez and Wilson (1998) summarized data for several anadromous fish species which, despite being subject to recent anthropogenic bottlenecks, still exhibit phylogeographic patterns reflecting post-glacial dispersal. The observed distribution of genetic variation can be explained without the invocation of an anthropogenic bottleneck over-riding the signal of post-glacial dispersal.

Within the Fraser, the present data support those of Brown *et al.* (1992a) in identifying the lower region as the most diverse. Because the Fraser and Columbia enter the Pacific Ocean only 500 km from each other, the potential contribution of inter-river migration to this diversity is of interest. Evidence for potential migration includes the presence of white sturgeon on (mostly the west coast of) Vancouver Island (D. Lane, personal communication), sturgeon tagged in the Columbia River and subsequently recaptured off the coast of northern Washington State (Galbreath 1985), and evidence that some Fraser River white sturgeon make marine migrations (Veinott *et al.* 1999). Several aspects of the present data reveal that white sturgeon in the lower Fraser are similar to those in the Columbia. The data cannot, however, be used to determine whether the similarity is due to migration, or a relatively short coalescence time. The upper limit to the lower Fraser region is the velocity barrier at Hell's Gate Rapids. White sturgeon are not believed able to migrate upstream of this barrier, but downstream movement has been recorded (McKenzie 2000). Divergence of this region from the rest of the Fraser, with uncertainty regarding exactly where the border is, suggests that the Fraser River below Hell's Gate is a distinct biogeographic region, but that it is not a single or closed breeding unit.

Sites between Hell's Gate and Fraser 7 grouped together, with neither marker type showing significant differences between them. The site upon which the two markers contrast is Fraser 9. Despite significant effort over 2 years of sampling, very few sturgeon were observed in the 80 km region south of the Nechako-Fraser confluence (McKenzie 2000). Yarmish and Toth (2001) noted that this region was broad and

shallow, lacking deep pools and channel structure. Those authors suggested that this region, as well as a similar region in the lower 60 km of the Nechako River act as migration barriers for white sturgeon. Tag and recapture data frequently revealed large movements (>32 km) within the upper Fraser, but no evidence of movement between the upper Fraser and the middle Fraser or the Nechako (Toth *et al.* 2000, Yarmish & Toth 2001). The authors of those studies proposed that the relatively large movements within the upper Fraser might be an adaptive response to the unique environment faced by these fish (i.e. lower temperature, seasonal ice and more sporadic anadromous food sources). Although microsatellite data did not reveal divergence here, mtDNA data are supported by tag and recapture data in identifying divergence between the upper and middle Fraser.

Nechako River white sturgeon are of special conservation interest as the stock consists mostly of older fish and exhibits low spawning success and recruitment. This is likely due to altered thermal and hydrographic regimes, and leaves sturgeon in this region susceptible to extirpation (McKenzie 2000). Microsatellite and mtDNA data concurred that the Nechako was distinct from the middle Fraser. While microsatellite data were unclear regarding distinction between the upper Fraser and the Nechako (majority bootstrap, but no significance), mtDNA data (specifically haplotype 7) provided much more conclusive evidence of this divergence. All Nechako sturgeon examined were from above river km 72, as sampling below this failed to produce a single fish (McKenzie 2000). This supports the suggestion that the lower Nechako acts as a migration barrier to white sturgeon.

Data presented here suggest the division of Fraser River white sturgeon into four biogeographic groups. These are: 1) the lower Fraser, below Hell's Gate, 2) the middle Fraser, between Hell's Gate and river km 553 (Fraser 7), 3) the upper Fraser, above the Nechako confluence, and 4) the Nechako River. These four groups are concordant with those suggested by tag and recapture and catch per unit effort data, and are separated by what have been identified as barriers to white sturgeon migration. The lack of significant among site within group variance indicates that structure on a finer scale than the one described is not detectable with the current data. The observation of slightly more variation in the upper Columbia than in the upper Fraser is what one would expect given that the Fraser was recently glaciated. Higher diversity in the lower Fraser than in the upper Fraser could be due to migration between rivers, or it could simply be that the lower Fraser has a larger N_e and thus loses fewer alleles to drift. Resolution of this issue as well as questions regarding post-glacial colonization sources of the Fraser River would require further sampling.

McPhail and Carveth (1993) suggested adoption of the evolutionarily significant unit (ESU) as the basic conservation element for this region's ichthyofauna. An ESU is defined as a population which is substantially reproductively isolated from conspecific populations, and which represents an important component of the evolutionary legacy of the species (Waples 1991). The present data revealed that the four groups identified are significantly isolated and thus meet the first condition. To address the second condition one should note that the environments, and thus selective regimes, faced by these groups are different. White sturgeon in the upper Fraser and Nechako grow more slowly, have to move greater distances to feed, and likely spend more time at a low metabolic rate under

winter ice (McKenzie 2000, Yarmish & Toth 2001). As Hell's Gate prevents upstream movement, sturgeon living above it are unlikely to have made marine migrations, while sturgeon living below it may have (Veinott *et al.* 1999). Based on the genetic data presented, combined with habitat and ecological data, the four groups identified here merit designation as ESUs.

CHAPTER 5 - CONCLUSIONS

This dissertation described genetic data for two anadromous fish species native to the Pacific coast of North America: coho salmon and white sturgeon. In each case, examining both nuclear microsatellites and mtDNA D-loop variation proved more informative than examining either marker alone. While similar molecular markers were examined in both species, sampling in the two studies was quite different, reflecting the question being asked in each case. Coho were sampled over their entire North American range, necessitating small, widely spread samples. Sturgeon were sampled from only the Columbia and Fraser rivers, allowing more fish in each system to be examined. Sampling over these two different scales yielded data with very different conservation implications.

The resolution provided by nuclear microsatellites and mtDNA was different in each study. In coho, microsatellites provided the greatest resolution. In sturgeon, mtDNA provided the greatest resolution. As only four of the simplest loci originally examined in sturgeon were used for population analysis, this result is probably an artifact. Given the complex and poorly understood nature of the white sturgeon genome, anonymous nuclear loci seem a poor choice of marker with which to characterize this species. The four microsatellite loci that were examined in white sturgeon were useful, however, in that they indicated a structure parallel to that of mtDNA. In doing so they lent confidence to extrapolation of mtDNA structure to population structure. In coho, differences in the evolutionary properties of the two marker types allowed each marker to illuminate an aspect of the species' evolution that the other marker did not.

Before comparison is made of the conservation relevance of these two data sets, limitations of applying neutral genetic data to conservation biology should be considered. An issue frequently raised is the assumption of selective neutrality of the markers being examined (Rand 1996). Selection is a factor that can never be completely ruled-out. The use of as many unlinked loci as possible is one way to minimize the effect that selection at individual loci might have on one's results. One rationale for ignoring potential selective forces acting on molecular markers is that the low N_e characteristic of many targets of conservation research will negate weak selection. As N_e is reduced, small or even moderate selective coefficients are easily overwhelmed by drift and or migration.

A second issue, which may be more difficult to dismiss, is the unclear relationship between neutral and adaptive variation. It seems unlikely that a simple relationship between the two exists (Lynch 1996, Lynch *et al.* 1999, Reed & Frankham 2001, Thelen & Allendorf 2001). What can be suggested is that if neutral divergence exists, the potential for adaptive divergence does also. In both of the case studies presented here, evidence from field studies was cited in order to suggest that the groups identified by neutral genetic variation were divergent for adaptive traits. A key factor in making such connections is understanding the biology and life history of the species in question (Waples 1998), and a lack of such knowledge necessitates some subjectivity in choosing analysis methods. In the white sturgeon study presented here, statistical significance of the differences among groups was used in place of biological significance to infer significant reproductive isolation. Arguments could be made for and against such an assumption. Accepting the above assumption in this case, and thus arguing that the

groups identified merit ESU status was partly based on the ethic of a conservative approach to protecting this species. Forced decisions based on incomplete data may be inevitable parts of conservation biology as a "crisis discipline" (Soule 1985, Meffe & Carroll 1997). Such limitations need to be recognized when suggesting the application of genetic or any other scientific data for management purposes (Hedrick 1996, Hedrick *et al.* 1996).

The white sturgeon data described variation over a small enough geographic scale as to make it directly useful to management. The four groups identified within the Fraser River are adjacent to each other or to migration barriers, and enough data has been collected to argue that these units merit ESU status. All of these units fall within a single political region, further facilitating management based on this data. The white sturgeon data, however, revealed nothing about how populations in the Fraser and Columbia relate to the Sacramento population, or to white sturgeon in rivers on Vancouver Island, northern British Columbia, or Alaska. Although, argument was made that the groups are adaptively divergent, whether protecting these groups would affect the evolutionary potential of the species is highly speculative. The conservation relevance of the white sturgeon data is that they identified groups within the Fraser River, between which gene flow is most limited. Protection of these groups individually should minimize the probability of the smaller groups being further reduced, and thus the chance of this species being eliminated from a region due to stochastic events.

The coho data, in contrast, describe variation on a continental scale. Evidence of genetic structure was observed at two different levels, and an explanation for this species' glacial

biogeography was offered. The distribution of genetic variance in the species, especially the south to north cline, identified regions among which coho's genetic resources are likely distributed. The samples are too small and too far separated to be of use in defining stocks. The conservation relevance of these data is that they identified groups within the species among which gene flow has historically been limited. These data are thus the best indication to date regarding which groups need to be protected in order to preserve the evolutionary potential of coho salmon.

The two species considered in this dissertation both diverged from their respective congeners in the North Pacific basin, probably during the Tertiary Period. The evolution of both species has likely been shaped by recurrent cycles of colonizing new habitat, diverging, and retreating to glacial refugia. Human activity over the last two centuries has almost certainly reduced the amount of variation within these species; however the distribution of existing variation seems to reflect these glacial cycles. The two case studies presented here illustrate different scales at which molecular genetic data may be applied to the interests of conservation biology. The different questions addressed in each case underline the importance of carefully defining the objectives of conservation research.

The potentials of these data sets to protect species other than coho salmon and white sturgeon, or the umbrella effects of these data sets, are likewise based on the geographic scale of each. The coho data support the existence of, and thus add weight to arguments for protecting, several biogeographic provinces along the Pacific coast of North America. Examining concordance or discordance among population structures of many species in

the context of past and present geography thus provides a powerful tool for conservation biologists (Walker & Avise 1998). An advantage of defining such biogeographic provinces, it that is affords us the opportunity to protect processes rather than individual species (Moritz 1999). The white sturgeon data define geographic units within the Fraser and Columbia rivers which should be managed as separate units. The potential umbrella effect of these data were demonstrated by a recent proposal (Anders 2000) involving transplantation of hatchery fish from Kootenay Lake into Slocan Lake (between Kootenay Lake and Arrow Lake in Fig. 16). Slocan Lake is home to a relict population of two white sturgeon with zero recruitment (RL&L 1997). The proposal suggested that release of hundreds of white sturgeon into Slocan Lake would be good for the species. The present data indicate that Kootenay Lake white sturgeon are distinct from those in the rest of the Columbia system. Risk of the transplanted sturgeon migrating down into the upper Columbia and hybridizing with populations there was thus used as a basis for rejecting the transplantation proposal. Species such as burbot (*Lota lota*), which currently inhabit Slocan Lake, likely benefited from this decision.

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Appendix 1 – Gel images



Figure 9. Gel photographs showing PCR products produced by *Oki1* (top) and *Oki2* (bottom). Superladder-Low 20bp Ladder (GenSura Labs Inc.) (indicated by *) was used to size products on each gel. Bands in the ladder are in 20bp increments. The 200bp band is indicated by > and <.



Figure 10. Gel photographs showing PCR products produced by *Oki3* (top) and *Oki10* (bottom). Superladder-Low 20bp Ladder (indicated by *) was used to size products on each gel. Bands in the ladder are in 20bp increments. The 200bp band is indicated by > and <.

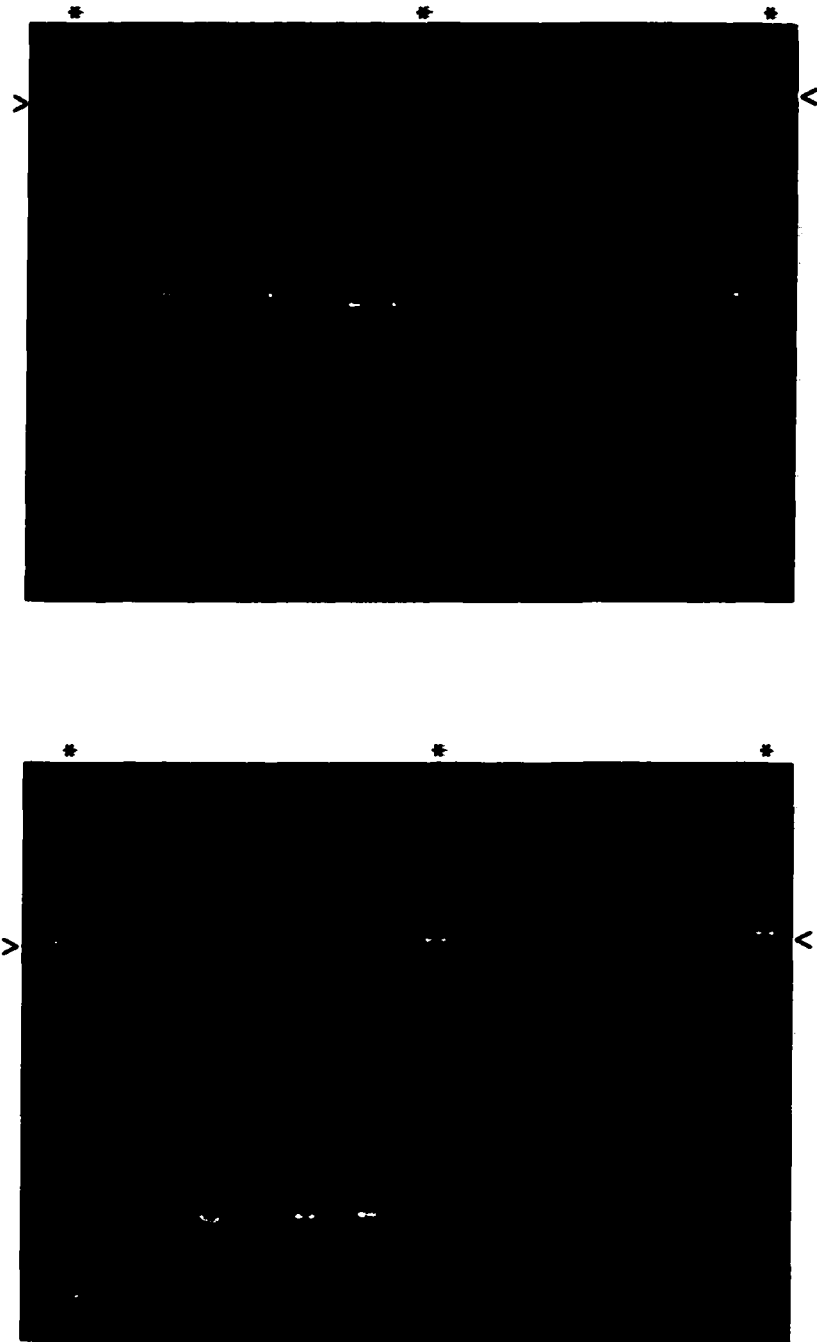


Figure 11. Gel photographs showing PCR products produced by *Oki11* (top) and *Oki13* (bottom). Superladder-Low 20bp Ladder (indicated by *) was used to size products on each gel. Bands in the ladder are in 20bp increments. The 200bp band is indicated by > and <.



Figure 12. Gel photographs showing PCR products produced by *Oki16* (top) and *Oki18* (bottom). Superladder-Low 20bp Ladder (indicated by *) was used to size products on each gel. Bands in the ladder are in 20bp increments. The 200bp band is indicated by > and <.



Figure 13. Gel photographs showing PCR products produced by *Oki20* (top) and *Omy77* (bottom). Superladder-Low 20bp Ladder (indicated by *) was used to size products on each gel. Bands in the ladder are in 20bp increments. The 200bp band is indicated by > and <.

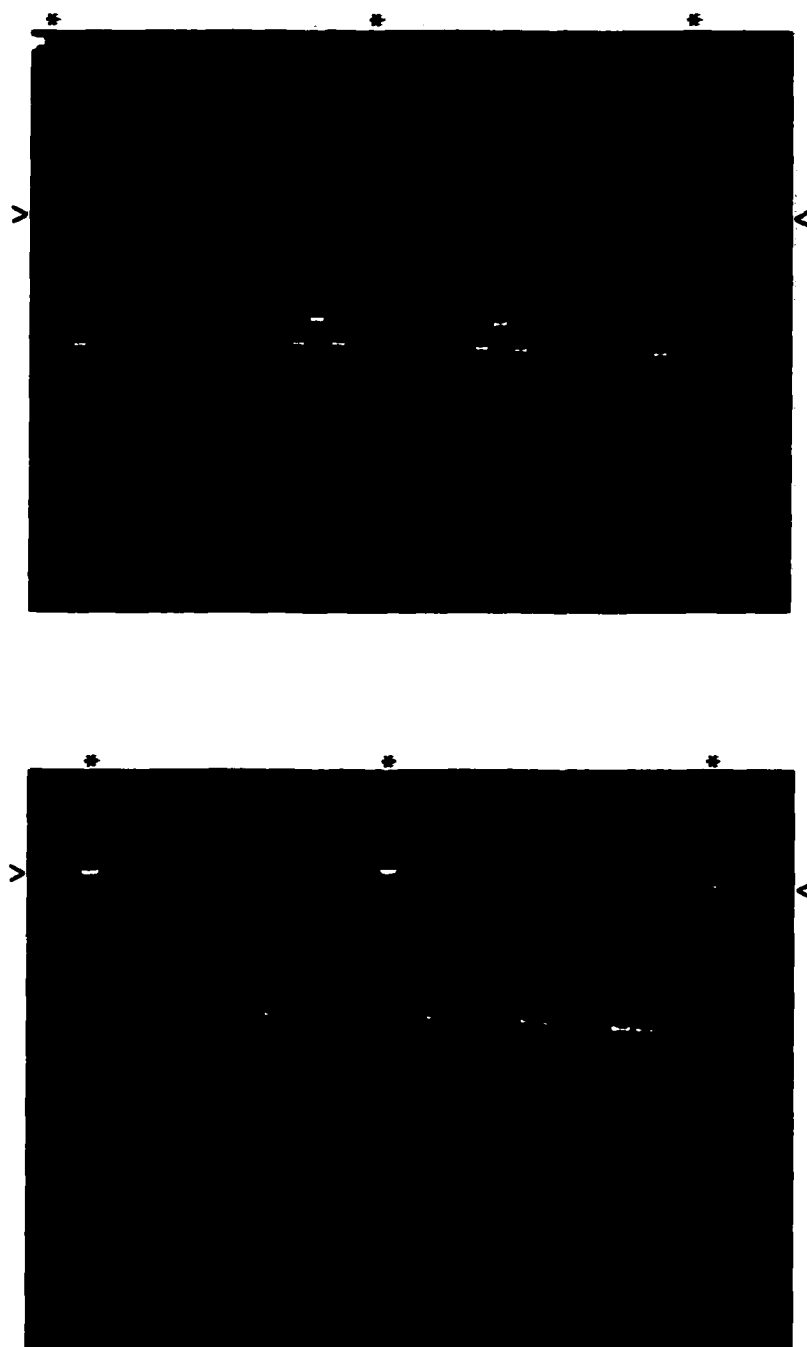


Figure 14. Gel photographs showing PCR products produced by *One11* (top) and *Ots3* (bottom). Superladder-Low 20bp Ladder (indicated by *) was used to size products on each gel. Bands in the ladder are in 20bp increments. The 200bp band is indicated by > and <.

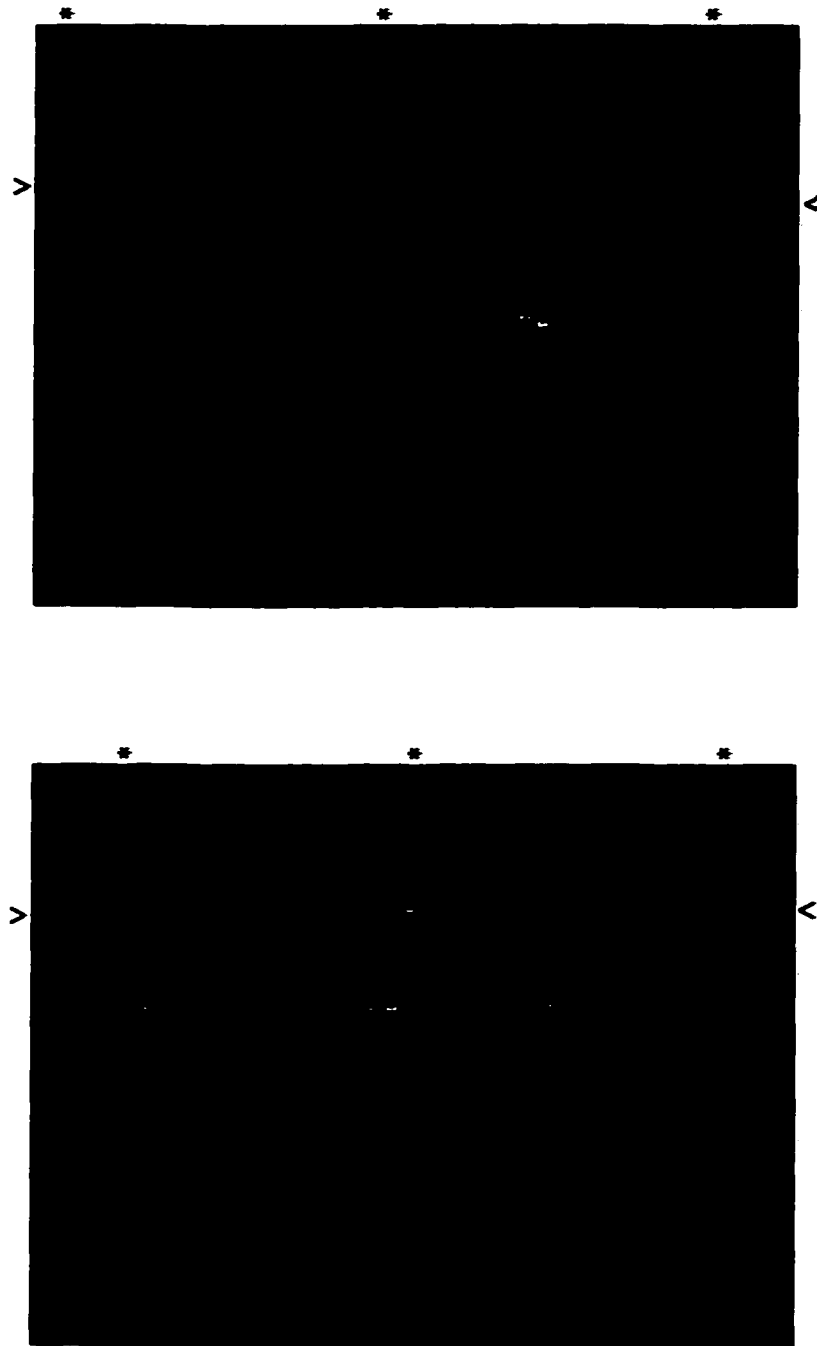


Figure 15. Gel photographs showing PCR products produced by *Ots4* (top) and *Ots72* (bottom). Superladder-Low 20bp Ladder (indicated by *) was used to size products on each gel. Bands in the ladder are in 20bp increments. The 200bp band is indicated by > and <.

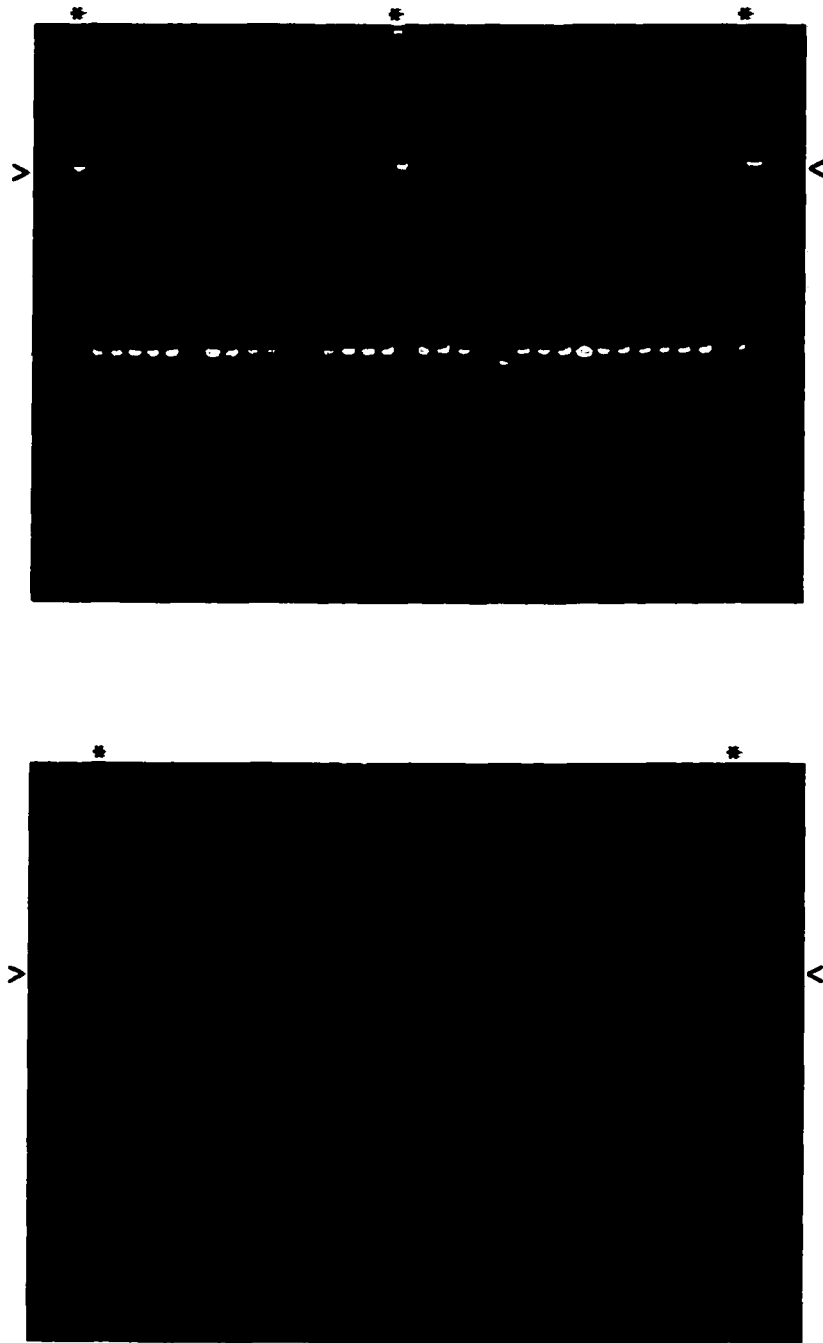


Figure 16. Gel photographs showing PCR products produced by *Ots9* (top) and *Ots101* (bottom). Superladder-Low 20bp Ladder (indicated by *) was used to size products on each gel. Bands in the ladder are in 20bp increments. The 200bp band is indicated by > and <.

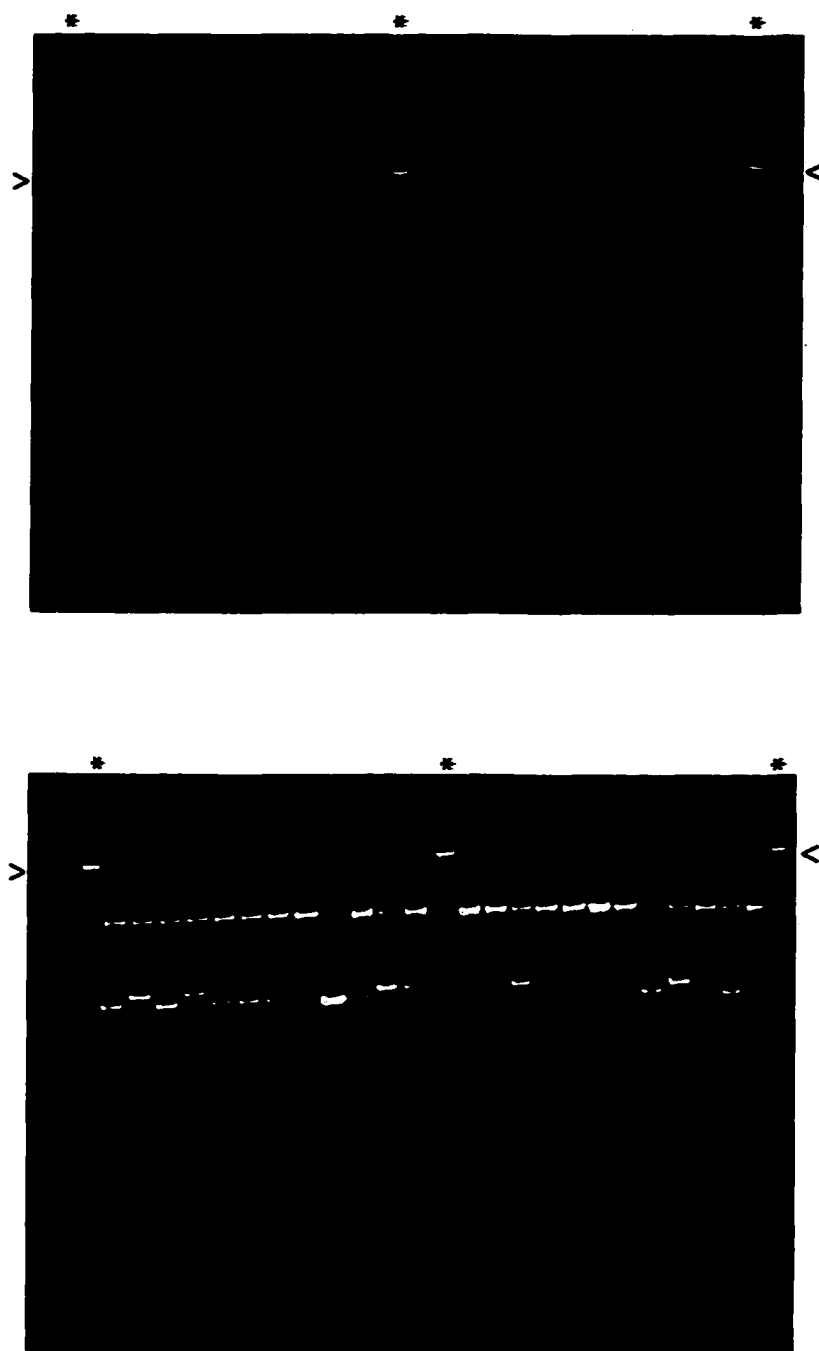


Figure 17. Gel photographs showing PCR products produced by *Ots103* (top) and *Ots105* (bottom). Superladder-Low 20bp Ladder (indicated by *) was used to size products on each gel. Bands in the ladder are in 20bp increments. The 200bp band is indicated by > and <.

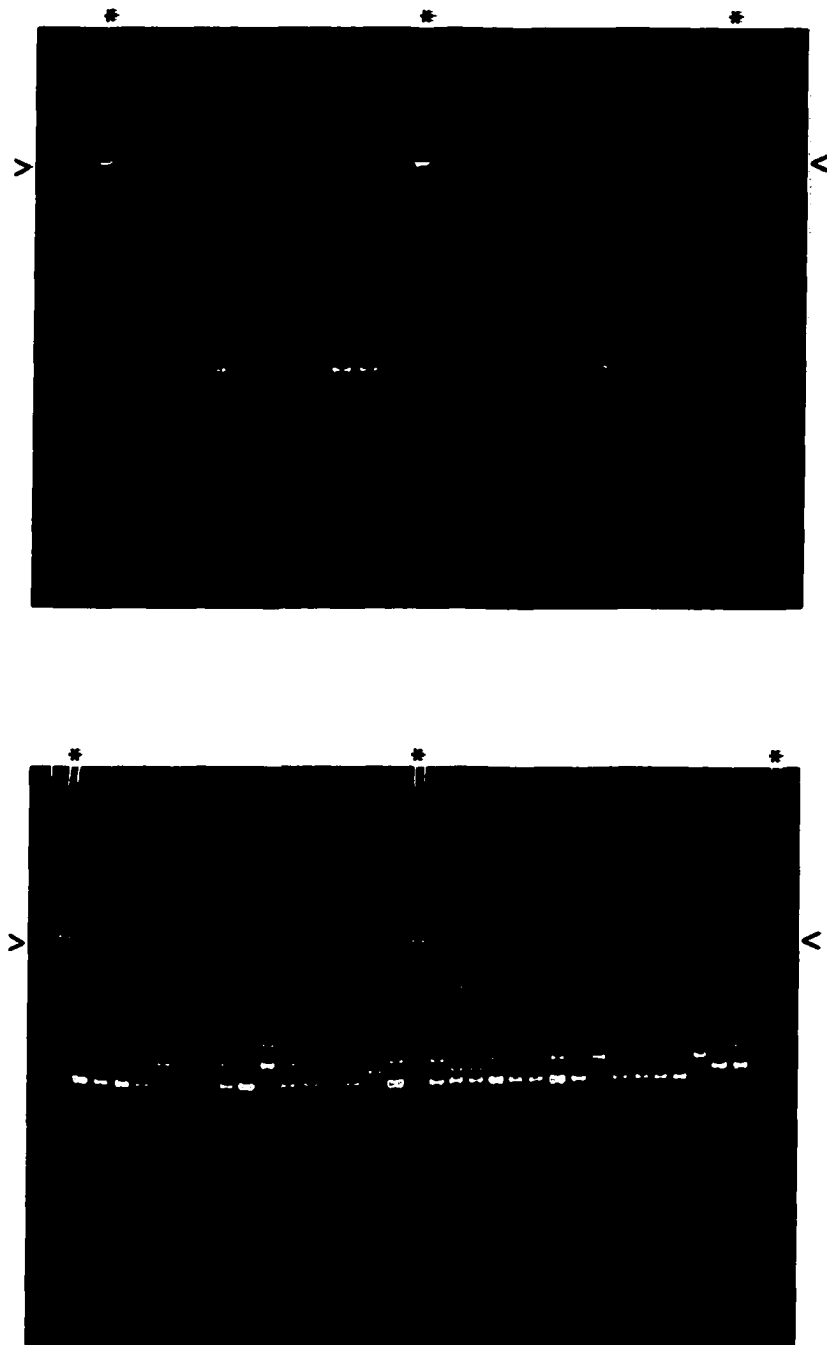


Figure 18. Gel photographs showing PCR products produced by $\mu 60$ (top) and $\mu 73$ (bottom). Superladder-Low 20bp Ladder (indicated by *) was used to size products on each gel. Bands in the ladder are in 20bp increments. The 200bp band is indicated by > and <.

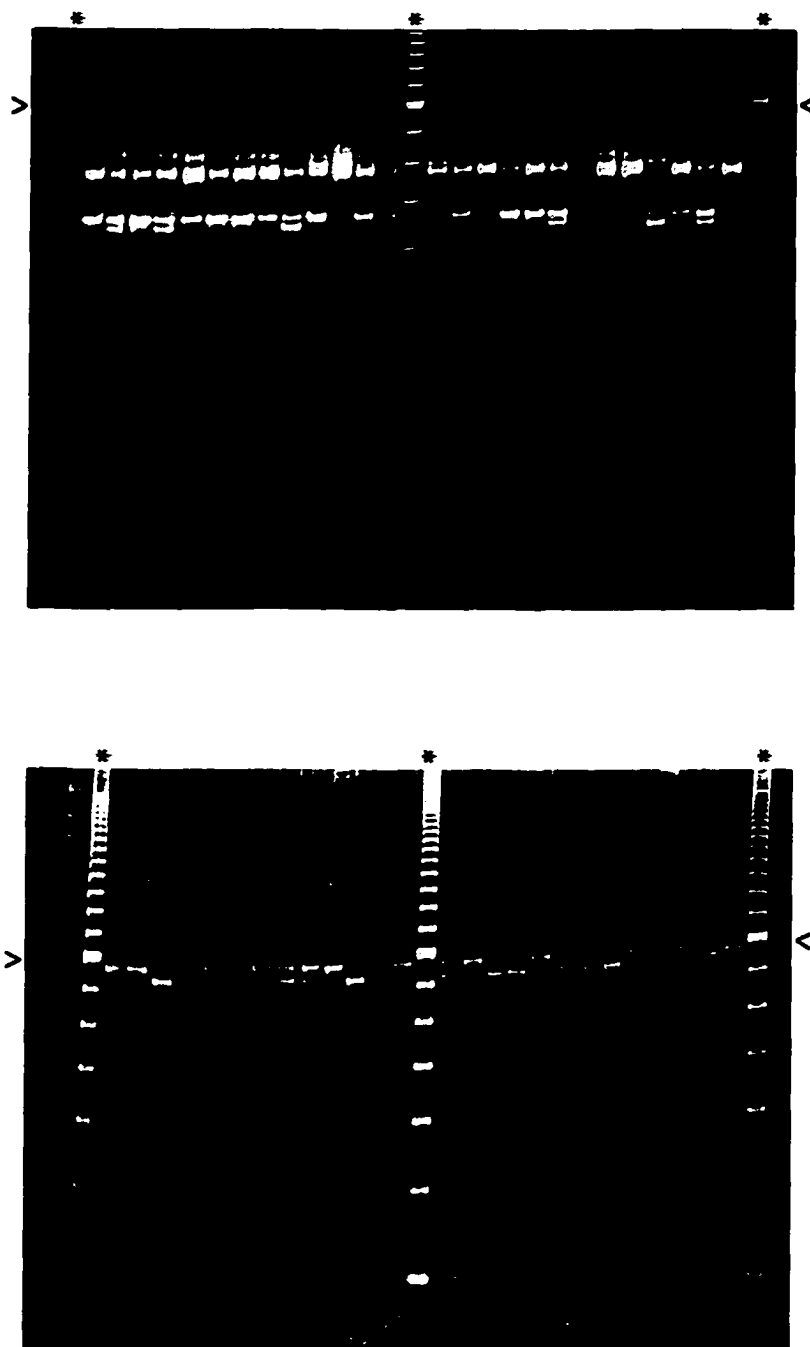


Figure 19. Gel photographs showing PCR products produced by *Atr1* (top) and *Atr2* (bottom). Superladder-Low 20bp Ladder (indicated by *) was used to size products on each gel. Bands in the ladder are in 20bp increments. The 200bp band is indicated by > and <.

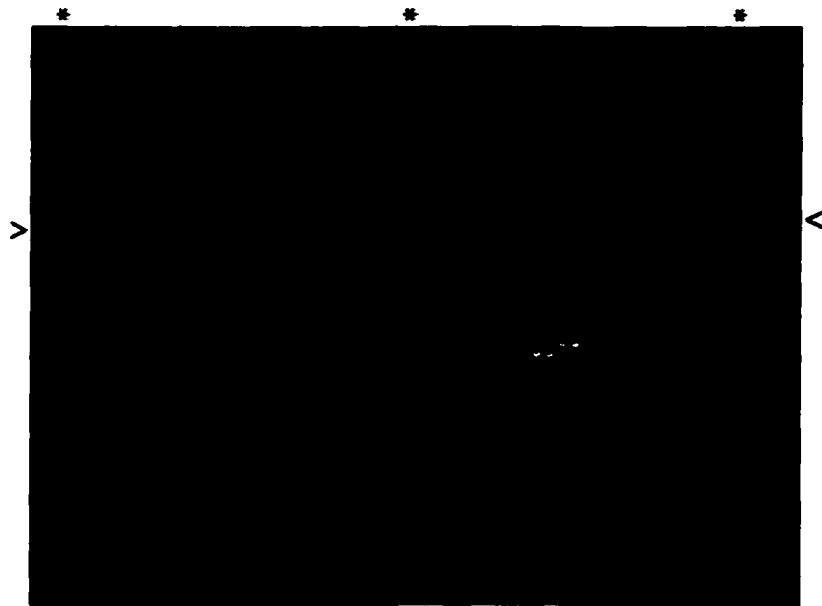


Figure 20. Gel photographs showing PCR products produced by *Atr3*. Superladder-Low 20bp Ladder (indicated by *) was used to size products on each gel. Bands in the ladder are in 20bp increments. The 200bp band is indicated by > and <.

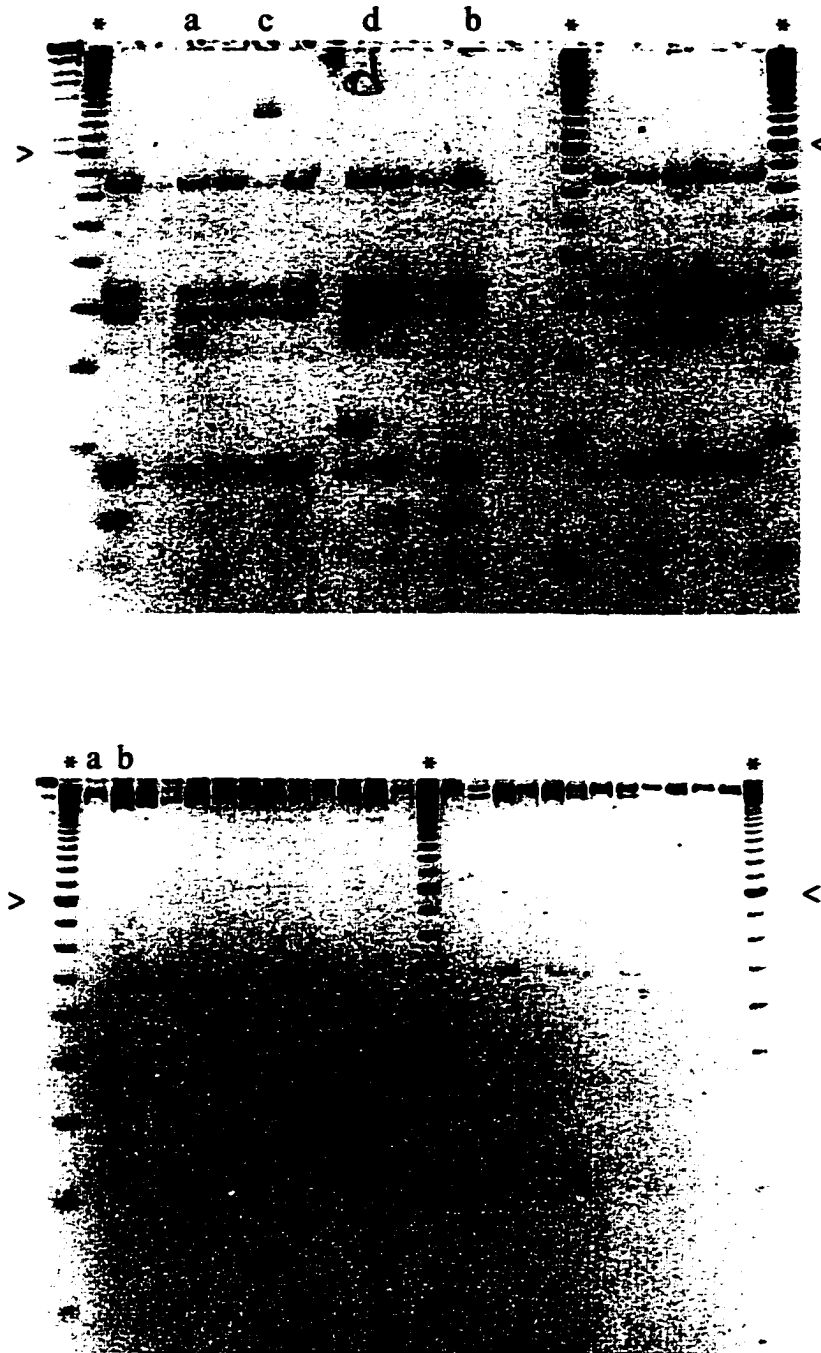


Figure 21. White sturgeon mtDNA control region RFLP haplotypes observed with the enzymes *Hsp92II* (top) and *SfcI* (bottom). Superladder-Low 20bp Ladder (indicated by *) was used to size products on each gel. Bands in the ladder are in 20bp increments. The 200bp band is indicated by > and <. Letters above the lanes indicate single-enzyme haplotypes (Table 11).

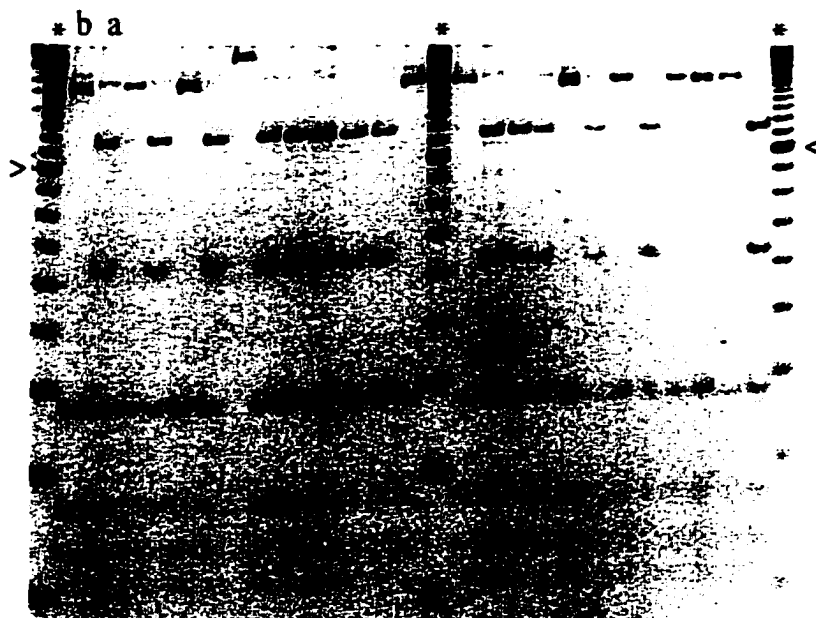


Figure 22. White sturgeon mtDNA control region RFLP haplotypes observed with the enzyme *MseI*. Superladder-Low 20bp Ladder (indicated by *) was used to size products on each gel. Bands in the ladder are in 20bp increments. The 200bp band is indicated by > and <. Letters above the lanes indicate single-enzyme haplotypes (Table 11).

Appendix 2. Observed allele frequencies for 20 microsatellite loci in 17 coho salmon sample sites.

	bp	Yukon	Kuskokwim	Kametolook	Theodore	Ophir Ck.	Nass	Sangan	Yakoun	Atnarko	Thompson	Quatse	Conuma	Capilano	Chehalis	Alsea	Trinity	Noyo
760	97	0.000	0.000	0.067	0.000	0.000	0.000	0.021	0.000	0.000	0.000	0.000	0.000	0.017	0.000	0.030	0.013	0.056
	99	0.000	0.000	0.000	0.058	0.125	0.057	0.167	0.063	0.125	0.047	0.156	0.042	0.121	0.083	0.152	0.025	0.000
	104	1.000	1.000	0.933	0.942	0.875	0.943	0.813	0.938	0.875	0.938	0.813	0.938	0.810	0.917	0.818	0.837	0.944
	108	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.016	0.031	0.021	0.052	0.000	0.000	0.125	0.000
773	134	0.395	0.340	0.466	0.380	0.200	0.278	0.219	0.344	0.391	0.422	0.547	0.281	0.274	0.464	0.352	0.115	0.361
	138	0.368	0.400	0.172	0.500	0.375	0.178	0.281	0.281	0.250	0.016	0.250	0.594	0.194	0.381	0.463	0.872	0.389
	142	0.237	0.260	0.362	0.120	0.425	0.544	0.500	0.375	0.359	0.563	0.203	0.125	0.532	0.155	0.185	0.013	0.250
Oki1	85	0.000	0.038	0.017	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.047	0.014	0.000
	89	0.000	0.000	0.000	0.000	0.000	0.011	0.010	0.000	0.000	0.000	0.047	0.000	0.000	0.013	0.094	0.000	0.000
	93	0.000	0.019	0.117	0.000	0.000	0.089	0.271	0.172	0.078	0.100	0.266	0.375	0.125	0.287	0.094	0.378	0.059
	97	0.447	0.442	0.367	0.173	0.079	0.378	0.302	0.406	0.391	0.250	0.313	0.177	0.516	0.175	0.109	0.149	0.029
	101	0.263	0.154	0.150	0.269	0.579	0.122	0.156	0.156	0.031	0.100	0.031	0.000	0.047	0.237	0.047	0.095	0.000
	104	0.211	0.135	0.050	0.096	0.053	0.100	0.010	0.109	0.281	0.067	0.000	0.052	0.156	0.100	0.094	0.054	0.000
	109	0.079	0.212	0.150	0.404	0.211	0.133	0.104	0.063	0.016	0.000	0.141	0.083	0.078	0.038	0.109	0.000	0.088
	112	0.000	0.000	0.050	0.038	0.079	0.078	0.000	0.016	0.094	0.233	0.047	0.104	0.047	0.013	0.078	0.189	0.118
	116	0.000	0.000	0.050	0.019	0.000	0.000	0.021	0.000	0.063	0.000	0.000	0.010	0.000	0.000	0.047	0.000	0.000
	120	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.031	0.050	0.000	0.063	0.000	0.013	0.078	0.122	0.059
	124	0.000	0.000	0.000	0.000	0.000	0.056	0.021	0.031	0.016	0.083	0.094	0.010	0.031	0.087	0.172	0.000	0.471
	128	0.000	0.000	0.000	0.000	0.000	0.033	0.083	0.031	0.000	0.000	0.063	0.125	0.000	0.025	0.000	0.000	0.118
	132	0.000	0.000	0.050	0.000	0.000	0.000	0.021	0.016	0.000	0.117	0.000	0.000	0.000	0.013	0.031	0.000	0.059
Oki2	159	0.000	0.000	0.000	0.000	0.000	0.067	0.000	0.000	0.094	0.141	0.031	0.089	0.048	0.378	0.250	0.295	0.222
	168	0.816	0.846	0.431	0.174	0.200	0.444	0.022	0.113	0.406	0.281	0.469	0.078	0.403	0.341	0.404	0.333	0.417

bp																		
	Yukon	Kuskokwim	Kametolook	Theodore	Ophir Ck.	Nass	Sangan	Yakoun	Atnarko	Thompson	Quatse	Conuma	Capilano	Chehalis	Alsea	Trinity	Noyo	
Okii2	174	0.184	0.154	0.569	0.826	0.750	0.489	0.933	0.548	0.391	0.484	0.313	0.833	0.516	0.256	0.173	0.179	0.194
(cont'd)	179	0.000	0.000	0.000	0.000	0.050	0.000	0.044	0.323	0.109	0.094	0.188	0.000	0.032	0.024	0.154	0.179	0.167
	187	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.016	0.000	0.000	0.000	0.000	0.000	0.000	0.019	0.013	0.000
	Yukon	Kuskokwim	Kametolook	Theodore	Ophir Ck.	Nass	Sangan	Yakoun	Atnarko	Thompson	Quatse	Conuma	Capilano	Chehalis	Alsea	Trinity	Noyo	
Okii3	70	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.010	0.000	0.000	0.000	0.000	0.000	
	72	0.361	0.385	0.117	0.000	0.425	0.044	0.000	0.000	0.047	0.000	0.000	0.000	0.119	0.045	0.000	0.000	
	75	0.639	0.615	0.867	1.000	0.575	0.900	1.000	1.000	0.922	1.000	1.000	0.906	0.821	0.924	1.000	1.000	
	78	0.000	0.000	0.000	0.000	0.000	0.033	0.000	0.000	0.031	0.000	0.000	0.094	0.060	0.000	0.000	0.000	
	80	0.000	0.000	0.017	0.000	0.000	0.022	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.030	0.000	0.000	
	Yukon	Kuskokwim	Kametolook	Theodore	Ophir Ck.	Nass	Sangan	Yakoun	Atnarko	Thompson	Quatse	Conuma	Capilano	Chehalis	Alsea	Trinity	Noyo	
Okii10	82	0.000	0.000	0.000	0.040	0.000	0.000	0.000	0.014	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	
	86	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.014	0.000	0.000	0.150	0.000	
	90	0.000	0.038	0.067	0.020	0.026	0.000	0.000	0.014	0.015	0.000	0.000	0.000	0.000	0.000	0.000	0.000	
	94	0.079	0.173	0.067	0.080	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	
	98	0.026	0.000	0.050	0.040	0.184	0.022	0.000	0.000	0.015	0.000	0.000	0.014	0.000	0.000	0.000	0.000	
	102	0.105	0.038	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.053	0.000	0.000	0.000	0.000	0.000	0.300	
	105	0.000	0.058	0.000	0.040	0.079	0.056	0.000	0.000	0.173	0.015	0.013	0.000	0.000	0.000	0.000	0.000	
	109	0.079	0.038	0.083	0.120	0.000	0.033	0.000	0.078	0.054	0.000	0.000	0.221	0.014	0.020	0.031	0.000	
	113	0.053	0.038	0.067	0.020	0.184	0.000	0.000	0.047	0.000	0.053	0.128	0.000	0.031	0.000	0.000	0.000	
	117	0.000	0.000	0.050	0.120	0.000	0.000	0.073	0.063	0.000	0.013	0.000	0.000	0.000	0.000	0.000	0.000	
	121	0.000	0.000	0.000	0.100	0.053	0.000	0.104	0.078	0.054	0.133	0.026	0.000	0.031	0.000	0.000	0.000	
	124	0.026	0.000	0.017	0.000	0.000	0.011	0.021	0.000	0.074	0.066	0.035	0.028	0.010	0.016	0.000	0.000	
	128	0.026	0.115	0.000	0.060	0.000	0.000	0.000	0.078	0.014	0.029	0.066	0.000	0.028	0.166	0.077	0.000	
	132	0.105	0.115	0.083	0.040	0.053	0.000	0.094	0.047	0.066	0.015	0.106	0.047	0.000	0.135	0.031	0.012	
	136	0.079	0.115	0.133	0.100	0.026	0.133	0.094	0.031	0.040	0.000	0.026	0.023	0.071	0.104	0.047	0.000	
	140	0.237	0.096	0.083	0.020	0.158	0.244	0.010	0.031	0.014	0.029	0.026	0.070	0.099	0.135	0.077	0.000	
	143	0.158	0.096	0.150	0.040	0.000	0.122	0.031	0.078	0.093	0.088	0.040	0.128	0.028	0.010	0.031	0.000	
	147	0.026	0.000	0.000	0.080	0.000	0.033	0.302	0.094	0.000	0.280	0.066	0.081	0.283	0.093	0.140	0.075	
	151	0.000	0.058	0.067	0.020	0.079	0.100	0.146	0.109	0.080	0.045	0.013	0.151	0.000	0.000	0.186	0.401	
	155	0.000	0.019	0.017	0.020	0.000	0.044	0.083	0.094	0.066	0.015	0.093	0.035	0.085	0.083	0.047	0.075	

bp																		
	Yukon	Kuskokwim	Kametolook	Theodore	Ophir Ck.	Nass	Sangan	Yakoun	Atnarko	Thompson	Quatse	Conuma	Capilano	Chehalis	Alsea	Trinity	Noyo	
Okii0	158	0.000	0.000	0.017	0.000	0.132	0.100	0.021	0.078	0.120	0.015	0.053	0.000	0.057	0.000	0.031	0.012	0.191
(cont'd)	162	0.000	0.000	0.000	0.040	0.026	0.044	0.010	0.047	0.000	0.000	0.053	0.081	0.042	0.010	0.124	0.088	0.000
	166	0.000	0.000	0.033	0.000	0.000	0.044	0.010	0.047	0.000	0.000	0.000	0.000	0.000	0.010	0.000	0.138	0.055
	170	0.000	0.000	0.017	0.000	0.000	0.011	0.000	0.000	0.000	0.000	0.000	0.000	0.085	0.010	0.031	0.000	0.109
	null	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.200	0.235	0.235	0.000	0.150	0.150	0.130	0.048	0.290
		Yukon	Kuskokwim	Kametolook	Theodore	Ophir Ck.	Nass	Sangan	Yakoun	Atnarko	Thompson	Quatse	Conuma	Capilano	Chehalis	Alsea	Trinity	Noyo
Okii1	73	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.087	0.000
	83	0.711	0.942	0.963	0.825	0.450	0.830	0.760	0.694	0.531	0.875	0.641	0.479	0.583	0.524	0.242	0.538	0.750
	87	0.289	0.058	0.037	0.150	0.550	0.148	0.240	0.306	0.469	0.125	0.313	0.521	0.383	0.429	0.742	0.375	0.250
	90	0.000	0.000	0.000	0.025	0.000	0.023	0.000	0.000	0.000	0.000	0.047	0.000	0.033	0.048	0.016	0.000	0.000
		Yukon	Kuskokwim	Kametolook	Theodore	Ophir Ck.	Nass	Sangan	Yakoun	Atnarko	Thompson	Quatse	Conuma	Capilano	Chehalis	Alsea	Trinity	Noyo
Okii3	90	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.047	0.013	0.016	0.000	0.000
	94	0.000	0.000	0.000	0.000	0.029	0.000	0.000	0.000	0.016	0.000	0.000	0.087	0.031	0.050	0.016	0.025	0.000
	97	0.921	0.808	0.783	0.673	0.735	0.778	0.684	0.406	0.887	0.790	0.776	0.880	0.719	0.762	0.887	0.837	0.333
	101	0.079	0.135	0.200	0.288	0.235	0.222	0.303	0.563	0.065	0.210	0.224	0.022	0.188	0.138	0.081	0.138	0.667
	105	0.000	0.000	0.017	0.038	0.000	0.000	0.013	0.016	0.000	0.000	0.000	0.011	0.016	0.025	0.000	0.000	0.000
	109	0.000	0.058	0.000	0.000	0.000	0.000	0.000	0.016	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
	114	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.032	0.000	0.000	0.000	0.000	0.013	0.000	0.000	0.000
		Yukon	Kuskokwim	Kametolook	Theodore	Ophir Ck.	Nass	Sangan	Yakoun	Atnarko	Thompson	Quatse	Conuma	Capilano	Chehalis	Alsea	Trinity	Noyo
Ots105	126	0.974	0.885	0.717	0.615	0.625	0.674	0.447	0.313	0.719	0.435	0.531	0.344	0.597	0.762	0.697	0.988	0.833
	130	0.026	0.115	0.283	0.385	0.375	0.326	0.553	0.688	0.281	0.565	0.469	0.656	0.403	0.238	0.303	0.013	0.167
		Yukon	Kuskokwim	Kametolook	Theodore	Ophir Ck.	Nass	Sangan	Yakoun	Atnarko	Thompson	Quatse	Conuma	Capilano	Chehalis	Alsea	Trinity	Noyo
Okii6	181	0.000	0.000	0.017	0.000	0.000	0.011	0.000	0.000	0.000	0.000	0.000	0.000	0.016	0.053	0.000	0.000	0.000
	191	0.105	0.135	0.250	0.019	0.125	0.443	0.208	0.484	0.047	0.297	0.188	0.213	0.094	0.513	0.727	0.400	0.088
	202	0.000	0.000	0.000	0.019	0.000	0.091	0.000	0.047	0.109	0.000	0.031	0.043	0.031	0.013	0.000	0.025	0.176
	219	0.132	0.250	0.250	0.000	0.000	0.034	0.531	0.219	0.063	0.000	0.094	0.266	0.016	0.171	0.045	0.025	0.000
	232	0.737	0.538	0.150	0.250	0.650	0.205	0.104	0.156	0.203	0.313	0.234	0.287	0.375	0.092	0.015	0.363	0.235
	243	0.026	0.077	0.283	0.712	0.175	0.057	0.146	0.063	0.125	0.172	0.031	0.160	0.359	0.145	0.182	0.162	0.000

bp																		
	Yukon	Kuskokwim	Kametolook	Theodore	Ophir Ck.	Nass	Sangan	Yakoun	Atnarko	Thompson	Quatse	Conuma	Capilano	Chehalis	Alsea	Trinity	Noyo	
Okil6	251	0.000	0.000	0.000	0.000	0.025	0.000	0.010	0.031	0.000	0.156	0.063	0.000	0.031	0.000	0.000	0.000	
(cont'd)	259	0.000	0.000	0.050	0.000	0.025	0.068	0.000	0.000	0.234	0.063	0.266	0.000	0.031	0.013	0.030	0.025	0.059
	270	0.000	0.000	0.000	0.000	0.000	0.091	0.000	0.000	0.219	0.000	0.094	0.032	0.047	0.000	0.000	0.000	0.441
Okil8	109	0.000	0.000	0.000	0.000	0.000	0.000	0.109	0.000	0.125	0.032	0.000	0.000	0.024	0.000	0.000	0.000	
	111	1.000	0.981	0.983	0.980	0.950	0.767	1.000	0.859	0.984	0.875	0.952	0.875	0.917	0.833	0.697	0.775	0.972
	113	0.000	0.019	0.017	0.020	0.050	0.233	0.000	0.031	0.016	0.000	0.016	0.125	0.083	0.143	0.288	0.225	0.028
	118	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.015	0.000	0.000	
Oki20	96	0.053	0.058	0.241	0.000	0.225	0.011	0.031	0.000	0.094	0.266	0.125	0.011	0.016	0.202	0.000	0.000	0.000
	100	0.947	0.942	0.759	1.000	0.650	0.977	0.969	1.000	0.906	0.609	0.875	0.989	0.984	0.774	0.953	1.000	1.000
	104	0.000	0.000	0.000	0.000	0.125	0.011	0.000	0.000	0.000	0.125	0.000	0.000	0.000	0.024	0.047	0.000	0.000
Omy77	113	0.000	0.000	0.000	0.000	0.000	0.106	0.016	0.000	0.000	0.063	0.109	0.000	0.000	0.000	0.000	0.000	
	126	0.579	0.846	0.767	0.731	0.875	0.800	0.883	0.906	0.741	0.953	0.797	0.783	0.917	1.000	1.000	0.759	1.000
	134	0.421	0.115	0.150	0.250	0.125	0.144	0.011	0.078	0.259	0.047	0.141	0.109	0.000	0.000	0.000	0.000	0.000
	139	0.000	0.038	0.083	0.019	0.000	0.056	0.000	0.000	0.000	0.000	0.000	0.000	0.083	0.000	0.000	0.241	0.000
One11	128	0.000	0.058	0.000	0.000	0.025	0.114	0.010	0.000	0.125	0.823	0.094	0.031	0.000	0.066	0.000	0.057	0.324
	139	1.000	0.942	1.000	1.000	0.975	0.886	0.990	1.000	0.875	0.177	0.906	0.969	1.000	0.934	1.000	0.943	0.676
Ots3	67	0.237	0.038	0.190	0.019	0.059	0.013	0.011	0.000	0.016	0.000	0.032	0.011	0.032	0.095	0.017	0.000	0.000
	70	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.048	0.000	0.000	0.000	0.000	0.000	0.000
	74	0.000	0.000	0.000	0.058	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
	76	0.000	0.000	0.000	0.000	0.000	0.013	0.000	0.000	0.016	0.000	0.016	0.000	0.000	0.000	0.000	0.000	0.000
	79	0.000	0.000	0.000	0.000	0.000	0.013	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.056
	82	0.000	0.000	0.069	0.000	0.000	0.000	0.000	0.000	0.081	0.000	0.000	0.000	0.000	0.012	0.000	0.051	0.056

bp																		
	Yukon	Kuskokwim	Kametolook	Theodore	Ophir Ck.	Nass	Sangan	Yakoun	Atnarko	Thompson	Quatse	Conuma	Capilano	Chehalis	Alsea	Trinity	Noyo	
Ots3	86	0.105	0.077	0.069	0.038	0.147	0.197	0.000	0.000	0.161	0.000	0.048	0.000	0.000	0.012	0.183	0.013	0.139
(cont'd)	88	0.053	0.058	0.034	0.135	0.176	0.447	0.500	0.328	0.403	0.129	0.323	0.557	0.500	0.500	0.117	0.077	0.278
	91	0.105	0.135	0.034	0.308	0.118	0.079	0.021	0.031	0.032	0.403	0.161	0.000	0.016	0.024	0.217	0.064	0.028
	94	0.447	0.673	0.483	0.308	0.206	0.145	0.383	0.406	0.210	0.306	0.274	0.364	0.145	0.238	0.300	0.628	0.222
	97	0.053	0.019	0.121	0.135	0.294	0.092	0.085	0.234	0.081	0.161	0.065	0.068	0.306	0.119	0.150	0.154	0.222
	102	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.032	0.000	0.000	0.000	0.017	0.013	0.000
		Yukon	Kuskokwim	Kametolook	Theodore	Ophir Ck.	Nass	Sangan	Yakoun	Atnarko	Thompson	Quatse	Conuma	Capilano	Chehalis	Alsea	Trinity	Noyo
Ots4	132	0.026	0.038	0.133	0.115	0.150	0.116	0.365	0.188	0.219	0.203	0.103	0.208	0.078	0.175	0.076	0.059	0.028
	138	0.895	0.962	0.867	0.885	0.850	0.884	0.635	0.766	0.766	0.609	0.862	0.792	0.859	0.688	0.909	0.941	0.750
	141	0.079	0.000	0.000	0.000	0.000	0.000	0.000	0.047	0.016	0.188	0.034	0.000	0.063	0.138	0.015	0.000	0.222
		Yukon	Kuskokwim	Kametolook	Theodore	Ophir Ck.	Nass	Sangan	Yakoun	Atnarko	Thompson	Quatse	Conuma	Capilano	Chehalis	Alsea	Trinity	Noyo
Ots7.2	138	1.000	0.923	0.750	0.712	0.775	0.644	0.563	0.625	0.797	0.766	0.531	0.240	0.781	0.663	0.742	0.825	1.000
	144	0.000	0.077	0.250	0.288	0.225	0.356	0.438	0.375	0.203	0.234	0.469	0.760	0.219	0.338	0.258	0.162	0.000
	151	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.013	0.000
		Yukon	Kuskokwim	Kametolook	Theodore	Ophir Ck.	Nass	Sangan	Yakoun	Atnarko	Thompson	Quatse	Conuma	Capilano	Chehalis	Alsea	Trinity	Noyo
Ots9	99	0.000	0.020	0.000	0.000	0.000	0.012	0.000	0.000	0.094	0.000	0.000	0.010	0.000	0.000	0.018	0.000	0.000
	103	1.000	0.980	0.983	1.000	0.975	0.942	1.000	1.000	0.906	1.000	0.891	0.969	1.000	1.000	0.982	0.925	1.000
	108	0.000	0.000	0.017	0.000	0.025	0.047	0.000	0.000	0.000	0.000	0.109	0.021	0.000	0.000	0.000	0.075	0.000
		Yukon	Kuskokwim	Kametolook	Theodore	Ophir Ck.	Nass	Sangan	Yakoun	Atnarko	Thompson	Quatse	Conuma	Capilano	Chehalis	Alsea	Trinity	Noyo
Ots101	101	0.000	0.000	0.050	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.031	0.000	0.000	0.000	0.000	0.000	0.000
	105	0.000	0.000	0.133	0.000	0.000	0.125	0.000	0.000	0.000	0.000	0.016	0.000	0.100	0.036	0.000	0.000	0.000
	109	0.000	0.000	0.133	0.058	0.100	0.080	0.000	0.109	0.000	0.000	0.031	0.075	0.000	0.071	0.000	0.000	0.000
	113	0.000	0.000	0.000	0.000	0.000	0.045	0.026	0.000	0.000	0.000	0.031	0.138	0.000	0.131	0.030	0.000	0.000
	117	0.000	0.000	0.050	0.000	0.025	0.114	0.064	0.031	0.047	0.141	0.016	0.313	0.233	0.107	0.136	0.138	0.029
	120	0.000	0.019	0.083	0.000	0.125	0.114	0.154	0.047	0.094	0.000	0.078	0.100	0.117	0.060	0.121	0.013	0.000
	124	0.000	0.000	0.000	0.058	0.000	0.080	0.282	0.109	0.094	0.000	0.125	0.000	0.083	0.060	0.076	0.125	0.000
	128	0.000	0.000	0.050	0.077	0.000	0.091	0.064	0.078	0.078	0.000	0.063	0.000	0.017	0.167	0.106	0.175	0.000
	132	0.000	0.000	0.067	0.077	0.050	0.045	0.013	0.078	0.047	0.000	0.063	0.050	0.050	0.107	0.076	0.000	0.000

bp																		
	Yukon	Kuskokwim	Kametolook	Theodore	Ophir Ck.	Nass	Sangan	Yakoun	Atmarko	Thompson	Quatse	Conuma	Capilano	Chehalis	Alsea	Trinity	Noyo	
Ots101	136	0.026	0.019	0.017	0.096	0.125	0.011	0.051	0.078	0.031	0.000	0.094	0.000	0.017	0.048	0.106	0.013	0.441
(cont'd)	140	0.053	0.038	0.000	0.077	0.075	0.000	0.000	0.031	0.109	0.000	0.047	0.063	0.000	0.024	0.015	0.000	0.000
	144	0.184	0.096	0.017	0.154	0.200	0.000	0.038	0.078	0.047	0.000	0.109	0.000	0.067	0.012	0.030	0.000	0.059
	147	0.000	0.058	0.033	0.058	0.100	0.080	0.103	0.031	0.016	0.000	0.063	0.013	0.017	0.024	0.000	0.013	0.000
	152	0.000	0.038	0.017	0.038	0.050	0.011	0.026	0.031	0.016	0.000	0.047	0.100	0.017	0.000	0.061	0.013	0.000
	156	0.000	0.000	0.033	0.000	0.000	0.000	0.000	0.016	0.000	0.000	0.016	0.013	0.000	0.000	0.000	0.000	0.088
	160	0.000	0.000	0.000	0.038	0.000	0.000	0.000	0.016	0.063	0.063	0.000	0.038	0.000	0.012	0.015	0.013	0.118
	166	0.000	0.096	0.017	0.096	0.000	0.023	0.013	0.016	0.063	0.297	0.031	0.000	0.017	0.012	0.030	0.262	0.059
	171	0.105	0.096	0.067	0.019	0.000	0.068	0.051	0.016	0.047	0.094	0.094	0.075	0.000	0.012	0.030	0.075	0.000
	176	0.079	0.154	0.000	0.019	0.025	0.011	0.064	0.063	0.125	0.141	0.000	0.000	0.033	0.000	0.015	0.087	0.000
	180	0.079	0.115	0.033	0.000	0.000	0.057	0.000	0.031	0.063	0.188	0.031	0.000	0.067	0.048	0.030	0.038	0.000
	184	0.158	0.115	0.017	0.058	0.000	0.011	0.026	0.031	0.000	0.078	0.000	0.000	0.050	0.036	0.030	0.000	0.088
	188	0.184	0.115	0.033	0.000	0.025	0.011	0.013	0.031	0.000	0.000	0.000	0.000	0.000	0.036	0.000	0.013	0.000
	192	0.105	0.019	0.017	0.058	0.100	0.011	0.000	0.016	0.016	0.000	0.000	0.000	0.017	0.000	0.076	0.013	0.059
	195	0.026	0.019	0.017	0.019	0.000	0.011	0.000	0.047	0.047	0.000	0.016	0.000	0.033	0.000	0.000	0.000	0.000
	200	0.000	0.000	0.017	0.000	0.000	0.000	0.013	0.016	0.000	0.000	0.000	0.000	0.017	0.000	0.000	0.000	0.000
	206	0.000	0.000	0.033	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.013	0.000
	211	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.033	0.000	0.000	0.000	0.000
	220	0.000	0.000	0.017	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.017	0.000	0.000	0.000	0.000
	225	0.000	0.000	0.017	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
	235	0.000	0.000	0.033	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
	239	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.015	0.000	0.000
	242	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.059
	251	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.025	0.000	0.000	0.000	0.000	0.000	0.000
		Yukon	Kuskokwim	Kametolook	Theodore	Ophir Ck.	Nass	Sangan	Yakoun	Atmarko	Thompson	Quatse	Conuma	Capilano	Chehalis	Alsea	Trinity	Noyo
Ots103	62	0.000	0.019	0.017	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
	70	0.000	0.000	0.033	0.019	0.000	0.012	0.000	0.031	0.000	0.000	0.083	0.033	0.000	0.000	0.000	0.000	0.000
	77	0.053	0.019	0.033	0.038	0.028	0.093	0.032	0.016	0.047	0.000	0.050	0.000	0.067	0.107	0.031	0.000	0.000
	81	0.132	0.404	0.033	0.077	0.056	0.058	0.064	0.000	0.000	0.000	0.017	0.133	0.000	0.000	0.016	0.000	0.000
	84	0.079	0.077	0.050	0.154	0.083	0.000	0.000	0.000	0.000	0.000	0.067	0.067	0.000	0.012	0.000	0.000	0.000
	89	0.053	0.000	0.133	0.173	0.278	0.163	0.000	0.000	0.000	0.000	0.011	0.050	0.071	0.063	0.000	0.000	0.000

bp		Yukon	Kuskokwim	Kametolook	Theodore	Ophir Ck.	Nass	Sangan	Yakoun	Atnarko	Thompson	Quatse	Conuma	Capilano	Chechalis	Alsea	Trinity	Noyo
Ots103	92	0.026	0.019	0.017	0.096	0.028	0.105	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.012	0.031	0.014	0.000
(cont'd)	97	0.000	0.000	0.000	0.038	0.139	0.000	0.000	0.000	0.047	0.017	0.017	0.000	0.000	0.060	0.172	0.000	0.000
	101	0.000	0.000	0.017	0.000	0.000	0.000	0.011	0.016	0.016	0.000	0.017	0.000	0.000	0.095	0.000	0.014	0.111
	104	0.000	0.000	0.000	0.000	0.083	0.000	0.053	0.219	0.000	0.000	0.133	0.056	0.067	0.012	0.203	0.000	0.083
	108	0.026	0.000	0.033	0.019	0.083	0.000	0.011	0.000	0.047	0.086	0.017	0.022	0.017	0.012	0.016	0.056	0.056
	112	0.053	0.038	0.033	0.000	0.000	0.047	0.000	0.000	0.063	0.379	0.050	0.267	0.017	0.190	0.016	0.014	0.222
	115	0.000	0.000	0.000	0.000	0.000	0.000	0.021	0.000	0.078	0.155	0.033	0.056	0.083	0.000	0.000	0.000	0.028
	118	0.000	0.000	0.000	0.000	0.000	0.058	0.000	0.047	0.000	0.000	0.050	0.111	0.083	0.036	0.016	0.014	0.083
	123	0.000	0.000	0.000	0.000	0.056	0.000	0.032	0.016	0.000	0.000	0.033	0.033	0.017	0.060	0.156	0.139	0.000
	126	0.000	0.019	0.017	0.000	0.000	0.012	0.000	0.031	0.000	0.000	0.083	0.078	0.050	0.071	0.063	0.097	0.028
	130	0.026	0.000	0.050	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.017	0.011	0.017	0.024	0.031	0.042	0.000
	134	0.000	0.019	0.000	0.000	0.028	0.012	0.000	0.000	0.031	0.000	0.017	0.011	0.083	0.024	0.000	0.014	0.000
	138	0.079	0.019	0.000	0.000	0.000	0.012	0.000	0.000	0.078	0.017	0.050	0.000	0.033	0.000	0.000	0.153	0.000
	142	0.026	0.019	0.017	0.000	0.000	0.070	0.000	0.047	0.000	0.000	0.000	0.000	0.000	0.024	0.016	0.028	0.000
	146	0.079	0.038	0.017	0.000	0.000	0.047	0.000	0.047	0.016	0.000	0.033	0.000	0.017	0.000	0.000	0.361	0.111
	150	0.000	0.019	0.000	0.000	0.000	0.000	0.000	0.063	0.000	0.069	0.050	0.000	0.017	0.024	0.078	0.014	0.000
	154	0.000	0.000	0.000	0.000	0.000	0.023	0.000	0.016	0.031	0.017	0.067	0.000	0.050	0.024	0.016	0.014	0.056
	158	0.026	0.019	0.033	0.038	0.000	0.081	0.043	0.063	0.063	0.000	0.033	0.044	0.067	0.024	0.000	0.000	0.000
	162	0.053	0.019	0.050	0.000	0.000	0.035	0.085	0.047	0.063	0.034	0.033	0.000	0.017	0.012	0.000	0.000	0.000
	166	0.026	0.000	0.017	0.038	0.000	0.012	0.032	0.078	0.094	0.000	0.017	0.000	0.000	0.000	0.000	0.000	0.000
	170	0.000	0.019	0.050	0.000	0.028	0.012	0.085	0.063	0.063	0.190	0.033	0.044	0.050	0.036	0.000	0.000	0.028
	174	0.000	0.058	0.050	0.000	0.028	0.035	0.085	0.031	0.000	0.000	0.000	0.000	0.017	0.036	0.016	0.000	0.000
	178	0.000	0.000	0.017	0.038	0.000	0.023	0.117	0.063	0.031	0.000	0.000	0.000	0.033	0.036	0.000	0.000	0.000
	182	0.079	0.038	0.017	0.000	0.000	0.035	0.085	0.016	0.016	0.000	0.000	0.000	0.017	0.000	0.000	0.000	0.111
	186	0.026	0.019	0.033	0.000	0.000	0.012	0.032	0.063	0.078	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
	190	0.053	0.019	0.033	0.077	0.028	0.012	0.064	0.016	0.047	0.017	0.000	0.000	0.033	0.000	0.000	0.014	0.000
	193	0.026	0.000	0.083	0.077	0.056	0.000	0.085	0.000	0.000	0.000	0.000	0.000	0.033	0.000	0.016	0.000	0.000
	199	0.000	0.000	0.017	0.019	0.000	0.012	0.011	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.016	0.000	0.028
	202	0.026	0.019	0.017	0.019	0.000	0.012	0.021	0.016	0.000	0.000	0.000	0.011	0.000	0.000	0.000	0.000	0.056
	206	0.000	0.000	0.000	0.000	0.000	0.000	0.011	0.000	0.000	0.017	0.000	0.000	0.017	0.000	0.000	0.000	0.000
	211	0.000	0.000	0.017	0.000	0.000	0.000	0.021	0.000	0.016	0.000	0.000	0.000	0.017	0.000	0.000	0.014	0.000
	214	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.047	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000

bp																	
	Yukon	Kuskokwim	Kametolook	Theodore	Ophir Ck.	Nass	Sangan	Yakoun	Atnarko	Thompson	Quatse	Conuma	Capilano	Chehalis	Alsea	Trinity	Noyo
Ots103	222	0.000	0.000	0.017	0.000	0.000	0.012	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
(cont'd)	225	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.016	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
	230	0.000	0.019	0.017	0.000	0.000	0.000	0.000	0.016	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
	235	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.011	0.033	0.000	0.031	0.000	0.000
	236	0.000	0.000	0.017	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
	242	0.000	0.019	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
	247	0.000	0.000	0.017	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
	250	0.000	0.038	0.000	0.058	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
	261	0.053	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
	275	0.000	0.000	0.000	0.019	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000

Appendix 3. Collection information for white sturgeon samples.

Target region	Sample number	Locale	River km	Date	Fork length (cm)	Floy tag colour	Floy tag #	Pit tag
Fraser R. 16-75km	1		22.0	04/06/00	39.0			
Fraser R. 16-75km	2		39.5	05/01/00	119.0			
Fraser R. 16-75km	3		39.5	05/01/00	68.0			
Fraser R. 16-75km	4		38.5	05/17/00	55.0			
Fraser R. 16-75km	5		16.0	05/17/00	75.0			
Fraser R. 16-75km	6		16.0	05/17/00	77.5			
Fraser R. 16-75km	7		16.0	05/17/00	72.0			
Fraser R. 16-75km	8		16.0	05/17/00	96.5			
Fraser R. 16-75km	9		16.0	05/17/00	76.0			
Fraser R. 16-75km	10		16.0	05/17/00	76.5			
Fraser R. 16-75km	11		16.0	05/17/00	89.0			
Fraser R. 16-75km	12		16.0	05/17/00	139.0			
Fraser R. 16-75km	13		16.0	05/17/00	73.0			
Fraser R. 16-75km	14		16.0	05/17/00	96.0			
Fraser R. 16-75km	15		16.0	05/17/00	115.0			
Fraser R. 16-75km	16		16.0	05/17/00	71.0			
Fraser R. 16-75km	17		16.0	05/17/00	93.5			
Fraser R. 16-75km	18		16.0	05/16/00	73.5			
Fraser R. 16-75km	19		16.0	05/16/00	77.0			
Fraser R. 16-75km	20		16.0	05/16/00	79.0			
Fraser R. 16-75km	21		16.0	05/16/00	107.0			
Fraser R. 16-75km	22		16.0	05/16/00	71.0			
Fraser R. 16-75km	23		16.0	05/16/00	75.0			
Fraser R. 16-75km	24		16.0	05/16/00	78.0			
Fraser R. 16-75km	25		16.0	05/16/00	69.0			
Fraser R. 16-75km	26		16.0	05/16/00	79.0			
Fraser R. 16-75km	27		16.0	05/16/00	79.0			
Fraser R. 16-75km	28		16.0	05/16/00	100.5			
Fraser R. 16-75km	29		16.0	05/16/00	81.0			
Fraser R. 16-75km	30		16.0	05/16/00	100.0			
Fraser R. 16-75km	31		16.0	05/16/00	82.0			
Fraser R. 16-75km	32		16.0	05/16/00	100.0			
Fraser R. 16-75km	33		16.0	05/16/00	75.0			
Fraser R. 16-75km	34		16.0	05/16/00	73.0			
Fraser R. 16-75km	35		16.0	05/16/00	76.0			
Fraser R. 16-75km	36		16.0	05/16/00	92.0			
Fraser R. 16-75km	37		42.0	05/10/00	99.5			
Fraser R. 16-75km	38		42.0	05/10/00	103.0			
Fraser R. 16-75km	39		37.5	05/10/00	99.0			
Fraser R. 16-75km	40		37.5	05/10/00	84.0			
Fraser R. 16-75km	41		37.5	05/10/00	88.0			
Fraser R. 16-75km	42		37.5	05/10/00	84.0			
Fraser R. 16-75km	43		37.5	05/10/00	57.0			
Fraser R. 16-75km	44		37.5	05/10/00	75.0			
Fraser R. 16-75km	45		37.5	05/10/00	60.0			
Fraser R. 16-75km	46		37.5	05/10/00	71.0			

Target region	Sample number	Locale	River km	Date	Fork length (cm)	Floy tag colour	Floy tag #	Pit tag
Fraser R. 16-75km	47		37.5	05/10/00	69.0			
Fraser R. 16-75km	48		37.5	05/10/00	69.0			
Fraser R. 16-75km	49		37.5	05/10/00	72.0			
Fraser R. 16-75km	50		37.5	05/10/00	97.0			
Fraser R. 16-75km	51		37.5	05/10/00	92.0			
Fraser R. 16-75km	52		37.5	05/10/00	106.0			
Fraser R. 16-75km	53		37.5	05/10/00	63.0			
Fraser R. 16-75km	54		42.0	05/10/00	66.0			
Fraser R. 16-75km	55		42.0	05/10/00	93.0			
Fraser R. 16-75km	56		42.0	05/10/00	64.5			
Fraser R. 78-123km	1		112.0	08/31/97	176.5	Y	0884	4158645103
Fraser R. 78-123km	2		91.0	11/04/97	87.5	Y	1524	4158651663
Fraser R. 78-123km	3		101.3	08/29/97	80.5	Y	0864	41585C2705
Fraser R. 78-123km	4		101.2	08/29/97	87.0	Y	0866	415969000C
Fraser R. 78-123km	5		81.5	11/09/97	174.0	Y	1609	4158462812
Fraser R. 78-123km	6		81.5	11/09/97	139.0	Y	1602	4158563668
Fraser R. 78-123km	7		90.3	08/29/97	170.0	Y	0871	415859614A
Fraser R. 78-123km	8		81.5	11/09/97	137.0	Y	1606	4158601D2A
Fraser R. 78-123km	9		123.4	11/05/97	177.5	Y	1528	41585B0779
Fraser R. 78-123km	10		123.5	11/07/97	151.0	Y	1539	41586C3534
Fraser R. 78-123km	11		91.2	08/10/97	69.5	Y	0820	41585C346C
Fraser R. 78-123km	12		81.7	11/03/97	182.0	Y	1513	41586F1467
Fraser R. 78-123km	13		81.5	11/09/97	57.0	Y	1549	4159172029
Fraser R. 78-123km	14		81.0-83.0	11/03/97	221.5	Y	1509	4158616352
Fraser R. 78-123km	15		81.0-83.0	11/03/97	164.0	Y	1514	4159114B69
Fraser R. 78-123km	16		90.9	11/04/97	144.0	Y	1527	4158552D34
Fraser R. 78-123km	17		81.6	11/05/96	178.0	Y	713	4158583159
Fraser R. 78-123km	18		112.1	08/13/97	174.0	Y	809	4158561748
Fraser R. 78-123km	19		101.3	08/10/97	142.5	Y	0824	4158453D26
Fraser R. 78-123km	20		90.8	11/08/97	117.0	Y	1540	41586B454F
Fraser R. 78-123km	21		90.2	08/30/97	62.5	Y	0874	7F7D365E11
Fraser R. 78-123km	22		81.5	11/09/97	96.0	Y	1603	4159785A01
Fraser R. 78-123km	23		82.5	11/09/97	154.5	Y	1548	415866C4009
Fraser R. 78-123km	24		112.5	11/04/97	100.0	Y	1529	41585B1C56
Fraser R. 78-123km	25		82.5	11/03/97	123.5	Y	1507	41584A154B
Fraser R. 78-123km	26		112.2	09/07/97	64.5	Y	1572	7F7D371939
Fraser R. 78-123km	27		81.5	11/09/97	212.5	Y	1546	41585F1006
Fraser R. 78-123km	28		82.5	11/09/97	192.0	Y	1550	4159132211
Fraser R. 78-123km	29		81.5	11/09/97	86.5	Y	1608	4158666737
Fraser R. 78-123km	30		101.2	08/29/97	124.0	Y	0865	41584D7D08
Fraser R. 78-123km	31		81.0-83.0	11/03/97	154.5	Y	1511	41586F5004
Fraser R. 78-123km	32		90.4	08/30/97	175.0	Y	0876	41585F3005
Fraser R. 78-123km	33		121.3	08/24/97	178.5	Y	0852	4158652C6C
Fraser R. 78-123km	34		90.4	09/03/97	192.5	Y	0895	41585E1012
Fraser R. 78-123km	35		82.5	11/09/97	164.0	Y	1610	4158621C6E
Fraser R. 78-123km	36		111.8	08/31/97	69.5	Y	0882	7F7D321B45
Fraser R. 78-123km	37		90.3	09/06/97	54.0	Y	1569	7F7D38123D
Fraser R. 78-123km	38		90.3	11/03/97	63.5	Y	1505	4158561F0E
Fraser R. 78-123km	39		90.2	08/30/97	197.5	Y	0875	4159204679

Target region	Sample number	Locale	River km	Date	Fork length (cm)	Floy tag colour	Floy tag #	Pit tag
Fraser R. 78-123km	40		90.2	08/30/97	55.5	Y	0881	7F7D292C44
Fraser R. 78-123km	41		112.3	08/09/97	160.0	Y	0831	4158703503
Fraser R. 78-123km	42		82.5	11/09/97	169.0	Y	1604	4159593D75
Fraser R. 78-123km	43		91.0	09/03/97	118.0	Y	0894	7F7D39462F
Fraser R. 78-123km	44		90.4	09/03/97	113.0	Y	1551	415871744D
Fraser R. 78-123km	45		91.0	11/08/97	167.5	Y	1544	4158633A57
Fraser R. 78-123km	46		90.4	08/29/97	161.5	Y	0869	41585C6366
Fraser R. 78-123km	47		90.2	08/30/97	53.5	Y	0878	7F7D322E72
Fraser R. 78-123km	48		123.0	08/24/97	131.0	Y	0854	4158704C62
Fraser R. 78-123km	49		91.0	08/29/97	60.0	Y	0868	7F7D38184A
Fraser R. 78-123km	50		91.0	11/04/97	107.5	Y	1525	415972620A
Fraser R. 78-123km	51		81.0-83.0	11/03/97	219.5	Y	1515	4158542348
Fraser R. 78-123km	52		91.2	08/10/97	67.0	Y	0819	41585A0B31
Fraser R. 78-123km	53		81.7	11/03/97	79.0	Y	1518	41586C496C
Fraser R. 78-123km	54		81.0-83.0	11/03/97	147.0	Y	1517	41586B6156
Fraser R. 169-185km	1		179.8	08/02/97	81.5	O	0896A	7F7D41363D
Fraser R. 169-185 km	2		179.8	08/02/97	77.0	Y	0741	7F7D353768
Fraser R. 169-185 km	3		179.8	08/02/97	91.5	Y	0742	7F7D365174
Fraser R. 169-185 km	4		182.5	09/05/97	161.0	Y	1565	41585F1C5A
Fraser R. 169-185 km	5		182.5	09/14/97	91.0	Y	0821	4158643C06
Fraser R. 169-185 km	6		182.5	09/09/97	83.5	Y	1583	7F7D502300
Fraser R. 169-185 km	7		182.5	09/11/97	139.0	Y	1592	4159524430
Fraser R. 169-185 km	8		178.8	08/23/97	90.0	Y	0802	7F7D376B24
Fraser R. 169-185 km	9		179.8	07/31/97	61.5	Y	0725	7F7D273057
Fraser R. 169-185 km	10		182.5	07/31/97	76.5	Y	0722	7F7D27015E
Fraser R. 169-185 km	11		181.3	09/11/97	58.0	Y	1595	41586E2F5F
Fraser R. 169-185 km	12		182.5	09/05/97	79.0	Y	1564	41591E1223
Fraser R. 169-185 km	13		179.8	07/31/97	119.0	Y	0730	7F7D434769
Fraser R. 169-185 km	14		179.8	08/04/97	114.0	Y	0847	7F7B03633E
Fraser R. 169-185 km	15		175.0	08/23/97	95.5	Y	0803	7F7D37743D
Fraser R. 169-185 km	16		182.5	09/09/97	130.0	Y	1584	41597E4E0E
Fraser R. 169-185 km	17		175.1	08/07/97	59.5	Y	0836	4158631E4E
Fraser R. 169-185 km	18		175.2	08/12/97	143.0	Y	0810	41596F4713
Fraser R. 169-185 km	19		182.5	09/08/97	143.0	Y	1577	41584E6654
Fraser R. 169-185 km	20		175.2	08/11/97	177.0	Y	0816	4158574F1D
Fraser R. 169-185 km	21		178.2	07/31/97	70.0	Y	0729	7F7D364A17
Fraser R. 169-185 km	22		182.5	09/08/97	166.0	Y	1576	415955210C
Fraser R. 169-185 km	23		182.5	09/05/97	92.5	Y	1559	4158560C67
Fraser R. 169-185 km	24		182.5	09/05/97	156.0	Y	1562	4158664617
Fraser R. 169-185 km	25		182.5	07/31/97	109.0	Y	0721	7F7D415553
Fraser R. 169-185 km	26		81.7	11/03/97	123.0	Y	1519	4158454269
Fraser R. 169-185 km	27		182.5	09/05/97	83.0	Y	1560	7F7D40305A
Fraser R. 169-185km	28		182.5	08/04/97	91.0	Y	0850	7F7B0C6F6B
Fraser R. 169-185 km	29		175.1	08/07/97	113.5	Y	0840	41585A1A6C
Fraser R. 169-185 km	32		182.5	09/09/97	117.0	Y	1580	41584F390C
Fraser R. 169-185 km	33		182.6	08/02/97	169.0	Y	0740	415850102E
Fraser R. 169-185 km	34		179.8	08/25/97	87.5	Y	0857	4158627571
Fraser R. 169-185 km	35		181.3	09/11/97	105.0	Y	1593	41584D0E1B
Fraser R. 169-185 km	36		175.1	08/07/97	100.0	Y	0838	4158676D51

Target region	Sample number	Locale	River km	Date	Fork length (cm)	Floy tag colour	Floy tag #	Pit tag
Fraser R. 169-185 km	37		182.5	09/09/97	101.5	Y	1578	41590D384D
Fraser R. 169-185 km	38		179.8	07/31/97	89.5	Y	0727	1F3B1E097F
Fraser R. 169-185 km	40		175.7	08/27/97	85.0	Y	0860	4158561271
Fraser R. 169-185 km	41		182.5	09/14/97	142.0	Y	1597	4158474614
Fraser R. 169-185 km	42		181.3	09/11/97	85.5	Y	1596	41585A4F52
Fraser R. 169-185 km	44		182.5	08/04/97	98.0	Y	0749	7F7B0C644F
Fraser R. 169-185 km	45		175.2	08/12/97	84.0	Y	0811	414847632E
Fraser R. 169-185 km	46		179.8	08/02/97	70.5	Y	0743	7F7D434D5A
Fraser R. 169-185 km	47		179.8	11/06/97	106.5	Y	1535	4158542566
Fraser R. 169-185 km	48		182.5	08/28/97	102.0	Y	0862	41586F0B52
Fraser R. 169-185 km	49		182.5	08/04/97	100.5	Y	0750	415851411E
Fraser R. 169-185 km	50		182.5	09/05/97	320.0	Y	1561	4159C4554
Fraser R. 169-185 km	51		180.2	09/28/96	69.0	Y	560	415A531727
Fraser R. 220-265km	1		254.5	09/21/97	102.5	Y	1084	7F7D432C02
Fraser R. 220-265km	2		254.5	08/15/97	135.0	Y	987	22236C3123
Fraser R. 220-265km	3		248.6	09/21/97	95.5	Y	1080	7F7D354110
Fraser R. 220-265km	4		233.6	09/20/97	112.5	Y	1068	7F7D432F2B
Fraser R. 220-265km	5		242.3	08/14/97	122.5	Y	978	222370580B
Fraser R. 220-265km	6		248.6	08/15/97	112.0	Y	984	222412625A
Fraser R. 220-265km	7		254.5	09/21/97	199.0	Y	1082	7F7D435015
Fraser R. 220-265km	8		248.6	09/21/97	78.0	Y	684	7F7D40326E
Fraser R. 220-265km	9		248.6	08/15/97	163.0	Y	983	22237E1A7A
Fraser R. 220-265km	10		229.2	08/14/97	95.0	Y	977	22235D6C34
Fraser R. 220-265km	11		242.3	08/14/97	100.0	Y	979	222417531C
Fraser R. 220-265km	12		233.6	08/13/97	172.0	Y	976	2224113014
Fraser R. 220-265km	13		248.6	08/19/97	128.0	Y	1015	7F7D363B17
Fraser R. 220-265km	14		254.5	09/20/97	119.0	Y	1071	7F7D344D47
Fraser R. 220-265km	15		248.6	08/19/97	111.0	Y	1016	7F7D380E30
Fraser R. 220-265km	16		248.6	08/19/97	87.0	Y	1017	7F7D435663
Fraser R. 220-265km	17		248.6	08/15/97	134.5	Y	982	222351504E
Fraser R. 220-265km	18		254.5	09/21/97	130.5	Y	1081	7F7D376E08
Fraser R. 220-265km	19		248.6	08/15/97	108.5	Y	0840A	2223474A45
Fraser R. 220-265km	20		254.5	08/15/97	120.0	Y	986	22234A7312
Fraser R. 220-265km	21		233.6	09/20/97	99.5	Y	1067	7F7D382041
Fraser R. 220-265km	22		248.6	09/21/97	128.0	Y	1078	7F7D365B76
Fraser R. 220-265km	23		248.6	08/13/97	132.5	Y	975	22240C432A
Fraser R. 220-265km	24		248.6	09/21/97	126.0	Y	1072	7F7D33730D
Fraser R. 220-265km	25		248.6	08/15/97	123.5	Y	985	222363575F
Fraser R. 220-265km	26		254.5	08/15/97	163.5	Y	989	2223586070
Fraser R. 220-265km	27		254.5	09/21/97	107.5	Y	1083	7F7D435378
Fraser R. 220-265km	28		242.3	08/15/97	138.0	Y	980	2224093D5E
Fraser R. 220-265km	29		233.6	09/20/97	82.0	Y	1069	7F7D273E6E
Fraser R. 220-265km	30		248.6	09/21/97	119.0	Y	1079	7F7D36400B
Fraser R. 220-265km	31		248.6	09/21/97	95.5	Y	1076	7F7D377640
Fraser R. 220-265km	32		248.6	09/21/97	104.0	Y	1077	7F7D433F28
Fraser R. 220-265km	33		233.6	09/20/97	107.0	Y	1065	7F7D41536A
Fraser R. 220-265km	34		248.6	09/21/97	124.0	Y	1073	7F7D371A4F
Fraser R. 220-265km	35		248.6	08/15/97	167.0	Y	981	222355120F
Fraser R. 220-265km	36		248.6	09/21/97	133.0	Y	1074	7F7D37644F

Target region	Sample number	Locale	River km	Date	Fork length (cm)	Floy tag colour	Floy tag #	Pit tag
Fraser R. 220-265km	37		254.5	08/15/97	97.0	Y	988	22234C0D15
Fraser R. 220-265km	38		254.5	09/20/97	94.0	Y	1070	7F7D270209
Fraser R. 220-265km	39		248.6	09/21/97	148.5	Y	1075	7F7D373472
Fraser R. 220-265km	40		233.6	09/20/97	88.0	Y	1066	7F7D275160
Fraser R. 220-265km	41		248.6	09/07/96	110.5	Y	688	4158531447
Fraser R. 220-265km	42		245	09/08/96	132.5	Y	680	7F7D336B26
Fraser R. 220-265km	43		248.6	09/07/96	64.5	Y	685	7F7D36543F
Fraser R. 220-265km	44		248.6	09/07/96	226.5	Y	690	7F7B0B3109
Fraser R. 220-265km	45		248.6	09/07/96	111	Y	682	7F7D413C0C
Fraser R. 220-265km	46		233.6	09/08/96	86	Y	681	7F7D375F75
Fraser R. 220-265km	47		248.6	09/08/96	107	Y	679	7F7D482C48
Fraser R. 220-265km	48		248.6	09/07/96	74.5	O	836A	7F7D401D2A
Fraser R. 220-265km	49		248.6	09/07/96	75.5	O	253	7F7D7A551D
Fraser R. 220-265km	50							
Fraser R. 266-335km	1		297.5	08/16/97	104.5	Y	990	2223441043
Fraser R. 266-335km	2		273.7	08/17/97	109.0	Y	1000	2224061129
Fraser R. 266-335km	3		285.1	08/17/97	117.0	Y	996	222409534C
Fraser R. 266-335km	4		282.6	08/18/97	172.5	Y	1011	7F7B0C6357
Fraser R. 266-335km	5		273.7	08/17/97	116.5	Y	997	2223542266
Fraser R. 266-335km	6		297.4	08/17/97	151.0	Y	851	222357426F
Fraser R. 266-335km	7		297.5	08/16/97	97.0	Y	992	2223615201
Fraser R. 266-335km	8		273.7	08/17/97	117.0	Y	1003	2224166D1D
Fraser R. 266-335km	9		273.6	08/18/97	159.5	Y	1012	2223631A59
Fraser R. 266-335km	10		297.5	08/16/97	133.5	Y	994	22235D6B39
Fraser R. 266-335km	11		273.7	08/19/97	104.0	Y	1005	222374045C
Fraser R. 266-335km	12		283.4	08/18/97	87.0	Y	1010	7F7D365969
Fraser R. 266-335km	13		273.7	08/19/97	121.0	Y	1021	7F7D263F0A
Fraser R. 266-335km	14		294.1	09/24/97	92.5	Y	1098	7F7D322C08
Fraser R. 266-335km	15		285.1	09/24/97	182.5	Y	1099	7F7D32303B
Fraser R. 266-335km	16		273.6	08/18/97	121.5	Y	1014	7F7E6C0D19
Fraser R. 266-335km	17		273.7	08/17/97	111.5	Y	998	22234C0C36
Fraser R. 266-335km	18		273.7	08/19/97	114.5	Y	1020	22234E0968
Fraser R. 266-335km	19		273.7	08/17/97	153.0	Y	999	22237F6715
Fraser R. 266-335km	20		317.5	09/13/97	135.5	Y	1061	7F7D364023
Fraser R. 266-335km	21		292.6	08/18/97	85.5	Y	1007	7F7D274307
Fraser R. 266-335km	22		273.7	08/17/97	122.0	Y	1002	222401023F
Fraser R. 266-335km	23		273.6	08/18/97	104.5	Y	1013	2224004371
Fraser R. 266-335km	24		304.7	07/31/97	102.5	Y	926	22237E5071
Fraser R. 266-335km	25		297.5	09/22/97	77.0	Y	1089	7F7D36390B
Fraser R. 266-335km	26		294.1	09/24/97	77.0	Y	1097	7F7D34450C
Fraser R. 266-335km	27		273.7	08/19/97	103.0	Y	1019	7F7D351D1F
Fraser R. 266-335km	28		318.5	07/31/97	68.5	Y	922	2224015416
Fraser R. 266-335km	29		316.4	08/03/97	92.5	Y	961	2223771D34
Fraser R. 266-335km	30		318.5	07/31/97	64.5	Y	923	22235B015A
Fraser R. 266-335km	31		318.5	07/31/97	69.5	Y	924	22240F635A
Fraser R. 266-335km	32		304.7	07/31/97	87.5	Y	925	22240F1E21
Fraser R. 266-335km	33		331.6	09/20/96	111.5	Y	518	4158594A18
Fraser R. 266-335km	34		301.4	09/17/96	104	Y	535	7F7D7A685E
Fraser R. 266-335km	35		305.2	09/17/96	106	Y	536	7F7D372245

Target region	Sample number	Locale	River km	Date	Fork length (cm)	Floy tag colour	Floy tag #	Pit tag
Fraser R. 266-335km	36		297.5	09/16/96	82	Y	547	7F7D265D6F
Fraser R. 266-335km	37		301.5	09/17/96	94.5	Y	537	7F7D37340C
Fraser R. 266-335km	38		319.7	09/15/96	153	Y	550	4158640609
Fraser R. 266-335km	39		315.4	09/15/96	98	Y	656	7F7D352F3E
Fraser R. 266-335km	40		301.5	09/16/96	108.5	Y	542	7F7D371E0B
Fraser R. 266-335km	41		297.7	09/16/96	89	Y	539	
Fraser R. 266-335km	42		331.6	09/20/96	123.5	Y	519	41586E382C
Fraser R. 266-335km	43		317.5	09/15/96	74.5	Y	658	7F7D430B11
Fraser R. 266-335km	44		297.5	09/16/96	88	Y	546	7F7D374E45
Fraser R. 266-335km	45		319.7	09/15/96	113.5	Y	651	4158714604
Fraser R. 266-335km	46		297.5	09/16/96	102	Y	545	7F7D433730
Fraser R. 266-335km	47		331.6	09/20/96	89	Y	517	7F7D772733
Fraser R. 266-335km	48		297.7	09/16/96	138	Y	538	
Fraser R. 266-335km	49		315.4	09/15/96	117.5	Y	655	7F7D372F6F
Fraser R. 266-335km	50		315.4	09/15/96	81.5	Y	652	
Fraser R. 336-480km	1		427.7	08/30/98	84.5	Y	1152	41247E3565
Fraser R. 336-480km	2		424.7	08/31/98	72.0	Y	1154	7F7D321425
Fraser R. 336-480km	3		433.2	08/30/98	94.5	Y	1136	412477322B
Fraser R. 336-480km	4		431.4	08/30/98	51.5	Y	1138	7F7D364F65
Fraser R. 336-480km	5		431.4	08/30/98	129.0	Y	1143	41250D7028
Fraser R. 336-480km	6		433.2	08/30/98	72.0	Y	1135	7F7D435408
Fraser R. 336-480km	7		436.5	08/30/98	59.5	Y	1133	7F7D39512C
Fraser R. 336-480km	8		427.7	08/30/98	57.5	Y	1146	7F7D380938
Fraser R. 336-480km	9		431.4	08/30/98	156.5	Y	1144	412510531F
Fraser R. 336-480km	10		424.7	09/01/98	116.5	Y	1159	41246C2F62
Fraser R. 336-480km	11		422.0	09/01/98	95.0	Y	1158	412510654C
Fraser R. 336-480km	12		419.5	09/01/98	57.5	Y	1156	7F7D322877
Fraser R. 336-480km	13		431.4	08/30/98	54.5	Y	1141	7F7D36536E
Fraser R. 336-480km	14		419.5	09/01/98	58.5	Y	1157	7F7D266B7C
Fraser R. 336-480km	15		433.2	08/30/98	108.5	Y	1137	41246F3862
Fraser R. 336-480km	16		447.5	09/02/98	55.5	Y	1163	7F7D41284B
Fraser R. 336-480km	17			06/11/98	68		FR 13	
Fraser R. 336-480km	18			06/11/98	64.5		FR 10	
Fraser R. 336-480km	19			06/11/98	92		FR 17	
Fraser R. 336-480km	20			06/11/98	67.8		FR 14	
Fraser R. 336-480km	21		445.6	08/28/98	118.0	Y	1130	412471031E
Fraser R. 336-480km	22		427.7	08/30/98	82.5	Y	1151	420E531A12
Fraser R. 336-480km	23		439.7	08/29/98	59.5	Y	1132	7F7D376940
Fraser R. 336-480km	24		431.4	08/30/98	61.0	Y	1142	7F7D377339
Fraser R. 336-480km	25			07/07/98	66.5		FR 43	
Fraser R. 336-480km	26			06/11/98	97		FR 20	
Fraser R. 336-480km	27			06/11/98	151		FR 11	
Fraser R. 336-480km	28			07/07/98	97.5		FR 48	
Fraser R. 336-480km	29			07/07/98	54.2		FR 50	
Fraser R. 336-480km	30			07/07/98	65		FR 40	
Fraser R. 336-480km	31			06/25/98	97.6		FR 16	
Fraser R. 336-480km	32			06/25/98	63.7		FR 29	
Fraser R. 336-480km	33			06/25/98	87.8		FR 22	
Fraser R. 336-480km	34			06/25/98	93.2		FR 24	

Target region	Sample number	Locale	River km	Date	Fork length (cm)	Floy tag colour	Floy tag #	Pit tag
Fraser R. 336-480km	35			06/11/98	145		FR 7	
Fraser R. 336-480km	36			06/11/98	89.7		FR 12	
Fraser R. 336-480km	37			06/11/98	70		FR 8	
Fraser R. 336-480km	38			06/11/98	183		FR 4	
Fraser R. 336-480km	39			06/11/98	95		FR 5	
Fraser R. 336-480km	40			06/11/98	74.5		FR 6	
Fraser R. 336-480km	41		445.6	08/28/98	57.0	Y	1131	7F7D270308
Fraser R. 336-480km	42		407.4	09/04/98	84.0	Y	1169	4124695950
Fraser R. 336-480km	43		427.7	08/30/98	50.0	Y	1147	22240C3D46
Fraser R. 336-480km	44		391.1	09/05/98	132.0	Y	1177	41246A7A37
Fraser R. 336-480km	45		428.4	08/29/98	38.5	Y	1134	7F7D38162D
Fraser R. 336-480km	46		410.2	09/04/98	128.5	Y	1166	4125097D5B
Fraser R. 336-480km	47		457.3	09/02/98	73.5	Y	1165	4124687D5D
Fraser R. 336-480km	48		460.1	09/02/98	157.5	Y	1164	4124737644
Fraser R. 336-480km	49		407.4	09/04/98	159.0	Y	1168	41246F3333
Fraser R. 336-480km	50		424.7	09/01/98	97.0	Y	1160	4125135C27
Fraser R. 480-554km	1			06/28/98	113		FR 28	
Fraser R. 480-554km	2			06/05/98	97		FR 1	
Fraser R. 480-554km	3			06/05/98	72		FR 2	
Fraser R. 480-554km	4			06/05/98	94.5		FR 3	
Fraser R. 480-554km	5			06/16/98	118		FR 15	
Fraser R. 480-554km	6			06/24/98	157		FR 23	
Fraser R. 480-554km	7			07/22/98	133.6		FR 52	
Fraser R. 480-554km	8			06/16/98	104		FR 9	
Fraser R. 480-554km	9			06/24/98	191		FR 31	
Fraser R. 480-554km	10			07/16/98	177.5		FR 47	
Fraser R. 480-554km	11			07/21/98	109		FR 49	
Fraser R. 480-554km	12			07/16/98	121		FR 44	
Fraser R. 480-554km	13			07/22/98	170		FR 45	
Fraser R. 480-554km	14			06/28/98	213		FR 30	
Fraser R. 480-554km	15			06/16/98	160		FR 18	
Fraser R. 480-554km	16			07/16/98	118.8		FR 46	
Fraser R. 480-554km	17		551	08/08/97	133.5	Y	969	22237B1010
Fraser R. 480-554km	18		552.6	08/07/97	122.5	Y	965	22236D0473
Fraser R. 480-554km	19		551	08/08/97	157.0	Y	968	2223436E50
Fraser R. 480-554km	20		552.6	08/06/97	81.0	Y	964	222407122A
Fraser R. 480-554km	21		552.6	08/07/97	148.5	Y	966	2223443579
Fraser R. 480-554km	22		552.6	08/07/97	150.5	Y	967	222409460B
Fraser R. 480-554km	23		502.8	10/14/97	106.0	Y	1112	41584D0073
Fraser R. 480-554km	24		553.0	08/21/97	117.0	O	70521	
Fraser R. 480-554km	25		552.7	10/22/97	61.5	O	70506	001 527 889
Fraser R. 480-554km	26		552.7	10/24/97	139.5	O	70509	7F7B0C6647
Fraser R. 480-554km	27		553.0	09/15/97	135.0	O	70504	001 802 372
Fraser R. 480-554km	28		552.7	10/22/97	185.0	O	70507	002 338 110
Fraser R. 480-554km	29		550	10/19/99	208	Y	5423	411B421378
Fraser R. 480-554km	30		550	04/09/99	155	Y	5227	001376025
Fraser R. 480-554km	31		550	04/09/99	150	Y	5229	401D5B5917
Fraser R. 480-554km	32		515	06/27/99	118	Y	5179	411B3D6E31
Fraser R. 480-554km	33		550	05/25/99	111	Y	5183	411B2C4216

Target region	Sample number	Locale	River km	Date	Fork length (cm)	Floy tag colour	Floy tag #	Pit tag
Fraser R. 480-554km	34		550	04/16/99	75	Y	5235	401D517E29
Fraser R. 480-554km	35		550	05/25/99	181	Y	5185	411B262D17
Fraser R. 480-554km	36		550	04/27/99	166	Y	5199	401D2E1530
Fraser R. 480-554km	37		542.5	05/11/99	216	Y	5187	411B425135
Fraser R. 480-554km	38		551	05/05/99	217	Y	5195	401D681F48
Fraser R. 480-554km	39		539	07/02/99	206	Y	5173	411B28767D
Fraser R. 480-554km	40		542.5	07/18/99	151	Y	5165	001859029
Fraser R. 480-554km	41		547	10/06/99	237	Y	5409	411B276126
Fraser R. 480-554km	42		539.5	08/10/99	176	Y	5090	401D2D0127
Fraser R. 480-554km	43		551	08/10/99	66	Y	5088	411B30014F
Fraser R. 480-554km	44		551	08/26/99	92.5	Y	5072	411B454134
Fraser R. 480-554km	45		542.5	05/05/99	261	Y	5189	411B3F6C62
Fraser R. 480-554km	46		551	07/18/99	218	Y	5167	411B3B7741
Fraser R. 480-554km	47		542	07/02/99	120	Y	5178	411B346717
Fraser R. 480-554km	48		542	05/25/99	280.5	Y	5181	411B453C4F
Fraser R. 480-554km	49		542	07/02/99	86.5	Y	5176	411B22576D
Fraser R. 480-554km	50		542	07/02/99	129	Y	5177	411B222769
Fraser R. 480-554km	51		550	05/05/99	134	Y	5191	411B37106D
Fraser R. 480-554km	52		539	08/10/99	101	Y	5092	411B402156
Fraser R. 480-554km	53		550	10/19/99	258	Y	5428	401D524358
Fraser R. 480-554km	54		542	07/16/99	214	Y	5169	411B2F0511
Fraser R. 480-554km	55		551	08/26/99	85	Y	5070	411B433C24
Fraser R. 480-554km	56		539	07/02/99	286	Y	5171	411B3E2344
Fraser R. 555-790km	1		609	10/07/95	194	Y	312	22236D1639
Fraser R. 555-790km	2		683.5	08/26/98	131.0	Y	1128	412479017D
Fraser R. 555-790km	3		670.0	08/26/98	239.0	Y	1129	4124772142
Fraser R. 555-790km	4		614.5	08/06/97	113.0	Y	962	2224041760
Fraser R. 555-790km	5		760.0	08/16/98	262.0	Y	1451	7F7B040028
Fraser R. 555-790km	6		760.0	08/17/98	130.0	Y	1125	4125034473
Fraser R. 555-790km	8		609.1	08/15/95	92.5	Y	309	7F7B037C6F
Fraser R. 555-790km	9		670	04/15/99	256	Y	5231	401D5A5371
Fraser R. 555-790km	10		670	07/21/99	228	Y	5161	411B357915
Fraser R. 555-790km	11		670	07/21/99	134	Y	5163	411B3F0D3B
Fraser R. 791-920km	1		888.6	09/27/97	136.0	Y	328	7F7D7B2121
Fraser R. 791-920km	2			1998				UF5
Fraser R. 791-920km	3			1998				UF6
Fraser R. 791-920km	4			1998				UF7
Fraser R. 791-920km	5			1998				UF8
Fraser R. 791-920km	6			1998				UF9
Fraser R. 791-920km	7		830	08/19/99	64	y	0025	501C144B5D
Fraser R. 791-920km	8		830	08/19/99	71.5	y	0024	50283B6C65
Fraser R. 791-920km	9		831.3	08/19/99	58	y	0023	50283B6E51
Fraser R. 791-920km	10		831.3	08/19/99	223	y	0022	5028364E1D
Fraser R. 791-920km	11		831	08/20/99	59.5	y	0002	5027797B55
Fraser R. 791-920km	12		831.3	08/20/99	57.5	y	0001	5028265144
Fraser R. 791-920km	13		829.95	08/21/99	54	y	0003	50283A5569
Fraser R. 791-920km	14		863.6	08/23/99	61	b	00097	5028364241
Fraser R. 791-920km	15		882.3	08/23/99	61	b	00100	5028381F05
Fraser R. 791-920km	16		882.3	08/23/99	72.5	y	0004	5028272D08

Target region	Sample number	Locale	River km	Date	Fork length (cm)	Floy tag colour	Floy tag #	Pit tag
Fraser R. 791-920km	17		882.3	08/23/99	75	y	0005	50277D7626
Fraser R. 791-920km	18		882.3	08/23/99	61	b	00099	502837513C
Fraser R. 791-920km	19		863.7	08/23/99	60	b	00098	502823341F
Fraser R. 791-920km	20	McGregor	1.6	08/24/99	52	b	00096	50274B0D63
Fraser R. 791-920km	21		882.6	08/25/99	146	y	0006	5027447327
Fraser R. 791-920km	22		900.5	08/25/99	131	y	0008	50283B0254
Fraser R. 791-920km	23		883.6	08/25/99	127.5	y	0007	5027545566
Fraser R. 791-920km	24		882.3	08/25/99	65	b	00095	502827623A
Fraser R. 791-920km	25	Bowron	0.4	08/28/99	52	b	00094	502835091A
Fraser R. 791-920km	26	Bowron	0.4	08/28/99	119	y	0010	502828734F
Fraser R. 791-920km	27	Bowron	0.4	08/28/99	117	y	0011	50282C5811
Fraser R. 791-920km	28	Bowron	0.4	08/28/99	114	y	0012	50282A7328
Fraser R. 791-920km	29		916.9	08/28/99	143	y	0009	5027256602
Fraser R. 791-920km	30		916.9	08/29/99	130	y	0013	50282F5941
Fraser R. 791-920km	31	Bowron	0.5	08/29/99	126	y	0014	50274F2E7B
Fraser R. 791-920km	32	Bowron	0.7	08/29/99	140.5	y	0015	5028011B27
Fraser R. 791-920km	33		916.9	08/30/99	105	y	0016	5028036A67
Fraser R. 791-920km	34		940.7	09/01/99	71	y	0017	5028284E4D
Fraser R. 791-920km	35		943.1	09/01/99	87.5	y	0018	5028264724
Fraser R. 791-920km	36		950.6	09/01/99	62	b	00093	5027761810
Fraser R. 791-920km	37		950.4	09/02/99	83	y	0019	502829735B
Fraser R. 791-920km	38		950.4	09/03/99	102	y	0021	5028002E77
Fraser R. 791-920km	39		950.4	09/03/99	124.5	y	0020	5028247314
Fraser R. 791-920km	40		831	09/04/99	102	y	0026	5027187F2D
Fraser R. 791-920km	41		831.3	09/04/99	77	b	00092	5027580F48
Fraser R. 791-920km	42		958.6	09/09/99	97	y	0028	501F7B1B17
Fraser R. 791-920km	43		1007.9	09/16/99	167	y	0029	5020205006
Nechako	1		126.5	08/20/95	215.5	Y	6	7F7B031610
Nechako	2		124.5	09/15/95	162.5	Y	13	7F7B0C4E1D
Nechako	3		110.1	08/18/95	109	Y	1	22234A7C59
Nechako	4		116.2	09/15/95	139.5	Y	20	7F7B0B1A3A
Nechako	5		110.1	08/18/95	134	Y	3	22236F2C51
Nechako	6		116.2	09/15/95	181	Y	18	7F7B0C4A4D
Nechako	7		124.9	09/16/95	160.5	Y	21	7F7B030A65
Nechako	8		116.5	08/21/95	152	Y	7	22240A5F63
Nechako	9		124.5	09/15/95	149	Y	14	7F7D7C631A
Nechako	10		116.5	08/21/95	155	Y	9	7F7D781A4D
Nechako	11		124.9	09/16/95	144	Y	22	7F7B0B1452
Nechako	12		115.2	09/16/95	153	Y	26	7F7B04052A
Nechako	13		107.5	08/18/95	165	Y	4	22235D2A63
Nechako	14		116.5	08/21/95	148.5	Y	8	2223420262
Nechako	15		91.5	06/11/95	96.5	O	4512	7F7D7D4335
Nechako	16		92.4	06/10/95	130.5	O	4508	7F7B0C3231
Nechako	17		92.4	06/10/95	123	O	4509	7F7D767322
Nechako	18		90.2	06/10/95	114.5	O	4511	7F7B0B1B5C
Nechako	19		93.1	06/10/95	114	O	4510	7F7D775A36
Nechako	20		92.4	06/17/95	181	O	4514	7F7B0C1874
Nechako	21		96.5	06/18/95	150	O	4515	7F7B0C6578
Nechako	22		114.9	09/16/95	175	Y	29	7F7B032A30

Target region	Sample number	Locale	River km	Date	Fork length (cm)	Floy tag colour	Floy tag #	Pit tag
Nechako	23		124.5	09/15/95	143.5	Y	10	7F7B0B1C28
Nechako	24		116.2	09/16/95	206	Y	25	7F7D7C6201
Nechako	25		114.9	09/16/95	178	Y	27	7F7D7A6A66
Nechako	26		125	09/14/95	137.5	Y	311	7F7B0B2E7E
Nechako	27		116.2	09/19/95	148	Y	31	7F7D7D4F7C
Nechako	28		125	09/15/95	150	Y	12	7F7B0B1041
Nechako	29		125	09/16/95	156.5	Y	23	7F7B027C16
Nechako	30		125.1	09/15/95	138.5	Y	11	7F7D7D373D
Nechako	31		116.2	09/15/95	167	Y	19	7F7B0C540B
Nechako	32		124.7	09/15/95	125	Y	16	7F7D7A3C1F
Nechako	33		116.2	09/16/95	129	Y	24	7F7B0B200A
Nechako	34		115.2	09/19/95	159.5	Y	30	7F7D7D2657
Nechako	35		116.2	09/15/95	215	Y	17	7F7B0C5763
Nechako	36		114.9	09/16/95	175.5	Y	28	7F7B0C3010
Nechako	37		116.2	09/08/96	168.5	Y	85	7F7B0C6856
Nechako	38		116.2	09/07/96	152	Y	80	7F7D784059
Nechako	39		116.2	09/07/96	151.5	Y	79	7F7D7D5904
Nechako	40		117.2	09/08/96	126	Y	83	7F7D781103
Nechako	41		116.5	09/08/96	171.5	Y	82	7F7B0C5B7A
Nechako	42		91.5	09/12/96	162.5	Y	91	7F7B0C6B60
Nechako	43		116.2	09/08/96	183	Y	84	7F7D7D4E08
Nechako	44		72.6	09/16/96	159	Y	93	7F7B0C6864
Nechako	45		91.5	09/12/96	133	Y	92	7F7D4F521F
Nechako	46		79.1	09/16/96	191	Y	94	7F7D43767B
Nechako	47		90.2	09/12/96	90	Y	89	7F7B03057D
Nechako	48		111.2	09/09/96	198	Y	86	7F7B033622
Nechako	49		109.4	09/10/96	135	Y	88	7F7D7D2E0E
Nechako	50		109.4	09/09/96	196.5	Y	87	7F7B0C4B3C
Lower Columbia	1		24-40	1998				
Lower Columbia	2		24-40	1998				
Lower Columbia	3		24-40					
Lower Columbia	4		24-40					
Lower Columbia	5		24-40					
Lower Columbia	6		24-40					
Lower Columbia	7		24-40					
Lower Columbia	8		24-40					
Lower Columbia	9		24-40					
Lower Columbia	10		24-40					
Lower Columbia	11		24-40					
Lower Columbia	12		24-40					
Lower Columbia	13		24-40					
Lower Columbia	14		24-40					
Lower Columbia	15		24-40					
Lower Columbia	16		24-40					
Lower Columbia	17		24-40					
Lower Columbia	18		24-40					
Lower Columbia	19		24-40					
Lower Columbia	20		24-40					
Lower Columbia	21		24-40					

Target region	Sample number	Locale	River km	Date	Fork length (cm)	Floy tag colour	Floy tag #	Pit tag
Lower Columbia	22		24-40					
Lower Columbia	23		24-40					
Lower Columbia	24		24-40					
Lower Columbia	25		24-40					
Lower Columbia	26		24-40					
Lower Columbia	27		24-40					
Lower Columbia	28		24-40					
Lower Columbia	29		24-40					
Lower Columbia	30		24-40					
Lower Columbia	31		24-40					
Lower Columbia	32		24-40					
Lower Columbia	33		24-40					
Lower Columbia	34		24-40					
Lower Columbia	35		24-40					
Lower Columbia	36		24-40					
Lower Columbia	37		24-40					
Lower Columbia	38		24-40					
Lower Columbia	39		24-40					
Lower Columbia	40		24-40					
Lower Columbia	41		24-40					
Lower Columbia	42		24-40					
Lower Columbia	43		24-40					
Lower Columbia	44		24-40					
Lower Columbia	45		24-40					
Lower Columbia	46		24-40					
Lower Columbia	47		24-40					
Lower Columbia	48		24-40					
Lower Columbia	49		24-40					
Lower Columbia	50		24-40					
Upper Columbia R.	1		0.1	12/18/97	137.5	O	30781	415864572D
Upper Columbia R.	2		0.1	12/16/97	114.0	O	30786	41597C5839
Upper Columbia R.	3		0.1	04/15/98	143.5	P	21889	7F7D4D1647
Upper Columbia R.	4		0.1	04/23/98	138.5	O	30992	7F7D1C5A66
Upper Columbia R.	5		0.1	04/22/98	178.0	O	1813	7F7D1C477C
Upper Columbia R.	6		0.1	04/21/98	117.0	O	30757	7F7D4D1C68
Upper Columbia R.	7		1.2	04/16/98	162.0	O	30765	4159531D46
Upper Columbia R.	8		2	04/21/98	174.0	O	31000	7F7D266702
Upper Columbia R.	9		0.1	04/15/98	136.0	O	30771	4158445F7C
Upper Columbia R.	10		2	04/21/98	144.0	O	30751	7F7D1C593C
Upper Columbia R.	11		0.1	04/22/98	119.5	O	30993	4159211167
Upper Columbia R.	12		2	04/21/98	139.0	O	30999	7F7D32157C
Upper Columbia R.	13		1.2	04/17/98	175.5	O	30762	4158562501
Upper Columbia R.	14		0.1	04/21/98	130.0	O	30753	7F7D187F2E
Upper Columbia R.	15		0.1	04/21/98	167.5	P	21278	7F7D1C237E
Upper Columbia R.	16		1.2	04/21/98	160.5	P	25770	7F7D1D0347

Target region	Sample number	Locale	River km	Date	Fork length (cm)	Floy tag colour	Floy tag #	Pit tag
Upper Columbia R.	17		1.2	04/14/98	207.0	O	30775	4158652113
Upper Columbia R.	18		0.1	04/21/98	144.0	O	30754	7F7B03226D
Upper Columbia R.	19		0.1	04/22/98	173.0	O	30994	7F7D372747
Upper Columbia R.	20		0.1	04/15/98	156.0	O	30772	7F7D4D3372
Upper Columbia R.	21		0.1	04/22/98	160.0	O	30995	7F7D1C282B
Upper Columbia R.	22		0.1	04/15/98	144.0	O	30770	41584E6A08
Upper Columbia R.	23		0.1	04/14/98	175.0	O	30924	41584C4404
Upper Columbia R.	24		1.2	04/21/98	130.5	O	30998	7F7D191025
Upper Columbia R.	25		0.1	04/21/98	150.5	P	23735	7F7D4F626F
Upper Columbia R.	26		0.1	04/21/98	136.0	O	30756	7F7D343852
Upper Columbia R.	27		2	04/21/98	142.0	O	30752	7F7D492B09
Upper Columbia R.	28		1	04/15/98	144.5	O	30769	4159671E26
Upper Columbia R.	29		0.1	04/16/98	146.0	O	30766	41586A5525
Upper Columbia R.	30		0.1	04/15/98	175.5	P	21894	7F7D502651
Upper Columbia R.	31		1.2	04/15/98	173.5	O	30768	4158683122
Upper Columbia R.	32		0.1	04/22/98	164.0	O	30996	7F7D4F725F
Upper Columbia R.	33							
Upper Columbia R.	34		1.2	04/17/98	126.0	O	30763	4158604D2D
Upper Columbia R.	35		0.1	04/17/98	153.5	O	30764	4158681418
Upper Columbia R.	36		0.1	04/21/98	148.5	O	30755	7F7D435878
Upper Columbia R.	37		1.2	04/15/98	280.0	O	30773	4158555B1E
Upper Columbia R.	38		1.2	04/22/98	146.5	P	25752	7F7D4F6677
Upper Columbia R.	39							
Upper Columbia R.	40		0.1	04/16/98	154.5	O	30767	41585B557E
Upper Columbia R.	41		0.1	08/06/98	157.0	O	30989	4159626D2D
Upper Columbia R.	42		0.1	08/06/98	154.0	O	30988	4158684960
Upper Columbia R.	43		0.1	08/06/98	137.0	O	30986	41595A391C
Upper Columbia R.	44		0.1	08/06/98	119.0	O	30987	415973275
Upper Columbia R.	45		0.1	08/06/98	137.0	O	30990	415847266E
Upper Columbia R.	46							
Upper Columbia R.	47		0.1	08/06/98	167.0	O	30985	41584A6C2A
Upper Columbia R.	48		0.1	11/10/98	147.5	O	32510	
Upper Columbia R.	49		0.1	11/10/98	176.5	O	32512	
Upper Columbia R.	50		0.1	08/06/98	143.0	O	30984	4158531750
Arrow Lakes	1		224.7	10/11/95	175.0	O	6747	7F7D0A3A66
Arrow Lakes	2		200.4	10/13/95	215.0	O	6746	7F7DOA4460
Arrow Lakes	3		181-10.6	08/10/95	184.0	O	6940	7F7D0D7764
Arrow Lakes	4		181.0	10/04/97	161.5	O	30799	4158666119
Arrow Lakes	5		223.2	10/02/97	199.0	O	30800	4158522117

Target region	Sample number	Locale	River km	Date	Fork length (cm)	Floy tag colour	Floy tag #	Pit tag
Arrow Lakes	6		181.0-0.1	10/06/97	179.0	O	30797	4158546F6D
Arrow Lakes	8		181.0-0.1	10/05/97	226.5	O	30798	415867575E
Arrow Lakes	9		183.5	10/23/98	180.5	O	32501	757B0C2A6B
Arrow Lakes	10		181.5	10/24/98	210.0	O	32502	7F7D520552
Arrow Lakes	11		181.0	10/27/98	196.5	O	32504	7F7D7D3342
Arrow Lakes	12		181.0	10/28/98	216.0	O	32508	4159673663
Arrow Lakes	13		181.0	10/28/98	184.0	O	32507	41586D6404
Arrow Lakes	14		181.0	10/27/98	208.0	O	32505	7F7B036047
Arrow Lakes	15		181.0	10/28/98	216.5	O	32506	7F7D7D783F
Arrow Lakes	16		181.0	10/29/98	214.5	O	32509	41586A7E77
Arrow Lakes	17		181.0-16.6	07/23/97	126.5	P	29864	7F7D432C07
Arrow Lakes	18		181.0	10/22/97	150.0	O	30792	4158693015
Arrow Lakes	19		181.0	10/24/97	192.5	O	30789	4158683235
Arrow Lakes	20		183.1	10/24/97	190.0	O	30790	415859106D
Arrow Lakes	21		181.0	10/22/97	172.5	O	30791	4158636864
Kootenay R.	1		0	08/20/96	123.0	P	29231	7F7D4F7176
Kootenay R.	2		0	08/20/96	164.0	O	30925	
Kootenay R.	3		0	08/20/96	140.0	P	8785	
Kootenay R.	4		0	08/20/96	152.0	O	30923	
Kootenay R.	5		0	08/20/96	179.0	O	30927	
Kootenay R.	6		0	10/01/96	149.5	O	31994	4158691A64
Kootenay R.	7		0	10/01/96	141.5	P	21954	7F7A003F17
Kootenay R.	8		0	10/01/96	137.5	P	21964	7F7D1C427F
Kootenay R.	9		0	10/01/96	140.5	Y	6964	41586F0314
Kootenay R.	10		0	10/01/96	145.5	O	31995	41586D4633
Kootenay R.	11		0	07/28/95	167.0	P	29222	7F7D216159
Kootenay R.	12							
Kootenay R.	13							
Kootenay R.	14							
Kootenay R.	15							
Kootenay R.	16							
Kootenay R.	17							
Kootenay R.	18		0	07/28/95	110.0	P	29221	7F7D4F382D
Kootenay R.	19							
Kootenay R.	20							
Kootenay R.	21							
Kootenay R.	22		0	08/20/96	105.5	O	30921	
Kootenay R.	23		0	08/20/96	187.5	O	30922	
Kootenay R.	24		0	10/01/96	140.5	P	21955	7F7D4D335E
Kootenay R.	25		0	08/20/96	155.0	O	30928	
Kootenay R.	26							
Kootenay R.	27		0	08/20/96	135.5	O	30929	
Kootenay R.	28		0	08/20/96	157.0	O	30920	
Kootenay R.	29							
Kootenay R.	30		0	10/01/96	137.0	O	31997	4158681E6A

Target region	Sample number	Locale	River km	Date	Fork length (cm)	Floy tag colour	Floy tag #	Pit tag
Kootenay R.	31		0	08/20/96	137.0	P	21964	
Kootenay R.	32		0	09/05/97	147.5	O	32150	
Kootenay R.	33		0	11/26/96	163.5	O	32071	41586B446C
Kootenay R.	34							
Kootenay R.	35		0.2	12/18/97	186.5	O ₂	30778	7F7A003763
Kootenay R.	36		0.2	04/17/98	95.0	O	30758	41595DOF30
Kootenay R.	37		0.2	04/17/98	153.0	O	30761	4158570E47
Kootenay R.	38		0.2	12/19/97	157.5	O	30777	4158590013
Kootenay R.	39		0.2	12/18/97	183.5	O	30779	415849236B
Kootenay R.	40		0.2	04/17/98	144.0	O	30760	41584B097D
Kootenay R.	41		2	11/21/97	162.0	O	30788	41586D4229
Kootenay R.	42		2	11/21/97	127.5	O	30787	4158507177
Kootenay R.	43		0	05/16/97	143.0	P	6553	7F7D490A04
Kootenay R.	44		0	05/16/97	178.0	P	23789	7F7D4E561D
Kootenay R.	45		0	05/16/97	164.0	P	29855	1F4C76217E
Kootenay R.	46		0	05/16/97	154.5	P	29856	7F7D49174B
Kootenay R.	47		0	05/16/97	148.5	P	29854	7F7D1E3570
Kootenay R.	48		0	05/16/97	147.0	P	23784	7F7D4E6D6F
Kootenay R.	49		0	05/16/97	141.5	P	29858	7F7D434D10
Kootenay R.	50		0	05/16/97	173.0	P	29857	1F6C77126C
Kootenay Lake	1			1998			KL95-1	
Kootenay Lake	2			1998			KL95-2	
Kootenay Lake	3			1998			KL95-3	
Kootenay Lake	4			1998			KL95-4	
Kootenay Lake	5			1998			KL95-5	
Kootenay Lake	6			1998			KL95-6	
Kootenay Lake	7			1998			KL95-7	
Kootenay Lake	8			1998			KL95-8	
Kootenay Lake	9			1998			KL95-10	
Kootenay Lake	10			1998			KL95-11	
Kootenay Lake	11			1998			KL95-12	
Kootenay Lake	12			1998			KL95-13	
Kootenay Lake	13			1998			KL95-14	
Kootenay Lake	14			1998			KL95-15	
Kootenay Lake	15			1998			KL95-16	
Kootenay Lake	16			1998			KL95-17	
Kootenay Lake	17			1998			KL95-18	
Kootenay Lake	18			1998			KL95-19	
Kootenay Lake	19			1998			KL95-20	
Kootenay Lake	20			1998			KL95-21	
Kootenay Lake	21			1998			KL95-22	
Kootenay Lake	22			1998			KL95-23	
Kootenay Lake	23			1998			KL95-24	
Kootenay Lake	24			1998			KL95-25	
Kootenay Lake	25			1998			KL95-27	
Kootenay Lake	26			1998			KL95-28	
Kootenay Lake	27			1998			KL95-29	
Kootenay Lake	28			1998			KL95-30	

Target region	Sample number	Locale	River km	Date	Fork length (cm)	Floy tag colour	Floy tag #	Pit tag
Kootenay Lake	29			1998			KL95-31	
Kootenay Lake	30			1998			KL95-32	
Kootenay Lake	31			1998			KL95-33	
Kootenay Lake	32			1998			KL95-34	
Kootenay Lake	33			1998			KL95-35	
Kootenay Lake	34			1998			KL95-36	
Kootenay Lake	35			1998			KL95-38	
Kootenay Lake	36			1998			KL95-39	
Kootenay Lake	37			1998			KL95-40	
Kootenay Lake	38			1998			KL95-41	
Kootenay Lake	39			1998			KL95-42	
Kootenay Lake	40			1998			KL95-43	
Kootenay Lake	41			1998			KL95-44	
Kootenay Lake	42			1998			KL95-45	
Kootenay Lake	43			1998			KL95-46	
Kootenay Lake	44			1998			KL95-47	
Kootenay Lake	45			1998			KL95-48	
Kootenay Lake	46			1998			KL95-49	
Kootenay Lake	47			1998			KL95-50	
Kootenay Lake	48			1998			96-KL-03 (22)	
Kootenay Lake	49			1998			96-KL-06 (33)	
Kootenay Lake	50			1998			96-KL-23 (64)	