

Exxon Valdez Oil Spill
Restoration Project Annual Report

Genetics of Populations of Pink Salmon
Inhabiting Prince William Sound

Restoration Project 97196
Annual Report

This annual report was prepared for peer review as part of the *Exxon Valdez* Oil Spill Trustee Council restoration program for the purpose of assessing project progress. Peer review comments have not been addressed in this annual report.

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Abstract: Allozyme and mitochondrial DNA (mtDNA) data were collected from 4, 34, 16, and 25 putative populations of pink salmon spawning throughout Prince William Sound (PWS) in 1992, 1994, 1995, and 1996, respectively. This annual report focuses on the 1996 samples which were selected to test for differences among streams and differences between timing and elevation within streams. Forty fish per collection were screened for haplotype variation at the ND5/ND6 region using six restriction enzymes; ten haplotypes were detected. Significant differences were detected both among streams (allozyme and mtDNA) and within streams (allozyme). These results are consistent with our analysis of 1994 samples where we found significant regional heterogeneity within upstream (allozymes and mtDNA) and tidal (allozymes) collections. We found no differences between upstream and tidal collections within streams and only one stream demonstrated early-late differences. This contrasts with 1994 analyses where we detected significant differences between upstream and tidal collections within Lagoon Creek (allozymes; not sampled in 1996) and within Koppen Creek (mtDNA; sampled in 1996). These results support managing native populations of pink salmon in PWS at the regional level, considering local subpopulation structure, rather than treating pink salmon as a single panmictic population in PWS.

Key Words: Allozymes, *Exxon Valdez* oil spill, genetics, mtDNA, *Oncorhynchus gorbuscha*, pink salmon, Prince William Sound, stock identification.

Project Data: (will be addressed in the final report)

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EXECUTIVE SUMMARY

- Allozyme and mitochondrial DNA (mtDNA) data were collected from 25 aggregates of pink salmon spawning in 1996 from Prince William Sound (PWS). Collection location and timing selections were made emphasizing early-late and upstream-tidal comparisons. Samples were collected from spawners from one hatchery, eight tidal, and seven upstream locations which included seven early- and eight late-spawning aggregations. For this annual report, we analyzed data only from those streams where we had early and late collections or upstream and tidal collections. Regional and inter-year analyses will be addressed in the final report.
- Inheritance of allozyme alleles was tested on 71 alleles from 31 loci using 17 single-pair matings. Three alleles (*bGALA*111*, *IDDH*134*, and *TPI-3*107*), and all alleles from *GDA**, *bHA**, and *GR** were found to be unreliable and were excluded from data analysis.
- We screened 65 allozyme loci from 48 to 100 fish per collection; 2400 fish were analyzed. Thirty-seven loci with frequencies for alternate alleles ≥ 0.01 in one or more populations and not excluded based on inheritance studies were used for population analyses.
- Haplotype data were collected from the ND5/ND6 region of mtDNA using six restriction enzymes on 40 fish per population for a total of 1000 fish. These enzymes yielded a total of ten haplotypes.
- We analyzed the data for genetic structure by organizing the 20 balanced collections hierarchically to test for homogeneity: among streams, within streams, between timing and between elevation within streams and between timing within elevation and between elevation within timing within streams.
- Significant differences were detected both among streams (allozyme and mtDNA) and within streams (allozyme). These results are consistent with our analysis of 1994 samples where we found significant regional heterogeneity within upstream (allozymes and mtDNA) and tidal (allozymes) collections. However, we found little variation partitioned within streams in the 1996 samples. We found no differences between upstream and tidal collections within streams and only Cabin Creek demonstrated early-late differences. This contrasts with 1994 analyses where we detected significant differences between upstream and tidal collections within Lagoon Creek (allozymes, not sampled in 1996) and within Koppen Creek (mtDNA, sampled in 1996). Samples to test for differences between timings were not collected in 1994.
- The results from the 1994 and 1996 samples support managing native populations of even-year pink salmon in PWS on a regional level, considering local subpopulation structure, rather than as a single panmictic population.

INTRODUCTION

On March 24, 1989, the supertanker *Exxon Valdez* ran aground on Bligh Reef in Prince William Sound (PWS), Alaska, spilling 41 million liters of crude oil. The oil slick, pushed by winds and currents, moved through western PWS and the western Gulf of Alaska, contaminating approximately 2000 km of coastal habitat (see overview in Wells et al. 1995), killing thousands of sea otters *Enhydra lutris* (Garrott et al. 1993; Bodkin and Udevitz 1993) and hundreds of thousands of seabirds (Ford et al. 1991), and adversely affecting many other taxa (e.g., Barber et al. 1995; Bowman et al. 1995; Bowyer et al. 1994; Duffy et al. 1994). Sublethal effects, including reproductive impairment (Ford et al. 1991) and chromosome damage (Hose 1994), were documented. In controlled incubation experiments, oiled substrate resulted in increased mortality of pink salmon *Oncorhynchus gorbuscha* to the eyed stage (Marty et al. 1997). Subsurface oil remained in some of the beaches in spite of the multi-billion dollar clean-up and restoration effort (Wolfe et al. 1994). Populations of some species including pink salmon may not be fully recovered (Craig et al. 1996).

Pink salmon is the most abundant North American species of Pacific salmon (Neave 1967; Heard 1991), making it an ecological cornerstone in biological communities of the Pacific Rim and an economic mainstay for many coastal communities. Pink salmon are both anadromous and semelparous: in their natural range, they make long oceanic migrations, home to their natal streams to spawn, and die at age two. Annual catches of pink salmon ranged from 46 to 128 million fish in Alaska alone during the period from 1985-1996.

Pink salmon, of both wild and hatchery origin, is one of the most abundant vertebrate species inhabiting the spill area. Historically, wild populations produced approximately five-hundred million pink salmon fry which emerged from streams throughout PWS each year to migrate seaward. Adult returns from these juvenile migrations averaged over 10 mil

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Genetics of Populations of Pink Salmon Inhabiting Prince William Sound

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Annual Report

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Abstract:

Allozyme and mitochondrial DNA (mtDNA) data were collected from 4, 34, 16, and 25 putative populations of pink salmon spawning throughout Prince William Sound (PWS) in 1992, 1994, 1995, and 1996, respectively. This annual report focuses on the 1996 samples which were selected to test for differences among streams and differences between timing and elevation within streams. Early and late samples were taken in five streams and upstream and tidal samples were taken in six streams. In addition, one hatchery and two streams were sampled and will be analyzed for the final report where we will test for regional structure of even-year pink salmon in PWS. Sixty-five allozyme loci were screened in up to 100 fish per population. Thirty-seven loci were used for population analyses because they had frequencies for alternate alleles ≥ 0.01 in one or more populations and were not excluded based on inheritance studies. Forty fish per collection were screened for haplotype variation at the ND5/ND6 region using six restriction enzymes; ten haplotypes were detected. Significant differences were detected both among streams (allozyme and mtDNA) and within streams (allozyme). These results are consistent with our analysis of 1994 samples where we found significant regional heterogeneity within upstream (allozymes and mtDNA) and tidal (allozymes) collections. We found no differences between upstream and tidal collections within streams and only one stream demonstrated early-late differences. This contrasts with 1994 analyses where we detected significant differences between upstream and tidal collections within Lagoon Creek (allozymes; not sampled in 1996) and within Koppen Creek (mtDNA; sampled in 1996). These results support managing native populations of pink salmon in PWS at the regional level, considering local subpopulation structure, rather than treating pink salmon as a single panmictic population in PWS.

Key Words: *Oncorhynchus gorbuscha*, pink salmon, stock identification, mtDNA, allozymes, Exxon Valdez, Prince William Sound, genetics

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Pink salmon, of both wild and hatchery origin, is one of the most abundant vertebrate species inhabiting the spill area. Historically, wild populations produced approximately five-hundred million pink salmon fry which emerged from streams throughout PWS each year to migrate seaward. Adult returns from these juvenile migrations averaged over 10 million fish annually. These returning wild-stock adults play a critical role in the total PWS ecosystem by conveying essential nutrients and minerals from the marine ecosystem to estuaries, freshwater streams, and terrestrial ecosystems. Both juveniles and adults are important sources of food for many fishes, birds, and mammals. Wild pink salmon also play a major role in the economy of PWS because of their contribution to commercial, sport, and subsistence fisheries in the area.

As much as 75% of wild pink salmon spawning within PWS occurs in intertidal areas (Helle et al. 1964; Roys 1971). This extensive use of intertidal areas made pink salmon susceptible to adverse effects from the oil spill. Pink salmon embryos and alevins suffered increased mortality, diminished growth, and a high incidence of somatic cellular abnormalities as a result of spawning ground contamination and rearing in oiled areas. Elevated mortality of embryos in the oiled streams continued through 1993, two generations after the oiling, implicating genetic damage (Bue et al. 1998). Also in 1989, the commercial harvest of pink salmon was shifted away from the hatchery and wild stocks in the oiled areas to target the wild stocks in eastern PWS (Geiger and Savikko 1990). This resulted in over-harvest and depletion of these stocks as evidenced by general run failures of eastern PWS populations of non-hatchery origin in 1991 (Geiger and Savikko 1992).

An array of conservation and restoration alternatives has been proposed for "species" impacted by the *Exxon Valdez* oil spill. However, species-based proposals often do not provide the resolution needed to sustain the conservation of genetically diverse aggregates of salmon

populations; it is essential to manage and restore these damaged pink salmon resources on a population basis in order to conserve between-population diversity (e.g., Cuenco et al. 1993; Waples 1995). Between-population diversity provides optimal production for species inhabiting diverse ecosystems such as PWS; highly diverse population mixes also provide a biological buffer to environmental change such as droughts, floods, major earthquakes, major shifts in oceanic conditions, and other catastrophic events that occur in Pacific Rim ecosystems. Our goal was to examine naturally occurring genetic markers to delineate the population structure of PWS pink salmon and to provide a genetic basis for fishery management and restoration programs.

A number of life history characteristics of pink salmon in PWS and environmental factors suggest that between-population genetic diversity could exist both temporally and spatially. Temporal differences in life history exist in both the timing of returns among regions within the Sound and within some streams. Fish return earliest in the northeast portion of PWS and later in the southwestern portion (Rugolo 1984). Within some streams, the numbers of fish entering over time is bimodally distributed (Helle et al. 1964; Wilcock, ADF&G Cordova per. com.) while the distribution is unimodal in others (Wilcock, ADF&G Cordova pers. com.). Spatial differences in the environment can be observed in the upstream and intertidal zones. Helle et al. (1964) found salt concentrations up to 9ppt at redd depths at the 11-foot tide level and temperature swings of 10°F within one hour at redd depths at the 8-foot tide level, well within the intertidal spawning areas of pink salmon. Upstream redds are not subject to these conditions. Lastly, pink salmon generally home to their natal streams. Selection for homing behavior can be explained by higher spawning success in natal streams than in non-natal streams. These differential success rates may be due to selection for individuals adapted to the conditions of their natal streams. For example, one condition that varies from stream to stream and region to region within the Sound is the temperature regime which is influenced by water source (glacier or rain) and stream length (Royce 1962; Sheridan 1962). This study was initiated because biological data raised questions about the genetic structure of pink salmon in PWS. Alternatively, these life history characteristics could also be the result of environmental factors, and pink salmon in PWS are actually composed of one panmictic population.

Our objective was to test for both temporal and geographical genetic structuring among even- and odd-year classes by examining genetic differences between early- and late-season spawners, upstream and intertidal spawners, and stream-of-spawning. Additionally, genetic positioning of the local hatchery stocks within this structure was of interest because the extensive releases of pink salmon fry in PWS in recent decades may have affected the partitioning of naturally occurring genetic diversity. Some fear that hatchery production may pose as much or more of a threat to native populations as the oil spill (see discussion in Gharrett and Smoker 1993).

Another important consideration is the fact that even- and odd-year classes have independent population structures because of the rigid two-year life cycle of pink salmon. For example, climactic, tectonic or other such events (such as the 1964 earthquake [Roys 1971] or the 1989 oil spill) may affect the population structure of one year class and cycle through subsequent generations, yet leave the alternate cycle of year-classes relatively unchanged. Therefore, population structure and conservation strategies must be independently assessed for the even- and odd-year classes.

Two categories of molecular markers have been used extensively to define population structure of salmonids: allozymes and mitochondrial DNA (mtDNA). Allozyme analysis remains

the preferred approach for study of population genetics of salmonids because of its power to resolve populations of many species in the tetraploid-derived family by assaying many nuclear loci rapidly and at low cost (Allendorf 1994). An additional advantage of allozymes is that many laboratories cooperate on inter-institutional examinations of pink salmon using this method, providing a support structure and a wealth of compatible data for potential comparisons among Pacific Rim populations (e.g., Seeb and Wishard 1977; Utter et al. 1980; Beacham et al. 1985, 1988; Gharrett et al. 1988; Shaklee et al. 1991; White and Shaklee 1991; Shaklee and Varnavskaya 1994).

The utility of the mtDNA approach to study genetic diversity of salmonid populations is controversial for reasons such as its relatively high cost and slow throughput (Allendorf 1994). Additionally, sometimes mtDNA data reveal less diversity than that detected through allozymes because mtDNA does not recombine and is maternally inherited as a single locus so that variation is absolutely linked (Smouse et al. 1994). However, haplotype data from PWS collections made in 1994 (Seeb et al. 1996) detected differences in one upstream-tidal comparison not detected with allozymes. We believed that the complementary use of the two techniques would provide optimal resolution of the population structure for this study.

Unlike mtDNA variation where banding patterns lead to unambiguous haplotypes, novel allozyme variation can be difficult to interpret. Therefore, in addition to collecting allozyme data from field collections, it is important to conduct experimental matings to verify the genetic basis of isozyme variation for putative allelic polymorphisms that are untested in pink salmon. In the examination of the 1994 collections, we identified numerous isozyme polymorphisms that were previously undescribed. The recently tetraploidized salmonids often express an abundance of isozymes from the duplicated loci, and new alleles can initially be difficult to score (cf., Marsden et al. 1987). Difficulty can arise in distinguishing among cryptic variation, single-locus variation from isolocus pairs, and phenotypic variation with a non-genetic basis. The genetic basis and state of duplication for these newly-found polymorphisms must be confirmed before they are incorporated into population structure analyses (e.g., see May et al. 1975; Seeb and Seeb 1986).

This annual report focuses on testing inheritance of new allozyme alleles and on the 1996 samples which were selected to test for differences among streams and differences between timing and elevation within streams. Allele frequencies from two stream collections and one hatchery collection made in 1996 are included in this report but were not analyzed because they did not contain upstream-tidal or early-late comparisons. These collections will be analyzed in the final report investigating regional and inter-annual variation in pink salmon. We assayed a total of 2400 individuals from 25 collections for variation at 65 allozyme loci and a subset of 40 individuals from each collection for variation at the ND5/ND6 region of mtDNA. We found genetic structuring among streams and between early and late collections from one creek.

OBJECTIVES

Our project objective is to define the genetic structure of pink salmon stocks in the EVOS-affected area of PWS. In this multi-year project we will test for:

1. genetic differences between spawners from the five primary management regions within PWS (Southeast, East, North, Southwest, Montague).

2. genetic differences between spawners from different streams within PWS.
3. genetic differences between upstream and intertidal spawners within the same streams.
4. genetic relationships between hatcheries and native populations.
5. genetic differences between temporally isolated spawners within the same streams.
6. genetic differences between odd- and even-year pink lineages.
7. inheritance of newly detected isozyme variants and loci.

In this report, we review the results for the 1995 and 1996 single-pair matings and the 1996 collections and address objectives 2, 3, 5, and 7. We addressed objectives 1, 2, 3, and 4 in even-year cohorts with the 1994 collections. We addressed objectives 2, 3, and 5 in odd-year cohorts with the 1995 collections. Samples to address objectives 1 and 4 in odd-year cohorts were collected in 1997. The study is ongoing, and objective 6 will be addressed in the final report.

METHODS

Inheritance Study

Single-pair matings were performed in 1995 and 1996 to confirm the genetic basis of novel variation observed in putative allozyme alleles detected in the population study. Eggs and milt from were taken from pink salmon returning to Armin F. Koernig Hatchery (AFK) in 1995 and from Solomon Gulch Hatchery (VFDA) in 1996. In each year, eggs from 100 females were placed in dry reclosable 4-L bags, and milt from 50 males was extracted into 50ml capped centrifuge tubes. Gametes were held on wet ice until matings were performed. Parental tissue samples from heart, liver, muscle, and vitreous humor from each parent were cross-referenced to their corresponding gametes, immediately frozen on dry ice, and stored at -80°C.

In 1995, we performed experimental matings and incubated eggs in two locations, AFK and Anchorage ADF&G Genetics Laboratory, to guard against catastrophic loss. At AFK we performed 12 single-pair matings and incubated them through egg yolk absorption in Heath trays in family lots. Fry from five families with at least 200 surviving fry were individually packaged into 4-L reclosable bags and shipped to Anchorage for rearing. For matings made at ADF&G Genetics Laboratory, gametes were shipped on wet ice from AFK to Anchorage. At the laboratory, AFK parents were assayed for variation at the following allozyme loci to identify the most useful single-pair matings to perform: *AK**; *sAAT-3**; *FH**; *G3PDH-1**; *G3PDH-2**; *G3PDH-3**; *bGALA**; *bHA**; *GAPDH-2**; *GDA**; *IDDH**; *sMDH-A1,2**; *sMDH-B1,2**; *mSOD**; and *sSOD-2** (see Table 1 for tissue/buffer combinations). Seventeen single-pair matings were performed, and embryos were incubated in Heath trays through egg yolk absorption.

In 1996, we shipped the gametes on wet ice from VFDA to Anchorage. We chose the best gametes to perform the 18 single-pair matings from VFDA parents. Grading criteria for eggs included the number of eggs available and presence of blood and broken eggs. Grading criteria for milt included quantity available, viscosity, and presence of blood and feces. Eggs were incubated through hatch.

During the incubation period in both 1995 and 1996, parents from all families were screened for all allozyme loci used in the population study to identify families with the most polymorphic alleles. Allozyme screening was done using the same methods as were used for the population study (see below). Due to limited rearing space, only those families whose parents contained the most polymorphic loci were reared in 20-L circular tanks until they were on feed (approximately one month). Eighteen families from the 1995 matings were then shipped to Fort Richardson Hatchery where they were raised by family in 70-L tanks to approximately 60mm total length. Eight families from the 1996 matings were reared to approximately 50mm total length in the 20-L tanks in the Anchorage Genetics laboratory. Of these, the most polymorphic eleven families from the 1995 matings and the most polymorphic six families from the 1996 matings were chosen for analysis. Tissues were dissected from up to 100 progeny from each family, placed in -80°C for storage, and analyzed for polymorphic loci. Genetic data were collected using the techniques of allozyme electrophoresis on all samples (Aebersold et al. 1987; Seeb et al. 1996). Nomenclature followed the American Fisheries Society standard (Shaklee et al. 1990).

Chi-squared tests were performed based on expected Mendelian ratios and observed genotype counts from progeny. Rejection criteria were set at an overall level of 0.05 and were adjusted for multiple tests within loci (Rice 1989).

Field Sampling – Population Structure

Tissues were collected from 48 to 100 individuals from each of 24 spawning aggregations from wild-stock streams and one hatchery in 1996 (Table 2; Figure 1). Sampling was designed to investigate early-late and upstream-tidal differences within streams. Primary consideration was given to the sampling of tributaries that routinely support large runs of fish on both even and odd years. The limited number of streams sampled did not allow for regional comparisons (Figure 1), however these collections will be used in combination with 1994 collections to make regional comparisons within even-year cohorts in the final report.

We chose five streams (Cabin, Mink, Meachum, Koppen, and Constantine) and sampled early in the spawning season (July 31 - August 11) and late in the spawning season (September 4 - 11) (Table 2) to test for temporal restrictions to gene flow within streams.

Finally, although a majority of pink salmon spawning in PWS occurs in areas of tidal influence, some larger tributaries also possess somewhat discrete aggregations that spawn in upstream areas above the influence of tides. Samples were collected from both tidal and upstream sites from six of these creeks (Mink, Paulson, Meachum, Koppen, Bernard, and Constantine) (Table 2; Figure 1). Hanning and Makaka Creeks were sampled to investigate regional comparisons and will be analyzed for inter-annual even-year variation in the final report. We also sampled Solomon Gulch Hatchery, and we will also analyze these samples in the final report to determine how hatcheries are related to wild populations.

Tissue samples from heart, liver, muscle, and vitreous humor from each individual were immediately frozen on dry ice and returned to Anchorage for storage at -80°C.

Allozyme Analysis

Genetic data were collected using the techniques of allozyme electrophoresis on all samples (Aebersold et al. 1987; Seeb et al. 1996). An extensive screening for resolution of allozyme phenotypes on 45 individuals collected in Erb Creek and Humpback Creek in 1991 and 1994 detected 77 putative loci in pink salmon within PWS (Seeb et al. 1996). Twelve loci were not screened in 1996. Those dropped due to poor resolution include *GAPDH-3**, *SIDHP-1**, *aMAN**, *NTP**, *PEPB-2**, and *PEPD-1**. The loci *ESTD**, *GAPDH-4**, *GAPDH-5**, *bHA**, *mMDH-1** were dropped due to lack of polymorphisms in the 1994 collections. Finally, *mMDH-2,3** was screened as a single locus (*mMDH-2**) rather than an isolocus (J. B. Shaklee, Washington Department of Fisheries, Olympia, pers. com.). The remaining 65 loci were screened for genetic variation in all 1996 collections except for the late Cabin Creek collection where no heart samples were available (Table 1). Nomenclature followed the American Fisheries Society standard (Shaklee et al. 1990).

Alleles present at frequencies above 0.01 in one or more collections and alleles that met inheritance criteria (see below) were used for data analysis. Alleles not meeting the minimum frequency criteria were pooled with the **100* allele to reduce statistical noise, thereby increasing our power to detect genetic structuring (see Shaklee and Varnavskaya 1994).

Individual genotypic data were summarized into allelic frequencies. For isoloci (*sMDH-A1,2**; *sMDH-B1,2**), allele frequencies were calculated using a multinomial model assuming independence of alleles at both loci. Tests for departure from Hardy-Weinberg were made using log-likelihood tests (Weir 1996) with the experimentwise significance level set at 0.05 and adjusted for multiple tests (Rice 1989). Observed and expected heterozygosities were computed using the reduced set of loci. Paired *t*-tests were used to test for differences in heterozygosities between upstream and tidal collections and early and late collections. Computations were performed using *S-plus* analytical software (Mathsoft, Inc., Seattle WA).

Hierarchical analyses using log-likelihood ratios to test for homogeneity within and among groups of pink salmon collections (modified from Smouse and Ward 1978) were performed using *S-plus*. We wanted to test both for differences between elevation within streams and within timing and differences between timing within streams and within elevation, therefore we used a dual hierarchy: a and b. The collections were organized hierarchically to test for homogeneity: 1) among and within all streams, 2) among all collections within streams, 3a) between early and late collections within streams, 3b) between tidal and upstream collections within streams, 4a) between early and late collections within elevation (tidal-upstream) within streams, and 4b) between tidal and upstream collection within timing (early-late) within streams. For the hierarchical analysis, if an allele was observed in a collection, we assumed that it existed within all collections, potentially at an infinitely small frequency. Therefore, the degrees of freedom and log-likelihood statistics are summable, and differences among and within collection subdivisions can be examined.

For the hierarchical analysis, comparisonwise significance levels were adjusted for multiple tests using a sequential Bonferroni adjustment (modified from Miliken and Johnson 1984 and Rice 1989) with the overall experimentwise significance level set at 0.05. The first step in the analysis was a sequentially adjusted test for differences at the first hierarchical level, i.e., between streams and within streams. If a significant difference was found within streams, then a

sequentially adjusted test was applied at the next level. Testing proceeded in this way through the hierarchy. If a test was not significant, then all remaining lower levels were combined, and a final sequentially adjusted multiple test of significance was performed.

For this report, we analyzed only those collections that were paired with either another elevation or another timing or both and excluded remaining collections. We analyzed the Cabin Creek collections separately because the late collection was missing data from loci expressed only in heart (heart samples were lost). For the Cabin Creek collections, we computed pairwise G-statistics using *S-plus*.

Two gene diversity analyses (Nei 1973) were performed using *S-plus*. The objective of these analyses was to determine the proportion of variation partitioned into each hierarchical level. The first analysis investigated diversity among elevations, then streams. The second analysis partitioned diversity by timing then streams. Isoloci were excluded.

In order to determine if the among collection components of variation were significant, F_{st} values were calculated and tested for significance per Weir and Cockerham (1984) using the FSTAT analysis program (Goudet 1995). Again, isoloci were excluded.

We investigated genetic similarities through multidimensional scaling (MDS, Lessa 1990) of Cavalli-Sforza and Edwards (1967) genetic distances. This ordination technique plots populations in multiple dimensions so that the plotted distances between collections closely match the observed distances in multidimensional space. Genetic distances were calculated using *S-plus* and the MDS was done using NTSYS (Version 1.80, Exeter software, Setauket, NY).

Mitochondrial DNA Analysis

A subset of 40 individuals from each of the 25 collections was assayed for variation at sites previously identified in the ND5/ND6 region (Fetzner et al. *submitted*). Genomic DNA was extracted using Puregene DNA isolation kits for animal tissues (Gentra Systems, Inc. P.O. Box 13159, Research Triangle, NC 27709-13159). This process included: 1) a cell lysis solution to break down cell and nuclear membranes; 2) a Proteinase K digest to denature proteins; 3) an RNase treatment to digest RNA; 4) protein precipitation to remove Proteinase K, RNase, and denatured proteins; 5) isopropanol to precipitate DNA; 6) 70% ethanol to wash DNA; and finally 7) a hydration solution to rehydrate DNA.

After extraction, DNA was amplified using the polymerase chain reaction. Amplified DNA was cut with six restriction enzymes found to detect haplotype polymorphisms (of the 30 screened in Fetzner et al. [*submitted*]; *Apa I*, *BstUI*, *EcoR V*, *Hinf I*, *Rsa I*, *Xba I*) and electrophoresed on agarose gels. Fragments were visualized under UV light, and a photographic record was made of each gel. The restriction sites detected for each enzyme were pooled as composite haplotypes for the statistical analyses.

Nucleotide (π) and haplotype (h) diversity measures (Nei 1987) were calculated for all collections using the restriction enzyme analysis package (*REAP*; McElroy et al. 1992). These measures estimate the number of nucleotide substitutions per site between DNA sequences (i.e., sequence divergence) and the amount of DNA polymorphism within collections, respectively. Analysis of variance (ANOVA) was used to determine if there was a significant correlation between allozyme heterozygosity and nucleotide and haplotype diversities.

For among collection variation, we again only used those collections that were paired with either another elevation or another timing or both and excluded remaining collections.

Nucleotide divergence among collections were calculated and used to derive an MDS plot. To test for heterogeneity among populations, Monte Carlo simulations with 10,000 replicates were performed (Roff and Bentzen 1989). To keep the mtDNA analysis comparable with the allozyme analysis, Cabin Creek collections were analyzed separately. Independent tests were performed to test for heterogeneity in a hierarchical manner following the levels identified in the log-likelihood analysis of the allozyme data. However, unlike the log-likelihood analysis, the χ^2 values for individual tests are not summable. Significance levels for multiple tests were adjusted using sequential Bonferroni techniques (Rice 1989). These analyses were made using the REAP analysis program.

An analysis of the distribution of molecular variance among the remaining qualifying collections was made using the AMOVA procedure in Arlequin (Excoffier et al. 1992, Schneider et al. 1997) and utilizing a matrix of Euclidean distances. Pairwise Euclidean distances were calculated as the total number of site changes between haplotypes. The AMOVA analysis calculates haplotypic diversity at different hierarchical levels. Haplotype correlation measures are expressed as Φ -statistics (Excoffier et al. 1992). Among elevations, Φ_{CT} is defined as the correlation of random haplotypes within the group of collections within elevation relative to that of random pairs of haplotypes drawn from the entire set of collections. For the analysis among collections within elevations, Φ_{SC} is the correlation of random haplotypes within collections relative to that of random pairs of haplotypes from the elevations. Finally for the within-collection analysis, Φ_{ST} is the correlation of random haplotypes within collections relative to that of random pairs of haplotypes drawn from the entire set of collections. The AMOVA analysis allows for only a two-level hierarchy, so we were unable to partition timings within elevations as in the preceding analyses. Rather, we performed two separate analyses, one based on elevation and one based on timing. The significance of the observed variance components and Φ -statistics were tested using a random permutation procedure in AMOVA. The permutation approach to significance testing avoids the parametric assumptions of normality and independence that are not met by molecular distance measures (Excoffier et al. 1992). The number of permutations was set at 1023 for each analysis.

RESULTS

Inheritance Study

We tested 71 alleles from 31 loci (Table 3) using chi-squared tests on expected Mendelian ratios and observed genotype counts from progeny of single-pair matings. Of these, the following alleles were expressed in progeny as would be expected under Mendelian inheritance: *sAAT-3*91*; *sAAT-4*210*; *sAAT-4*290*; *sAAT-4*-10*; *ADA-2*110*; *ADA-2*90*; *sAH*115*; *AK*-145*; *CK-A2*82*; *CK-C2*105*; *FDHG*132*; *FH*136*; *FH*45*; *G3PDH-1*60*; *G3PDH-2*120*; *G3PDH-2*90*; *bGALA*91*; *GPI-B1,2*200*; *sIDHP-2*125*; *sIDHP-2*134*; *sMDH-A1,2*50*; *sMDH-B1,2*129*; *sMDHB-1,2*63*; *mMEP-1*123*; *mMEP-2*70*; *PEPB-1*138*; *PEPB-1*200*; *PEPD-2*120*; *PEPD-2*80*; *PEPLT*108*; *PGDH*96*; *PGDH*86*; *mSOD*32* and all common alleles from these loci (Table 4). Alleles that did not produce expected genotype counts in at least one family were: *GDA*100*; *GDA*130/108*; *GDA*155/113*; *GDA*189/118*; *GDA*167/115*;

*GDA*222/123; bGALA*111; bHA*100; bHA*200; GR*114; IDDH*134; TPI-3*107* (Table 4). These alleles (or loci) were excluded from the analyses.

Allozymes

Variation and heterozygosity

Variation was detected at 79% (48/61) of the allozyme loci not excluded through the inheritance study (loci excluded: *bGALA**, *GDA**, *GR* and *IDDH**). Eleven polymorphic loci (Appendix A) and 13 monomorphic loci were dropped because alleles were present at frequencies below 0.01 in all collections. The screening also yielded 34 rare alleles (<0.01 in each collection) which were excluded from analyses. The remaining thirty-seven loci in the 1996 data set (*mAAT-1**; *sAAT-1,2**; *sAAT-3**; *sAAT-4**; *ADA-1**; *ADA-2**; *MAH-2**; *MAH-4**; *CK-A2**; *CK-C1**; *CK-C2**; *FDHG**; *GAPDH-2**; *G3PDH-1**; *G3PDH-2**; *G3PDH-3**; *GPI-B1,2**; *mIDHP-1**; *sIDHP-2**; *LDH-B1*; *LDH-B2*; *sMDH-A1,2**; *sMDH-B1,2**; *mMEP-1**; *PEPA**; *PEPB-1**; *PEPD-2**; *PEPLT**; *PGDH**; *PGM-2**; *mSOD**; *sSOD1*; *TPI-2**) met our minimum frequency criteria and did not fail the inheritance tests. In contrast to data analysis of 1994 collections, we excluded *sAH**, *MAH-3**, *bGALA**, *G3PDH-1**, *GDA**, *sIDDH**, *LDH-A2**, *NTP**, *bHA**, and *LDH-A2** and included *MAH-2**, *CK-C1**, *CK-C2**, *GAPDH-2**, *LDH-B1**, and *PEPA** in 1996 data analysis based on the same criteria and the results from the inheritance study.

Observed heterozygosities based on 37 loci varied over a relatively narrow range (mean 0.092, range 0.0723 to 0.1036; Table 5). No significant differences in heterozygosities were observed using paired *t*-tests between tidal and upstream (mean tidal = 0.092, mean upstream = 0.092, *t* = 0.386, *df* = 22, *P* = 0.885) or early and late (mean early = 0.091, mean late = 0.092, *t* = 0.453, *df* = 10, *P* = 0.764) collections.

Hardy-Weinberg expectations

Genotypic frequencies were tested for departures from Hardy-Weinberg (H-W) expectations. No collection had an overall deviation from H-W. We made 671 tests, of which 8 were significant when comparisonwise significance level was set to 0.05, well within the range of positive results expected. The significant deviations were spread over six loci, and no locus deviated from H-W in more than two collections. The only highly significant test was for *PGDH** in the Koppen early, upstream collection, where we observed two *PGDH*86/86* homozygotes and only four heterozygotes with the *86 allele.

G-test of population differentiation for Cabin Creek

The G-statistic test between the early and late collections from Cabin Creek was significant (*G* = 59.9, *df* = 27, *P* = 0.0003). Loci that had the significant allele frequency differences between the two collections, in order of significance, were: *ADA-2**, *sIDHP-2**, *sAAT-3**, *GPI-B1,2**, and *LDH-B2**.

Hierarchical analysis using log-likelihood ratios

The hierarchical analysis using log-likelihood ratios detected highly significant differences among streams ($P < 0.0001$), and significant differences within streams ($P = 0.027$; Table 6; Appendix B). However, when we tested for differences between elevation and timing within each stream, we did not detect any differences.

MDS analysis

The MDS analysis portrayed a result similar to that obtained in the hierarchical analysis (Figure 2). Some stream-to-stream structuring is apparent from the plot. The collections from Constantine cluster on the left portion of the plot, Meachum collections cluster on the upper-right portion, and Paulson on the forward-right portion of the plot. There does not appear to be any clustering of collections by timing or elevation. Cavalli-Sforza and Edwards chord distances between collections ranged from 0.030 to 0.058.

Gene diversity analysis

We performed two hierarchical gene diversity analyses excluding isoloci. The first hierarchical analysis was stratified by collection, elevation, and stream. The second hierarchical analysis was stratified by collection, timing, and stream. By far the majority of the variation (99.39%) occurred within collections (Tables 7 and 8). In the first analysis the remaining heterogeneity was divided among collections within elevations (0.26%), between elevations within streams (0.17%), and among streams (0.19%). In the second analysis heterogeneity was divided among collections within timing (0.26%), between timing within streams (0.16%), and among streams (0.19%).

Although most of the variation observed was within collections, the among collection components were significant (overall F_{st} was significantly different from zero, $P = 0.002$). Loci most indicative of the lack of panmixia ($P = 0.001$) were *mAAT-1**, *G3PDH-2**, and *PEPLT**.

Mitochondrial DNA

Forty individuals from each of the 25 collections were examined for variation at ND5/ND6 using six restriction enzymes previously identified to reveal polymorphisms in pink salmon (Table 9). Ten unique haplotypes were defined from 960 individuals detected with the six restriction enzymes tested (Table 10). Five of the haplotypes (VI, VII, XX, XXI, and XXIII) had overall frequencies less than 0.01 (nine or fewer individuals observed within all populations combined). The two rarest haplotypes, XX and XXI, were observed only once each. In contrast to analysis of 1994 samples, we did not detect haplotype XV (ACBAAA; detected once in 1994) but we did detect one each of haplotypes XX and XXI and three haplotype XXIII's which were not observed in 1994 collections.

Haplotype and nucleotide diversity

Haplotype diversity (h) ranged from 0.0975 in Koppen Creek early, upstream, to 0.6215 in Constantine Creek late, tidal, and averaged 0.377 (Table 10). Nucleotide diversity values (π) ranged from 0.0011 in Koppen Creek early, upstream, to 0.0092 in Meachum Creek late, upstream, and averaged 0.0049. In paired t-tests, significant differences between timings were found for both h ($t = 0.974$, $df = 16$, $P = 0.033$) and π ($t = 0.978$, $df = 16$, $P = 0.028$) with lower values in the early collections compared with late collections ($h = 0.321$ early, 0.439 late; $\pi = 0.0039$ early, 0.0060 late). No such differences were detected between elevations (h : $t = 0.337$, $df = 18$, $P = 0.739$; π : $t = 0.579$, $df = 18$, $P = 0.579$). No correlation between allozyme heterozygosity and haplotype diversity or nucleotide diversity was found ($F = 0.043 - 0.052$, $df = 24$, $P = 0.82 - 0.84$)

Heterogeneity detected by Monte Carlo tests

A Monte Carlo test among all collections did not yield a significant test statistic (Table 6). No within stream tests were significant (within stream tidal vs upstream collection or early vs late collections) indicating overall homogeneity in haplotype frequencies within and among streams. No differences were detected between the early and late collections from Cabin Creek ($P = 0.70$).

AMOVA analyses

An AMOVA analysis that partitioned the molecular variation by elevation and by timing was also performed. Again, the majority of the variation in both analyses (98.2% for analysis by elevation and 97.6% for analysis by timing) was within collections (Table 11). The variance component for within collections was significant for both analyses (Table 11). No other variance components were more extreme than expected by chance alone.

Genetic similarities among collections

An MDS plot was generated using nucleotide divergence among collections (Figure 3). Consistent with the AMOVA and hierarchical Monte-Carlo analyses, no patterns for timing or elevation were evident in the MDS plot. We also did not see any clustering of streams, indicating that the significant “within collections” components of the AMOVAs were not due to systematic differences among streams.

DISCUSSION

Understanding the genetic structure of Pacific salmon populations is critical to their management and conservation. For example, managing on too fine a scale may adversely affect the fishing industry and waste management resources, while managing on too large a scale may result in loss of genetic adaptations and diversity (see Mundy et al. 1993). Here we report our findings in an examination of the 1996 even-year lineage of populations of pink salmon that inhabit PWS, Alaska.

Inferences from studies showing genetic homogeneity for allozymes over vast geographic distances (e.g., Shaklee and Varnavskaya 1994) lead some to suggest that pink salmon populations within PWS, spanning only 100 kilometers, should be genetically homogenous. In contrast, implications from other allozyme studies (Lane et al. 1990) suggest that pink salmon populations in PWS might be substantially heterogeneous. Our objective was to generate molecular genetic data to support or reject these alternatives.

Three recent and major factors have impacted these populations. The *Exxon Valdez* oil spill of 1989 adversely affected pink salmon through a combination of direct lethal effects, sublethal effects, and alterations in fishing pressure (Bue et al. 1996). Further, the major tectonic upheaval of 1964 produced bottlenecks in some populations. However, arguably one of the most serious factors influencing population structure may be deleterious effects of hatchery/wild-stock interactions and the potential erosion of locally adapted genotypes (Gharrett and Smoker 1993). PWS is the center of one of the world's largest aquacultural industries. Six-hundred million pink salmon fry of hatchery origin are released annually. Alaska Department of Fish and Game has been grappling with management of the wild populations in face of intractable hatchery/wild-stock interactions for nearly a decade. The *Exxon Valdez* oil spill-related damage to wild populations, coupled with full-scale hatchery egg takes, exacerbated wild-stock conservation concerns.

Despite all the forces potentially inducing pink salmon in PWS to stray, barriers to gene flow were detected among collections in 1996 as they were detected in 1995 (Habicht et al. 1998) and 1994 (Seeb et al. 1997) collections. The differences in allele frequencies, although small relative to those found in other species (e.g. sockeye; Seeb et al. 1996), were unlikely due to Type II error. The *P*-value calculated in the hierarchical analysis, a conservative analysis because all alleles observed are assumed to exist in all collections thereby inflating the degrees of freedom, for among 1996 streams was less than 0.001. Further, genetic distances were within the range considered biologically significant for pink salmon (Shaklee and Varnavskaya 1994). Shaklee and Varnavskaya (1994) argued that pink salmon populations from the Pacific coast of Russia represent those that evolved *in situ* because of the lack of anthropomorphic activities except harvest (no hatcheries or stock transfers). Using identical methods to ours, the genetic distances they found among populations up to 3,000 ocean km apart (0.040 to 0.055) were similar to the distances we detected among the collections within PWS no more than 70 ocean km apart (0.030 to 0.058). Shaklee and Varnavskaya (1994) concluded that the Russian collections are not part of a single, panmictic stock based on slight, but significant heterogeneity in allelic composition among the eight Russian collections.

In addition, the pattern of genetic relationships detected among our collections is consistent with biological observations. Significant differences among streams revealed by allozymes (Table 6) are consistent with biological data that indicate that pink salmon generally home to their natal streams (Helle et al. 1964). Another indication that spawners from different streams are genetically different is the variation in timing of returns to different creeks within the Sound. For example, fish spawning in the eastern region enter the Sound and eastern streams earlier than fish spawning in the southwestern region enter the Sound and spawn in southwestern streams. Even within regions, run timing can vary substantially between nearby streams. For example, even-year fish numbers in Koppen Creek peak during the first week in August, while fish numbers in Allen Creek peak four weeks later (J. Wilcock ADF&G unpublished data). These two creeks are both located within the same bay.

In odd-year pink salmon we found genetic differentiation between early and late spawners in two of the three creeks tested (Koppen and Olsen). During odd years, both of these creeks have bimodal distributions in the number of fish in the streams over time. By contrast, Koppen Creek has a unimodal distribution during even years, as do the other streams in which we investigated temporal separation in this study (Cabin, Constantine, Mink, and Meachum). Therefore, the biological data might predict lack of separation between early and late fish within these creeks. This was true for all creeks with mtDNA data and all except Cabin Creek with allozyme data. Other creeks within the Sound such as Chase Creek, Beartrap River, Olsen Creek, Harrison Lagoon, Pablo Creek, and Halverson Creek have bimodal distributions in even years, and may therefore have distinct early and late runs (J. Wilcock ADF&G unpublished data).

We excluded the early and late Cabin Creek collections in the hierarchical analysis because the late collection was missing loci expressed only in heart tissue. The allozyme G-statistic test between early and late collections from Cabin Creek was significant, but the mtDNA exact test of population differentiation was not. The G-statistic was significant even after adjusting the critical value for the nine early-late comparisons possible within streams and timings. Cabin Creek may be an example of a system with early and late spawners that could be missed if the cumulative run-timing data was relied on solely. Cumulative run-timing data may not identify all systems that have distinct early and late spawners if run timing varies from year to year and the timing differences between early and late spawners is small. In such systems, shifting bimodal peaks could result in a cumulative unimodal peak if the early and late peaks overlap across years (e.g. early fish in a late year come in during the same calendar week and late fish from an early year). Mean timing of return varies from year to year as a result of climactic conditions.

Although we did not find any difference with mtDNA data between early and late fish in Cabin Creek with the Mote Carlo simulations or the hierarchical AMOVA, we did find higher levels of haplotype diversity and nucleotide diversity in the late collections relative to the early collections. This phenomena could be explained in two ways. First we may have a type two error (P -values = 0.028 to 0.033) or we may have mixed samples (early and late) in the late collection. If there are restrictions to gene flow between early and late collections and our early collections are pure, but our late collections contain both early and late fish, we might expect these results. The mixed samples in the late collections would cloud the differences between early and late collections leading to our inability to detect them in our tests for restrictions to gene flow, while increasing the number of haplotypes present in the late collections. Collecting mixed samples in the late collection is highly possible, because females guard their nests after they have spawned and may have been sampled along with late-spawning fish. The allozyme data do not show an increase in heterozygosity between early and late collections. However, heterozygosity would not be expected to increase in a mixed sample, it would simply be the average heterozygosity of the mixture components.

We did not to detect any significant differences in mtDNA haplotype frequencies among streams in the 1996 collections or between early and late collections within Cabin Creek as were detected with allozymes. This inability of mtDNA data to distinguish among collections when allozyme data do is similar to our results from 1995 collections where mtDNA was unable to distinguish between early and late spawning collections while allozymes were able to detect differences (Habicht et al. 1998). These results were unexpected because mtDNA is maternally inherited and therefore has a smaller effective population size leading to higher genetic drift than allozymes (Avice and Vrijenhoek 1987). Further, mtDNA lacks repair mechanisms (Wilson et al.

1985) present in nuclear DNA resulting in faster mutation rates than allozymes. Finally, mtDNA can detect barriers to gene flow in cases where only males stray which would be missed by nuclear markers (Melnick and Hoelzer 1992). Three hypotheses might explain our inability to detect differences with mtDNA when they were detectable using allozymes: higher straying rates in females than in males, bottlenecks or extinctions and recolonizations, or lack of statistical power. Higher straying rates in females could homogenize mtDNA allele frequencies because of strict maternal inheritance, while allozyme heterogeneity might be maintained if males stray little (Allendorf 1994). However, evidence from coded-wire tag data indicates that straying rates of pink salmon in PWS is similar for males and females (Habicht, unpublished data). Other studies have observed low mtDNA variation in populations with high allozyme variation and have attributed these results to historical bottlenecks or extinction and subsequent recolonizations (reviewed in Allendorf 1994). MtDNA haplotypes in this study were variable; we found ten haplotypes of which three had frequencies greater than 5% (Table 10). Lastly, the lack of significant tests in the mtDNA data analysis could be due to reduced statistical power resulting from the lower allele counts observed per population using mtDNA, a single locus. We analyzed 40 fish per population for mtDNA data which translates to 40 allele counts per population; conversely, we analyzed 48 to 100 fish per population using allozymes which translates to 96 to 200 allele counts per locus, with 37 different loci analyzed. When we increased the number of samples analyzed from the 1994 samples from 40 to 100 in three collections, two of the three pair-wise comparisons that were previously insignificant became significant (P -values changed from 0.0490 to 0.0039, 0.0292 to 0.0135, and 0.0155 to 0.0033: critical values adjusted for multiple tests = 0.005) (Habicht et al. 1998).

The 1996 collections do not demonstrate any restrictions to gene flow between intertidal and upstream spawners. The lack of differences between tidal and upstream collections in 1996 contrasts somewhat with our results from pink salmon collected in 1994 (Seeb et al. 1996). In 1994 collections, differences were detected between tidal and upstream collections using both the allozyme (Lagoon Creek; not tested in 1996) and mtDNA (Koppen Creek; tested in 1996) data sets. Interestingly, the upstream collections made in 1996 were done further upstream than the collections made in 1994 when they were made just above the high tide zone. Where differences were detected in 1994, they were large (the upstream collections were the most dispersed in the MDS analyses). However, four of the five upstream-tidal comparisons made in 1994 and all six comparisons made in 1996 were not significant within each data set. We did not detect differences with mtDNA in Koppen Creek in 1996 ($P = 0.050$) as were detected in 1994 ($P = 0.002$) indicating that if there are differences here, they are not very robust. However, when data from both years are pooled, we did detect significant differences between upstream and tidal collections at Koppen Creek ($P = 0.005$). The frequency of the II haplotype was higher in the tidal collections in both years (1994: 20% tidal, 0% upstream; 1996: 15% tidal, 5% upstream).

From the even-year data we might conclude that restricted gene flow between tidal and upstream fish appears in few streams. Two assumptions of this conclusion are that we sampled representative streams within the Sound and that the fish collected in tidal and upstream sections were indeed spawning there. The first assumption seems reasonable as we have collections from tidal and upstream reaches from streams in all regions with relatively long streams (north, east, and southeast regions). The second assumption is more difficult because fish destined for upstream spawning must pass through the tidal zone before spawning and drift through the tidal zone after spawning as they are flushed from the stream. Although we tried to collect fish that

appeared to be on their spawning grounds, it was difficult, using seines, to select specific individuals. Natural otolith marks may provide a way to separate tidally reared from non-tidally reared pink salmon because tidally reared embryos would be subjected to large and uniform temperature fluctuations as tidal water warms the incubation substrate every six hours (Helle 1964) which might leave systematic marks in the otoliths (T. Joyce ADF&G Cordova, pers. comm.).

It is also important to note that the genes we study are probably selectively neutral. They likely identify barriers to gene flow, but not functional genetic differences between collections. However, if barriers to gene flow are detected in these selectively neutral genes, then it is possible that genes under selection pressure will diverge much more quickly if the environments between populations differ. Therefore small, yet significant heterogeneity in non-selected genes may underestimate the magnitude of the adaptive genetic differentiation that may be present.

Data indicating high straying of hatchery fish into wild streams within the Sound collected in 1997 (T. Joyce, ADF&G Cordova unpublished data) is surprising given the amount of genetic heterogeneity detected in this study. All hatchery fish were otolith marked before release in 1996, therefore hatchery fish could be differentiated from wild fish when they returned in 1997. Fish from 13 streams along the migration path taken by pink salmon entering the Sound or in close proximity to hatcheries were sampled for otoliths once a week over a four week period. Within these streams, hatchery fish composed between 26% and 97% of the fish. If this straying pattern is representative of all streams and the strays are successfully reproducing, then we would not expect to detect any barriers to gene flow.

Because we do find barriers to gene flow with molecular markers, it is likely that the straying data can not be extrapolated to either previous years or to the entire Sound or hatchery fish are not successfully reproducing. The high hatchery stray rates may not be representative of earlier years because of the high proportions of hatchery fish relative to wild fish in 1997 compared with previous years. In 1997, the hatchery-to-wild return ratios were almost twice the mean ratios since accurate measurements were taken in 1989 (5.2 vs 2.9 hatchery fish per wild fish; Morstadt et al. 1998). The data may not be extrapolated to other streams within the Sound, especially those streams on the eastern Sound because of the lack of representative streams in the otolith study. Streams with high probabilities of containing hatchery strays were chosen in the 1997 study because the objective of the study was to compare coded-wire-tag extrapolations to otolith tag data, not to document hatchery straying (T. Joyce, ADF&G, Cordova, pers. comm.). Finally, there are differences in return timing of fish within the Sound, both regionally and interregionally that are difficult to explain without functional genetic differences among pink salmon from different streams.

Our objectives were to test for barriers to gene flow as a result of regional, elevational, or temporal isolation. Although our objectives did not include developing management strategies to preserve observed heterogeneity, our results can be and have been incorporated into the management of pink salmon within PWS to conserve some of the heterogeneity we have described. Managers of the resource are eager to use information on population structure in guiding their management strategies (James Brady, Regional Supervisor, ADF&G Anchorage, pers. comm.). For example, these data provide managers with the evidence to reject the hypothesis that pink salmon in PWS are a single interbreeding population as has been suggested by hatchery operators. Based on our data, this fishery would best be managed on as fine a scale as possible. Given the financial constraints on the Department, our study upholds their current

management strategy of trying to meet escapement goals throughout the season assessed on a region-by-region basis. It also validates concerns managers have regarding specific pink salmon runs within the Sound. For example, managers are concerned about wild pink salmon returns to the small Coghill district in Northwestern PWS where fisheries targeting hatchery returns to Wally Noerenberg Hatchery are suspected of intercepting wild fish bound for the Coghill district.

In addition to fishery management actions, these data also have application in the assessment of fish transport permits. For example, these data can be used to support recommendations on fish transport requests such as changing hatchery broodstocks, transplanting stocks within the Sound, or supplementing streams.

These data show that the even-year lineage of pink salmon in PWS has a shallow genetic structure relative to other salmonids (in contrast to the structure of sockeye salmon populations from a similar geographic range in Cook Inlet, Alaska, for example; Seeb et al. 1997), however, barriers to gene flow do exist. The commercial harvest of pink salmon fluctuated dramatically between six and 44 million fish during the years since the oil spill. The instability of the run size is due to an array of anthropogenic and natural factors. Maintenance of genetic diversity will play a key role in ameliorating the effects of this instability. Our data confirm that harvest- and hatchery-management decisions made for conservation purposes should best be made on a population-specific rather than species-specific basis. Expansion of this study to include comparisons among years both within and between year-classes is continuing; the analysis of data from multiple year classes will allow us to better test the appropriateness of current management and hatchery practices.

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Table 1. Enzymes, loci, and primary tissue-buffer combinations used to screen for allozyme variation from samples collected in 1996. Enzyme nomenclature follows Shaklee et al. (1990), and locus abbreviations are given.

Enzyme	Enzyme Number	Locus	Tissue	Buffer ¹
Aspartate aminotransferase	2.6.1.1	<i>sAAT-1,2*</i>	Heart	ACEN 7
		<i>sAAT-3*</i>	Eye	TG
		<i>sAAT-4*</i>	Liver	TBCL
		<i>mAAT-1*</i>	Heart	ACEN 7
		<i>mAAT-2*</i>	Heart	ACEN 7
Adenosine deaminase	3.5.4.4	<i>ADA-1*</i>	Muscle	AC 6.1
		<i>ADA-2*</i>	Muscle	AC 6.1
Aconitate hydratase	4.2.1.3	<i>mAH-1*</i>	Heart	ACEN 7
		<i>mAH-2*</i>	Heart	ACEN 7
		<i>mAH-3*</i>	Heart	ACEN 7
		<i>mAH-4*</i>	Heart	ACEN 7
		<i>sAH*</i>	Liver	TG
Adenylate kinase	2.7.4.3	<i>AK*</i>	Muscle	ACE 7
Alanine aminotransferase	2.6.1.2	<i>ALAT*</i>	Muscle	ACE 7
Creatine kinase	2.7.3.2	<i>CK-A1*</i>	Muscle	TG
		<i>CK-A2*</i>	Muscle	TG
		<i>CK-B*</i>	Eye	TG
		<i>CK-C1*</i>	Eye	TG
		<i>CK-C2*</i>	Eye	TG
Formaldehyde dehydrogenase	1.2.1.1	<i>FDHG*</i>	Liver	TBCL
Fumarate hydratase	4.2.1.2	<i>FH*</i>	Muscle	ACE 7
B -N-Acetylgalactosaminidase	3.2.1.53	<i>bGALA*</i>	Muscle	TG
Glyceraldehyde-3-phosphate	1.2.1.12	<i>GAPDH-1*</i>	Muscle	AC 6.1
		<i>GAPDH-2*</i>	Heart	ACEN 7
Guanine deaminase	3.5.4.3	<i>GDA*</i>	Liver	ACEN 6.8
			Liver ²	TG ²
Glycerol-3-phosphate dehydrogenase	1.1.1.8	<i>G3PDH-1*</i>	Muscle	TG
		<i>G3PDH-2*</i>	Heart	ACEN 6.8
		<i>G3PDH-3*</i>	Heart	ACEN 7
Glucose-6-phosphate isomerase	5.3.19	<i>GPI-B1,2*</i>	Muscle	TG
		<i>GPI-A*</i>	Muscle	TG
Glutathione reductase	1.6.4.2	<i>GR*</i>	Heart	ACEN 6.8
N-Acetyl-B-glucosaminidase ²	3.2.1.53	<i>bHA*²</i>	Liver ²	ACE 6.8 ²
Isocitrate dehydrogenase (NADP+)	1.1.1.42	<i>mIDHP-1*</i>	Heart	ACEN 7
		<i>mIDHP-2*</i>	Heart	ACEN 7
		<i>sIDHP-2*</i>	Liver	ACE 6.8
L-Iditol dehydrogenase	1.1.1.14	<i>sIDDH*</i>	Liver	TBCL

Table 1. Continued.

Enzyme	Enzyme Number	Locus	Tissue	Buffer ¹
L-Lactate dehydrogenase	1.1.1.27	<i>LDH-A1*</i>	Muscle	TG
		<i>LDH-A2*</i>	Muscle	TG
		<i>LDH-B1*</i>	Eye	TG
		<i>LDH-B2*</i>	Liver	TG
		<i>LDH-C*</i>	Eye	TG
Malate dehydrogenase	1.1.1.37	<i>sMDH-A1,2*</i>	Liver	AC 6.8
		<i>sMDH-B1,2*</i>	Muscle	AC 6.1
		<i>mMDH-2*</i>	Heart	ACEN 7
Malic enzyme (NADP+)	1.1.1.40	<i>mMEP-1*</i>	Muscle	ACE 7
		<i>mMEP-2*</i>	Muscle	ACE 7
Mannose-6-phosphate isomerase	5.3.1.8	<i>MPI*</i>	Heart	TBE
Cytosol non-specific Dipeptidase	3.4.13.1	<i>PEPA*</i>	Muscle	TG
Tripeptide aminopeptidase	3.4.11.4	<i>PEPB-1*</i>	Heart	TG
X-pro-dipeptidase	3.4.13.9	<i>PEPD-2*</i>	Heart	ACEN 6.5
Peptidase-LT	3.4.-.-	<i>PEPLT*</i>	Muscle	TG
Phosphogluconate dehydrogenase	1.1.1.44	<i>PGDH*</i>	Heart	ACEN 7
Phosphoglycerate kinase	2.7.2.3	<i>PGK-1*</i>	Muscle	ACE 7
		<i>PGK-2*</i>	Muscle	ACE 7
Phosphoglucomutase	5.4.2.2	<i>PGM-2*</i>	Heart	TG
Superoxide dismutase	1.15.1.1	<i>sSOD-1*</i>	Heart	ACEN 6.8
		<i>sSOD-2*</i>	Heart	ACEN 6.8
		<i>mSOD*</i>	Heart	ACEN 6.8
Triose-phosphate isomerase	5.3.1.1	<i>TPI-1*</i>	Liver	TG
		<i>TPI-2*</i>	Liver	TG
		<i>TPI-3*</i>	Muscle	TG
		<i>TPI-4*</i>	Muscle	TG

¹Buffers: AC: amine-citric acid buffer, pH 6.8 (Clayton and Tretiak 1972) modified with EDTA (E), NAD (N), or both (Harris and Hopkinson 1976); TBCL: Tris-citric acid gel, pH 8.7 and lithium hydroxide-boric acid electrode buffer, pH 8.0 (Ridgway et al. 1970); TC4: Tris-citric acid buffer pH 5.8 (Schaal and Anderson 1974); TG: Tris-glycine buffer, pH 8.5 (Holmes and Masters 1970). TBE: (Boyer et al. 1963).

²Only used in single-pair matings to confirm Mendelian ratios.

Table 2. Pink salmon collected from Prince William Sound in 1996. Map numbers refer to Figure 1. Run timing is denoted by E and L and correspond to collections made early and late relative to the historical run curves derived from aerial surveys for each creek. All fish were screened for allozyme variation. Forty fish from each collection were screened for mtDNA variation.

Sample #	Map #	Location name	Elevation	Region	Run	Sample Date	N
1	1	Cabin Creek	Tidal	Montague	E	8/11/96	52
2	1	Cabin Creek	Tidal	Montague	L	9/4/96	48
3	2	Hanning Creek	Tidal	Montague	L	9/4/96	100
4	3	Mink Creek	Tidal	North	E	7/31/96	100
5	3	Mink Creek	Tidal	North	L	9/6/96	100
6	3	Mink Creek	Upstream	North	E	7/31/96	100
7	3	Mink Creek	Upstream	North	L	9/6/96	100
8	4	Paulson Creek	Tidal	North	L	9/7/96	100
9	4	Paulson Creek	Upstream	North	L	9/8/96	100
10	5	Meachum Creek	Tidal	North	E	8/1/96	100
11	5	Meachum Creek	Tidal	North	L	9/7/96	100
12	5	Meachum Creek	Upstream	North	E	8/2/96	100
13	5	Meachum Creek	Upstream	North	L	9/7/96	100
14	6	Solomon Gulch	Hatchery	East	L	8/14/96	100
15	7	Koppen Creek	Tidal	East	E	8/7/96	100
16	7	Koppen Creek	Tidal	East	L	9/9/96	100
17	7	Koppen Creek	Upstream	East	E	8/7/96	100
18	7	Koppen Creek	Upstream	East	L	9/9/96	100
19	8	Bernard Creek	Tidal	Southeast	E	8/9/96	100
20	8	Bernard Creek	Upstream	Southeast	E	8/9/96	100
21	9	Makaka Creek	Upstream	Southeast	E	8/11/96	100
22	10	Constantine Creek	Tidal	Southeast	E	8/8/96	100
23	10	Constantine Creek	Tidal	Southeast	L	9/11/96	100
24	10	Constantine Creek	Upstream	Southeast	E	8/8/96	100
25	10	Constantine Creek	Upstream	Southeast	L	9/10/96	100

Table 3. Relative mobilities (percent distance traveled relative to the common allele mobility on buffers in Table 1) of alleles tested for Mendelian inheritance in pink salmon progeny. Relative allele mobilities for *GDA** are given first for TG buffer followed by ACEN 6.8 buffer.

Locus	Allele designation					
	2	3	4	5	6	7
<i>sAAT-3</i> *	91					
<i>sAAT-4</i> *	210	290	-10			
<i>ADA-2</i> *	110	90				
<i>sAH</i> *	115					
<i>AK</i> *	-145					
<i>CK-A2</i> *		82				
<i>CK-C2</i> *	105					
<i>FDHG</i> *	132					
<i>FH</i> *	136		45			
<i>G3PDH-1</i> *		60				
<i>G3PDH-2</i> *	120	90				
<i>GDA</i> *	130/108	155/113		189/118	167/115	222/123
<i>bGALA</i> *	111	91				
<i>bHA</i> *	200					
<i>GPI-B1,2</i> *	200					
<i>GR</i> *	114					
<i>IDDH</i> *	134					
<i>sIDHP-2</i> *	125	134				
<i>sMDH-A1,2</i> *			50			
<i>sMDH-B1,2</i> *	129	63				
<i>mMEP-1</i> *	123					
<i>mMEP-2</i> *	70					
<i>PEPB-1</i> *	138		200			
<i>PEPD-2</i> *	120	80				
<i>PEPLT</i> *	108					
<i>PGDH</i> *		96	86			
<i>mSOD</i> *		32				
<i>TPI-3</i> *		107				

Table 4. Genotype counts of progeny from single-pair matings designed to test for Mendelian inheritance of putative allozyme alleles. Relative mobilities for each allele number for each locus is in Table 3. Broodlines include matings from parents collected at AFK hatchery in 1995 (AFK 95) and VFDA hatchery in 1996 (VFDA 96). Probability (*P*) calculated from chi-squared tests on expected Mendelian ratios and observed genotype counts. Dashes (-) indicate none observed.

Locus	Broodline	Dam X Sire	Parental Genotypes ¹		Progeny Genotype Counts								<i>P</i> ²	
			Dam	Sire	11	12	22	13	33	23	14	24		34
<i>sAAT-3*</i>	AFK95	14X92	12	22	-	40	51	-	-	-	-	-	-	0.2489
	AFK95	20X78	11	12	48	48	-	-	-	-	-	-	-	1.0000
	AFK95	21X63	12	11	42	55	-	-	-	-	-	-	-	0.1869
	AFK95	28X80	12	12	23	42	34	-	-	-	-	-	-	0.0946
	AFK95	29X92	11	12	27	19	-	-	-	-	-	-	-	0.2382
	AFK95	103X53	12	11	53	36	-	-	-	-	-	-	-	0.0715
	AFK95	104X54	11	12	57	37	-	-	-	-	-	-	-	0.0391
	AFK95	114X64	12	11	26	24	-	-	-	-	-	-	-	0.7773
	VFDA96	5X29	12	12	32	32	28	-	-	-	-	-	-	0.0119
	VFDA96	9X31	12	11	42	39	-	-	-	-	-	-	-	0.7389
	VFDA96	20X32	12	11	23	18	-	-	-	-	-	-	-	0.4349
<i>sAAT-4*</i>	AFK95	20X78	12?	24?	-	8	17	11	-	12	-	-	-	0.3208
	AFK95	21X63	22	12	-	42	43	-	-	-	-	-	-	0.9136
	AFK95	29X92	14?	12	17	12	-	-	-	-	7	8	-	0.1307
	AFK95	43X53	12	12	9	25	19	-	-	-	-	-	-	0.1392
	AFK95	103X53	22	12	-	35	40	-	-	-	-	-	-	0.5637
	AFK95	104X54	12	22	-	24	30	-	-	-	-	-	-	0.4142
	AFK95	120X66	12	12	13	37	19	-	-	-	-	-	-	0.4951
	VFDA96	2X26	23	12	-	8	14	8	-	13	-	-	-	0.4136
	VFDA96	9X31	13	12	18	20	-	14	-	10	-	-	-	0.3080
	VFDA96	14X39	12	22	-	13	12	-	-	-	-	-	-	0.8415
VFDA96	16X27	12	11	25	29	-	-	-	-	-	-	-	0.5862	
VFDA96	20X32	12	12	7	16	9	-	-	-	-	-	-	0.8825	
<i>sAH*</i>	AFK95	8X62	12	11	42	51	-	-	-	-	-	-	-	0.3507
<i>ADA-2*</i>	AFK95	43X53	13	11	48	-	-	50	-	-	-	-	-	0.8399
	AFK95	103X53	13	11	35	-	-	50	-	-	-	-	-	0.0983
	AFK95	120X66	11	13	24	-	-	32	-	-	-	-	-	0.2850
	VFDA96	14X39	12	11	21	16	-	-	-	-	-	-	-	0.4111
<i>AK*</i>	AFK95	28X80	11	12	54	43	-	-	-	-	-	-	-	0.2640
<i>CK-A2*</i>	VFDA96	20X32	11	13	21	-	-	23	-	-	-	-	-	0.7630
<i>CK-C2*</i>	AFK95	103X53	12	11	42	48	-	-	-	-	-	-	-	0.5271
<i>FDHG*</i>	AFK95	43X53	12	11	45	52	-	-	-	-	-	-	-	0.4772
<i>FH*</i>	AFK95	14X92	14	11	46	-	-	-	-	-	42	-	-	0.6662
	VFDA96	14X39	11	12	24	13	-	-	-	-	-	-	-	0.0705

Table 4. Continued.

Locus	Broodline	Cross	Parental		Progeny Genotype Counts										P^2	
			Genotypes ¹		11	12	22	13	33	23	14	24	34			
<i>G3PDH-1*</i>	AFK95	20X78	13	11	48	-	-	51	-	-	-	-	-	-	0.7629	
	VFDA96	2X26	11	13	41	-	-	42	-	-	-	-	-	-	0.9126	
	VFDA96	5X29	11	13	44	-	-	47	-	-	-	-	-	-	0.7532	
<i>G3PDH-2*</i>	AFK95	29X92	13	11	20	-	-	20	-	-	-	-	-	-	1.0000	
	VFDA96	16X27	11	12	24	19	-	-	-	-	-	-	-	-	0.4458	
<i>GDA*</i>	AFK95	8X62	11	12	45	42	-	-	-	-	-	-	-	-	0.7477	
	AFK95	14X92	23	22	-	-	1	-	36	45	-	-	-	-	0.0000 \square	
	AFK95	20X78	11	12	50	47	-	-	-	-	-	-	-	-	0.7607	
	AFK95	21X63	11	12	48	36	9	1	-	-	-	-	-	-	0.0000 \square	
	AFK95	28X80	12	11	42	45	-	-	-	-	-	-	-	-	0.7477	
	AFK95	29X92	11	17	25	1	-	-	-	-	-	-	-	-	0.0000 \square	
	AFK95	103X53	22	27	-	21	10	-	-	-	-	-	-	-	0.0000 \square	
	AFK95	104X54	15	11	29	6	12	-	-	-	-	-	-	-	0.0000 \square	
	AFK95	114X64	23	22	-	-	25	-	4	21	-	-	-	-	0.0000 \square	
	AFK95	120X66	25	12	-	31	14	-	-	-	-	-	-	-	0.0000 \square	
	VFDA96	2X26	12	11	27	5	3	33	-	-	-	-	-	-	0.0000 \square	
	VFDA96	9X31	12	12	17	35	25	-	-	-	-	-	-	-	0.3168	
	VFDA96	14X39	11	22	-	35	-	-	-	-	-	-	-	-	1.0000	
	VFDA96	16X27	12	12	18	32	18	12	3	1	-	-	-	-	0.0000 \square	
	VFDA96	20X32	12	12	11	17	4	2	1	1	-	-	-	-	0.0000 \square	
	<i>bGALA*</i>	AFK95	103X53	12	11	51	23	-	-	-	-	-	-	-	-	0.0011 \square
		VFDA96	2X26	11	12	45	30	-	-	-	-	-	-	-	-	0.0833
		VFDA96	5X29	13?	11	43	-	-	35	-	-	-	-	-	-	0.3625
		VFDA96	14X39	12?	12	16	12	2	-	-	-	-	-	-	-	0.0008 \square
<i>bHA*</i>	AFK95	20X78	11	11	46	30	-	-	-	-	-	-	-	-	0.0000 \square	
<i>GPI-B1,2*</i>	VFDA96	2X26	1111	1211	47	31	-	-	-	-	-	-	-	-	0.0700	
<i>GR*</i>	AFK95	8X62	11	11	93	5	-	-	-	-	-	-	-	-	0.0000 \square	
	AFK95	14X92	11	11	76	12	-	-	-	-	-	-	-	-	0.0000 \square	
	AFK95	28X80	11	11	94	5	-	-	-	-	-	-	-	-	0.0000 \square	
	AFK95	43X53	11	11	80	16	-	-	-	-	-	-	-	-	0.0000 \square	
<i>IDDH*</i>	AFK95	21X63	12	11	100	-	-	-	-	-	-	-	-	-	0.0000 \square	
<i>sIDHP-2*</i>	AFK95	8X62	12	11	45	38	-	-	-	-	-	-	-	-	0.4423	
	AFK95	20X78	12	12	19	59	20	-	-	-	-	-	-	-	0.1286	
	AFK95	28X80	11	13	58	-	-	42	-	-	-	-	-	-	0.1050	
	AFK95	29X92	11	12	18	27	-	-	-	-	-	-	-	-	0.1797	
	AFK95	104X54	11	12	37	49	-	-	-	-	-	-	-	-	0.1957	
	VFDA96	2X26	11	22	-	72	-	-	-	-	-	-	-	-	1.0000	
	VFDA96	5X29	12	12	17	45	17	-	-	-	-	-	-	-	0.4650	
<i>sMDH-A1,2*</i>	AFK95	20X78	1111	1411	45	-	-	-	-	-	54	-	-	-	0.3637	

Table 4. Continued.

Locus	Broodline	Cross	Parental		Progeny Genotype Counts								P^2	
			Dam	Sire	11	12	22	13	33	23	14	24		34
<i>sMDH-B1,2*</i>	AFK95	14X92	1311	1111	35	-	-	54	-	-	-	-	-	0.0440
	AFK95	29X92	1211	1111	28	18	-	-	-	-	-	-	-	0.1404
	AFK95	120X66	1111	1311	40	-	-	48	-	-	-	-	-	0.3918
<i>mMEP-1*</i>	VFDA96	16X27	12	12	27	32	15	-	-	-	-	-	-	0.0727
	VFDA96	20X32	12	11	23	21	-	-	-	-	-	-	-	0.7630
<i>mMEP-2*</i>	VFDA96	9X31	11	12	39	42	-	-	-	-	-	-	-	0.7389
<i>PEPB-1*</i>	AFK95	43X53	11	12	53	44	-	-	-	-	-	-	-	0.3608
	VFDA96	2X26	11	12	37	33	-	-	-	-	-	-	-	0.6326
	VFDA96	16X27	14	11	35	-	-	-	-	48	-	-	-	0.1485
	VFDA96	20X32	12	11	18	14	-	-	-	-	-	-	-	0.4795
<i>PEPD-2*</i>	AFK95	8X62	11	13	49	-	-	42	-	-	-	-	-	0.4617
	AFK95	20X78	11	13	49	-	-	47	-	-	-	-	-	0.8382
	AFK95	28X80	13	11	48	-	-	44	-	-	-	-	-	0.6764
	AFK95	29X92	12	13	12	13	-	10	-	11	-	-	-	0.9330
	AFK95	43X53	23	11	-	54	-	43	-	-	-	-	-	0.2610
	AFK95	103X53	12	11	41	48	-	-	-	-	-	-	-	0.4581
	AFK95	104X54	12	11	47	48	-	-	-	-	-	-	-	0.9183
	AFK95	114X64	12	12	9	18	14	-	-	-	-	-	-	0.4007
	AFK95	120X66	12	11	47	42	-	-	-	-	-	-	-	0.5961
	VFDA96	2X26	33	13	-	-	-	47	32	-	-	-	-	0.0915
	VFDA96	5X29	23	12	-	10	15	9	-	7	-	-	-	0.3628
	VFDA96	9X31	22	12	-	37	41	-	-	-	-	-	-	0.6506
	VFDA96	14X39	11	12	19	16	-	-	-	-	-	-	-	0.6121
	<i>PEPLT*</i>	VFDA96	16X27	33	11	-	-	-	65	-	-	-	-	-
VFDA96		5X29	11	12	38	38	-	-	-	-	-	-	-	1.0000
<i>PGDH*</i>	AFK95	29X92	13	11	17	-	-	29	-	-	-	-	-	0.0668
	AFK95	104X54	13	11	45	-	-	50	-	-	-	-	-	0.6075
	AFK95	120X66	11	13	54	-	-	36	-	-	-	-	-	0.0528
	VFDA96	2X26	33	11	-	75	-	-	-	-	-	-	-	1.0000
	VFDA96	5X29	13	14	21	-	-	24	-	-	20	-	22	0.9398
	VFDA96	9X31	13	11	30	-	-	41	-	-	-	-	-	0.1854
	VFDA96	14X39	33	13	-	-	-	17	19	-	-	-	-	0.7389
<i>mSOD*</i>	AFK95	104X54	13	11	47	-	-	43	-	-	-	-	-	0.6730
<i>TPI-3*</i>	AFK95	43X53	11	13	98	-	-	-	-	-	-	-	-	0.0000 \square
	AFK95	103X53	11	13	90	-	-	-	-	-	-	-	-	0.0000 \square
	AFK95	120X66	11	13	51	-	-	34	-	-	-	-	-	0.0598
	VFDA96	2X26	11	13	48	-	-	32	-	-	-	-	-	0.0736

¹? = parental genotype was not scorable, but was inferred through the genotypes of their progeny.

²+ = genotypes also seen in progeny: 15, 17, 25, 26, 27, 55 and/or 57; \square = significant deviation from expected after adjusting for multiple tests within loci (Rice 1987).

Table 5. Observed and expected heterozygosities calculated from 37 polymorphic loci from pink salmon collected in 1996 from PWS.

Stream	Timing	Elevation	Observed Heterozygosity		Expected Heterozygosity	
			<i>H_o</i>	Std. Dev	<i>H_e</i>	Std. Dev
Cabin Cr.	Early	Tidal	0.0929	0.0344	0.0937	0.0006
	Late	Tidal	0.0723	0.0270	0.0673	0.0005
Hanning Cr.	Late	Tidal	0.0956	0.0337	0.0974	0.0003
Mink Cr.	Early	Tidal	0.0895	0.0327	0.0870	0.0003
	Late	Tidal	0.0991	0.0353	0.0981	0.0003
	Early	Upstream	0.0879	0.0314	0.0872	0.0003
	Late	Upstream	0.0935	0.0327	0.0934	0.0004
Paulson Cr.	Late	Tidal	0.0868	0.0306	0.0883	0.0003
	Late	Upstream	0.0869	0.0288	0.0925	0.0003
Meachum Cr.	Early	Tidal	0.0906	0.0348	0.0898	0.0003
	Late	Tidal	0.0909	0.0315	0.0912	0.0003
	Early	Upstream	0.0894	0.0325	0.0912	0.0003
	Late	Upstream	0.0894	0.0299	0.0909	0.0003
Solomon Gulch	Late	Hatchery	0.0900	0.0322	0.0895	0.0003
Koppen Cr.	Early	Tidal	0.0931	0.0339	0.0926	0.0003
	Late	Tidal	0.0902	0.0337	0.0876	0.0003
	Early	Upstream	0.0856	0.0289	0.0916	0.0003
	Late	Upstream	0.0941	0.0337	0.0936	0.0003
Bernard Cr.	Early	Tidal	0.0908	0.0337	0.0903	0.0003
	Early	Upstream	0.0919	0.0307	0.0944	0.0003
Makaka Cr.	Early	Upstream	0.0918	0.0345	0.0930	0.0003
Constantine Cr.	Early	Tidal	0.0945	0.0335	0.0967	0.0003
	Late	Tidal	0.0981	0.0378	0.0947	0.0003
	Early	Upstream	0.0993	0.0365	0.0998	0.0003
	Late	Upstream	0.1036	0.0391	0.1035	0.0003

Table 6. Hierarchical analysis of 1996 pink salmon collections in PWS using log-likelihood ratios for allozyme data and Monte Carlo simulation probabilities for mtDNA data. Comparisonwise significance levels (α_c) were adjusted for multiple tests done within the same test groups (Test) using sequential Bonferonni adjustments (modified from Miliken and Johnson [1984] and Rice [1989]). Asterisks indicate significance at experimentwise $\alpha = 0.05$.

Source of Variation	Allozyme data					mtDNA data		
	df	Overall	<i>P</i>	α_c	Test	<i>P</i>	α_c	Test
Among Streams	220	359.61	0.000 *	0.025	1	0.065	0.050	1
Within Streams	616	685.12	0.027 *	0.050	1			
Mink Creek	132	142.4	0.253	0.013	2	0.516	0.007	2
Between Timing	44	58.4	0.072	0.006	3	0.823	0.010	2
Within Timing	88	84.05	0.599	0.050	3			
Early (upstream vs tidal)	44	41.09	0.597	0.025	3	0.462	0.006	2
Late (upstream vs tidal)	44	42.96	0.516	0.013	3	0.144	0.000	2
Between Elevation	44	41.82	0.565	0.017	3	0.078	0.000	2
Within Elevation	88	100.64	0.168	0.008	3			
Tidal (early vs late)	44	46.35	0.376	0.010	3	1.000	0.050	2
Upstream (early vs late)	44	54.29	0.138	0.007	3	0.833	0.013	2
Paulson Creek (upstream vs tidal)	44	48.42	0.299	0.017	2	0.885	0.017	2
Meachum Creek	132	138.2	0.338	0.025	2	0.025	0.000	2
Between Timing	44	52.86	0.169	0.006	4	0.154	0.001	2
Within Timing	88	85.34	0.560	0.017	4			
Early (upstream vs tidal)	44	45.07	0.427	0.013	4	0.263	0.002	2
Late (upstream vs tidal)	44	40.27	0.632	0.050	4	0.048	0.000	2
Between Elevation	44	46.5	0.370	0.008	4	0.033	0.000	2
Within Elevation	88	91.71	0.372	0.010	4			
Tidal (early vs late)	44	41.53	0.578	0.025	4	0.261	0.001	2
Upstream (early vs late)	44	50.18	0.242	0.007	4	0.178	0.001	2
Koppen Creek	132	158.8	0.056	0.010	2	0.017	0.000	2
Between Timing	44	55.24	0.119	0.013	5	0.150	0.000	2
Within Timing	88	103.51	0.124	0.010	5			
Early (upstream vs tidal)	44	56.81	0.093	0.008	5	0.124	0.000	2
Late (upstream vs tidal)	44	46.7	0.362	0.025	5	0.029	0.000	2
Between Elevation	44	51.49	0.204	0.017	5	0.050	0.000	2
Within Elevation	88	107.26	0.080	0.007	5			
Tidal (early vs late)	44	42.77	0.524	0.050	5	0.044	0.000	2
Upstream (early vs late)	44	64.49	0.024	0.006	5	0.330	0.006	2
Bernard Creek (upstream vs tidal)	44	35.2	0.826	0.050	2	0.906	0.025	2

Table 6. Continued

Source of Variation	Allozyme data					mtDNA data		
	DF	Overall	<i>P</i> - value	α_c	Test	<i>P</i> - value	α_c	Test
Constantine Creek	132	162.1	0.039	0.008	2	0.042	0.000	2
Between Timing	44	61.85	0.039	0.006	6	0.020	0.000	2
Within Timing	88	100.22	0.176	0.017	6			
Early (upstream vs tidal)	44	42.02	0.557	0.050	6	0.707	0.008	2
Late (upstream vs tidal)	44	58.2	0.074	0.008	6	0.104	0.000	2
Between Elevation	44	56.16	0.103	0.013	6	0.278	0.003	2
Within Elevation	88	105.91	0.094	0.010	6			
Tidal (early vs late)	44	44.95	0.432	0.025	6	0.062	0.000	2
Upstream (early vs late)	44	60.96	0.046	0.007	6	0.071	0.000	2

Table 7. Gene diversity analysis (Nei 1973) by locus of 1996 data among streams, between elevations within streams, among collections within elevations, and within collections.

Locus	Absolute gene diversity		Relative gene diversity			
	Total	Within collections	Within Collections	Among Collections Within Elevations	Between Elevations Within Streams	Among Streams
<i>sAAT-3*</i>	0.3120	0.3100	0.9936	0.0012	0.0018	0.0034
<i>sAAT-4*</i>	0.5149	0.5121	0.9947	0.0023	0.0024	0.0006
<i>ADA-1*</i>	0.0010	0.0010	0.9950	0.0030	0.0010	0.0010
<i>ADA-2*</i>	0.1449	0.1440	0.9937	0.0020	0.0013	0.0030
<i>mAH-2*</i>	0.0246	0.0244	0.9929	0.0020	0.0016	0.0035
<i>mAH-4*</i>	0.0786	0.0782	0.9950	0.0014	0.0027	0.0009
<i>mAAT-1*</i>	0.0091	0.0090	0.9885	0.0024	0.0057	0.0034
<i>CK-A2*</i>	0.0126	0.0125	0.9953	0.0013	0.0018	0.0015
<i>CK-C1*</i>	0.0085	0.0084	0.9962	0.0017	0.0011	0.0009
<i>CK-C2*</i>	0.0054	0.0053	0.9940	0.0019	0.0019	0.0022
<i>FDHG*</i>	0.0171	0.0170	0.9952	0.0011	0.0022	0.0015
<i>GAPDH-2*</i>	0.0318	0.0316	0.9930	0.0040	0.0013	0.0018
<i>PEPA*</i>	0.0015	0.0015	0.9928	0.0033	0.0026	0.0020
<i>G3PDH-1*</i>	0.2856	0.2840	0.9944	0.0015	0.0028	0.0014
<i>G3PDH-2*</i>	0.1961	0.1941	0.9898	0.0034	0.0023	0.0045
<i>G3PDH-3*</i>	0.0145	0.0144	0.9947	0.0008	0.0007	0.0038
<i>mIDHP-1*</i>	0.0065	0.0065	0.9937	0.0023	0.0017	0.0023
<i>sIDHP-2*</i>	0.4565	0.4537	0.9940	0.0026	0.0023	0.0012
<i>LDH-B1*</i>	0.0108	0.0108	0.9952	0.0031	0.0004	0.0013
<i>LDH-B2*</i>	0.0169	0.0168	0.9940	0.0033	0.0015	0.0011
<i>PEPB-1*</i>	0.2303	0.2290	0.9942	0.0024	0.0013	0.0022
<i>PEPLT*</i>	0.2227	0.2201	0.9883	0.0055	0.0019	0.0043
<i>mMEP-1*</i>	0.3966	0.3936	0.9926	0.0055	0.0009	0.0009
<i>PGDH*</i>	0.4071	0.4058	0.9967	0.0009	0.0006	0.0017
<i>PGM-2*</i>	0.0040	0.0040	0.9932	0.0040	0.0015	0.0013
<i>PEPD-2*</i>	0.6131	0.6101	0.9951	0.0023	0.0010	0.0017
<i>mSOD*</i>	0.0209	0.0208	0.9959	0.0022	0.0017	0.0002
<i>sSOD-1*</i>	0.0020	0.0020	0.9935	0.0015	0.0030	0.0020
<i>TPI-2*</i>	0.0311	0.0309	0.9959	0.0010	0.0024	0.0007
Overall	4.0765	4.0516	0.9939	0.0026	0.0017	0.0019

Table 8. Gene diversity analysis (Nei 1973) by locus of 1996 data among streams, between timing within streams, among collections within timing, and within collections.

Locus	Absolute gene diversity		Relative gene diversity			
	Total	Within Collections	Within Collections	Among Collections Within Timing	Between Timing Within Streams	Among Streams
<i>sAAT-3*</i>	0.3120	0.3100	0.9936	0.0023	0.0007	0.0034
<i>sAAT-4*</i>	0.5149	0.5121	0.9947	0.0037	0.0010	0.0006
<i>ADA-1*</i>	0.0010	0.0010	0.9950	0.0020	0.0010	0.0010
<i>ADA-2*</i>	0.1449	0.1440	0.9937	0.0020	0.0012	0.0030
<i>mAH-2*</i>	0.0246	0.0244	0.9929	0.0029	0.0007	0.0035
<i>mAH-4*</i>	0.0786	0.0782	0.9950	0.0040	0.0001	0.0009
<i>mAAT-1*</i>	0.0091	0.0090	0.9885	0.0069	0.0012	0.0034
<i>CK-A2*</i>	0.0126	0.0125	0.9953	0.0023	0.0008	0.0015
<i>CK-C1*</i>	0.0085	0.0084	0.9962	0.0026	0.0001	0.0009
<i>CK-C2*</i>	0.0054	0.0053	0.9940	0.0024	0.0013	0.0022
<i>FDHG*</i>	0.0171	0.0170	0.9952	0.0026	0.0006	0.0015
<i>GAPDH-2*</i>	0.0318	0.0316	0.9930	0.0030	0.0023	0.0018
<i>PEPA*</i>	0.0015	0.0015	0.9928	0.0039	0.0013	0.0020
<i>G3PDH-1*</i>	0.2856	0.2840	0.9944	0.0038	0.0004	0.0014
<i>G3PDH-2*</i>	0.1961	0.1941	0.9898	0.0047	0.0010	0.0045
<i>G3PDH-3*</i>	0.0145	0.0144	0.9947	0.0013	0.0003	0.0038
<i>mIDHP-1*</i>	0.0065	0.0065	0.9937	0.0029	0.0012	0.0023
<i>sIDHP-2*</i>	0.4565	0.4537	0.9940	0.0029	0.0019	0.0012
<i>LDH-B1*</i>	0.0108	0.0108	0.9952	0.0020	0.0014	0.0013
<i>LDH-B2*</i>	0.0169	0.0168	0.9940	0.0027	0.0021	0.0011
<i>PEPB-1*</i>	0.2303	0.2290	0.9942	0.0023	0.0013	0.0022
<i>PEPLT*</i>	0.2227	0.2201	0.9883	0.0053	0.0021	0.0043
<i>mMEP-1*</i>	0.3966	0.3936	0.9926	0.0013	0.0051	0.0009
<i>PGDH*</i>	0.4071	0.4058	0.9967	0.0009	0.0006	0.0017
<i>PGM-2*</i>	0.0040	0.0040	0.9932	0.0043	0.0010	0.0013
<i>PEPD-2*</i>	0.6131	0.6101	0.9951	0.0015	0.0018	0.0017
<i>mSOD*</i>	0.0209	0.0208	0.9959	0.0025	0.0013	0.0002
<i>sSOD-1*</i>	0.0020	0.0020	0.9935	0.0035	0.0005	0.0020
<i>TPI-2*</i>	0.0311	0.0309	0.9959	0.0026	0.0007	0.0007
Overall	4.0765	4.0516	0.9939	0.0026	0.0016	0.0019

Table 9. Restriction enzymes, length of recognition sequence (r), and approximate fragment sizes detected in ND5/ND6 haplotypes in 1996 collections.

Restriction Enzyme	r (bp)	Haplotype	Fragment sizes (bp)
<i>Apa I</i>	6	A	1240, 1170
		B	1240, 710, 460
		C	1170, 935, 305
<i>BstUI</i>	4	A	1624, 791
		B	1191, 791, 433
		C	1134, 791, 490
<i>EcoRV</i>	6	A	2400
		B	1500, 900
<i>Hinf I</i>	4	A	800, 500, 350, 300, 225 ¹
		B	1025, 500, 350, 300, 225
		C	500, 450, 350 ¹ , 300, 225 ¹
<i>Rsa I</i>	4	A	1564, 338, 300, 130, 40, 38
		C	1564, 430, 338, 40, 38
<i>Xba I</i>	6	A	2400
		B	1700, 700

¹ There are two fragments of the indicated size in these patterns.

Table 10. Haplotype counts for 1996 collections from Prince William Sound (E = early, L = late; T = tidal spawning, U = upstream spawning, H = hatchery). Haplotype designations after Fetzner et al. (*submitted*): I = AAAAAA, II = ACAAAA, III = AAABAA, IV = ABAAAA, V = AABAAA, VI = BAAAAA, VII = AAACAA, XX = ACAAAB, XXI = AAAACA, XXIII = CAAACA. Order of restriction enzymes is *Apa I*, *BstUI*, *EcoR V*, *Hinf I*, *Rsa I*, *Xba I*. Haplotype diversity (h) and nucleotide diversity (π) are given.

Sampling Site	ND5/ND6 Haplotypes											h	π
	I	II	III	IV	V	VI	VII	XX	XXI	XXIII			
Bernard Cr.	E T	28	5	3	1	3	0	0	0	0	0	0.4886	0.0064
	E U	29	6	3	1	1	0	0	0	0	0	0.4506	0.0057
Cabin Cr.	E T	31	7	0	2	0	0	0	0	0	0	0.3709	0.0042
	L T	29	6	3	1	1	0	0	0	0	0	0.4506	0.0057
Constantine Cr.	E T	33	4	1	1	0	1	0	0	0	0	0.3114	0.0037
	E U	36	2	0	1	0	0	0	1	0	0	0.1886	0.0026
	L T	22	11	2	2	2	0	1	0	0	0	0.6215	0.0083
	L U	30	5	2	0	0	2	1	0	0	0	0.4215	0.0053
Hanning Cr.	L T	33	3	1	1	2	0	0	0	0	0	0.3139	0.0039
Koppen Cr.	E T	31	4	4	1	0	0	0	0	0	0	0.3835	0.0047
	E U	38	1	1	0	0	0	0	0	0	0	0.0975	0.0011
	L T	29	8	0	0	0	2	0	0	1	0	0.4367	0.0060
	L U	34	3	3	0	0	0	0	0	0	0	0.2696	0.0032
Makaka Cr.	E U	34	4	0	2	0	0	0	0	0	0	0.2684	0.0031
Meachum Cr.	E T	31	3	1	1	3	0	1	0	0	0	0.3911	0.0049
	E U	35	2	3	0	0	0	0	0	0	0	0.2291	0.0027
	L T	31	6	0	0	0	0	2	0	0	1	0.3785	0.0056
	L U	27	4	5	2	0	0	0	0	0	2	0.5203	0.0092
Mink Cr.	E T	32	5	2	1	0	0	0	0	0	0	0.3456	0.0041
	E U	25	7	5	2	0	1	0	0	0	0	0.5671	0.0075
	L T	32	6	1	0	0	1	0	0	0	0	0.3405	0.0040
	L U	27	4	7	1	0	1	0	0	0	0	0.5089	0.0067
Paulson Cr.	L T	30	4	3	2	0	1	0	0	0	0	0.4241	0.0053
	L U	33	3	3	1	0	0	0	0	0	0	0.3114	0.0038
Solomon Gulch	L H	32	2	6	0	0	0	0	0	0	0	0.3392	0.0042

Table 11. Hierarchical analysis of molecular variation (AMOVA) observed in Prince William Sound pink salmon collections from 1996.

a. Elevation

Variance Component	Observed Partition		P^1	Φ -statistic
	Variance	% Total		
Among elevation	0.001	0.30	0.187	$\Phi_{CT} = 0.003$
Among collections within elevation	0.003	1.46	0.025	$\Phi_{SC} = 0.015$
Within collections	0.195	98.24	0.007	$\Phi_{ST} = 0.018$

b. Timing

Variance Component	Observed Partition		P^1	Φ -statistic
	Variance	% Total		
Among timing	0.002	0.90	0.068	$\Phi_{CT} = 0.009$
Among collections within timing	0.003	1.52	0.014	$\Phi_{SC} = 0.015$
Within collections	0.192	97.58	0.001	$\Phi_{ST} = 0.024$

¹Probability of having a more extreme variance component and Φ -statistic than the observed value by chance alone (1,023 permutations)

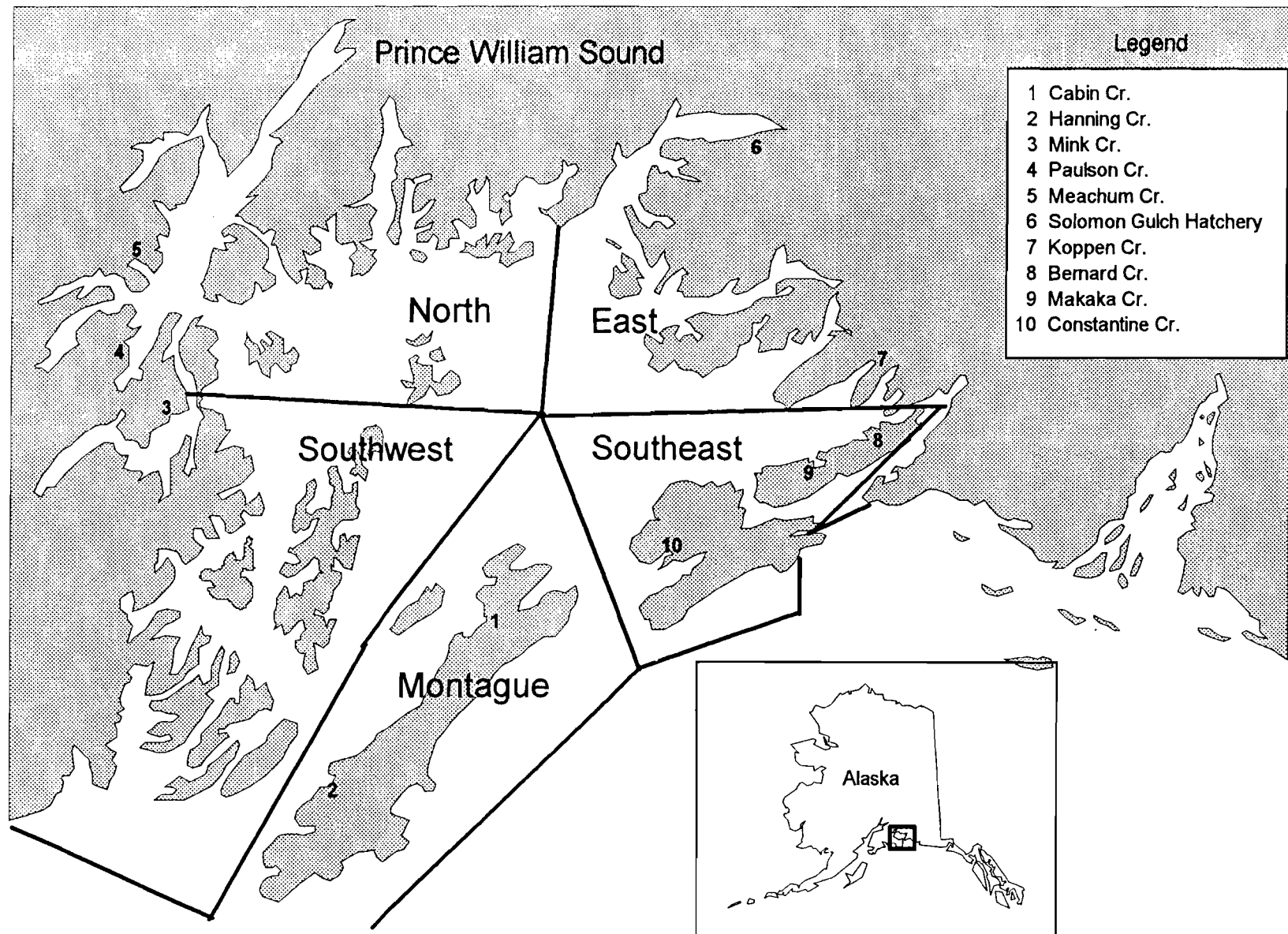


Figure 1. Locations and biological regions within Prince William Sound, Alaska where pink salmon were sampled in 1996 for genetic analysis.

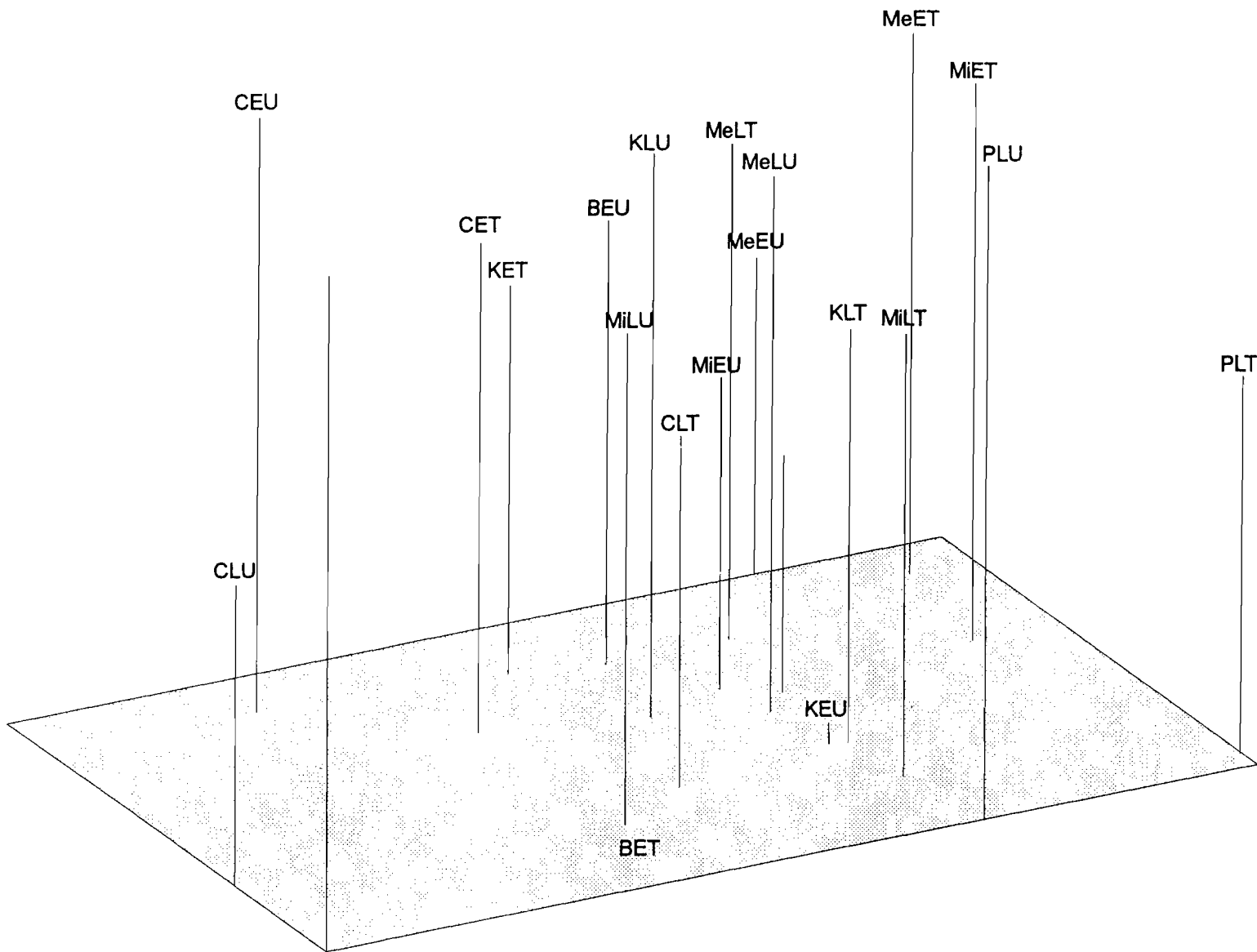


Figure 2. Multidimensional scaling analysis using Cavalli-Sforza and Edwards (1967) chord distances, calculated from 37 allozyme loci. In the three letter abbreviations for collections, the first letter represents stream (K - Koppen, Me - Meachum, C - Constantine, P - Paulson, B - Bernård, and Mi - Mink), the second letter represents timing (E - Early, L - Late), and the last letter represents elevation (U - upstream, T - Tidal).

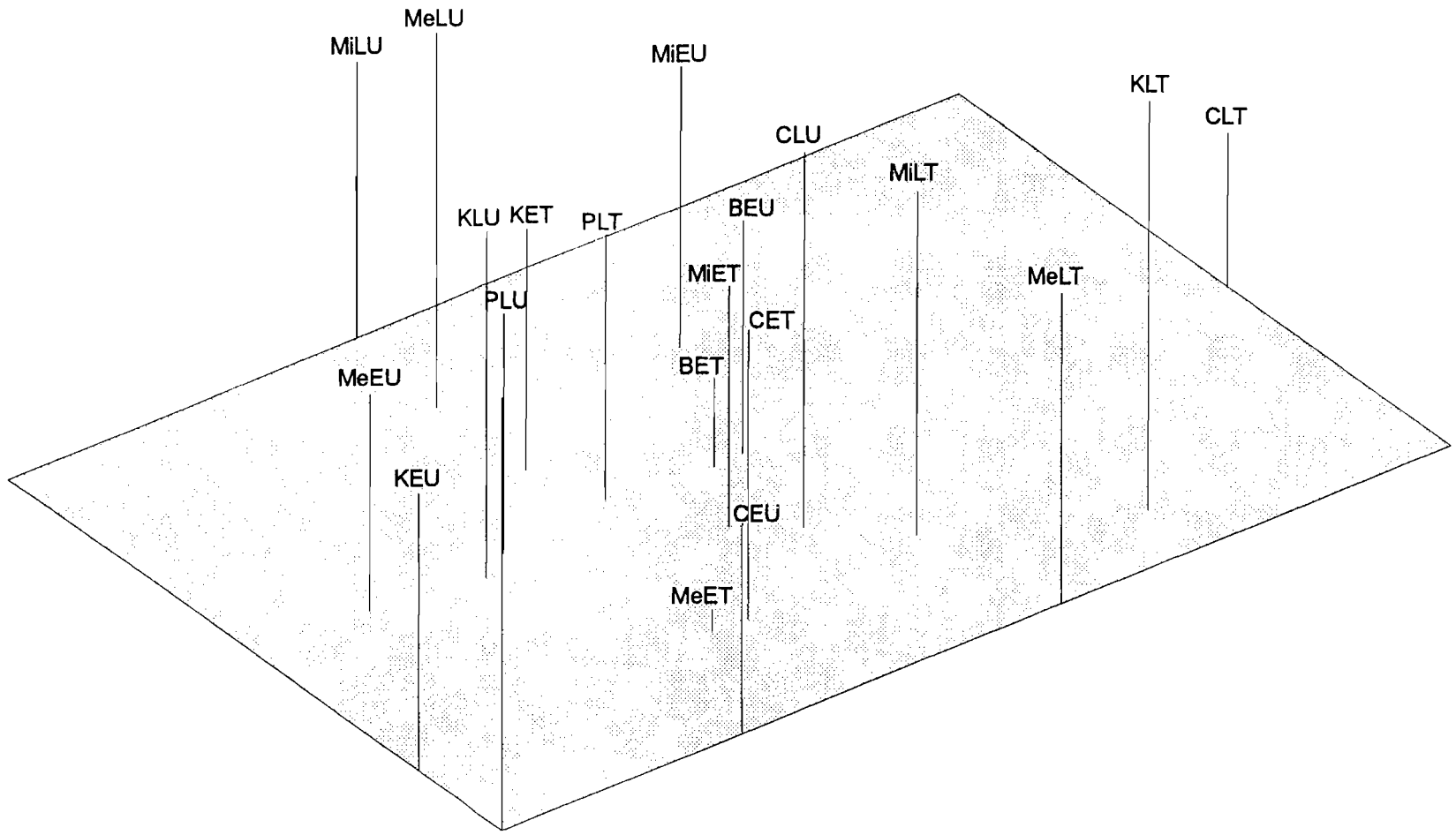


Figure 3. Multidimensional scaling analysis using nucleotide divergence (Nei 1987) among collections, calculated from mtDNA restriction site data. In the three letter abbreviations for collections, the first letter represents stream (K - Koppen, Me - Meachum, C - Constantine, P - Paulson, B - Bernard, and Mi - Mink), the second letter represents timing (E - Early, L - Late), and the last letter represents elevation (U - upstream, T - Tidal)

Appendix A. Allele frequency estimates of polymorphic allozyme loci for pink salmon collected from Prince William Sound, Alaska in 1996. Within the population names, "E" designates collections made early, and "L" designates collections made late in the spawning cycle; "T" designates collections made in tidal zones, "U" designates collections made in upstream zones, and "H" designates a collection made from hatchery broodstock. Mobilities are based on buffers in Table 1. Blanks indicate no data.

Population	<i>sAAT-1,2*</i>			<i>sAAT-3*</i>		
	N	100	83	N	100	91
Cabin Cr. E. 96 T.	52	1.0000	0.0000	47	0.7872	0.2128
Cabin Cr. L. 96 T.				46	0.9022	0.0978
Hanning Cr. L. 96 T.	99	0.9924	0.0076	100	0.7850	0.2150
Mink Cr. E. 96 T.	100	0.9950	0.0050	97	0.8041	0.1959
Mink Cr. L. 96 T.	99	0.9975	0.0025	93	0.8226	0.1774
Mink Cr. E. 96 U.	99	0.9949	0.0051	95	0.8158	0.1842
Mink Cr. L. 96 U.	100	0.9925	0.0075	99	0.8434	0.1566
Paulson Cr. L. 96 T.	100	0.9950	0.0050	95	0.8263	0.1737
Paulson Cr. L. 96 U.	100	0.9925	0.0075	100	0.8450	0.1550
Meachum Cr. E. 96 T.	100	1.0000	0.0000	98	0.7908	0.2092
Meachum Cr. L. 96 T.	100	0.9950	0.0050	88	0.7955	0.2045
Meachum Cr. E. 96 U.	100	1.0000	0.0000	97	0.8041	0.1959
Meachum Cr. L. 96 U.	99	0.9975	0.0025	96	0.8229	0.1771
Solomon Gulch L. 96 H.	99	1.0000	0.0000	100	0.8100	0.1900
Koppen Cr. E. 96 T.	100	0.9975	0.0025	100	0.8100	0.1900
Koppen Cr. L. 96 T.	100	0.9925	0.0075	96	0.8333	0.1667
Koppen Cr. E. 96 U.	100	1.0000	0.0000	99	0.8333	0.1667
Koppen Cr. L. 96 U.	100	0.9925	0.0075	81	0.8333	0.1667
Makaka Cr. E. 96 U.	100	0.9900	0.0100	97	0.8041	0.1959
Bernard Cr. E. 96 T.	98	1.0000	0.0000	98	0.7959	0.2041
Bernard Cr. E. 96 U.	98	1.0000	0.0000	100	0.7750	0.2250
Constantine Cr. E. 96 T.	100	0.9925	0.0075	100	0.7650	0.2350
Constantine Cr. L. 96 T.	100	0.9975	0.0025	94	0.8404	0.1596
Constantine Cr. E. 96 U.	100	0.9925	0.0075	100	0.7400	0.2600
Constantine Cr. L. 96 U.	99	0.9798	0.0202	83	0.7349	0.2651

Population	sAAT-4*					ADA-1*		
	N	100	210	290	-10	N	100	86
Cabin Cr. E. 96 T.	49	0.4694	0.5204	0.0102	0.0000	52	1.0000	0.0000
Cabin Cr. L. 96 T.	47	0.4362	0.5638	0.0000	0.0000	48	1.0000	0.0000
Hanning Cr. L. 96 T.	98	0.3929	0.6020	0.0051	0.0000	100	1.0000	0.0000
Mink Cr. E. 96 T.	99	0.4343	0.5404	0.0202	0.0051	100	1.0000	0.0000
Mink Cr. L. 96 T.	100	0.3950	0.5800	0.0150	0.0100	100	1.0000	0.0000
Mink Cr. E. 96 U.	98	0.4643	0.5204	0.0102	0.0051	100	1.0000	0.0000
Mink Cr. L. 96 U.	100	0.4400	0.5400	0.0200	0.0000	100	1.0000	0.0000
Paulson Cr. L. 96 T.	98	0.4235	0.5561	0.0102	0.0102	100	1.0000	0.0000
Paulson Cr. L. 96 U.	100	0.4200	0.5550	0.0200	0.0050	100	1.0000	0.0000
Meachum Cr. E. 96 T.	99	0.4545	0.5253	0.0101	0.0101	99	1.0000	0.0000
Meachum Cr. L. 96 T.	99	0.4192	0.5505	0.0253	0.0051	97	1.0000	0.0000
Meachum Cr. E. 96 U.	100	0.4550	0.5250	0.0100	0.0100	96	1.0000	0.0000
Meachum Cr. L. 96 U.	99	0.4798	0.4949	0.0202	0.0051	99	1.0000	0.0000
Solomon Gulch L. 96 H.	100	0.5300	0.4550	0.0150	0.0000	96	1.0000	0.0000
Koppen Cr. E. 96 T.	100	0.5200	0.4650	0.0150	0.0000	100	1.0000	0.0000
Koppen Cr. L. 96 T.	99	0.4747	0.5101	0.0152	0.0000	100	1.0000	0.0000
Koppen Cr. E. 96 U.	100	0.5800	0.6100	0.0100	0.0000	100	0.9950	0.0050
Koppen Cr. L. 96 U.	99	0.4747	0.5152	0.0101	0.0000	100	1.0000	0.0000
Makaka Cr. E. 96 U.	100	0.4650	0.4950	0.0400	0.0000	100	0.9900	0.0100
Bernard Cr. E. 96 T.	100	0.3850	0.5850	0.0300	0.0000	98	1.0000	0.0000
Bernard Cr. E. 96 U.	99	0.4747	0.5152	0.0101	0.0000	100	1.0000	0.0000
Constantine Cr. E. 96 T.	100	0.4400	0.5350	0.0200	0.0050	100	1.0000	0.0000
Constantine Cr. L. 96 T.	100	0.4100	0.5850	0.0050	0.0000	100	1.0000	0.0000
Constantine Cr. E. 96 U.	99	0.5051	0.4747	0.0202	0.0000	100	0.9950	0.0050
Constantine Cr. L. 96 U.	96	0.4219	0.5521	0.0260	0.0000	100	1.0000	0.0000

Population	ADA-2*				mAH-1*			mAH-2*		
	N	100	110/116	90/96	N	100	32	N	100	135
Cabin Cr. E. 96 T.	52	0.9808	0.0192	0.0000	52	1.0000	0.0000	52	0.9904	0.0096
Cabin Cr. L. 96 T.	48	0.8958	0.0312	0.0729						
Hanning Cr. L. 96 T.	99	0.8939	0.0354	0.0707	100	0.9950	0.0050	100	0.9850	0.0150
Mink Cr. E. 96 T.	100	0.9600	0.0150	0.0250	68	1.0000	0.0000	87	0.9828	0.0172
Mink Cr. L. 96 T.	99	0.9242	0.0404	0.0354	97	1.0000	0.0000	97	0.9845	0.0155
Mink Cr. E. 96 U.	100	0.9300	0.0300	0.0400	98	1.0000	0.0000	99	0.9899	0.0101
Mink Cr. L. 96 U.	100	0.9050	0.0450	0.0500	100	1.0000	0.0000	100	0.9950	0.0050
Paulson Cr. L. 96 T.	100	0.9600	0.0050	0.0350	98	1.0000	0.0000	96	1.0000	0.0000
Paulson Cr. L. 96 U.	100	0.9450	0.0150	0.0400	99	0.9949	0.0051	99	1.0000	0.0000
Meachum Cr. E. 96 T.	99	0.9293	0.0253	0.0455	100	1.0000	0.0000	100	1.0000	0.0000
Meachum Cr. L. 96 T.	96	0.9167	0.0521	0.0312	98	1.0000	0.0000	98	0.9796	0.0204
Meachum Cr. E. 96 U.	98	0.9133	0.0204	0.0663	100	1.0000	0.0000	100	0.9850	0.0150
Meachum Cr. L. 96 U.	100	0.9400	0.0250	0.0350	99	1.0000	0.0000	99	0.9949	0.0051
Solomon Gulch L. 96 H.	95	0.9368	0.0263	0.0368	99	0.9949	0.0051	99	0.9949	0.0051
Koppen Cr. E. 96 T.	100	0.8900	0.0400	0.0700	99	1.0000	0.0000	96	0.9896	0.0104
Koppen Cr. L. 96 T.	98	0.9286	0.0306	0.0408	98	0.9949	0.0051	98	0.9898	0.0102
Koppen Cr. E. 96 U.	100	0.9500	0.0250	0.0250	97	1.0000	0.0000	99	1.0000	0.0000
Koppen Cr. L. 96 U.	100	0.9300	0.0250	0.0450	100	1.0000	0.0000	100	0.9850	0.0150
Makaka Cr. E. 96 U.	98	0.9490	0.0255	0.0255	97	1.0000	0.0000	100	0.9900	0.0100
Bernard Cr. E. 96 T.	97	0.9227	0.0206	0.0567	100	1.0000	0.0000	100	0.9950	0.0050
Bernard Cr. E. 96 U.	100	0.9000	0.0450	0.0550	91	1.0000	0.0000	84	0.9702	0.0298
Constantine Cr. E. 96 T.	100	0.9050	0.0250	0.0700	100	1.0000	0.0000	100	0.9750	0.0250
Constantine Cr. L. 96 T.	100	0.8950	0.0100	0.0950	99	1.0000	0.0000	98	0.9796	0.0204
Constantine Cr. E. 96 U.	100	0.9150	0.0300	0.0550	75	0.9933	0.0067	84	0.9702	0.0298
Constantine Cr. L. 96 U.	100	0.9000	0.0150	0.0850	99	0.9949	0.0051	98	0.9847	0.0153

Population	sAH*					mAH-4*		
	N	100	115	88/86	110	N	100	81
Cabin Cr. E. 96 T.	51	0.9902	0.0098	0.0000	0.0000	52	0.9423	0.0577
Cabin Cr. L. 96 T.	48	1.0000	0.0000	0.0000	0.0000			
Hanning Cr. L. 96 T.	100	0.9950	0.0000	0.0050	0.0000	100	0.9450	0.0550
Mink Cr. E. 96 T.	99	1.0000	0.0000	0.0000	0.0000	89	0.9382	0.0618
Mink Cr. L. 96 T.	100	0.9950	0.0000	0.0050	0.0000	98	0.9439	0.0561
Mink Cr. E. 96 U.	99	0.9949	0.0000	0.0051	0.0000	99	0.9646	0.0354
Mink Cr. L. 96 U.	100	0.9950	0.0000	0.0050	0.0000	100	0.9650	0.0350
Paulson Cr. L. 96 T.	99	0.9949	0.0000	0.0051	0.0000	100	0.9750	0.0250
Paulson Cr. L. 96 U.	100	1.0000	0.0000	0.0000	0.0000	99	0.9545	0.0455
Meachum Cr. E. 96 T.	100	1.0000	0.0000	0.0000	0.0000	100	0.9550	0.0450
Meachum Cr. L. 96 T.	100	1.0000	0.0000	0.0000	0.0000	97	0.9588	0.0412
Meachum Cr. E. 96 U.	100	1.0000	0.0000	0.0000	0.0000	100	0.9700	0.0300
Meachum Cr. L. 96 U.	100	0.9950	0.0000	0.0050	0.0000	99	0.9495	0.0505
Solomon Gulch L. 96 H.	94	1.0000	0.0000	0.0000	0.0000	99	0.9596	0.0404
Koppen Cr. E. 96 T.	100	1.0000	0.0000	0.0000	0.0000	96	0.9844	0.0156
Koppen Cr. L. 96 T.	100	1.0000	0.0000	0.0000	0.0000	97	0.9536	0.0464
Koppen Cr. E. 96 U.	100	0.9950	0.0000	0.0000	0.0050	90	0.9222	0.0778
Koppen Cr. L. 96 U.	98	1.0000	0.0000	0.0000	0.0000	100	0.9500	0.0500
Makaka Cr. E. 96 U.	100	1.0000	0.0000	0.0000	0.0000	100	0.9650	0.0350
Bernard Cr. E. 96 T.	100	0.9950	0.0050	0.0000	0.0000	100	0.9600	0.0400
Bernard Cr. E. 96 U.	98	1.0000	0.0000	0.0000	0.0000	100	0.9650	0.0350
Constantine Cr. E. 96 T.	100	1.0000	0.0000	0.0000	0.0000	100	0.9600	0.0400
Constantine Cr. L. 96 T.	100	1.0000	0.0000	0.0000	0.0000	99	0.9596	0.0404
Constantine Cr. E. 96 U.	99	0.9949	0.0000	0.0051	0.0000	85	0.9765	0.0235
Constantine Cr. L. 96 U.	100	0.9950	0.0000	0.0050	0.0000	98	0.9745	0.0255

Population	mAAT-1*				AK*			CK-A1*		
	N	-100	-83	-108	N	-100	-145	N	100	66
Cabin Cr. E. 96 T.	52	0.9904	0.0096	0.0000	52	1.0000	0.0000	52	1.0000	0.0000
Cabin Cr. L. 96 T.					48	1.0000	0.0000	48	1.0000	0.0000
Hanning Cr. L. 96 T.	97	0.9845	0.0155	0.0000	100	1.0000	0.0000	97	1.0000	0.0000
Mink Cr. E. 96 T.	100	1.0000	0.0000	0.0000	100	1.0000	0.0000	100	1.0000	0.0000
Mink Cr. L. 96 T.	99	0.9899	0.0051	0.0051	100	1.0000	0.0000	100	0.9950	0.0050
Mink Cr. E. 96 U.	99	0.9949	0.0051	0.0000	100	1.0000	0.0000	98	1.0000	0.0000
Mink Cr. L. 96 U.	92	0.9891	0.0109	0.0000	100	1.0000	0.0000	100	1.0000	0.0000
Paulson Cr. L. 96 T.	100	0.9700	0.0300	0.0000	100	1.0000	0.0000	100	1.0000	0.0000
Paulson Cr. L. 96 U.	99	1.0000	0.0000	0.0000	100	1.0000	0.0000	96	1.0000	0.0000
Meachum Cr. E. 96 T.	100	1.0000	0.0000	0.0000	100	1.0000	0.0000	97	1.0000	0.0000
Meachum Cr. L. 96 T.	100	1.0000	0.0000	0.0000	97	1.0000	0.0000	100	1.0000	0.0000
Meachum Cr. E. 96 U.	99	1.0000	0.0000	0.0000	100	1.0000	0.0000	98	1.0000	0.0000
Meachum Cr. L. 96 U.	100	1.0000	0.0000	0.0000	100	1.0000	0.0000	100	1.0000	0.0000
Solomon Gulch L. 96 H.	99	0.9848	0.0152	0.0000	97	0.9948	0.0052	96	1.0000	0.0000
Koppen Cr. E. 96 T.	99	1.0000	0.0000	0.0000	100	1.0000	0.0000	100	1.0000	0.0000
Koppen Cr. L. 96 T.	96	0.9948	0.0052	0.0000	100	1.0000	0.0000	96	1.0000	0.0000
Koppen Cr. E. 96 U.	100	0.9850	0.0150	0.0000	100	1.0000	0.0000	97	1.0000	0.0000
Koppen Cr. L. 96 U.	100	0.9950	0.0000	0.0050	100	1.0000	0.0000	98	1.0000	0.0000
Makaka Cr. E. 96 U.	97	0.9897	0.0103	0.0000	100	1.0000	0.0000	100	1.0000	0.0000
Bernard Cr. E. 96 T.	100	0.9950	0.0050	0.0000	99	1.0000	0.0000	99	1.0000	0.0000
Bernard Cr. E. 96 U.	100	1.0000	0.0000	0.0000	100	1.0000	0.0000	100	1.0000	0.0000
Constantine Cr. E. 96 T.	100	1.0000	0.0000	0.0000	100	1.0000	0.0000	100	1.0000	0.0000
Constantine Cr. L. 96 T.	99	0.9949	0.0051	0.0000	100	1.0000	0.0000	100	1.0000	0.0000
Constantine Cr. E. 96 U.	99	1.0000	0.0000	0.0000	100	1.0000	0.0000	100	1.0000	0.0000
Constantine Cr. L. 96 U.	99	0.9899	0.0101	0.0000	100	1.0000	0.0000	100	1.0000	0.0000

Population	CK-A2*				CK-C1*			CK-C2*		
	N	100	82	135	N	100	92	N	100	105
Cabin Cr. E. 96 T.	52	1.0000	0.0000	0.0000	47	0.9894	0.0106	44	0.9886	0.0114
Cabin Cr. L. 96 T.	48	1.0000	0.0000	0.0000	47	0.9894	0.0106	47	0.9894	0.0106
Hanning Cr. L. 96 T.	97	0.9948	0.0052	0.0000	96	1.0000	0.0000	94	1.0000	0.0000
Mink Cr. E. 96 T.	98	1.0000	0.0000	0.0000	100	0.9950	0.0050	100	0.9900	0.0100
Mink Cr. L. 96 T.	100	0.9900	0.0000	0.0100	94	0.9894	0.0106	94	1.0000	0.0000
Mink Cr. E. 96 U.	98	0.9949	0.0051	0.0000	100	0.9950	0.0050	100	0.9950	0.0050
Mink Cr. L. 96 U.	100	1.0000	0.0000	0.0000	96	1.0000	0.0000	99	1.0000	0.0000
Paulson Cr. L. 96 T.	100	0.9950	0.0000	0.0050	97	0.9948	0.0052	97	1.0000	0.0000
Paulson Cr. L. 96 U.	96	0.9948	0.0000	0.0052	96	0.9948	0.0052	97	0.9948	0.0052
Meachum Cr. E. 96 T.	97	0.9897	0.0103	0.0000	100	1.0000	0.0000	100	0.9900	0.0100
Meachum Cr. L. 96 T.	100	0.9950	0.0050	0.0000	83	0.9940	0.0060	83	0.9880	0.0120
Meachum Cr. E. 96 U.	98	1.0000	0.0000	0.0000	96	0.9844	0.0156	97	0.9948	0.0052
Meachum Cr. L. 96 U.	100	1.0000	0.0000	0.0000	97	0.9948	0.0052	97	1.0000	0.0000
Solomon Gulch L. 96 H.	96	0.9896	0.0104	0.0000	97	1.0000	0.0000	98	0.9847	0.0153
Koppen Cr. E. 96 T.	100	0.9950	0.0050	0.0000	99	1.0000	0.0000	99	1.0000	0.0000
Koppen Cr. L. 96 T.	94	0.9894	0.0000	0.0106	96	0.9948	0.0052	98	1.0000	0.0000
Koppen Cr. E. 96 U.	97	0.9948	0.0052	0.0000	100	0.9950	0.0050	100	1.0000	0.0000
Koppen Cr. L. 96 U.	98	0.9949	0.0000	0.0051	80	1.0000	0.0000	79	0.9937	0.0063
Makaka Cr. E. 96 U.	100	1.0000	0.0000	0.0000	96	0.9896	0.0104	97	1.0000	0.0000
Bernard Cr. E. 96 T.	99	0.9949	0.0051	0.0000	97	0.9948	0.0052	96	1.0000	0.0000
Bernard Cr. E. 96 U.	100	0.9850	0.0150	0.0000	74	0.9932	0.0068	69	1.0000	0.0000
Constantine Cr. E. 96 T.	100	0.9950	0.0050	0.0000	97	1.0000	0.0000	99	1.0000	0.0000
Constantine Cr. L. 96 T.	100	0.9950	0.0000	0.0050	98	0.9949	0.0051	97	1.0000	0.0000
Constantine Cr. E. 96 U.	100	0.9850	0.0150	0.0000	94	1.0000	0.0000	89	1.0000	0.0000
Constantine Cr. L. 96 U.	100	0.9850	0.0100	0.0050	48	1.0000	0.0000	50	1.0000	0.0000

Population	FDHG*				GAPDH-2*			
	N	100	132	57	N	100	127	87
Cabin Cr. E. 96 T.	51	1.0000	0.0000	0.0000	52	1.0000	0.0000	0.0000
Cabin Cr. L. 96 T.	48	1.0000	0.0000	0.0000				
Hanning Cr. L. 96 T.	95	1.0000	0.0000	0.0000	98	0.9847	0.0102	0.0051
Mink Cr. E. 96 T.	94	0.9894	0.0106	0.0000	100	0.9750	0.0100	0.0150
Mink Cr. L. 96 T.	99	0.9798	0.0202	0.0000	99	0.9646	0.0253	0.0101
Mink Cr. E. 96 U.	99	0.9899	0.0051	0.0051	99	0.9949	0.0000	0.0051
Mink Cr. L. 96 U.	99	0.9949	0.0051	0.0000	100	0.9600	0.0300	0.0100
Paulson Cr. L. 96 T.	99	0.9949	0.0051	0.0000	100	0.9750	0.0250	0.0000
Paulson Cr. L. 96 U.	98	0.9898	0.0102	0.0000	100	0.9950	0.0050	0.0000
Meachum Cr. E. 96 T.	100	0.9950	0.0050	0.0000	99	0.9848	0.0101	0.0051
Meachum Cr. L. 96 T.	98	0.9898	0.0051	0.0051	99	0.9899	0.0051	0.0051
Meachum Cr. E. 96 U.	100	0.9950	0.0050	0.0000	100	0.9900	0.0050	0.0050
Meachum Cr. L. 96 U.	100	0.9850	0.0150	0.0000	98	0.9796	0.0102	0.0102
Solomon Gulch L. 96 H.	93	0.9946	0.0054	0.0000	98	0.9847	0.0051	0.0102
Koppen Cr. E. 96 T.	100	0.9800	0.0200	0.0000	100	0.9900	0.0000	0.0100
Koppen Cr. L. 96 T.	100	0.9800	0.0200	0.0000	99	0.9949	0.0000	0.0051
Koppen Cr. E. 96 U.	100	1.0000	0.0000	0.0000	100	0.9900	0.0000	0.0100
Koppen Cr. L. 96 U.	95	0.9895	0.0105	0.0000	99	0.9798	0.0152	0.0051
Makaka Cr. E. 96 U.	100	0.9950	0.0050	0.0000	100	0.9750	0.0050	0.0200
Bernard Cr. E. 96 T.	100	0.9900	0.0100	0.0000	99	0.9949	0.0051	0.0000
Bernard Cr. E. 96 U.	99	0.9798	0.0152	0.0051	100	0.9800	0.0100	0.0100
Constantine Cr. E. 96 T.	100	1.0000	0.0000	0.0000	100	0.9900	0.0050	0.0050
Constantine Cr. L. 96 T.	100	0.9950	0.0050	0.0000	97	0.9845	0.0052	0.0103
Constantine Cr. E. 96 U.	99	1.0000	0.0000	0.0000	100	0.9650	0.0200	0.0150
Constantine Cr. L. 96 U.	99	0.9949	0.0051	0.0000	99	1.0000	0.0000	0.0000

Population	PEPA*				G3PDH-1*			
	N	100	109	93	N	100	-151	-52
Cabin Cr. E. 96 T.	52	1.0000	0.0000	0.0000	52	0.8365	0.0000	0.1635
Cabin Cr. L. 96 T.	48	0.9896	0.0104	0.0000				
Hanning Cr. L. 96 T.	100	1.0000	0.0000	0.0000	100	0.8450	0.0000	0.1550
Mink Cr. E. 96 T.	99	1.0000	0.0000	0.0000	100	0.8200	0.0050	0.1750
Mink Cr. L. 96 T.	100	1.0000	0.0000	0.0000	100	0.7800	0.0050	0.2150
Mink Cr. E. 96 U.	99	1.0000	0.0000	0.0000	100	0.8450	0.0000	0.1550
Mink Cr. L. 96 U.	100	1.0000	0.0000	0.0000	100	0.8700	0.0050	0.1250
Paulson Cr. L. 96 T.	100	0.9950	0.0000	0.0050	100	0.8350	0.0050	0.1600
Paulson Cr. L. 96 U.	95	0.9947	0.0053	0.0000	100	0.8550	0.0000	0.1450
Meachum Cr. E. 96 T.	100	1.0000	0.0000	0.0000	99	0.8131	0.0000	0.1869
Meachum Cr. L. 96 T.	99	1.0000	0.0000	0.0000	100	0.8200	0.0000	0.1800
Meachum Cr. E. 96 U.	98	1.0000	0.0000	0.0000	100	0.8050	0.0000	0.1950
Meachum Cr. L. 96 U.	99	0.9949	0.0000	0.0051	100	0.7750	0.0000	0.2250
Solomon Gulch L. 96 H.	97	1.0000	0.0000	0.0000	99	0.8131	0.0000	0.1869
Koppen Cr. E. 96 T.	100	1.0000	0.0000	0.0000	100	0.8300	0.0000	0.1700
Koppen Cr. L. 96 T.	95	1.0000	0.0000	0.0000	100	0.8650	0.0050	0.1300
Koppen Cr. E. 96 U.	100	1.0000	0.0000	0.0000	100	0.8250	0.0000	0.1750
Koppen Cr. L. 96 U.	100	1.0000	0.0000	0.0000	100	0.7900	0.0000	0.2100
Makaka Cr. E. 96 U.	100	0.9950	0.0000	0.0050	100	0.8100	0.0000	0.1900
Bernard Cr. E. 96 T.	99	1.0000	0.0000	0.0000	100	0.7950	0.0000	0.2050
Bernard Cr. E. 96 U.	100	1.0000	0.0000	0.0000	100	0.8450	0.0000	0.1550
Constantine Cr. E. 96 T.	97	1.0000	0.0000	0.0000	100	0.8100	0.0000	0.1900
Constantine Cr. L. 96 T.	100	1.0000	0.0000	0.0000	100	0.8350	0.0000	0.1650
Constantine Cr. E. 96 U.	100	0.9900	0.0100	0.0000	100	0.8350	0.0000	0.1650
Constantine Cr. L. 96 U.	100	1.0000	0.0000	0.0000	100	0.8750	0.0000	0.1250

Population	G3PDH-2*				G3PDH-3*		
	N	100	120	90	N	100	90
Cabin Cr. E. 96 T.	52	0.9038	0.0192	0.0769	52	0.9423	0.0577
Cabin Cr. L. 96 T.							
Hanning Cr. L. 96 T.	100	0.9000	0.0100	0.0900	100	0.9900	0.0100
Mink Cr. E. 96 T.	94	0.9255	0.0000	0.0745	100	1.0000	0.0000
Mink Cr. L. 96 T.	100	0.9300	0.0250	0.0450	100	0.9950	0.0050
Mink Cr. E. 96 U.	81	0.9074	0.0432	0.0494	100	0.9900	0.0100
Mink Cr. L. 96 U.	98	0.9031	0.0204	0.0765	98	0.9949	0.0051
Paulson Cr. L. 96 T.	98	0.9286	0.0000	0.0714	99	0.9899	0.0101
Paulson Cr. L. 96 U.	99	0.8990	0.0202	0.0808	99	0.9848	0.0152
Meachum Cr. E. 96 T.	97	0.9227	0.0000	0.0773	100	0.9950	0.0050
Meachum Cr. L. 96 T.	99	0.9040	0.0152	0.0808	99	1.0000	0.0000
Meachum Cr. E. 96 U.	100	0.9050	0.0450	0.0500	100	0.9950	0.0050
Meachum Cr. L. 96 U.	98	0.9082	0.0255	0.0663	99	1.0000	0.0000
Solomon Gulch L. 96 H.	97	0.9381	0.0206	0.0412	99	0.9949	0.0051
Koppen Cr. E. 96 T.	97	0.8711	0.0309	0.0979	100	0.9850	0.0150
Koppen Cr. L. 96 T.	100	0.9450	0.0100	0.0450	98	0.9949	0.0051
Koppen Cr. E. 96 U.	100	0.8700	0.0500	0.0800	99	0.9949	0.0051
Koppen Cr. L. 96 U.	100	0.8250	0.0300	0.1450	100	0.9900	0.0100
Makaka Cr. E. 96 U.	100	0.9200	0.0200	0.0600	100	0.9950	0.0050
Bernard Cr. E. 96 T.	100	0.8900	0.0150	0.0950	100	0.9750	0.0250
Bernard Cr. E. 96 U.	100	0.8950	0.0200	0.0850	100	0.9850	0.0150
Constantine Cr. E. 96 T.	100	0.8450	0.0300	0.1250	100	0.9950	0.0050
Constantine Cr. L. 96 T.	99	0.8636	0.0404	0.0960	100	0.9950	0.0050
Constantine Cr. E. 96 U.	99	0.8283	0.0455	0.1263	97	0.9948	0.0052
Constantine Cr. L. 96 U.	99	0.8838	0.0455	0.0707	98	1.0000	0.0000

Population	GPI-B1,2*				GPI-A*			
	N	100	200	25	N	100	91	88
Cabin Cr. E. 96 T.	52	1.0000	0.0000	0.0000	52	1.0000	0.0000	0.0000
Cabin Cr. L. 96 T.	48	0.9740	0.0208	0.0052	48	1.0000	0.0000	0.0000
Hanning Cr. L. 96 T.	100	0.9900	0.0100	0.0000	100	1.0000	0.0000	0.0000
Mink Cr. E. 96 T.	100	0.9875	0.0125	0.0000	100	0.9950	0.0000	0.0050
Mink Cr. L. 96 T.	100	0.9925	0.0075	0.0000	100	1.0000	0.0000	0.0000
Mink Cr. E. 96 U.	100	0.9925	0.0075	0.0000	100	1.0000	0.0000	0.0000
Mink Cr. L. 96 U.	100	0.9850	0.0125	0.0025	100	1.0000	0.0000	0.0000
Paulson Cr. L. 96 T.	100	0.9950	0.0050	0.0000	100	1.0000	0.0000	0.0000
Paulson Cr. L. 96 U.	100	0.9925	0.0075	0.0000	100	0.9950	0.0050	0.0000
Meachum Cr. E. 96 T.	98	0.9949	0.0051	0.0000	98	1.0000	0.0000	0.0000
Meachum Cr. L. 96 T.	100	1.0000	0.0000	0.0000	99	1.0000	0.0000	0.0000
Meachum Cr. E. 96 U.	100	0.9950	0.0050	0.0000	100	1.0000	0.0000	0.0000
Meachum Cr. L. 96 U.	100	0.9825	0.0150	0.0025	100	1.0000	0.0000	0.0000
Solomon Gulch L. 96 H.	100	0.9875	0.0125	0.0000	100	0.9950	0.0050	0.0000
Koppen Cr. E. 96 T.	100	0.9900	0.0100	0.0000	100	0.9950	0.0050	0.0000
Koppen Cr. L. 96 T.	100	0.9900	0.0100	0.0000	100	1.0000	0.0000	0.0000
Koppen Cr. E. 96 U.	100	0.9975	0.0025	0.0000	100	1.0000	0.0000	0.0000
Koppen Cr. L. 96 U.	100	0.9900	0.0075	0.0025	100	0.9950	0.0000	0.0050
Makaka Cr. E. 96 U.	100	0.9950	0.0050	0.0000	100	0.9950	0.0050	0.0000
Bernard Cr. E. 96 T.	99	1.0000	0.0000	0.0000	99	0.9949	0.0051	0.0000
Bernard Cr. E. 96 U.	100	0.9975	0.0025	0.0000	100	1.0000	0.0000	0.0000
Constantine Cr. E. 96 T.	100	0.9900	0.0100	0.0000	100	1.0000	0.0000	0.0000
Constantine Cr. L. 96 T.	100	0.9950	0.0050	0.0000	100	1.0000	0.0000	0.0000
Constantine Cr. E. 96 U.	100	0.9950	0.0050	0.0000	100	1.0000	0.0000	0.0000
Constantine Cr. L. 96 U.	100	0.9900	0.0100	0.0000	100	1.0000	0.0000	0.0000

Population	mIDHP-1*				mIDHP-2*		
	N	100	53	69	N	100	118
Cabin Cr. E. 96 T.	52	0.9904	0.0000	0.0096	52	1.0000	0.0000
Cabin Cr. L. 96 T.							
Hanning Cr. L. 96 T.	100	1.0000	0.0000	0.0000	100	1.0000	0.0000
Mink Cr. E. 96 T.	100	1.0000	0.0000	0.0000	100	1.0000	0.0000
Mink Cr. L. 96 T.	98	1.0000	0.0000	0.0000	98	1.0000	0.0000
Mink Cr. E. 96 U.	99	1.0000	0.0000	0.0000	99	1.0000	0.0000
Mink Cr. L. 96 U.	100	0.9850	0.0050	0.0100	100	1.0000	0.0000
Paulson Cr. L. 96 T.	100	0.9950	0.0000	0.0050	100	1.0000	0.0000
Paulson Cr. L. 96 U.	100	0.9900	0.0100	0.0000	100	1.0000	0.0000
Meachum Cr. E. 96 T.	96	1.0000	0.0000	0.0000	96	1.0000	0.0000
Meachum Cr. L. 96 T.	100	1.0000	0.0000	0.0000	100	1.0000	0.0000
Meachum Cr. E. 96 U.	100	1.0000	0.0000	0.0000	100	1.0000	0.0000
Meachum Cr. L. 96 U.	100	1.0000	0.0000	0.0000	100	1.0000	0.0000
Solomon Gulch L. 96 H.	99	1.0000	0.0000	0.0000	99	1.0000	0.0000
Koppen Cr. E. 96 T.	99	0.9949	0.0000	0.0051	99	1.0000	0.0000
Koppen Cr. L. 96 T.	100	1.0000	0.0000	0.0000	100	1.0000	0.0000
Koppen Cr. E. 96 U.	100	1.0000	0.0000	0.0000	100	0.9950	0.0050
Koppen Cr. L. 96 U.	100	1.0000	0.0000	0.0000	100	1.0000	0.0000
Makaka Cr. E. 96 U.	100	1.0000	0.0000	0.0000	100	1.0000	0.0000
Bernard Cr. E. 96 T.	100	1.0000	0.0000	0.0000	100	1.0000	0.0000
Bernard Cr. E. 96 U.	100	1.0000	0.0000	0.0000	100	1.0000	0.0000
Constantine Cr. E. 96 T.	100	0.9950	0.0000	0.0050	100	1.0000	0.0000
Constantine Cr. L. 96 T.	97	0.9948	0.0052	0.0000	99	1.0000	0.0000
Constantine Cr. E. 96 U.	100	0.9950	0.0000	0.0050	100	1.0000	0.0000
Constantine Cr. L. 96 U.	99	0.9848	0.0051	0.0101	99	1.0000	0.0000

Population	SIDHP-2*					LDH-A1*		
	N	100	125/130	76/90	141/166	N	-100	-250
Cabin Cr. E. 96 T.	51	0.7451	0.2549	0.0000	0.0000	52	1.0000	0.0000
Cabin Cr. L. 96 T.	47	0.5745	0.4255	0.0000	0.0000	48	1.0000	0.0000
Hanning Cr. L. 96 T.	100	0.6000	0.4000	0.0000	0.0000	100	1.0000	0.0000
Mink Cr. E. 96 T.	99	0.6212	0.3788	0.0000	0.0000	100	1.0000	0.0000
Mink Cr. L. 96 T.	99	0.6061	0.3939	0.0000	0.0000	99	1.0000	0.0000
Mink Cr. E. 96 U.	99	0.6566	0.3384	0.0000	0.0051	100	1.0000	0.0000
Mink Cr. L. 96 U.	96	0.6927	0.3073	0.0000	0.0000	100	1.0000	0.0000
Paulson Cr. L. 96 T.	99	0.6162	0.3838	0.0000	0.0000	100	1.0000	0.0000
Paulson Cr. L. 96 U.	99	0.6061	0.3889	0.0000	0.0051	98	1.0000	0.0000
Meachum Cr. E. 96 T.	100	0.6500	0.3500	0.0000	0.0000	100	1.0000	0.0000
Meachum Cr. L. 96 T.	98	0.6684	0.3316	0.0000	0.0000	100	1.0000	0.0000
Meachum Cr. E. 96 U.	99	0.6111	0.3838	0.0051	0.0000	100	1.0000	0.0000
Meachum Cr. L. 96 U.	99	0.6818	0.3182	0.0000	0.0000	100	1.0000	0.0000
Solomon Gulch L. 96 H.	100	0.7650	0.2350	0.0000	0.0000	97	0.9948	0.0052
Koppen Cr. E. 96 T.	99	0.6616	0.3384	0.0000	0.0000	100	1.0000	0.0000
Koppen Cr. L. 96 T.	99	0.6465	0.3535	0.0000	0.0000	96	1.0000	0.0000
Koppen Cr. E. 96 U.	100	0.6150	0.3850	0.0000	0.0000	100	1.0000	0.0000
Koppen Cr. L. 96 U.	98	0.6531	0.3469	0.0000	0.0000	100	1.0000	0.0000
Makaka Cr. E. 96 U.	99	0.5606	0.4343	0.0000	0.0051	100	1.0000	0.0000
Bernard Cr. E. 96 T.	96	0.6302	0.3698	0.0000	0.0000	100	1.0000	0.0000
Bernard Cr. E. 96 U.	98	0.7347	0.2602	0.0051	0.0000	100	1.0000	0.0000
Constantine Cr. E. 96 T.	100	0.7000	0.3000	0.0000	0.0000	98	1.0000	0.0000
Constantine Cr. L. 96 T.	100	0.5850	0.4150	0.0000	0.0000	100	1.0000	0.0000
Constantine Cr. E. 96 U.	99	0.6717	0.3283	0.0000	0.0000	100	1.0000	0.0000
Constantine Cr. L. 96 U.	99	0.6212	0.3788	0.0000	0.0000	100	1.0000	0.0000

Population	LDH-B1*				LDH-B2*			
	N	100	86	153	N	100	151	124
Cabin Cr. E. 96 T.	52	1.0000	0.0000	0.0000	52	1.0000	0.0000	0.0000
Cabin Cr. L. 96 T.	48	1.0000	0.0000	0.0000	48	0.9688	0.0000	0.0312
Hanning Cr. L. 96 T.	99	0.9899	0.0000	0.0101	100	0.9950	0.0000	0.0050
Mink Cr. E. 96 T.	100	0.9900	0.0000	0.0100	100	0.9950	0.0000	0.0050
Mink Cr. L. 96 T.	98	0.9949	0.0000	0.0051	100	0.9900	0.0050	0.0050
Mink Cr. E. 96 U.	100	0.9900	0.0000	0.0100	100	0.9900	0.0000	0.0100
Mink Cr. L. 96 U.	100	1.0000	0.0000	0.0000	100	1.0000	0.0000	0.0000
Paulson Cr. L. 96 T.	91	0.9890	0.0055	0.0055	100	0.9950	0.0000	0.0050
Paulson Cr. L. 96 U.	100	1.0000	0.0000	0.0000	100	0.9900	0.0000	0.0100
Meachum Cr. E. 96 T.	99	0.9899	0.0000	0.0101	100	0.9750	0.0000	0.0250
Meachum Cr. L. 96 T.	100	0.9950	0.0000	0.0050	100	0.9950	0.0000	0.0050
Meachum Cr. E. 96 U.	76	0.9868	0.0000	0.0132	100	0.9800	0.0000	0.0200
Meachum Cr. L. 96 U.	100	1.0000	0.0000	0.0000	100	0.9950	0.0000	0.0050
Solomon Gulch L. 96 H.	100	1.0000	0.0000	0.0000	100	0.9950	0.0000	0.0050
Koppen Cr. E. 96 T.	98	1.0000	0.0000	0.0000	100	0.9900	0.0000	0.0100
Koppen Cr. L. 96 T.	97	0.9948	0.0000	0.0052	100	1.0000	0.0000	0.0000
Koppen Cr. E. 96 U.	100	1.0000	0.0000	0.0000	100	0.9950	0.0000	0.0050
Koppen Cr. L. 96 U.	100	1.0000	0.0000	0.0000	100	0.9850	0.0050	0.0100
Makaka Cr. E. 96 U.	98	0.9949	0.0051	0.0000	100	0.9900	0.0000	0.0100
Bernard Cr. E. 96 T.	100	0.9900	0.0000	0.0100	100	0.9950	0.0000	0.0050
Bernard Cr. E. 96 U.	100	0.9900	0.0000	0.0100	100	0.9900	0.0000	0.0100
Constantine Cr. E. 96 T.	100	0.9900	0.0000	0.0100	100	0.9950	0.0000	0.0050
Constantine Cr. L. 96 T.	99	1.0000	0.0000	0.0000	100	1.0000	0.0000	0.0000
Constantine Cr. E. 96 U.	100	1.0000	0.0000	0.0000	100	0.9900	0.0000	0.0100
Constantine Cr. L. 96 U.	100	0.9850	0.0000	0.0150	100	0.9750	0.0000	0.0250

Population	PEPB-1*				PEPLT*			
	N	100	138	200	N	100	108	90
Cabin Cr. E. 96 T.	51	0.8431	0.1471	0.0098	51	0.8137	0.0784	0.1078
Cabin Cr. L. 96 T.	40	0.8375	0.1250	0.0375	48	0.8750	0.0833	0.0417
Hanning Cr. L. 96 T.	100	0.8650	0.1100	0.0250	100	0.8750	0.0900	0.0350
Mink Cr. E. 96 T.	100	0.9050	0.0850	0.0100	99	0.9293	0.0303	0.0404
Mink Cr. L. 96 T.	99	0.8636	0.1061	0.0303	100	0.8450	0.0750	0.0800
Mink Cr. E. 96 U.	100	0.9100	0.0650	0.0250	70	0.8500	0.0643	0.0857
Mink Cr. L. 96 U.	100	0.8550	0.1100	0.0350	70	0.8286	0.1000	0.0714
Paulson Cr. L. 96 T.	100	0.8650	0.1150	0.0200	100	0.8800	0.0400	0.0800
Paulson Cr. L. 96 U.	100	0.8350	0.1500	0.0150	94	0.8830	0.0479	0.0691
Meachum Cr. E. 96 T.	98	0.8622	0.1122	0.0255	95	0.9316	0.0421	0.0263
Meachum Cr. L. 96 T.	100	0.8850	0.0900	0.0250	98	0.9184	0.0408	0.0408
Meachum Cr. E. 96 U.	100	0.9100	0.0850	0.0050	98	0.9082	0.0561	0.0357
Meachum Cr. L. 96 U.	100	0.8600	0.1100	0.0300	99	0.8636	0.0909	0.0455
Solomon Gulch L. 96 H.	100	0.8150	0.1400	0.0450	97	0.8763	0.0876	0.0361
Koppen Cr. E. 96 T.	100	0.8450	0.1050	0.0500	100	0.9150	0.0500	0.0350
Koppen Cr. L. 96 T.	100	0.8850	0.0950	0.0200	95	0.8895	0.0684	0.0421
Koppen Cr. E. 96 U.	100	0.8700	0.0750	0.0550	100	0.8900	0.0350	0.0750
Koppen Cr. L. 96 U.	100	0.8600	0.1150	0.0250	99	0.8939	0.0808	0.0253
Makaka Cr. E. 96 U.	100	0.8400	0.1350	0.0250	98	0.8827	0.0510	0.0663
Bernard Cr. E. 96 T.	100	0.9150	0.0500	0.0350	98	0.8724	0.0459	0.0816
Bernard Cr. E. 96 U.	100	0.8800	0.1000	0.0200	99	0.8838	0.0657	0.0505
Constantine Cr. E. 96 T.	100	0.8700	0.0950	0.0350	97	0.8093	0.0825	0.1082
Constantine Cr. L. 96 T.	100	0.8650	0.0950	0.0400	100	0.8700	0.0750	0.0550
Constantine Cr. E. 96 U.	100	0.8150	0.1550	0.0300	100	0.9000	0.0650	0.0350
Constantine Cr. L. 96 U.	99	0.8636	0.1162	0.0202	100	0.7850	0.1400	0.0750

Population	sMDH-A1, 2*					sMDH-B1, 2*			
	N	100	148	-32	50	N	100	124	66
Cabin Cr. E. 96 T.	52	0.9856	0.0000	0.0000	0.0144	52	1.0000	0.0000	0.0000
Cabin Cr. L. 96 T.	48	0.9896	0.0000	0.0000	0.0104	48	0.9948	0.0052	0.0000
Hanning Cr. L. 96 T.	100	0.9850	0.0000	0.0000	0.0150	100	0.9875	0.0100	0.0025
Mink Cr. E. 96 T.	100	0.9800	0.0050	0.0000	0.0150	100	0.9925	0.0050	0.0025
Mink Cr. L. 96 T.	100	0.9750	0.0000	0.0000	0.0250	100	0.9950	0.0025	0.0025
Mink Cr. E. 96 U.	100	0.9900	0.0025	0.0000	0.0075	100	0.9975	0.0025	0.0000
Mink Cr. L. 96 U.	100	0.9775	0.0000	0.0000	0.0225	100	0.9850	0.0075	0.0075
Paulson Cr. L. 96 T.	100	0.9950	0.0000	0.0000	0.0050	100	0.9925	0.0075	0.0000
Paulson Cr. L. 96 U.	100	0.9850	0.0000	0.0000	0.0150	100	0.9900	0.0050	0.0050
Meachum Cr. E. 96 T.	100	0.9875	0.0025	0.0000	0.0100	100	0.9975	0.0025	0.0000
Meachum Cr. L. 96 T.	100	0.9725	0.0000	0.0000	0.0275	100	0.9850	0.0125	0.0025
Meachum Cr. E. 96 U.	100	0.9900	0.0000	0.0000	0.0100	100	0.9900	0.0100	0.0000
Meachum Cr. L. 96 U.	100	0.9825	0.0000	0.0000	0.0175	100	0.9975	0.0025	0.0000
Solomon Gulch L. 96 H.	100	0.9825	0.0000	0.0000	0.0175	100	0.9950	0.0050	0.0000
Koppen Cr. E. 96 T.	100	0.9850	0.0000	0.0000	0.0150	100	0.9900	0.0050	0.0050
Koppen Cr. L. 96 T.	100	0.9800	0.0025	0.0000	0.0175	100	0.9950	0.0050	0.0000
Koppen Cr. E. 96 U.	100	0.9850	0.0025	0.0000	0.0125	100	0.9950	0.0050	0.0000
Koppen Cr. L. 96 U.	100	0.9975	0.0000	0.0000	0.0025	100	0.9900	0.0075	0.0025
Makaka Cr. E. 96 U.	100	0.9850	0.0025	0.0000	0.0125	100	0.9925	0.0050	0.0025
Bernard Cr. E. 96 T.	100	0.9800	0.0025	0.0000	0.0175	100	0.9950	0.0050	0.0000
Bernard Cr. E. 96 U.	100	0.9725	0.0025	0.0000	0.0250	100	0.9950	0.0050	0.0000
Constantine Cr. E. 96 T.	100	0.9775	0.0075	0.0025	0.0125	100	0.9900	0.0050	0.0050
Constantine Cr. L. 96 T.	100	0.9775	0.0025	0.0000	0.0200	100	0.9900	0.0100	0.0000
Constantine Cr. E. 96 U.	100	0.9850	0.0000	0.0000	0.0150	100	0.9925	0.0075	0.0000
Constantine Cr. L. 96 U.	99	0.9773	0.0025	0.0000	0.0202	100	0.9875	0.0100	0.0025

Population	mMEP-1*				mMDH-2*			MPI*		
	N	100	123	84	N	100	228	N	100	94
Cabin Cr. E. 96 T.	52	0.7596	0.2404	0.0000	47	1.0000	0.0000	52	0.9904	0.0096
Cabin Cr. L. 96 T.	48	0.7188	0.2812	0.0000				39	1.0000	0.0000
Hanning Cr. L. 96 T.	95	0.6474	0.3526	0.0000	100	1.0000	0.0000	100	0.9900	0.0100
Mink Cr. E. 96 T.	100	0.7800	0.2200	0.0000	97	1.0000	0.0000	95	1.0000	0.0000
Mink Cr. L. 96 T.	100	0.7300	0.2700	0.0000	98	1.0000	0.0000	100	1.0000	0.0000
Mink Cr. E. 96 U.	100	0.7850	0.2150	0.0000	100	1.0000	0.0000	99	1.0000	0.0000
Mink Cr. L. 96 U.	100	0.7100	0.2900	0.0000	100	1.0000	0.0000	100	1.0000	0.0000
Paulson Cr. L. 96 T.	99	0.7424	0.2576	0.0000	100	1.0000	0.0000	100	1.0000	0.0000
Paulson Cr. L. 96 U.	98	0.7245	0.2755	0.0000	48	1.0000	0.0000	99	1.0000	0.0000
Meachum Cr. E. 96 T.	99	0.6970	0.3030	0.0000	98	1.0000	0.0000	100	1.0000	0.0000
Meachum Cr. L. 96 T.	99	0.7475	0.2525	0.0000	100	1.0000	0.0000	95	0.9947	0.0053
Meachum Cr. E. 96 U.	98	0.6429	0.3571	0.0000	100	1.0000	0.0000	100	1.0000	0.0000
Meachum Cr. L. 96 U.	100	0.7550	0.2450	0.0000	96	1.0000	0.0000	98	1.0000	0.0000
Solomon Gulch L. 96 H.	97	0.7474	0.2526	0.0000	97	1.0000	0.0000	98	0.9949	0.0051
Koppen Cr. E. 96 T.	100	0.7050	0.2950	0.0000	98	1.0000	0.0000	100	1.0000	0.0000
Koppen Cr. L. 96 T.	100	0.7550	0.2450	0.0000	94	0.9947	0.0053	100	1.0000	0.0000
Koppen Cr. E. 96 U.	100	0.6850	0.3150	0.0000	100	1.0000	0.0000	100	1.0000	0.0000
Koppen Cr. L. 96 U.	99	0.7374	0.2576	0.0051	98	1.0000	0.0000	100	1.0000	0.0000
Makaka Cr. E. 96 U.	100	0.7300	0.2700	0.0000	100	0.9950	0.0050	99	1.0000	0.0000
Bernard Cr. E. 96 T.	99	0.7172	0.2828	0.0000	100	1.0000	0.0000	100	1.0000	0.0000
Bernard Cr. E. 96 U.	100	0.7400	0.2600	0.0000	100	1.0000	0.0000	100	1.0000	0.0000
Constantine Cr. E. 96 T.	99	0.7980	0.2020	0.0000	100	1.0000	0.0000	100	1.0000	0.0000
Constantine Cr. L. 96 T.	100	0.6950	0.3050	0.0000	98	1.0000	0.0000	100	1.0000	0.0000
Constantine Cr. E. 96 U.	100	0.7300	0.2700	0.0000	100	1.0000	0.0000	100	1.0000	0.0000
Constantine Cr. L. 96 U.	99	0.6667	0.3333	0.0000	50	1.0000	0.0000	49	1.0000	0.0000

Population	PGDH*					PGK-2*			
	N	100	108	96	86	N	100	122	85
Cabin Cr. E. 96 T.	52	0.7212	0.0000	0.2404	0.0385	52	0.9904	0.0000	0.0096
Cabin Cr. L. 96 T.	47	0.7021	0.0000	0.2553	0.0426	48	1.0000	0.0000	0.0000
Hanning Cr. L. 96 T.	100	0.6650	0.0000	0.2700	0.0650	93	1.0000	0.0000	0.0000
Mink Cr. E. 96 T.	50	0.7200	0.0200	0.2300	0.0300	100	1.0000	0.0000	0.0000
Mink Cr. L. 96 T.	97	0.7062	0.0000	0.2629	0.0309				
Mink Cr. E. 96 U.	100	0.7400	0.0000	0.2450	0.0150	100	1.0000	0.0000	0.0000
Mink Cr. L. 96 U.	100	0.7200	0.0000	0.2250	0.0550	100	1.0000	0.0000	0.0000
Paulson Cr. L. 96 T.	100	0.7250	0.0000	0.2600	0.0150	100	1.0000	0.0000	0.0000
Paulson Cr. L. 96 U.	100	0.7000	0.0000	0.2500	0.0500				
Meachum Cr. E. 96 T.	98	0.7449	0.0000	0.2398	0.0153				
Meachum Cr. L. 96 T.	100	0.7350	0.0000	0.2300	0.0350	100	1.0000	0.0000	0.0000
Meachum Cr. E. 96 U.	100	0.7350	0.0000	0.2600	0.0050	100	0.9950	0.0050	0.0000
Meachum Cr. L. 96 U.	100	0.7700	0.0000	0.2200	0.0100	100	1.0000	0.0000	0.0000
Solomon Gulch L. 96 H.	99	0.7374	0.0000	0.2323	0.0303				
Koppen Cr. E. 96 T.	100	0.7800	0.0000	0.2000	0.0200	100	1.0000	0.0000	0.0000
Koppen Cr. L. 96 T.	99	0.7374	0.0000	0.2424	0.0202	100	1.0000	0.0000	0.0000
Koppen Cr. E. 96 U.	100	0.7700	0.0000	0.1850	0.0450				
Koppen Cr. L. 96 U.	100	0.7450	0.0000	0.2200	0.0350	100	1.0000	0.0000	0.0000
Makaka Cr. E. 96 U.	100	0.6650	0.0000	0.2950	0.0400	100	1.0000	0.0000	0.0000
Bernard Cr. E. 96 T.	98	0.7500	0.0000	0.2245	0.0255	99	1.0000	0.0000	0.0000
Bernard Cr. E. 96 U.	100	0.7100	0.0050	0.2650	0.0200	100	1.0000	0.0000	0.0000
Constantine Cr. E. 96 T.	99	0.6970	0.0000	0.2778	0.0253	100	1.0000	0.0000	0.0000
Constantine Cr. L. 96 T.	99	0.7020	0.0051	0.2626	0.0303	100	1.0000	0.0000	0.0000
Constantine Cr. E. 96 U.	100	0.7100	0.0050	0.2400	0.0450	100	1.0000	0.0000	0.0000
Constantine Cr. L. 96 U.	100	0.6900	0.0000	0.2550	0.0550				

Population	PGM-2*							PEPD-2*			
	N	100	155	137	25	250	178	N	100	120	80
Cabin Cr. E. 96 T.	52	0.9904	0.0096	0.0000	0.0000	0.0000	0.0000	52	0.4231	0.2596	0.3173
Cabin Cr. L. 96 T.	48	1.0000	0.0000	0.0000	0.0000	0.0000	0.0000				
Hanning Cr. L. 96 T.	100	0.9950	0.0050	0.0000	0.0000	0.0000	0.0000	99	0.5909	0.1919	0.2172
Mink Cr. E. 96 T.	100	1.0000	0.0000	0.0000	0.0000	0.0000	0.0000	100	0.5200	0.2550	0.2250
Mink Cr. L. 96 T.	100	0.9800	0.0000	0.0000	0.0050	0.0000	0.0150	100	0.5600	0.1900	0.2500
Mink Cr. E. 96 U.	100	0.9950	0.0000	0.0000	0.0000	0.0000	0.0050	100	0.5050	0.2900	0.2050
Mink Cr. L. 96 U.	100	1.0000	0.0000	0.0000	0.0000	0.0000	0.0000	100	0.5450	0.2100	0.2450
Paulson Cr. L. 96 T.	100	1.0000	0.0000	0.0000	0.0000	0.0000	0.0000	100	0.5500	0.2000	0.2500
Paulson Cr. L. 96 U.	100	0.9900	0.0050	0.0000	0.0000	0.0000	0.0050	100	0.5050	0.1750	0.3200
Meachum Cr. E. 96 T.	100	0.9900	0.0050	0.0000	0.0000	0.0050	0.0000	100	0.4800	0.2850	0.2350
Meachum Cr. L. 96 T.	100	1.0000	0.0000	0.0000	0.0000	0.0000	0.0000	99	0.5606	0.2222	0.2172
Meachum Cr. E. 96 U.	100	1.0000	0.0000	0.0000	0.0000	0.0000	0.0000	100	0.5350	0.2850	0.1800
Meachum Cr. L. 96 U.	100	0.9850	0.0050	0.0000	0.0050	0.0000	0.0050	100	0.5650	0.1950	0.2400
Solomon Gulch L. 96 H.	97	1.0000	0.0000	0.0000	0.0000	0.0000	0.0000	99	0.5455	0.2071	0.2475
Koppen Cr. E. 96 T.	100	0.9950	0.0050	0.0000	0.0000	0.0000	0.0000	100	0.5450	0.2700	0.1850
Koppen Cr. L. 96 T.	100	0.9950	0.0000	0.0000	0.0000	0.0000	0.0050	100	0.4550	0.2800	0.2650
Koppen Cr. E. 96 U.	100	1.0000	0.0000	0.0000	0.0000	0.0000	0.0000	100	0.5350	0.2550	0.2100
Koppen Cr. L. 96 U.	100	1.0000	0.0000	0.0000	0.0000	0.0000	0.0000	99	0.5404	0.2323	0.2273
Makaka Cr. E. 96 U.	100	0.9900	0.0050	0.0000	0.0000	0.0000	0.0050	100	0.5100	0.2400	0.2500
Bernard Cr. E. 96 T.	100	0.9950	0.0050	0.0000	0.0000	0.0000	0.0000	100	0.5000	0.2650	0.2350
Bernard Cr. E. 96 U.	100	0.9950	0.0000	0.0050	0.0000	0.0000	0.0000	100	0.5150	0.2400	0.2450
Constantine Cr. E. 96 T.	100	0.9950	0.0050	0.0000	0.0000	0.0000	0.0000	100	0.5050	0.2100	0.2850
Constantine Cr. L. 96 T.	96	1.0000	0.0000	0.0000	0.0000	0.0000	0.0000	100	0.4800	0.2350	0.2850
Constantine Cr. E. 96 U.	100	0.9950	0.0000	0.0000	0.0000	0.0000	0.0050	100	0.5150	0.2400	0.2450
Constantine Cr. L. 96 U.	100	1.0000	0.0000	0.0000	0.0000	0.0000	0.0000	100	0.5300	0.2300	0.2400

Population	<i>mSOD*</i>				<i>sSOD-1*</i>				
	N	100	145	16	N	100	176	15	140
Cabin Cr. E. 96 T.	52	0.9904	0.0096	0.0000	52	1.0000	0.0000	0.0000	0.0000
Cabin Cr. L. 96 T.									
Hanning Cr. L. 96 T.	100	0.9950	0.0050	0.0000	100	1.0000	0.0000	0.0000	0.0000
Mink Cr. E. 96 T.	100	0.9950	0.0050	0.0000	100	0.9950	0.0000	0.0050	0.0000
Mink Cr. L. 96 T.	100	0.9850	0.0150	0.0000	100	1.0000	0.0000	0.0000	0.0000
Mink Cr. E. 96 U.	98	0.9847	0.0153	0.0000	98	1.0000	0.0000	0.0000	0.0000
Mink Cr. L. 96 U.	100	0.9900	0.0100	0.0000	100	1.0000	0.0000	0.0000	0.0000
Paulson Cr. L. 96 T.	100	0.9950	0.0050	0.0000	100	1.0000	0.0000	0.0000	0.0000
Paulson Cr. L. 96 U.	100	0.9800	0.0100	0.0100	100	1.0000	0.0000	0.0000	0.0000
Meachum Cr. E. 96 T.	100	0.9950	0.0050	0.0000	100	0.9900	0.0100	0.0000	0.0000
Meachum Cr. L. 96 T.	100	0.9950	0.0050	0.0000	100	0.9950	0.0050	0.0000	0.0000
Meachum Cr. E. 96 U.	100	0.9750	0.0250	0.0000	100	1.0000	0.0000	0.0000	0.0000
Meachum Cr. L. 96 U.	100	0.9900	0.0100	0.0000	100	0.9950	0.0000	0.0050	0.0000
Solomon Gulch L. 96 H.	99	1.0000	0.0000	0.0000	99	1.0000	0.0000	0.0000	0.0000
Koppen Cr. E. 96 T.	99	0.9949	0.0051	0.0000	99	1.0000	0.0000	0.0000	0.0000
Koppen Cr. L. 96 T.	98	0.9847	0.0153	0.0000	100	1.0000	0.0000	0.0000	0.0000
Koppen Cr. E. 96 U.	100	0.9950	0.0050	0.0000	100	0.9900	0.0050	0.0000	0.0050
Koppen Cr. L. 96 U.	100	0.9800	0.0200	0.0000	100	0.9950	0.0000	0.0050	0.0000
Makaka Cr. E. 96 U.	100	0.9900	0.0100	0.0000	100	1.0000	0.0000	0.0000	0.0000
Bernard Cr. E. 96 T.	100	0.9900	0.0050	0.0050	100	1.0000	0.0000	0.0000	0.0000
Bernard Cr. E. 96 U.	100	0.9850	0.0100	0.0050	100	1.0000	0.0000	0.0000	0.0000
Constantine Cr. E. 96 T.	99	0.9899	0.0051	0.0051	100	0.9950	0.0000	0.0050	0.0000
Constantine Cr. L. 96 T.	99	0.9949	0.0051	0.0000	100	1.0000	0.0000	0.0000	0.0000
Constantine Cr. E. 96 U.	99	0.9899	0.0101	0.0000	99	1.0000	0.0000	0.0000	0.0000
Constantine Cr. L. 96 U.	100	0.9750	0.0250	0.0000	99	1.0000	0.0000	0.0000	0.0000

Population	TPI-2*			TPI-3*		
	N	-100	110	N	100	92
Cabin Cr. E. 96 T.	51	0.9902	0.0098	51	1.0000	0.0000
Cabin Cr. L. 96 T.	48	0.9792	0.0208	48	1.0000	0.0000
Hanning Cr. L. 96 T.	100	0.9750	0.0250	100	1.0000	0.0000
Mink Cr. E. 96 T.	99	0.9848	0.0152	99	1.0000	0.0000
Mink Cr. L. 96 T.	100	0.9850	0.0150	100	1.0000	0.0000
Mink Cr. E. 96 U.	100	0.9800	0.0200	100	1.0000	0.0000
Mink Cr. L. 96 U.	100	0.9900	0.0100	100	1.0000	0.0000
Paulson Cr. L. 96 T.	100	0.9800	0.0200	100	1.0000	0.0000
Paulson Cr. L. 96 U.	100	1.0000	0.0000	100	1.0000	0.0000
Meachum Cr. E. 96 T.	100	0.9900	0.0100	100	0.9950	0.0050
Meachum Cr. L. 96 T.	100	0.9800	0.0200	100	1.0000	0.0000
Meachum Cr. E. 96 U.	100	0.9950	0.0050	100	1.0000	0.0000
Meachum Cr. L. 96 U.	100	0.9850	0.0150	100	1.0000	0.0000
Solomon Gulch L. 96 H.	100	0.9900	0.0100	100	1.0000	0.0000
Koppen Cr. E. 96 T.	100	0.9850	0.0150	100	1.0000	0.0000
Koppen Cr. L. 96 T.	100	0.9900	0.0100	50	1.0000	0.0000
Koppen Cr. E. 96 U.	100	0.9700	0.0300	96	1.0000	0.0000
Koppen Cr. L. 96 U.	100	0.9850	0.0150	100	1.0000	0.0000
Makaka Cr. E. 96 U.	98	0.9847	0.0153	98	1.0000	0.0000
Bernard Cr. E. 96 T.	100	0.9750	0.0250	100	0.9950	0.0050
Bernard Cr. E. 96 U.	100	0.9800	0.0200	100	1.0000	0.0000
Constantine Cr. E. 96 T.	100	0.9950	0.0050	100	0.9950	0.0050
Constantine Cr. L. 96 T.	100	0.9900	0.0100	100	1.0000	0.0000
Constantine Cr. E. 96 U.	99	0.9697	0.0303	99	1.0000	0.0000
Constantine Cr. L. 96 U.	99	0.9747	0.0253	99	1.0000	0.0000

Appendix B. Hierarchical analysis using likelihood ratios for pink salmon collected in 1996 from Prince William Sound. Within the Overall columns, asterisk indicates significance at the 0.05 level after adjusting for multiple comparisons (modified from Miliken and Johnson [1984] and Rice [1989]).

Source of Variation	DF	<i>sAAT-1,2*</i>	DF	<i>sAAT-3*</i>	DF	<i>sAAT-4*</i>	DF	<i>ADA-1*</i>	DF	<i>ADA-2*</i>	DF	<i>mAH-2*</i>	DF	<i>mAH-4*</i>	DF	<i>mAAT-1*</i>
Among Streams	5	17.167	5	12.631	15	18.217	5	3.645	10	24.699	5	16.385	5	3.19	5	13.974
Within Streams	14	18.05	14	10.72	42	35.46	14	5.54	28	26.52	14	17.36	14	15.34	14	23.79
Mink Creek	3	1.03	3	1.1	9	5.45	3	0	6	5.7	3	1.65	3	2.49	3	2.95
Between Timing	1	0	1	0.72	3	0.84	1	0	2	3.29	1	0.17	1	0.02	1	1.13
Within Timing	2	1.03	2	0.38	6	4.61	2	0	4	2.4	2	1.46	2	2.46	2	1.81
Early (upstream vs tidal)	1	0	1	0.08	3	0.93	1	0	2	1.81	1	0.35	1	1.44	1	1.39
Late (upstream vs tidal)	1	1.03	1	0.3	3	3.68	1	0	2	0.59	1	1.11	1	1.02	1	0.42
Between Elevation	1	0.5	1	0.36	3	2.07	1	0	2	1.9	1	1.28	1	2.43	1	1.13
Within Elevation	2	0.52	2	0.73	6	3.37	2	0	4	3.78	2	0.36	2	0.05	2	1.81
Tidal (early vs late)	1	0.33	1	0.21	3	1.13	1	0	2	2.89	1	0.01	1	0.05	1	1.39
Upstream (early vs late)	1	0.19	1	0.52	3	2.24	1	0	2	0.89	1	0.35	1	0	1	0.42
Paulson Creek																
(upstream vs tidal)	1	0.2	1	0.24	3	1	1	0	2	1.13	1	0	1	1.24	1	8.34
Meachum Creek	3	4.51	3	0.73	9	4.18	3	0	6	6.76	3	6.7	3	1.17	3	0
Between Timing	1	4.18	1	0.18	3	2.68	1	0	2	3.85	1	0.54	1	0.35	1	0
Within Timing	2	0.33	2	0.54	6	1.5	2	0	4	2.9	2	6.16	2	0.81	2	0
Early (upstream vs tidal)	1	0	1	0.1	3	0	1	0	2	0.9	1	4.18	1	0.62	1	0
Late (upstream vs tidal)	1	0.33	1	0.44	3	1.5	1	0	2	2	1	1.98	1	0.19	1	0
Between Elevation	1	0.33	1	0.5	3	0.78	1	0	2	2.25	1	0	1	0.04	1	0
Within Elevation	2	4.16	2	0.23	6	3.39	2	0	4	4.5	2	6.69	2	1.12	2	0
Tidal (early vs late)	1	2.77	1	0.01	3	2.06	1	0	2	2.38	1	5.66	1	0.03	1	0
Upstream (early vs late)	1	1.39	1	0.22	3	1.33	1	0	2	2.12	1	1.03	1	1.09	1	0
Koppen Creek	3	5.36	3	0.55	9	9.2	3	2.77	6	5.94	3	4.32	3	8.88	3	6.6
Between Timing	1	3.97	1	0.18	3	0.49	1	1.38	2	0.25	1	1.29	1	0.02	1	1.02
Within Timing	2	1.38	2	0.37	6	8.69	2	1.38	4	5.67	2	3.02	2	8.84	2	5.58
Early (upstream vs tidal)	1	1.38	1	0.37	3	8.49	1	1.38	2	5.52	1	2.84	1	8.82	1	4.15
Late (upstream vs tidal)	1	0	1	0	3	0.2	1	0	2	0.15	1	0.18	1	0.02	1	1.43
Between Elevation	1	0.14	1	0.18	3	4.69	1	1.38	2	2.79	1	0.17	1	4.47	1	1
Within Elevation	2	5.22	2	0.36	6	4.5	2	1.38	4	3.14	2	4.15	2	4.4	2	5.6
Tidal (early vs late)	1	1.05	1	0.36	3	0.82	1	0	2	1.94	1	0	1	3.17	1	1.42
Upstream (early vs late)	1	4.17	1	0	3	3.68	1	1.38	2	1.2	1	4.15	1	1.23	1	4.18
Bernard Creek																
(upstream vs tidal)	1	0	1	0.25	3	4.8	1	0	2	1.88	1	3.71	1	0.06	1	1.38
Constantine Creek	3	6.95	3	7.85	9	10.83	3	2.77	6	5.11	3	0.98	3	1.5	3	4.52
Between Timing	1	0.62	1	1.57	3	4.55	1	1.38	2	4.33	1	0.75	1	0	1	4.18
Within Timing	2	6.33	2	6.26	6	6.27	2	1.38	4	0.77	2	0.21	2	1.5	2	0.34
Early (upstream vs tidal)	1	0	1	0.33	3	2.98	1	1.38	2	0.46	1	0.07	1	0.81	1	0
Late (upstream vs tidal)	1	6.33	1	5.93	3	3.29	1	0	2	0.31	1	0.14	1	0.69	1	0.34
Between Elevation	1	3.46	1	4.34	3	4.12	1	1.38	2	0.67	1	0	1	1.49	1	0.34
Within Elevation	2	3.49	2	3.5	6	6.7	2	1.38	4	4.44	2	0.97	2	0.01	2	4.17
Tidal (early vs late)	1	1.05	1	3.49	3	3.97	1	0	2	2.1	1	0.09	1	0	1	1.39
Upstream (early vs late)	1	2.44	1	0.01	3	2.73	1	1.38	2	2.34	1	0.88	1	0.01	1	2.78

Source of Variation	DF	CK-A2*	DF	CK-C1*	DF	CK-C2*	DF	FDHG*	DF	GAPDH-2*	DF	PEPA*	DF	G3PDH-1*	DF	G3PDH-2*
Among Streams	10	17.316	5	3.398	5	9.446	5	7.159	10	15.683	5	7.25	5	5.357	10	27.593
Within Streams	28	28.52	14	12.36	14	12.44	14	14.48	28	38.02	14	6.97	14	17.31	28	58.56
Mink Creek	6	8.31	3	2.82	3	4.4	3	2.8	6	10.87	3	0	3	6.12	6	13.59
Between Timing	2	4.14	1	0	1	4.06	1	0.46	2	6.96	1	0	1	0.03	2	0.08
Within Timing	4	4.16	2	2.82	2	0.34	2	2.34	4	3.89	2	0	2	6.08	4	13.51
Early (upstream vs tidal)	2	1.38	1	0	1	0.34	1	0.39	2	3.81	1	0	1	0.29	2	11.7
Late (upstream vs tidal)	2	2.78	1	2.82	1	0	1	1.95	2	0.08	1	0	1	5.79	2	1.81
Between Elevation	2	4.16	1	1.07	1	0.36	1	2.21	2	0.59	1	0	1	4.35	2	2.99
Within Elevation	4	4.14	2	1.74	2	4.03	2	0.58	4	10.27	2	0	2	1.76	4	10.59
Tidal (early vs late)	2	2.74	1	0.4	1	2.66	1	0.58	2	1.56	1	0	1	1.02	2	8.05
Upstream (early vs late)	2	1.4	1	1.34	1	1.37	1	0	2	8.71	1	0	1	0.74	2	2.54
Paulson Creek																
(upstream vs tidal)	2	0	1	0	1	1.38	1	0.35	2	2.95	1	1.44	1	0.17	2	5.71
Meachum Creek	6	4.55	3	4.44	3	3.54	3	1.72	6	1.27	3	0	3	1.46	6	14.58
Between Timing	2	0.36	1	0.12	1	0.12	1	0.7	2	0.21	1	0	1	0.16	2	0.36
Within Timing	4	4.18	2	4.31	2	3.42	2	1.01	4	1.06	2	0	2	1.29	4	14.2
Early (upstream vs tidal)	2	2.8	1	4.3	1	0.31	1	0	2	0.35	1	0	1	0.04	2	13.4
Late (upstream vs tidal)	2	1.38	1	0.01	1	3.11	1	1.01	2	0.71	1	0	1	1.25	2	0.8
Between Elevation	2	4.18	1	1.78	1	2.12	1	0.66	2	0.2	1	0	1	0.89	2	8.89
Within Elevation	4	0.37	2	2.65	2	1.41	2	1.05	4	1.07	2	0	2	0.57	4	5.68
Tidal (early vs late)	2	0.37	1	1.58	1	0.03	1	0	2	0.34	1	0	1	0.03	2	4.15
Upstream (early vs late)	2	0	1	1.07	1	1.38	1	1.05	2	0.73	1	0	1	0.54	2	1.53
Koppen Creek	6	7.34	3	2.6	3	3.12	3	6.63	6	9.03	3	0	3	4.59	6	19.02
Between Timing	2	6.95	1	0	1	1.5	1	0.46	2	4.85	1	0	1	0	2	2.97
Within Timing	4	0.38	2	2.58	2	1.61	2	6.17	4	4.18	2	0	2	4.58	4	16.05
Early (upstream vs tidal)	2	0	1	1.37	1	0	1	5.58	2	0	1	0	1	0.01	2	1.25
Late (upstream vs tidal)	2	0.38	1	1.21	1	1.61	1	0.59	2	4.18	1	0	1	4.57	2	14.8
Between Elevation	2	0.34	1	0	1	1.48	1	3.74	2	4.17	1	0	1	2.55	2	7.18
Within Elevation	4	6.99	2	2.59	2	1.63	2	2.88	4	4.85	2	0	2	2.03	4	11.82
Tidal (early vs late)	2	4.22	1	1.42	1	0	1	0	2	0.33	1	0	1	1.25	2	6.77
Upstream (early vs late)	2	2.77	1	1.17	1	1.63	1	2.88	2	4.52	1	0	1	0.78	2	5.05
Bernard Creek																
(upstream vs tidal)	2	1.03	1	0.03	1	0	1	0.21	2	3.1	1	0	1	1.69	2	0.25
Constantine Creek	6	7.29	3	2.47	3	0	3	2.77	6	10.8	3	5.53	3	3.28	6	5.41
Between Timing	2	3.45	1	1.67	1	0	1	2.77	2	3.51	1	2.8	1	1.56	2	3.87
Within Timing	4	3.83	2	0.79	2	0	2	0	4	7.27	2	2.72	2	1.71	4	1.52
Early (upstream vs tidal)	2	1.05	1	0	1	0	1	0	2	3.03	1	2.72	1	0.42	2	0.66
Late (upstream vs tidal)	2	2.78	1	0.79	1	0	1	0	2	4.24	1	0	1	1.29	2	0.86
Between Elevation	2	2.93	1	1.09	1	0	1	0	2	0.66	1	2.74	1	1.56	2	0.79
Within Elevation	4	4.35	2	1.37	2	0	2	2.76	4	10.12	2	2.78	2	1.71	4	4.6
Tidal (early vs late)	2	2.77	1	1.37	1	0	1	1.38	2	0.37	1	0	1	0.42	2	1.1
Upstream (early vs late)	2	1.58	1	0	1	0	1	1.38	2	9.75	1	2.78	1	1.29	2	3.5

Source of Variation	DF	G3PDH-3*	DF	GPI-B1,2*	DF	mlDHP-1*	DF	sIDHP-2*	DF	LDH-B1*	DF	LDH-B2*	DF	PEPB-1*	DF	PEPLT*
Among Streams	5	13.174	5	7.865	10	16.099	5	4.715	5	6.005	5	4.399	10	16.012	10	28.118
Within Streams	14	9.44	14	15.11	28	20.81	14	19.46	14	18.56	14	19.61	28	31.33	28	48.99
Mink Creek	3	2.78	3	1.02	6	8.3	3	3.96	3	3.31	3	2.78	6	6.73	6	12.03
Between Timing	1	0	1	0	2	4.18	1	0.04	1	1.9	1	1.05	2	4.77	2	5.86
Within Timing	2	2.78	2	1.02	4	4.12	2	3.92	2	1.4	2	1.72	4	1.95	4	6.16
Early (upstream vs tidal)	1	2.78	1	0.51	2	0	1	0.7	1	0	1	0.34	2	1.86	2	5.46
Late (upstream vs tidal)	1	0	1	0.51	2	4.12	1	3.22	1	1.4	1	1.38	2	0.09	2	0.7
Between Elevation	1	1.07	1	0	2	4.15	1	3.44	1	0.21	1	0	2	0.92	2	3.37
Within Elevation	2	1.7	2	1.02	4	4.15	2	0.52	2	3.1	2	2.78	4	5.79	4	8.64
Tidal (early vs late)	1	1.38	1	0.51	2	0	1	0.09	1	0.32	1	0	2	2.78	2	7.33
Upstream (early vs late)	1	0.32	1	0.51	2	4.15	1	0.43	1	2.78	1	2.78	2	3.01	2	1.31
Paulson Creek (upstream vs tidal)	1	0.2	1	0.2	2	4.16	1	0.01	1	1.48	1	0.34	2	1.17	2	0.29
Meachum Creek	3	2.75	3	8.74	6	0	3	2.11	3	3.82	3	4.99	6	6.04	6	6.84
Between Timing	1	2.75	1	0.38	2	0	1	1.54	1	2.36	1	4.88	2	1.49	2	1.9
Within Timing	2	0	2	8.36	4	0	2	0.57	2	1.45	2	0.11	4	4.55	4	4.94
Early (upstream vs tidal)	1	0	1	0	2	0	1	0.49	1	0.07	1	0.11	2	3.99	2	0.72
Late (upstream vs tidal)	1	0	1	8.36	2	0	1	0.08	1	1.38	1	0	2	0.56	2	4.22
Between Elevation	1	0	1	3.81	2	0	1	0.08	1	0.09	1	0.09	2	0.61	2	4.12
Within Elevation	2	2.74	2	4.92	4	0	2	2.01	2	3.72	2	4.9	4	5.42	4	2.71
Tidal (early vs late)	1	1.37	1	2.81	2	0	1	0.14	1	0.35	1	2.95	2	0.54	2	0.63
Upstream (early vs late)	1	1.37	1	2.11	2	0	1	1.87	1	3.37	1	1.95	2	4.88	2	2.08
Koppen Creek	3	1.49	3	2.42	6	2.79	3	1.07	3	2.81	3	3.32	6	7.14	6	10.25
Between Timing	1	0.14	1	0.33	2	1.39	1	0.11	1	1.39	1	0.2	2	5.45	2	5.64
Within Timing	2	1.35	2	2.07	4	1.39	2	0.94	2	1.42	2	3.12	4	1.68	4	4.6
Early (upstream vs tidal)	1	1.03	1	1.93	2	1.39	1	0.93	1	0	1	0.34	2	1.12	2	3.57
Late (upstream vs tidal)	1	0.32	1	0.14	2	0	1	0.01	1	1.42	1	2.78	2	0.56	2	1.03
Between Elevation	1	0.15	1	1.36	2	1.39	1	0.35	1	1.41	1	0.2	2	0.18	2	0.64
Within Elevation	2	1.34	2	1.05	4	1.39	2	0.71	2	1.39	2	3.12	4	6.95	4	9.6
Tidal (early vs late)	1	1.01	1	0	2	1.39	1	0.1	1	1.39	1	2.78	2	2.94	2	0.76
Upstream (early vs late)	1	0.33	1	1.05	2	0	1	0.61	1	0	1	0.34	2	4.01	2	8.84
Bernard Creek (upstream vs tidal)	1	0.51	1	1.37	2	0	1	5.42	1	0	1	0.34	2	4.36	2	2.16
Constantine Creek	3	1.71	3	1.36	6	5.56	3	6.89	3	7.14	3	7.84	6	5.89	6	17.42
Between Timing	1	0.34	1	0	2	2.81	1	5.98	1	0.2	1	0.51	2	0.8	2	2.82
Within Timing	2	1.36	2	1.36	4	2.74	2	0.91	2	6.93	2	7.33	4	5.08	4	14.59
Early (upstream vs tidal)	1	0	1	0.68	2	0	1	0.37	1	2.78	1	0.34	2	3.34	2	9.11
Late (upstream vs tidal)	1	1.36	1	0.68	2	2.74	1	0.54	1	4.15	1	6.99	2	1.74	2	5.48
Between Elevation	1	0.31	1	0	2	1.03	1	0.01	1	0.19	1	5.1	2	4.04	2	3.26
Within Elevation	2	1.39	2	1.36	4	4.52	2	6.87	2	6.94	2	2.73	4	1.84	4	14.15
Tidal (early vs late)	1	0	1	0.68	2	2.77	1	5.77	1	2.76	1	1.38	2	0.07	2	3.99
Upstream (early vs late)	1	1.39	1	0.68	2	1.75	1	1.1	1	4.18	1	1.35	2	1.77	2	10.16

Source of Variation	DF	sMDH-A1,2*	DF	sMDH-B1,2*	DF	mMEP-1*	DF	PGDH*	DF	PGM-2*	DF	PEPD-2*	DF	mSOD*	DF	sSOD-1*
Among Streams	5	5.521	5	2.237	5	3.723	10	15.378	5	4.955	10	16.019	5	0.964	5	8.37
Within Streams	14	19.11	14	7.9	14	25.42	28	26.27	14	16.29	28	27.17	14	13.78	14	7.28
Mink Creek	3	4.8	3	1.53	3	4.4	6	5.8	3	6.62	6	6.91	3	1.4	3	0
Between Timing	1	3.71	1	0.14	1	4.18	2	3.08	1	1.05	2	5.98	1	0.1	1	0
Within Timing	2	1.08	2	1.39	2	0.2	4	2.72	2	5.56	4	0.93	2	1.29	2	0
Early (upstream vs tidal)	1	1.03	1	0.34	1	0.01	2	0.77	1	1.38	2	0.68	1	1.09	1	0
Late (upstream vs tidal)	1	0.05	1	1.05	1	0.19	2	1.95	1	4.18	2	0.25	1	0.2	1	0
Between Elevation	1	0.58	1	0.14	1	0.06	2	0.32	1	1.05	2	0.86	1	0.12	1	0
Within Elevation	2	4.21	2	1.39	2	4.33	4	5.47	2	5.56	4	6.04	2	1.27	2	0
Tidal (early vs late)	1	1.03	1	0.34	1	1.35	2	0.39	1	4.18	2	2.46	1	1.05	1	0
Upstream (early vs late)	1	3.18	1	1.05	1	2.98	2	5.08	1	1.38	2	3.58	1	0.22	1	0
Paulson Creek (upstream vs tidal)	1	2.11	1	0.2	1	0.16	2	4.1	1	1.38	2	2.44	1	0.34	1	0
Meachum Creek	3	4.92	3	4.96	3	7.7	6	6.9	3	2.77	6	8.93	3	4.32	3	4.51
Between Timing	1	4.01	1	0.09	1	6.36	2	2.49	1	1.38	2	6.29	1	1.03	1	0.34
Within Timing	2	0.91	2	4.86	2	1.33	4	4.4	2	1.38	4	2.63	2	3.29	2	4.16
Early (upstream vs tidal)	1	0	1	1.93	1	1.3	2	1.26	1	0	2	2.05	1	2.95	1	2.78
Late (upstream vs tidal)	1	0.91	1	2.93	1	0.03	2	3.14	1	1.38	2	0.58	1	0.34	1	1.38
Between Elevation	1	0.62	1	0.09	1	0.49	2	4.11	1	1.38	2	0.72	1	2.97	1	4.17
Within Elevation	2	4.29	2	4.86	2	7.2	4	2.78	2	1.38	4	8.2	2	1.35	2	0.34
Tidal (early vs late)	1	3.45	1	2.93	1	1.26	2	1.61	1	0	2	2.93	1	0	1	0.34
Upstream (early vs late)	1	0.84	1	1.93	1	5.94	2	1.17	1	1.38	2	5.27	1	1.35	1	0
Koppen Creek	3	5.68	3	0.31	3	3.14	6	4.99	3	2.77	6	6.2	3	3.12	3	2.77
Between Timing	1	0.48	1	0.11	1	2.87	2	1.86	1	1.38	2	2.86	1	2.99	1	1.39
Within Timing	2	5.19	2	0.2	2	0.26	4	3.12	2	1.38	4	3.34	2	0.12	2	1.37
Early (upstream vs tidal)	1	0.09	1	0	1	0.18	2	2.1	1	0	2	0.42	1	0	1	1.37
Late (upstream vs tidal)	1	5.1	1	0.2	1	0.08	2	1.02	1	1.38	2	2.92	1	0.12	1	0
Between Elevation	1	2.67	1	0.11	1	0.26	2	3	1	1.38	2	1.33	1	0.09	1	1.38
Within Elevation	2	3	2	0.2	2	2.87	4	1.97	2	1.38	4	4.86	2	3.02	2	1.38
Tidal (early vs late)	1	0.07	1	0	1	1.27	2	1.04	1	1.38	2	4.51	1	1.07	1	0
Upstream (early vs late)	1	2.93	1	0.2	1	1.6	2	0.93	1	0	2	0.35	1	1.95	1	1.38
Bernard Creek (upstream vs tidal)	1	0.54	1	0	1	0.26	2	0.96	1	0	2	0.33	1	0.34	1	0
Constantine Creek	3	1.06	3	0.9	3	9.76	6	3.52	3	2.75	6	2.36	3	4.26	3	0
Between Timing	1	0.97	1	0.7	1	6.84	2	0.3	1	1.36	2	0.06	1	1.01	1	0
Within Timing	2	0.09	2	0.2	2	2.91	4	3.21	2	1.38	4	2.29	2	3.25	2	0
Early (upstream vs tidal)	1	0.09	1	0.2	1	2.55	2	1.71	1	1.38	2	1.02	1	0.34	1	0
Late (upstream vs tidal)	1	0	1	0	1	0.36	2	1.5	1	0	2	1.27	1	2.91	1	0
Between Elevation	1	0.04	1	0.07	1	2.26	2	2.95	1	1.36	2	1.86	1	2.94	1	0
Within Elevation	2	1.02	2	0.82	2	7.49	4	0.57	2	1.38	4	0.49	2	1.32	2	0
Tidal (early vs late)	1	0.71	1	0.68	1	5.6	2	0.19	1	0	2	0.4	1	0	1	0
Upstream (early vs late)	1	0.31	1	0.14	1	1.89	2	0.38	1	1.38	2	0.09	1	1.32	1	0

Source of Variation	DF	TPI-2*	DF	Overall	P - value	αc	Test
Among Streams	5	2.951	220	359.61	0.000	* 0.025	1
Within Streams	14	16.41	616	685.12	0.027	* 0.050	1
Mink Creek	3	0.69	132	142.4	0.253	0.013	2
Between Timing	1	0.35	44	58.4	0.072	0.006	3
Within Timing	2	0.33	88	84.05	0.599	0.050	3
Early (upstream vs tidal)	1	0.13	44	41.09	0.597	0.025	3
Late (upstream vs tidal)	1	0.2	44	42.96	0.516	0.013	3
Between Elevation	1	0	44	41.82	0.565	0.017	3
Within Elevation	2	0.69	88	100.64	0.168	0.008	3
Tidal (early vs late)	1	0	44	46.35	0.376	0.010	3
Upstream (early vs late)	1	0.69	44	54.29	0.138	0.007	3
Paulson Creek (upstream vs tidal)	1	5.58	44	48.42	0.299	0.017	2
Meachum Creek	3	2.15	132	138.2	0.338	0.025	2
Between Timing	1	1.66	44	52.86	0.169	0.006	4
Within Timing	2	0.48	88	85.34	0.560	0.017	4
Early (upstream vs tidal)	1	0.34	44	45.07	0.427	0.013	4
Late (upstream vs tidal)	1	0.14	44	40.27	0.632	0.050	4
Between Elevation	1	0.4	44	46.5	0.370	0.008	4
Within Elevation	2	1.74	88	91.71	0.372	0.010	4
Tidal (early vs late)	1	0.69	44	41.53	0.578	0.025	4
Upstream (early vs late)	1	1.05	44	50.18	0.242	0.007	4
Koppen Creek	3	2.42	132	158.8	0.056	0.010	2
Between Timing	1	1.17	44	55.24	0.119	0.013	5
Within Timing	2	1.24	88	103.51	0.124	0.010	5
Early (upstream vs tidal)	1	1.04	44	56.81	0.093	0.008	5
Late (upstream vs tidal)	1	0.2	44	46.7	0.362	0.025	5
Between Elevation	1	1.17	44	51.49	0.204	0.017	5
Within Elevation	2	1.24	88	107.26	0.080	0.007	5
Tidal (early vs late)	1	0.2	44	42.77	0.524	0.050	5
Upstream (early vs late)	1	1.04	44	64.49	0.024	0.006	5
Bernard Creek (upstream vs tidal)	1	0.11	44	35.2	0.826	0.050	2
Constantine Creek	3	5.46	132	162.1	0.039	0.008	2
Between Timing	1	0	44	61.85	0.039	0.006	6
Within Timing	2	5.45	88	100.22	0.176	0.017	6
Early (upstream vs tidal)	1	4.07	44	42.02	0.557	0.050	6
Late (upstream vs tidal)	1	1.38	44	58.2	0.074	0.008	6
Between Elevation	1	5.02	44	56.16	0.103	0.013	6
Within Elevation	2	0.43	88	105.91	0.094	0.010	6
Tidal (early vs late)	1	0.34	44	44.95	0.432	0.025	6
Upstream (early vs late)	1	0.09	44	60.96	0.046	0.007	6