2006 Arctic Yukon Kuskokwim Sustainable Salmon Initiative Project Final Report[1]

Landscape Genetics of AYK salmon populations

by:

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ABSTRACT:

An important question in species conservation is to what extent does landscape heterogeneity similarly influence the spatial distribution of genetic diversity in closely related and sympatric species? In this study we combined classic population genetics with landscape genetic methods to address this question for Chinook, chum and coho salmon from Norton Sound and the Yukon and Kuskowkim rivers: three contiguous watersheds encompassing over 1 million km^2 in subarctic North America. We compared and contrasted both the spatial patterns of population structure and the extent to which nine habitat attributes from four general categories (spatial isolation, habitat size, climate, and ecology) explained population structure. We found broadly similar, but unexpected, spatial patterns of population structure for each species despite some differences in the level of population differentiation likely attributable to life history. Notably, the three major watersheds did not form the first level of hierarchical population structure as predicted but rather each species exhibited a single coastal population group and one or more inland population groups. In addition, some inland population groups were inconsistent with the waterway network, suggesting that extant population structure may also be influenced by historical events. Two types of multivariate analysis suggested that region-wide population structure of each species was partially explained by multiple attributes including indicators of spatial isolation, habitat size and climate. However, only one attribute, precipitation, was identified in all species, suggesting that the population genetic response to environmental changes will probably vary among species. Overall, our results suggest conservation planners should not assume environmental changes will similarly influence the spatial distribution of genetic diversity in closely related and sympatric species.

PRESS RELEASE

The study “Landscape Genetics of AYK salmon populations” compared the level and patterns of genetic diversity in Chinook, coho, and chum salmon from three major watersheds (Norton Sound and the Yukon and Kuskokwim rivers) of the Arctic-Yukon-Kuskokwim region. The primary objective was to assess if and how genetic population structure is influenced by environmental factors, namely variation in habitat. To that end we combined classic population genetic and landscape genetics methods to address the question does habitat heterogeneity similarly influence the spatial distribution of genetic diversity in each species across the three watersheds? The results from the analysis support three general conclusions that have implications for conservation.

First, we found broadly similar, but unexpected, patterns of population structure for each species despite some differences in the level of population structure likely attributable to life history. Notably, the three major watersheds did not form the first level of hierarchical population structure as predicted but rather each species exhibited a single coastal population group and one or more inland population groups. In addition, some inland population groups were inconsistent with the waterway network, suggesting that extant population structure may also be influenced by historical events. Collectively, these results suggest that the spatial scale of conservation should first focus regionally at the coastal versus inland population dichotomy rather than at the level of the three watersheds which is the present scale of management.

Second, the results suggested that region-wide population structure of each species was partially explained by multiple habitat attributes including indicators of spatial isolation, habitat size and climate. There were similarities and differences among species, supporting a growing number of studies that show population structure may be best explained by multiple factors including variables that can influence population size as well as indicators of spatial isolation and climate that may influence population connectivity. The present study suggested precipitation may partially explain the region-wide population structure of all species. However, the fact that other habitat variables may also influence population structure and that these variables differ among species suggests that environmental changes are unlikely to similarly influence each species. Thus, conservation planners should not assume environmental changes will similarly influence the population structure of each species in the AYK region.

Third, the results of the study also varied with spatial scale. That is, the region-wide results were not supported at the coastal and inland scales. In fact, with the exception of the coastal coho populations, the analyses were generally inconclusive for the coastal and inland populations of each species. Thus, the study results can be used to infer the influence of habitat variation on population structure at a coarse scale (region wide) but further study including more population samples and more precise data on habitat variation will be needed for a fine scale assessment.

PROJECT EVALUATION:

Objective 1: Estimate the influence of spatial, environmental, ecological and life history factors on intra- and inter-population genetic diversity in Chinook, chum, and coho, salmon from the Yukon and Kuskokwim rivers, and Norton Sound. This objective was met at the region-wide (over all watersheds) scale. We examined nine habitat attributes representing four general categories (spatial isolation, habitat size, climate, and ecology). Our results suggested that the level and spatial patterns of extent population structure are likely influenced by a combination of environmental factors, life history and historical events. Further research is needed, however, to examine additional factors such as temperature and to examine a finer spatial scale using more precise estimates of habitat heterogeneity and more population samples. For a complete report and discussion of the results see Appendix 1.

Objective 2: Create a GIS database of genetic data for spatially-referenced Chinook, chum, and coho salmon populations that are freely accessible through the Alaska Geospatial Data Clearing House (http://agdc.usgs.gov/) or on DVD from the project investigators. This database will be constructed so that it can routinely be updated with additional populations and genetic data. Rather than post our data on the Alaska Geospatial Data Clearing House we created a Google web map and posted the data on our (USFWS Conservation Genetics Laboratory) web site (http://alaska.fws.gov/fisheries/genetics/CGL_googlemap.html). This web map provides all the downloadable data layers described in the project objective but is also more informative and useful to a wider range of interests. In addition, the web map is more easily maintained and updated on our web site than if we attempted to post the data on the Geospatial Data Clearing House.

Project delay: The final report was delayed 15 months. This project was scheduled as a two-year study with a completion date of July 1, 2008 and a final report due date of August 1, 2008. Two factors contributed to the 15 month delay. First, we underestimated the time required to build and test the ArcGIS database and analyze the data. These steps required about eight additional months to complete. Many of the population sample locations did not have spatial coordinates (latitude and longitude) so determining their location required detailed examination of field records including a trip to Whitehorse, Yukon Territory to meet with Canadian Department of Fisheries and Oceans staff regarding upper Yukon River samples. The sample locations that did have coordinates often did not list the datum and thus required verification in ArcGIS and, when necessary, conversion to the NAD83 datum to assure the locations were accurately represented on the map. We experienced delays integrating the Canadian GIS data for the upper Yukon River with US GIS data for the lower and middle Yukon River. This problem was unexpected because we assumed the integrated data was available through the Alaska Geospatial Data Clearinghouse. In fact, most of the environmental data layers were not integrated and required detailed modifications after merging to assure the Canadian and US locations were measured at the same map scale and all trans-boundary features (lines and polygons) were seamless. Unanticipated data analysis was required including programming using the computer language R and the testing and use of new software for landscape genetic analysis. In addition, some analysis was performed in ArcGIS and required testing and interaction with technical support at ESRI. These steps in data analysis were necessary to complete the study but were unforeseen and not accounted for in the project timeline. The second factor contributing to the delay concerned accessibility and dissemination of the data (objective two). As the project progressed it became clear that simply posting the data layers on the Alaska Geospatial Data Clearinghouse web site would not adequately convey the study to the non-scientific public. Rather, it was determined that an independent website with a detailed map and project description as well as downloadable data would be more useful to a wider range of interests. Developing the map required “outside” expertise and was contracted to Geographic Resource Solutions Inc of Anchorage Alaska. This project required an additional six months. We feel the online web map is a much better product for disseminating the study to a broad audience as opposed to simply posting the data layers on a web site intended mostly for the scientific community.

DELIVERABLES:

The following deliverables disseminate the findings from this study: 1) four progress reports and a final report available through the AYKSSI program or from the authors, 2), a manuscript for submission to a peer-reviewed journal (Appendix 1 of the final report), 3) genotype and allele frequency data in a Excel (Microsoft Office version 11) spreadsheet available from the authors, 4) a Google web map that is accessible through the USFWS Region Seven web site (http://alaska.fws.gov/fisheries/genetics/CGL_googlemap.html). The web map contains a project summary, data layers that can be opened and closed in the Google map environment, downloadable data layers in *.kml (Google earth) and *.shp (ArcGIS) format, a downloadable project report, and a downloadable interactive pdf version of the web map.

PROJECT DATA SUMMARY:

Genotype and allele frequency data are archived in an Excel (Microsoft Office version 11) spreadsheet available from the authors (Conservation Genetics Laboratory, U.S. Fish & Wildlife Service, 1011 East Tudor Road, Anchorage, Alaska, USA 99503. ph: (907) 786-3858, email: jeffrey_olsen@fws.gov). A Google web map that is accessible through the USFWS Region Seven web site (http://alaska.fws.gov/fisheries/genetics/CGL_googlemap.html). The web map contains a project summary, data layers that can be opened and closed in the Google map environment, downloadable data layers in *.kml (Google earth) and *.shp (ArcGIS) format, a downloadable project report, and a downloadable interactive pdf version of the web map.

APPENDIX 1: Manuscript for submission to *Conservation Genetics*

Comparative landscape genetic analysis of co-occurring Pacific salmon species from subarctic North America

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Running title:

Abstract

An important question in species conservation is to what extent does landscape heterogeneity similarly influence the spatial distribution of genetic diversity in closely related and sympatric species? In this study we combined classic population genetics with landscape genetic methods to address this question for three salmon species (*Oncorhynchus tshawytscha*, *O. kisutch*, *and O. keta*) from three contiguous watersheds encompassing over 1 million km^2 in subarctic North America. We compared and contrasted both the spatial patterns of population structure and the extent to which nine habitat attributes from four general categories (spatial isolation, habitat size, climate, and ecology) explained population structure. We found broadly similar, but unexpected, spatial patterns of population structure for each species despite some differences in the level of population differentiation likely attributable to life history. Notably, the three major watersheds did not form the first level of hierarchical population structure as predicted but rather each species exhibited a single coastal population group and one or more inland population groups. In addition, some inland population groups were inconsistent with the waterway network, suggesting that extant population structure may also be influenced by historical events. Two types of multivariate analysis suggested that region-wide population structure of each species was partially explained by multiple attributes including indicators of spatial isolation, habitat size and climate. However, only one attribute, precipitation, was identified in all species, suggesting that the population genetic response to environmental changes will probably vary among species. Overall, our results suggest conservation planners should not assume environmental changes will similarly influence the spatial distribution of genetic diversity in closely related and sympatric species.

Introduction

Identifying the factors influencing population structure is important for understanding how populations evolve and for predicting how they may change in the face of environmental perturbations. Multi-species analysis using landscape genetics methods (Manel et al. 2003; Storfer et al. 2007) can provide important insights in this regard. For example, common patterns of population structure among co-occurring species that exhibit different life histories have revealed landscape features (and evidence of historical processes) that have broad taxonomic influence (e.g., Petren et al. 2005; Gagnon and Angers 2006). On the other hand, contrasting patterns of population structure among species from the same landscape have shown the importance of species ecology and life history and demonstrate the danger in generalizing the role of habitat on genetic diversity (e.g., Whitely et al. 2004; Short and Caterino 2009). Multi-species analyses are particularly relevant for conservation of closely related and co-occurring species for which it may seem reasonable to assume that landscape heterogeneity similarly influences the spatial distribution of genetic diversity (Marten et al. 2006). Here we question this assumption by examining the interacting roles of habitat and life history on population structure of three species of Pacific Salmon (Oncorhynchus spp.) in a pristine subarctic environment in North America.

Pacific salmon are found in most river systems on the west coast of North America between 40ºN and 68ºN (Groot and Margolis 1991). Five species are anadromous, philopatric and semelparous. Along the west coast of Alaska above 60ºN, three species, Chinook (*O. tshawytscha*), coho (*O. kisutch*), and chum (*O. keta*) salmon, are sufficiently abundant to support commercial, subsistence, and sport fisheries. Each species exhibits some unique life history traits that, in addition to habitat and demographics, may differentially influence gene flow and genetic

drift. Based on these traits, and abundance, we predict the level of population structure from least to most will be chum < coho < Chinook. For example, juvenile chum salmon migrate to the ocean after leaving their gravel nest whereas juvenile Chinook and coho salmon spend a year or more in freshwater. In addition, chum salmon are substantially more abundant in the fishery and in adult escapement estimates (Brannian et al. 2006). The lack of freshwater specialization and greater abundance should favor higher gene flow and a lower rate of genetic drift, respectively, and thus a lower level of population structure in chum relative to Chinook and coho salmon (Quinn 2005). Chinook and coho salmon are more similar in terms of juvenile life history and adult abundance, however, the former mature almost exclusively at four years whereas the later mature at between three and seven years. The lack of age structure in coho salmon should favor higher gene flow and a lower level of population structure relative to Chinook salmon (Quinn 2005).

The three species broadly overlap in three contiguous watersheds which vary in size and habitat complexity. Norton Sound is the smallest (~ 50,000 km^2) and least complex (four ecoregions) watershed, consisting of many unconnected and relatively short (mean length ~110 km, Figure 1) coastal rivers. The Kuskokwim River watershed is larger (~151,000 km^2) and more complex (six ecoregions) than Norton Sound, extending into the interior of Alaska over 1,500 rkm from the mouth. The Yukon River watershed is the largest (858,000 km^2) and most complex (22 ecoregions) of the three watersheds, traversing Alaska with headwaters in British Columbia over 3,000 rkm from the mouth. Combined, the three watersheds encompass over 1 million km^2 and 24 ecoregions, three of which are common to each watershed. Based on the broad physical and ecological differences among watersheds, we predict that the three watersheds will form the first level of hierarchical population structure of each species.

We combined population genetic and landscape genetics methods to address the question does landscape heterogeneity similarly influence the spatial distribution of genetic diversity in subarctic populations of Chinook, chum and coho salmon? Our objectives were threefold. First, we assessed if the level of population divergence from least to most was chum < coho < Chinook as predicted based on the life history differences. Second, we assessed if the three watersheds form the first level of hierarchical population structure in each species. More generally, we assessed if the patterns of hierarchical population structure in each species were congruent. Finally, we assessed and compared the extent to which habitat features from four general categories (spatial isolation, habitat size, climate, and ecology) explained population structure in each species. The results were evaluated in the context of current management and conservation efforts with an emphasis on environmental perturbations from factors such as climate change.

Materials and Methods

Genetic data

The genetic data consisted of microsatellite genotypes drawn mostly from genetic baselines developed for mixed-stock analysis and to describe population structure (e.g., Flannery et al. 2006, Crane et al. 2007, Olsen et al. 2008). For the present study, we added genotypes for coho and Chinook salmon from Norton Sound following the protocol of Crane et al. (2007) and Seeb et al. (2007). The genotypes represented 13, 12, and eight loci for Chinook (47 locations), chum (53 locations), and coho salmon (28 locations), respectively (Table 1, Figure 1, Appendices S1-S3). The sample sizes ranged from 21 to 116 and averaged approximately 85 for each species. A geographic information system (GIS) data layer of sample locations was created using latitude and longitude (North American Datum 83) from a GPS or a physical description of the location.

No data was available for coho salmon from the upper Yukon River because there is little evidence of coho spawning in that area.

Habitat data

Habitat data in the form of GIS data layers were obtained from the Alaska geospatial data clearing house (http://agdc.usgs.gov/) and the Canadian GeoBase (http://www.geobase.ca/geobase/en/index.html). We examined nine variables associated with the watershed environment (Appendix 1). These variables reflected four general categories (spatial isolation, habitat size, climate, and ecology) that may affect population structure by influencing gene flow or genetic drift or both. Increasing spatial isolation is expected to decrease gene flow in migratory and philopatric species. Spatial isolation was evaluated using four indictors: waterway distance to the coast, median pairwise waterway distance from each location to all other locations (similar to connectivity), elevation, and migration difficulty (waterway distance to the coast x elevation, see Quinn 2005). All estimates of waterway distance were computed in ArcGIS™ (ESRI) version 9.2 using National Hydrologic Dataset (NHD) flowlines. Increasing habitat size may correspond with larger population size which should result in lower genetic drift. Habitat size was evaluated using two indicators: the length of the home river for each sample and the U.S. Geological Service (USGS) Hydrologic Unit Code (HUC) level four subbasin area (and it's equivalent from the Canadian GeoBase). Although finer scale HUC units are available, we chose level four because it is equivalent to the finest scale freely available from the Canadian GeoBase. Climate was evaluated using regional estimates of mean annual precipitation for areas in Alaska and northwest Canada. The amount of precipitation in this area is positively correlated to the magnitude and frequency of flooding (Jones and Fahl 1994) which decreases river stability. Less stable rivers are believed to promote higher gene flow (Quinn 2005). Ecology was

evaluated using two categorical indicators: ecoregion and permafrost region. Ecoregions are spatial zones in which biotic and abiotic features such a vegetation, geology, minerals, physiography, and land cover are relatively homogeneous. Local adaptation may favor homing to ecoregion and thus greater gene flow within versus between ecoregions. We used ecoregions defined by Gallant et al. (1995) and the Ecological Stratification Working Group (1996) because the two data sets represent Alaska and the Yukon territory, respectively, and are based on the same habitat criteria. Permafrost regions are spatial zones with varying vertical and horizontal distribution of permafrost. The extent of permafrost can influence stream biogeochemistry (MacLean et al. 1999) and thus, like ecoregion, populations may locally adapt to permafrost region. Our samples represented permafrost regions from the circum-arctic permafrost and ground ice data layer (Heginbottom et al. 1993). We converted the categorical indicators of ecology into measures of ecological distance for each location relative to all other locations. We did this by computing the mean pairwise distance from each location to all other locations (similar to median waterway distance above) except that in this case values of 0 and 1 were used for population pairs from the same and from different regions, respectively.

Intra-population diversity

Estimates of allele frequency, allelic richness (A_r), and observed and expected heterozygosity (H_o, H_e) were computed for each locus and population using the computer program FSTAT version 2.9.3 (Goudet 2001). Estimates of private allele richness (pA_r) were computed for each locus in each population using the computer program HP-RARE version 1.0 (Kalinowski 2005). Randomization tests were used to test for conformity to Hardy-Weinberg equilibrium (HWE) for each locus and population combination and to test for genotypic disequilibrium among locus pairs over all populations. These tests were performed using FSTAT and GenePop version 4.0.7 (Rousset 2007), respectively, and the threshold for statistical significance ($\alpha = 0.05$) was

corrected (α/k) for k-simultaneous tests using the sequential Bonferroni method (Rice 1989). Two values of k were used for the HWE test to evaluate each population over all k-loci and each locus over k-populations.

Population divergence

The level of population divergence was first estimated using F_{ST} (Wright 1943), which was computed over all populations and for each population pair, over all loci, according to Weir and Cockerham (1984) using FSTAT. The null hypothesis (global F_{ST} not greater than zero) was tested by bootstrap sampling of loci. We also computed $F2_{ST}$ to assess if locus polymorphism was influencing the level of population divergence as estimated by F_{ST} (McDonald 1994). Estimates of $F2_{ST}$ were derived by pooling all but the most common allele at each locus to create bi-allelic loci.

Landscape genetic analysis

We used hierarchical Analysis of Molecular Variance (AMOVA, Excoffier et al. 2005) to evaluate the spatial patterns of population structure for each species. First, we grouped populations by watershed and used the program ARLEQUIN version 3.01 (Excoffier et al. 2005) to estimate how much variation exists within (F_{SC}) and among (F_{CT}) the three population groups. The level of group differentiation, F_{CT}, should be maximized under this grouping strategy if the three watersheds form the first level of hierarchical population structure. Next, we used the program SAMOVA (Spatial Analysis of Molecular Variance, Dupanloup et al. 2002) version 1.0 that incorporates spatial data (x and y coordinates) for each population. SAMOVA performs a series of AMOVA analyses in which population groups are defined through a simulated annealing procedure that identifies geographically homogeneous groups which are maximally differentiated. The number of groups (k) is a user defined variable so we began with k = 2 and

increased k until F_{CT} was maximized and F_{SC} was minimized. Because latitude and longitude data do not reflect the true spatial relationships in a riverine system, we derived surrogate x and y coordinates by using the pairwise waterway distance matrix to project the position of the populations on a multidimensional scaling (MDS) plot and then spatially reference populations using MDS axes one and two values (Manni et al., 2004).

We used the program BARRIER version 2.2 (Manni et al. 2004) to complement the SAMOVA results. BARRIER uses Monmonier's algorithm to detect areas of abrupt change in population structure that may reflect partial barriers to gene flow. Our interests here were two fold: assess if population structure associated with the watersheds was significant enough to be consistent with a genetic barrier, and assess if putative genetic barriers for each species are congruent. Simulations suggest the Monmonier's approach is better than SAMOVA for identifying barriers, particularly when population structure follows an isolation-by-distance pattern (Dupanloup et al. 2002; Manni et al. 2004). We used the values from the MDS axes one and two as described above for x and y coordinates. To account for isolation by distance in each species we used a matrix of residuals rather than F_{ST} as suggested by Manni et al. (2004). In order to determine the robustness of each barrier, we generated 100 matrices of residuals by bootstrap sampling of loci. The pairwise F_{ST} values, bootstrap sampling, and computation of residuals used in the BARRIER analyses were derived using R-scripts (R 2.8.1, http://www.r-project.org/) written by the author and J. Bromaghin (USFWS, Anchorage Alaska).

The SAMOVA and BARRIER results suggested a single coastal and one or more inland population groups nested within the region-wide population structure of each species (see below). Therefore, we conducted tests of differences in estimates of A_r, H_e, F_{ST}, $F2_{ST}$, and pA_r among the coastal and inland populations of each species. We used a pairwise randomization test in FSTAT

to evaluate the first four variables and a Mann-Whitney test in R 2.8.1 to evaluate pA_r using each locus as an observation.

We used the method of Foll and Gaggiotti (2006) as implemented in the program GESTE version 2.0 to evaluate the influence of indicators of spatial isolation, habitat size, climate and ecology on population structure in each species. The program computes population-specific estimates of F_{ST} by estimating the genetic differentiation between each local population and the overall metapopulation. A hierarchical Bayesian method is used to relate the estimates of F_{ST} to location-specific estimates of environmental attributes under a generalized linear model. We chose this approach as our primary method because recent studies suggest it may be more informative when using location-specific environmental data (e.g., Kittkein and Gaggiotti 2008) and because it tests multiple variables simultaneously. All combinations of variables were considered and models were evaluated using estimates of posterior probability, the 95% highest probability density interval (HPDI), and the estimate of unexplained variance (σ^2, Foll and Gaggiotti 2006). As suggested by the authors, we used 10 pilot runs of 5000 iterations to obtain the parameters of the proposal distributions. We also used an additional burn in of 50000 iterations and a thinning interval of 20. Estimates were derived from a sample size of 10000. The analyses were performed over all populations (region wide) and separately for the coastal and inland populations in two phases. In the first phase, all variables were included. In the second phase, we included only those variables with a cumulative posterior probability (the posterior probability of all models containing each variable) of 0.10 or greater in phase one. We used the results from the second phase analysis to select and evaluate the highest probability models.

To complement the approach of Foll and Gaggiotti (2006) we conducted a series of partial Mantel tests (Smouse et al. 1986) in which we controlled for the influence of pairwise waterway distance while testing the influence of each habitat feature on estimates of pairwise genetic divergence [$F_{st}/(1 - F_{st})$]. We converted the location-specific habitat data into pairwise estimates by computing pairwise differences for distance to the coast, elevation, and migration difficulty and pairwise averages for precipitation, subbasin area, and river length. Ecoregion and permafrost region were treated as binary variables in which population pairs from the same and different regions were assigned values of 0 and 1, respectively. We used the program IBD version 1.52 (Bohonak 2002) to perform the tests at the region-wide scale and separately for the coastal and inland populations.

Results

Intra-population genetic diversity

The mean estimates of heterozygosity (H_e) and allelic richness (A_r) were 0.75, 0.85, 0.37 and 10.1, 11.1, 2.9 for Chinook, chum, and coho salmon, respectively (Appendices S1-S3). Fifty (Chinook), 53 (chum), and 10 (coho) population x locus combinations deviated from Hardy-Weinberg equilibrium (HWE) at $\alpha = 0.05$ (Appendices S1-S3). When the α-level was adjusted for multiple tests, the number of significant tests declined to 12 (Chinook), 19 (chum), and 1 (coho) for multiple loci, and 8 (Chinook), 14 (chum), and 1 (coho) for multiple populations. Significant tests were not indicative of deviations of HWE at any specific locus or population.

Population divergence

The comparison of F_{ST} estimates did not support the prediction that the relative level of population structure for the three species is chum < coho < Chinook. Rather, the 95% confidence intervals indicated F_{ST} for coho was significantly larger than for Chinook and chum salmon

(Figure 2). The difference in values of F_{ST} for the later two species was not statistically significant, indicating chum = Chinook < coho. The values of $F2_{ST}$ were larger than F_{ST} for each species but the intra-specific differences were not statistically significant. The $F2_{ST}$ value for coho was significantly larger than for Chinook but not for chum salmon.

Landscape genetic analysis

The genetic variation among groups (F_{CT}) was not maximized when populations were grouped by watershed (Table 2). In fact, F_{CT} was actually lower than F_{SC} (within-group variation) for Chinook and chum salmon. The SAMOVA analysis showed that the largest estimates of F_{CT} were derived assuming k=2 groups for each species. However, for both Chinook and chum salmon one group contained no more than two populations and the estimates of F_{SC} were similar to the watershed groupings. So we increased k until the estimate of F_{SC} declined substantially. This point occurred at k=6 for both Chinook and chum salmon and k=2 for coho salmon (Table 2). The results suggested a single multi-population coastal group and one (coho) or more (Chinook and chum) inland groups consisting of one or more populations. The inland population groups also revealed some spatial inconsistencies. For example, Chinook populations 5 and 6 and chum populations 9 and 10 are part of a middle Yukon River population group despite being closer by waterway to the coastal population group. Coho populations 23 and 24 in the upper Kuskokwim River appear to be more closely related to the middle-upper Yukon River population group.

The BARRIER results indicated partial gene flow barriers at points separating most population groups revealed by SAMOVA (Figure 3). No barriers were found separating the three watersheds but barriers were identified between the coastal group and adjacent inland groups. Most barriers were strongly supported by bootstrap sampling. Of the 100 bootstrap replicates, twelve of the 15 barriers (all species) occurred at least 80 times and all 15 barriers occurred at

least 50 times. The strongest barriers (i.e., those identified first and having the highest bootstrap support) for Chinook and chum salmon encapsulated populations furthest from the ocean in the upper Yukon and Kuskokwim rivers whereas for coho salmon the strongest barrier separated the coastal population group from the middle-upper Yukon River populations. Barrier six for Chinook and chum salmon supported the relative isolation of populations 5 and 6 (Chinook) and 9 and 10 (chum) from the geographically closest coastal populations. Similarly, barrier two for coho salmon supported the isolation of populations 23 and 24 in the upper Kuskokwim River from adjacent lower river populations

The estimates of H_e, A_r, and mean private allele richness over loci (pA_r) differed significantly ($P < 0.05$) between the coastal and inland populations and were larger for the coastal populations (Table 3). The values of F_{ST}, and $F2_{ST}$ were larger for the inland populations compared to the coastal populations; however, the differences were only significant ($P < 0.05$) for Chinook and chum salmon.

The results from the program GESTE version 2.0 showed that no single habitat variable was strongly correlated to the population-specific F_{ST} values at the region-wide scale. However, one variable, precipitation (Prec), had a cumulative posterior probability greater than 0.9 (Table 4) and contributed to the highest probability (HP) models for each species (Table 5). The regression coefficient for Prec was negative which is consistent with the expectation that F_{ST} will be lower (gene flow higher) in areas of higher precipitation. The region-wide HP models also included an indicator of spatial isolation but the variables differed among species. These variables were distance from the coast (Coastdist) for Chinook, elevation (Elev) for chum, and median distance to all other populations (Meddist) for coho. In each instance, the regression coefficients indicated a positive correlation with F_{ST} as would be expected if gene flow decreases with increasing isolation. The all-populations HP model for Chinook also included an indicator of habitat size,

277 subbasin area (SBA), which was negatively correlated with F_{ST}. The posterior probabilities for
278 the region-wide HP models were low to moderate, ranging from 0.19 (coho) to 0.63 (chum).
279 Nevertheless, the models fit the data reasonable well as indicated by the moderate estimates of
280 unexplained variance (σ^2, range = 0.43-0.44) and the fact that the upper bounds of the 95%
281 highest probability density intervals (HPDI) were less than one (Foll and Gaggiotti 2006).
282 The highest HP model was for Coastal coho salmon (P = 0.90, Table 5). That model included
283 only the variable Meddist and a constant. The regression coefficient indicated Meddist was
284 positively correlated with F_{ST} and the estimates of σ^2 and the HPDI were low, indicating the
285 model fit the data well. The coastal Chinook model included two of the three variables (Prec,
286 SBA) identified in the region-wide Chinook model, however the estimate of σ^2 was relatively
287 high and the upper bound of the HPDI was greater than one. The results for coastal chum and
288 inland populations of all species were inconclusive. For example, the regression coefficients for
289 coastal chum were inconsistent with expectations, indicating a negative rather than positive
290 correlation between the variables (Elev, EcoR) and F_{ST}. No variables were identified for inland
291 populations of Chinook and coho salmon. For chum salmon, the highest probability model
292 included Elev and a constant, however, the posterior probability of the model was low (P = 0.18).
293 The region-wide partial Mantel tests indicated that genetic divergence was significantly
294 correlated with the habitat factors included in the HP models (Table 5) for each species when
295 controlling for waterway distance (Table 6). In addition, genetic divergence was correlated with
296 many of the factors not included in the HP models. Interestingly, both Chinook and coho genetic
297 divergence was not significantly correlated with waterway distance when controlling for
298 Coastdist. For chum salmon the correlation coefficient for waterway distance was low compared
299 to Coastdist but significant.

The partial Mantel tests for coastal Chinook salmon populations revealed the same two habitat factors (Prec, SBA) that were included in the HP model. For coastal chum salmon, the tests revealed one factor (Elev) included in the HP model and two factors, Prec and permafrost region (PermR) not included the HP model. For coastal coho salmon the tests revealed one factor, river length (RL), and it was not included in the HP model. Genetic divergence was significantly correlated with waterway distance in all partial Mantel tests of coastal populations in all species. Interestingly, the comparable location-specific indicator of waterway distance (Meddist) was included only in the HP model for coastal coho. The partial Mantel tests for the inland populations revealed two significant factors each for Chinook (Prec, Coastdist), chum (Coastdist, SBA) and coho (Coastdist, PermR) salmon. Waterway distance was not significant in any of the tests for inland coho salmon, nor was it significant for Chinook salmon when controlling for Coastdist.

Discussion

Life history and population divergence

We compared estimates of F_{ST} for each species in order to assess if life history traits predict the level of population divergence. The evaluation of F_{ST} suggested the relative order of species in terms of population divergence is chum = Chinook < coho rather than the predicted chum < coho < Chinook. The estimates of $F2_{ST}$, although larger than F_{ST}, also indicated chum = Chinook and Chinook < coho but not chum < coho. Both F_{ST} and $F2_{ST}$ suggested the population divergence in Chinook is lower than expected compared to chum and coho. Many factors could explain this outcome but we feel two factors stand out; location and species ecology. First, the study location is near the northern extent of the range for each species. The cold subarctic climate likely limits life history variation which has been shown to be positively correlated to genetic diversity in

Pacific salmon (Waples et al. 2001). Our predicted species order was based on relatively few life history traits. This is particularly relevant for Chinook salmon because the subarctic populations appear to exhibit much lower life history diversity than has evolved in populations from the Pacific Northwest and British Columbia (Taylor 1990; Waples et al. 2001). For example, the cold northern climate likely inhibits the evolution of winter and spring seasonal adult returns that have evolved in the south. Although chum exhibit a seasonal dichotomy in adult return, the run timing modes are separated by weeks, not months and are not complete barriers to gene flow (Olsen et al. 2008). Finally, the fact that Chinook exhibited lower genetic diversity than coho may also reflect ecological differences. In particular, coho occupy a wider array of freshwater habitat types throughout their range than the other species (Sandercock 1991). So despite the fact that the overall abundance of coho and Chinook appear to be similar in the fishery and escapement (Brannian et al. 2006; Clark et al. 2006), the effective size of coho salmon populations may be smaller (genetic drift greater) assuming they spawn in more areas.

Hierarchical population structure

Contrary to our prediction, the SAMOVA and BARRIER results suggested that the three watersheds do not form the first level of hierarchical population structure. Rather, the results showed that hierarchical population structure for each species occurs primarily along the latitudinal axes dominated by the Yukon River, rather than the much shorter longitudinal axes that defines the watershed positions. In fact, the SAMOVA results revealed a single population group for each species that consisted of all or most of the Norton Sound and Kuskowkim River watersheds and the lower Yukon River. The location of boundaries separating these coastal populations from the inland populations were similar among species and were identified as partial gene flow barriers, some of which likely reflect historical processes that have similarly influenced each species (see below).

347 The fact that population structure among the inland populations was higher than for coastal
348 populations suggests populations in the middle to upper Yukon River are more isolated and gene
349 flow is limited and heterogeneous. Indeed, the relatively high values of F_{ST} and low values of
350 intra-population diversity for the inland populations compared to the coastal populations (Table
351 3) suggested greater spatial structuring and lower gene flow occur inland. In addition to the
352 habitat features discussed below, these differences between the coastal and inland populations
353 may reflect differences in the complexity of freshwater migration. For example, studies of chum
354 and Atlantic salmon (*Salmo salar*) suggest gene flow is greater among populations closer to the
355 coast because the migration is shorter and less navigationally complex than for populations
356 further inland (Primmer et al. 2006; Olsen et al. 2008). The results from this study, suggested
357 populations high in the Yukon River drainage are most likely to be genetically isolated.
358 The SAMOVA and BARRIER results revealed some population boundaries between the
359 coastal and inland population groups that are possibly indicative of historical events. Three
360 barriers stand out: barrier six for Chinook and chum and barrier two for coho (Figure 3). In each
361 instance the populations above the barrier are part of an inland population group to which they
362 are not closely connected via waterway. This outcome is unlikely to have resulted from
363 contemporary gene flow and genetic drift but, given the glacial history of the region, vicariance
364 or post-glacial secondary contact are possible explanations. Vicariance would involve a change
365 in the tributary network through stream capture following glacial recession. For example, part of
366 the area around each barrier was ice covered during the late Wisconsin period (Kaufman and
367 Manley 2004). Barrier six for Chinook and chum are geographically proximate and occur in the
368 Koyukuk River, a lower Yukon River tributary, with headwaters approximately 9 km from the
369 upper Chandalar River, a middle Yukon River tributary. Barrier two for coho salmon occurs in
370 the upper Kuskokwim River and is located near the middle Tanana River, a middle Yukon River

371 tributary. Glacial recession followed by isostatic rebound could have resulted in stream captures
372 in both areas (e.g., a branch of the Chandalar River by the Koyukuk River and a branch of the
373 Tanana River by the Kuskokwim River). Vicariance induced by glacial recession has been used
374 to explain similar results for chum salmon elsewhere in Alaska (Seeb and Crane 1999).
375 Alternatively, the three barriers (and other barriers between the coastal and inland groups) may
376 reflect post-glacial secondary contact. The three watersheds are part of a hypothesized northern
377 glacial refugium (Beringia) for Pacific salmon and other freshwater fishes (Lindsey and McPhail
378 1986, Taylor 1990). It is not known if, or to what extent, Pacific salmon occupied the region
379 during glaciation. However, there is evidence some salmon populations in the area may have
380 survived the last glaciation in small numbers (e.g., Smith et al. 2003). The general geographic
381 congruence among species regarding the location of barriers between the coastal and inland
382 groups may reflect the edge of post glacial colonization into the putative northern refugium by
383 populations from a southern refugium (e.g., Cascadia, Lindsey and McPhail 1986). The fact that
384 both the coastal and inland populations exhibited private alleles (Table 3) is consistent with
385 secondary contact. Finally, while both vicariance and secondary contact may explain the location
386 of the barriers, we lack data to assess which explanation is most likely. There are no geological
387 studies supporting stream capture and a complete evaluation of secondary contact would require
388 the inclusion of southern refugium populations.

389 **Habitat features and population structure**

390 Two general trends related to spatial scale and habitat variation were apparent in the results of the
391 multivariate analyses conducted using GESTE. First, the influence of habitat features on the
392 degree of population structure for each species varied with scale. In particular, we found little
393 evidence of consistency within species in the habitat variables identified in the highest
394 probability (HP) models for the region-wide, coastal, and inland population groups. This trend

suggests that spatial scale plays an important role in how and if habitat influences population structure of sub-arctic Pacific salmon. The apparent scale dependence observed here is consistent with other landscape genetic studies (e.g., Dionne et al. 2008; Dillane et al. 2008). Second, the influence of habitat features on the degree of population structure was more complex (involved a greater number of variables) at the region-wide scale versus the smaller coastal and inland scales. This trend was also apparent in the partial Mantel test results. A reasonable explanation is that some of the habitat features such as precipitation operate on regional scale and are less likely to influence gene flow or population size at the smaller scales represented by the coastal and inland groups. For both trends it is important to note that negative results do not necessarily indicate lack of correlation at the smaller scales and that unexamined habitat features may contradict these trends. Nonetheless, the results underscore the importance of considering scale when assessing the impact of habitat diversity on population structure.

Evidence of a link between habitat and population structure was generally strongest at the region-wide scale. Here, we found similarities and differences among species in the habitat features identified in the HP models. One variable, precipitation, was included in the region-wide HP models and was a significant variable in the partial Mantel tests for each species. The negative regression coefficient for precipitation is consistent with the expectation that F_{ST} will be lower in areas of higher precipitation because rivers in these areas exhibit a greater magnitude and frequency of flooding (Jones and Fahl 1994). More flooding decreases river stability and may promote higher gene flow (Quinn 2005). The influence of climate-related factors such as precipitation on population structure and species diversity is of growing interest in conservation due to the possible impacts climate change (e.g., Hassol et al. 2005). Factors such as precipitation and temperature may have broad influence particularly for aquatic species like salmon. Although sufficient temperature data was not available for this study, a recent landscape

419 genetic analysis of Atlantic salmon (*Salmo salar*) revealed a correlation between air temperature
420 and population-specific F_{ST} (Dionne et al. 2008).

421 Four habitat features identified in the region-wide HP models were not shared among species.
422 However, three of these four variables (elevation, Coastdist, Meddist) are indicators of spatial
423 isolation. The variables for chum and Chinook (elevation and Coastdist), respectively) while
424 positively correlated ($r^2 = 0.91$) may not be interchangeable as they could reflect species
425 differences when combined with the other model variables. For example, elevation may be more
426 a deterrent to gene flow for chum salmon because they appear to be less likely to ascend partial
427 water flow barriers than Chinook (Salo 1991). On the other hand, Coastdist may be a better
428 indicator of genetic isolation for Chinook because they are strong swimmers and less inhibited by
429 partial flow barriers. It should also be noted that the inclusion of elevation and Coastdist in the
430 models for chum and Chinook, respectively, could partially reflect the signature of the historical
431 events hypothesized above. For coho, Meddist based on waterway distance to other populations
432 may be most appropriate because there is little evidence coho occur in the upper portion of the
433 Yukon River furthest from the coast and at the highest elevations. Finally, Chinook were the
434 only species in which an indicator of habitat size (subbasin area) was included in the region-wide
435 model. The fact that subbasin area was negatively correlated with F_{ST} is consistent with the
436 notion that population size is positively correlated with habitat size (e.g., Dillane et al. 2008).
437 Consequently, populations occupying small subbasins may exhibit higher rates of genetic drift
438 and thus larger values of F_{ST} compared to populations from large subbasins. The inclusion of
439 subbasin area in the Chinook model but not the chum and coho models suggests Chinook
440 population size, and hence population structure, is more sensitive to habitat size. Regarding
441 chum, their populations are generally much more abundant than Chinook populations and thus
442 are probably less likely to be influenced by factors influencing genetic drift compared to factors

influencing gene flow. Coho, on the other hand, appear to be similar in abundance to Chinook (Brannian et al. 2006). It could be that the subbasin scale examined here is too coarse for coho given that they presumably occupy a wider array of freshwater habitat type compared to Chinook (Sandercock 1991). In addition, the ability to occupy a wide range of habitat type suggests coho populations may be more densely distributed across the landscape. More densely distributed populations may be more sensitive to gene flow because neighboring populations will be less far apart.

With the exception of coastal coho, the models for the coastal and inland spatial scales were either not strongly supported (coastal Chinook) or inconclusive (coastal chum and inland populations for each species) compared to the region-wide models. This outcome could be due to a number of factors including low precision or accuracy in measuring each variable, incomplete population sampling across the landscape, and the limited number of habitat features evaluated. For the coastal Chinook and chum the results could also be due to the low level of genetic structure among coastal populations ($F_{ST} < 0.01$). Relatively high gene flow among most populations may inhibit detecting the influence of habitat heterogeneity with our samples.

Of the three species, coho appeared to be the most influenced by waterway connectivity (Meddist). In fact, Meddist was the only variable correlated with population structure of coastal coho. This single-variable model had the highest *P*-value of all models examined across species and spatial scales. In addition, the partial Mantel tests showed that coho had fewer habitat features that were significantly correlated with population structure when controlling for waterway distance. It is not clear why coho population structure appears to be more influenced by waterway distance, however as pointed out above the results may reflect the ability to occupy a wider range of habitat compared to chum and Chinook. It may be that coho population structure is simply less influenced by other habitat features. What ever the reason, the results

indicate that considering waterway distance alone may partially explain population structure in some instances, but that the inclusion of other habitat features and the use of multivariate methods that consider more that two variables simultaneously can provide a better assessment of the influence of habitat on population structure.

Summary and implications for conservation

We combined population genetic and landscape genetics methods to address the question does landscape heterogeneity similarly influence the spatial distribution of genetic diversity in subarctic populations of Chinook, chum and coho salmon? First, we found broadly similar, but unexpected, patterns of population structure for each species despite some differences in the level of population structure likely attributable to life history. Notably, the three major watersheds did not form the first level of hierarchical population structure as predicted but rather each species exhibited a single coastal population group and one or more inland population groups. In addition, some inland population groups were inconsistent with the waterway network, suggesting that extant population structure may also be influenced by historical events. Collectively, these results suggest that the spatial scale of conservation should first focus regionally at the coastal-inland population dichotomy rather than at the level of the three watersheds which is the present scale of management.

Second, two types of multivariate analysis suggested that region-wide population structure of each species was partially explained by multiple attributes including indicators of spatial isolation, habitat size and climate. However, only one attribute, precipitation, was identified in all species, suggesting that the population genetic response to environmental changes will probably vary among species. These results support a growing number of landscape genetic studies that show population structure may be best explained by multiple factors including variables that can influence population size and hence genetic drift (e.g., habitat size) as well as

indicators of spatial isolation and climate that may influence gene flow (Manier and Arnold 2006; Dillane et al. 2008; Dionne et al. 2008; Kittlein and Gaggiotti 2008). The results from these studies provide a better understanding of the factors influencing population structure and thus are more useful than simple isolate-by-distance models in a management and conservation context.

Third, the results of the multivariate analysis varied with spatial scale and with species. These results also corroborate recent studies that reveal the importance of considering spatial scale in landscape genetic analyses (Dillane et al. 2008; Dionne et al. 2008) and caution against assuming that shared habitat features will similarly influence the population structure of closely related species (Short and Caterino 2009). Although precipitation may partially explain the region-wide population structure of all species, the fact that the other variables in the region-wide models differ among species suggests that changes in precipitation are unlikely to similarly influence each species. Equally important is the fact that the region-wide models were not supported at the coastal and inland scales. A finer scale analysis may be needed at these smaller scales including more population samples and more precise data on habitat heterogeneity.

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Literature Cited

Bohonak AJ (2002) IBD (isolation by distance); a program for analysis of isolation by distance. *J. Hered.,* **93**, 153-154.

Brannian LK., Evenson MJ, Hilsinger JR (2006) Escapement goal recommendations for select Arctic-Yukon-Kuskokwim region salmon stocks, 2007. Alaska Department of Fish and Game, Fishery Manuscript No. 06-07, Anchorage. Available via http://www.sf.adfg.state.ak.us/FedAidPDFs/fm06-07.pdf.

Crane P, Molyneaux D, Lewis C, Wenburg J (2007) Genetic variation among coho salmon populations from the Kuskokwim Region and application to stock-specific harvest estimation. Alaska Fisheries Technical Report No. 96, U.S. Fish and Wildlife Service, Anchorage. Available via http://alaska.fws.gov/fisheries/genetics/reports.htm.

Dillane E, McGinnity P, Coughlan JP, et al (2008) Demographics and landscape features determine intrariver population structure in Atlantic salmon (*Salmo salar* L.): the case of the River Moy in Ireland. *Mol. Ecol.,* **17**, 4786-4800.

Dionne M, Caron F, Dodson JJ, Bernatchez L (2008) Landscape genetics and hierarchical genetic structure in Atlantic salmon: the interaction of gene flow and local adaptation. *Mol. Ecol.,* **17**, 2382-2396.

Dupanloup I, Schneider S, Excoffier L (2002) A simulated annealing approach to define the genetic structure of populations. *Mol. Ecol.,* **11,** 2571-2581.

Ecological Stratification Working Group (1996) A National Ecological Framework for Canada. Agriculture and Agri-Food Canada, Research Branch, Centre for Land and Biological Resources Research and Environment Canada, State of Environment Directorate, Ottawa/Hull. 125 p. Available via

537 http://sis.agr.gc.ca/cansis/publications/ecostrat/intro.html.
538 Excoffier L, Laval G, Schneider S (2005) Arlequin ver. 3.0: An integrated software program for
539 population genetic data analysis. *Evol. Bioinform. Online*, **1**, 47-50.
540 Flannery B, Beacham T, Wetklo M, Smith C, Templin B, Antonovich A, Seeb L, Miller S, Schlei
541 O, Wenburg JK (2006) Run timing, migratory patterns, and harvest information of Chinook
542 salmon stocks within the Yukon River. Alaska Fisheries Technical Report No. 92, U.S.
543 Fish and Wildlife Service. Available via
544 http://alaska.fws.gov/fisheries/genetics/reports.htm.
545 Foll M, Gaggiotti O (2006) Identifying the Environmental Factors That Determine the Genetic
546 Structure of Populations. *Genetics*, **174**, 875-891.
547 Gagnon M-, Angers B (2006) The determinant role of temporary proglacial drainages on the
548 genetic structure of fishes. *Mol. Ecol.*, **15**, 1051-1065.
549 Gallant AL, Binnian EF, Omernik JM, Shasby MB (1995) Ecoregions of Alaska US Geological
550 Survey Professional Paper 1567, 73 p. Available via
551 http://pubs.er.usgs.gov/usgspubs/pp/pp1567.
552 Goudet J (2001) FSTAT, a program to estimate and test gene diversities and fixation indices
553 (version 2.9.3). Available via http://www.unil.ch/izea/softwares/fstat.html.
554 Groot C, Margolis L (1991) Pacific salmon life histories. University of British Columbia Press,
555 Vancouver BC.
556 Hassol SJ, Berner J, Callaghan TV, Fox S, Furgal C, Hoel AH et al (2005) Arctic Climate Impact
557 Assessment. Cambridge University Press, Cambridge. Available via
558 http://www.acia.uaf.edu/.
559 Heginbottom JA, Brown J, Melnikov ES, Ferrians Jr OJ (1993) Circum-arctic map of permafrost
560 and ground ice conditions in Proceedings of the Sixth International Conference on

561 Permafrost, Wushan, Guangzhou, China: South China University Press, Vol. 2: 1132-1136.
562 Available via http://nsidc.org/data/docs/fgdc/ggd318_map_circumarctic/brown.html
563 Jones SH, Fahl CB (1994) Magnitude and frequency of floods in Alaska and conterminous basins
564 of Canada. US Geological Survey Water-Resources Investigations Report, 93–4197, 122 p.
565 Available via http://pubs.er.usgs.gov/usgspubs/wri/wri934179.
566 Kalinowski ST (2005) HP-RARE 1.0: a computer program for performing rarefaction on
567 measures of allelic richness. *Mol. Ecol. N.*, **5**, 187-189.
568 Kaufman DS, Manley WF (2004) Pleistocene maximum and late Wisconsin glacier extents
569 across Alaska, U.S.A. In: Ehlers J, Gibbard PL (eds) Quarternary Glaciations Extent and
570 chronology Part II: North America, Elsevier B.V. 440p.
571 Kittlein MJ, Gaggiotti OE (2008) Interactions between environmental factors can hide isolation
572 by distance patterns: a case study of Ctenomys rionegrensis in Uruguay. *Proc. Roy. Soc.*
573 *Lond. B*, **275**, 2633-2638.
574 Lindsey CC, McPhail JD (1986) Zoogeography of fishes of the Yukon and Mackenzie basins. In:
575 Hocutt CH, Wiley EO (eds) The zoogeography of North American freshwater fishes,
576 Wiley, New York, pp639-674.
577 MacLean R, Oswood MW, Irons JG, McDowell WH (1999) The effect of permafrost on stream
578 biogeochemistry: A case study of two streams in the Alaskan (U.S.A.) taiga.
579 *Biogeochemistry*, **47**, 239-267.
580 Manel S, Schwartz MK, Luikart G, Taberlet P (2003) Landscape genetics: combining landscape
581 ecology and population genetics. *TREE*, **18**, 189-197.
582 Manier MK, Arnold SJ (2006) Ecological correlates of population genetic structure: a
583 comparative approach using a vertebrate metacommunity. *Proc. Roy. Soc. Lond. B*, **273**,
584 3001-3009.

585 Manni F, Guerard E, Heyer E (2004) Geographic Patterns of (Genetic, Morphologic, Linguistic)
586 Variation: How Barriers Can Be Detected by Using Monmonier's Algorithm. *Hum. Biol.,*
587 **76**, 173-190.
588 Marten A, Brändle M, Brandl R (2006) Habitat type predicts genetic population differentiation in
589 freshwater invertebrates. *Mol. Ecol.*, **15**, 2643-2651.
590 McDonald JH (1994) Detecting natural selection by comparing geographic variation in protein
591 and DNA polymorphisms. In: Golding B (ed) Non-neutral evolution: theories and
592 molecular data, Chapman and Hall, New York, pp. 88-100.
593 Olsen JB, Flannery BG, Beacham TD, et al (2008) The influence of hydrographic structure and
594 seasonal run timing on genetic diversity and isolation-by-distance in chum salmon
595 (Oncorhynchus keta). *Can. J. Fish. Aquat. Sci.,* **65**, 2026-2042.
596 Petren K, Grant PR, Grant BR, Keller L (2005) Comparative landscape genetics and the adaptive
597 radiation of Darwin's finches: the role of peripheral isolation. *Mol. Ecol.*, **14**, 2943-2957.
598 Primmer CR, Veselov AJ, Zubchenko A, Poututkin A, Bakhmet I, Koskinen MT (2006) Isolation
599 by distance within a river system: genetic population structuring of Atlantic salmon, Salmo
600 salar, in tributaries of the Varzuga River in northwest Russia. *Mol. Ecol.,* **15,** 653-666.
601 Quinn TP (2005) The behavior and ecology of Pacific salmon and trout. University of
602 Washington Press, Seattle, WA..
603 Rice WR (1989) Analyzing tables of statistical tests. *Evolution*, **43**, 223-225.
604 Rousset F (2008) genepop'007: a complete re-implementation of the Genepop software for
605 Windows and Linux. *Mol. Ecol. Res.*, **8**, 103-106.
606 Sandercock FK (1991) Life history of coho salmon. In: Groot C, Margolis L (eds) Pacific salmon
607 life histories, University of British Columbia Press, Vancouver BC, pp 392-446.
608 Seeb LW, Antonovich A, Banks MA, Beacham TD, Bellinger MR, Blankenship SM, et al (2007)

609 Development of a standardized DNA database for Chinook salmon. *Fisheries* **32**, 540-552.
610 Short AEZ, Caterino MS (2009) On the validity of habitat as a predictor of genetic structure in
611 aquatic systems: a comparative study using California water beetles. *Mol. Ecol.*, **18**, 403-
612 414.
613 Smith CT, Nelson RJ, Wood CC, Koop BF (2001) Glacial biogeography of North American coho
614 salmon (*Oncorhynchus kisutch*). *Mol. Ecol.*, **10**, 2775-2785.
615 Smouse PE, Long JC, Sokal RR (1986) Multiple regression and correlation extensions of the
616 Mantel test matrix correspondence. *Syst. Zool.*, **35**, 627-632.
617 Storfer A, Murphy MA, Evans JS, et al (2006) Putting the `landscape' in landscape genetics.
618 *Heredity*, **98**, 128-142.
619 Taylor EB (1990) Phenotypic Correlates of Life-History Variation in Juvenile Chinook Salmon,
620 Oncorhynchus tshawytscha. *J. Anim. Ecol.*, **59**, 455-468.
621 Waples RS, Gustafson RG, Weitkamp LA, et al (2001) Characterizing diversity in salmon from
622 the Pacific Northwest. *J. Fish Biol.*, **59**, 1-41.
623 Weir BS, Cockerham CC (1984) Estimating F-statistics for the analysis of population structure.
624 *Evolution*, **38**, 1358-1370.
625 Whiteley AR, Spruell P, Allendorf F (2004) Ecological and life history characteristics predict
626 population genetic divergence of two salmonids in the same landscape. *Mol. Ecol.*, **13**,
627 3675-3688.

Table 1. Sample information, population specific F_{ST}, and habitat variables for Chinook, chum and coho salmon in the Yukon River, Kuskokwim, River and Norton Sound. Latitude and longitude are reported as decimal degrees (North American Datum 1983). Variable abbreviations are given in Appendix 1. Chum salmon locations are prefixed with s or f to denote summer and fall run timing.

Location	ID	n	Year	Lat NAD83	Long NAD83	Elev (m)	Prec (cm)	ER	PF	SBA (km^2)	RL (km)	Coastdist (km)	Meddist (km)	Migdiff	F_{ST}
								Chinook							
Yukon R.															
Andreafsky R.	1	107	2003	62.117	-162.807	6	43	ER3	PF5	35479	231	202	1644	1167	0.0072
Anvik R.	2	30	2002	62.649	-160.396	24	43	ER2	PF2	10093	242	553	1747	13270	0.0430
Gisasa R.	3	99	2001	65.253	-157.712	52	38	ER3	PF3	7941	160	957	2003	49386	0.0111
Tozitna R.	4	110	2003	65.515	-152.208	153	43	ER3	PF5	4215	208	1251	1861	191374	0.0315
Henshaw Ck.	5	96	2001	66.557	-152.210	137	38	ER2	PF1	4434	35	1634	2679	223917	0.0482
SF Koyukuk R.	6	31	2003	66.849	-151.061	221	43	ER3	PF5	5993	290	1755	2800	387085	0.0446
Kantishna R.	7	100	2005	64.738	-149.996	91	38	ER2	PF3	18381	261	1347	1917	122394	0.0407
Chena R.	8	116	2001	64.794	-147.922	132	38	ER2	PF3	11578	178	1545	2115	203210	0.0506
Salcha R.	9	44	2004	64.536	-146.286	245	38	ER4	PF5	5734	251	1668	2238	408225	0.0461
Beaver Ck.	10	87	1997	65.769	-146.776	265	38	ER4	PF4	20936	478	1872	1892	496009	0.0445
Chandalar R.	11	90	2003	66.986	-146.393	158	38	ER8	PF3	5747	411	1744	1742	275587	0.0316
Sheenjek R.	12	45	2003,04,06	67.092	-144.201	185	25	ER8	PF3	12302	467	1861	1859	344374	0.0395
Chandindu R.	13	101	2004	64.292	-139.469	496	38	ER10	PF4	12683	103	2238	2235	1109880	0.0416
Klondike R.	14	86	2001,02,03	64.052	-139.443	303	38	ER4	PF4	12683	236	2252	2250	682430	0.0620
Stewart R.	15	91	1997	63.363	-139.515	310	30	ER4	PF4	12683	734	2348	2346	728034	0.0423
Mayo R.	16	84	1992,2003	63.616	-135.899	520	38	ER10	PF4	6860	70	2642	2640	1373781	0.0316
Pelly R.	17	90	1997	62.785	-137.335	451	30	ER9	PF4	5379	810	2530	2528	1141018	0.0378
Earn R.	18	52	2003,04	62.734	-134.698	578	38	ER10	PF4	18229	128	2764	2761	1597422	0.0495
Blind Ck.	19	101	2003,04	62.194	-133.181	811	38	ER10	PF6	18229	69	2920	2918	2368396	0.0453
Tatchun R.	20	91	1996,97	62.281	-136.301	512	30	ER9	PF4	19885	98	2625	2623	1344196	0.0390
Nordenskiold R.	21	95	2003	62.102	-136.302	517	30	ER9	PF4	19885	272	2662	2660	1376179	0.0800
Little Salmon R.	22	77	1987,97	62.079	-135.360	611	38	ER9	PF7	19885	72	2756	2754	1684146	0.0339
Big Salmon R.	23	88	1987,97	61.438	-133.496	781	43	ER5	PF7	6835	247	2966	2964	2316519	0.0326
Takhini R.	24	73	1997,2002	60.647	-136.113	669	30	ER11	PF7	7341	126	3087	3085	2065284	0.0605
Nisutlin R.	25	47	1987,97	60.162	-132.725	683	38	ER11	PF7	17893	349	3105	3103	2120856	0.0513
Kukskokwim R.															
MF Goodnews R.	26	106	2005	59.157	-161.393	11	64	ER1	PF6	59769	96	18	2416	196	0.0040
NF Goodnews R.	27	106	2006	59.129	-161.478	3	64	ER1	PF6	59769	138	9	2407	28	0.0054
Arolik R.	28	101	2005	59.563	-161.486	53	64	ER1	PF6	59769	61	46	2261	2448	0.0025

Kanektok R.	29	101	2005	59.740	-161.021	119	64	ER1	PF6	59769	150	76	2283	9017	0.0012
Eek R.	30	88	2002	60.164	-161.118	61	64	ER1	PF6	59769	296	171	2324	10427	0.0029
Kwethluk R.	31	92	2001	60.494	-161.096	24	64	ER1	PF2	59769	220	229	2374	5375	0.0032
Kisaralik R.	32	91	2005	60.857	-161.242	4	43	ER7	PF2	59769	187	166	2311	733	0.0046
Tuluksak R.	33	94	1994	61.044	-160.585	15	43	ER1	PF2	59769	148	260	2406	3898	0.0043
Aniak R.	34	43	2005	61.583	-159.491	15	43	ER2	PF2	16200	217	335	2480	5019	0.0036
Salmon R.	35	86	2002	61.067	-159.175	117	89	ER1	PF5	16200	85	432	2578	50700	0.0012
George R.	36	91	2002	61.942	-157.697	87	64	ER3	PF3	16200	150	484	2629	42052	0.0047
Kogrukluk R.	37	93	1993/2005	60.838	-157.840	117	64	ER3	PF6	16604	105	736	2882	86149	0.0023
Stony R.	38	90	1994	61.771	-156.588	61	64	ER2	PF3	24231	315	564	2710	34394	0.0077
Tatlawiksuk R.	39	92	2005	61.935	-156.194	79	64	ER2	PF3	24231	130	598	2744	47485	0.0344
Cheeneetnuk R.	40	88	2002	61.812	-156.011	105	64	ER2	PF5	24231	113	615	2761	64549	0.0050
Gagaryah R.	41	106	2006	61.619	-155.647	160	64	ER2	PF5	24231	102	650	2796	104147	0.0072
Takotna R.	42	78	2005	62.968	-156.097	111	43	ER3	PF5	5767	203	869	3014	96327	0.0080
Salmon R.	43	94	1995	62.892	-154.577	119	43	ER2	PF3	15768	148	928	3074	110213	0.0354
Norton Sound															
Pilgrim R.	44	52	2006	65.103	-164.825	7	38	ER6	PF5	13242	101	41	3214	300	0.0106
Snake R.	45	21	2006	64.538	-165.546	8	43	ER6	PF2	11891	50	14	2835	114	0.0206
Unalakleet R.	46	80	2005	63.865	-160.717	14	38	ER3	PF2	13047	172	4	2065	56	0.0202
Golsovia R.	47	57	2006	63.562	-161.070	0	38	ER7	PF5	13047	88	42	2019	0	0.0327
								Chum							
Yukon R.															
sAndreafsky R.	1	100	2004	62.117	-162.807	5.8	43	ER3	PF5	35479	231	202	1509	1167	0.0099
sAtchuelinguk R.	2	88	1989	61.958	-162.827	0.0	43	ER3	PF2	16860	72	193	1478	0	0.0175
sTozitna R.	3	100	2002	65.515	-152.208	153.0	43	ER3	PF5	4215	208	1251	1627	191374	0.0033
sAnvik R.	4	89	1988	62.649	-160.396	24.0	43	ER2	PF2	10093	242	553	1573	13270	0.0063
sCalifornia Ck.	5	43	1997	64.092	-157.696	91.4	43	ER3	PF5	25061	52	1115	2136	101980	0.0122
sNulato R.	6	93	2003	64.728	-158.207	39.5	43	ER3	PF3	15237	133	826	1732	32652	0.0065
sMelozitna R.	7	99	2003	64.838	-155.612	174.0	43	ER3	PF3	7035	434	1009	1646	175529	0.0042
sGisasa R.	8	100	2003	65.253	-157.712	51.6	38	ER3	PF3	7941	160	957	1812	49386	0.0052
sJim R.	9	100	2002	66.790	-151.201	198.0	38	ER3	PF5	5993	113	1740	2594	344442	0.0160
sSF Koyukuk R.	10	91	1996	66.614	-151.597	160.0	38	ER2	PF1	5993	290	1689	2544	270311	0.0175
sHenshaw Ck.	11	100	2003	66.557	-152.210	137.0	38	ER2	PF1	4434	35	1634	2489	223917	0.0023
sChena R.	12	98	1994	64.884	-146.696	198.0	38	ER3	PF5	5422	178	1669	2017	330469	0.0220
sSalcha R.	13	100	1994	64.536	-146.286	244.7	38	ER4	PF5	5734	251	1668	2017	408225	0.0203
sBig Salt R.	14	39	2001	65.885	-150.144	152.0	43	ER3	PF5	8046	79	1395	1583	212059	0.0326
fClearwater Ck.	15	70	1990	64.102	-145.561	312.1	38	ER2	PF3	13147	50	1723	2071	537714	0.0451

fToklat R.	16	100	1994	64.455	-150.315	115.0	38	ER2	PF3	18381	170	1431	1779	164568	0.0219
fKantishna R.	17	100	2001	64.738	-149.996	90.9	38	ER2	PF3	18381	261	1347	1695	122394	0.0310
fSheenjek R.	18	100	1989	66.740	-144.569	136.0	25	ER8	PF3	14556	467	1760	1871	239365	0.0297
fBlack R.	19	100	1995	66.664	-144.731	134.0	25	ER8	PF3	14556	538	1743	1855	233561	0.0298
fChandalar R.	20	100	2001	67.018	-146.465	169.0	38	ER8	PF3	5747	411	1750	1862	295791	0.0197
fTatchun R.	21	89	1992	62.281	-136.301	512.0	30	ER9	PF4	19885	98	2625	2737	1344196	0.0339
fPelly R.	22	50	1993	62.785	-137.335	451.0	30	ER9	PF4	18229	810	2530	2642	1141018	0.0844
fBig Ck.	23	89	1995	62.614	-136.982	464.0	30	ER9	PF4	19885	122	2561	2673	1188421	0.0427
fMinto Ck.	24	86	1989	63.702	-135.867	591.0	38	ER10	PF4	6860	22	2659	2771	1571457	0.0418
fKluane R.	25	99	2001	61.530	-139.317	742.0	38	ER12	PF6	25821	165	2759	2870	2046873	0.0637
fDonjek R.	26	57	1994	62.553	-139.517	518.0	38	ER4	PF4	25821	322	2544	2656	1317820	0.0841
fFishing Branch	27	100	1997	66.531	-139.250	373.0	43	ER14	PF2	23565	192	2542	2654	948336	0.0341
fTeslin R.	28	97	1992	61.022	-134.154	721.0	38	ER11	PF7	5040	508	2946	3058	2124269	0.0709
Kuskokwim R.															
sMF Goodnews R.	29	88	2007	59.157	-161.393	10.8	64	ER1	PF6	59769	96	18	2312	196	0.0067
sKanektok R.	30	82	2007	59.740	-161.021	119.0	64	ER1	PF6	59769	150	76	2179	9017	0.0059
sKwethluk R.	31	92	2007	60.494	-161.096	23.5	64	ER1	PF2	59769	220	229	2271	5375	0.0038
sTuluksak R.	32	90	2007	61.044	-160.585	15.0	43	ER1	PF2	59769	148	260	2302	3898	0.0039
sSalmon R.	33	87	2007	61.063	-159.194	129.0	89	ER1	PF5	16200	85	433	2475	55900	0.0037
sHolokuk R.	34	47	2007	61.525	-158.542	36.0	64	ER2	PF5	16200	86	393	2435	14159	0.0041
sGeorge R.	35	95	2007	61.942	-157.697	86.9	64	ER3	PF3	16200	150	484	2526	42052	0.0036
sKogrukluk R.	36	90	2007	60.838	-157.840	117.1	64	ER3	PF6	16604	105	736	2778	86149	0.0052
sTatlawiksuk R.	37	90	2007	61.935	-156.194	79.4	64	ER2	PF3	24231	130	598	2640	47485	0.0058
sTakotna R.	38	82	2007	62.968	-156.097	110.9	43	ER3	PF5	5767	203	869	2911	96327	0.0057
fBig R.	39	82	2008	62.467	-155.050	206.0	43	ER3	PF3	15768	221	977	3019	201307	0.0359
fSF Kuskokwim	40	93	2008	63.004	-154.273	131.8	43	ER2	PF3	15768	260	959	3001	126494	0.0304
Norton Sound															
Agiapuk R.	41	96	2005	65.223	-165.729	7.4	38	ER6	PF5	13242	120	21	2947	156	0.0200
Eldorado R.	42	93	2005	64.573	-164.937	7.2	51	ER6	PF2	11891	54	10	2554	73	0.0066
Fish R.	43	48	2005	64.624	-163.354	1.3	43	ER6	PF2	11891	146	4	2349	5	0.0075
Niukluk R.	44	77	2005	64.803	-163.450	7.6	43	ER3	PF5	11891	97	38	2383	287	0.0129
Koyuk R.	45	43	2005	65.139	-161.390	8.7	43	ER3	PF5	12797	259	85	2179	740	0.0180
Kwiniuk R.	46	88	2005	64.784	-162.238	28.9	43	ER3	PF5	12797	89	33	2232	953	0.0100
Nome R.	47	90	2005	64.497	-165.218	13.9	43	ER6	PF2	11891	65	6	2612	86	0.0059
Pikmiktalik R.	48	92	2005	63.237	-162.582	6.0	38	ER7	PF2	13047	79	5	1629	29	0.0066
Pilgrim R.	49	91	2005	65.103	-164.825	7.3	38	ER6	PF5	13242	101	41	3005	300	0.0059
Shaktoolik R.	50	94	2005	64.382	-160.963	22.3	43	ER7	PF5	13047	171	17	1949	390	0.0079
Snake R.	51	90	2005	64.538	-165.546	8.1	43	ER6	PF2	11891	50	14	2625	114	0.0092

Unalakleet R.	52	87	2005	63.865	-160.717	14.0	38	ER3	PF2	13047	172	4	1856	56	0.0067
Ungalik R.	53	49	2005	64.528	-160.784	29.2	43	ER7	PF5	12797	175	12	2045	365	0.0053
							Coho								
Yukon R.															
Archuelinguk R.	1	43	2005	62.176	-163.719	12.1	43	ER7	PF2	35479	72	146	1355	1767	0.0584
Andreafsky R.	2	92	1998	62.117	-162.807	5.8	43	ER3	PF5	35479	231	202	1358	1167	0.0440
Anvik R.	3	54	2002	62.649	-160.396	24.0	43	ER2	PF2	10093	242	553	1654	13270	0.0565
Rodo R.	4	51	2005	64.272	-158.723	50.2	43	ER3	PF2	15237	84	761	1785	38170	0.0567
Clear Ck.	5	41	2004	66.221	-155.541	86.7	43	ER3	PF5	18417	39	1415	2425	122679	0.1600
Kantishna R.	6	116	2001	64.738	-149.996	90.9	38	ER2	PF3	18381	261	1347	2357	122394	0.2780
Nenana R.	7	85	1997	64.502	-149.119	113.4	38	ER2	PF3	10078	237	1465	2475	166076	0.2460
Otter Ck.	8	99	2003/04	64.487	-149.162	118.0	38	ER2	PF3	10078	6	1468	2479	173216	0.2120
Clearwater Ck.	9	95	1997	64.062	-145.470	319.9	38	ER2	PF3	13147	50	1733	2744	554452	0.2970
Porcupine R.	10	97	1998	67.565	-139.835	241.0	25	ER13	PF2	14556	770	2131	3142	513690	0.3170
Fishing Branch	11	108	2000	66.531	-139.250	373.0	43	ER14	PF2	23565	192	2542	3553	948336	0.3520
Kuskokwim R.															
MF Goodnews R.	12	100	2004	59.157	-161.393	10.8	64	ER1	PF6	59769	96	18	1441	196	0.0280
Arolik R.	13	85	1997	59.563	-161.486	53.0	64	ER1	PF6	59769	61	46	1286	2448	0.0783
Kanektok R.	14	100	2004	59.740	-161.021	119.0	64	ER1	PF6	59769	150	76	1308	9017	0.0407
Kwethluk R.	15	99	2004	60.494	-161.096	23.5	64	ER1	PF2	59769	220	229	1304	5375	0.0210
Kisaralik R.	16	52	2004	60.762	-160.580	48.1	64	ER1	PF2	59769	187	228	1303	10940	0.0317
Tuluksak R.	17	97	2004	61.044	-160.585	15.0	43	ER1	PF2	59769	148	260	1336	3898	0.0249
Salmon R.	18	97	2004	60.955	-159.395	184.3	89	ER1	PF2	16200	85	457	1533	84203	0.0259
George R.	19	99	2004	61.942	-157.697	86.9	64	ER3	PF3	16200	150	484	1559	42052	0.0253
Kogrukluk R.	20	100	2004	60.838	-157.840	117.1	64	ER3	PF6	16604	105	736	1811	86149	0.0319
Tatlawiksuk R.	21	98	2004	61.935	-156.194	79.4	64	ER2	PF3	24231	130	598	1674	47485	0.0424
Takotna R.	22	99	2004	62.968	-156.097	110.9	43	ER3	PF5	5767	203	869	1944	96327	0.0517
SF Kuskokwim	23	96	2004	63.010	-154.375	130.0	43	ER2	PF3	15768	260	948	2024	123295	0.1430
Highpower Ck.	24	38	2004/05	63.408	-153.127	206.0	38	ER2	PF3	13229	220	1172	2247	241373	0.2440
Norton Sound															
Pilgrim R.	25	99	2006	65.103	-164.825	7.3	38	ER6	PF5	13242	101	41	3003	300	0.1400
Snake R.	26	98	2006	64.538	-165.546	8.1	43	ER6	PF2	11891	50	14	2624	114	0.1260
Shaktoolik R.	27	100	2006	64.374	-161.067	12.7	43	ER7	PF5	13047	171	9	1939	120	0.0622
Pikmiktalik R.	28	100	2006	63.237	-162.582	6.0	38	ER7	PF2	13047	79	5	1627	29	0.0592

Table 2. AMOVA results for populations when grouped by watershed (3w) using Arlequin version 3.01 and when grouped to maximize F_{CT} (among-group variation) using SAMOVA version 1.0. The bold values indicate the grouping strategy when F_{SC} (within-group variation) first declines substantially relative to F_{CT}. The numbers in each group indicate sample ID in Table 1

Species	Groups	Group composition	F_{ST}	F_{CT}	F_{SC}
Chinook	3w	[1-25] [26-43] [44-47]	0.032	0.012	0.020
	2	[1-20,22-47] [21]	0.053	0.031	0.023
	3	[1-20,22-23,25-47] [21] [24]	0.049	0.027	0.022
	4	[1-20,22-23,25-44,46-47] [21] [24] [45]	0.047	0.025	0.022
	5	[1-20,22-23,25-38,40-44,46-47] [21] [24] [39] [45]	0.044	0.024	0.021
	6	**[1-4,26-38,40-47] [5-12] [13-14] [15-20,22-25] [21] [39]**	**0.033**	**0.024**	**0.009**
	7	[1-4,26-38,40-47] [5-12] [13-14] [15-20,22-23,25] [21] [24] [39]	0.033	0.025	0.008
	8	[1-4,26-38,40-47] [5-9] [10-12] [13-14] [15-20,22-23,25] [21] [24] [39]	0.033	0.026	0.007
chum	3w	[1-28] [29-40] [41-53]	0.019	0.009	0.011
	2	[1-24,27-53] [25-26]	0.039	0.030	0.009
	3	[1-24,27-53] [25] [26]	0.037	0.027	0.009
	4	[1-24,27-38,40-53] [25] [26] [39]	0.031	0.023	0.009
	5	[1-24,27,29-38,40-53] [25] [26] [28] [39]	0.028	0.020	0.008
	6	**[1-8,11,29-38,41-53] [9-10,14-24,27] [12-13] [25-26] [28] [39-40]**	**0.020**	**0.020**	**0.000**
	7	[1-8,11,29-38,41-53] [9-10,14,18-24,27] [12-13] [15-17] [25-26] [28] [39-40]	0.019	0.020	-0.001
	8	[1-8,11,29-38,41-53] [9-10,14,15,18-24,27] [12-13] [16] [17] [25-26] [28] [39-40]	0.019	0.020	-0.001
coho	3w	[1-11] [12-24] [25-28]	0.112	0.062	0.054
	2	**[1-5,12-22,25-28] [6-11,23-24]**	**0.162**	**0.141**	**0.025**
	3	[1-5,12-22,25-28] [6-11,23] [24]	0.159	0.138	0.025
	4	[1-5,12-22,25-28] [6,9-11,23] [7-8] [24]	0.154	0.135	0.022

Table 3. Comparison of genetic diversity between coastal and inland groups for Chinook, chum and coho salmon. Diversity estimates include mean heterozygosity (H_e), mean allelic richness (A_r), and mean private allelic richness (pA_r) over loci, F_{ST}, and binned F_{ST} ($F2_{ST}$).

			Intra-population			Inter-population	
Species	(N) [pops]		H_e	A_r	pA_r	F_{ST}	$F2_{ST}$
Chinook							
Coastal	(25) [1-4,26-38,40-47]		0.769	10.9	3.5	0.008	0.009
Inland	(22) [5-25,39]		0.719	9.2	1.1	0.033	0.035
		p	0.001	0.001	0.002	0.001	0.001
Chum							
Coastal	(32) [1-8,11,29-38,41-53]		0.866	11.9	3.6	0.003	0.003
Inland	(21) [9-10,12-28,39-40]		0.830	9.9	1.2	0.018	0.026
		p	0.001	0.001	0.005	0.001	0.004
Coho							
Coastal	(20) [1-6,12-22,25-28]		0.408	3.0	1.9	0.022	0.019
Inland	(8) [6-11,23-24]		0.254	2.4	0.6	0.038	0.056
		p	0.001	0.001	0.030	0.689	0.444

Table 4. Cumulative posterior probability (*P*) of all models identified by GESTE containing each habitat variable. Coastal and inland populations are shown in Table 2. Variable abbreviations are given in Appendix 1.

	P		
Factor	Chinook	Chum	Coho
All samples			
Elev	0.225	0.737	0.352
Prec	0.996	0.981	0.914
Coastdist	0.860	0.136	0.326
Meddist	0.044	0.035	0.608
SBA	0.609	0.047	0.053
RL	0.044	0.060	0.058
Migdiff	0.151	0.306	0.142
EcoR	0.066	0.034	0.174
PermR	0.039	0.089	0.054
Coastal samples			
Elev	0.226	0.389	0.055
Prec	0.680	0.088	0.061
Coastdist	0.117	0.183	0.047
Meddist	0.347	0.051	0.989
SBA	0.437	0.047	0.054
RL	0.064	0.036	0.096
Migdiff	0.310	0.241	0.045
EcoR	0.090	0.429	0.057
PermR	0.066	0.113	0.049
Inland samples			
Elev	0.085	0.696	0.112
Prec	0.038	0.052	0.082
Coastdist	0.061	0.342	0.132
Meddist	0.074	0.097	0.094
SBA	0.040	0.210	0.090
RL	0.035	0.137	0.092
Migdiff	0.073	0.420	0.121
EcoR	0.034	0.081	0.161
PermR	0.038	0.098	0.160

Table 5. Summary of highest probability (*P*) generalized linear models relating habitat variables to genetic differentiation (population-specific F_{ST}). σ^2 is the posterior mode of unexplained variance associated with each model and the 95% HPDI is the 95 percent highest probability interval. Coastal and inland populations are shown in Table 2. Variable abbreviations are given in Appendix 1.

	Regression coefficient for model factors									
	Const	Elev	Prec	Coastdist	Meddist	SBA	EcoR	*P*	σ^2	95% HPDI
Region wide										
Chinook	-4.11		-0.56	0.39		-0.32		0.45	0.44	0.25: 0.66
Chum	-4.37	0.58	-0.37					0.63	0.43	0.26; 0.62
Coho	-2.45		-0.42		0.63			0.19	0.45	0.19; 0.77
Coastal										
Chinook	-5.15		-0.62			-0.48		0.21	0.65	0.27; 1.10
Chum	-5.07	-0.33					-0.23	0.28	0.23	0.11; 0.36
Coho	-3.06				0.60			0.90	0.27	0.11; 0.50
Inland										
Chinook	-3.36							0.62	0.21	0.10; 0.35
Chum	-3.83	0.44						0.18	0.44	0.19; 0.72
Coho	-1.34							0.57	0.42	0.10; 0.92

Table 6. Partial Mantel test correlations (r) of pairwise genetic divergence [$F_{ST}/(1 - F_{ST})$] with habitat factors, controlling for pairwise waterway distance (factor c/dist) and vice versa (dist c/factor). Coastal and inland populations are shown in Table 2. Only habitat factors that were statistically significant for at least one species are shown. Bold r – values indicate factors included in the highest probability models in Table 5. Variable abbreviations are given in Appendix 1.

	Chinook		chum		coho	
	dist c/factor	factor c/dist	dist c/factor	factor c/dist	dist c/factor	factor c/dist
Factor	*r*	*r*	*r*	*r*	*r*	*r*
Region wide						
Elev diff	0.34***	0.30***	0.45***	**0.57*** **	0.40***	0.49***
Prec avg	0.58***	**-0.47*** **	0.67***	**-0.41*** **	0.47***	**-0.23***
Coastdist diff	0.11	**0.35*** **	0.22**	0.55***	0.10	0.73***
SBA avg	0.55***	**-0.30** **	0.63***	-0.04	0.49***	-0.06
RL avg	0.56***	0.17	0.66***	0.37**	0.50***	0.23
Migdiff diff	0.35***	0.30**	0.46***	0.59***	0.30***	0.58***
EcoR	0.52***	0.08*	0.61***	0.12*	0.49***	0.13*
PermR	0.53***	0.07**	0.62***	0.08*	0.52***	0.09
Coastal						
Elev diff	0.46**	0.03	0.26***	**-0.17** **	0.57***	-0.12
Prec avg	0.31*	**-0.41** **	0.23**	-0.25*	0.50***	-0.28
SBA avg	0.33*	**-0.33***	0.21**	-0.09	0.50***	-0.13
RL avg	0.46**	-0.03	0.21**	<0.01	0.53***	-0.36*
PermR	0.46**	0.05	0.22**	-0.10*	0.57***	-0.06
Inland						
Prec avg	0.66***	-0.27*	0.70***	0.05	0.12	-0.20
Coastdist diff	0.24	0.36***	0.59**	0.23*	-0.18	0.44*
SBA avg	0.67***	0.23	0.77***	0.47**	0.09	-0.10
PermR	0.64***	-0.01	0.73***	-0.05	-0.01	0.49*

*$P < 0.05$; ** $P < 0.01$; *** $P < 0.001$

Figure Captions

Figure 1. Sample locations for Chinook, chum and coho salmon in the Norton Sound (green), Yukon River (beige) and Kuskowim River (blue) watersheds. Sample details and habitat information are listed by sample ID for each species in Table 1.

Figure 2. The estimates of F_{ST} and $F2_{ST}$ for Chinook, chum and coho. The bars denote 95% confidence intervals.

Figure 3. Population groups and inferred gene flow barriers for Chinook, chum and coho salmon. Symbols indicate sample locations, symbol numbers indicate the sample ID for each species in Table 1. Different symbols indicate population groups defined by SAMOVA (red and black denote coastal and inland groups, respectively). Arrows indicate the locations of barriers (red lines or triangles). Numbers indicate the order in which barriers were identified (strongest putative barriers first) and the robustness of the inferred barrier based on 100 bootstrap samples (in parentheses).

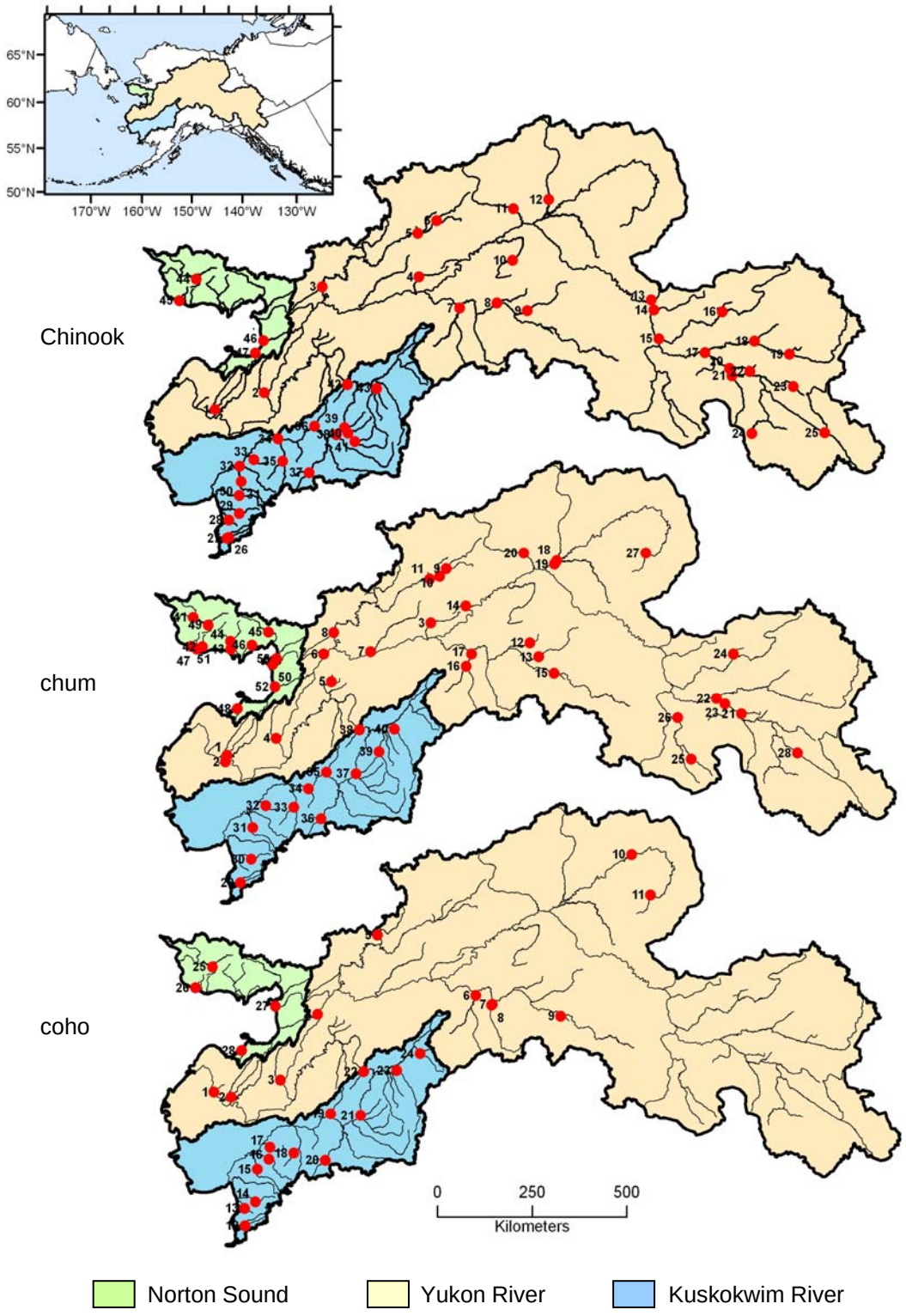
65°N
60°N
55°N
50°N
170°W
160°W
150°W
140°W
130°W
Chinook
chum
coho
0
250
500
Kilometers
Norton Sound
Yukon River
Kuskokwim River

Figure 1.

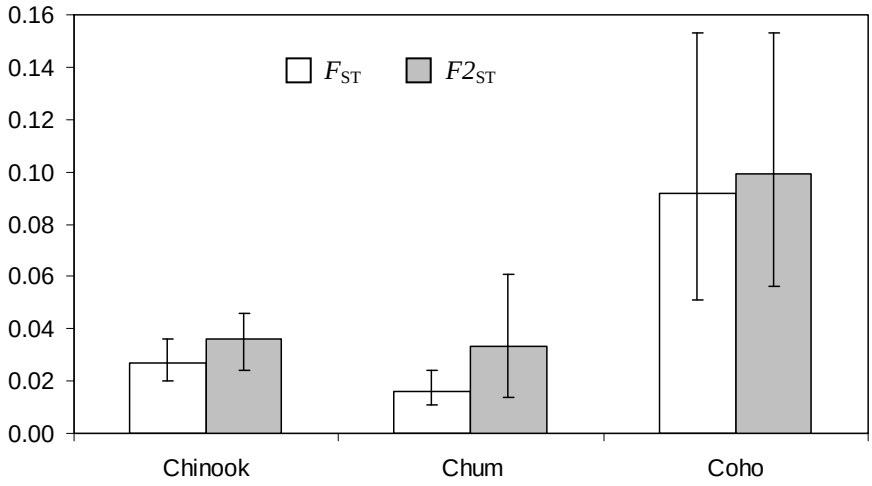

Figure 2.

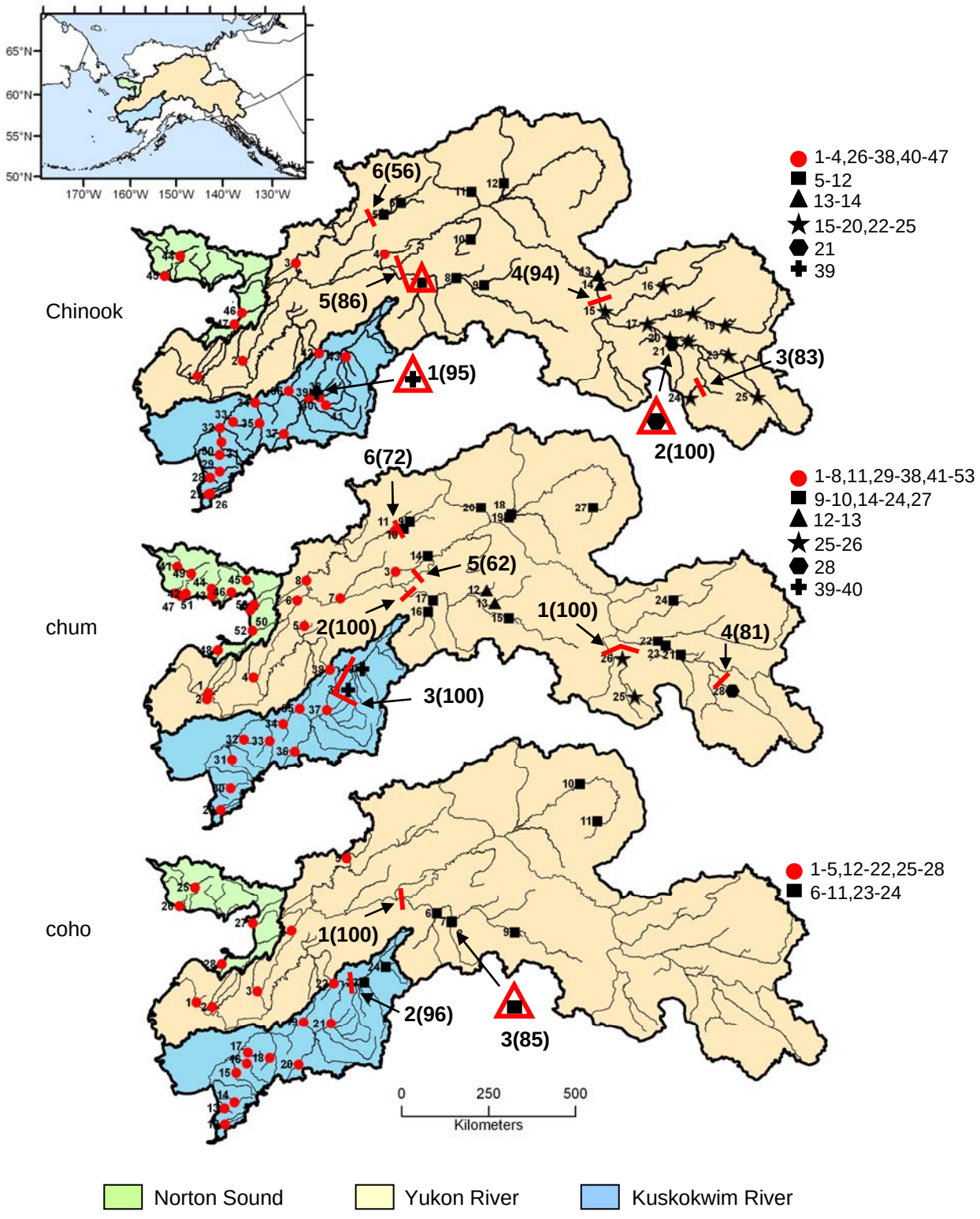
65°N
60°N
55°N
50°N
170°W
160°W
150°W
140°W
130°W
Chinook
chum
coho
6(56)
5(86)
4(94)
1(95)
3(83)
2(100)
6(72)
5(62)
2(100)
1(100)
4(81)
3(100)
1(100)
2(96)
3(85)
1-4,26-38,40-47
5-12
13-14
15-20,22-25
21
39
1-8,11,29-38,41-53
9-10,14-24,27
12-13
25-26
28
39-40
1-5,12-22,25-28
6-11,23-24
0
250
500
Kilometers
Norton Sound
Yukon River
Kuskokwim River

Figure 3.

Appendix A. Habitat categories (italicized) and variables.

Variable	Description
Spatial isolation	
Coastdist	Shortest waterway distance to coast
Meddist	For each location, the median pairwise waterway distance to all other locations
Elev	Elevation (m)
Migdiff	Migration difficulty (Elev x Coastdist)
Habitat size	
RL	River length (km)
SBA	Subbasin area (km^2) – the USGS hydrologic unit level 4 and equivalent for the Canadian section of the Yukon River.
Climate	
Prec	Annual precipitation (cm)
Ecology	
EcoR	Ecoregion: ER1 – Ahklun and Kilbuck Mountains, ER2 – Interior Bottomlands, ER3 – Interior Forested Lowlands and Uplands, ER4 – Interior Highlands, ER5 – Pelly Mountains, ER6 – Seward Peninsula, ER7 – Subarctic Coastal Plains, ER8 – Yukon Flats, ER9 – Yukon Plateau Central, ER10 – Yukon Plateau North, ER11 – Yukon Southern Lakes, ER12 – Ruby Range, ER13 – Old Crow Range, ER14 – Ogilvie Mountains
PermR	Permafrost region: PF1 – Continuous permafrost extent with high ground ice content and thick overburden, PF2 – Continuous permafrost extent with medium ground ice content and thick overburden, PF3 – Discontinuous permafrost extent with low ground ice content and thick overburden, PF4 – Discontinuous permafrost extent with low ground ice content and thin overburden and exposed bedrock, PF5 – Discontinuous permafrost extent with medium ground ice content and thick overburden, PF6 – Sporadic permafrost extent with low ground ice content and thick overburden, PF7 – Sporadic permafrost extent with low ground ice content and thin overburden and exposed bedrock