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ARTICLE

Divergent life-history races do not represent Chinook salmon coast-wide: the importance of scale in Quaternary biogeography

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Abstract: The dynamic Quaternary geology of the Pacific Ring of Fire created substantial challenges for biogeography. Fish life history and population genetic variation were shaped by climate change, repeated formation and subsidence of ice sheets, sea-level change, volcanism and tectonics, isostatic rebound, and now human activities. It is widely recognized in Chinook salmon (*Oncorhynchus tshawytscha*) that parallel evolution and phenotypic plasticity have obscured range-wide patterns of life-history segregation with evolutionary lineage, yet the idea of the lineages themselves persists. We employed a large, internationally standardized, microsatellite data set to explore population structure at coast-wide scale and test for two divergent lineages, whether or not related to life history. We found at least 27 distinct lineages. However, relationships among groups were poorly resolved — essentially a star phylogeny. We found pervasive isolation by distance among groups, complicating cluster analysis. Only in the interior Columbia River (east of the Cascade Mountains) is there a deep genetic bifurcation that supports both the two-lineage hypothesis and the life-history segregation hypothesis. This broad-scale perspective helps reconcile different views of Chinook salmon phylogeography and life-history distribution.

Résumé : La géologie quaternaire dynamique de la ceinture de feu du Pacifique est à l'origine d'importants défis sur le plan biogéographique. Le cycle biologique des poissons et la variabilité génétique de leurs populations ont été modelés par les changements climatiques, la formation et le retrait répétés de calottes glaciaires, les variations du niveau de la mer, le volcanisme et la tectonique, le relèvement isostatique et, aujourd'hui, l'activité humaine. S'il est largement admis que, chez le saumon quinnat (*Oncorhynchus tshawytscha*), l'évolution parallèle et la plasticité phénotypique ont masqué des patrons de ségrégation des cycles biologiques en fonction de la lignée évolutionnaire à la grandeur de l'aire de répartition, la notion des lignées comme telles persiste toutefois. Nous avons employé un grand ensemble de données de microsatellites normalisées à l'échelle internationale pour explorer la structure des populations à l'échelle de la côte et vérifier s'il y a présence de deux lignées divergentes, reliées ou non au cycle biologique. Nous avons trouvé au moins 27 lignées distinctes. Toutefois, les relations entre groupes étaient mal résolues, définissant essentiellement une phylogénie en forme d'étoile. Nous avons observé un isolement par la distance répandu parmi les groupes qui complique l'analyse topologique. Une bifurcation génétique marquée n'a été observée que dans la partie intérieure du fleuve Columbia (à l'est des monts Cascade), ce qui appuie tant l'hypothèse de la présence de deux lignées que celle d'une ségrégation des cycles biologiques. Cette perspective facilite le rapprochement d'opinions divergentes concernant la phylogéographie et la répartition des cycles biologiques du saumon quinnat. [Traduit par la Rédaction]

Introduction

The Quaternary zoogeography of the west coast of North America is especially complicated by the volatile earth history of this region. In particular, euryhaline species such as salmonids, sticklebacks, and others often show complex patterns of morphological and life-history variation that is influenced by selective pressures and historical contingencies as well as phenotypic plasticity and parallel evolution (Taylor et al. 1996; McCusker et al. 2000; Johnson and Taylor 2004). Chinook salmon (*Oncorhynchus tshawytscha*) population structure is often characterized as a primary dichotomy between "stream-type" and "ocean-type" life histories (Gilbert 1912, 1922) that were once thought to represent distinct "lineages" or evolutionary "races" (Healey 1983, 1991). It is now widely recognized that this pattern of strict segregation of life-history types with distinct genetic lineage is substantially confounded by parallel evolution and phenotypic plasticity (Waples et al. 2004; Beacham et al. 2006). Fish with stream-type life history generally rear in freshwater streams, undergo smoltification as yearlings, and quickly migrate to sea. By contrast, ocean-type fish migrate downstream almost immediately as subyearling fry or parr but spend an extended period in estuarine habitats. Stream-type fish have an early adult return migration for semelparous spawning (spring or summer run), whereas ocean-type fish return later, in late summer or fall. Nearly all Chinook salmon genetic

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studies continue to consider life history because of its importance for interpretation of population structure, yet the ocean-type and stream-type terms are used inconsistently to refer to life-history traits in individual fish, to populations, or to genetic lineages.

Stream-type and ocean-type life histories were originally described only from patterns of scale annuli that indicated yearling and subyearling juvenile migrations, respectively (Gilbert 1912, 1922). For a long time, adult return (or spawn time) was considered synonymous with lineage or race (Mason 1965). Healey (1991) synthesized juvenile and adult life histories to develop a new racial model; stream types were derived from a northern glacial refuge, and ocean types were from a southern refuge. Healey's (1991) inferred contact zone was at latitude 56°N. He also inferred from low harvest rates that the stream-type lineage exhibits a distinct, offshore marine migration (Myers et al. 1987; Trudel et al. 2009; Weitkamp 2010).

Myers et al. (1998) analyzed Chinook salmon allozyme data from California to western Alaska; the results seemed to support Healey's racial model, and subsequent genetic studies supported a genetic dichotomy in British Columbia (Teel et al. 2000; Beacham et al. 2003) and in the Columbia River (Rasmussen et al. 2003; Waples et al. 2004; Narum et al. 2004, 2010). Despite support for two principal lineages, frequent parallel evolution of life history complicated the Healey (1991) hypothesis and led Myers et al. (1998) and Waples et al. (2004) to offer a refinement that emphasized different scales of evolutionary divergence. Their interpretation was strongly driven by the compelling distinctiveness of sympatric lineages in the interior Columbia Basin. The southern–coastal lineage and the northern–interior lineage of Healey (1991) were each thought to have an ancestral predisposition for life-history type, but with frequent parallel evolution of adult return time and juvenile outmigration, especially in the southern–coastal lineage. In this view, stream-type and ocean-type represented evolutionary lineages, irrespective of life history of individuals and populations, which might exhibit phenotypic plasticity, parallel evolution, or population-level polymorphism. Despite other examples of life-history parallelism in fishes (Reznick et al. 1996; Colosimo et al. 2005; Duponchelle et al. 2008), many salmon biologists did not adopt the lineage definition of Waples et al. (2004), and most continue to use the terms as life-history descriptors (Buchanan et al. 2009; Copeland and Venditti 2009; MacFarlane 2010), irrespective of geography or genetic affiliation, often citing both Healey (1991) and Waples et al. (2004). Waples et al. (2004) maintained that Chinook salmon were characterized by two (or a few) genetically discrete and distinct lineages, and that idea persists in research and management, particularly in the USA (e.g., "Two distinct types or races among Chinook salmon have evolved."; NOAA Office of Protected Resources, http://www.nmfs.noaa.gov/pr/species/fish/chinooksalmon.htm).

Waples et al. (2004) found support for Healey's ocean-type – stream-type hypothesis in the interior Columbia Basin, and to a lesser extent the Fraser River, but the authors were less clear about more northern populations. In addition to abundant parallelism, they suggested that on a broader geographic scale, Healey's hypothesis was further complicated for four principal reasons: (*i*) the extremely divergent upper Willamette River populations suggest that Healey's hypothesis of only two major lineages might be too simplistic, (*ii*) the genetic affinity between interior Columbia and interior Fraser populations is not as strong as would be predicted assuming a common origin for all stream-type populations, (*iii*) interior Fraser populations are not as strongly separated genetically from other Chinook salmon in British Columbia as are the stream- and ocean-type populations in the interior Columbia, and (*iv*) Healey did not include the full range of life-history diversity within the ocean-type populations. Waples et al. (2004) assumed ocean- and stream-type populations derive from separate lineages, perhaps — but not necessarily — related to northern and southern glacial refugia (p. 395). Explanation of their results suggested they viewed the lineages as a deep evolutionary feature of Chinook salmon related to range-wide biogeography and postglacial recolonization.

Beacham et al. (2006) suggested a minimum of two refugia, northern and southern, during the last glaciation, but were referring to Beringia, represented by contemporary populations in the Yukon and the Northern Gulf Coast of Southeast Alaska, versus all populations to the south, including those of the interior Fraser and Columbia basins. They also speculated that existing populations in southeast Alaska, British Columbia, and Washington might be derived primarily from the southern Columbia River refuge, with perhaps some contribution from a coastal British Columbia refuge.

Various scenarios have been proposed for two or three principal refugia that might coincide with two or a few major lineages in Chinook salmon. In the current study we address three principal questions: (*i*) What are the most divergent genetic groupings supported by currently available genetic data? (*ii*) How do the divergent lineages observed in the Columbia River relate to broader geographic diversity in Chinook salmon? Specifically, how do those populations relate to those of the Fraser River, Central British Columbia, and Southeast Alaska? (*iii*) Finally, what phylogeographic inferences can be drawn, and what are the limitations? We consider life-history variation in the context of potential predisposition of ancestral lineages that might have arisen from glacial refugia (Waples et al. 2004); however, we recognize parallel evolution and phenotypic plasticity (Beacham et al. 2006) and focus instead on the lineages themselves. Our goal is to provide a framework for understanding patterns of population genetic structure and life-history variation in Chinook salmon with the hope of eventually connecting those patterns with the specific processes that shaped them.

Materials and methods

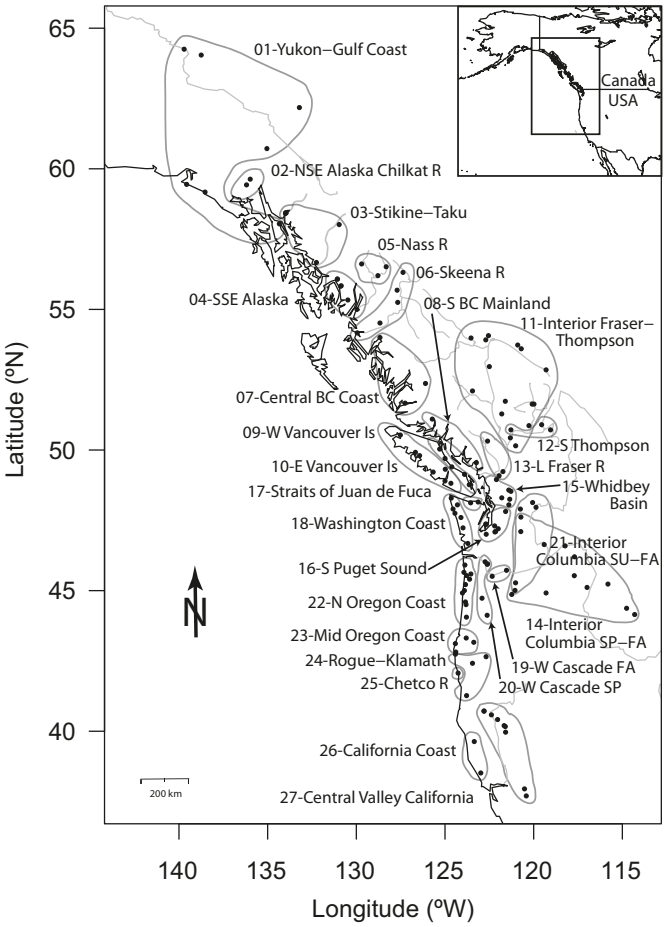
Sample collections, shared data, and quality control

The genotypic data analyzed here came from multiple laboratories and included both previously published (Beacham et al. 2006; Seeb et al. 2007; Narum et al. 2007*b*, 2008, 2010) and unpublished data. Our ability to combine these data sets and thus conduct a broader and more geographically balanced analysis than would otherwise be possible is based on the use of standardized markers and allele nomenclature adopted by all the contributing laboratories (Moran et al. 2006; Seeb et al. 2007).

Tissue samples were taken in a variety of ways and included wild adults and juveniles, as well as hatchery brood stocks. We originally examined 302 collections representing 168 sites (putative populations) within 45 regions or previously recognized lineages (Seeb et al. 2007). Our final analyses omitted some mixed-origin hatchery stocks. Ultimately, we examined 19 679 individual fish distributed among 280 collections from 144 sites and 45 regions–lineages ("Regions" hereafter; Fig. 1; Table 1). In most cases, these represent distinct geographic regions; however, in a few cases, distinct genetic groups overlap in distribution, such as the mid- and upper Columbia spring run and interior Columbia Basin late-summer – fall run. In general, sample sizes from each location were greater than 100 individuals (mean 130.5, standard deviation 44.9) and typically included multiple temporal replicates taken in different years between 1985 and 2005.

We employed 13 microsatellite loci (Table 2) and the same convention for standardization of genotypic data used by the Genetic Analysis of Pacific Salmonids (GAPS) Consortium (Seeb et al. 2007). The data analyzed here are part of what is now a larger data set used by the GAPS collaborators and regional fishery management agencies for a diverse range of applications, including identification of conservation units, stock-specific harvest impacts, habitat use, predation, and migration. Previous analyses of these micro-

Fig. 1. Map of collection sites depicting the broadest, most inclusive groups showing genetic cohesiveness (>70% bootstrap support; see Fig. 4). SU, summer; FA, fall; SP, spring.



satellite loci (Seeb et al. 2007; Narum et al. 2008; four common loci with Beacham et al. 2006) revealed no systematic patterns of linkage disequilibrium or departures from Hardy–Weinberg–Castle (HWC) genotypic expectations (Castle 1903). Nevertheless, we took several measures to evaluate data quality and test for violations of population genetic assumptions.

Quality assurance and quality control (QA–QC) of interagency data are detailed in Moran et al. (2006). The current study also included independent QA–QC testing of the combined data set. For example, replicate population samples, taken in different years, were pooled for all the analyses presented here, though we tested the assumption that replicates came from single populations (data not shown). In addition to tests for departures from HWC genotypic expectations, we tested for evidence of genotypic disequilibrium (GD, or compound linkage disequilibrium; Weir 1979) and potential genetic linkage among loci. These tests were done by using the Markov chain Monte Carlo (MCMC) methods described by Guo and Thompson (1992) and implemented in the program GENEPOP (Raymond and Rousset 1995). We also tested for departures from neutral expectation (loci potentially under selection) by using the F_{ST} outlier method of Beaumont and Nichols (1996) as implemented in the software application Lositan (Antao et al. 2008). We removed one locus, *Ots*G474, from our final data set because of an extreme departure from neutral expectation (most analyses were carried out with and without *Ots*G474). We used a simulated Fisher's exact test (Raymond and Rousset 1995) of allele-frequency differences between all pairs of collections and sites. Finally, a leave-one-individual-out jackknife procedure (MCMC in the ONCOR software package; Kalinowski 2007) was used to evaluate population and regional self-assignment and to identify potential sample quality problems. These procedures provided basic biological information at the same time that they tested for potential laboratory or sampling errors.

Regions, lineages, and the distribution of genetic diversity

To examine population genetic structure and diversity in the context of life-history variation and latitude, we used Weir and Cockerham's (1984) F_{ST} estimator, θ_{ST}, and Cavalli-Sforza and Edwards's (CSE) chord distance (Cavalli-Sforza and Edwards 1967) estimated with the programs FSTAT (Goudet 2001) and PHYLIP (Felsenstein 2005), respectively. Many analyses were conducted using multiple metrics that were found to produce similar results. For reporting purposes, and to allow comparisons, it was essential to be consistent with previous studies. For example, F_{ST} is typically used for isolation by distance (IBD), whereas CSE chord distance is commonly used for cluster analysis. A fundamental problem is to pick an appropriate metric for both fine-scale and higher-order relationships. A mutationally explicit metric for microsatellite loci, such as R_{ST}, might be more appropriate for higher order relationships (Goldstein et al. 1995). However, the GAPS allele nomenclature is not consistent with an inferred repeat unit increment for all loci, and in some cases imperfect repeats preclude any repeat-unit inference (see Seeb et al. 2007). For these reasons, and because genotypic data were obtained from multiple laboratories, it was essentially impossible to confidently calculate a metric that incorporated repeat-unit information (Moran et al. 2005). We also applied the G'_{ST} metric, which effectively normalizes disparate heterozygosities, relative to the untransformed G_{ST} (multilocus F_{ST}). Although the shape of the curve changed slightly, the overall pattern of IBD was similar (data not shown). For that reason, and because of recent caveats (Meirmans and Hedrick 2011) and criticism regarding the use of G'_{ST} (Whitlock 2011), we opted for the more traditional and more widely used F_{ST} approach. Again, we applied a variety of alternative metrics with no effect on our central conclusions.

Multivariate clustering and ordination were used for evaluation of barriers to gene flow and IBD. Diversity within sites was estimated as expected heterozygosity (H_S). The model-based clustering method in STRUCTURE version 2.3.2 (Pritchard et al. 2000) was used to estimate the minimum number of clusters represented. Five replicates were run for each iteration of K = 1 to K = 21, the estimated log-likelihoods [ln(PrK)] averaged, and ΔK calculated using the method of Evanno et al. (2005) to determine the most likely value of K. STRUCTURE was designed to sort individuals into populations rather than into groups of populations or lineages (Kalinowski 2010). Nevertheless, there is heuristic appeal to the notion that if the two-lineage pattern were a dominant element of Chinook salmon population structure, then STRUCTURE would probably reveal that pattern. To display STRUCTURE results on a map, ArcMap GIS software (ESRI) was used to perform inverse-distance-weighted interpolation with the Geostatistical Analyst extension. Every pixel represents an average of the cluster 1 Q values (STRUCTURE analysis where K = 2) from a minimum of 10 individuals and maximum of 15 individuals within the standard search neighborhood. We used a default option of power = 2, which controls the influence of known values on the interpolated values. We classified interpolated Q values into three categories of assignment to cluster 1 (0%–30%, >30%–70%, and >70%–100%). We then color-coded these categories to visualize underlying data from individual populations on our interpolated map. This analysis represents an heuristic method for identifying genetic discontinuities by displaying the geographical distribution of inferred ancestry. We compared the model-based clustering results with estimates of K from 26 distance-based clustering methods (estimates based on the first 10 principle component axes extracted from microsatellite allele frequencies and implemented in the

Table 1. Collection information, summary statistics, and available life-history data for Chinook salmon from 144 sample sites in 45 Regions and 27 Groups, including sample size (N) heterozygosity (H_S), allelic richness (AR), inbreeding index (F_{IS}), number of pairwise locus combinations (out of 66 pairs) exhibiting genotypic disequilibrium (GD), mean proportional ancestry ($\overline{Q}$), and three principal characters associated with stream-type and ocean-type life histories (life-history data provided by Fisheries and Oceans Canada and NOAA–Fisheries (including Healey 1983; Myers et al. 1998; Waples et al. 2004)).

Site No.	Site name	Region No.	Region name[a]	Group No.	Group name[b]	Latitude	Longitude	N	Collection year(s)	H_S	AR	F_{IS}	$\overline{Q}$	GD	Run[c]	Subyearling smolts (%)	Marine harvest rate (%)
001	Klondike River	01	Yukon	01	Yukon–Gulf Coast	064.04400	–138.74600	106	1995–2003	0.764	10.173	–0.007	0.894	0	SU	—	—
002	Chandindu River	01	Yukon	01	Yukon–Gulf Coast	064.25278	–139.70972	283	1998–2004	0.759	10.372	0.013	0.922	1	SU	—	—
003	Blind Creek	01	Yukon	01	Yukon–Gulf Coast	062.17778	–133.20972	160	2003–2004	0.784	11.116	0.003	0.872	0	SU	—	—
004	Whitehorse Rapids Fish Hatchery	01	Yukon	01	Yukon–Gulf Coast	060.71800	–135.04200	242	1985–1997	0.718	9.289	–0.008	0.901	0	SU	0	—
005	Situk River	02	North Gulf Coast Situk R	01	Yukon–Gulf Coast	059.44600	–139.56910	132	1988–1992	0.797	10.731	0.006	0.919	0	SP–SU	98	—
006	Klukshu River	03	North Gulf Coast Alsek R	01	Yukon–Gulf Coast	059.17220	–138.52930	141	1989–1990	0.816	11.193	0.018	0.917	0	—	—	—
007	Tahini River	04	NSE Alaska Chilkat R	02	NSE Alaska Chilkat R	059.63150	–135.98290	141	1992–2004	0.787	10.316	0.017	0.894	0	—	—	—
008	Big Boulder Creek	04	NSE Alaska Chilkat R	02	NSE Alaska Chilkat R	059.42820	–136.19060	144	1992–2004	0.805	11.591	–0.004	0.910	1	—	—	—
009	King Salmon River	05	NSE Alaska King Salmon R	01	Yukon–Gulf Coast	058.04300	–134.34085	144	1989–1993	0.781	8.347	0.013	0.924	11	—	—	—
010	Andrew Creek	06	SSE Alaska Stikine R	03	Stikine–Taku	056.66820	–132.25030	144	1989–2004	0.848	14.477	–0.001	0.824	0	—	—	—
011	Cripple Creek	07	SSE Alaska	04	SSE Alaska	056.07870	–131.06850	144	1988–2003	0.870	15.257	–0.002	0.718	0	—	—	—
012	Clear Creek	07	SSE Alaska	04	SSE Alaska	056.07870	–131.06850	144	1989–2004	0.867	15.077	0.007	0.721	1	—	—	—
013	King Creek	07	SSE Alaska	04	SSE Alaska	055.84080	–130.85080	143	2003	0.853	13.639	0.009	0.731	3	—	—	—
014	Chickamin River	07	SSE Alaska	04	SSE Alaska	055.82270	–130.89430	50	1990	0.864	14.573	–0.014	0.839	0	—	—	—
015	Keta River	07	SSE Alaska	04	SSE Alaska	055.33540	–130.47720	144	1989–2003	0.879	14.438	0.006	0.733	0	—	—	—
016	Nahlin River, upper	08	Taku R	03	Stikine–Taku	058.43520	–133.96640	144	1989–2004	0.846	13.722	0.01	0.810	0	SU	<1	—
017	Tatsatua Creek	08	Taku R	03	Stikine–Taku	058.43520	–133.96640	142	1989–1990	0.852	13.690	0.015	0.789	0	SU	<1	—
018	Nakina River	08	Taku R	03	Stikine–Taku	058.41960	–133.99230	142	1989–1990	0.845	14.207	0.007	0.818	0	SU	<1	—
019	Kowatua Creek	08	Taku R	03	Stikine–Taku	058.41960	–133.99230	144	1989–1990	0.850	13.800	0.011	0.781	0	SU	<1	—
020	Little Tahltan River	08	Taku R	03	Stikine–Taku	058.01667	–130.96667	140	1989–1990	0.859	14.819	0.022	0.793	0	SP	—	—
021	Owegee River	09	Nass R	05	Nass R	056.61667	–129.70000	81	1996	0.809	12.052	0.024	0.828	1	SU	<1	25
022	Damdochax River	09	Nass R	05	Nass R	056.51667	–128.31667	65	1996	0.822	12.453	–0.018	0.846	0	SU	<1	25
023	Kwinageese River	09	Nass R	05	Nass R	056.20000	–128.78333	73	1996	0.799	11.418	–0.007	0.765	0	SU	<1	25
024	Kincolith River	09	Nass R	05[d]	Nass R	055.00000	–129.96667	155	1996	0.849	13.358	0.015	0.812	1	SU	<1	25
025	Sustut River	10	Upper Skeena R	06	Skeena R	056.31667	–127.36667	155	2001	0.830	11.524	–0.005	0.935	0	SU	3.4	57

Table 1 (*continued*).

Site No.	Site name	Region No.	Region name[a]	Group No.	Group name[b]	Latitude	Longitude	*N*	Collection year(s)	H_S	AR	F_{IS}	$\overline{Q}$	GD	Run[c]	Subyearling smolts (%)	Marine harvest rate (%)
026	Fort Babine Hatchery	10	Upper Skeena R	06	Skeena R	055.68333	–127.70000	61	1996	0.869	14.619	0.02	0.816	0	SU	3.4	57
027	Bulkley River	10	Upper Skeena R	06	Skeena R	055.25000	–127.66667	142	1999	0.785	10.143	–0.003	0.882	1	SP	3.4	<<50
028	Kitsumkalum River, lower	11	Lower Skeena R	06	Skeena R	054.51667	–128.66667	142	2001	0.859	14.688	0.004	0.856	0	SU	3.3	57
029	Ecstall River	11	Lower Skeena R	06[d]	Skeena R	054.16667	–129.95000	141	2000–2002	0.813	11.116	0.031	0.670	0	SU	>3.4	57
030	Kitimat River Hatchery	12	Central BC Coast	07	Central BC Coast	054.00000	–128.66667	141	1997	0.869	15.196	0.01	0.661	0	SU	88	>50
031	Atnarko Hatchery	12	Central BC Coast	07	Central BC Coast	052.36667	–126.10000	144	1996	0.852	14.397	0.02	0.501	0	SU	86	48
032	Wannock Hatchery	12	Central BC Coast	07[d]	Central BC Coast	051.66667	–127.25000	144	1996	0.821	13.494	–0.013	0.329	0	FA	99	38
033	Klinaklini River	13	South BC Mainland	08	South BC Mainland	051.10000	–125.71667	144	1997	0.836	13.354	0.018	0.600	0	FA	—	—
034	Porteau Cove Hatchery	13	South BC Mainland	08	South BC Mainland	049.55000	–123.23333	154	2003	0.838	12.318	–0.006	0.580	6	FA	—	—
035	Marble Hatchery	14	West Vancouver Is	09	West Vancouver Is	050.53333	–127.51667	144	1996–2000	0.846	11.455	–0.014	0.659	0	FA	—	—
036	Tahsis River	14	West Vancouver Is	09	West Vancouver Is	049.91667	–126.66667	195	1996–2003	0.835	13.293	–0.007	0.933	0	FA	—	—
037	Conuma Hatchery	14	West Vancouver Is	09	West Vancouver Is	049.80000	–126.43333	143	1997	0.839	12.967	–0.002	0.906	2	FA	>75	—
038	Robertson Creek Hatchery	14	West Vancouver Is	09	West Vancouver Is	049.31667	–124.98333	164	1996–2003	0.863	13.433	0	0.676	0	FA	—	—
039	Tranquil River	14	West Vancouver Is	09	West Vancouver Is	049.21667	–125.66667	195	1996–1999	0.848	14.200	0.007	0.809	4	FA	—	—
040	Sarita Hatchery	14	West Vancouver Is	09	West Vancouver Is	048.90000	–125.00000	160	1997–2001	0.830	13.347	0.01	0.806	15	FA	—	—
041	Nitinat River Hatchery	14	West Vancouver Is	09	West Vancouver Is	048.81667	–124.66667	144	1996	0.819	12.283	–0.001	0.833	1	FA	—	—
042	Quinsam River Hatchery	15	East Vancouver Is	10	East Vancouver Is	050.03333	–125.30000	164	1996–1998	0.853	13.275	0.031	0.292	0	FA	99	—
043	Puntledge River Hatchery FA	15	East Vancouver Is	10	East Vancouver Is	049.70000	–125.00000	192	2000–2001	0.853	13.960	0.007	0.129	3	FA	—	—
044	Big Qualicum Hatchery	15	East Vancouver Is	10	East Vancouver Is	049.40000	–124.61667	144	1996	0.852	14.087	0.02	0.162	1	FA	100	—
045	Nanaimo River Hatchery FA	15	East Vancouver Is	10	East Vancouver Is	049.13333	–123.90000	192	1998–2002	0.855	13.047	0	0.179	0	FA	95	>50
046	Cowichan River Hatchery	15	East Vancouver Is	10	East Vancouver Is	048.76667	–123.63333	200	1999–2000	0.844	13.793	0.002	0.149	0	FA	—	—
047	Salmon River SP	16	Upper Fraser R	11	Interior Fraser–Thompson	054.06667	–122.55000	134	1997	0.833	12.720	–0.013	0.934	0	SP	—	—

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Table 1 (*continued*).

Site No.	Site name	Region No.	Region name[a]	Group No.	Group name[b]	Latitude	Longitude	*N*	Collection year(s)	H_S	AR	F_{IS}	$\overline{Q}$	GD	Run[c]	Subyearling smolts (%)	Marine harvest rate (%)
048	Torpy River	16	Upper Fraser R	11	Interior Fraser–Thompson	053.73333	–120.90000	85	2001	0.813	12.255	–0.019	0.952	0	FA	—	—
049	Morkill River	16	Upper Fraser R	11	Interior Fraser–Thompson	053.60000	–120.70000	154	2001	0.819	12.176	–0.025	0.938	2	FA	—	—
050	Swift River	16	Upper Fraser R	11	Interior Fraser–Thompson	052.85000	–119.30000	162	1996	0.791	10.040	0.051	0.930	0	FA	—	—
051	Stuart River	17	Mid-Fraser R	11	Interior Fraser–Thompson	053.98333	–123.53333	161	1996	0.863	15.174	0.04	0.912	0	FA	—	—
052	Nechako River	17	Mid-Fraser R	11	Interior Fraser–Thompson	053.91667	–122.70000	163	1996	0.867	14.883	0.01	0.896	0	FA	—	—
053	Quesnel River	17	Mid-Fraser R	11	Interior Fraser–Thompson	052.96667	–122.50000	144	1996	0.859	14.136	0.025	0.916	0	FA	—	—
054	Chilko River	17	Mid-Fraser R	11	Interior Fraser–Thompson	052.10000	–123.45000	178	1995–2002	0.853	14.036	–0.002	0.885	0	FA	<1	<10
055	Chilcotin River, upper	17	Mid-Fraser R	11	Interior Fraser–Thompson	051.73333	–121.60000	161	2001	0.836	12.486	0.007	0.844	3	SP	—	<10
056	Raft River	18	North Thompson R	11	Interior Fraser–Thompson	051.63333	–119.98333	79	2001–2002	0.847	13.994	–0.019	0.824	0	SU	—	—
057	Clearwater River	18	North Thompson R	11	Interior Fraser–Thompson	051.63333	–120.08333	154	1997	0.842	13.049	0.006	0.864	0	FA	—	—
058	Lower Adams River Hatchery	19	South Thompson R	12	South Thompson R	050.90000	–119.55000	46	1996	0.827	14.120	0.04	0.739	0	FA	25–75	>50
059	Middle Shuswap Hatchery	19	South Thompson R	12	South Thompson R	050.71667	–119.05000	125	1997	0.858	12.141	–0.002	0.801	0	FA	—	—
060	Thompson River, lower	19	South Thompson R	12	South Thompson R	050.71667	–121.28333	154	2001	0.807	16.187	–0.006	0.687	0	FA	34	—
061	Deadman River Hatchery	20	Lower Thompson R	11	Interior Fraser–Thompson	051.28333	–121.80000	173	1996–1999	0.828	11.466	0.002	0.920	0	SP	—	—
062	Louis Creek	20	Lower Thompson R	11	Interior Fraser–Thompson	050.86667	–120.26667	182	2001	0.760	8.670	–0.023	0.941	0	FA	—	—
063	Nicola River Hatchery	20	Lower Thompson R	11	Interior Fraser–Thompson	050.43333	–121.31667	142	1998–1999	0.820	11.381	–0.006	0.940	0	SP	<1	—
064	Spius Creek Hatchery	20	Lower Thompson R	11	Interior Fraser–Thompson	050.15000	–121.01667	136	1996–1998	0.813	11.183	0.024	0.899	0	SP	—	—
065	Birkenhead Hatchery	21	Lower Fraser R	13	Lower Fraser R	050.31667	–122.60000	140	1996–2003	0.711	9.219	–0.005	0.313	0	SP	<25	<1
066	Maria Slough	21	Lower Fraser R	13[d]	Lower Fraser R	049.23333	–121.73333	190	1999–2001	0.813	9.869	–0.01	0.708	49	SU	—	—
067	Chilliwack River Hatchery	21	Lower Fraser R	13	Lower Fraser R	049.08333	–121.95000	194	1998–1999	0.859	14.747	0.003	0.527	0	FA	—	—
068	North Fork Nooksack Hatchery	22	Nooksack R	15	Whidbey Basin	048.95000	–122.10000	139	1998–1999	0.844	11.978	0.011	0.213	4	SP–SU	93	59

Table 1 (*continued*).

Site No.	Site name	Region No.	Region name[a]	Group No.	Group name[b]	Latitude	Longitude	*N*	Collection year(s)	H_S	AR	F_{IS}	$\overline{Q}$	GD	Run[c]	Subyearling smolts (%)	Marine harvest rate (%)
069	Skagit River, upper	23	Whidbey Basin	15	Whidbey Basin	048.57623	–121.40436	56	1998	0.874	14.354	–0.031	0.293	12	SU	87	42
070	Cascade River, upper	23	Whidbey Basin	15	Whidbey Basin	048.53171	–121.28224	47	1998	0.881	14.451	0.006	0.255	1	SP	—	—
071	North Fork Stillaguamish Hatchery	23	Whidbey Basin	15	Whidbey Basin	048.30000	–121.80000	350	1996–2004	0.882	14.762	0.004	0.213	0	SU	97	65
072	Suiattle River	23	Whidbey Basin	15	Whidbey Basin	048.25000	–121.35000	154	1989–1999	0.877	14.545	0.009	0.261	1	SP	35	74
073	Sauk River	23	Whidbey Basin	15	Whidbey Basin	048.05000	–121.40000	115	1994–1995	0.877	15.154	0.002	0.244	0	FA	55	74
074	Skykomish River	24	South Puget Sound FA	16[d]	South Puget Sound	047.81450	–121.58279	44	2004–2005	0.876	15.857	–0.007	0.346	0	SU	>75	40
075	Soos Creek Hatchery	24	South Puget Sound FA	16	South Puget Sound	047.30000	–122.20000	184	1998–2004	0.824	13.692	–0.007	0.169	0	FA	—	—
076	South Prairie Creek	24	South Puget Sound FA	16	South Puget Sound	047.10000	–122.15000	104	1998–2002	0.816	13.700	0.015	0.195	0	FA	97	71
077	Voights Creek Hatchery	24	South Puget Sound FA	16	South Puget Sound	047.08755	–122.18654	95	1998	0.825	14.435	0.004	0.156	0	FA	—	—
078	Clear Creek Hatchery	24	South Puget Sound FA	16	South Puget Sound	047.00428	–122.67700	141	2005	0.818	13.915	0.002	0.231	0	FA	—	—
079	Hupp Springs Hatchery	25	South Puget Sound SP	16	South Puget Sound	047.37175	–122.70246	94	2002	0.792	10.244	–0.02	0.345	10	SU	80	80
080	White River Hatchery	25	South Puget Sound SP	16	South Puget Sound	047.20000	–122.00000	152	1998	0.816	10.836	0.005	0.327	2	SU	80	80
081	Dungeness River	26	Straits of Juan de Fuca	17	Straits of Juan de Fuca	048.15000	–123.13000	132	2004	0.849	12.723	0.012	0.230	0	FA	>95	—
082	Elwha River	26	Straits of Juan de Fuca	17	Straits of Juan de Fuca	048.12151	–123.55473	173	2004–2005	0.846	13.289	0.021	0.249	0	SU	35	60
083	Makah National Fish Hatchery	27	Washington Coast	18	Washington Coast	048.28972	–124.64889	138	2001–2003	0.861	13.592	–0.01	0.228	0	FA	—	—
084	Sol Duc River Hatchery	27	Washington Coast	18[d]	Washington Coast	048.05000	–124.30000	96	2003	0.870	13.717	–0.01	0.188	4	SP	—	—
085	Quillayute River	27	Washington Coast	18	Washington Coast	047.90195	–124.54603	108	1995–1996	0.890	14.641	0.013	0.259	0	FA	92	—
086	Hoh River	27	Washington Coast	18	Washington Coast	047.75000	–124.44000	120	2004–2005	0.892	14.956	0.021	0.299	0	FA	>95	—
087	Queets River	27	Washington Coast	18	Washington Coast	047.60000	–124.10000	80	1996–1997	0.894	15.100	0.014	0.281	0	FA	99	70
088	Humptulips Salmon Hatchery	27	Washington Coast	18	Washington Coast	047.23167	–123.98500	83	1990	0.881	14.434	–0.004	0.238	0	FA	99	—
089	Forks Creek Hatchery	27	Washington Coast	18	Washington Coast	046.67798	–123.71068	142	2005	0.885	14.941	0	0.149	0	FA	—	—
090	Tucannon River	28	Snake R SP–SU	14	Interior Columbia Basin SP–SU	046.20343	–117.69961	135	2003	0.812	11.885	–0.002	0.872	8	SP	0	—

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Table 1 (*continued*).

Site No.	Site name	Region No.	Region name[a]	Group No.	Group name[b]	Latitude	Longitude	*N*	Collection year(s)	H_S	AR	F_{IS}	$\overline{Q}$	GD	Run[c]	Subyearling smolts (%)	Marine harvest rate (%)
091	Imnaha River	28	Snake R SP–SU	14	Interior Columbia Basin SP–SU	045.11350	–116.99017	144	1998–2003	0.840	12.995	–0.013	0.894	1	SP	0	1
092	Minam River	28	Snake R SP–SU	14	Interior Columbia Basin SP–SU	045.53135	–117.71023	144	1994–2003	0.845	13.824	0.005	0.884	0	SP	0	1
093	Secesh River	28	Snake R SP–SU	14	Interior Columbia Basin SP–SU	045.23283	–115.81200	144	2001–2003	0.836	12.452	0.013	0.884	0	SP	0	1
094	West Fork Yankee Fork River	28	Snake R SP–SU	14	Interior Columbia Basin SP–SU	044.37217	–114.75986	60	2005	0.825	10.984	–0.024	0.946	17	SP	0	1
095	East Fork Salmon River	28	Snake R SP–SU	14	Interior Columbia Basin SP–SU	044.15031	–114.30559	144	2004–2005	0.831	12.487	0.016	0.916	9	SP	0	1
096	John Day River	29	Mid and Upper Columbia SP	14	Interior Columbia Basin SP–SU	044.91639	–119.30111	143	2000–2004	0.851	13.971	–0.018	0.869	0	SP	0	1
097	Wenatchee River, spring	29	Mid and upper Columbia SP	14	Interior Columbia Basin SP–SU	047.61473	–120.72046	62	1993	0.839	13.657	0.041	0.849	0	SP	0	1
098	Cle Elum Hatchery	30	Yakima R	14	Interior Columbia Basin SP–SU	047.09985	–120.72596	199	1998	0.862	13.393	0.022	0.850	0	SP	0	1
099	Warm Springs National Fish Hatchery	31	Deschutes R SP	14	Interior Columbia Basin SP–SU	044.86451	–121.23515	143	2002–2003	0.771	11.105	–0.007	0.854	0	SP	0	1
100	Methow River	32	Interior Columbia Basin SU–FA	21	Interior Columbia Basin SU–FA	048.13219	–120.06029	143	1992–1994	0.874	15.969	–0.006	0.135	0	SU	71	68
101	Wells Hatchery	32	Interior Columbia Basin SU–FA	21	Interior Columbia Basin SU–FA	047.96314	–119.86782	144	1993	0.876	15.860	–0.018	0.101	1	SU	—	—
102	Wenatchee River SU–FA	32	Interior Columbia Basin SU–FA	21	Interior Columbia Basin SU–FA	047.90000	–120.75000	135	1993	0.870	15.762	0.007	0.102	0	SU	88	68
103	Hanford Reach	32	Interior Columbia Basin SU–FA	21	Interior Columbia Basin SU–FA	046.63834	–119.40788	284	1999–2001	0.892	17.082	0.009	0.135	0	F	97	39
104	Lyons Ferry Hatchery	32	Interior Columbia Basin SU–FA	21	Interior Columbia Basin SU–FA	046.59133	–118.22483	186	2002–2003	0.877	15.718	0.013	0.122	2	FA	98	36
105	Deschutes River, lower	32	Interior Columbia Basin SU–FA	21	Interior Columbia Basin SU–FA	045.27721	–121.02007	144	1999–2002	0.878	16.036	0.017	0.092	6	FA	96	28
106	Deschutes River, upper	32	Interior Columbia Basin SU–FA	21	Interior Columbia Basin SU–FA	045.00841	–121.05319	144	1998–2002	0.868	14.768	0.006	0.081	0	FA	96	28

Table 1 (*continued*).

Site No.	Site name	Region No.	Region name[a]	Group No.	Group name[b]	Latitude	Longitude	*N*	Collection year(s)	H_S	AR	F_{IS}	$\overline{Q}$	GD	Run[c]	Subyearling smolts (%)	Marine harvest rate (%)
107	Spring Creek National Fish Hatchery	33	Spring Cr Group tule	19	West Cascade FA	045.72246	–121.53223	144	2001–2002	0.833	13.940	0.002	0.149	0	FA	—	—
108	North Santiam Hatchery	34	Willamette R SP	20	West Cascade SP	044.73002	–122.91264	143	2002–2004	0.821	13.036	0.005	0.105	12	SP	<25	55
109	McKenzie River Hatchery	34	Willamette R SP	20	West Cascade SP	044.12320	–122.62369	142	2002–2004	0.823	12.827	0.009	0.096	0	SP	<25	55
110	Lewis River FA	35	West Cascade FA	19	West Cascade FA	045.95000	–122.60000	93	2003	0.888	15.959	0.007	0.142	0	FA	97	53
111	Sandy River	35	West Cascade FA	19	West Cascade FA	045.50882	–122.33901	124	2002–2004	0.899	16.598	0.002	0.129	0	FA (late)	27	53
112	Kalama Falls Hatchery SP	36	West Cascade SP	20	West Cascade SP	046.02392	–122.73801	144	2004	0.870	15.013	0.032	0.258	0	SP	—	24
113	Lewis River Hatchery SP	36	West Cascade SP	20	West Cascade SP	045.93687	–122.61920	144	2004	0.874	15.081	–0.012	0.462	7	SP	—	24
114	Necanicum River Hatchery	37	North Oregon Coast	22	North Oregon Coast	045.91066	–123.87874	77	2005	0.854	13.116	0.034	0.167	4	FA	Prevalent	—
115	Nehalem River	37	North Oregon Coast	22	North Oregon Coast	045.65000	–123.93333	151	2000–2002	0.820	11.773	0.01	0.105	0	SU–FA	99	52
116	Wilson River	37	North Oregon Coast	22	North Oregon Coast	045.59147	–123.54154	139	2005	0.872	14.251	0.003	0.121	0	FA	99	—
117	Kilchis River	37	North Oregon Coast	22	North Oregon Coast	045.53357	–123.78603	58	2000–2005	0.872	14.115	0.013	0.110	0	FA	Prevalent	—
118	Trask River	37	North Oregon Coast	22	North Oregon Coast	045.40703	–123.61339	162	2005	0.880	14.510	0.011	0.172	0	FA	97	52
119	Nestucca River Hatchery	37	North Oregon Coast	22	North Oregon Coast	045.21583	–123.84528	130	2004–2005	0.864	13.457	0.018	0.101	9	FA	94	—
120	Salmon River FA	37	North Oregon Coast	22	North Oregon Coast	045.00276	–123.90506	102	2003	0.883	14.357	0.018	0.150	0	FA	87	64
121	Siletz River	37	North Oregon Coast	22	North Oregon Coast	044.91667	–124.01667	165	2000	0.888	14.761	0.012	0.142	0	FA	99	—
122	Yaquina River	37	North Oregon Coast	22	North Oregon Coast	044.59742	–123.84930	136	2005	0.875	14.023	0.027	0.134	1	FA	100	—
123	Alsea River	37	North Oregon Coast	22	North Oregon Coast	044.50285	–123.81402	168	2004	0.872	14.030	0.026	0.132	2	FA	>90	52
124	Siuslaw River	37	North Oregon Coast	22	North Oregon Coast	044.05626	–123.79269	159	2001	0.893	15.686	0.044	0.167	0	FA	97	—
125	South Coos River	38	Mid-Oregon Coast	23	Mid-Oregon Coast	043.31450	–123.80456	50	2000	0.884	15.194	0.03	0.124	0	FA	100	—
126	South Umpqua Hatchery	38	Mid-Oregon Coast	23[d]	Mid-Oregon Coast	043.16318	–123.37731	134	2002	0.872	15.169	0.01	0.102	0	FA	Prevalent	—
127	Coquille River	38	Mid-Oregon Coast	23	Mid-Oregon Coast	043.11667	–124.41667	141	2000	0.872	14.704	0.029	0.167	0	FA	99	52

Table 1 (*concluded*).

Site No.	Site name	Region No.	Region name[a]	Group No.	Group name[b]	Latitude	Longitude	*N*	Collection year(s)	H_S	AR	F_{IS}	$\overline{Q}$	GD	Run[c]	Subyearling smolts (%)	Marine harvest rate (%)
128	Sixes River	38	Mid-Oregon Coast	23	Mid-Oregon Coast	042.81604	–124.39204	124	2000–2005	0.869	14.032	0.032	0.121	0	FA	97	52
129	Elk River Hatchery	38	Mid-Oregon Coast	23	Mid-Oregon Coast	042.73889	–124.41281	141	2004	0.864	13.126	0.005	0.102	0	FA	97	52
130	Cole M. Rivers Hatchery	39	Rogue R	24	Rogue–Klamath	042.65000	–122.68333	142	2004	0.844	13.693	0.004	0.088	0	SP	93	65
131	Applegate Creek	39	Rogue R	24	Rogue–Klamath	042.41667	–123.45000	143	2004	0.847	14.108	0.005	0.096	3	FA	96	65
132	Chetco River	40	Chetco R	25	Chetco R	042.06757	–124.26043	137	2004	0.854	13.171	0.023	0.070	0	FA	100	65
133	Klamath River FA	41	Klamath R	24	Rogue–Klamath	041.26667	–123.78333	128	2004	0.803	12.356	0.042	0.084	0	FA	87	—
134	Trinity River Hatchery SP	41	Klamath R	24	Rogue–Klamath	040.71667	–122.80000	144	1992	0.783	10.595	0.02	0.057	0	SP	90	65
135	Trinity River Hatchery FA	41	Klamath R	24	Rogue–Klamath	040.71667	–122.80000	144	1992	0.796	11.042	0.012	0.048	0	FA	>75	65
136	Eel River	42	California Coast	26	California Coast	039.63333	–123.35000	137	2000–2001	0.780	11.977	0.007	0.159	1	FA	>90	65
137	Russian River	42	California Coast	26	California Coast	038.51667	–122.98333	144	2001	0.807	12.533	0.02	0.139	16	FA	Prevalent	—
138	Sacramento Hatchery WI	43	Central Valley WI	27	Central Valley California	040.58333	–122.38333	135	1992–2004	0.696	7.490	0.033	0.064	0	WI	>85	54
139	Battle Creek FA	44	Central Valley FA	27	Central Valley California	040.41667	–122.03333	144	2002–2003	0.842	14.755	0.057	0.109	0	FA	Prevalent	—
140	Stanislaus River FA	44	Central Valley FA	27	Central Valley California	037.95000	–120.51667	76	2002	0.855	15.035	–0.008	0.074	0	FA	>85	68
141	Tuolumne River FA	44	Central Valley FA	27	Central Valley California	037.70000	–120.41667	68	2002	0.838	14.555	0.01	0.062	0	FA	Prevalent	—
142	Mill Creek SP	45	Central Valley SP	27	Central Valley California	040.20000	–121.66667	91	2002–2003	0.834	13.632	0.037	0.076	5	SP	Prevalent	—
143	Deer Creek SP	45	Central Valley SP	27	Central Valley California	040.16667	–121.60000	53	2002	0.831	13.455	0.047	0.059	0	SP	87	68
144	Butte Creek SP	45	Central Valley SP	27	Central Valley California	039.96667	–121.58333	144	2002–2003	0.804	12.258	0.032	0.073	0	SP	>85	68
Mean								130.47		0.840	17.471	0.008		1.694			
SD								44.87		0.037	1.787	0.016		5.136			
Min.								44	1985	0.696	7.490	–0.031		0			
Max.								350	2005	0.89933	17.0823	0.057		49			

Note: SP, spring; SU, summer; FA, fall; WI, winter; SSE Alaska, southern Southeast Alaska.

[a]Regions were identified a priori based on a combination of genetic similarity, run timing, and geographic features.

[b]Groups were identified primarily based on the results of the genetic analyses presented here; however, some samples (footnoted) did not fall cleanly into the Region identified at data submission.

[c]Differences exist among agencies in designation of nominal return time. Moreover, systems with extensive estuaries make it difficult to consistently identify freshwater entry.

[d]Population is placed in this group based on geography and history; however, our analyses did not provide strong support (Fig. 2).

Table 2. Genetic Analysis of Pacific Salmonids (GAPS) consortium Chinook salmon microsatellite loci (Seeb et al. 2007) with numbers of alleles observed, heterozygosities (H_S), and F statistics (θ_{ST} and θ_{IS}; Weir and Cockerham 1984).

Locus	No. of alleles	H_S	θ_{ST}	θ_{IS}
*Ogo*2	27	0.737	0.097	0.007
*Ogo*4	22	0.765	0.120	0.000
*Oki*100	46	0.935	0.026	0.007
*Omm*1080	71	0.946	0.026	0.023
*Ots*201	53	0.906	0.050	0.006
*Ots*208	56	0.935	0.031	0.002
*Ots*211	42	0.917	0.044	0.003
*Ots*212	36	0.864	0.068	0.005
*Ots*213	51	0.925	0.042	0.008
*Ots*3M	19	0.713	0.129	0.006
*Ots*9	9	0.562	0.097	0.011
*Ots*G474[a]	19	0.526	0.189	–0.004
*Ssa*408	39	0.879	0.063	0.018
Overall	490	0.840	0.063	0.008

[a]Omitted from most final analyses because of an extreme departure from neutrality.

NbClust library of the R statistical package, R Development Core Team 2012).

Similarly, with several spatial analyses, we looked for apparent barriers to gene flow that might correspond to previously suggested geographic contact zones between hypothesized ancestral lineages (latitude 56°N, the Columbia River, etc.; Healey 1991; Waples et al. 2004). Monmonier's (1973) algorithm, implemented in the Barriers computer program (Manni et al. 2004), used Delaunay triangulation and Voronoi tessellation to infer geographic boundaries, in this case, barriers to gene flow (expressed as the first principle coordinate axis derived from pairwise transformed F_{ST} estimates). Landscape connectivity and IBD were explored by plotting F_{ST} against waterway distance. We then tested for statistical significance with Kendall's rank correlation coefficient (τ) as implemented in the R statistical package. In contrast with the IBD analysis, Monmonier's algorithm was unconstrained by waterway paths, potentially revealing prehistoric drainage capture. Monmonier's algorithm infers putative barriers to gene flow by identifying larger-than-expected allele-frequency differences over smaller-than-expected geographic distances (Monmonier 1973). As an alternative ordination procedure, we performed a factorial correspondence analysis (FCA) on the allele-frequency data by using the program GENETIX version 4.03 (Belkhir et al. 2004). Finally, analysis of molecular variance (AMOVA, implemented in the software package Arlequin; Excoffier et al. 1992; Excoffier and Lischer 2010) was used to quantify the proportion of variance explained by dividing our samples into two groups based on latitude (56°N), on model-based clustering, and on neighbor-joining analysis. Statistical significance for AMOVA was evaluated by permutation.

Results

Quality control studies conducted on an earlier version of the GAPS baseline showed interlaboratory genotyping concordance greater than 0.95 (on average, across all labs and loci, fewer than five scored alleles in 100 differed between laboratories; Seeb et al. 2007). Detailed explanations can be found in Moran et al. (2006) for the QA–QC procedures in individual laboratories and the errors that were observed in blind genotyping tests across laboratories.

The loci examined here exhibited between 9 and 71 alleles each (*Ots*9 and *Omm*1080, respectively), with a mean of 37.7 alleles per locus (Table 2) and heterozygosities ranging from 0.526 (*Ots*G474) to 0.946 (*Omm*1080), with a mean of 0.840. Most pairwise allele-frequency differences between sites were highly significant. Those that were not were generally between sites within a river basin (data not shown). This gave us confidence in pooling collections within sites. Significant departures from expected HWC genotypic proportions were observed (uncorrected $\alpha = 0.05$), but for the most part, those departures were broadly distributed among loci and sites. They also represented both heterozygote excesses and deficits (See Table 1 for F_{IS} estimates for all sites), but many more deficits were observed than excesses (40/144 deficits versus 4/144 excesses). We attribute these heterozygote deficits primarily to null alleles and upper allele dropout, the effects of which are commonly observed in microsatellite data sets. This view is supported by the regional distribution of HWC departures, for example, *Omy*1080 in Northern Oregon Coast sites and *Ssa*408 on the North Gulf Coast, in southern Southeast (SSE) Alaska, and the Taku River. Despite potential problem loci such as *Omy*1080, *Ssa*408, and to a lesser extent, *Oki*100, we elected not to eliminate any loci due to HWC departures.

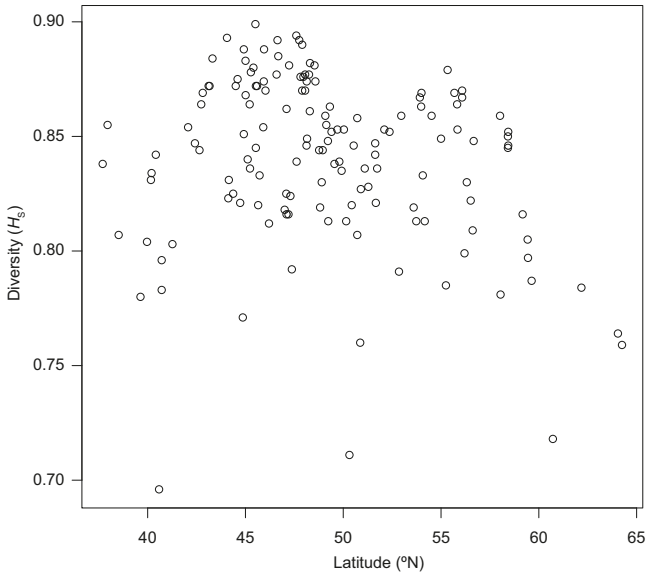
We also observed some nonrandom segregation of genotypes. Approximately one-third of our sample sites (42/144) exhibited significant GD for one or more pairs of loci. The number of locus pairs per collection site showing GD ranged from 0 to 49 (Table 1). Individual pairs of loci exhibited disequilibrium at between 0 (several pairs of loci) and 22 (*Ots*201 and *Ots*208) sample sites. The samples examined here were not collected with the present study in mind and likely varied substantially in how well they represent all of the individuals and families returning to each site. Because of this limitation and the numerous possible causes for GD, it is not possible for us to make biological inferences based on this result. Nevertheless, finer-scale population studies have examined these same loci and not found evidence of substantial GD (Narum et al. 2008; Smith and Engle 2011), and in the current study, we did not observe patterns in the GD tests that compelled us to remove loci (no apparent linkage) or sample sites (no obvious family effects) from subsequent analyses.

Neutrality testing among populations suggested that *Ots*G474 departed significantly from neutral expectation, exhibiting the highest F_{ST} (0.202) and the lowest heterozygosity (0.507) of any locus examined. Indeed, the 156 allele at *Ots*G474 had an estimated F_{ST} substantially higher than any other single allele in the study (0.302). Modeling of F_{ST} and heterozygosity (Beaumont and Nichols 1996) showed this difference to be highly significant ($P < 4 \times 10^{-6}$), and *Ots*G474 was omitted from further analyses. *Ogo*2 and *Ogo*4 were also found to depart from neutrality ($P = 1.7 \times 10^{-3}$ and 1.6×10^{-3}, respectively), but were much less extreme than *Ots*G474, consistent with results of Narum et al. (2008). Neither did *Ogo*2 and *Ogo*4 show extreme F_{ST} values for individual alleles, and so they were retained.

Diversity within populations (H_S) showed a general decline with increasing latitude, but was slightly bimodal. Results suggested a primary peak at 46°N and another at 56°N (Fig. 2). The latter is driven by relatively high diversity estimates in SSE Alaska populations (Keta and Chickamin rivers and Clear and Cripple creeks, SSE Alaska, Group 4). The southerly peak in diversity derives primarily from three regions: the Washington Coast, the Whidbey Basin in northern Puget Sound, and to a lesser extent, the interior Columbia River late-summer and fall populations. These peaks in diversity did not seem correlated with population boundaries nor to patterns of connectivity at either regional or coast-wide scales (see results for neighbor-joining and Monmonier's analyses below).

We observed strong genetic IBD, despite considerable variance in that relationship (Fig. 3; Kendall's $\tau = 0.3052$, $P < 2.2 \times 10^{-16}$). Genetic similarity decreased quickly with distance, but attenuated between 500 and 1000 km. By about 2000 km, pairwise F_{ST} nearly stabilized at 0.1 but continued to increase all the way up to the maximum distances observed in this study, over 11 300 km (from Central Valley, California, to the Yukon; $F_{ST} = 0.193$).

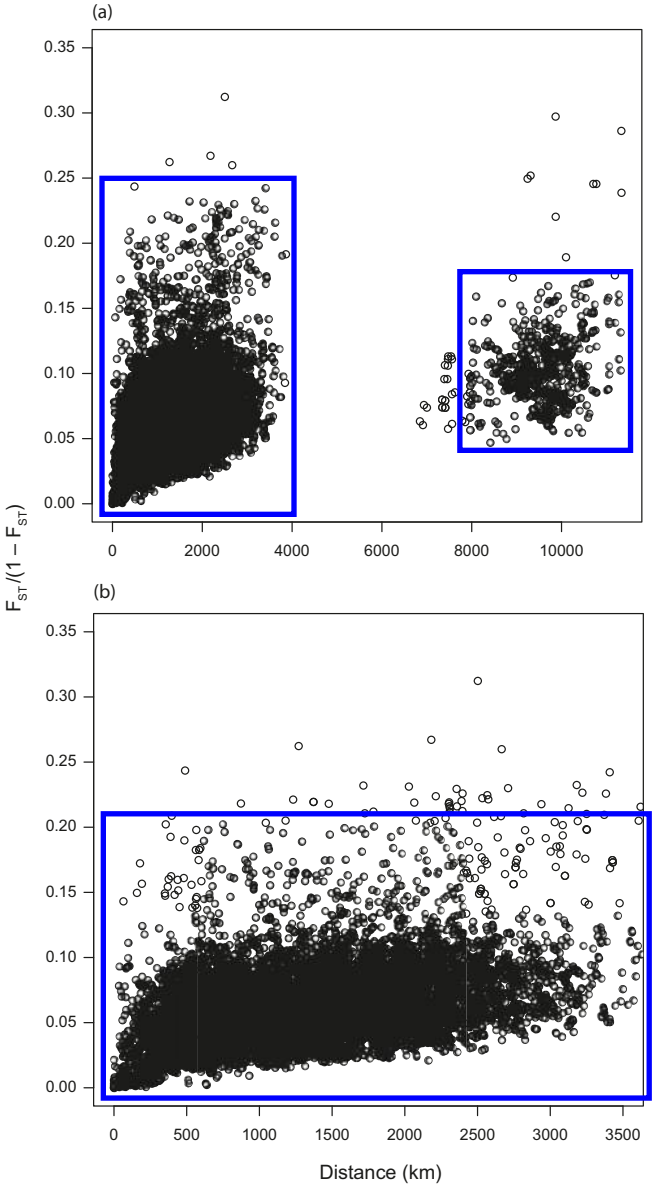
Fig. 2. Genetic diversity (H_S) observed in 144 populations of Chinook salmon. A general trend of decline in H_S at the peripheries of the range was punctuated by peaks at 46°N and 56°N.



Neighbor-joining cluster analysis produced 27 terminal groups that were distinct, as reflected by relatively high bootstrap support (>70%); however, deeper nodes were not well supported, often below 20% (Fig. 4 and Supplemental Appendix S1[1] created with FigTree 1.3.1; Rambaut 2009). Previous studies showed similar results, and although they tended to identify the same terminal clusters with high bootstrap support, they sometimes showed substantially different branching order in basal nodes (Fig. 5). The pattern revealed was consistent with the IBD described above. In general, geographically proximate groups of sites clustered together in the neighbor-joining dendrogram. The most noteworthy exception to this pattern was the near complete genetic isolation of sympatric interior Columbia Basin spring- and early-summer-run (Group 14) versus late-summer- and fall-run populations (Group 21). FCA results might be interpreted as showing two groups separated along FC axis 1, one north and one south, with central populations that are intermediate (Supplemental Appendix S2[1]). Alternatively, one might infer three groups, one north, one interior that includes a few northern populations, and one south. In both cases, Central British Columbia Coast, South British Columbia Mainland, and Lower Fraser are intermediate, as are other populations (central to both axes of the FCA plot, Supplemental Appendix S2[1]).

In results of sequential model-based cluster analysis (Evanno et al. 2005), the mean ln(Pr(X/K)) continued to increase steeply with increasing K, reaching an apparent plateau at approximately K = 11 (Supplemental Appendix S3[1]). However, the second-order derivative of that curve (ΔK) supported an estimate of K = 2, with additional peaks at 11, 14, and 17, and a huge peak at 19, although the variance becomes quite large at that point. When proportional membership ($\overline{Q}$) values from model-based clustering (STRUCTURE) were plotted for individuals in populations and genetic groups (where K = 2), there appeared to be a northern group of populations with similar $\overline{Q}$ values that transitioned into a southern group and extended from southern British Columbia to California (Fig. 6 and 7). Sites in southern British Columbia and the lower Fraser River were intermediate in $\overline{Q}$ value. General concordance between these results from model-based clustering and

Fig. 3. Isolation by distance inferred from pairwise estimates of F_{ST}. Panel (*a*) includes all sites, whereas panel (*b*) omits the Yukon River populations. Despite initial attenuation at 500 to 1000 km, isolation by distance continued a positive trend, even at the greatest distances observed (>11 000 km).

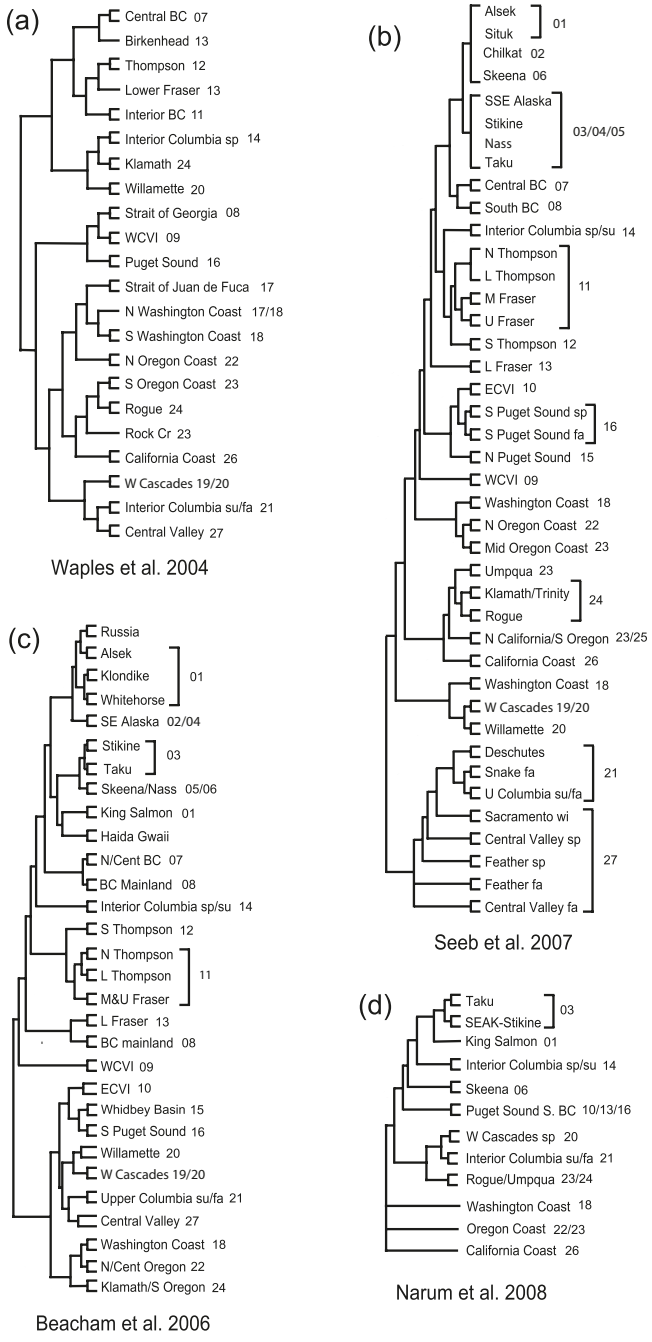


the FCA plot (Supplemental Appendix S2[1]) could be observed in the way that populations with intermediate proportional membership ($\overline{Q}$ values between 30% and 70% cluster 1) were found in an intermediate region of the FCA plot. Populations with $\overline{Q}$ values at the extreme ranges (0%–30% and 70%–100%) were found in separate FCA clusters. This level of concordance was not observed between results from model-based clustering and the neighbor-joining cluster analysis (Fig. 4). Populations with similar $\overline{Q}$ values often lacked cohesiveness in the tree; however, $\overline{Q}$ values were generally similar within regions. Distance-based clustering indices gave a wide variety of estimates of minimum K. Of 26 population-level clustering indices, 9 estimated K = 2, whereas 11 estimated more than 20 distinct clusters.

[1]Supplementary data are available with the article through the journal Web site at http://nrcresearchpress.com/doi/suppl/10.1139/cjfas-2012-0135.

Fig. 4. Neighbor-joining, bootstrap-consensus cluster analysis of Cavalli-Sforza and Edwards's (CSE) chord distance shows genetic relationships among groups (in bold) and sites (with region numbers). Clusters are collapsed with greater than 70% bootstrap support (>700/1000 replicates). The length of the collapsed branch reflects the relative number of sites in the group (Fig. 1; Table 1). Gray dots indicate three classes of group-level mean $\overline{Q}$ value, similar to the interpolation map (Fig. 7). Complete, uncollapsed figure available electronically in the supplementary Appendix S1[1].

Fig. 5. Stylized dendrograms depicting genetic relationships among Chinook salmon populations revealed in previous studies as compared with the current study. Different studies tended to identify the same, well-supported terminal clusters. However, branching order among those groups differed among studies and bootstrap values were low on basal nodes.



Monmonier's triangulation and tessellation analysis failed to provide support for a two-lineage model of Chinook salmon population structure. Instead it revealed barriers that correlated with sites, regions, and groups distributed throughout the range examined here (Table 1). The first two barriers, a and b, distinguished Sacramento winter run (Region 43) and Birkenhead Hatchery (Region 21), respectively (Fig. 8). Barrier c, the strongest barrier that separated groups of populations, united the Yukon–Gulf Coast populations (Group 1) and separated them from all other populations to the south. Barrier d distinguished Interior Columbia Basin spring and early-summer populations (Group 14) from all others, including interior Fraser. Barrier e distinguished the single population King Salmon River in northern Southeast Alaska, and f separated the lower Thompson River (Region 20) from the other Thompson and Fraser River populations. Barrier g isolated Central Valley California fall and spring populations (Group 27) from all others. Barrier h ran down the center of Vancouver Island (separating Group 9 from Group 10), continued south between the Puget Sound (Group 16) and the lower Columbia River (West Cascade Groups 19 and 20), then formed a loop to unite Cle Elum Hatchery (Site 98) and Wenatchee River spring (Site 97). Barrier i separated the Interior Fraser – Thompson (Group 11) from coastal populations, and barrier j, the 10th and final barrier possible with this software implementation, separated Keta River (Site 15) from other sites in Southeast Alaska. It is worth noting that gaps in sampling in the presence of IBD might result in spurious barriers, but not likely false negative results (Manni et al. 2004; e.g., failure to detect the most significant postglacial contact zones).

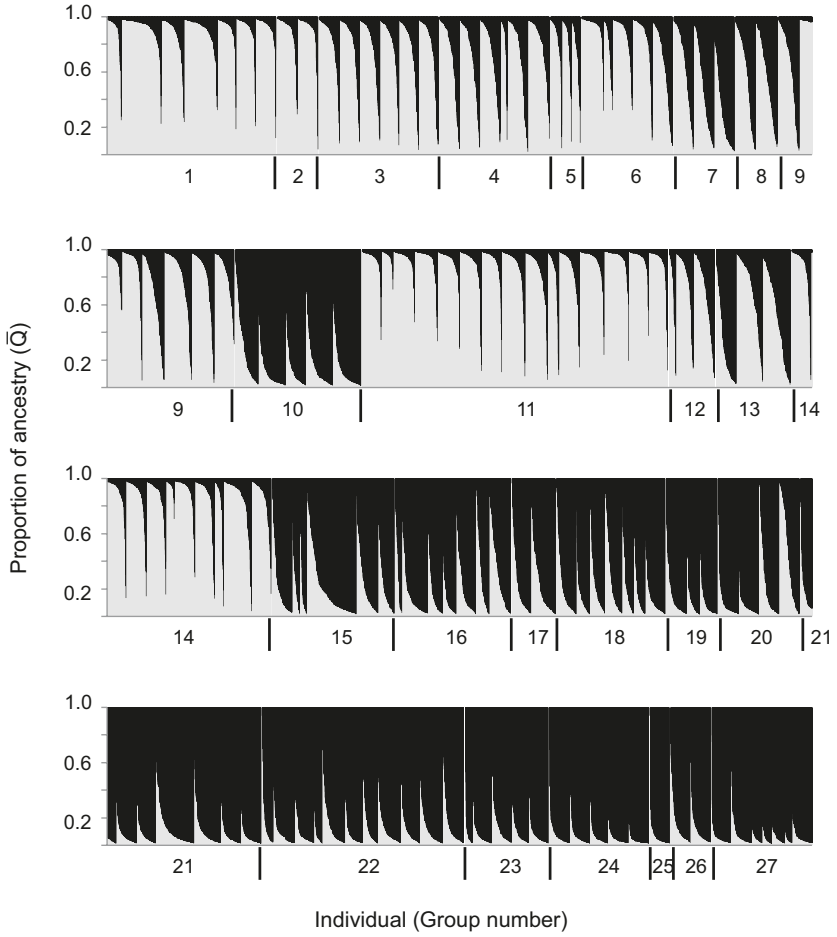
Monmonier's and neighbor-joining did, in some cases, reveal genetic differences between life-history types at the smaller geographic scale of individual river basins or localized regions (spring-run versus fall-run populations in Puget Sound, Central Valley California, or lower Columbia River), but did not support deep genetic divisions nor persistent reproductive isolation that might indicate lineages or races such as those seen when comparing interior Columbia River spring-run versus fall-run populations (Narum et al. 2007*a*). Even if the two groups suggested by model-based clustering (STRUCTURE) represent biologically relevant entities, it is more difficult to infer a deep evolutionary division consistent with "lineages" or "races" (Kalinowski 2010). Moreover, all populations showed a degree of mixed ancestry, consistent with the dominant pattern of IBD. Finally, AMOVA showed that our 27-group model (Fig. 4) described more than two and a half times the variation (4.32%) as that explained by the two-lineage STRUCTURE model (1.56%) or a two-lineage, latitude 56°N model (1.66%).

Discussion

Genetic lineages

We found both mutual support as well as contradiction among different methods used to evaluate the genetic structure of Chinook salmon of the west coast of North America. We also found important caveats related to IBD, clustering, and local adaptation. Model-based cluster analysis agreed with neighbor joining (distance-based clustering) in that population $\overline{Q}$ values were generally similar within the genetic and regional groups that were identified by neighbor-joining and bootstrap analysis. Moreover, all individuals showed a degree of shared ancestry, consistent with IBD. Methods differed, however, with respect to one of our central questions about the number of ancestral lineages that best characterize Chinook salmon and how those lineages were distributed on the landscape. Model-based clustering (STRUCTURE) showed a bimodal distribution of $\overline{Q}$ values, and ΔK supported two clusters. However, neighbor-joining and Monmonier's analysis conflicted fundamentally with that result. The dendrogram showed no long or well-supported internal branches, and previous studies estimated different sister group relationships among regions. Puget Sound and West Cascade populations were intermediate in $\overline{Q}$ value (0.3–0.7), yet clustered with other populations in their respective regions and showed high bootstrap support, that is, they were not intermediate in fitted neighbor-joining chord distance. Monmonier's triangulation–tessellation analysis also failed to support two divergent lineages except perhaps the Beringian versus Pacific coastal populations (third predicted barrier and the first-order barrier to separate groups of populations). That putative contact zone is in Southeast Alaska,

Fig. 6. Coefficient of ancestry values ($\bar{Q}$) for every individual from 144 sites and 27 groups (group numbers on the *x* axis appear in Table 1).



separating the Yukon and Gulf Coast from all populations to the south, including Fraser and Columbia River populations. This Beringian contact zone is a pattern widely observed in fishes of the west coast (McPhail and Lindsey 1986), including sockeye salmon (*Oncorhynchus nerka*, Withler 1985; Wood et al. 1994; Bickham et al. 1995), coho salmon (*Oncorhynchus kitsuch*) Small et al. 1998; Smith et al. 2001), and rainbow trout (*Oncorhynchus mykiss*, McCusker et al. 2000), as well as Chinook salmon (Gharrett et al. 1987; Guthrie and Wilmont 2004). Gharrett et al. (1987) speculated whether genetic similarity in the Yukon and Southeast Alaska was due to colonization of the Yukon from the Gulf Coast and Southeast Alaska or vice versa. Our results showed both similar allele frequencies and patterns of depressed diversity that suggested a small Beringian clade might have been isolated and then later invaded Southeast Alaska through Holocene river capture (see Gharrett et al.'s 1987 figure 3 and associated references).

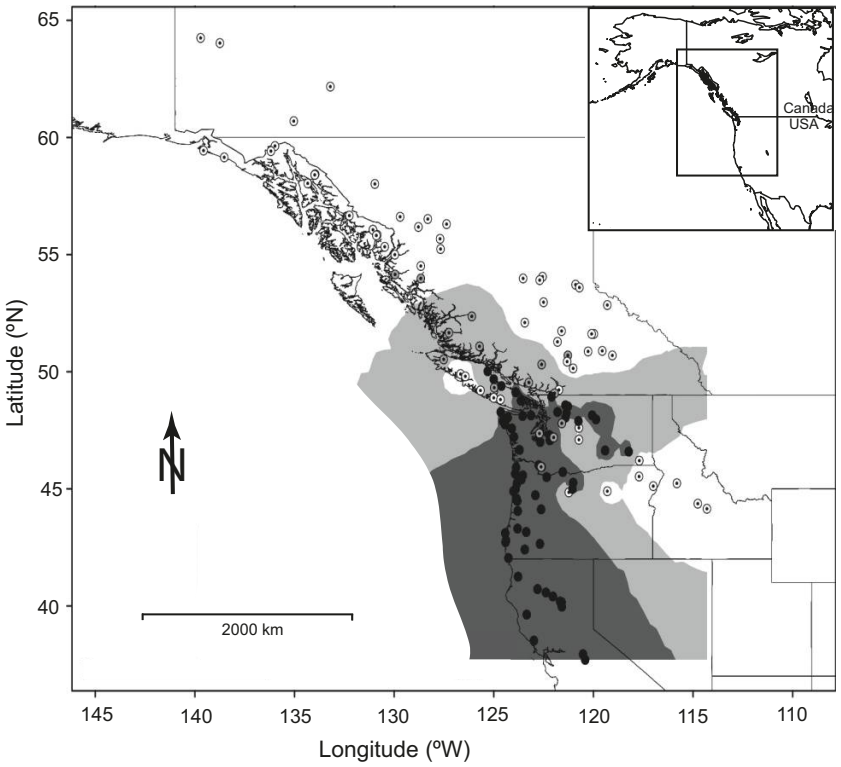
Beacham et al. (2006) hypothesized that Chinook salmon might have had multiple southern refugia (i.e., coastal British Columbia), similar to the scenario Wood et al. (1994) proposed for sockeye salmon. The location and structure of putative coastal refugia is less clear than for Beringia, but the preponderance of evidence from multiple sources, including results of our study, makes the existence of such a refuge nearly indisputable. Parts of Haida Gwaii and Vancouver Island were thought to be ice-free at the height of the Fraser Glaciation and provided refuge for plants (Pojar 1980; Warner et al. 1982) and at least some freshwater fishes (McPhail and Carveth 1992). It seems likely that the genetic complexity and diversity observed in our Southeast Alaska and British Columbia Coast populations are best explained by multiple coastal refugia. This interpretation would be consistent with suggestions of numerous other studies in species such as sockeye salmon (Wood et al. 1994) coho salmon (Small et al. 1998; Smith et al. 2001), rainbow trout (McCusker et al. 2000), as well as Chinook salmon (Beacham et al. 2006; Templin et al. 2011). In contrast, McLean et al. (1999) proposed that eulachon (*Thaleichthys pacificus*) radiated from a single refuge based on low sequence divergence between mtDNA haplotype groups (0.4%) relative to that of rainbow smelt (*Osmerus mordax*), which dispersed from multiple refugia (0.7%; Bernatchez 1997).

Model-based clustering and FCA seemed to suggest a contact zone between genetic groups of Chinook salmon populations in Georgia Basin, whereas Monmonier's analysis and neighbor joining suggested a contact zone in the Gulf Coast region of Southeast Alaska. FCA showed a north–south, interior–coastal separation similar to that found with model-based clustering, but the northern group was divided to form a third cluster. Before attempting to reconcile these disparate results, it is important to recognize some caveats. For example, IBD can undoubtedly bias identification of genetic groups (Meirmans 2012) and is a concern for both ordination and clustering. STRUCTURE in particular was shown to produce unpredictable results under IBD. Another important caveat is that STRUCTURE models HWC populations, and its performance with deeper evolutionary lineages can be "pathological" (Kalinowski 2010).

Temporal scale of phylogeographic processes and life-history divergence

Beyond genetic modeling, there is even more fundamental uncertainty in our expectations regarding the genetic effects of

Fig. 7. Isopleth interpolation map of $\bar{Q}$ values among Chinook salmon populations. The circles indicate collection locations, and three shading levels correspond to three ranges of average population assignment to cluster 1 where $K = 2$. Population circles are categorized as having 0%–30% (black), >30%–70% (gray), or >70%–100% (white) probability of membership ($\bar{Q}$) to cluster 1 (Table 1).



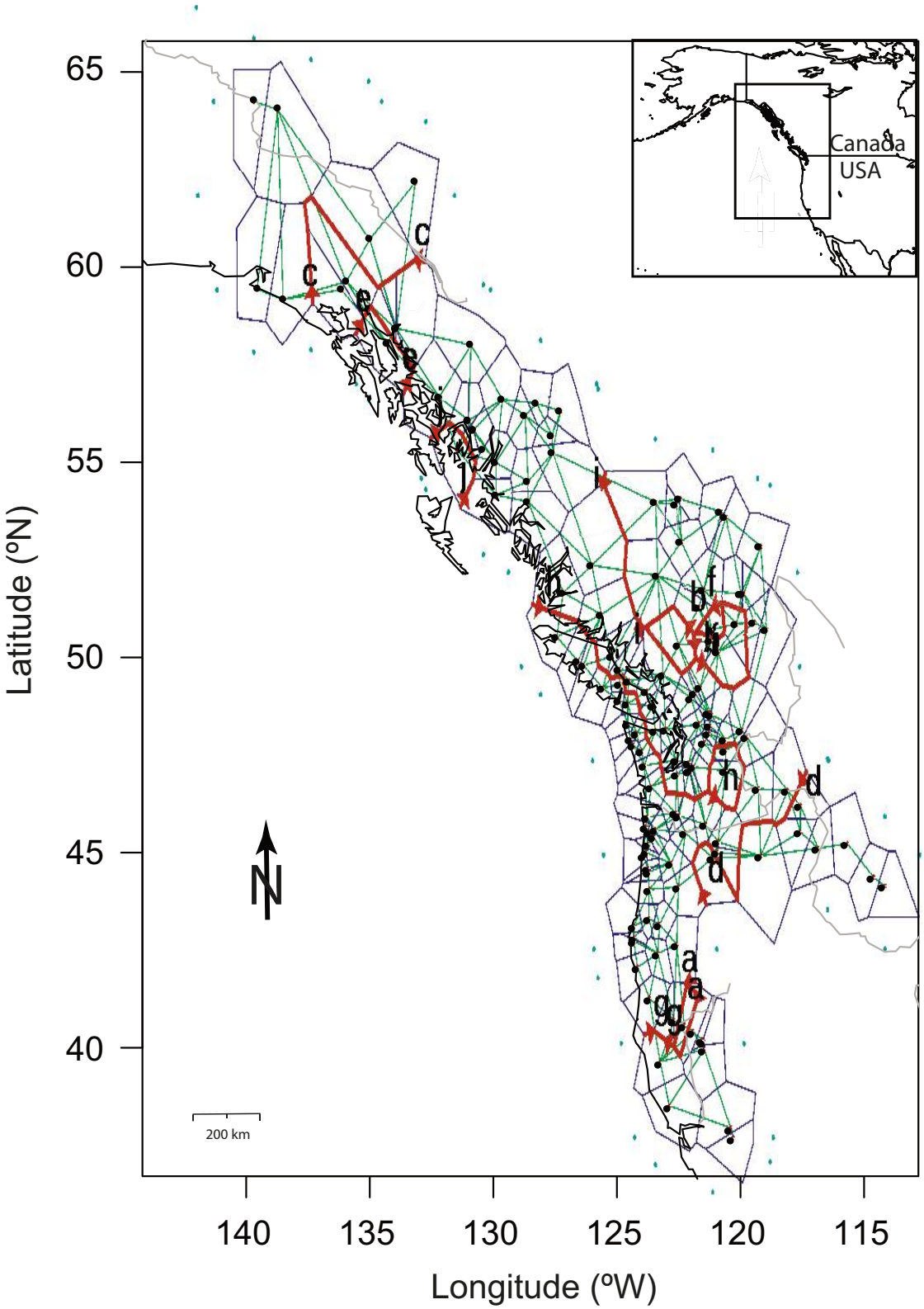
Earth history. Under the contraction–expansion model of Quaternary biogeography (Hewitt 1996), we expect that (1) the highest diversity should be found in regions that remained ice-free, and (2) the distribution of intraspecific polymorphism in northern regions should be dictated by ice-free refugia and postglacial colonization routes. Implicit in expectation 2 is the notion that divergent lineages will date the glacial periods that caused isolation of different groups in different refugia. However, Taberlet et al. (1998) showed that for many European species, lineages often substantially predate the Pleistocene and the last glacial maximum (see also Aldenhoven et al. 2010). Thus, the structure of divergent lineages is often a simple function of more general coalescent processes rather than Quaternary biogeography and long isolation in glacial refugia.

These caveats not withstanding, it seems unlikely that the principal results of any of our analyses can be dismissed as completely artifactual. Instead, we propose that disparate results reveal processes happening at different temporal scales. It might be that some of the patterns we observed are due to pre-Pleistocene processes, followed by IBD and basin–subbasin structure as a result of Pleistocene and Holocene processes, including temporary isolation and postglacial dispersal or differential survival and local adaptation. However, any potential signal there might be from two lineages — whether due to isolation in glacial refugia, simple coalescence, or some other process — has apparently been diminished over much of the range because of subsequent contact and differential mixing (extensive in the Fraser and Central British Columbia, almost nonexistent in the interior Columbia River Basin; Waples et al. 2004). Further, contemporary patterns of gene flow, and perhaps selection and divergence, have resulted in the current pattern of IBD superimposed on basin–subbasin structure. These results suggest that the traditional two-lineage model, widely held for Chinook salmon, is less meaningful than the 27-group model we present here. This view of increased diversity is further reinforced by the enormous life-history variation that is now evident. Even populations thought to be "fixed" for life-history type can exhibit latent or rare life-history variants such as hold-over yearling smolts from interior Columbia fall-run populations (Healey 1991; Connor et al. 2005) and subyearling migrants from interior Columbia River spring-run populations (Copeland and Venditti 2009). The success of such alternative strategies might be limited under the current environmental regime (essentially no returning adults in the latter example; Taylor 1990). However, such latent variability could represent an important buffer to environmental change at a larger temporal scale (Slatkin 1974) and could explain the persistence of life-history diversity, despite widespread depression and extirpation of local populations (Gustafson et al. 2007). This diversity also shows differences in the genetic basis of expression. For example, alternative maturation timing, strongly influenced by environment (and probably nonadditive gene-by-environment interaction), is common both within and among Chinook salmon populations (Taylor 1991; Beckman and Dickhoff 1998). Clearly, changing environmental conditions, including anthropogenic change, can alter the selective regime and place constraints on life-history expression (Waples et al. 2004; Crozier et al. 2008) with concomitant loss of diverse ancestral life-history forms (Reimers 1973; Bottom et al. 2005).

Spatial scale in genetic and phenotypic diversity

Chinook salmon life-history types are frequently referred to as "lineages" or "races" in much of the recent literature, which implies the existence of clearly separated, species-wide, ancestral groups. Not coincidentally, these studies almost all focus on interior Columbia River Basin populations, where the Healey model is supported by both divergent lineages and strong life-history segregation. Studies outside the interior Columbia use the terms stream type and ocean type to refer to yearling and subyearling juvenile migrants and sometimes relate them to adult return;

Fig. 8. Monmonier's triangulation (blue) and tessellation (green) of allele-frequency differences among sample sites based on pairwise F_{ST}. Putative barriers to gene flow (red) are ordered by decreasing importance from a to j. The algorithm optimizes barriers to reflect larger-than-expected allele-frequency difference over smaller-than-expected geographic distance.



however, marine migration and harvest rates are not generally considered. This application of terms is incompatible with the Waples et al. (2004) interpretation of marine migration as a highly conserved trait in the stream-type lineage. In our life-history analysis, only Birkenhead Hatchery in the lower (not interior) Fraser River shares with the interior Columbia spring run the low marine harvest rates that indicate a unique offshore migration pattern (Table 1). Although data are sparse for northern populations, rivers as far north as the Skeena and Nass have marine harvest rates as high as 25%–57%, compared with 1% in the interior Columbia spring and early-summer run. Deep evolutionary divergence of just a few lineages is not supported by range-wide genetic data, and extensive life-history diversity within apparent lineages complicates any inference about ancestral predisposition.

Our results therefore argue strongly against the use of terms "Supra-group" ocean-type and stream-type "lineages" (Waples et al. 2001, I, Section III); even though our results and others (Beacham et al. 2006; Seeb et al. 2007) strongly support the population groupings of Waples et al. (2001). Our most recent compilation of Chinook salmon life-history information (Table 1) reinforces the view that these traits are too plastic or too evolutionarily labile to segregate in a meaningful way with ancestral lineages (Beacham et al. 2006). Agreeing with Utter et al. (1989), however, we do not suggest that genetic differences are lacking between populations that differ in life-history type. We identified many of those differences here, and other work cited above strongly supports such observations at various scales — just not at the broadest, range-wide scale.

In more general terms, our results emphasize the importance of spatial scale in sampling to obtain a complete picture of range-wide genetic and phenotypic diversity. Multiple analytical approaches can provide insight into processes acting at different temporal and spatial scales.

Population genetics and biogeography

Glacial events have clearly served to reduce overall molecular genetic diversity across many North American fish species (Bernatchez and Wilson 1998), and our data also suggested reduced intrapopulation diversity in Chinook salmon at the most northern latitudes, consistent with expectation 1 of the contraction–expansion model (Hewitt 1996). However, the high diversity we observed at latitude 46°N, in Whidbey Basin (Group 15), was unexpected, considering this region was covered by more than a kilometre of ice at the height of the Fraser Glaciation (McPhail and Lindsey 1986). Lacking highly diverse potential donor populations, this diversity must be the result of recolonization from multiple sources.

Biogeographic inference was also complicated by a peak in diversity at 56°N, far to the north of the southern extent of ice sheets at the last glacial maximum. This northern peak in diversity is not consistent with widespread recolonization from the interior Columbia River spring–early-summer-run populations, none of which were particularly diverse themselves (Winans 1989; Narum et al. 2010; the current study, but see Beacham et al. 2006). The interior basins of the Fraser and Columbia rivers must have shared Chinook salmon migrants at some low level, either through former, perhaps early Pleistocene connections (Martin et al. 2010) or via long-distance strays (Ford 1998); however, it is almost certainly not the case that the Fraser Basin and the rest of Cascadia (north to the Stikine River) were extensively recolonized by fish from the upper Columbia, as suggested for most fish species by McPhail and Lindsey (1986). If so, one would expect populations in the Fraser and Thompson rivers (Groups 11 and 12), and in regions further north, to nest within Columbia River populations. Yet much of the genetic data supports the opposite, with all the interior Columbia River spring-run populations nested among groups to the north (Beacham et al. 2006) or at least sister to the Fraser (the current study). It is unclear whether peaks in genetic diversity at latitude 56°N represented the location of a coastal refuge itself or a contact zone between formerly isolated populations. However, even if increased diversity is due to a contact zone, none of our results support the persistence of two deeply divergent genetic lineages coming in contact at latitude 56°N. Monmonier's analysis estimated a barrier farther north, whereas model-based cluster analysis inferred a transition in $\overline{Q}$ value proportions far to the south, in Georgia Basin.

In addition to the historical contingencies of postglacial recolonization and serial demographic bottlenecks, local adaptation and selection almost certainly affect the distribution and structure of these lineages through the success of strays, particularly long-distance strays (Olsen et al. 2010*a*, 2010*b*). These forces of demography and selection might also drive patterns of postglacial recolonization or confound former patterns of recolonization (Holliday et al. 2010). For example, interior Columbia late-summer–fall populations might also have had access to the Fraser–Thompson along with the spring–early-summer populations, but only the spring–early-summer fish persisted. This would undoubtedly change our impression of directionality of colonization.

In addition to the unknown effects of selection and demography, the geologic history of this region is especially complex and dynamic. Waples et al. (2008) reviewed geologic, climatic, and tectonic forces in the Pacific Northwest that have undoubtedly contributed to genetic patterns. Cascadia has experienced repeated catastrophic floods, advance and retreat of continental and grounded, marine ice sheets, isostatic rebound, and changing sea level that profoundly influenced fishes (McPhail and Lindsey 1986). Particularly important were the large proglacial lakes that formed repeatedly and provided the opportunity for invasion and secondary contact among multiple inland river systems throughout Cascadia (McPhail and Lindsey 1986). The lakes themselves might have provided glacial refugia for salmonids. The consequence is that salmon phylogeography is highly susceptible to post hoc hypotheses. There will always be multiple hypothetical explanations for any observed genetic pattern, and although such explanations are often intuitively appealing, they are generally untestable, much like those of the repeated catastrophic events that shaped them (Baker 2002).

Although the Chinook salmon populations of the Interior Columbia Basin spring–early-summer Group 14 (Table 1) were genetically and phenotypically distinct (94% bootstrap support), their ancestral affinities to other Groups were obscured by poor resolution of basal nodes in the dendrogram. Multiple studies show consistent genetic similarities between populations in the interior Columbia River and the Fraser–Thompson River systems; however, bootstrap support is invariably low and sister group relationships vary. In our study, 41.8% of bootstrap replicates united the Fraser–Thompson cluster and the interior Columbia Basin spring–early-summer-run populations. Only 10.5% bootstrap support was observed for the separation of northern and interior populations from the southern and coastal, putatively ancestral, ocean-type populations (Healey 1991). This unresolved "star phylogeny" means that even if one fully accepted microsatellite allele-frequency variation as strongly indicative of historical biogeography, it would not be possible to say with confidence that northern and interior regions were more closely related to one another than they were to coastal and southern lineages, even if that were the "true" evolutionary relationship (complicated by nonequilibrium conditions and intermittent gene flow). Poor resolution of the basal relationships among Chinook salmon lineages confounded our attempts to test the suggestion of Waples et al. (2004) that a postglacial invasion of the Fraser from northern British Columbia might explain what they saw as lack of genetic affinity with the interior Columbia Basin. Beacham et al. (2006) found interior Columbia spring run to be closer to the central British Columbia and Alaska cluster than to the Fraser, whereas

Seeb et al. (2007) and our analysis found interior Columbia and Fraser to be sister groups that were joined to a British Columbia – Alaska cluster. Only dense nuclear haplotypes and a better understanding of Earth history events will permit full dissection of the genetic landscape and evolutionary history of Chinook salmon, especially where repeated vicariance and secondary contact events have occurred.

Despite limited resolution of the basal nodes of our dendrogram, excellent discrimination of terminal groups provided interesting differences between our microsatellite results and previous allozyme studies. For example, Waples et al. (2004, p. 394) noted that interior Columbia populations show some similarities to the upper Klamath River. However, as indicated above, our microsatellite results suggested that the interior Columbia Basin spring–early-summer-run populations were related to populations in British Columbia and Alaska, but were not at all similar to those in the Klamath (Group 24), which clustered tightly with the Rogue River (98.2% bootstrap support). Although sister to the Rogue River, the Klamath–Trinity system was genetically distinct with microsatellites, although not as divergent as with allozymes (Waples et al. 2004). Previous allozyme data also suggested (albeit with low bootstrap support) that the upper Willamette River population might be sister to interior Columbia and Klamath river populations (Waples et al. 2004). Those results also contrasted with our analysis, which strongly united upper Willamette River with geographically proximate West Cascade spring-run populations (97.9% bootstrap support). Finally, microsatellite data showed a closer affinity than was seen with allozymes between the Interior Columbia Basin spring–early-summer-run (Group 14) and Interior Fraser–Thompson (Group 11) populations. The lack of affinity with allozymes was a principal caveat that Waples et al. (2004) had for the Healey model (see above).

Differential sample coverage alone cannot fully reconcile allozyme and microsatellite results, but, non-neutrality might; however, further studies are needed to understand potentially similar selective pressures in the Willamette and Snake rivers. Beacham et al. (2006) found similar differences in British Columbia populations when comparing their microsatellite data with the allozyme data of Teel et al. (2000). Such differences not withstanding, the same regional groups are largely supported by different genetic marker classes, albeit with somewhat different sister group relationships that vary from study to study.

Implications for fishery management, conservation, and evolutionary biology

Given our results, "stream-type" and "ocean-type" Chinook salmon should not be considered distinct "lineages" and are perhaps best abandoned as descriptors. Even their use as life-history designations is confusing. Juvenile life-history diversity based on age at sea entry is better described as "subyearling" and "yearling" migration. Evolutionary lineage is better described as adult return time **combined with location** (e.g., Interior Columbia spring run.) This might seem like a semantic issue of terminology, yet it has fundamental importance to the way questions about Chinook salmon evolution are framed and how results are interpreted. Explicit recognition of group-specific life-history diversity is essential for effective conservation and recovery because much current habitat restoration targets life-history types rather than the specific populations or lineages that are the legally protected entities. Ultimately, such insight leads to a deeper understanding of rates of phenotypic evolution, gene-by-environment interaction, and the habitat needs of imperiled populations of both Chinook salmon and other fishes.

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