Genetic structure, migration, and patterns of allelic richness among coho salmon (*Oncorhynchus kisutch*) populations of the Oregon Coast

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Abstract: Genotypic data from eight microsatellite loci are used to infer population structure, effective population size, migration rates, and patterns of allelic richness among wild and hatchery populations of Oregon coastal coho salmon, *Oncorhynchus kisutch*. Corroborating the results of a previous study, we found relatively weak genetic structure among coho from different river basins, although some geographically and ecologically defined clades are supported. Contemporary migration rates among basins appear to be high and asymmetrical. Hatchery populations tended to resemble the wild populations from which they were founded, but presented significantly lower levels of allelic richness. Allelic richness was also low in Oregon coastal lake populations and peaked in the central region of the evolutionarily significant unit among wild river populations. We suggest that the observed patterns may reflect both current source–sink dynamics and post-Pleistocene colonization events.

Résumé : Les données génotypiques provenant de huit locus microsatellites nous ont servi à déduire la structure de la population, la taille effective de la population, les taux de migration et les patrons de richesse allélique chez des populations sauvages et de pisciculture de saumons coho, *Oncorhynchus kisutsch*, de la région côtière de l'Oregon. Nous trouvons une structure génétique relativement faible parmi les saumons coho des divers bassins versants, ce qui corrobore les résultats d'une étude antérieure; néanmoins, il y a évidence de quelques clades définis géographiquement ou écologiquement. Les taux de migration actuels d'un bassin à l'autre semblent être élevés et asymétriques. Les populations de pisciculture tendent à ressembler aux populations sauvages dont elles sont issues, mais elles affichent des taux significativement plus bas de richesse allélique. La richesse allélique est également basse dans les populations lacustres de la côte de l'Oregon et elle atteint son maximum dans la région centrale de l'unité évolutive significative parmi les populations sauvages d'eau courante. Nous pensons que les patrons observés sont le reflet à la fois de la dynamique actuelle de type source–drain et des événements de la colonisation après le pléistocène.

[Traduit par la Rédaction]

Introduction

The life histories of Pacific salmon (*Oncorhynchus* spp.) present unique challenges for management and conservation. For example, the tendency for adult salmon to return to their natal streams as they prepare to spawn is believed to isolate populations over a spatial scale and mediate genetic divergence of locally adapted stocks (Taylor 1991). Moreover, in some species, fixed maturation ages, combined with semelparity, limits matings among individuals from different brood years to events involving less abundant precocial individuals (jacks). For example, most coho salmon (*Oncorhynchus kisutch*) mature and spawn at age 3+ years, although a fraction return to spawn at age 2+ years. Consequently, temporally isolated subpopulations can occur within a single watershed.

Given the potential for population structure at multiple scales, the rapid decline of many Pacific salmon stocks in the late 1980s prompted managers and conservation biologists to consider demographic independence and genetic distinctiveness as key criteria for the establishment of management units (Allendorf and Phelps 1981; Waples 1991; Utter et al. 1993). Allozyme studies (e.g., Utter et al. 1973; Beacham et al. 1985; Weitkamp et al. 1995) provided the first source of genetic data for the delineation of the 52 Pacific salmon evolutionarily significant units (ESUs; Waples 1991) now recognized by the US Endangered Species Act. However, the statistical power provided by allozyme data to discriminate among populations varies greatly for Pacific salmon species (Utter 1991), limiting the general applicability of these markers.

Advances in molecular genetic technology have since allowed researchers to uncover previously undetected levels of genetic diversity within and among populations of Pacific salmon. For example, highly polymorphic microsatellite markers have elucidated large levels of genetic structure among coho salmon within and among river basins of California (Bucklin et al. 2007), Oregon (Ford et al. 2004), Brit-

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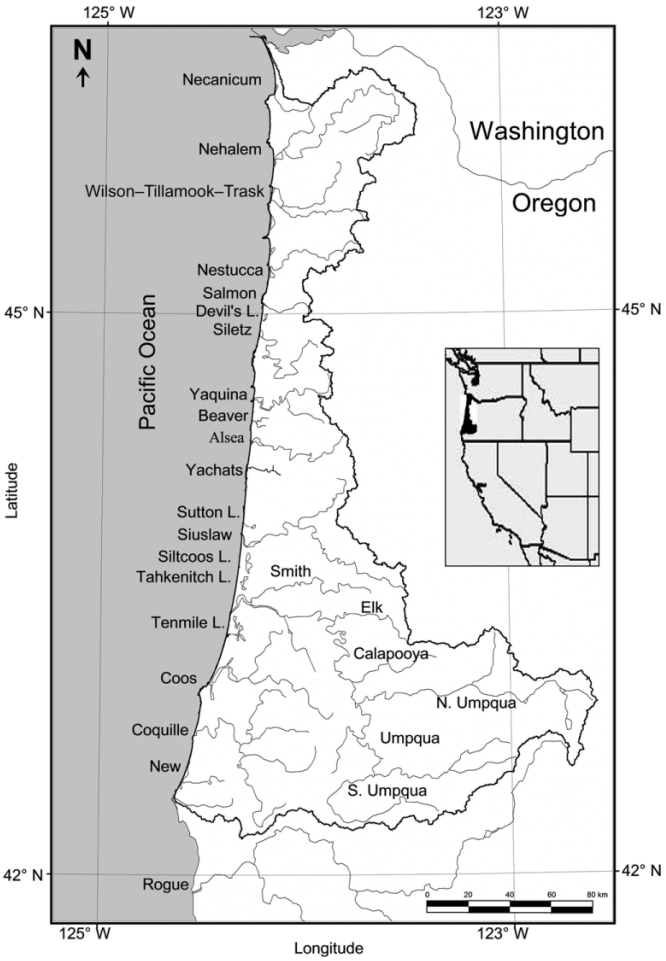
ish Columbia (Small et al. 1998; Beacham et al. 2001), and Alaska (Olsen et al. 2003). Over a larger scale, Smith et al. (2001) used mtDNA sequence data and microsatellite markers to describe patterns of coho genetic diversity throughout the species' North American range. A latitudinal cline of mtDNA haplotype diversity led Smith et al. (2001) to hypothesize that early Pleistocene glaciations had reduced the North American distribution of coho salmon to southern refugia in California and (or) Oregon. Latitudinal clines of genetic diversity in other nearshore fishes have similarly been described (e.g., Adams et al. 2006; Gysels et al. 2004). Only three coho populations from California and Oregon were considered by Smith et al. (2001), thus limiting the resolution of analyses in this region.

Recently, Ford et al. (2004) used seven microsatellite loci to more thoroughly characterize the genetic structure of coho salmon populations from the Oregon coast. In addition to structure analyses, the authors tested for a signal of genetic introgression from an aquacultural operation, which utilized non-native broodstock on the central Oregon coast. Their findings generally supported previously hypothesized population complexes and clearly acknowledged the potentially confounding effects of anthropogenic activities over coho salmon genetic diversity.

In this study, we use data from eight microsatellite loci to characterize genetic structure within and among putative coho salmon populations from 23 river basins of the Oregon Coastal Coho (OCC) ESU, as well as a single basin (Rogue River) from the Northern California – Southern Oregon ESU (Fig. 1). We utilize temporally replicated samples of wild populations from five river basins to estimate the effective number of breeders, immigrant fractions, and the percentage of genetic variation apportioned among river basins, broodyears, and within basin sampling sites. Directional migration rates among wild coho populations are estimated through a Bayesian assignment method (Wilson and Rannala 2003), and in a final analysis, we examine latitudinal patterns of allelic richness among wild and hatchery coho populations of the Oregon coast.

Fig. 1. Map of rivers from which tissue samples were collected. The Oregon Coastal Coho evolutionarily significant unit is outlined in bold. Inset shows location on the US west coast.



Materials and methods

Sampling and genotyping

During the spawning seasons of 2002, 2003, and 2004, tissue samples were collected from expired, presumably wild origin coho salmon spawners from 24 coastal Oregon river basins. Wild origin fish were distinguished from hatchery coho through the presence of an intact adipose fin, which is removed from nearly all coastal Oregon hatchery coho prior to release (84%, 96%, and 97% marked for brood years 2002, 2003, and 2004, respectively). In 2004, samples were also collected from adipose fin-clipped coho returning to five Oregon hatcheries. Tissue samples were preserved in 95% ethanol, and the collection location and date were recorded together with the length and sex of each fish sampled. From the 2002 collection, samples from all rivers were included in our analyses. Samples from four basins in the 2003 collection (Nehalem, Yachats, Smith, and Coos) and five basins in the 2004 collection (Nehalem, Yachats, Smith, Coos, and Coquille) were also included in our analyses. Genomic DNA was extracted through DNEasy (Qiagen Inc., Valencia, California) or Chelex – proteinase K (Estoup et al. 1993) protocols, and separate polymerase chain reactions were carried out in 5 μL volumes on a MJ Research thermocycler to amplify eight microsatellite loci, utilizing fluorescently labeled primers (*One13*, Scribner et al. 1996; *Ots2*, Banks et al. 1999; *p53*, de Fromentel et al. 1992; *Oki16*, Smith et al. 1998; *Ots215*, Greig et al. 2003; *Ots520*, Naish and Park 2002; *Ots3*, Banks et al. 1999; *Ocl8*, Condrey and Bentzen 1998). PCR products were separated via polyacrylamide gel electrophoresis on an ABI 3730XL genotyper and (or) MJ Research Basestation and binned according to size with either GeneMapper or Cartographer software. A minimum of 96 samples were analyzed at all loci on both genotyping platforms to allow for bin adjustments and consistent size scoring.

Statistical analyses

We used the program FSTAT (Goudet 1995) to calculate the per-locus and overall heterozygosity for each population, as well as performed permutation tests (1000 iterations) to detect departures from Hardy–Weinberg equilibrium (HWE). The program GENETIX (Belkhir et al. 2004) was used to carry out permutation tests (1000 iterations) to detect linkage disequilibrium among loci. Sequential Bonfer-

Table 1. Various data collected for all populations: mean sample sizes across loci, deviation from Hardy–Weinberg proportions (F_{IS}), observed and expected heterozygosities (H_O and H_E, respectively), latitude of river (at mouth), origin, and ecotype.

Basin	Mean n	F_{IS}	H_O	H_E	Latitude (°N)	Origin	Ecotype
Alsea	83.5	0.094	0.731	0.801	44.25	Wild	River
Beaver Creek*	31.6	0.069	0.733	0.774	44.31	Wild	River
Coos	178.5	0.099	0.729	0.807	43.21	Wild	River
Coquille	41.8	0.197	0.648	0.794	43.07	Wild	River
Devil's	37.3	0.110	0.669	0.741	44.57	Wild	Lake
Necanicum	30.0	0.115	0.696	0.771	46.01	Wild	River
Nehalem	162.1	0.089	0.708	0.775	45.40	Wild	River
Nestucca	55.4	0.089	0.714	0.776	45.09	Wild	River
New*	42.8	0.055	0.728	0.761	42.56	Wild	River
Rogue	44.4	0.092	0.672	0.730	42.25	Wild	River
Salmon	42.8	0.072	0.730	0.777	45.02	Wild	River
Siletz	46.4	0.120	0.685	0.769	44.54	Wild	River
Siltcoos	26.9	0.103	0.692	0.754	43.52	Wild	Lake
Siuslaw	130.6	0.161	0.683	0.811	44.00	Wild	River
Smith	90.5	0.109	0.722	0.805	43.40	Wild	River
Sutton	34.0	0.097	0.688	0.749	44.04	Wild	Lake
Tahkenitch*	31.1	0.069	0.725	0.765	43.48	Wild	Lake
Tenmile	57.6	0.073	0.739	0.789	43.33	Wild	Lake
Tillamook*	13.3	0.082	0.698	0.728	45.33	Wild	River
Trask*	18.9	0.021	0.750	0.744	45.33	Wild	River
Umpqua	275.25	0.074	0.757	0.816	43.40	Wild	River
Wilson*	31.1	0.072	0.739	0.782	45.33	Wild	River
Yachats*	20.3	0.050	0.770	0.789	44.18	Wild	River
Yaquina	111.6	0.166	0.668	0.796	44.37	Wild	River
Temporal replicates							
Coos 2003	54.6	0.093	0.731	0.798	43.21	Wild	River
Coos 2004*	80.3	0.047	0.775	0.808	43.21	Wild	River
Coquille 2004	44.9	0.055	0.723	0.757	43.07	Wild	River
Nehalem 2003*	121.9	0.021	0.790	0.803	45.40	Wild	River
Nehalem 2004	41.4	0.184	0.648	0.780	45.40	Wild	River
Smith 2003	58.0	0.079	0.734	0.789	43.40	Wild	River
Smith 2004	67.5	0.077	0.740	0.794	43.40	Wild	River
Yachats 2003*	35.0	0.060	0.768	0.803	44.18	Wild	River
Yachats 2004*	33.9	0.073	0.732	0.777	44.18	Wild	River
Hatcheries							
Coos 2004*	91.0	0.005	0.797	0.789	43.21	Hatchery	River
Coquille 2004*	47.1	0.007	0.794	0.780	43.07	Hatchery	River
Cow Creek 2004*	42.8	0.027	0.806	0.818	43.40	Hatchery	River
Nehalem 2004	28.3	0.100	0.703	0.764	45.40	Hatchery	River
Salmon 2004*	50.0	0.002	0.750	0.741	45.02	Hatchery	River
Total	2434.0						

Note: Samples were collected in 2002, except where indicated.

*No significant difference ($p = 0.05$) from Hardy–Weinberg equilibrium (HWE) after sequential Bonferroni correction.

roni corrections (Rice 1989) were made to adjust the initial critical value of 0.05 to account for multiple comparisons made during these tests.

Pairwise values for Weir and Cockerham's inbreeding coefficient, θ, were calculated for all wild 2002 samples with the program GENETIX (Belkhir et al. 2004), and we used a permutation test with 1000 iterations to assess the statistical significance of these estimates. Similarly, we calculated all pairwise θ values for all major tributaries of the Umpqua River to assess structure within this basin. We used the program GDA (Lewis and Zaykin 2001) to perform an analysis of molecular variance (AMOVA) on data from four temporally replicated populations (Nehalem, Yachats, Smith, and Coos), simultaneously estimating the percentage of total genetic covariance explained by allele frequency differences among river basins, years, and within-basin sampling sites for each year.

We used the maximum likelihood phylogeny inference program, CONTML, in the PHYLIP analysis package (Felsenstein 2005) to construct trees depicting the structure of

coho salmon genetic diversity among all 24 basins sampled in 2002. Five hatchery populations and temporal replicates (2003, 2004) of wild populations from five river basins were also included in this analysis. We used the program SEQBOOT, also in the PHYLIP package, to bootstrap the data and estimate statistical support for the topology of the best maximum likelihood tree. We displayed trees with the program TREEVIEW (Page 1996).

For the five populations that were sampled in multiple years, the number of breeders, N_B, was estimated through the methods of Waples (1990):

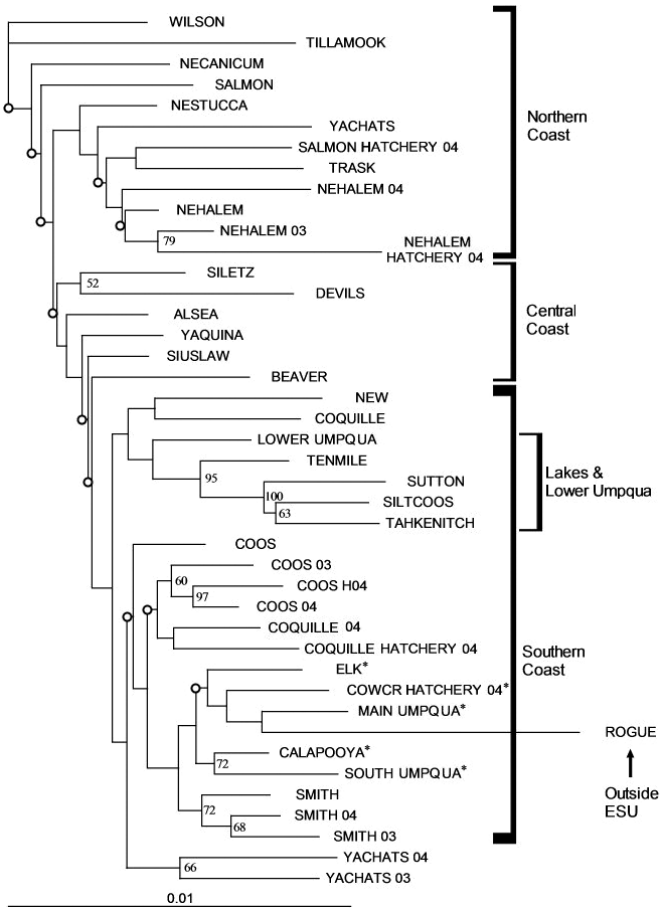
$$\widehat{N}_B = \frac{b}{2(\widehat{F} - 1/S)}$$

where $\widehat{F}$ is an estimator of the standardized temporal variance in allele frequencies, $1/S$ is a sampling error correction factor, and b is the number of generations between samples, adjusted to account for the relative contribution of jacks to the population. Values of b were calculated according to the methods of Tajima (1992). N_B was then used to estimate m, the per-population immigrant fraction, according to the temporal F_{ST} method (Ford et al. 2004).

Using only data from 2002, we applied a Bayesian method to estimate directional migration rates among wild coho salmon populations. This method, described by Wilson and Rannala (2003) and implemented in the program BAYESASS, relaxes several assumptions carried in the temporal F_{ST} method (e.g., constant and symmetrical geneflow between population pairs, HWE) and is designed to provide an estimate of recent migration rates. By inferring the ancestry of each sample through Markov chain Monte Carlo methods, BAYESASS provides directional estimates of migration, which may be used to infer source–sink dynamics. However, computational limits of the program necessitated some data pooling. A minimum number of pooling steps were made, utilizing evidence for natural clades identified through the maximum likelihood inference of coho population structure. Briefly, (*i*) the lower Umpqua and neighboring coastal lakes were pooled into a single clade; (*ii*) all other Umpqua tributaries were pooled into a single clade; and (*iii*) the Wilson and Tillamook rivers were pooled together as a single clade. Also, the number of alleles present at the *Oki16* locus exceeded the computational limits of the program. Thus, data from this marker were not included in the analysis. Lastly, the current version of BAYESASS limits the maximum number of populations considered to 19. We therefore performed the analysis twice, first excluding the northernmost population (Necanicum) and then excluding the southernmost population (Rogue). We used the default prior values (allele frequency, migration rate, and inbreeding coefficient all set at 0.15) and performed three million steps (999 999 burn-in) with a sampling frequency of 2000.

Allelic richness, a measure of genetic diversity that accounts for variable sample sizes through rarefaction, was calculated for all loci in all populations with the program FSTAT (Goudet 1995). An analysis of variance, carried out with the program S-PLUS 7.0 (Insightful Corp., Seattle, Washington), was used to test for associations between each population's mean allelic richness (across loci) and the following explanatory variables: "latitude" of entry from the ocean into the spawning river (river mouth), sampling "year", "ecotype" (river or lake), and "origin" (hatchery or wild). All variables were treated as fixed effects, and all variables were categorical, except for latitude, which was continuous. Owing to the unbalanced design of our study (e.g., absence of lake hatcheries and temporal replication for only wild fish from rivers), we used type III sums of squares to assess the significance of variables included in our models, but could not estimate the significance of third- and fourth-order interaction terms. We included all first-order interactions, with the exception of ecotype × year (not estimable), in an initial full model, then manually removed insignificant terms to obtain our final reduced model. We then used linear regression analysis to test for a cline in allelic richness among wild coho populations, using the continuous explanatory variable latitude.

Fig. 2. Maximum likelihood tree depicting structure among Oregon coastal coho salmon (*Oncorhynchus kisutch*) populations. Open circles indicate branches of length not significantly different from zero ($\alpha = 0.05$). Values for nodes that received bootstrap support greater than 50% are presented. All samples were collected in 2002, unless otherwise indicated (03, from 2003; 04, from 2004). An asterisk (*) indicates a tributary or hatchery of the Umpqua River drainage.



Results

The eight microsatellites we used to characterize Oregon coastal coho salmon populations presented high yet variable

Table 2. Effective number of breeders (N_B) and corresponding immigrant fractions (m) for five Oregon coastal coho salmon (*Oncorhynchus kisutch*) populations as calculated by the temporal F_{ST} method (Ford et al. 2004), under 10% and 25% jack contributions.

	10% jacks		25% jacks		
Basin	N_B	m	N_B	m	Bayesian m*
Nehalem	170 (117, 245)	0.05 (0.02, 0.10)	76 (53, 110)	0.12 (0.06, 0.22)	0.06 (0.02, 0.10)
Yachats	150 (81, 348)	0.06 (0.02, 0.14)	66 (35, 153)	0.14 (0.05, 0.32)	0.32 (0.29, 0.33)
Smith	378 (210, 824)	0.02 (0.01, 0.06)	171 (95, 373)	0.05 (0.02, 0.12)	0.15 (0.06, 0.28)
Coos	384 (238, 674)	0.02 (0.01, 0.05)	172 (107, 301)	0.05 (0.02, 0.11)	0.19 (0.15, 0.24)
Coquille	168 (98, 324)	0.06 (0.02, 0.12)	71 (41, 137)	0.13 (0.05, 0.28)	0.31 (0.28, 0.33)

Note: For all estimates, 95% confidence intervals are reported in parentheses.
*Immigrant fraction as calculated through the Bayesian method of Wilson and Rannala (2003).

Table 3. Analysis of variance (ANOVA) table testing for association between the explanatory variables origin, ecotype, year, and latitude with mean allelic richness of Oregon coastal coho salmon (*Oncorhynchus kisutch*) populations.

	df	Sum of squares	Mean squares	F	Pr(F)
Origin	1	0.9782	0.9782	4.4301	0.043
Ecotype	1	1.8633	1.8633	8.4384	0.007
Year	2	0.2716	0.1358	0.6150	0.547
Latitude	1	0.0045	0.0045	0.0203	0.888
Error	32	7.0661	0.2208		

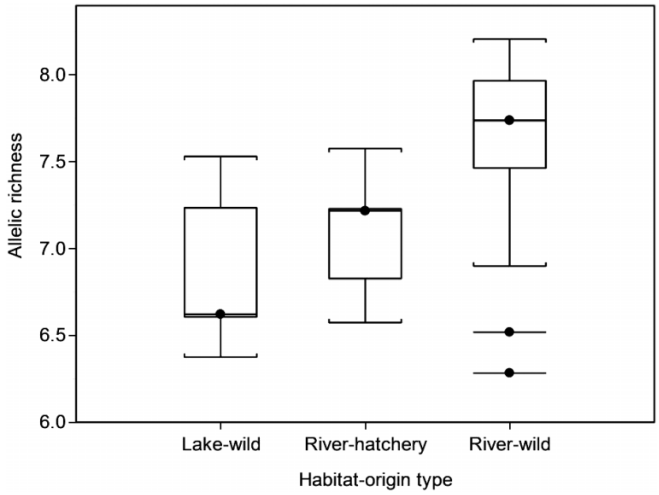
Note: See text for variable descriptions.

levels of polymorphism, with between 10 and 71 alleles (mean = 30.12, standard deviation (SD) = 18.52). Per-locus heterozygosities ranged from 85.2% to 60.2%, with a rating of 72.8% overall (Table 1). Even after sequential Bonferroni corrections, approximately 64% of the wild populations did not conform to HWE expectations across all loci, whereas only one of five hatchery populations differed significantly from expected HWE genotypic frequencies. After making sequential Bonferroni adjustments to an initial critical value of 0.05, we detected significant evidence for linkage disequilibrium for only 0.7% of locus pairs, considering all possible locus pair combinations across all populations.

Population structure

Pairwise θ values at the basin level ranged from 0.002 to 0.068, with an overall θ value of 0.021 (95% confidence interval (CI) = 0.016, 0.027; $p < 0.0001$). Highest values tended to occur between the northerly Trask population and those of rivers and coastal lakes from the southern extreme of the ESU (see Appendix A, Table A1). Within the Umpqua River, pairwise θ values ranged between 0.003 to 0.015, with an overall value of 0.015 (95% CI = 0.010, 0.022; $p < 0.0001$). Highest pairwise θ values within this basin occurred between the Smith River and south fork Umpqua populations, followed by values associated with the lower Umpqua and all other Umpqua tributaries. For the Nehalem, Yachats, Smith, and Coos rivers, simultaneous hierarchal analyses indicated that 97.33% of the observed genetic variance could be attributed to differences among individuals. Most of the remaining 2.67% of genetic variance could be explained by allele frequency differences among basins (52.8%), followed by differences among sites within basins (29.5%), and lastly, differences observed among temporal replicates (17.7%).

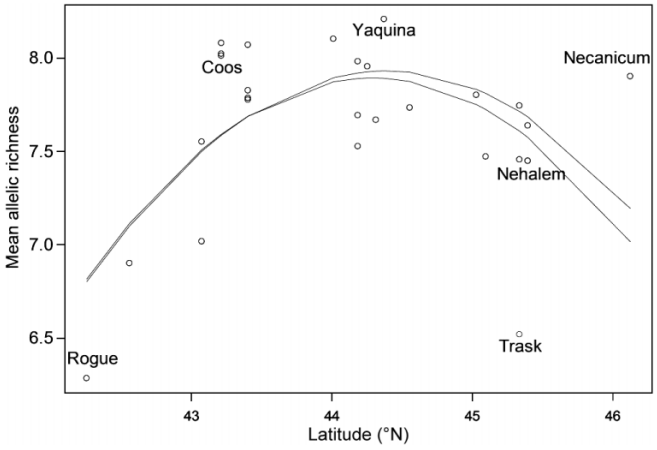
Fig. 3. Box plots depicting the range of mean allelic richness observed among coho (*Oncorhynchus kisutch*) populations from three habitat origin types: lake-wild, river-hatchery, river-wild. Boxes enclose the 25th through 75th quartile range, and whiskers are drawn to the nearest value not beyond the standard span from quartiles (i.e., 1.5 × interquartile range).



In agreement with our analyses of genetic variance, the maximum likelihood tree inferred from our data suggests that only weak structure exists among coho salmon samples from different river basins of the OCC ESU, as many internal branch lengths are short or do not significantly differ from zero (Fig. 2). However, statistically supported clades generally reflect geographic relationships among basins. For example, the coastal lakes flanking the mouth of the Umpqua River form a clade together with the lower reaches of this river. Nearby Sutton Lake also falls into this group, whereas the more distant Devil's Lake does not, but instead appears to be most similar to its proximal Siletz River. The Coos, Umpqua, Smith, and Coquille rivers appear to form a southern group, whereas the Nehalem, Tillamook, Wilson, Necanicum, Nestucca, Trask, and Salmon rivers form a loosely defined northern group.

Samples collected from the same river in different years tended to form clades, although interannual Coquille samples alternately grouped with neighboring rivers to the north and south (Fig. 2). The Yachats River population presents

Fig. 4. Relationship between mean allelic richness of wild, river-rearing Oregon coastal coho salmon (*Oncorhynchus kisutch*) populations and the latitude at which they enter freshwater spawning grounds. The upper curve includes the Trask River sample point; the lower curve does not.



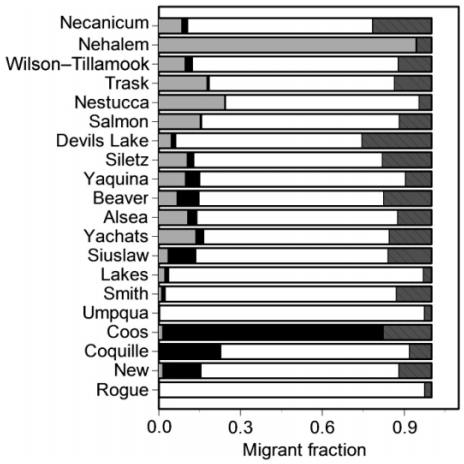
another exception, as it does not fit neatly on the tree in a geographic context, but instead aligns with distant southern and northern populations between years.

In all but one case, hatchery coho salmon populations appear most similar to wild fish returning to the river where they are located (Fig. 2). The exception to this pattern is the Salmon River hatchery stock, which appears to be most similar to the Trask River wild population. Unlike other hatchery stocks considered here, the Salmon River hatchery population was not established from native fish from the river on which it operates. Instead it was founded by Siletz River hatchery stock (Salmon River Hatchery operations plan, Oregon Department of Fish and Wildlife, ODFW), which was heavily supplemented with Trask River coho during the years 1968–1977 (Beidler 1987). In concert, the pairwise θ value between the Salmon and Trask wild populations is the lowest observed between any two populations (Appendix A, Table A1), evidence that suggests that hatchery-mediated genetic introgression of Trask River stock may have occurred into the wild Salmon River coho population.

Migration

Estimates of the effective number of breeders, based on the methods of Waples (1990), ranged from 66 to 384 individuals for the five populations examined (Table 2). Immigrant fraction estimates for these populations ranged from 0.02 to 0.14. The immigrant fraction point estimate in the Smith River, as calculated through the Bayesian assignment procedure implemented in BAYESASS (Wilson and Rannala 2003), exceeded those calculated through the temporal F_{ST} method of Ford et al. (2004) (Table 2), largely as a result of migration from the Umpqua and Lakes – Lower Umpqua migrant sources. In general, the Bayesian migration estimates tended to be higher, although estimates for the Nehalem River did not follow this pattern (Table 2). The Nehalem and Coos populations appeared to be the primary migrant sources for most basins, followed by the Umpqua and Lakes – Lower Umpqua (Appendix A, Table A2). Notably, our estimates for the Rogue River population indicate that strays from this basin account for less than 0.01% of the individuals present in any basin of the OCC ESU and that less than 0.01% of the Rogue population originated from any basin of the OCC ESU. This degree of isolation is not observed for any population within the OCC ESU. The BAYESASS program provided very consistent results between runs, with overlapping 95% CIs for all repeated estimates. Directional migration rate estimates among 20 population groups are presented in Appendix A (Table A2).

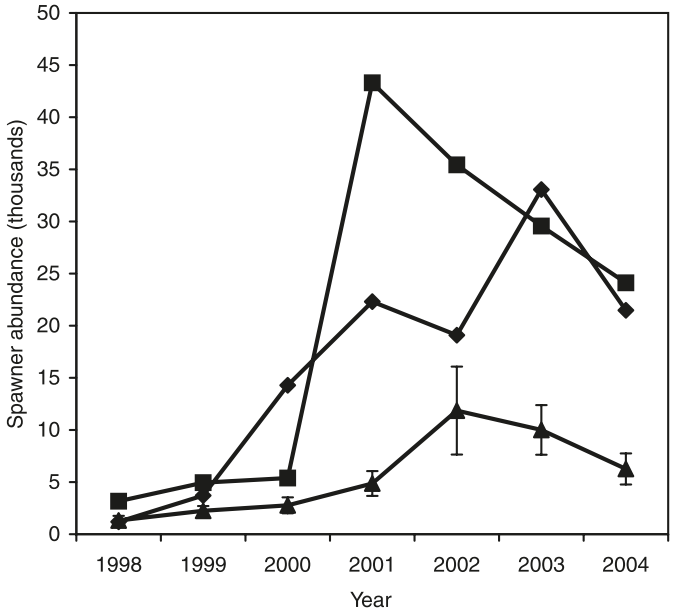
Fig. 5. Oregon coho (*Oncorhynchus kisutch*) populations ordered from north (top) to south (bottom) as composed by individuals homing to their natal river (open) and migrants from the Nehalem (light gray), Coos (black), and all other sources combined (dark gray). Migrant contributions estimated with the program BAYESASS (Wilson and Rannala 2003).



Allelic richness

Considerable variation in mean allelic richness was observed among Oregon coastal coho salmon populations. An analysis of variance indicated that first-order interaction terms for the explanatory variables year, origin, latitude, and ecotype were not significantly associated with variability in allelic richness ($p > 0.05$). Accordingly, the interaction terms were removed from the model, and a subsequent analysis of variance (ANOVA) identified both origin and ecotype to be significantly associated with variation in mean population allelic richness ($F_{[1,32]} = 4.430$, $p = 0.043$ and $F_{[1,32]} = 8.438$, $p = 0.007$, respectively; Table 3). Neither year nor latitude appeared to be significant ($F_{[2,32]} = 0.615$, $p = 0.547$ and $F_{[1,32]} = 0.020$, $p = 0.888$, respectively Table 3). Given these results, we then collapsed the data into three categories: WildRiver, WildLake, and HatcheryRiver, recognizing that each of these population "types" could be making substantially different contributions to the overall mean of allelic richness. A Scheffé's multiple comparisons analysis indicated that mean allelic richness of wild lake rearing populations is significantly lower than wild river rearing populations (Fig. 3). One potential outlier, the Trask River population, presented markedly low mean allelic richness for a wild river population (Fig. 4). When this sample is removed, the Scheffé's multiple comparisons analysis suggests that wild river populations present significantly

Fig. 6. Spawner abundance of coho salmon (*Oncorhynchus kisutch*) in the Nehalem (◆) and Coos (■) rivers, plotted together with the mean spawner abundance of 13 other Oregon Coastal Coho evolutionarily significant unit (OCC ESU) populations (▲, Necanicum, Tillamook, Nestucca, Salmon, Siletz, Yaquina, Alsea, Yachats, Siuslaw, Coquille, Tenmile Lake, Tahkenitch Lake, Siltcoos Lake) for the years 1998 through 2004. Error bars indicate standard error of mean estimate. Adapted from Oregon Department of Fisheries and Wildlife data (oregonstate.edu/Dept/ODFW/spawn/cohoabund.htm).



higher mean allelic richness than both wild lake and hatchery river origin coho.

Given the small sample sizes of both lake and hatchery populations and the disparate patterns of allelic richness observed between these groups and wild river coho salmon, linear regression analysis of mean allelic richness was conducted only for the latter. A latitudinal cline in neutral genetic diversity, peaking in the central region of the OCC ESU, can be observed by plotting mean allelic richness of wild river coho populations against the latitude at which they enter freshwater spawning grounds (Fig. 4). Initially, a model with a single linear term, latitude, was evaluated, but this variable alone was not significantly associated with variation in allelic richness ($F_{[1,26]} = 0.3509$, $p = 0.5587$). Given the curvature observed in the data (Fig. 4), a linear regression model containing a quadratic latitudinal term was tested and found to carry high significance, explaining 33.1% of the variation observed in population mean allelic richness ($F_{[2,25]} = 6.184$, $p = 0.007$):

$$\mu\{\text{Richness}|\text{Latitude}\} = -501.93 + 23.02 \times \text{Latitude} - 0.26 \times \text{Latitude}^2$$

Moreover, when the potentially outlying Trask River sample was removed from this analysis, the model fit improved considerably, explaining 43% of the variation ($F_{[2,24]} = 9.048$, $p = 0.001$).

Discussion

Population structure and migration

The relatively weak genetic structure observed among coho salmon from Oregon coastal rivers suggests that migration among these populations has acted to reduce the effects of genetic drift and divergence. Tagging studies have suggested that during spawning migrations, coho may stray into non-natal streams more frequently than some other Pacific salmonids (Shapovalov and Taft 1954; Quinn 2005). Moreover, past human activities have served to mediate migration among Oregon coho populations through the practice of hatchery stock transfers. Disentangling the relative influence of these two sources of migration is complicated by the shared ancestry of many hatchery and wild coho populations, as well as the unpredictable nature of genetic introgression from introduced hatchery stocks.

The immigrant fraction values we have estimated through the temporal F_{ST} method approximate those reported by Ford et al. (2004), although a direct comparison can only be made for the Smith River, which presents nearly identical values. Immigrant fractions were highest in the Yachats and Coquille populations, that in 2002 presented the lowest spawner abundance counts for the five populations examined (data not shown). Curiously, the temporal F_{ST} method provides a rather high m value for the large Nehalem population. It should be kept in mind, however, that several assumptions of the temporal F_{ST} method, namely HWE and symmetrical geneflow among populations, might not be met. By applying the Bayesian method of Wilson and Rannala (2003), we provide directional migration rate estimates that are not contingent on these assumptions.

Bayesian migration rate estimates tended to be higher than those of the temporal F_{ST} method and suggest that two of the larger populations function as migrant sources for numerous smaller populations (Fig. 5 and Appendix A, Table A2). Moreover, source–sink dynamics appear to be influenced by distance, as smaller basins appear to receive more migrants from the Coos in the south, whereas the Nehalem functions as the principal migrant source in the north (Fig. 5). Consequently, populations of the central coast, such as those from the Yaquina River, Alsea River, and Beaver Creek, receive relatively balanced immigrant contributions from the major source populations.

Two noteworthy sources of error may be compromising the accuracy of our Bayesian migration rate estimates. First, simulations performed by Wilson and Rannala (2003) indicate that their method lacks power when either few loci (less than 20) are employed or when population structure is weak. Given the nature of our data set, caution must therefore be taken when interpreting these results. The influence of unmarked hatchery coho salmon may constitute a second source of error in our migration rate estimates. Most notably, in 1999, the Nehalem hatchery released 53 080 unmarked hatchery coho smolts. Given estimated smolt-to-adult survival rates of 4% to 8% (Logerwell et al. 2003), this hatchery cohort likely produced between 2123 and 4246 unmarked coho adults returning in 2002, a portion of which may have strayed into neighboring basins, thereby elevating the estimate of wild migrants from the Nehalem River. This event may also have generated major allele fre-

quency changes within the Nehalem River population, affecting the Nehalem temporal F_{ST} estimate of m. In contrast, such confounding circumstances are not associated with the Coos source population, as only 139 unmarked Coos River hatchery smolts were released in 1999. Despite these factors, we believe that our results provide a useful index of migration rates and represent the first attempt at quantitatively describing source–sink dynamics among Oregon coho populations.

Dramatic census size increases, recorded for most coastal Oregon coho salmon populations during the sampling period of 1998–2002 (Fig. 6), have probable relevance to our findings. It is likely that the relatively high contemporary migration rates that we are reporting are the result of a spilling over effect, as the larger Coos and Nehalem populations responded more quickly to favorable conditions and provided large numbers of migrants to neighboring populations in 2002. Again, hatchery influence over coho population dynamics on the Nehalem River cannot be ignored and may have contributed to this population's rapid census size increase. Nevertheless, wild coho smolt production on the north fork of this river was estimated to be twice that of any other coastal Oregon site monitored by ODFW in 1999.

Regardless of the source, admixture resulting from migration would generate a transient signal of nonrandom mating. Such a scenario would serve to explain the major departures from HWE that we have detected in the majority of wild populations. Although recent population expansions may be increasing this effect, it seems that high levels of geneflow among populations may be characteristic of Oregon coho salmon, as our $F_{ST}(\theta)$ estimates corroborate previously reported values for Oregon coho (Ford et al. 2004), yet are much lower than values reported for coho at more extreme locations of the species' North American distribution (Olsen et al. 2003; Bucklin et al. 2007).

The temporal and spatial scales over which natural populations form discrete units are seldom predictable and often dynamic. Whereas major departures from HWE were observed when all individuals from a given basin were considered as a single population, most hatchery populations conformed to HWE expectations. Again, this observation suggests that considerable admixture or genetic substructure, not present in hatchery populations, exists within natural coho populations.

To evaluate the possibility of within-basin substructure, we conducted a hierarchical analysis of genetic covariance and tested for conformance with HWE expectations at the level of within-basin sampling sites for the Nehalem, Yachats, Smith, and Coos populations. Hierarchical analyses of genetic covariance provided only limited evidence for within-basin substructure, when contrasted with covariance levels associated with amon- basin differences. However, among-site covariance did exceed among-year covariance; thus, it can be inferred that precocial males (jacks) mediate a higher level of geneflow among brood-year populations than occurs among spawning sites within the same basin. Concomitantly, nearly a third of all putative subpopulations did not conform to genotypic frequency expectations under HWE, even after sequential Bonferroni corrections. Thus, within-basin substructure appears to be both weak and more complex than a temporally stable system of spatially defined demographic units. Unfortunately, the use of carcass samples precluded our ability to detect for multiple, temporally structured populations within spawning years at sampling sites.

In all but one case, hatchery coho salmon populations appeared to be most similar to wild fish of the same river. This result is perhaps not surprising, as the hatchery populations examined were founded by local wild stock, with the exception of the Salmon River hatchery population. Moreover, the Coquille, Coos, and Cow Creek hatchery stocks receive regular supplementation from native wild fish. Although small sample sizes preclude statistical analyses, each of these three hatcheries presented higher allelic richness than both the Nehalem and Salmon hatchery populations, which do not incorporate wild stock into their breeding programs. Overall, the general pattern suggests that hatchery populations possess substantially lower levels of allelic richness than wild river populations.

Allelic richness

Founder effects, bottlenecks, and inbreeding may all contribute to the relatively low allelic richness observed in Oregon hatchery coho salmon populations. However, these processes may also act over natural populations. Coho salmon from Oregon rivers have been shown to be more diverse than more northerly populations with both allozymes (Wehrhahn and Powell 1987) and mtDNA sequence data (Smith et al. 2001). These findings have been interpreted as a signal of bottlenecks and founder effects from a limited number of post-Pleistocene colonizations by coho from Oregon and California refugia. Interestingly, the coastal lakes flanking the mouth of the Umpqua River are also believed to be of late Pleistocene origin (Cooper 1958; Johnson et al. 1985), far younger than most rivers along the Oregon coast. These basins therefore became available for colonization by coho during the same period that more northerly, glaciated rivers of Washington, British Columbia, and Alaska became inhabitable. Founder effects may then also serve to explain the relatively low levels of allelic richness observed in coho populations from Oregon coastal lakes, as compared with neighboring populations.

The highest levels of allelic richness were found in river populations from the central region of the OCC ESU. Interestingly, it appears that coho salmon populations of this region receive the most balanced contributions from the two primary, geographically distant migrant sources of the ESU: the Nehalem and Coos river populations (Fig. 5).

Only one population from another ESU was included in our analyses, that of the Rogue River in southern Oregon, and it presented the lowest level of allelic richness observed among our samples. While sampling across additional ESUs could certainly broaden the scope of our findings, the intensive within-ESU sampling strategy we have employed has provided sufficient resolution to detect both continuous and categorical patterns of allelic richness that might otherwise have been overlooked or misinterpreted.

In conclusion, our findings suggest that both natural and anthropogenic forces have served to shape the contemporary patterns of coho salmon genetic diversity along the Oregon coast. Relatively high migration rates from a limited number of large, geographically distant source populations appear to

modulate spatial genetic structure while maintaining elevated levels of allelic richness within the core of the OCC ESU. In concert with local adaptations, the source–sink dynamics we have described may very well represent a long-standing ecological mechanism responsible for generating and maintaining genetic diversity in Oregon coastal coho salmon populations.

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Appendix A

Tables A1 and A2 appear on the following pages.

Table A1. Pairwise θ values for Oregon coastal coho salmon (*Oncorhynchus kisutch*) populations as defined by basins (data above diag-

	Umpqua	Yaquina	Yachats	Wilson	Trask	Tillamook	Tenmile	Tahkenitch	Sutton	Smith	Siuslaw	Siltcoos
Alsea	0.010	0.014	0.015	0.020	0.021	0.025	0.031	0.031	0.032	0.015	0.006	0.032
Beaver	0.015	0.011	0.016	0.022	0.014	0.025	0.043	0.028	0.039	0.026	0.007	0.032
Coos	0.013	0.013	0.025	0.037	0.044	0.032	0.018	0.020	0.027	0.010	0.011	0.021
Coquille	0.026	0.025	0.040	0.047	0.066	0.038	0.023	0.031	0.035	0.022	0.021	0.028
Devil's	0.035	0.022	0.045	0.021	0.029	0.023	0.064	0.047	0.046	0.045	0.023	0.035
Necanicum	0.013	0.008	0.008	0.016	0.019	0.009*	0.030	0.031	0.041	0.019	0.011	0.032
Nehalem	0.020	0.015	0.014	0.011	0.006*	0.024	0.051	0.039	0.042	0.028	0.012	0.037
Nestucca	0.016	0.014	0.006*	0.016	0.004*	0.030	0.036	0.034	0.034	0.024	0.010	0.032
New	0.026	0.024	0.041	0.053	0.061	0.062	0.028	0.028	0.027	0.028	0.024	0.024
Salmon	0.022	0.015	0.024	0.010	0.002*	0.017	0.054	0.044	0.049	0.035	0.015	0.040
Siletz	0.015	0.016	0.019	0.018	0.013	0.022	0.047	0.040	0.040	0.028	0.013	0.028
Siltcoos	0.028	0.021	0.044	0.032	0.053	0.055	0.017	0.007*	0.005*	0.030	0.018	—
Siuslaw	0.007	0.006	0.011	0.015	0.020	0.020	0.026	0.015	0.021	0.011	—	
Smith	0.007	0.022	0.019	0.039	0.043	0.032	0.021	0.028	0.033	—		
Sutton	0.028	0.029	0.047	0.043	0.064	0.059	0.019	0.009	—			
Tahkenitch	0.025	0.024	0.037	0.041	0.056	0.056	0.019	—				
Tenmile	0.026	0.034	0.029	0.058	0.068	0.062	—					
Tillamook	0.024	0.019	0.041	0.020	0.031	—						
Trask	0.025	0.020	0.019	0.015	—							
Wilson	0.027	0.016	0.027	—								
Yachats	0.015	0.020	—									
Yaquina	0.016	—										
Umpqua	—											

*Not significantly different from zero at $p < 0.05$ with 1000 permutations.

Table A2. Directional migration rates among coho (*Oncorhynchus kisutch*) populations of the Oregon coast, as estimated by the program

Source	Necanicum	Nehalem	Wilson–Tillamook	Trask	Nestucca	Salmon	Devil's	Siletz	Yaquina	Beaver
Necanicum	0.678	0.000	0.002	0.003	0.001	0.002	0.002	0.002	0.001	0.003
Nehalem	0.086	0.945	0.098	0.179	0.243	0.154	0.047	0.106	0.100	0.069
Wilson–Tillamook	0.010	0.025	0.754	0.017	0.006	0.011	0.159	0.007	0.009	0.009
Trask	0.003	0.001	0.002	0.679	0.001	0.002	0.003	0.002	0.001	0.003
Nestucca	0.005	0.001	0.003	0.007	0.709	0.003	0.004	0.006	0.004	0.013
Salmon	0.003	0.007	0.007	0.005	0.004	0.723	0.005	0.010	0.003	0.003
Devil's	0.003	0.001	0.003	0.004	0.002	0.002	0.683	0.003	0.002	0.003
Siletz	0.004	0.001	0.005	0.006	0.002	0.002	0.004	0.691	0.002	0.005
Yaquina	0.005	0.003	0.011	0.022	0.006	0.005	0.009	0.014	0.753	0.037
Beaver	0.004	0.000	0.003	0.004	0.001	0.002	0.003	0.002	0.001	0.676
Alsea	0.020	0.005	0.010	0.016	0.003	0.039	0.010	0.025	0.028	0.008
Yachats	0.004	0.001	0.002	0.004	0.001	0.002	0.003	0.002	0.001	0.003
Siuslaw	0.006	0.001	0.012	0.004	0.002	0.002	0.006	0.009	0.010	0.012
Lakes – lower Umpqua	0.019	0.002	0.007	0.006	0.004	0.005	0.016	0.016	0.015	0.030
Smith	0.018	0.001	0.008	0.005	0.002	0.008	0.005	0.006	0.003	0.004
Umpqua	0.104	0.002	0.039	0.021	0.005	0.024	0.015	0.069	0.004	0.033
Coos	0.021	0.003	0.027	0.008	0.003	0.006	0.017	0.025	0.053	0.081
Coquille	0.003	0.001	0.003	0.005	0.002	0.005	0.003	0.003	0.001	0.004
New	0.004	0.001	0.003	0.005	0.002	0.002	0.006	0.003	0.007	0.005
Rogue	—	0.001	0.003	0.004	0.002	0.003	0.003	0.004	0.002	0.004

Note: First column (Source) lists source of migrants (e.g., migration rate from Alsea to Beaver = 0.008).

onal) and tributaries of the Umpqua River (lower right inset).

Siletz	Salmon	New	Nestucca	Nehalem	Necanicum	Devil's	Coquille	Coos	Beaver	Alsea
0.013	0.014	0.034	0.008	0.016	0.012	0.030	0.030	0.018	0.013	—
0.009	0.014	0.033	0.008	0.014	0.014	0.026	0.041	0.025	—	
0.029	0.034	0.022	0.027	0.027	0.019	0.042	0.011	—		
0.043	0.048	0.022	0.041	0.049	0.033	0.058	—			
0.019	0.021	0.050	0.027	0.021	0.025	—				
0.010	0.008	0.038	0.010	0.013	—					
0.015	0.013	0.046	0.008	—						
0.009	0.008	0.038	—							
0.039	0.052	—								
0.009	—									
—										

Inset: Smith	South Umpqua	Calapooya	Elk	Main Umpqua	Cow Creek hatchery	
					0.004	Main Umpqua
				0.007	0.004	Elk
			0.008	0.012	0.020	Calapooya
		0.004	0.009	0.013	0.017	South Umpqua
	0.020	0.010	0.010	0.015	0.016	Smith
0.012	0.030	0.024	0.014	0.025	0.027	Lower Umpqua

BAYESASS (Wilson and Rannala 2003).

Alsea	Yachats	Siuslaw	Lakes – lower Umpqua	Smith	Umpqua	Coos	Coquille	New	Rogue
0.002	0.004	0.001	0.000	0.001	0.000	0.001	0.002	0.002	—
0.108	0.138	0.036	0.024	0.013	0.002	0.016	0.003	0.017	0.002
0.007	0.009	0.015	0.002	0.003	0.001	0.008	0.004	0.006	0.002
0.002	0.004	0.002	0.001	0.001	0.000	0.001	0.002	0.002	0.001
0.005	0.020	0.001	0.001	0.002	0.001	0.002	0.004	0.005	0.001
0.003	0.004	0.004	0.001	0.001	0.001	0.001	0.004	0.002	0.001
0.002	0.004	0.001	0.001	0.001	0.000	0.001	0.002	0.002	0.001
0.004	0.005	0.002	0.001	0.002	0.001	0.001	0.002	0.004	0.001
0.006	0.009	0.032	0.002	0.010	0.001	0.009	0.004	0.005	0.002
0.002	0.004	0.001	0.001	0.001	0.000	0.001	0.002	0.002	0.001
0.735	0.005	0.007	0.002	0.002	0.003	0.026	0.006	0.004	0.002
0.002	0.680	0.001	0.001	0.001	0.000	0.001	0.002	0.002	0.001
0.002	0.008	0.705	0.001	0.004	0.002	0.002	0.007	0.004	0.001
0.033	0.033	0.048	0.933	0.037	0.002	0.103	0.018	0.047	0.002
0.009	0.007	0.002	0.008	0.847	0.011	0.014	0.008	0.004	0.002
0.040	0.021	0.034	0.007	0.059	0.970	0.002	0.010	0.022	0.003
0.034	0.029	0.102	0.014	0.013	0.003	0.809	0.226	0.140	0.002
0.002	0.010	0.002	0.001	0.001	0.001	0.002	0.691	0.005	0.001
0.002	0.008	0.002	0.001	0.001	0.001	0.001	0.003	0.725	0.002
0.004	0.005	0.002	0.000	0.002	0.000	0.001	0.005	0.004	0.971