Genetic Analyses Provide Insight into the Early Ocean Stock Distribution and Survival of Juvenile Coho Salmon off the Coasts of Washington and Oregon

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Abstract.—Estimating the stock proportions of mixed-stock fishery samples by means of genetic stock identification has played an important role in the management of salmon fisheries. In addition, stock identification of individual fish has applications for population studies, forensic cases, and management issues. We examined 11 microsatellite DNA loci in 84 populations of coho salmon *Oncorhynchus kisutch* sampled at 78 locations from southern British Columbia to northern California to construct a database of microsatellite allele frequencies. We then evaluated the applicability of the database for estimating stock proportions in a mixed fishery and assigning individuals to their regions of origin. The loci were highly polymorphic: observed heterozygosity ranged from 0.754 to 0.943. Using genetic distance calculations, we identified six major geographic regions and 15 smaller subregions into which the populations grouped. Computer simulations and a sample of 143 coho salmon with known origins showed that the database was sufficient to make accurate stock proportion estimates to the 15 subregions. For the sample of fish with known origins, individual assignments to region of origin were 82.5% accurate for all samples and 97.8% accurate for those where *P* was greater than 0.95. We used the database to estimate stock proportions and densities of 2,344 coho salmon sampled over eight summers in a juvenile marine ecology study conducted off the coasts of Washington and Oregon. Columbia River juveniles were caught at higher densities than coastal fish throughout the summer. Fish from Columbia River and coastal sources were captured both north and south of their points of sea entry in early summer and at higher densities than in late summer. September catch of Columbia River juveniles was correlated with adult abundance in the following year, indicating that year-class strength for this stock is largely set during the first summer in the ocean.

Estimating the stock proportions of mixed-stock samples by means of genetic stock identification (GSI) has played an important role in salmon research and fishery management by providing information about the stock composition of captured fish (Shaklee et al. 1999). Although making estimates of stock proportions will continue to be a valuable use of genetic data for fisheries research, the recent discovery of highly polymorphic microsatellite loci has also made stock identification of individual fish a reality (Hansen et al. 2001). Stock identification of individual fish has applications for population studies (e.g., identifying strays or immigrants in a population: Hansen et al.

2001), forensic issues (e.g., the catch of fish from protected stocks: Withler et al. 2004), and management issues (e.g., identifying a fish as originating from a particular stock [Beacham et al. 2005] or run type [Olsen et al. 2000]). Individual stock identification is most applicable to studies encompassing small geographic areas where all possible source populations have been sampled, as has been done successfully for Barkley Sound sockeye salmon *Oncorhynchus nerka* (Beacham et al. 2002) and Fraser River steelhead *O. mykiss* (Beacham et al. 2004). In larger geographic areas, where sampling of every possible source population is not practical, individual assignments will have to be made to a predefined region of origin instead of a population of origin.

Genetic databases of allozyme variation have been constructed and used successfully for GSI of most Pacific salmon *Oncorhynchus* spp. (Shaklee et al.

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1999). For coho salmon *O. kisutch*, Teel et al. (2003) used an allozyme frequency baseline to estimate the stock composition of juvenile coho salmon mixtures caught in marine waters off Washington and Oregon. However, with the advent of molecular techniques to examine highly variable DNA loci, there is a need to construct new baselines to exploit the advantages these loci offer for GSI. Coho salmon are of interest because many of their populations are considered "threatened" under the Endangered Species Act (ESA; Good et al. 2005). A database of microsatellite DNA loci and a major histocompatibility complex (MHC) locus has been used effectively for stock identification of coho salmon mixtures in British Columbia (Beacham et al. 2001). In addition, Withler et al. (2004) tested a baseline of coho salmon microsatellite DNA data for use in forensic cases in British Columbia. These baselines did include some samples from Washington and the Columbia River but none from further south.

Our primary purpose for constructing a baseline of microsatellite DNA data for coho salmon was for stock identification in a multiyear study of the early ocean life history of Pacific salmon off the coasts of Washington and Oregon (Brodeur et al. 2003). This study was motivated by the recognition that marine survival, particularly during the first months at sea, may be as important as freshwater survival to the number of salmon in a given year-class that return to spawn (Pearcy 1992; Bradford 1995). Factors that contribute to early marine survival of coho salmon (e.g., food availability, levels of competition, abundance of predators, and oceanographic conditions) can vary among marine areas at regional and local scales (Emmett and Brodeur 2000; Hobday and Boehlert 2001; Logerwell et al. 2003; Beamish et al. 2004; Brodeur et al. 2004; De Robertis et al. 2005). Understanding how these factors contribute to differences in survival rates among coho salmon populations requires information on behavioral differences among stocks, including migration patterns and habitat use. Developing a genetic baseline sufficient for GSI is a key element in process-oriented field studies and is necessary to enumerate stock abundances in sampled areas.

The primary objective of our study was to construct a database of microsatellite allele frequencies for coho salmon populations from southern British Columbia to northern California. We then evaluated our ability to estimate stock proportions in mixed-stock samples as well as our ability to assign individual fish to their most likely region of origin. After validation of the baseline, we utilized it to estimate the origin of over 2,300 juvenile coho salmon sampled over eight summers in nearshore areas off the Washington and Oregon coasts.

Stock identification information was used to document fine-scale spatial distributions of stocks and to examine the empirical relationship between the abundance of Columbia River, Oregon coast, and Washington coast coho salmon juveniles during their first summer at sea and the abundance of adults from these stocks during the following year.

Methods

Sample collection.—Samples of juvenile or adult coho salmon were collected from streams and hatcheries ranging from southern British Columbia to northern California (Figure 1). Fish were sampled from 84 populations at 78 locations, 51 of which were sampled in multiple years (Table 1). Samples were
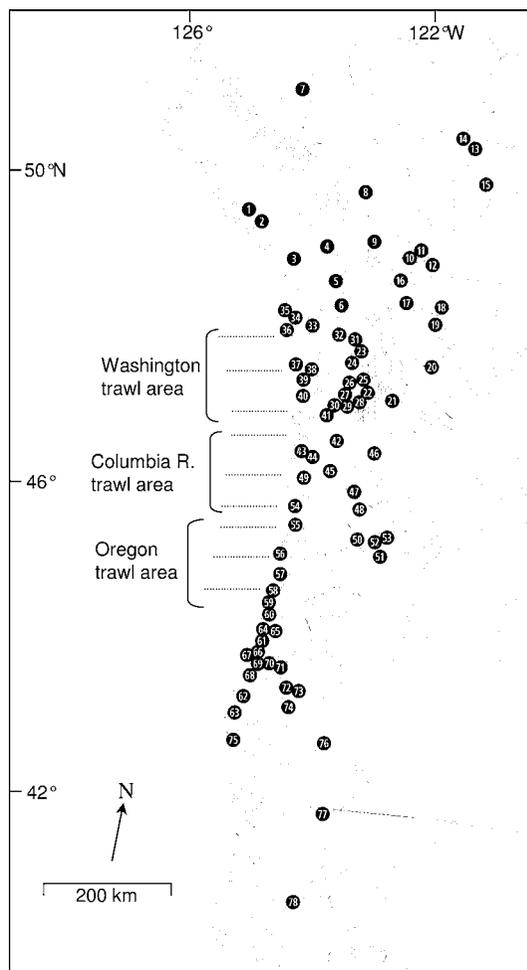

FIGURE 1.—Sample locations and ocean trawl areas and transects (dashed lines) used to evaluate the stock composition of juvenile coho salmon sampled off the coasts of Washington and Oregon. Location numbers are defined in Table 1.

TABLE 1.—Sample information for Pacific coast coho salmon samples analyzed for microsatellite DNA variation. Map codes are used in Figure 1.

Map code	Region, subregion, and location	Sample size	Number of samples pooled	Life stage sampled
	South British Columbia region			
	West coast Vancouver Island subregion			
1	Tranquil Creek Hatchery	81	3	Adult
2	Upper Kennedy River Hatchery	72	3	Adult
3	Nitinat River Hatchery	95	4	Adult
	East coast Vancouver Island subregion			
4	Nanaimo River Hatchery	96	4	Adult
5	Cowichan Fish Hatchery	89	3	Adult
6	Goldstream Salmon Hatchery	96	1	Adult
	South British Columbia coast subregion			
7	Homathko River	73	2	Adult
8	Tenderfoot Creek Hatchery	91	2	Adult
9	Capilano Salmon Hatchery	79	3	Adult
	Lower Fraser River subregion			
10	Inch Creek Hatchery	78	3	Adult
11	Chehalis River Hatchery	87	3	Adult
12	Chilliwack Hatchery	82	3	Adult
	Mid-Fraser–Thompson River subregion			
13	Dunn Creek	76	4	Adult
14	Bridge Creek	90	3	Adult
15	Bessette Creek	79	5	Adult
	Puget Sound region			
	Puget Sound (without Hood Canal) subregion			
16	Nooksack Hatchery	95	2	Parr
17	Ennis Creek, Samish River	140	4	Adult
18	Skagit Hatchery	87	2	Parr
19	Fortson Creek	41	1	Adult
20	Grizzly Creek, Snoqualmie River	105	2	Adult
21	Soos Creek Hatchery	450	6	Adult, parr
22	Minter Creek Hatchery	40	1	Adult
	Hood Canal subregion			
23	Quilcene Hatchery	141	3	Adult
24	Rockybrook Creek, Dosewallips River	32	1	Adult
25	Big Beef Creek	134	2	Adult, smolt
26	Hatchery Creek, Duckabush River	78	1	Adult
27	John Creek, Hamma Hamma River	86	1	Adult
28	Dewatto River	115	2	Adult
29	George Adams Hatchery	91	1	Adult
30	Kirkland and Fir Creek, Skokomish River	94	1	Adult
	Washington coast region			
	Strait of Juan de Fuca subregion			
31	Snow Creek	137	3	Adult
32	Dungeness Hatchery	47	1	Parr
33	Elwha Hatchery	186	2	Adult
	North Washington coast subregion			
34	Hoko River	76	1	Adult
35	Makah Hatchery	143	4	Adult
36	Sol Duc Hatchery (summer run)	96	2	Parr
36	Sol Duc Hatchery (fall run)	94	2	Parr
36	Sol Duc River (summer run)	95	2	Parr
37	Clearwater River	117	2	Adult, smolt
38	Queets River	156	2	Adult, parr
39	Quinault Hatchery	139	3	Adult
	South Washington coast subregion			
40	Humptulips Hatchery (early run)	47	1	Parr
41	Bingham Creek Hatchery, Chehalis River	66	1	Parr
42	Hope Creek, Chehalis River	44	1	Parr
43	Nemah Hatchery	94	2	Parr
44	Naselle Hatchery	94	2	Parr
	Columbia River subregion			
45	Elochoman Hatchery (early run)	42	1	Parr
45	Elochoman Hatchery (late run)	46	1	Parr
46	Cowlitz Hatchery	137	2	Parr
47	Fallert Creek (Kalama) Hatchery (early run)	92	2	Parr
47	Kalama Falls Hatchery (late run)	83	2	Parr
48	Lewis Hatchery (early run)	46	1	Parr
48	Lewis Hatchery (late run)	48	1	Parr
49	Big Creek Hatchery	88	1	Parr
50	Clackamas River (early run)	54	1	Adult

TABLE 1.—Continued.

Map code	Region, subregion, and location	Sample size	Number of samples pooled	Life stage sampled
50	Clackamas River (late run)	31	1	Adult
51	Eagle Creek Hatchery	96	1	Adult
52	Sandy Hatchery	95	1	Parr
53	Bonneville Hatchery	94	1	Parr
	Oregon coast region			
	North-central Oregon coast subregion			
54	Nehalem Hatchery	92	1	Parr
55	Trask Hatchery	94	1	Parr
56	Devil's Lake	60	2	Adult
57	Siletz River	69	2	Adult
58	Yaquina River	66	2	Adult
59	Beaver Creek	64	2	Adult
60	Alsea River	62	2	Adult
61	Siuslaw River	150	2	Adult
62	Coos River	76	3	Parr
63	Bethel Creek, New River	30	1	Parr
	Oregon lakes complex subregion			
64	Sutton Creek	48	1	Adult
65	Mercer Lake	28	1	Adult
66	Siltcoos Lake	53	2	Adult
67	Tahkenitch Lake	34	2	Adult
68	Ten Mile Lake	75	3	Adult, parr
	Umpqua River subregion			
69	Mainstem Umpqua River	53	2	Adult
70	Smith River, Umpqua River	128	4	Adult, parr
71	Elk Creek, Umpqua River	30	2	Adult
72	Calapooya River, Umpqua River	34	2	Adult
73	Rock Creek, North Umpqua River	55	2	Parr
74	South Fork, Umpqua River	67	2	Adult
	South Oregon–north California coast subregion			
75	Elk River	23	1	Parr
76	Cole Rivers Hatchery (Rogue stock)	34	1	Parr
77	Irongate Hatchery	106	1	Parr
78	Trinity River Hatchery	102	1	Parr

collected from populations that potentially migrate to areas off the coasts of Washington and Oregon during the summer. Not every potential population could be sampled, so we attempted to at least include samples from the largest coho salmon populations in each geographic region.

In addition, we analyzed 2,344 juvenile coho salmon that were captured in 16 National Marine Fisheries Service (NMFS) coastal pelagic trawl surveys from 1998 to 2005. As described more fully by Teel et al. (2003), annual surface trawls were made over 6–10-d periods in late June and late September at stations along nine transects oriented perpendicular to shore and extending from 1 to 50 km offshore (Figure 1). Surface trawls were conducted with a Nordic 264-rope trawl (see Krutzikowsky and Emmett 2005 for a detailed description). For this study, samples were grouped into one of three trawl areas, each of which contained three transects: Washington (47°55′N, 47°32′N, 47°00′N), Columbia River (46°40′N, 46°10′N, 45°44′N), and Oregon (45°29′N, 45°03′N, 44°40′N). Five transects were sampled every year (47°55′N, 47°00′N, 46°10′N, 45°29′N, 44°40′N). The

remaining four transects were sampled as time and weather allowed. Coho salmon were classified as juveniles in their first year of marine residence based upon length criteria used in previous studies (Pearcy and Fisher 1990; Teel et al. 2003). Fish with fork lengths less than or equal to 330 mm in June or 450 mm in September were considered to be juveniles. A subset of samples ($N = 143$) contained fish that had been implanted with coded wire tags (CWTs) and was used to test the accuracy of stock identifications made with the baseline.

Data collection.—Tissues samples were collected from a variety of sources: fin, muscle, or operculum tissue preserved in a 100% solution of ethanol; muscle tissue stored at −80°C that had previously been analyzed for allozyme variation; and scales that had been dried on paper and stored at room temperature. Genomic DNA was isolated from the tissue samples with Wizard genomic DNA purification kits (Promega Corp.) used according to the manufacturer's instructions. The isolated genomic DNA was used in polymerase chain reactions (PCRs) to amplify 11 microsatellite loci (Table 2). The resulting PCR

TABLE 2.—Annealing temperatures and primer references for the 11 microsatellite DNA loci used to evaluate coho salmon stock composition.

Locus	Annealing temperature (°C)	Reference
Ocl8	60	Condrey and Bentzen 1998
Oki1	58	Smith et al. 1998
Oki10	60	Smith et al. 1998
Oki23	58	Spidle et al. 2000
One13	58	Scribner et al. 1996
Ots3	47	Banks et al. 1999
Ots103	54	Small et al. 1998
Ots213	58	Greig et al. 2003
Ots505 NWFSC	54	Naish and Park 2002
OtsG422	58	Williamson et al. 2002
P53	58	de Fromentel et al. 1992

products were analyzed with an Applied Biosystems 310 or 3100 capillary electrophoresis system. Gene-Scan (Applied Biosystems 2001a) and Genotyper (Applied Biosystems 2001b) software programs were used to determine the size and number of alleles observed at each locus. We genotyped 7,175 fish from known populations and 2,344 fish from ocean trawl samples.

Population statistical analyses.—The observed allele frequencies for the baseline samples were tested for conformance to expected Hardy–Weinberg proportions with a Fisher's exact test (Guo and Thompson 1992) in GENEPOP (Raymond and Rousset 1995). The sequential Bonferroni method (Rice 1989) was used to adjust the critical significance level for multiple tests.

After testing for conformance to expected Hardy–Weinberg proportions, samples collected from the same location in different years were pooled together as recommended by Waples (1990). The total number of alleles observed, allelic richness (a measure of the number of alleles observed that takes into account the size of each sample), and observed heterozygosity for each locus were computed with the program FSTAT (Goudet 1995).

Cavalli-Sforza and Edwards (1967) chord distances among populations were calculated over 1,000 bootstrap replicates with the program PHYLIP (Felsenstein 2005). We then used PHYLIP to create a consensus neighbor-joining tree.

Baseline validation: simulations.—The program Genetic Mixture Analysis (GMA; Kalinowski 2003) was used to conduct mixed-stock proportion and individual assignment simulations. These simulations were performed to test the adequacy of the baseline to make such estimates of a mixed-stock sample. Mixture proportion simulations were conducted by creating hypothetical mixtures comprised solely of fish from a single region or subregion. Such a mixture is useful for

determining which regions are likely to receive misallocations. In addition, mixture proportion and individual assignment simulations were conducted on simulated mixtures that contained unequal proportions of samples from the regions or subregions. For all simulations, mixtures were generated with a sample size of 200 genotypes drawn in equal proportions from a region's baseline populations. Mean estimated percentage contributions and individual assignments were calculated over 100 bootstrap resamplings of the baseline. Baseline populations were grouped into 6 geographic regions and 15 subregions, the boundaries of which were determined by the results of genetic distance calculations (Figure 2) and analyses of simulated mixtures. We attempted to identify regions and subregions where mixture proportion estimates of simulated mixtures with 100% contribution from one region or subregion would be at least 90% accurate. Unless noted otherwise, the region we refer to as the Oregon coast includes all Oregon coastal samples except for those identified in the south Oregon–north California region (Table 1). Also, the region we refer to as Puget Sound includes samples from Hood Canal, whereas the Puget Sound subregion does not include samples from Hood Canal.

Baseline validation: samples of known origin.— Mixture proportions and individual assignments were estimated with the programs GMA and cBayes (Beacham et al. 2005) for the sample of 143 CWT-implanted coho salmon recovered in the trawl survey. Mixture proportion estimates and individual assignments were made to the most likely region and subregion of origin. Mixture proportions were estimated by means of mixed-stock analyses and by summing all of the individual assignments made to each region. In addition, we made individual assignments of these fish to a single region versus all other regions for each of the three regions that comprised most of the CWT sample (Washington coast, Columbia River, Oregon coast). Standard deviations for the mixture proportion estimates and probability values for the individual assignments were also calculated. These results were compared with those of the actual region and subregion of origin, as revealed by the CWT data, to determine the accuracy of the mixture estimates and individual assignments. More accurate results were generated by cBayes than by GMA; therefore, only results from cBayes are presented for the actual mixtures. However, because cBayes is not capable of performing simulations, we present simulation results produced by GMA.

Ocean distribution and abundance.—Proportional estimates of stock-groups (region of origin) of juvenile coho salmon caught in coastal surface trawls were made with cBayes. Stock-specific proportional esti-
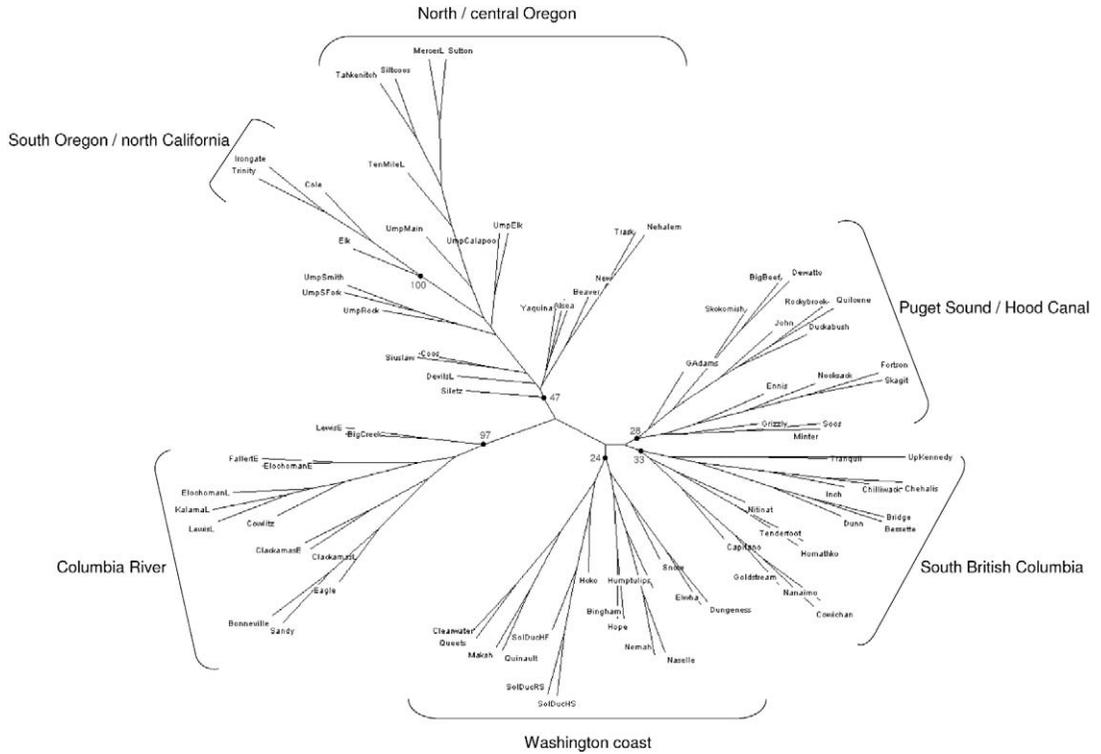
FIGURE 2.—Neighbor-joining dendrogram generated from Cavalli-Sforza and Edwards' (1967) chord distances for 84 coho salmon samples collected within six regions of the Pacific coast. Bootstrap values (%) for the regions are shown.

mates were converted to a standardized density value by multiplying the proportional estimate times the total sample size and dividing by the number of kilometers trawled to obtain the sample. This allowed us to compare the relative abundances of stocks among trawl areas, seasons, and years, standardized to sampling effort. Juvenile density was compared with adult coho salmon abundance data reported by the Pacific Fishery Management Council to manage coho salmon fisheries in the Oregon Production Index (OPI) area (PFMC 2006). Adult abundance data (returns + harvest) were for the years 1999–2005 (1-year lag behind the juvenile sampling years) and included Columbia River hatchery fish and hatchery and natural spawners from Oregon coast populations. Because the OPI management data for Washington coast populations only included ocean escapements for four coho salmon index stocks, counts of adult returns to Washington coast hatcheries (WDFW 2006) were added to the abundance estimates.

Results

Population Diversity

The number of alleles observed at each locus ranged from 20 to 74, and allelic richness values ranged from

5.1 to 8.6 (Table 3). Of all loci, *OtsG422* had the largest number of observed alleles, the highest allelic richness, and the highest heterozygosity. Baseline allele frequencies for the 11 microsatellite loci examined in 84 coho salmon populations are available upon request (D.M.V., unpublished data).

After correcting for multiple comparisons, 4.8% of all tests for conformance to Hardy–Weinberg equilib-

TABLE 3.—Number of alleles observed, allelic richness, and observed heterozygosity for the 11 microsatellite DNA loci over all coho salmon populations sampled.

Locus	Number of alleles observed	Allelic richness	Observed heterozygosity
Ocl8	29	7.2	0.871
Oki1	22	6.0	0.803
Oki10	53	8.3	0.926
Oki23	28	7.2	0.867
One13	22	6.9	0.863
Ots3	24	5.1	0.754
Ots103	64	8.6	0.802
Ots213	43	5.5	0.761
Ots505 NWFSC	20	5.8	0.795
OtsG422	74	8.6	0.943
P53	25	5.8	0.829
All loci	404		0.838

rium were significant. A majority of the significant tests (68.2%) occurred at the locus *Ots103*. This locus is known to have null alleles (Beacham et al. 2001), which could explain the high number of significant tests we observed. Even so, it has been shown that accurate stock composition estimates can be made by including the observed allele frequencies for this locus in a baseline (Beacham et al. 2001).

The results of the chord distances computed among samples show geographic clustering (Figure 2). Six major groups can be identified: south British Columbia, Puget Sound, Washington coast, Columbia River, Oregon coast, and south Oregon–north California coast. Bootstrap support was extremely high for the Columbia River (99%) and south Oregon–north California coast (100%) groups but was considerably lower for the other four groups (22–38%). There was also evidence of further clustering within each of these major groups. For example, within the south British Columbia group, all of the Fraser and Thompson River samples clustered together. Within the Puget Sound group, all of the Hood Canal samples formed a cluster separate from the other Puget Sound samples. The Washington coast group can be further divided into Strait of Juan de Fuca, north Washington coast, and south Washington coast clusters. The one exception is the Hoko River, which drains into the Strait of Juan de Fuca. Our sample from the Hoko River clustered with north Washington coast samples. This is not surprising,

since the Hoko River enters the Strait of Juan de Fuca near its westernmost end and is geographically close to the northern coast of Washington. Therefore, we included the Hoko River in the north Washington coast subregion for subsequent analyses. The two most northerly Oregon coast samples clustered together (Nehalem and Trask hatcheries), but they also clustered closely with several samples from the central Oregon coast. All but one (Devil's Lake) of the Oregon coast samples collected from lake-rearing populations formed a cluster. The remaining central Oregon coast samples did not form any distinctive clusters.

Baseline Validation: Simulations

Results from the analyses of the simulated mixtures are summarized in Table 4. Very accurate stock composition estimates were obtained for each of the 6 regions and 15 subregions. Stock composition estimates ranged from 95.1% to 99.8% for the six regions and from 92.2% to 99.9% for the 15 subregions for simulated mixtures in which the true proportion of each region or subregion was 100%. For four of the five subregions with estimates that were less than 95% accurate, the largest proportion of misallocation was to a geographically adjacent subregion. For the south Washington coast, the subregion with the largest proportion of misallocation was Puget Sound. Estimates of simulated mixtures with varying proportions of each region or subregion were also highly accurate.

TABLE 4.—Actual and mean estimated mixture proportions (SD) for Pacific coast coho salmon sampled from 6 regions and 15 subregions, and the region of largest misallocation (estimates <95%) in analyses of simulated mixtures. Each simulated mixture had a sample size of 200 and along with the baseline was resampled 100 times.

Region or subregion	Actual proportion	Estimated proportion	Region of largest misallocation	Actual proportion	Estimated proportion
Regions					
South British Columbia	100.0	95.7 (1.7)		0.0	0.5 (0.4)
Puget Sound	100.0	96.5 (1.4)		10.0	10.7 (2.6)
Washington coast	100.0	95.1 (1.9)		15.0	15.4 (2.9)
Columbia River	100.0	98.1 (1.0)		50.0	49.0 (3.6)
Oregon coast	100.0	97.1 (1.1)		20.0	19.5 (3.1)
South Oregon–north California coast	100.0	99.8 (0.3)		5.0	5.0 (1.5)
Subregions					
West coast Vancouver Island	100.0	97.2 (1.3)		0.0	0.1 (0.2)
East coast Vancouver Island	100.0	97.2 (1.2)		0.0	0.1 (0.2)
South British Columbia coast	100.0	93.1 (2.7)	Puget Sound	0.0	0.1 (0.3)
Lower Fraser River	100.0	96.6 (1.9)		0.0	0.1 (0.2)
Mid-Fraser–Thompson River	100.0	99.9 (0.2)		0.0	0.0 (0.1)
Puget Sound (without Hood Canal)	100.0	96.1 (1.4)		5.0	6.0 (1.9)
Hood Canal	100.0	92.2 (2.6)	Puget Sound	5.0	4.6 (1.9)
Strait of Juan de Fuca	100.0	95.4 (1.9)		5.0	4.7 (1.6)
North Washington coast	100.0	95.7 (1.8)		5.0	5.7 (2.0)
South Washington coast	100.0	92.6 (2.5)	Puget Sound	5.0	4.4 (1.6)
Columbia River	100.0	98.0 (1.1)		50.0	48.8 (3.3)
North-central Oregon coast	100.0	95.4 (1.7)		10.0	11.2 (2.7)
Oregon lakes complex	100.0	93.6 (2.4)	North-central Oregon coast	5.0	4.3 (1.7)
Umpqua River	100.0	93.4 (2.3)	North-central Oregon coast	5.0	4.7 (1.8)
South Oregon/north California coast	100.0	99.8 (0.3)		5.0	5.1 (1.6)

TABLE 5.—Simulated mixture proportions for Pacific coast coho salmon samples in 6 regions and 15 subregions, percentage of correct individual assignments, and the region of largest misallocation for estimates less than 95% accurate. Each simulated mixture was composed of unequal proportions of samples from each region or subregion, had a sample size of 200, and along with the baseline was resampled 100 times.

Region or subregion	Mixture proportion	Percentage of correct individual assignments	Region of largest misallocation
Regions			
South British Columbia	0.0		
Puget Sound	10.0	83.7	Washington coast
Washington coast	15.0	86.8	Puget Sound
Columbia River	50.0	95.8	
Oregon coast	20.0	90.1	Washington coast
South Oregon/north California coast	5.0	98.4	
Mean		90.1	
Subregions			
West coast Vancouver Island	0.0		
East coast Vancouver Island	0.0		
South British Columbia coast	0.0		
Lower Fraser River	0.0		
Mid-Fraser–Thompson River	0.0		
Puget Sound (without Hood Canal)	5.0	77.0	Hood Canal
Hood Canal	5.0	75.4	Puget Sound
Strait of Juan de Fuca	5.0	82.7	Puget Sound
North Washington coast	5.0	79.7	Puget Sound
South Washington coast	5.0	75.2	Puget Sound
Columbia River	50.0	95.2	
North-central Oregon coast	10.0	86.1	Umpqua River
Oregon lakes complex	5.0	81.6	North-central Oregon coast
Umpqua River	5.0	77.5	North-central Oregon coast
South Oregon–north California coast	5.0	98.6	
Mean		82.9	

Individual assignment simulations produced accuracy rates ranging from 83.7% to 98.4% (mean = 90.1%) for the six regions and from 75.2% to 98.6% (mean = 82.9%) for the 15 subregions (Table 5). The Puget Sound region had the lowest accuracy rate for the regional simulation, whereas the south Washington coast subregion was lowest for the subregional simulation. The south Oregon–north California coast had the highest accuracy rate for both the regional and subregional simulations.

Baseline Validation: Samples of Known Origin

Mixture proportion estimates of the CWT sample are shown in Table 6. For the mixed-stock analyses, the subregion with the largest difference between estimated and actual percentages was the Columbia River, for which the actual value was overestimated by 6.2%. The Columbia River was the subregion with the highest actual proportion (58.0%) in the mixture. Four out of six subregions that were not represented in the CWT sample were estimated by the mixed-stock analyses to be present in the mixture in small proportions (south British Columbia coast, Hood Canal, Strait of Juan de Fuca, and the Oregon lakes complex). However, as indicated by the standard deviations, only the Hood Canal estimate was significantly greater than zero. The estimates obtained by summing the individual assignments were similar to estimates from the mixed-stock analyses. The Puget Sound and Columbia River estimates were overestimated by an even greater percentage, whereas the Oregon coast estimate was more accurate. Of the six subregions that were not represented in the CWT samples, only one was estimated to be present in the mixture by the individual assignment method (Hood Canal).

Accuracy rates of the individual assignments of CWT samples are shown in Table 7. Varying degrees of success were achieved depending upon the criteria used. As expected, estimates were more accurate for regional assignments than for subregional assignments, but only by a small margin. Over all 143 samples, 82.5% were correctly assigned to regions of origin, whereas 81.1% were correctly assigned to subregions. A 97.8% accuracy rate was achieved for individual regional assignments for which P was greater than 0.95. However, only 90 of the 143 assignments met that criterion. Likewise, a 98.8% accuracy rate was achieved for individual subregional assignments with P-values greater than 0.95. Only 84 of 143 subregional assignments met that criterion. The highest levels of

TABLE 6.—Actual composition proportions and proportions estimated by means of mixed-stock analyses and by summing individual assignments of a mixture consisting of 143 coded-wire tagged coho salmon sampled from 6 regions and 15 subregions of the Pacific coast.

Region or subregion	Actual proportion	Mixed-stock analyses (SD)	Summed individual assignments
Regions			
South British Columbia	1.4	0.8 (1.1)	0.0
Puget Sound	2.8	4.9 (2.3)	6.3
Washington coast	23.1	15.9 (3.5)	17.5
Columbia River	58.0	64.2 (4.4)	65.7
Oregon coast	11.2	13.4 (3.5)	9.8
South Oregon–north California coast	3.5	0.7 (0.7)	0.7
Subregions			
West coast Vancouver Island	0.7	0.1 (0.4)	0.0
East coast Vancouver Island	0.7	0.1 (0.4)	0.7
South British Columbia coast	0.0	0.5 (0.9)	0.0
Lower Fraser River	0.0	0.0 (0.2)	0.0
Mid-Fraser–Thompson River	0.0	0.0 (0.1)	0.0
Puget Sound (without Hood Canal)	2.8	0.4 (0.9)	2.8
Hood Canal	0.0	4.5 (2.1)	3.5
Strait of Juan de Fuca	0.0	0.1 (0.3)	0.0
North Washington coast	11.2	6.7 (2.5)	7.7
South Washington coast	11.9	9.2 (2.9)	9.1
Columbia River	58.0	64.2 (4.4)	65.7
North-central Oregon coast	2.8	2.3 (2.1)	2.8
Oregon lakes complex	0.0	0.1 (0.3)	0.0
Umpqua River	8.4	11.0 (3.0)	7.0
South Oregon–north California coast	3.5	0.7 (0.7)	0.7

accuracy were obtained when considering the simpler question of whether or not an individual fish originated from a particular region versus all other regions. For the three regions considered in this analysis, the estimates ranged from 98.2% to 99.1% for assignments with P-values greater than 0.95.

Ocean Distribution and Abundance

Densities (proportional estimate × sample size/km trawled) of ocean-caught juveniles in the three trawl areas off Washington and Oregon varied among stock-groups and between months (Figure 3). Most coho salmon juveniles were from the Washington coast,

TABLE 7.—Results of individual assignment estimates for 143 coded-wire-tagged coho salmon from 6 Pacific coast regions and 15 subregions. Criteria used, percent of correct assignments to region, and total number assigned under those criteria are presented. Single-region estimates considered whether an individual originated from a particular region versus all other regions.

Criterion	Percent correct overall	Percent correct ($P > 0.95$)	N ($P > 0.95$)
Six regions	82.5	97.8	90
15 subregions	81.1	98.8	84
Single regions			
Washington coast	90.2	98.2	111
Columbia River	90.9	99.1	109
Oregon coast	92.3	98.2	112

Columbia River, and Oregon coast stock-groups. These three stock-groups were distributed in all three trawl areas; however, the Washington coast stock density in the Oregon trawl area in June was very low (0.03 ± 0.01). Columbia River juveniles were caught in the highest densities in all three trawl areas in both June and September. The highest densities of Columbia River fish were caught in June in Washington-area trawls (1.52 ± 0.05) and the lowest were caught in September in the Oregon trawl area (0.15 ± 0.01). Densities of Washington coast fish were highest in the Washington trawl area in both June (0.71 ± 0.04) and September (0.10 ± 0.02). In June, Oregon coast juveniles were found at their highest densities in the Oregon (0.40 ± 0.02) and Washington trawl areas (0.32 ± 0.04) and at the lowest density in the area of the Columbia River (0.13 ± 0.02). Puget Sound coho salmon were only abundant in September in the Washington trawl area (0.31 ± 0.03). All of the density estimates made for the south Oregon–north California region had values at or near zero and standard deviations that included zero; therefore, that region is not included in these results.

Juvenile density also varied among years (Figure 4; Table 8). Juveniles from the Columbia River were the most abundant stock-group in all surveys in June except during 2005, when Washington coast juveniles were estimated at higher densities. The Columbia River was the most abundant stock-group in September of
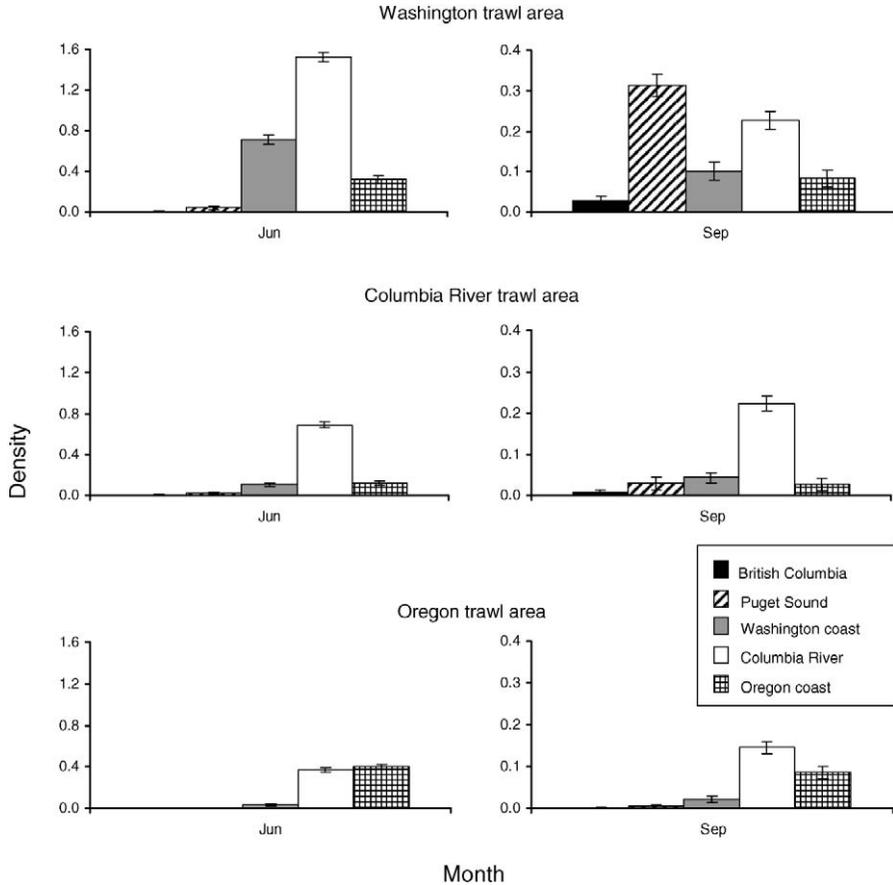
FIGURE 3.—Density (proportional estimate × sample size/km trawled; ±SD) of juvenile coho salmon caught in marine trawls during June and September of 1998–2005 within three Pacific coast areas. Samples were pooled by year. Note the different y-axis scales between June and September graphs.

1998–2000, whereas Puget Sound was the most abundant stock-group in September of 2001–2003. September densities for 2004 and 2005 were lower than in previous years for almost all stock-groups. Columbia River, Oregon coast, and Washington coast juveniles decreased in density from June to September in all years.

Ocean Survival

Densities of Columbia River juveniles in September were highly correlated with adult returns to the Columbia River the following year ($r^2 = 0.77$, $P = 0.005$; Figure 5). Correlations were weaker and nonsignificant for adult returns and abundances of Columbia River juveniles in June ($r^2 = 0.14$; $P = 0.20$), Oregon coast juveniles in June ($r^2 = 0.30$, $P = 0.10$) and September ($r^2 = 0.04$; $P = 0.34$), and Washington coast juveniles in June ($r^2 = 0.28$; $P = 0.11$) and

September ($r^2 = 0.06$; $P = 0.29$). Adult abundance estimates are shown in Table 9.

Discussion

The results presented here indicate that these 11 microsatellite loci and the corresponding baseline will be sufficient for conducting mixed-stock analyses and for making individual assignment estimates of coho salmon along the Washington and Oregon coasts. The loci are highly polymorphic and show good conformance to Hardy–Weinberg expectations. In addition, these loci can be used to analyze samples that were stored under less-than-ideal circumstances, such as archived scale samples. Many of the central Oregon coast samples used in this study were dried scale samples. Seven of these loci have been used to genotype historical scale samples collected in 1975 and 1985 (Ford et al. 2004), and all 11 loci have been
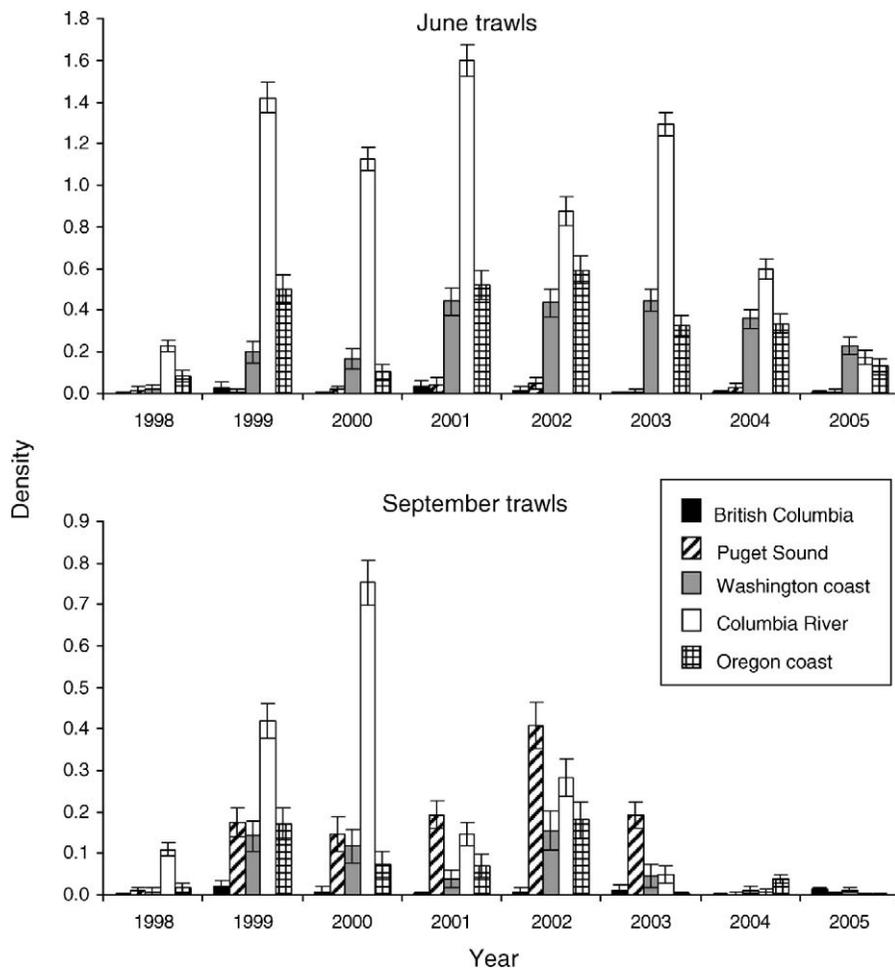
FIGURE 4.—Density (proportional estimate × sample size/km trawled; ±SD) of juvenile coho salmon caught in marine trawls off the Pacific coast during June and September of 1998–2005. Samples from three trawl areas were pooled. Note the different y-axis scales between the June and September graphs.

used to genotype scales dating back to 1976 (D.M.V., unpublished data).

Population Structure

Based upon our genetic population structure results (Figure 2), we identified six major groupings of populations and several additional finer-scale population groups, but only the Columbia River and South Oregon–north California groups were supported with high bootstrap values. Relatively weak geographic population structure among coho salmon populations has also been observed in several other genetic studies ranging from California to Alaska (Bartley et al. 1992; Small et al. 1998; Olsen et al. 2003; Teel et al. 2003; Ford et al. 2004).

Our genetic population structure results also have

similarities and differences compared with previous determinations of evolutionarily significant units (ESUs) under the ESA (Weitkamp et al. 1995; Good et al. 2005). When being considered for listing under the ESA, coho salmon populations were grouped into several ESUs, each of which represented a group of populations believed to (1) be substantially reproductively isolated and (2) contribute substantially to the ecological or genetic diversity of the species (Weitkamp et al. 1995). Two of the subregions we identified—the north-central Oregon coast and the south Oregon–north California coast—are identified as ESUs. Teel et al. (2003) found similar population structure using allozyme variation for coho salmon populations in Oregon and California. Second, similar to Ford et al. (2004), who analyzed seven loci for many

TABLE 8.—Number of kilometers trawled and juvenile coho salmon densities (proportional estimate × sample size/km trawled) for trawls conducted off the Washington and Oregon coasts.

Year	Distance trawled (km)	Stock-group					
		South British Columbia	Puget Sound	Washington coast	Columbia River	Oregon coast	South Oregon–north California
June							
1998	132.2	0.003	0.016	0.023	0.227	0.085	0.000
1999	122.7	0.030	0.007	0.198	1.420	0.502	0.001
2000	99.5	0.003	0.020	0.168	1.125	0.101	0.001
2001	139.8	0.036	0.039	0.441	1.600	0.523	0.001
2002	145.6	0.015	0.050	0.435	0.877	0.593	0.001
2003	201.9	0.004	0.007	0.445	1.293	0.325	0.001
2004	181.2	0.006	0.028	0.358	0.597	0.335	0.000
2005	111.6	0.005	0.008	0.229	0.173	0.131	0.000
September							
1998	122.9	0.002	0.010	0.008	0.109	0.018	0.000
1999	161.5	0.022	0.174	0.141	0.420	0.172	0.000
2000	92.8	0.008	0.148	0.117	0.752	0.072	0.001
2001	144.3	0.002	0.193	0.039	0.145	0.070	0.000
2002	132.6	0.007	0.409	0.155	0.282	0.180	0.000
2003	100.7	0.009	0.191	0.045	0.049	0.003	0.000
2004	150.7	0.001	0.002	0.012	0.007	0.038	0.006
2005	135.5	0.012	0.003	0.012	0.001	0.002	0.000

of the samples used in the present study, we found that samples from the Oregon lakes population complex (identified by Nickelson 2001; not considered to be an ESU) formed a distinct cluster. The Oregon lakes complex comprises three watersheds that have large lake systems: Siltcoos, Tahkenitch, and Tenmile lakes. Third, populations from Puget Sound and the Strait of Georgia are identified as a single ESU, and our samples from Puget Sound are most closely related to samples from south British Columbia. However, like Beacham et al. (2001), we further divided those populations into smaller subregions. Lastly, our designation of the north Washington coast, south Washington coast, and Columbia River as distinct subregions concurs with the ESU designation.

Our study provides new information on the genetic relationships of coho salmon in the Strait of Juan de Fuca and adjacent coastal and Puget Sound populations. In the absence of genetic data for Strait of Juan de Fuca populations, Weitkamp et al. (1995) considered environmental data and ocean migration patterns inferred from CWT recoveries and included coho salmon from the Elwha River and other eastern Strait of Juan de Fuca populations in the Puget Sound ESU. Subsequently, cluster analysis based on microsatellite and MHC loci (Beacham et al. 2001) also supported inclusion of the Elwha River in the Puget Sound ESU. However, our analysis, which used more loci and included data from four populations within the Strait of Juan de Fuca, indicated that coho salmon in the strait are genetically more similar to coastal populations than to those in Puget Sound.

Baseline Validation

We were able to use simulations and a mixed sample of fish with known origins to evaluate the use of baseline data in generating proportional estimates and individual assignments to region of origin. For the mixture simulations, all 6 regions and 10 of 15 subregions had estimated proportions greater than 95% when the true proportion was 100%. The estimates of the simulated mixture composed of different proportions from the regions or subregions were very accurate relative to the actual proportions. These estimates had low standard deviations and never differed from the true proportion by more than 1.2%. This indicates that the baseline will be sufficient to make accurate estimates of stock proportions of a mixed fishery for these 6 regions or 15 subregions.

The accuracy of the individual assignment simulations varied among the different regions and subregions and was lower overall than that of the mixture proportion simulations. At the regional level, assignments were 90% accurate overall. Columbia River and south Oregon–north California coast assignments were greater than 95% accurate. However, individual assignments made to the subregional level were considerably less accurate, indicating that individual assignments will need to be made to the regional level to obtain adequate accuracy rates.

While simulations are a common way to test baselines of genetic data for their adequacy to make accurate stock identifications, use of a mixture of fish with known origins can also be a valuable way to test a baseline (Brodziak et al. 1992; Teel et al. 2003). A real
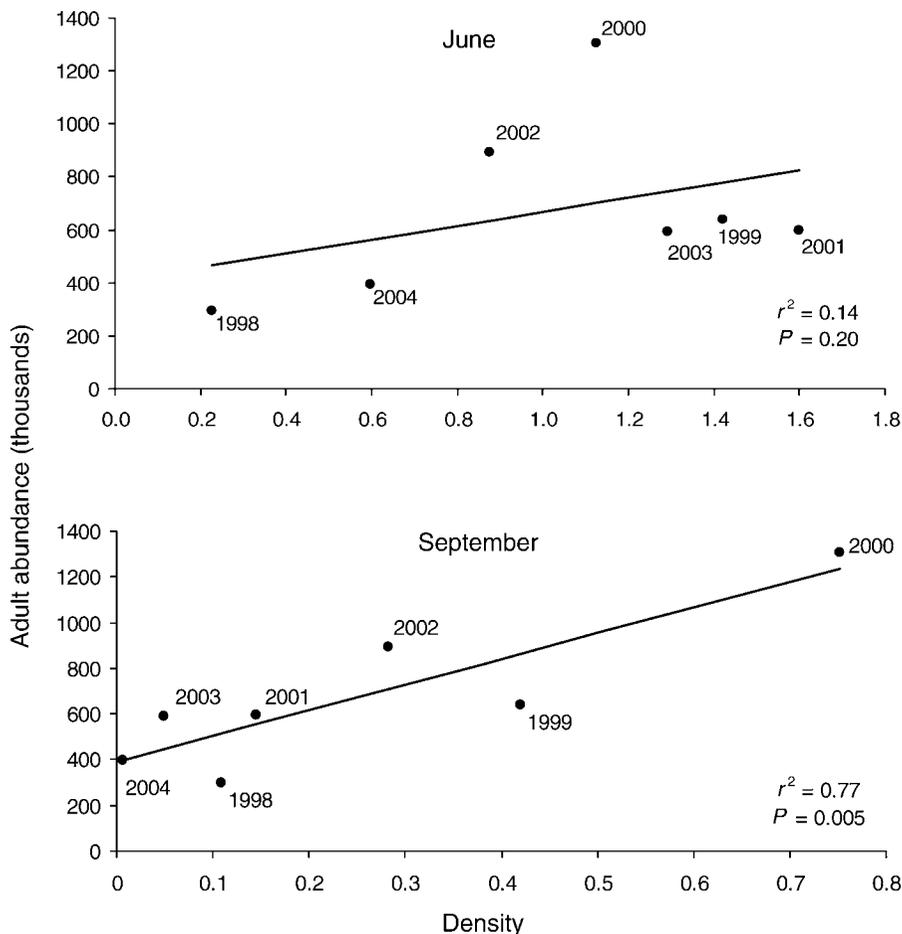
FIGURE 5.—Correlation between the density (proportional estimate × sample size/km trawled) of Columbia River juvenile coho salmon caught in June and September marine trawls (1998–2005) and the abundance of Columbia River adult coho salmon 1 year later. Data points are labeled with the juvenile sampling year.

mixture may have characteristics that are not present in simulated mixtures, such as fish that originate from populations that are not in the baseline or fish with alleles that are not found in the baseline samples. In fact, 58 of the 143 fish in the CWT sample we used originated from populations that were not represented

in the baseline, and two alleles that were present in the CWT sample were not observed in the baseline samples. Despite this, the mixture proportion estimates of the CWT sample are close to the actual mixture proportions and are a marked improvement over the accuracy achieved by Teel et al. (2003), who used allozyme allele frequencies to estimate the stock composition of 41 CWT coho salmon.

It is generally thought that mixed-stock analysis will provide more accurate mixture proportion estimates than by simply summing individual assignments (Manel et al. 2005). However, when making individual assignments of a mixture sample, Bayesian methods can estimate mixture proportions first and use those results as prior probabilities for the individual assignments, resulting in more accurate assignments (Masuda and Pella 2004). Similar to Potvin and Bernatchez

TABLE 9.—Annual estimates (thousands) of adult coho salmon abundance within three Pacific coast areas.

Year	Washington coast	Columbia River	Oregon coast
1999	135.5	295.6	66.7
2000	144.5	638.1	92.9
2001	314.4	1,304.2	211.5
2002	305.3	596.5	349.1
2003	298.6	893.7	316.9
2004	200.9	592.0	219.7
2005	242.9	394.3	161.2

(2001), we found that summing the individual assignments of the CWT sample provided proportional estimates that were similar to those produced by mixed-stock analysis. The ability to make individual assignments to region of origin will be useful for analyses of both mixtures and individuals.

The individual assignment results of the CWT sample further demonstrate that accurate assignments can be made to the regional level but with the caveat that acceptance of only those assignments with *P*-values greater than 0.95 will reduce the number of samples assigned. To assign individuals to six regions for which *P* was greater than 0.95, we had to reject 53 (37.1%) of the 143 assignments. The percentage of samples that will be rejected under these criteria will no doubt vary among different mixtures depending upon the true stock composition of the mixtures. Mixtures that contain a high proportion of fish from regions that are more distinct, such as the Columbia River or south Oregon–north California coast, would be expected to have a lower number of assignments rejected because *P* is less than 0.95. However, rejection of individual assignments with *P*-values less than 0.95 introduces a bias into the estimates, as assignments of fish originating from less-differentiated regions are more likely to be rejected. Therefore, to avoid this bias, any analyses that use individual assignments to estimate stock proportions should use all the assignments to make the proportional estimates.

While having a sample of fish with known origins is useful for testing the baseline, our CWT sample is not representative of the composition of mixtures we would expect to analyze with this baseline. Obviously, CWT fish would not need to undergo genetic analyses to determine their origin. Also, our CWT sample consisted of fish that all originated from a hatchery. This is not surprising given the fact that very few wild coho salmon populations are routinely tagged (Weit-kamp and Neely 2002). Actual mixtures will no doubt contain both hatchery- and wild-origin fish. How this might affect the accuracy of mixture proportion and individual assignment estimates is unclear. Extensive stock transfers between hatcheries, a practice that was formerly common with coho salmon (Weitkamp et. al 1995), can create populations that have a mixed-stock ancestry, which could confound estimates. Thus, a mixture that includes wild-origin fish may be expected to produce more accurate mixture proportion and individual assignment estimates than a mixture that only contains hatchery-origin fish. This may partially explain why the accuracy of our CWT sample estimates was lower than that obtained in the simulations.

The individual assignment tests that attempted to determine whether an individual originated from a particular region or not provided the most accurate results. Assignments such as these will be useful for applications focused on coho salmon from a single region only. For example, it may be particularly valuable to know whether a fish originated from the Puget Sound region, the Columbia River, or the south Oregon–north California region, all of which are ESUs protected under the ESA (Good et al. 2005).

Ocean Distribution, Abundance, and Survival

The use of microsatellite data to identify the origins of juveniles sampled at sea provides a tool to estimate stock-specific densities of coho salmon. The use of the same sampling gear deployed in a consistent manner over a span of eight summers allowed us to compare relative stock abundances among areas and across seasons and years. Results from our analyses of samples grouped bycatch location and averaged over years clearly reflected fish movements in the weeks immediately after sea entry (Figure 3). Juveniles from the Columbia River, as well as from both Oregon and Washington coast rivers, were present in all three sampling areas in June. Studies conducted off the Oregon and Washington coasts in the early 1980s found that after entering the ocean in the spring, coho salmon from the Columbia River and adjacent coastal rivers initially moved to the south and were probably advected by coastal surface currents before reversing and moving north later in the summer (Pearcy and Fisher 1988). In our study, most Columbia River fish have moved north to the Washington coast by June, where we captured them at more than twice the rate than in the area of the Columbia River mouth. Some Oregon coast coho salmon also migrate northward, and their abundance in the Washington trawl area was similar to that estimated for the Oregon trawl area. Consistent with earlier allozymes results (Teel et al. 2003), we identified Puget Sound juveniles that had moved south along the coast. The longer migration distance required for Puget Sound coho salmon to reach our study area probably explains why they were virtually absent until the end of summer, when they were found off the Washington coast in densities greater than other stock-groups.

Our results indicate that the adult abundance of particular Columbia River brood years is largely set by the end of the first ocean summer and can be forecasted by estimating the abundances of juveniles. Estimates of Columbia River juvenile density in September were highly correlated with the number of adults either captured in fisheries or returning to freshwater the following year (Figure 5). This relationship provides new and stock-specific evidence to support the "critical

first summer" hypothesis that early marine phase mortality is vital for determining coho salmon adult abundance (Hartt 1980; Pearcy 1992). Fisher and Pearcy (1988) suggested that coho salmon year-class success is probably determined early in summer, shortly after smolts leave freshwater. However, our data indicate that trawls conducted in late June occurred prior to the decisive mortality for the brood years of coho salmon we studied. Instead, our results are more consistent with the Beamish and Mahnken (2001) hypothesis that despite very high predation-based mortality immediately after ocean entry, coho salmon year-class strength is not set until after the end of summer. In the Beamish and Mahnken (2001) model, major mortality occurs when ocean environmental conditions during the summer prevent juveniles from growing to a critical size. Although Beamish and Mahnken (2001) argued that insufficient summer growth leads to high mortality in late autumn and winter, our findings demonstrate that for Columbia River coho salmon, year-class size is determined by the end of September.

It is also worth considering our results in the context of the work of Hartt and Dell (1986), who concluded from tagging studies that Columbia River and other southern stocks are highly migratory soon after ocean entry and comprise a substantial proportion of juveniles found north along the coastal shelf as far as the Gulf of Alaska. However, the survival signal we detected was derived by sampling juveniles that remained in local coastal waters for several months after ocean entry. It is therefore apparent that summer resident juveniles represent a major portion of the Columbia River coho salmon population. This conclusion supports the perspective presented by Pearcy and Fisher (1988), who found that many coho salmon from southern sources are not highly migratory during their first summer in the ocean.

In contrast to our findings for Columbia River coho salmon, shifts in summer abundances of Oregon and Washington coast juveniles were poor predictors of the adult abundances of those stocks. Juveniles from the coastal stocks, particularly those from Oregon, typically constituted only a small fraction of our catches. It may be that density estimates for these fish are not sufficiently sensitive to year-to-year changes in abundance. One explanation for these differences may be the much smaller volume of coho salmon production in coastal streams compared with that of the Columbia River. An alternative explanation is that our trawl surveys were not conducted over a broad enough region to sample the core marine habitats of coho salmon from Oregon and Washington coast rivers. Oregon coho salmon have a more southerly marine

distribution than Columbia River fish. In recent juvenile salmon surveys conducted in southern Oregon and northern California nearshore areas, coho salmon from the Oregon coast were predominant (Brodeur et al. 2004), although relatively few juveniles were captured. Furthermore, analyses of CWT coho salmon showed that Oregon coast adults are caught at much higher rates in southern Oregon and California fisheries than are Columbia River fish, which are primarily harvested in fisheries within our study area (Weitkamp and Neely 2002). Weitkamp and Neely (2002) also demonstrated that the marine migration patterns of Washington coast coho salmon populations were very different from those of Columbia River and Oregon coast populations, as much of their harvest occurred in Canadian fisheries. Therefore, current ocean research programs in British Columbia (Beamish et al. 2003; Trudel et al. 2004) are expected to sample more juveniles from Washington coast populations than our study.

We presented a new microsatellite DNA baseline and provided empirical data on the level of accuracy to expect when estimating mixture proportions and assigning individual coho salmon to a region of origin. We then used genetic estimates to enumerate relative abundances of Columbia River and coastal stocks sampled in an ongoing marine ecology study conducted off Oregon and Washington. We anticipate that genetic identification of individuals will have broad applicability to the ongoing study, which includes numerous process-oriented investigations (e.g., Emmett and Brodeur 2000; Schabetsberger et al. 2003; Emmett et al. 2004, 2006; Brodeur et al. 2005; De Robertis et al. 2005; Krutzikowsky and Emmett 2005). Genetic data will be useful for examining patterns of migration, habitat use, and survival as well as for studying stock-specific rates of growth, early maturity in males, diet, parasitic infections, and disease occurrence.

Acknowledgments

References

Applied Biosystems. 2001a. ABI Prism GeneScan analysis software, version 3.7 for the Windows NT platform. Applied Biosystems, Foster City, California.

Applied Biosystems. 2001b. ABI Prism Genotyper 3.7 NT software. Applied Biosystems, Foster City, California.

Banks, M. A., M. S. Blouin, B. A. Baldwin, V. K. Rashbrook, H. A. Fitzgerald, S. M. Blankenship, and D. Hedgecock. 1999. Isolation and inheritance of novel microsatellites in Chinook salmon (*Oncorhynchus tshawytscha*). Journal of Heredity 90:281–288.

Bartley, D. M., B. Bentley, P. G. Olin, and G. A. E. Gall. 1992. Population genetic structure of coho salmon (*Oncorhynchus kisutch*) in California. California Fish and Game 78:88–104.

Beacham, T. D., J. R. Candy, B. McIntosh, C. MacConnachie, A. Tabata, K. Kaukinen, L. Deng, K. M. Miller, and R. E. Withler. 2005. Estimation of stock composition and individual identification of sockeye salmon on a Pacific Rim basis using microsatellite and major histocompatibility complex variation. Transactions of the American Fisheries Society 134:1124–1146.

Beacham, T. D., J. R. Candy, K. J. Supernault, T. Ming, B. Deale, A. Schulze, D. Tuck, K. H. Kaukauna, J. R. Irvine, K. M. Miller, and R. E. Wither. 2001. Evaluation and application of microsatellite and major histocompatibility complex variation for stock identification of coho salmon in British Columbia. Transactions of the American Fisheries Society 130:1116–1149.

Beacham, T. D., K. D. Le, and J. R. Candy. 2004. Population structure and stock identification of steelhead trout (*Oncorhynchus mykiss*) in British Columbia and the Columbia River based on microsatellite variation. Environmental Biology of Fishes 69:95–109.

Beacham, T. D., B. McIntosh, and C. MacConnachie. 2002. Microsatellite identification of individual sockeye salmon in Barkley Sound, British Columbia. Journal of Fish Biology 61:1021–1032.

Beamish, R. J., and C. Mahnken. 2001. A critical size hypothesis to explain natural regulation of salmon abundance and the linkage to climate and climate change. Progress in Oceanography 49:423–437.

Beamish, R. J., C. Mahnken, and C. M. Neville. 2004. Evidence that reduced early marine growth is associated with lower marine survival of coho salmon. Transactions of the American Fisheries Society 133:26–33.

Beamish, R. J., I. A. Pearsall, and M. C. Healey. 2003. A history of the research conducted on the early marine period of Pacific salmon off Canada's Pacific coast. North Pacific Anadromous Fish Commission Bulletin 3:1–40.

Bradford, M. J. 1995. Comparative review of Pacific salmon survival rates. Canadian Journal of Fisheries and Aquatic Sciences 52:1327–1338.

Brodeur, R. D., J. P. Fisher, R. L. Emmett, C. A. Morgan, and E. Casillas. 2005. Species composition and community structure of pelagic nekton off Oregon and Washington under variable oceanographic conditions. Marine Ecology Progress Series 298:41–57.

Brodeur, R. D., J. P. Fisher, D. J. Teel, R. L. Emmett, E. Casillas, and T. W. Miller. 2004. Juvenile salmonid distribution, growth, condition, origin, and environmental and species associations in the northern California current. U.S. National Marine Fisheries Service Fishery Bulletin 102:25–46.

Brodeur, R. D., K. W. Myers, and J. H. Helle. 2003. Research conducted by the United States on the early ocean life history of Pacific salmon. North Pacific Anadromous Fish Commission Bulletin 3:89–131.

Brodziak, J., B. Bentley, D. Bartley, G. A. E. Gall, R. Gomulkiewicz, and M. Mangel. 1992. Tests of genetic stock identification using coded wire tagged fish. Canadian Journal of Fisheries and Aquatic Sciences 49:1507–1517.

Cavalli-Sforza, L. L., and A. W. F. Edwards. 1967. Phylogenetic analysis: models and estimation procedures. American Journal of Human Genetics 19:233–257.

Condrey, M. J., and P. Bentzen. 1998. Characterization of coastal cutthroat trout (*Oncorhynchus clarki clarki*) microsatellites and their conservation in other salmonids. Molecular Ecology 7:787–789.

de Fromentel, C. C., F. Pakdel, A. Chapus, C. Baney, P. May, and T. Soussi. 1992. Rainbow trout P53 cDNA cloning and biochemical characterization. Gene 112:241–245.

De Robertis, A., C. A. Morgan, R. A. Schabetsberger, R. W. Zabel, R. D. Brodeur, R. L. Emmett, C. M. Knight, G. K. Krutzikowsky, and E. Casillas. 2005. Columbia River plume fronts II: distribution, abundance, and feeding ecology of juvenile salmon. Marine Ecology Progress Series 299:33–44.

Emmett, R. L., and R. D. Brodeur. 2000. Recent changes in the pelagic nekton community off Oregon and Washington in relation to some physical oceanographic conditions. North Pacific Anadromous Fish Commission Bulletin 2:11–20.

Emmett, R. L., R. D. Brodeur, and P. M. Orton. 2004. The vertical distribution of juvenile salmon and associated fishes in the Columbia River plume. Fisheries Oceanography 13:392–402.

Emmett, R. L., G. K. Krutzikowsky, and P. Bentley. 2006. Abundance and distribution of pelagic piscivorous fishes in the Columbia River plume during spring/early summer 1998–2003: relationship to oceanographic conditions, forage fishes, and juvenile salmonids. Progress in Oceanography 68:1–26.

Felsenstein, J. 2005. PHYLIP (Phylogeny Inference Package), version 3.6. Department of Genome Sciences, University of Washington, Seattle. Available: http://evolution.genetics.washington.edu/phylip.html. (October 2005).

Fisher, J. P., and W. G. Pearcy. 1988. Growth of juvenile coho salmon (*Oncorhynchus kisutch*) in the ocean off Oregon and Washington, USA, in years of differing coastal

upwelling. Canadian Journal of Fisheries and Aquatic Sciences 45:1036–1044.

Ford, M. J., D. Teel, D. M. Van Doornik, D. Kuligowski, and P. W. Lawson. 2004. Genetic population structure of central Oregon coast coho salmon (*Oncorhynchus kisutch*). Conservation Genetics 5:797–812.

Good, T. P., R. S. Waples, and P. Adams, editors. 2005. Updated status of federally listed ESUs of West Coast salmon and steelhead. NOAA Technical Memorandum NMFS-NWFSC-66.

Goudet, J. 1995. FSTAT, version 1.2: a computer program to calculate *F*-statistics. Journal of Heredity 86:485–486.

Greig, C., D. P. Jacobson, and M. A. Banks. 2003. New tetranucleotide microsatellites for fine-scale discrimination among endangered Chinook salmon (*Oncorhynchus tshawytscha*). Molecular Ecology Notes 3:376–379.

Guo, S. W., and E. A. Thompson. 1992. Performing the exact test of Hardy–Weinberg proportions for multiple alleles. Biometrics 48:361–372.

Hansen, M. M., E. Kenchington, and E. E. Nielsen. 2001. Assigning individual fish to populations using microsatellite DNA markers. Fish and Fisheries 2:93–112.

Hartt, A. C. 1980. Juvenile salmonids in the oceanic ecosystem: the first critical summer. Pages 25–37 *in* W. J. McNeil and D. C. Himsworth, editors. Salmonid ecosystems of the North Pacific. Oregon State University Press, Corvallis.

Hartt, A. C., and M. B. Dell. 1986. Early oceanic migrations and growth of juvenile Pacific salmon and steelhead trout. International North Pacific Fisheries Commission Bulletin 47:1–105.

Hobday, A. J., and G. W. Boehlert. 2001. The role of coastal ocean variation in spatial and temporal patterns in survival and size of coho salmon (*Oncorhynchus kisutch*). Canadian Journal of Fisheries and Aquatic Sciences 58:2021–2036.

Kalinowski, S. T. 2003. Genetic mixture analysis 1.0. Department of Ecology, Montana State University, Bozeman. Available: http://www.montana.edu/kalinowski. (October 2005).

Krutzikowsky, G. K., and R. L. Emmett. 2005. Diel differences in surface trawl fish catches off Oregon and Washington. Fisheries Research 71:365–371.

Logerwell, E. A., N. Mantua, P. W. Lawson, R. C. Francis, and V. N. Agostini. 2003. Tracking environmental processes in the coastal zone for understanding and predicting Oregon coho (*Oncorhynchus kisutch*) marine survival. Fisheries Oceanography 12:554–568.

Manel, S., O. E. Gaggiotti, and R. S. Waples. 2005. Assignment methods: matching biological questions with appropriate techniques. Trends in Ecology and Evolution 20:136–142.

Masuda, M., and J. Pella. 2004. Identification of source populations of mixture individuals from their genotypes. North Pacific Anadromous Fish Commission Technical Report 5:103–105.

Naish, K. A., and L. K. Park. 2002. Linkage relationships for 35 new microsatellite loci in Chinook salmon *Oncorhynchus tshawytscha*. Animal Genetics 33:312–327.

Nickelson, T. E. 2001. Population assessment: Oregon coast coho salmon ESU. Northwest region research and monitoring program. Oregon Department of Fish and Wildlife, Portland.

Olsen, J. B., P. Bentzen, M. A. Banks, J. B. Shaklee, and S. Young. 2000. Microsatellites reveal population identity of individual pink salmon to allow supportive breeding of a population at risk of extinction. Transactions of the American Fisheries Society 129:232–242.

Olsen, J. B., S. J. Miller, W. J. Spearman, and J. K. Wenburg. 2003. Patterns of intra- and inter-population genetic diversity in Alaskan coho salmon: implications for conservation. Conservation Genetics 4:557–569.

Pearcy, W. G. 1992. Ocean ecology of North Pacific salmonids. University of Washington Press, Seattle.

Pearcy, W. G., and J. P. Fisher. 1988. Migrations of coho salmon, *Oncorhynchus kisutch*, during their first summer in the ocean. U.S. National Marine Fisheries Service Fishery Bulletin 86:173–195.

Pearcy, W. G., and J. P. Fisher. 1990. Distribution and abundance of juvenile salmonids off Oregon and Washington, 1981–1985. NOAA Technical Report NMFS 93.

PFMC (Pacific Fishery Management Council). 2006. Coho salmon abundance in the Oregon Production Index area. PFMC. Available: http://www.pcouncil.org/salmon/salpre.html. (February 2006).

Potvin, C., and L. Bernatchez. 2001. Lacustrine spatial distribution of landlocked Atlantic salmon populations assessed across generations by multilocus individual assignment and mixed-stock analyses. Molecular Ecology 10:2375–2388.

Raymond, M., and F. Rousset. 1995. GENEPOP (version 1.2): population genetics software for exact tests and ecumenicism. Journal of Heredity 86:248–249.

Rice, W. R. 1989. Analyzing tables of statistical tests. Evolution 43:223–225.

Schabetsberger, R., C. A. Morgan, R. D. Brodeur, C. L. Potts, W. T. Peterson, and R. L. Emmett. 2003. Prey selectivity and diel feeding chronology of juvenile Chinook (*Oncorhynchus tshawytscha*) and coho (*O. kisutch*) salmon in the Columbia River plume. Fisheries Oceanography 12:523–540.

Scribner, K. T., P. A. Crane, W. J. Spearman, and L. W. Seeb. 1996. DNA and allozyme markers provide concordant estimates of population differentiation: analyses of U.S. and Canadian populations of Yukon River fall-run chum salmon (*Oncorhynchus keta*). Canadian Journal of Fisheries and Aquatic Sciences 55:1748–1758.

Shaklee, J. B., T. D. Beacham, L. Seeb, and B. A. White. 1999. Managing fisheries using genetic data: case studies from four species of Pacific salmon. Fisheries Research 43:1–34.

Small, M. P., T. D. Beacham, R. E. Withler, and R. J. Nelson. 1998. Discriminating coho salmon (*Oncorhynchus kisutch*) populations within the Fraser River, British Columbia, using microsatellite DNA markers. Molecular Ecology 7:141–155.

Smith, C. T., B. F. Koop, and R. J. Nelson. 1998. Isolation and characterization of coho salmon (*Oncorhynchus kisutch*) microsatellites and their use in other salmonids. Molecular Ecology 7:1614–1616.

Spidle, A. P., T. P. Quinn, and P. Bentzen. 2000. GenBank accession number AF272822. *Oncorhynchus kisutch*

microsatellite *Oki23* sequence. Available: http://www. ncbi.nlm.nih.gov. (April 2006).

Teel, D. J., D. M. Van Doornik, D. R. Kuligowski, and W. S. Grant. 2003. Genetic analysis of juvenile coho salmon (*Oncorhynchus kisutch*) off Oregon and Washington reveals few Columbia River wild fish. U.S. National Marine Fisheries Service Fishery Bulletin 101:640–652.

Trudel, M., D. W. Welch, J. F. T. Morris, J. R. Candy, and T. D. Beacham. 2004. Using genetic markers to understand the coastal migration of juvenile coho (*Oncorhynchus kisutch*) and Chinook salmon (*O. tshawytscha*). North Pacific Anadromous Fish Commission Bulletin 5:52–54.

Waples, R. S. 1990. Temporal changes of allele frequencies in Pacific salmon: implications for mixed-stock fishery analysis. Canadian Journal of Fisheries and Aquatic Sciences 47:968–976.

WDFW (Washington Department of Fish and Wildlife). 2006. Adult coho salmon returns to Washington coast hatcheries. Washington Department of Fish and Wildlife,

Olympia. Available: http://wdfw.wa.gov/hat/escape/ escape.htm.12

Weitkamp, L., and K. Neely. 2002. Coho salmon (*Oncorhynchus kisutch*) ocean migration patterns: insight from marine coded-wire tag recoveries. Canadian Journal of Fisheries and Aquatic Sciences 59:1100–1115.

Weitkamp, L. A., T. C. Wainwright, G. J. Bryant, G. B. Milner, D. J. Teel, R. G. Kope, and R. S. Waples. 1995. Status review of coho salmon from Washington, Oregon, and California. NOAA Technical Memorandum NMFS-NWFSC-24.

Williamson, K. S., J. F. Cordes, and B. May. 2002. Characterization of microsatellite loci in Chinook salmon (*Oncorhynchus tshawytscha*) and cross-species amplification in other salmonids. Molecular Ecology Notes 2:17–19.

Withler, R. E., J. R. Candy, T. D. Beacham, and K. M. Miller. 2004. Forensic DNA analysis of Pacific salmonid samples for species and stock identification. Environmental Biology of Fishes 69:275–285.