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ARTICLE

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Abstract

Identification of population-specific run timing is an important component of salmonid fisheries management and was a major focus of our study. Population structure of steelhead *Oncorhynchus mykiss* was examined in the Skeena River of northern British Columbia. Variation at 14 microsatellites was surveyed in 3,062 steelhead sampled from 17 populations in the drainage. During 1998–2010, 6,691 individuals were sampled in a lower river test fishery to obtain information on relative abundance and time of arrival of specific populations near the river mouth. The genetic differentiation index F_{ST} calculated over all populations and loci was 0.021; individual locus values ranged from 0.017 to 0.045. Differentiation in steelhead allele frequencies among populations was approximately 14 times the differentiation observed among years within populations. A regional structuring of populations was the general pattern observed, with steelhead populations from the upper portion of the drainage clustering together in 87% of dendrograms evaluated and those in the lower portion of the drainage clustering together in 100% of dendrograms. The 17 populations sampled were arranged in nine reporting groups for genetic stock identification applications. The estimated stock composition of a simulated known-origin mixture was within 2% of the correct estimate for seven of the nine reporting groups present in the mixture. The stock composition of an actual known-origin sample was estimated within 2% of the correct estimate for eight of the nine reporting groups present. Application to actual samples from the test fishery indicated that upper drainage populations generally migrated through the lower river earlier than other populations, whereas lower river populations typically migrated later. Genetic mixed-stock analysis can assist managers in regulating fisheries to maintain productivity of Skeena River steelhead.

Conservation of genetic diversity has proven to be an important objective in the management of many Pacific salmon species. Determination of population structure within a species is a major step in identifying management units or conservation units needed to manage fisheries and conserve genetic diversity of exploited species. A common and effective method to determine population structure and subsequent conservation units is through the analysis of genetic variation.

Steelhead *Oncorhynchus mykiss* (anadromous rainbow trout) are found in all major coastal river systems in British Columbia. In the Skeena River, summer-run steelhead enter the drainage between June and October, mature in the river (often overwintering in lakes, deep canyon locations, or main-stem locations), and spawn in mid-May to late June. Winter-run fish enter the river between late October and mid-May and spawn subsequently in May and June. In the Skeena River watershed, steelhead undergo smoltification between ages 1 and 6, spend 1–4 years at sea, and may repeat spawn as many as four times (Chudyk 1976; M. Beere, personal observation). In general, tributary streams upstream of the Zymoetz River (Figure 1) have only summer-run

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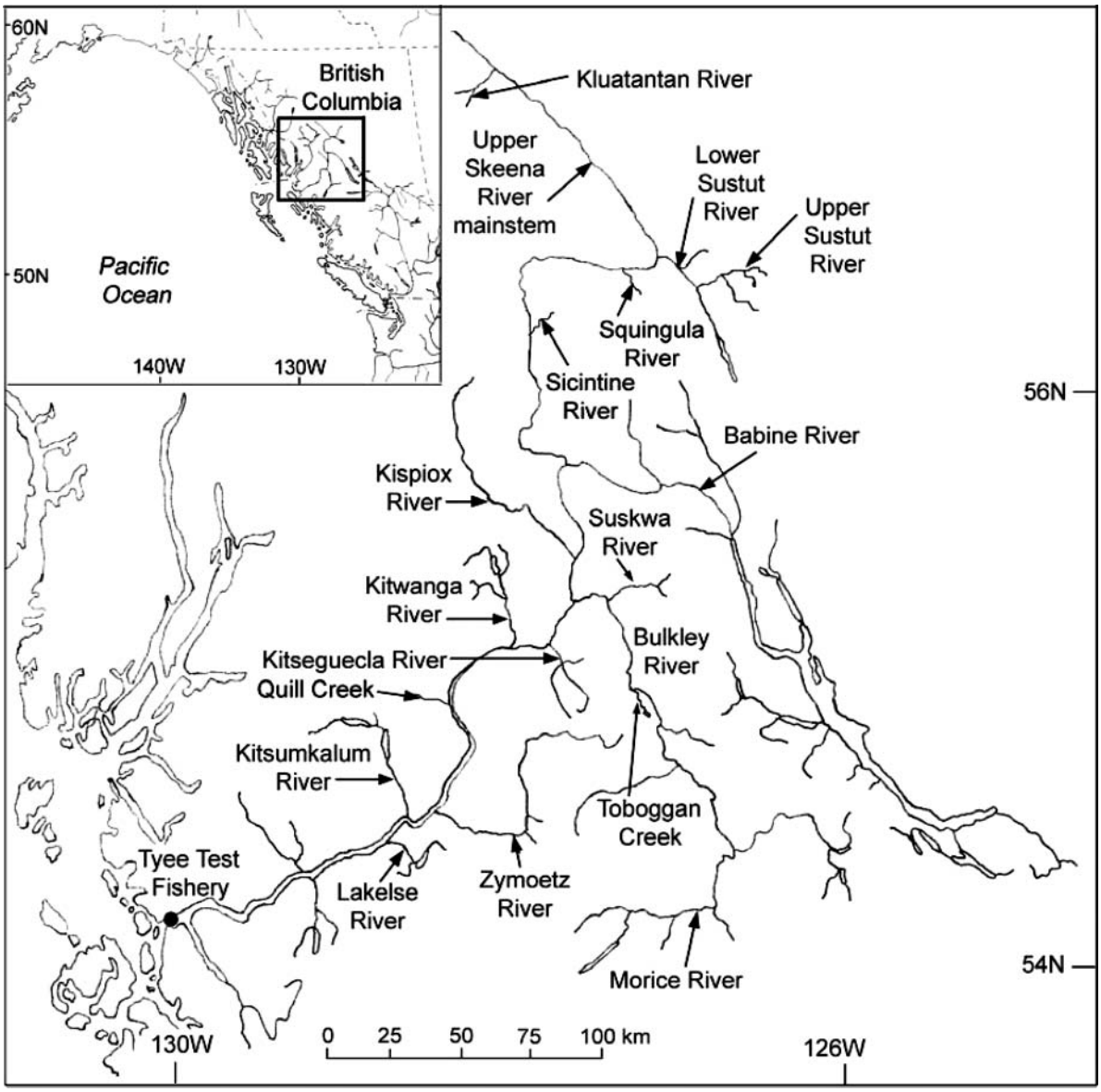

FIGURE 1. Locations of the 17 steelhead populations in the Skeena River drainage, British Columbia, that were sampled and subsequently analyzed for population structure and run timing. The Tyee test fishery location at the mouth of the river is also indicated.

populations, whereas those downstream may have summer-run and winter-run populations.

Steelhead abundance has become of increasing concern to fisheries managers because the status of many populations in British Columbia may require increased emphasis on conservation (Slaney et al. 1996). In the Skeena River, a mixed-stock salmon fishery is directed at sockeye salmon *O. nerka* and pink salmon *O. gorbuscha*, and summer-run steelhead are harvested as bycatch because they overlap in their migration timing to a significant degree with the sockeye salmon. This complicates management of the sockeye salmon-directed fishery (Sprout and Kadowaki 1987). Management of the Skeena River fishery is complex because it involves federal and provincial agencies as well as several user groups (Hilborn and Walters 1977). Sprout and Kadowaki (1987), by using simplified run-timing curves, indicated that a number of populations would probably be harvested in the fishery; however, the harvest rates of individual populations were unknown because there were few techniques available in the 1980s to identify individual populations. Improvement in identifying specific populations and their relative timing through the lower river fishery would aid considerably in management of the fishery. Currently, the management focus is to ensure the continued viability and productivity of existing populations and, after conservation requirements for specific populations have been obtained, to allow for limited exploitation of target populations, either through the recreational fishery

or aboriginal harvest. At present, First Nations harvests occur throughout the watershed because conservation concerns have not been expressed for the majority of populations in recent years. Steelhead retention is not permitted in the recreational fishery, although it is assumed that some low degree of incidental mortality occurs.

Determination of population structure of exploited species typically incorporates results from surveys of genetic variation. In British Columbia, surveys of genetic variation have been used to describe population structure in steelhead (Parkinson 1984; Taylor 1995; Beacham et al. 1999, 2000, 2004; Heath et al. 2001, 2008; Hendry et al. 2002). Microsatellite variation was initially examined among steelhead populations in the Skeena River to resolve population structure (Beacham et al. 2000). Additional microsatellites beyond those reported by Beacham et al. (2000, 2004) have been subsequently surveyed, and the baseline used to identify specific populations has been considerably enhanced. The ability to identify specific populations in mixed-stock fisheries may be possible, enabling the identification of the relative timing of specific populations through the lower Skeena River. Information on steelhead timing and abundance is of interest to both federal and provincial agencies as well as recreational fishery and environmental organizations.

An important requirement in genetic stock identification of mixed-stock fishery samples is the accuracy of the estimated stock composition to the smallest practical unit. In mixed-stock salmon fisheries, managers frequently request high-resolution estimates of stock composition, which in many cases may require identification of salmon spawning in specific rivers. This capability is possible in many applications for species with a high degree of genetic differentiation among populations, such as sockeye salmon (Beacham et al. 2011a), but as the level of genetic differentiation among populations decreases, reliable population-specific estimates of stock composition may not be available. In these instances, populations with limited genetic differentiation are typically pooled together in a reporting region or group. It may be possible subsequently to refine estimates within a specific reporting group as baseline sample size is increased (Beacham et al. 2011b) or as additional genetic markers are incorporated into the estimation procedure. Accuracy of estimated stock compositions in a management application can thus improve as the baselines and suites of genetic markers employed in estimating stock composition are enhanced.

In this study, we evaluated the population structure of steelhead in the Skeena River by surveying variation at 14 microsatellites, and we assessed the utility of the microsatellites for steelhead stock identification applications in the Skeena River drainage. This assessment was conducted by examining the accuracy and precision of estimated stock compositions via analysis of simulated mixtures and estimation of stock composition of samples collected during 10 years of sampling from a test fishery in the lower river; the mixtures were resolved using a 17-population baseline incorporating populations throughout the Skeena River drainage.

METHODS

Collection of DNA samples and laboratory analysis.—Fishery samples of returning adults in the Skeena River were collected from a gill-net test fishery (Jantz et al. 1990), which has been conducted annually since 1955 at Tyee in the tidal portion of the Skeena River. The test fishery has provided a relative index of abundance in-season for all species migrating past the fishery. Until 2002, a 365-m (1,200-ft), fibrous nylon gill net of varying mesh sizes was deployed daily during slackwater tidal periods. The net was set perpendicular to the water flow and was usually left drifting for 1 h before being retrieved. In 2002, the gill net was replaced by a monofilament net that could intercept salmon swimming at greater depths. Five years of data from both nets were used to standardize catch per unit effort (CPUE) between the sampling gears. The CPUE was obtained by multiplying the total fishing time by the surface area of the net to provide an index of abundance (expressed in terms of catch per unit surface area per hour).

Tissue samples from the baseline populations (see Waples and Gaggiotti 2006) were collected from mature steelhead and, in some instances, from juveniles. The main methods of sampling included electrofishing of juveniles and angling of adults, although enumeration fences (weirs) were used at some locations in some years. Populations, year of sampling, and number of fish analyzed in the baseline populations are outlined in Table 1. Further sampling details were outlined by Beacham et al. (1999, 2000). Samples were preserved in 95% ethanol and sent to the Molecular Genetics Laboratory at the Pacific Biological Station, where DNA was extracted from the tissue samples using one of a variety of methods, including a chelex resin protocol outlined by Small et al. (1998), a Qiagen 96-well Dneasy procedure, or a Promega Wizard SV96 Genomic DNA Purification System. Once the extracted DNA was available, variation was surveyed at 14 microsatellite loci: *Ogo4* (Olsen et al. 1998); *Oke4* (Buchholz et al. 2001); *Omm1008* and *Omm1037* (Rexroad et al. 2002); *Omm1276* (Rexroad and Palti 2003); *Omm5140* (Coulibaly et al. 2005); *Ots1*, *Ots2*, and *Ots9* (Banks et al. 1999); *Oki10* (Smith et al. 1998); *One111* and *One114* (Olsen et al. 2000); *Omy325* (O'Connell et al. 1997); and *Ssa408* (Cairney et al. 2000). Four of these loci (*Omm1008, Omm1037, Omm1276*, and *Omm5140*) had not been included in previous surveys of variation in Skeena River steelhead.

In general, polymerase chain reaction (PCR) DNA amplifications were conducted using a DNA Engine Cycler Tetrad2 (BioRad, Hercules, California) in 6-μL volumes consisting of 0.15 units of *Taq* polymerase, 1 μL of extracted DNA, 1 × PCR buffer (Qiagen, Mississauga, Ontario), 60 μM of each nucleotide, 0.40 μM of each fluorescently labeled primer, and deionized H_2O. The thermal cycling profile involved one cycle of 15 min at 95°C, followed by 30–40 cycles of 20 s at 94°C, 30–60 s at 47–65°C, and 30–60 s at 68–72°C (depending on the locus). Microsatellites were size fractionated in an ABI 3730 capillary DNA sequencer, and genotypes were scored

TABLE 1. Collection years (sample sizes in parentheses) for 17 steelhead populations in the Skeena River drainage of British Columbia. Asterisks denote years in which juveniles were sampled.

Stock reporting group	Population	Years of sampling (sample size)	Total sample size
Upper Skeena River	Lower Sustut River	1997 (13), 2003 (59), 2005* (76)	148
	Upper Skeena River main stem	2005* (143), 2010* (118)	261
	Kluatantan River	2005* (74)	74
	Squingula River	2010* (118)	118
	Sicintine River	2010* (84)	84
Sustut River	Sustut River	1992 (13), 1994 (48), 1996 (50), 1997 (71), 1998 (50), 1999 (92), 2000 (100), 2001 (100)	524
Babine River	Babine River	1991 (19), 1992 (18), 1995 (36), 1996 (31), 1997 (28), 1998 (126)	258
Morice River	Morice River	1991 (20), 1992 (41), 1995 (22), 1996 (36), 1997 (20), 1998 (46), 2003 (65), 2004 (75)	325
Middle Skeena River	Toboggan Creek	1998 (128)	128
	Quill Creek	2010* (42)	42
	Kispiox River	1992 (20), 1995 (30), 1998 (35), 2003 (46)	131
	Kitwanga River	2001 (140)	140
Suskwa River	Suskwa River	2009* (206)	206
Kitseguecla River	Kitseguecla River	1998 (13), 2005* (235)	248
Lower Skeena River	Kitsumkalum River	2004 (145), 2005 (41)	186
	Lakelse River	2004 (78)	78
Zymoetz River	Zymoetz River	1993 (16), 1995 (18), 1997 (38), 1999 (39)	111

by GeneMapper version 3.0 (Applied Biosystems, Foster City, California) using an internal lane sizing standard.

Data analysis.—All annual samples available for a location were combined to estimate population allele frequencies, as was recommended by Waples (1990). Each population at each locus was tested for departure from Hardy–Weinberg equilibrium using Genetic Data Analysis (GDA; Lewis and Zaykin 2001). Critical significance levels for simultaneous tests were evaluated by using the Bonferroni adjustment ($\alpha = 0.05/17 = 0.0029$; Rice 1989). Weir and Cockerham's (1984) genetic differentiation index F_{ST} was calculated for each locus over all populations by use of FSTAT version 2.9.3.2 (Goudet 1995). The significance of the multilocus F_{ST} value over all samples was determined by jackknifing over loci. The Cavalli-Sforza and Edwards (CSE) chord distance (Cavalli-Sforza and Edwards 1967) was used to estimate genetic distances among all populations.

An unrooted neighbor-joining tree based upon CSE chord distance was generated using NJPLOT (Perriere and Gouy 1996). Bootstrap support for the major nodes in the tree was evaluated based upon 500 replicate trees with the CONSENSE program in PHYLIP software (Felsenstein 1993). Computation of the number of alleles observed per locus was carried out with GDA. Allele frequencies for all location samples surveyed in this study are available at the Molecular Genetics Laboratory website (www.pac.dfo-mpo.gc.ca/science/facilities-installations/pbs-sbp/mgl-lgm/data-donnees/index-eng.htm).

The distribution of genetic variation in steelhead populations within the Skeena River drainage was evaluated with a hierarchical gene diversity analysis for the following groups: (1) among populations within the drainage and (2) among sampling years within populations. The analysis was conducted with GDA. To maintain a balanced design, we required populations included in the analysis to be represented by two or more years of samples. To reduce sampling error in estimating allele frequencies, years within populations included in the analysis were restricted to those in which at least 40 individuals had been sampled. Populations (and years of sampling) included in the analysis were Kitsumkalum River (2003 and 2005), Morice River (1992, 1998, 2003, and 2004), Lower Sustut River (2003 and 2005), Sustut River (1994 and 1996–2001), and upper Skeena River main stem (2005 and 2010). Negative variance components were set to zero in the hierarchical gene diversity analysis.

Estimation of stock composition.—We used ONCOR (Kalinowski et al. 2007) to estimate stock composition of simulated single-population samples. All loci were considered to be in Hardy–Weinberg equilibrium, and expected genotypic frequencies were determined from the observed allele frequencies at each locus. The Rannala and Mountain (1997) correction to baseline allele frequencies was implemented, and precision of the stock compositions was calculated by bootstrapping (100 simulations) over observed baseline population sample sizes and a mixture size of 100 fish. Each of the 17 populations sampled was tested individually, and a target of 90% accuracy was

required for remaining as a separate reporting group (similar to the procedure outlined by Seeb and Crane 1999). If the target of 90% accuracy was not achieved, then the previously outlined cluster analysis of CSE chord distance values between populations was used to select potential aggregates of populations (reporting group) to achieve the 90% accuracy target. These reporting groups were enlarged until the approximately 90% accuracy target was achieved in the simulations.

Analysis of fishery samples was conducted with a Bayesian procedure (BAYES) as outlined by Pella and Masuda (2001). A new version of BAYES was developed as a C-based program (cBAYES; Neaves et al. 2005). In the analysis, eight Monte Carlo Markov chains (20,000 iterations/chain) of estimated stock compositions were produced, with initial starting values for each chain set at 0.90 for a particular population, which was different for each chain. Estimated stock compositions were considered to have converged when the shrink factor was less than 1.2 for the eight chains (Pella and Masuda 2001). The last 1,000 iterations from each of the eight chains were then combined, and for each fish the probability of originating from each population in the baseline was determined. These individual probabilities were summed over all fish in the sample and divided by the number of fish sampled to provide the point estimate of stock composition. Standard deviations of estimated stock compositions were determined from the last 1,000 iterations from each of the eight chains incorporated in the analysis. A simulated sample of 100 known-origin fish from multiple populations and multiple reporting groups was developed to evaluate accuracy of estimated stock compositions and was analyzed with cBAYES. An actual mixture sample of 100 known-origin fish was also developed for analysis. In this case, the mixture sample was created by removing a known number of fish from selected populations, and the baseline allele frequencies for each population in the baseline were recalculated by excluding the fish that had been selected for the mixture sample.

Migration timing.—All 6,691 steelhead caught during the 1998, 2000, 2001, and 2003–2010 test fisheries were sampled and analyzed for microsatellite variation. Within each year, samples were stratified into 13 periods: June 1–15 and 16–30; July 1–14, 15–21, and 22–28; July 29–August 4; August 5–11, 12–18, and 19–25; August 26–September 1; and September 2–8, 9–15, and 16–30. The period CPUE index was determined (sum of daily CPUEs within the period) and was then multiplied by the estimated period stock proportions and apportioned to the nine reporting groups outlined in Table 1. Stock-specific period CPUEs were then averaged over the 11 years of operation of the test fishery, and the results were summarized to provide an estimate of relative timing and abundance by reporting group.

Median day of migration through the test fishery for each reporting group was determined by pooling all fish sampled in the 11 years of sampling into a single sample, and individuals were allocated to a specific reporting group based upon individual assignment probability. Individuals were assigned to a specific population, which was estimated to have the highest probability of correct assignment. The assigned reporting group and day of capture in the test fishery were determined for each individual, and the total number of individuals assigned to each reporting group was determined. For each reporting group, the number of individuals sampled in each day was collated, and the median day of migration through the test fishery was determined as the day at which 50% of the total number of individuals sampled in the reporting group was attained; the number of fish identified for each reporting group was summed cumulatively for each successive day of test fishery operation.

RESULTS

Variation Within and Among Populations

Variation was observed in the number of alleles at the 14 microsatellite loci surveyed in the study. The fewest number of alleles was observed at *Omm5140* (9 alleles), and the greatest number of alleles observed at *Omy325* (31 alleles; Table 2). Lower heterozygosity was observed at those loci with fewer alleles. Observed and expected heterozygosities were in close agreement for the loci surveyed. Genotypic frequencies of the loci surveyed typically conformed to those expected under Hardy–Weinberg equilibrium. One significant test over the 17 populations was observed for each of the following loci: *Ogo4*, *Oke4*, *One111*, *One114*, *Oki10*, *Ots2*, *Omm1037*, and *Omm1276*.

Hierarchical gene diversity analysis of the 14 loci surveyed was used to evaluate the distribution of genetic variation among populations and among sampling years within populations. The amount of variation within populations ranged from 91.5% (*Oke4*) to 98.9% (*Omm5140*), the average for an individual locus being 97.1% (Table 3). Variation among populations within

TABLE 2. Number of alleles observed, expected heterozygosity (H_e), observed heterozygosity (H_o), and genetic differentiation index (F_{ST}; SD in parentheses) based on 14 microsatellite loci examined in steelhead from 17 Skeena River populations.

Locus	Alleles	H_e	H_o	F_{ST}
Omm5140	9	0.80	0.80	0.021 (0.005)
Oke4	14	0.75	0.73	0.045 (0.018)
One111	16	0.72	0.72	0.025 (0.009)
Ots9	18	0.75	0.76	0.016 (0.003)
Ogo4	19	0.69	0.69	0.012 (0.003)
Omm1276	19	0.81	0.80	0.018 (0.004)
Omm1008	20	0.84	0.85	0.013 (0.003)
Ssa408	21	0.88	0.88	0.025 (0.008)
Ots1	22	0.60	0.60	0.020 (0.006)
Oki10	23	0.72	0.69	0.031 (0.010)
Ots2	28	0.84	0.83	0.017 (0.005)
Omm1037	28	0.91	0.89	0.022 (0.006)
One114	30	0.89	0.88	0.017 (0.005)
Omy325	31	0.72	0.70	0.022 (0.006)
All loci				0.021 (0.002)

TABLE 3. Hierarchical gene diversity analysis based on 14 microsatellite loci from steelhead belonging to five populations within the Skeena River drainage. The analysis was performed with Genetic Data Analysis software (Lewis and Zaykin 2001). The time difference between the earliest and latest samples included for specific populations ranged from 1 to 12 years. Significant ($P < 0.01$) values for a given locus are shown in bold italics.

Locus	Within populations	Among years within populations	Among populations within drainage
Ogo4	0.9887	0.0000	***0.0113***
Oke4	0.9153	0.0032	***0.0815***
Oki10	0.9672	0.0041	***0.0287***
Omm1008	0.9796	0.0057	***0.0147***
Omm1037	0.9707	0.0051	***0.0242***
Omm1276	0.9806	0.0002	***0.0192***
Omm5140	0.9888	0.0000	***0.0112***
Omy325	0.9663	0.0017	***0.0320***
One111	0.9621	0.0000	***0.0379***
One114	0.9735	0.0015	***0.0250***
Ots1	0.9712	0.0012	***0.0276***
Ots2	0.9767	0.0024	***0.0209***
Ots9	0.9810	0.0005	***0.0185***
Ssa408	0.9700	0.0015	***0.0285***
Total	0.9710	0.0019	***0.0271***

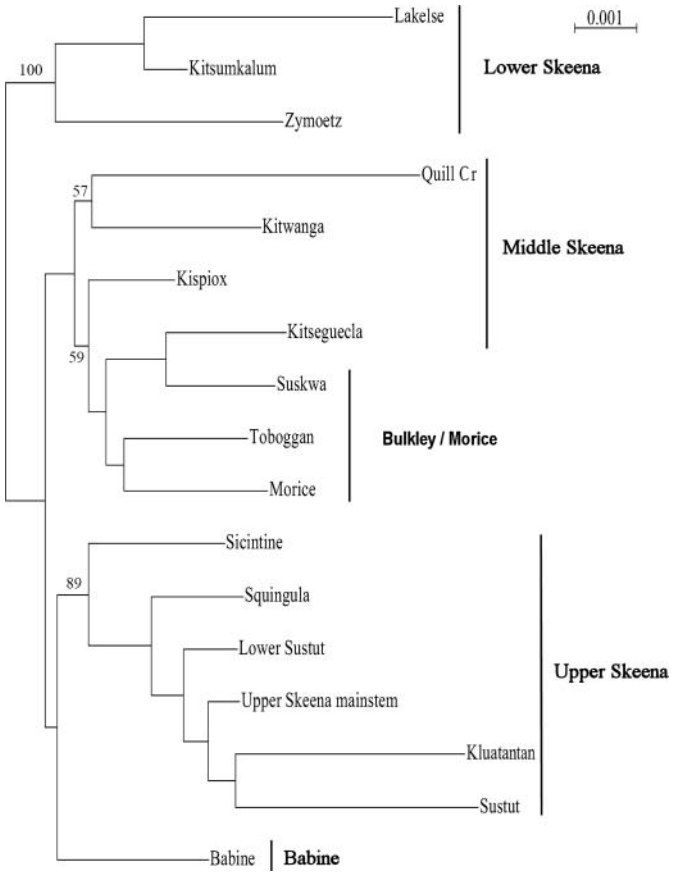

FIGURE 2. Unrooted neighbor-joining dendrogram outlining population structure of 17 Skeena River steelhead populations (listed in Table 1).

the Skeena River drainage accounted for 2.7% of observed variation. The variation among sampling years within populations was the smallest source of variation observed, accounting for 0.2% of all variation. Differentiation among populations within the drainage was approximately 14 times the differentiation observed among years within populations. For the time intervals surveyed in our study, annual variation in microsatellite allele frequencies was relatively minor compared with differences among populations within the Skeena River drainage.

Population Structure

There was genetic differentiation among the 17 steelhead populations sampled in the Skeena River drainage. The F_{ST} value calculated over all populations and loci was 0.021, with individual locus values ranging from 0.012 (*Ogo4*) to 0.045 (*Oke4*; Table 2). The most distinctive population sampled originated from the Sustut River in the upper portion of the Skeena River drainage (mean pairwise F_{ST} value = 0.032; Table 4). The next most distinctive population was the Zymoetz River population ($F_{ST} = 0.029$) in the lower portion of the drainage, followed by the Kluatantan River population ($F_{ST} = 0.025$) in the upper drainage. The lowest mean F_{ST} value (0.012) was observed for the Sicintine River population in the upper drainage, followed by the Squingula River population ($F_{ST} = 0.013$) and the Lower Sustut River ($F_{ST} = 0.014$), both in the upper drainage.

A geographically based structuring of populations within the Skeena River drainage was the general pattern observed in our survey. The six steelhead populations spawning in the upper portion of the drainage clustered together in 89% of dendrograms evaluated, indicative that these populations were more similar to each other than to populations in other areas of the drainage (Figure 2). The population from the Babine River, located downstream of the six upper drainage populations, was more similar to those six populations than to populations further downstream. The Morice River and middle drainage populations clustered as a single group. The three steelhead populations spawning in the lower portion of the drainage clustered together in 100% of dendrograms evaluated (Figure 2).

Accuracy of Estimated Stock Compositions

Analysis of simulated single-population samples indicated that reasonably accurate (>90% average) estimates of population-specific composition would be achieved for 8 of the 17 populations surveyed in the study (Table 5). Using the populations arranged by the nine reporting groups outlined in Table 1, accurate estimates of reporting group composition were generally achieved across populations. Aside from the Sustut River population, all upper drainage populations were combined into a single reporting group, which considerably improved the accuracy of estimated stock compositions. Four middle

TABLE 4. Pairwise genetic differentiation index (F_{ST}) values averaged over 14 microsatellite loci from steelhead in 17 Skeena River drainage populations (population codes [PCs]: 1 = Babine River, 2 = Kispiox River, 3 = Kitseguecla River, 4 = Kitsumkalum River, 5 = Kitwanga River, 6 = Kluatantan River, 7 = Lower Sustut River, 8 = Lakelse River, 9 = Morice River, 10 = Quill Creek, 11 = Sicintine River, 12 = Squingula River, 13 = Suskwa River, 14 = Sustut River, 15 = Toboggan Creek, 16 = upper Skeena River main stem, 17 = Zymoetz River).

PC	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
2	0.0110															
3	0.0128	0.0103														
4	0.0138	0.0108	0.0204													
5	0.0180	0.0107	0.0146	0.0190												
6	0.0251	0.0308	0.0256	0.0256	0.0372											
7	0.0135	0.0114	0.0176	0.0136	0.0185	0.0115										
8	0.0219	0.0213	0.0256	0.0098	0.0221	0.0320	0.0220									
9	0.0133	0.0075	0.0143	0.0167	0.0167	0.0303	0.0166	0.0227								
10	0.0140	0.0127	0.0231	0.0140	0.0183	0.0356	0.0211	0.0236	0.0173							
11	0.0086	0.0072	0.0105	0.0113	0.0130	0.0159	0.0034	0.0180	0.0108	0.0170						
12	0.0132	0.0093	0.0153	0.0117	0.0157	0.0114	0.0021	0.0210	0.0153	0.0199	0.0037					
13	0.0148	0.0079	0.0079	0.0166	0.0172	0.0256	0.0143	0.0252	0.0121	0.0205	0.0102	0.0127				
14	0.0352	0.0341	0.0418	0.0306	0.0371	0.0217	0.0116	0.0369	0.0414	0.0393	0.0203	0.0159	0.0373			
15	0.0148	0.0042	0.0105	0.0159	0.0150	0.0328	0.0138	0.0220	0.0078	0.0205	0.0087	0.0132	0.0090	0.0388		
16	0.0149	0.0118	0.0178	0.0139	0.0190	0.0103	0.0027	0.0237	0.0159	0.0223	0.0058	0.0023	0.0156	0.0163	0.0145	
17	0.0295	0.0265	0.0314	0.0205	0.0289	0.0360	0.0289	0.0208	0.0298	0.0360	0.0220	0.0216	0.0282	0.0458	0.0278	0.0272

TABLE 5. Mean (SD in parentheses) estimates of percentage composition for single-population samples (correct = 100%) from Skeena River steelhead populations. The reporting group designation includes the sum of percentage allocations to all populations in the group as outlined in Table 1.

Stock reporting group	Population	Population percentage	Reporting group percentage
Upper Skeena River	Lower Sustut River	64.4 (5.7)	94.1 (3.1)
	Upper Skeena River main stem	82.3 (3.9)	98.0 (1.5)
	Kluatantan River	77.1 (4.1)	99.1 (0.9)
	Squingula River	60.7 (5.0)	93.7 (2.5)
	Sicintine River	54.8 (4.8)	84.7 (3.8)
Sustut River	Sustut River	98.8 (1.0)	98.8 (1.0)
Babine River	Babine River	95.2 (2.0)	95.2 (2.0)
Morice River	Morice River	96.0 (2.1)	96.0 (2.1)
Middle Skeena River	Toboggan Creek	80.5 (4.3)	90.0 (3.4)
	Quill Creek	58.7 (4.8)	81.0 (4.2)
	Kispiox River	69.4 (4.9)	82.3 (4.4)
	Kitwanga River	92.6 (2.8)	96.7 (1.9)
Suskwa River	Suskwa River	92.2 (3.2)	92.2 (3.2)
Kitseguecla River	Kitseguecla River	95.0 (2.5)	95.0 (2.5)
Lower Skeena River	Kitsumkalum River	90.4 (2.9)	94.2 (2.4)
	Lakelse River	80.4 (3.4)	98.4 (1.1)
	Zymoetz River	92.6 (2.4)	92.6 (2.4)

drainage populations were combined into a reporting group; the Morice River, Suskwa River, and Kitseguecla River populations were retained as distinct populations. Two reporting groups were retained for the three lower river populations; the Lakelse River population did not display sufficient resolution from the Kitsumkalum River population at the current level of baseline development.

Accuracy and precision of estimated stock composition were evaluated for a multipopulation, multireporting group simulated mixture of steelhead as may be encountered in Skeena River mixed-stock fishery sampling. The estimated stock composition of the mixture was within 2 percentage points of the correct percentage for seven of the nine reporting groups present in the mixture (Table 6). In addition, analysis of an actual known-origin sample indicated that estimated stock compositions were within 2 percentage points of actual percentages for eight of the nine reporting groups (Table 6). Analysis of the single-population and multipopulation mixtures indicated that reliable estimates of stock composition by reporting group should be provided by the 14 microsatellites we evaluated.

Population-Specific Run Timing

Steelhead typically arrive at the lower river test fishery in late June, peaking in daily abundance in late July or early August (Figure 3). The large majority of returning summer-run steelhead pass through the lower river from late July to the beginning of September, with virtually all of the run migrating through the lower river by late September or early October. The earliest returning population originates from the Sustut River in the upper portion of the drainage, and peak abundance typically was observed around July 24 (Figure 4); the median date of migration

TABLE 6. Mean (SD in parentheses) estimates of percentage stock composition for a simulated mixture of 100 steelhead and a known-origin mixture of 100 individuals as may be encountered in the Skeena River. Expected reporting group composition is the sum of allocations to individual populations in the reporting group as outlined in Table 1. The known-origin sample was developed by randomly removing individual fish from selected populations, re-estimating allele frequencies for all populations in the baseline, and then using this modified baseline to estimate stock composition in the sample of known origin.

	Simulated mixture			Known-origin mixture		
Population	True	Population	Reporting group	True	Population	Reporting group
Sustut River	10	10.8 (3.3)	10.8 (3.3)	15	16.7 (3.9)	16.7 (3.9)
Lower Sustut River	10	10.9 (3.4)	13.7 (4.8)	10	2.5 (2.3)	6.5 (3.7)
Babine River	25	23.8 (5.0)	23.8 (5.0)	20	18.8 (4.6)	18.8 (4.6)
Morice River	20	16.2 (4.5)	16.2 (4.5)	20	20.1 (5.0)	20.1 (5.0)
Kitseguecla River	5	4.3 (3.2)	4.3 (3.2)	5	5.4 (3.5)	5.4 (3.5)
Toboggan Creek	5	4.8 (3.6)	5.9 (3.6)	5	6.4 (3.6)	6.4 (3.6)
Suskwa River	5	4.2 (2.7)	4.2 (2.7)	5	5.0 (3.2)	5.0 (3.2)
Kitsumkalum River	10	6.5 (3.3)	11.1 (4.1)	10	7.4 (3.5)	10.7 (3.9)
Zymoetz River	10	10.0 (3.5)	10.0 (3.5)	10	10.0 (3.4)	10.0 (3.4)

for the Sustut River population was July 28 (Figure 5). The Sustut River population accounted for an average of 5% of the run during 1998–2010 (Table 7). Other upper drainage populations were typically earlier in migration timing than those in the middle and lower portions of the drainage, peaking in abundance during the first week of August. Median date of migration for upper drainage populations was August 6, and they accounted for an average of about 16% of total returns. All populations from the upper portion of the drainage accounted for 21% of the steelhead returns to the Skeena River.

The Babine River population is geographically located between populations in the upper and middle portions of the drainage. The peak of abundance for this population typically occurred in the lower river test fishery around August 14, and

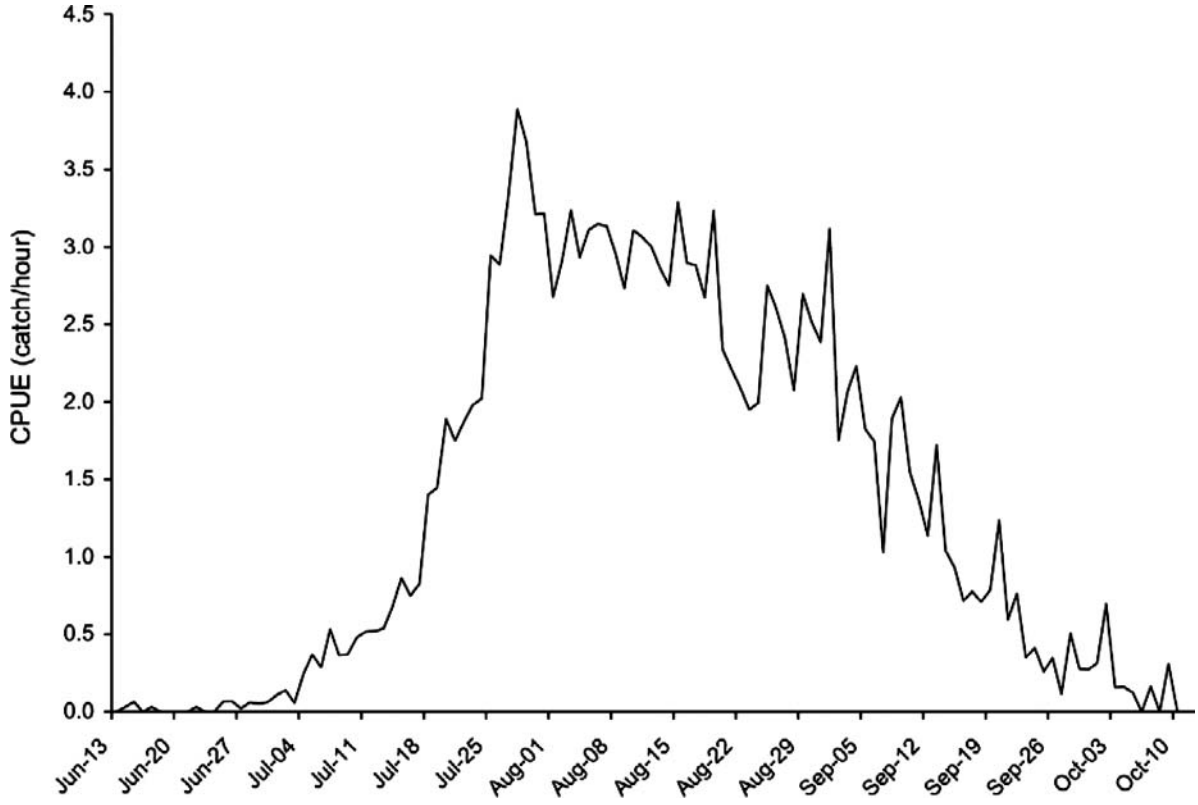

FIGURE 3. Average daily catch per unit effort (CPUE; catch/h) of Skeena River steelhead in the Tyee test fishery at the Skeena River mouth, 1998–2010.

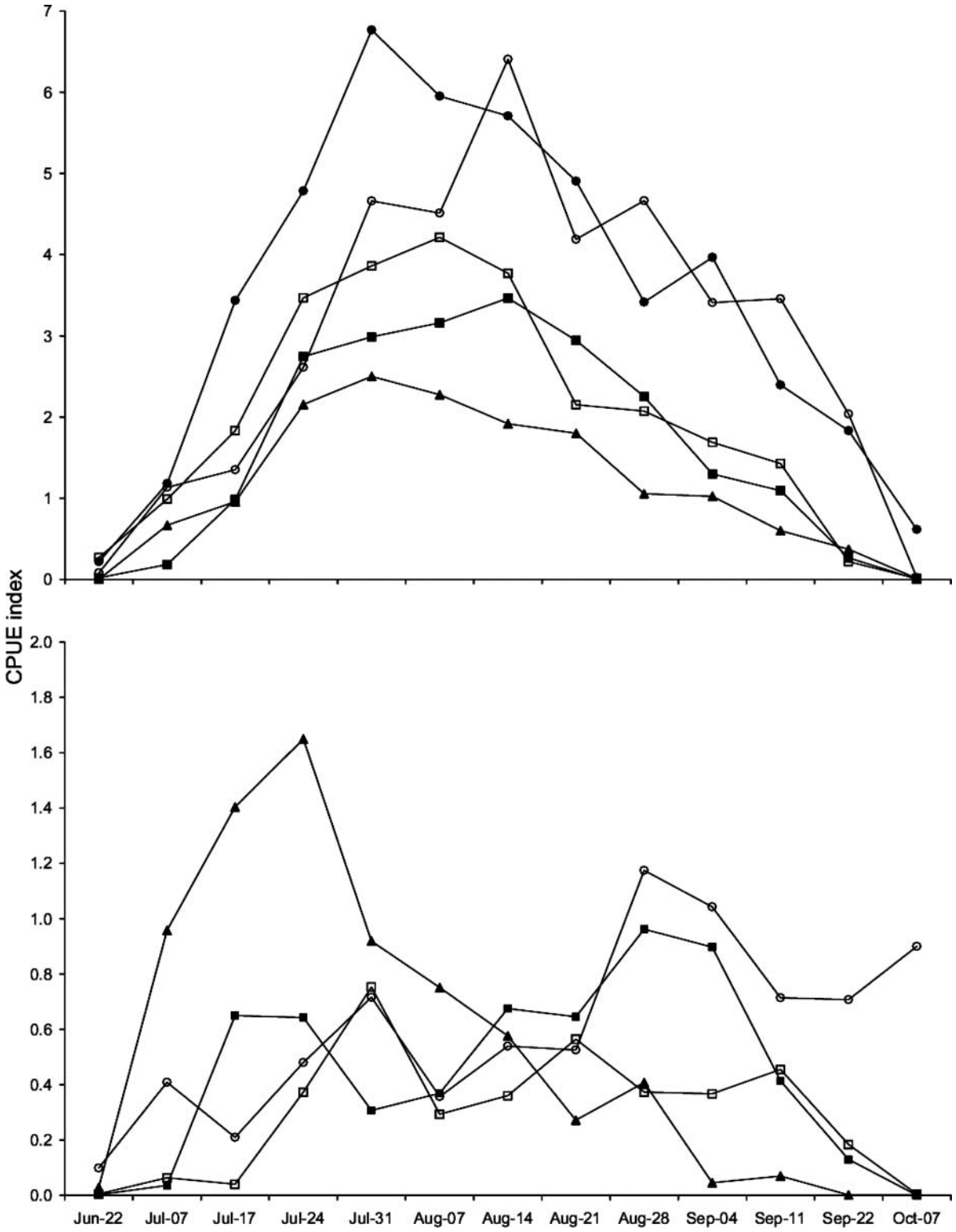

FIGURE 4. Total average weekly index of steelhead abundance (catch per unit effort [CPUE]; catch/h) by reporting group (see Table 1) based upon returns to the lower Skeena River test fishery, 1998–2010: **(A)** the more abundant groups were Babine River (filled squares), Zymoetz River (filled triangles), upper Skeena River (open squares), middle Skeena River (open circles), and Morice River (filled squares); **(B)** the less-abundant groups were Kitseguecla River (filled squares), Sustut River (filled triangles), Suskwa River (open squares), and lower Skeena River (open circles). Biweekly intervals are used at the beginning and end of the season, and the remaining intervals are weekly. Dates plotted along the *x*-axis are midpoints of the intervals.

TABLE 7. Estimated percent stock composition (SD in parentheses) of Skeena River steelhead obtained from a lower river test fishery during 1998–2010; stock composition was estimated with a 17-population baseline incorporating variation at 14 microsatellites. All 6,691 steelhead caught in the test fishery were sampled and analyzed.

Reporting group	Estimated stock composition (%)
Upper Skeena River	15.6 (0.9)
Sustut River	4.9 (0.4)
Babine River	14.1 (0.8)
Morice River	25.4 (0.9)
Middle Skeena River	22.0 (1.3)
Suskwa River	2.4 (0.5)
Kitseguecla River	3.2 (0.5)
Lower Skeena River	4.4 (0.4)
Zymoetz River	8.0 (0.4)

the median date of passage was August 8. This population constituted about 14% of the returns during 1998–2010.

Several populations were present in the Morice River and the central portion of the Skeena River drainage. The Morice River population was estimated as the single largest contributor to drainage returns, accounting for 25% of all returning steelhead during 1998–2010. Peak abundance of the population was estimated to occur near July 31, and the median date of passage was August 7. Peak abundance of populations in the middle Skeena River reporting group was estimated to occur about 2 weeks later (August 14) than that of the Morice River population, and this group of populations contributed 22% of returns during the study period. For the Suskwa River population, which spawns in a tributary of the Morice River, peak migration timing through the lower river test fishery (July 31) was estimated to be similar to that of the Morice River population. The Suskwa River population, however, contributed substantially less to overall returns (2%) than the Morice River population. The Kitseguecla River population, spawning in a tributary of the Skeena River, displayed a later peak week of abundance (August 28; Figure 4) than did other populations from the general middle portion of the drainage. It was estimated to have contributed only about 3% of returns during the study period.

Three populations were surveyed in the general lower portion of the drainage. The most distinctive was the Zymoetz River population. Peak abundance for this population was estimated to occur near July 31, and the median date of passage was August 7. This peak week of abundance was about 4 weeks earlier than that observed for the two populations in the Lower Skeena River reporting group (i.e., Kitsumkalum and Lakelse rivers). The estimated peak abundance for the Kitsumkalum River and Lakelse River populations occurred on August 28, and the

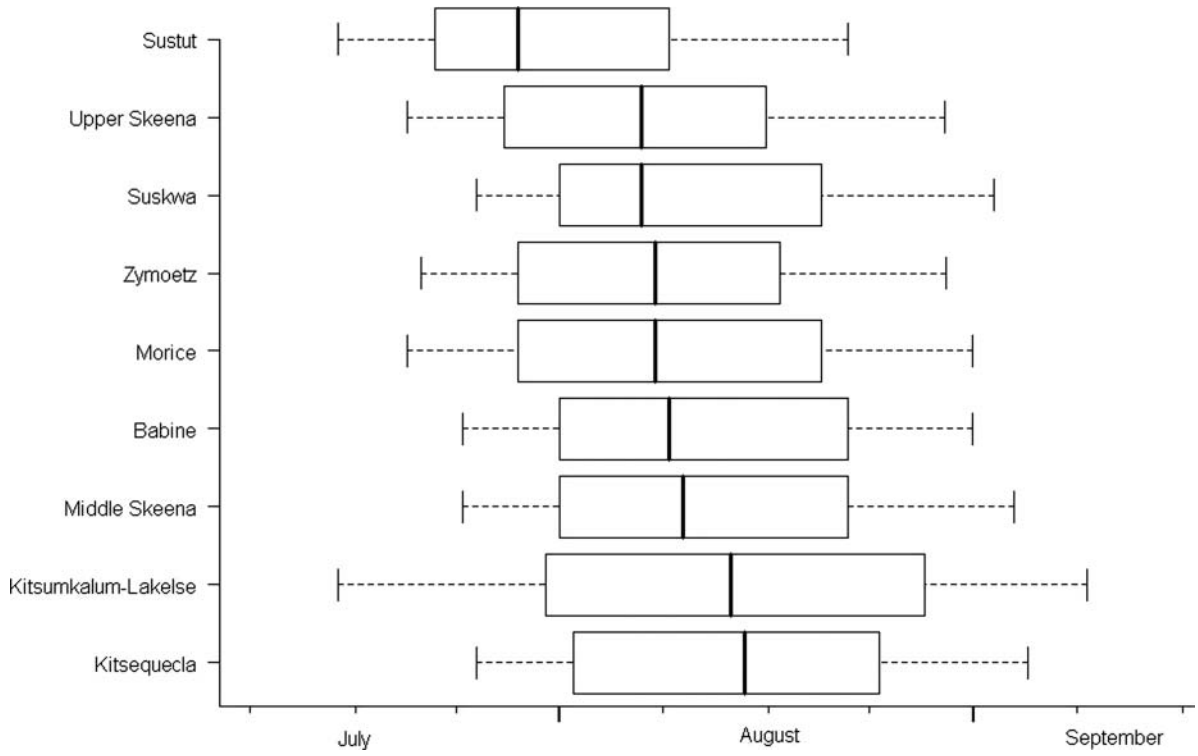

FIGURE 5. Box-and-whisker plots of migration timing distribution for Skeena River steelhead by reporting group (see Table 1) based upon returns to the Tyee test fishery, 1998–2010. Each plot presents the median (solid line within box), upper and lower quartiles (boundaries of box), and 10th and 90th percentiles (ends of whiskers).

estimated median time of passage was August 13 (Figure 5). The Zymoetz River population was estimated to have contributed 8% of the returns to the river during 1998–2010, about double the contribution of the Kitsumkalum River and Lakelse River populations combined (Table 7). There was a general pattern of upper river populations displaying earlier migration timing than lower river populations, but variation was certainly apparent among populations and reporting groups.

DISCUSSION

Population Structure

Initial evaluation of genetic population structure of Skeena River steelhead through analysis of allozyme variation was reported by Parkinson (1984). Results from that study indicated that Skeena River populations were distinct from those in southern British Columbia, but there was limited evidence for population structure within the drainage. Subsequent application of minisatellites was reported by Taylor (1995), who observed significant differentiation among the Babine River, Morice River, and Sustut River populations. Later analyses of microsatellites indicated significant differentiation among populations within the drainage and some regional structure or tributary structure within the drainage (Beacham et al. 2000; Heath et al. 2001, 2002). Our results considerably expanded the number of populations surveyed from five (Heath et al. 2001, 2002) or eight populations (Beacham et al. 2000, 2004) to 17 populations surveyed throughout the drainage. The number of individuals we analyzed in the population survey tripled to approximately 3,000, and four new microsatellites were included in the survey. This expanded survey indicated genetic differentiation among populations spawning in the upper, middle, and lower portions of the drainage, and genetically distinct populations were observed in all three geographic regions of the drainage. However, the level of differentiation among populations in the Skeena River drainage was typically less than that observed among steelhead populations in other major river drainages (e.g., the Snake River in Idaho; Nielsen et al. 2009) and in coastal regions of California (Nielsen et al. 1997; Aguilar and Garza 2006) and was also less than that observed in local populations within a small river drainage near San Francisco, California (Pearse et al. 2009).

In the present study, both juveniles and adults were sampled to obtain estimates of allele frequencies for the 14 microsatellites surveyed. Samples derived from adults were the preferred method of obtaining DNA samples because this generally precludes nonrandom (family) sampling of juveniles (Hansen et al. 1997; Wenburg et al. 1998), avoids the potential of mixing juvenile rainbow trout and juvenile steelhead (Parkinson 1984), and avoids the problem of juveniles potentially rearing in nonnatal streams (Scrivener et al. 1994; Daum and Flannery 2011). However, access to returning adults was quite difficult in many tributaries in which steelhead returned to spawn, particularly the tributaries in the upper portion of the Skeena River drainage. Many of the tributaries were remote and difficult to access, and steelhead were in low abundance. Under these circumstances, samples from juveniles were used for DNA samples because we wanted to have as complete a baseline as possible for subsequent stock identification applications. For the samples from juveniles, there was little evidence to suggest that nonrandom or family sampling of juveniles had occurred because genotypic frequencies were generally in Hardy–Weinberg equilibrium for the loci surveyed in individual samples. However, because observed F_{ST} values were lowest for upper drainage populations, where the estimates of allele frequencies were derived entirely from juvenile samples, it is possible that some juveniles were rearing in nonnatal tributaries, which may have had some effect of homogenization of allele frequencies among populations.

The results of our study indicated that allele frequencies were stable within five populations over the time frame (maximum = 12 years) we evaluated. Differentiation of allele frequencies among the five populations evaluated within the drainage was approximately 14 times greater than that of annual variation within populations, indicative of the relative stability of allele frequencies over time. Annual variation in allele frequencies has been reported previously for steelhead (Parkinson 1984; Reisenbichler et al. 1992; Heath et al. 2002). For many populations, it is typically difficult to sample enough individuals (preferably adults) within a year to obtain adequate sample sizes for estimation of allele frequencies. We restricted analysis of annual variation to only those populations with at least 40 individuals sampled in each of at least 2 years. If annual sample sizes are small relative to the number of alleles observed at a locus, then annual estimates of allele frequencies may be subject to sampling error, which may inflate estimates of temporal variation, as outlined by Beacham and Withler (2010). Stability of population structure among the five populations surveyed was probably indicative of stability within the Skeena River drainage, which would allow application of baseline samples collected during one or more years to estimation of stock composition from sampling mixed-stock fisheries, which may or may not overlap the annual sampling distribution of baseline population sampling.

Stock Identification

The number of fish sampled in a baseline population probably influenced the accuracy of estimated stock compositions. For example, fewer than 100 individuals were sampled for the Quill Creek, Lakelse River, and Kluatantan River populations, and accuracy of simulated single-population fishery samples was typically less than 80% for population-specific estimates. The Kluatantan River population was among the more distinct populations sampled, so estimated accuracy from the simulated single-population samples would typically have been expected to be greater than 90%, as was observed for the Sustut River and Zymoetz River populations, which had comparable F_{ST} values. Increased accuracy of estimated population-specific stock compositions would probably be achieved with larger baseline sample sizes available for those populations with smaller numbers

of fish surveyed, such as the Lakelse River population (Beacham et al. 2011b). The ability to identify populations with moderate numbers of individuals analyzed, such as the Kispiox River population, would probably be enhanced with larger numbers of fish analyzed in the baseline sample as well. Increased accuracy of estimated population-specific stock compositions from upper Skeena River drainage populations would also probably be achieved if additional adult samples were available from these populations rather than the current preponderance of juvenile samples, which may mute genetic differentiation present in the spawning populations because juveniles rearing in nonnatal streams may have been included in samples collected to characterize populations.

Evaluation of genetic stock identification applications initially involves analysis of simulated mixtures to evaluate accuracy and precision of estimated stock compositions. Our analysis of simulated single-population samples generally indicated that accurate estimates of stock composition would be available if the 17-population baseline was organized into nine reporting groups. These nine reporting groups corresponded well to proposed steelhead conservation units in the Skeena River drainage (Tautz et al. 2011). Analysis of simulated and known-origin, multiple reporting group mixtures within the bounds of stock compositions likely to be observed in actual mixed-stock fishery samples from the Skeena River indicated that reliable estimates of stock composition were obtained. However, even if reliable estimates of stock composition are obtained from analysis of simulated mixtures, inaccurate estimates of stock composition can potentially still be obtained from real fisheries applications if a sizeable portion of the mixed-stock sample has been derived from populations or regions that are inadequately represented in the baseline. No populations of significant abundance are known to be unrepresented in the current baseline; thus, estimates of stock composition of actual fishery samples with the current baseline should be reliable.

Considerable variation in relative abundance of the various reporting groups was observed in the sampling of the lower river test fishery during 1998–2010, but estimated stock compositions by reporting group aligned closely with management expectations. The Morice River population was estimated to comprise 25% of the returning steelhead during this period; it was the largest single population observed in the drainage, which fits with observations from spawning ground enumerations (Schwarz and Bonner 2011). The Sustut River population, enumerated at a weir, was estimated to account for about 5% of returns, in line with weir counts. The Zymoetz River population was estimated to be twice as abundant as the other two lower drainage populations (Kitsumkalum and Lakelse rivers) combined. The Zymoetz River is a much more productive watershed than the other two tributaries because it is less glacial than the Kitsumkalum River and much longer and more diverse than the Lakelse River. The Zymoetz River drainage is also known to support both summer-run and winter-run steelhead populations. Thus, we would expect higher steelhead production from the Zymoetz River drainage than from the other two drainages.

Conservation of specific populations can be of concern in the management of Skeena River steelhead. For example, the upper Sustut River steelhead population was considered depressed (in the conservation concern zone) during 2005–2008. During this period, the upper Sustut River population contributed 4.4–7.2% of the Tyee test fishery samples. However, populations of special concern will probably vary over time. Currently, there are no known populations of special conservation concern. Steelhead stock assessment in Skeena River drainage is limited (for logistic and practical reasons) to the upper Sustut River weir, the Moricetown mark–recapture estimate (Bulkley and Morice rivers), the Kloiya River winter-run (resistivity counter) abundance estimate, and the Tyee test fishery. A drainage escapement goal of 36,000–40,000 fish (Ward et al. 1992) has been met for 8 of the past 56 years of Tyee test fishery operation.

The timing of various reporting groups of steelhead through the lower river fishery generally indicated that upper drainage populations displayed the earliest timing of migration, followed by middle drainage populations, with the lower river populations generally displaying the latest timing. The most distinctive population surveyed in the study originated from the Sustut River in the upper portion of the drainage. Steelhead from this population return early through the lower river, migrate some 560 km from the river mouth to the spawning grounds, and ascend about 1,524 m in elevation during the migration, making them among the highest-elevation-migrating steelhead in North America. In the lower portion of the drainage, Zymoetz River steelhead were also genetically distinct. Zymoetz River summer-run steelhead (the more abundant component of this population) pass through the lower river earlier than other lower river populations because they have a longer migration route to the spawning grounds than the other lower drainage populations (i.e., Kitsumkalum and Lakelse rivers). Differences in timing of spawning migration may restrict gene flow among geographically proximate populations, resulting in increased distinctiveness of either early run or late-run populations in a region.

In summary, the application of microsatellite variation provided reliable estimates of stock composition among steelhead sampled in the lower Skeena River test fishery. The ability to identify timing of passage of specific populations through the lower river provides fishery managers with the opportunity of managing fisheries so that exploitation on populations of concern can be reduced while at the same time providing opportunities for harvest of the more abundant sockeye salmon. Ideally, from the provincial perspective, selective fisheries that minimize bycatch mortality are desired. Genetic stock identification will continue to become a tool of increasing importance in the management and assessment of Pacific salmon fisheries.

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