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ARTICLE

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Abstract
Determination of run timing is an important component of salmonid fisheries management and was the major focus of the current study. Population structure of Sockeye Salmon *Oncorhynchus nerka* was examined in the Skeena River, northern British Columbia. Variation at 14 microsatellites was surveyed for 27 populations in the drainage. There were 9,473 individuals sampled in a lower river test fishery during 2000–2011 in order to provide information on relative abundance and time of arrival of specific populations or stocks near the mouth of the river. Within-lake or within-river tributary structuring of populations was the general pattern observed, with 10 populations from Babine Lake clustering together in 91% of dendrograms evaluated, and two populations from Lakelse Lake clustering together in 100% of dendrograms evaluated. The 27 populations sampled were arranged in 12 reporting groups for genetic stock identification applications. The estimated stock composition of known-origin mixtures was within 2% of the correct estimate for all 12 reporting groups present in the mixtures. Sockeye Salmon typically began arriving at the test fishery on the lower Skeena River by June 10, peaking in daily abundance in late July or early August, and finished migrating past the test fishery by mid-September. Relative timing of the 12 reporting groups, from earliest to latest, was as follows: Lakelse Lake, Alastair Lake, Zymoetz River, Morice Lake, Kispiox River, Sustut Lake, Babine Lake, Slamgeesh Lake, Motase Lake, Bear Lake, Kitsumkalum Lake, and Kitwanga Lake. Genetic mixed-stock analysis, coupled with a test fishery in the lower river, can assist managers in regulating fisheries directed at Skeena River Sockeye Salmon.

Sockeye Salmon *Oncorhynchus nerka* returning to the Skeena River watershed in northern British Columbia support the second largest Sockeye Salmon fishery in British Columbia, second only to the Fraser River fishery in southern British Columbia. Management of the Skeena River Sockeye Salmon fishery is complex, as there can be overlapping timing of return of Sockeye Salmon, Pink Salmon *O. gorbuscha*, Chinook Salmon *O. tshawytscha*, Coho Salmon *O. kisutch*, Chum Salmon *O. keta*, all species subject to federal management, as well as steelhead *O. mykiss*, subject to provincial management. Management of the Sockeye Salmon fishery thus involves both federal and provincial agencies, as well as many user groups, each with their own economic and social objectives (Hilborn and Walters 1977; Sprout and Kadowaki 1987). The

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underlying priority in management of the fishery is one of conservation first of stocks and species of conservation concern, and secondarily where and when possible, allowing for harvest of more abundant stocks of Sockeye Salmon.

The Skeena River drainage includes Babine Lake, the largest natural lake in British Columbia, as well as a number of smaller lakes. In the 1960s, spawning channels and flow controls were established on the two major Babine Lake spawning tributaries located at Pinkut Creek and Fulton River in order to increase the number of juvenile Sockeye Salmon rearing in Babine Lake (Ginetz 1977). The first significant returns of Sockeye Salmon from the enhancement facilities occurred in 1975 (Wood et al. 1998). Approximately 90% of all Skeena River Sockeye Salmon production originates from Babine Lake, compared with less than 80% before the construction of enhancement facilities (West and Mason 1987; Wood et al. 1998). Assessment of the Sockeye Salmon abundance returning to Babine Lake is an important factor in the management of Skeena River Sockeye Salmon and is an ongoing process (Cox-Rogers and Spilsted 2012). As part of the assessment, Sockeye Salmon escapement to Babine Lake has been determined annually at a counting fence since 1949 (West and Mason 1987). Thus, a measure of the absolute abundance of Sockeye Salmon returning to Babine Lake is available on an annual basis.

One of the objectives of managing salmon fisheries in British Columbia is to ensure conservation of biodiversity of the existing returning populations. In essence, this objective requires that no population is consistently overexploited and requires more information for mixed-stock fisheries management than has traditionally been available for fisheries managers. Increasing the number of smolts produced from Pinkut Creek and Fulton River in Babine Lake was undertaken to increase Sockeye Salmon production. The expectation was that surplus production would be harvested in marine fisheries or freshwater fisheries downstream from Babine River in order to harvest fish of higher flesh quality, and thus obtain greater economic benefits from the surplus production. The evolution of British Columbia salmon fisheries is one of combined mixed-stock marine harvesting and mixed-stock freshwater harvesting as salmon migrate from the open ocean to the river spawning grounds. Past and current societal use of the salmon resource supports both marine and in-river harvesting by different harvesting sectors. Societal support for more terminal salmon fisheries, in order to minimize mixed-stock impacts, is a more recent yet emerging theme in British Columbia salmon fishery management. Enhancement of Sockeye Salmon production in the Skeena River was limited to Babine Lake facilities, and harvesting of surplus production required the exploitation of Babine Lake-origin Sockeye Salmon in mixed-stock fisheries, resulting in less productive populations becoming potentially subject to overexploitation. The identification of timing of the return of specific populations from information gained through fisheries is thus a key component of reducing exploitation on populations of conservation concern. For Skeena River Sockeye Salmon, initial research on run timing centered on tagging migrating individuals either in marine commercial fishery areas or in the Skeena River drainage (Aro and McDonald 1968; Smith and Jordan 1973; Takagi and Smith 1973). Fishery managers have used biological markers based on variation at allozymes, frequency of occurrence of parasites, and age compositions to estimate the proportion of Babine Lake Sockeye Salmon in mixed-stock samples (Rutherford et al. 1999). Microsatellite genetic markers were subsequently applied on a trial basis for stock identification of Skeena River Sockeye Salmon (Beacham et al. 2000), and they are now the main method of stock identification used for Sockeye Salmon in the Skeena River drainage and elsewhere in British Columbia (Beacham et al. 2005a).

Determination of spawning escapement is one of the key pieces of information required in the assessment of the status of specific salmon populations. As approximately 90% of production of Skeena River Sockeye Salmon originates from Babine Lake (Wood et al. 1998) and because escapement is enumerated with a counting fence, much of the total escapement to the Skeena River drainage is estimated with the accuracy associated with a counting fence. The accuracy of the Babine River fence counts themselves should be quite good for most years as the fence is placed in the river prior to migration and counting ends well towards the end of migration. All fish are physically counted as they pass the fence each day the fence is in operation, and none can escape past the counting traps. In some years, high water precludes installing the fence until 2 or 3 weeks after migration begins, and thus the front ascending limb of the migration is not counted. However, smoothing and various historical filling routines are used to adjust escapement counts in those years.

There is a wide geographic range to other spawning populations in the drainage (Figure 1), and there are considerable challenges in determining spawning escapements in non-Babine Lake tributaries. Visual estimates of escapements may underestimate actual escapement, and in an era of declining financial resources for salmonid assessments, in which ground site visits or overflights may not be conducted in every year to estimate tributary escapement, alternative methods of escapement estimation for smaller populations may be required. The Skeena River watershed provides an ideal opportunity for the estimation of Sockeye Salmon escapements through a lower Skeena River test fishery and application of genetic stock identification techniques, as escapement for one large genetically distinct stock (Babine Lake: Beacham et al. 2000) is estimated with the accuracy associated with a counting fence. Sampling of the test fishery in proportion to run abundance should thus provide a means to estimate escapement of smaller populations within the drainage.

In the current study, we evaluated the population structure of Sockeye Salmon in the Skeena River by surveying variations at 14 microsatellites, and also assessed the utility of the microsatellites for identification of the timing of return of Sockeye Salmon populations in the Skeena River drainage. This assessment was conducted by examining the accuracy and precision of estimated

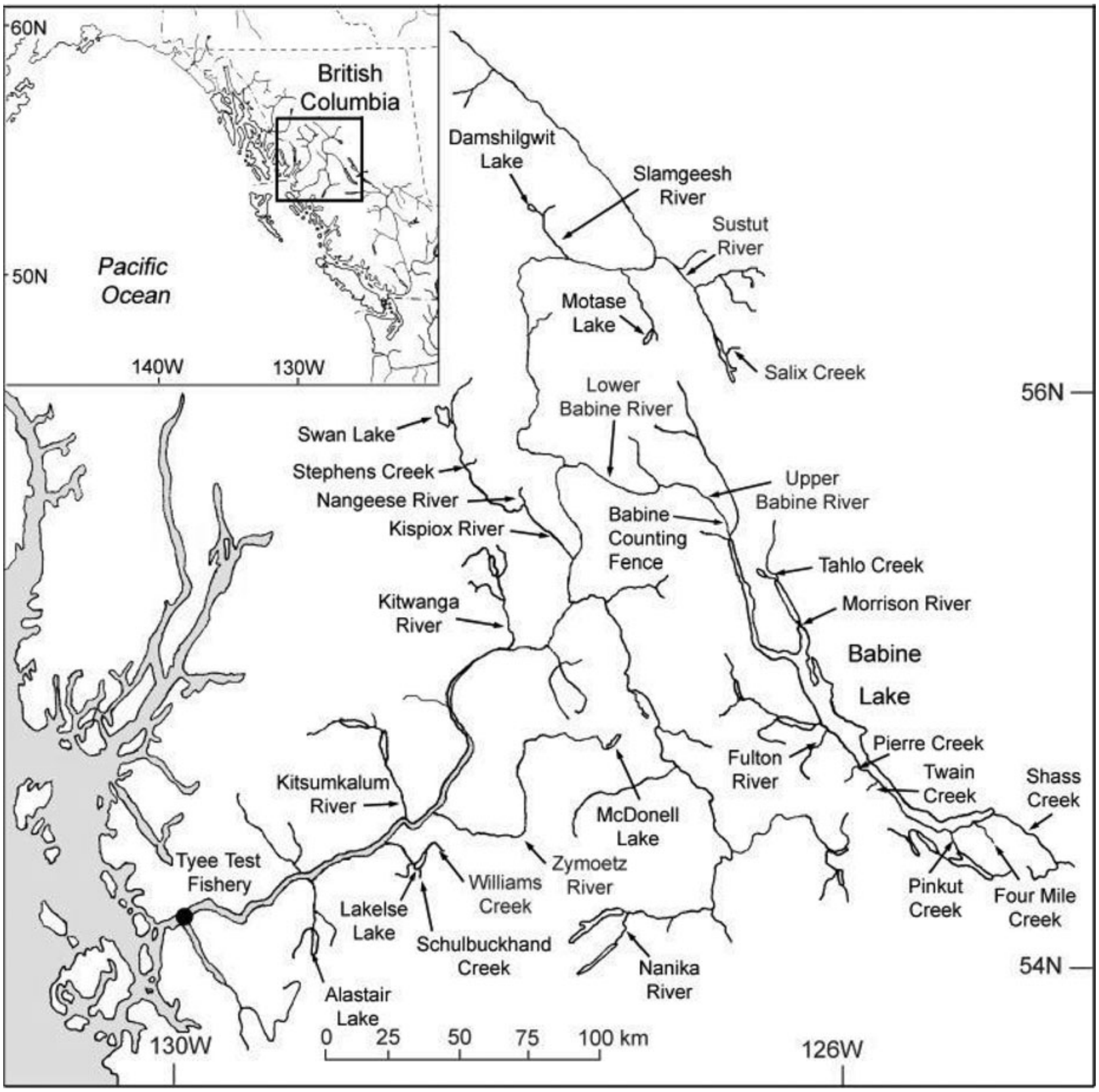

FIGURE 1. Locations of the 27 Sockeye Salmon populations sampled in the Skeena River drainage, as well as the Tyee test fishery at the mouth of the river.

stock compositions through analysis of known-origin and simulated mixtures and estimating the timing of return through analysis of samples collected during 12 years of sampling from a test fishery in the lower river; the mixtures were resolved by using a 27-population baseline incorporating populations throughout the Skeena River drainage.

METHODS

Fishery samples of returning adults in the Skeena River were collected with a gill-net test fishery at Tyee (Jantz et al. 1990). Summarized briefly, the test fishery at Tyee has been conducted since 1955 in the tidal portion of the Skeena River (Figure 1) and has provided a relative index of abundance in season for all species migrating past the fishery. Until 2002, a 1,200-ft (365 m) fibrous nylon gill net of varying mesh size was deployed daily during slack-water tidal periods. In 2002, the gill net was replaced by a monofilament net to replace the multifilament net material as it was no longer available. Five years of deploying both nets were conducted to standardize CPUE between the sampling gears.

The test fishery CPUE indices were daily average catch (*C*) per hour (*E*) values (*C*/*E*) calculated from the two or three daily test-fishery sets (drifts), which occurred for 1-h periods at slack tide intervals. Average daily catch per hour in the test fishery (the daily test index) was assumed proportional to the passing daily abundance of salmon entering the Skeena River (equation 1) as

$$C/E = qN, \tag{1}$$

where q was the catchability coefficient and N was abundance passing into the river. There was no way to calculate the catchability coefficient on a daily basis at the test fishing site, but annual catchability (equation 2) was calculated at the end of the season using upstream accounting of the number of salmon that passed the test fishery (e.g., spawning ground escapement counts of which 90% are counted through a counting fence at Babine Lake), i.e.:

$$\text{Annual } q = (\text{cumulative } C/E)/(\text{upstream spawning count } N). \tag{2}$$

Plots of annual upstream spawning N against annual cumulative test fishery C/E displayed positive correlations of varying magnitude depending upon the time periods evaluated (Cox-Rogers and Jantz 1993), which by extension we assumed applied to daily N and daily C/E at the test-fishing site. However, several factors can affect catchability in the test fishery that can add variability to the relationship between C/E and passing abundance (Cox-Rogers and Jantz 1993). These factors include saturation of the fishing gear when passing salmon abundance levels are very high, unaccounted size selectivity of the sampling gear (a multipanel gill net), and distributional access of fish to the sampling gear. Unfortunately, we have had difficulty separating and quantifying these interacting factors with respect to assessing accuracy and precision of the daily C/E indices at the test-fishery site. The variance inherent in plots of annual N against annual cumulative C/E were provided by Cox-Rogers and Jantz (1993). Daily, weekly, and seasonal CPUE indices of abundance were available from the test fishery. Tissue samples were obtained from representative numbers of Sockeye Salmon sampled in the test fishery, and genetic analysis of these samples was conducted in proportion to weekly run abundance.

Tissue samples from Sockeye Salmon sampled in the test fishery were preserved in 95% ethanol and sent to the Molecular Genetics Laboratory at the Pacific Biological Station of Fisheries and Oceans Canada in Nanaimo, British Columbia. Tissue samples from the baseline populations were collected from mature Sockeye Salmon. Stock identification reporting groups, populations within reporting groups, year of sampling, and number of fish analyzed in the baseline populations are described in Table 1. Fourteen microsatellites (Beacham et al. 2005a) were surveyed with an ABI 3730 capillary DNA sequencer, and genotypes were scored by GeneMapper software 3.0 (Applied Biosystems, Foster City, California) using an internal lane sizing standard as described by Beacham et al. (2005a).

Baseline population data analysis.—All annual samples available for 27 baseline locations (Figure 1) were combined to estimate population allele frequencies, as was recommended by Waples (1990). Cavalli-Sforza and Edwards (1967) chord distance (CSE) was used to estimate genetic distances among all populations in the baseline used for stock identification applications. An unrooted neighbor-joining tree based upon CSE was generated using NJPLOT (Perriere and Gouy 1996). Bootstrap support for the major nodes in the tree was evaluated with the CONSENSE program from PHYLIP based upon 500 replicate trees (Felsenstein 1993).

Determination of reporting groups.—A mixture sample of 50 known-origin fish was developed for each population in the baseline where existing sample sizes permitted development of the sample. The mixture sample was created by removing 50 fish from a population, and the baseline allele frequencies for that population in the baseline were recalculated by excluding the fish that had been selected for the mixture sample. Each of the 27 populations sampled was tested individually, with a target of 90% accuracy required for remaining as a separate reporting group or stock, similar to the procedure described by Seeb and Crane (1999). If the target of 90% accuracy was not achieved, then the previously outlined cluster analysis of CSE values between populations was used to select potential aggregates of populations (reporting group or stock) to achieve the 90% accuracy target. These reporting groups or stocks were enlarged until the approximately 90% accuracy target was achieved in the analysis. For the four populations (Motase Lake, Zymoetz River, Twain Creek, and Shass Creek) where sample size was insufficient to allow for removal of individuals from the baseline, 50 simulated multilocus genotypes were used in the analysis for these populations.

Estimation of stock composition.—Analysis of fishery samples was conducted with a Bayesian procedure (BAYES) as described by Pella and Masuda (2001). A C-based version of the program was developed (Neaves et al. 2005) and used for estimation of stock composition. In the analysis, eight 20,000-iteration Monte Carlo Markov chains of estimated stock compositions were produced, for which initial starting values for each chain was 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 <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.

Migration timing.—Samples were available from the test fishery conducted during 2000–2011, and a total of 9,473 fish were analyzed for microsatellite variation during the study. Within a year, samples were stratified into 16 weekly periods: June 3–9, June 10–16, June 17–23, June 24–30, July 1–7,

TABLE 1. Stock reporting groups, populations within stock reporting groups, years of sampling, and population sample size for 27 Sockeye Salmon populations in the Skeena River drainage of British Columbia. Juveniles from all spawning populations reared in lakes, except for those sampled from spawning populations in the Zymoetz River, Nangeese River, and Kispiox River.

Stock reporting group	Populations	Years	Sample size
Alastair Lake	Alastair Lake	1987, 1988, 1994, 1998, 2006	323
Lakelse Lake	Williams Creek	1987, 1988, 1994, 2005, 2006	388
	Schulbuckhand Creek	1988, 2005	94
Zymoetz River	McDonell Lake	1987, 1988, 1994, 2002	256
	Zymoetz River	2006	63
Kitwanga Lake	Kitwanga River	1998, 2008, 2009	488
Kitsumkalum Lake	Kitsumkalum River	1994, 2006	162
Kispiox River	Stephens Creek	2001, 2004	193
	Swan Lake	1988, 1994, 2006	262
	Nangeese River	2002, 2005, 2006, 2007	151
	Kispiox River	2002, 2005, 2009	252
Motase Lake	Motase Lake	1987	39
Morice Lake	Nanika River	1988, 1994, 2003	129
Bear Lake	Salix Creek	1987, 1988	82
Sustut Lake	Sustut River	1993, 2000, 2001, 2006	333
Slamgeesh River	Slamgeesh River	2006, 2008	443
	Damshilgwit Lake	2004	202
Babine Lake	Lower Babine River	1987, 1994	137
	Upper Babine River	1987, 1994, 2006	246
	Morrison River	1988, 1994	98
	Fulton River	1985, 1987, 1990, 1994	375
	Pinkut Creek	1985, 1987, 1990, 1994	311
	Four Mile Creek	1987, 1988, 2006	177
	Pierre Creek	1987, 1988, 2006	215
	Tahlo Creek	1987, 1988, 1994	185
	Shass Creek	1987	64
	Twain Creek	1987, 1990	75

July 8–14, July 15–21, July 22–28, July 29–August 4, August 5–11, August 12–18, August 19–25, August 26–September 1, September 2–8, September 9–15, and September 16–22. The period CPUE index was determined (sum of daily CPUE indices within a week), then the period CPUE index was averaged over the 12 years of the study. This resulting average CPUE index was multiplied by the estimated-period stock proportions and apportioned to the 12 reporting groups in Table 1. Stock-specific period CPUE indices were summed over the 12 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 Tyee test fishery for each reporting group was determined by indentifying individuals in an annual sample to a specific reporting group based upon individual assignment probability. Individuals were assigned to a specific population that 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 then the total number of individuals assigned to each reporting group was determined in each of the 12 annual samples collected during 2000–2011. Individual identifications by reporting group were then summed over all 12 annual samples. 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

Population Structure

Significant genetic differentiation was observed among Sockeye Salmon populations sampled in the different stocks or reporting groups. The greatest differentiation was observed in the Kitwanga Lake, Sustut Lake, Zymoetz River, and Lakelse Lake stocks, in which the average pairwise F_{ST} values was >0.1200 for these stocks (Table 2). The average pairwise F_{ST}

TABLE 2. Mean pairwise F_{ST} values averaged over 14 microsatellite loci from 12 stocks or regional reporting groups of Sockeye Salmon in Table 1 that were sampled at 27 locations within the Skeena River drainage. Comparisons were conducted between individual populations in each stock or reporting group. Values in bold italic text on the diagonal are comparisons among populations within each stock or region. F_{ST} values are listed below the diagonal, with SD values above the diagonal. Mean F_{ST} values at the bottom of the table are mean values among the 12 reporting groups. A dash along the diagonal indicates that it was not possible to determine within reporting group pairwise mean F_{ST} values because only a single population was sampled. A dash (–) for SD indicates that it was not possible to determine because each reporting group contained only a single population.

Reporting group	Alastair Lake	Babine Lake	Bear Lake	Kispiox River	Kitsumkalum Lake	Kitwanga Lake	Lakelse Lake	Morice Lake	Motase Lake	Slamgeesh River	Sustut Lake	Zymoetz River
Alastair Lake	–	(0.0045)	–	(0.0237)	(0.0041)	–	(0.0051)	–	–	(0.0006)	–	(0.0065)
Babine Lake	0.0571	***0.0048***	(0.0051)	(0.0176)	(0.0052)	(0.0058)	(0.0046)	(0.0049)	(0.0062)	(0.0048)	(0.0063)	(0.0056)
Bear Lake	0.0652	0.0531	**–**	(0.0138)	(0.0007)	–	(0.0042)	–	–	(0.0004)	–	(0.0087)
Kispiox River	0.0802	0.0568	0.0376	***0.0402***	(0.0129)	(0.0139)	(0.0242)	(0.0187)	(0.0093)	(0.0155)	(0.0369)	(0.0349)
Kitsumkalum Lake	0.0563	0.0489	0.0494	0.0530	***0.0013***	(0.0047)	(0.0049)	(0.0026)	(0.0002)	(0.0006)	(0.0013)	(0.0071)
Kitwanga Lake	0.0962	0.1037	0.1190	0.1091	0.1092	**–**	(0.0043)	–	–	(0.0069)	–	(0.0020)
Lakelse Lake	0.1022	0.1239	0.1086	0.1172	0.0882	0.1769	***0.0022***	(0.0013)	(0.0033)	(0.0023)	(0.0010)	(0.0077)
Morice Lake	0.0992	0.0938	0.0580	0.0841	0.0921	0.1696	0.1443	**–**	–	(0.0029)	–	(0.0072)
Motase Lake	0.1035	0.0871	0.0458	0.0670	0.0868	0.1620	0.1561	0.0847	**–**	(0.0016)	–	(0.0035)
Slamgeesh River	0.0623	0.0477	0.0092	0.0335	0.0452	0.0994	0.1028	0.0603	0.0484	***0.0008***	(0.0005)	(0.0062)
Sustut Lake	0.1423	0.1349	0.0889	0.1260	0.1491	0.1839	0.1936	0.1414	0.1352	0.0893	**–**	(0.0052)
Zymoetz River	0.0967	0.1183	0.1359	0.1370	0.1322	0.1391	0.1611	0.1657	0.1671	0.1136	0.1636	***0.0000***
Mean F_{ST}	0.0874	0.0841	0.0701	0.0820	0.0828	0.1335	0.1341	0.1085	0.1040	0.0647	0.1407	0.1398

value among the 12 stocks or reporting groups identified was 0.1026. Within a stock, average pairwise F_{ST} values were typically <0.0050. The exception was in the Kispiox River stock, where the lake-type populations (juveniles rear in lakes; Stephens Creek, Swan Lake) were differentiated from the river-type populations (juveniles rear in freshwater backchannels during their first year; Nangeese River, Kispiox River).

A lake-based or tributary-based structuring of Sockeye Salmon populations within the Skeena River drainage was the general pattern observed in the survey. The 10 Babine River populations clustered together in 91% of dendrograms evaluated, as did the two Lakelse Lake populations (99%) and two Zymoetz River populations (100%), indicative that these populations were more similar to each other than to populations in other areas of the drainage (Figure 2). Five populations in the upper portion of the Skeena River drainage, upstream from the Babine River junction, clustered as a group, and two populations in the Slamgeesh River clustered in 85% of dendrograms evaluated. Generally, populations within lakes or tributaries were genetically distinct from other populations sampled in different lakes or tributaries within the Skeena River drainage.

Accuracy of Estimated Stock Compositions

Analysis of known-origin, single-population samples indicated that reasonably accurate (>90% average) estimates of population-specific composition would be achieved for 8 of the 27 populations surveyed in the study (Table 3). When the populations were arranged by the 12 reporting groups shown in Table 1, accurate estimates of reporting-group composition were generally achieved across populations. All 10 Babine River populations were combined into a single reporting group, which considerably improved the accuracy of estimated stock compositions for the Babine River drainage. Lake-based or tributary-based populations were combined into reporting groups for Lakelse Lake, Zymoetz River, Kispiox River, and Slamgeesh River. The 12 reporting groups in Table 1 comprised separate tributaries of the Skeena River drainage.

Accuracy and precision of estimated stock composition were evaluated for two multipopulation, multireporting-group, known-origin mixtures of Sockeye Salmon as may be encountered in Skeena River mixed-stock fishery sampling. The estimated stock composition of the mixture was within one percentage point of the correct estimate for six of the eight reporting groups present in mixture 1 and all of the seven reporting groups present in mixture 2 (Table 4). In particular, accurate estimation of stock composition for the reporting groups present only in small proportions (2–7%) was observed, although 95% confidence limits for the estimate typically included zero. As Babine Lake-origin Sockeye Salmon were expected to dominate any mixed-stock samples, it was necessary that accurate estimation of low-abundance reporting groups be achieved. Analysis of the single- and multipopulation mixtures indicated that reliable estimates of stock composition determined by reporting group should be provided by the 14 microsatellites evaluated in the study.

Run Timing

Sockeye Salmon typically begin arriving at the Tyee test fishery by June 10, peak in daily abundance in late July or early August, and finish migrating past the test fishery by mid-September (Figure 3). A decline in abundance observed near July 24 likely reflected the effect of marine commercial fisheries catch, as fishery openings tend to be directed towards peak abundance of the run. The large majority of returning Sockeye

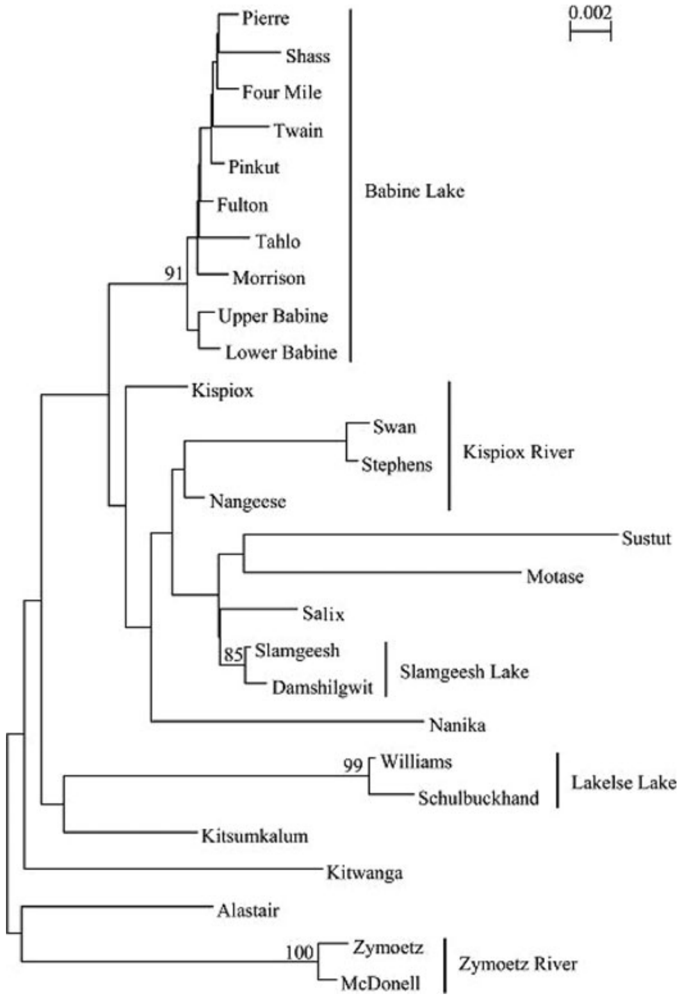

FIGURE 2. Unrooted neighbor-joining dendrogram outlining the population structure of 27 Sockeye Salmon populations in the Skeena River drainage. Values on the dendrogram refer to bootstrap support (the percentage of dendrograms where populations to the right of the value clustered together).

Salmon pass through the lower river from mid-July through mid-August, and virtually all of the run has migrated through the lower river by early September. Of the 12 reporting groups defined in the study, the earliest returning group originated from Lakelse Lake in the lower portion of the Skeena River drainage (Figure 1). Peak abundance of this population during 2000–2011 was observed, on average, during the week beginning June 17 (Figure 4a), and the median date of migration was June 21 (Figure 5). The Lakelse Lake population accounted for an average of 1.4% of the Sockeye Salmon returning to the test fishery sampling location (Table 4). Two other lower river populations, Alastair Lake and Zymoetz River, also displayed a relatively early time of return to the test fishery. Peak abundance of the Alastair Lake population was observed during the week of June 24th, and peak abundance of the Zymoetz River population was observed during the week beginning July 1 (Figure 4a). The two populations accounted for 2.6% and 0.9% of returns to the test fishery, respectively (Table 5). The peak of abundance of the Morice Lake (Nanika River) population occurred during the week of July 8, and the population accounted for an average of 1.2% of total returns during 2000–2011 (Table 5). The peak abundance of the Kispiox River stock, located in the middle portion of the Skeena River drainage, occurred during the week of July 15 (Figure 4b), and this stock accounted for 2.4% of drainage escapement (Table 5).

Four populations or stocks were included in the middle-timed group of returning Sockeye Salmon. Peak abundance of the Sustut Lake population, located in the upper portion of the Skeena River drainage, was observed during the week of July 15, and a median date of passage for the population through the lower river test fishery was estimated as July 20. Peak abundance of the Motase Lake population was estimated as July 15 (Figure 4c), and the median date of passage was July 26 (Figure 5). However, as this population was estimated to have accounted for only 0.1% of drainage escapement (eight fish identified in the 9,473 fish analyzed) (Table 5), there was likely uncertainty over the precise timing of this population through the lower river test fishery. In contrast, the returns of Sockeye Salmon to the Skeena River were dominated by individuals of Babine Lake origin, as this stock accounted for about 87% of Skeena River drainage escapement. Peak abundance of the stock was estimated to have occurred during the week of July 22 (Figure 4b), and the median date of passage through the lower river test fishery was July 24 (Figure 5). Peak abundance of the Slamgeesh Lake stock, located in the upper portion of the Skeena River drainage, was estimated to occur during the weeks of July 22 and July 29 (Figure 4b), and the median date of passage was estimated as July 25. This stock accounted for 0.9% of drainage escapement (Table 5).

Three populations were included in the later-timed group migrating through the lower river test fishery. The peak abundance of the Bear Lake population was estimated to have occurred during the week of July 29 (Figure 4c), and the median date of passage was estimated as August 2 (Figure 5). The peak abundance of the Kitsumkalum Lake population was estimated to have occurred during the week of July 29, and the median date of passage was estimated as August 3 (Figure 5). The populations accounted for 0.8% and 2.0% of drainage escapement, respectively. The latest migrating population originated from Kitwanga Lake (Figure 5). The peak abundance of this population occurred during the week beginning August 5, and this population accounted for 0.3% of drainage escapement.

Median dates of passage through the test fishery were estimated by pooling of individuals across 12 years of sampling by reporting group. Given that there may be variation in timing of return among years, it may be that pooling individuals across years increases variance in the median date of passage relative to that observed in an individual year, with extended tails of the distribution of individuals. Annual sample sizes by reporting group only permitted an evaluation of the effect of pooling for the Babine Lake stock. Median date of passage through the

TABLE 3. Mean (SD in parentheses) estimates of percentage composition for single-population, known-origin samples (correct = 100%) from Skeena River Sockeye Salmon populations. The reporting-group designation includes the sum of percentage allocations to all populations in the group as shown in Table 1. Each known-origin sample was developed by removing 50 individual fish from the selected population to develop the sample, allele frequencies estimated for the remaining fish in the baseline population sample, and then using this modified baseline to estimate stock composition in the sample of known origin. Sample sizes for four populations (Motase Lake, Zymoetz River, Twain Creek, and Shass Creek) were too small to allow for the removal of individuals from the baseline, so 50 simulated multilocus genotypes were used in the analysis for these populations.

Stock reporting group	Population	Population percentage (SD)	Reporting group percentage (SD)
Alastair Lake	Alastair Lake	100.0 (1.7)	100.0 (1.7)
Lakelse Lake	Williams Creek	86.8 (8.9)	100.0 (1.4)
	Schulbuckhand Creek	39.0 (13.5)	100.0 (1.5)
Zymoetz River	McDonell Lake	97.4 (5.6)	100.0 (2.6)
	Zymoetz River	34.1 (4.6)	100.0 (2.5)
Kitwanga Lake	Kitwanga River	98.0 (2.5)	98.0 (2.5)
Kitsumkalum Lake	Kitsumkalum River	99.9 (1.9)	99.9 (1.9)
Kispiox River	Stephens Creek	85.6 (13.2)	100.0 (1.7)
	Swan Lake	96.9 (4.8)	98.0 (4.0)
	Nangeese River	12.2 (9.3)	78.7 (7.1)
	Kispiox River	68.0 (7.2)	78.2 (7.0)
Motase Lake	Motase Lake	98.0 (2.0)	98.0 (2.0)
Morice Lake	Nanika River	100.0 (2.7)	100.0 (2.7)
Bear Lake	Salix Creek	98.1 (5.9)	98.1 (5.9)
Sustut Lake	Sustut River	100.0 (1.9)	100.0 (1.9)
Slamgeesh Lake	Slamgeesh River	55.8 (11.7)	90.1 (8.6)
	Damshilgwit Lake	34.3 (11.3)	88.4 (9.2)
Babine Lake	Lower Babine River	11.1 (11.6)	96.5 (3.3)
	Upper Babine River	53.6 (14.0)	100.0 (1.4)
	Morrison River	44.8 (15.8)	100.0 (3.5)
	Fulton River	60.0 (13.4)	100.0 (1.4)
	Pinkut Creek	35.2 (16.6)	100.0 (1.6)
	Four Mile Creek	43.9 (12.2)	100.0 (1.4)
	Pierre Creek	46.2 (13.8)	99.9 (1.7)
	Tahlo Creek	70.5 (11.2)	100.0 (2.3)
	Shass Creek	31.2 (10.2)	100.0 (0.4)
	Twain Creek	23.3 (9.2)	99.6 (1.4)

lower river fishery ranged from July 19 to July 31 during 2000–2011 (Figure 6), illustrating that some annual variation in timing of return occurred. The average duration during this 12-year period in which 25% to 75% of the stock migrated past the test fishery was 21 d, and was 40 d for migration of the 10% to 90% portion of the stock. With individuals pooled over 12 years, the duration in which 25% to 75% of the stock migrated past the test fishery was 21 d, and that for the 10% to 90% portion of the stock was 42 d. There was little evidence to suggest that pooling of individuals across sampling years inflated variance in timing of passage through the test fishery.

DISCUSSION

Population Structure

Initial evaluation of genetic population structure of Skeena River Sockeye Salmon through analysis of microsatellite variation was reported by Beacham et al. (2000, 2005b). The results from the current study expanded the number of populations surveyed from 17 populations surveyed by Beacham et al. (2000) and 24 populations surveyed by Beacham et al. (2005b) to 27 populations surveyed throughout the drainage. The three new populations added to those presented by Beacham et al. (2005b) (Zymoetz River, Slamgeesh River, and Damshilgwit Lake), as well as additional sampling in previously surveyed populations, revealed a consistent population structure within the Skeena River drainage. The Zymoetz River population, which spawns in the main-stem Zymoetz River, was genetically most similar to the McDonell Lake population in the same river drainage. The two additional new populations, Slamgeesh River and Damshilgwit Lake, are both located in the Slamgeesh River drainage, and both populations were most similar genetically to each other. Structuring of populations was either lake-based or tributary-based, and this structure permitted the designation

TABLE 4. Estimated percentage stock composition (SD in parentheses) of two known-origin mixtures of 100 Sockeye Salmon each that may be encountered in the Skeena River. Expected reporting-group composition is the sum of allocations to individual populations in the reporting group as shown in Table 1. The known-origin samples were 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 samples of known origin.

Population	Actual%	Estimate (SD)
Mixture 1		
Population:		
Alastair Lake	5	5.0 (2.1)
Williams Creek	7	6.8 (2.6)
McDonell Lake	3	3.8 (2.1)
Zymoetz River	1	0.2 (0.9)
Kitsumkalum River	6	7.1 (2.6)
Kitwanga River	4	4.0 (2.0)
Stephens Creek	6	0.8 (2.0)
Damshilgwit Lake	3	0.4 (1.0)
Lower Babine River	15	10.6 (5.4)
Pierre Creek	25	1.3 (3.0)
Fulton River	25	34.2 (6.8)
Reporting group:		
Alastair Lake	5	5.0 (2.1)
Lakelse Lake	7	7.0 (2.6)
Zymoetz River	4	4.0 (2.1)
Kitsumkalum Lake	6	7.1 (2.6)
Kitwanga Lake	4	4.0 (2.0)
Kispiox River	6	6.7 (2.8)
Slamgeesh Lake	3	2.5 (1.7)
Babine Lake	65	63.7 (4.9)
Mixture 2		
Population:		
Swan Lake	5	4.7 (2.2)
Motase Lake	2	1.7 (1.5)
Nanika River	5	5.0 (2.2)
Salix Creek	3	3.2 (2.1)
Sustut River	5	5.9 (2.3)
Slamgeesh River	7	3.6 (3.4)
Upper Babine River	15	20.7 (5.7)
Four Mile Creek	10	13.3 (4.9)
Morrison River	10	0.1 (0.4)
Pinkut Creek	23	0.4 (1.5)
Tahlo Creek	15	2.1 (3.3)
Reporting group:		
Kispiox River	5	4.7 (2.2)
Motase Lake	2	1.8 (1.5)
Morice Lake	5	5.0 (2.2)
Bear Lake	3	3.2 (2.1)
Sustut Lake	5	5.9 (2.3)
Slamgeesh Lake	7	6.6 (2.8)
Babine Lake	73	72.8 (4.4)

of 12 reporting groups for the subsequent analysis of the test fishery samples.

Stock Identification

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. For Sockeye Salmon, this may require identification of salmon spawning in specific lakes, or in some cases, among populations within lakes. However, within lakes, there is typically limited genetic differentiation among populations, unless there are differences in timing of return among lake populations, or differences between lake-spawning and tributary-spawning populations (Varnavskaya et al. 1994). Lower reporting-group accuracy was observed for two populations (Nangeese River and Kispiox River) within the four-population Kispiox River stock. Juveniles from both the Nangeese River and Kispiox River populations do not rear in lakes, and spawning escapements for these two populations constituted less than 5% of the Kispiox River escapement. Therefore, as the Kispiox River stock was estimated as constituting an average of 2.4% of drainage escapement, the Nangeese River and Kispiox River populations constituted about 0.1% of drainage escapement. The level of reporting-group misidentification related to these two populations was not considered to have introduced demonstrable errors on the results observed in the study. Populations with limited genetic differentiation are typically pooled together in a reporting group, as was done for the 10 populations surveyed within the Babine River drainage in the study. Accuracy of estimated stock compositions in a management application can improve as baselines and the suites of genetic markers employed in estimating stock composition are enhanced.

An evaluation of a genetic stock identification application initially involves analysis of either simulated mixtures or known-origin samples to evaluate accuracy and precision of estimated stock compositions. In the current study, analysis of either simulated or known-origin, single-population samples indicated that accurate estimates of stock composition would be available if the 27-population baseline was organized into 12 reporting groups. Analysis of known-origin, multireporting-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 by reporting group. No populations of significant abundance are known to be unrepresented in the current baseline, and thus estimates of stock composition of actual fishery samples with the current baseline should be reliable. For example, the contribution of Babine Lake Sockeye Salmon to the average 2000–2011 escapement measured at the test fishery was estimated at 87% of drainage escapement, which agreed well with the 90% estimate reported earlier by West and Mason (1987) and Wood et al. (1998).

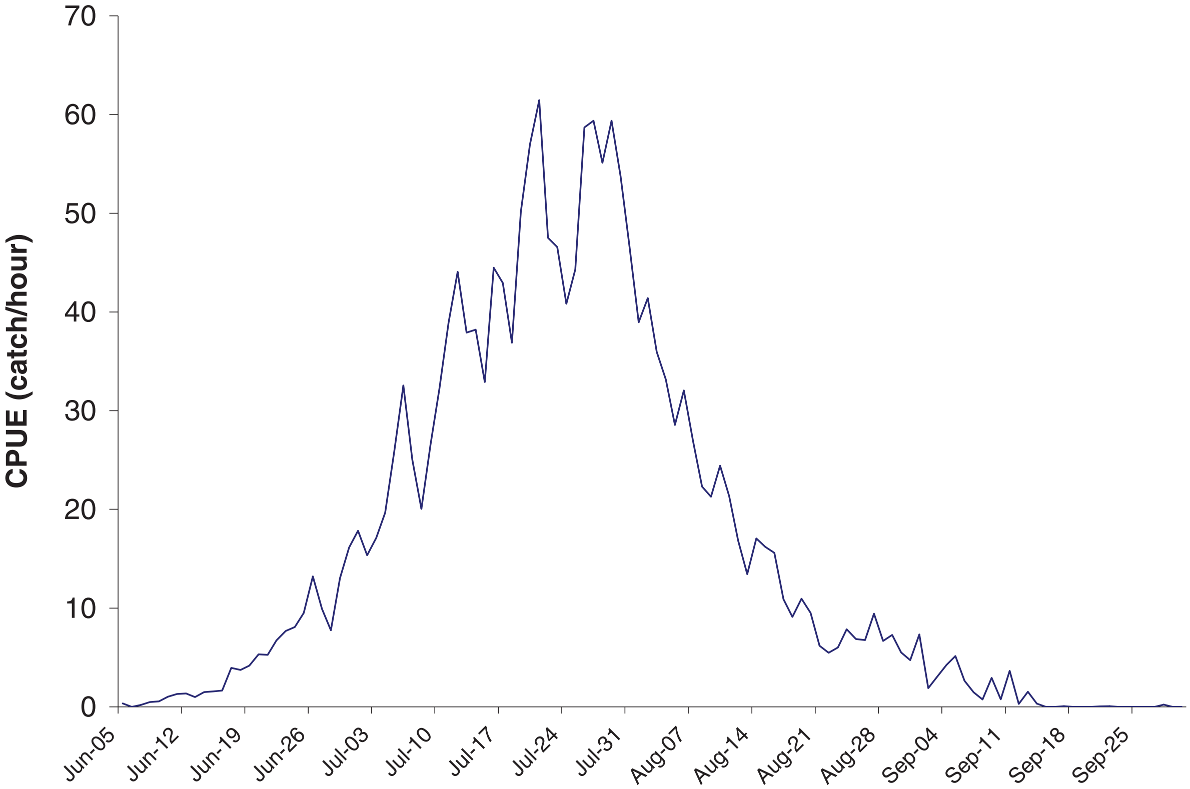

FIGURE 3. Average daily CPUE (catch/h) of Sockeye Salmon in the lower river test fishery, 2000–2011.

In the current study, timing of return of 12 stocks of Skeena River Sockeye Salmon was determined at a lower river test fishery. However, marine fisheries that targeted Skeena River Sockeye Salmon prior to their arrival at the test fishery were conducted. In essence, timing of the escapement from the marine fisheries was estimated at the test fishery, not the timing of return of the entire stock. If the timing of return of the entire stock was required, then a series of run reconstructions would be necessary

TABLE 5. Estimated percentage stock composition (SD in parentheses) of Skeena River Sockeye Salmon obtained from a lower river test fishery during 2000–2011 and estimated with a 27-population baseline incorporating variation at 14 microsatellites. Sockeye Salmon were analyzed in proportion to weekly run abundance within the year.

	Year												
Reporting group	2000	2001	2002	2003	2004	2005	2006	2007	2008	2009	2010	2011	Average
N	986	1,181	794	907	653	724	996	664	736	573	664	595	789
Alastair Lake	1.3	1.5	0.8	4.1	4.8	6.3	2.0	3.4	0.4	0.4	2.9	3.5	2.6 (0.6)
Lakelse Lake	0.8	2.0	0.4	1.1	3.4	2.7	1.3	1.1	0.4	0.7	1.2	2.0	1.4 (0.4)
Zymoetz River	0.3	0.3	1.1	1.7	0.6	2.2	0.4	0.9	0.0	0.7	0.7	1.3	0.9 (0.3)
Kitwanga Lake	0.0	0.1	0.0	0.3	0.1	0.0	0.0	0.0	0.3	0.5	2.5	0.0	0.3 (0.2)
Kitsumkalum Lake	0.5	1.2	1.5	6.5	2.6	2.1	0.2	0.9	1.1	1.5	3.9	1.7	2.0 (0.5)
Kispiox River	1.5	1.6	3.7	3.3	2.4	3.1	1.4	2.2	4.5	2.1	1.7	1.9	2.4 (0.6)
Motase Lake	0.1	0.1	0.0	0.2	0.0	0.3	0.0	0.0	0.0	0.4	0.1	0.4	0.1 (0.1)
Morice Lake	0.5	1.4	2.0	1.7	0.4	0.3	0.2	2.2	1.5	1.9	1.6	1.2	1.2 (0.4)
Bear Lake	1.3	1.8	0.6	0.9	1.0	0.3	0.6	0.0	0.9	1.7	0.5	0.7	0.8 (0.4)
Sustut Lake	0.2	0.1	0.3	0.9	0.5	0.3	0.2	0.8	0.1	0.6	0.9	0.7	0.5 (0.2)
Slamgeesh Lake	0.2	0.0	0.9	0.9	0.6	0.3	0.9	0.1	0.8	4.1	0.8	0.9	0.9 (0.4)
Babine River	93.0	90.0	88.6	78.4	83.7	82.2	92.7	88.5	89.9	85.5	83.2	85.6	86.8 (1.3)

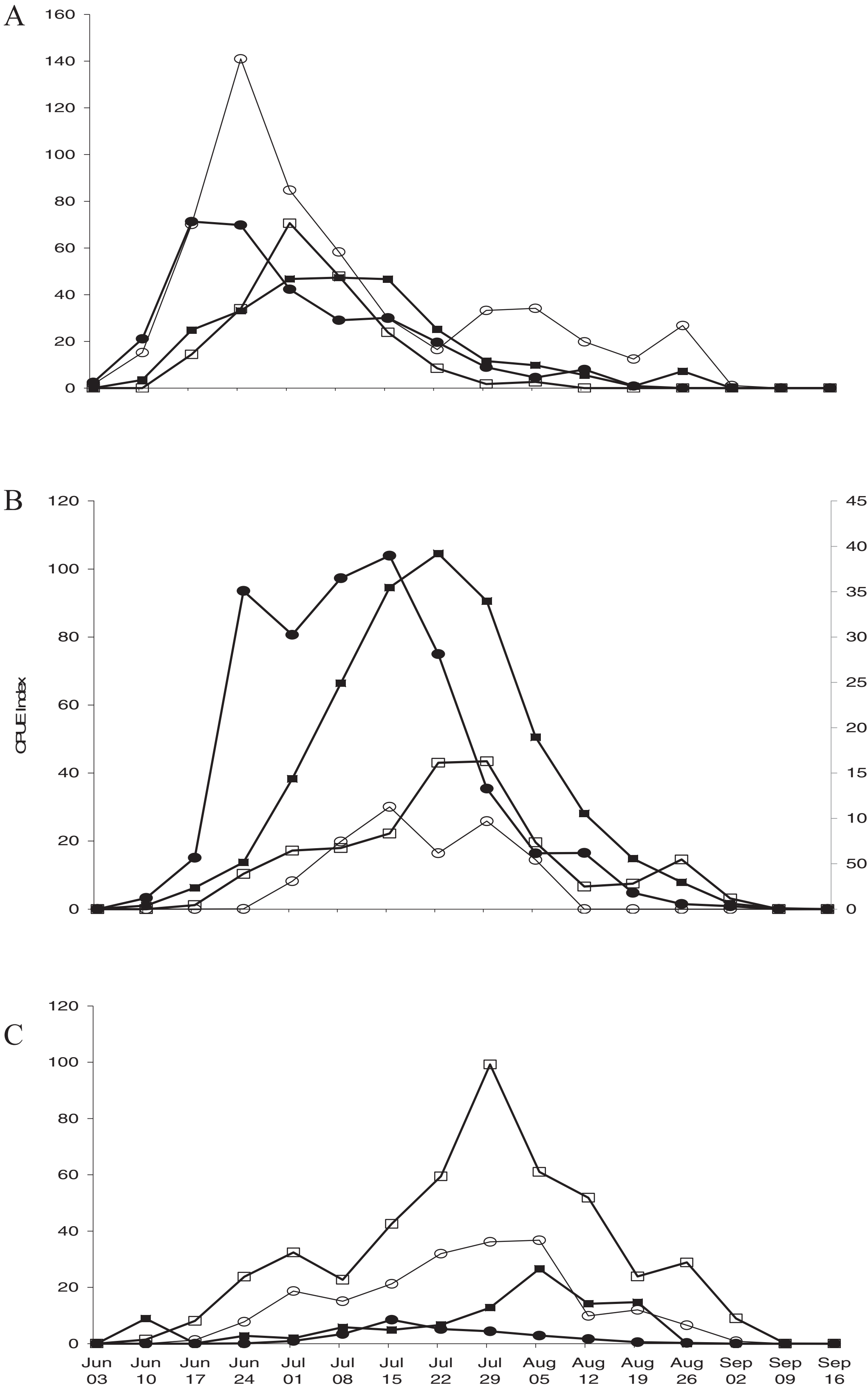

FIGURE 4. Total average weekly index of abundance by reporting group (Table 1) based upon returns to the lower river test fishery, 2000–2011. (**A**) Returning groups were Lakelse Lake (filled circle), Alastair Lake (open circle), Zymoetz River (open square), and Morice Lake (filled square). (**B**) Returning groups were Kispiox River (filled circle), Sustut Lake (open circle), Slamgeesh Lake (open square), and Babine Lake (filled square). Scale to the right refers to Babine Lake only. (**C**) Returning groups were Motase Lake (filled circle), Bear Lake (open circle), Kitsumkalum Lake (open square), and Kitwanga Lake (filled square). Date plotted along the *x*-axis is the beginning day of a week.

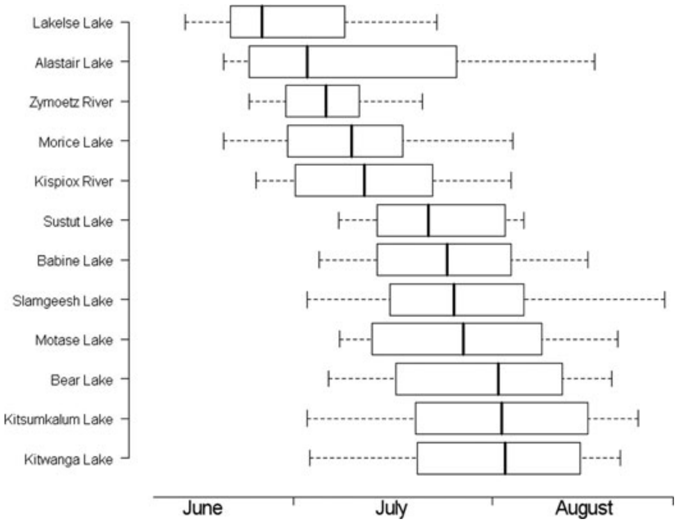

FIGURE 5. Migration timing distribution of Skeena River Sockeye Salmon by reporting group (Table 1) based upon returns to the lower river test fishery, 2000–2011. Each box plot presents the median (solid line), upper and lower quartiles (upper and lower box boundaries), and 10th and 90th percentiles.

to move the escapements back to the fishing grounds prior to any commercial exploitation of the return. Fishery exploitation can influence estimated abundance and timing, as declining daily abundance typically observed near July 24 may have reflected the effect of marine commercial fisheries catch.

Populations spawning in tributaries in the lower portion of the Skeena River drainage (Lakelse Lake, Alastair Lake, and Zymoetz River) displayed an earlier timing of return than did those in other portions of the drainage. A similar early timing of return has also been observed in the Zymoetz River population of steelhead (Beacham et al. 2012). The prespawning Sockeye Salmon typically hold in the lakes in each drainage for an extended period before entering streams to spawn. An early timing of return was perhaps related to stream flows and water temperatures in the tributary streams.

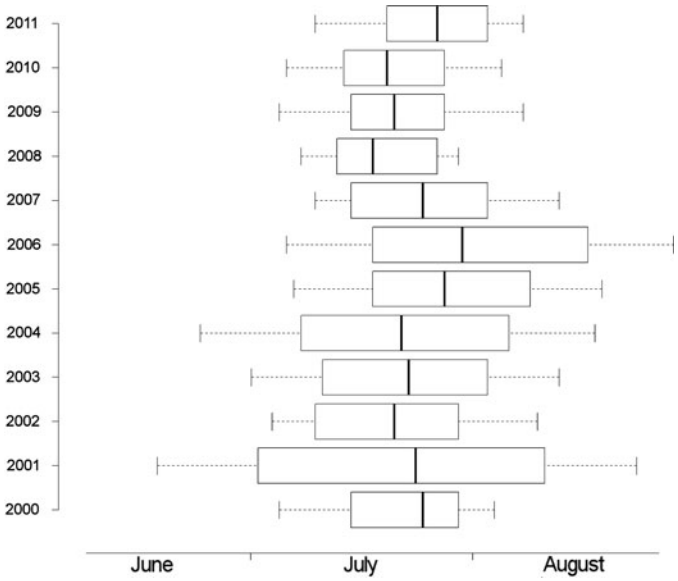

FIGURE 6. Annual migration timing distribution of Babine Lake Sockeye Salmon based upon returns to the lower river test fishery, 2000–2011. Each box plot presents the median (solid line), upper and lower quartiles (upper and lower box boundaries), and 10th and 90th percentiles.

In the Skeena River, an estimate of Sockeye Salmon escapement to Babine Lake is obtained directly from a counting fence, whereas visual surveys are typically used to estimate escapement in other Skeena River tributaries. There has been a discrepancy in non-Babine Lake escapements estimated from visual surveys and those estimated from the Tyee test fishery using stock identification techniques (Rutherford et al. 1999), and this discrepancy has continued through changes in the technology used for stock identification. Non-Babine Lake escapements are always consistently fewer when estimated visually than when estimates are derived from the test fishery coupled with stock identification. This continuing discrepancy in non-Babine Lake escapements may be due to several sources. First, the proportion of Babine Lake-origin fish may be consistently underestimated through stock identification techniques, thus inflating the estimate of the non-Babine Lake proportion. This bias seems unlikely, as testing of known-origin samples provided evidence of accurate determination of the Babine Lake component in mixed-stock samples. Secondly, samples from the test fishery may underrepresent the Babine Lake component due to smaller average size of Babine-origin individuals or high abundance during the main return period of the Babine Lake stock, saturating the net used in the test fishery (Cox-Rogers and Jantz 1993). Variable mesh size would likely preclude reduced vulnerability of Babine Lake-origin fish to the gear, and there is little evidence to suggest that vulnerability to capture is significantly impaired during periods of large returning abundance. For example, if catchability in the test fishery changes, then large returns to Babine Lake should not necessarily be associated with higher indices of abundance at the Tyee test fishery. Rutherford et al. (1999) demonstrated that there was clearly a relationship between the test fishery index of abundance and the Babine Lake fence count. Thus, it seems unlikely that the discrepancy in escapement estimates is due to unrepresentative sampling in the test fishery. Thirdly, expansion of the Babine Lake fence count to a drainage escapement assumes that mortality en route to the spawning grounds is either zero or the same mortality occurred in the non-Babine Lake stocks as in the Babine Lake stock. For a consistent bias to occur in which the non-Babine Lake stock escapement is overestimated at the test fishery, then enroute mortality of the non-Babine Lake stocks would have to be higher than that of the Babine Lake stock. There is no evidence available to evaluate this scenario, and it remains as a viable but still untested hypothesis. Finally, visual estimates of escapement may simply underestimate the actual abundance of Sockeye Salmon on the spawning grounds (Brett 1952). This factor seems to be the most likely explanation of the continuing discrepancy between non-Babine Lake escapement estimated at the test fishery and at the spawning grounds. In fact, in run reconstructions by the Pacific Salmon Commission, non-Babine Lake visual escapement estimates are currently expanded by a factor of 3.56, which is thought to account for visual underestimation of the escapement and missing survey sites (S. Cox-Rogers, personal observation).

A test fishery coupled with genetic stock identification of migrating salmon can provide a powerful fishery assessment and management tool to estimate escapement past the test fishery. If an absolute measure of abundance is available from a population that constitutes a major portion of the return, then the abundance of the major population is divided by its seasonal proportional contribution to the test fishery, providing an estimate of drainage escapement. Escapement of smaller populations is estimated by multiplying the drainage escapement by the seasonal proportional contribution to the test fishery. These circumstances apply to the Skeena River Sockeye Salmon test fishery, where returns are dominated by individuals originating from Babine Lake. Information on the timing of return is used to structure fishery openings to target productive stocks like Babine Lake, with the fishery closed to minimize exploitation of stocks of conservation concern. Stock-specific timing, harvest rates, and escapement abundance are obtained by the application of genetic stock identification to samples derived from both commercial and test fisheries.

Similar circumstances apply to the Nass River in northern British Columbia, where most of the drainage occurs in more remote areas of the province. Returns to the Nass River are dominated by Meziadin Lake-origin individuals, and smaller populations are present in the drainage (Beacham and Wood 1999). In 2009, discrepancies began to occur between estimated Kwinageese River escapement at the lower Nass River test fishery and abundance observed on the spawning grounds, with far fewer Sockeye Salmon reaching the spawning grounds than were estimated to be at the test fishery. This discrepancy prompted a survey of the Kwinageese River in July 2011, where a previously unknown rockslide had caused a 3-m-high waterfall to form, effectively blocking passage to most of the Sockeye Salmon. A helicopter was used shortly thereafter to place concrete blocks in a pool at the base of the waterfall, raising the level of the pool by a meter, allowing passage of the salmon over the waterfall. Based upon the estimated stock composition in the lower Nass River test fishery, assessment staff had confidence that Sockeye Salmon originating from the Kwinageese River were actually in the lower Nass River, narrowing the location where the loss of salmon was occurring. The test fishery results were important in the management and assessment of all Nass River Sockeye Salmon, as managers had subsequently restricted fishery openings to permit passage of Kwinageese River salmon after spawning escapement had declined dramatically in 2009.

The application of genetic stock identification technology to a salmon test fishery can provide a powerful and cost-effective method of estimating relative population abundance and timing for application in fishery management. For example, stock composition estimated through genetic analysis, along with daily harvest counts, have been the primary sources of information used to manage a Chinook Salmon fishery in the lower Columbia River (Shaklee et al. 1999). Similarly, if fisheries exploit a mixture of populations that have overlapping run timing, determination of the timing of run components that enter a river drainage may allow for the development of a management regime that targets a specific component of the return (Doctor et al. 2010). The application of genetic stock identification to abundance information derived from test or commercial fisheries in a river drainage is a fundamental tool in the management of fisheries in British Columbia (Beacham et al. 2004), Alaska (Smith et al. 2005; Flannery et al. 2010), and the Columbia River (Shaklee et al. 1999). One limitation of the technique is precise estimation of stock composition for populations with low ($<5\%$) relative abundance in the fishery, but precision can be improved by increasing the number of fish sampled in the test fishery, as well as adding more informative genetic markers in estimation of stock composition. More generally, marine applications of genetic stock identification to test or commercial fishery samples can provide managers with accurate information on where and when to conduct fisheries to either exploit or avoid specific stocks of salmon. As costs for genetic analysis of individuals will likely decline in the near future as more automated procedures are applied in laboratory analysis, with new and additional genetic markers providing increased resolution among individual populations, it is likely that genetic stock identification will play an increasing role in salmon fisheries management applications.

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