Estimation of Stock Composition and Individual Identification of Sockeye Salmon on a Pacific Rim Basis Using Microsatellite and Major Histocompatibility Complex Variation

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Abstract.—The variation at 14 microsatellite loci and one major histocompatibility complex (MHC) locus was surveyed for over 48,000 sockeye salmon *Oncorhynchus nerka* sampled from 299 localities ranging from the Columbia River to Japan. For the microsatellite loci, the number of alleles observed at a locus was related to the power of the locus in providing accurate estimates of stock composition of single-population mixtures. In an analysis of single-population mixtures where the Pacific Rim baseline was used for estimation of stock identification, 80% accuracy for the average population was achieved by employing approximately 80 alleles in the analysis. Increasing the accuracy of estimated stock compositions to 90% for the average population required approximately 400 microsatellite alleles. When all loci were used to estimate stock compositions, estimates were above 80% for all sampling sites or populations, above 90% for the lake of origin, and generally above 95% for the region of origin. Analysis of known-origin samples indicated that accurate lake or regional estimates of stock composition were obtained. The accuracy of identification of individual fish to the correct lake of origin was above 90%, regardless of whether the lakes were geographically widespread or within a single watershed. The estimated stock compositions of mixed-fishery samples from the western Bering Sea, from the continental shelf near Kodiak Island in the Gulf of Alaska, from Southeast Alaska, and from Johnstone Strait in southern British Columbia were markedly different among samples. These stock compositions reflected geographical variation in fishery locations and variation in the migration pathways of either juvenile or maturing sockeye salmon. Variation of DNA enabled us to estimate accurately the origin of individual fish and the composition of mixed-stock samples from any location in the Pacific Rim distribution of sockeye salmon.

Sockeye salmon *Oncorhynchus nerka* have a wide distribution in the Pacific Rim spawning grounds, ranging from Japan, eastern Russia, Alaska, British Columbia, and Washington, to the Columbia River. During their marine life history phase, populations from many geographic areas may overlap in their oceanic distributions, particularly in the rearing areas in the Gulf of Alaska and the Bering Sea (Margolis 1963). During spawning migrations, the mix of populations becomes less diverse the closer the populations are to their spawning grounds, culminating in the returning sockeye salmon spawning in their natal

stream. Determining the origins of sockeye salmon in a sample of fish is thus most difficult for samples taken from immature salmon in northern marine feeding areas where there can potentially be a complex mixture of populations in the sample, with the level of difficulty decreasing as the potential for admixture of populations declines.

Several methods of stock identification currently exist for sockeye salmon; scale pattern analysis (Cook and Guthrie 1987), parasites (Margolis 1963), allozymes (Seeb et al. 2000), minisatellites (Beacham et al. 1995), microsatellites (Beacham and Wood 1999), and major histocompatibility complex (MHC) variation (Miller et al. 2001) are all potentially available for application to specific problems. Different techniques can to applied to stock identification problems depending on the

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geographic scale and the degree of resolution required in the application. Genetic methods of stock identification have several advantages over other techniques, among them the level of differentiation among populations and the stability of the genetic characters surveyed. Although allozymes proved successful initially in local applications (e.g., Seeb et al. 2000), DNA-level variation has been demonstrated to be effective in applications involving more complex mixtures of populations, allowing identification to the individual population in complex regional assemblages of populations (Beacham et al. 2004b, 2005). These genetic differences among populations are generally stable over time frames of interest in management applications. For example, differences among populations for Fraser River sockeye salmon were about 20 times greater than annual variation within populations for microsatellite loci, and 28 times greater than that for an MHC locus (Beacham et al. 2004b). As annual variation in allele frequencies in salmonid microsatellite and MHC loci is substantially less than differentiation among populations (Beacham and Wood 1999; Tessier and Bernatchez 1999; Beacham et al. 2000a, 2000b; Miller et al. 2001), there is no requirement for annual updating of baseline populations once sufficient surveys have been conducted to characterize adequately the genetic differentiation among populations.

The key requirement for the application of any stock identification technique is the accuracy of estimation of stock composition to the smallest practical unit. In some cases this can be to the local area, in many cases it requires identification to the river or lake of origin, and in the most demanding cases it will require the identification of individual sockeye salmon to the river or lake of origin. Surveys of variation at allozyme loci have demonstrated that the nursery lake is a key component in sockeye salmon population structure (Wood et al. 1994; Wood 1995). The requirement for increased population discrimination relative to that of other techniques led our laboratory initially to evaluate minisatellite (Beacham et al. 1995), microsatellite (Beacham and Wood 1999; Beacham et al. 2000a, 2000b), and MHC variation (Miller et al. 2001). Population-specific stock composition estimates of sockeye salmon have been available with microsatellite analysis in a local area (Beacham et al. 1998), within a river drainage (Beacham and Wood 1999), or between river drainages (Beacham et al. 2000b). Microsatellites can provide regional estimates as well,

but can also provide population-specific estimates in some applications if the survey of baseline populations has been adequate (Beacham et al. 2001; Beacham et al. 2003; Beacham et al. 2004b).

Rapid, accurate identification of individual Pacific salmon to their lake or river of origin is crucial to our understanding of their population-specific responses to recent climatic regime shifts in the north Pacific Ocean (Welch et al. 2000; Mueter et al. 2002). Identification of either freshwater or marine biotic and abiotic factors responsible for the shifting fortunes of salmon populations requires identification of individual fish sampled in freshwater or on the high seas to population of origin. Juveniles typically rear in one of hundreds of nursery lakes for at least 1 year before undertaking ocean migrations. For this species, the dramatic increases produced by climate change in some populations have been offset by severe declines in others (Hilborn et al. 2003). The potential intermingling of salmon throughout their marine existence necessitates identification of individual fish from mixed-population samples for delineation of population-specific migration pathways and marine feeding areas (Brodeur et al. 2003), and for the evaluation of physiological status during spawning migrations (Cooke et al. 2004). The holy grail of sockeye salmon stock identification is the determination of lake origin of individual fish from mixed-population samples obtained from any location throughout the species range.

In the current study, we evaluate the utility of using the variation at 14 microsatellite loci and one MHC locus for lake-specific identification of sockeye salmon over its natural range. This evaluation is conducted by examining the accuracy and precision of estimated stock compositions through an analysis of simulated mixtures and samples from fisheries in coastal British Columbia. Mixtures were resolved using a 299-population baseline incorporating populations from Japan, Russia, Alaska, British Columbia, and Washington. We demonstrate that sufficient population allele frequency variation exists at microsatellite and MHC loci in sockeye salmon to enable a highly accurate identification of individual fish to lake of origin on a Pacific Rim basis.

Methods

Collection of DNA samples and laboratory analysis.—Tissue samples were collected from adult fish in sockeye salmon populations from the Pacific Rim, and DNA was extracted from the samples as described by Withler et al. (2000). For the

survey of baseline populations, polymerase chain reaction (PCR) products at 14 microsatellite loci— *Ots2, Ots3* (Banks et al. 1999); *Ots100, Ots103, Ots107,* and *Ots108* (Beacham et al. 1998; Nelson and Beacham 1999); *Oki1* (two loci), *Oki6, Oki10, Oki16,* and *Oki29* (Smith et al. 1998 and unpublished); *One8* (Scribner et al. 1996); and *Omy77* (Morris et al. 1996)—were size fractionated on denaturing polyacrylamide gels, and allele sizes were determined with the ABI 377 automated DNA sequencer. Genetic variation at the MHC class II *DAB*-β1 locus (Miller et al. 2001) was surveyed by denaturing gradient gel electrophoresis (DGGE). β1 alleles were separated by DGGE with the Bio-Rad (Hercules, California) D Gene or D Code electrophoresis systems, with conditions determined by the methods of Miller et al. (1999). Fluorescently multiplexed- (FM-) DGGE (Miller et al. 2000) was used in the population survey.

Baseline populations and population structure.—The baseline survey consisted of an analysis of over 48,000 sockeye salmon from 299 populations from Japan, Russia, Alaska, British Columbia, and Washington. The sampling sites or populations surveyed in each geographic region are outlined in the Appendix; one population is included from Japan, 53 populations from Russia, 51 populations from Alaska, 190 populations from British Columbia, and four populations from Washington. The geographic regions outlined in the Appendix are indicated in Figure 1. Information on regional population structure has been outlined previously for sockeye salmon populations on the western coast of Vancouver Island (Beacham et al. 2002), the Fraser River (Beacham et al. 2004b), coastal British Columbia (Beacham et al., in press), the Nass and Skeena rivers (Beacham et al. 2000b), and northern British Columbia (Beacham et al. 2004a). A regional population structure was observed in the Pacific Rim analysis of microsatellite variation, populations within lakes and river drainages generally being more similar to each other compared with populations in other lakes or river drainages. Allele frequencies for all population surveyed in this study are available on the internet (http://www-sci.pac.dfo-mpo.gc.ca/mgl/default_e.htm).

Estimation of stock composition.—The evaluation of the Pacific Rim baseline for stock composition determination initially included an analysis of simulated fishery samples. Single-population mixtures (mixtures containing simulated multilocus genotypes derived entirely from a single population) were simulated for populations spanning the Pacific Rim distribution of sockeye salmon surveyed, and the entire 299-population baseline was used to estimate the stock composition of each mixture. Genotypic frequencies were determined for each locus in each population, and the statistical package for the analysis of mixtures software program (SPAM, version 3.7; Debevec et al. 2000) was used to es-
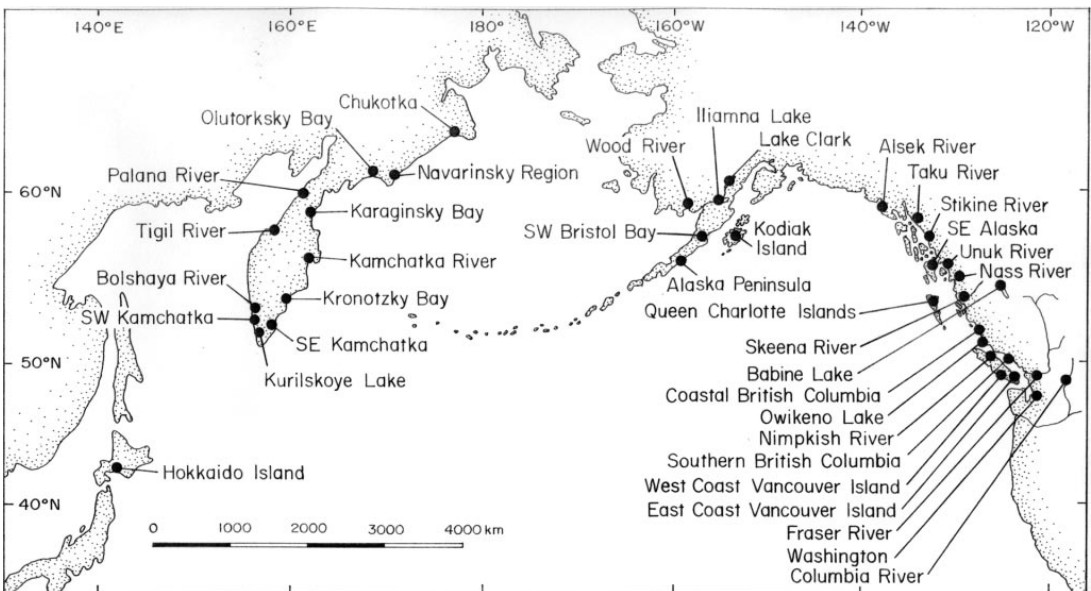

FIGURE 1.—Map indicating the geographic regions referred to in Appendix.

timate stock composition of simulated mixtures. The Rannala and Mountain (1997) correction to baseline allele frequencies was used in the analysis in order to avoid the occurrence of fish in the mixed sample from a specific population having an allele not observed in the baseline samples from that population. All loci were considered to be in Hardy–Weinberg equilibrium, and expected genotypic frequencies were determined from the observed allele frequencies. Reported stock compositions for simulated fishery samples are the bootstrap mean estimates of each mixture of 150 fish analyzed, mean and variance estimates derived from 100 simulations. Each baseline population and simulated fishery sample was sampled with replacement in order to simulate random variation involved in the collection of the baseline and fishery samples.

The accuracy of estimates of stock composition was first evaluated for each microsatellite and MHC locus individually for five stocks of current or historical (Owikeno Lake) major regional sockeye salmon production. This analysis was intended to compare the power of the MHC locus for stock identification relative to that of individual microsatellite loci. For the microsatellite loci only, the effect of the number of alleles observed at a locus on the accuracy of estimated stock compositions was evaluated for each of the 14 loci individually. Mean accuracy of estimated stock compositions for 28 single-population mixtures spanning a Pacific Rim distribution was compared with the number of alleles observed at each microsatellite locus. Analysis of subsequent simulated single-population mixtures for these 28 populations employed the full set of 14 microsatellite loci and one MHC locus. The effect of allele number on the accuracy of estimated stock compositions of single-population mixtures was evaluated for the most difficult and easiest of the populations to resolve. This was conducted by sequentially adding microsatellite loci to the analysis beginning with the locus with least number of alleles (*Oki1a*) and ending with the locus with the greatest number (*Oki10*). Six additional simulated multipopulation mixtures were evaluated, and accuracy and precision of estimated stock compositions were determined on the basis of both population and geographic region.

Analysis of simulated mixtures provided the initial evaluation of the utility of the baseline for stock composition analysis. The key assumption in the simulations is that the baseline used will be representative of populations present when it is applied to mixed-stock fishery samples. The next stage in the evaluation was to estimate stock com-

position of known-origin samples that were completely independent of the baseline used in the estimation. Samples from freshwater test fisheries were analyzed for five major rivers (Fraser, Skeena, Nass, Stikine, and Taku) in British Columbia. These test fisheries occurred in the lower part of each river, and it was assumed that all fish sampled in the test fisheries were native to the drainage in which the test fishery was conducted. Two additional known-origin samples (Barkley Sound and northern British Columbia–Southeast Alaska) were also evaluated using the Pacific Rim baseline, and these samples were initially provided to our laboratory as a test of accuracy of stock composition estimates on a local basis. For the northern British Columbia–Southeast Alaska known sample, origins of fish from Southeast Alaska were known to specific lakes as spawning ground samples were used to develop the sample. However, test fishery samples were used from the Nass and Skeena rivers, so individual lakes of origin were unknown in this case. Accuracy of the northern British Columbia–Southeast Alaska sample with a regional baseline was outlined by Beacham et al. (2005).

Analysis of the simulated mixtures was conducted entirely with SPAM. However, analysis of actual fishery samples was conducted with both SPAM and a Bayesian procedure (BAYES) as outlined by Pella and Masuda (2001). When SPAM was used in the analysis, the reported stock compositions for actual fishery samples were point estimates for each mixture analyzed (variance estimates derived from 100 bootstrap simulations). For BAYES, the initial FORTRAN-based computer program as outlined by Pella and Masuda (2001) required large amounts of computer analytical time when applied to stock identification problems with a baseline as comprehensive as employed in the current study. Given this limitation, a new version of the program was developed by our laboratory as a C-based program (cBAYES, available from our laboratory website). In the analysis, four 20,000-iteration Monte Carlo–Markov chains of estimated stock compositions were produced, and initial starting values for each chain was set at 0.90 for a particular population that was different for each chain. Estimated stock compositions were considered to have converged when the shrink factor was less than 1.2 for the four chains (Pella and Masuda 2001), and thus the starting values were considered to be irrelevant. Stock composition estimates converged before 20,000 iterations, and no further improvements in the es-

timates were observed in excess of 20,000 iterations. Therefore, 20,000 iterations were set as the standard in the analysis. The last 1,000 iterations from each of the four chains were then combined, and the mean and standard deviations of estimated stock compositions were determined. Accuracy and precision of estimated stock compositions of known samples were compared with both analytical procedures.

Four marine fishery samples of unknown composition from widely different geographic origins were analyzed to compare the performance of the baseline in estimating stock compositions. One fishery sample was obtained on 17–18 June 2002 from immature sockeye salmon in waters near coastal Russia in the western Bering Sea (54.2°N, 164.5°E), one sample during November 1997 from juvenile salmon waters near Kodiak Island in the northern Gulf of Alaska, one sample on 14 August 2002 from a fishery on maturing fish near Tree Point in Southeast Alaska, and one sample on 24 August 2004 from a migration pathway (Johnstone Strait) to the Fraser River in southern British Columbia. It was expected that widely divergent estimates of stock composition should be obtained from these four geographically distinct samples.

The accuracy of identification of individuals to a particular lake of origin was evaluated with cBAYES only. Multiple spawning locations were sampled in some lakes, and representative samples were removed from the baseline data. These samples provided for individual classification of a multipopulation mixture sample of known origin that was independent of the baseline. This method of creating a mixture of known origin relies on the fact that differentiation among populations within lakes at microsatellite loci is considerably less than the level of differentiation among populations in different lakes (Beacham et al. 2004b). Identification of individual fish to lake of origin was conducted with cBAYES, the lake of origin determined as the one with the highest probability of assignment. The analysis was restricted to those individuals scored at 10 or more loci in each of the test populations.

Results

Comparisons among Loci

The number of alleles observed at the 14 microsatellite loci surveyed ranged from 8 to 83; 15 alleles were observed at the MHC locus (Table 1). A determination of the relative power of individual loci in practical stock identification applications

TABLE 1.—Number of alleles among 299 sockeye salmon samples for 14 microsatellite loci and a major histocompatibility complex locus.

Locus	Number of alleles
Oki1a	8
Oki1b	10
Ots107	15
Omy77	20
Ots2	26
Ots3	26
Oki16	26
Ots108	29
Ots103	30
One8	32
Ots100	33
Oki6	37
Oki29	39
Oki10	83
DAB-β1	15

can be of prime importance. The initial comparision centered on five productive stocks with a Pan-Pacific distribution of lake of origin. The MHC locus was more effective for stock identification than 13 of the 14 microsatellite loci surveyed (Table 2). Although only 15 alleles were observed at the MHC locus, allele frequency differentiation among sockeye salmon from these lakes provided considerable power to discriminate these lakes from all other lakes and rivers surveyed in the study.

A range in the number of alleles observed among the microsatellite loci allowed a comparison of the effect of allele number on the relative power of the locus to estimate stock composition of representative single-population samples (populations were located throughout the Pacific Rim distribution of sockeye salmon; Table 3). The number of alleles observed at a locus was significantly related to the power of the locus in providing accurate estimates of stock composition of single-population mixtures ($r^2 = 0.75$; $P < 0.01$; Figure 2). Estimated stock compositions of single-population mixtures for loci with 15 or fewer alleles were less than 25%, for loci with 20–40 alleles about 50%, and for a locus with more than 80 alleles about 70%. In general, loci with more alleles present provided greater resolution of single-population mixtures than did loci with fewer alleles.

Analysis of Simulated Single-Population Mixtures

Analysis of simulated mixtures composed of a single population or sampling site resulted in estimates above 80% for the sampling site or population, above 90% for the lake of origin, and generally above 95% for the region of origin (Table

TABLE 2.—Mean estimated percentage stock compositions of single-stock mixtures (correct = 100%) for five stocks of major regional current or historical sockeye salmon production. Stock composition included the sum of allocations to all populations sampled within the lake drainage system. Stocks included in the analyses were Kurilskoye Lake (Kamchatka), Iliamna Lake (western Alaska), Babine Lake (northern British Columbia), Owikeno Lake (central British Columbia), and Quesnel Lake (Fraser River). Estimates were calculated with single loci for 14 microsatellite loci and one major histocompatibility complex locus. Simulations were conducted using a 299-population baseline, 150 fish in the mixture sample, and 100 resamplings in the mixture and baseline samples. Standard deviations are given in parentheses.

Locus	Kurilskoye	Iliamna	Babine	Owikeno	Quesnel	Mean
Oki1a	9.3 (12.4)	21.5 (22.6)	64.5 (25.0)	29.5 (29.0)	27.0 (24.8)	30.4 (22.8)
Oki1b	10.5 (18.6)	13.9 (18.8)	18.2 (22.7)	11.8 (15.9)	40.6 (26.5)	19.0 (20.5)
Ots107	11.9 (17.5)	7.3 (15.4)	18.9 (21.7)	34.0 (26.3)	53.7 (27.6)	25.2 (21.7)
Omy77	54.4 (25.0)	80.9 (19.3)	89.2 (8.8)	37.2 (18.9)	55.3 (16.0)	63.4 (17.6)
Ots2	71.4 (14.5)	36.3 (21.6)	48.9 (22.8)	33.8 (21.4)	79.5 (10.4)	54.0 (18.1)
Ots3	35.2 (22.5)	50.4 (25.5)	70.1 (21.3)	11.4 (19.0)	50.4 (25.6)	43.5 (22.8)
Oki16	48.2 (20.0)	47.2 (19.5)	77.8 (14.0)	85.0 (7.6)	57.6 (17.9)	63.2 (15.8)
Ots108	61.1 (14.4)	40.0 (16.0)	55.3 (12.4)	72.0 (11.0)	83.0 (6.7)	62.3 (12.1)
Ots103	66.7 (11.1)	40.5 (17.1)	71.3 (11.1)	24.1 (16.5)	85.0 (5.8)	57.5 (12.3)
One8	64.9 (14.6)	58.2 (19.6)	71.6 (14.0)	53.4 (19.2)	58.0 (25.0)	61.2 (18.5)
Ots100	78.9 (9.2)	66.9 (11.8)	80.4 (8.1)	88.9 (4.8)	87.2 (8.5)	80.5 (8.5)
Oki6	42.1 (23.7)	14.3 (19.5)	74.0 (17.7)	56.3 (21.5)	57.6 (17.9)	48.9 (20.1)
Oki29	49.9 (16.5)	73.4 (10.9)	80.4 (8.0)	66.7 (12.6)	79.8 (6.9)	70.0 (10.6)
Oki10	61.7 (12.0)	70.8 (8.5)	64.4 (10.9)	60.8 (11.6)	88.1 (6.9)	69.6 (10.0)
DAB-β1	86.7 (10.2)	84.6 (10.1)	85.4 (19.1)	65.0 (15.8)	80.5 (10.8)	80.5 (13.2)

TABLE 3.—Mean estimated percentage compositions of single-population mixtures (correct = 100%) for 28 representative populations of sockeye salmon from the Pacific Rim distribution of populations calculated with 14 microsatellite loci and one major histocompatibility complex locus. The lake designation includes percentages allocated to all populations within a lake, and the region designation includes allocations to all populations in the region. Simulations were conducted using a 299-population baseline, 150 fish in the mixture sample, and 100 resamplings in the mixture and baseline samples. Standard deviations are given in parentheses.

| Population	Region	Allocation		
		Population	Lake	Region
Abira River	Hokkaido Island	95.7 (1.7)	95.7 (1.7)	95.7 (1.7)
Tigil River	Tigil River basin	95.0 (2.0)	95.0 (2.0)	95.0 (2.0)
Plotnikova	Bolshaya River basin	90.9 (3.3)	90.9 (3.3)	94.9 (2.0)
Kirushutk	Kurilskoye Lake	80.5 (4.8)	96.7 (1.7)	96.7 (1.7)
Paratunka	Southeastern Kamchatka	91.9 (2.4)	91.9 (2.4)	91.9 (2.4)
Elovka	Kamchatka River	94.5 (2.1)	94.5 (2.1)	96.9 (1.4)
Laguna Anana	Olutorksky Bay	94.2 (2.7)	94.2 (2.7)	97.8 (1.3)
Painter Creek	Alaska Peninsula	89.9 (3.2)	89.9 (3.2)	89.9 (3.2)
Mission Creek	Wood River	91.7 (2.5)	97.7 (1.4)	98.4 (1.1)
Lynx Creek	Wood River	92.0 (2.6)	92.0 (2.6)	94.9 (1.9)
Knutson Bay	Iliamna Lake	87.6 (4.1)	96.9 (1.5)	96.9 (1.5)
Kijik River	Lake Clark	88.4 (3.3)	95.6 (1.8)	95.6 (1.8)
Ruth Lake	Southwest Bristol Bay	90.1 (3.2)	90.1 (3.2)	90.1 (3.2)
Meadow (late)	Kodiak Island	83.3 (4.6)	95.4 (1.9)	95.8 (1.8)
Hetta	Southeast Alaska	98.3 (1.1)	98.3 (1.1)	99.0 (1.2)
Neskataheen	Alsek River	98.5 (1.2)	98.5 (1.2)	99.9 (0.1)
Little Tatsamenie	Taku River	89.7 (4.0)	97.3 (1.8)	97.7 (1.2)
Tahlran	Stikine River	98.7 (1.1)	98.7 (1.1)	99.6 (0.5)
Meziadin Beach	Nass River	89.4 (4.0)	98.6 (1.2)	98.7 (1.2)
Pinkut Creek	Babine Lake	86.2 (5.2)	99.5 (0.7)	99.5 (0.7)
Copper River	Queen Charlotte Islands	97.1 (1.4)	97.1 (1.4)	97.1 (1.4)
Inziana River	Owikeno Lake	87.1 (4.7)	99.2 (0.8)	99.2 (0.8)
Canoona Lake	Central British Columbia	94.7 (2.0)	94.7 (2.0)	95.2 (2.0)
Henderson Lake	West Coast Vancouver Island	97.8 (1.4)	97.8 (1.4)	99.6 (0.5)
Sakinaw Lake	South British Columbia	97.5 (1.3)	97.5 (1.3)	97.6 (1.3)
Chilko Lake	Fraser River	97.4 (1.8)	98.8 (0.8)	99.9 (0.2)
Lake Washington	Washington	96.3 (1.5)	96.3 (1.5)	96.4 (1.5)
Okanagan River	Columbia River	99.6 (0.6)	99.6 (0.6)	99.6 (0.5)
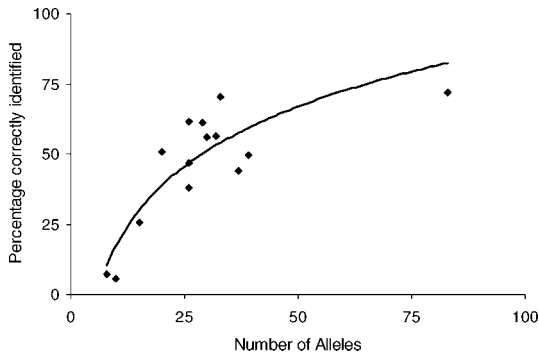
FIGURE 2.—Relationship between the number of alleles observed at a microsatellite locus and the accuracy obtained for single-population mixtures using only a single locus and the Pacific Rim baseline for 28 populations of sockeye salmon (the populations are described in Table 3).
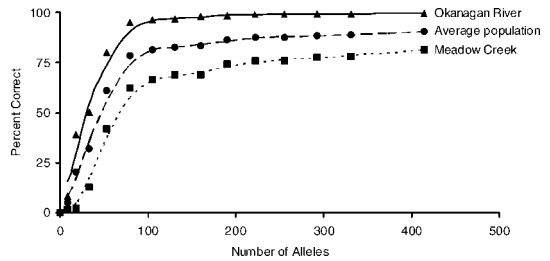

FIGURE 3.—Relationship between the number of microsatellite alleles used in estimating stock compositions and the accuracy obtained for single-population mixtures of Okanagan River, an average population, and Meadow Creek (late) sockeye salmon.

3). Samples had been analyzed from multiple spawning sites within a lake for a number of lakes in the survey, and for the results outlined in Table 3, these included Kurilskoye Lake (Kirushutk sampling site), Lake Aleknagik (Mission Creek), Iliamna Lake (Knutson Bay), Lake Clark (Kijik River), Karluk Lake (Meadow Creek late), Meziadin Lake (beach spawners), Babine Lake (Pinkut Creek), Owikeno Lake (Inziana River), and Chilko Lake (Chilko River). Estimates of stock composition for the individual sampling site within a lake ranged from 80% to 90% of the simulated mixture, but estimated stock composition for the lake was always in excess of 90%. Accurate estimates of stock composition by lake of origin will be available as long as a particular lake is represented in the baseline used in the stock composition estimation.

The number of microsatellite alleles used in the stock composition analysis directly influenced the average accuracy obtained in resolving single-population mixtures. For populations difficult to identify, such as late-run Meadow Creek sockeye salmon from Karluk Lake on Kodiak Island (Table 3), increasing the number of microsatellite alleles to the maximum 414 alleles available resulted in the maximum accuracy of estimates for this population (Figure 3). For distinct populations, such as Okanagan River (Table 3), 97% accuracy in estimated stock compositions was achieved by employing approximately only 100 alleles. For the average population, increasing the number of alleles employed in stock composition analysis consistently increased the accuracy of the estimates. For estimates up to 80% accuracy, each additional

allele used in the estimation increased accuracy by about 1%, so that an 80% accuracy for the average population was achieved by employing approximately 80 alleles in the analysis. Increasing the accuracy of estimated stock compositions to 90% for the average population required approximately 400 microsatellite alleles. Further diminishing returns in accuracy per allele added would be expected by employing more than 400 alleles in the stock composition analysis.

Analysis of Simulated Multipopulation Mixtures

Six fishery mixture samples were simulated, and stock compositions were estimated for the individual site and regions. Estimated stock compositions of a simulated mixture containing fish from Russia and Alaska were usually within 1% of the specific site or population, and within 1% of the specific region of origin (Table 4, mixture 1). Similar results were observed for a mixture comprising Japanese, Russian, and Alaskan sockeye salmon (Table 4, mixture 2). For example, for the four populations from Southeast Alaska, estimates of the individual population contributions were within 0.5% of the actual values, as was the regional estimate (20%) for Southeast Alaska. Mixtures containing populations from British Columbia and Russia were usually within 1% on both a population and region basis, the exceptions being populations from lakes having multiple populations or sampling sites in the baseline (Table 4, mixture 3). Accurate estimates of stock composition on both a population and regional basis were obtained for analysis of mixtures containing only Fraser River populations (Table 4, mixture 4). Similar results were observed for mixtures containing populations from Southeast Alaska to Washington, with both population and regional estimates usually within 1% of actual values (Table 4, mixture 5). Regional

TABLE 4.—Estimated percentage stock compositions of simulated mixtures of sockeye salmon as may be encountered in marine samples. Each mixture of 150 fish was generated 100 times with replacement, and stock compositions of the mixtures were estimated by resampling each of the 299 baseline populations with replacement to obtain a new distribution of allele frequencies. Standard deviations are given in parentheses. The expected regional composition is obtained by adding the true population components; the estimated regional composition is listed in the Region column for each mixture.

Population (region)	True	Estimated Population	Estimated Region
Mixture 1			
Woody Island (Iliamna)	10	7.6 (2.4)	9.8 (2.6)
Hansen Creek (Wood River)	5	4.6 (2.0)	
Lynx Creek (Wood River)	5	4.4 (1.8)	9.6 (2.5)
Karluk Lake (Kodiak Island)	5	4.0 (1.8)	
Linda Creek (Kodiak Island)	5	3.9 (1.6)	10.7 (2.5)
Painter Creek (Alaska Peninsula)	5	4.7 (2.0)	4.7 (2.0)
Gavrushka River (Kurilskoye Lake)	10	6.5 (2.4)	
Oladochnaya Bay (Kurilskoye Lake)	10	7.3 (2.6)	19.0 (3.0)
Plotnikova River (Bolshaya River)	10	10.0 (2.7)	10.5 (2.7)
Elovka River (Kamchatka River)	10	10.0 (2.6)	
Kamchatka River (Kamchatka River)	10	8.5 (2.6)	20.0 (3.5)
Lake Anana (Olutorksky Bay)	10	9.1 (2.6)	
Lake Potat (Olutorksky Bay)	5	4.2 (1.7)	14.1 (3.0)
Mixture 2			
McDonald (Southeast Alaska)	5	4.5 (1.8)	
Petersburg (Southeast Alaska)	5	4.9 (1.5)	
Red Bay (Southeast Alaska)	5	5.1 (1.9)	
Sitkoh (Southeast Alaska)	5	4.8 (1.7)	19.6 (3.4)
Kijik River (Lake Clark)	10	9.0 (2.5)	9.7 (2.3)
Mission Creek (Wood River)	10	9.3 (2.3)	10.0 (2.3)
Ruth Lake (Southwest Bristol)	10	8.4 (2.6)	8.4 (2.6)
Up. Station (Kodiak Island)	10	9.0 (2.4)	9.8 (2.5)
Kirushutk (Kurilskoye)	10	7.8 (2.5)	10.9 (2.7)
Avachinsky (Southeast Kamchatka)	20	17.8 (2.9)	17.8 (2.9)
Abira River (Hokkaido Island)	10	9.8 (2.7)	9.8 (2.7)
Mixture 3			
Nahatlatch (Fraser)	20	19.5 (3.4)	19.6 (3.5)
Fulton River (Babine Lake)	20	16.5 (3.5)	20.0 (3.4)
Klukshu River (Alsek River)	20	19.3 (3.5)	19.9 (3.2)
Lake Anana (Olutorksky Bay)	20	18.5 (3.3)	19.5 (3.2)
Gavrushka Bay (Kuril Lake)	20	14.4 (2.8)	18.9 (3.2)
Mixture 4			
Fennell (Fraser)	20	19.6 (3.4)	
Gates Creek (Fraser)	20	20.0 (3.5)	
Birkenhead River (Fraser)	20	19.6 (3.2)	
Horsefly River (Fraser)	20	18.3 (3.6)	
Little Adams River (Fraser)	20	17.7 (3.5)	99.7 (0.5)
Mixture 5			
Baker Lake (Washington)	10	9.3 (2.3)	9.5 (2.3)
Great Central (West Coast Vancouver Island)	10	9.7 (2.7)	10.0 (2.6)
Ashlum River (Owikeno Lake)	5	2.9 (1.8)	5.4 (2.1)
Bowser Lake (Nass River)	10	10.0 (2.4)	10.2 (2.4)
McDonnell Lake (Skeena River)	10	10.0 (2.3)	10.1 (2.3)
Chutine Lake (Stikine River)	10	8.0 (2.3)	11.1 (2.4)
Lake Trapper (Taku River)	15	13.4 (2.8)	14.2 (3.0)
Copper River (Queen Charlotte Islands)	10	9.2 (2.3)	9.2 (2.3)
Hugh Smith (Southeast Alaska)	10	9.5 (2.2)	
Kah Sheets (Southeast Alaska)	10	9.6 (2.5)	19.5 (3.2)
Mixture 6			
Okanagan River (Columbia)	10	10.0 (2.4)	10.0 (2.4)
Bowron River (Fraser)	15	14.7 (3.1)	15.1 (3.1)
Devon Lake (British Columbia Central)	5	4.7 (1.7)	4.9 (1.7)
Alastair Lake (Skeena River)	15	14.7 (3.0)	14.8 (3.0)
Shakes Creek (Stikine River)	5	3.4 (1.7)	5.1 (1.8)
Karta Lake (Southeast Alaska)	10	9.9 (2.6)	10.4 (2.6)
Fuel Dump Island (Iliamna Lake)	10	7.5 (2.6)	9.6 (2.7)
Lake Thumb (Kodiak Island)	10	7.1 (2.3)	8.9 (2.2)
Dvu-Yurtochnaya R (Kamchatka River)	15	13.2 (3.1)	14.6 (3.0)
Abira River (Hokkaido Island)	5	5.0 (1.8)	5.0 (1.8)

TABLE 5.—Estimated percentage stock compositions of 200 fish each for Fraser River (sampled in 2004), Skeena River (2003), Nass River (2001), Stikine River (2001), and Alsek River (2001) sockeye salmon obtained from fisheries within each river system and estimated with a 299-population baseline incorporating variation at 14 microsatellite loci and one major histocompatibility complex locus. Estimated stock compositions were derived from both SPAM and cBAYES (see text; standard deviations in parentheses). Known-origin samples were also available from Barkley Sound (three lakes sampled in 2002 [$N = 100$ fish]) on the west coast of Vancouver Island (WCVI) and Southeast Alaska (sampled 2002 [$N = 494$], incorporating 16 lakes in Southeast Alaska as well as the Skeena River and Nass River in northern British Columbia).

Region	Actual	SPAM	cBAYES
Fraser River	100.0	98.5 (1.5)	99.2 (0.8)
Skeena River	100.0	92.9 (2.5)	93.9 (1.7)
Nass River	100.0	93.1 (3.4)	98.2 (1.3)
Stikine River	100.0	86.4 (3.0)	85.6 (3.1)
Alsek	100.0	94.4 (2.8)	97.3 (1.7)
Barkley Sound			
Sproat Lake	32.0	29.1 (5.8)	28.2 (5.1)
Great Central Lake	22.0	20.4 (4.7)	19.2 (4.6)
Henderson Lake	46.0	44.7 (6.3)	51.6 (5.5)
Other WCVI	0.0	5.8 (4.1)	0.0 (0.2)
Southeast Alaska			
Skeena River	32.7	31.4 (2.1)	29.8 (2.2)
Nass River	37.8	38.6 (2.7)	40.1 (2.3)
Hetta	2.2	2.4 (0.7)	2.5 (0.7)
Hugh Smith	3.0	3.4 (1.0)	3.6 (1.0)
Kah Sheets	1.6	1.6 (0.6)	1.6 (0.6)
Karta	2.6	2.6 (0.7)	2.7 (0.7)
Kegan	1.0	1.1 (0.5)	1.1 (0.5)
Klakas	0.6	0.5 (0.3)	0.5 (0.3)
Kunk	0.6	0.4 (0.4)	0.5 (0.3)
Kutlaku	1.0	0.8 (0.4)	0.9 (0.4)
Luck	2.4	2.0 (0.7)	2.1 (0.7)
Mahoney	3.0	3.0 (0.7)	3.1 (0.8)
MacDonald	2.6	2.1 (0.9)	2.5 (0.9)
Petersburg	0.6	0.6 (0.4)	0.6 (0.3)
Red Bay	1.4	1.2 (0.5)	1.2 (0.5)
Salmon Bay	3.0	3.4 (0.9)	3.7 (0.9)
Shipley	0.8	0.8 (0.4)	0.8 (0.4)
Thoms	2.6	2.4 (0.7)	2.4 (0.7)
All southeastern Alaska	29.5	28.8 (2.2)	29.8 (2.0)

compositions of a simulated mixture of fish from the entire Pacific Rim distribution of sockeye salmon, ranging from the Columbia River in North America to Japan, were generally within 1% of the actual regional contribution (Table 4, mixture 6). Accurate estimates of stock composition should be available when the baseline is applied to any sample drawn from the Pacific Rim distribution of Pacific salmon, particularly if the objective is to obtain an estimate of the local regional contribution to the sample.

Analysis of Known-Origin Mixtures

Analysis of the simulated 100% Fraser River mixture outlined in Table 3 indicated that sockeye salmon from this drainage should be well differentiated from other regional groups of sockeye salmon. The validity of this finding was tested by analyzing fishery samples from this drainage, as well as from four other major river drainages in British Columbia (Nass, Skeena, Stikine, and Alsek rivers). The expectation would be that 100% of each sample should be allocated to populations within the drainage, as these were samples taken from fish caught within the drainage and thus their river of origin was known with a high probability. Stock composition of the Fraser River sample estimated with the Pacific Rim baseline was at least 98.5% Fraser River origin (Table 5). This analysis confirmed the results of analysis of simulated samples and indicated that Fraser River estimated stock compositions should have little bias. Estimated stock compositions of fishery samples from the Nass, Skeena, and Alsek rivers were at least 93% to river of origin, while the sample from the Stikine River was estimated at approximately 86% Stikine River origin. Approximately 11% of the fish in this sample were estimated to have origi-

TABLE 6.—Percentage of individual sockeye salmon correctly identified to their lake of origin for eight lakes ranging from Kamchatka, Russia, to British Columbia (BC), Canada, using variation at 14 microsatellite loci and one major histocompatibility complex locus. Individuals had to be scored for at least 10 loci for inclusion in the analysis (N = the number of fish analyzed).

Geographic area	Lake	Sampling site	N	% Correct
Kamchatka, Russia	Kurilskoye	Far North Bay	54	94.4
Bristol Bay, Alaska	Iliamna	Fuel Dump Island	97	95.9
Kodiak Island, Alaska	Karluk	Shore spawners	94	95.7
Alsek River, BC	Kluksu	Outlet weir	311	92.6
Skeena River, BC	Babine	Four Mile Creek	76	98.7
Central Coast, BC	Owikeno	Sheemahant Creek	250	97.6
Vancouver Island, BC	Sproat	Gracie Creek	69	100.0
Fraser River, BC	Quesnel	Middle Horsefly River	143	100.0

nated from the Taku River, an adjacent river to the north of the Stikine River drainage.

Analysis of the known-origin sample derived from three populations from Barkley Sound on the western coast of Vancouver Island indicated that the contributions of specific lakes were each underestimated by about 2% for SPAM-based estimates, but all fish in the sample were identified as western coast Vancouver Island in origin (Table 5). Estimates based on cBAYES were slightly less accurate than SPAM-based estimates on an individual-lake basis, but quite similar on a regional basis. Estimated stock compositions of the Southeast Alaska–northern British Columbia known sample were usually within 0.4% for the 16 specific lake components, the regional estimates being within 1% for SPAM-based estimates and within 2–3% for cBAYES-based estimates (Table 5). Analyses of both of these samples indicated that reasonably accurate, lake-specific estimates of stock composition should be possible when the Pacific Rim baseline is used for analysis, in agreement with the results from the analysis of simulated multipopulation mixtures.

High-sea fishery samples are likely to contain fish from populations not in the baseline, or even

perhaps regions not presently in the baseline. The value of having an adequate baseline for stock identification applications was evaluated for the known-origin sample from the Fraser River. Limiting the baseline to include only three Fraser River populations (Weaver Creek, Stellako River, and Fennell River) reduced the accuracy of the estimates to 80.3% Fraser River composition (SD = 4.1%) for a SPAM-based estimate and 85.0% (SD = 2.5%) for a cBayes-based estimate, compared with the greater than 98.5% estimate incorporating the full baseline.

Identification of Individuals

The Pacific Rim distribution of sampled populations provided an opportunity to test the accuracy of identification of individual sockeye salmon to a specific lake of origin. The accuracy of identification of individual fish to correct lake of origin was greater than 90%, regardless of whether the lakes were geographically widespread (Table 6) or within a single watershed (Table 7). Individuals correctly assigned to specific lakes had a probability of assignment ranging from 30% to 100% for a mixture containing a geographically wide-ranging collection of populations (Figure 4). However, for the Fraser River, where analysis of both simulated and actual mixed-fishery samples indicated that accuracy was usually within 1% of actual values, almost 90% of the individuals correctly identified had a probability of assignment greater than 0.80. Fraser River sockeye salmon were identified with a high degree of accuracy, and high probabilities of assignment were associated with the individuals. Misidentifications of Fraser River individuals were always to other lakes in the drainage (Table 7). Some individuals were incorrectly identified in both the Pacific Rim and Fraser River mixtures, yet the probability of assignment to a specific lake was greater than 0.80 (Figure 4).

TABLE 7.—Percentage of individual sockeye salmon correctly identified to their lake of origin within the Fraser River and to the Fraser River drainage for five sampling sites using variation at 14 microsatellite loci and one major histocompatibility complex locus. The entire Pacific Rim baseline was used in the analysis (N = the number of fish analyzed from each site).

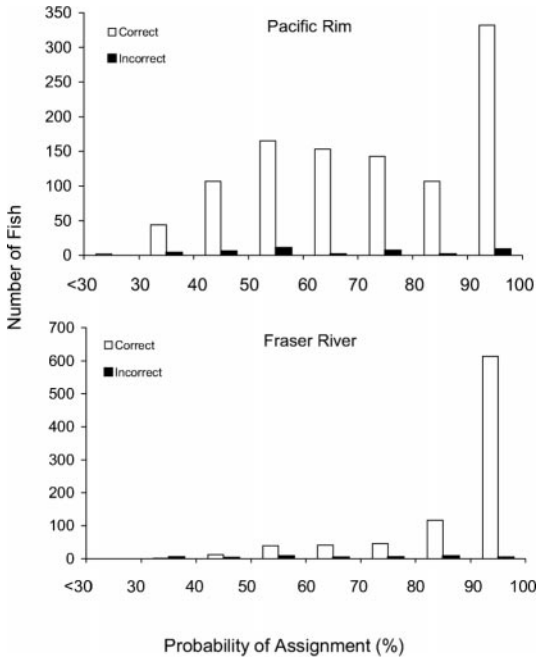| Lake	Sampling site	N	% Correct to lake	% Correct to Fraser River
Shuswap	Eagle River (early)	182	97.3	100.0
Chilko	Chilko (south end)	311	95.5	100.0
Trembleur	Forfar Creek	128	95.3	100.0
Adams	Cayenne Creek	89	100.0	100.0
Quesnel	McKinley Creek	196	93.9	100.0

FIGURE 4.—Frequency distributions for the probability of assignment of sockeye salmon to their lake of origin correctly ($N = 1,053$) and incorrectly ($N = 41$) for individuals in a Pacific Rim mixture of populations as well as in a Fraser River population mixture (correct: $N = 869$; incorrect: $N = 37$).

These fish, accounting for about 1% of the fish tested, were likely true strays, as their identified natal origin was usually from a location geographically adjacent to the origin of the test samples. These results constitute the first accurate identification of salmonid individuals to a specific lake of origin over their species' range.

Analysis of Marine Samples

Analysis of simulated mixtures and known samples of sockeye salmon suggested that accurate estimates of stock composition should be obtained when applied on a Pacific Rim basis. We tested model performance by analyzing four marine samples of sockeye salmon obtained from geographically distinct regions within the Pacific Rim baseline. Russian-origin sockeye salmon dominated the sample obtained from the western Bering Sea, comprising 93% of the fish sampled. The main geographic regions of origin were all geographically adjacent to the location of the sample (Kamchatka River, 29%; Chukotka, 28%; Olutorksky Bay, 14%; Navarinsky, 7%; Karaginsky Bay, 6%; Figure 5). Sockeye salmon originating from the

western coast of Kamchatka comprised 8% of the sampled fish (Kurilskoye Lake, 4%; Bolshaya River, 4%). Salmon from North America were estimated to have comprised 7% of the mixture, primarily originating from the Alaska Peninsula.

Markedly different origins of juvenile salmon were observed from the sample obtained near Kodiak Island in the Gulf of Alaska. Juveniles of Fraser River origin dominated the sample, comprising 41% of the sample (Figure 5). Juveniles from Southeast Alaska were a significant component of the sample (22%). Sockeye salmon from rivers in northern British Columbia were also observed in the sample (Alsek River, 5%; Stikine River, 8%; Nass River, 3%; Skeena River–Babine Lake, 8%). Virtually all of the sample was estimated to have originated from locations south and east of Kodiak Island, consistent with the concept of a juvenile migration pattern following the continental shelf in a north and westerly direction.

The origin of sockeye salmon in a mid-August fishery on maturing fish at Tree Point in Southeast Alaska was estimated to be primarily from Babine Lake (63%) and the Nass River (20%; Figure 5). Sockeye salmon from adjacent areas were also estimated to be present (Southeast Alaska, 4%; Stikine River, 4%; Skeena River, 1%). Sockeye salmon from more southern areas in British Columbia were also estimated to be present, although in very minor amounts (central-coastal British Columbia, 1%; Fraser River, 2%; southern British Columbia, 2%).

Johnstone Strait in southern British Columbia is a major migration route of sockeye salmon returning to the Fraser River. Sockeye salmon sampled from this location in late August 2004 were estimated to have originated entirely from the Fraser River (Figure 5), a result completely consistent with their abundance and timing relative to other populations in southern British Columbia. As expected, when all four samples were considered, markedly different origins of sockeye salmon were observed in samples with a wide geographic distribution.

Discussion

Reliable, accurate, effective, and practical methods of stock identification are a key requirement in the determination of migration pathways for juvenile sockeye salmon, assessment of the status of juvenile and immature sockeye salmon in marine feeding areas, and management of fisheries that target sockeye salmon during their spawning migration. The most effective stock identification

Western Bering Sea
N=62

- ☐ Bolshaya River Basin
- ▨ Kurilskoye Lake
- ◼ Kronotzky Bay
- ▨ Kamchatka River Basin
- ▧ Olutorsky Bay
- ▨ Navarinsky Region
- ▦ Chukotka
- ▨ Alaska Pennisula
- ◼ Other

Kodiak Island
N=92

- ▥ Southeast Alaska
- ▦ Alsek River
- ▨ Stikine River
- ▨ Nass River
- ☐ Babine Lake
- ▦ Owikeno Lake
- ▨ Fraser River
- ◼ Other

Southeast Alaska
N=103

- ▥ Southeast Alaska
- ▨ Stikine River
- ▨ Nass River
- ☐ Babine Lake
- ◼ Other
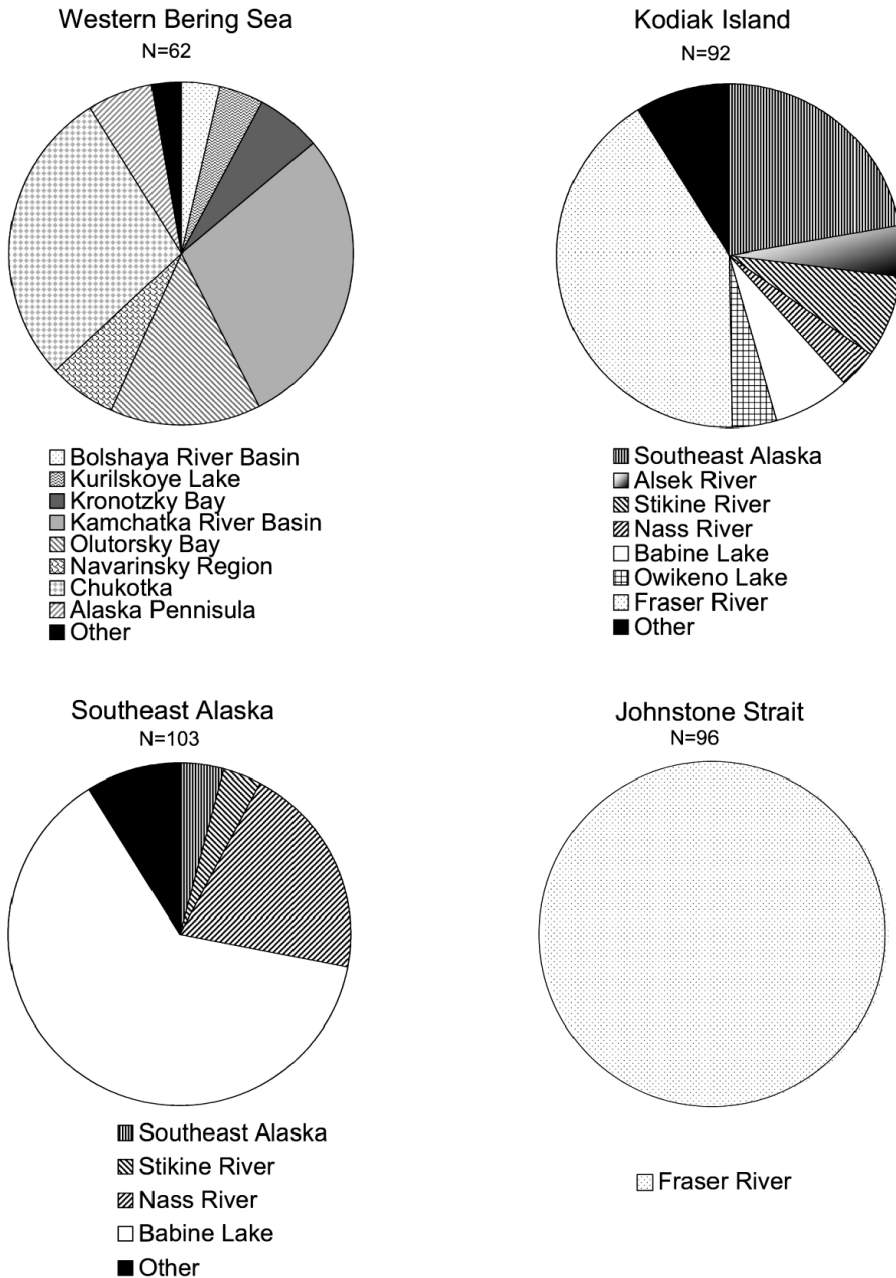
Johnstone Strait
N=96

- ▨ Fraser River

FIGURE 5.—Estimated stock compositions of four mixed-stock samples of sockeye salmon obtained from the western Bering Sea, on the continental shelf near Kodiak Island, near Tree Point in Southeast Alaska, and in Johnstone Strait in southern British Columbia.

techniques for sockeye salmon are those that provide reliable discrimination among populations, and simultaneously provide the ability to identify populations regardless of whether the applications are local, regional, national, or international in scope (international applications potentially in-

volving mixtures of Asian and North American populations). Ideal methods for mixed-stock analysis are those based on biological variation in characters which differ substantially among populations, show little temporal or annual variation within populations relative to population differ-

ences, and can be screened in a rapid, nonlethal, and cost-effective manner for both baseline and mixed-population samples. The survey of microsatellite DNA and MHC loci meet these criteria, and population differentiation can be readily used for in-season fishery management decisions requiring stock composition analysis (Beacham et al. 2004c).

Loci used in stock composition estimation are assumed to be in Hardy–Weinberg equilibrium (HWE) in the baseline populations (Debevec et al. 2000). In our survey, the *Oki10* locus was not in HWE in all populations. Genotypic frequencies conform to HWE for populations in southern British Columbia (Beacham et al. 2002, 2004b), show some level of nonconformance (10–20%) to HWE for populations in central and northern British Columbia and Southeast Alaska (Beacham et al. 2005; in press), and increase nonconformance to 40% for Russian populations (Beacham et al., unpublished). Since 83 alleles were observed at *Oki10* in our survey, it would not be practical to use observed genotypic frequencies given the number of fish sampled per population, as there will very likely be fish in the mixture from a population displaying *Oki10* genotypes not observed in the baseline sample. Beacham et al. (2001) illustrated that the accuracy of stock composition estimates was enhanced by assuming HWE distribution of genotypic frequencies for loci at which observed genotypic frequencies did not conform to those expected under HWE. The accuracy of estimated stock compositions of known samples was generally quite close to actual population values, so inclusion of a locus not in HWE in all populations did not induce significant bias in the estimated population contributions. In particular, contributions of Russian-origin populations were estimated with the same degree of accuracy as were those for populations from other regions.

The MHC locus contributed significantly to identification of sockeye salmon, especially when the problem was to discriminate among different potential lakes of origin, compared with discrimination among populations within a lake. Genetic differentiation among populations within a lake was usually more pronounced at microsatellite loci than at the MHC locus, but among sockeye salmon from different lakes, greater genetic differentiation was observed at the MHC locus than at the microsatellite loci (Miller et al. 2001). In regional salmon stock identification applications, MHC loci provide more stock discrimination power than most microsatellite loci (Beacham et al. 2001, 2004b).

The number of alleles observed at a microsatellite locus was clearly related to the power of the locus in providing accurate estimates of stock composition of single-population mixtures when there was a Pacific Rim distribution of the baseline populations. Loci with larger numbers of alleles were more effective in providing more accurate estimates of stock composition than were loci with smaller numbers of alleles. The cumulative number of alleles used in mixed-stock analysis directly influenced the accuracy of the estimated stock compositions. O'Reilly et al. (2004) reported that a measure of genetic differentiation among populations declined with increasing number of alleles observed at the locus, and that this resulted in a reduced ability to discriminate among samples. Kalinowski (2002) had previously suggested that equivalent information can be obtained by examining either a few loci with many alleles or more loci with more moderate numbers of alleles. Our results support that observation. For example, the mean accuracy of estimated stock compositions for single-population mixtures obtained by employing *Oki10* with approximately 80 alleles (72%) was similar to the results obtained (78%) by employing the five loci with the fewest number of alleles (79 alleles total). The use of more than 100 alleles for stock composition estimation resulted in diminishing returns for accuracy per allele employed, but variance of the estimates was also reduced. The number of alleles or loci to employ in stock identification applications is dependent upon the level of accuracy and precision required, as well as the cost of the analysis. For example, applications requiring identification of individuals to specific lakes will require more information (loci) than regional estimates of stock composition.

Known-origin samples provide an effective test of the ability of a technique to provide reliable estimates of stock composition. Estimated stock compositions of samples derived from fisheries in the lower part of the drainage for five major rivers in British Columbia were generally above 90% for the drainage under examination, except for the Stikine River in northern British Columbia. In this case, 11% of the sample was estimated to have been derived from the Taku River, another major river drainage north of the Stikine River. Previous analyses of population structure in these two rivers had indicated that genetic differentiation between river-rearing juvenile life history types in the two rivers was limited (Beacham et al. 2004a). The

ability to discriminate accurately between these two drainages was reduced when river-rearing life history types comprised a substantial portion of the sample. However, reduced distinctiveness of river-rearing sockeye salmon was restricted to the Taku and Stikine rivers. River-rearing populations were also quite common on the Kamchatka Peninsula, yet these populations were able to be identified with a high degree of accuracy.

Accurate estimates of stock composition were obtained for the two other known-origin samples analyzed, particularly for the sample containing sockeye salmon from 16 lakes in Southeast Alaska, as well as from the Nass River and Skeena River. The estimated components for individual lakes were generally within 0.2–0.4% of actual values, reflecting the level of differentiation (mean pairwise $F_{ST} = 0.10$) observed between populations in the individual lakes. Lake-specific estimates of stock composition should be possible for samples containing Southeast Alaskan sockeye, provided that the appropriate lakes are included in the baseline used to resolve the mixtures.

Two analytical models (SPAM, cBAYES) were used to provide estimates of stock composition for the mixed-fishery samples. While cBAYES provided marginally more accurate results than did SPAM, in essence there was little difference in estimated stock compositions between the two methods. We generally find that as long as the baseline used in stock composition analysis is extensive, such that fish in the mixture are presumably well represented by the baseline populations, there is little difference between SPAM and cBAYES estimates. However, in cases where the baseline is only partially complete for the application in which it is used, our experience indicates that cBAYES estimates tend to be more accurate and more reflective of expected stock compositions. This result was illustrated in the analysis of the known-origin Fraser River sample, where when an incomplete Fraser River baseline was used in the analysis, higher accuracy was obtained from cBayes compared with SPAM.

Evaluation of a technique and a baseline for mixed-stock analysis initially consists of an evaluation of simulated mixtures to determine whether the level of population differentiation is sufficient for a reliable estimation of stock composition. The next step is an evaluation of the accuracy of estimated stock compositions of known-origin, mixed-stock samples that are independent of the baseline. In our study, analysis of simulated mixtures suggested that accurate estimates of stock

composition should be obtained with a Pacific Rim baseline, and estimated stock compositions of known-origin samples were within reasonable levels of accuracy. Inaccurate estimates of stock composition can still be produced in mixed-stock fishery samples even when the baseline has passed the simulated mixtures and known-origin mixtures evaluation. This could occur if a significant portion of the mixed-fishery sample is derived from unrepresented populations or regions in the baseline. The final stage of evaluation is to apply the baseline to estimate stock compositions of fishery samples and to determine if the results are biologically reasonable. In our study, the four mixed-stock fishery samples analyzed were from widely divergent geographic locations, and as such inferences can be drawn about what stocks are likely to be in the samples. Sockeye salmon sampled in the western Bering Sea in June would largely be expected to be of Russian origin, and this was precisely the result obtained in our study. Similarly, juvenile sockeye salmon sampled during November on the continental shelf near Kodiak Island would reasonably be expected to have originated from populations to the south and east, given the northern and western migration pattern of juveniles (French et al. 1976), and these results were observed in our study. At Tree Point in Southeast Alaska, fisheries conducted in mid-August are known to intercept Skeena River (primarily Babine Lake) and Nass River stocks (Pella et al. 1993), and it is expected that sockeye salmon from these two rivers should dominate catches in this location at this time. Finally, sockeye salmon migrating through Johnstone Strait in southern British Columbia in late August would be expected to be of Fraser River origin (Verhoeven and Davidoff 1962), and these were the results observed in our study. Application of microsatellite and MHC variation clearly provided reliable estimates of stock composition for a local group of sockeye salmon even when there is a potential of a Pacific Rim distribution of populations contributing to the fishery sample.

Identification of individuals to a specific lake, river, or region is the most demanding stock identification application, and has been conducted previously in a limited geographic area (Beacham et al. 2002). A number of applications are possible with accurate individual stock identification over a Pacific Rim distribution of populations. Identification of fish to lake of origin enables prosecution of those involved in the illegal harvest and sale of salmonids (Withler et al. 2004). A determination

of marine influences on the overall abundance and geographic variation in salmon spawning migrations is now possible with concerted effort on marine sampling. DNA-based identification of individual salmon and the monitoring of their pathways and fates throughout their marine existence can provide the key to a treasure-trove of information on the biology of adaptation in the face of rapid environmental change.

Some baseline enhancement will be beneficial if the Pacific Rim baseline is to be employed in some applications in local areas in the Pacific Rim. Baseline coverage in Russia is adequate, but in Alaska, samples from major populations in the Copper River drainage, Cook Inlet, as well as additional samples from Bristol Bay, are required to account for populations originating from these areas. All significant populations from British Columbia have been included in the survey, but some coastal populations from Washington, although population sizes are small (Gustafson and Winans 1999), could be added to the baseline. In summary, although additional populations can be added to the baseline in local areas, microsatellite and MHC variation provides the most powerful stock identification technique available for application to sockeye salmon on a Pacific Rim basis.

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Appendix follows

Appendix 1: Sampling Sites or Populations Surveyed

TABLE A.1.—Spawning location, nursery lake, sample collection years, number of fish sampled per year, and total number of fish sampled for over 48,000 sockeye salmon surveyed from 299 sites (allele frequencies for all location samples surveyed in this study are available at http://www-sci.pac.dfo-mpo.gc.ca/mgl/default_e.htm).

Sampling site	Nursery lake	Years	Number	Total
Columbia River				
1. Okanagan River	Okanagan	1993, 1997, 1998, 1999, 2000, 2001, 2002	70, 94, 38, 15, 41, 50, 194	502
2. Wenatchee Lake	Wenatchee	1988	68	68
Washington				
3. Lake Washington	Washington	2000	201	201
4. Baker Lake	Baker	1991	92	92
5. Ozette Lake	Ozette	1995	50	50
Upper Fraser				
6. Bowron River	Bowron	1999, 2000, 2001	65, 100, 100	265
7. Stellako River	Stellako	1992, 1995, 1996, 1998, 1999, 2000	99, 143, 35, 100, 88, 117	582
8. Middle River	Trembleur	1993, 1996, 1997, 1998, 2000, 2001	40, 41, 51, 99, 100, 105	436
9. Nadina River	Francois	1986, 1992, 1999, 2000	39, 99, 100, 118	356
10. Pinchi Creek	Stuart	1999	74	74
11. Tachie River	Stuart	1995, 1996, 1997, 1999, 2000, 2001	92, 96, 56, 11, 100, 105	460
12. Kuzkwa River	Tezzeron	2001	105	105
13. Chilko River	Chilko	1992, 1996, 1997, 1998, 1999, 2000, 2001	99, 60, 148, 119, 100, 122, 100, 110	858
14. Chilko Lake (south)	Chilko	1996, 1997, 2001	110, 101, 200	411
15. Horsefly River (mixed)	Quesnel	1985, 1986, 1993, 1996, 1997, 1998, 1999	77, 96, 97, 98, 95, 101, 118	682
16. Lower Horsefly River	Quesnel	2001	200	200
17. Middle Horsefly River	Quesnel	2001	200	200
18. Upper Horsefly River	Quesnel	2000, 2001	102, 400	502
19. Roaring River	Quesnel	2001	100	100
20. Wasko Creek	Quesnel	2001	100	100
21. Blue Lead Creek	Quesnel	2001	100	100
22. McKinley Creek	Quesnel	2001	200	200
23. Mitchell River	Quesnel	1993, 1994, 1997, 1998, 2001	44, 18, 20, 114, 205	401
24. Portage Creek	Seton	1986, 1997, 1998, 1999	98, 115, 72, 47	332
25. Gates Creek	Anderson	1986, 1992, 1995, 1999, 2000	91, 49, 60, 103, 100	403
26. Nahatlatch River	Nahatlatch	1996, 1997	106, 132	238
Early Stuart				
27. Kynock Creek	Trembleur	1994, 1997	74, 98	172
28. Gluskie Creek	Trembleur	1997	149	149
29. Forfar Creek	Trembleur	1997	152	152
30. Dust Creek	Takla	1988, 1991, 1997	24, 44, 105	173
31. Porter Creek	Takla	2000	15	15
32. Hudson Bay Creek	Takla	2000	18	18
33. Blackwater Creek	Takla	2000	20	20
Lower Fraser				
34. Birkenhead River	Lillooet	1992, 1997, 1998, 1999, 2001	99, 136, 48, 100, 41, 100	524
35. Weaver Creek	Harrison	1982, 1986, 1992, 1996, 1998, 1999, 2000, 2001	139, 81, 49, 101, 46, 100, 100	699
36. Big Silver Creek	Harrison	2000, 2002	100, 100	200
37. Cogburn Creek	Harrison	2003	28	28
38. Harrison River	None	1986, 1995, 2000	132, 50, 100	282
39. Douglas Creek	Harrison	2003	16	16
40. Pitt River	Pitt Lake	1986, 2000, 2001	145, 100, 100	345
41. Widgeon Slough	None	2002	97	97
42. Cultus Lake	Cultus	1992, 1995, 1999, 2000, 2001	61, 69, 84, 34, 56	304
43. Chilliwack River	Chilliwack	1996, 2001, 2003	59, 100, 51	210
44. Chilliwack River (upper)	Chilliwack	2003	21	21
Thompson River				
45. Lower Adams	Shuswap	1982, 1990, 1995, 1996, 1998, 1999	100, 50, 103, 97, 102, 115	567
46. Upper Adams	Adams	1996, 2000	278, 100	378
47. Little River	Shuswap	2002	88	88
48. Lower Shuswap	Mara	1983, 1986, 1990, 1996, 1998, 1999, 2002	30, 36, 28, 5, 99, 85, 36	319

Appendix 1: Sampling Sites or Populations Surveyed

TABLE A.1.—Continued.

Sampling site	Nursery lake	Years	Number	Total
49. Middle Shuswap	Mabel	1986, 2002	147, 100	247
50. Little Shuswap	Shuswap	1994	81	81
51. Scotch Creek	Shuswap	1994, 1995, 1996, 1999, 2000	100, 77, 112, 83, 100	472
52. Seymour River	Shuswap	1986, 1996, 1999	143, 107, 86	336
53. Eagle River (early)	Shuswap	2000, 2002	100, 100	200
54. Eagle River (late)	Shuswap	1990, 2002	80, 100	180
55. Cayenne Creek	Adams	2000	100	100
56. Fennell Creek	North Barriere	1996, 1999, 2000, 2001	199, 100, 100, 94	493
57. Raft River	Kamloops	1996, 2000, 2001	101, 100, 100	301
58. North Thompson	Kamloops	2003	104	104
Vancouver Island				
59. Sproat Lake	Sproat	1987, 1990, 1992	80, 99, 100	279
60. Sproat at Snow	Sproat	2002	68	68
61. Sproat at Gracie	Sproat	2002	71	71
62. Sproat at Antler	Sproat	2002	60	60
63. Great Central	Great Central	1987, 1990, 1992	94, 100, 122	316
64. Great Central at Forestry	Great Central	2002	19	19
65. Great Central at Fawn	Great Central	2002	76	76
66. Great Central at McBride	Great Central	2002	115	115
67. Great Central at North	Great Central	2002	108	108
68. Great Central at Forest2	Great Central	2002	116	116
69. Henderson	Henderson	1988, 1993, 1995, 2002	100, 100, 12, 29	350
70. Hobiton	Hobiton	1992	81	81
71. Kennedy	Kennedy	1986	91	91
72. Tributary	Quatse	2003	197	197
73. Schoen	Schoen	2003	29	29
74. Trawl[a,b]	Woss	1985, 2001, 2002	80, 112, 101	293
75. Trawl[a]	Vernon	2001, 2002	77, 290	367
76. Trawl[a]	Nimpkish	2001, 2002, 2003	56, 42, 95	203
Southern mainland				
77. Klinaklini River	Devereux	1998, 2002	219, 106	325
78. Phillips River	Phillips	2002	205	205
79. Trawl[a]	Village Bay	2003	18	18
80. Lakeshore	Sakinaw	1998, 2000, 2001	81, 20, 12	113
81. Heydon	Heydon	2003	176	176
82. Glendale	Glendale	2003	188	188
Central Coast				
83. Tributary	Devon	1985, 1999	100, 100	200
84. Tributary	Mikado	1986, 1999	100, 62	162
85. Tributary	Lowe	1986	40	40
86. Tributary	Banks	1986	41	41
87. Canoona River	Canoona	1986	100	100
88. Tezwa River	Kitlope	1986	40	40
89. Atnarko River	Tenas	1985	80	80
90. Atnarko River	Lonesome	1997	100	100
91. Tributary	Namu	1999	93	93
92. Mary Cove Creek	None	1999	78	78
93. Lagoon Creek	Lagoon	1999	50	50
94. Lakeshore	Kimsquit	1986	81	81
95. Tributary	Tankeeah	1986, 2001, 2002	100, 30, 31	161
96. Tributary	Klemtu	2002	27	27
97. Tributary	Koeye	1986	80	80
98. Bella Coola (mixed)	Several	2003	223	223
99. Marble Creek	Owikeno	2001, 2002	25, 96	121
100. Inziana River	Owikeno	1997, 2000, 2001, 2002	50, 151, 100, 97	398
101. Washwash River	Owikeno	1997, 2000, 2001, 2002	63, 91, 114, 99	367
102. Ashlulm River	Owikeno	2000, 2001, 2002	25, 82, 94	201
103. Dallery River	Owikeno	2000, 2001, 2002	32, 33, 95	160
104. Genesee River	Owikeno	2000, 2001, 2002	7, 35, 88	130

Appendix 1: Sampling Sites or Populations Surveyed

TABLE A.1.—Continued.

Sampling site	Nursery lake	Years	Number	Total
105. Neechanz River	Owikeno	2000, 2001, 2002	69, 110, 96	275
106. Amback River	Owikeno	2000, 2001, 2002	92, 100, 58	250
107. Sheemahant River	Owikeno	2000, 2001, 2002	43, 100, 113	256
108. Wannock	Owikeno	2002	86	86
109. Docee River (mixed)	Long	1989, 1998, 1999, 2000, 2001	60, 200, 49, 81, 100	490
110. Smokehouse Creek	Long	2001, 2002	56, 205	261
111. Canoe Creek	Long	2001, 2002	39, 100	139
		Queen Charlotte Islands		
112. Mercer Creek	Mercer	1983	41	41
113. Yakoun River	Yakoun	1989, 1993	61, 99	160
114. Awun River	Awun	1995	80	80
115. Naden River	Eden	1995	98	98
116. Copper Creek	Skidegate	1993, 1996, 2001	85, 95, 10	190
		Nass River		
117. Bonney	Fred Wright	1987, 1994, 1996, 1998, 1999, 2001	76, 81, 93, 100, 82, 107	539
118. Kwinageese	Fred Wright	1987, 2000, 2001	81, 48, 65	194
119. Meziadin (fishway)	Meziadin	1987, 1996, 2001	100, 111, 264	475
120. Meziadin (beach spawning)	Meziadin	2001	188	188
121. Tintina Creek	Meziadin	2001, 2002	51, 50	101
122. Hanna Creek	Meziadin	2001, 2002	49, 100	149
123. Damdochax	Damdochax	1987, 1994, 1998, 1999, 2000, 2001	100, 81, 100, 89, 50, 140	560
124. Bowser	Bowser	1986, 1987, 1994, 1998, 1999, 2000, 2001	80, 72, 81, 100, 160, 82, 222	797
125. Gingit	None	1987, 1988, 1997	73, 93, 169	335
126. Brown Bear	None	1997	40	40
127. Zolzap	None	1996, 1997	36, 24	60
		Skeena River		
128. McDonell Lake	McDonell	1987, 1988, 1994, 2002	81, 75, 60, 71	287
129. Williams Creek	Lakelse	1987, 1988, 1994	83, 98, 100	281
130. Schulbuckhand Creek	Lakelse	1988	77	77
131. Alastair Lake	Alastair	1987, 1988, 1994, 1998	75, 21, 100, 83	279
132. Kitwanga River	Kitwanga	1998	98	98
133. Kitsumkalum River	Kitsumkalum	1994	77	77
134. Stephens Creek	Stephens	2001	200	200
135. Nangeese River	None	2002	33	33
136. Kispiox River	None	2002	56	56
137. Motase Lake	Motase	1987	49	49
138. Swan Lake	Swan	1988, 1994	100, 81	181
139. Bear	Bear	1987, 1988	45, 71	116
140. Sustut	Sustut	1993, 2000, 2001	93, 47, 100	240
141. Nanika River	Morice	1988, 1994	75, 63	138
142. Lower Babine River	Babine	1987, 1994	50, 100	150
143. Upper Babine River	Babine	1987, 1994	81, 99	180
144. Pinkut Creek	Babine	1985, 1987, 1990, 1994	200, 99, 100, 100	499
145. Fulton River	Babine	1985, 1987, 1990, 1994	95, 193, 100, 100	488
146. Morrison River	Babine	1988, 1994	76, 100	176
147. Shass Creek	Babine	1987	78	78
148. Twain Creek	Babine	1987, 1990	100, 54	154
149. Tahlo Creek	Babine	1987, 1988, 1994	78, 85, 90	253
150. Four Mile Creek	Babine	1987, 1988	88, 55	143
151. Pierre Creek	Babine	1987, 1988	84, 79	163
		Unuk River		
152. Border Lake	Border	1987	50	50
		Stikine River		
153. Tuya River	Tuya	1996	46	46
154. Tahltan	Tahltan	1987, 1996, 2002	21, 405, 48	474
155. Upper Stikine (mixed)	Tuya, Tahltan	1996	368	368
156. Scud River	None	1985, 1987, 2000, 2001	60, 81, 49, 186	376
157. Iskut River	None	1985, 2002	50, 37	87
158. Chutine River	None	1985, 2000, 2001, 2002	50, 17, 200, 104	371
159. Christina Lake	Christina	1984	51	51

Appendix 1: Sampling Sites or Populations Surveyed

TABLE A.1.—Continued.

Sampling site	Nursery lake	Years	Number	Total
160. Verrett River	None	1986, 2000, 2001, 2002	116, 145, 40, 26	327
161. Porcupine River	None	2000, 2001	20, 50	70
162. Bugleg Creek	None	2001	42	42
163. Shakes Creek	None	2001, 2002	44, 6	50
164. Bronson Slough	None	2001	26	26
165. Devil's Elbow	None	2001	58	58
166. Mainstem Stikine River	None	2001	144	144
167. Craig River	None	2001	39	39
168. Katete River	None	2001	25	25
169. Twin River	None	2002	23	23
Taku River				
170. Kuthai	Kuthai	1986, 1987	75, 40	115
171. Little Tatsamenie	Tatsamenie	1985, 1987, 1993	80, 70, 49	199
172. Big Tatsamenie	Tatsamenie	1992, 1993	100, 51	151
173. Hackett	None	1985, 1987	61, 30	91
174. Little Trapper	Little Trapper	1992	70	70
175. Tuskwa	None	2000	134	134
176. King Salmon	None	2000	12	12
177. Tulsequah	None	2000	43	43
178. Shustahini	None	2000	13	13
179. Takwahoni	None	2000	31	31
Alsek River				
180. Klukshu River (mixed)	Klukshu	1992, 2000	76, 238	314
181. Klukshu River (early)	Klukshu	2000, 2001, 2002	85, 95, 48	228
182. Klukshu River (late)	Klukshu	2000, 2001, 2002	167, 95, 49	311
183. Neskataheen	Neskataheen	2000, 2001, 2002	346, 206, 40	592
184. Lower Tatshenshini	None	2000, 2001, 2003	14, 24, 41	79
185. Upper Tatshenshini	None	2001, 2002, 2003	27, 126, 171	324
186. Kudwat Creek	None	2001	83	83
187. Detour Creek	None	2001	22	22
188. Stinky Creek	None	2001	64	64
189. Mainstem Alsek River[c]	None	2001	32	32
190. Mainstem Alsek River[d]	None	2001	27	27
191. Stanley Creek	None	2001	10	10
192. Blanchard River	Blanchard	2001	23	23
193. O'Connor Creek	None	2001	22	22
194. Kane Creek	None	2001	26	26
Southeast Alaska				
195. Hugh Smith	Hugh Smith	1992, 2000	95, 200	295
196. Heckman	Heckman	1992, 2000	100, 200	300
197. McDonald	McDonald	1992, 2000	100, 187	287
198. Karta	Karta	1992, 2000	100, 175	275
199. Thoms	Thoms	2000	212	212
200. Kutlaku	Kutlaku	2000	203	203
201. Red Bay	Red Bay	2000	201	201
202. Sitkoh	Sitkoh	2000, 2001	343, 40	383
203. Petersburg	Petersburg	2000	193	193
204. Salmon Bay	Salmon Bay	2000	197	197
205. Sarkar	Sarkar	2000	45	45
206. Luck	Luck	2000	200	200
207. Hetta	Hetta	2000, 2002	206, 108	314
208. Klakas	Klakas	2000	200	200
209. Kegan	Kegan	2000	196	196
210. Mahoney	Mahoney	2002	71	71
211. Kah Sheets	Kah Sheets	2002	105	105
212. Kunk	Kunk	2002	107	107
213. Shipley	Shipley	2002	105	105
214. Chilkat	Chilkat	1981	49	49

Appendix 1: Sampling Sites or Populations Surveyed

TABLE A.1.—Continued.

Sampling site	Nursery lake	Years		Number	Total
Kodiak Island					
215. Meadow (late)	Karluk	1999		112	112
216. Meadow (early)	Karluk	1999		100	100
217. Lower Thumb	Karluk	1999		110	110
218. Upper Thumb	Karluk	1999		100	110
219. Shoreline	Karluk	1999		98	98
220. Midway Beach	Frazer	1995		101	101
221. Linda Creek	Frazer	1995		112	112
222. Stumble Creek	Frazer	1995		18	18
223. Caida Beach	Frazer	1995		31	31
224. Summit Creek	Frazer	1995		35	35
225. Pinnell Creek	Frazer	1995		35	35
226. Outlet Beach	Frazer	1995		85	85
227. Fish pass weir	Frazer	1995		15	15
228. Upper Station	Upper Station	1995		60	60
229. Connecticut Creek	Red	1999		75	75
Bristol Bay					
230. Knutson Bay	Iliamna	1992, 1997		53, 100	153
231. Fuel dump	Iliamna	1991		49, 48	97
232. Gibraltar	Iliamna	1991		54	54
233. Woody Island	Iliamna	1991, 1992		51, 50	151
234. Copper River	Iliamna	1991, 1992		51, 47	98
235. Chinkelyes	Iliamna	1991		59	59
236. Kijik	Lake Clark	2000		101	101
237. Little Kijik	Lake Clark	2000		100	100
238. Tazimina	Six Mile	1992		50	50
239. Mission Creek	Aleknagik	1998		100	100
240. Hansen Creek	Aleknagik	1998		100	100
241. Bear Creek	Aleknagik	1999		100	100
242. Lynx Creek	Nerka	1998		100	100
243. Outlet river	Ruth	1995		100	100
Alaskan Peninsula–Aleutian Islands					
244. Painter Creek	Mother Goose	2000		100	100
245. Lake Andrew	Lake Andrew	1994		75	75
Chukotka					
246. Krutaya	Pekulney-skoye	2001		25	25
247. Kautayam	Pekulney-skoye	2001		25	25
248. Mangiskon Lake	Pekulney-skoye	2001		25	25
249. Podarok Lake	Pekulney-skoye	2001		25	25
250. Kakanaut Bay	Pekulney-skoye	2001		20	20
251. Kakanaut River	Pekulney-skoye	2001		25	25
252. Vaamochka Lake	Vaamochka	2001		30	30
253. Vaamochka River	Vaamochka	2001		24	24
Olutorksy Bay					
254. Ilir	Ilir	2001, 2002		49, 94	143
255. Potat Lake	Potat	2001		54	54
256. Vatit Lake	Vatit	2001, 2002		49, 52	101
257. Anana Lake	Anana	2001		48	48
258. Anana Lagoon	Anana	2002		180	180
Navarinsky region					
259. Severnaya Lagoon	Severnaya	2002		100	100
Kamchatka River basin					
260. Shapina River	None	1998		69	69
261. Kamchatka River	None	1998, 2001, 2003		78, 57, 55	190

Appendix 1: Sampling Sites or Populations Surveyed

TABLE A.1.—Continued.

Sampling site	Nursery lake	Years	Number	Total
262. Kitilgina River	None	1998	50	50
263. Shapina River (late)	None	1998	28	28
264. Elovka River	None	2002, 2003	55, 120	175
265. Dvu-Yurtochnaya River	Dvu-Yurto-chnaya	2001, 2003	56, 99	155
266. Kireevna River	None	2003	104	104
267. Kurajechnoe River	None	2003	118	118
268. Tvashka River	None	2003	99	99
269. Kultuchnaya River	Azabachie	1998	31	31
270. Bushujka River	Azabachie	2001	24	24
271. Athl Creek	Azabachie	1996	20	20
272. Rybovodnij Creek	Azabachie	1996	15	15
273. Orishkin Bay	Azabachie	2003	30	30
274. Snovidovskay Bay	Azabachie	2003	30	30
275. Lotnaya River	Azabachie	1996	19	19
Kronotzky Bay				
276. Zhupanova River	None	2003	44	44
Southeastern Kamchatka				
277. Listvenichnaya River	Listvenich-noye	1998	38	38
278. Sarannaya River	Sarannoye	1998	35	35
279. Paratunka River	Dalnee–Blijnee	2002	71	71
Kurilskoye Lake				
280. Vichenkiya River	Kurilskoye	2000	100	100
281. Gavrushka River	Kurilskoye	2000	55	55
282. Kirushutk River	Kurilskoye	1989, 2000	72, 49	121
283. South Bay	Kurilskoye	1989, 2000	53, 50	103
284. Ozernaya Bay	Kurilskoye	2000	50	50
285. Close North Bay	Kurilskoye	2000	103	103
286. Far North Bay	Kurilskoye	2000	54	54
287. Oladochnaya Bay	Kurilskoye	1989, 2000	45, 49	93
288. Khakitzin Bay	Kurilskoye	2000	53	53
289. Gavrushka Bay	Kurilskoye	1989, 2000	35, 55	90
290. Gavrushka at Cape Tugumink	Kurilskoye	2000	54	54
291. Etamink River	Kurilskoye	2000	55	55
Southwestern Kamchatka				
292. Golygina River	None	2002	52	52
Bolshaya River basin				
293. Bolshaya River	None	1999, 2001	34, 79	113
294. Bistraya River	None	1998	25	25
295. Plotnikova River	None	1998, 2001	50, 97	147
296. Kluchevka River	None	2001	50	50
Tigil River basin				
297. Tigil River	None	2002	101	101
Palana River basin				
298. Palana River	Palana	2002	49	49
Japan				
299. Abira River	None	1994	75	75

[a] Juvenile sampled from midwater trawl.
[b] Adult sample (1985), juvenile samples other years.
[c] Upstream from confluence of Alsek and Tatshenshini rivers.
[d] Downstream from confluence of Alsek and Tatshenshini rivers.