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**Estimation of stock composition of sockeye salmon in the North Pacific Ocean**

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### Abstract

Variation at 14 microsatellite and one major histocompatibility complex (MHC) loci was surveyed in over 48,000 sockeye salmon (*Oncorhynchus nerka*) sampled from 298 localities ranging from the Columbia River to Japan. The observed regional population structure enabled an evaluation of the utility of using microsatellite and MHC variation for estimation of stock composition of sockeye salmon in mixed-stock fisheries. Stock compositions were estimated for a series of simulated and actual fishery samples, with the 298-population baseline used to estimate stock compositions. Application of microsatellite and MHC variation clearly has the potential to provide reliable estimates of stock composition for sockeye salmon originating from a specific lake even when there is a potential of a Pacific Rim distribution of populations contributing to the fishery sample.

### Introduction

Reliable, accurate, effective, and practical methods of stock identification are a key requirement in the assessment and management of Pacific salmon fisheries and populations. Stock identification of sockeye salmon (*Oncorhynchus nerka*) is of particular concern to many management agencies, given the economic value of sockeye salmon fisheries. Several methods of stock identification currently exist for sockeye salmon, with 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 MHC variation (Miller et al. 2001) all potentially available for applications to specific problems. Genetic methods of stock identification have several advantages, among them the level of differentiation among populations and the stability of the genetic characters surveyed. 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,b; Miller et al. 2001; Beacham et al. 2004), 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 requirement for increased population discrimination relative to that of other techniques that led us to evaluate minisatellite (Beacham et al. 1995), microsatellite (Beacham and Wood 1999; Beacham et al. 2000a,b), 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). Allozyme-based applications generally provide regional estimates of stock composition in a species, provided that there is a regional basis in population structure (Shaklee et al. 1999). Population-specific estimates of sockeye stock composition can sometimes be required in management decisions, as are regional-specific estimates in more wide ranging applications, and these were unlikely to be available using allozymes for stock composition analysis (Wood et al. 1994). Microsatellites can provide regional estimates as well, but may possibly provide population-specific estimates in some applications if the survey of baseline populations has been adequate (Beacham et al. 2001, Beacham et al. 2003). This greater population discrimination ability is a consequence of the higher heterozygosity and the larger number of alleles at microsatellite loci compared with allozyme loci. With respect to sockeye salmon, no relatively local regional population structure is apparent when population structure is examined with allozymes (Wood et al 1994; Gustafson and Winans 1999), and applications in stock composition estimation in marine fisheries have been limited.

In the current study, we evaluate the utility of using variation at 14 microsatellite and one MHC loci for regional stock identification of sockeye salmon. This evaluation is conducted by examining the accuracy and precision of estimated stock compositions through analysis of

simulated mixtures and samples from fisheries in coastal British Columbia, with the mixtures resolved using a 298-population baseline incorporating populations from Japan, Russia, Alaska, British Columbia, and Washington.

## Materials and Methods

### Collection of DNA samples and laboratory analysis

Tissue samples were collected from adult fish from sockeye salmon populations in the Pacific Rim and DNA extracted from the samples as described by Withler et al. (2000). For the survey of baseline populations, 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 unpub.), *One8* (Scribner et al. 1996), and *Omy77* (Morris et al. 1996) were size fractionated on denaturing polyacrylamide gels and allele sizes determined with the ABI 377 automated DNA sequencer. Allele sizes were determined with Genescan 3.1 and Genotyper 2.5 software (PE Biosystems, Foster City, CA). Genetic variation at the MHC class II *DAB-β1* locus (Miller et al. 2001) was surveyed by denaturing gradient gel electrophoresis (DGGE).  $\beta1$  alleles were separated by DGGE with the Bio-Rad (Hercules, CA) 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

The baseline survey consisted of analysis of over 48,000 sockeye salmon from 298 populations from Japan, Russia, Alaska, British Columbia, and Washington (Table 1). Allele frequencies and sample sizes for all locations surveyed in this study are available at [http://www-sci.pac.dfo-mpo.gc.ca/mgl/default\\_e.htm](http://www-sci.pac.dfo-mpo.gc.ca/mgl/default_e.htm).

### Estimation of stock composition

Genotypic frequencies were determined at each locus in each population and the statistical package for the analysis of mixtures software program (SPAM version 3.7) was used to estimate stock composition of each mixture (Debevec et al. 2000). 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. Each baseline population was resampled with replacement in order to simulate random variation involved in the collection of the baseline samples before the estimation of stock composition of each simulated mixture. Simulated fishery samples of 150 fish were generated by randomly resampling with replacement the baseline populations in each drainage. Estimated stock composition of a simulated mixture was then determined, and the whole process was repeated 100 times to estimate the mean and standard deviation of the individual stock composition estimates.

## Results and Discussion

The regional structure observed in sockeye salmon populations resulted in good discrimination among sockeye salmon from different lakes and regions in the Pacific Rim distribution of the species. 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 2). 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 2, these included Kuril Lake (Kirushutk sampling site), Lake Aleknagik (Mission Creek), Iliamna Lake (Knutson Bay), Lake Clark (Kijik River), Karluk Lake (Meadow Creek late), and Owikeno Lake (Inziana River). Estimates of stock composition for the individual sampling site within a lake ranged from 80-90% 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.

In analysis of samples from marine fisheries, it is rare to have sockeye salmon from only a single region present in the samples. We evaluated whether the genetic differentiation observed among the 298 sampling sites or populations included in the baseline was sufficient for mixed-stock analysis aimed at estimating population, lake or regional contributions to fishery samples. Three 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 3, mixture 1). Similar results were observed for a mixture comprised of Japanese, Russian, and Alaskan sockeye salmon (Table 3, 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. Regional 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 3, mixture 3). 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.

Ideal technologies for mixed-stock analysis are those based on biological variation in characters which differ substantially among stocks, show little temporal or annual variation within stocks relative to stock differences, and can be screened in a rapid, non-lethal, and cost-effective manner for both baseline and mixed-stock samples. The PCR-based survey of single-locus allele frequencies at microsatellite DNA and MHC loci meet these criteria, and can be readily used for in-season fishery management decisions requiring stock composition analysis.

Application of microsatellite and MHC variation clearly has the potential to provide 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. Regardless of the current baseline status, the results outlined in the present study are an example of the power of microsatellite and MHC variation that will likely be applied to an increasing number of species and fisheries for which the management concerns of identifying population structure and detecting specific populations or stocks in mixed-stock fisheries arise.

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Table 1. Regions and number of populations sampled within regions included in a survey of 14 microsatellite and one MHC loci in sockeye salmon.

Region	Number of populations	Populations
Hokkaido Is	1	Abira R.
Northwestern Kamchatka	2	Tigil R., Zupanova R.
Western Kamchatka	4	Bolshaya R., Bistraya R., Plotnikova R., Kluchevka R.
Kuril Lake	12	Vichenkiya R., Gavrushka R., Kirushutk R., Ozernaya Bay, South Bay, Close North Bay, Far North Bay, Oladochnaya Bay, Khakitzin Bay, Gavrushka Bay, Gavrushka@Cape Tugumink, Etamink River
Southwestern Kamchatka	1	Galigina River
Southeastern Kamchatka	3	Listvenichnaya River, Saranaya River, Avachinsky River
Eastern Kamchatka	24	Shapina River, Kamchatka River, Kitilgina River, Shapina River, Elovka River, Dvu-Yurtochnaya River, Kireevna River, Kurajechnoe River, Tvashka River, Kultuchnaya River, Bushujka River, Athl Creek, Rybovodnij Creek, Orishkin Bay, Snovidovskay, Lotnaya River, Krutaya, Kaytayam, Mangiskon Lake, Podarok Lake, Kakanaut Bay, Kakanaut River, Vaamochka Lake, Vaamochka River
Bering Sea Coast	6	Iilir, Potat Lake, Vatit Lake, Anana Lake, Anana Lagoon, Severnaya Lagoon
Alaska Peninsula	2	Lake Andrew, Painter Creek
Wood River	4	Mission Creek, Hansen Creek, Bear Creek, Lynx Creek
Iamna Lake	6	Knutson Bay, Fuel Dump, Gibraltar, Woody Island, Copper River, Chinkelyes
Lake Clark, Six Mile Lake	3	Kijik, Little Kijik, Tazimina
Southwest Bristol Bay	1	Ruth Lake
Kodiak Island	15	Meadow Creek (early & late), Lower Thumb, Upper Thumb, Karluk Shoreline, Midway Beach, Linda Creek, Stumble Creek, Caida Beach, Summit Creek, Pinnell Creek, Outlet Beach, Fish pass weir, Upper Station, Connecticut Creek
Southeast Alaska	20	Hugh Smith, Heckman, McDonald, Karta, Thoms, Kutlaku, Red Bay, Sitkoh, Petersburg, Salmon Bay, Sarkar, Luck, Hetta, Klakas, Kegan, Mahoney, Kah Sheets, Kunk, Shipley, Chilkat
Alsek River	15	Klukshu River (early, late & mixed), Neskataheen, Lower Tatshenshini, Upper Tatshenshini, Kudwat Creek, Detour Creek, Stinky Creek, mainstem Alsek River (2 sites), Stanley Creek, Blanchard River, O'Connor Creek, Kane Creek
Taku River	10	Kuthai, Little Tatsamenie, Big Tatsamenie, Hackett, Little Trapper, Tuskwa, King Salmon, Tulsequah, Shustahini, Takwahoni
Stikine River	17	Tuya River, Tahltan, Upper Stikine mixed, Scud River, Iskut River, Chutine River, Christina Lake, Verrett River, Porcupine River, Bugleg Creek, Shakes Creek, Bronson Slough, Devil's Elbow, Mainstem Stikine River, Craig River, Katete River, Twin River
Unuk River	1	Border Lake
Queen Charlotte Islands	5	Mercer Creek, Yakoun River, Awun River, Naden River, Copper Creek
Nass River	11	Bonney, Kwinageese, Meziadin (fishway, shore), Tintina Creek, Hanna Creek, Damdochax, Bowser, Gingit, Brown Bear, Zolzap
Skeena River	14	McDonnell Lake, Williams Creek, Schulbuckhand Creek, Alastair Lake, Kitwanga River, Kitsumkalum River, Stephens Creek, Nangeese River, Kispiox River, Motase Lake, Swan Lake, Bear, Sustut, Nanika River, Lower Babine River, Upper Babine River, Pinkut Creek, Fulton River, Morrison River, Shass Creek, Twain Creek, Tahlo Creek, Four Mile Creek, Pierre Creek
Babine Lake	10	Devon, Mikado, Lowe, Banks, Canoona, Kitlope, Tenas, Lonesome, Namu, Mary Cove Creek, Lagoon Creek, Kimsquit, Tankeeah, Klemtu, Koeye, Bella Coola, Docee River, Smokehouse Creek, Canoe Creek
Coastal British Columbia	19	Marble Creek, Inziana River, Washwash River, Ashlulm River,
Owikeno Lake	10	

		Dallery River, Genesee River, Neechanz River, Amback River, Sheemahant River, Wannock
Southern BC	6	Klinaklini River, Phillips River, Village Bay, Sakinaw, Heydon, Glendale
West coast Vancouver Is.	14	Sproat Lake (4 sites), Great Central Lake (6 sites), Henderson Lake, Quatse Lake, Hobiton Lake, Kennedy Lake
East coast Vancouver Is.	1	Schoen Lake
Nimpkish River	3	Nimpkish Lake, Woss Lake, Vernon Lake
Fraser River	53	Bowron River, Stellako River, Middle River, Nadina River, Pinchi Creek, Tachie River, Kuzkwa River, Chilko River, Chilko Lake, Roaring River, Horsefly River (4 sites), Wasko Creek, Blue Lead Creek, Gates Creek, McKinley Creek, Mitchell River, Portage Creek, Nahatlatch River, Kynock Creek, Dust Creek, Gluskie Creek, Forfar Creek, Porter Creek, Hudson Bay Creek, Blackwater Creek, Birkenhead River, Weaver Creek, Big Silver Creek, Harrison River, Douglas Creek, Pitt River, Widgeon Slough, Cultus Lake, Chilliwack River (2 sites), Cogburn Creek, Lower Adams, Upper Adams, Little River, Lower Shuswap, Middle Shuswap, Little Shuswap, Scotch Creek, Seymour River, Eagle River (early, late), Cayenne Creek, Fennell Creek, Raft River, North Thompson
Washington	3	Lake Washington, Baker Lake, Ozette Lake
Columbia River	2	Okanagan River, Wenatchee

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Table 2. Mean estimated percentage stock compositions of single population mixtures (correct = 100%) for 15 representative populations of sockeye salmon mostly from Russia and western Alaska calculated with 14 microsatellite loci and one MHC 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 298-population baseline, 150 fish in the mixture sample and 100 resamplings in the mixture sample and baseline samples. Standard deviation is in parentheses.

Sampling site	Population	Lake	Region	Region
Abira River	95.7 (1.7)	95.7 (1.7)	95.7 (1.7)	Hokkaido Island
Tigil	95.0 (2.0)	95.0 (2.0)	95.0 (2.0)	Northwest Kamchatka
Plotnikova	90.9 (3.3)	90.9 (3.3)	94.9 (2.0)	West Kamchatka
Kirushutk	80.5 (4.8)	96.7 (1.7)	96.7 (1.7)	Kuril Lake
Avachinsky	91.9 (2.4)	91.9 92.4)	91.9 (2.4)	Southeast Kamchatka
Elovka	94.5 (2.1)	94.5 (2.1)	96.9 (1.4)	East Kamchatka
Laguna Anana	94.2 (2.7)	94.2 (2.7)	97.8 (1.3)	Bering Sea
Painter Creek	89.9 (3.2)	89.9 (3.2)	89.9 (3.2)	Alaska Peninsula
Mission Creek	91.7 (2.5)	97.7 (1.4)	98.4 (1.1)	Wood River
Lynx Creek	92.0 (2.6)	92.0 (2.6)	94.9 (1.9)	Wood River
Knutson Bay	87.6 (4.1)	96.9 (1.5)	96.9 (1.5)	Iliamna Lake
Kijik River	88.4 (3.3)	95.6 (1.8)	95.6 (1.8)	Lake Clark
Ruth Lake	90.1 (3.2)	90.1 (3.2)	90.1 (3.2)	Southwest Bristol Bay
Meadow (late)	83.3 (4.6)	95.4 (1.9)	95.8 (1.8)	Kodiak Island
Inziana River	87.1 (4.7)	99.2 (0.8)	99.2 (0.8)	Owikeno Lake

Table 3. 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 298 baseline populations with replacement to obtain a new distribution of allele frequencies. Standard deviation is in parentheses. Expected regional composition is obtained by adding true population components, with estimated regional composition listed in the Region column for each mixture.

Population/Region	Mixture 1			Mixture 2			
	True	Estimated		Population/Region	True	Estimated	
		Population	Region			Population	Region
Woody Is. (Iliamna)	10	7.6 (2.4)	9.8 (2.6)	McDonald (SE Alaska)	5	4.5 (1.8)	
Hansen Cr. (Wood R.)	5	4.6 (2.0)		Petersburg (SE Alaska)	5	4.9 (1.5)	
Lynx Cr. (Wood R.)	5	4.4 (1.8)	9.6 (2.5)	Red Bay (SE Alaska)	5	5.1 (1.9)	
Karluk_Lake (Kodiak Is.)	5	4.0 (1.8)		Sitkoh (SE Alaska)	5	4.8 (1.7)	19.6 (3.4)
Linda Cr. (Kodiak Is.)	5	3.9 (1.6)	10.7 (2.5)	Kijik R. (L. Clark)	10	9.0 (2.5)	9.7 (2.3)
Painter Cr. (Alaska Pen.)	5	4.7 (2.0)	4.7 (2.0)	Mission Cr. (Wood R.)	10	9.3 (2.3)	10.0 (2.3)
Gavrushka R. (Kuril L.)	10	6.5 (2.4)		Ruth Lake (SW Bristol)	10	8.4 (2.6)	8.4 (2.6)
Oladochnaya B. (Kuril L.)	10	7.3 (2.6)	19.0 (3.0)	Up. Station (Kodiak Is.)	10	9.0 (2.4)	9.8 (2.5)
Plotnikova R. (W. Kam.)	10	10.0 (2.7)	10.5 (2.7)	Kirushutk (Kuril L.)	10	7.8 (2.5)	10.9 (2.7)
Elovka R. (E. Kam.)	10	10.0 (2.6)		Avachinsky (S.E. Kam.)	20	17.8 (2.9)	17.8 (2.9)
Kamchatka R. (E. Kam.)	10	8.5 (2.6)	20.0 (3.5)	Abira R. (Hokkaido Is.)	10	9.8 (2.7)	9.8 (2.7)
L. Anana (Bering Sea)	10	9.1 (2.6)					
L. Potat (Bering Sea)	5	4.2 (1.7)	14.1 (3.0)				
Mixture 3							
Okanagan R. (Columbia)	10	10.0 (2.4)	10.0 (2.4)				
Bowron R. (Fraser)	15	14.7 (3.1)	15.1 (3.1)				
Devon L. (BC Central)	5	4.7 (1.7)	4.9 (1.7)				
Alastair L. (Skeena R.)	15	14.7 (3.0)	14.8 (3.0)				
Shakes Cr. (Stikine R.)	5	3.4 (1.7)	5.1 (1.8)				
Karta L (SE Alaska)	10	9.9 (2.6)	10.4 (2.6)				
Fuel Dump Is (Iliamna L)	10	7.5 (2.6)	9.6 (2.7)				
L. Thumb (Kodiak Is.)	10	7.1 (2.3)	8.9 (2.2)				
Dvu-Yurtochnaya R (EK)	15	13.2 (3.1)	14.6 (3.0)				
Abira R. (Hokkaido Is.)	5	5.0 (1.8)	5.0 (1.8)				