Sockeye salmon (*Oncorhynchus nerka*) return after an absence of nearly 90 years: a case of reversion to anadromy

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Abstract: We document the recent reappearance of anadromous sockeye salmon (*Oncorhynchus nerka*) that were thought to have been extirpated by the construction of hydroelectric dams on the Coquitlam and Alouette rivers in British Columbia, Canada, in 1914 and 1927, respectively. Unexpected downstream migrations of juveniles during experimental water releases into both rivers in 2005 and 2006 preceded upstream return migrations of adults in 2007 and 2008. Genetic (microsatellite and mitochondrial DNA) markers and stable isotope (δ^{34}S and ^{87}Sr/^{86}Sr) patterns in otoliths confirm that both the juvenile downstream migrants and adult upstream migrants were progeny of nonanadromous sockeye salmon (kokanee) that inhabit Coquitlam and Alouette reservoirs. Low genetic diversity and evidence of genetic bottlenecks suggest that the kokanee populations in both reservoirs originated from relatively few anadromous individuals that residualized after downstream migration was largely prevented by the construction of dams. Once given an opportunity for upstream and downstream migration, both populations appear capable of reverting to a successful anadromous form, even after 25 generations.

Résumé : Nous apportons des informations sur la réapparition récente des saumons rouges (*Oncorhynchus nerka*) anadromes qu'on croyait extirpés par la construction de barrages sur les rivières Coquitlam et Alouette en Colombie-Britannique, Canada, respectivement en 1914 et en 1927. Des migrations inattendues vers l'aval de jeunes saumons durant des vidanges expérimentales d'eau dans les deux rivières en 2005 et 2006 ont précédé des migrations de retour vers l'amont en 2007 et 2008. Les marqueurs génétiques (microsatellites et ADN mitochondrial) et les patrons d'isotopes stables (δ^{34}S et ^{87}Sr/^{86}Sr) dans les otolithes confirment que tant les jeunes migrateurs vers l'aval que les migrateurs adultes vers l'amont sont des rejetons de saumons rouges non anadromes (kokanis) qui habitent les réservoirs Coquitlam et Alouette. La faible diversité génétique et des indications de goulots d'étranglement génétiques laissent croire que les populations de kokanis des deux réservoirs sont issues d'un petit nombre d'individus anadromes qui sont demeurés sur place lorsque la migration vers l'aval a été en grande partie bloquée par la construction des barrages. Une fois la possibilité rétablie de migrations vers l'amont et l'aval, les deux populations semblent capables de revenir avec succès à une forme anadrome, même après 25 générations.

[Traduit par la Rédaction]

Introduction

Life history diversity contributes to population resilience in variable environments (e.g., Hilborn et al. 2003; Schindler et al. 2010), yet human actions and natural processes increasingly threaten migratory phenotypes in salmonids (Gustafson et al. 2007; Waples and Hendry 2008). The species sockeye salmon, *Oncorhynchus nerka*, is widely distributed throughout the North Pacific and occurs as three distinctive ecotypes:

(*i*) anadromous lake-type sockeye salmon, which typically rear in lakes for 1 year before migrating to the ocean where they typically spend the next 2 years before returning to fresh water to spawn and die; (*ii*) anadromous sea- or river-type sockeye salmon, which usually rear in rivers for several weeks to months before migrating to the ocean where they spend 2 to 3 years and then return to fresh water; and (*iii*) nonanadromous kokanee, which spend their entire life in fresh water (Burgner 1991; Wood et al. 2008). Kokanee pop-

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ulations are known to have evolved from anadromous lake-type sockeye salmon where barriers have impeded anadromous migration (Ricker 1938, 1959; Krogius 1981). Genetically distinct kokanee populations can also evolve and coexist in sympatry with the freshwater phase of lake-type sockeye salmon (Foote 1989; Wood and Foote 1996).

Because kokanee retain the ability to osmoregulate in seawater even after being land-locked for thousands of generations (Foote et al. 1994), it seems plausible that they could revert to an anadromous ecotype given the opportunity. Considerable evidence for such reversion exists, but well-documented examples of "sea-run kokanee" are rare. Foerster (1947) marked and released hatchery-reared age-1 kokanee from Kootenay Lake, B.C., into Sweltzer Creek (draining Cultus Lake, B.C.), forcing them to migrate downstream to the Fraser River. Of the 63 874 juveniles released, 0.12% survived to adulthood, with an estimated 74 caught in the fishery and 17 returning to the lake as 5-year-olds, 1 year older than the typical age of return for anadromous sockeye salmon (Foerster 1947). Hatchery-reared progeny of 1942 brood-year kokanee from Lake Chelan in Washington State were released as 18-month-old juveniles in the Entiat River, but only 0.004% survived to return as adults. The populations of kokanee in Kootenay and Chelan lakes must have been non-anadromous for about 10 000 years because high natural waterfalls block their return migration. In another experiment, hatchery-reared progeny of the 1944 brood-year kokanee from Wenatchee Lake, also in Washington State, were marked and planted back into Wenatchee Lake as 12-month-old juveniles and into Icicle Creek (a tributary of the Wenatchee River) as 18-month-old juveniles; 0.27% and 0.5% were later recovered as anadromous adults, respectively (Fulton and Pearson 1981). Ricker (1972) speculated that these kokanee had been recently derived from anadromous sockeye salmon in Wenatchee Lake and that Lake Wenatchee kokanee may have diverged from sockeye salmon only within the past 90 years. Up to 2.8% of hatchery-reared kokanee released in Lake Toro and forced to migrate to sea survived to return as anadromous adults (Urawa and Kaeriyama 1999). The parent kokanee had been transplanted from Lake Sikotshu, which in turn had originated from anadromous sockeye salmon that were transplanted from the Kuril Islands in the late 1800s and as recently as 1925–1940 (Urawa and Kaeriyama 1999). Although limited, these observations collectively suggest that adaptations to marine life are lost after a long period of isolation in fresh water.

Understanding the potential for kokanee to revert to anadromy could aid in the recovery of anadromous sockeye runs, many of which face imminent extirpation (Slaney et al. 1996; Gustafson et al. 2007; Waples and Hendry 2008). It is therefore important to document empirical evidence of the biotic and abiotic conditions under which one ecotype is favoured over another and to identify conditions under which kokanee can successfully revert to anadromy.

In this paper we investigate the extent to which kokanee in the Coquitlam and Alouette reservoirs may have reverted to anadromy under a modified regime of water outflow. Both rivers once drained natural lakes and supported sizeable runs of sockeye salmon that provided a major food supply to local aboriginal people in the area (Hirst 1991). The main runs in both rivers were early (April–May up to July), although later

runs were also present (Bengeyfield et al. 2001; Koop 2001). Anadromous sockeye salmon used to spawn along the shores of the Alouette and Coquitlam lakes and adjoining tributaries (Hirst 1991; Koop 2001). Gold Creek, an inlet tributary of Alouette Lake, was one of the spawning grounds (Hirst 1991). By the 1930s, following construction of hydroelectric dams in the mid 1910s and late 1920s, native anadromous sockeye salmon had disappeared entirely from the Alouette and Coquitlam rivers, respectively.

In 2007 and 2008, for the first time in nearly 90 years, anadromous adults reappeared in both rivers migrating upstream as far as the dams. These adult upstream migrants (AUM) were presumed to be associated with unprecedented observations of *O. nerka* juvenile downstream migrants (JDM) in both rivers in 2005 and 2006, which apparently had been triggered by experimental manipulations of water releases past the dams (Baxter and Bocking 2006; Humble et al. 2006). Alternatively, the AUM might have been strays from nearby populations, or sea- or river-type sockeye salmon that evolved from lake-type Alouette sockeye salmon and persisted in the Alouette River after dam construction prevented access to the nursery lake.

Our first objective is to document these unusual events including relevant demographic information for AUM and JDM with respect to estimates of abundance, size, age, migration timing, and marine survival. We then compare these demographic characteristics with data available for other populations of sockeye salmon that emigrated from the Fraser River in the same year.

Our second objective is to assess, using genetic and isotopic markers, whether the JDM and the AUM were progeny of the kokanee known to inhabit each reservoir. We tested this hypothesis in two complementary ways. First, we compared the microsatellite DNA (μsatDNA) and mitochondrial DNA (mtDNA) of the unknown samples (i.e., JDM and AUM) with reference samples from kokanee in the reservoirs and from other populations of sockeye salmon and kokanee in nearby river systems. Second, we measured stable isotope ratios of sulfur ($^{34}S/^{32}S$, expressed as $\delta^{34}S$) and strontium ($^{87}Sr/^{86}Sr$) in otoliths to determine whether the isotopic signature was consistent with that expected in the anadromous progeny of kokanee (hereafter referred to as "sea-run kokanee"). The otolith core is formed from the yolk, which reflects the feeding environment of the maternal parent (Kalish 1990), so sea-run kokanee should not have a marine signature in the otolith core.

Our third objective is to elucidate the evolutionary history of sockeye salmon and kokanee in the Alouette and Coquitlam rivers by compiling historical accounts and examining genetic data. We searched the literature and government databases for stocking and catch records to assess whether Alouette and Coquitlam kokanee might have originated from a native or introduced kokanee population. Lastly, we compared indices of allelic richness and genetic diversity in Alouette and Coquitlam kokanee with indices for nearby sockeye salmon populations, looking for evidence of population bottlenecks or rapid genetic drift. Bottlenecks would be expected if the Alouette and Coquitlam kokanee populations had originated from "residual" sockeye salmon (the non-anadromous progeny of anadromous sockeye salmon), which were likely rare in the original population, but which could

have survived to spawn after dams prevented spawning by anadromous fish.

Materials and methods

Study sites

Coquitlam and Alouette reservoirs are oligotrophic, relatively small (12 and 16 km^2) but deep (maximum depths of 187 and 140 m), located in the steep terrain of the Coast Mountains at 49.3°N latitude, at a distance to the ocean of 60 and 72 km, respectively (Fig. 1). Both are coastal reservoirs where the majority of the inflow results from seasonal storms and spring snow melt. The bulk of the outflow from both reservoirs is diverted to other water bodies via tunnels to produce hydroelectricity.

Alouette Reservoir is formed by a 21 m dam constructed at the south end of the original lake at the natural outlet into the Alouette River, which drains into the Pitt River before entering the Fraser River (Conlin et al. 2000a). The 17 km long reservoir comprises two basins separated by a narrow section corresponding to the former two lakes "Upper and Lower Lillooet Lake" (Conlin et al. 2000a). Most of the outflow is diverted through a 1 km tunnel at the north end of Alouette Lake into Stave Reservoir where power generation occurs. Outflow at the original outlet into the Alouette River is controlled by a low-level outlet (LLO, underwater release), a crest gate (surface water release), and a free crest weir (surface water release) (BC Hydro 2009). Water can spill over the free crest weir if the water level is greater than 125.5 m, but such spills are rare. Based on BC Hydro records from 1984, it occurred only in 1986 (3 days in November) and 1995 (5 days in November and December) (B. Wilson, BC Hydro Ruskin Dam & Generating Station, 10600 Wilson Street, Mission, BC V4S 1B4, unpublished data).

The 12 km long Coquitlam Reservoir is formed by a 30 m dam constructed across the original outlet into the Coquitlam River at the south end of the lake (Conlin et al. 2000b). In contrast with the Alouette Reservoir, there is no crest gate at the Coquitlam dam for releasing surface water into the river. Water spills to the Coquitlam River are solely controlled by the LLO and a free crest weir. Over the full length of the records, water spill over the free crest weir occurred only in 1990 (3 days in November), 1991 (3 days August–September), 1995 (15 days August–September), and 1996 (3 days in January). The Coquitlam River runs through the municipality of Port Coquitlam before entering the Fraser River and the Pacific Ocean. Most of the outflow is diverted for power generation into Buntzen Lake through a tunnel at the southwest side of the reservoir, 4 km from the dam. Public access to the Coquitlam watershed has been restricted since the 1880s because it supplies drinking water to the Greater Vancouver Metropolitan Area via a water intake 300 m from the dam on the east side of the lake (Conlin et al. 2000b; BC Hydro 2005).

Fish monitoring and collection and experimental water releases

As part of the Alouette and Coquitlam Water Use Plans, rotary screw traps (RSTs) have been used to monitor the downstream migrations of coho (*Oncorhynchus kisutch)*, chum (*Oncorhynchus keta)*, and Chinook salmon (*Oncorhynchus tshawytscha)* and steelhead trout (*Oncorhynchus mykiss)*. In the Alouette River, RSTs were deployed 16 km downstream of the dam every year since 1998 (Cope 2010). In the Coquitlam River, RSTs were deployed at 1, 4, and 7 km downstream of the dam every year since 2000 (Derek et al. 2010). Returning adults were enumerated visually by stream walk in the Coquitlam River and by trapping in the Alouette River. After sockeye salmon were observed returning to the Alouette River trap in 2007, that trap was modified to better handle returns in 2008 (Backle 2008), and a new trap was installed in the Coquitlam River in 2008.

As part of a program to reintroduce coho salmon in 2005 and steelhead trout in 2006, the hydroelectric company of British Columbia (BC Hydro) in concert with the Alouette River Management Society experimentally manipulated water release from the Alouette Dam. In 2005, water was released via the crest gate over the spillway for 1 month (3 May – 3 June), and flow at the gate was maintained between 2.2 and 2.8 m^3·s^{-1} (Baxter and Bocking 2006). In 2006, the water was released over 2 weeks (11–31 May), with flow at the gate ranging from 2.2 to 3.5 m^3·s^{-1} (Humble et al. 2006). The water depth at the gate during surface water release averaged ~1 m (1 standard deviation (SD) = 0.26). The outflow through the LLO was gradually decreased when the experiment began and was maintained at zero flow for the majority of the experimental water releases. In both years, RSTs located approximately 1.5 km downstream of the Alouette Dam were used to obtain a sample of the salmonid migrants. Traps were checked daily in the morning, and all species of fish within the holding box were counted. Total numbers of JDM in 2005 and 2006 were based on estimates of trap efficiency obtained in mark and recapture experiments with coho (42%, 2005) and with JDM (35%, 2006). Experimental water releases in the Coquitlam Reservoir consisted of opening the LLO and fish valves. In 2005, water flow at the gate was maintained experimentally at ~6.5 m^3·s^{-1} for 10 days (21 April – 1 May). A second water release of 23 days (21 April – 14 May) occurred in 2006, when flow at the gate was ~6.1 m^3·s^{-1} (G. Lewis, 2755 Lougheed Highway, Port Coquitlam, BC V3B 5Y9, personal communication, 2010). The depth at which the LLO opened ranged from 5.0 to 6.7 m in 2005 and 3.0 to 3.7 m in 2006. In both years, RSTs were used to monitor all salmonid migrants, including the JDM.

In 2005 and 2006, tissue samples and fork length measurements were collected from a random sample of JDM in both the Alouette and Coquitlam rivers. Fish scales for ageing were collected from random samples of the Alouette JDM in 2005 and 2006. BC Hydro employees first noticed sockeye salmon-like spawners in the Alouette and Coquitlam rivers attempting to ascend past the dams in the late summer of 2007, and they collected tissues for DNA analysis, scales for ageing, otoliths, and postorbital fork lengths. In 2008, AUM from both rivers were sampled only for fork length, DNA, and scales for ageing before being transported and released upstream into their respective reservoirs (Table 1a). Corresponding samples were collected from kokanee in both reservoirs.

Genetic markers

Microsatellites (µsatDNA) and mitochondrial DNA (mtDNA) were analyzed to determine whether samples of JDM and AUM (Table 1a) were more closely related to kokanee in their respec-

Fig. 1. Location of sockeye salmon (open circles) and kokanee (solid circles) populations sampled for the genetic and isotopic markers studies. Genetic study on the lower Fraser River and Chilko Lake sockeye salmon on the upper Fraser: Alouette Reservoir (1), Coquitlam Reservoir (2), Widgeon Slough (3), Pitt River (4),Weaver (5), Harrison Rapids (6), Big Silver Creek (7), Chilliwack Lake (8), Cultus Lake (9), Lillooet Lake – Birkenhead River (10), Chilko Lake (11). Isotopic markers study: Alouette Reservoir (1), Sakinaw Lake (12), Sproat Lake (13), and Nimpkish Lake (14).
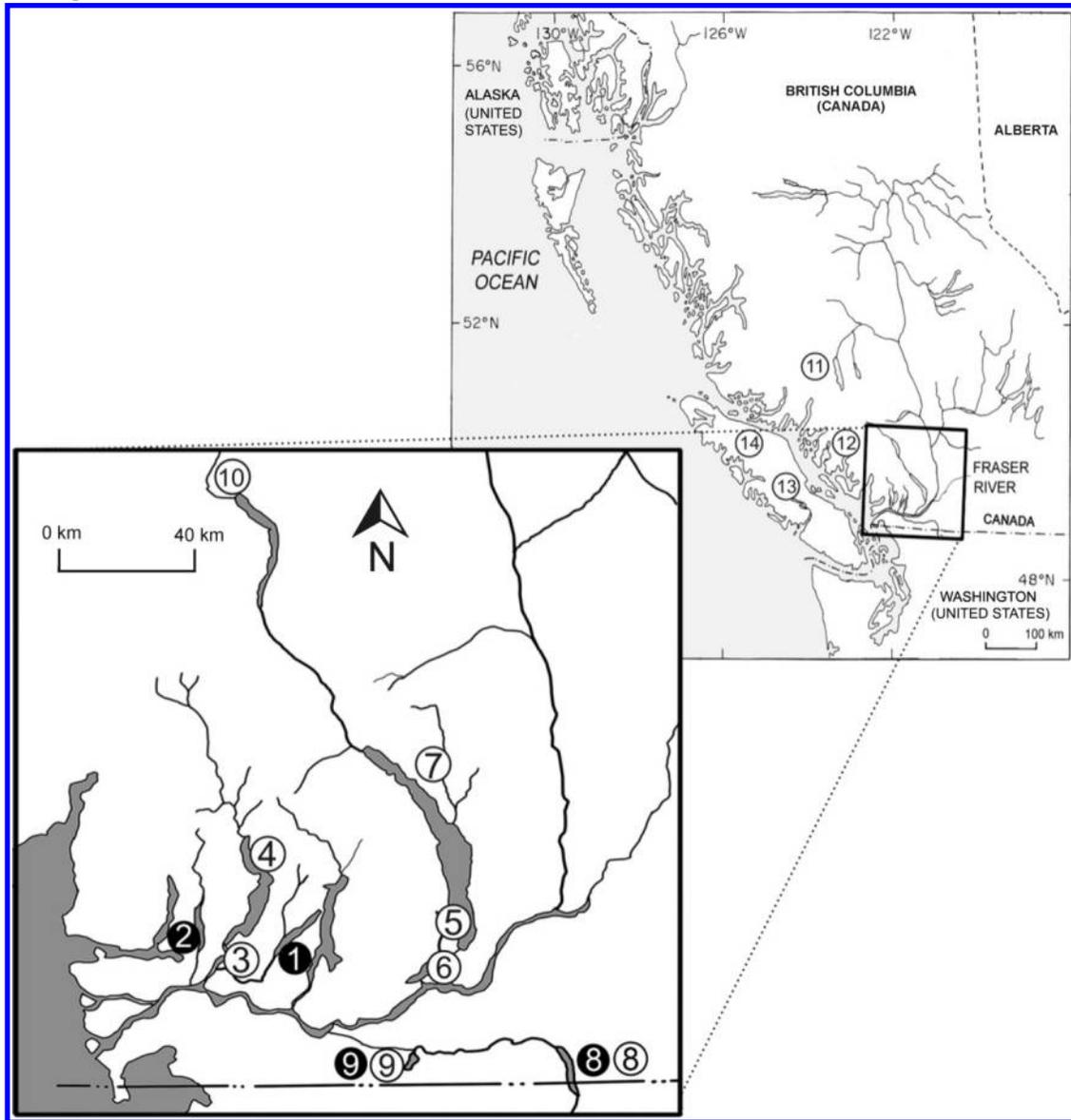
tive river systems than to anadromous sockeye salmon spawning in neighbouring rivers (referred to as the reference populations; Table 1*b*). For each AUM sampled, we determined a multilocus genotype at 14 microsatellite loci (*Ots2*, *Ots3*, *Ots100*, *Ots103*, *Ots107*, *Ots108*, *Oki1a*, *Oki1b*, *Oki6*, *Oki10*, *Oki16*, *Oki29*, *One8*, and *Omy77*; Beacham et al. 2005) and a composite haplotype based on two genes (cytochrome *b* (*cytb*) and NADH dehydrogenase subunit 1(*ND1*)) in mitochondrial DNA (as described in Wood et al. 2008). Polymerase chain reaction (PCR) amplification of mitochondrial genes *ND1* and *cytb* was accomplished with primer pairs LGL 290 GGGCCTAAGCCCTTTTTCTCA, LGL 560 GGCRGCTTTTGGTTATTAG and LGL 287 GAGCTAGGGCAGGCTCA, LGL 765 GAAAAACCAYCGTTGTWATTCAACT, respectively. The *cytb* PCR product was approximately 1300 base pairs, whereas the amplified segment of the *ND1* gene was approximately 859 base pairs. Genetic data

for the 10 reference populations are from published µsatDNA (Beacham et al. 2005) and mtDNA (Wood et al. 2008) databases and additional analyses conducted as part of this study.

The extent of genetic divergence between groups of fish was assessed by testing for differences in allelic and haplotypic frequencies based on pairwise F_{ST} values calculated for each sample over all loci or haplotypes combined. The pairwise F_{ST} value is the genetic variance attributable to differentiation between samples. F_{ST} values can range from 0 (no detectable divergence between samples) to 1 (complete divergence). Critical significance levels for simultaneous pairwise population differentiation one-tailed tests were evaluated using Bonferroni adjustment ($0.05/240 \times 2 = 0.000417$) in FSTAT version 2.9.3.2 (Goudet 2001). An unrooted, consensus neighbor-joining tree based on 1000 replicate trees was generated with the CONSENSE program from PHYLIP (Fel-

Table 1. Sample collection data for (*a*) juvenile downstream migrants (JDM) and adult upstream migrants (AUM) caught in the Alouette and Coquitlam rivers; and (*b*) reference samples for genetic analysis from kokanee and anadromous sockeye salmon populations in the lower Fraser River.

(*a*) Samples of unknown origin (caught below reservoir).

	Year migration	μsatDNA (*n*)	mtDNA (*n*)	δ^{34}S (*n*)	^{87}Sr/^{86}Sr (*n*)	Population estimate of the migrants (*N*)
JDM						
Alouette River	2005	190	25			7 900[a]
	2006	48	55			5 064[b]
	2007	44	0			62 923
	2008	10	0			8 257
Coquitlam River	2005	0	0			~1 500[c]
	2006	41	46			~800[c]
	2007	0	0			NA
	2008	3	0			NA
AUM						
Alouette River	2007	18	8	13	10	28[d]
	2008	53	27			54[d]
Coquitlam River	2007	2	1			NA
	2008	10	10			10[e]

(*b*) Samples of known origin.

	μsatDNA (*n*, years)	mtDNA (*n*, years)	δ^{34}S (*n*, years)	^{87}Sr/^{86}Sr (*n*, years)
Kokanee				
Alouette Reservoir	86 (2000, 2002)	122 (2005, 2006)	3 (2007)	5 (2007)
Coquitlam Reservoir	59 (2004, 2005)	133 (2002, 2004, 2005, 2006)		
Cultus Lake	32 (2006, 2007)	21 (2007)		
Chilliwack Lake	100 (2004)	23 (2002, 2004)		
Sockeye				
Widgeon Slough	82 (2002)	45 (1997, 2003)		
Pitt River	68 (2005)	33 (2004)		
Weaver Creek	60 (1992)	48 (1992, 2000)		
Harrison Rapids	132 (1986)	25 (1997)		
Birkenhead River	100 (1998)	25 (1992)		
Big Silver Creek	95 (2002)	25 (2002)		
Chilliwack Lake	88 (2004)	25 (2001, 2004)		
Cultus Lake	161 (2005)	25 (1985)		
Chilko Lake (upper Fraser)	122 (1999)	23 (1992)		
Sproat Lake			5 (2006)	5 (2006)
Sakinaw Lake			2 (2005)	7 (2003, 2005)
Nimpkish Lake			1 (2006)	4 (2006)

Note: Sample size is represented by *n*; population estimates are represented by *N*. Data in part *b* include an outgroup (Chilko Lake sockeye salmon) from the upper Fraser River and reference otolith samples for isotope analysis from kokanee in the Alouette Reservoir and anadromous sockeye salmon in Sproat, Sakinaw, and Nimpkish lakes.

[a]Baxter and Bocking 2006.

[b]Humble et al. 2006.

[c]G. Lewis, 2755 Lougheed Highway, Port Coquitlam, BC V3B 5Y9, personal communication, January 2011.

[d]Backle 2008.

[e]M. Coulter-Boisvert, Fisheries and Oceans Canada, Delta, BC V3M 6A2, personal communication, January 2011.

senstein 1993). The Chilko River sockeye salmon population was included as an outgroup.

Genetic similarity among populations was also revealed by multidimensional scaling (MDS) with the monotonic Kruskal loss function in SYSTAT (2004). MDS allows genetic similarities among populations to be visualized in two dimensions without the added challenge of imposing a phylogenetic tree. Two similarity matrices were created, one for μsatDNA data and the other for mtDNA data, based on Cavalli-Sforza and Edwards (1967) chord distances between each pair of populations. This distance measure is appropriate when differences arise by genetic drift rather than by mutation (Felsenstein 2005). To facilitate comparison of grouping patterns in the μsatDNA and mtDNA data, MDS values from dimension 2 of the mtDNA analysis were plotted against MDS values from dimension 1 of the μsatDNA analysis. These particular

dimensions were complementary (least redundant) in the sense that they provided the greatest separation of individual populations in a two-dimensional projection.

Assignment of individual genotypes for the unknown AUM samples was conducted using Bayesian methods from the program cBAYES (Neaves et al. 2005). The cBAYES program was run with eight chains through 20 000 iterations, and each fish was assigned to the baseline sample to which it had the highest probability of membership.

Standardized allelic richness (El Mousadik and Petit 1996) in the AUM samples was compared with that in the reference populations. The software program Bottleneck (Cornuet and Luikart 1996) was used to compare gene diversity (expected heterozygosity) at each locus in the AUM sample with that expected, given the same number of alleles assuming mutation–drift equilibrium. The calculation was performed using the infinite alleles model of locus evolution. For each sample, a one-tailed Wilcoxon test was performed to determine whether the observed number of loci showing excess heterozygosity was significantly higher than expected by chance, which would indicate a recent loss of alleles consistent with a bottleneck in population size. To correct for multiple tests, a P value less than 0.0042 was required to reject the null hypothesis with 95% confidence.

Isotopic markers

Otoliths from 13 AUM in the Alouette River in 2007 (Table 1a) were cleaned in de-ionized water, dried, embedded in resin (Buehler 20–8130 epoxide resin with Buehler 20-8132 hardener), cured overnight at 62 °C in a drying oven, and polished on both sides to expose growth bands and the core portion of the otolith accreted during juvenile growth. Distribution of sulfur isotopes in otoliths, from the core to the outer edge of the otoliths, was analyzed by secondary ion mass spectrometry (SIMS) at University of California – Los Angeles with methods similar to those reported by Godbout et al. (2010). Usually two spots were analyzed in each of three zones: the core (pre-exogenous), the first year of growth (exogenous feeding in fresh water), and the last 2 years of growth. Data were corrected for instrumental mass fractionation determined throughout each analytical session from replicate analysis of the outer edge of the sockeye salmon otolith assuming a marine $^{34}S/^{32}S$ of 0.04505, or $\delta^{34}S$ (V-CDT) = +20‰ relative to V-CDT $^{34}S/^{32}S$ = 0.044163 (Ding et al. 2001). All $^{34}S/^{32}S$ ratios were expressed as $\delta^{34}S$ values, the deviation in per mil (‰) relative to the Canyon Diablo Troilite (CDT) standard.

$$\delta^{34}S = \left[\frac{(^{34}S/^{32}S)_{sample}}{(^{34}S/^{32}S)_{CDT}} - 1 \right] \times 1000$$

To supplement our comparison, we used $\delta^{34}S$ in otoliths from three kokanee caught in the Alouette Reservoir and eight wild adult sockeye salmon from Sakinaw, Sproat, and Nimpkish lakes (Godbout et al. 2010), hereafter referred to as kokanee and wild sockeye salmon of known maternal origin, respectively (Table 1b). We also measured the strontium isotope ratio ($^{87}Sr/^{86}Sr$) in otoliths of 10 AUM (Table 1a), 4 Alouette kokanee, and 16 wild sockeye salmon from Sakinaw, Sproat, Nimpkish lakes, respectively (Table 1b) by laser ablation multicollector inductively coupled plasma mass

spectrometry (LA-MC-ICPMS; Agilent Technologies 7200A ICPMS, coupled with a Nd:YAG 213 nm laser, New Ware Research UP213 at University of California – Davis, Davis, California) with specific instrument, laser, and interference corrections as applied to otoliths (Barnett-Johnson et al. 2005). Two or three laser spots were analyzed in each of the three zones (core, first, and last 2 years of growth). Approximately 30 $^{87}Sr/^{86}Sr$ ratios were measured for each laser spot (60 μm). $^{87}Sr/^{86}Sr$ ratios were normalized to $^{88}Sr/^{86}Sr$ = 0.1194 to account for any natural or machine-induced fractionation. External precisions (reproducibility) were based on repeated measurements of an in-house gastropod shell standard. The daily mean value of $^{87}Sr/^{86}Sr$ measurements for the standard ranged from 0.70921 to 0.70924 (1 SD < 0.00006; daily n >5), which is close to the global marine $^{87}Sr/^{86}Sr$ value of 0.70918.

The life histories of the various groups (Alouette AUM, Alouette Lake kokanee, and wild sockeye salmon of known origin) were confirmed by testing for differences in $\delta^{34}S$ and $^{87}Sr/^{86}Sr$ in analyses of variance (ANOVAs in Proc GLM; SAS Institute Inc. 2008). Subsequently, multiple t tests with Tukey–Kramer adjustment (LSMEANS in Proc GLM; SAS Institute Inc. 2008) were used to test for differences in the mean values of $\delta^{34}S$ and $^{87}Sr/^{86}Sr$ in the core, in the last 2 years of growth, and in the mean differences between the core and last 2 years of growth (DIFF), among AUM, kokanee, and sockeye salmon.

Results

Evidence for anadromous migrations

Mark–recapture estimates of JDM abundance in the Alouette River were 7900 in 2005 and 5064 in 2006 (Table 1a) (Baxter and Bocking 2006; Humble et al. 2006). Mark–recapture estimation was not successful in the Coquitlam River, but tentative estimates of 1500 and 800 JDM have been suggested for 2005 and 2006, respectively (G. Lewis, 2755 Lougheed Highway, Port Coquitlam, BC V3B 5Y9, personal communication, 2010). In both 2005 and 2006, most JDM in the Alouette River were age 1 with a median fork length of 8.0 cm (Fig. 2). JDM in the Coquitlam River comprised three size groups with median fork lengths of 7.7, 16.1, and 19.9 cm. Although these fish have not been aged, the three size groups likely correspond to ages 1, 2, and 3 years of age, respectively. Sockeye salmon smolts from Chilko and Cultus lakes were primarily age 1 in both 2005 and 2006 (Fig. 2). In 2005, average size was similar in Alouette JDM and Chilko smolts (7 cm) and 3 cm longer in Cultus smolts (10 cm); in 2006, Alouette JDM averaged 1 cm less than Chilko smolts (8 cm), and again 3 cm less than Cultus smolts (10 cm) (Fig. 2).

Counts of AUM in the Alouette River were 28 in 2007 and 54 in 2008, but some might have been missed in 2007 as no monitoring program was in place (their return was unexpected). In 2007, all aged fishes were age 4 (or more specifically, 1.2, where the digits indicate the number of winters spent in fresh water and at sea, respectively, excluding the first winter, while the fish is an unhatched egg (Burgner 1991); in 2008, 32% were age 4 (both 1.2 and 2.1), 55% were age 5 (1.3 and 2.2), and 13% could not be aged (Table 2). The overall mean ($\pm$1 standard error, SE) length of

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Fig. 2. Length distribution of juvenile downstream migrants (JDM) from the Alouette and Coquitlam rivers and anadromous sockeye smolts from Chilko and Cultus lakes in 2005 (left panels) and 2006 (right panels). Numbers beside each mode indicate estimated age. Note that the size distribution of the 2-year-old JDM from Alouette River in 2006 is based on fish selected to be larger than 14 cm (*).
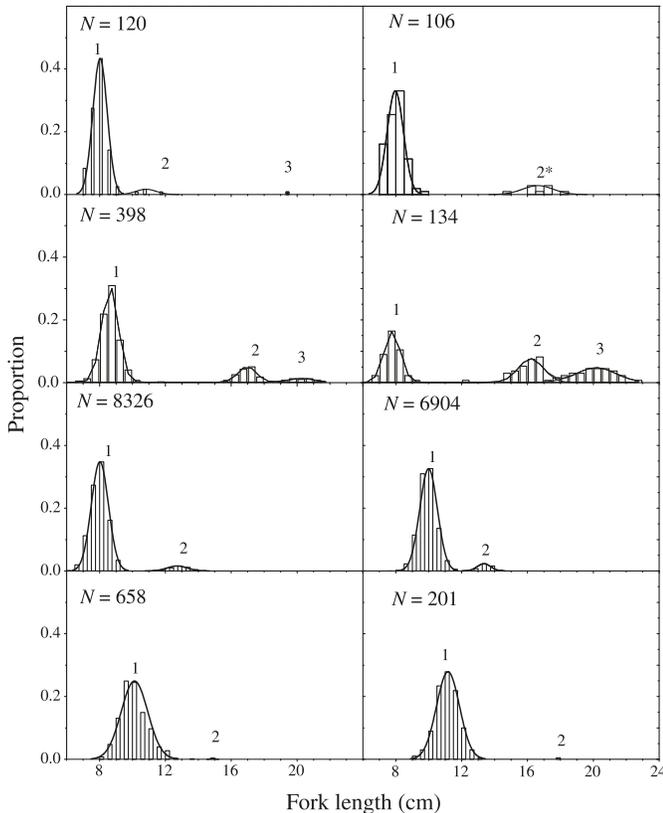
the returning adults was 59.7 ± 0.66 cm. Regardless of freshwater age, returning adults that had spent 3 years at sea (age *x*.3) were on average 4 cm longer than those returning after only 2 years at sea (*x*.2) (Table 2).

No AUM were reported in the Coquitlam River in 2007, perhaps owing to a lack of monitoring as there was not yet any expectation of returns. In 2008, 10 AUM were observed (M. Coulter-Boisvert, Fisheries and Oceans Canada, Delta, British Columbia, personal communication, 2011), ranging in size from 56.0 to 69.5 cm; ages 4 and 5 adults were equally represented among the six fish that could be aged. Coquitlam and Alouette adults of the same sea age were similar in size (Table 2). In contrast, adult kokanee that remained within the Alouette reservoir their entire life were on average less than half the length of the AUM in Alouette River at the same total age (Fig. 3).

Evidence for sea-run kokanee

μsatDNA variation within samples

Allelic frequencies did not differ significantly among samples of kokanee, JDM, and AUM collected within the same drainage (Table 3). In contrast, allelic frequencies differed significantly in pairwise comparisons between all 12 reference populations of sockeye salmon and kokanee (Table 3; Fig. 4*a*). The mean F_{ST} value in pairwise comparisons be-

tween kokanee populations (0.13) was similar to that of sockeye salmon populations (0.11). Kokanee populations in the Alouette and Coquitlam reservoirs were more similar to one another than to other populations in the lower Fraser River (Table 3; Fig. 4*a*). Kokanee and sockeye salmon populations in the Chilliwack drainage were the most distinctive (although relatively similar to one another) because of their unusual allelic frequencies and low levels of diversity. The three populations within the Pitt River drainage (Alouette kokanee, Upper Pitt sockeye salmon, and Widgeon Slough sockeye salmon) were genetically diverse, with the Pitt sockeye salmon population being more similar to sockeye salmon populations of the Harrison River drainage than to the other Pitt River populations. This analysis confirms that genetic distinctions among populations are sufficient to permit accurate individual identifications of AUM and JDM fish.

mtDNA

F_{ST} values for pairwise comparisons based on mtDNA haplotype frequencies generally support inferences based on μsatDNA (Table 3). Plotting multidimensional scaling values for dimension 1 of μsatDNA against dimension 2 for mtDNA reveals nonoverlapping geographic clusters associated with seven distinct nursery lakes (Alouette, Coquitlam, Cultus, Chillliwack, Lillooet (the Birkenhead River sample), Harrison (the Big Silver and Weaver Creek samples), and Pitt lakes) and two sea-type populations (Widgeon Slough and Harrison Rapids) (Fig. 4*b*). This plot also shows that the Alouette group is more similar to the Coquitlam group than to any other group. JDM and AUM are more closely related to the kokanee within the same drainage. The greater variation along the *Y* axis within the Coquitlam samples is due to the small sample size (Table 1*a*); only 11 Coquitlam AUM were analyzed for mtDNA, which accounts for the apparent (but statistically insignificant) difference among Coquitlam kokanee, JDM, and AUM (Fig. 4).

Genetic assignment of AUM

cBAYES assigned all AUM specimens to the kokanee population within the same drainage after comparing their multilocus genotypes to genetic data for 12 reference populations. This result confirms that the AUM were not strays from other rivers.

Isotopic markers

Otoliths of AUM from the Alouette River typically had low values of $\delta^{34}S$ (~5‰) and $^{87}Sr/^{86}Sr$ (~0.7042) in the core and in the first year of growth, as in kokanee, but high values of $\delta^{34}S$ (20‰) and $^{87}Sr/^{86}Sr$ (~0.7093) in the last 2 years of growth, as in anadromous sockeye salmon (Figs. 5*a*, 5*b*). Plotting mean values of $\delta^{34}S$ and $^{87}Sr/^{86}Sr$ in the core against mean values in the last 2 years of growth reveals three distinct groups (Figs. 6*a*, 6*b*). Mean $\delta^{34}S$ and $^{87}Sr/^{86}Sr$ in the core of otoliths in AUM (~5.59‰, 0.7043) were not significantly different than that in kokanee (5.18‰, $P < 0.95$; and 0.7045, $P < 0.33$), but were lower than that in sockeye salmon (~19.2‰, $P < 0.0001$; and 0.7082, $P < 0.0001$), which confirms that the AUM were the progeny of nonanadromous females. It is therefore impossible for the AUM to have been the progeny of sea- or river-type sockeye salmon that might have persisted in the Alouette River after
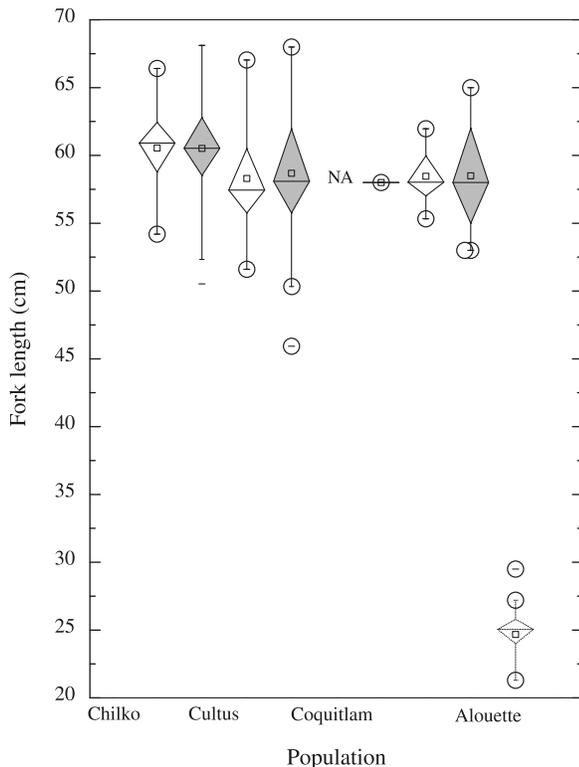
Table 2. Age composition (x.x) and mean fork length (FL ± 1 standard error, SE) at age of the adult upstream migrants (AUM) in Alouette River and Coquitlam River in 2007 and 2008.

Adults of unknown origin (AUM)	Migration year	Age proportion (FL±1 SE)				
		1.2	2.1	1.3	2.2	Unknown
Alouette River	2007 (n = 28)	0.5 (58.5±0.53)	—	—	—	0.5
	2008 (n = 53)	0.30 (58.5±1.0)	0.02 (52.0)[a]	0.23 (62.6±0.8)	0.32 (58.4±1.0)	0.13 (61.4±1.9)
Coquitlam River	2007	NA	NA	NA	NA	NA
	2008 (n = 10)	0.10 (58.0)[a]	—	—	0.30 (57.8±1.6)	0.60 (60.8±1.9)

Note: Sample size is indicated by n.

[a]There was only one fish, so there is no SE.

Fig. 3. Box plot comparison of fork length (cm) of age 4 (1.2) adults returning to Chilko Lake, Cultus Lake, Coquitlam River, and Alouette River in 2007 (open diamonds) and 2008 (light grey diamonds) and Alouette kokanee collected from the lake in 2007 (open diamond, dotted line, lower right). Fork lengths (FL) for Chilko sockeye salmon were estimated from postorbital fork length (pof) based on a conversion equation specific to Chilko Lake: FL_{Chilko} (male) = 1.0054 × pof + 6.7876; FL_{Chilko} (female) = 1.0934 × pof + 0.39262 (S. Cox-Rogers, Fisheries and Oceans Canada, 417 – 2nd Avenue West, Prince Rupert, BC V8J 1G8, unpublished data). Fork lengths for anadromous adults returning to the Alouette River in 2007 and Cultus Lake in 2007 and 2008 were estimated using a general conversion equation: FL (male) = 1.0555 × pof + 4.6563; FL (female) = 1.0625 × pof +2.1976 (S. Cox-Rogers, unpublished data).

which was not the case for kokanee (DIFF = –1.72‰, $P <$ 0.18) or sockeye salmon (DIFF = –0.96‰, $P <$ 0.22). The $^{87}Sr/^{86}Sr$ DIFF of both the AUM (0.0049, $P <$ 0.0001) and sockeye salmon (0.00095, $P <$ 0.0001) were significantly different than zero and significantly different from each other ($P <$ 0.0001).

Evolutionary history of the Alouette and Coquitlam kokanee populations

Historical records

We attempted to assess whether kokanee existed sympatrically with sockeye salmon prior to dam construction or whether the existing kokanee population is recently derived from sockeye salmon since the construction of the dam. Historical records confirm that prior to the construction of the dams, natural lakes in both the Alouette and Coquitlam drainages supported sizeable populations of anadromous sockeye salmon (Wilson et al. 2003; Bengeyfield et al. 2001). After dam construction, sockeye salmon returning from the ocean in either system would have had no possibility to access the reservoirs (J. Bruce BC Hydro, 6911 Southpoint Drive (Floor E04), Burnaby, BC V3N 4X8, personal communication, 2010). We were unable to find any record of kokanee having existed in these natural lakes.

Kokanee were first documented in Alouette Lake in 1951. No sampling has been conducted in Coquitlam Reservoir (because of the restricted access), but kokanee were first documented in Buntzen Lake (immediately downstream via the tunnel) in 1955 (D. Jesson, BC Ministry of Environment, Surrey, British Columbia, unpublished data), which suggests that kokanee may have been in Coquitlam Reservoir by this time too. Our search of an electronic database (http://a100. gov.bc.ca/pub/fidq/stockedSpeciesSelect.do) and hardcopy files (D. Jesson, BC Ministry of Environment, Surrey, British Columbia, unpublished data) for either Coquitlam or Alouette produced no records that kokanee were stocked in either system from 1894 to present.

The fact that male kokanee in Alouette Reservoir resemble "residual sockeye salmon" (as described by Ricker 1938) in that they lack secondary sexual characteristics (Wilson et al. 2003) suggests a recent origin from anadromous sockeye salmon. Although we cannot rule out that kokanee existed sympatrically with sockeye salmon in the original natural lakes, as they do in some other lakes in the Lower Fraser (e.g., Chilliwack Lake), all the available evidence is consistent with a more recent origin.

Genetic data: genetic diversity and bottlenecks

Allelic richness was lower (<7) in all four kokanee popu-

dam construction. The mean $\delta^{34}S$ and $^{87}Sr/^{86}Sr$ during the last 2 years of growth were also significantly higher in AUM (20.00‰ and 0.7091) than in kokanee (6.90‰, $P <$ 0.0001; and 0.7048, $P <$ 0.0001), but not significantly different than in anadromous sockeye salmon (21.15‰, $P =$ 0.76; and 0.7092, $P =$ 0.92). Finally, $\delta^{34}S$ DIFF of the AUM was significantly different from zero (DIFF = 14.41‰, $P <$ 0.0001),

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Table 3. F_{ST} values for pairwise comparisons between juvenile downstream migrants (JDM), adult upstream migrants (AUM), and reference mitochondrial DNA (below diagonal).

	Alouette_K	Alouette_JDM	Alouette_AUM	Coquitlam_K	Coquitlam_JDM	Coquitlam_AUM
Alouette_K	—	0.002	0.004	**0.050**	**0.055**	**0.037**
Alouette_JDM	0.000	—	0.000	**0.045**	**0.051**	**0.036**
Alouette_AUM	0.000	0.000	—	**0.042**	**0.047**	**0.033**
Coquitlam_K	**0.143**	**0.120**	**0.088**	—	0.000	0.000
Coquitlam_JDM	**0.245**	**0.191**	**0.120**	–0.009	—	0.000
Coquitlam_AUM	**0.686**	**0.594**	**0.408**	0.045	0.021	—
Chilliwack_K	**0.986**	**0.981**	**0.966**	**0.651**	**0.697**	**0.735**
Cultus_K	**0.916**	**0.884**	**0.805**	**0.565**	**0.540**	**0.356**
Big Silver	**0.271**	**0.203**	0.110	0.020	0.014	0.076
Birkenhead	**0.955**	**0.938**	**0.894**	**0.598**	**0.607**	**0.533**
Chilliwack	**0.907**	**0.874**	**0.795**	**0.542**	**0.539**	**0.454**
Cultus	**0.820**	**0.764**	**0.643**	**0.411**	**0.369**	**0.155**
Harrison	**0.765**	**0.697**	**0.561**	**0.285**	**0.254**	0.102
Pitt	**0.474**	**0.393**	**0.269**	0.043	0.047	0.009
Weaver	**0.449**	**0.377**	**0.272**	**0.081**	**0.068**	–0.008
Widgeon	0.000	0.000	0.000	**0.096**	**0.138**	**0.463**

Note: Population is anadromous sockeye salmon unless denoted otherwise. Bold font indicates that the pairwise F_{ST} value is significantly greater than zero

Fig. 4. (*a*) Unrooted, consensus neighbour-joining dendrogram based on chord genetic distance showing phylogenetic relationships among reference samples of kokanee (solid circles) and anadromous sockeye salmon (open circles) from the lower Fraser River and juvenile downstream migrants (downward triangles) and adult upstream migrants (upward triangles) in the Alouette and Coquitlam rivers. The Chilko Lake sockeye salmon population is included as an outgroup. (*b*) Multidimensional scaling values (MDS) from matrix of chord distances among populations based on mitochondrial DNA (*Y* axis) plotted against corresponding MDS values based on microsatellite DNA (*X* axis). Location labels are as in Fig. 1. Dotted circles group populations rearing in the same nursery lake.
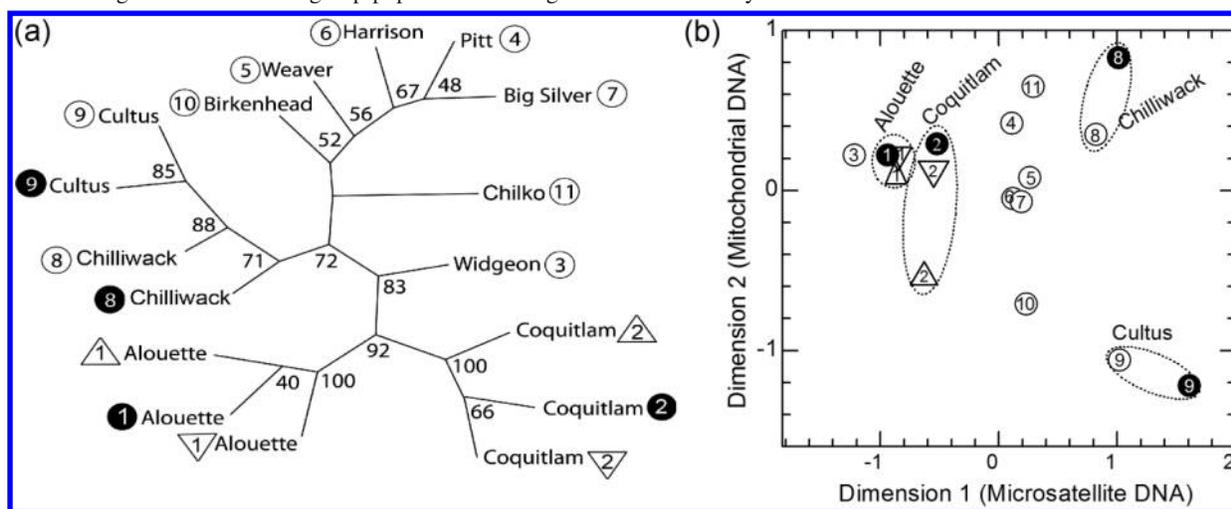
lations than in most sockeye salmon populations that we examined in the lower Fraser River (Table 4). Among sockeye salmon populations, Widgeon Slough in the Pitt River drainage and Cultus and Chilliwack lakes in the Chilliwack River drainage had unusually low levels of allelic richness and gene diversity. After accounting for multiple comparisons, four samples had significant levels of excess heterozygosity compared with expectations for populations in mutation–drift equilibrium (Table 4). These samples included kokanee in the Alouette and Coquitlam reservoirs, Cultus Lake kokanee, and Pitt River sockeye salmon.

The excess heterozygosity in the Alouette and Coquitlam kokanee samples suggests that abundance had been very low (i.e., bottlenecked) in the recent past, consistent with the hypothesis that they are recently derived from residual sockeye

salmon that remained in the reservoir after dam construction. Low levels of diversity at microsatellite loci and fixation of a single mitochondrial haplotype in the Alouette kokanee population are also consistent with this scenario. The Coquitlam population has retained greater diversity at microsatellite loci and a greater diversity of mitochondrial haplotypes. These results suggest that the Alouette and Coquitlam kokanee populations were established independently, likely from distinct anadromous sockeye salmon populations that once inhabited the Alouette and Coquitlam rivers.

Discussion

Our results based on genetic and isotopic markers confirm that the anadromous AUM in the Alouette and Coquitlam

populations of kokanee (K), and anadromous sockeye salmon in the lower Fraser River based on microsatellite DNA (above diagonal) and

Chilliwack_K	CultusK	Big Silver	Birkenhead	Chilliwack	Cultus	Harr	Pitt	Weaver	Widgeon
0.190	0.148	0.092	0.113	0.134	0.184	0.096	0.096	0.112	0.186
0.183	0.141	0.089	0.105	0.129	0.172	0.091	0.091	0.105	0.187
0.177	0.138	0.085	0.102	0.127	0.169	0.085	0.087	0.105	0.203
0.150	0.108	0.068	0.070	0.095	0.147	0.073	0.071	0.084	0.196
0.153	0.104	0.071	0.072	0.089	0.139	0.072	0.073	0.085	0.206
0.139	0.099	0.053	0.057	0.085	0.136	0.058	0.054	0.072	0.200
—	0.145	0.123	0.115	0.164	0.166	0.126	0.116	0.162	0.257
0.698	—	0.089	0.081	0.098	0.091	0.090	0.069	0.099	0.265
0.843	0.638	—	0.036	0.102	0.129	0.023	0.023	0.040	0.180
0.838	0.532	0.721	—	0.090	0.119	0.034	0.038	0.045	0.180
0.159	0.453	0.640	0.538	—	0.099	0.110	0.103	0.090	0.224
0.639	0.026	0.455	0.476	0.423	—	0.126	0.124	0.106	0.278
0.618	0.360	0.311	0.184	0.335	0.250	—	0.026	0.044	0.186
0.544	0.426	0.097	0.479	0.346	0.276	0.118	—	0.050	0.174
0.455	0.309	0.132	0.397	0.283	0.172	0.094	−0.004	—	0.199
0.971	0.831	0.134	0.909	0.820	0.679	0.601	0.301	0.299	—

($P < 0.05$ after Bonferroni correction).

Fig. 5. (*a*) Transmitted light micrograph of a polished otolith from an age-4 adult upstream migrant (AUM) to Alouette River in 2007. Ion probe pits (1–18, white circles) from sulfur isotope analysis and MC-ICPMS pits (1–8, white squares) from strontium isotope analysis. (*b*) Spatial distribution of the mean (±1 standard error, SE) ratio of strontium isotopes (open squares) and mean (±1 SE) ratio of sulfur isotopes (solid circles) in the (*i*) core–pre-exogenous, (*ii*) first year, and (*iii*) last 2 years of growth.
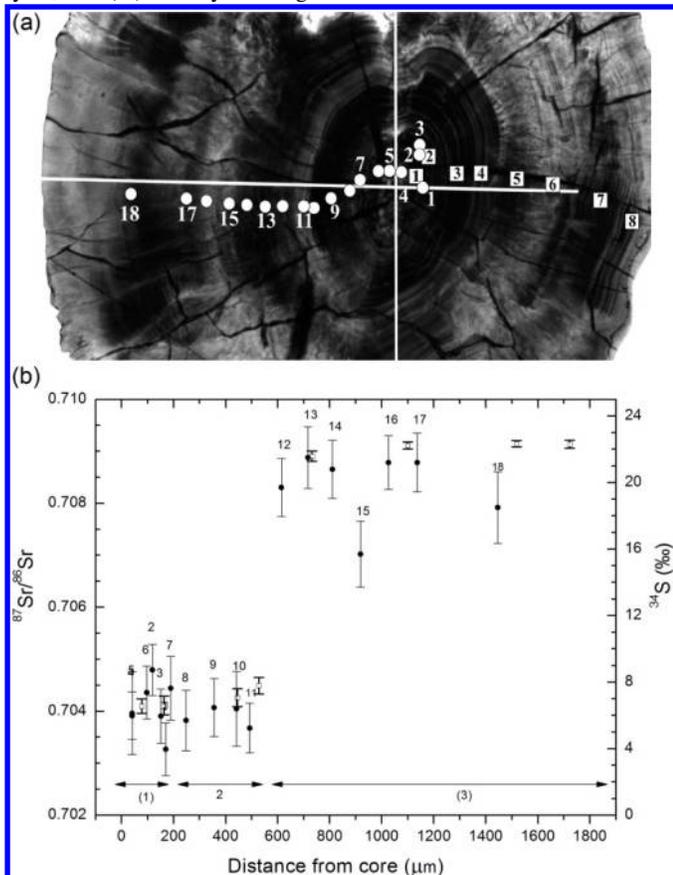
Fig. 6. Mean (±1 standard error, SE) ratio of stable isotopes of (*a*) $\delta^{34}S$ and (*b*) $^{87}Sr/^{86}Sr$ in the last 2 years of growth (*Y* axis) plotted against values in the core of the otolith (*X* axis) of Alouette adult upstream migrants (AUM), Alouette kokanee, and wild anadromous sockeye salmon from other populations in British Columbia. Ellipses illustrate groupings identified by analysis of variance (ANOVA).
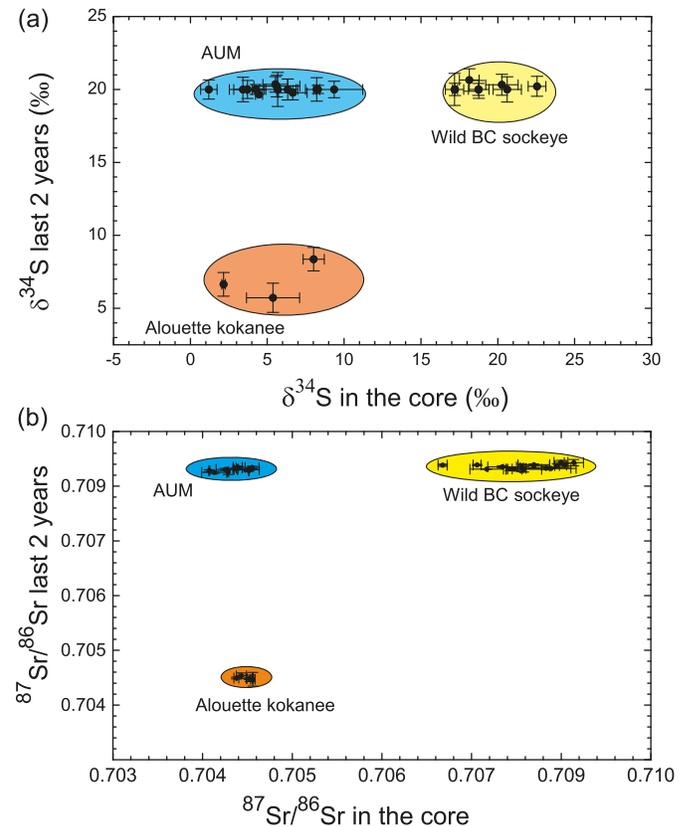
Table 4. Comparison of genetic diversity in reference populations of kokanee and sockeye salmon in the lower Fraser River.

| Population | Mitochondrial DNA | | Microsatellite DNA | | |
	No. of haplotypes	Gene diversity	Allelic richness	Expected heterozygosity	Probability of bottleneck
Kokanee					
Alouette	1	0.00	5.8	0.64	**0.0004**
Coquitlam	5	0.40	6.9	0.67	**0.0006**
Chilliwack	2	0.09	6.2	0.63	0.0595
Cultus	3	0.50	6.8	0.69	**0.0017**
Sockeye					
Big Silver	2	0.22	8.1	0.71	0.0067
Birkenhead	2	0.22	8.7	0.72	0.0968
Chilliwack	3	0.48	6.0	0.62	0.0453
Cultus	3	0.61	6.7	0.59	0.1788
Harrison Rapids	3	0.59	8.8	0.71	0.1338
Pitt	4	0.58	9.4	0.73	**0.0021**
Weaver	5	0.69	8.3	0.66	0.0676
Widgeon	1	0.00	4.1	0.51	0.0290

Note: Sample sizes and descriptions are given in Table 1. Bold font indicates a statistically significant probability of a recent bottleneck (after correction for multiple comparisons).

rivers in 2007 and 2008 are sea-run kokanee originating from local nonanadromous (kokanee) populations. The possibility that these fish were strays is implausible because of the extent of genetic differentiation among populations in the lower Fraser River. In addition, the freshwater isotopic signature in otolith cores of the AUM ruled out the possibility of an Alouette sea- or river-type sockeye salmon. The genetic evidence for recent population bottlenecks in both the Alouette and Coquitlam kokanee populations, together with the lack of secondary sexual characteristics of Alouette male kokanee and the absence of historical records of kokanee in these reservoirs until mid-century, further suggests that these populations are recently derived from anadromous runs that were extirpated by the dams 20 to 25 generations ago.

The fact that JDM were ~5- to 10-fold more abundant in the Alouette River than in the Coquitlam River suggests that kokanee are more abundant in the Alouette Reservoir, perhaps as a result of lake fertilization that has occurred annually since 1999. Alternatively, given that sockeye salmon smolts migrate nocturnally and orient to the surface during downstream migration (Wood et al. 1993), the lower number of JDM in the Coquitlam River might be caused by the LLO being located 3 to 7 m below the water surface.

Whether nonanadromous ecotypes could be used to recreate anadromous populations that have become extinct depends in part on their survival and reproductive capacity. At this time, it is not known whether AUM transported in the Alouette Reservoir in 2008 reproduced successfully. Comparison of their body size, migration route, and marine survival to the corresponding data for other sea-run kokanee and anadromous sockeye salmon populations suggests that the AUM may contribute to the restoration of the anadromous ecotype of *O. nerka* in Alouette Reservoir.

Body size of adult sea-run kokanee from the Alouette Reservoir was similar to that of sockeye salmon returning to Chilko and Cultus lakes and to that of other North American sockeye salmon populations at the same latitude, and thus

they could be expected to have similar fecundity (McGurk 2000). Migratory behaviour of sea-run kokanee juveniles seems to be similar to that of sockeye salmon. Acoustic tracking of 19 Alouette JDM showed that their migration rates to the lower Fraser River and into Juan de Fuca Strait were similar to that of juvenile salmon (Baxter and Bocking 2006). These results are consistent with the findings of Wood et al. (2011) that acoustically tagged sockeye salmon and kokanee dispersed from a marine release site near Sakinaw Lake, British Columbia, at the same rate and tended to follow the same migration route.

Smolt-to-adult survival of Alouette sea-run kokanee (corrected for harvest, including all age classes) was 0.57% in sea-entry year 2005 and 0.84% in 2006. These rates are lower than those observed in Chilko sockeye salmon (1.53% and 3.97%), but similar to those in Cultus sockeye salmon (0.68% and 1.35%) in the same years. Lower marine survival of sea-run kokanee may be related to the relatively late timing of the experimental water releases, as earlier downstream migration appeared to be associated with higher marine survival. Chilko smolts emigrated 10 days earlier in 2005 and 7 days earlier in 2006 than Cultus smolts (T. Cone, Fisheries and Oceans Canada, Annacis Island, British Columbia, unpublished data). Chilko smolts also migrated downstream at a faster pace, requiring only 7 days on average to reach the mouth of the Fraser River from Chilko Lake (Crittenden 1994; D. Welch, Kintama Research, Nanaimo, British Columbia, personal communication, 2011) compared with 4 to 5.6 days from Cultus Lake (Welch et al. 2009), despite the sevenfold greater travel distance from Chilko Lake. At this rate of travel, 50% and 60% of Chilko Lake smolts (compared with only 10% and 35% of Cultus Lake smolts) would have already reached the mouth of the Fraser River by the time water was first spilled from the Alouette Reservoir in 2005 and 2006, respectively.

Comparison of marine survival rates in different years is complicated by annual and decadal fluctuations in marine cli-

mate. We note that survival rates of Alouette sea-run kokanee that migrated volitionally in sea-entry years 2005 and 2006 were higher than those sea-run kokanee forced to migrate in experiments in the 1940s with kokanee populations that had been isolated for ~10 000 years (0.004% for Lake Chelan, 0.12% for Kootenay lake kokanee released from Cultus Lake; total sea-run kokanee in the fishery/number yearlings). However, within the same period (1933–1936; Foerster 1936), marine survival rate of the Kootenay Lake kokanee released from Cultus Lake was 15- to 24-fold lower than that of Cultus Lake sockeye salmon.

Our study confirms that kokanee isolated from anadromous sockeye salmon for at least 80 to 90 years can revert to anadromy. Additional work is needed to compare the marine survival, growth, migratory behaviour, and reproductive capacity of sea-run kokanee that have been isolated for various amounts of time.

Acknowledgements

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