

# Revisiting evolutionary dead ends in sockeye salmon (*Oncorhynchus nerka*) life history

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**Abstract:** This study challenges recent hypotheses about sockeye salmon (*Oncorhynchus nerka*) colonization based on life history and broadens the pathways that investigators should consider when studying sockeye colonization of novel habitats. Most sockeye populations exhibit lake-type life histories. Riverine populations are thought to be more likely to stray from their natal stream to spawn and therefore colonize new habitat. We examined genetic relationships among five geographically proximate sockeye populations from the Aniakchak region of the Alaska Peninsula, Alaska. Specifically, we sought to determine if the genetic population structure was consistent with the hypothesis that a riverine population colonized a recently available upriver volcanic caldera lake, and whether recent volcanism led to genetic bottlenecks in these sockeye populations. Heterozygosity and allelic richness were not higher in the riverine population. Patterns of genetic divergence suggested that the geographically proximate riverine sockeye population did not colonize the lake; the caldera populations were more genetically divergent from the downstream riverine population ( $F_{ST} = 0.047$ ) than a lake-type population in a different drainage ( $F_{ST} = 0.018$ ). Our results did not suggest the presence of genetic bottlenecks in the caldera populations.

**Résumé :** Notre étude remet en question quelques hypothèses récentes sur la colonisation du saumon rouge (*Oncorhynchus nerka*) basées sur le cycle biologique et ouvre de nouvelles perspectives que les chercheurs devront prendre en considération lorsqu'ils étudient la colonisation de nouveaux habitats par le saumon rouge. La plupart des populations de saumons rouges ont des cycles biologiques de type lacustre. On croit que les populations d'eau courante sont plus susceptibles de s'éloigner de leur cours d'eau natal lors de la fraye et ainsi de coloniser de nouveaux habitats. Nous examinons les relations génétiques de cinq populations de saumons rouges rapprochées géographiquement dans la région d'Aniakchak de la péninsule de l'Alaska, Alaska. En particulier, nous cherchons à savoir si la structure génétique des populations s'accorde avec l'hypothèse qui veut qu'une population d'eau courante ait colonisé un lac volcanique de caldeira d'amont qui est récemment devenu disponible; nous voulons aussi voir si l'activité volcanique récente a produit des goulots d'étranglement génétiques chez ces populations de saumons rouges. L'hétérozygotie et la richesse allélique ne sont pas plus élevées dans la population d'eau courante. Les patrons de divergence génétique laissent croire que la population d'eau courante de saumons rouges située à proximité n'a pas colonisé le lac; les populations de la caldeira divergent plus génétiquement de la population d'eau courante d'aval ( $F_{ST} = 0,047$ ) que d'une population de type lacustre d'un autre bassin versant ( $F_{ST} = 0,018$ ). Nos résultats n'indiquent aucun goulot d'étranglement génétique chez les populations de la caldeira.

[Traduit par la Rédaction]

## Introduction

Anadromous sockeye salmon (*Oncorhynchus nerka*) are thought to have two general life history strategies. The first strategy (lake-type) includes the use of a lake as a nursery where young sockeye rear for 1–2 years after emergence. Populations are often locally adapted to spawning sites within a lake (Foerster 1968; Burgner 1991; Wood 1995). The second strategy (sea- and river-type) includes the use of riverine habitats, instead of lakes, for rearing. These sockeye

migrate to the ocean either several months (sea-type or ocean-type; Gilbert 1913) or 1–2 years (river-type; Semko 1954) after emergence. All of these strategies involve migration to the ocean for the majority of growth, so the important habitat differences among these strategies are in the freshwater phase.

A number of investigators have studied these alternative life histories (e.g., Wood et al. 1987; Eiler et al. 1992; Wood et al. 1994). River-type and sea-type (both hereafter "riverine") sockeye spawn in glacial runoff habitat and rear

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downstream in “side-channel river habitat” (Gustafson and Winans 1999). This contrasts with lake-type sockeye that typically spawn in tributaries, outlets, or beaches and rear in the adjacent lake (Burgner 1991). In broad-scale genetic studies, there is less genetic differentiation among riverine than among lake-type populations, suggesting that natal homing may be less precise in riverine sockeye (Wood 1995; Gustafson and Winans 1999; Beacham et al. 2004). However, a different pattern was observed in the Kamchatka Peninsula where riverine populations were genetically distinct (Beacham et al. 2006a). Riverine sockeye populations tend to have higher levels of genetic diversity than lake-type populations, measured as heterozygosity and allelic richness (Gustafson and Winans 1999; Beacham et al. 2004, 2006b). Wood (1995) suggested that riverine sockeye were the principal colonists of new habitats following the retreat of glaciers.

During periods of glacial maxima, coastal Alaska and Canada were mostly covered by ice. The majority of freshwater lakes in this area arose since the last glaciation (Imbrie and Imbrie 1979; Pielou 1991). Hence, most lower lying areas that lake-type sockeye presently use to spawn and rear were probably blocked by glaciers, and thus suitable habitat for sockeye to exhibit a lake-type life history was limited. Riverine sockeye persisted in glacial refugia in northern and southern refuges and possibly in other areas (Varnavskaya et al. 1994a; Wood et al. 1994; Beacham et al. 2006a). As the retreat of the Cordilleran ice sheet opened coastal habitats about 10 000 years ago, sockeye rapidly colonized new freshwater habitats and, in many cases, adopted a lake-type life history (Wood 1995). Colonization and establishment of new sockeye populations occurs when, instead of homing to their natal habitats, individuals stray and spawn in a freshwater location previously uninhabited by sockeye. Straying to new habitats may not result in the establishment of new populations in all cases, as the potential colonists may be maladapted to the new freshwater environments. Lake-type sockeye specialize in the use of freshwater habitats more than any other Pacific salmon species (Burgner 1991). Lake-type sockeye use many lake habitats for spawning, including tributaries, outlets, outwash fans, upwelling zones, and beaches (Burgner 1991; Wood 1995). Compared with lake-type, riverine sockeye are thought to be the persistent, parental lineage, which colonize new habitat more readily because of higher rates of straying. Lake-type sockeye are specialized for temporary environments and are thought to be less able to colonize because of their low straying rates. As a result, they have been referred to as evolutionary dead ends (Wood 1995).

Sockeye have diversified within the past 10 000 years from very few populations residing in glacial refugia to thousands of locally adapted populations along the entire coast of the North Pacific Ocean. Several factors can affect population size and structure in sockeye salmon. First, populations may become established via the colonization of only a few individuals (Wood 1995; Milner et al. 2000). Small initial size may lead to founder effects and genetic bottlenecks impacting the population structure of sockeye populations (Ramstad et al. 2004). Second, geologic events have the potential of obstructing returning salmon from reaching their natal sites to spawn or affecting the survival of eggs and juveniles

(Ricker 1950; Leider 1989). Third, natural barriers such as waterfalls and rapids have been found to reduce effective population size ( $N_e$ ) in sockeye spawning above barriers (Habicht et al. 2004). Severe reductions in  $N_e$  can result in a genetic bottleneck that may be detectable for decades after the demographic constriction (Cornuet and Luikart 1996; Ramstad et al. 2004).

Many studies have examined genetic structure of sockeye populations that were colonized 7000 – 10 000 years ago (e.g., Varnavskaya et al. 1994b; Habicht et al. 2004; Ramstad et al. 2004), but few studies have addressed systems colonized more recently (Burger et al. 1997; Woody et al. 2000). In the present study, we investigated the genetic relationships among five geographically proximate sockeye salmon populations on the Alaska Peninsula. This area contains both recently colonized lake-type populations, as well as a downriver population that exhibits the riverine life history. Using microsatellite markers, we addressed two questions. (i) Are genetic relationships consistent with patterns suggesting that the riverine population colonized lake habitats within a volcanic caldera? (ii) Do the caldera populations show genetic indications of recent bottlenecks?

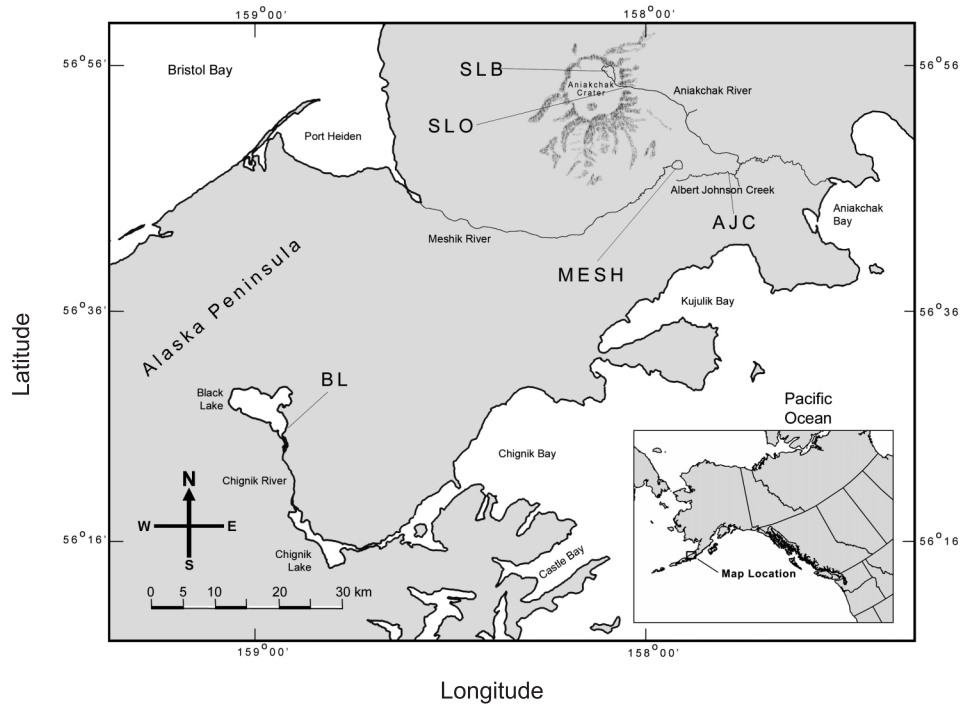
## Materials and methods

### Study area

Aniakchak National Monument and Preserve (ANMP) in southwestern Alaska provides a unique system in which to study the interactions of sockeye life history strategies. Several recent cataclysmic geologic events have taken place within ANMP (Fig. 1). A massive volcanic eruption 3650 years ago formed a large caldera (Aniakchak Caldera) that filled with water creating a lake similar to Crater Lake in Oregon (McGimsey et al. 1994; Pearce et al. 2004). Approximately 1800 years ago (VanderHoek and Myron 2004), the caldera wall collapsed resulting in a large flood and the formation of the Aniakchak River, which connects the caldera lake (Surprise Lake, elevation 321 m) with the Pacific Ocean through “The Gates”, a chasm breaching the caldera wall (Hubbard 1931; see Fig. 1). A large fluvial plain was established when the passing flood waters dropped sediment as the water velocity slowed where the Aniakchak emerges from more deeply incised bedrock channels to relatively flat lowlands. Several smaller eruptions have occurred, including well-documented events approximately 500 years ago and in 1931 (Hubbard 1931; McGimsey et al. 1994; Neal et al. 2001). These smaller eruptions probably affected spawning, rearing, and incubating conditions and may have impacted or eliminated any sockeye populations present in the caldera during that time (Hubbard 1932). Sockeye salmon spawning habitat of current populations in the Aniakchak caldera may have been available for colonization of current populations as early as about 1800 years ago (based on access following the flood) or as recently as 76 years ago (based on the timing of the most recent eruption). Adult sockeye caldera populations are all lake-type, although some spawn along Surprise Lake beaches and some spawn in the Surprise Lake outlet in riverine habitats (Fig. 1).

The only other known sockeye population in the Aniakchak River drainage spawns in Albert Johnson Creek (Fig. 1), the largest tributary of the Aniakchak River. This

**Fig. 1.** Map of Aniakchak National Monument and Preserve and Black Lake showing the five study populations (inset: location in Alaska, USA): MESH, Meshik Lake; BL, Black Lake; SLB, Surprise Lake beaches; SLO, Surprise Lake outlet; AJC, Albert Johnson Creek.



creek is located at the base of the volcano (~27 m elevation) and cuts east through the fluvial flood plain. Adults of these sockeye are riverine, having no juvenile access to Surprise Lake, which is the only lake in the drainage. Another sockeye salmon population occurs in Meshik Lake near the headwaters of Albert Johnson Creek. This lake is on the other side of the peninsular divide and drains into the Bering Sea (Fig. 1). Although Meshik Lake is geographically proximate to Albert Johnson Creek (3.5 km), mouth-to-mouth distance between the two drainages around the Alaska Peninsula is approximately 1200 km. A fifth population, Black Lake, is part of the Chignik River drainage and has a large, commercially important, lake-type sockeye run. The mouth of the Chignik River is located approximately 120 km southwest of the mouth of the Aniakchak River (Fig. 1). Black Lake and Meshik Lake populations serve as ecological outgroups providing perspective on the genetic relationships found among Aniakchak River drainage populations.

### Sample collection

We conducted the genetic sampling of spawning sockeye adults in both Albert Johnson Creek and the caldera (Surprise Lake beaches and outlet) in early August (2001–2003). The Alaska Department of Fish and Game sampled Black Lake sockeye adults in July (2002–2003) at the Black Lake outlet. A National Park Service field crew sampled Meshik Lake juveniles in July (2003). A small amount (approximately 1 cm<sup>2</sup>) of fin tissue was collected from each adult fish. In the case of Meshik Lake, whole juvenile fish were collected. All fish were sampled using a beach seine. Samples were stored in 100% ethanol and brought to the USGS Molecular Ecology Laboratory (Alaska Science Center, Anchorage, Alaska) for DNA analyses.

### Molecular data collection

Total genomic DNA was extracted from intact fin clips using Puregene DNA Isolation Kits<sup>®</sup> (Gentra Systems, Inc.). Six tetranucleotide microsatellites were analyzed: *One102*, *One105*, *One108*, *One109*, *One110*, and *One115* (Olsen et al. 2000). Multiplexes for these markers were developed by G.K. Sage (USGS Alaska Science Center, Anchorage, Alaska). Polymerase chain reaction (PCR) amplifications were conducted in 10 µL volumes using approximately 50 ng of genomic DNA, 0.1–0.2 µL of Taq<sup>®</sup> DNA polymerase (Perkin Elmer), and buffer (Scribner et al. 1996) for 35–40 cycles (Table 1). Gel electrophoresis and visualization of microsatellite alleles were performed using LI-COR Model 4200<sup>®</sup> and IR2 automated fluorescent DNA sequencers (Middendorf et al. 1992). Sizing was performed using Gene ImageIR version 3.00 (LI-COR, Lincoln, Nebraska). All allele size standards were calibrated to the M13 ladder and other known sockeye standards. Every gel was independently proofed by other researchers, and all questionable samples were rerun. Ten percent of all samples were independently amplified a second time and visualized for quality control purposes.

### Molecular data analysis

Genotypic disequilibrium and Hardy–Weinberg equilibrium (HWE) tests were conducted using GENEPOP version 3.4 (Raymond and Rousset 1997). Statistical significance levels for multiple comparisons were set using sequential Bonferroni tests (Rice 1989). ARLEQUIN version 1.1 (Schneider et al. 1997) was used to test for differences between sampling years at the same location. If no significant interannual differences were detected, sampling years were pooled and reanalyzed with ARLEQUIN to test for differences in

**Table 1.** Loci and multiplexes used with thermal regime for PCR amplifications, size range, number of alleles, and expected heterozygosity.

Locus	Thermal regime		Size range	No. of alleles	$H_e$
Multiplex 1	94° 2 min				
<i>One102</i>	94° 15 s	40 cycles	197–261	17	0.853
<i>One105</i>	56° 15 s		128–152	7	0.558
<i>One115</i>	72° 30 s		179–243	17	0.898
	72° 30 min				
Multiplex 2	94° 2 min				
<i>One108</i>	94° 15 s	35 cycles	177–257	21	0.890
<i>One109</i>	54° 15 s		124–180	15	0.871
<i>One110</i>	72° 30 s		220–304	27	0.910

pairwise allele frequencies between populations. Values of expected heterozygosity for each locus were generated using Microsatellite Analyzer (MSA; Dieringer and Schlotterer 2003). Populations were then compared in a pairwise fashion, and in each comparison, a paired  $t$  test was conducted with the pairs of locus heterozygosity values in SAS version 8 (SAS Institute Inc., Cary, North Carolina).

Genetic distance values reflecting the proportion of shared alleles between individuals and groups of individuals can be used to graphically depict genetic relationships and population structure. Allele frequency data were used to create 2000 genetic distance matrices based on Cavalli-Sforza and Edwards' (1967) genetic chord distance using GENEDIST from PHYLIP (Felsenstein 1993). Neighbor-joining (NJ) trees were generated using the NEIGHBOR application of PHYLIP from each distance matrix. A consensus tree was created using CONSENSE from PHYLIP. SEQBOOT from PHYLIP was used to bootstrap allelic relationships creating 2000 trees depicting the five populations (Felsenstein 1985). TreeView version 1.6.6 (Page 1996) was used to visualize the consensus NJ tree with bootstrap values.

To compare our data with those of other recent sockeye salmon studies from different localities (Withler et al. 2000; Ramstad et al. 2004; Habicht et al. 2004), five different measures were used to detect a bottleneck signature. These tests were conducted with sampling years pooled for populations with multiple samples. Genotypic disequilibrium was tested using GENEPOP to infer gametic phase disequilibrium (Waples and Smouse 1990), which may be present in populations that have experienced a recent and acute bottleneck (Habicht et al. 2004). Differences in allelic diversity (Nei et al. 1975; Allendorf 1986) were estimated using FSTAT version 2.9.3.2 (Goudet 1995) to calculate population allelic richness (alleles per population adjusted for number of individuals sampled), as rare alleles may be lost after a bottleneck. This test requires comparing possibly bottlenecked populations with a putatively non-bottlenecked population. Pairwise comparisons of populations were estimated for differences in allelic richness using paired  $t$  tests in SAS. We calculated Garza and Williamson's  $M$  values using AGAR<sub>ST</sub> version 2.9 (Garza and Williamson 2001). This metric measures allelic "vacancies" within the allelic range and is expressed as a decimal between zero and one. Bottlenecked populations are expected to have more vacancies than non-

bottlenecked populations. Any loci exhibiting alleles outside the four-base-pair repeat motif were excluded from this test (Garza and Williamson 2001). Mode shifts in allele frequency class distributions (Luikart et al. 1998) and heterozygosity excess (Cornuet and Luikart 1996) due to the loss of rare alleles were tested in comparison to Nei's allelic diversity (Nei et al. 1975) using BOTTLENECK (Piry et al. 1998). BOTTLENECK employs the Wilcoxon signed-rank test to detect heterozygosity excess. The output consisted of results obtained under two different mutation models to calculate the comparison expected heterozygosity if the populations were in mutation-drift equilibrium: the infinite allele model (IAM) and the stepwise mutation model (SMM; Cornuet and Luikart 1996).

Genotypic disequilibrium, mode shift in allele frequency class distribution, and heterozygosity excess are best at detecting recent and acute bottlenecks, whereas reduced allelic diversity and Garza and Williamson's  $M$  value are capable of detecting less severe bottlenecks for a longer time after the demographic constriction (Habicht et al. 2004; Ramstad et al. 2004). All results were analyzed for evidence of bottlenecks and compared with other sockeye studies that used similar analyses (Withler et al. 2000; Habicht et al. 2004; Ramstad et al. 2004).

## Results

All five sockeye populations were polymorphic at all loci (total of 576 individuals; Table 2). Allelic polymorphism ranged from 7 to 27, and allelic size ranged from 124 to 304 base pairs over all loci (Table 1). Number of alleles per locus ranged from 2 to 19 (Table 2). Of 72 tests performed, only five were out of HWE ( $P < 0.05$ ; Table 2). No inter-annual genetic variation was detected in any population ( $P > 0.05$ ), so years were combined for populations with multiple collections for pairwise  $F_{ST}$  comparisons, bottleneck tests, and genetic diversity comparisons. All five populations were significantly genetically differentiated ( $P < 0.001$ ). Pairwise  $F_{ST}$  values ranged between 0.0112 and 0.0570 (Table 3). The Black Lake population had higher average heterozygosity than Surprise Lake, Albert Johnson Creek, and Meshik Lake populations (Table 4), though this difference was not statistically significant in the paired  $t$  tests between pairs of loci

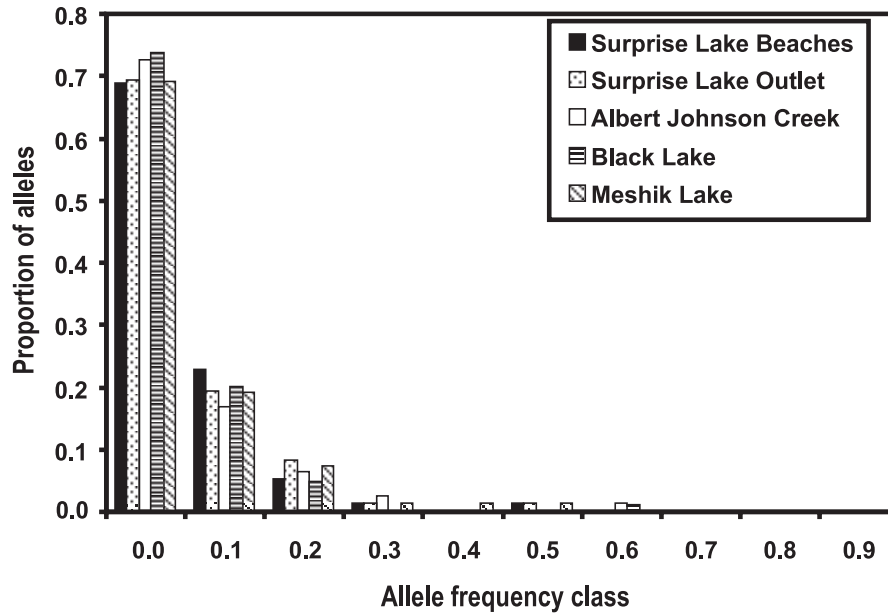
**Table 2.** Microsatellite data collection summary.

Population and year		Number of genotyped individuals per locus					
		<i>One102</i>	<i>One105</i>	<i>One108</i>	<i>One109</i>	<i>One110</i>	<i>One115</i>
<b>Surprise Lake beaches</b>							
2001	<i>n</i>	44	54	53	54	54	51
	<i>A</i>	10	3	15	10	14	13
	H-W	+	+	+	+	+	+
2002	<i>n</i>	42	41	43	43	43	40
	<i>A</i>	10	3	15	8	14	10
	H-W	-	+	+	+	+	+
2003	<i>n</i>	53	53	51	52	49	54
	<i>A</i>	11	3	13	10	13	13
	H-W	+	+	+	+	+	-
Years combined	<i>n</i>	139	148	147	149	146	145
	<i>A</i>	12	3	18	12	15	14
	H-W	+	+	+	+	+	-
<b>Surprise Lake outlet</b>							
2001	<i>n</i>	18	26	25	28	28	24
	<i>A</i>	9	3	11	11	16	13
	H-W	+	+	+	+	+	+
2002	<i>n</i>	35	43	43	43	41	41
	<i>A</i>	12	4	10	10	13	12
	H-W	+	+	+	+	+	+
2003	<i>n</i>	47	48	46	48	46	48
	<i>A</i>	9	5	10	8	13	12
	H-W	-	+	+	+	+	+
Years combined	<i>n</i>	100	117	114	119	115	113
	<i>A</i>	12	5	13	12	17	13
	H-W	-	+	+	+	+	+
<b>Albert Johnson Creek</b>							
2001	<i>n</i>	21	29	28	29	29	27
	<i>A</i>	9	2	10	10	12	13
	H-W	-	+	+	+	+	+
2002	<i>n</i>	27	26	34	34	30	25
	<i>A</i>	10	4	11	11	11	12
	H-W	+	+	+	+	+	+
2003	<i>n</i>	52	55	55	56	54	51
	<i>A</i>	11	4	10	12	18	15
	H-W	+	+	+	+	+	+
Years combined	<i>n</i>	89	85	100	101	95	88
	<i>A</i>	14	4	12	12	19	15
	H-W	+	+	+	+	+	+
<b>Black Lake</b>							
2002	<i>n</i>	40	50	48	49	50	45
	<i>A</i>	11	4	16	12	14	16
	H-W	+	+	+	+	+	+
2003	<i>n</i>	40	43	44	43	43	38
	<i>A</i>	12	4	16	12	17	12
	H-W	+	+	+	+	+	+
Years combined	<i>n</i>	91	97	108	104	107	99
	<i>A</i>	13	5	18	13	19	16
	H-W	+	+	+	+	+	+
<b>Meshik Lake</b>							
2003	<i>n</i>	85	91	91	91	91	91
	<i>A</i>	11	4	14	11	13	15
	H-W	+	+	+	-	+	+

**Note:** *n*, number of individuals genotyped; *A*, number of alleles; H-W, Hardy-Weinburg equilibrium (+, no significant deviation; -, significant deviation;  $\alpha = 0.05$ ).



**Fig. 3.** Allele class frequency distribution for each population.



**Table 6.** Population comparisons of allelic richness and *P* values (bold = significant; initial  $\alpha = 0.0083$ ).

Comparison	Paired mean difference	<i>P</i>
Black Lake vs.		
Surprise Lake beaches	2.359	<b>0.0008</b>
Meshik Lake	2.493	0.0165
Surprise Lake outlet	2.255	0.0337
Albert Johnson Creek	1.611	0.1437
Albert Johnson Creek vs.		
Surprise Lake outlet	0.644	0.2264
Surprise Lake beaches	0.747	0.5119

**Microsatellite polymorphism**

The levels of allelic variability found in populations in this study were within the normal range of variation described previously for Bristol Bay sockeye salmon populations (Habicht et al. 2004; Olsen et al. 2004) with the exception of *One110*. This locus exhibited more variability than previously reported because of a two-base-pair variant that is present in all of the Pacific Ocean populations sampled in our study. This variant was not reported by other investigators.

**Colonizing population of the caldera**

Beacham et al. (2004) found a riverine population that grouped closely with three upriver lake-type populations in a NJ tree based on Cavalli-Sforza and Edwards' chord distance. They also found that riverine populations had more alleles and increased heterozygosity compared with lake-type populations in the same drainage. In the present study, we found the caldera populations to be more genetically similar to a lake-type population in an adjacent drainage, Black Lake, than to a riverine population in the same drainage (Albert Johnson Creek). We also found that numbers of alleles and observed levels of heterozygosity were not significantly

higher for riverine sockeye than for lake-type sockeye in this system.

The caldera populations are more genetically similar to Black Lake sockeye than Albert Johnson Creek or Meshik Lake populations, despite the fact that Albert Johnson Creek is within the Aniakchak Drainage. Several circumstances could explain this pattern. First, the actual colonizing population may have been a riverine population that was not included in the populations surveyed. However, Albert Johnson Creek contains the only known riverine sockeye in Aniakchak National Monument and Preserve, and there are no other documented riverine populations within 250 km of the Aniakchak River mouth. Second, Albert Johnson Creek sockeye may stray less than typical riverine sockeye. Albert Johnson Creek is spring fed, which differs from many studied riverine systems in which sockeye spawn in glacial runoff habitat (Gustafson and Winans 1999). Quinn (1984) found that lake-type sockeye that spawn in glacially influenced habitats were more likely to stray than lake-type sockeye that spawn in streams with less year-to-year variability in habitat quality. Third, even if Albert Johnson Creek individuals strayed to the Caldera, they may be maladapted to this new and different environment and unable to successfully colonize. Fourth, straying in riverine sockeye populations may occur frequently among riverine populations but rarely with lake-type populations, as suggested by Gustafson and Winans (1999). Fifth, Black Lake sockeye were sampled on a single day as they entered Black Lake at the outlet. Black Lake is a silty, shallow lake that is not conducive to beach spawning, but there are multiple tributary spawning aggregates identified (Phinney 1970). The vast majority of these identified spawning populations are in the Alec River drainage on the east side of Black Lake (G. Ruggerone, Natural Resources Consultants Inc., 1900 West Nickerson Street, Suite 207, Seattle, WA 98119, USA, personal communication, 2004). This drainage is fed from snowmelt runoff and may have variable year-to-year flow. These sockeye may exhibit an increased straying rate compared with that of other

lake-type populations in response to this habitat variability. Sixth, Black Lake contains a much larger population of sockeye. The annual escapement at Black Lake is on the order of a million fish, whereas aerial surveys of the Aniakchak River drainage indicate typical returns for Albert Johnson Creek, the Surprise Lake Outlet, and the Surprise Lake Beaches of fewer than 10 000 fish each. If the Black Lake population has a greater than typical lake-type straying rate in addition to a very large population size, it may exert a powerful genetic influence through migration to the Aniakchak drainage, despite the geographic distance between these drainages. This influence may overwhelm migrants originating from Albert Johnson Creek, which is a much smaller population in nonglacially influenced habitat.

These results suggest that lake-type populations may not always be evolutionary dead ends. Large lake-type populations may also be the colonizers of newly accessible habitats. Our results, unlike previously published accounts (Wood 1995; Beacham et al. 2004, 2006b), suggest that riverine sockeye may not be fully responsible for the long-term persistence of this species over evolutionary time. The interaction of both of these life history strategies working in concert may contribute to long-term persistence through oscillating climate patterns. Wood (1995) suggested that although all extant populations are important, riverine sockeye should receive special conservation emphasis compared with lake-type sockeye because of their colonizing role. Beacham et al. (2006a), as well as the results of this study, question the universal colonization role of riverine sockeye. We suggest that lake-type populations may also colonize new habitats. Thus managers and investigators must consider multiple pathways in sockeye colonization.

### **Bottlenecks and geologic activity**

The results for heterozygosity excess under the two mutation-model assumptions (IAM and SMM) were contradictory. Microsatellites, in general, and tetranucleotide repeat markers, in particular, which were the basis of the present study, are expected to conform closer to the SMM (Shiver et al. 1993). Using the SMM, no heterozygosity excess was depicted. Also, all five of the study populations, including Black Lake, exhibited significant heterozygosity excess under the IAM. This contradicted all other bottleneck measures, indicating that this mutation model may not be appropriate for the markers used in this study. Taken together, these results indicate that the caldera populations did not go through a bottleneck as a result of the 1931 eruption (15 generations ago).

The reduced allelic richness in the Surprise Lake beach spawning population in relation to Black Lake sockeye may be an effect of (i) a bottleneck after the much larger eruption that occurred 500 years ago (100 generations ago), (ii) the original colonization after the flood (360 generations ago), (iii) the tendency for larger populations to exhibit higher genetic diversity (Wright 1940; Rosensweig 1995; Vellend 2003), or (iv) the result of the 300 m elevation climb that is necessary to reach the caldera. Habicht et al. (2004) found that populations above migration barriers (waterfalls and rapids) exhibited reduced heterozygosity compared with populations below the barriers, but neither of the caldera populations had significantly lower allelic richness com-

pared with that of Albert Johnson Creek. This test for genetic bottlenecks is the only test of the five tests used in this study that involved comparison with another population, and results could vary depending on the population chosen for the comparison.

The lack of strong evidence for recent bottlenecks in the caldera populations is surprising in a system with recent volcanic disturbance. Our results differed from those obtained by Ramstad et al. (2004) in an analysis of Lake Clark sockeye (another drainage in southwestern Alaska). Lake Clark was formed after a glacial retreat 12 000 – 15 000 bp (Stilwell and Kaufman 1996), though at least one population may have been established only 100–200 bp (Ramstad et al. 2004). Six out of 11 populations surveyed had reduced  $M$  values, and the investigators attributed this reduction, along with reduced allelic diversity, to founder effects (Ramstad et al. 2004).

Withler et al. (2000) found no evidence to support a substantial genetic effect of rock slides that severely disrupted sockeye runs in a Fraser River drainage, British Columbia, between 1913–1914. These authors state: "... it is not clear whether the apparent lack of genetic bottlenecks is due to the fact that population sizes did not become as small as estimated after the rockslides, whether effective population sizes were bolstered by increasing gene flow among streams at low fish densities, or whether rapid expansion of population sizes once recovery was initiated prevented a great loss of genetic diversity (p. 1996)". Any one of these situations could apply to the sockeye that spawn at Surprise Lake beaches. Also, demographic bottlenecks caused by single-year events may be difficult to detect in sockeye salmon because of their overlapping generations (Waples 1991; Habicht et al. 2004).

This study of sockeye salmon in the Aniakchak River drainage sheds new light on genetic population structure found between different life history strategies and among populations. Populations that spawn in a volcanic caldera with documented eruptions 76 and 500 years ago left no genetic evidence of population bottlenecks. A large lake-type population appears to have greater genetic association with a population in a recently colonized lake than a more proximate riverine population. This result may indicate that large lake-type populations are more important in colonization events than previously reported.

Several other studies have documented subdivision of sockeye salmon populations over short time scales (e.g., Hendry et al. 2000; Woody et al. 2000; Kinnison et al. 2002), after natural colonization events (e.g., Wilmot and Burger 1985; Varnavskaya et al. 1994b; Habicht et al. 2004), and across major life history groupings (e.g., Wood 1995; Gustafson and Winans 1999; Beacham et al. 2006a). This is the first study to document population genetic structure covering all three aspects in the same group of sockeye salmon. Our study was conducted on a small number of populations at one locality, but our findings are similar to those of other recent research showing genetic differentiation between populations spawning in different habitats of the same lake (Beacham et al. 2004, 2006b). However, unlike the findings in the Beacham et al. (2006b) study, the Aniakchak riverine sockeye population did not exhibit increased heterozygosity and allelic richness compared with lake-type populations in



the same area. Wood (1995) suggested that riverine sockeye populations stray more frequently and, therefore, are most likely to colonize new areas. Results from this study bring into question these expectations when looking at factors contributing to genetic population structure in sockeye salmon during colonization events. These results should broaden the colonization pathways considered by other investigators when looking at genetic population structure, sockeye colonization, and restoration in novel habitats.

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