

Preliminary Analysis of Sockeye Salmon Colonization in Glacier Bay Inferred from Genetic Methods

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Abstract. Several species of Pacific salmon have colonized recently deglaciated streams and lakes in Glacier Bay. New populations result from colonization by straying salmon that fail to home to their natal streams to spawn. Little is known about the manner in which colonization occurs. We used population genetics methods to evaluate the possible colonization mechanisms of sockeye salmon populations in streams of different ages in and around park waters. We conclude that new populations are derived from multiple sources, involve an intermediate number of colonizers, and are subject to recurrent immigration.

Introduction

Numerous watersheds in Glacier Bay now provide spawning and rearing habitat for several species of Pacific salmon (Milner and Bailey, 1989); however, little is known about these recently colonized populations. Glacier Bay National Park and Preserve provides a rare opportunity to study the successful result of straying by salmonids in their natural environment under minimal human influence. Our study evaluates colonization mechanisms among streams of different ages within and adjacent to park waters through analysis of genetic variation among and within sockeye salmon (*Oncorhynchus nerka*) populations. We address the questions of whether colonization is recurrent or a one-time event and whether the initial colonization events involve few or many immigrants.

Methods

Tissue samples of sockeye salmon were collected on or near spawning grounds from seven watersheds within and adjacent to Glacier Bay over several years (fig. 1). The Gull watershed is small—fish collected intertidally in the mouth and in the short outlet were in full spawning condition and presumably would have spawned in the lake had water flow not been restrictive at the time of sampling. The watersheds sampled have been ice-free for different lengths of time: (1) the youngest system (Gull) for several decades, (2) the “medium-aged” systems (Vivid, N. Berg, and Seclusion) for less than 200 years, and (3) the oldest systems (Neva, Hoktaheen, and Ford Arm) for presumably greater than 10,000 years (Milner and others, 2000).

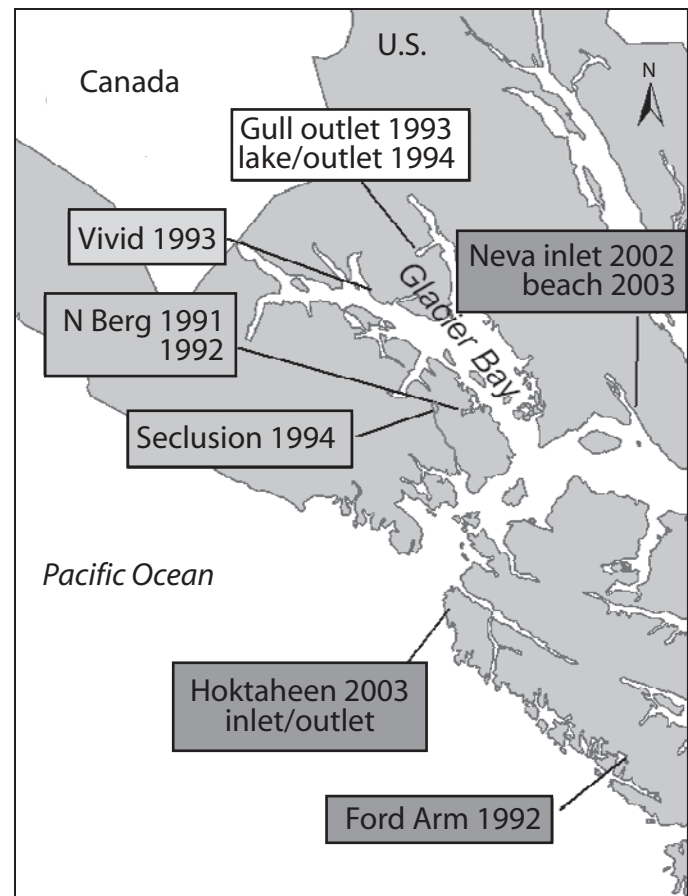


Figure 1. Location and sampling year of sockeye salmon tissue collections in and around Glacier Bay, Alaska.

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We isolated DNA from heart, muscle, or skin tissue and specific regions of the DNA were targeted and amplified using the polymerase chain reaction. Genetic variation was assessed using: (1) restriction site analysis of the mitochondrial DNA (mtDNA) ND1/ND2 region cut with four restriction enzymes, and (2) genotypes of six nuclear microsatellite loci (*Omy77*, *One102*, *One109*, *Ots3*, *Ots107*, and *uSat60*). Forty fish per collection were used to assess mtDNA variation and 50 fish per collection were used to genotype microsatellite loci, except for Gull 1993 (n=32) and Neva 2002 (n=48). Microsatellite genotypes were obtained from LI-COR DNA Analyzer gel images and mtDNA haplotypes were obtained from ethidium bromide-stained agarose gels.

The number and relative frequencies of mtDNA haplotypes and microsatellite alleles were estimated for each collection. Genetic distance was calculated from these frequencies and summarized with “unweighted pair group method with arithmetic means” (UPGMA) trees to obtain a visual representation of population structure. Heterozygosity of microsatellite loci and mtDNA haplotype diversity were estimated for each collection.

Results

Mitochondrial DNA

A total of eight mtDNA haplotypes were observed in the collections; one to five haplotypes were observed in each collection. The three core haplotypes common to populations throughout the geographic distribution of the species (Churikov and others, 2001) occurred in all watersheds except Vivid and Neva. Three haplotypes, all at low frequency, were unique to Glacier Bay collections; one rare haplotype was unique to Hoktaheen inlet, an older, adjacent watershed. Large differences in haplotype frequencies were observed between collections in and adjacent to Glacier Bay (figs. 2 and 3). The only significant year-to-year differences within watersheds occurred between Gull 1993 and 1994, possibly due to the very small sample size in 1993. The Hoktaheen drainage contains genetically distinct inlet and outlet populations. Haplotype diversity, a measure of genetic variation, did not differ between the younger populations within Glacier Bay and the older populations adjacent to Glacier Bay.

Nuclear DNA

All collections were variable at all six microsatellite loci. Eleven alleles were unique to Glacier Bay populations: three were rare (1 percent allele frequency), six occurred at low frequency (2-8 percent), and two had frequencies greater than 10 percent in at least one collection. Five of the seven alleles unique to the older, adjacent populations were rare (allele frequency <1 percent in collections). Although not statistically

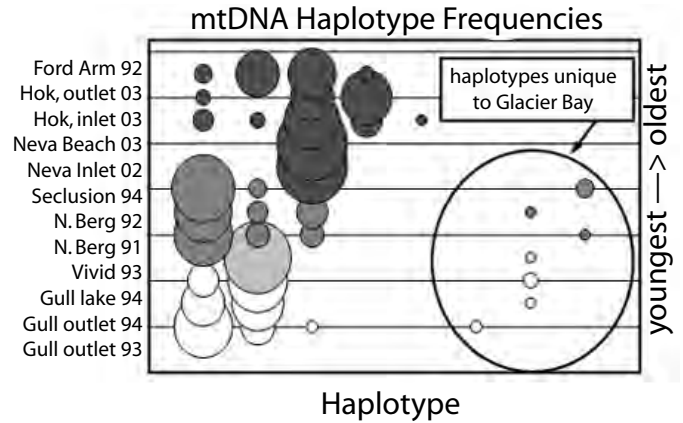


Figure 2. mtDNA haplotype frequencies of sockeye salmon collected in and around Glacier Bay. Circle size indicates relative frequency.

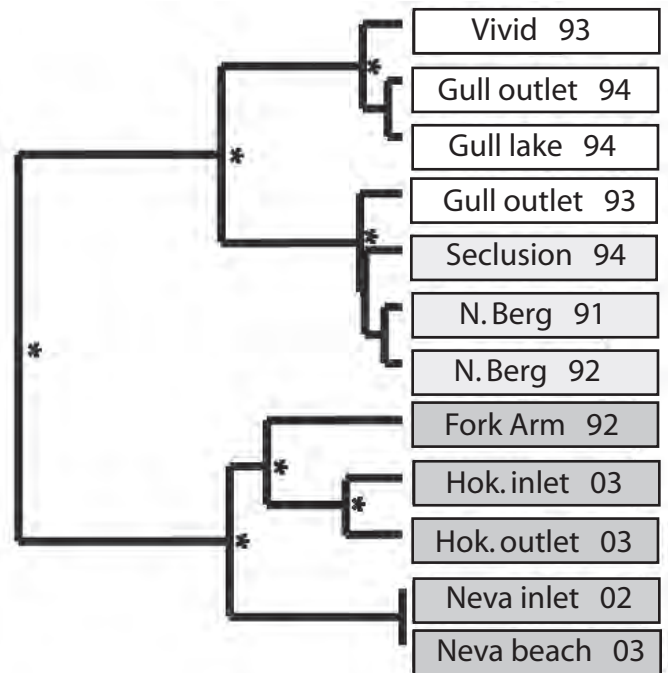


Figure 3. Structure of sockeye populations in and around Glacier Bay based on genetic distance of mtDNA haplotype frequencies, depicted as a UPGMA tree. Statistically significant groupings, $P < 0.02$, are denoted with a “*”.

significant, the number of microsatellite alleles was highest in the youngest populations (fig. 4). Heterozygosity, another measure of genetic variation, also did not differ among populations. With the exception of the collections from two years in N. Berg, all multi-year collections and populations were heterogeneous due to significant allele frequency differences.

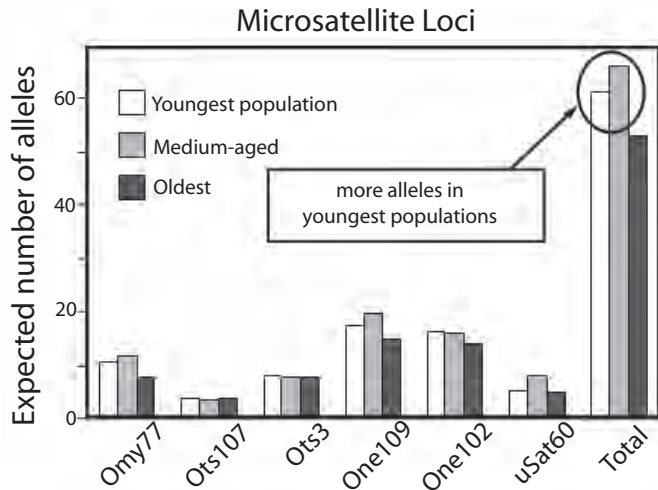


Figure 4. Number of alleles, with sample size differences taken into account, per microsatellite locus under the infinite alleles model for the youngest, medium-aged, and oldest populations in and around Glacier Bay, Alaska.

Discussion and Conclusions

Various measures of genetic variation, e.g., heterozygosity, number of microsatellite alleles and mtDNA haplotypes, and haplotype diversity, are similar in newer populations within Glacier Bay and older populations adjacent to Glacier Bay. This suggests that the number of colonizers must be more than a few fish. Reduced variation would be expected if colonization was restricted to a small number of fish, which would carry only a portion of the variation existing in donor populations. On the other hand, the allele and haplotype frequencies differed among populations both within and outside Glacier Bay, which could only have occurred if the number of immigrants in new populations was not large. A large number of immigrants would result in homogeneity, i.e. similar haplotype and allele frequencies between populations. Thus, we conclude that an intermediate number of immigrant sockeye salmon, not quantifiable with these data, colonized new freshwater habitat in Glacier Bay and that gene flow after colonization must be low because these populations remain heterogeneous. Additional analyses may provide ballpark estimates for the number of fish colonizing recently deglaciated watersheds.

Although not statistically significant, the total number of alleles at the six microsatellite loci was greater in the populations in the lower part of Glacier Bay. These populations were colonized presumably less than 200 years ago, a period of less than 50 generations of sockeye salmon during which migrants could contribute new genetic variation. Given the slight increase in the number of alleles and haplotypes present in these “medium-aged” populations, some degree of recurrent colonization appears to have occurred. As populations age, however, the relative success of

immigrants that introduce new genetic variation wanes, and genetic drift due to stochastic population size fluctuations and the reproductive isolation characteristic of salmon play more important evolutionary roles.

Although Seclusion Lake drains into marine waters outside Glacier Bay, and N. Berg empties into lower Glacier Bay, the headwaters of these systems lie in close proximity to one another. Given the dynamic nature of watersheds during deglaciation and the genetic similarity of the sockeye salmon from these two locations, we can speculate that these two watersheds were connected during the time of colonization.

Our results indicate that populations within Glacier Bay were formed from multiple sources by an intermediate number of fish, probably repeatedly over time. This strategy of colonization maximizes genetic diversity on which selection can act (Krueger and others, 1981) and may in part explain the rapid rate and expansion of salmonid colonization in recently deglaciated watersheds of Glacier Bay. The entrance to Glacier Bay intersects Icy Strait, a major migratory corridor between oceanic and coastal waters for many populations of salmon in northern and central southeast Alaska (Elling and Macy, 1955). Thus, the opportunity exists for many stocks to contribute immigrants to Glacier Bay.

Management Implications

The colonization of salmon in Glacier Bay profoundly affects the evolution of stream ecology in this region. Salmonids are an important nutrient resource for many organisms in Glacier Bay, including bears, birds, insects, plants, and humans. On a broader scale, salmon are a valuable component to the health of the coastal environment and human economies of the North Pacific region. Improved understanding of salmon population dynamics is of interest to resource managers and agencies within and beyond the National Park Service.

Acknowledgments

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