INFORMATION TO USERS

This manuscript has been reproduced from the microfilm master. UMI films the text directly from the original or copy submitted. Thus, some thesis and dissertation copies are in typewriter face, while others may be from any type of computer printer.

The quality of this reproduction is dependent upon the quality of the copy submitted. Broken or indistinct print, colored or poor quality illustrations and photographs, print bleedthrough, substandard margins, and improper alignment can adversely affect reproduction.

In the unlikely event that the author did not send UMI a complete manuscript and there are missing pages, these will be noted. Also, if unauthorized copyright material had to be removed, a note will indicate the deletion.

Oversize materials (e.g., maps, drawings, charts) are reproduced by sectioning the original, beginning at the upper left-hand corner and continuing from left to right in equal sections with small overlaps. Each original is also photographed in one exposure and is included in reduced form at the back of the book.

Photographs included in the original manuscript have been reproduced xerographically in this copy. Higher quality 6" x 9" black and white photographic prints are available for any photographs or illustrations appearing in this copy for an additional charge. Contact UMI directly to order.

UMI

A Bell & Howell Information Company
300 North Zeeb Road, Ann Arbor MI 48106-1346 USA
313/761-4700 800/521-0600

Ecological, Morphological, Genetic, and Life History Comparison of Two Sockeye Salmon Populations, Tustumena Lake, Alaska

by

Carol Ann Woody

A dissertation submitted in partial fulfillment
of the requirements for the degree of

Doctor of Philosophy

University of Washington

1998

Approved by ______________________________
Chairperson of Supervisory Committee

____

____

____

Program Authorized
to Offer Degree Fisheries

Date 12/18/98

UMI Number: 9916735

UMI
300 North Zeeb Road
Ann Arbor, MI 48103

In presenting this dissertation in partial fulfillment of the requirements for the Doctoral degree at the University of Washington, I agree that the Library shall make its copies freely available for inspection. I further agree that extensive copying of this dissertation is allowable only for scholarly purposes, consistent with "fair use" as prescribed in the U.S. Copyright Law. Requests for copying or reproduction of this dissertation may be referred to University Microfilms, 1490 Eisenhower Place, P.O. Box 975, Ann Arbor, MI 48106, to whom the author has granted "the right to reproduce and sell (a) copies of the manuscript in microform and/or (b) printed copies of the manuscript made from microform."

Signature ______

Date 17 Dec 1998

University of Washington

Abstract

Ecological, Morphological, Genetic, and Life History Comparison of Two Sockeye Salmon Populations, Tustumena Lake, Alaska

by Carol Ann Woody

Chairperson of the Supervisory Committee
Associate Professor Christian E. Grue
USGS Fisheries Cooperative Unit, School of Fisheries

Populations can differ in both phenotypic and molecular genetic traits. Phenotypic differences likely result from differential selection pressures in the environment, whereas differences in neutral molecular markers result from genetic drift associated with some degree of reproductive isolation. Two sockeye salmon, *Oncorhynchus nerka*, populations were compared using both phenotypic and genotypic characters, and causal factors were examined. Salmon spawning in a short (< 3 km), shallow (< 21 cm), clear, homogenous spring-fed study site spawned later, were younger, smaller, and produced fewer and smaller eggs than salmon spawning in a longer (~ 80 km), deeper, stained, diverse, precipitation-dominated stream. Run timing differences were associated with differences in stream thermal regimes. Age and size at maturity differences are likely due to differences in age-specific mortality rates. Fish in the shallow spring-fed system suffered higher adult predation rates and exhibited greater egg to fry survival compared to fish in the precipitation-fed system. Salmon in both streams exhibited non-random nest site selection for deeper habitats and smaller substrates (≥ 2 to < 64 mm mean diameter) relative to available habitat; fish from the precipitation system avoided low velocity habitats containing fine (< 2 mm) substrates. Genetic comparisons of six microsatellite loci indicated that run time was a more effective reproductive isolating mechanism than geographical distance. Differences between and within the tributary spawning populations are discussed in terms of selection, genetic drift, and the homogenizing effects of gene flow. This study indicates important adaptive differences may exist between proximate spawning groups of salmon which should be considered when characterizing populations for conservation or management purposes.

TABLE OF CONTENTS

LIST OF FIGURES

LIST OF TABLES

ACKNOWLEDGMENTS

The success of this project was due to the combined efforts of many wonderful people. Special thanks goes to Dr. Leslie Holland-Bartels, Branch Chief of the Fisheries and Marine Mammals Division, Alaska Biological Science Center, U. S. Geological Survey (USGS), Biological Resources Division (BRD), for her dedication in obtaining funding for this research. I am grateful to Dr. Christian Grue, Leader, Washington Cooperative Fish and Wildlife Research, and Barbara Funke, Unit Manager, for their many hours of time and effort in administering the project.

My Reading Committee, Dr. Paul Bentzen, Dr. Chris Foote, Dr. Christian Grue, and Dr. Leslie Holland-Bartels, provided valuable insight and criticism on the manuscripts. Dr. Foote was an exceptional sounding board for organizing my thoughts and ideas and his positive feedback provided motivation during periods of frustration. Dr. Eric Knudsen, Fisheries Team Leader, USGS-BRD, provided careful reviews of the spring research proposals and final manuscripts. Jeff Olsen of the Marine Molecular Biotechnology Laboratory, University of Washington, taught me the art of microsatellite analysis. Joel Reynolds, Lucinda Tear, Donna Robertson, and Mark Udevitz provided statistical support and advice. Mary Whalen assisted with graphics, logistics, and otolith readings. The U.S. Fish and Wildlife Service (USFWS), particularly the wonderful staff at the Kenai Fishery Resource Office and the Kenai National Wildlife Refuge provided critical logistical and technical support. Pat Shields of the Alaska Department of Fish and Game (ADF&G) verified otolith readings. Dr. Lisa Seeb (ADF&G) provided laboratory space to finish the microsatellite analysis. Ken Tarbox (ADF&G) provided verbal input and many faxes regarding the commercial fishery of Cook Inlet. The USFWS Water Resources Division installed and monitors hydrologic gauging stations on my study sites. Gari Fandri of the Cook Inlet Aquaculture Association provided valuable advice and field assistance. The Youth Conservation Corps assisted with weir monitoring operations.

This work could not have been accomplished without a special group of people who camped, worked, and shared an indescribable wilderness experience, through terrific storms, forest fires, and charging brown bears, special thanks to: Dan Nelson, Mary Whalen and Cricket, Bob Maloney, Kurt, Steve Hendricks, and Matt Nemeth. My invaluable emotional support crew: Lucinda Tear, Scott Martin, Kevin Kumagai, Holiday Sloan, Mike Ward, Kristina Ramstad, George Durner, Mary Whalen, Alyssa Rieschauer, Jeff Olsen, Pam Jensen, Steve Amstrup, Julia Meka, and last and best, Joel Reynolds, thank you.

Funding for this research was provided by the Alaska Biological Science Center of the U. S. Geological Survey (formerly the U. S. Fish and Wildlife Service (USFWS) and National Biological Survey/Service) through the Washington Cooperative Fish and Wildlife Research Unit in the School of Fisheries at the University of Washington.

DEDICATION

To Leslie Holland-Bartles: your support throughout my entire graduate career, both in terms of securing funding and in your steadfast belief in my potential, have made this work possible. Thank you for the opportunity. I hope to do the same for a young, promising, female scientist.

Chapter I:

Ecological and Morphological Comparison of Two Sockeye Salmon Populations, Tustumena Lake, Alaska

Introduction

Sockeye salmon, *Oncorhynchus nerka*, vary widely across populations in potentially adaptive traits such as run timing (Ricker 1972; Brannon 1987), migration behavior (Raleigh 1971; Brannon 1972; Wilmont and Burger 1985), morphology (Foerster 1968; Blair et al.1993), age at maturity (Healy 1987), and fecundity and egg size (Foerster 1968; Beacham and Murray 1993). A genetic basis has been demonstrated in salmonids for many of these traits (e.g. run timing, *O. mykiss*, Siitonen and Gall 1989, and *O. gorbuscha*, Gharrett and Smoker 1993; fry migration behavior, *O. nerka*, Raleigh 1971; morphology, *O. kisutch*, Taylor and McPhail 1985a; age at maturity, *O. tshawytscha*, Hankin 1993, and *O. mykiss*, Gall et al.1988; egg size, *O. mykiss*, Bromage et al.1990; see review by Taylor 1991). In a few cases, an environmental mechanism has been strongly correlated to phenotypic variation across populations, suggesting adaptation to local conditions. For example, return time of salmonids to natal streams has been correlated to incubation regimes experienced by their progeny; adults returning to cool streams generally spawn earlier than those returning to warmer ones (Burger 1985; Brannon 1987; Heggberget 1988). This behavior is thought to have evolved to coordinate fry emergence time with increased food production in spring (Brannon 1987). However, our understanding of potentially adaptive relationships between sockeye salmon and their freshwater natal habitats is limited. The alarming decline of historically productive salmon populations (Nehlsen et al. 1991) and numerous failed efforts to transplant self-sustaining anadromous sockeye salmon runs (see review by Wood 1995) underscores the need for research to assist conservation efforts.

Sockeye salmon populations originating from specific rearing lakes can usually be differentiated from each other both phenotypically and genetically (Marriot 1964; Foerster 1968; Varnavskaya et al.1994; Wood et al.1994; Wood 1995); therefore, the rearing lake is frequently used to define populations for commercial fishery management. However, sockeye salmon originating from different tributaries to a common rearing lake often exhibit phenotypic and genetic differences, which may be related to differences in natal habitats. For example, Foskett (1958) documented differences in time of migration, age, and size of sockeye originating from different tributaries to glacial Owikeno Lake, British Columbia. Gard et al. (1987) found that Karluk Lake sockeye originating from short, steep, narrow, shallow streams with small substrates were 91% spring spawners while low gradient, wide, deep streams with relatively larger substrates contained both spring and fall runs. The late run populations were larger and older than those in spring runs. Varnavskaya et al. (1994a) found differences in allozyme frequencies among populations of sockeye salmon within nine lake systems. The greatest differences were observed among populations using different spawning habitats and those exhibiting different run timing. Habitat differences were acknowledged in each of these studies, but only qualitatively. Rogers (1987) provided some quantification of potentially important habitat variables by noting that sockeye salmon returning to small (< 7 m wide, < 4 km long), shallow (< 20 cm) streams were younger and smaller than fish returning to larger tributaries. Quantitative information is necessary to begin to evaluate the strength and importance of morphometric-habitat relationships.

The primary objective of this study was to compare potentially adaptive traits of two sockeye salmon populations that spawn in different tributaries to Tustumena Lake, Alaska. The secondary objective was to quantify abiotic and biotic factors that could influence any observed differences (e.g., potential selection mechanisms). Past research within the Tustumena watershed focused on factors influencing sockeye salmon fry production within the lake (Koenings and Burkett 1987; Kyle 1992); adult spawning population distribution (Burger et al. 1995); and a genetic comparison among populations spawning in different habitats (Burger et al. 1997). Sockeye salmon spawning in the Kasilof River at the outlet of the lake are genetically distinct from inlet tributary spawning populations, among which significant differences have not been detected (Burger et al. 1997). Research quantifying tributary spawning sockeye salmon phenotypes and habitat parameters has not yet been conducted.

Study Site

Tustumena Lake, southcentral Alaska (Figure 1.1), is about 295 km^2 with a watershed of 1,376 km^2 which drains ($\approx 2.13 \times 10^9$ m^3/yr) to Cook Inlet via the Kasilof River. The lake is glacial, extremely turbid, cold (temperaures for the ice-free period average between 6 and 10°C), and unproductive (chlorophyll *a* average = 0.45 µg/l; Kyle 1992).

The Cook Inlet fishery harvests an estimated 2 million Tustumena Lake sockeye salmon annually, and an average of 200 thousand fish escape the fishery to spawn within the Tustumena drainage (Ken Tarbox 1997, personal communication, Alaska Department of Fish and Game, Soldotna, Alaska). Sockeye salmon spawn primarily in seven main tributaries and two beach areas of Tustumena Lake (Burger et al. 1995). Two streams were selected for a comparative study based on preliminary stream surveys, Glacier Flats and Nikolai creeks, as they were hydrologically and geomorphically different (Figure 1.1; Table 1.1), yet similar to other streams within the watershed. Glacier Flats was covered by the Tustumena glacier as recently as 2,000 years ago (Karlstrom 1964). The stream is a first order, monomorphic, relic glacial channel located on a low relief outwash floodplain situated downslope of the Tustumena glacier. The stream is fed by upwelling groundwater which moderates hydrologic regimes. It varies annually in length (2-6 km) and watershed boundaries are undefined. It most closely resembles the description of a groundwater fed slough (palustrine channel type, spring-fed) as described by Paustian et al. (1992). Historic aerial escapement estimates and weir counts indicate an average of 32,000 sockeye salmon annually spawn in Glacier Flats Creek (Kyle 1992). Nikolai Creek is an older (14,000 years old, Reger 1993) fourth order, heterogeneous, sinuous, stained, valley bottom stream. The stream is about 80 linear km long and drains a watershed of 142 km^2. Water inputs primarily originate in precipitation events, and water temperature and discharge may fluctuate drastically in a 24-h period (Figure 1.2). Historic aerial escapement surveys indicate an average of 16,000 sockeye salmon spawn annually in Nikolai Creek (Kyle 1992). The stream is comprised of several distinct channel types; however, for the purposes of this study sampling efforts were limited to the first 4 km of the mainstem and the first 4 km of the east and west forks (Figure 1.1).

The mainstem of Nikolai Creek (Figure 1.1, section 1) is approximately 7 linear km from the mouth to the first fork. This portion of the stream has a complex riparian area including sloughs, spring-fed tributaries, and side channels. High flows are not contained within the active channel; therefore, this portion of the stream is classified as a floodplain channel type (Paustian et al. 1992) (Table 1.1). The first 4 km of the east fork (Figure 1.1, section 2) falls within the palustrine channel type (bog), characterized by a single, low velocity, highly sinuous, sandy channel occurring in a low-relief wetland. The west fork of Nikolai Creek (Figure 1.1, section 3) is a mixed control channel (Paustian et al. 1992). The lower 2 km resemble the Nikolai mainstem with the upper transitional section becoming more constrained by inclusions of boulder and bedrock, limiting floodplain development. Glacier Flats and Nikolai creeks were considered to be ideal for comparison as potential selection regimes appeared different (e.g. temperature, discharge); therefore, the potential for adaptive differences between the populations appeared high (Brannon 1987).

Methods

Habitat Characterization

Habitat Use, Availability, and Relative Use

Habitat use in 1994 was determined by recovery of tagged females (tagging described in phenotypic methods) on redds where spawning or active nest defense were observed. Male sockeye salmon neither select the nest site, nor exhibit strong site fidelity; therefore, the habitat use data are for females only. Nest site water velocity (cm/s) and depth (cm) were measured at the undisturbed, upstream portion of each redd. Surface composition of spawning substrate was characterized using a modified Wolman pebble count (Wolman 1954; Kondolf and Li 1992). One hundred or more random substrate samples from undisturbed gravel around each redd were measured along the medial axis and classified into one of eight categories ($p_1 < 2$; $p_2 \geq 2$ to < 4; $p_3 \geq 4 < 8$; $p_4 \geq 8$ to < 16; $p_5 \geq 16 < 32$; $p_6 \geq 32$ to < 64; $p_7 \geq 64$ to < 128; $p_8 \geq 128$ mm). Temperatures of the water column and within each redd (from the gravel surface to 10 cm into the nest pocket) were measured (± 0.1°C) at each site. Hydrologic gauging stations were installed on each stream in October 1994 to monitor annual discharge and intergravel thermal regimes.

A more detailed resource use analysis was conducted in 1995 by quantifying habitat potentially available to spawning salmon (depth, velocity, substrate) in addition to nest site (used) data. Available habitat were characterized prior to initiation of the spawn run at 60 randomly selected points within the first 4 km of each channel type (15 sites/km). Then, habitat used by female sockeye salmon was characterized based on data from up to 100 randomly selected spawning females from within the same stretches of river. Habitat features were measured as described for the 1994 spawning season.

Cumulative distribution functions were developed (Cleveland 1993) to examine whether depth or velocity resource availability and use differed among channels, and to compare used and available habitat within a channel. Among channel comparisons were tested with Kolmogorov-Smirnov (KS) two-sample tests, using a Bonferroni adjusted alpha ($\alpha / 3$). Non-random habitat selection was determined by comparing used and available distributions with a Kolmogorov-Smirnov two-sample test ($\alpha = 0.05$). Substrate frequency data for available, used (across channel), and used vs. available (within channel), were compared using a chi-square test of homogeneity. Analysis included frequency data in the eight substrate categories previously described.

Fish may be limited in their use of a particular resource due to its availability; therefore, relative use provides an indication of habitat features fish may select for or against if availability were to change. This type of index was initially developed by Savage (1931) and has been applied in fisheries for assessing the impacts of altered stream flow regimes on fish habitat (Baldrige and Amos 1981; Orth and Maughan 1982). Relative use (used habitat/ available habitat) of depth, velocity, and substrate by sockeye salmon within each channel was examined. Used and available habitat data were categorized and, because of unequal sample sizes, were standardized by determining percent frequency within each category. Frequency histograms were developed and a relative use curve determined by dividing individual percent use categories by the corresponding percent available category.

Resource Use Models

Resource selection functions were developed for Glacier Flats Creek, Nikolai mainstem, and Nikolai west fork; the east fork was dropped from the modeling exercise because so few fish nested in that particular channel ($n = 5$). The models were used to compare selection parameters among channels and to evaluate the relative probability a female would select a given site based on available and used habitat data for that channel. Resource selection functions were based on logistic regression following Design I, Sampling Protocol A, as outlined in Manley et al. (1993). Used and available data from 1995 were incorporated into the analysis as: depth, depth^2, velocity, velocity^2, and substrate categories were combined: $p_1 < 2$; $p_{234} \geq 2$ to < 16; $p_{56} \geq 16$ to < 64; $p_7 \geq 64$ to < 128, and $p_8 \geq 128$ mm. The number of substrate categories was reduced from the original eight to five categories to increase the residual degrees of freedom and, therefore, the precision of the probability of use estimates. The continuous variables, depth and velocity, were incorporated into the model as quadratic functions because fish used a specific range of each of these resources, i.e., the function was not linear.

First, a correlation analysis was conducted to ascertain variable independence. A correlation coefficient $|r| > 0.60$ was considered to indicate some linear dependence between variables. Therefore, correlated variables were not included together in a model to avoid bias and inflated parameter estimate variance due to multicollinearity (Neter et al. 1996). Second, logistic regression (SAS Proc Logistic, descending) was used to select the best eight models for a one-variable model, two-variable model, ... , up to the full model (SAS Institute 1989). Models were compared using the Akaike Information Criterion (AIC = - 2 log [L(O)] + 2K; K = number of parameters in the model; Akaike 1973). The model with the lowest AIC value is generally considered the "best" profile of variables that will estimate the relative probability an individual will use a particular site. Reduced or nested models with similar AIC values were compared to the full model using a log-likelihood ratio test (Hosmer and Lemeshow 1989). The final model for each channel was chosen with consideration given to both the AIC and the biology of the species. Models were compared to determine whether the probability of use by female sockeye salmon was affected by similar habitat variables in each channel.

Phenotypic Comparisons

Selected phenotypic traits (run timing, body length, body depth, degree of ripeness upon stream entry, fecundity, egg size, age and size at maturity) were compared between the Glacier Flats and Nikolai creek populations in 1994. These traits were selected for study because they may be related to physical and biotic differences in the streams (Brannon 1987; Rogers 1987; Gall et al. 1988; Hankin et al. 1993). Each run was monitored and sampled at picket weirs established approximately 0.5 km upstream of each stream mouth (Figure 1.1). Weirs were installed prior to initiation of each run and removed when runs diminished to less than 1% of the run maximum.

Sockeye migrants were counted and sexed as they passed over a flash-board in the weir. About 50 fish (25 males, 25 females) were randomly netted from a holding pen in the weir throughout the day for phenotypic characterization. Fish were lightly anesthetized with MS 222 (approximately 1 g/ 8 L of water) and classified as to ripeness (ripe: fish which have ovulated or completed spermatogenesis extrude gametes readily when pressure is applied to the ventral sides; non-ripe: if otherwise). Morphometric traits of body length (midorbit of eye to hypural plate) and body depth (anterior insertion of the dorsal fin to the abdomen) were made to the nearest millimeter with a caliper.

Nest site selection and an estimate of the number of fish taken by bears was determined through a mark-recapture study (Seber 1962). Fish selected at the weir for phenotypic characterization were tagged with a numbered, color-coded, 40-mm Peterson disk on the left side of the dorsal fin. Tagging operations in Nikolai Creek took place 16-31 July and 9-16 August and recovery surveys were made 25-31 July, and 1-4, 10-14, and 19-22 August. Tagging operations in Glacier Flats Creek took place 10-18 and 24-30 August and recovery efforts began 19 August; the entire stream was surveyed twice weekly from 19 August to 14 September. More fish were tagged in Nikolai Creek (1,201) compared to Glacier Flats (700) because the run into Nikolai Creek was much larger than anticipated based on prior escapement data (Kyle 1992); therefore, a larger sample size was necessary.

Recovered salmon were categorized as spawning (S), completed spawning (O), dead (D), bear killed (B), or pre-spawning (G); pre-spawning fish were released after their number and location were noted. Otoliths were extracted from recaptured fish (S, O, D, B) for age determination, tags removed, and location of capture noted. Tags recovered from fresh, bear-killed salmon or tags found on bear middens within the immediate stream banks (0-3 m from stream edge) were classified as bear kills. Otoliths were also collected from tagged carcasses found impinged upon weirs.

Fecundity was determined in the field by sacrificing 69 ripe females collected at each wier (Nikolai: n = 34; Glacier: n = 35). Egg masses were removed and 500 eggs were counted, blotted dry, weighed (mg), and average egg weights calculated: total weight of 500 eggs/500. Fecundity was estimated by: total weight of egg mass/ average individual egg weight. Analysis of covariance (ANCOVA) was performed to compare linear models of fecundity as a function of female length.

Egg samples were collected throughout each run to determine egg weight, both from ripe females sampled at the weir and from tagged females recaptured during spawning. A total of 204 egg samples were collected from Glacier Flats females and 147 from Nikolai Creek females with each sample being comprised of 30 or more eggs. Samples were immediately preserved in 10% buffered formalin and weighed about 2 months later in the laboratory. Thirty formalin-preserved eggs from each sample were blotted dry and weighed (± 1 µg) to estimate individual egg weights. Analysis of covariance was used to compare linear models of egg weight as a function of female length for the two populations.

Age determinations from otoliths were made from a dry, then a "wet" (25% glycerin solution for 3-24 h) reading of the saggita annuli (Kim and Robertson 1968). A second expert reader verified ages. The European age designation system was used with the first number representing the number of winters spent in freshwater and the second number representing the number of winters spent in the ocean. For example, an adult sockeye aged as 1.2 years spent one winter in freshwater after hatching, and then spent two winters in oceanic feeding grounds before returning to spawn. Age composition of populations was compared with a chi-square analysis. Length at age data were compared using ANOVA; significantly different means were further analyzed using a post-hoc Tukey test.

In 1995, unlike 1994, weirs were not installed to examine stream entry characters, nor were fish tagged. However, morphometric data and otoliths were collected from up to 60 randomly selected spawning or post-spawning females on established redds within the first 4 km of each study channel (Glacier Flats, Nikolai, main stem, and Nikolai westfork). Males obviously paired with an established female were sampled in a similar fashion. All data were collected, processed, and analyzed in a manner similar to 1994. Chi-square analysis was used to compare age frequency composition between streams. Analysis of variance was used to compare morphometric differences among channels.

Morphometric-Habitat Relationships

The relationship between female morphometric traits (length, depth) and nest site variables (depth, velocity, substrate) was examined using ANCOVA. Male sockeye salmon do not exhibit nest site fidelity as do females. Thus, direct nest site morphometric-habitat comparisons are less valid. However, ANCOVA was used to compare body depth of males adjusted for length among channel types, and results were compared to the female morphometric-habitat results.

Results

Habitat Characterization

Habitat Use, Availability, and Relative Use

Distributions of available habitat (depth and velocity) differed among channels. Glacier Flats and Nikolai west fork were shallow (Figure 1.3) and similar in their depth distributions (Kolmogorov-Smirnov two-sample test [KS], $p = 0.378$), compared to the mainstem, which contained more deep habitat (KS, $p = 0.0001$ vs. Glacier; $p = 0.001$ vs. west fork). Glacier Flats Creek contained a narrower range of velocities and more low velocity habitat than both the Nikolai west fork (KS, $p < 0.001$) and mainstem (KS, $p = 0$), which did not differ from each other (KS, $p = 0.28$; Table 1.2; Figure 1.3).

Fish may be limited in their use of a particular resource due to its availability. Therefore, relative use provides an indication of habitat features fish may select for or against if availability were to change. The relative use graphs (percent used/ percent available; Figure 1.3) indicated that fish in all channels generally used deeper, faster water and small to medium (≥ 2 to < 64 mm) substrate disproportionate to availability, indicating selection. Comparisons of used vs. available (velocity and depth) habitat distributions indicated that female sockeye salmon in all channels exhibited non-random selection for deeper waters than that available (KS, $p \leq 0.013$ all comparisons; Table 1.2; Figure 1.3). Glacier Flats females randomly selected nest sites relative to water velocity (KS, $p = 0.735$; Table 1.2; Figure 1.3). In contrast, fish in both Nikolai channels exhibited non-random selection relative to velocity and tended to avoid low velocity habitats (KS, west, $p = 0.001$; mainstem, $p = 0.016$).

Available nest substrate composition differed significantly (chi-square; $r = 2$, $c = 7$; $p < 0.001$) among study channels. Glacier Flats available habitat contained more fine substrates (< 2 mm) and less cobble boulder (≥ 128 mm) compared to Nikolai west (chi-test; $r = 2$, $c = 7$; $p < 0.001$), while Nikolai main was significantly different than both (chi-test; Glacier, $r = 1$, $c = 7$; $p < 0.0001$; Nikolai west, $r = 1$, $c = 7$; $p < 0.0001$) with an intermediate composition of fine and large substrate compared to the other channels. Used and available substrate comparisons differed significantly within all study channels, indicating non-random selection (chi-test; $r = 1$, $c = 7$; $p < 0.001$, all comparisons, Figure 1.3). Fish in all channels selected small (≥ 2 to $= 16$ mm) and medium (≥ 16 to < 16 mm) substrates in greater frequency than their availability (Figure 1.3). Used nest substrate composition also differed significantly among channels (chi-test, $r = 2$, $c = 7$; $p < 0.0001$), with the most obvious difference being in the use of fine substrate. Glacier Flats nests contained more fines (< 2 mm) than expected, while Nikolai west and main females used less than expected. In general, fish used small and medium gravel more than expected based on availability.

Resource Use Models

Resource selection models indicate that the relative probability a female would select a site based on habitat resources (depth, velocity, substrate) varied among channels. The probability a female would select a given site in Glacier Flats Creek was most determined by the presence of small and medium sized substrate (≥ 2 to < 64 mm; Table 1.3). Note that these substrate sizes were highly negatively correlated ($|r| = 0.72$) with the presence of fine silt and sand (< 2 mm; Appendix B) in the Glacier Flats correlation matrix, and that highly correlated parameters were not included together in the models (see methods). Nikolai west fish selected nest sites based primarily on velocity and avoided sites comprised of cobble and boulder substrates (≥ 64 mm mean diameter), sizes which were negatively correlated ($|r| \geq 0.60$) with small and medium gravel sizes (Table 1.3; Appendix B). Nikolai mainstem females selected against sites comprised of sand and silt substrates, which were negatively correlated with medium gravel sizes ($|r| = 0.68$); Table 1.3; Appendix B).

Phenotypic Comparisons

Stream entry patterns were derived from daily weir monitoring in 1994 (Figure 1.4). Adult sockeye salmon movement into Nikolai Creek began approximately 25 days earlier and lasted twice as long as the run into Glacier Flats. A total of 63,723 adult sockeye passed the Nikolai weir and 10,347 passed the Glacier Flats weir. Sex ratios of spawning adults differed between streams with 1.1:1 and 1.6:1 females to males observed in Nikolai and Glacier Flats, respectively. Most females that passed through the Nikolai weir had not ovulated and therefore were classified as "green" (1 ripe: 3.5 green females); in contrast, the majority of Glacier Flats females had ovulated (1 ripe: 0.5 green; Table 1.4).

Significant differences were found between Nikolai (N) and Glacier Flats (G) creeks when comparing fish depth (males), fecundity, and egg weight, even after adjustment for fish length (Table 1.5). Returning Nikolai males increased their depth more with length, while Nikolai females were more fecund ($\bar{x}_N = 4,103$ vs. $\bar{x}_G = 2,970$ eggs/female), and had larger eggs ($\bar{x}_N = 88$ vs. $\bar{x}_G = 78$ mg/egg) than Glacier Flats fish.

Age composition differed between populations (Figure 1.5). The majority of Glacier Flats sockeye salmon returned to spawn at age 1.2, whereas most Nikolai Creek fish spent an additional year in the ocean, returning at age 1.3. No differences in age composition were detected between sexes within a stream in either year so further analyses pooled data across sexes in each stream. The stream populations differed with respect to how long they spent in freshwater (chi-square test of homogeneity, 1994: $p = 0.016$, 1995: $p = 0.000$) and how long they spent in saltwater (chi-square, 1994: $p = 0.000$, 1995: $p = 0.000$), with Nikolai fish spending more time in both systems (Figure 1.5).

Stream populations differed in 1994 length at age in both sexes (ANOVA: females, $p = 0.000$; males, $p = 0.000$; Table 1.6). Compared to Glacier Flats males, Nikolai males were larger than fish of the same age and similar in size to Glacier males that had spent an additional year at sea (N 2.2 vs. G 1.3, 2.3). A similar relationship was observed for females.

Morphometric-Habitat Relationships

Of the habitat variables (water depth, water velocity, substrate composition), only water depth explained a significant amount of variation in log of female body depth. Controlling for this covariate, female body depth still differed significantly among study channels (ANCOVA, $p = 0.026$), with the deepest bodied fish found in the deepest channels. Female body length also differed among channels (ANCOVA, $p = 0.001$) but was not significantly associated with any quantified habitat variables. Male sockeye salmon do not exhibit strong nest site fidelity as females do, thus the direct relationship between male morphology and habitat variables was not explored. However, comparisons of male length and depth among channels indicated a similar relationship of shallow bodied fish in the shallow channels (Glacier Flats and the Nikolai west fork) and deeper bodied fish in the Nikolai mainstem (ANOVA; p = 0.001; Table 1.7).

Discussion

The Tustumena watershed has been influenced by glaciation events which affected the evolution of many contemporary sockeye salmon ecosystems (Karlstrom 1964; Milner and Baily 1989; Wood 1994), and findings from my study may be pertinent to similar channel types. The Tustumena tributaries in this study have depths, substrate composition, temperatures, and discharge rates within published ranges for other tributaries used by the species, although some nest site velocities were higher than previously documented (Burner 1951; Kerns and Donaldson 1968; Olsen 1968; Bazarkin 1990a; Bazarkin 1990b). Research similar to my study, where relative use and the relative probability of use were determined based on quantified parameters, is lacking in the salmon literature. It is important to consider these relationships as habitat rehabilitation efforts based on demonstrated habitat preference would likely be more successful than efforts based on general tributary measures. In my study, water depth, velocity, and substrate composition were important variables contributing to the differences observed in habitat use, while temperature and water depth appeared to be related to adaptive variation in phenotypes.

Water depth was a key habitat parameter relative to nest site selection (Table 1.2; Figure 1.3) and also explained a significant amount of variation in female body depth (ANCOVA, p = 0.026). Patterns of selection by salmon for deeper nest sites relative to their availability, and phenotypic patterns of shallow bodied fish in shallow channels and deeper bodied fish in deeper channels (Table 1.7) may be adaptive responses to predation. Selecting deeper rather than shallow sites in which to nest would likely reduce the chance of detection by predators, as the fish would not protrude from the water, and might reduce capture probability as a fish would have a larger escape range.

Bear predation of tagged fish in Glacier Flats Creek (shallow, clear, homogenous) was estimated at 33%, while in the Nikolai mainstem (deep, diverse, stained), about 2% of tagged fish were captured by bears (Table 1.4). These are certainly underestimates of the total number of fish taken by predators in both systems as only one species was considered, *Ursus arctos*, and only kills found within 3 m of the stream bank were documented. Sub-dominant bears and many other species of salmon predators were observed in the area (e.g. eagles, gulls, osprey, wolverine, fox, wolves, coyotes, marten, mink) which carry fish away from the stream (> 3 m) to feed. In a shallow, homogenous, clear system, such as Glacier Flats, predators can easily detect and capture prey, however, in a deeper, diverse, stained stream, such as Nikolai Creek mainstem, detection and capture are likely more difficult.

Other characteristics observed in Glacier Flats fish, but not in fish spawning in the Nikolai Creek mainstem, were the rapid deposition of gametes (3.5 days versus 6 days; Table 1.4) and smaller fish size (Table 1.6). Rapid reproduction would likely increase fitness when the probability of predation is high. The smaller size of Glacier Flats females and males would be advantageous relative to predation in a shallow stream as smaller, more slender fish would be less visible than larger, deeper fish, particularly when negotiating shallow riffle areas. Smaller fish also have higher burst swimming speeds (Yates 1983), a handy trait when avoiding predators.

Current velocity was a significant determinant in nest site selection for the precipitation fed Nikolai channels, but not for Glacier Flats. Nikolai fish likely need to select higher surface velocity regions to ensure sufficient intergravel water flow for embryonic survival, as the two are related. Glacier Flats is a low velocity spring-fed system with a high percentage of fine substrates (< 2 mm). Here, sockeye salmon likely focus on regions of upwelling versus areas of high surface velocity to increase the probability of embryonic survival.

The consistent correlation of a phenotypic trait with specific habitat features (late spawning runs in warmer systems; older larger fish in larger systems) may indicate important adaptive differences and should be researched further (Endler 1986, Futuyma 1986). Such findings would impact management of sockeye salmon originating from a single lake and provide insight for rehabilitation efforts.

Ecologically Based Adaptations

Run Timing

Run timing is a precise (Brannon 1987), heritable behavior (Busack and Gall 1980; Siitonen and Gall 1989), which is correlated with natal stream incubation regimes; early runs return to colder systems than late runs (Sheridan 1962; Ricker 1972; Burger et al.1985; Brannon 1987; Heggberget 1988). Findings from my study corroborate this pattern: Nikolai Creek averaged 1.4°C colder than Glacier Flats during the 1994 incubation period (August to April) (Figure 1.2) and the spawn run began 25 days earlier (Figure 1.4).

Age and Size at Maturity

Age at maturity is an environmentally affected, heritable trait in salmonids (Gall et al. 1988; Peterman et al. 1986; Rogers 1987; Hankin et al. 1993). The amount of time a sockeye salmon spends in freshwater may be independent of the factors which determine marine age. For example, in a 27-year data set of 20 Wood River sockeye populations, freshwater age was most often determined by rearing lake temperature and fish density, while marine age was highly correlated ($|r| > 0.80$) with parental marine age (Rogers 1987). Similar observations have been made for other Alaskan and British Columbia sockeye salmon populations (Larkin and Macdonald 1968; Rogers 1984; Peterman 1985). Rogers' (1987) study indicated that ocean age was heritable, and he suggested that differential reproductive success of small and large individuals in the natal environment could account for the differences in age composition. That study also found that small (< 5 m wide and < 2 km long), shallow (< 20 cm) streams were dominated by small 2-ocean fish whereas larger, deeper tributaries were dominated by 3-ocean fish (Rogers 1987). Similar observations have been made for 78 chum salmon populations in British Columbia (Beacham and Murray 1987). Results from my study were similar, as Glacier Flats Creek is a small (mean width = 6.9 m, < 4 km long), shallow (mean = 20.6 cm) stream dominated by 2-

ocean fish, while Nikolai Creek is larger (mean width = 5.7 m, ≈ 80 km long), deeper (mean = 32 cm), and dominated by 3-ocean fish.

Ocean age is a pivotal life history trait for salmon because it is the most significant determinant of size at maturity (Healy 1986), which is, itself, positively correlated with fecundity and egg size (Beacham 1982; Healy and Heard 1984; this study), all factors affecting fitness. Age- and size-specific mortality rates can cause rapid evolutionary change in a species' life history traits (Reznick 1982, 1983; Stearns 1992) and would seem particularly important in a semelparous species. Assuming that Nikolai and Glacier Flats populations experience similar mortality rates in the shared lake-rearing and marine environments, it is possible that differential selection among channels can effect phenotypic variation in age at maturity.

Predators can affect the phenotypic expression of the genotype in their prey (Reznik 1982, 1983; Endler 1991). Life history theory (Stearns 1992) predicts, and empirical studies with iteroparous Poecilids (Reznik 1982, 1983) have demonstrated, that high predation on sexually mature adult fish can select for smaller, early maturing fish which produce smaller offspring. High predation pressure on adults of a semelparous species, such as sockeye salmon, could feasibly effect a similar and more rapid result. Because brown bears exhibit site fidelity (Glenn and Miller 1980; Schoen and Beier 1985), it is reasonable to assume consistent annual predation pressure within the study channels. Adult sockeye salmon spawning in Glacier Flats certainly suffer predation rates in excess of the 33% documented in my study, which could contribute to the evolution of younger, smaller fish. Differential selection in Glacier Flats by predators may also favor smaller (therefore younger) and more slender fish as predation rates are likely higher on bigger (therefore older) fish, as they would be more visible and have reduced swimming ability (Yates 1983). Predation does not appear to be as strong a selective mechanism in the Nikolai Creek mainstem because it is deeper, stained and diverse, affording fish more refuge from predators.

Nikolai Creek sockeye salmon generally spend an additional year in the ocean, attain greater length for the same age (Table 1.7) and are more fecund than Glacier Flats salmon (mean fecundity = 4,103 vs. 2,970 in Glacier Flats). Adult mortality due to predation is apparently lower in the Nikolai study channels, however, mortality during the embryonic stage is likely greater in Nikolai Creek than in Glacier Flats Creek. Nikolai Creek is colder in the winter and subject to high discharge events in the fall and spring(Figure 1.2), factors which increase mortality during incubation and emergence stages (Bams 1972; Tyler and Gibbons 1973; Murray and Beacham 1986; Murray and McPhail 1988; Beacham and Murray 1990). Larger female size would be advantageous in Nikolai Creek because larger females dig deeper nests (van den Burghe and Gross 1984), which may situate embryos below the level of mortality induced by scour (Montgomery et al. 1996). Nikolai Creek females were more fecund, and higher egg production combined with gametes deposited in a typical series of redds (Burgner 1991) would help offset high embryonic mortality due high discharge or extreme temperatures. Thus, in the more environmentally extreme Nikolai Creek, females may increase their fitness by staying in the ocean longer, growing larger, providing greater care through construction of deeper nests, and producing more eggs.

Delayed maturity in Nikolai females may also decrease the instantaneous mortality rate of emergent fry. In my study, older larger females produced larger eggs than younger smaller females. Larger eggs produce larger fry (Gall 1974) and larger fry have a survival advantage as they can attain higher burst swimming speeds; a fitness advantage when escaping predators (Taylor and McPhail 1985b). Nikolai Creek has a greater abundance of emergent fry predators in comparison to Glacier Flats Creek (Woody 1998). Thus, the larger egg size I observed in Nikolai Creek females could increase fitness by providing a swimming advantage for fry escaping predators.

Resource Use Models

All the models exhibit some similar features. Water depth is a significant parameter with a positive coefficient in all the models as fish require specific minimum depths in which to navigate and spawn and deeper waters often provide refuge from predators. However, increasing depth was only important to fish up to a point, then a decline in availability and use occurred (Figure 1.3). Thus, a negative coefficient is associated with the depth^2 parameter, which was significant in the mainstem and Glacier models. In these study channels, depths greater than 50 cm were not generally used and often indicated silt-filled pools (Glacier Flats) or areas subject to scour (Nikolai mainstem), which would be unsuitable for developing embryos. Velocity is an important model parameter in Nikolai Creek channels because intergravel water flow, which affects survival of embryos, is related to surface water velocity and gravel permeability in Nikolai, whereas Glacier Flats Creek is fed by upwelling springs. The probability of use in Glacier Flats is likely more influenced by upwelling groundwater locations and gravel permeability than surface water velocity. Velocity is more important in the west fork of Nikolai than in the mainstem; fish in the west fork prefer higher velocity water but it is more limited in availability than in the mainstem. The large coefficients associated with percent substrate composition in all the models reflect the strong influence these parameters have on the relative probability a female will use a site for egg deposition. The greater the percentage of substrate within the ≥ 2 to < 64 range, the greater the relative probability a female will use a site.

Conclusions

Significant differences in habitat availability and use, both between and within tributaries, was observed for two sockeye salmon populations of Tustumena Lake, Alaska. Females in study channels exhibited non-random selection for deeper sites; random selection relative to velocity in spring areas, and non-random selection against low velocity sites in a precipitation dominated system. Fish exhibited specific habitat preferences relative to what was available; larger deeper fish preferred deeper water in which to spawn compared to smaller fish. This preference may have evolved due to high predation in the shallow clear system.

Significant differences were also observed between the populations in run time and age and size at maturity and are believed to be, in part, adaptations to freshwater natal habitats. Run timing differences were attributed to differences in stream thermal regimes during embryonic development phases. Differences in age and size at maturity are hypothesized to have evolved in response to different mortality rates on adults and embryos of the two populations. High predation on adults in the small, clear, shallow spring-fed stream have may have selected younger, smaller, more slender, rapidly spawning fish. In the large, stained, deep, precipitation fed system, adult mortality is apparently lower, but embryonic mortality due to annual flooding and freezing is likely higher, contributing to selection for larger females which can bury embryos deeper (to help mitigate mortality due to scour) and produce more eggs (to compensate for the higher embryonic mortality).

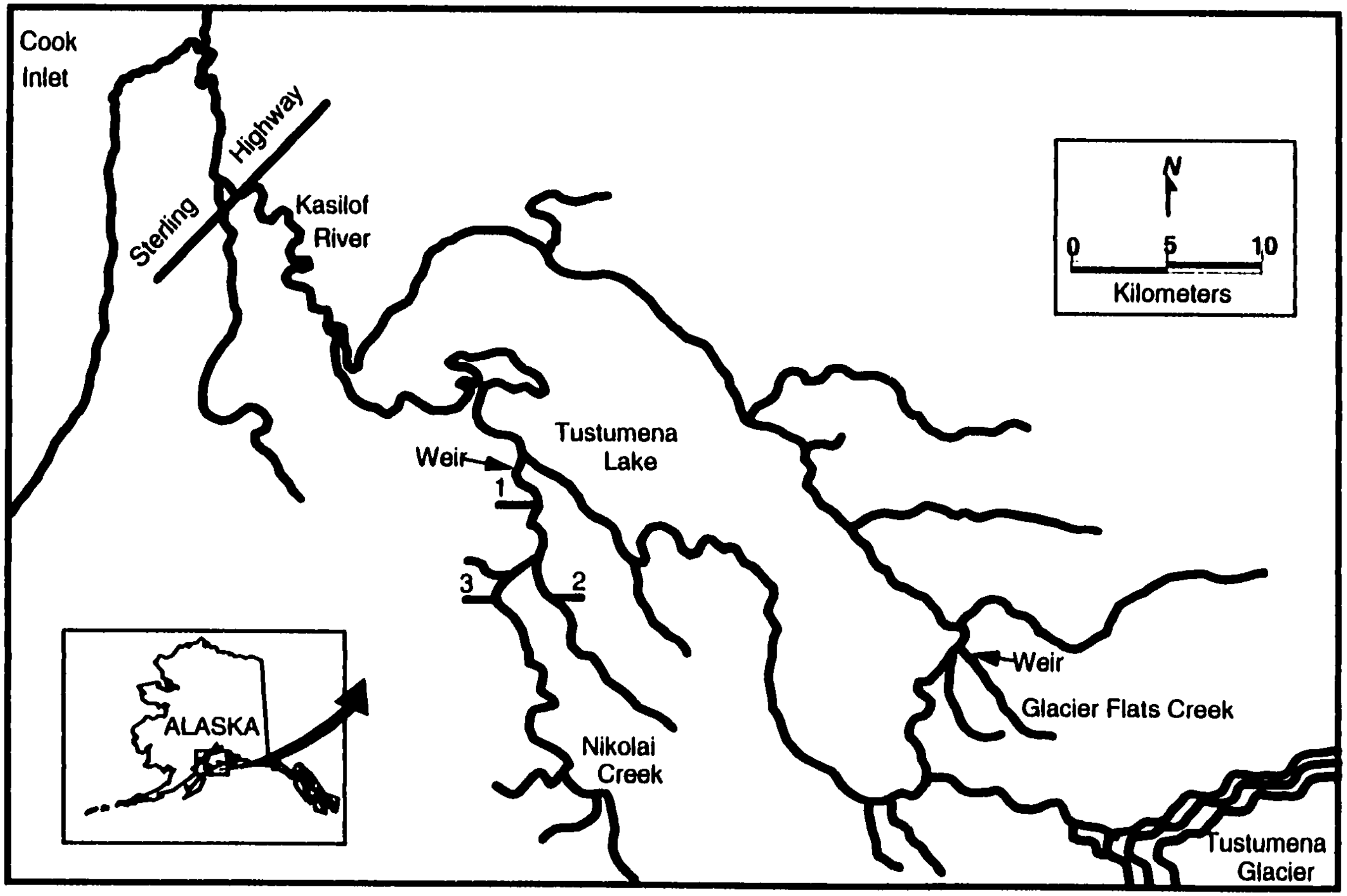


Figure 1.1. Study channel and weir locations used in comparing proximate sockeye salmon populations, Tustumena Lake, Alaska, 1994 to 1995. Nikolai Creek channel types are: 1 = mainstem, floodplain; 2 = east fork, palustrine; 3 = west fork, mixed control. Lines indicate upper boundary of study reaches. Glacier Flats Creek comprised a single palustrine study channel.

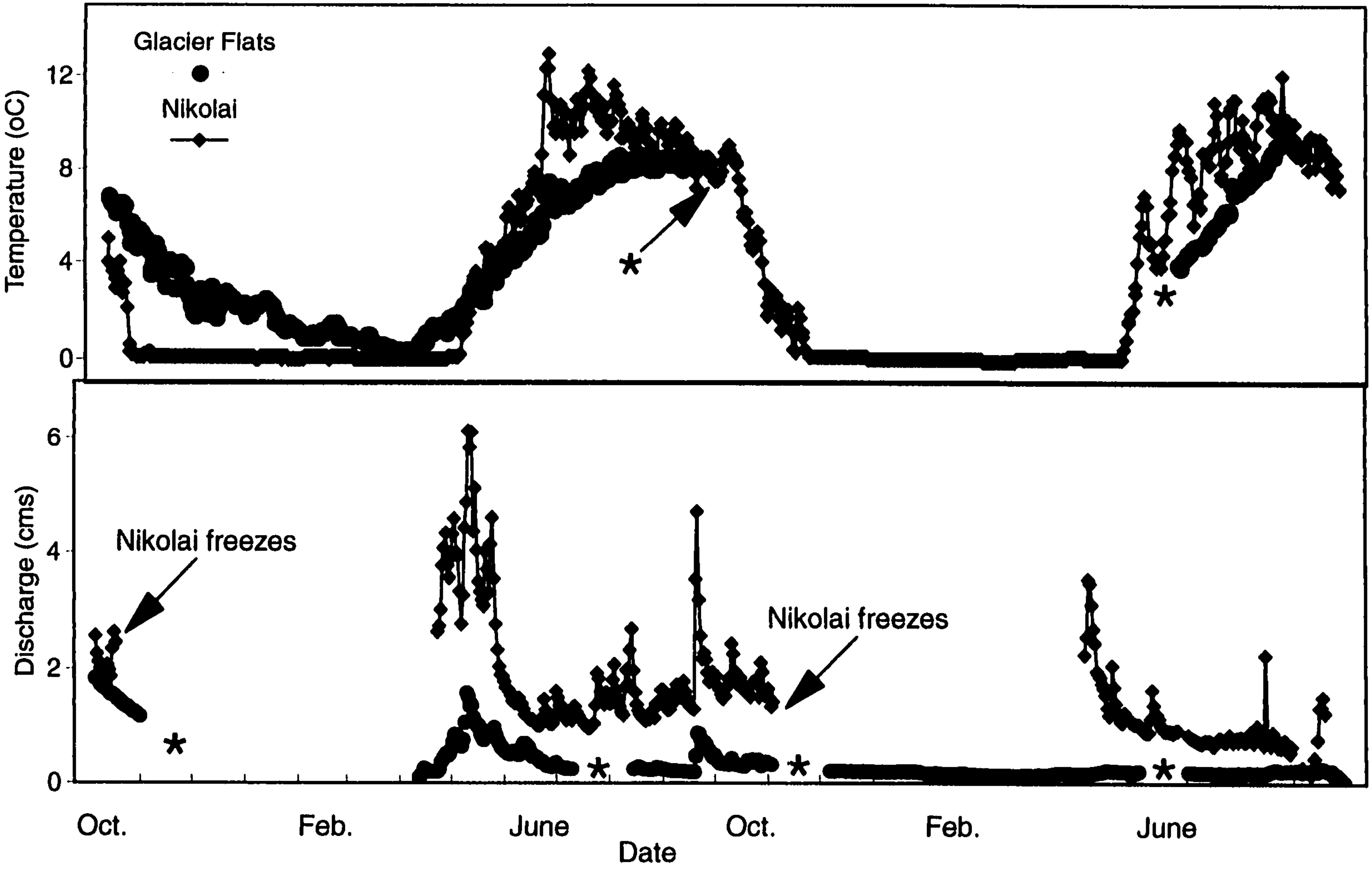


Figure 1.2. Mean daily stream temperature (°C) and discharge (cms) data collected for Glacier Flats and Nikolai creeks, Tustumena watershed, Alaska, 1994 to1996. The * indicates missing data from Glacier Flats due to vandalism of probes by bears.

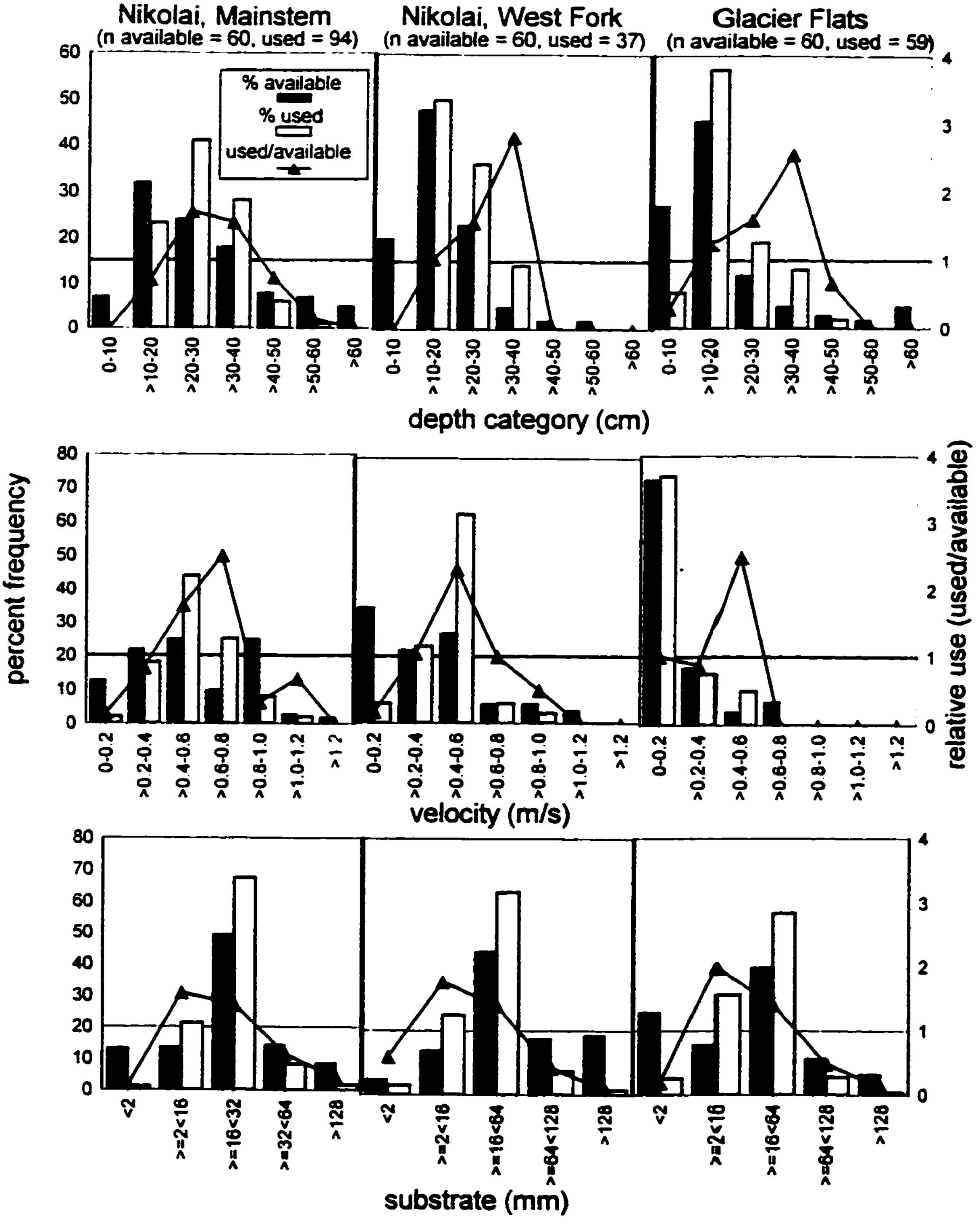


Figure 1.3. Use, availability, and relative use (used/available) of water depth,velocity and substrate categories by sockeye salmon in Nikolai and Glacier Flats creeks, Tustumena Lake watershed, Alaska, 1995. Relative use values greater than one indicate selection.

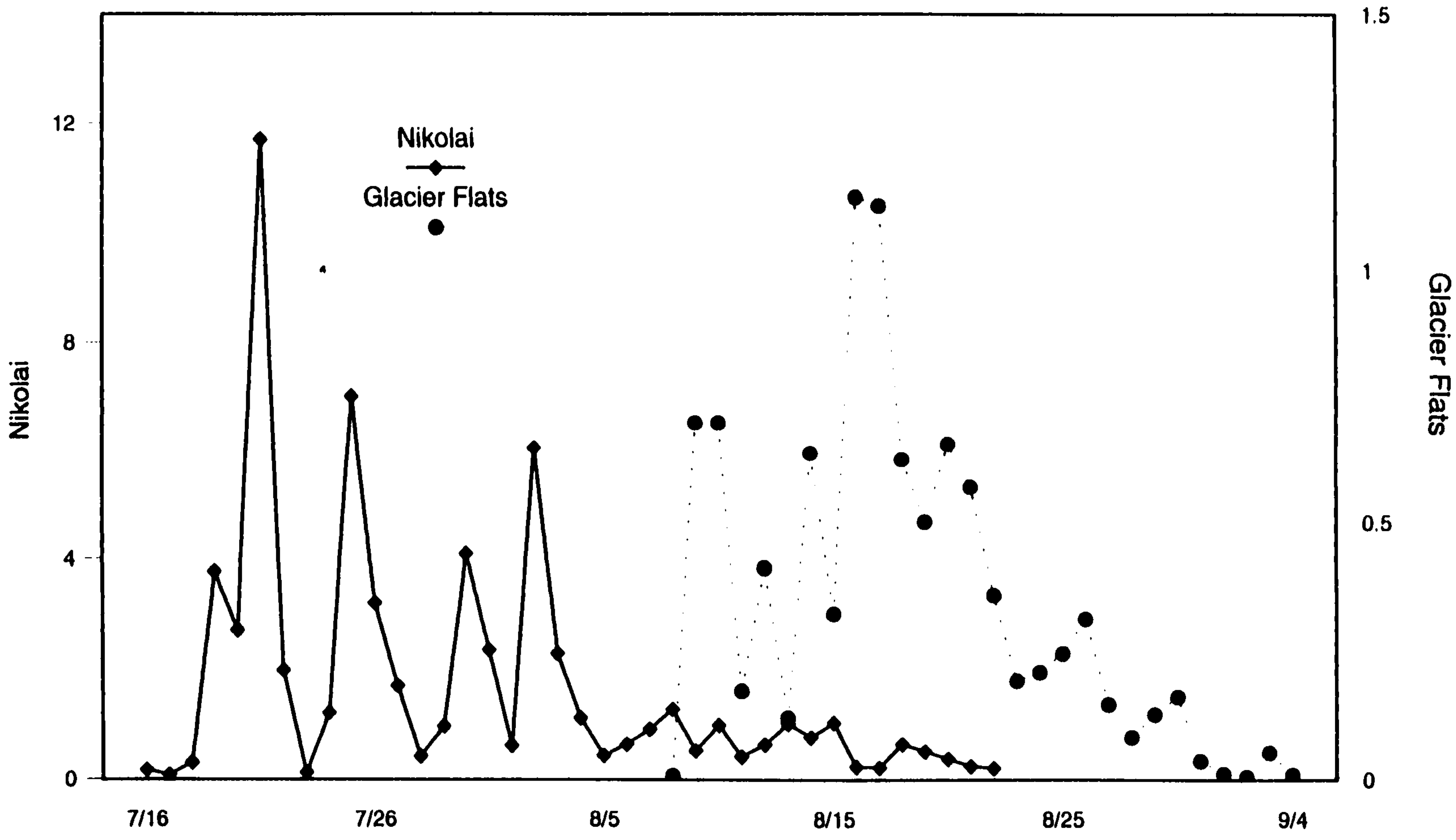


Figure 1.4. Daily weir counts of sockeye salmon (thousands) entering Nikolai and Glacier Flats creeks, Tustumena Lake watershed, Alaska, 1994.

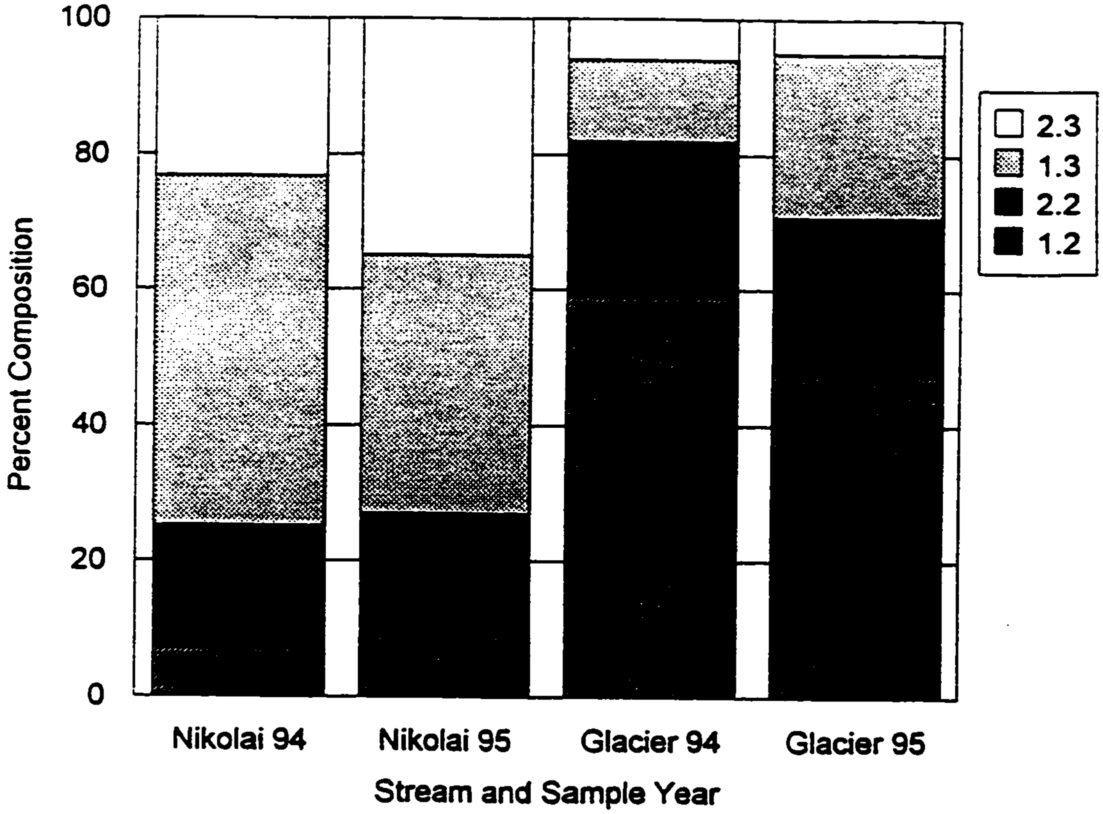


Figure 1.5. Percent age at maturity of sockeye salmon returning to Glacier Flats and Nikolai creeks, Tustumena Lake watershed, Alaska, 1994 and 1995.

Table 1.1. Summary of general habitat data for Nikolai and Glacier Flats creeks, Tustumena Lake, Kenai Peninsula, Alaska, 1994 and 1995. Channel type determinations based on Paustian et al. (1992). Bankful width and water depth are mean values.

Stream	Channel type (location)	Bankful width (m)	Water depth (cm)	Width:depth	Sinuosity [a]	Gradient (%)
Nikolai	Floodplain (mainstem)	7.6	29.9	25 (high)	1.5	1.2
	Mixed control (west fork)	6.1	18.4	33 (high)	1.2	2.1
	Palustrine (east fork)	3.3	47.9	6.9 (low)	1.8	1.4
Glacier Flats	Palustrine	6.9	20.5	33.7 (high)	1.3	0.5

[a] Sinuosity = ratio of actual stream length to valley length; low sinuosity < 1.2; moderate ≥ 1.2 to < 1.4; high ≥ 1.4 to < 1.5; very high ≥ 1.5

Table 1.2. Summary of cumulative distribution function comparisons of used and available sockeye salmon nest site depth and velocity. Kolmogorov-Smirnov two-sample tests were used to compare distributions with $\alpha = 0.05$ for within channel comparisons, and a Bonferroni adjusted $\alpha = 0.05/3 = 0.167$ for comparisons among channels.

Channel Comparison	Habitat comparison	Variable	K-S	p-value
Among channels:	Available vs. Available			($\alpha = 0.0167$)
Glacier vs. Nikolai west		depth	0.167	0.378[a]
Glacier vs. Nikolai main			0.4	<0.001
Nikolai west vs. Nikolai main			0.367	0.001
Glacier vs. Nikolai west		velocity	0.4	<0.001
Glacier vs. Nikolai main			0.6	0
Nikolai west vs. Nikolai main			0.267	0.028[a]
Within channel	Used vs. Available			($\alpha = 0.05$)
Glacier		depth	0.28	0.012
Nikolai west			0.32	0.013
Nikolai main			0.3	0.009
Glacier		velocity	0.11	0.735[a]
Nikolai west			0.379	0.002
Nikolai main			0.283	0.016
Among channels, 1994	Used vs. Used; 1994			($\alpha = 0.0167$)
Glacier vs. Nikolai west		depth	0.467	<0.001
Glacier vs. Nikolai main			0.484	0
Nikolai west vs. Nikolai main			0.275	<0.001
Glacier vs. Nikolai west		velocity	0.878	<0.001
Glacier vs. Nikolai main			0.792	0
Nikolai west vs. Nikolai main			0.439	0.018[a]
Among channels, 1995	Used vs. Used; 1995			($\alpha = 0.0167$)
Glacier vs. Nikolai west		depth	0.275	0.045[a]
Glacier vs. Nikolai main			0.848	0
Nikolai west vs. Nikolai main			0.467	<0.001
Glacier vs. Nikolai west		velocity	0.76	<0.001
Glacier vs. Nikolai main			0.578	0
Nikolai west vs. Nikolai main			0.436	<0.001

[a] indicates channel-habitat comparison was not significantly different

Table 1.3. Resource selection probability functions developed for female sockeye salmon spawning in Glacier Flats Creek and two Nikolai Creek channels, the west fork and the mainstem, Tustumena Lake, Alaska, 1995. Substrate categories are coded: $p_1 = < 2$; $p_{234} = \geq 2$ to < 16; $p_{56} \geq 16$ to < 64; $p_7 \geq 64$ to < 128, and $p_8 = \geq 128$ mm. Positive model coefficients indicate that the resource selection probability function increases with increasing variable values.

Channel	Resource selection probability model
Glacier Flats Creek	$w(x) = \exp(9.41[p_{234}] + 5.94\,[p_{56}] + 0.188\,[\text{depth}] - 0.003\,[\text{depth}^2])$
Nikolai Creek, west fork	$w(x) = \exp(31.27\,[\text{velocity}] + 0.31[\text{depth}] - 40.23\,[p_7] - 28.47\,[p_8] - 24.43\,[\text{velocity}^2])$
Nikolai Creek, mainstem	Model 1. $w(x) = \exp(-78.6\,[p_1] - 8.37\,[p_7])$
	Model 2. $w(x) = \exp(10.05\,[\text{velocity}] + 10.26\,[p_{56}] + 6.12\,[p_{234}] + 0.46\,[\text{depth}] - 0.065\,[\text{depth}^2] - 9.5\,[\text{velocity}^2])$

Table 1.4. Weir counts of sockeye salmon, tagging information, spawning condition at stream entry, and mean number of days until recaptured as either spawning or spawned-out individuals, Glacier Flats and Nikolai creeks, Tustumena Lake, Alaska, 1994. Recovery condition presented as percent killed by bears, spawning and spawned out. Green at weir and ripe at weir indicate spawning condition of individuals when tagged; n = number recaptured.

					Condition at recovery				
Stream	Sex	Weir Count (# tagged)	Ripe at weir (%)	Number of tag recoveries	Bear killed (%)	Mean number of days until ripe fish observed spawning (n)	Mean number of days until non-ripe fish observed spawning (n)	Mean number of days until ripe fish observed spawned out (n)	Mean number of days until non-ripe fish observed spawned out (n)
Glacier Flats	male	3,706 (350)	91	199	38	6.8 d (25)	ND	11.8 d (35)	12 d (2)
	female	5,612 (350)	66	242	29	3.25 d (8)	7.1 d (6)	8.9 d (78)	10.6 d (39)
Nikolai	male	30,018 (600)	74	91	1[a]	6.4 d (24)	10.2 d (5)	6.4 d (14)	9 d (3)
	female	33,158 (601)	22	101	1[a]	2.6 d (12)	6 d (23)	5.9 d (10)	8.7 d (35)

[a] The diverse brushy terrain made it difficult to locate and survey all bear middens along Nikolai Creek, whereas the level grassy banks along Glacier Flats Creek facilitated estimates of fish mortality due to bears. Thus, the Nikolai Creek bear kill estimate is likely an underestimate of bear take.

Table 1.5. Summary of ANCOVA results comparing Nikolai and Glacier Flats creeks with respect to fish depth, fecundity, and individual egg weight, each adjusted for fish length.

ANCOVA response	Coefficient	Ho: Nikolai = Glacier Flats	Linear Model (R^2) Nikolai (n)	Linear Model (R^2) Glacier Flats (n)
depth (♂)	intercept	0.007	0.68 (437)	0.59 (319)
	slope	0.003		
depth (♀)	intercept	0.094	0.62 (133)	0.58 (204)
	slope	0.093		
fecundity	intercept	0.002	0.093 (34)	0.144 (35)
	slope	0.623		
egg weight	intercept	0.047	0.215 (147)	0.186 (204)
	slope	0.698		

Table 1.6. Results of multiple comparison tests of differences between mean lengths (mm) at age (ANOVA; Tukey test; $\alpha = 0.05$) for populations of sockeye salmon returning to Glacier Flats (G) and Nikolai (N) creeks, Tustumena watershed, 1994. Populations joined by a solid line were not significantly different. Sample sizes: females, $n_G = 191$, $n_N = 146$; males, $n_G = 112$, $n_N = 159$.

Creek	G	G	N	N	G	G	N	N
Age	1.2	2.2	1.2	2.2	1.3	2.3	1.3	2.3
Male length	398	399	408	434	445	450	470	482
Female length	398	402	421[a]	438	445	450	466	468[a]

[a] significant differences observed between sexes within a stream (ANOVA; $p < 0.05$).

Table 1.7. Analysis of variance and Tukey test results ($\alpha = 0.05$) comparing mean body length and depth of sockeye salmon among study channels, Tustumena Lake, Alaska. Means joined by a line were not significantly different. Study channel mean depths included to illustrate the relationship of shallow-bodied fish in shallow channels, deeper-bodied fish in deeper channels.

	Nikolai west fork	Glacier Flats Creek	Nikolai mainstem
Male length	420	423	486
Male depth	124	138	162
Female length	415	414	462
Female depth	100	104	111
Study channel water depth	18	21	30

Chapter II:

Temporal Variation of Genotypic and Phenotypic Traits of Two Sockeye Salmon Populations in Tustumena Lake, Alaska

Introduction

Sockeye salmon generally spawn in tributaries to lakes where their young rear for one to two years before migrating to oceanic feeding grounds. Adults return to their respective nursery lakes at maturity, segregate to their streams of origin, reproduce, and die soon thereafter. Returning adults are spatially and temporally precise (Hartman and Raleigh 1966; Ricker 1972; Hasler and Scholz 1983; Brannon 1987) and molecular genetic studies indicate significant differentiation has occurred among lake-originating populations (Utter 1984; Foote 1989; Varnavskaya et al. 1994a, 1994b; Wood 1995). As a result, the nursery lake is used as the basic unit for conservation and management purposes.

Defining sockeye salmon populations by nursery lake of origin may not accurately reflect a more complex population structure. Adults may return to the same nursery lake, although they may ultimately spawn in very different habitats such as lake shores, small streams, large rivers, or spring areas. Precise homing can reproductively isolate populations which may then accrue genetic differences through time, either through random genetic events (drift, mutation) or adaptation to differing selection regimes. When within-lake population structure has been examined, researchers have frequently documented significant genetic and phenotypic differences among populations spawning in different habitats (Raleigh 1971; Taylor 1991; Blair et al. 1993; Varnavskaya et al. 1994a; Burger et al.1995; Wood 1995). For example, Varnavskaya et al. (1994a) found significant genetic differentiation among populations using littoral versus tributary spawning habitats. In the Wood River system of Alaska, Rogers (1987) observed that small streams less than 20 cm deep, 5 m wide, and 2 km long contained predominantly small, 2-ocean fish while larger streams had higher percentages of larger 3-ocean fish. Blair et al. (1993) observed that river spawning sockeye salmon of the Kvichak River system of Alaska were older and larger at the same age than fish that spawned along island beaches. Size is positively correlated to age at maturity, which has been shown to be heritable in salmonids (Gjerde 1984; Gall 1988; Hankin et al. 1993). The differences observed among these populations indicate that there is little successful gene flow among populations spawning in different habitats.

Studies which have further organized within-lake population comparisons by run time into a particular spawning habitat indicate that temporal differences among populations also contribute to genetic structure. For example, Wilmot and Burger (1985) found significant differences in allele frequencies of three enzyme coding loci among early and late spawning sockeye salmon from tributaries of the Karluk and Russian rivers of Alaska. Varnavskaya et al. (1994a) compared allozyme allelic frequencies within nine lakes throughout the species' range and found the greatest within-lake variation between early and late spawning runs. Differences in spawning time among populations may restrict gene flow, perhaps as effectively as geographical isolation.

Temporal subdivision of a salmon population returning to spawn in the same habitat could significantly affect our interpretation of population structure depending on our sampling regime. If a population is subdivided, then sampling at different points in time would more accurately characterize the population versus sampling at one point in time. A single tributary-spawning population of anadromous sockeye salmon is generally comprised of individuals that spawn and die at different times and this time period may encompass a few weeks or many months (Ricker 1972; Burgner 1991). If a population is genetically panmictic, then a single day of sampling could theoretically provide sufficient information to characterize that population. However, run timing in salmonids has an heritable component (Siitonen and Gall 1989). If an individual has inherited a tendency to return at a specific time and the run is protracted, this would limit gene flow among fish spawning within a single stream. Fish that spawn at the beginning of a run will not have the opportunity to reproduce with fish that spawn at the end of a run and vice versa. Therefore, differences in run time may be an important barrier to gene flow both within and among populations. Accurate characterization of variation within and between populations may depend as much on when populations are sampled as where they are sampled.

To date, there is little information regarding variation within populations, both genetic and phenotypic, relative to sockeye salmon run time. Some evidence of genetically-based structure relative to run time within a stream exists for salmonids.

Tallman (1986) sampled a population of chum salmon (*O. keta*) in Bush Creek, Vancouver Island, Canada. The October component of the run spawned below a waterfall that was impassable until November when freshets allowed late arriving fish to ascend and spawn in the upper watershed. Tallman (1986) observed significant heritable differences in incubation rate and emergence time of progeny from early and late spawning Bush Creek salmon. Leary et al. (1989) surveyed variation in protein loci relative to run timing in a hatchery population of rainbow trout (*O. mykiss*) and found significant differences among progeny produced by early, mid, and late spawning run components. Taylor (1980) marked four distinct temporal components of a pink salmon (*O. gorbuscha*) run in Auke Creek, Alaska, and found that each group used a different portion of the stream for spawning. Gharrett and Smoker (1993) demonstrated that early spawning adults in Auke Creek produced early emigrating fry and late spawning adults produced late emigrating fry. These studies indicate that temporal patterns of a spawning population contribute to within-stream variation in both genotypic and phenotypic traits.

Variation in molecular genetic traits to discriminate among salmon populations has historically been examined using allozymes, mitochondrial DNA, and randomly amplified polymorphic DNA (RAPDs) (review: O'Connell and Wright 1997). The ability to distinguish among populations using genetic markers is limited by the level of variation inherent in that marker; markers with a low level of variation have low resolving power while highly variable markers provide higher resolution. Microsatellites are a relatively new tool in the field of molecular genetics (Tautz 1989;

Weber 1989). They are found in nuclear DNA and consist of short (1-6 base pair, bp), simple, tandem repeats of nucleotide sequences (O'Connell and Wright 1997). Microsatellites generally exhibit Mendelian inheritance (Wright 1993) and appear to be non-coding and selectively neutral (Burke and Bruford 1987; Love et al. 1990; but see Jackson 1995). The high level of polymorphism exhibited by most microsatellite loci may offer finer resolution of population structure than allowed by other molecular markers (Sanchez et al. 1995; McConnell et al. 1997). Microsatellite data have recently been used to resolve questions regarding genetic differentiation among salmonid populations (Estoup et al. 1993; Olsen et al. 1998). However, information regarding temporal variation of microsatellite markers within a population has not yet been assessed, nor have microsatellite data been combined with or compared to ecologically-based data.

The purpose of this study was to examine population variation relative to temporal patterns of two tributary-spawning sockeye salmon populations. The question addressed was whether gene flow occurred in both time and space between and within two proximate salmon populations. Sockeye salmon from two tributaries to Tustumena Lake, Alaska, were sampled at the peak and at the end of the 1994 spawning run. Complementary data sets composed of allelic frequencies of neutrally selective microsatellite markers and phenotypic traits of mid-orbit hypural length and body depth were collected and compared. The neutral molecular markers were used to evaluate the influence of drift and gene flow, while the run time and morphological data likely reflect the influence of selection. Results are discussed in terms of population conservation.

Study Site

Tustumena Lake, located on the Kenai Peninsula of Alaska, represents an extreme freshwater sockeye salmon habitat (Figure 2.1). Water temperatures during the ice-free period average between 6.3-10.1°C (Kyle 1992). The lake is very turbid (52 nephelometric turbidity units) due to runoff from the Tustumena glacier and, as a result, is relatively unproductive (chlorophyll a average = 0.45 µg/L) compared to other sockeye salmon nursery lakes (Keonings and Burkett 1987). The lake is fed by 11 tributaries, which are used by sockeye salmon for spawning. Two streams were selected for this study, Glacier Flats and Nikolai creeks (Figure 2.1), because prior research indicated that the sockeye salmon populations spawning within the streams differed in potentially adaptive traits such as run time (Kyle 1992; Burger et al.1995) and Kyle (1992) indicated size differences existed between the populations. Although phenotypic traits differ, mitochondrial DNA and allozyme data collected from the two populations did not indicate molecular genetic differentiation (Burger et al. 1997). Because the populations appeared to be somewhat isolated reproductively based on the phenotypic evidence, and because microsatellites may provide higher resolution of population genetic structure (Sanchez et al.1995; McConnell et al. 1997), we thought the populations were ideal for examining temporal variation.

Glacier Flats Creek is a first order, relic glacial channel which was covered by the Tustumena Glacier as recently as 2,000 years ago (Karlstrom 1964). It is low gradient (0.5%) and monomorphic, averaging 6.9 m wide and 20.6 cm deep (Woody 1998). The length of the stream varies annually (2 to 4 km) as it is fed entirely from clear, upwelling groundwater which also tempers thermal and flow variations. Nikolai Creek is a fourth order, highly diverse, tannin-stained, valley bottom stream which is about 80 km in total length. The system is estimated to be 14,000 years old (Reger 1993). It averages 7.6 m wide and 29.9 cm deep in the lower 7 km portion of the main channel (Woody 1998). Water inputs are mainly derived from precipitation, which can cause dramatic fluctuations in flow and temperature regimes. The number of fish spawning within each stream differs. In 1994, 10,347 sockeye salmon ascended Glacier Flats Creek to spawn while 63,723 were counted past the Nikolai Creek weir (Woody 1998).

Methods

Prespawning migrant sockeye salmon were sampled at weirs established in each stream approximately 0.5 km upstream of the lake (Figure 2.1). Weirs were installed prior to the beginning of each run and were removed after salmon stopped entering Glacier Flats Creek (0 fish/week), while the Nikolai Creek weir was removed after fewer than 200 fish/week were observed. Salmon were netted from a collection chamber in the weir, lightly anesthetized with MS 222 (1 to 2 g/ 8 L water), classified as ripe (ovulation completed; gametes easily extruded with light pressure to the ventral sides) or non-ripe, and a small fin clip (≈ 5 cm^2) was collected from the dorsal fin for genetic analysis. Mid-orbit hypural length and body depth (measured from the anterior insertion of the dorsal fin to the abdomen) were measured for each fish (± 3 mm). Morphometrics were collected only from fully mature individuals, as individual depth increases with the development of secondary sexual characteristics. After sampling, fish were placed in fresh water, allowed to recover from the anesthetic, and released upstream of the weir. Approximately 50 males and 50 females were sampled over the course of two to three days at the beginning and latter portion of each run. Sampling dates are coded as follow: Nikolai I = 16-19 July; Nikolai II = 9-10 August; Glacier I = 10-11 August; and Glacier II = 24-25 August 1994.

Fin clips for microsatellite (Bentzen et al. 1991; O'Connell and Wright 1997) genetic comparison were removed from the dorsal fin of each fish and preserved in 100% ethanol. Genomic DNA was obtained for polymerase chain reaction (PCR) using a rapid cell lysis protocol modified from Hoelzel and Green (1994). Approximately 3 mg of tissue was cut from each sample and placed in a centrifuge tube containing 100 μL of a lysis solution of 10mM Tris HCL (pH 9.5), 50 mM KCL, and 0.5% TWEEN 20. One μL of proteinase K (10mg/mL) was added to each tube and samples were incubated for about 20 h at 37°C. Samples were then heated to 95°C for 15 min, centrifuged for 5 min at 17,600 X g, then stored at -20°C until used for PCR.

Microsatellite amplifications were carried out using primers designed by Scribner et al. (1996) and O'Reilly et al. (1996) in multiplex combinations adapted from Olsen et al. (1996). DNA samples were diluted 1:1 with lysis buffer prior to the PCR. Two PCRs were conducted for each sample. Each 10 µL PCR contained 1-0.5 µL diluted DNA sample, 10mM Tris-HCL (pH 9.0), 50 mM KCl, 1.5 mM $MgCl_2$, 0.8 mM dNTPs, 0.5-1.0 U *Taq* polymerase, and 0.08-0.19 µM forward and reverse primers for each of three microsatellite primer pairs. The following profile was used for amplification in a Perkin Elmer 9600 thermocycler: 1 cycle of 94°C (2 min) + 7 cycles of 94°C (1 min) → 58°C (30 sec) → 72°C (15 sec) + 18 cycles of 94°C (30 sec) → 58°C (30 sec) → 72°C (15 sec). The PCR products were stored at 4°C until use.

One µL from each triplex PCR was combined in a vial containing approximately 4 µL of loading buffer (0.60 µL 50 mM EDTA, 3.15 µL formamide, and 0.25 µL [1.0 fmol] Perkin-Elmer GS 350 internal size standard). Samples were then denatured at 95°C for 3 min, placed on ice, then electrophoresed on a 6% denaturing polyacrylamide gel for 9 h using an Applied Biosystems Incorporated (ABI) 373A™ genescanner (ABI 1993). Electrophoretic data were analyzed using Genotyper™ software (ABI 1994).

Analyses

Tests for departure from Hardy-Weinburg equilibrium and for heterogeneity in allele frequencies among groups of sockeye salmon were carried out using the program GENEPOP 3.1 (Raymond and Rousset 1995). Unbiased estimates of corresponding

P-values were derived using a Markov chain method (Dememorization = 1000; Batches = 300; Iterations = 1000/batch) modified from Guo and Thompson (1989).

Unbiased hierarchical F statistics (Wright 1969; Weir and Cockerham 1984) were calculated to measure the extent of genetic differentiation (F_{ST}) among temporal run components using the program FSTAT (Goudet 1995). Test of the significance of F-statistics over all loci were calculated by permuting (1,000 iterations) alleles within totals. Estimates of number of migrants (*Nm*: Wright 1951; Hudson et al. 1992) per generation for significant F_{ST} values were calculated using

$$= \frac{1}{4}\left(\frac{1}{F_{ST}} - 1\right)$$

Multivariate analyses of variance (MANOVA) were used to compare the joint distributions of length and depth among populations (Tabachnick and Fidell 1996). Males and females were analyzed separately due to dimorphism in secondary sexual characters. If a significant difference was found across the populations, all pairwise tests among temporal samples were conducted. To control for the multiple comparisons, these pairwise tests were conducted with a conservative significance level given by the Bonferroni correction, $\alpha = 0.05/6 = 0.008$.

Results

Significant differences were detected in the joint distributions of fish length and depth across the four temporal sample groups of each sex ($P \approx 0$). Investigation of residuals and within-population variance-covariance matrices showed no departures from the assumptions of the MANOVA. Pairwise comparisons indicated that fish from the two Nikolai Creek sample groups were longer and deeper than both Glacier Flats Creek sample groups ($P \approx 0$) (Figure 2.2). Nikolai early run fish were larger than Nikolai late run fish (both males and females; $P \approx 0$). Within the Glacier Flats sample groups, early-run females were longer on average, but not deeper, than the late-run females ($P = 0.001$), while the male sample groups did not differ ($P = 0.039$, compared to Bonferroni adjusted $\alpha = 0.008$).

The six microsatellite loci surveyed were highly polymorphic. The mean number of alleles per microsatellite locus (± SE) was 11.3 ± 2.4, and ranged from four (Oneμ11) to 20 (Ssa85) (Appendix D). Expected heterozygosity (H_E) among loci (populations combined) ranged from 0.24 (Oneμ1) to 0.83 (Oneμ2) and averaged 0.61. We did not include locus Oneμ14 in our average heterozygosity estimates as it departed significantly from Hardy-Weinburg equilibrium. A deficit of heterozygotes, relative to expected frequencies, was observed in the Glacier Flats females from both temporal components, and in the early run males of both streams (Table 2.1). Hardy-Weinburg equilibrium is an assumption of the statistical comparisons we made regarding genetic differentiation (Goudet 1995; Raymond and Rousset 1995). In the absence of other evidence of non-random mating, an excess of homozygotes observed at a microsatellite locus usually indicates the presence of a null, or non-amplifying, allele (Callen 1993; Pemberton et al 1995). However, the deviation observed in Oneμ 14 suggests a more complex phenomenon than the simple presence of one or more null alleles and for this reason we did not use Oneμ14 in subsequent statistical comparisons. The mean expected heterozygosity (excluding Oneμ14) among all Glacier Flats and Nikolai subgroups (early female, early male, late female, late male) was 0.57 ± 0.018 and 0.58 ± 0.28, respectively (Table 2.1).

Tests of genic differentiation within temporal samples (I, II) indicated no significant difference in allele frequencies between sexes comprising early or late run components within a stream. When sexes were pooled within temporal samples, pairwise comparisons indicated significant differences between streams and run components ($P = 0.008$) at one or two loci for all tests (Table 2.2), with two exceptions: Nikolai I and II did not differ at any loci nor did Nikolai II and Glacier I. When samples within a stream were combined, significant differences between Nikolai and Glacier Flats remained detectable only at locus Ssa85 (Table 2.2).

Analyses of genetic differentiation based on F_{ST} generally paralleled the results of the genic differentiation tests, except for the within-stream comparisons. Estimates of F_{ST} were not significant between Glacier I and II ($F_{ST} = 0.003$; $P = 0.114$), but were significant between Nikolai I and II ($F_{ST} = 0.006$; $P = 0.007$; Figure 2.3). No difference ($F_{ST} = 0$) was observed between the Nikolai late (II) and Glacier early (I) samples which were sampled at similar times (Figure 2.3). However, F_{ST} estimates for other pairwise comparisons between streams were significantly greater than zero and tended to increase with increasing temporal separation between samples (Figure 2.3). The largest F_{ST} value ($F_{ST} = 0.011$; $P = 0.001$) was observed between Nikolai I and Glacier II, the two samples most separated in time. The estimated number of migrants per generation between the different temporal components was highest between Nikolai II and Glacier I as no genetic differentiation was detected. Numerical estimates for the number of migrants per generation (*Nm*) for F_{ST} values greater than zero were highest between Nikolai I and Nikolai II and between Nikolai I and Glacier I, with an estimated *Nm* = 41 migrants per generation. The lowest level of migration was between Nikolai I and Glacier II, the most temporally separated comparison groups, which were estimated to share about 23 migrants per generation.

Discussion

Populations that are reproductively isolated may evolve differences through random genetic events (drift and mutation), which affect the genotype, and through selection, act on the phenotype (Futuyma 1986; Hartl and Clark 1997). Rates of evolution differ between these three processes. Mutation rates of microsatellite loci have been estimated to be 10^{-3} to 10^{-5} per generation (see review by O'Connell and Wright 1997). The rate of genetic drift is inversely related to population size; it can be rapid in small, reproductively isolated populations. Selection on phenotypes may also occur rapidly, sometimes within a few generations (Reznik 1982; Siitonen and Gall 1989; Stearns 1992). Low rates of migration (gene flow) among populations are sufficient to diminish or eliminate differentiation based on neutral genetic variation; however, distinct subpopulations with unique, coadapted gene complexes can occur even in the presence of gene flow if selection is present (Endler 1977).

Microsatellite markers allow examination of genetic differentiation due to random genetic events, and the homogenization of gene frequencies due to gene flow. Mutation as a diversifying evolutionary force is likely to be weak on time scales relevant to this study. The recent founding of Glacier Flats (≈ 2,000 years ago) and Nikolai (≈ 10,000 years ago) creeks, combined with our evidence of gene flow among the study populations, discounts mutation and implicates drift as the prime cause of population differentiation among study groups. The data indicate a high rate of gene flow between the two stream populations when they overlap in run time (NII and GI, Figure 2.3), which prevents drift and effectively homogenizes allele frequencies. Gene flow diminishes with increasing temporal separation, and a small but significant degree of genetic differentiation due to drift is apparent within and between the populations (Figure 2.3). The largest genetic difference is between the early run Nikolai fish and the late run Glacier fish whose spawning times differ by about a month. Female salmon returning to Nikolai Creek begin spawning 2-6 days after entering the stream and can survive up to two weeks after spawning (Woody 1998). It would not be feasible for Glacier Flats sockeye salmon, which do not begin spawning until the second week of August, to successfully spawn with the early run Nikolai fish as these would have already completed their reproductive cycle and died. Therefore, these two sample groups are more reproductively isolated from each other by time than by geographic distance. It is feasible that Nikolai Creek fish could stray to and reproduce in Glacier Flats Creek in July, but fish generally do not enter Glacier Flats to spawn until the second week of August (Kyle 1992; Woody 1998).

Variation in run timing of salmon populations into natal habitats indicates adaptive differences among populations. Run timing is an heritable trait in salmonids (Siitonen and Gall 1989) and is correlated with natal stream temperatures during embryonic phases. Early runs of salmon return to relatively cool streams and late runs return to warmer ones in a particular geographic area (Sheridan 1962; Ricker 1972; Burger et al. 1985; Heggberget 1988; Brannon 1987; Woody 1998). Adult run time is adaptive because adult spawn timing is related to the thermal regimes their embryos experience, and stream temperatures directly affect the rate of embryonic development, size at hatching, and survival (Tang et al. 1987; Beacham and Murray 1990; Murray et al. 1990; Woody 1998). Development rate of embryos is somewhat plastic (Weatherly and Gill 1995), is genetically controlled (Murray and McPhail 1988; Murray et al. 1990; Wood and Foote 1990; Woody 1998), and is adaptive in that embryos and larvae from populations native to cold waters may exhibit greater fitness at low temperatures than those from warmer waters and vice versa (Beacham and Murray 1988). The time of year a salmon embryo hatches and subsequently emerges is considered an important transitional period, especially at northern latitudes. If sockeye salmon fry emerge before primary production begins in the rearing lake (e.g. before day length increases or ice break-up), they may not survive if yolk reserves are insufficient to sustain them (McCart 1967; Bilton and Robins 1971). If emergence is asynchronous with peak emergence and emigration of other fry, vulnerability to predation may increase (Godin 1981; Brannas 1995).

Glacier Flats Creek is a clear, shallow, spring-fed stream which is warmer during the embryonic development period than Nikolai Creek; consequently, the spawn run begins later (Woody 1998). Glacier Flats embryos also incubate at a slower rate than Nikolai Creek embryos (Woody 1998). If Nikolai Creek fish strayed into the warmer Glacier Flats in mid-July, their progeny would develop, hatch, and emerge to feed in a still frozen rearing lake (Woody 1998), with limited food resources due to lack of light and cold temperatures (Wetzel 1983). Conversely, if fish from Glacier Flats strayed into Nikolai in late August, their progeny would experience colder temperatures, emerge later (Woody 1998), therefore risking a higher probability of predation (Godin 1981; Brannas 1995), and miss opportunity for growth in the short lake growing season. Spawning success of strays into either system is most likely dependent on timing of gamete deposition with a thermal regime conducive to embryonic fitness requirements.

Sufficient gene flow occurs between the early August sample groups (NII and GI) to homogenize microsatellite allele frequencies, but phenotypically, Nikolai fish are significantly larger than the Glacier Flats fish (Figure 2.2). Assuming the two populations share similar lake and oceanic habitats, the differences are likely due to differential selection in natal habitats. Researchers have observed a positive correlation between fish size and age at maturity, which has a genetic component (Hankin et al. 1993; Heath et al. 1994), and natal tributary size (Beacham and Murray 1987; Rogers 1987; Blair et al. 1993; Woody 1998), suggesting a fitness advantage of larger size in larger systems and vice versa. Nikolai Creek is a larger system than

Glacier Flats and Nikolai fish are older and larger at the same age than Glacier Flats fish (Woody 1998).

The within-stream size difference between Nikolai I fish (larger) and Nikolai II fish (smaller) may be due to the higher rate of gene flow between the Nikolai II fish and the smaller Glacier I fish (Figure 2.3). Because allele frequencies are identical between the Nikolai II and Glacier I (Figure 2.3) fish, and because Glacier Flats fish are smaller than Nikolai fish, it is likely that some of the small fish observed in the latter portion of the Nikolai run are successfully reproducing strays from Glacier Flats Creek. Because there is an apparent fitness advantage of large size in large tributaries, selection may be preventing homogenization of phenotypes, which would explain the intermediate size of Nikolai II fish.

The difference in Nikolai I and II body size may also be influenced by differences in habitat use. Nikolai Creek is comprised of several distinct channels and salmon that spawned in the first 7 km of Nikolai Creek were larger on average and spawned in deeper, faster water than salmon that spawned in a shallower upper tributary (Woody 1998). A significant relationship between fish depth and spawning site water depth was also observed. Therefore, the phenotypic differences between the early and late run fish into Nikolai may also be related to differences in spawning habitat use; early run fish may be using the deeper, faster waters for spawning, while smaller fish that use the upper watershed may enter the stream later.

Conclusions

Salmon populations are currently in a state of serious decline. Conservation and management efforts, although well intentioned, may not be accurately characterizing differences among populations. Molecular genetic markers are frequently used to characterize populations; however, sampling regimes rarely take into account ecological traits which might influence genetic variation. This study indicates that spawn run time, an important adaptive trait, may influence genetic structure; therefore, research results on a given population may be influenced by limited temporal scope in sampling regimes. Accurate characterization of salmon populations should include information on run timing, sampling at different points in the run, and collection of basic phenotypic data. The increasing reliance upon molecular genetic information to characterize populations and the rapid decline of salmon populations makes consideration of ecologically significant characters critical.

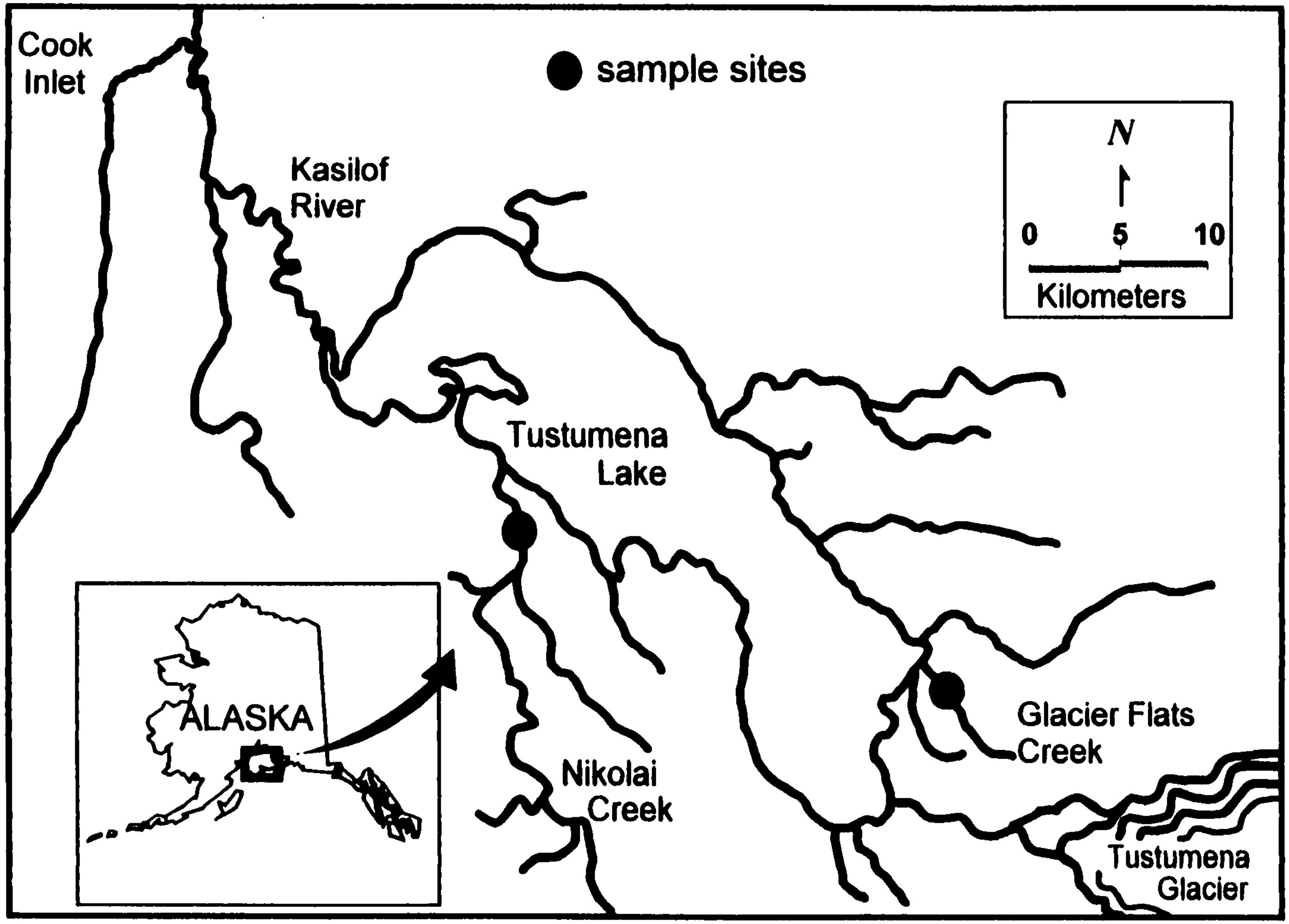


Figure 2.1. Sample sites (weir) for genotypic and phenotypic characterization of Nikolai and Glacier Flats creeks sockeye salmon populations, Tustumena Lake, Alaska, 1994.

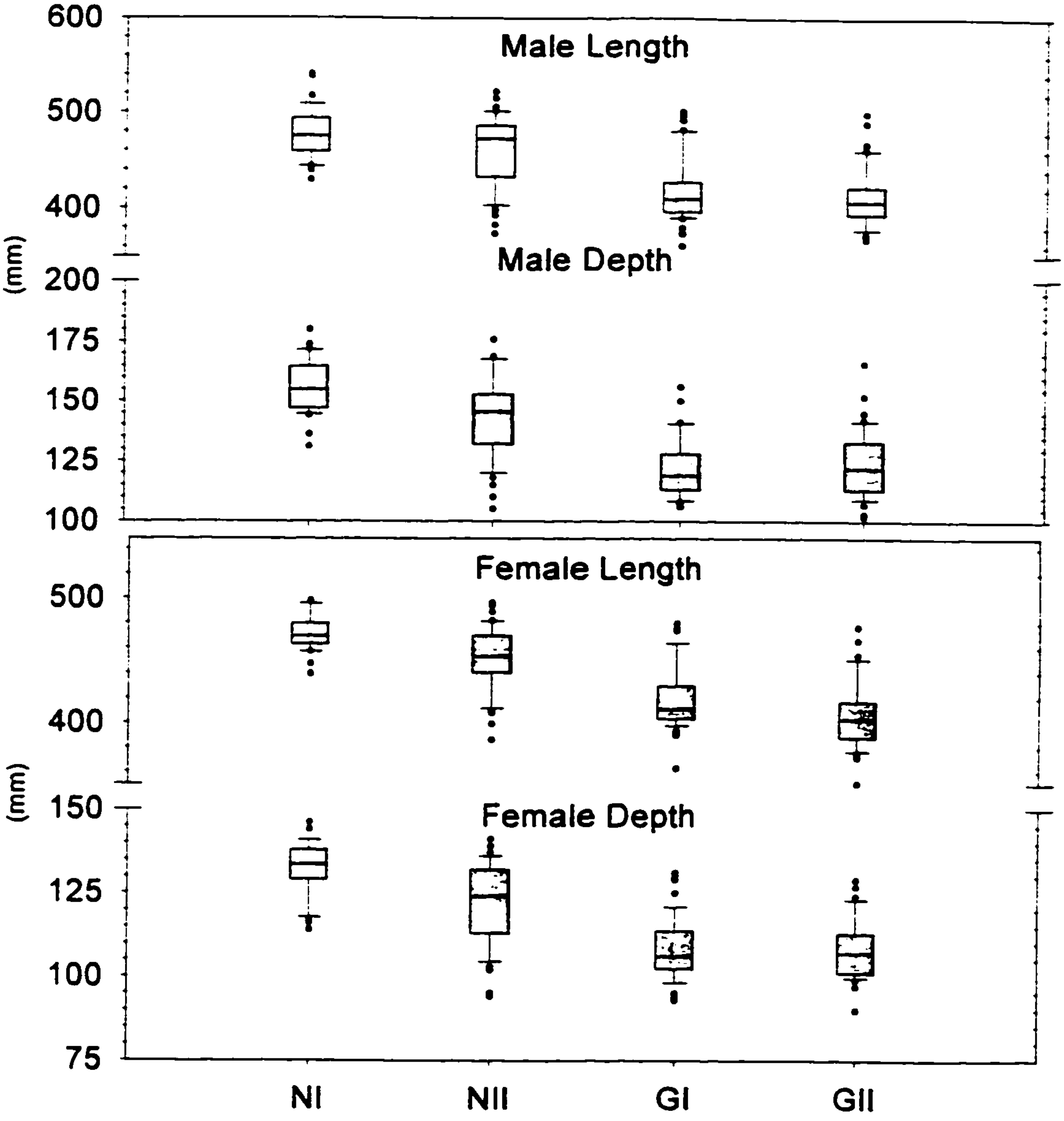
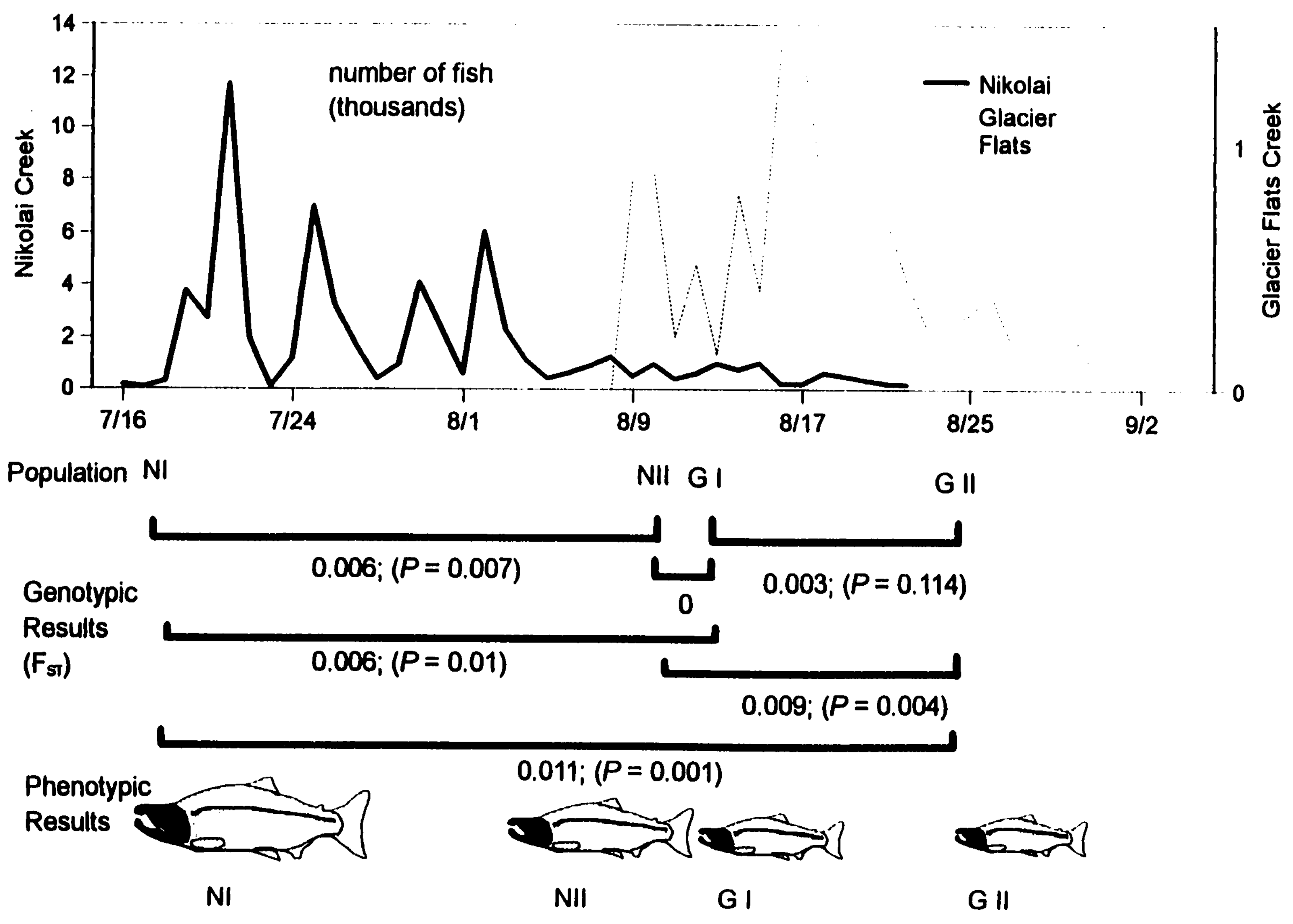


Figure 2.2. Box plots of length and depth distributions of sockeye salmon sampled from Nikolai and Glacier Flats creeks, Tustumena Lake watershed, Alaska, 1994. The line in the center of each box indicates the median value, shaded portions indicate the interquartile range (from the 25th to 75th percentiles). Whiskers extend to the minimum and maximum observed values, unless such values exceed 1.5 * the interquartile range (Cleveland 1993). In this case, these more extreme observations are marked by dots. Sample populations are as follow: NI = early Nikolai run; NII = Nikolai late run; GI = Glacier early run; GII = Glacier late run.

Figure 2.3. Sockeye salmon stream entry patterns in thousands of fish, sampling dates, F_{ST} values, and relative size of sockeye salmon spawning in Nikolai and Glacier Flats creeks, Tustumena Lake watershed, Alaska, 1994. Sample dates are coded as: NI = Nikolai, July 16-19; NII = Nikolai August 9-10; GI = Glacier Flats sampling dates 10-11; GII= Glacier sampling dates 24 - 25 August 1994. Genotypic results are F_{ST} and corresponding P values, lines indicate comparison made. Phenotypic differences among sample groups indicated by size (not to scale) of fish schematic.



14
12
10
8
6
4
2
0
Nikolai Creek
number of fish
(thousands)
Nikolai
Glacier
Flats
1
0
Glacier Flats Creek
7/16
7/24
8/1
8/9
8/17
8/25
9/2
Population NI
NII G I
G II
0.006; (P = 0.007)
0
0.003; (P = 0.114)
Genotypic
Results
(F_{ST})
0.006; (P = 0.01)
0.009; (P = 0.004)
0.011; (P = 0.001)
Phenotypic
Results
NI
NII
G I
G II

Table 2.1. Hardy-Weinberg probability-test results for temporal groups of Tustumena Lake sockeye salmon originating from Nikolai or Glacier Flats creeks. Sampled run components are: Nikolai I = July 16-19 and II = August 9-10; Glacier I = August 10 -11 and II= 24 - 25 August 1994. H_E = expected heterozygosity; (*P*) = probability value that the subgroup is in Hardy Weinburg equilibrium.

Population	Run time	Sex	n		Oneμ1	Oneμ11	Oneμ14	Oneμ12	Oneμ8	Ssa85	Average H_E [b]
Nikolai	I	♀	53	H_E	0.21	0.51	0.64	0.81	0.68	0.78	0.598
				(*P*)	(0.504)	(0.951)	(0.017)	(0.015)	(0.991)	(0.014)	
	I	♂	52	H_E	0.21	0.64	0.67	0.85	0.73	0.77	0.64
				(*P*)	(1)	(0.194)	(0.001)[a]	(0.609)	(0.342)	(0.086)	
	II	♀	51	H_E	0.13	0.51	0.80	0.77	0.60	0.53	0.508
				(*P*)	(1)	(0.054)	(0.069)	(0.472)	(0.648)	(0.087)	
	II	♂	49	H_E	0.26	0.50	0.69	0.78	0.68	0.72	0.588
				(*P*)	(0.098)	(0.686)	(0.098)	(0.947)	(0.576)	(0.374)	
Glacier	I	♀	48	H_E	0.15	0.41	0.81	0.80	0.67	0.66	0.538
				(*P*)	(0.023)	(1)	(0.000)[a]	(0.615)	(0.013)	(0.836)	
	I	♂	43	H_E	0.34	0.53	0.79	0.81	0.74	0.70	0.62
				(*P*)	(0.211)	(0.495)	(0.008)[a]	(0.279)	(0.929)	(0.002)[a]	
	II	♀	49	H_E	0.31	0.37	0.80	0.79	0.61	0.67	0.55
				(*P*)	(0.491)	(1)	(0.000)[a]	(0.327)	(0.459)	(0.558)	
	II	♂	46	H_E	0.30	0.50	0.77	0.80	0.67	0.57	0.568
				(*P*)	(0.465)	(0.139)	(0.020)	(0.024)	(0.025)	(0.518)	

[a] Indicates significant deviation from expected equilibrium proportions after application of a sequential Bonferroni, initial $\alpha=0.008$.

[b] Average heterozygosity does not include data from locus Oneμ14.

Table 2.2. Allelic differentiation among temporally distinct sockeye salmon spawning groups from Glacier Flats and Nikolai creeks, Tustumena Lake, Alaska, 1994. Numbers indicate sampling dates: Nikolai I = 16-18 July; Nikolai II = 9-10 August; Glacier I = 9-12 August; Glacier II = 10-11 August 1994. Significant genic differences are indicated by P-values determined using Fishers exact test computed using a modified Markov Chain method (SE < 0.01); Bonferroni adjusted initial $\alpha = 0.01$.

Pairwise Comparison	Oneμ1	Oneμ11	Oneμ2	Oneμ8	Ssa85
Glacier I x Glacier II	--	--	0.000	--	--
Nikolai I x Nikolai II	--	--	--	--	--
Glacier I x Nikolai I	--	--	0.008	--	0.001
Glacier I x Nikolai II	--	--	--	--	--
Glacier II x Nikolai I	0.003	--	--	--	0.000
Glacier II x Nikolai II	--	--	0.000	--	--
Glacier x Nikolai	--	--	--	--	0.000

Chapter III:

Early Ecology of Sockeye Salmon Fry Emigrating from Two Tributaries to Tustumena Lake, Alaska

Introduction

Sockeye salmon (*Oncorhynchus nerka*) generally return to lakes at maturity and then segregate to natal tributaries. Females select a nest site, a mate, and then bury their eggs in a series of nests, or redd. Females defend the nest site from superimposition by other spawning females until they die or are too weak to maintain position in the stream. Embryos develop over winter and hatch as alevins after a specific number of thermal units have been realized (Beacham and Murray 1987; Murray and McPhail 1988). Alevins remain in the gravel absorbing their large yolk sacs until spring or early summer, when they emerge as fry and emigrate to the rearing lake (Bams 1969). A genetic component has been documented for the time at which salmonids spawn (Bams 1976; Siitonen and Gall 1989), the number and size of eggs (Beacham and Murray 1987; Bromage et al.1990), the number of thermal units embryos require to hatch and emerge (Beacham and Murray 1989), and the direction of their emigration (up or downstream; Raleigh 1967). These characters are thought to be part of an intricate series of adaptations which ensure that some fry reach their rearing lake at a time appropriate for their survival (Bams 1969; Godin 1981; Brannon 1987).

Mortality while embryos are incubating is high (~ 90%) and predators (Foote and Brown 1998), high discharge (Holtby and Healy 1986; Montgomery et al. 1996), poor water quality caused by intrusion of sediments into nest sites (McNeil 1968; see review by Chapman 1988; Rubin 1998), and extremely cold temperatures (McNeil 1966; Beacham and Murray 1987; Murray and McPhail 1987) all contribute to embryonic mortality during the incubation phase.

The time during which fry emerge from gravels and emigrate to the rearing lake is also a highly vulnerable period. Sockeye salmon fry first emerge at night (Godin 1981), gradually fill their gas bladder at the stream surface (Bams 1969) and once they attain neutral buoyancy, they emigrate to a lake, frequently *en masse* (Beacham and Star 1982; Holtby et al. 1989). Fry negotiating inlet tributaries emigrate at night, while those migrating upstream from outlet spawning areas migrate during the day (Raleigh 1967). High predation rates have been observed for emigrants, with predators consuming from 59% to 85% of fry emigrating from tributaries (Foerster 1968; Ruggerone and Rogers 1992). Aggregation behavior and nocturnal movements are considered anti-predator strategies as synchronous emigration decreases the individual's probability of predation (Brännäs 1995) and visual acuity of piscivores diminishes with decreasing light intensity (Ginetz and Larkin 1975). The ability of fry to avoid predation during emigration also depends upon their size and stage of development. Larger fry are better able to avoid predators (Parker 1971; Taylor and McPhail 1985), while fry emigrating with large yolk reserves are subject to higher predation rates (Fresh and Schroder 1987).

Tustumena Lake is located on the Kenai Peninsula of Alaska and contributes about 20% to the Cook Inlet commercial sockeye salmon catch. Numerous studies regarding sockeye salmon production relative to limnological conditions in the lake have been conducted (see summary by Kyle 1992). Less well understood are the environmental factors which affect the early ecology and survival of sockeye salmon fry within lake tributaries. Over 60% of the sockeye salmon returning to the Tustumena Lake watershed spawn in clear-water tributaries (Burger et al. 1995), and significant phenotypic differences in heritable traits have been observed among adults spawning in different tributaries (Woody 1998). For example, Nikolai Creek is a diverse, large, variable discharge system and returning adults are significantly older, larger at the same age, and produce more and larger eggs than fish from a smaller, nearby spring-fed system, Glacier Flats Creek (Kyle 1992; Woody 1998). Other researchers have observed a similar pattern of large size in large watersheds (Beacham and Murray 1987; Rogers 1987) and it is thought these traits are adaptive. One potential evolutionary advantage of being larger in a large watershed has been attributed to the fact that larger females can bury their eggs deeper than smaller fish (van den Berghe and Gross 1984); therefore, embryonic mortality due to scour during high discharge would be less for deep versus shallow nests (Montgomery et al. 1996). Large eggs generally produce large fry (Beacham and Murray 1986) which have higher sustained and burst swimming ability than small fish (Brett 1965; Taylor and McPhail 1985). Superior swimming ability would likely facilitate emigration through a large, high discharge system and would be an evolutionary advantage to avoid predators (Taylor and McPhail 1985).

The purpose of this study was to compare the early life history and corresponding environmental conditions experienced by two sockeye salmon populations in an effort to understand factors contributing to the differences observed in adult size, egg size, and fecundity. To do so I (1) estimated egg to fry survival for both populations, (2) examined factors contributing to mortality during early life history, (3) evaluated fry emigration patterns relative to adult run time, spring discharge, thermal regime, and daylight, (4) compared emigrant fry size and condition between populations, and (5) determined the relative abundance, species composition, and size of predators in the first 0.5 km of each stream outlet.

Study Site

Tustumena Lake is the fourth largest lake in Alaska with an estimated watershed of 1,376 km^2 which drains into Cook Inlet via the Kasilof River (Figure 3.1). The lake is 40 km long, 8 km wide, has a mean depth of 124 m and a maximum depth of 320 m (Kyle 1992). It is one of the most turbid salmon systems in the world (40-57 NTUs) due to glacial runoff; consequently, less than 1% of the lake volume is in the euphotic zone (Koenings and Burkett 1987). All five species of eastern Pacific salmon spawn within the system; however, sockeye salmon predominate with escapements averaging 200,000 fish annually (Ken Tarbox, personal communication, Alaska Department of Fish and Game, Commercial Fisheries Division, Soldotna, Alaska). Sockeye salmon primarily spawn in two lake shore regions (Burger et al.1995) and five clear-water tributaries. Two clear-water streams were selected for this study, Glacier Flats and Nikolai creeks (Figure 3.1).

Glacier Flats Creek is predominantly fed from upwelling groundwater, does not freeze completely in the winter, drains an indeterminate area, and is of variable length (3-4 km) depending on groundwater recharge (Kyle 1992). Nikolai Creek drains a watershed of 142 km^2, is about 80 linear km long, water regimes are dominated by precipitation events, and thermal regimes are determined by ambient temperatures. Nikolai Creek is a more extreme system relative to thermal and discharge regimes. During the 1994-1995 water year (October 1994 to1995) Nikolai temperatures averaged 3.8°C (SE = 0.23) and discharge averaged 0.99 m^3/s (SE = 0.068), whereas Glacier averaged 4.0°C (SD = 0.15) and 0.64 m^3/s (SE = 0.037) (Figure 3.2).

Methods

Sockeye salmon fry emigration in each stream was monitored using a fyke net installed approximately 0.5 km from each stream outlet. A trap was installed 13 April 1995 in Glacier Flats Creek. The trap fished 1.14 m of a 9.1 m wide stream section near the stream center. The Nikolai Creek trap was installed near the right stream bank (looking downstream) the day after ice break-up began (24 April), and fished 0.8 m of an 8.4 m wide stream section. Both traps were fished daily and continuously from 2200 to 0500 hours. Traps were checked hourly, at which time fry were removed, counted, and released.

Emigrant fry abundance was estimated using a simple stratified design for mark-recapture (M-R) data (Carlson et al. 1998). A known number of fry captured in the fyke trap were dyed in a solution of Bismark Brown (0.5 to1 g dye/ 7 L water) for about 3 h, held overnight in fresh water to account for handling mortality, then released in low velocity water (0.0-0.3 m/s) about 0.05 km upstream at 2400 to 0100 h. Two to three mark-recapture efforts were conducted weekly, or when traps were modified. The Glacier Flats trap was modified from 14-16 May to prevent debris clogging, and the Nikolai trap was moved on 21 May in an attempt to increase trapping efficiency. Monitoring of traps was discontinued when the number of fry captured in an evening averaged fewer than 100 fry/night over a 3-d period.

Sampling efforts for each stream were divided into strata which corresponded with a 5 to 7-d sample period or a trap modification period. The stratum and total fry out-migration estimates were based on methodologies developed by Carlson et al. (1998) for mark-recapture population estimates of salmon smolt. The following notation was used in the estimation methods:

h: stratum index (capture period and a corresponding M-R trial)

L: number of strata or periods ($h = 1, 2, \ldots, L$)

M_h; number of marked fry released in h

M: total number of marked fry released ($= \Sigma M_h$)

m_h: number of marked fry recovered in stratum h

u_h: number of unmarked fry captured in stratum h

n_h: total number of fry captured in stratum $h (= m_h + u_h)$

U_h: total population size of fry in stratum h, excluding marked releases and minus observed mortality

N_h: total population size of fry in stratum h, including marked releases $(=M_h + U_h)$

U: total population size of fry, excluding marked releases $(= \Sigma\ U_h)$

N: total population size of fry, including marked releases $(= \Sigma\ N_h)$

p_h: population proportion of marked fry in stratum h $(=M_h/N_h)$

e_h: fry capture probability (trap efficiency) in stratum h $(= n_h/N_h)$

The population size ($\hat{U}_h$) of each stratum (h) was estimated using an approximately unbiased Peterson estimate (Seber 1982; Carlson et al.1998) of

$$\hat{U}_h = \hat{N}_h - M_h = \frac{u_h(M_h + 1)}{m_h + 1}$$

and an approximately unbiased variance estimate of

$$v(\hat{U}_h) = \frac{(M_h + 1)(u_h + m_h + 1)(M_h - m_h)u_h}{(m_h + 1)^2(m_h + 2)}.$$

The total fry abundance estimate was therefore

$$\hat{U} = \sum_{h=1}^{L} \hat{U}_h ,$$

with a variance estimate of

$$v(\hat{U}) = \sum_{h=1}^{L} v(\hat{U}_h).$$

The 95% confidence intervals (CI) were estimated based on asymptotic approximations (Seber 1982; Krebs 1989; Carlson et al. 1998) with the estimator of each strata

$$\hat{U}_h \pm 1.96\sqrt{v(\hat{U}_h)}$$

and for the total population estimate

$$\hat{U} \pm 1.96\sqrt{v(\hat{U})}\ .$$

Short-term mortality due to marking and handling was determined by marking a known quantity of fish and then transferring them to freshwater for observation; after 24 h, the number of dead fry were counted. Mortality estimates were made once or twice weekly. Estimated survival for each stratum (h) was

$$\hat{S}h = \frac{a_h}{A_h},$$

where $\hat{S}h$ is the estimated survival, a_h is the number surviving after the 24-h holding period, and A_h is the number initially marked.

Egg to fry survival was estimated by calculating total egg production for each stream in 1994 (number of females × mean number of eggs/female; Woody 1998), then dividing the total number of fry estimated to have emigrated from each system by the total number of eggs.

Fry emigration patterns were compared to 1994 adult escapement patterns to determine if peak out-migration was separated by a month, as the peak adult run times were in 1994, or if emergence was synchronous. Correlation analysis was used to examine the relationship between fry emigration pattern and average daily discharge. Emigration patterns were monitored for 24 h on four occasions to estimate percent fry emigrating during daylight.

Size and condition of fry from the two streams were determined by anesthetizing 30 fry every 3 d in a lethal dose of MS222, then preserving fish directly in 10% buffered formalin. Samples were processed in the laboratory about 2 mos after preservation. Preserved fry were rinsed in fresh water, blotted dry, weighed individually on an analytical balance (0.01 mg), and measured (total length; 0.1 mm) using a dissecting microscope combined with a microcomputer-based digital image analysis system and Optimus™ image analysis software (Bioscan, Inc., Seattle, WA). Condition factor for each fish was calculated using $K = 100 \times W/L^3$ (Wootton 1990) with K = condition factor, W = weight, and L = length. The condition factor provides an index of well-being of a fish with higher K values indicating which fish are heavier for their length. Weight, length, and condition factor were compared between populations using a student's t-test (with pooled sample variance estimate, when an F-test for homogeneity of variance supported such an assumption). Within-stream comparisons were made among early, peak, and late emerging fry using an ANOVA and post-hoc Tukey "honestly significant difference test" (Zar 1984).

The size of yolk sac attached to emigrating fry and the frequency of occurrence were examined. Yolk sacs were removed from fry collected at early, peak, and late emigration times. Each sac was weighed and categorized as: no yolk sac; small, 4.0 to < 10.0 mg; medium, 10.0 to < 20.0; large, ≥ 20.0 mg. A chi-square test of homogenity was used to compare frequency of occurrence between populations.

The relative abundance and size of resident fishes within the first 0.05 km of each stream was estimated using minnow traps. Five traps were baited with commercially preserved salmon eggs in perforated film canisters and set for 24 h in each stream on 23, 26, 27, and 28 May. Traps were checked at the end of each 24-h period and any captured fish were anesthetized, identified, measured (total length, mm), and released. Traps were set in a new location for each sampling period in depths ranging from 0.1 to 1 m. Catch per unit effort (CPUE), mean CPUE (catch/h/set), and standard error were determined to provide information on relative abundance. Mean length (total, mm) and standard error were calculated for each species observed and compared between streams.

Results

Fry Estimates

The Glacier Flats fry trap was monitored a total of 52 d. Trap capture efficiency in Glacier Flats generally ranged from 10 to 15% over the nine mark-recapture temporal strata (Table 3.1). Lower trap efficiencies occurred from 14-16 May (efficiency = 4%) when the trap mouth was reduced due to debris accumulation, and from 30 May to 9 June (7%), which was the end of the out-migration period. The Nikolai Creek trap was monitored a total of 57 days. High discharge, bed-load movement, debris, and ice flows dictated that the Nikolai trap be situated in a protected area which reduced capture efficiency. Capture efficiencies in Nikolai ranged from 1 to 8%, which resulted in higher variance and wider confidence intervals around individual stratum and total population estimates (Table 3.1). An estimated 1,356,285 (± 148,469) sockeye salmon fry emigrated from Glacier Flats Creek to Tustumena Lake, and 3,731,988 (± 736,386) emigrated from Nikolai Creek. Egg to fry survival rates were estimated at 9.5% for Glacier Flats and 2.8% for Nikolai (Table 3.2).

Handling mortality was generally low. The initial dye test in Glacier Flats Creek resulted in a mortality of 11.5% of the total fry marked; however, after experimenting with dye concentrations and exposure time, mortality was reduced substantially. Survival ranged from 97.7 to 100% and averaged 98.9% in Glacier Flats, and ranged from 93 to 100% and averaged 98% in Nikolai Creek.

Emigration Patterns

Time of peak escapement of adults into each stream (1994) differed by about one month. However, peak emigration of their progeny occurred in the same week, 6-13 May 1995 (Figure 3.3). The majority of fry from both populations emigrated during darkness. The percent of the total emigrating during daylight over a 24-h period ranged from < 1% to 5% and averaged 1% in Glacier Flats Creek, while in Nikolai ranges were 1% to 19% and averaged 5%. The highest number of diurnal emigrants in Glacier Flats were observed in June, the end of the emigration period, while the Nikolai high (19%) occurred during the first spring freshet. The number of fry emigrating was significantly correlated with discharge in Nikolai ($\rho = 0.71$), but not in Glacier Flats ($\rho = 0.24$).

Size and Condition of Emigrants

Glacier Flats fry weighed less (average 111 mg vs. 117 mg; $P < 0.001$) and were not as long (average 26.8 vs. 27.3 mm; $P < 0.001$) as Nikolai Creek fry, although Glacier Flats fry were significantly heavier for their length than Nikolai Creek fry (average condition factor of 0.580 vs. 0.570; $P < 0.001$; Table 3.3). Within-stream comparisons of the early, peak, and late portions of each population indicated no significant difference in Glacier Flats fry weights or lengths, although the early Glacier Flats migrants had a significantly higher condition factor than later emigrating fry (Table 3.3). Nikolai Creek fry exhibited a different pattern as early emigrants weighed significantly less (108 mg; $P < 0.001$) and were not as long (26.2 cm; $P < 0.001$) on average as the peak and late out-migrants (Table 3.3). However, the condition factor of Nikolai Creek fry did not differ among temporal components ($P = 0.17$).

The highest frequency of Nikolai fry with large yolk sacs attached were observed during 24-28 April, which corresponded to the period of ice break-up and the first spring freshet (early columns in Figure 3.4). Comparison of early, peak, and late emigration components indicated a higher frequency of fry with large yolk sacs observed in Nikolai Creek (chi-square test of homogenity, $P < 0.001$) compared to the majority of Glacier Flats fry which had fully absorbed their yolk sacs prior to emigration (Figure 3.4).

Resident Fish

The relative abundance and size of resident fishes within the first 0.5 km of each stream mouth differed between streams. More and larger resident fish were captured per unit of effort in Nikolai Creek compared to Glacier Flats Creek (Table 3.4). A total of 309 resident fish were captured in Nikolai Creek for 477 h of effort, while 10 were captured in Glacier Flats Creek for 480 h. The Nikolai relative abundance is an underestimate as traps were so full of fish when checked after the initial 24-h set, no more fish could have fit inside. All four species captured in Nikolai Creek are known predators of sockeye salmon fry: *Salvelinus malma* (Roos 1960), *Cottus* spp. (Kline et al. 1993; Foote and Brown 1998), *O. mykiss* (Ginetz and Larkin 1976), and *O. kisutch* (Ruggerone and Rogers 1992). A similar species composition was observed in Glacier Flats Creek, although no cottids were observed and one three-spine stickleback (*Gasterosteus aculeatus*) was captured.

Discussion

The highest mortalities experienced by Pacific salmon (*Oncorhynchus* spp.) occur during early life history stages and frequently exceed 90% (Hartman et al. 1962; Foerster 1968). Mortality during incubation is primarily due to abiotic factors such as extreme temperatures (Murray and McPhail 1988; Beacham and Murray 1990), scour in decreased water quality (Chapman 1988). After fry emerge from gravels, they generally emigrate to rearing areas, and being naïve, often suffer high mortality due to predation (Roos 1960; Foerster 1968; Fresh and Schroder 1987). The lower estimated egg to fry survival observed in Nikolai Creek compared to Glacier Flats Creek is likely due, in part, to the more extreme hydrologic regimes in Nikolai Creek and the greater abundance of predators.

Incubation temperature affects development rates, growth, and survival of salmonid embryos and alevins. Incubation studies have shown embryo survival to emergence is highest for sockeye salmon incubated at 8°C (79% survival) with survival declining toward both temperature extremes (38% at 2°C) (Murray and McPhail 1988). Sockeye salmon embryos incubated between 6 to10°C have shown > 90% survival, while only 70% survival occurred at temperatures below 4°C (Combs 1965); only 50% survival has been observed in embryos incubated at 1°C (Beacham and Murray 1990). Intra-gravel temperatures at the Nikolai monitoring site averaged 0.3°C between 6 October 1996 and 30 April 1995 (Figure 3.2) with 186 consecutive d of temperatures less than 0.5°C, of which 44 d were at or slightly below 0°C, indicating ice formation within gravel interstices. Glacier Flats temperatures during the same period were warmer, averaging 2.2°C with fewer than 16 d (total) of temperatures below 0.5°C (Figure 3.2) and no recorded zero or subzero temperatures. It is reasonable to conclude the lower egg to fry survival in Nikolai Creek is partly attributable to extremely cold temperatures.

High discharge events during the incubation period can decrease embryo survival through scouring which can crush or dislodge developing embryos or alevins (McNeil 1966; Lisle 1989); a high positive correlation has been found between peak seasonal discharge and salmonid fry mortality (Holtby and Healy 1986). Salmon have apparently evolved mechanisms to minimize mortality due to scour. For example, some researchers have observed that large salmon are capable of digging deeper nests than smaller fish (van den Berghe and Gross 1984), and larger, older fish generally predominate in larger rivers (Rogers 1987), including Nikolai Creek (Woody 1998). Eggs buried below the depth of scour are protected from mechanical dislodgment and crushing. Chum salmon egg burial depths, scour depths, and potential egg loss for various discharge rates in Kennedy Creek, Washington, have been shown to be associated (Montgomery et al. 1996). In that system, salmon buried their eggs at an average depth greater than the average scour depth at bank-full discharge, and greater than average flood events could cause significant increases in embryo mortality.

While scour does not occur in the spring-fed Glacier Flats Creek, it is an important force in Nikolai Creek. Fall and spring freshets regularly occur during the incubation period (Figure 3.2, Table 3.5), and during water year 1995 the creek exceeded bank-full (≈ 4 cms) over 10 consecutive d during the early and peak spring fry emigration. That early high flows and scour disturbed still developing alevins is seen in the high frequency of large yolk sacs observed on Nikolai fry compared to Glacier Flats fry (Figure 3.4) and the higher percent of fry emigrating during daylight (16%). It does not make evolutionarily sense for fry to emerge early or emigrate during daylight with a large yolk sac. The presence of a large yolk reduces the swimming ability of fry (Bams 1967) and increases their vulnerability to predation (Fresh and Schroder 1987), as does early and late emergence relative to peak emergence (Brännäs 1995). Daylight emigration can increase susceptibility to predation as most piscivores locate their prey visually, and predation has been shown to be inversely related to light intensity (Ginetz and Larkin 1976). Recall the high relative abundance of piscivores observed in the first 0.5 km of Nikolai Creek (Table 3.4). The Nikolai Creek early emigrants were likely from nests which were not deep enough to escape scour during ice break-up, or emerged early due to diminishing water quality in the gravel. The fact that no fry with large yolk sacs were observed at peak emigration (Figure 3.4), which, relative to predation, is the more evolutionarily stable emergence time (Brännäs 1995), indicates that the early emerging fry were not volitional.

Spring discharge increases may be an important trigger to synchronize fry emergence in Nikolai Creek. The high correlation of fry numbers with discharge has been observed in other salmonid systems (Whitler 1952; Holtby et al. 1989). Asynchronous emergence relative to peak numbers can increase the risk of predation (Brännäs 1995) and fry may be more vulnerable to predation in streams versus lakes (Roos 1960), as well as at low water velocities and turbidities (Ginetz and Larkin 1976; Gregory 1993). The high correlation between the number of fry emigrating and discharge observed in Nikolai Creek may be adaptive given the greater abundance of predators. Emigrating at high discharge would allow more rapid negotiation of the clear-water stream habitat to the relative safety of the very turbid Tustumena Lake, and some cover might be afforded by increased turbidity levels at high flows.

Size and Condition of Emigrant Fry

Nikolai Creek fry were longer and heavier at emergence than Glacier Flats fry (Table 3.3). This is attributed to the larger egg size of Nikolai Creek females (Table 3.2), as larger eggs produce larger fry (Beacham and Murray 1986). Although Nikolai fry were larger, Glacier Flats fry had a higher condition factor (Table 3.3). This may be attributable to the extended, low incubation regime in Nikolai Creek which decreases yolk to tissue conversion efficiency during development (Beacham and Murray 1989).

Resident Species

Predation can be an important source of mortality during egg deposition and during emigration of juvenile sockeye salmon to the rearing lake. Foote and Brown (1998) determined sculpins (*Cottus aleuticus* and *C. cognatus*) actively moved to sockeye salmon spawning sites prior to initiation of spawning, reached densities of greater than 100 sculpins per nest, and consumed up to 15% of the sockeye salmon eggs on certain spawning beaches with gravel and cobble substrate. Foerster (1968) estimated mortality of emigrating sockeye salmon fry from Scully Creek, B.C., by Dolly Varden char (*Salvelinus malma*), cutthroat trout (*O. clarki*), yearling coho (*O. kisutch*), and sculpins (*Cottus* spp.) at 64 to 85% of the total fry available to them.

Predation rates on salmonid fry are affected by abundance of both predators and prey (Fresh and Schroder 1987), water clarity, light, water velocity, turbidity (Ginetz and Larkin 1976; Gregory 1993), size and developmental stage of fry (Parker 1971; Fresh and Schroder 1987), and emergence timing relative to peak emergence (Brännäs 1995). With the exception of one stickleback observed in Glacier Flats Creek (Table 3.4), all the resident fish captured are known predators of sockeye salmon fry.

Annual spawning runs and spring fry emigration from tributaries to Tustumena Lake represent a predictable, high quality food resource to resident piscivores. The higher relative abundance and larger size of predators in Nikolai compared to Glacier Flats is not surprising considering 1994 adult run characteristics. The 1994 spawning escapement into Nikolai Creek was six times larger than the Glacier Flats run (63,723 vs. 10,374); Nikolai females were more fecund (mean = 4,103 eggs/female vs. 2,970) and had larger eggs compared to Glacier Flats females (Woody 1998). Nikolai Creek represents a more significant food resource, apparently attracts more and larger resident piscivores, and as a result, predation may be considered a more significant source of mortality for Nikolai Creek fry than for Glacier Flats fry.

Conclusions

Comparison of the early ecology of sockeye salmon originating from a small, spring-fed stream versus a larger, precipitation-fed system indicated higher egg to fry survival in the spring system. It is hypothesized that the difference in survival is due, in part, to the less extreme hydrologic regime and the lower relative abundance of predators in the spring-fed system.

The potential evolutionary advantages of being an older, larger female producing more and larger eggs in the larger, precipitation-fed Nikolai Creek are: (1) larger females dig deeper nests, which would increase the probability of some embryos surviving annual high discharge events in Nikolai Creek, (2) higher fecundity would increase the probability of some fry surviving to emergence given the Nikolai characteristics of scour and extreme cold during the incubation period, and (3) larger eggs produced larger fry in Nikolai Creek, which would be an advantage in negotiating the high velocity system and in avoiding the more numerous and larger predators in that system.

The potential evolutionary advantage for both populations to emerge at or just after ice break-up in the lake is related to the short growing season in south-central Alaska. Tustumena Lake is cold, turbid, and relatively unproductive. Entering the lake as soon as primary production begins to increase in spring would allow fry the longest growing season possible. Adult spawn timing appears coordinated to this emergence period, as peak spawning of adults in the colder Nikolai Creek occurred a month earlier than peak spawning in the warmer Glacier Flats Creek. Because embryonic development and emergence are a function of temperature, progeny in both streams emerged at a similar time.

Variation among populations in heritable life history traits such as run time, age and size at maturity, fecundity, egg and progeny size indicate variation in fitness (Stearns 1992). It is unlikely that in Nikolai Creek the survival rate of progeny originating from smaller, less fecund, late spawning females with smaller eggs would be higher than that for the significantly older and larger fish which dominate the system. Research to identify patterns of adaptation (e.g. large fish in large watersheds) and their correlates (high discharge, predators, temperature) will facilitate salmonid rehabilitation efforts through the matching of phenotypes to environments.

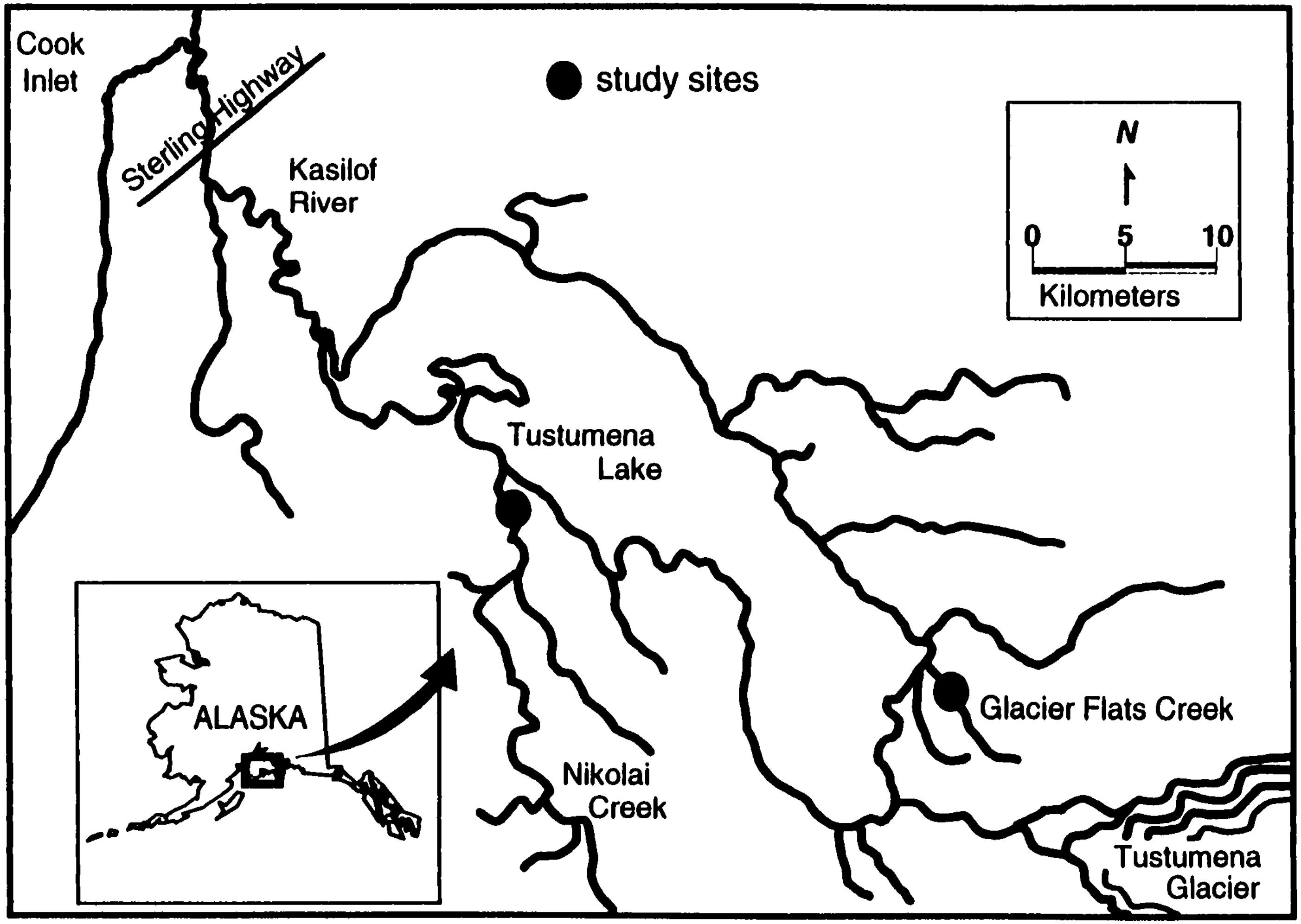


Figure 3.1. Sample sites where fyke nets were established to monitor sockeye salmon fry outmigration, Tustumena Lake watershed, Alaska, 1995.

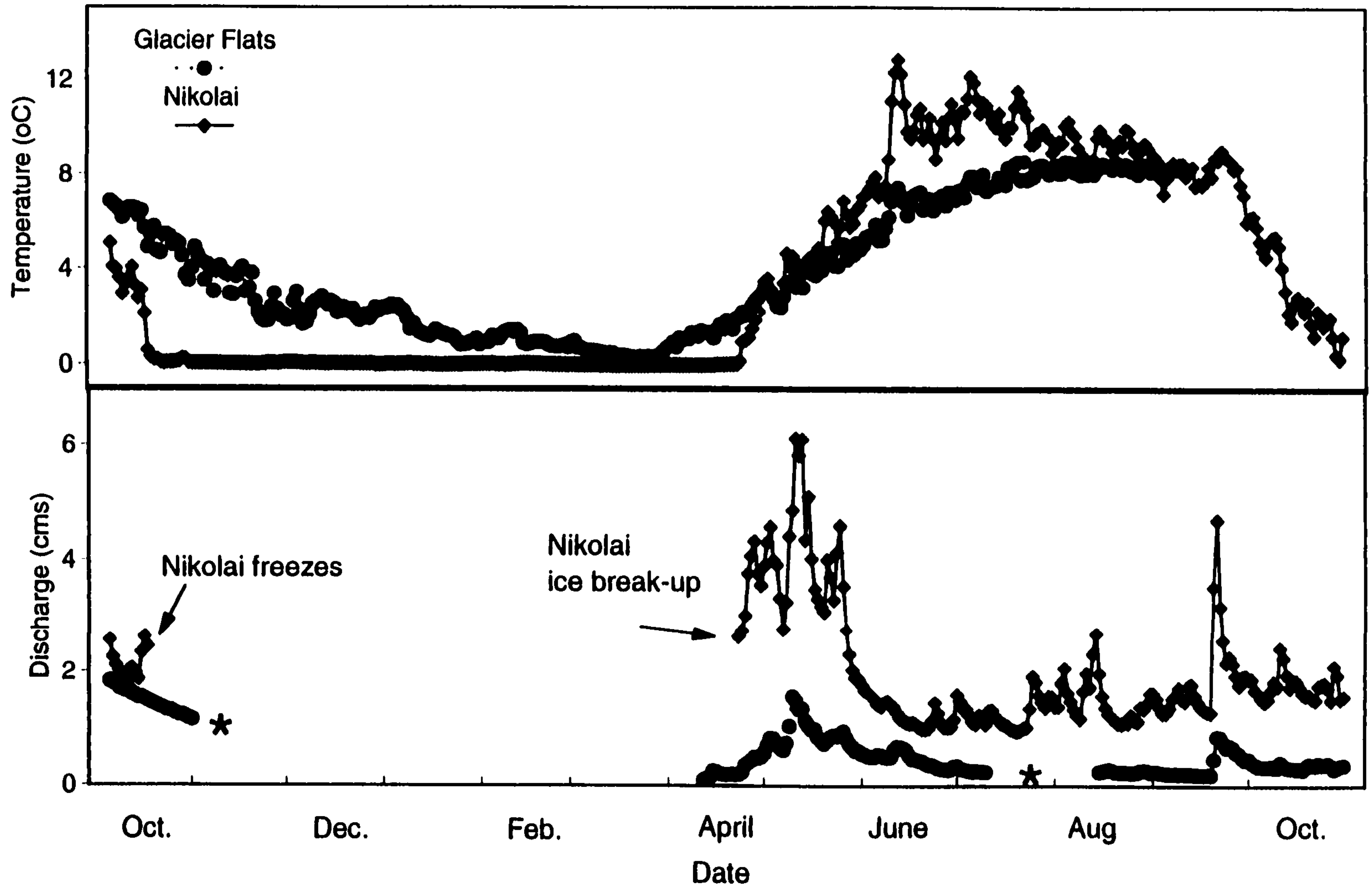


Figure 3.2. Thermal and discharge regimes for water year 1995, in Glacier Flats and Nikolai creeks, Tustumena Lake watershed, Alaska. Glacier Flats remained ice-free during the winter, however, asterisks indicate data gaps due to vandalism of probes by bears.

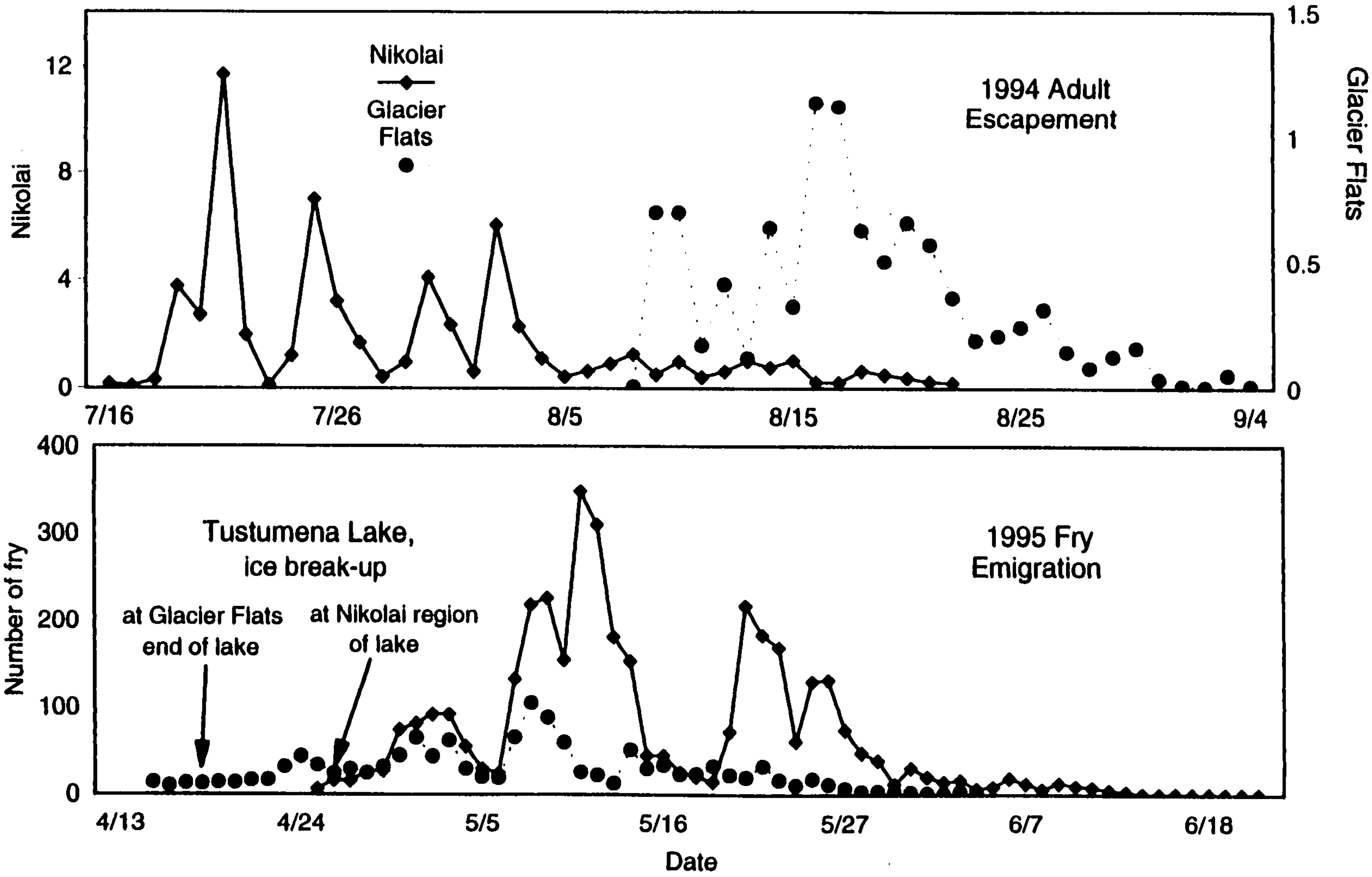


Figure 3.3. Adult sockeye salmon escapement (thousands) and run time distribution into Glacier Flats and Nikolai creeks, Tustumena Lake watershed, 1994 (top graph). Lake break-up timing, spring emigration timing and estimated number of progeny (thousands), 1995 (bottom graph).

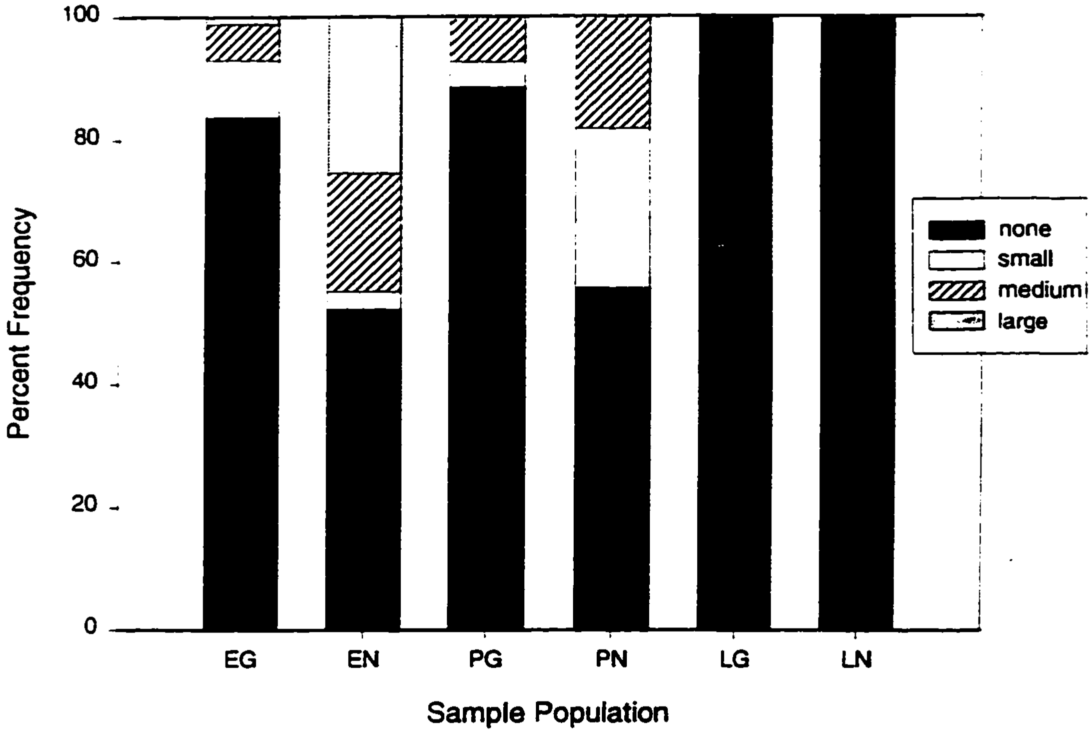


Figure 3.4. Size and percent frequency occurrence of yolk sac on sockeye salmon fry from the early (E), peak (P) or late (L) portion of the Glacier Flats (G) and Nikolai (N) creek spring emigration, Tustumena Lake watershed, 1995. Sample dates and sizes (n) for Glacier Flats are as follow: EG, 15 - 20 April, n = 87; PG, 8 - 12 May, n = 96; LG, 29 May - 4 June, n = 87; for Nikolai Creek: EN, 24 - 28 April, n = 88; PN, 9 - 13 May, n = 62; LN 7 - 14 June, n = 85. Categories for yolk sac classification are: none = no yolk sac; small, 4.0 to < 10.0; medium, 10.0 to < 20.0; large ≥ 20.0 mg.

Table 3.1. Summary of mark-recapture data of sockeye salmon fry emigrating from Nikolai and Glacier Flats creeks, tributaries to Tustumena Lake, Alaska. Trap efficiency trials were conducted two or three times weekly. A single trap site was used in each stream and marked fry were released 0.5 km upstream.

Period	Stratum (h)	# Marked (M_h)	# Recovered (m_h)	Unmarked captures (u_h)	Total captures (n_h)	Capture efficiency (e_h)	Estimated total (U_h)	Variance	Lower 95% CI	Upper 95% CI
Glacier Flats Creek										
15 to 20 April	1	97	61	12,296	12,357	0.15	78,932	8.39E+7	60,979	96,886
21 to 26 April	2	200	20	17,503	17,523	0.10	167,529	1.14E+09	101,242	233,815
27April to 1 May	3	213	26	24,922	24,948	0.12	197,530	1.22E+09	129,099	265,961
2 to 6 May	4	200	30	27,103	27,133	0.15	175,732	8.17E+08	119,705	231,760
7 to 13 May	5	400	38	37,246	37,284	0.10	382,965	3.31E+09	270,145	495,785
14 to 16 May	6	275	12	5,441	5,453	0.04	109,933	8.25E+08	53,650	166,216
17 to 24 May	7	1186	124	19,332	19,456	0.10	183,577	2.41E+08	153,160	213,994
25 to 29 May	8	807	78	4,363	4,441	0.10	44,645	2.29E+7	35,269	54,022
30 May to 4 June	9	512	38	751	789	0.07	9,883	2.37E+6	6,864	12,903
Total estimates							1,356,285	7.75E+09	1,183,696	1,528,874
Nikolai Creek										
25 to 29 April	1	310	24	7,289	7,313	0.08	90,675	2.92E+08	57,194	124,156
30 April to 6 May	2	902	26	13,445	13,471	0.03	449,661	7.02E+09	285,452	613,870
7 to 14 May	3	2294	16	12,795	12,811	0.01	1,727,325	1.65E+11	931,790	2,522,860
15 to 20 May	4	695	12	4,172	4,184	0.02	223,362	3.5E+09	107,278	339,447
21 to 26 May	5	2119	32	13,904	13,936	0.02	893,227	2.32E+10	594,979	1,191,475
27 May to 1 June	6	1623	39	5,525	5,564	0.02	224,315	1.21E+09	156,259	292,371
2 to 5 June	7	1187	53	2,073	2,126	0.04	45,606	3.70E+7	33,678	57,534
6 to 21 June	8	644	16	2,051	2,067	0.02	77,817	3.3E+08	42,198	113,436
Total estimates							3,731,988	2E+11	2,854,803	4,609,356

Table 3.2. Egg to fry survival estimates for progeny of sockeye salmon spawning in Glacier Flats and Nikolai creeks, Tustumena Lake, Alaska, 1994.

Stream	Number of females 1994	Mean fecundity	Mean egg wt. (mg)	Estimated egg deposition	Estimated number of fry	Percent survival
Glacier Flats	4,798	2,790	75	13,386,420	1,356,285	10
Nikolai	32,992	4,103	90	135,366,176	3,731,988	2.8

Table 3.3. Summary of average weight (mg), total length (mm), and condition factor of fry emigrating from Glacier Flats and Nikolai creeks, Tustumena Lake watershed, Alaska, 1995. Samples (n = 30) were collected every 3 d at each site throughout the emigration period. The first two rows of data include all fry sampled spring of 1995, whereas the last rows are specific to the dates indicated.

Stream	Sample period	n	Weight (SE)	Length (SE)	Condition (SE)
Glacier Flats	all dates	638	111 (0.712)	26.8 (0.045)	0.580 (2.41E-3)
Nikolai	all dates	457	117 (0.985)	27.3 (0.066)	0.570 (3.92E-3)
Glacier Flats	early (15 to 20 April)	87	115 (0.156)	26.7 (0.114)	0.606 (4.93E-3)
	peak (8 to 12 May)	96	110 (0.167)	26.7 (0.124)	0.574 (5.83E-3)
	late (29 May to 4 June)	87	113 (0.193)	26.9 (0.118)	0.579 (0.006)
Nikolai	early (24 to 28 April)	88	108 (0.317)	26.3 (0.261)	0.568 (1.28E-2)
	peak (9 to 13 May)	62	118 (0.236)	27.2 (0.128)	0.583 (9.39E-3)
	late (7 to 14 June)	85	117 (0.183)	27.6 (0.124)	0.559 (5.01E-3)

Table 3.4. Observed frequency, catch per unit effort, and size of fish captured in minnow traps set in Glacier Flats and Nikolai creeks, Tustumena Lake watershed, Alaska. Five traps were set in each stream for about 24 h on 23, 26, 27, and 28 May 1995. Nikolai Creek was fished a total of 477 h and Glacier Flats a total of 480 h. Length measures are total length in mm.

Stream		Dolly Varden	Sculpin	Rainbow trout	Three-spine stickleback	Coho salmon
Nikolai Creek						
	total captured	190	115	3	0	1
	Length mean (SE)	127 (1.24)	57 (1.48)	114 (6.3)	—	90
	CPUE mean (SE)	0.392 (0.147)	0.234 (0.058)	0.006 (0.004)	—	0.002
Glacier Flats Creek	total captured	6	0	2	1	1
	Length mean (SE)	81 (13.1)	—	71 (4)	51	126
	CPUE mean (SE)	0.0125 (0.024)	NA	0.004 (0.003)	0.002	0.002

References

Adkison, M. D. 1995. Population differentiation in Pacific salmon: local adaptation, genetic drift, or the environment? Canadian Journal of Fisheries and Aquatic Sciences 52:2762-2777.

Akaike, H. 1973. Information theory and an extension of the maximum likelihood principle. Pages 267 - 281 *in* B.N. Petran and F. Csaki, editors. International symposium on information theory, 2nd edition. Akadeniai Kiadi, Budapest, Hungary.

Alaska Department of Fish and Game. 1998. Regional information report number 5J98:01.

Applied Biosystems Incorporated. 1993. Genescan 672 software. Users manual revision A. Foster City, California.

Applied Biosystems Incorporated. 1994. Genotyper 1.1 DNA fragment analysis software. Users manual revision A. Foster City, California.

Bagenal, T. B. 1969. Relationship between egg size and fry survival in brown trout *Salmo trutta* L. Journal of Fish Biology 1:349-353.

Baldrige, J. E., and D. Amos. 1982. A technique for determining fish habitat suitability criteria: a comparison between habitat utilization and availability. Pages 251-258 *in* N. B. Armantrout, editor. Acquisition and utilization of aquatic habitat inventory information. American Fisheries Society, Bethesda, Maryland.

Bams, R. A. 1967. Differences in performance of naturally and artifically propagated sockeye salmon migrant fry, as measured with swimming and predation tests. Journal of the Fisheries Research Board of Canada 24:1117-1153.

Bams, R. A. 1969. Adaptations of sockeye salmon associated with incubation in stream gravels. Pages 71-87 *in* T. G. Northcote, editor. H. R. MacMillan Lectures in Fisheries, Symposium on salmon and trout in streams. University of British Columbia, Vancouver.

Bams, R. A. 1972. A quantitative evaluation of survival to the adult stage and other characteristics of pink salmon (*Oncorhynchus gorbuscha*) produced by a revised hatchery method which simulates natural conditions. Journal of the Fisheries Research Board of Canada 24:1117-1153.

Bams, R. A. 1976. Survival and propensity for homing as affected by presence or absence of locally adapted paternal genes in two transplanted populations of pink salmon (*Oncorhynchus gorbuscha*). Journal of the Fisheries Research Board of Canada 33:2716-2725.

Bazarkin, V. N. 1990a. Hydrologic regimes of various types of spawning grounds of sockeye salmon, *Oncorhynchus nerka*. Journal of Icthyology 30(4):31-39.

Bazarkin, V. N. 1990b. Features of the ecology of salmons of the genus *Oncorhynchus* during the spawning period in the lower reaches of the Kamchatka River. Journal of Icthyology 30(2):43-50.

Beacham, T. D., and C. B. Murray. 1986. Comparative developmental biology of chum salmon (*Oncorhynchus keta*) from the Fraser River, British Columbia. Canadian Journal of Fisheries and Aquatic Sciences 43:252-262.

Beacham, T. D., and C. B. Murray. 1987. Adaptive variation in body size, age, morphology, egg size, and developmental biology of chum salmon (*Oncorhynchus keta*) in British Columbia. Canadian Journal of Fisheries and Aquatic Sciences 44:244-261.

Beacham, T. D., and C. B. Murray. 1988. Variation in developmental biology of pink salmon (*Oncorhynchus gorbuscha*) in British Columbia. Canadian Journal of Zoology 66:2634-2648.

Beacham, T. D., and C. B. Murray. 1989. Variation in developmental biology of sockeye salmon (*Oncorhynchus nerka*) and chinook salmon (*O. tshawytscha*) in British Columbia. Canadian Journal of Fisheries and Aquatic Sciences 67:2081-2089.

Beacham, T. D., and C. B. Murray. 1990. Temperature, egg size and development of embryos and alevins of five species of Pacific salmon: a comparative analysis. Transactions of the American Fisheries Society 119:927-945.

Beacham, T. D., and C. B. Murray. 1993. Fecundity and egg size variation in North American Pacific salmon (*Oncorhynchus*). Journal of Fish Biology 42:485-508.

Beacham, T. D., and P. Starr. 1982. Population biology of chum salmon, *Oncorhynchus keta*, from the Fraser River, British Columbia. U. S. National Marine Fisheries Service Fishery Bulletin 80:813-825.

Bell, G. 1980. The costs of reproduction and their consequences. American Naturalist 116:45-76.

Bentzen, P., A. S. Harris, and J. M. Wright. 1991. Cloning of hypervariable minisatellite and simple sequence microsatellite repeats for DNA fingerprinting of important aquacultural species of salmonids and tilapia. Pages 242-263 *in* T. Burke, G. Dolf, A. J. Jefferies, and R. Wolff, editors. DNA fingerprinting: approaches and applications. Birkhauser Verlag, Switzerland.

Bilton, H. T., and G. L. Robins. 1971. Response of young sockeye salmon (*Oncorhynchus nerka*) to prolonged periods of starvation. Journal of the Fisheries Research Board of Canada 30:1-5.

Bishop, S. M. 1990. Morphometric differences among spawning populations of sockeye salmon (*Oncorhynchus nerka*) in the Wood River Lake system. Masters thesis. University of Washington, Seattle, Washington.

Blair, G. R., D. E. Rogers, and T. P. Quinn. 1993. Variation in life history characteristics and morphology of sockeye salmon in the Kvichak River system, Bristol Bay, Alaska. Transactions of the American Fisheries Society 122:550-559.

Bradford, M. J., and R. M. Peterman. 1987. Maternal size effects may explain positive correlations between age at maturity of parent and offspring sockeye salmon (*Oncorhynchus nerka*). Pages 90-100 *in* H. D. Smith, L. Margolis and C.C. Wood, editors. Sockeye salmon (*Oncorhynchus nerka*) population biology and future management. Canadian Special Publications of Fisheries and Aquatic Sciences 96, Canadian Government Publishing Centre, Ottawa, Canada.

Brännäs, E. 1995. First access to territorial space and exposure to strong predation pressure: a conflict in early emerging Atlantic salmon (*Salmo salar* L.). Evolutionary Ecology 9:411-420.

Brannon, E. L. 1972. Mechanisms controlling migration of sockeye salmon fry. International Pacific Salmon Fisheries Commission, Bulletin 21.

Brannon, E. L. 1987. Mechanisms stabilizing salmonid fry emergence timing. Pages 120-124 *in* H. D. Smith, L. Margolis and C. C. Wood, editors. Sockeye salmon (*Oncorhynchus nerka*) population biology and future management. Canadian Special Publications of Fisheries and Aquatic Sciences 96, Canadian Government Publishing Centre, Ottawa, Canada.

Brett, J. R. 1965. The relation of size to rate of oxygen consumption and sustained swimming speed of sockeye salmon (*Oncorhynchus nerka*). Journal of the Fishery Research Board of Canada 6:1491-1501.

Brett, J. R. 1986. Production energetics of a population of sockeye salmon, *Oncorhynchus nerka*. Canadian Journal of Zoology 64:555-564.

Bromage, N., P. Hardiman, J. Jones, J. Springate, and V. Bye. 1990. Fecundity, egg size, and total egg volume differences in 12 stocks of rainbow trout, *Oncorhynchus mykiss* Richardson. Aquaculture and Fisheries Management 21:269-294.

Burger, C. V., R. L. Wilmot, and D. B. Wangaard. 1985. Comparison of spawning areas and times for two runs of chinook salmon in the Kenai River, Alaska. Canadian Journal of Fisheries and Aquatic Sciences. 42:693-700.

Burger, C. V., J. E. Finn, and L. Holland-Bartels. 1995. Pattern of shoreline spawning by sockeye salmon in a glacially turbid lake: evidence for subpopopulation differentiation. Transactions of the American Fisheries Society 124:1-15.

Burger, C. V., W. J. Spearman, and M. A. Cronin. 1997. Genetic differentiation of sockeye salmon subpopulations from a geologically young Alaskan lake system. Transactions of the American Fisheries Society 126:926-938.

Burgner, R. L. 1987. Factors influencing age and growth of juvenile sockeye salmon (*Oncorhynchus nerka*) in lakes. Pages 129-142 *in* H. D. Smith, L. Margolis and C. C. Wood, editors. Sockeye salmon (*Oncorhynchus nerka*) population biology and future management. Canadian Special Publications of Fisheries and Aquatic Sciences 96, Canadian Government Publishing Centre, Ottawa, Canada.

Burgner, R. L. 1991. Life history of sockeye salmon (*Oncorhynchus nerka*). Pages 1- 117 *in* C. Groot and L. Margolis, editors. Pacific salmon life histories. University of British Columbia Press, Vancouver, British Columbia.

Burke, T., and M. W. Bruford. 1987. DNA fingerprinting in birds. Nature 327:149-152.

Burner, C. J. 1951. Characteristics of spawning nests of Columbia River salmon. Fishery Bulletin of the U. S. Fish and Wildlife Service 52:97-110.

Busack, C. A., and G. A. E. Gall. 1980. Ancestry of artificially propagated California rainbow trout strains. California Fish and Game 66:17-24.

Callen, D. F., A. D. Thompson, Y. Shen, H. A. Phillips, R. I. Richards, J. C. Mulley, and G. R. Sutherland. 1993. Incidence and origin of "null" alleles in the $(AC)_n$ microsatellite markers. American Journal of Human Genetics 52:922-927.

Carlson, S. R., L. G. Coggins, and C. O. Swanton. 1998. A simple stratified design for mark-recapture estimation of salmon smolt runs. Alaska Fishery Research Bulletin *In Press.*

Chapman, D. W. 1988. Critical review of variables used to define effects of fines in redds of large salmonids. Transactions of the American Fisheries Society 117:1-21.

Cleveland, W. S. 1993. Visualizing data. Hobart Press. Summit, New Jersey.

Combs, B. D. 1965. Effect of temperature on the development of salmon eggs. Progressive Fish Culturist 3:134-137.

Darwin, C. 1859. On the origin of species by means of natural selection, or the preservation of favoured races in the struggle for life. John Murray, London.

Duston, J., and N. R. Bromage. 1986. Photoperiodic mechanisms and rhythms of reproduction in the female rainbow trout. Fish Physiology and Biochemistry 2:35-64.

Endler, J. A. 1977. Geographic variation, speciation and clines. Princeton University Press. Princeton, New Jersey.

Endler, J. A. 1986. Natural selection in the wild. Monographs in population biology 21. Princeton University Press, Princeton, New Jersey.

Endler, J. A. 1991. Interactions between predator and prey. Pages 169-196 *in* J. R. Krebs and N. B. Davies, editors. Behavioral ecology. Blackwell Scientific Publications, Oxford.

Estoup, A., P. Presa, F. Krieg, D. Vaiman, and R. Guyomard. 1993. $(CT)_n$ and $(GT)_n$ microsatellites: a new class of genetic markers for *Salmo trutta* L. (brown trout). Heredity 71:488-496.

Fagerlund, U. H. M., J. R. McBride, and I. V. Williams. 1995. Stress and tolerance. Pages 461-493 *in* C. Groot, L. Margolis and W. C. Clarke, editors. Physiological ecology of Pacific salmon. University of British Columbia Press, Vancouver, British Columbia.

Fleming, I. A., and M. R. Gross 1989. Evolution of adult female life history and morphology in a Pacific salmon (coho: *Oncorhynchus kisutch).* Evolution 43:141-157.

Fleming, I. A., and M. R. Gross. 1990. Latitudinal clines: a trade-off between egg number and size in Pacific salmon. Ecology 1:1-11.

Foerster, R. E. 1968. The sockeye salmon, *Oncorhynchus nerka*. Bulletin of the Fisheries Research Board of Canada 162.

Foote, C. J. 1988. Male mate choice dependent on male size in salmon. Behavior 106: 63-80.

Foote, C. J. 1990. An experimental comparison of male and female spawning territoriality in a Pacific salmon. Behavior 115:283-314.

Foote, C. J., and G. S. Brown. 1998. The ecological relationship between slimy sculpins (*Cottus cognatus*), coastrange sculpins (*C. aleuticus*) and beach spawning sockeye salmon (*Oncorhynchus nerka*) in Iliamna Lake, Alaska. Canadian Journal of Fisheries and Aquatic Sciences 55:1-10.

Foote, C. J., C. C. Wood, and R. E. Withler. 1989. Biochemical genetic comparison of sockeye salmon and kokanee, the anadromous and nonanadromous forms of *Oncorhynchus nerka*. Canadian Journal of Fisheries and Aquatic Sciences 46:149-158.

Foskett, D. R. 1958. The Rivers Inlet sockeye salmon. Journal of the Fishery Research Board of Canada 15:867-889.

Fresh, K. L., and S. L. Schroder. 1987. Influence of the abundance, size, and yolk reserves of juvenile chum salmon (*Oncorhynchus keta*) on predation by freshwater fishes in a small coastal stream. Canadian Journal of Fisheries and Aquatic Sciences 44:236-243.

Futuyma, D. J. 1986. Evolutionary biology, Second edition. Sinauer Associates, Inc. Sunderland, Massachusetts.

Gall, G. A. E. 1974. Influence of size of eggs and age of female in hatchability and growth on rainbow trout. California Fish and Game 60(1):26-35.

Gall, G. F., J. Baltodano, and N. Huang. 1988. Heritability of age at spawning for rainbow trout. Aquaculture 68:93-102.

Gard, R. 1971. Brown bear predation on sockeye salmon at Karluk Lake, Alaska. Journal of Wildlife Management 35:193-204.

Gard, R., B. Drucker, and R. Fagen. 1987. Differentiation of subpopulations of sockeye salmon (*Oncorhynchus nerka*) from the Karluk River System, Alaska. Pages 408-418 *in* H. D. Smith, L. Margolis , and C. C. Wood, editors.

Sockeye salmon (*Oncorhynchus nerka*) population biology and future management. Canadian Special Publication of Fisheries and Aquatic Sciences 96. Canadian Government Publishing Centre, Ottawa, Canada.

Gharrett, A. J., and W. W. Smoker. 1993. A perspective on the adaptive importance of genetic infrastructure in salmon populations to ocean ranching in Alaska. Fisheries Research 18:45-58.

Ginetz, R. M., and P. A. Larkin. 1976. Factors affecting rainbow trout (*Salmo gairdneri*) predation on migrant fry of sockeye salmon (*Oncorhynchus nerka*). Journal of the Fisheries Research Board of Canada 33:19-24.

Gjerde, D. 1984. Response to individual selection for age at sexual maturity in Atlantic salmon. Aquaculture 38:229-240.

Glenn, L. P., and L. H. Miller. 1980. Seasonal movements of an Alaska Peninsula brown bear population. Pages 307-312 *in* C. J. Martinka and K. L. McArther, editors. Bears-their biology and management. U. S. Government Printing Office, Washington, D. C.

Godin, J. J. 1981. Migrations of salmonid fishes during early life history phases: daily and annual timing. Pages 22-45 *in* E. L. Brannon and E. O. Salo, editors. Proceedings of the salmon and trout migratory behavior symposium. School of Fisheries, University of Washington, Seattle, Washington.

Goudet, J. 1995. F-stat Version 1.2 A computer program to calculate F-statistics. Journal of Heredity 86:485-486.

Gregory, R. S. 1993. Effect of turbidity on the predator avoidance behaviour of juvenile chinook salmon (*Oncorhynchus tshawytscha*). Canadian Journal of Fisheries and Aquatic Science 50:241-246.

Guo, S. W., and E. A. Thompson. 1992. Performing the exact test of Hardy-Weinburg proportions for multiple alleles. Biometrics 48:361-372.

Hankin, D. G., J. W. Nicholas, and T. W. Downey. 1993. Evidence for inheritance of age of maturity in chinook salmon (*Oncorhynchus tshawytscha*). Canadian Journal of Fisheries and Aquatic Sciences 50:347-358.

Hartl, D. L., and A. G. Clark. 1997. Principles of population genetics, 3rd edition. Sinauer Associates, Inc. Sunderland, Massachusetts.

Hartman, W. L., and R. F. Raleigh. 1966. Tributary homing of sockeye salmon in Brooks and Karluk lakes, Alaska. Journal of Fisheries Research Board of Canada 21:485-504.

Hartman, W. L., C. W. Strickland, and D. T. Hoopes. 1962. Survival and behavior of sockeye salmon fry migrating into Brooks Lake, Alaska. Transactions of the American Fisheries Society 91:133-139.

Hasler, A. D., and A. T. Scholz. 1983. Olfactory imprinting and homing in salmon. Springer-Verlag, Berlin.

Healey, M. C. 1986. Optimum size and age at maturity in Pacific salmon and effects of size selective fisheries. Canadian Special Publications in Fisheries and Aquatic Sciences 89:39-52.

Healey, M. C. 1987. The adaptive significance of age and size at maturity in female sockeye salmon (*Oncorhynchus nerka*). Pages 110-117 *in* H. D. Smith, L. Margolis, and C. C. Wood, editors. Sockeye salmon (*Oncorhynchus nerka*) population biology and future management. Canadian Special Publication of Fisheries and Aquatic Sciences 96, Canadian Government Publishing Centre, Ottawa, Canada.

Healey, M. C., and W. R. Heard. 1984. Inter- and intrapopulation variation in the fecundity of chinook salmon (*Oncorhynchus tshawytscha*) and its relevance to life history theory. Canadian Journal of Fisheries and Aquatic Sciences 41:476-483.

Heggberget, T. G. 1988. Timing of spawning in Norwegian Atlantic salmon (*Salmo salar*). Canadian Journal of Fisheries and Aquatic Sciences 45:845-849.

Hoelzel, A. R., and A. Green. 1994. Analysis of population-level variation by sequencing PCR-amplified DNA. *in* A. R. Hoelzel, editor. Molecular Genetic Analysis of Populations. A Practical Approach. Oxford University Press.

Holtby, L. B, and M. C. Healy. 1986. Selection for adult size in female coho salmon (*Oncorhynchus kisutch*). Canadian Journal of Fisheries and Aquatic Sciences 43:1946-1959.

Holtby, L. B., T. E. McMahon, and J. C. Scrivener. 1989. Stream temperatures and inter-annual variability in the emigration timing of coho salmon (*Oncorhynchus kisutch*) smolts and fry and chum salmon (*O. keta*) fry from Carnation Creek, British Columbia. Canadian Journal of Fisheries and Aquatic Sciences 8:1396-1405.

Hoopes, D. T. 1972. Selection of spawning sites by sockeye salmon in small streams. Fishery Bulletin 70(2):447-458.

Horral, R.M. 1981. Behavioral stock-isolating mechanisms in Great Lakes fishes with special reference to homing and site imprinting. Canadian Journal of Fisheries and Aquatic Sciences 38:1481-1496.

Hosmar, D. W., and S. Lemeshow. 1989. Applied logistic regression. John Wiley and Sons, New York, New York.

Jackson, T. R. 1995. Linkage analysis of molecular markers and a search for quantitative trait loci for upper temperature tolerance in rainbow trout (*Oncorhynchus mykiss*). Doctoral Dissertation, University of Guelph, Canada.

Jeffreys, A. J., N. J. Royle, V. Wilson, and Z. Wong. 1988. Spontaneous mutation rates to new length alleles at tandem-repetitive hypervariable loci in human DNA. Nature 322:278-281.

Karlstrom, T. N. V. 1964. Quaternary geology of the Kenai lowland and glacial history of the Cook Inlet Region, Alaska. Geological Survey professional paper 443. United States Government Printing Office, Washington, D.C.

Kerns, O. E. Jr., and J. R. Donaldson. 1968. Behavior and distribution of spawning sockeye salmon on island beaches on Iliamna Lake, Alaska, 1965. Journal of the Fishery Research Board of Canada 25(3):485-494.

Kim, W. S., and K. Roberson. 1968. On the use of otoliths of sockeye salmon for age determination. Pages 151-168 *in* R. L. Burgner, editor. Further studies of Alaska sockeye salmon. University of Washington Publications in Fisheries, New Series, Volume 3. Seattle, Washington.

Kline, T.C. Jr., and five coauthors. 1993. Recycling of elements transported upstream by runs of Pacific salmon: II. $\delta^{15}N$ and $\delta^{13}C$ evidence in the Kvichak River watershed, Bristol Bay, southwestern Alaska. Canadian Journal of Fisheries and Aquatic Sciences 50:2350-2365.

Koenings, J. P. and R. D. Burkett. 1987. Population characteristics of sockeye salmon (*Oncorhynchus nerka*) smolts relative to temperature regimes, euphotic volume, fry density and forage base within Alaskan Lakes. Pages 216-234 *in* H. D. Smith, L. Margolis and C. C. Wood, editors. Sockeye salmon population biology and future management. Canadian Special Publication of Fisheries and Aquatic Sciences 96:216-234.

Kondolf, C. M., and S. Li. 1992. The pebble count technique for quanitifying surface bed material size in instream flow studies. Rivers 3(2):80-87.

Krebs, C. J. 1989. Ecological methodology. Harper and Row, New York, New York.

Kyle, G. B. 1992. Summary of sockeye salmon (*Oncorhynchus nerka*) investigations in Tustumena Lake, 1981-1991. Alaska Department of Fish and Game, Fisheries Rehabilitation and Enhancement Division Report 122, Juneau. Alaska.

Larkin, P. A. 1970. Management of Pacific salmon in North America. Pages 223-226 *in* A century of fisheries in North America. N. G. Benson, editor. American Fisheries Society, Washington, D.C.

Larkin, P. A., and J. G. MacDonald. 1968. Factors in the population biology of the sockeye salmon of the Skeena River. Journal of Animal Ecology 37:229-258.

Leary, R. F., F. W. Allendorf, and K. L. Knudsen. 1989. Genetic differences among rainbow trout spawned on different days within a single season. The Progressive Fish Culturist 51:10-19.

Lisle, T.E. 1989. Sediment transport and resulting deposition in spawning gravels, north coastal California. Water Resources Research 25:1303-1319.

Lorenz, J. M., and J. H. Eiler. 1989. Spawning habitat and redd characteristics of sockeye salmon in the glacial Taku River, British Columbia and Alaska. Transactions of the American Fisheries Society 118:495-502.

Love, J. M., A. M. Knight, M. A. McAleer, and J. A. Todd. 1990. Towards construction of a high resolution map of the mouse genome using PCR-analyzed microsatellites. Nucleic Acids Research 18:4123-4130.

Manley, B. F., L. L. McDonald, and D. Thomas. 1993. Resource selection by animals: statistical design and analysis for field studies. Chapman and Hall, New York, New York.

Marriott, R. A. 1964. Stream catalog of the Wood River Lake system, Bristol Bay, Alaska. U. S. Fish and Wildlife Service Scientific Report 494. Anchorage, Alaska.

McBride, D. N., and A. Brogle. 1983. Catch, escapement, age, sex and size data for salmon (*Oncorhynchus spp.)* returns to the Yakutat area, 1984. Alaska Department of Fish and Game Technical Report 101, Anchorage, Alaska.

McCart, P. 1967. Behavior and ecology of sockeye salmon fry in the Babine River. Journal of the Fishery Research Board of Canada 24:375-428.

McConnell, S. D. J., D. E. Ruzzante, P. T. O'Reilly, L. Hamilton, and J. M. Wright. 1997. Microsatellite loci reveal highly significant genetic differentiation among Atlantic salmon (*Salmo salar* L.) stocks from the east coast of Canada. Molecular Ecology 6:1075-1089.

McNeil, W. J. 1966. Effect of the spawning bed environment on reproduction of pink and chum salmon. U. S. Fish and Wildlife Service Fishery Bulletin 64:495-523.

McNeil, W. J. 1968. Migration and distribution of pink salmon spawners in Sashin Creek in 1965 and survival of their progeny. U. S. Fish and Wildlife Service, Fishery Bulletin 66:575-586.

Montgomery, D. R., J. M. Buffington, N. P. Peterson, D. Schuett-Hames, and T. P. Quinn. 1996. Stream-bed scour, egg burial depths, and the influence of salmonid spawning on bed surface mobility and embryo survival. Canadian Journal of Fisheries and Aquatic Sciences 53:1061-1070.

Morrison, J. K., and C. E. Smith. 1986. Altering the spawning cycle of rainbow trout by manipulating water temperature. Progressive Fish Culturist 48:52-54.

Murray, C. B., and J. D. McPhail. 1988. Effect of incubation temperature on the development of five species of Pacific salmon (*Oncorhynchus*) embryos and alevins. Canadian Journal of Zoology 66:266-273.

Murray, C. B., T. D. Beacham, and J. D. McPhail. 1990. Influence of parental stock and incubation temperature on the early development of coho salmon (*Oncorhynchus kisutch*) in British Columbia. Canadian Journal of Zoology 68:347-358.

Nehlsen, W., J. E. Williams, and J. A. Lichatowich. 1991. Pacific salmon at the crossroads: stocks at risk from California, Oregon, Idaho, and Washington. Fisheries 2:4-21.

Neter, J., M. H. Kuter, C. J. Nachtsheim, and W. Wasserman. 1996. Applied linear statistical models. Fourth edition. Irwin, Chicago, Illinois.

O'Connell, M., and J. M. Wright. 1997. Microsatellite DNA in fishes. Reviews in Fish Biology and Fisheries 7:331-363.

O'Reilly, P. T., L. C. Hamilton, S. K. McConnell, and J. M. Wright. 1996. Rapid analysis of genetic variation in Atlantic salmon (*Salmo salar*) by PCR multiplexing of dinucleotide and tetranucleotide microsatellites. Canadian Journal of Fisheries and Aquatic Sciences 53:2292-2298.

Olsen, J. B., J. K. Wenburg, and P. Bentzen. 1996. Semi-automated multilocus genotyping of Pacific salmon (*Oncorhynchus* spp.) using microsatellites. Molecular Marine Biology and Biotechnology 5:259-272.

Olsen J. B., L. W. Seeb, P. Bentzen, and J. E. Seeb. 1998. Genetic interpretation of broad-scale microsatellite polymorphism in odd-year pink salmon. Transactions of the American Fisheries Society 127:535-550.

Olsen, J. C. 1968. Physical environment and egg development in a mainland beach area and an island beach area of Iliamna Lake. Pages 169-197 *in* R.L. Burgner, editor. Further studies of Alaska sockeye salmon. University of Washington-Publications in Fisheries-New Series, Volume III, Seattle, Washington.

Orth, D. J., and O. E. Maughan. 1986. In defense of the instream flow incremental methodology. Canadian Journal of Fisheries and Aquatic Sciences 43:1092 - 1093.

Parker, R. R. 1971. Size selective predation among juvenile salmonid fishes in a British Columbia Inlet. Journal of the Fisheries Research Board of Canada 28:1503-1510.

Parsons, B. G. M., and W. A. Hubert. 1988. Influence of habitat availability on spawning site selection by kokanees in streams. North American Journal of Fisheries Management 8:426-431.

Paustian, S. J., and 13 coauthors. 1992. A channel type users guide for the Tongass National Forest, Southeast Alaska. U.S.D.A. Forest Service Alaska Region R10-TP-26, Juneau, Alaska.

Pemberton, J. M., J. Slate, D. R. Bancroft, and J. A. Barrett. 1995. Non-amplifying alleles at microsatellite loci: a caution for parentage and fingerprinting studies. Molecular Ecology 4:519-520.

Peterman, R. M. 1985. Patterns of interannual variation in age at maturity of sockeye salmon (*Oncorhynchus nerka*) in Alaska and British Columbia. Canadian Journal of Fisheries and Aquatic Sciences 42:1595-1607.

Peterman, R. M., M. J. Bradford, and J. L. Anderson. 1986. Environmental and parental influences on age at maturity in sockeye salmon (*Oncorhynchus* *nerka*) from the Fraser River, British Columbia. Canadian Journal of Fisheries and Aquatic Sciences 43:269-274.

Pielou, F. C. 1994. After the ice age: the return of life to glaciated North America. University of Chicago Press, Chicago, Illinois.

Raleigh, R. F. 1967. Genetic control in the lakeward migrations of sockeye salmon (*Oncorhynchus nerka*). Journal of the Fishery Research Board of Canada 24:2613-2622.

Raleigh, R. F. 1971. Innate control of migrations of salmon and trout fry from natal gravels to rearing areas. Ecology 2:291-297.

Raymond, M., and F. Rousset. 1995 Genepop (v.1.2): population genetics software for exact tests and ecumenicism. Journal of Heredity 86:248-249.

Reger, R. D. 1993. Late Wisconsin glaciation of the Cook Inlet region with emphasis on Kenai lowland. Abstract presented at the 20th annual conference of the Alaskan Anthropological Association, Anchorage, Alaska.

Reznick, D. N. 1982. The impact of predation on life history evolution in Trinidadian guppies. Genetic basis of observed life history patterns. Evolution 36:1236-50.

Reznik, D. N. 1983. The structure of guppy life histories: the trade-off between growth and reproduction. Ecology 64:862-73.

Ricker, W. E. 1972. Hereditary and environmental factors affecting certain salmonid populations. Pages 27-160 *in* R. C. Simon and P. A. Larkin, editors. The stock concept in Pacific salmon. H.R. McMillian Lectures in Fisheries, University of British Columbia, Vancouver.

Ricker, W. E. 1980. Causes of the decrease in age and size of chinook salmon (*Oncorhynchus tshawytscha*). Canadian Technical Report of Fisheries and Aquatic Sciences 944:1-25.

Riddell, B. E. 1993. Spatial organization of Pacific salmon: what to conserve? Pages 23-41 *in* J. G. Cloud and G. H. Thorgaard, editors. Genetic conservation of salmonid fishes. Plenum, New York.

Rogers, D. E. 1987. The regulation of age at maturity in Wood River sockeye salmon (*Oncorhynchus nerka*). Pages 78-89 *in* H. D. Smith, L. Margolis and C. C. Wood, editors. Sockeye salmon (*Oncorhynchus nerka*) population biology and future management. Canadian Special Publications of Fisheries and Aquatic Sciences 96, Canadian Government Publishing Centre, Ottawa, Canada.

Roos, J. F. 1960. Feeding habits of the Dolly Varden, *Salvelinus malma* (Walbaum), at Chignik, Alaska. Transactions of the American Fisheries Society 88:253-260.

Rosenau, M. L., and J. D. McPhail. 1987. Inherited differences in agonistic behavior between two populations of coho salmon. Transactions of the American Fisheries Society 116:646-654.

Rubin, J. F. 1998. Survival and emergence pattern of sea trout fry in substrata of different compositions. Journal of Fish Biology 53:84-92.

Ruggerone, G. T., and D. E. Rogers. 1992. Predation on sockeye salmon fry by juvenile coho salmon in the Chignik Lakes, Alaska: implications for salmon management. North American Journal of Fisheries Management 12:87-102.

Sanchez, J. A., C. Clabby, D. Ramos, G. Blanco, F. Flavin, E. Vazquez, and R. Powell. 1996. Protein and microsatellite single locus variability in *Salmon salar* L. (Atlantic salmon). Heredity 77:423-432.

SAS Institute. 1989. SAS/STAT user's guide, version 6.03. SAS Institute, Cary, North Carolina.

Savage, R. E. 1931. The relation between the feeding of the herring of the east coast of England and the plankton of the surrounding waters. Fishery Investigation, Ministry of Agriculture, Food and Fisheries, Series 2, 12:1-88.

Schoen, J. W., and L. Beier. 1985. Brown bear habitat preferences and brown bear logging and mining relationships in southeast Alaska. Alaska Department of Fish and Game, Federal Aid to Wildlife Restoration Project W-22-3, Job 4.17R, Juneau, Alaska.

Scott, D. B. C. 1979. Environmental timing and the control of reproduction in teleost fish. Symposium of the Zoological Society of London 44:105-139.

Scribner, K. T., J. Gust, and R. L. Fields. 1996. Isolation and characterization of novel microsatellite loci: cross species amplification and population genetic applications. Canadian Journal of Fisheries Aquatic Sciences 53:833-841

Seber, G. A. F. 1982. The estimation of animal abundance and related parameters, second edition. Charles Griffin and Company Ltd., London.

Shaeffer, W. M., and P. F. Elson. 1975. The adaptive significance of variation in life history among local populations of Atlantic salmon in North America. Ecology 56:321-333.

Sheridan, W. L. 1962. Relation of stream temperature to timing of pink salmon escapements in southeastern Alaska. Pages 87-102 *in* N. J. Wilimovsky, editor. Symposium on pink salmon, MacMillian Lectures in Fisheries. University of British Columbia, Vancouver, British Columbia.

Siitonen, L., and G. A. E. Gall. 1989. Response to selection for early spawn date in rainbow trout, *Salmo gairdneri*. Aquaculture 78:153-161.

Sowden, T. R., and G. Power. 1985. Prediction of rainbow trout embryo survival in relation to groundwater seepage and particle size of spawning substrates. Transactions of the American Fisheries Society 114:804-812.

Stearns, S. C. 1990. The evolutionary significance of phenotypic plasticity. Bioscience 39: 436-445.

Stearns, S. C. 1992. The evolution of life histories. Oxford University Press, New York, New York

Tabachnick, B. G., and L. S. Fidell. 1996. Using multivariate statistics. Third edition. HarperCollins Publishers Inc. New York, New York.

Tallman, R. F. 1986. Genetic differentiation among seasonally distinct spawning populations of chum salmon, *Oncorhynchus keta*. Aquaculture 57:211-217.

Tallman, R. F., and M. C. Healey. 1991. Phenotypic differentiation in seasonal ecotypes of chum salmon, (*Oncorhynchus keta)*. Canadian Journal of Fisheries and Aquatic Sciences 48:661-671.

Tang, J., M. D. Bryant, and E. L. Brannon. 1987. Effect of temperature extremes on the mortality and development rates of coho salmon embryos and alevins. Progressive Fish Culturist 49:167-174.

Tautz, D. 1989. Hypervariability of simple sequences as a general source for polymorphic DNA markers. Nucleic Acids Research 17:6463-6471.

Taylor, E. B. 1991. A review of local adaptation in Salmonidae with particular reference to Pacific and Atlantic salmon. Aquaculture 98:185-207.

Taylor, E. B., and J. D. McPhail. 1985a. Burst swimming and size-related predation of newly emerged coho salmon *Oncorhynchus kisutch*. Transactions of the American Fisheries Society 114:546-551.

Taylor. E. B., and J. D. McPhail. 1985b. Variation in body morphology among British Columbia populations of coho salmon, *Oncorhynchus kisutch*. Canadian Journal of Fisheries and Aquatic Sciences 42:2020-2028.

Taylor. S. G. 1980. Marine survival of pink salmon fry from early and late spawners. Transactions of the American Fisheries Society 109:79-82.

Tyler, R. W., and D. R. Gibbons. 1973. Observation of the effects of logging on salmon producing tributaries on the Staney Creek watershed and the Thorne River watershed and of logging in the Sitka district. Fisheries Research Institute Report 7307, University of Washington, Seattle, Washington.

U. S. Fish and Wildlife Service and Cook Inlet Aquaculture Association. 1997. Environmental assessment, Tustumena Lake sockeye salmon enhancement program, Kenai National Wildlife Refuge. Kenai Fishery Resource Office, Kenai, Alaska.

Utter, F. M., J. E. Seeb, and L. W. Seeb. 1993 Complementary uses of ecological and biochemical genetic data in identifying and conserving salmon populations. Fisheries Research 18:59-76.

Utter, F. M., P. Aebersold, J. Helle, and G. Winans. 1984 Genetic characterization of populations in the southeastern range of sockeye salmon. Pages 17-32 *in* J. Walton and D. Huston, editors. Proceedings of the Olympic wild fish conference. Port Angeles, Washington.

van den Berghe, E. P, and M. R. Gross. 1984. Female size and nest depth in coho salmon (*Oncorhynchus kisutch*). Canadian Journal of Fisheries and Aquatic Science 41:204-206.

van den Berghe, E. P., and M. R. Gross. 1989. Natural selection resulting from female breeding competition in a Pacific salmon (coho: *Oncorhynchus kisutch*). Evolution 43:125-140.

Varnavskaya, N. V., and six coauthors. 1994a. Genetic differentiation of subpopulations of sockeye salmon (*Oncorhynchus nerka*) within lakes of Alaska, British Columbia, and Kamchatka, Russia. Canadian Journal of Fisheries and Aquatic Sciences 51 (Supplement 1):147-157.

Varnavskaya, N. V., C. C. Wood, and R. J. Everett. 1994b. Genetic variation in sockeye salmon (*Oncorhynchus nerka*) populations of Asia and North America. Canadian Journal of Fisheries and Aquatic Sciences 51 (Supplement 1):132-146.

Waters, T. F. 1995. Sediment in streams; sources, biological effects and control. American Fisheries Society, Monograph 7, Bethesda, Maryland.

Weatherley, A. H. and H. S. Gill. 1987. The biology of fish growth. Academic Press, London.

Weatherley, A. H., and H. S. Gill. 1995. Growth. Pages 103-152 *in* C. Groot, L. Margolis and W. C. Clarke, editors. Physiological ecology of Pacific Salmon. University of British Columbia Press, Vancouver, British Columbia.

Weber, J. L., and P. E. May. 1989. Abundant class of human DNA polymorphisms which can be typed using the polymerase chain reaction. American Journal of Human Genetics 44:388-396.

Weir, B. S., and C. C. Cockerman. 1984. Estimating F-statistics for the analysis of population structure. Evolution 38:1358-1370.

Wilmont, R. L., and C. V. Burger. 1985. Genetic differences among populations of Alaskan sockeye salmon. Transactions of the American Fisheries Society 114:236-243.

Withler, F. C. 1952. Sockeye reproduction in a tributary of Babine Lake, 1950-51. Fishery Research Board of Canada, Pacific Progress Report, No. 91. P13-16.

Wolman, M. G. 1954. A method of sampling coarse river-bed material. Transactions of the American Geophysical Union 35(6):951-956.

Wood, C. C. 1995. Life history variation and population structure in sockeye salmon. Pages 195-216 *in* J. L. Nielsen, editor. Evolution and the aquatic ecosystem: defining unique units in population conservation. American Fisheries Society, Symposium 17, Bethesda, Maryland.

Wood, C. C., B. E. Riddell, D. T. Rutherford, and R. E. Withler. 1994. Biochemical genetic survey of sockeye salmon (*Oncorhynchus nerka*) in Canada. Canadian Journal of Fisheries and Aquatic Sciences 51(Supplement 1): 114-131.

Woody, C. A. 1998. Ecologic, morphologic, genetic, and life history comparison of two proximate sockeye salmon populations, Tustumena Lake, Alaska. Doctoral dissertation. University of Washington, Seattle, Washington.

Wooton, R. J. 1990. Ecology of teleost fishes. Chapman and Hall Inc., New York, New York.

Wright, J. M. 1993. DNA fingerprinting of fishes. Pages 1-73 *in* Hochachka and Mommsen, editors. Biochemistry and molecular biology of fishes. Volume 2. Elsevier Science Publishers B. V., Amsterdam.

Wright, S. 1969. Evolution and the genetics of populations. Volume 2. The theory of gene frequencies. University of Chicago Press, Chicago, Illinois.

Yates, G. T. 1983. Hydromechanics of body and caudal fin propulsion. Pages 177-212 *in* Webb, P. W. and D. Weihs, editors. Fish biomechanics. Praeger Publishers Division. Westport, Connecticut.

Appendix A. Mean and variance of used and available sockeye salmon nest site data, Nikolai and Glacier Flats creeks, Tustumena Lake, Alaska, 1995. Available habitat data for Nikolai were collected from three selected channel types representative of approximately 50% of the total stream length, while Glacier Flats data were collected from the entire stream length.

		Nikolai Mainstem			Nikolai East Fork			Nikolai West Fork			Glacier Flats		
Habitat Variable	Statistic	Used 1994	Used 1995	Available 1995	Used 1994	Used 1995	Available 1995	Used 1994	Used 1995	Available 1995	Used 1994	Used 1995	Available 1995
	n	59	60	60	2	5	60	15	29	60	82	60	60
Water Velocity	mean	58	62	54	44	48	39	42	46	36	13	14	16
(cm/s)	range	12-113	25-111	3-120	38-49	37-53	5-107	9 - 56	17-98	0-112	0-82	0-50	0-73
	s^2	671	373	960	na	88	152	146	266	830	177	185	344
Water Depth	mean	26.7	30.3	29.9	33	32.6	47.9	19.2	22.5	18.35	17.9	19.7	20.6
(cm)	range	10 - 52	13 - 55	4.5 - 104	30 - 36	23 - 50	8 - 97	11 - 34	12 - 38	1.5 - 55	7 - 47	9 - 48	2 - 94
	s^2	79.6	71.38	326.41	na	103.8	338.23	44.3	47.3	106.5	48	66.1	354.5
Water Column	mean	13.3	9.21	12.7	11	7.8	7.5	13.78	9.1	6	11.2	8.5	8.6
Temperature	range	9.4 - 17.7	7.5 - 10.5	9.9 - 16.4	10.4 - 11.6	7.5 - 9.0	4.1 - 9.8	12.5 - 17.1	8 - 11	2.4 - 11.9	8.3 - 13.6	5.4 - 15	5.5 - 13
(°C)	s^2	2.85	0.79	3.66	na	0.45	3.39	1.29	0.6	6.39	2.5	6.9	4.7
Intragravel	mean	12.2	10	10.8	10.7	• nd	• nd	12.7	• nd	• nd	9.5	7.6	• nd
Temperature	range	9.8 - 14.8	9.6 - 10.6	6.8 - 14.3	10.2 - 11.2	• nd	• nd	11.6 - 14.3	• nd	• nd	6.3 - 12.8	4.1 - 12.5	• nd
(°C)	s^2	1.64	0.03	2.34	na	• nd	• nd	0.66	• nd	• nd	2	5.1	• nd

Appendix B. Pearson correlation coefficients ($|r| \geq 0.60$) for habitat parameters used in developing resource selection probability functions for sockeye salmon, Tustumena Lake, Alaska, 1995. Substrate parameters are represented by p_1 through p_8 and represent mean median diameters as follow: $p_1 < 2$ mm; $p_{234} \geq 2$ to < 16 mm; $p_{56} \geq 16$ to < 64 mm; $p_7 \geq 64 < 128$ mm, and $p_8 > 128$ mm.

Channel	Correlated parameters	Pearson correlation coefficient $|r|$
Nikolai, mainstem	p_1, p_{56}	0.68
Nikolai, west fork	p_{234}, p_7	0.60
	p_{56}, p_8	0.78
Glacier Flats Creek	p_1, p_{56}	0.72
	p_7, p_8	0.64

Appendix C. Log-likelihood (-2 Log L) ratio tests of full and reduced resource function models. A reduced model with fewer variables may provide similar and simplified results in a resource selection probability function. A chi-square value >0.05 indicates that the removal of a parameter(s) from the full model is significant and, therefore, should not be removed.

Channel	Variables in full model	Variables in reduced model	-2 Log L full model	-2 Log L reduced model	Deviance	df	chi-sq (P)
Nikolai mainstem	depth, depth^2, velocity, velocity^2, p_{234}, p_{56}[a]	depth, depth^2, velocity, p_{234}, p_{56}	89.771	93.967	4.20	1	0.041
		depth, depth^2, p_{234}, p_{56}	89.771	96.63	6.86	2	0.032
		depth, depth^2, p_{56}	89.771	106.589	16.82	3	0.001
Nikolai west fork	depth, velocity, velocity^2, p_7, p_8[a]	velocity, velocity^2, p_7, p_8	27.808	40.855	13.05	1	0.000
		depth, velocity, velocity^2, p_7	27.808	48.874	21.07	1	0.000
		velocity, velocity^2, p_7	27.808	56.006	28.20	2	0.000
		depth, p_7, p_8	27.808	56.538	28.73	2	0.000
Glacier Flats	depth, depth^2, velocity, velocity^2, p_{234}, p_{56}	depth, depth^2, velocity, p_{234}, p_{56}	99.71	103.821	4.11	1	0.043
		depth, depth^2, p_{234}, p_{56}[a]	99.71	104.619	4.91	2	0.086

[a] Best model.

Appendix D. Allele frequencies for early and late run, male and female, tributary spawning sockeye salmon originating from Glacier Flats and Nikolai creeks, Tustumena Lake, Alaska, 1994.

Locus Allele(bp)		Glacier Flats Creek ♀ Early	♀ Late	♂ Early	♂ Late	Nikolai Creek ♀ Early	♀ Late	♂ Early	♂ Late	Early Run ♀♂Glacier	♀♂Nikolai	Late Run ♀♂Glacier	♀♂Nikolai
Oneμ1	n =	48	47	43	46	53	50	52	48	91	105	93	98
110		0.000	0.000	0.000	0.011	0.000	0.000	0.000	0.000	0.000	0.000	0.005	0.000
112		0.083	0.106	0.151	0.120	0.066	0.060	0.115	0.104	0.115	0.090	0.113	0.082
114		0.917	0.819	0.802	0.826	0.887	0.930	0.885	0.854	0.863	0.886	0.823	0.893
116		0.000	0.021	0.023	0.000	0.047	0.010	0.000	0.010	0.011	0.024	0.011	0.010
118		0.000	0.053	0.023	0.043	0.000	0.000	0.000	0.031	0.011	0.000	0.048	0.015
Oneμ11	n =	46	46	43	45	53	50	51	48	88	104	91	98
146		0.054	0.043	0.081	0.089	0.094	0.090	0.069	0.042	0.067	0.082	0.066	0.066
150		0.728	0.750	0.616	0.656	0.623	0.610	0.637	0.604	0.674	0.630	0.703	0.607
156		0.207	0.207	0.302	0.244	0.283	0.300	0.284	0.354	0.253	0.284	0.225	0.327
158		0.011	0.000	0.000	0.011	0.000	0.000	0.010	0.000	0.006	0.005	0.005	0.000
Oneμ14	n =	47	49	43	42	53	50	52	48	90	105	101	98
129		0.106	0.041	0.198	0.107	0.066	0.070	0.096	0.073	0.150	0.071	0.081	0.071
133		0.000	0.020	0.000	0.024	0.000	0.020	0.019	0.010	0.000	0.022	0.010	0.015
135		0.149	0.173	0.174	0.190	0.170	0.190	0.154	0.135	0.161	0.181	0.162	0.163
137		0.011	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.006	0.000	0.000	0.000
139		0.000	0.000	0.023	0.000	0.009	0.010	0.000	0.000	0.011	0.000	0.005	0.005
141		0.043	0.061	0.023	0.012	0.009	0.000	0.000	0.021	0.033	0.038	0.005	0.010
143		0.000	0.031	0.012	0.000	0.028	0.010	0.019	0.010	0.006	0.016	0.024	0.010
145		0.213	0.153	0.035	0.202	0.358	0.210	0.183	0.010	0.128	0.176	0.271	0.112
147		0.287	0.347	0.337	0.214	0.104	0.230	0.250	0.500	0.311	0.286	0.176	0.362
149		0.011	0.000	0.012	0.024	0.028	0.020	0.019	0.021	0.011	0.011	0.024	0.020
151		0.128	0.163	0.186	0.179	0.198	0.210	0.173	0.177	0.156	0.170	0.186	0.194
153		0.000	0.000	0.000	0.000	0.009	0.000	0.019	0.000	0.000	0.000	0.014	0.000
155		0.011	0.000	0.000	0.012	0.009	0.020	0.019	0.031	0.006	0.005	0.014	0.026
161		0.043	0.010	0.000	0.036	0.009	0.010	0.048	0.010	0.022	0.022	0.029	0.010

		Glacier Flats Creek				Nikolai Creek				Early Run		Late Run	
Locus Allele(bp)		♀ Early	♀ Late	♂ Early	♂ Late	♀ Early	♀ Late	♂ Early	♂ Late	♀♂ Glacier	♀♂ Nikolai	♀♂ Glacier	♀♂ Nikolai
Oneμ2	n =	47	45	43	45	50	48	51	47	90	101	90	95
256		0.000	0.000	0.000	0.000	0.010	0.000	0.000	0.000	0.000	0.005	0.000	0.000
262		0.032	0.000	0.000	0.000	0.010	0.000	0.010	0.011	0.017	0.010	0.000	0.005
264		0.064	0.178	0.035	0.178	0.090	0.094	0.127	0.064	0.050	0.109	0.178	0.079
266		0.085	0.089	0.174	0.044	0.060	0.125	0.059	0.085	0.128	0.059	0.067	0.105
268		0.096	0.100	0.047	0.111	0.050	0.073	0.039	0.074	0.072	0.045	0.106	0.074
270		0.309	0.278	0.267	0.300	0.190	0.250	0.304	0.202	0.289	0.248	0.289	0.226
272		0.043	0.067	0.151	0.122	0.090	0.104	0.098	0.085	0.094	0.094	0.094	0.095
274		0.000	0.022	0.000	0.022	0.020	0.000	0.029	0.032	0.000	0.025	0.022	0.016
276		0.064	0.033	0.035	0.011	0.070	0.031	0.029	0.021	0.050	0.050	0.022	0.026
278		0.266	0.156	0.267	0.133	0.280	0.302	0.206	0.351	0.267	0.243	0.144	0.326
280		0.043	0.067	0.012	0.056	0.090	0.000	0.059	0.043	0.028	0.074	0.061	0.021
282		0.000	0.011	0.012	0.000	0.030	0.021	0.039	0.021	0.006	0.035	0.006	0.021
Oneμ8	n =	45	42	43	41	50	40	51	43	88	101	83	83
194		0.011	0.024	0.047	0.000	0.020	0.038	0.020	0.035	0.028	0.020	0.012	0.036
196		0.000	0.000	0.000	0.000	0.000	0.025	0.000	0.012	0.000	0.000	0.000	0.018
198		0.133	0.143	0.163	0.195	0.100	0.100	0.118	0.174	0.148	0.109	0.169	0.139
200		0.244	0.357	0.233	0.207	0.230	0.262	0.206	0.256	0.239	0.218	0.283	0.259
202		0.000	0.000	0.000	0.000	0.000	0.013	0.010	0.000	0.000	0.005	0.000	0.006
204		0.456	0.381	0.419	0.402	0.460	0.400	0.490	0.349	0.438	0.475	0.392	0.373
206		0.089	0.071	0.070	0.061	0.100	0.063	0.078	0.105	0.080	0.089	0.066	0.084
208		0.011	0.000	0.023	0.024	0.010	0.013	0.000	0.000	0.017	0.005	0.012	0.006
210		0.000	0.000	0.000	0.012	0.000	0.000	0.000	0.000	0.000	0.000	0.006	0.000
212		0.000	0.000	0.000	0.000	0.000	0.000	0.010	0.012	0.000	0.005	0.000	0.006
214		0.022	0.024	0.047	0.049	0.060	0.063	0.029	0.035	0.034	0.045	0.036	0.048
224		0.033	0.000	0.000	0.049	0.020	0.025	0.039	0.023	0.017	0.030	0.024	0.024

Locus Allele(bp)		Glacier Flats Creek				Nikolai Creek				Early Run		Late Run	
		♀ Early	♀ Late	♂ Early	♂ Late	♀ Early	♀ Late	♂ Early	♂ Late	♀♂ Glacier	♀♂ Nikolai	♀♂ Glacier	♀♂ Nikolai
	n =	45	44	41	37	48	37	51	44	86	99	81	81
*Ssa*85													
121		0.000	0.000	0.000	0.000	0.000	0.000	0.020	0.000	0.000	0.010	0.000	0.000
129		0.033	0.068	0.061	0.041	0.083	0.027	0.029	0.045	0.047	0.056	0.056	0.037
133		0.000	0.000	0.000	0.000	0.010	0.014	0.010	0.000	0.000	0.010	0.000	0.006
135		0.167	0.159	0.220	0.189	0.198	0.108	0.206	0.136	0.192	0.202	0.173	0.123
137		0.500	0.466	0.439	0.486	0.229	0.500	0.324	0.386	0.471	0.278	0.475	0.438
139		0.111	0.091	0.159	0.122	0.156	0.122	0.157	0.148	0.134	0.157	0.105	0.136
141		0.000	0.023	0.000	0.000	0.125	0.027	0.010	0.023	0.000	0.066	0.012	0.025
143		0.078	0.068	0.037	0.054	0.063	0.027	0.088	0.080	0.058	0.076	0.062	0.056
145		0.033	0.034	0.037	0.000	0.031	0.041	0.029	0.034	0.035	0.030	0.019	0.037
147		0.011	0.011	0.000	0.054	0.000	0.000	0.010	0.011	0.006	0.005	0.031	0.006
149		0.022	0.034	0.000	0.000	0.010	0.027	0.010	0.000	0.012	0.010	0.019	0.012
151		0.000	0.000	0.000	0.041	0.000	0.000	0.010	0.011	0.000	0.005	0.019	0.006
159		0.022	0.000	0.000	0.000	0.031	0.014	0.029	0.045	0.012	0.030	0.000	0.031
165		0.000	0.000	0.000	0.000	0.000	0.014	0.000	0.000	0.000	0.000	0.000	0.006
171		0.000	0.000	0.000	0.000	0.000	0.014	0.000	0.011	0.000	0.000	0.000	0.012
173		0.022	0.023	0.037	0.014	0.010	0.027	0.049	0.045	0.029	0.030	0.019	0.037
175		0.000	0.000	0.000	0.000	0.042	0.000	0.000	0.000	0.000	0.020	0.000	0.000
177		0.000	0.011	0.000	0.000	0.010	0.014	0.010	0.011	0.000	0.010	0.006	0.012
179		0.000	0.011	0.000	0.000	0.000	0.027	0.000	0.011	0.000	0.000	0.006	0.019
181		0.000	0.000	0.012	0.000	0.000	0.000	0.010	0.000	0.006	0.005	0.000	0.000

CAROL ANN WOODY

EDUCATION

Ph.D. Fisheries, 1998, University of Washington, Seattle.
Dissertation title: Ecological, Morphological, Genetic, and Life History Comparison of Two Sockeye Salmon Populations, Tustumena Lake, Alaska.

M.S. Aquatic Ecology, 1988, with honors, University of Wisconsin, La Crosse.
Thesis title: Reproductive biology, growth, and verification of three fish hosts of *Magnonaias nervosa* (Rafinesque, 1820) (Bivalvia:Unionidae) in the east channel of navigation pool 10, upper Mississippi River.

B.S. Fishery and Wildlife Science, 1983, Utah State University, Logan.

EMPLOYMENT HISTORY

Research Fishery Biologist. GS-486-11. September 1993 to present. USGS-Biological Research Division, Alaska Biological Science Center, 1011 E. Tudor Road, Anchorage, AK 99503-6199. Responsibilities center on planning, conducting and reporting independent research regarding the ecology, genetics, life history, and patterns of adaptive significance of fish populations.

Fish Biologist. November 1992 - June 1993. Fisheries Research Institute. University of Washington, Box 357980, Seattle, WA 98195. Responsible for the data compilation, analysis, and preparation of three manuscripts regarding thermal tolerance and preference in coho salmon (see publications).

Fish Biologist. June 1992 - March 1993. HARZA Northwest Inc. 2353 130th Ave. Bellevue, WA 98005. Responsible for designing, conducting and reporting results of fish population and habitat assessment surveys using SCUBA. Provided input to local and international fish habitat impact assessments regarding timber harvest, dam construction, and other anthropogenic activities.

Biological Technician (Fisheries). October 1991 - March 1992. Fishery Research Institute, University of Washington, Box 357980, Seattle, WA 98195. Assisted Ph.D. student John Konecki in conducting thermal tolerance, behavioral preference, and egg incubation research on coho salmon in Washington. Assisted in studies to understand the ecology of sockeye salmon and their habitats in Iliamna Lake, Alaska.

Fish and Wildlife Biologist. January 1988 - October 1991. GS-9. U.S. Forest Service, Tongass National Forest, Stikine Area, P.O. Box 309, Petersburg, AK 99833. Responsible for the design, implementation, and reporting of the District fish and wildlife program. Duties included deer population census; bald eagle population mapping and the sampling of individuals for baseline heavy metal concentrations; moose habitat enhancement; black bear range mapping; chum salmon stream-side egg incubation projects; stream side rehabilitation; fishing trail and educational exhibit design and construction. Provided input and recommendations to the timber harvest program to minimize impacts of harvest on fish habitat.

Fishery Research Assistant. April 1986 - June 1988. University of Wisconsin, La Crosse, WI 54601, in cooperation with the U.S. National Fishery Research Laboratory, 2630 Fanta Reed Road, La Crosse, WI 54601. Designed, conducted, analyzed, and published original research on the life history and biology of a commercially exploited freshwater mussel as part of a Masters research project.

Peace Corps Volunteer (Fisheries). October 1983 - August 1985. Peace Corps Fisheries Volunteer (Ecuador, South America). U.S. Peace Corps, Washington, D.C. 20526.

Other Experience

June 1983 - August 1983. Biological Technician. U.S. Fish and Wildlife Service, Waterfowl Population Surveys, MBMO, Columbia, MO 65201.

May 1982 - May 1983. Biological Technician. Utah State University, Ecology and Range Departments. Logan, UT 84322.

June 1980 - September 1980 and April 1981 - September 1981. Research Technician. Kemp's Atlantic Ridley Turtle Recovery Project. Tamaulipas, Mexico. Administered by the Gladys Porter Zoo, 500 Ringgold St., Brownsville, TX 78520.

June 1979 - Sept 1979. Fisheries Technician. Utah Division of Wildlife Resources. 1596 So. Temple, Salt Lake City, UT 84116.

SOCIETY AND COMMITTEE PARTICIPATION

Office Held – President-elect, Alaska Chapter of the American Fisheries Society-1998.
Committee Member – American Fisheries Society, Endangered Species Committee

PUBLICATIONS

Woody, C. A., J. Olsen, P. Bentzen, and J. Reynolds. In Review. Temporal variation in genetic and phenotypic traits of two sockeye salmon populations, Tustumena Lake, Alaska. Transactions of the American Fisheries Society.

Woody, C. A. In review. Bears and salmon: considering other species in biological escapement assessments. Ecosystem considerations in fishery management. Proceedings of the conference of the Western Division of the American Fisheries Society.

Konecki, J. T., C. Woody, and T. P. Quinn. 1995. Temperature preference in two populations of juvenile coho salmon (*Oncorhynchus kisutch*). Environmental Biology of Fishes. 44: 417 - 421.

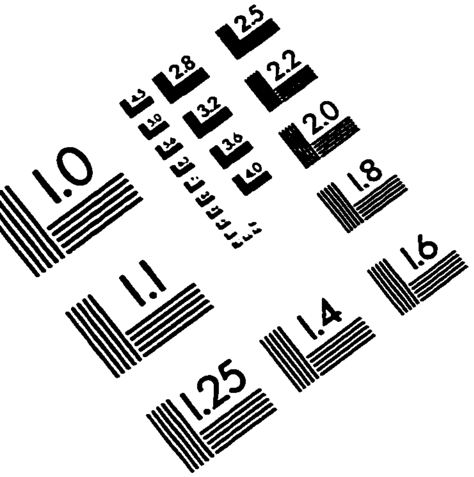
Konecki, J. T., C. Woody, and T. P. Quinn. 1995. Critical thermal maxima of coho salmon (*Oncorhynchus kisutch*) fry under field and laboratory acclimation regimes. Canadian Journal of Zoology. 73: 993 - 996.

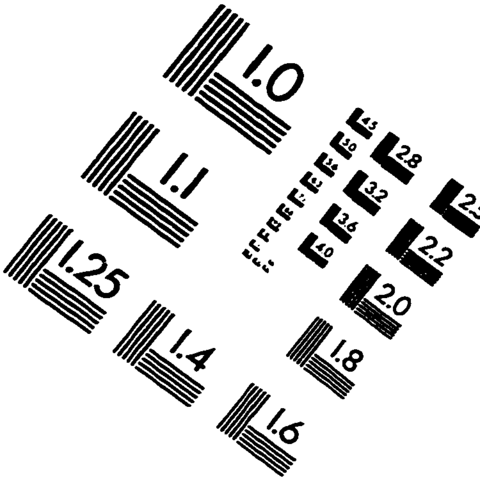
Konecki, J. T., C. Woody, and T. P. Quinn. 1995. Influence of temperature on incubation rates of coho salmon (*Oncorhynchus kisutch*) from ten Washington populations. Northwest Science, 69(2): 126-132.

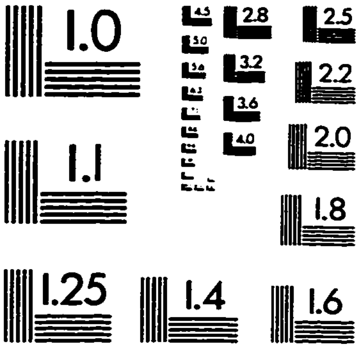
Woody, C. A. and L. Holland - Bartels. 1993. Reproductive characteristics of a population of washboard mussels, *Megalonaias nervosa* (Rafinesque 1820), in the upper Mississippi River. Journal of Freshwater Ecology. 8: 57 - 66.

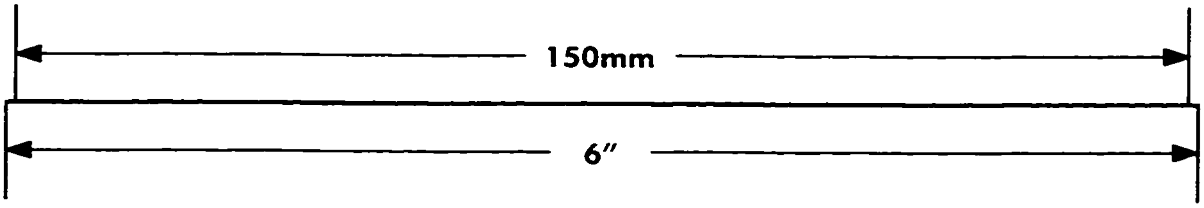
Woody, C. A. and S. Riefensthul. 1991. Streamside incubation of chum salmon eggs at two streams on Kuiu Island, Alaska. Proceedings of the 15th N.E. Pacific pink and chum salmon workshop. Pacific Salmon Commission. Vancouver, B.C.

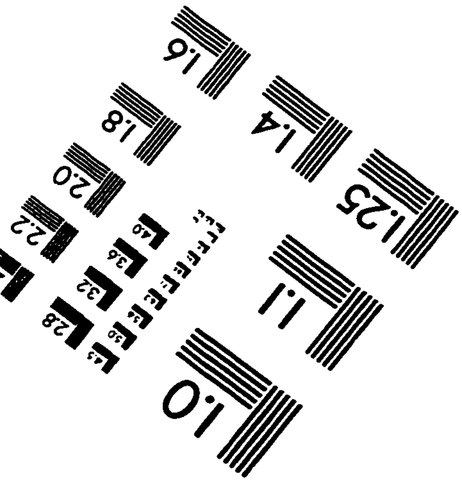
IMAGE EVALUATION TEST TARGET (QA-3)











APPLIED IMAGE . Inc
1653 East Main Street
Rochester, NY 14609 USA
Phone: 716/482-0300
Fax: 716/288-5989