SAFS-UW-0701
March 2007

Alaska Salmon Research 2006

ANNUAL REPORT

Alaska Salmon Program
University of Washington
School of Aquatic & Fishery Sciences

http://fish.washington.edu/alaska

The recommended format for citing this report is as follows:

Alaska Salmon Program. 2007. Alaska salmon research 2006. Univ. Washington, School of Aquatic & Fishery Sciences, SAFS-UW-0701. Seattle.

It was not practical to list authorship for the numerous report components written by faculty and staff. The following authors contributed significantly to the report:

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Acknowledgments

A project of this scope owes a great debt to a wide range of individuals and agencies. The biggest debt is to the Fisheries Research Institute faculty and staff who founded the program, set up the data collection systems, and maintained the program until the current faculty staff and students were lucky enough to inherit it. William F Thompson, Robert "Bud" Burgner, Ole Mathisen, and Don Rogers deserve special mention. Equally important were the visionary members of the processing industry, who saw the need, found the people to do the work, and provided the majority of the funding for over 50 years. Our research would not be possible without the active support of the local communities and agencies, especially the communities of Aleknagik, Iliamna, and Pedro Bay, but addditionally the Wood–Tikchik State Park authorities, Alaska Department of Fish and Game, Bristol Bay Science and Research Institute, Bristol Bay Native Association, and Bristol Bay Economic Development Corporation.

We thank program member Gordon Holtgrieve for his assistance in generating the maps displayed on pages 35-38.

The current supporters of the teaching and research include the Bristol Bay Processors, Chignik Regional Aquaculture Association, Gordon and Betty Moore Foundation, National Science Foundation, NOAA Fisheries, Pew Institute of Ocean Sciences, and the University of Washington.

Ole Mathisen, 1919-2007

Ole Alfred Mathisen passed away on March 12, 2007, at the age of 88. He was born in Oslo, Norway on February 9, 1919, and studied zoology at the University of Oslo. During World War II he served in the Norwegian Underground Service. He came to the USA after the war to continue his studies at the University of Washington and earned his PhD in Fisheries Biology in 1955.

He was a Professor at the College of Fisheries, University of Washington, teaching and conducting research, from 1955 to 1982. During this time he spent summers in Bristol Bay, Alaska studying the population dynamics of sockeye salmon. In 1983, he became the Dean of the College of Fisheries and Ocean Science, University of Alaska in Juneau. He served as a visiting scholar at the University of Moscow during 1960–1961 and also was a Fulbright Scholar in Norway during 1965–1966 and in Malaysia during 1988–1989.

During his professional life Ole participated in many scientific expeditions to regions ranging from the Bikini Atoll to the Antarctic to South America and the African continent. After his retirement from the University of Alaska he built a log cabin near Friday Harbor on San Juan Island, Washington where he continued his research and many professional activities.

Tom Quinn of the Alaska Salmon Program and School of Aquatic & Fishery Sciences faculty member, credits Ole with helping to establish one of the longest-running and most comprehensive research programs of its kind, paving the way for modern conservation and sustainable fisheries:

> To say that Ole Mathisen cast a big shadow would be quite an understatement. He was one of the true pioneers of the Fisheries Research Institute, building not only the research program but the cabins as well. Both were built on solid foundations and are strong today. Ole Mathisen, Bud Burgner, Don Bevan and Don Rogers were exceptional scientists, who had great insights into the ecology of salmon. They came into areas that were very poorly known, prior to Alaska's statehood, and designed long-term research programs that have yielded a rich storehouse of knowledge about the interactions between salmon, density, and climate. Before there was talk about climate change, those men were establishing datasets on lake level, ice-breakup, temperature, and host of other things that now reveal the process of global warming. Terms like conservation biology, ecosystem management, and biodiversity were not part of their lexicon either but there writings clearly showed their commitment to conservation and sustainable fisheries, salmon runs, and the ecosystems on which they depend. With the passing of Ole Mathisen we have lost a giant in Pacific Northwest fisheries science but his legacy lives on in the programs he helped start.

He is survived by his wife of 58 years, Randi, his two children and their spouses, Sven and Gro and granddaughters, Karine and Benedikte of Oslo, Norway and Heidi and Klaus and grandchildren Kristiaan and Annika of Seattle and many friends and former students all over the world.

Remembrances may be sent to the Nordic Heritage Museum, 3014 NW 67th Street, Seattle WA 98117 (http://www.nordicmuseum.org).

1. Introduction

The year 2006 marked the 61st year of field work in Bristol Bay for our program and marks the continued growth of both the field program and analytic work conducted at the University of Washington. In the summer of 2006, we saw a new high for activity in our field camps with 2,830 person days—we had a full field season in the Chignik–Black Lake system for the second consecutive year, had a significantly longer field season at Iliamna Lake, and taught the AERA undergraduate field ecology class for the eighth year at the Aleknagik and Iliamna camps. The core of our program research remains focused on the biology and management of the salmon of western Alaska, but we continue to broaden the scope of the program with the work of professors Lorenz Hauser (University of Washington), who pursues genetic studies, and Gunnar Knapp (University of Alaska Anchorage) and Chris Costello (University of California at Santa Barbara), who conduct economic studies. In addition to the UW faculty, staff, and students, we also now have ongoing research and teaching participation with Professor Milo Adkison (University of Alaska Juneau) and Carl Walters (University of British Columbia).

This report provides an overview of the research and teaching activities conducted under the umbrella of the Alaska Salmon Program—the name we use at the UW to represent the various activities centered around our field facilities in Bristol Bay and the Chignik Lake system. It is organized into general themes, and within each theme, brief summaries of our activities and any major results are presented. We expect that few readers will read this report from cover to cover, but rather will read specific topics based upon their individual interests. Much of the material reported herein is also on our website, http://fish.washington.edu/alaska. In addition, reference maps for the general research areas and specific study sites are provided on pages 35-39.

Since 1946, our work has been largely funded by the processing industry of Bristol Bay, and the program would have disappeared many years ago without their continued financial and political support. The University of Washington has also supported the program over the last 60 years through combinations of funding for facilities and staff salaries. The UW support increased considerably when we began teaching an undergraduate course in Alaska in 1999. We received a major increase in funding in 2005 with significant grants from the National Science Foundation, the Gordon and Betty Moore Foundation, and the Pew Institute of Ocean Sciences.

The Alaska salmon research program was initiated in 1947 under the auspices of the Fisheries Research Institute (FRI), which was originally affiliated with the UW Graduate School. In 1958, it became a department within the newly organized College of Fisheries. By the mid-1980s, FRI was a division within the School of Fisheries, and by the mid-1990s, when school divisions were eliminated, FRI as an institutional unit ceased to exist. However, we continue to use the term FRI in our relationships with outside organizations for our Alaskan salmon work.

2. Fisheries Management

Introduction

Preseason and inseason forecasting continue to be central features of our fisheries management activities. Preseason forecasts are very important to processors and fishermen for planning their capacity for the coming season, and the conservation concerns about Kvichak have meant that the preseason forecast has special importance with regard to whether the fisheries in Naknek and Egegik operate in restricted boundaries at the beginning of the season. In addition, we have a number of projects associated with escapement goals and are working closely with ADFG on methods for evaluating alternative harvest strategies. While the traditional analysis of escapement goals has been focused only on maximum harvest, the need to increase profitability in the processing and harvesting industries has caused us to explore the economic implications as well as the biological implications of harvest strategies.

2006 Preseason Review

The 2006 forecast was 14 percent lower than the observed inshore returns to Bristol Bay (Table 2.1). The largest differences between the forecasted and observed returns can be attributed to the Nushagak and Egegik districts. In the Nushagak district, we predicted only 3.9 million fish to return to the Wood River and actual production was 11.6 million. The forecast error in the Wood River system was due to the large returns of both the 1.2 and 1.3 age classes; this may imply an increase in ocean survival between 2005 and 2006 that our preseason model would not have detected. The error in the Egegik forecast continues to plague our accuracy—our forecast in 2006 was 4.5 million higher than the observed returns. The work by Bob Lessard may hold clues about where the error in the Egegik forecast is occurring. Alternatively, our forecast for the Kvichak River system was in line with observed returns. Our forecast of 2 million fish of the 1.2 age class to the Kvichak River system came under scrutiny because the parent escapement was only 700,000; however, the high survival rate is commensurate with historical recruits-per-spawner at low densities for that system.

Table 2.1. Difference in millions between the 2006 preseason forecast and the observed number of sockeye salmon returning to Bristol Bay, Alaska, by river system and age class. A negative means the preseason forecast was lower than the observed returns, and vise versa.

District	Ages				
River	1.2	1.3	2.2	2.3	Total
Naknek/Kvichak	0.0	-1.8	1.0	0.2	-0.6
Kvichak	-0.6	-1.0	0.4	-0.1	-1.3
Naknek	1.1	-1.2	0.4	0.4	0.6
Alagnak	-0.5	0.4	0.2	0.0	0.1
Egegik	2.0	-0.2	3.6	-0.9	4.5
Ugashik	-0.5	-0.3	0.7	0.1	0.1
Nushagak	-4.2	-4.1	-0.5	-0.9	-9.6
Wood R.	-4.1	-2.6	-0.5	-0.4	-7.7
Nushagak	0.0	-0.6	0.0	-0.4	-1.0
Igushik	-0.1	-0.8	0.0	0.0	-0.9
Togiak	-0.1	-0.1	-0.1	-0.1	-0.4
Totals	-2.7	-6.5	4.8	-1.4	-5.9

2007 Preseason Forecast

The 2007 Bristol Bay forecast is 35.32 million fish (Table 2.2) for a total catch of 28.3 million with an estimated weight of 161.6 million lb. While the expected number of fish harvested is fewer than last year, the pounds of fish harvested will be very similar if we see average-sized fish for their age. We produced forecasts for all nine major rivers (Kvichak, Alagnak, Naknek, Egegik, Ugashik, Wood, Igushik, Nushagak–Mulchatna, and Togiak). We use only the ages 1.2, 1.3, 2.2, and 2.3 to produce the forecasts. To determine the catch in pounds for each age class, we subtracted the escapement proportional to the age-specific forecast, then multiplied this forecasted catch by the average weight of 2- or 3-ocean fish.

Inseason Forecasting 2006

Three topics arose during the inseason forecasting in 2006: fish size, offshore distribution at Port Moller, and Port Moller genetics.

Table 2.2. The 2007 preseason forecast of the number of sockeye salmon in millions returning to the Bristol Bay, Alaska, by river system and age class.

District	Ages				
River	1.2	1.3	2.2	2.3	Total
Naknek/Kvichak	3.41	5.07	1.79	0.99	11.26
Kvichak	2.41	0.56	0.97	0.20	4.14
Naknek	0.79	3.36	0.57	0.74	5.46
Alagnak	0.21	1.15	0.25	0.05	1.66
Egegik	1.86	2.48	2.58	2.05	8.97
Ugashik	2.99	1.83	0.82	0.28	5.92
Nushagak	2.49	5.5	0.17	0.17	8.33
Wood R.	2.10	3.44	0.11	0.12	5.77
Nushagak	0.18	1.08	0.03	0.02	1.31
Igushik	0.21	0.98	0.03	0.03	1.25
Togiak	0.13	0.64	0.03	0.04	0.84
Totals	10.88	15.52	5.39	3.53	35.32

First, fish size was the dominant topic during the 2006 inseason forecasting. The fish were extremely small for their age, which resulted in a number of questions about the accuracy of the Port Moller index because of changes in the selectivity of the test fishery net. In fact, the Port Moller index proved to be accurate throughout most of season, with consistent forecasts of 35–45 million fish. Further, fish size did not affect the data we received from the fishing districts. This is because our inseason model uses total returns to the five major districts, regardless of whether the fish are observed in the catch or the escapement.

Second, the distribution of fish offshore from Port Moller did create issues for our inseason model. The distribution of fish offshore normally looks like a single bell-shaped curve, with the peak of the distribution occurring between stations 4 and 8. The curve can be skewed to the inside or the outside, but our model integrates across all the stations to get a daily index based on the assumption that distribution has only one peak. In 2006, however, the fish were distributed in two peaks offshore. We were able to reconfigure the inseason model to account for the anomalous distribution, which ultimately led to more accurate forecasts beginning in July.

Third, the reason for the second peak in the offshore distribution was apparent as genetics information was collected and analyzed. On the basis of genetics information, the fish located farthest offshore, and representing the second peak in the distribution, were almost entirely fish bound for the Nushagak district. We continue to see the genetics data as a valuable asset to improving the accuracy of our inseason forecasting model although this season we will need to begin addressing issues surrounding the sampling design.

Escapement Goal Analysis

RB Lessard (research scientist)

Prior to each fishing season, Bristol Bay managers set target escapement goals for sockeye salmon entering each river system. The targets reflect biological conservation objectives and optimal yield objectives. In recent years, escapement targets have also captured long-term sustainability goals within accepted ranges of variability. Goals are set by the Alaska Board of Fisheries and are based on the scientific advice of research staff at ADFG. The UW School of Aquatic and Fishery Sciences faculty and staff routinely work with ADFG on run reconstruction, forecasting, and escapement goal analysis. Software has been developed for the purpose of analyzing Bristol Bay sockeye population trends and establishing alternative escapement goals through the analysis of models that predict population trends.

The traditional approach to setting escapement goals has been to use Ricker or Beverton–Holt stock–recruitment relationships to calculate the spawning stock size that produces the highest average catch. In our current work, we are developing models and software to incorporate multiple objectives more easily when establishing escapement goals. The models predict population trends at intermediate stages of life history so that model output can be compared with data sources other than spawning escapement and total adult returns. One of the key advantages of using an explicit life-history model is that it separates freshwater and ocean phases and is sensitive to the contrast in adult age classes, leading to greater sensitivity in detecting density dependence. The software includes policy search tools capable of setting policy variables that emphasize more objectives than simply average yield. Examples of objectives include the economic value of the catch as a function variable, and fixed industry costs as well as social and economic costs of high inter-annual catch variability.

The software first estimates parameters that predict the best statistical model fit to empirical trends. The model that uses the estimated parameters is then treated as the best predictor of system behavior. The software can then be used to find maximum sustained yield (MSY) harvest rates (U_{MSY}), fixed escapements (S_{MSY}), and threshold harvest rate policies. Policy variables are estimated by predicting the population dynamics of a system using estimated parameters and then using the model predictions to find policy variables that optimize desired catch objectives.

The software includes several different models of the life history of Bristol Bay sockeye, each of which makes distinct assumptions about sockeye behavior, the environment, and the statistical nature of the data. Each model can be used to predict population trends and then to establish escapement goals. There is a built-in feature that performs Markov Chain Monte Carlo (MCMC) simulations. The uncertainty in policy variables (U_{MSY} and S_{MSY}) can be estimated from the parameter values drawn from MCMC simulations.

The current phase of software development was demonstrated at a workshop in Anchorage in December 2006. ADFG managers used the software in hands-on exercises of escapement goal analysis of Bristol Bay stocks. Workshop attendees fit models to data, performed MCMC simulations, and compared escapement targets that would have been obtained from traditional Ricker and Beverton–Holt analyses with those that were obtained from the new software (Figs. 2.1 and 2.2).

The life-history models at the core of the software are being used as the basis for exploring various issues of concern regarding the ecology and management of Bristol Bay sockeye. They are designed to explore environmental, economic, industrial, and ecological questions equally well. The policy search tool is a flexible environment for

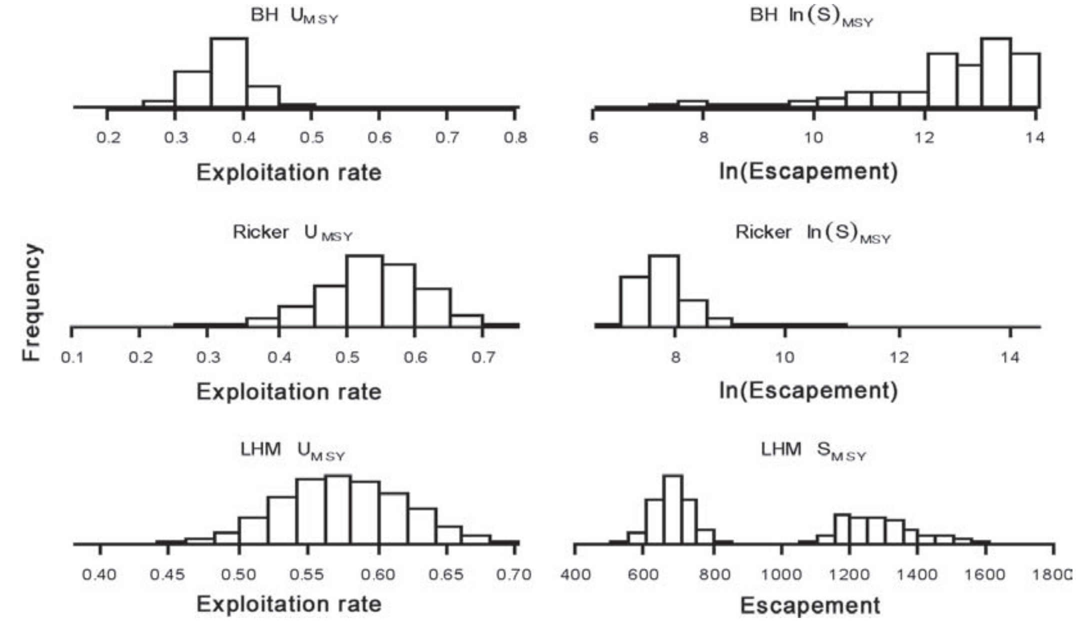


Figure 2.1. Posterior distributions of estimated U_{MSY} and S_{MSY} obtained from random samples of Markov Chain Monte Carlo (MCMC) simulated parameter estimates. Histograms represent the relative probability that policy variables on the x-axis are true optima. Beverton-Holt and Ricker S_{MSY} are shown in log-scale, illustrating the failure of those approaches to detect density dependence and leading to extremely high S_{MSY} estimates.

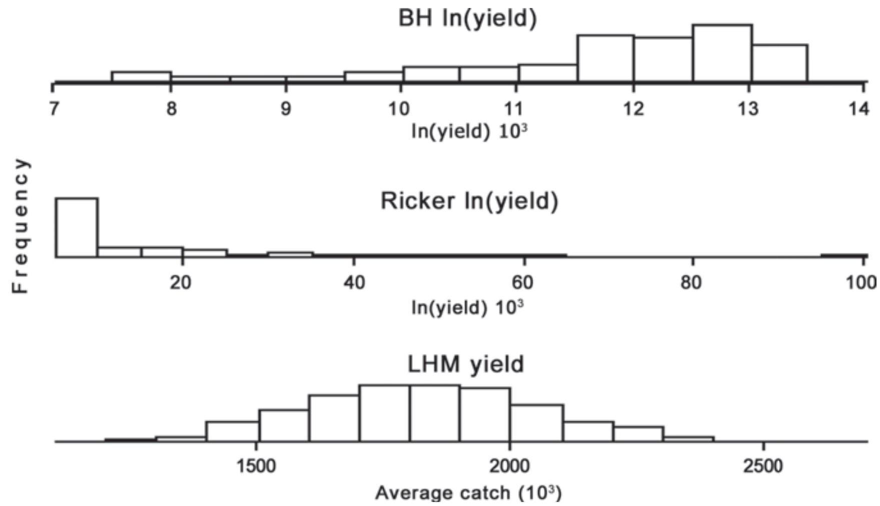


Figure 2.2. Posterior estimate of yield obtained from random samples of MCMC simulated parameters estimates. Histograms show the relative probability of realizing the yield values on the x-axis.

formulating policies that meet complex economic and biological objectives. As an integrated software suite, the tools are useful for escapement goal analysis for the purpose of scientific research as well as for teaching and workshop environments.

Marine Density Dependence and Pacific Salmon Production

N Taylor (research scientist)

Marine competition may affect survival and growth of Pacific salmon. Interspecific competition, in particular with pink salmon, has been shown to influence growth and survival of other salmon species but in some cases, intraspecific competition is more important (Ruggerone and Nielsen 2004). The effects of both kinds of competition are important with regard to total salmon production, which—in large part due to hatcheries—has been increasing for the last 50 years (Rogers and Ruggerone 1993, Rogers 2001).

Hatchery releases have increased in the last 25 years and there is considerable debate about how such releases affect wild salmon stocks. While some authors defend hatcheries (Brannon et al. 2004), increased hatchery outputs have corresponded with decreased Snake River spring chinook (Levin et al. 2001); also, hatchery fish survive poorly (Hilborn 1992) and, at best, appear to replace wild stocks with no overall increase in population size (Sweeting et al. 2003, Zaporozhets and Zaporozhets 2004). Pacific salmon hatchery releases are huge in the Pacific with approximately 5 billion fry released annually (42%, 37%, 11%, and 10% from Japan, the USA, Russia, and Canada, respectively [North Pacific Anadromous Fisheries Commission]). Given their considerable overlap in oceanic distribution (Ruggerone et al. 2003, Seeb et al. 2004), such large hatchery releases may affect growth and survival of distant salmon stocks if there are ocean density-dependent effects.

As part of a large collaboration with researchers at the University of British Columbia, Simon Fraser University, and the UW, we created a spatially explicit model that includes density-dependent effects on growth and survival on overlapping ocean stocks. The model was parameterized using known distributions of sockeye, chum, and pink salmon (Tagaki et al. 1981, Ruggerone et al. 2003, Seeb et al. 2004, Armstrong et al. 2005) and fit to data for 135 Pacific salmon stocks. The reconstructions show that worldwide hatchery returns are now 150 million fish per year with wild numbers remaining more of less constant at approximately 500 million fish (Fig 2.3). Total reconstructed wild and hatchery Pacific salmon biomasses are now approximately 3 and 1.5 million tons, respectively (Fig 2.4). Hatchery production now comprises approximately 30% of total Pacific salmon biomass.

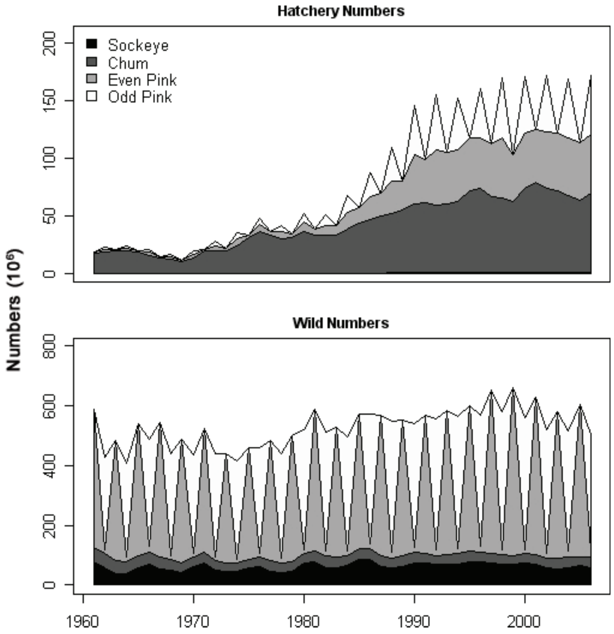


Figure 2.3. Total reconstructed returns (millions of fish), 1960–2006, for hatchery (top), and wild pink, chum, and sockeye salmon (bottom).

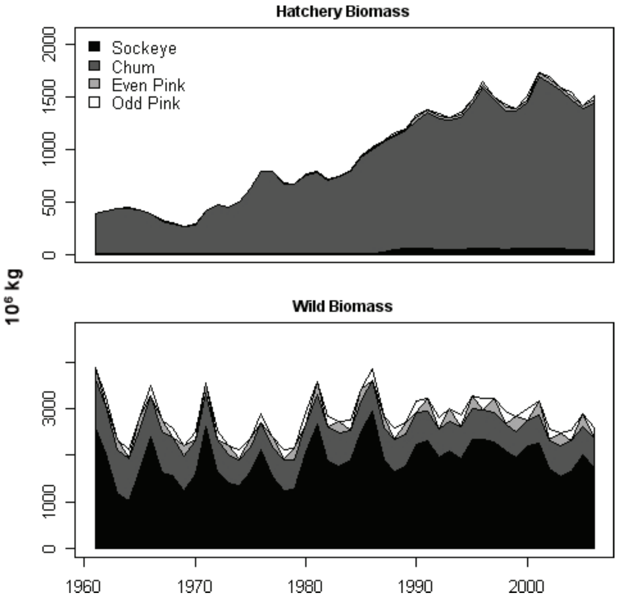


Figure 2.4. Total reconstructed biomass (in millions of kg), 1960–2006, for hatchery (top) and wild (bottom) Pacific salmon stocks.

Long-Term Fishery Selection on Length and Age at Maturity of Sockeye Salmon in Bristol Bay, Alaska

N Kendall (graduate student), T Quinn (adviser)

Certain types of fishing gear, specifically gillnets, often selectively remove individuals with respect to size, and can thus alter the distribution of life-history traits such as size and age at maturity among the fish surviving to breed. An increasing body of literature has warned of negative evolutionary changes resulting from fishery exploitation on wild populations. An economically and biologically important sockeye salmon gillnet fishery has been located at the Wood River system, Nushagak fishing district of Bristol Bay, for over 100 years. Past research suggested that this fishery is selective for size and age of sockeye based on gillnet mesh size and the timing of the fishery. However, fishing pressure and fishery management have varied greatly among years—owing to run size fluctuations, evolving fishing techniques and technology, and increased knowledge, such as of the effects of different mesh sizes on the size of fish caught—and long-term patterns of selection have not been examined.

We are investigating the magnitude and nature of gear selectivity by the Nushagak district gillnet fishery on length and age at maturity of the sockeye salmon across 6 decades (1946–2006) to quantify underlying fishery selection. The life-history patterns. age and size at maturity and size at age, of sockeye will be examined in the lake system as a whole as well as in individual spawning populations within the system. This project has two components. The first is a historical review of size- and age-selective fishing of the Nushagak district and Wood River system sockeye based on fishery data collected by UW and ADFG. The second component entails an assessment of the extent to which natural variation in size and age among discrete spawning populations within the Wood River system results in different exploitation rates, and a model of the effects of fishing on different life-history traits of the populations.

Since 1960, 18–78% of the sockeye salmon run has been caught by the fishery in a given year. This strong variability in the strength of the fishery results in differing yearly selection pressure on the sockeye as a whole. Fishery management strategies, including tactical measures (e.g., gillnet mesh size and material type regulations), harvest strategies, and fleet management and allocation techniques have varied over time.

In the past, gillnets were highly selective on larger, 3-ocean sockeye of both sexes because of mesh size and fishery timing (Burgner 1964). To assess these patterns in more detail over time, we calculated yearly vulnerability profiles, which describe the proportion of fish of a given length caught by the fishery in a given year (1946–2006). These values are scaled to 1 to be comparable between years. Our results show large variation in vulnerability to the fishery based on fish length, but these patterns also vary considerably among years, and between males and females. Vulnerability patterns have not always followed bell-shaped curves often used to characterize gillnet selectivity (Fig. 2.5).

We have also calculated standardized selection differentials, which describe the differences in mean length between fish who escape through the fishery to spawn versus those in the total run, before fishery selection. This value is divided by the standard deviation of the length of fish in the total run, allowing comparisons between years. These selection differentials reveal that the fishery has been more selective on females than on males over time, though it has become less size-selective on both males and females in recent years (Fig. 2.6). This may be due to the high exploitation rate of the fishery in more recent years and changing gillnet mesh-size regulations.

We are currently examining exploitation by the fishery of specific spawning populations. We will also assess whether and how fishery selectivity affects biocomplexity within the sockeye salmon populations of Wood River system. To do so, we have assembled the long-term data

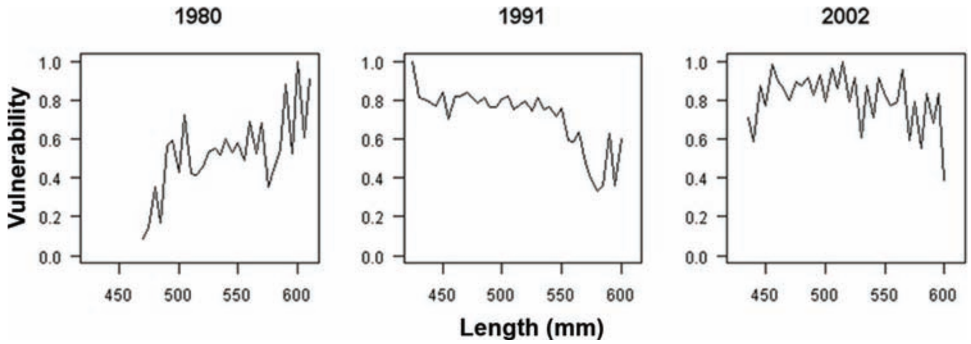


Figure 2.5. Vulnerability profiles for female Nushagak fishing district sockeye salmon for the years 1980, 1991, and 2002, showing different fishery exploitation patterns over time. Sufficient data to calculate vulnerability is not available for some lengths.

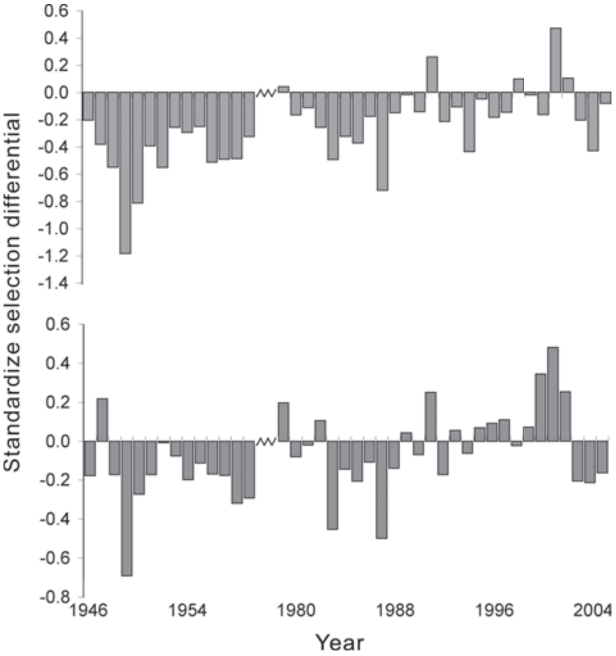


Figure 2.6. Standardized selection differentials of mean length, 1946–1959 and 1979–2005, for female and male sockeye salmon in the Nushagak fishing district, Bristol Bay, Alaska. Positive values indicate longer fish escaping to spawn; negative values show shorter fish escaping. Note y-axis magnitude differences for males vs. females.

on age composition among populations and all available data on length at age and morphology among populations. In 2005 and 2006, we took measurements on length at age in many populations that had not been sampled recently so that we could best estimate the overall size distribution (hence vulnerability to the fishery) of each spawning population. Finally, we will evaluate how fishing technology and management tools and techniques, including fishery opening schedules and gillnet regulations, can affect fishery selectivity and spawning population exploitation, and thus life-history traits and sustainable fishery yields. The goal of this analysis is to gain a greater understanding of fishery selectivity and its past and future effects on Wood River system spawning populations.

The Effects of Temporally Biased Fishing on Migration Patterns of the Wood River Sockeye Population, Bristol Bay, Alaska

KK Doctor (graduate student), T Quinn (adviser)

Sockeye salmon returning to the Wood River system are often subject to temporally biased fishing pressure that may target later returning individuals. To determine the effect that this fishing pressure may have on the discrete spawning populations within the Wood River system, we must define the temporal structure of their migration patterns. Depending on the migratory structure of the population, the selective depletion of individuals caused by temporally biased fishing pressure could act in different ways. Two scenarios are plausible:

1. All populations migrate through the fishery and upriver at the same time, even though they spawn at different times. Thus the populations are randomly distributed as they pass through the fishery and the harvest rate is applied equally to all populations.
2. Populations are temporally segregated in their migration timing through the fishery and upriver (e.g., early spawning populations might also migrate earlier than populations that spawn later). In this case, higher harvest rates late in the season would differentially intercept certain populations within the system.

To test these scenarios, we conducted a tagging study in the Wood River system during the 2006 upriver migration and spawning season. The migration period was divided into five distinct time periods and approximately 2,800 sockeye were tagged in each period (for a total of 14,000 sockeye). Tagged fish were then resighted in approximately 50 spawning sites (creeks, rivers, and beaches) throughout the Wood River system to determine whether temporal segregation existed in the upriver migration of the spawning populations. Preliminary analysis has been done to examine the following:

1. whether migration timing is correlated with arrival timing within a single spawning site, and
2. whether upriver migration timing varies systematically by habitat (e.g., creek, river, and lake beach), lake (Aleknagik vs. Nerka, etc.), or among spawning populations.

To determine whether migration timing paralleled timing of arrival, we analyzed data from Hansen Creek, where we were able to get the date of arrival for all the tags recovered. This data showed significant differences in arrival time between the first and the third migration periods (Fig. 2.7). This timing difference indicated that arrival date at Hansen Creek was correlated with the migration timing through the Wood River; thus, the first fish to migrate through the river were also the first to arrive at the spawning grounds. However, tags from all the migration periods were recovered in Hansen Creek (among the earliest spawning populations). These results tend to support the hypothesis that a temporally biased fishery would selectively remove later returning individuals of all populations if this pattern of arrival date were true for other populations.

Data were also analyzed to see whether locally adapted spawning populations are organized in their upriver migration timing by habitat and lake system. The analysis

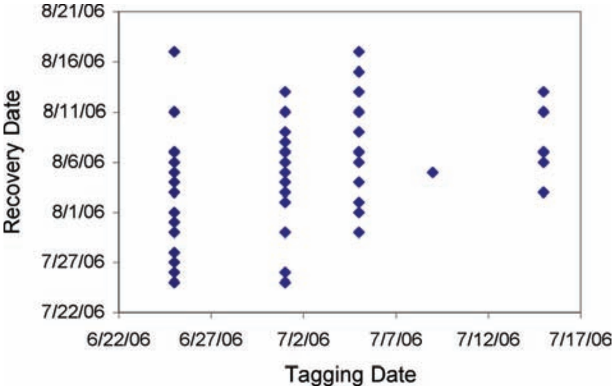


Figure 2.7. Number of tags recovered by tagging date (migration period) upon arrival at Hansen Creek, Wood River system, Bristol Bay, Alaska.

shows significant differences between habitats (Fig. 2.8). More tags from the first migration periods were recovered in creeks than from the later migration periods and, conversely, more tags recovered in the rivers were from the later migration periods. This suggests that creek spawners migrate through the Wood River before river spawners. The comparison between lake systems show no significant difference in the migration timing of spawners to Aleknagik, Nerka, and the upper lakes (aggregated in this analysis owing to small sample sizes; Fig. 2.9).

The results of this study may be confounded by some sampling bias in the river and beach spawning populations, as follows:

1. Sockeye salmon in creeks tended to spawn early and those in rivers and beaches tended to spawn late; our sampling efforts tended to favor the former part of the spawning season (creeks) over the latter part of spawning season (beaches).

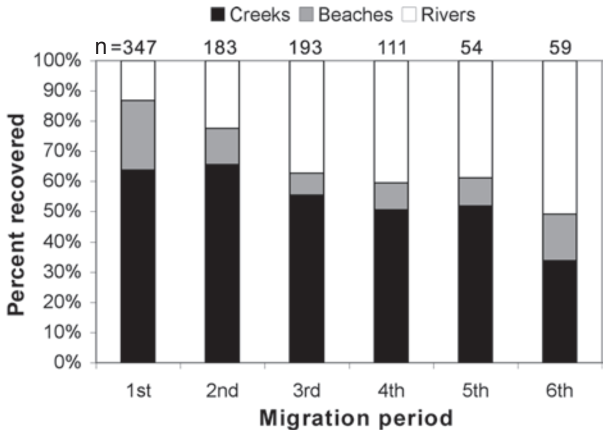


Figure 2.8. Percentage of tags from each migration period recovered in each spawning habitat (creeks, rivers, and beaches). Total number of tags recovered per period (n) is given in the top row of the graph.

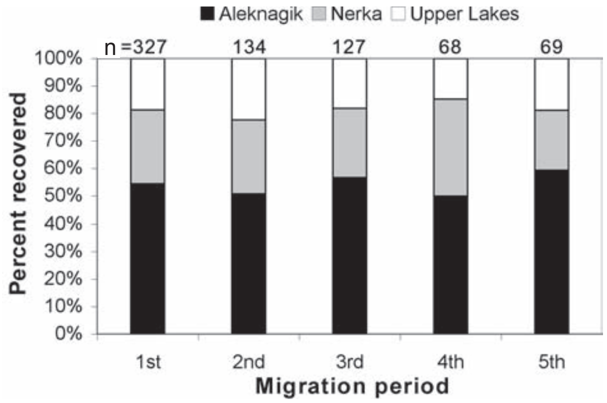


Figure 2.9. Percentage of tags from each migration period recovered in each lake system. Total number of tags recovered per period (n) is given in the top row.

2. The three types of spawning grounds differ from lake to lake. Our spawning efforts also varied between lakes and tended to heavily favor Lake Aleknagik and Lake Nerka sites. Thus, tag recoveries were underrepresented in the upper lakes, and the populations there comprise mostly beach spawners (which were difficult to sample).
3. The probability of seeing a tagged fish, given that it was present, was higher in creeks than in beaches and rivers, which was due to visibility and physical parameters of the spawning habitat.

Further analysis is being conducted to account for these biases in analysis of the data to test the hypotheses.

Fishery-Induced Delayed Mortality in Sockeye Salmon: Incidence and Consequences of Gillnet-Related Injury in Spawning Salmon at Natal Streams

M Baker (graduate student), D Schindler (adviser)

Commercial salmon fisheries are managed to meet escapement targets sufficient to ensure an adequate number of migrating adults reach natal streams to spawn. Many salmon counted in the escapement, however, suffer injuries related to their interaction with the fishery and ultimately fail to contribute to the reproductive capacity of escaped stocks (Fig. 2.10). Collateral mortality of target species that escape is rarely quantified and, while fishery-related mortality is included implicitly in the management of exploited populations of salmon, it has not been explicitly considered. The effects of this unaccounted mortality may have important implications for the estimation of stock–recruitment relationships, the designation of escapement targets in exploited populations, and evolutionary selection.

Figure 2.10. A female sockeye salmon exhibiting visible signs of gillnet-related injury (the severity of injury was ranked moderate).

Sockeye salmon in Bristol Bay, Alaska are caught with gillnets. The goals of our research are to estimate the incidence of gillnet-related injury among spawning adults at natal streams, determine the severity of injury and whether such injuries indicate a size-selective bias, investigate the physiological consequences of such injuries, and estimate the effect of fishery-related injury on prespawning mortality and reproductive success. We are also working to incorporate the effects of fishery-related delayed mortality into modeling of the population dynamics of exploited stocks. Damage to escaped stocks is an important consequence of the fishery directly relevant to escapement targets, especially if the incidence of injury varies from year to year. Distinguishing between total escapement (all fish that migrate past the fishery) and effective escapement (fish that are likely to survive the migration and spawn) should be considered in determining the relationship between spawning stock size and juvenile recruitment.

We conducted a series of beach seine samples at the mouths of creeks throughout the lower part of the Wood River system (see maps, p. 35-37) to estimate the incidence of gillnet-related injury among spawning adults, sampling between 200 and 500 fish at each site. Findings indicated substantial rates of injury ranging from 4% to 37%. Differences in the incidence of scarring between creeks were closely correlated with historical records for the timing of peak spawning activity ($R^2 = 0.93$). Creeks with later spawning populations exhibited significantly higher rates of scarring, perhaps related to differential holding times off the mouths of creeks or differential timing of the migration of these populations through the fishery.

To determine the effects of fishery-related injury on prespawning mortality and reproductive potential, we conducted a mark–recapture study, monitoring longevity, stream residence time, and spawning success. At the mouth of Pick Creek, Lake Nerka, 200 sockeye salmon (100 non-injured and 100 injured—roughly half with minor injuries and half with moderate to severe injuries) were anesthetized, measured and photographed, tagged with individually coded 3-cm Petersen disk tags, and released. Regular creek walks were conducted to monitor the fish throughout their lifespans (July 17–August 25).

A mark–recapture model developed by Lady and Skalski (1998) was adapted and used to develop a nonparametric estimator for stream life, based on conditional survival probabilities from one sampling event to the next. Subsequently, maximum likelihood estimation was used to derive survival and detection probabilities. Notable differences were observed between fish suffering from moderate and severe injuries as compared with those in the control group or suffering only minor injuries. Virtually all (98%) non-injured fish and the vast majority (92%) of fish with minor injuries were resighted at least once during the course of the survey, and most fish were observed repeatedly over the course of several weeks. Most moderately and severely injured fish were never resighted after the initial tagging and none were observed beyond the initial 2 weeks of the study. Total survival post-tagging, or longevity, was estimated to be less than 2 days on average for severely or moderately injured fish while fish with minor or no injuries lived an average of 18 days (Fig. 2.11). While pre-spawning mortality was highly correlated with the severity of injury, fungal infection of damaged tissue by a common water mold (*Saprolegnia* spp.) explained more of the variance in post-tagging survival and appears to be the proximate cause of premature death. Present in almost all freshwater systems in Alaska, *Saprolegnia* is a common affliction among salmon that are severely stressed or have compromised epidermal tissue, as is the case of most fish suffering gillnet-related injuries.

Surprisingly, fish with minor injuries lived slightly longer on average than those fish without injury. On average, however, uninjured fish had a longer stream residence time, which was our proxy for spawning success (Fig. 2.12). The enhanced post-tagging survival and reduced stream residence time exhibited by fish with minor injuries is likely linked to delayed maturation in response to stress due to fishery-related injuries. Fish with minor injuries entered the creek a full week later than those without injury and commonly exhibited visible signs of delayed maturity with regard to morphology and coloring. A subsequent tagging study was conducted to more closely examine the instream behavior of salmon with minor injuries to determine their ability to secure and defend territory, attract a mate, and successfully spawn. Additionally, we have begun to analyze blood samples to determine whether differences in hormonal levels related to stress and reproductive maturation exist between salmon that have experienced gillnet-related injury and those that have not. Such analyses will further examine the relationship between gillnet injury, physiological stress, and the suppression or delay of sexual maturity.

Since gillnets are size-selective, fishery-related damage to escaped stocks may also exert important evolutionary

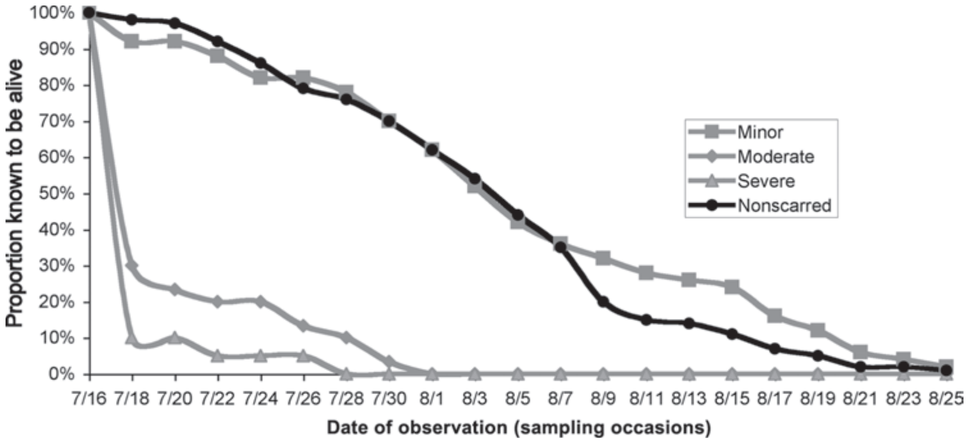


Figure 2.11. Plot of longevity (post-tagging survival) as a function of severity of gillnet-related injury, representing the relative proportions of fish known to be alive at any given sampling occasion over time.

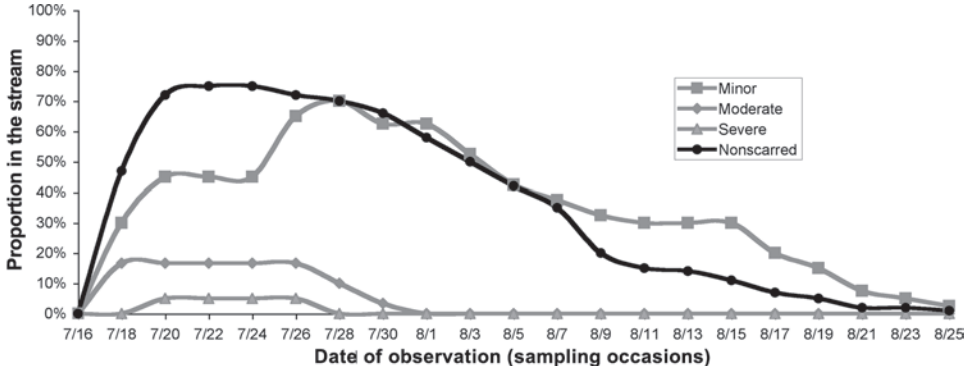


Figure 2.12. Plot of stream residence (time in stream) as a function of severity of gillnet-related injury, representing the relative proportion of fish assumed to be instream based on estimated detection and survival probabilities.

pressures on the morphology of exploited populations. While the length distributions of non-injured salmon are bimodal, representing the differences between 2- and 3-ocean fish (Fig. 2.13), the length distribution of injured fish is unimodal, largely reflecting larger 3-ocean fish. Thus, fishery-related scarring may be disadvantageous for a life-history strategy of longer ocean residence.

Research will continue to explore (1) fluctuations over time in the incidence and severity of gillnet injury, (2) the relationship between incidence of injury and intensity of fishing effort, (3) whether scarring has a size or sex-selective bias, (4) the effect of scarring on reproductive potential and spawning success, and (5) the causal mechanisms that lead to pre-spawning mortality in fish injured by the gillnet fishery.

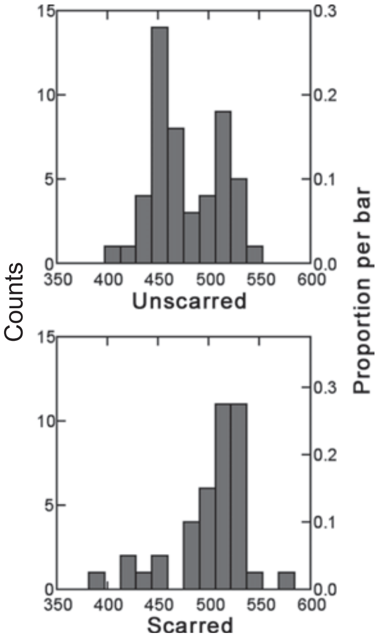


Figure 2.13. Plot of length distributions for injured and non-injured salmon.

3. Salmon Behavior and Ecology

Research on behavior and ecology has been a key component of the overall program of investigations on western Alaska sockeye salmon since the inception of the program. The numerous long- and short-term studies being conducted on adult and juvenile salmon are designed to address pressing questions related to management, and also broader questions related to the functioning of the ecosystem and the evolution of the fishes and other organisms that occupy it.

Starting with the sockeye salmon at sea on their homeward migration, we have recently investigated processes that affect (or correlate with) the timing of return migration (Hodgson et al. 2006), describing the general tendency for runs in the northern part of the range of sockeye salmon to be early after a warm spring, and the opposite pattern in southern areas. We have also studied the extent to which the fisheries in Bristol Bay (with emphasis on Egegik and Ugashik) have been selective for timing. The exploitation rate tends to be higher at the end than the beginning of the run, and evidence indicates that the escapements and indeed the runs as a whole may be getting earlier over the years (Quinn et al. in press). These projects motivated the large-scale study to test the hypothesis that all populations within the Wood River system migrate at the same time against the predictions that early spawning salmon migrate early, or that salmon spawning in certain types of habitats migrate earlier than others (see p. 7). Further research is planned to investigate the possible linkage between arrival date on the spawning grounds and spawning site selection, and the connection between migration date and body size variation within and among populations within systems.

We have studied the patterns of reproductive success and natural and sexual selection that salmon experience on the spawning grounds. Striking variation in longevity (days alive in the stream) has been shown among populations and this variation has been linked to the intensity of bear predation on newly arrived salmon (Carlson 2006). We have also demonstrated that populations differ in the balance between selective predation by bears on large salmon and greater reproductive success of large salmon if they are not killed. These differences in selection intensity seem to result in the variation in life-history traits seen among populations. In some cases, notably Hansen Creek, the selective effects of bear predation are augmented by selection from stranding at the shallow mouth of the creek. This stranding is most prevalent and also most size-selective when lake levels are low. Efforts to study processes on the spawning grounds have also included work on the extent to which females are able to spawn completely under conditions of high density. This work—comparing Wood River, Iliamna, and Alagnak populations—documented extremely high rates of egg retention (incomplete spawning and total spawning failure for some females) in some cases, especially in the Alagnak system, where spawning densities were very high. However, it appears that elevated water temperatures also affect pre-spawning mortality.

We have been investigating the movements of adult sockeye salmon on the spawning grounds, looking at the interface between homing and spawning-site selection. Results have shown limited movements by adult salmon, including males, and remarkably fine-scale homing to the natal site (Rich et al. 2006, Quinn et al. 2006). These studies on the behavior of the salmon themselves have been complemented with research on the ramifications of digging by salmon and carcass decomposition for the flux of nutrients in small streams. This research has revealed that adult salmon not only import nutrients from the ocean to the stream but also dislodge insects and organic material from the sediment, causing them to drift downstream. In addition, there is evidence for adaptation by the aquatic insects to emerge and avoid the disturbance caused by the salmon (Moore et al. in prep.).

In recent years, we have continued to study the ecology of juvenile sockeye salmon in lakes Aleknagik (Schindler et al. 2005a), Iliamna (Rich 2006), and the Chignik–Black lake system. These investigations have used our long-term data to determine the relative roles of temperature and density in controlling the growth of juvenile sockeye. Interestingly, growth in Lake Aleknagik is more strongly influenced by fry density than it is in Iliamna Lake, where temperature seems to be the primary factor controlling growth. However, both factors play a role in each lake, and in Iliamna the density of fry and yearlings affects fry growth. In Black and Chignik lakes, shifts in the use of each lake by sockeye salmon and sticklebacks may be changing, as the rivers and lakes in this system are undergoing rapid and substantial natural changes. In support of these studies, we have expended considerable effort in entering primary records into our relational database and checking them for errors. This database will greatly facilitate future research on the patterns of production from these lakes.

Besides these large-scale studies, we are undertaking a wide variety of smaller-scale studies, each designed to address specific issues or questions in sockeye salmon behavior and ecology. Examples include analysis of morphology and genetics to assist in distinguishing Dolly Varden from Arctic char, migrations of threespine sticklebacks, distribution of juvenile rainbow trout and coho salmon in different streams, spawning behavior of adult and jack sockeye salmon (Allen et al. in press), and predation on sockeye salmon by harbor seals in Iliamna Lake.

Spawning Ground Surveys

Wood River System

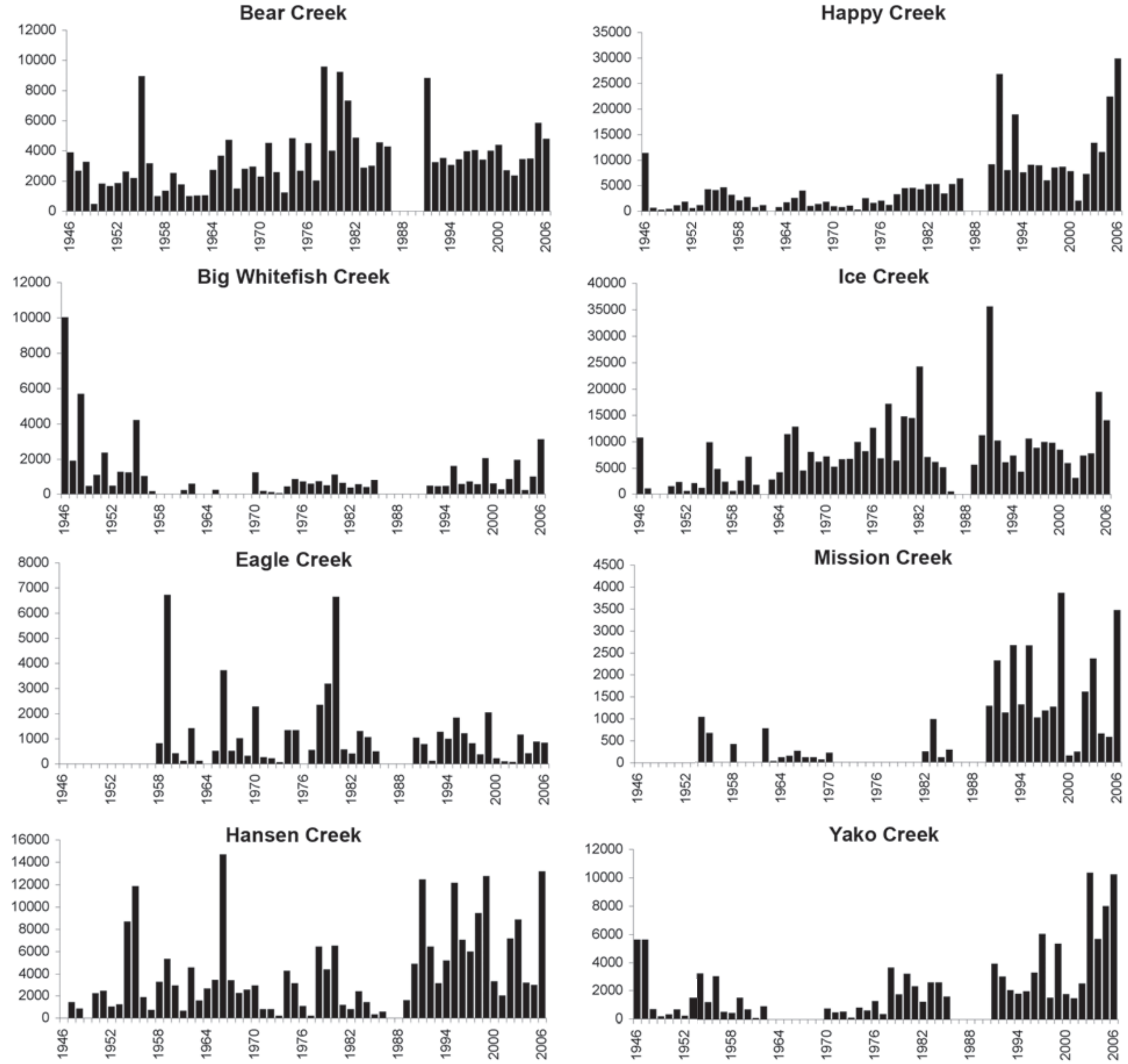
The Fisheries Research Institute's (FRI) Bristol Bay research program began with spawning ground surveys in the Wood River Lakes in 1946 to determine the number and distribution of sockeye salmon spawning in this system. During the early 1950s, methods were established to enumerate and sample the commercial catches, escapements (through the use of observation towers), and the number of smolts produced. By the late 1950s, we had established several important measurements, which have been maintained to the present, in order to characterize each year's environment for spawning adults and rearing juveniles. To characterize the fine-scale population variability among individual spawning sites, we have surveyed about 25 small creek populations to monitor year-to-year changes in spawner densities, age composition, sex ratios, and predation rates by bears for several decades now. Historically, these surveys were integrated across all small stream habitats and were sub-sampled with index reaches on the larger streams. Starting in 2005, we surveyed many of our historical sites on multiple occasions to evaluate whether spawning run timing has changed over the last few decades.

We also began mapping the spatial distributions of spawning sockeye on finer spatial scales by estimating abundance in each stream in successive 200-m sections. By monitoring population dynamics at the fine spatial scales, we aim to evaluate how habitat use changes with population density, and to improve our understanding of habitat quality in sites throughout the Wood River system.

A record high number (4.0 million) of sockeye escaped into the Wood River in 2006. The spatial distribution of these fish was not uniform across the spawning habitats of the Wood River system. Despite the fact that there were nearly four times the long-term average number of spawners in the system, survey counts in our standard spawning streams averaged only 2.7 times the long-term average, and only 2.0 times the average density observed in the previous ten years (Figure 3.1). The highest relative densities were seen in tributaries of Lake Aleknagik, which were 3.8 and 2.8 times their average for the long term and the last10 years, respectively. Tributaries of Lake Nerka were only 1.7 and 1.3 times their average for long-term and last 10 years, respectively. Our single index streams in lakes Beverley and Kulik had densities that approached four times the long-term and 10-year averages.

In 2006, in collaboration with ADFG, we conducted aerial surveys of the Wood River system to enumerate spawning populations on beaches and in major rivers. Aerial surveys coupled with our annual foot surveys (described previously) of spawner density in smaller streams allow us to estimate the distribution of spawners throughout the lake system. Using the aerial survey data and the foot survey data, we have expanded the estimates of sockeye spawners by lake and habitat type. The observational data indicated that a much larger proportion of the record escapement returning to the Wood River lakes in 2006 went to the upper lakes (i.e., Beverly and Kulik) than in recent years, with average escapements of 1.25 million sockeye. The upper lakes spawning areas are dominated by beach habitat. Thus, it is no surprise that our estimates show beach habitat receiving 60% of the total escapement in 2006, followed by rivers and creeks at 22% and 18%, respectively. Distribution of escapement broken down by lake would therefore follow this same pattern with Lake Beverly being estimated to have received 36% of the total escapement and the three other major Wood River lakes (Aleknagik, Nerka, and Kulik) getting approximately 20% each of the total escapement. All other lakes in the drainage were estimated to receive 1% or less of the total escapement.

The age composition of spawners in the Wood River system comprised a mix of age 1.2 fish (i.e., one freshwater year of growth and 2 marine years of growth), followed by 1.3 fish, in 2006 (Appendix B). In general, populations from rivers and large streams were dominated by 1.3 fish. However, populations spawning on beaches were distinctly dominated by 1.2 fish, suggesting that 2007 might produce large numbers of 1.3 fish spawning on these beaches. These estimates of the age composition of spawners in


Bear Creek

Happy Creek

Big Whitefish Creek

Ice Creek

Eagle Creek

Mission Creek

Hansen Creek

Yako Creek

Figure 3.1. Historical total peak sockeye counts for Aleknagik streams, 1946–2006. similar figures showing long-term trends in tributary streams of lakes Nerka, Little Togiak, Beverley, and Kulik are given in Appendix D.

2006 included our surveys of all major spawning beaches on Lake Beverley, which had not been sampled for over a decade.

Proportions of males that were jacks (i.e., 1.1 age fish) in Wood River spawning sites were much lower in 2006 than that observed in the previous 4 years. Only Lynx and Teal creeks produced relatively large numbers of jacks in 2006, as has been observed for several years at these sites (Appendix B).

Kvichak River System

Each year since 1956, we have collected scales or otoliths from spawned-out sockeye salmon from several major spawning grounds in the Kvichak River system. In recent years, aerial surveys were conducted to determine the distribution of the escapement among the many spawning grounds. ADFG did not conduct a survey in 2006; therefore, our observations on the distribution of the escapement of 3.1 million fish in 2006 were dependent on our ground observations made while collecting otoliths.

We continued this work by sampling fish sites we have sampled annually at Copper River, Knutson Creek, Gibraltar Creek, Chinkelyes Creek (two important rivers and large creeks), two representative island beaches—Woody and Fuel Dump—the mainland beach at Knutson Bay, and a system of spring-fed ponds in Pedro Bay. Additionally, surveys for presence and absence along several other island spawning beaches were made. Sockeye were present at the following spawning beaches: Flat Island No. 2, Cottonwood Point, Southwest Woody Island No. 1, Southwest

Woody Island No. 4, and Painted Rock on Porcupine Island. Densities at the river and creek sites appeared, at least qualitatively, to be moderate, and obtaining otolith samples from spawned-out carcasses was accomplished with ease at all sites (except for females at Gibraltar Creek). Additionally, we were able to obtain a sample of late-spawning beach fish from Knutson Bay in October.

Hansen Creek Daily Runs and Bear Predation

K Denton, H Rich, S Carlson (graduate students), T Quinn (adviser)

Hansen Creek, a small tributary to Lake Aleknagik, has been the focus of long-term research on sockeye salmon spawning behavior, life history, ecology and evolution, with special emphasis on bear predation. In 2006, the run to Hansen Creek of 20,440 fish was much larger than the 3,928 spawners seen in the 2-km creek in 2005 (Table 3.1). This creek has shown a clear, 4-yr cycle, having had large peak runs in 1987, 1991, 1995, 1999, and 2003. This year's high run may indicate a shift in the cycle, as 2006 was the pre-peak run yet was significantly larger than the 11,162 fish that returned in the "peak" year of 2003. Although 2006 was not expected to be a peak year, a large run was consistent with the high number of jacks observed in 2005. Larger than average returns of jacks to Hansen Creek also occurred in 1998 and 2002 ("pre-peak" years in the cycle), constituting 3.5% and 2.8% of the males in those years, respectively. On the basis of long-term data, jacks are 1.7% of the males in Hansen Creek, but in 2005 there were a record number of jacks—33.8% of all the males (H. Rich, unpubl. data). A high percentage of jacks in the male population usually forecasts a higher than normal return in the next year.

Two other noteworthy phenomena of the Hansen Creek run in 2006 were the small average size of the fish and the high proportion of females in the escapement. In 2006, the average fish length was only 404 mm (mid-eye to hypural plate), as opposed to the average of 444 mm from 2001 to 2005. This decrease in average size is most likely a result of increased competition in the marine phase of the life cycle, which is corroborated by the high returns to Hansen Creek and the Wood River system as a whole. The return in 2006 was composed of 65% females, as compared with an average of 54% for the time period 2001-2005. The reason for this increase in percentage is probably due to a combination of the smaller average body size and the influence of commercial fishing. Gillnet fisheries often harvest the larger bodied males more efficiently than the smaller females, an occurrence which may have been exacerbated by the small body size of the fish in 2006.

Table 3.1. Number of bear-killed salmon and other sources of mortality combined, by sex and section of Hansen Creek, 2006

Section	Status	Female	Male	Combined
Mouth	Bear	295	133	428
	Other	2,989	2,041	5,030
Lower	Bear	742	365	1,107
	Other	2,787	1,123	3,910
Middle	Bear	333	227	560
	Other	2,086	768	2,854
Pond	Bear	399	387	786
	Other	3,047	1,646	4,693
Upper	Bear	37	27	64
	Other	553	244	797
Subtotal	Bear	1,806	1,139	2,945
	Other	11,462	5,822	17,284
Grand total		13,268	6,961	20,229

Predation rate by bears is density-dependent on an interannual basis, and the rate in 2006 was about 14% (run size of 20,440), consistent with the trend seen in previous years (Fig. 3.2). Predation in Hansen Creek and elsewhere in the system (e.g., Pick and Bear creeks) is size-selective—larger fish are more vulnerable than smaller fish (Quinn and Buck 2001). In addition, males are generally more likely to be killed than females. The detailed studies at Hansen Creek are being applied to the more extensive but less intensive sampling that we conduct in association with the annual creek surveys throughout the system. The resulting data demonstrate that the level of predation is a decreasing function of stream size (especially width), and the age structure and morphology of sockeye salmon are clearly related to habitat and predation (Quinn et al. 2001a).

Finally, the mouth of Hansen Creek is very shallow and a large fraction of the sockeye salmon become stranded there and die without reaching the spawning areas upstream in the creek (Carlson and Quinn in press). In 2006, roughly 30% of the salmon died at the mouth and the mortality rate was, as usual, higher for males than females (because their longer and deeper bodies are less maneuverable in shal-

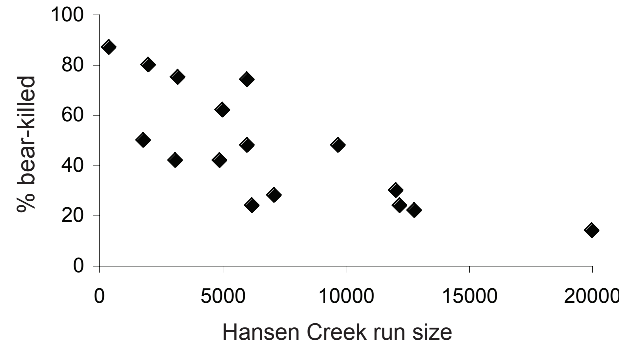


Figure 3.2. Effect of spawning run size on the kill rate by bears in Hansen Creek. Modified from Rogers et al. 2003.

low water). Analysis indicated that the mortality is consistently size-selective, and in years when the lake level is low, the mortality rate and the strength of selection against large fish increase. Lake level in late July is correlated with spring (May) air temperatures—probably because this affects the rate of snow melt and rainfall in July. Thus, the ecology of this stream is affected by a complex combination of climate-driven and density-related processes.

Pre-Spawning Mortality and Egg Retention: A Component in Density-Dependent Population Regulation in Pacific Salmon

T Quinn, H Rich, Jr (UW), D Eggers, J Clark (ADFG)

The combination of exceptionally large returns (without precedent in 50 years) and low fishing rates resulted in salmon densities on the Alagnak River system's spawning grounds that were about 11.5-fold (in 2004) and 9.0-fold (in 2005) greater than the average through 2003. In 2006, the run to the Alagnak River system (1.8 million) was above average but smaller than in the previous two years. The extraordinary Alagnak River "over-escapements" in 2004 and 2005, and the contrasting runs there in 2006 and in the other Bristol Bay systems, provided a rare opportunity to assess the prevalence of egg retention and spawning failure. Our primary goal was to quantify the prevalence of pre-spawning mortality and incomplete spawning, comparing the levels in Alagnak River system populations with populations elsewhere in Bristol Bay where salmon runs approximated the escapement goals. Our secondary goal was to test the hypothesis that larger females would have a lower frequency of incomplete spawning and spawning failure. We assumed that they would be competitively superior to smaller females, and also tend to arrive earlier than smaller females and so should be more likely to complete spawning.

In 2006, we sampled dead female sockeye salmon at two adjacent locations, Funnel Creek and Moraine Creek, within Katmai National Park. Considering the total egg production of those females, we estimated that only about 3% of the potential egg deposition was lost in this year, contrasted with much higher levels of lost potential egg deposition in 2004 (23%) and 2005 (43%). Furthermore, we found, contrary to our original hypothesis, that larger females did not retain significantly fewer eggs than smaller females. Instead, for both Funnel and Moraine creeks in 2006, it was the larger females that retained eggs (average body size of partially spawned females and spawning failures was 429 mm vs. 413 mm for spawned-out fish).

In 2006, we also collected egg retention data from four locations within the Kvichak River watershed to act as "pseudo-controls," as we have done in previous years. Egg retention rates in Iliamna Lake populations were low, about 2%, and lower than they have been in recent years (5-20%). Conditions in 2006 were much cooler and wetter than in the previous two years in the Bristol Bay region. The lower rates of egg retention in 2006 in the Alagnak River system might be explained by either the lower density or lower temperatures, but the lower rates in the Iliamna Lake populations, where density was, if anything, higher in 2006, seem best explained by the cooler, wetter conditions. We hope to continue this work in the future to better understand the dynamics of spawning success and failure in relation to salmon density and climate in these systems.

A and C Creeks

A and C creeks, located in Little Togiak Lake, are two of the smallest salmon runs we regularly monitor and are at the extreme of several dimensions of adaptation, including depth of water (shallow), intensity of bear predation (high), and life expectancy after stream entry (short). Since 1996, we have attempted to monitor these streams daily, marking every individual fish and recording their location in the creeks. In the last several years, graduate students have been using these systems for their graduate research: Jocelyn Lin is studying genetic differentiation between lake and creek spawning fish (p. 49), and Stephanie Carlson used the data in her analysis of senescence rates (p. 16). A major programmatic objective is to be able to pedigree the populations: that is, to determine who the parents were for each individual returning in a generation. This will allow us to determine how many individuals, and what habitats, produce successful offspring, and calculate several factors important to genetic differentiation, such as the effective population size. In addition, we should be able to calculate the heritability of phenotypic traits, both morphology and behavior, from pedigree data. We first obtained near-complete genetic samples in 2003, and we continued complete genetic sampling in 2004, 2005, and 2006. The offspring from 2003 spawning will return in 2007 and 2008.

A and C creeks are normally characterized by extremely intense bear predation—A Creek in particular often being completely cleaned out by bears several times in the season—and 2006 was no exception. In A Creek, 56% of fish were killed by bears and in C Creek bear kills constituted 58% of the dead fish. While this rate is high compared with other larger spawning streams, it is a rather moderate rate for A and C creeks relative to 2004, when 98% and 73% of fish in A and C creeks, respectively, were killed by bears, and 2005, when the bear kill rate was only 6% and 13% in A and C creeks, respectively. Prior to 2004, there was a beaver dam on C Creek about 200 m from the lake. This dam broke down during the 2004 season and, since then, we have seen a number of fish colonize the area above the dam, providing excellent data on how quickly new habitats are colonized. Figure 3.3 shows the number of fish entering, and the number of fish still alive in A and C creeks for 2006.

The Evolutionary Effects of Bear Predation on Salmon Life History and Morphology

S Carlson (graduate student, PhD completed), T Quinn (adviser)

The power of selection to drive evolution has captivated evolutionary biologists since Darwin. It is often noted that conspecific populations differ in phenotypic traits, and divergent selection appears to be a critical force generating this biological diversity. Until recently, most research focused on the role of resource competition in driving divergence, but other factors may also be important. The overarching goal of this dissertation research was to examine the role of natural selection in the form of predation in driving adaptive population divergence.

To achieve this goal, we investigated the effects of predation from bears on the evolution of salmon. This research was carried out on sockeye salmon in the Wood River Lakes system. Previous research in this system has demonstrated that the percent of salmon killed by bears varies among populations, as does the tendency of bears to kill salmon early or late in their reproductive life. This previous research laid the foundation for the current study by enabling us to test whether trait divergence among populations was related to the local predation intensity.

A comparative approach was employed to quantify trait divergence among populations, and to then relate trait divergence with predation intensity. The focus was on salmon life-history traits (reproductive lifespan, rates of senescence) as well as morphological traits (body size and shape). Results demonstrate that among population variation in senescence rates, body size and shape is closely associated with the degree of predation experienced. In particular, variation in senescence was related to the extent to which bears killed salmon that exhibited little senescence; populations senesce at slower rates when they have been historically exposed to bear predation that selectively targets fish showing more advanced senescence. Variation in body size and shape was also related to the intensity of bear predation; populations are smaller and more shallow-bodied when they have been exposed to more intense bear predation. In general, this dissertation study contributed to a small but growing body of research demonstrating the importance of divergent selection due to predation in driving adaptive population divergence.

Spatial Distribution and Dynamics of Pink and Chum Salmon in Streams Dominated by Sockeye Salmon: Insights into the Processes of Straying and Colonization

G Pess (graduate student), T Quinn (adviser)

Salmonids can quickly colonize new habitats and establish

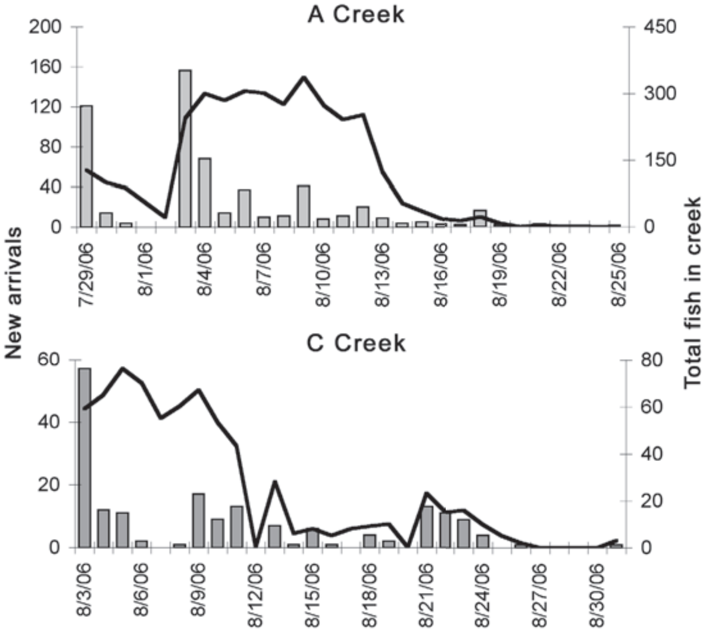


Figure 3.3. Number of fish entering (▮) and total fish in creek (—) in A and C creeks, Little Togiak Lake, for 2006.

populations (Milner and York 2001, Hendry et al. 2004a) but the key factors that determine salmonid colonization (and recolonization rates after blockages are removed) are not well understood. One hypothesis is that straying and the establishment of populations is related to the compatibility between specific life-history variation and the hydrologic, geographic, and ecological characteristics that determine stream habitat complexity (Quinn 1984, Allendorf and Waples 1996, Burger et al. 2000).

The relationship between straying, habitat characteristics, and salmon colonization is being investigated by examining the correlation between the occurrence of small salmonid spawning aggregates of pink and chum salmon, habitat characteristics, and competing, numerically dominant sockeye salmon. The study scale ranges from stream reach to watershed, in a series of different streams in the Wood River system, Alaska. We hypothesize that pink and chum salmon occurrence in the Wood River system will be greatest over time where (1) habitat conditions for spawning are most suitable, (2) competition with adult spawning sockeye is lowest, and (3) distance to a pink and chum salmon source population is shortest.

The hypothesis focuses on two scales—stream and reach within stream—and two forms of fish data—occurrence and abundance. The first approach focuses on the stream scale and utilizes long-term (e.g., >30 years) presence/absence data for pink and chum salmon. Pink and chum salmon occurrence was used as an indicator of salmon colonists because these species' populations are relatively low in many of the smaller streams throughout the Wood River system, yet they have been documented in 22 streams for over 35 years by the Alaska Salmon Program. The second analysis focuses on the reach scale and uses spatially explicit pink and chum abundance data collected in 2005 and 2006. Each scale will utilize similar descriptive and statistical techniques to determine the correlations between fish occurrence/abundance and physical habitat characteristics and adult sockeye densities.

The Wood River system is an excellent area to explore the relationship between straying, habitat, and colonization because the habitat condition and salmonid populations have not been altered by anthropogenic influences such as land development, hatchery production, and invasive species (Hilborn et al. 2003). The main influence on salmon populations has been harvest, which has been well managed, and catch and return estimates have been well documented since the 1960s (Hilborn et al. 2003). In addition, much research has already been conducted to examine the effects of other variables that influence salmon populations, such as climate variability (Hilborn et al. 2003). Also, the Wood River has a diversity of stream and habitat types that facilitate comparing salmon occurrence among streams (T. Quinn, pers. comm.).

This analysis will increase our understanding of the relative importance and interaction of variables that lead to natural salmon colonization in a pristine setting, variables such as habitat condition, competition, and population source. The combination of multiple reference-habitat locations, long-term data, and relatively unaltered salmon populations to answer questions related to salmon colonization and salmon issues is unique. Thus, the analysis will allow us to understand how natural salmon colonization occurs over time and in multiple settings. The analysis will also provide empirical data that will help develop models to answer applied questions about what may transpire once barriers are removed for fish passage, and how different fish management strategies may effect salmon recolonization. This could aid in prioritizing what barriers and actions are needed to increase the rate of salmon recovery across areas where populations are threatened or endangered.

During the summers of 2005 and 2006, we collected habitat data on 30 streams throughout Lake Aleknagik and Lake Nerka. We measured stream characteristics including stream channel width, depth, habitat type, streambed particle size, wood loading, and cover for juvenile and adult salmonids. Each of the 30 streams had three to four sections measured that ranged in length between 50 m and 300 m. The data will be used to identify what characteristics correspond with the occurrence of other species besides sockeye, including pink and chum salmon.

Preliminary results indicated that a wide range of stream habitat characteristics exists for salmonids in the Wood River system. Bankfull width (m), a surrogate for stream power, ranged between 2.5 m and 25 m, while stream channel gradients ranged from <1% to 5% in stream reaches surveyed for spawning sockeye. Preliminary results correlating the occurrence of pink and chum salmon over a 30-year time period with habitat characteristics revealed that drainage area (km^2) may be an important factor in developing suitable habitat for species besides sockeye (Fig. 3.4). Pink salmon consistently occur in relatively small drainage areas (>20 km^2), whereas these same species tend not to occur in smaller watersheds (<6 km^2), based on historical spawner survey records. Pink

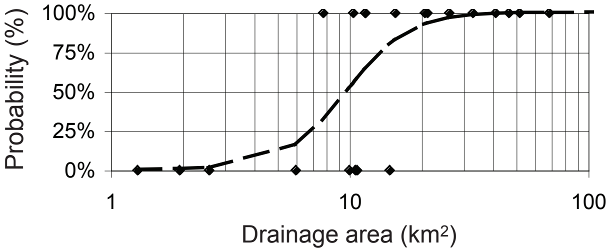


Figure 3.4. Logistic regression of probability of occurrence of pink salmon in streams entering lakes Aleknagik and Nerka.

and chum occurrence also decreases as spawning sockeye density increases (Fig. 3.5). Variation in occurrence is large at lower sockeye densities; however, as sockeye densities increase to greater than 0.3 per m^2, the occurrence of pink and chum salmon declines to less than 25%. Even though sockeye spawning density data suggest density-dependence effects, reach-scale analysis revealed differences in peak spawning locations for sockeye and pink salmon (Fig. 3.6). The proportion of sockeye spawning in upper Ice Creek is greater than in lower Ice Creek while pink salmon exhibit their highest densities in the lower portion of Ice Creek. Future research will involve an analysis of the potential mechanisms associated with these preliminary results.

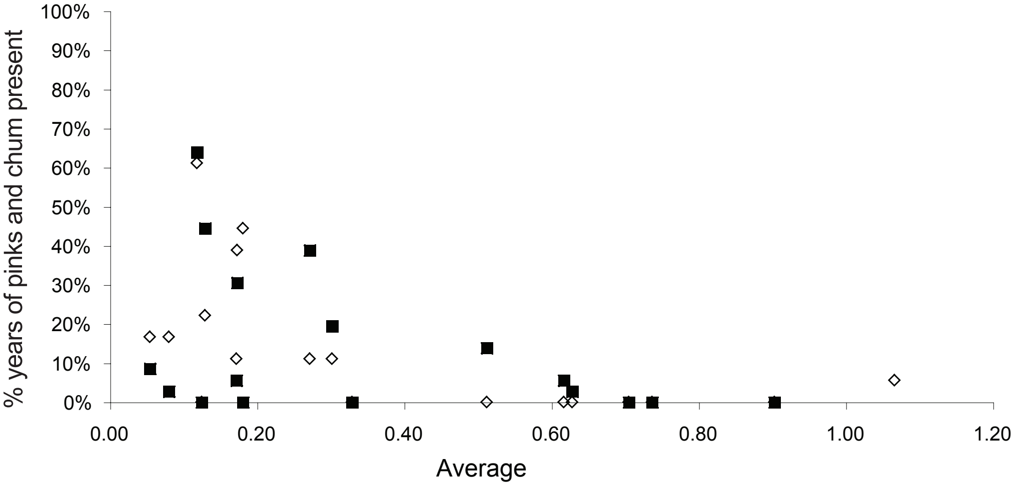


Figure 3.5. The occurrence of pink and chum salmon from 1968 to 2003 in lakes Aleknagik and Nerka versus mean sockeye spawning density (fish/m^2). ■ = chum occurrence; ◇ = pink salmon.

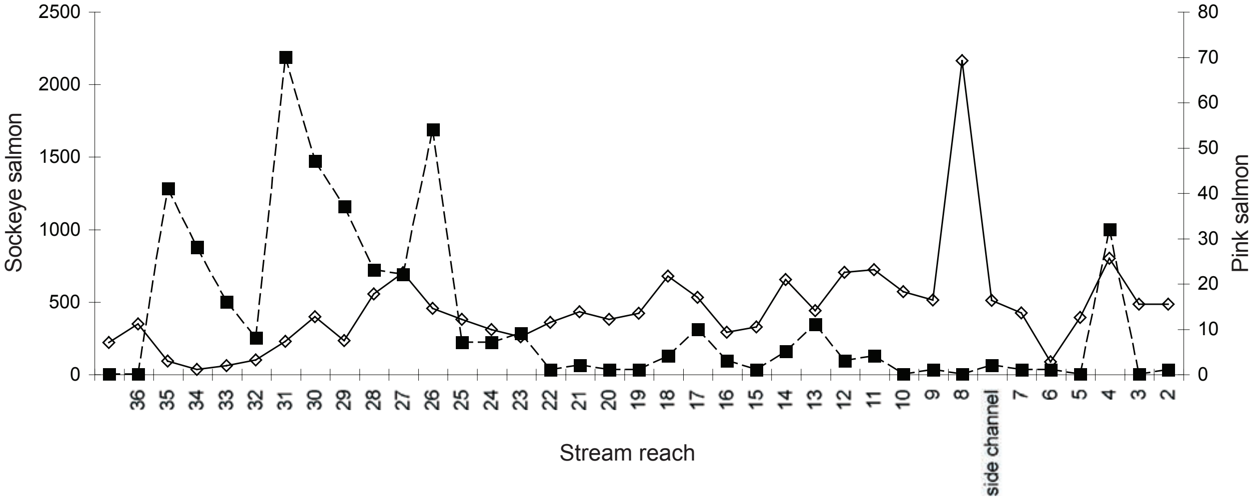


Figure 3.6. Reach scale differences in the proportion of pink and sockeye salmon spawning in Ice Creek, a tributary of Lake Aleknagik, 2005. —◇— = sockeye salmon. –■– – = pink salmon. Water flow goes from right to left so stream reach 2 is approximately rkm 5.0, while stream reach 36 is the mouth of Ice Creek.

4. Lake Ecosystems and Nutrients

Introduction

We have continued monitoring environmental and limnological conditions in the lakes of the Wood River system and in Iliamna Lake. Many of these records are now continuous for spring and summer seasons for over 50 years, and we have made extending these valuable records a programmatic priority. One of the striking features of these long-term records is the large changes in environmental conditions associated with climate warming during the last century. Climate warming has been especially notable in many parts of Alaska, and it appears to be having a wide array of effects on the physical and biological aspects of the spawning and nursery habitats for salmon and other aquatic species. Some of these responses are described in more detail in the following research descriptions in this section.

The year 2006 was one of the coldest years in the last decade but was about average compared with the last 50 years (Table 4.1). Thus, 2006 provided a very interesting year of observations that enabled us to test our understanding of some of the climate-driven changes in the lake ecosystems observed over the duration of our datasets. In addition to maintaining our routine environmental and limnological monitoring, we have initiated paleolimnological research to reconstruct historical sockeye salmon escapement densities over the last several centuries. This research is enabling us to better understand the responses of sockeye populations to long-term variation in climatic and ocean conditions.

Environmental Conditions and Limnology

Thermal Conditions

Bristol Bay was relatively cold in 2006 compared with the last decade and, therefore, was an anomaly from the long-term warming trend observed over our period of records. The springs of 2002–2005 were substantially milder than average as reflected by the timing of spring ice breakup and spring water temperatures. In general, the date of spring ice breakup has advanced considerably and is about 9 days earlier now than it was in 1962. However, in 2006, spring ice breakup occurred on June 3 and May 20 in lakes Aleknagik and Iliamna, respectively. Statistical time-series analyses of the long-term changes in spring breakup date on Lake Aleknagik (Fig. 4.1) show that the Pacific Decadal Oscillation and a long-term warming trend associated with global warming have contributed about equally to the trend towards earlier ice breakup dates (Schindler et al. 2005a). Conditions in 2006 were clearly an anomaly from this trend and were about average considering the long-term record. The trend towards earlier spring ice breakup dates are paralleled by the considerably warmer spring water temperatures in Lake Aleknagik (Fig. 4.1). In 2006, lake temperatures were considerably colder than those observed for most of the last decade. Between 1993 and 2005, spring water temperatures in all but one year (1999) were warmer than average. However, substantially warmer spring conditions do not carry over directly into equally warmer summer conditions. In fact, surface water temperatures in July and August of 2003–2005 were only subtly warmer than the long-term averages in Lake Aleknagik. In 2006, water temperatures were on target or slightly colder than the 50-year average conditions in Lake Aleknagik (Table 4.1).

Thermal conditions in Iliamna Lake have also been showing a steady warming trend over the last 5 decades that parallels the observed increases in spring air temperatures (Fig. 4.2). Since 1962, average spring air temperatures have warmed more than 2°C and water temperatures have warmed about 3°C. Ice-free data have been collected each year since 1956 by FRI and ADFG personnel. Data are collected from local area residents and pilots across the different regions of the Iliamna Lake area. Records reveal an east-to-west pattern, with the east end becoming ice free earlier than the western end of the lake, near the outlet at Igiugig. In 2006, we saw the latest ice-free date we have recorded since 1999—May 20, about 20 days later than the previous five years but very close to the long-term average (Fig. 4.3).

In 2006, the mean August air temperature at Iliamna was 11.6°C, the 11th coolest year since 1950. August of 2006 was the second wettest in the 52-year period of

Table 4.1. Summary of environmental variables and conditions in the Wood River system in 2006 compared with long-term average conditions (1950–2006).

	Year	Date									
1. Date of ice breakup 1949–	2006	6/3									
	average (1949–2006)	5/28									
	range (1949–2006)	4/28–6/17									
			25–Jun	14–Jul	2–Aug	31–Aug					
2. Water surface temperature 0–20m 1958–2006	2006		8	10	11	13					
	average (1958–2006)		6	12	13	12					
	range (1958–2006)		3.8–13.7	8.1–18.0	9.4–18.8	9.7–16.0					
3. Water transparency Secchi depth (m) 1962–	2006		5	5	7	9					
	average (1962–2006)		8	8	9	9					
	range (1962–2006)		4.8–10.5	4.7–12.3	6.3–10.9	5.8–12.1					
4. Water conductivity (micromhos/cm) 1968–	2006		40	41	40	40					
	average (1968–2006)		39	39	38	39					
	range (1968–2006)		31.1–52.1	32.0–42.6	32.5–40.5	32.2–47.9					
			June 1–15	June 16–30	July 1–15	July 16–31	Aug. 1–15	Aug. 16–31	Sept. 1–15	Sept. 16–30	
5. Average daily solar radiation (gm cal^{-1} cm^{-1})	2006			349	358	206	109	292			
	average (1963–2006)		403	383	374	332	274	254	204		
	range (1963–2006)		272–588	205–572	212–543	192–485	109–402	142–421	114–282		
6. Lake level (cm) of Lake Nerka 1952–	2006		183	183	126	84	64	67	87	102	
	average (1952–2005)		148	153	131	105	86	81	82	91	
	range (1952–2005)		84–227	97–218	74–199	52–172	34–173	30–184	29–161	76–102	
		5–Jun	11–Jun	25–Jun	5–Jul	14–Jul	24–Jul	2–Aug	11–Aug	21–Aug	31–Aug
7. Chlorophyll "a", 0–20m (mg m^{-2}) 1963–	2006	4	14	33	54		29	6	11	7	
	average (1963–2005)			28		25		20			23
	range (1963–2005)			10–45		10–43		6–37			5–38
			June		July		August		September		
8. Total zooplankton density 0–60m (10^3 m^{-2}) 1967–	2006		305		450		768		982		
	average (1967–2000)		259		284		399		434		
	range (1967–2000)		66 – 337		101 – 487		100 – 768		125 – 982		

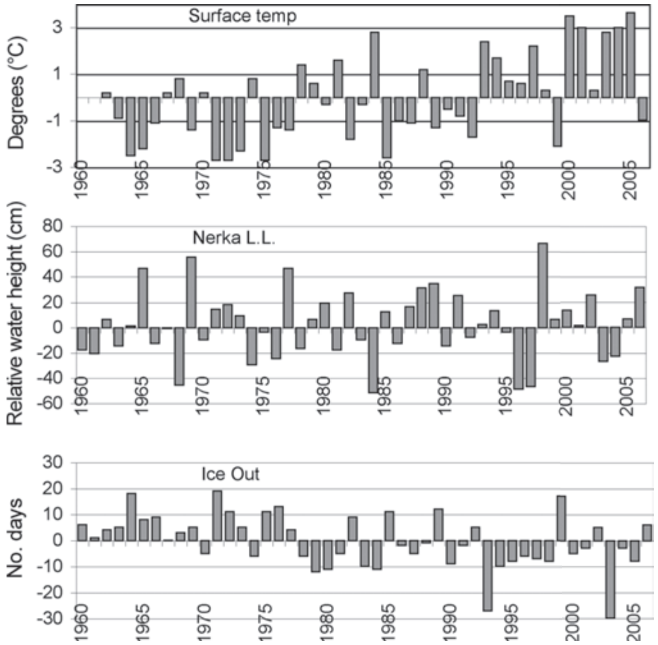


Figure 4.1. Time series of spring environmental indicators from the Wood River System. Spring (June 22–25) water temperatures are given as the anomaly from the long-term mean (6.4°C). Water level at Lake Nerka is given as the anomaly from the long-term spring (June 6–30) mean (151 cm). Ice breakup date is given as the number of days before/after May 28.

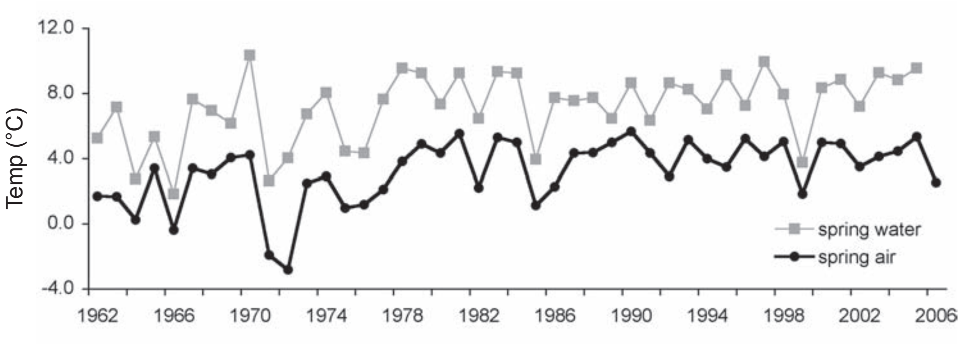


Figure 4.2. Average spring water temperatures (June 1–15) recorded at outlet of Iliamna Lake at Igiugig (water temperature data collected by ADFG during annual smolt enumeration project) and average spring air temperatures (March–June) recorded at Intricate Bay on Iliamna Lake.

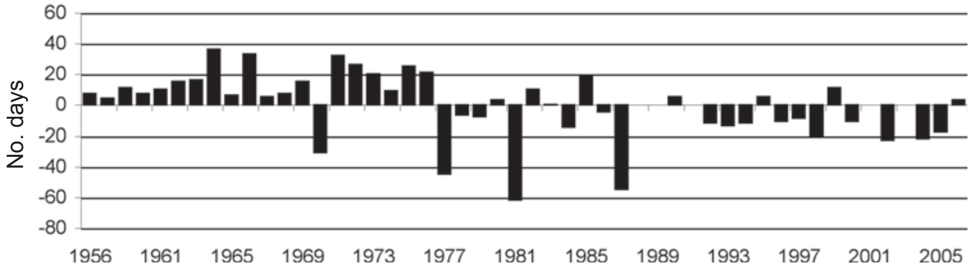


Figure 4.3. Time series of ice breakup date for Iliamna Lake given as the number of days before/after the long-term average date of May 17.

record at King Salmon, and it was the fifth wettest in the 57 years of records at Iliamna village. Similarly, in mid-August of 2006, Iliamna Lake was much cooler than in 2004 or 2005, with average temperature at 5-15 m depth in Knutson Bay and Pedro Bay being 10.0°C and 9.8°C, respectively (Fig. 4.4).

Between 2003 and 2006, water transparency in Lake Aleknagik as measured by Secchi depth was lower than average, possibly owing to a prolonged spring phytoplankton bloom. Water conductivity during recent years has not varied much from long-term average conditions (Table 4.1).

Lake Level

We have used the lake level in Lake Nerka as our integrated measure of hydrology throughout the Wood River System. Lake levels at Nerka were lower than average during 2003–2005, especially during July and August when summer rainfall was scarce (Table 4.1). Late August water levels were especially low in 2004 and the same trajectory was observed in 2005, but intense rains in early September brought the water levels up quickly in the lakes and creeks throughout the system. Although conditions were extremely dry during 2003–2005, water level did not approach the record lows observed earlier in our records. In 2006, water level was substantially above average through June, but because of relatively low rainfall and a thin snowpack, levels were below average in July and early August. Similar to 2005, September was a very wet month and lake levels increased to above-average levels through September. Although our data collection did not continue past mid-September, water levels were reported to be exceptionally high through mid-November owing to continued fall rains in 2006.

Zooplankton and Aquatic Insects

We have monitored zooplankton and emerging insect abundance in Lake Aleknagik since 1967 as a means for assessing temporal trends in the primary prey for juvenile sockeye salmon and their competitors (e.g., sticklebacks; see Appendix C). The observed warming trend in water temperatures is strongly and positively associated with enhanced zooplankton densities throughout the summer (Fig. 4.5). In 2003–2005, total crustacean zooplankton densities were substantially higher than the long-term averages, and these differences were most pronounced late in the season (August and September) when sockeye fry are located in pelagic habitats and feeding almost exclusively on zooplankton. The taxa that appear to be benefiting most from this warming trend are the cladocerans *Eubosmina* and *Daphnia*, which are important prey for sockeye throughout their range (Fig. 4.5; Schindler et al. 2005a). These taxa are found at relatively low densities in the spring and reach peak densities in August and September (Fig. 4.5). In 2003–2005, *Eubosmina* and *Daphnia* densities were approximately double the long-term means for August and September. Both cyclopoid and calanoid copepods, which are generally more abundant early in the summer, were found at densities comparable with the long-term means in Lake Aleknagik (Fig. 4.5). In 2006, the colder environmental conditions translated into substantially reduced zooplankton abundances compared with most other years in the last decade. Although total crustacean densities in 2006 were higher than the long-term average, *Eubosmina* and *Daphnia* were substantially lower in density than the past few years. However, 2006 cladoceran densities were approximately equal to the long-term averages for Lake Aleknagik (Fig. 4.5).

Sockeye Fry Abundance and Size

Wood River

We have sampled juvenile sockeye fry in the Wood River system in August of each year since 1958 by townetting at night. The resulting data are collected to monitor growth of juvenile sockeye during their freshwater residency. A formal analysis of this dataset showed that the climate warming trends evident in the ice breakup dates and in water temperatures are associated with improved growing conditions for juvenile sockeye from 1962 to

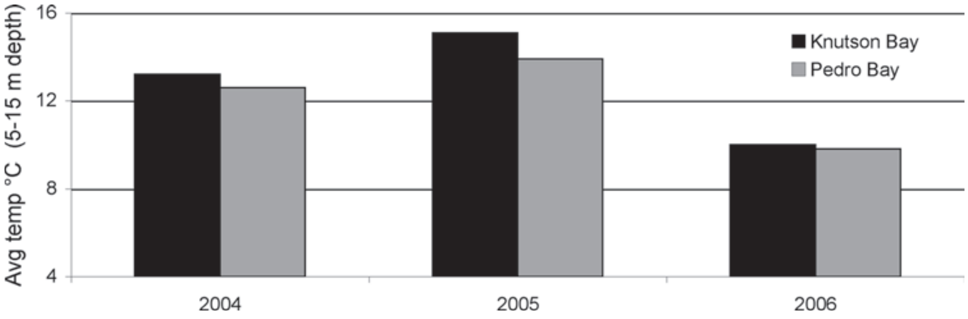


Figure 4.4. Average water temperatures (5- to 15-m depth) in mid–August (Aug 14–17) at two locations within Iliamna Lake.

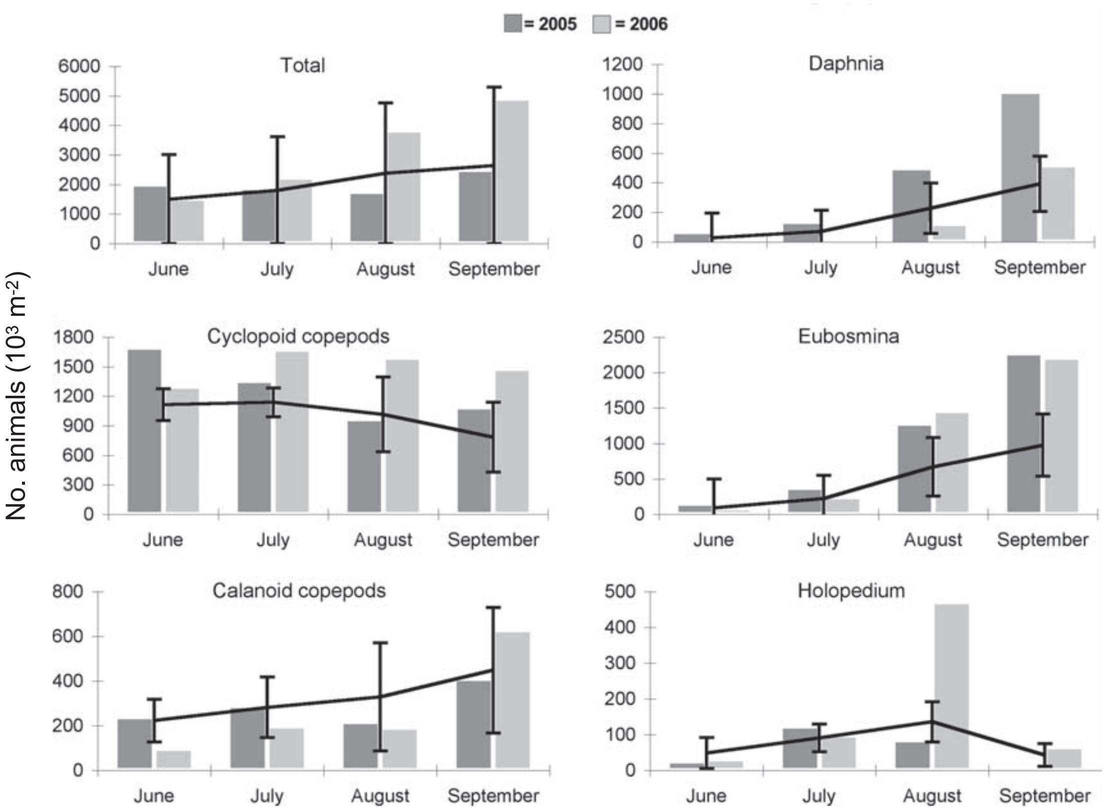


Figure 4.5. Monthly zooplankton densities in Lake Aleknagik from 1967 to 2000 (lines with standard deviations) compared with densities observed in 2005 and 2006.

2002 (Schindler et al. 2005a). The specific mechanisms accounting for the enhanced growing conditions have not been pinpointed yet, but they appear to be a combination of a longer growing season, increased water temperatures, and increased zooplankton abundance—all of which should yield higher growth of juvenile sockeye in lakes. These improved growing conditions for juvenile sockeye are associated with the long-term population buildup in the Wood River since the 1960s. As escapements have increased during this time period, there has also been increased competition among juvenile sockeye in the Wood River system, a process that partially obscures the positive effects of a warmer climate (Schindler et al. 2005a).

The enhanced growing conditions for juvenile sockeye continued through 2003–2005. Ice breakup dates were substantially earlier than normal during this time period and were associated with above-average densities of cladoceran zooplankton, the primary prey of juvenile sockeye. Juvenile sockeye growth was particularly high in 2003 when they were almost as large as the previous observed maximum in 1973 despite the relatively high escapement to the Wood River in 2002 (1.3 million). Juveniles were especially large throughout Lake Nerka and Little Togiak Lake. Juvenile sockeye were a little smaller than average in Lake Aleknagik in 2004, but larger than average in other Wood River lakes (Fig. 4.6). In 2005, juveniles were larger than average in all Wood River lakes sampled. Thus, despite the larger than average escapements to the Wood River in recent years, growth rates of juvenile sockeye have tended to be higher than average during the last decade. The potential for decreased growth rates of juvenile sockeye in response to the recent increases in escapement appears to be compensated by enhanced growing conditions from climate warming.

In 2006, the late ice breakup, cool summer temperatures, and moderate zooplankton densities combined to produce growth rates of sockeye that were substantially lower than those observed in the last decade, but about equal to the long-term mean in lakes throughout the Wood River system (Fig. 4.6). In addition to our routine sampling of fry from lakes Aleknagik, Nerka, and Little Togiak, in 2006 we reinitiated our fry sampling in the upper lakes (Beverley and Kulik). By September 1, the average size of sockeye fry among the five lakes (mean = 55 mm, std dev. = 1.5) was remarkably similar but there is considerable year-to-year variation in all of the lakes. Much of this variation does not appear to be coherent among lakes, suggesting that density-dependent processes are not synchronized at the river scale, but rather, they are responses to densities in each of the five nursery lakes.

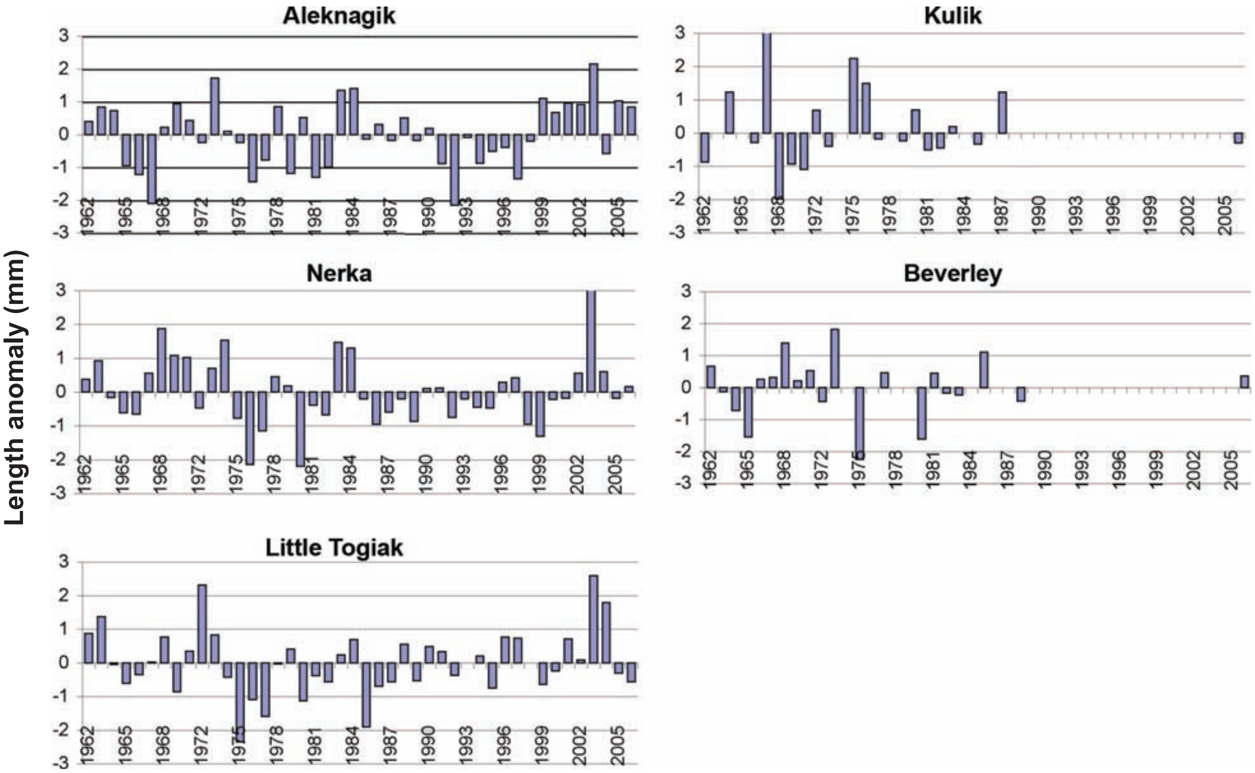


Figure 4.6. Size of sockeye fry on September 1, 1962–2006 for all Wood River lakes. All fish were sampled with night townet surveys. Annual length anomalies (measured as fork length, mm) are based on the long-term average (Aleknagik, 55.12; Nerka, 56.31; Little Togiak, 52.42; Kulik, 54.41; and Beverley, 55.58). Kulik sockeye in 1967 were 10.9 mm larger than the average.

Kvichak

In 2006, we were able to reinstate beach seining operations for juvenile sockeye in the eastern end of Iliamna Lake. Beach seine sites were chosen to closely approximate historically established sites, and to match the geographic areas of our townetting index sites. Sampling juveniles in the littoral areas of the lake gives an early indication of relative abundance, size, and growth trajectory of the new cohort (sampling conducted July 6–27, 2006). In general, fry size increased through sampling rounds as catches decreased (Fig. 4.7), presumably reflecting movement to limnetic areas of the lake.

We have sampled sockeye fry in the Kvichak system in August of each year since 1962 (1961 brood year) by townetting at night in Iliamna Lake (similar monitoring was done in Lake Clark until 1995) (Table 4.2). Catch rates of sockeye fry in August townetting surveys have been consistently lower than average since 1994, coincident with the lower escapements to the Kvichak River during this time period (Fig. 4.8). Townet catches are used to generate an index of relative abundance for fry each year, and the index value for fry abundance for 2006 was low, with the index rank being the 10th lowest on record since 1962 (Fig. 4.8). The parent escapement from 2005 was small (2.3 million spawners), and this result is not unexpected; interestingly, we did see higher catches of age 1 yearling sockeye than we have seen since 2001, and these yearlings are progeny of the 2004 parent escapement of 5.5 million. Additionally, the 2006 spring air temperatures were cooler than average—much cooler than we have seen since 1999—and may have had a negative impact on fry production.

The relatively large fry body sizes seen during the previous 10 years indicate good growth conditions due to

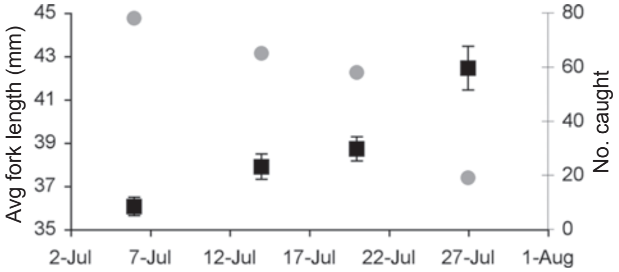


Figure 4.7. Number of sockeye fry caught (gray circle) and average length of fry (black square +/- SE mean) from beach seining in the eastern end of Iliamna Lake, 2006.

Table 4.2. Mean townet catches and lengths (on September 1 in mm) of sockeye salmon fry in Lakes Iliamna and Clark (geometric mean of 20-min tows), 1961–2005.

		Iliamna Lake (tows in areas 7 and 8 only)		Lake Clark	
Brood year	Kvichak escapement (10^6)	Mean catch	Mean length	Mean catch	Mean length
61	3.7	90	53	13	50
62	2.6	12	45	54	50
63	0.3	5	54	3	50
64	1.0	7	62	2	50
65	24.3	170	53	23	52
66	3.8	67	57	15	47
67	3.2	78	62	47	59
68	2.6	43	62	9	50
69	8.4	386	61	11	55
70	13.9	127	44	20	38
71	2.4	4	50	15	41
72	1.0	3	58	17	48
73	0.2	2	71	12	57
74	4.4	491	54	80	55
75	13.1	252	49	105	49
76	2.0	16	53	--	--
77	1.3	11	61	--	--
78	4.1	339	62	65	56
79	11.2	282	53	60	48
80	22.5	134	61	26	59
81	1.8	37	52	58	46
82	1.1	9	68	18	57
83	3.6	242	64	40	56
84	10.5	147	46	84	51
85	7.2	63	54	16	49
86	1.2	10	60	--	--
87	6.1	79	63	11	56
88	4.1	22	58	21	48
89	8.3	181	55	19	47
90	7.0	336	54	-	-
91	4.2	_	56	20	47
92	4.7	135	57	27	61
93	4.0	64	57	26	55
94	8.3	83	55	21	54
95	10.0	126	62		
96	1.5	23	67		
97	1.5	-	-		
98	2.3	57	46		
99	6.2	38	44		
00	1.8	159	58		
01	1.1	4	57		
02	0.7	25	62		
03	1.7	36	64		
04	5.5	23	61		
05	2.3	13	52		
06	3.1				

warmer temperatures and relatively low fish densities. Fry size at the end of the first growing season is influenced to a large degree by temperatures experienced during early emergence. The adjusted mean length of fry caught in 2006 Iliamna Lake townet operations (52 mm) reflects the pattern of cooler springs and smaller fry (Fig. 4.9). The 2006 adjusted mean was 5 mm smaller than the long-term average (57 mm), and about 7 mm smaller than we have seen on average over the last 10 years. The smaller sizes of fry this year match fry sizes seen from the 1998 (46 mm) and 1999 (54 mm) brood years—the 1998 brood experienced exceptionally cold temperatures during the 1999 summer (coldest on record from 1985 to present), and the 1999 brood occurred at relatively high density in the lake in 2000 in response to the substantial (6.2 million) escapement.

Our analyses of the long-term smolt data collected by ADFG has shown an increasing tendency for smolts to leave after their first year of growth. This trend towards younger smolts is associated with their increased body condition in the spring of migration and a shift towards earlier spring ice breakup dates as has been observed in the Wood River System (Schindler et al. 2005a). However, the link between this shift in the age structure of the smolt population and the recent poor performance of the Kvichak sockeye stock appears to be weak.

Arctic Char Predation

Arctic char concentrate in the interconnecting rivers of the Wood River System to prey on sockeye salmon smolts during their spring migration to sea. We conducted several detailed studies of the effects of char predation on sockeye smolts during the 1950s to 1970s, and since then, have sampled the char in Little Togiak River annually on an opportunistic basis to monitor long-term trends in predation rates during the spring smolt migration.

Since 1990, there has been a general increase in the average length of char in the Little Togiak River, and during 2002–2006, average lengths of char were substantially larger than the long-term average of 436 mm TL (Table 4.3).

From 2000 to 2005, we sampled char diets non-lethally and have tagged and released most sampled fish. Recapture rates in subsequent years have been too small to be useful for population estimates, suggesting that the Little Togiak River char populations are quite large or that these individuals migrate throughout the larger lake system. In 2002–2006, predation rates on sockeye smolts and fry were about normal. To date, we have detected no notable long-term trends in predation rates on smolts and fry in this river. In 2005, char were especially difficult to catch off the mouth of the Little Togiak River and at several other sites in Lake Nerka. In 2006, catch rates seemed to be more normal.

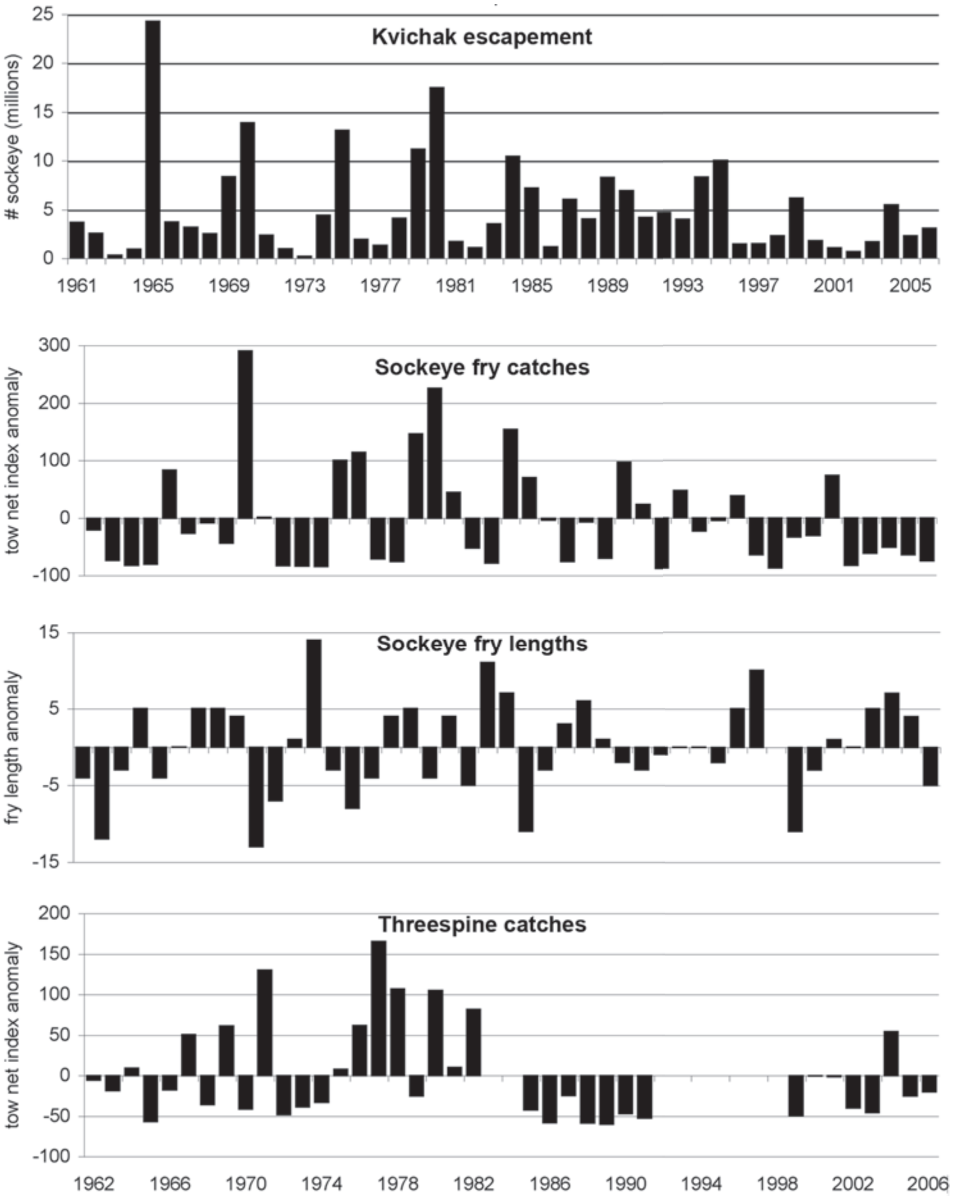


Figure 4.8. Kvichak River escapement (1961–2006), Iliamna Lake townet index for sockeye fry catches (dev. from mean), sockeye fry length (dev. from mean), and townet index for threespine stickleback catches (dev. from mean; 1962–2006).

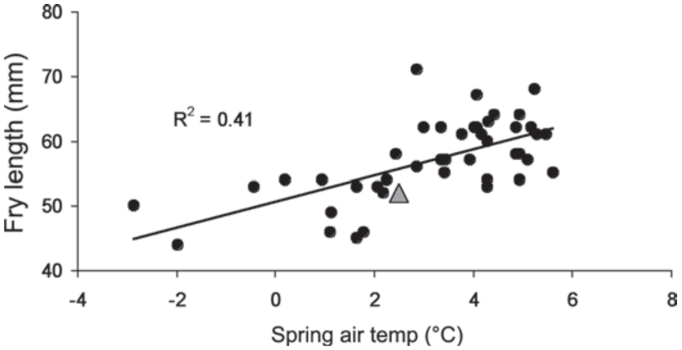


Figure 4.9. Relationship between Iliamna Lake sockeye fry length on Sept. 1 and average spring (March–June) air temperatures. (2006 is gray triangle point.)

Table 4.3. Occurrence and numbers of juvenile sockeye in stomachs of Arctic char collected by hook and line from Little Togiak River during the spring. Since 2000, all char diets were sampled by gastric lavage, and then fish were tagged and released.

Year	Date of ice-out	Range in sampling dates	No. char examined	Mean length (mm)	% char with:		Mean no.		
							Per char		Sockeye
					Fry	Smolt	Fry	Smolt	escape. year-2
72	8-Jun	6/26–7/10	82	446	34	60	2.8	4.5	55
73	2-Jun	6/19–7/3	121	446	34	44	1.9	2.9	24
74	22-May	6/11–6/25	64	429	19	39	0.8	1.6	14
75	8-Jun	6/22–7/13	71	415	9	36	0.2	1.8	14
76	10-Jun	6/19–7/13	96	418	11	56	0.4	2.2	48
77	1-Jun	6/11–7/11	325	403	30	17	7	0.4	30
78	22-May	6/7–6/25	316	437	7	42	0.2	1.5	18
79	16-Jun	6/6–6/22	178	438	32	25	1.8	1.2	26
80	17-May	6/9–6/25	278	459	--	81	--	9.4	45
81	23-May	6/12–6/25	124	415	3	31	0.1	1.4	44
82	6-Jun	6/17–7/5	105	450	18	61	1.8	6.4	81
83	18-May	6/19–7/3	78	424	0	14	0	0.3	60
84	17-May	6/20–7/2	56	408	0	18	0	0.4	36
85	8-Jun	6/15–7/6	60	437	22	30	1.6	1.2	31
86	26-May	6/16–7/5	61	437	21	56	0.4	2.7	17
87	23-May	6/14–7/5	51	451	6	78	0.1	4.9	21
88	27-May	6/16–6/29	43	431	7	26	0.1	0.8	21
89	9-Jun	6/20–7/15	105	388	37	38	2.2	1.3	15
90	19-May	6/7–6/24	72	391	35	11	1.8	0.3	19
91	26-May	6/20–7/7	48	415	4	35	0.9	2.5	15
92	2-Jun	6/15–7/11	79	425	0	46	0	1.9	29
93	1-May	6/7–6/18	124	429	9	19	0.6	0.4	19
94	18-May	6/14–6/29	52	420	0	15	0	0.2	35
95	20-May	6/11–6/13	3	468	66	66	2.3	2	19
96	22-May	6/16–6/24	40	429	0	42	0	1.1	24
97	21-May	6/13–6/24	28	445	0	11	0	0.3	28
98	20-May	6/15–6/25	22	435	9	36	0.1	2.8	23
99	14-Jun	6/28–7/1	12	469	17	50	0.4	0.9	45
00	23-May	6/20–6/29	67	430	0	48	0	1.4	53
01	25-May	6/13–6/22	41	451	15	34	3.7	1.7	21
02	2-Jun	6/19–6/29	45	466	11	38	0.9	0.8	ND
03	28-April	6/17–6/25	60	473	0	57	0	2.2	ND
04	25-May	6/10–6/28	56	459	4	63	0.1	2.3	ND
05	20-May	6/12–6/24	28	478	25	39	2.7	1.7	ND
06	3-Jun	6/19–7/1	36	485	0	61	0	2.3	ND
Means	3-Jun		88	436	15	40	1.1	2	31

Sockeye Salmon as a Food Resource for Resident Stream Fishes in Nursery Ecosystems

We are investigating the importance of sockeye salmon as a prey resource for fishes that are full-time residents in lakes and streams used by this species for spawning habitats. We are especially interested in evaluating whether the importance of sockeye tissues varies substantively among resident fish species (e.g., arctic grayling versus rainbow trout), and whether this importance varies among years according to sockeye density on the spawning grounds.

For this report, we focused on our efforts in several creeks draining into Lake Nerka that provide substantial habitat for rainbow trout and grayling. Resident fishes are surveyed at least twice per year (before and after sockeye arrival) with small seines to assess their diets, size distributions, and species composition in the stream.

We find that the feeding rate of arctic grayling and rainbow trout increases over fourfold once sockeye have entered streams and initiated spawning activities (Fig. 4.10). However, the compositional changes in the diet before and after sockeye entry are different between the two resident fishes. While both grayling and rainbow trout feed heavily on stream invertebrates prior to salmon arrival, diet composition of rainbow trout shifts to become dominated by sockeye resources after their entry to the stream (Fig. 4.10). After sockeye entry to streams, more than 80% of rainbow trout diets is composed of sockeye eggs, flesh, and maggots. This shift is more radical than that for grayling, which do switch feeding modes to include a modest amount of sockeye eggs and fly maggots from salmon carcasses, but benthic invertebrates remain the dominant component of the diet. We infer that grayling feeding rates on benthic invertebrates increase after sockeye arrival because of their increased availability due to sockeye nest-digging activities. Bioenergetics modeling of the potential growth responses of these enhanced feeding rates during salmon residence in streams suggests that most of the annual growth of rainbow trout and grayling occurs during this short window of the year.

Comparison of the feeding rates of resident fishes among years with variable sockeye escapement densities demonstrates that the foraging subsidy from sockeye is scaled by their density (Fig. 4.11). In years with high sockeye densities, the subsidy of eggs is severalfold higher than in years with low sockeye density. This effect is especially marked in grayling, where their consumption of eggs is virtually

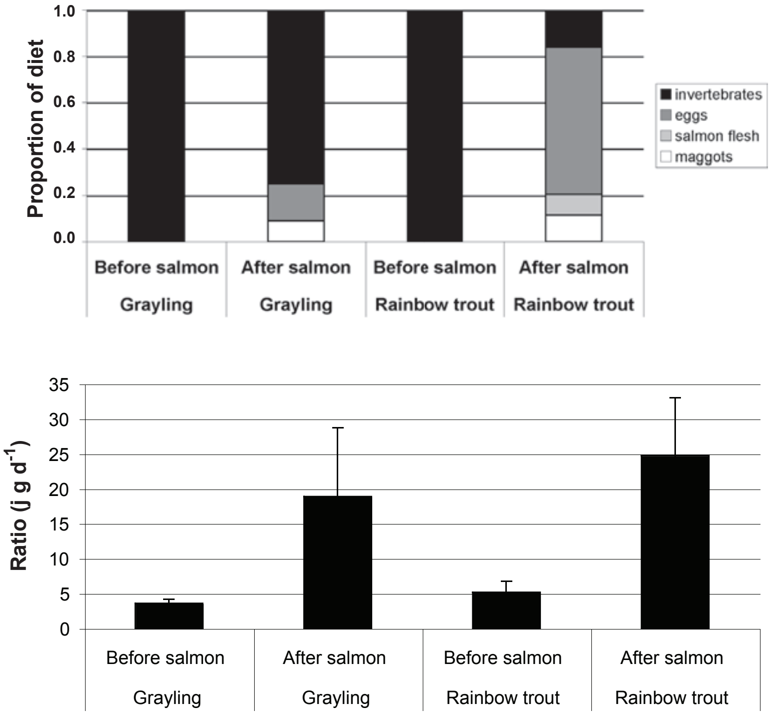


Figure 4.10. (A) Diet composition and (B) feeding rate for Arctic grayling and rainbow trout before and after the entry of sockeye salmon into small streams on Lake Nerka. From MD Scheuerell, JW Moore, DE Schindler, CJ Harvey. Varying effects of anadromous salmon on the trophic ecology of resident stream fishes in Alaska, unpubl. ms.

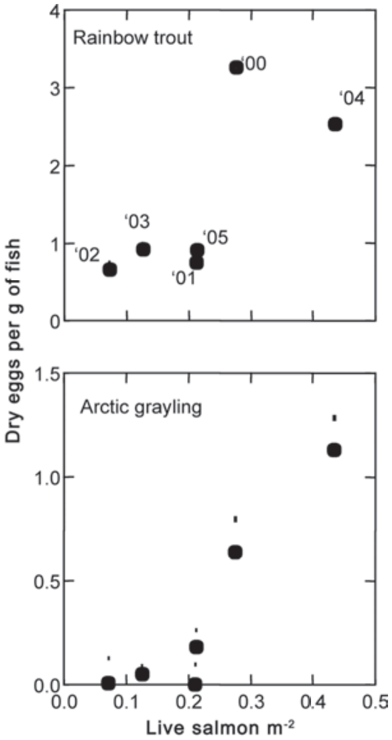


Figure 4.11. Feeding rate of rainbow trout and arctic grayling on sockeye salmon eggs in Hidden Creek, Alaska, 2000–2005. Consumption rates are standardized for the body mass of predators. Samples are based on at least 25 individuals in each year. From Moore et al. in prep.

nil during years with relatively low sockeye densities. We are still exploring the mechanistic basis for these patterns, but we hypothesize that sockeye densities have a nonlinear effect on egg feeding by resident fishes. This effect is due to the increasing importance of redd superimposition as a mechanism for making sockeye eggs available to resident fishes as sockeye populations increase in density (Moore et al. in review.). These results demonstrate the importance of sockeye escapement for providing marine-derived prey subsidies to freshwater fish communities. Interestingly, it appears that there is substantial variation in the density-dependent effect of sockeye on resident fish feeding, when comparing among streams. In Hidden Lake Creek, this relationship is characterized by a power function with which the inflection point coincides when redd superimposition occurs. In Lynx Creek, the importance of eggs in the diet of rainbow trout is an asymptotic function of sockeye density, suggesting that spawning habitat is extremely limiting for sockeye, thereby making eggs available to resident fish at much lower spawning densities (Fig. 4.12, Lynx Creek diets).

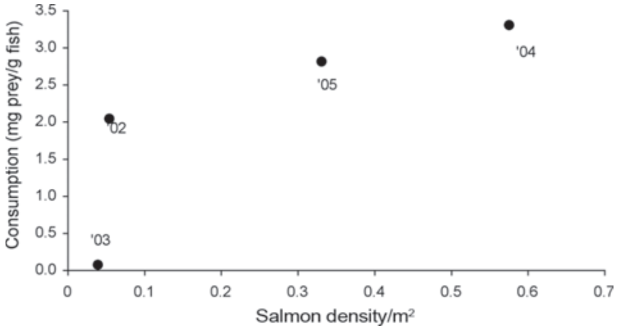


Figure 4.12. Consumption of salmon eggs by rainbow trout as a function of sockeye spawner density in Lynx Creek, Alaska, 2002–2005.

The Role of Marine-Derived Nutrients on the Movement, Diet, and Growth of Dolly Varden Char

K Denton (graduate student), T Quinn (adviser)

Individual Pacific salmon accumulate up to 99% percent of their final adult mass at sea. When they return to their natal rivers to spawn and die, the marine derived nutrients (MDN) in their bodies are released into freshwater ecosystems. The ways in which these nutrients affect primary and secondary production in streams has been well studied, but research into the effects of returning salmon on resident fish populations is less extensive.

Bristol Bay, Alaska is home to two economically important fisheries: commercial, largely for sockeye salmon, and recreational, for resident fish. Our research investigates the ecological link between these two fisheries. The objectives of this study are to document changes in Dolly Varden char diet, growth, and movement patterns, and relate them to sockeye arrival and abundance.

In this study, we are focusing on a series of spring-fed ponds adjacent to the northeast corner of Iliamna Lake. The ponds have very clear water and range in size from 100 m² to 2,000 m² and are about 0.5 m deep. The ponds are the seasonal home of Dolly Varden char and returning adult sockeye salmon.

In the summers of 2005 and 2006, char were captured (size range 57-343 mm) with a stick seine and 612 of them were PIT-tagged. PIT tags—individually coded tags about the size of a grain of rice—are surgically inserted into a fish's body cavity and subsequently read electronically. In 2006, there was a recapture event approximately every 3 days, and captured fish length, weight, diet, and location were documented.

Preliminary results indicate that before salmon arrived, a few small char (121 mm) were in the pond complex. Approximately 2 weeks after salmon started returning to the ponds, many larger char (161 mm) entered the complex (Fig. 4.13). Char diets also changed drastically during this time period. Before salmon arrived, diets were constituted almost entirely of aquatic macroinvertebrates, mostly larval and adult chironomids. After salmon began spawning, char diets shifted entirely to salmon eggs. Along with this shift in diet, radically different growth rates were observed over the same time period. After salmon arrived, char grew almost ten times faster than before salmon were in the system (Fig. 4.14). In fact, larger char often actually lost weight prior to salmon arrival, indicating that the nutrient subsidy salmon provide to resident fish is crucial to their yearly growth cycle.

The next step in this study will be to use over-winter recaptures from 2005–2006 and recaptures that will be collected in summer 2007 to model yearly growth rates in an effort to estimate the percentage of yearly growth a char accumulates due to MDN. Over-winter recapture rates will also enable us to address survival in this project.

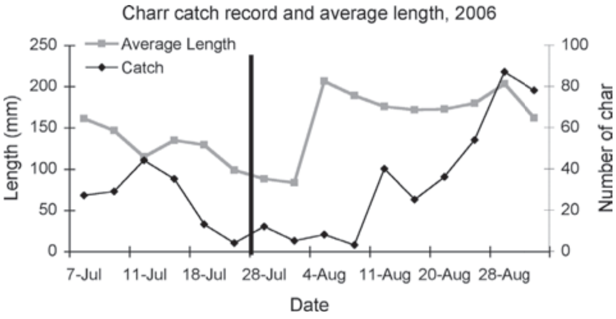


Figure 4.13. Catch records and average size of char throughout July and August of 2006. The vertical black line indicates arrival of salmon to the ponds.

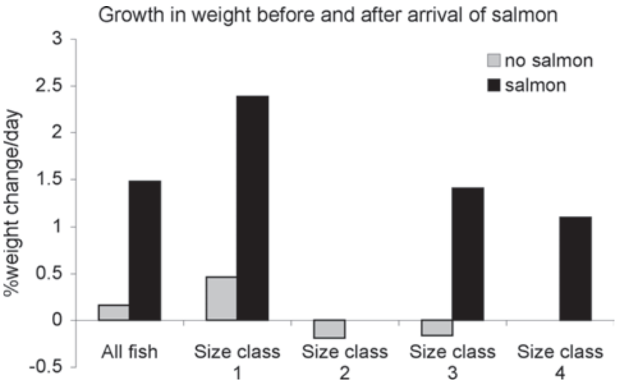


Figure 4.14. Percent weight change per day for char before and after the arrival of salmon. Size class 1: 0-140 mm; size class 2: 141-180 mm; size class 3: 181-240 mm; size class 4: >241 mm.

Reconsidering the Effect of Salmon on Ecosystem Metabolism

GW Holtgrieve (graduate student), D Schindler (adviser)

Pacific salmon represent one of the most widely acknowledged examples of biologically controlled spatial subsidies and are a stunning example of habitat connectivity by itinerant animals. Upon their migration from the ocean to natal habitats, where they eventually spawn and die, salmon can import a large quantity of nutrients, organic matter, and energy to coastal freshwater and riparian ecosystems (Naiman et al. 2002, Schindler et al. 2003). In areas with sizable salmon runs, the effect of these subsidies is transmitted across all trophic levels, and many species have adapted their life-history strategies to capitalize on this consistent resource (Gende et al. 2002).

Three main mechanisms have been proposed to describe how salmon alter freshwater ecosystem function: (1) increased primary production and subsequent secondary production as a result of nitrogen (N) and/or phosphorus (P) released from live and dead salmon, (2) increased secondary production via direct consumption of salmon tissues and eggs, and (3) physical habitat modification through bioturbation (Schindler et al. 2003, Moore 2006). Currently, the dominant model of how salmon affect stream primary productivity is one of “bottom-up” forcing in which MDN subsidies of N and P increase in situ primary productivity and, in turn, subsidize upper trophic levels including prey that support recruitment of juvenile salmon (Stockner 2003). Despite its general appeal, this hypothesis has the least direct evidence in its support and, in fact, has remained untested at the ecosystem scale.

Beginning in 2005, we sought test the hypothesis that salmon increase stream primary productivity by examining the effect of spawning sockeye on net ecosystem metabolism—the balance of respiration and photosynthesis. To do so, we have employed an integrative approach by measuring the concentration and isotopic composition of dissolved oxygen ($[O_2]$ and $\delta^{18}O_2$) and carbon dioxide ($[CO_2]$). This worked initially focused on Pick Creek in the Wood River System, Bristol Bay, Alaska before and after salmon entered the system. Pick Creek is an important salmon stream with historical sockeye runs of greater than 20,000 fish. In 2005, salmon entered the stream on July 17th and peak density was 0.65 salmon per m^2 on August 16th. In 2006, the number of streams was expanded to cover a range of salmon densities so as to better predict salmon effects and potential thresholds.

Our results show that, as expected, salmon added substantial nutrients (N and P) to the stream water in Pick Creek (Fig. 4.15A). Nitrogen stable isotopes (^{15}N) can be used to track the fate of nutrients from salmon, and we observed an increase in the $\delta^{15}N$ of periphyton, demon-

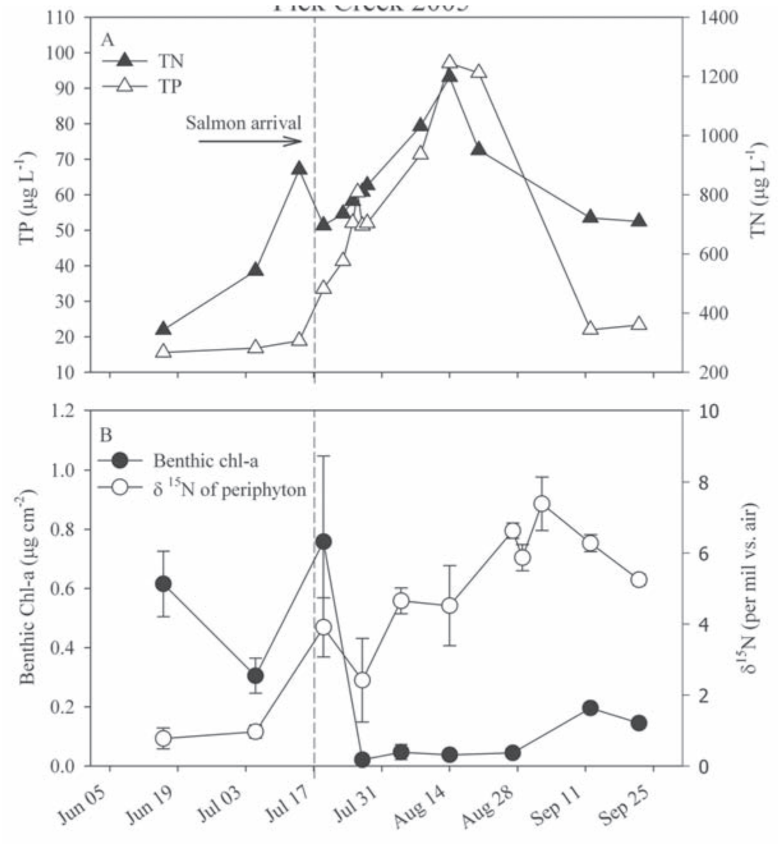


Figure 4.15. Total concentration of nitrogen and phosphorus in unfiltered water samples from Pick Creek over most of the open-water season 2005: (A) chlorophyll–*a* content per unit area and (B) δ^{15}N of periphyton (mean ±1 SE). Salmon entered the stream on July 17 with nearly complete senescence by early September

strating that nutrients from salmon are being incorporated into algal tissues (Fig. 4.15B). In spite of the increase in available nutrients, biomass of benthic primary producers in Pick Creek declined after the arrival of salmon (Fig. 4.15B) as a result of the high disturbance from nest-digging activities.

Using an oxygen isotope mass balance model of net ecosystem metabolism, we found that, contrary to the current paradigm, natural densities of salmon did not increase net primary production. Rather, photosynthesis roughly equaled respiration prior to salmon spawning but once salmon entered the system, respiration increased while primary production decreased (Table 4.4). Integrated ecosystem respiration exceeded production by two- to sevenfold depending on the assumed gas exchange rate.

Metabolism by salmon, decay of carcasses, or physical suspension of in situ organic material which is then respired by bacterial heterotrophs are mechanisms by which salmon can increase overall heterotrophic respiration within a stream. We estimated the amount of carbon mineralized via respiration in excess of pre-salmon conditions from July 17 to August 28 and compared this with the carbon content of returning salmon (~450 g C fish^{-1}). C in salmon tissues accounted for roughly 37% of total mineralized C in the stream over this time period, suggesting that much of the observed increase in respiration was driven by heterotrophic microorganisms fueled by mobilized sediments and organic matter.

In conclusion, it appears that although nutrient concentrations in Pick Creek increase significantly owing to spawning salmon, and algae incorporate these nutrients into their tissues, widespread uptake by biota is limited by the abundance of primary producers because of the intense bioturbation effects by salmon (Moore 2006). The net result is a decrease in primary production and a substantial shift to a dominantly net heterotrophic state (respiration » production). Nutrient inputs to these systems via salmon are undoubtedly significant and are propagated throughout the stream and riparian habitats. However, we suggest changes to the current model of how salmon and MDN affect stream ecosystems to one that more fully considers the role of salmon as living species interacting with their environment rather than focusing on the specific resources they might provide.

Table 4.4. Reaeration and ecosystem metabolic rates in Pick Creek, 2005.

Date	Model[a]	K_2[b] (hr^{-1})	R[c] (µmoles O_2 $liter^{-1}$ hr^{-1})	GPP[c] (µmoles O_2 $liter^{-1}$ hr^{-1})	NPP[c] (µmoles O_2 $liter^{-1}$ hr^{-1})
08-Jul-05	SRM	0	51	44	-7
	MET	1	163	153	-10
	EDM	1	227	216	-11
16-Aug-05	SRM	0	94	24	-70
	MET	0	185	67	-118
	EDM	1	282	114	-168
29-Aug-05	SRM	0	NA[d]	NA[d]	NA[d]
	MET	0	123	23	-100
	EDM	1	194	55	-139

[a] Competing gas exchange models used to calculate rates of respiration and production. SRM=surface renewal model; MET=meta-analysis model; EDM=energy dissipation model.

[b] Reaeration coefficent of gas excahnge.

[c] R=respiration; GPP=gross primary production; NPP=net primary production=GPP-R.

[d] Does not include SRM due to artifactual errors in isotope mass balance.

Impacts of Salmon Nest-Digging on Stream Ecosystems

JW Moore (graduate student; completed PhD), D Schindler (adviser)

Pacific salmon can have large impacts on freshwaters when they return to their home streams and lakes to spawn and die. For example, salmon move massive quantities of nutrients from the ocean to coastal ecosystems during their spawning migration (Moore and Schindler 2004). These salmon-derived nutrients may help support coastal productivity and biodiversity (Schindler et al. 2003).

Further, anadromous salmon may have large impacts on freshwater spawning habitats because they often dig large nests and spawn at high densities (Moore 2006). A female Pacific salmon digs at least one nest (redd) in which she lays and buries her eggs (Fig. 4.16). Depending on the size, species, and location of spawning salmon, a single salmon redd can cover between 1 m^2 and 17 m^2 (Groot and Margolis 1991), and be up to 35 cm deep (Steen and Quinn 1999). For example, in three creeks in the Wood River system, Alaska, female sockeye salmon dig nests in the gravel substrate that cover approximately 2.1–4.1 m^2 and are on average 20 cm deep (Steen and Quinn 1999, Peterson and Foote 2000). In addition, in some years in the Wood River system, salmon spawning in high densities in certain streams may disturb all available habitat.

This research has been focused on how salmon nest-digging changes streams. Previously, we used small-scale experiments to learn that salmon nest-digging dislodges silt, algae, and benthic invertebrates on a small spatial scale (Moore et al. 2004). We followed up this study by examining how this behavior influences streams at larger spatial and temporal scales. These studies have provided insight into the diverse and dramatic ways in which salmon nest-digging affects stream ecosystems.

To investigate the ecological importance of salmon nest-digging in streams, we have compared the seasonal dynamics of streams across a gradient of sockeye salmon density. We examined 10 streams that spanned a natural range in salmon density, studying these streams across multiple years with different escapements. For up to five summers for each stream, we sampled a suite of stream

Figure 4.16. A female sockeye salmon digging her redd. She uses body and tail undulations to displace large sediments and dislodge small sediments into the water column. Note the plume of dislodged fine sediments drifting downstream of the female. Photo by D Schindler.

ecosystem variables every 7-14 days. During each sampling event, we measured suspended sediments and total nitrogen and phosphorus in water at the stream outflows, and we quantified periphyton biomass and benthic invertebrate community composition with Surber samplers.

During nest-digging, salmon dislodge fine sediments into the water column where they subsequently drift to downstream lakes (Fig. 4.16). The concentration of suspended particulate matter in stream water drastically increases as soon as salmon enter streams and start to dig their nests (Fig. 4.17). Over the entire season, this nest-digging exports up to 1 kg of dry matter per m^2 of streambed from streams. In addition, for a given stream in years with higher salmon densities, higher levels of fine sediments are exported. Thus, salmon nest-digging influences fluxes of fine sediments, changing sediment dynamics of stream ecosystems (Moore et al. in press). Fine sediments have been observed to negatively affect early life-history stages of salmon (Tappell and Bjornn 1983), suggesting that this nest-digging might lead to feedback loops across generations of salmon (Montgomery et al. 1996).

Salmon also increase the export of nutrients such as nitrogen and phosphorus from streams when they dig their nests to spawn (Moore et al. in press). For example, in Pick Creek, a stream with high densities of spawning salmon, concentrations of total phosphorus increase fivefold and concentrations of total nitrogen double when salmon enter streams and spawn. Over the entire season, this nest-digging exports large quantities of nutrients. In fact, in some streams and in some years, salmon export as much phosphorus as is brought back in their carcasses. A bioassay experiment suggested that the exported nutrients are used by primary producers and fuel primary productivity of downstream lakes.

During nest-digging, salmon can bury or dislodge algae attached to substrates. This periphyton is the base of the stream food web, directly or indirectly contributing to a variety of invertebrates and fishes. In streams and years with high densities of salmon, algal biomass decreases dramatically when salmon enter streams and churn up the substrates. In general, when there is 0.1 salmon per m^2 or more, algal biomass plummets to about 10-20% of pre-salmon abundance (Fig. 4.18). While previous studies have suggested that salmon carcasses can fuel periphyton

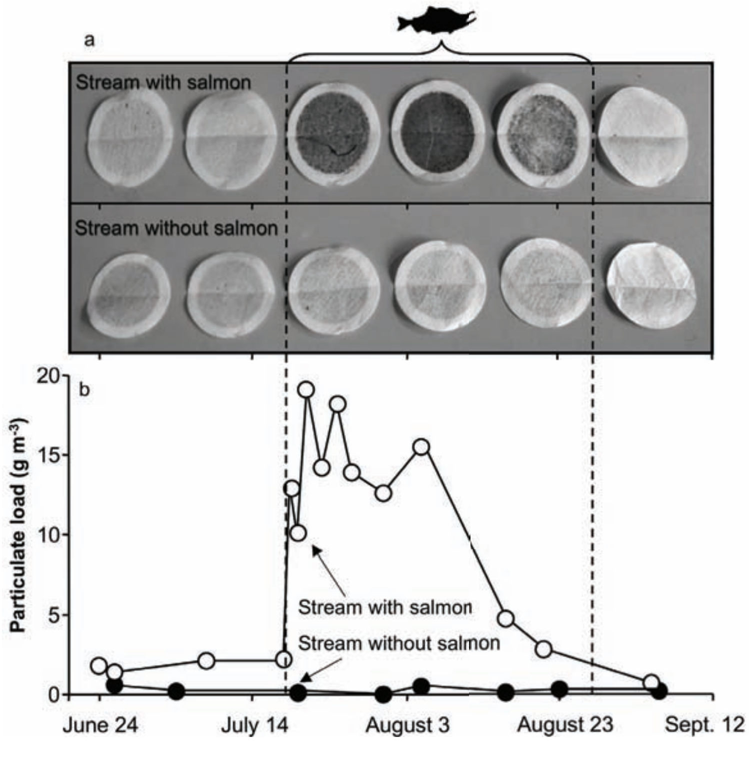


Figure 4.17. The impact of bioturbation by spawning salmon on the concentrations of total suspended particulate matter in the outflows of two Alaskan creeks. The dashed vertical lines indicate spawning period in the stream with salmon. (a) Seasonal progression of particulate load: Pictured are GF/F filters (pore size = 0.7 μm) used to filter 2 L of water throughout the 2002 summer from Pick Creek (top), which has high densities of spawning sockeye salmon mid-summer, and Cottonwood Creek (bottom), a nearby stream without salmon. (b) Seasonal dynamics of concentrations of suspended particulate matter in the same two streams in 2003. Points represent mean of two replicate grab samples of 2 L of water from stream outflows that were filtered through GF/F filters, dried, and weighed. No substantial changes in discharge occurred during the salmon spawning period.

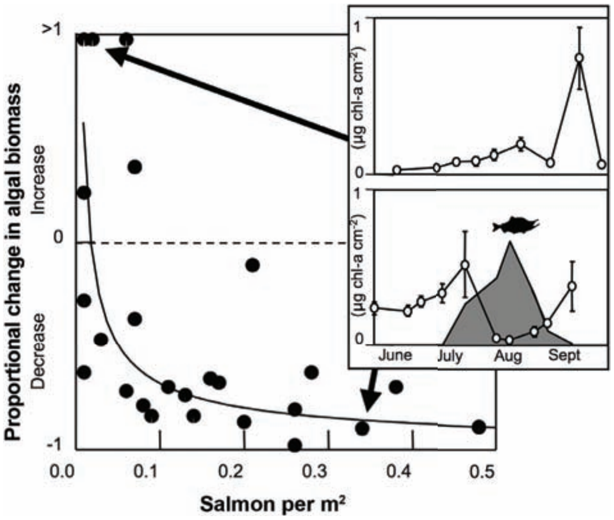


Figure 4.18. The impact of spawning salmon on periphyton abundance. Each point represents the proportion change in biomass of algae from before to during salmon spawning for a given stream year. Thus, any point above the dashed line represents a stream and year where algal biomass increased during the season, while any point below the line represents a stream and year when algal biomass decreased during the season. This change in algal biomass is plotted against the maximum observed spawning density of salmon for that stream–year. The inset shows two example time-series of the seasonal dynamics of algal biomass, corresponding to summary points on the main graph.

growth (Naiman et al. 2002), we have observed that any possible fertilization by salmon is overwhelmed by the disturbance caused by their nest-digging.

Salmon nest-digging also has large impacts on the benthic invertebrates that inhabit stream bottoms. Benthic invertebrates such as mayflies disappear from streams when high densities of salmon enter and spawn. Two mechanisms may drive this pattern. First, salmon nest-digging might be a direct source of mortality, crushing or dislodging benthic insects. In addition, our data suggest that salmon nest-digging constrains the phenologies of benthic invertebrates. Specifically, insects emerge into terrestrial adults before high densities of salmon start spawning in streams. Thus, predictable and severe disturbance from nest-digging salmon may drive local adaptation of insect emergence timing.

Through physically modifying stream habitats during nest-digging, salmon are acting as ecosystem engineers (Moore 2006). This ecosystem engineering has dramatic impacts on a variety of stream dynamics. It controls the seasonal movements of fine sediments and nutrients, moving enormous quantities of this matter out of streams into downstream lakes. In addition, this nest-digging has dramatic impacts on benthic communities, acting as a predictable and severe disturbance of periphyton and benthic invertebrates. Previous studies of the impacts of salmon on streams have focused on how salmon carcasses can fertilize streams. Our studies challenge this paradigm, and suggest that salmon affect streams primarily through physical modification of stream habitats during spawning.

The Link Between Salmon and Birds: Reproductive Success and Stable Isotopes of Tree Swallows

LX Payne (research scientist), D Schindler

Although salmon are well known as an important food source for direct consumers (e.g., grizzly bears), the extent to which salmon and salmon-derived nutrients are important to secondary consumers—especially birds—is poorly understood. More than 100 species of birds nest in Wood–Tikchik State Park; at least 60% of these rely on insects during the energy-intensive chick-rearing period. The principal objective of this pilot project, which started in 2006, is to determine the importance of salmon to the avian community in Wood–Tikchik State Park.

Tree swallows (Fig. 4.19) are long-distance migrants that breed across North America. They rely on aerial insects (especially near aquatic sites), and are demonstrated indicators of the health of aquatic systems. Swallows feed on salmon indirectly, by consuming aerial insects that have taken up nutrients originating from salmon carcasses. The extent to which salmon subsidize tree swallow diets is unknown but can be inferred using stable isotopes.

For this study, we will quantify the extent of salmon-derived nutrients in tree swallow diets using several feathers taken from each juvenile. This relatively non-invasive technique is adequate because all nutritional inputs to juveniles (and therefore, into their feathers) necessarily originate from localized food sources around their nest box; tree swallows feed within 400 m of their nest boxes. We will also explore the link between salmon subsidies and the ecological dynamics of tree swallows by monitoring growth rates and fledgling mass to estimate the effects of salmon on swallow recruitment rates.

Figure 4.19. Tree swallow adult. Photo by J Bailey.

Specific questions we will address are as follows:

1. is it possible to differentiate, using stable isotopes, among tree swallow juveniles raised along salmon versus non-salmon streams?
2. Do juvenile tree swallows from salmon versus non-salmon sites grow at different rates?
3. How does insect production vary among sites (throughout the nesting season)?

This study of ecosystem linkages, in a relatively pristine area with healthy salmon runs and intact bird communities, is also important because it provides baseline information for understanding and comparing with either degraded ecosystems or ecosystems under uncertain climate scenarios.

In 2006, we monitored 45 tree swallow nest boxes located at seven sites (Fig. 4.20): along three salmon streams, two non-salmon streams, and two muskegs (wet meadows) in the central Nerka area. Nest boxes were built and installed in summer 2005 to accommodate breeding swallows by spring 2006 (as birds arrive in May). Nest-box occupancy was limited to tree swallows in 2006 (exceptionally, three nest boxes had wasp nests) and occupancy was modest (42%) this first year, as is common during the first year of most next-box studies. We anticipate tree swallow occupancy to at least double over the next few years.

Most of the seven sites showed early evidence of nesting activity (i.e., partial to complete nests), with highest nesting activity at nest boxes along salmon streams, moderate activity at muskegs, and lowest activity along non-salmon streams.

Across all sites, many nests were abandoned, probably owing to cold late-spring temperatures and consequently low aerial insect availability (swallows commonly abandon nesting efforts if aerial insects are scarce). However, 39 chicks (Fig. 4.21) were produced at 12 nests, at two salmon stream sites (n = 11 nests) and at one muskeg site (3 chicks from a single nest).

Figure 4.20. Researchers user ladder to check contents of nests, which are installed at least 10 feet from the ground to avoid bears. Photo by E Schindler.

Chick growth rates varied, but sample sizes were too small to make meaningful comparisons by site type. About half of the observed breeding females were young (based on plumage), so nest success in 2006 was likely influenced by age/experience of parents. Larger sample sizes will be necessary to make statistical comparisons, so we built and installed 35 more nest boxes at the end of the 2006 field season.

In anticipation of increased nest box occupancy and higher chick production for 2007–2008, we should have large enough samples to be able to test whether tree swallows have differential stable isotope signatures among site types, and whether growth rates of juvenile swallows vary predictably by site type.

Results from this study will pave the way to being able to answer the larger question: Can we determine the extent to which songbirds are subsidized by salmon-derived nutrients by sampling juvenile songbird feathers in various habitats?

Climate and Density-Dependent Controls over Growth and Life History of Sockeye Salmon in Iliamna Lake, Alaska

H Rich, Jr. (graduate student, Master's completed), T Quinn (adviser)

Since 1962, the Alaska Salmon Program has been conducting townet operations to study the relative abundance, distribution, and growth of juvenile sockeye salmon in Iliamna Lake. In this study, we used long-term data (1962–2005) on juvenile sockeye salmon growth in Iliamna Lake to determine the relative roles of climate and

Figure 4.21. Tree swallow juveniles, about 2 weeks old. Photo by P Lisi.

density in controlling growth and life-history transitions in this species. The Iliamna Lake populations of sockeye salmon include fish that migrate to sea after either one or two full growing seasons in the lake, allowing us to study competitive interactions between these two year classes. Iliamna Lake and its tributaries not only have had remarkably large runs of sockeye salmon during the time period we are studying, but also have shown cycles of abundance (Eggers and Rogers 1987), and in recent years the runs have been very low. These changes in density, unrelated to degradation in habitat quality or access, have taken place during a period of dramatic shifts in climate (Mantua et al. 1997, Hilborn et al. 2003), making this an ideal system in which to study the interplay between these processes. Accordingly, the objectives of this study were to quantify the relative effects of climate and density on the size of juvenile sockeye salmon at the end of their first growing season in Iliamna Lake. We predicted that warmer conditions would be positively correlated with fry size at the end of the first summer whereas density of juvenile sockeye salmon (within and between brood years) was predicted to correlate negatively with size.

We used a class of Bayesian time-series models known as dynamic linear models (DLM; Pole et al. 1994) to quantify the relative effects of different factors on the growth of juvenile sockeye in their first year of life: the density of their parents (and so, presumably, the abundance of fry), the density of older conspecifics from the previous year's cohort, and temperatures the sockeye experienced as newly emerged fry. We compared alternative models through the use of cumulative Bayes factors (H), which represent the odds in favor of one model relative to another while accounting for model complexity (Berger and Pericchi 1996). The DLM for the 44-year time series (1962–2005), which included spring air temperature and fry density as predictors in explaining variation in sockeye fry length, provided the best fit to the observed data for this model group (Fig. 4.22). The positive effect of air temperature was about three times as large as the negative effect of fry density (mean effects: 7.15 mm for temperature and -2.40 mm for density). For the 39-year time series (1962–2000), for which estimates of yearling density were also available, the best models had both spring air temperature and density estimates from both age classes of sockeye juveniles as predictors (Fig. 4.22). The positive effect of temperature was the strongest predictor variable (about 40% greater than yearling density and about 2.5 times greater than fry density).

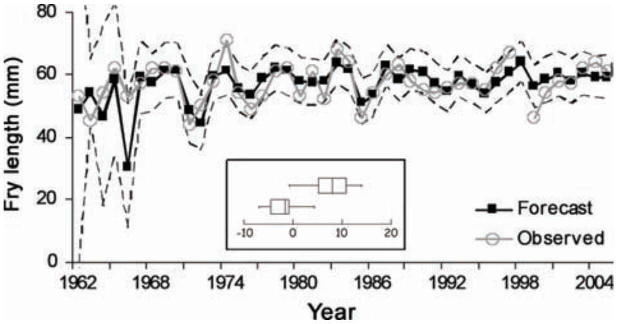


Figure 4.22. Model output showing model forecast fit to observed data and the 90% prediction intervals for the fry density–spring air model. Effect size plot inset shows mean effect size over the time series for spring air temperatures (top plot) and fry density (lower plot). Model forecast to observed fit $r^2 = 0.32$ (increases to 0.47 if outlier is removed).

In the past decade, the Kvichak/Iliamna system has seen the combined effects of mild temperatures and reduced intraspecific competition. The two "peak" year returns since 1995 (6.2 million in 1999 and 5.5 million in 2004) were small compared with the peak years in the past. Concurrent with this reduction in spawner densities, environmental conditions have warmed considerably. Both of these factors have influenced fry size at the end of the first growing season, which affects the proportion of the cohort that migrates to sea as 1-year-olds (Burgner 1987; Fig. 4.23, $r^2 = 0.48$). We have seen increasing proportions of age 1 smolts leaving this system, which is due to both increases in temperature and relaxation of density effects. Indeed, over the smolt migration years of 1993–2000, approximately 72% of outmigrants were age 1, compared with the average of 48% age 1 smolts from the 1963–1992 smolt years. The link between this shift in age structure of the smolt population and its consequences for adult productivity remain uncertain (Schindler 2006, pers comm. and unpubl. data).

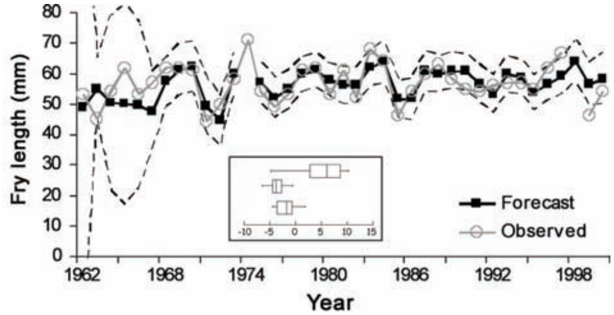


Figure 4.23. Model output showing model forecast fit to observed data and the 90% prediction intervals for the fry density–yearling density–spring air model. Effect size plot inset shows mean effect size over the time series for spring air temperatures (top plot), yearling density (middle plot), and fry density (lower plot). Model forecast to observed fit $r^2 = 0.33$.

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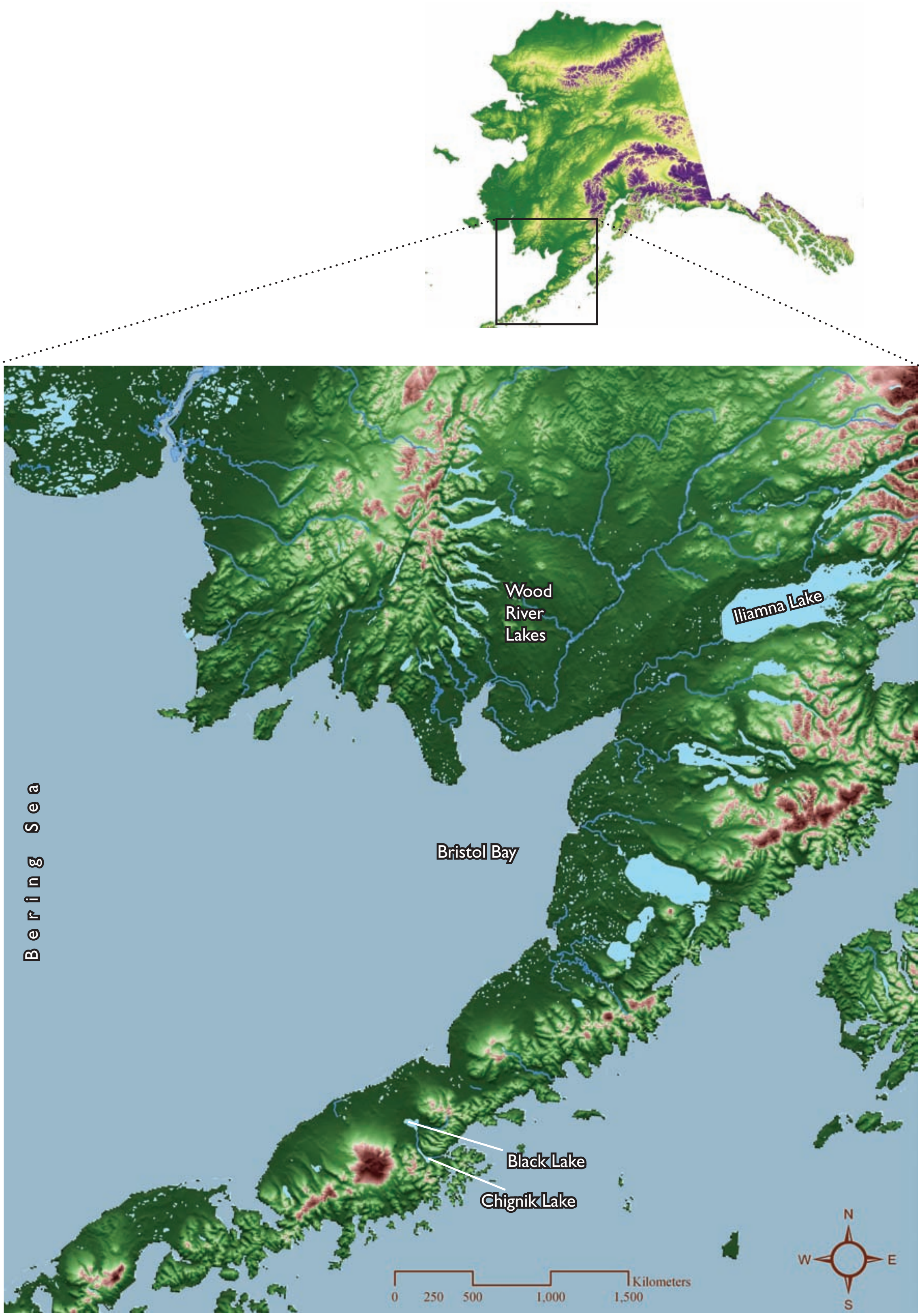
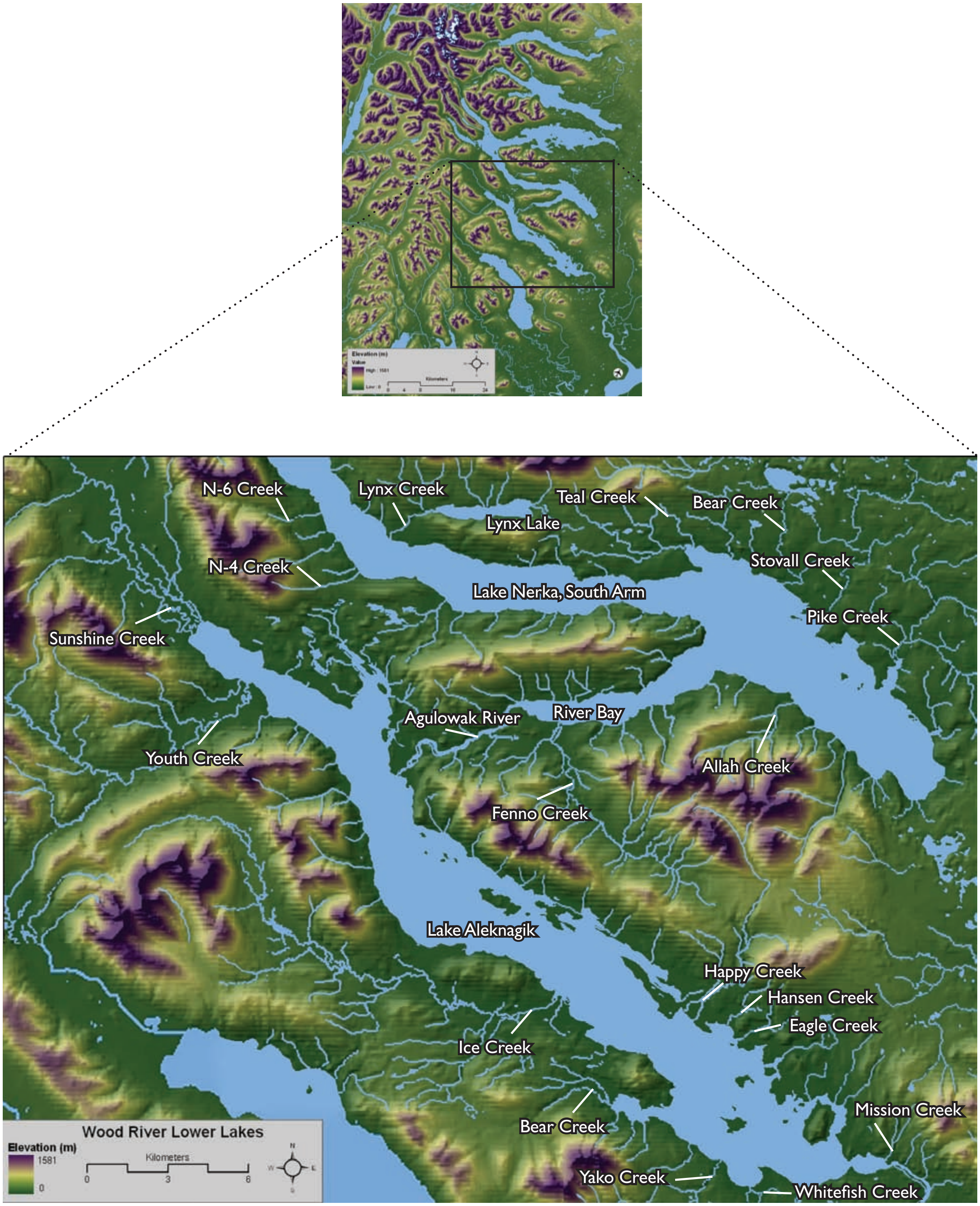
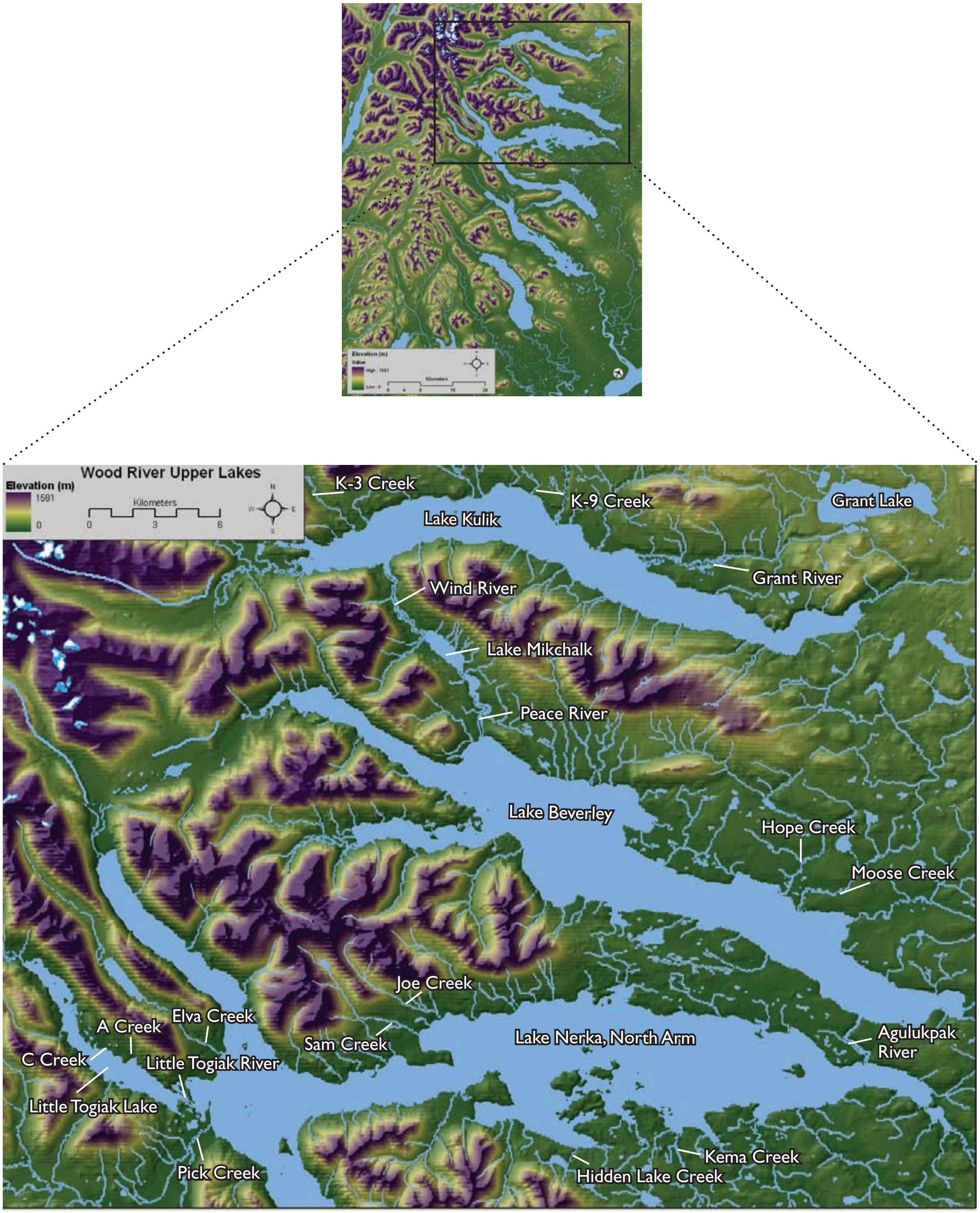
Maps



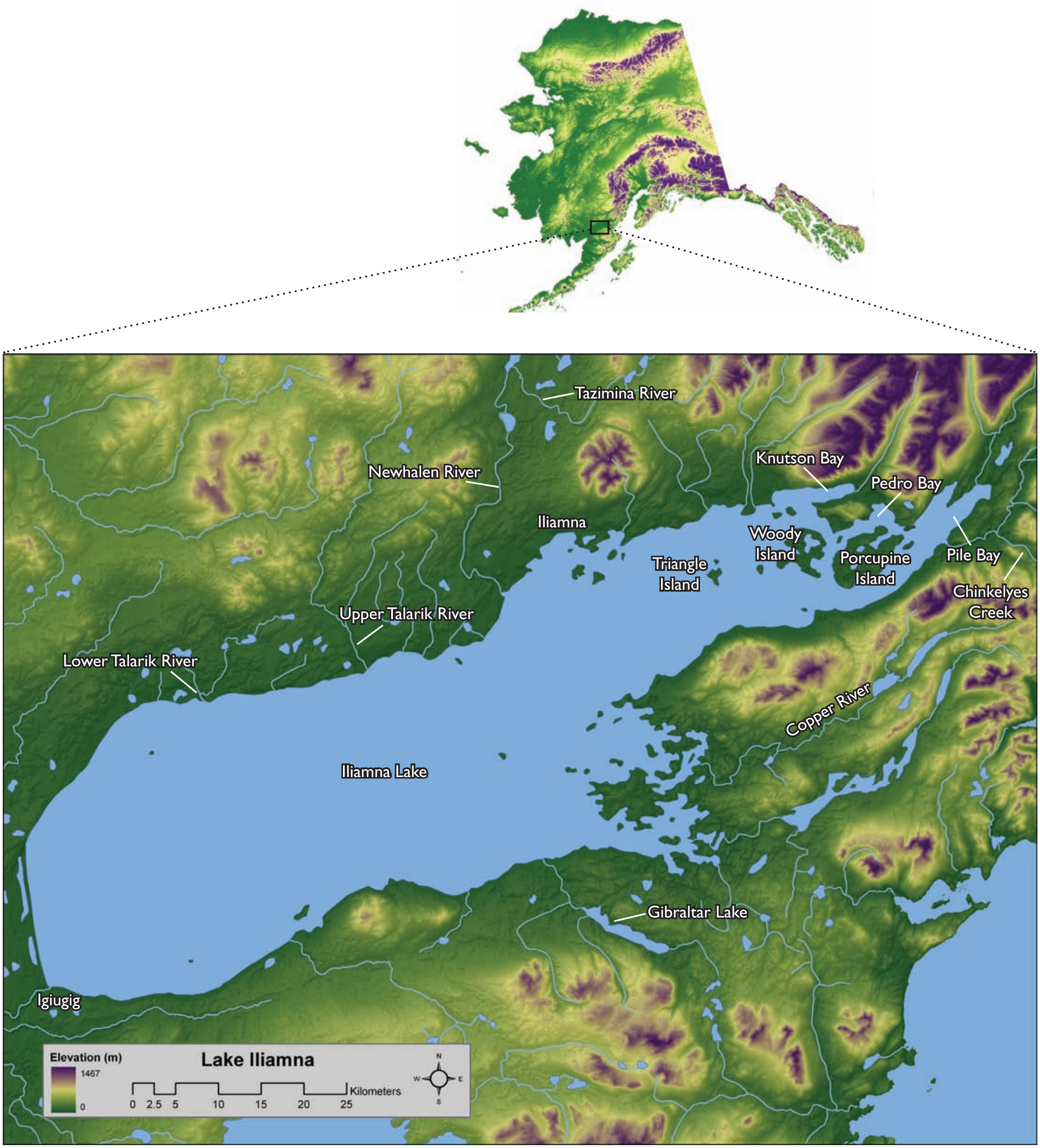
Map of the Alaska Salmon Program's three major research areas: Wood River lakes, Iliamna Lake, and the Chignik lake system.



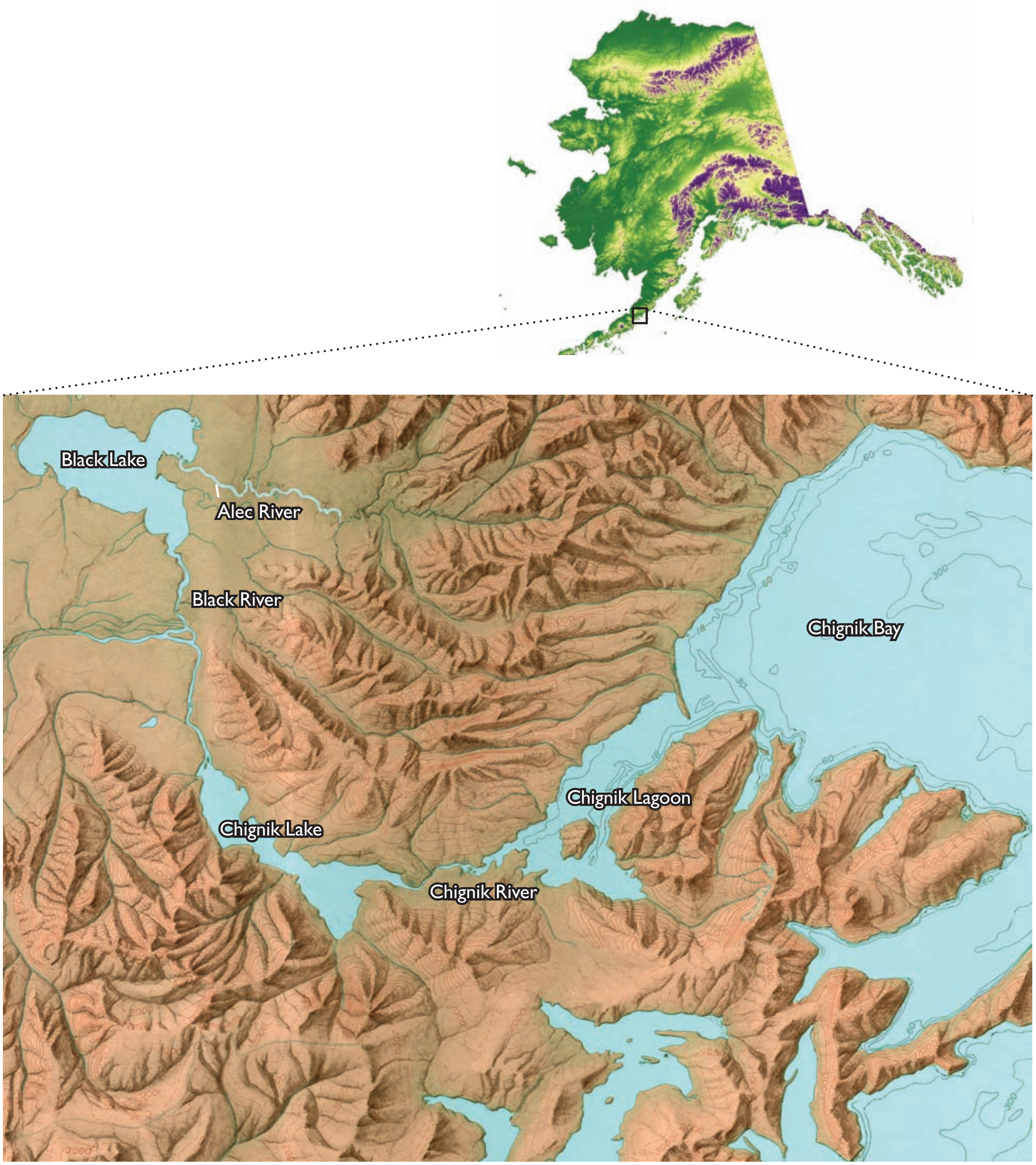
Detail map of lower Wood River lakes.



Detail map of upper Wood River lakes.



Detail map of Iliamna Lake.



Detail map of Chignik and Black lakes.

Mechanisms Behind Cyclic Sockeye Populations

P Lisi (undergraduate/technician), D Schindler (adviser)

Sockeye salmon often oscillate in abundance by many orders of magnitude periodically, and it has been suggested (Ricker 1950, Ward and Larkin 1964, Levy and Wood 1992) that delayed density dependence may play a role in these variations in abundance. Such patterns have been termed cyclic dominance, which is evident in the Kvichak River system in Bristol Bay, Alaska.

Cyclic dominance has been under debate for the past 50 years, yet no scientific consensus as to what causes the fluctuations in salmon populations has been reached. Eggers and Rogers (1987) used modeling to suggest that commercial fishing maintains the dominant line of sockeye in cyclic populations. Alternatively, Ward and Larkin (1992) proposed that depensatory agents independent of the fishery suppress the production from small escapements. However, little empirical evidence supports the mechanisms behind either hypothesis.

Interactions independent of the fishery could be explained by observing how juveniles of different ages share available resources—from fry emergence to smolt migration to sea. Using a beach seine and townet, we caught smolt and fry during June and July 2006 at Lake Aleknagik. Lake Aleknagik is not a system where strong cyclic sockeye populations occur. Yet we can still assess how cohorts partition available resources. We examined the gut contents of smolt and fry to calculate a percentage overlap in their diet. We found a significant overlap in diet from June 21 to July 3 (Fig. 4.24). Smolt and fry diets did not overlap on June 12; however, the results are likely due to a low sample size during this period (n = 4).

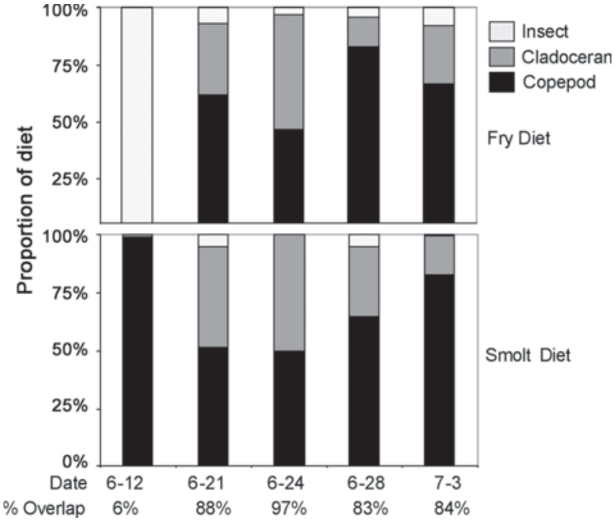


Figure 4.24. Diet overlap between fry and smolt in Lake Aleknagik during the summer of 2006.

These data suggest a competitive foraging arena between broods during a critical window in a juvenile salmon's lifecycle. When broods suppress insect and zooplankton populations, they likely decrease their own growth and survival. If we apply this concept to other sockeye-dominated systems with different lake morphology, productivity, and stronger cycle years, we may be able to better understand the mechanisms that drive cyclic dominance.

Movements of Sculpin to Sockeye Salmon Spawning Sites on Island Beaches in Iliamna Lake.

J Hill (undergraduate/technician), H Rich, T Quinn (advisers)

Iliamna Lake supports two species of sculpin: the coastrange sculpin and the slimy sculpin. Previous research suggested that sculpin move to perennial sockeye salmon spawning locations on island beaches in Iliamna Lake at least 6 days prior to spawning. The objective of this study was to measure the relative abundance of sculpin at both a perennial sockeye spawning site and neighboring non-spawning sites prior to and during spawning. Sampling was conducted with egg-baited minnow traps in the eastern part of Iliamna Lake at island beach locations.

On the basis of previous studies, we expected to see an increase in relative abundance of sculpins at the spawning site prior to salmon arriving on the spawning beach. Also expected was a corresponding decrease in abundance at the neighboring non-spawning sites, as we hypothesized that sculpin would move to take advantage of the egg resource. The increase in sculpin abundance at the spawning location prior to spawning was not observed conclusively. However, a dramatic decrease in abundance at the non-spawning sites immediately following the initiation of spawning was noted (Fig. 4.25). A similarly dramatic

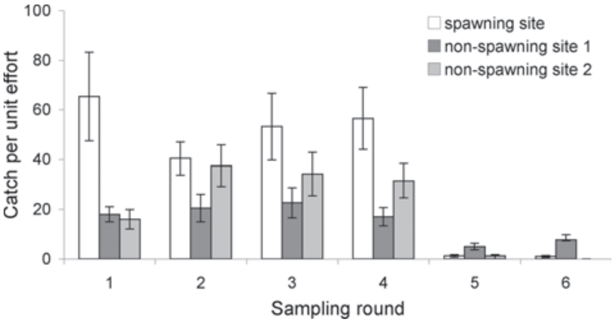


Figure 4.25. Mean catch (± SE) of sculpins at spawning and non-spawning beach sites in Iliamna Lake, Alaska, July to mid-August, 2006.

Continued from p. 36

decrease in abundance at the spawning site was caused by sculpin not entering the traps, which was due to the availability of eggs in salmon redds. The decrease in abundance at the non-spawning sites suggests that sculpin were moving off the non-spawning sites in response to nearby spawning activity by salmon. Related work this summer revealed that some individually marked sculpins moved approximately 800 m from location of post-marking release. Proposed future work includes (1) direct measurement of relative abundance of sculpins on the spawning ground during spawning and (2) continued investigation of sculpin movement capabilities and distances traveled to exploit the egg resource.

Rapid Restructuring of the Pelagic Fish Community in the Chignik Lake System: The Result of Habitat Loss, Climate Change, or Both?

P Westley (graduate student), R Hilborn (adviser)

Local habitat change is often driven by evolution of natural processes such as tectonics, volcanic activity, geomorphology, and hydrology. Rapid change in the geomorphology of Black Lake, Alaska, provides a unique opportunity to investigate organism and community response to rapid, large-scale physical changes to aquatic habitats. The Chignik Lake system is situated on the south side of the Alaska Peninsula (56°16'N Lat., 158°50'W), and produces the vast majority of the sockeye salmon in the region. The system consists of two interconnected lakes draining into the Gulf of Alaska (see map, p. 39). Chignik Lake is small (22 km^2), relatively deep (64 m), and is surrounded by precipitous mountains. In contrast, the upper lake, Black Lake, is larger (41 km^2) and extremely shallow (3 m maximum depth) and turbid, resting in a shallow tundra depression. Black Lake drains via the Black River into Chignik Lake. The outlet of Chignik Lake flows into a semi-enclosed estuary, Chignik Lagoon, and eventually into the Gulf of Alaska (Narver 1966, Dahlberg 1968, Ruggerone 1989).

For 50 years, University of Washington researchers, first through the Fisheries Research Institute (FRI) and more recently through the Alaska Salmon Program, have worked in the Chignik Lake system with the goal of understanding the physical and biological factors that control sockeye salmon production. During this time, rapid environmental changes in Black Lake have been documented (Ruggerone et al. 1992, Ruggerone 1994, Ruggerone et al. 1999, Chasco et al. 2003, Ruggerone 2003). Largely because of channel migration of the West Fork of the Black River, Black Lake is losing volume (Papanicolaou et al. 2006). Lake depth has decreased dramatically since the 1950s, resulting in a volume loss of approximately 50%, which in turn has greatly reduced the amount of available rearing area for juvenile sockeye salmon and other non-anadromous fishes such as sticklebacks (threespine and ninepsine) and pond smelt.

Through the use of a long-term database, we show that the pelagic fish community in Chignik Lake has shifted from one dominated by juvenile sockeye salmon to one that includes high abundances of competitor species. We hypothesize that conditions upstream in Black Lake, such as reduced water volume and rearing area, as well as warmer temperatures from climatic fluctuations, have stimulated increased emigration of fish from Black Lake to Chignik Lake. However, disentangling the proximate mechanisms driving these changes in community structuring is difficult as climate change and reduction of Black Lake volume are occurring simultaneously. Analyses to quantify the effects of habitat loss and climate fluctuations are ongoing.

Following an extensive investigation of lake carrying capacities, Narver (1966) states that an analysis of niches in the Chignik Lake ecosystem showed the pelagic zone was completely dominated by juvenile sockeye salmon. It is clear how Narver arrived at this conclusion. At least 80% of the total catch per tow in Chignik Lake during the 1960s and 1970s constituted sockeye salmon (Fig. 4.26). In contrast, the pelagic zone of Black Lake frequently had a high percentage of non-sockeye species, approximately 50% on average. Largely because of funding shortfalls, townet sampling did not consistently occur from 1973 to 1992. A dramatic increase in sticklebacks and pond smelt in the townet catches of Chignik Lake is evident upon continuation of sampling in the early 1990s. Relative abundance of sticklebacks and pond smelt also increased in Black Lake, but less dramatically than in Chignik Lake. Non-metric multidimensional scaling (MDS) was employed to quantify the community composition in the Chignik lakes and to avoid biases due to non-independent relationships between trends in species' relative abundances (Litzow 2006). Additionally, MDS is robust to large numbers of zeroes observed for several species during early time periods. Relative abundance (based on catch-per-unit-effort) of species in each lake and year was taken as 'sample' assemblages. The Bray-Curtis procedure provides a formal quantitative method for investigating co-occurrence or dissimilarity of relative abundance of multiple species in time and space. Samples between lake and year were measured by Bray-Curtis dissimilarities calculated based on the natural log-transformed abundances. The Bray-Curtis index ranges from 0 to 1, where 0 indicates complete dissimilarity among community composition (no species shared), and 1 represents total agreement on relative abundance of species. Sample pairs were then

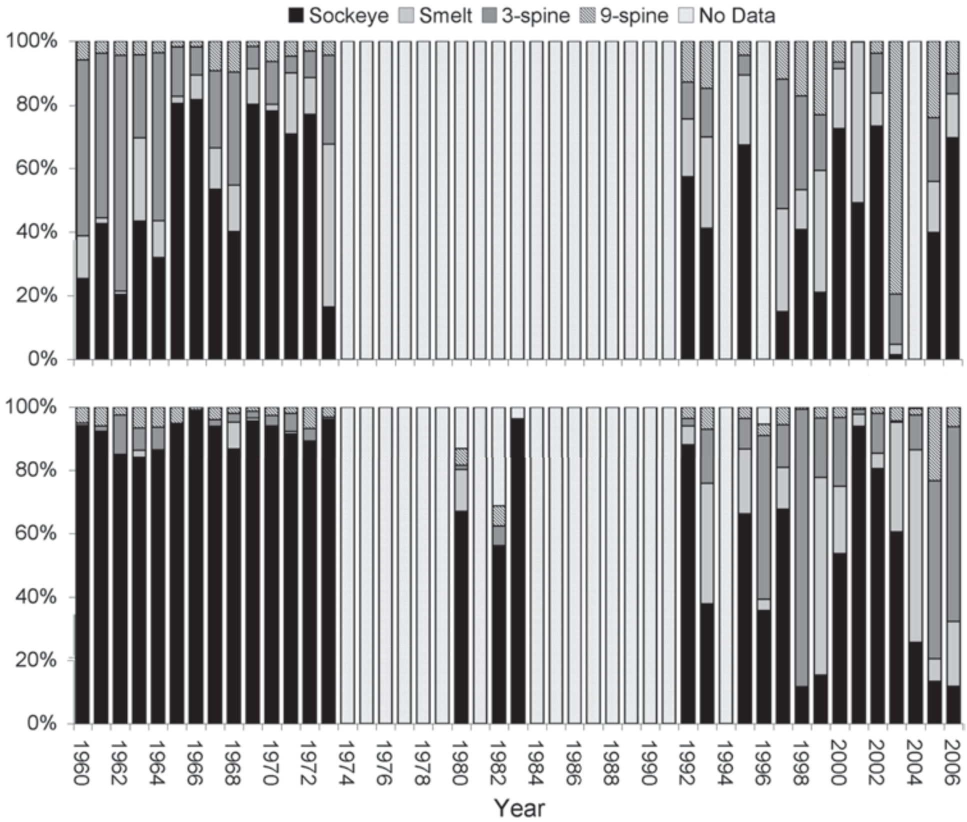


Figure 4.26. Composition of townet catches from the pelagic region of Black Lake (top) and Chignik Lake (bottom) between 1960 and 2006.

plotted in the software package (PRIMER), whereby sample location on the MDS plot maximally corresponds to dissimilarity index, and plot stress (0 to 1) indicates lack of agreement in placement and dissimilarity. Clearly, the Chignik Lake community clustered by itself from 1960 to 1973 (Fig. 4.27), but after 1992 it clustered with the Black Lake community. Statistical tests corroborate the visual representation of Figure 4.27, and suggest that the Chignik community during the early period (1960–1973) was significantly different (ANOSIM, r = 0.633, p <0.01) than recent years (1992–2006). Interestingly, the community in Chignik Lake during the early period was significantly different than the community in Black Lake (r = 0.758, p <0.01), but it is not significantly different in recent years (r = 0.212, p = .07). Thus, it appears that the Chignik pelagic community, which historically was distinct from the community in Black Lake, is now similar in species composition and relative abundances.

Sampling of interlake movement of fishes in 2005 and 2006 and analysis of a long-term database provide preliminary evidence of increased downstream movement of sticklebacks and pond smelt, especially in warm years, which may explain the shift in pelagic community of Chignik Lake. The summer of 2006 was markedly cooler and wetter than 2005, and these climate conditions correspond to large differences in extent of downstream fish movement out of Black Lake. In 2005, nearly 750,000 sticklebacks and pond smelt were caught leaving Black Lake, whereas less than 5,000 sticklebacks and pond smelt were caught in 2006. Additionally, demographics of fish leaving Black Lake were different among years, and were categorized by large numbers of young-of-the-year fish in 2005 and mostly adult fish in 2006 (Fig. 4.28). Taken as a whole, these data suggest that warm climatic conditions are conducive for resident fish recruitment and provide an intriguing alternative (or contributing) mechanism underlying the rapid restructuring of the Chignik Lake pelagic fish community.

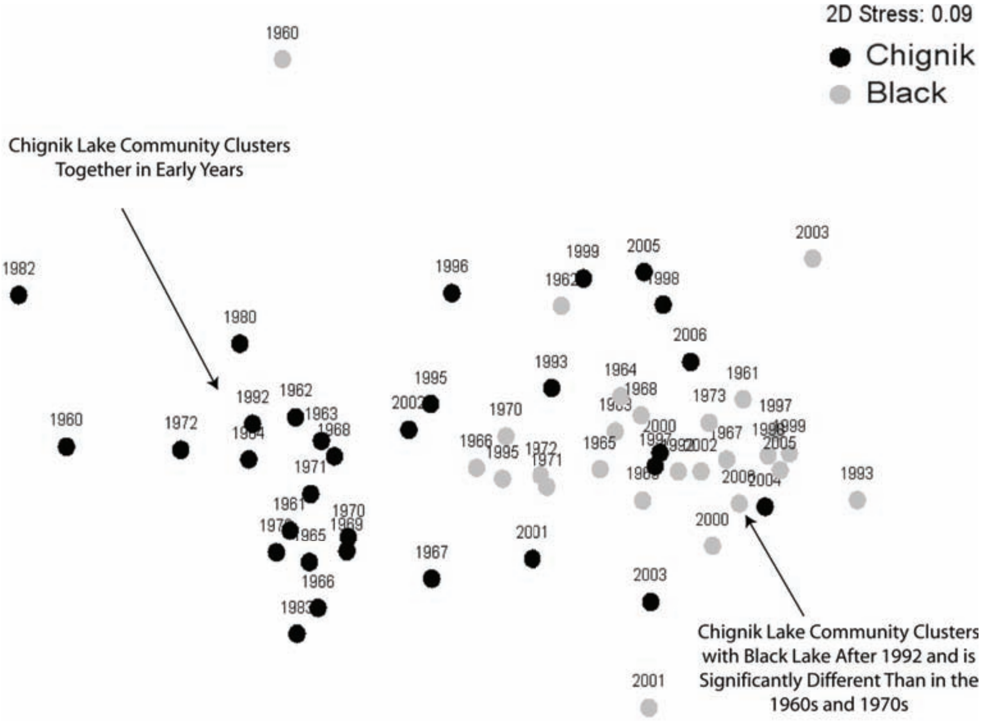


Figure 4.27. An MDS plot of the pelagic fish community in Chignik Lake (black points) and Black Lake (grey points) between 1960 and 2006. Statistically, the Chignik Lake community clusters distinctly from Black Lake until 1992. After 1992, the communities in the lakes are more similar.

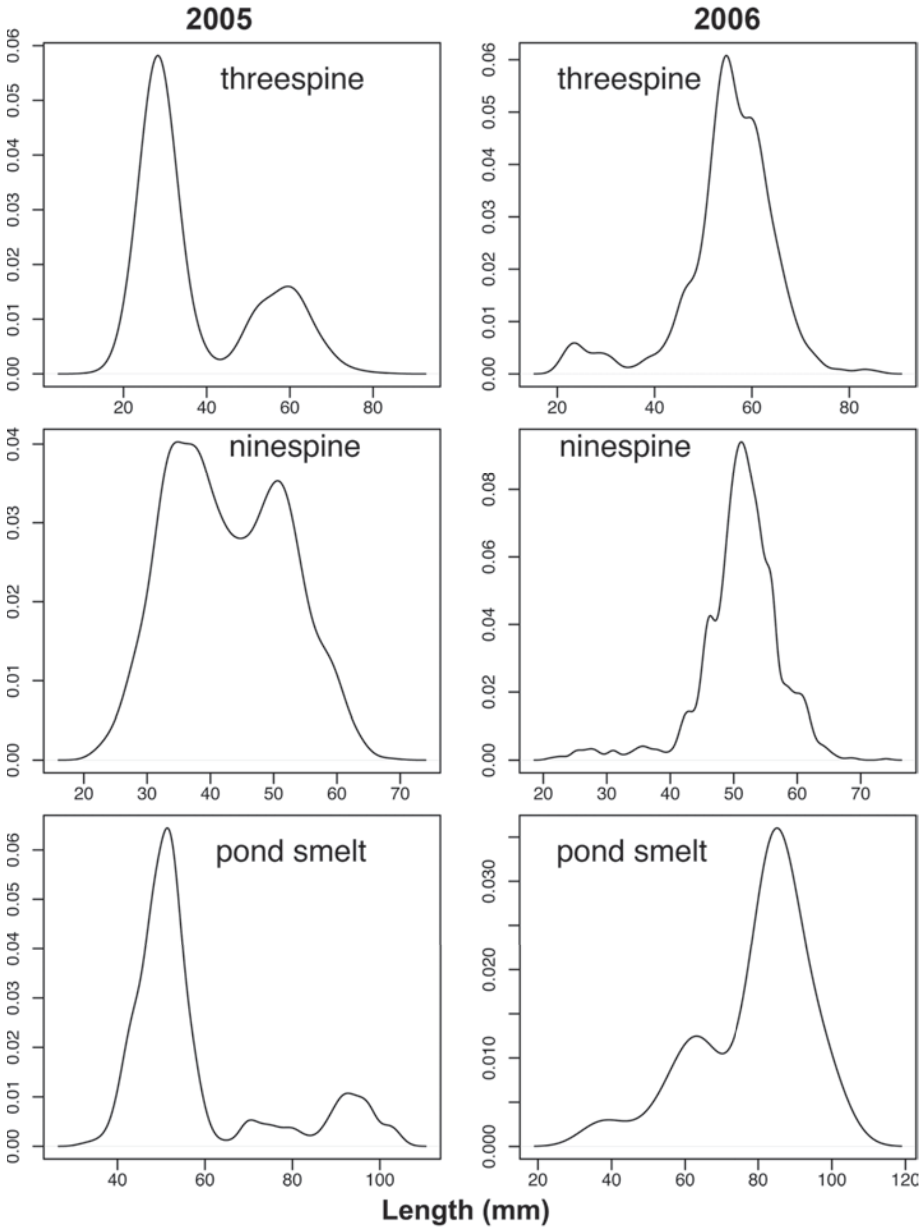


Figure 4.28. Length-frequency of threespine sticklebacks, ninespine sticklebacks, and pond smelt caught in the Black River during 2005 and 2006, plotted as density functions for graphical purposes.

5. Biocomplexity

September 1, 2004 marked the beginning of a 5-year grant from the National Science Foundation to explore the biocomplexity of the Bristol Bay salmon resource, the communities that depend on it, and the management system. This project is built around our longstanding research projects on salmon, their ecosystem, and their management. This work has been ongoing since 1946 but we have expanded the scope of activities by bringing in a geneticist and two economists. This project is described in the context of five themes:

1. evolution and maintenance of phenotypic and genetic diversity;
2. climate and forcing on different adaptations;
3. the role of marine derived nutrients in freshwater productivity;
4. harvest policies, catch stability, and economic resilience; and
5. fleet composition, fishermen's behavior, and resilience to natural and anthropogenic stress.

The overriding theme of this project is that fish, fishermen, and communities evolve and adapt to the conditions they face. By understanding how the fish and their ecosystem have evolved and adapted, and how the fishermen, processors and their communities adapt to the ecological and economic circumstances, as well as the management system, we hope to provide better advice to the managers on how to take full advantage of the biological and economic resilience of the ecosystem.

Theme 1: Evolution and Maintenance of Genetic and Phenotypic Diversity

A core component of the biocomplexity project is the investigation of the current population structure of sockeye salmon, and the ways in which this structure has evolved. Our investigations and those of our collaborators have spanned a range of spatial and temporal scales to consider the patterns and processes of sockeye salmon biodiversity in Bristol Bay. At a mechanistic level, we have demonstrated the restricted movements of individual adult sockeye salmon of both sexes once they settle in specific areas of a stream (Hansen Creek, flowing into Lake Aleknagik), and their tendency to return to these areas after displacement (Stewart et al. 2004, Rich et al. 2006). Most recently, experimental thermal marking of embryonic salmon otoliths allowed us to show extremely fine-scale homing to natal sites within this very small stream system (Quinn et al. 2006). These studies of homing at fine spatial scales, combined with work on isolation of temporally discrete breeding groups within a stream conducted by collaborators (Hendry et al. 2004b), open up the possibility of exceptionally complex population structure in a single creek. We know that salmon arriving early tend to be larger than those arriving later, and that they tend to selectively settle and breed in certain areas of some creeks. We plan to combine datasets on these phenomena to shed light on the interplay between arrival timing and nest-site use in one creek.

The work on spatial and temporal aspects of homing led us to compare the genetic structure of sockeye salmon in three small streams, in close proximity within a single bay of Lake Aleknagik: Happy, Hansen, and Eagle creeks (see map, p. 36). Adult sockeye salmon in Happy and Hansen creeks are similar in spawning timing but differ in size and morphology (Happy Creek fish being older, larger for their age, and deeper-bodied for their length than in Hansen Creek), whereas fish in Hansen and Eagle creeks are similar in size and shape but differ in timing (Eagle Creek fish spawn later than those in Happy and Hansen creeks). We collected DNA samples for microsatellite analysis from early and late fish in Happy and Hansen creeks, and fish from Eagle Creek similar in timing to the late collections from the other creeks. These data demonstrated a lack of genetic differentiation despite morphological variability, suggesting the presence of strong selection pressures maintaining phenotypic differentiation (Lin et al. p. 50).

At a somewhat broader scale, we are investigating the levels of gene flow between pairs of populations spawning in creeks and nearby beaches. Building on previous work showing that sockeye salmon (especially males) spawning in creeks are much less deep-bodied than those spawning in beaches (Blair et al. 1993, Hamon et al. 2000, Quinn et al. 2001b), we are collecting data on size and shape of sockeye salmon spawning in two small creeks flowing into Little Togiak Lake (A Creek and C Creek), and the sockeye salmon spawning on beaches in the lake right at the outlet of each creek. Data from three brood years (2002–2004) showed strong differentiation between beach and creek spawners as well as higher differentiation between the populations in the two creeks than between the beach populations (Lin and Hauser, this page). More importantly, however, the genetic data provided evidence of considerable annual variation in straying rates, and the A Creek population showed signs of complete replacement by immigrants in 2004. In addition, we have collected similar data from creek and beach spawners in Lynx Creek, in Lake Nerka, Yako Creek in Lake Aleknagik, and Knutson Creek in Iliamna Lake (see maps, pp. 36-38). These samples have been screened for genetic diversity and will be analyzed to test the generality of the findings from A and C creeks in an effort to determine the relative rates of gene flow between proximate but different habitats (i.e., creek and beach) and between more distant but similar habitats (i.e., beach-to-beach and creek-to-creek).

At a still broader scale, we have been collaborating with geneticists at ADFG who have been examining possible differences in timing of adult and smolt migrations between sockeye salmon from Lake Clark and Iliamna Lake. These scientists have had considerable success in differentiating sockeye salmon from these two lake systems, but it appears that the timing of adult and smolt migrations does not differ between these population complexes (Habicht et al. 2005). We are currently in the process of standardizing molecular genetic methods between their and our laboratories (Hauser et al., pp. 52-53), and hope to exchange data more readily in the near future. Such data exchange will greatly improve our genetic database, which will allow a more thorough investigation of genetic diversity of Alaskan sockeye salmon. Finally, our collections have contributed to a review of population structure of sockeye salmon across their entire distribution (Beacham et al. 2006).

Relationship Between Ecological and Genetic Differentiation in Sockeye Salmon of the Wood River Lakes

J Lin (graduate student), R Hilborn, T Quinn, L Hauser (adviser)

Biocomplexity can be defined as the properties arising from the interactions of biological systems with each other and their environment. The complexity of such interactions depends crucially on the diversity within systems, or in population ecology terms, the extent of phenotypic and genetic variation among populations. Although genetic variation at small geographic scales has been demonstrated in many sockeye populations (Wood 1995), knowledge of relationships between gene flow, population history, and phenotypic differentiation is limited. Our research uses genetic data from beach and stream ecotypes of sockeye salmon in the Wood River Lakes system to examine the relationship between ecological and genetic differentiation in these fish.

In 2002–05, samples were obtained from throughout the Wood River system (Table 5.1) but analysis was

Table 5.1. Collection information for 15 sockeye salmon spawning sites in Bristol Bay. Reproductive ecotypes are abbreviated as follows: B = beach spawning, S = stream spawning. Sample sizes are separated by year.

			Year				
Sample	System	Ecotype	2002	2003	2004	2005	2006
A Beach	Wood River	B	34	4	64	21	0
A Creek	Wood River	S	34	32	496	444	585
C Beach	Wood River	B	33	31	54	18	---
C Creek	Wood River	S	26	28	383	280	473
Little Togiak north end	Wood River	B	---	---	53	87	---
Little Togiak south end	Wood River	B	---	---	56	69	---
Lynx Mouth Beach	Wood River	B	---	---	54	99	---
Lynx Creek	Wood River	B	---	---	50	100	---
Lynx Lake Beach	Wood River	S	---	---	50	---	---
N4 Beach	Wood River	B	---	---	50	100	105
N4 Creek	Wood River	S	---	---	52	51	---
Yako Beach	Wood River	B	---	---	51	100	102
Yako Creek	Wood River	S	---	---	229		100
Knutson Bay Beach	Iliamna Lake	B	---	---	100	---	14
Knutson Creek	Iliamna Lake	S	---	---	98	---	31
Anvil Bay Beach	Wood River	B	---	---	---	100	---

performed primarily on those from Little Togiak Lake. The lake has two creeks supporting sockeye salmon runs—A Creek and C Creek—and sockeye salmon also spawn off the mouths of these creeks and in several other locations throughout the lake. Microsatellite data from these creeks and beaches were used to address several basic issues concerning genetic patterns in sockeye salmon ecotypes. Our objectives were to (1) test whether geographically proximate ecotypes are genetically differentiated, (2) quantify patterns of differentiation between populations and see whether they are similar for beach and stream spawners, and (3) determine patterns and rates of straying among populations within and between ecotypes.

Genetic data from 12 microsatellite markers and samples from two creeks (A and C) and four beaches (A, C, North, South) in Little Togiak Lake were collected for 3 consecutive years (2002–04). These data showed that differentiation was high and significant between beach and creek spawners from each location (mean F_{ST} across years at A = 0.0481, mean F_{ST} across years at C = 0.0253). Moreover, samples of beach spawners showed low but significant differentiation (F_{ST} =0.007), whereas stream spawners showed higher differentiation (F_{ST}=0.0382). In summary, we found differentiation between ecotypes and within the stream ecotype.

To identify putative strays among creeks, we used clustering analyses by the likelihood programs STRUCTURE (Pritchard et al. 2000; Fig. 5.1) and BAPS (Corander et al. 2004). The majority of strays in both creeks were identified as stream spawners, suggesting that straying between creeks is more frequent than between habitats. Interestingly, beach-origin males that strayed into the creeks had shallow body depths, whereas stream-origin males that strayed onto the beaches were deeper-bodied than the creek spawners yet more shallow-bodied than other beach spawners. This finding indicated that morphology had some bearing on whether or not the fish strayed into a different type of spawning habitat.

Genetic Differentiation among Phenotypically Distinct Sockeye Salmon Populations

J Lin (graduate student), E Ziegler (undergraduate student), L Hauser, T Quinn (advisers)

Phenotypic variation in length, depth, age at maturity, return timing, and morphology among populations is commonly observed in sockeye salmon and is generally interpreted as evidence for adaptation to local environmental conditions facilitated by accurate homing of each population to natal habitats. However, the degree of straying among such populations is poorly understood; further, it is uncertain whether selection pressures in different habitats suffice to maintain the genetic basis of heritable adaptive traits despite gene flow, which can reduce genetic differentiation. Such questions are central to understanding the demographic dynamics of the entire stock complex of Bristol Bay sockeye salmon (e.g., time to recolonization after extinction, resilience to environmental and anthropogenic disturbance, and the effect of selective fisheries).

Genetic studies on Pacific salmon usually concentrate on spatial rather than temporal variation. However, run

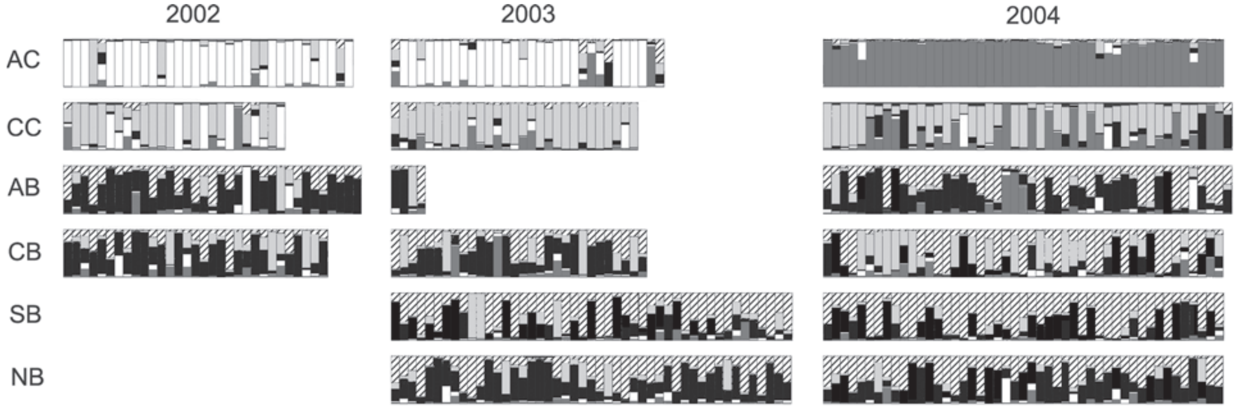


Figure 5.1. Population contribution to each genotype estimated by the multilocus clustering program, STRUCTURE. Different grayscale colors and patterns represent different populations as determined by the program. Each bar represents an individual fish, and the patterns in the bar show the inferred mixed population ancestry of that fish. Thus, a hybrid individual will have multiple patterns within its bar, and a stray individual will differ in pattern from the majority of other individuals within the sample. Note the relative homogeneity of A Creek sockeye (AC02–AC04) and the immigrants in C Creek (individuals with different colors and patterns, CC02–CC04). Note also the difference between AC02/AC03 and AC04, represented by different colors and patterns. In contrast, beach spawners appear to be a mixture of several populations.

timing is a highly heritable trait (Smoker et al. 1998, Quinn et al. 2000), indicating that sockeye will return to their natal streams during the same period of the run as their parents did. Such constraints to gene flow create the possibility for genetic divergence and thus local adaptation between early- and late-arriving individuals (Hendry and Day 2005).

We tested for significant genetic variation among sockeye salmon populations in three geographically proximate creeks in Lake Alekagnik (Happy, Hansen and Eagle creeks, Fig. 5.2). Fish of the three creeks differ significantly in their run timing, morphology, and life history, suggesting local adaptation to their habitat although the rate of straying between rivers is largely unknown. Furthermore, we tested for temporal genetic differentiation within runs in two of the creeks. About 100 fin clips were collected from sockeye salmon returning in the first and last week of the run in Happy and Hansen creeks, and only from early fish in Eagle Creek, where the run is later than the other two creeks. The samples were stored in 95% ethanol for genetic analyses. DNA was extracted from about 50 individuals in each sample using Qiagen DNeasy 96-well silica membrane-based kits, following the manufacturer's protocol. Genotypic variation was determined at four microsatellite loci (Olsen et al. 2000) on a MegaBace 1000 automated sequencer.

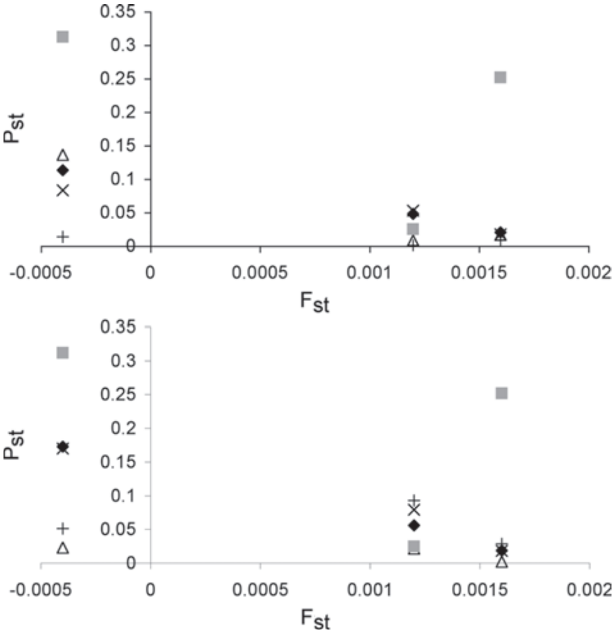


Figure 5.2. P_{ST} versus F_{ST} in females (top) and males (bottom). F_{ST} between Eagle and Happy creeks was -0.0004, F_{ST} between Hansen and Happy creeks was 0.0012, and F_{ST} between Eagle and Hansen creeks was 0.0016. ◆ = body length, Δ = standardized body depth, X = 2-ocean-length, + = 3-ocean-length by a cross, ■ = spawn timing.

Genetic diversity was high and comparable among the five samples, with expected heterozygosities per locus exceeding 85% and more than 15 alleles per locus in each sample (Table 5.2). Most loci fulfilled population genetic expectations of randomly mating populations (Hardy–Weinberg equilibrium), although some significant deviations also occurred (Table 5.2). Despite this high variability and reasonablyarge sample sizes, measures of genetic differentiation among all samples were small and not significant (F_{ST} over all samples = 0.0009). Pairwise F_{ST} estimates between samples were also low (F_{ST} = -0.0004 to 0.0016), with no values significantly different from zero. A power analysis (POWSIM, Ryman and Palm 2006) suggested that our genetic data were sufficiently powerful to detect differentiation as low as F_{ST} = 0.002 with almost 90% probability. This level of differentiation corresponds to about four generations of complete isolation (no migration) among three populations of a genetically effective size approximately equal to the harmonic mean of census numbers in the three streams (n = 1500). Alternatively, under migration-drift equilibrium in an island model of migration, this level of differentiation would equate to a gene flow of about 120 fish per generation, or about 10% of the population size. In reality, migration rates and time since divergence interact, and the populations probably have been separated for a longer time with lower migration rates. However, the lack of differentiation provides a framework of migration and divergence time parameters against which phenotypic differentiation can be compared.

Happy Creek had larger, older individuals, a finding consistent with a prior study on comparative morphology of sockeye salmon from creeks, beaches, and rivers (Quinn

Table 5.2. Hierarchical AMOVA showing total differentiation (F_{ST}), differentiation among samples within groups (F_{SC}), and between groups (F_{CT}). Groups are based on ecotype (beach versus creek spawners), location (A versus C) and year (2002 versus 2003 versus 2004). The percentage of genetic differentiation due to differences between the respective groups (F_{CT}/F_{ST}) is also given as a percentage.

	Ecotype	P	Location	P	Year	P
SNPs						
F_{ST}	0.032	0.000	0.030	0.000	0.028	0.000
F_{SC}	0.025	0.000	0.028	0.000	0.031	0.000
F_{CT}	0.007	0.020	0.002	0.259	-0.003	0.844
F_{CT}/F_{ST}	21%		6%		-12%	
Micros						
F_{ST}	0.035	0.000	0.030	0.000	0.029	0.000
F_{SC}	0.022	0.000	0.029	0.000	0.032	0.000
F_{CT}	0.014	0.000	0.001	0.369	-0.003	0.976
F_{CT}/F_{ST}	39%		2%		-11%	

et al. 2001b). Stream survey data showed that spawning occurs later in Eagle Creek than in Hansen and Happy creeks. After finding these significant differences among the creeks, we calculated a measure of phenotypic differentiation (P_{ST}) for spawning timing and for each morphological trait measured so that we could directly compare P_{ST} and F_{ST} values. P_{ST} values were generally significantly different from zero (P_{ST} = -0.014 to 0.31) whereas F_{ST} values were not. No correlations were apparent between the obtained P_{ST} and F_{ST} values (Fig. 5.2), thereby demonstrating that the differences in the phenotypic traits analyzed had no detectable effect on patterns of neutral genetic variation in Happy, Hansen, and Eagle creeks. The significant phenotypic differentiation, however, suggested that strong divergent selection occurs on the phenotypic traits despite any homogenizing effects of gene flow. These results illustrated an interesting contrast with the A and C creeks situation, in which gene flow does not occur between creeks with morphologically similar spawners.

In summary, our results suggest that complex demographic dynamics exist for sockeye salmon populations in the Wood River system, even on a very small geographic scale. Beach spawners showed considerable genetic similarity and may employ a generalist strategy with some flexibility in selection of spawning site and thus high colonization potential. Creek spawners, alternatively, may adopt multiple strategies. In A and C creeks, spawners appeared to be reproductively isolated and more reliant on local adaptation. However, straying among Happy, Hansen, and Eagle creeks appeared substantial enough to homogenize neutral allele frequencies among those creeks. Our results therefore suggest considerable diversity in adaptive strategies on a small geographic scale. By collecting more genetic data from Wood River sockeye, we hope to develop a clearer picture of this species' population dynamics at different ecological and geographical scales. This type of knowledge may be useful for theoretical purposes and may also be important for understanding and predicting the resilience of sockeye salmon to environmental and human-induced perturbations.

Comparison of SNPs and Microsatellites in Detecting Genetic Diversity and Differentiation of Sockeye Salmon Populations

L Hauser (PI); JG Rhydderch, LR Newton (research technicians); J Lin (graduate student); C Habicht (postdoctoral researcher, ADFG); J Seeb (PI, ADFG)

SNPs (single nucleotide polymorphisms) have attracted considerable interest as a molecular marker because sample screening can be performed rapidly and because data are readily transferable among laboratories (a major problem with microsatellites). Furthermore, because SNPs are often found in coding genes, they may be under selection and often reveal larger genetic differentiation than strictly neutral markers such as microsatellites. Because of this higher population differentiation and the speed of screening, SNPs have been largely adopted for mixed stock analyses and fisheries forecasting by our collaborators at ADFG, providing an excellent opportunity for direct data comparisons between our laboratories. However, inferences about migration rates and population divergence times are difficult with SNPs because of the complicating influence of selection on coding genes. Furthermore, SNPs have not been tested on relatively small-scale population differentiation. In this study, we compared our microsatellite dataset from A and C creeks and four beaches in Little Togiak Lake with data from 20 SNPs for the same samples.

SNP sequences were provided by the Conservation Genetics Laboratory at the ADFG, Anchorage, Alaska. We opted for a novel and cheaper technology of SNP assay provided by KBiosciences, United Kingdom. Out of 43 sequences supplied by ADFG, 10 assays failed, 5 were polymorphic, and the remaining 28 provided useful data. Eight of these loci are currently undergoing final optimization, and we present data for the remaining 20 loci. Furthermore, our data are being confirmed by ADFG to establish the rate of genotyping error between laboratories.

Initially, estimates of genotyping error are encouraging; the average genotyping error per locus was 0.29% for SNPs, compared with 0.73% for microsatellites. Furthermore, SNP genotyping error occurred at only three of the 20 loci, and we are confident that we will be able to eliminate these in routine screening. It therefore appears that SNPs will provide data that are not only comparable among labs, but also virtually error free (barring clerical errors in spreadsheets and sample handling).

Genetic diversity was much lower in the di-allelic SNPs (expected heterozygosity H_E = 0.28, average number of alleles N_A = 1.9) compared with multi-allelic microsatellites (H_E = 0.77, N_A = 10.1). However, patterns of genetic diversity among populations were comparable, with creek spawners showing lower diversity in both marker systems (data not shown).

Overall, the F_{ST} values were similar between the two marker systems (microsatellite F_{ST} = 0.030, SNP F_{ST} = 0.027, both $p < 0.001$). Hierarchical analyses quantifying differentiation between ecotypes (beach versus creek), location (A versus C) and year (2002 versus 2003 versus 2004) provided similar patterns, though SNP appeared to reveal slightly more, but not significant, differentiation between locations (Table 5.2). Patterns of pairwise tests between samples were highly correlated (Mantel test, p = 0.001), though pairwise differentiation with SNPs was less likely to be significant than with the more variable microsatellites (SNPs: 37/55 significant tests; microsatellites: 51/55 significant tests; $p < 0.05$).

Assignment tests showed considerable difference between the two marker sets: Self-assignment using a Bayesian approach (GeneClass, Piry et al. 2004) was more successful with microsatellites (46.8% of individuals correctly assigned to their sample) than with SNPs (25% of individuals correctly assigned to their sample). Furthermore, clustering approaches (STRUCTURE) that were so revealing with microsatellites (Fig. 5.1) showed no patterns of differentiation at all. This discrepancy is probably due to the lower variability of SNPs and due to the small number of SNPs used so far. We are working on getting all 43 SNP loci from ADFG to function correctly in our lab, and will then repeat the analysis.

In summary, even the small number of SNPs revealed similar patterns of genetic diversity and differentiation as microsatellites. However, with the limited number of SNP loci available here, fewer tests for genetic differentiation were significant, and assignment and clustering procedures were inefficient. Nevertheless, our preliminary data demonstrate that SNPs will be a useful addition to our molecular toolbox.

Theme 2: Climate Forcing on the Success of Alternative Adaptations

Climate changes can alter the spawning success, growth, and survival of sockeye salmon during all points in their life cycle. We are in a unique position to retrospectively evaluate the biological responses to changes in climate during the freshwater phase of their lives. In particular, we have already shown that growth rates of juvenile sockeye have been enhanced owing to climate warming in southwestern Alaska (Schindler et al. 2005a, Rich 2006). Other obvious climate effects relevant to sockeye are the effects of hydrology on the relative access to lake, river, and stream spawning habitats. In particular, we expect that streams become less available to spawning sockeye during relatively dry periods because lower stream flows (1) increase the probability of fish stranding at creek mouths while attempting to gain access to spawning areas (e.g., Quinn and Buck 2001, Carlson and Quinn, in press) and (2) make fish more vulnerable to bear predation in shallow water. In Iliamna Lake, preliminary analyses show that the contributions from beach-spawning populations have declined over the last 4 decades (Hilborn et al. 2003). We have not done similar analyses for the Wood River system, but expect that increases in hydrologic flows will increase the contributions from stream spawning populations. Because juveniles spawned from all habitat types compete in common feeding grounds (i.e., lakes) before migrating to the ocean, we expect that declines in beach populations may compensate for increases from stream populations. We hypothesize that populations spawning in similar habitat types will exhibit more coherent responses in population dynamics to changes in climate than populations spawning in less similar habitats, and this is consistent with analysis of abundance patterns of Iliamna Lake populations (Stewart et al. 2003).

By evaluating patterns of population coherence at increasingly finer scales of population structure (i.e., fishing districts→individual lakes→habitat types→individual locations), Lauren Rogers has begun to quantify the spatial scales that are relevant to understanding population dynamics. Rogers' analyses show that population dynamics of individual creeks within the Wood River system are no more coherent than the fishing districts within Bristol Bay. However, creeks within specific nursery lakes do show more coherence than random pairs of streams within the Wood River system, suggesting that environmental effects may be common to each nursery lake.

Studying the mechanisms leading to biocomplexity in freshwater habitats is convenient. Mechanisms relevant to spawning behavior are especially easy to observe and, thus, we have a wealth of knowledge about local adaptations in freshwaters and how these respond to changing climatic conditions. In contrast, we have very limited capacity to study mechanisms for producing biocomplexity in marine systems. However, Susan Johnson's dissertation research (p. 54) is using the stable isotope characteristics of archived sockeye scales to reconstruct sockeye marine feeding histories for the last few decades in each major fishing district. In particular, stable isotopes provide information about trophic position and productivity of food webs supporting salmon growth. Johnson's initial data suggest that the trophic positions of sockeye from different districts have responded to climate in a variety of ways over the last 50 years. In particular, populations whose dynamics are most responsive to climate variation also appear to show the largest variation in trophic position over this timeframe. This result suggests that the trophic ecology of different salmon stocks is not uniform in the ocean and may provide important mechanisms through which climate may have stock-specific effects on population dynamics of sockeye.

Our paleolimnology research (Biocomplexity Theme 3, p. 57) has been providing some new insights into whether individual stock components have responded differently to climate forcing over the last few centuries. Although incomplete, these analyses suggest that the biocomplexity observed in the 20th century by inspecting the spatial diversity of sockeye catch within Bristol Bay was not abnormal when compared with the population dynamics inferred from paleolimnology over the last 5 centuries.

Using Stable Isotopes to Investigate Biocomplexity in the Ocean—Linking Freshwater Spawning Strategies To Marine Foraging

S Johnson (graduate student), D Schindler (adviser)

Biocomplexity is the diversity of life-history patterns and local adaptations that buffer the amalgamation of populations from perturbations (Hilborn et al. 2003). For example, in freshwater systems of Bristol Bay, sockeye salmon populations contain diverse freshwater adaptations—including differences in spawning location or habitat, timing of freshwater migration, body size and shape at maturity (e.g., Quinn and Foote, 1994), time rearing in freshwater, and time at sea (Quinn et al. 2001b)—that likely contribute to the long-term sustainability of the fishery.

In freshwater systems of Bristol Bay, sockeye salmon spawn in various habitats including lakeshore beaches, creeks, and rivers (Demory et al. 1964, Marriott 1964, Quinn 2005). There are striking morphological differences in mature salmon that spawn in these different habitat types. For instance, male sockeye from beach habitats are deeper bodied than those that spawn in shallow creeks (Quinn et al. 2001b). Additionally, there are differences in years spent at sea among sockeye populations that spawn in different habitat types (Rogers 1987, Blair et al. 1993, Quinn et al. 2001b). For example, beach-spawning populations have fewer older (age 3 ocean) salmon than creek-spawning populations in the Wood River system (Quinn et al. 2001b).

It is less clear whether different populations also have distinct marine ecologies, which also may contribute to biocomplexity and sustainability. There may be adaptations to the marine environment that are at least partially responsible for the success of sockeye salmon in Bristol Bay, and for the variation in recruitment among populations in a given period of time. Variation in size-at-age appears to be partially determined by freshwater habitat characteristics of the spawning adults, so we wanted to determine what aspects of sockeye foraging ecology at sea might produce this variation. In particular, we hypothesized that big fish (e.g., beach spawners) feed at higher trophic levels than smaller fish (e.g., creek spawners) to attain their respective body sizes.

Stable isotope analysis was used to test for differences in foraging ecology among sockeye salmon populations. The heavy nitrogen isotope (^{15}N) is a useful tool to investigate foraging ecology and trophic position. ^{15}N accumulates between 1.3‰ and 5.3‰ (average = 3.5) per trophic transfer. Therefore, higher ^{15}N values indicate feeding at higher trophic levels. Populations were sampled across habitat types (stream, river, and lake beach spawners) that display morphological differences reflecting differences in weight at length.

Among spawning locations, larger fish of the same age feed at a higher trophic level, as predicted (Fig. 5.3). An ANCOVA was performed to test for an interaction between age and body depth (a surrogate for body weight) and it was not significant ($p = 0.483$). This allowed us to remove the interaction term and test for an age effect. This analysis revealed a significant difference between the salmon ages ($p = 0.001$). In other words, for any given body depth, ocean age 2 fish had a higher ^{15}N than ocean age 3 fish. Additionally, within a given spawning location, larger salmon do not feed at higher trophic levels as was expected. In fact, for a given spawning location, younger fish, which were smaller, had higher ^{15}N values than older fish. For example, average ^{15}N for Hansen Creek salmon was highest for ocean age 1 (jacks) fish (11.57) followed by ocean age 2 fish (11.24) and ocean age 3 fish (11.02) (Fig. 5.4). This pattern of younger fish having higher ^{15}N was consistent across all of the study locations, indicating that fish returning to spawn earlier feed at higher trophic levels. These data suggest that earlier maturing fish take more risks by feeding at a higher trophic level to obtain the energy needed for migration and spawning than fish that will spend more time growing at sea.

This study links foraging ecology at sea to observed life-history variation in freshwater associated with spawning. These results suggest that biocomplexity is a feature of the marine phase of the sockeye salmon life cycle.

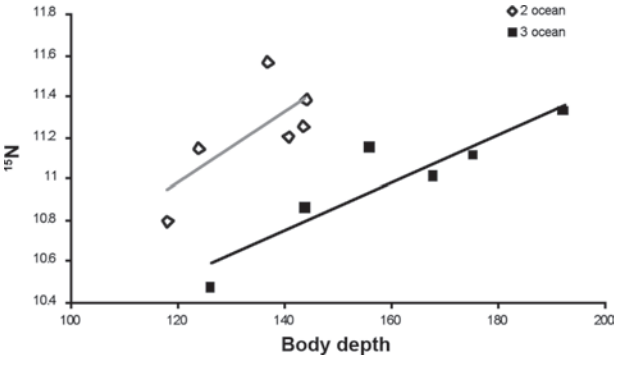


Figure 5.3 ^{15}N as a function of salmon body depth across spawning locations: shown for ocean age 2 fish (◇) and ocean age 3 fish (■). Each data point is the average of all salmon sampled for a particular location (e.g., Pick Creek) in that age group. The regression r^2 values for ocean age 2 and 3 salmon are 0.53 and 0.84, respectively. ANCOVA results show that ocean age 2 fish have significantly higher levels of ^{15}N than ocean age 3 fish for a given depth.

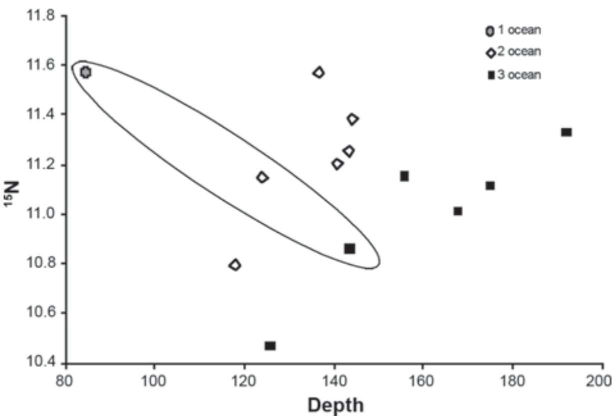


Figure 5.4. ^{15}N as a function of salmon body depth across spawning locations: shown for ocean age 1 fish (●), ocean age 2 fish (◇), and ocean age 3 fish (■). Each data point is the average of all salmon sampled for a particular location (e.g., Hansen Creek) in that age group (see Fig. 4.3). Circled points are all data from Hansen Creek showing that ocean age 1 fish have the highest ^{15}N followed by ocean age 2 then ocean age 3 fish in that creek. This trend of higher ^{15}N in younger fish was true for each individual location.

Synchrony and Fine-Scale Biocomplexity Among Sockeye Salmon Populations in the Wood River System

L Rogers (graduate student) and D Schindler (adviser)

Salmon populations in the Pacific Northwest and Alaska vary over 50-70 year periods in response to the Pacific Decadal Oscillation (PDO), a climate phenomenon that affects both oceanic and terrestrial environmental conditions (Mantua et al. 1997). Bristol Bay, Alaska, has seen high sockeye salmon productivity during positive phases of the PDO, and diminished productivity during negative phases. However, across watersheds or even among neighboring creeks within the same watershed, individual stocks or populations do not appear to respond uniformly to climatic variation (Hilborn et al. 2003, Rogers and Schindler in review). These asynchronous responses may be important for the overall sustainability of the fishery since some salmon populations appear to thrive under certain environmental conditions while others do not. In this ongoing research, we are investigating how climatic variation affects sockeye salmon at different spatial and temporal scales, and whether populations spawning in close proximity or with similar life-history strategies respond more coherently to changing climate conditions.

One way of exploring how populations are affected by climate variation is to analyze patterns of synchrony or covariation among populations. The general expectation is that populations become more correlated in their dynamics with increasing spatial proximity because of exposure to common environmental conditions (Liebhold et al. 2004). An alternative hypothesis is that populations experience climate differently depending on spawning and rearing habitat features or life-history strategies, which would then influence the coherence of populations over time.

To explore the patterns of productivity among populations of sockeye salmon, we analyzed 50 years of spawner survey data for nine stream populations within the Wood River System. The streams included in this analysis were Bear, Hansen, Happy, and Ice creeks, which drain into Lake Aleknagik; and Fenno, Hidden Lake, Kema, Lynx, and Pick creeks, which drain into Lake Nerka (see maps, p. 38-39). We calculated indices of productivity for each population based on reconstructed brood tables, and then computed correlations among populations (Rogers and Schindler in review). To test whether the degree of correlation in population productivity could be related to geographic proximity or similarity in age composition, we used Mantel tests, which test for a linear relationship between two similarity matrices (Legendre and Legendre 1998). Geographic proximity was measured as the straight-line distance between stream mouths. Similarity in age composition was calculated using Whittaker's index of association (Legendre and Legendre 1998) on the average age composition of the spawners in each population.

We found that stream-spawning populations of sockeye salmon exhibit a limited degree of coherence in their productivity over time (mean r = 0.45). Figure 5.5 shows that substantial variability remains among populations (shown here in terms of total recruits over time) despite their close proximity in spawning and nursery habitats. Correlations between stream populations decreased with geographic distance (Fig. 5.6) (Mantel test: $r_M = -0.622$, $p < 0.01$), with distance measured as the straight-line distance between stream mouths. This suggests that processes affecting the productivity of sockeye salmon are shared by populations in close proximity. However, within a single lake, correlation was not significantly related to distance (Mantel test: Nerka $r_M = -0.406$, $p = 0.15$; Aleknagik $r_M = 0.106$, $p = 0.66$). That is, the apparent relationship between coherence in productivity and geographic distance was explained by a lake-specific effect, whereby populations rearing in the same lake were more correlated than populations rearing in separate lakes. This suggests that sockeye populations are subject to synchronizing processes at the lake scale (Rogers and Schindler in review).

Correlations between stream populations increased with similarity in age composition, though not signifi-

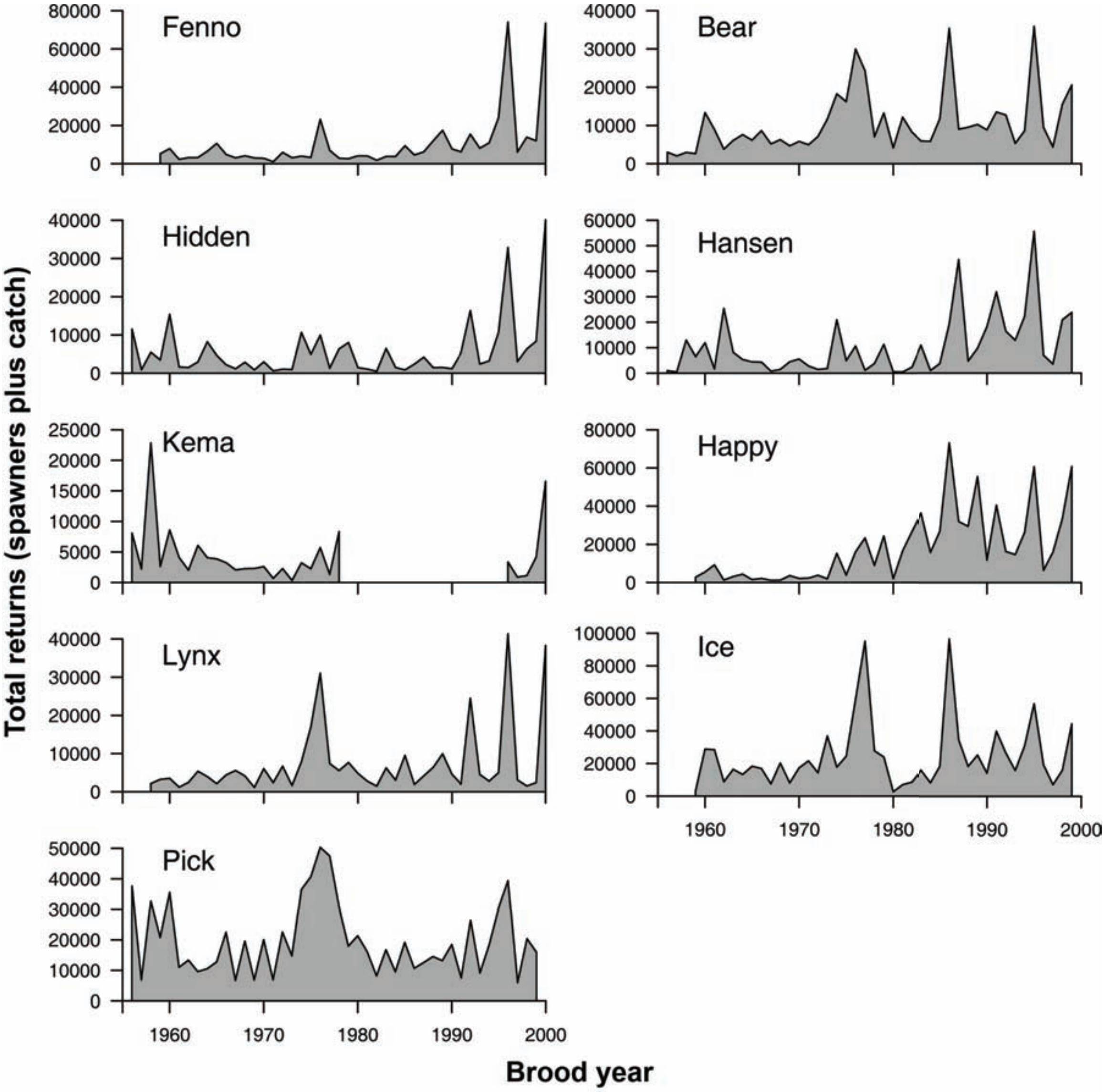


Figure 5.5. Time-series of returns (sum of fish on the spawning grounds and those intercepted by the fishery) to the nine study streams, plotted by brood year (Rogers and Schindler in review).

cantly (Mantel test: $r_M = 0.277$, $p = 0.07$). This suggests that populations sharing similar life-history traits, such as freshwater residency time and age at maturity, may respond more coherently to changes in climate conditions. However, populations within Lake Nerka or within Lake Aleknagik are more similar to one another in their age compositions than comparing across lakes, suggesting again that this may be a lake effect.

Sockeye salmon spend 1 or 2 years rearing in lakes as juveniles, during which time they are subject to density- and prey-dependent growth (Schindler et al. 2005a), which in turn may affect their marine survival (Koenings et al. 1993). Exposure to these common growing conditions may synchronize the productivity of populations using a common lake. Although only a few kilometers apart, lakes Nerka and Aleknagik may show differential responses to a common regional driver such as climate (Magnuson et al. 2004), potentially resulting in incoherent patterns of prey density and juvenile growth between lakes. Alternatively, populations rearing in a common lake could share other life history attributes, such as timing of ocean entry as smolts, or ocean migration patterns, which could also synchronize their productivity over time.

Using data from the past 50 years, future research will build on these findings by explicitly modeling the responses of different populations of sockeye salmon to specific climate drivers. This modeling will help us determine which climate drivers are important for sockeye salmon

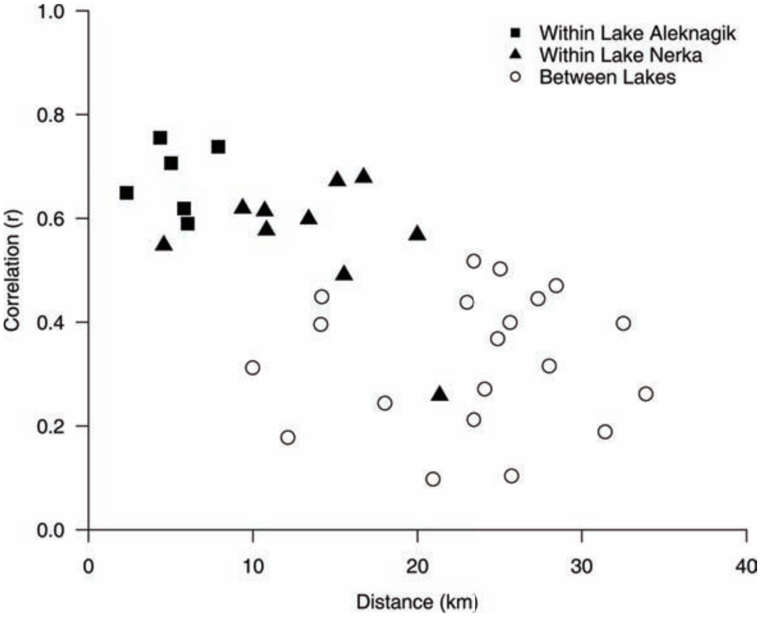


Figure 5.6. Pearson product–moment correlation coefficients calculated among all pairwise comparisons of stream productivity indices, plotted against geographic distance between stream mouths, measured as the crow flies. Filled symbols represent comparisons among populations that rear in a common lake, whereas open symbols represent comparisons among populations using different rearing lakes (Rogers and Schindler in review).

productivity in the Wood River System and across Bristol Bay, and whether different populations are sensitive to different climate drivers. This research will improve our understanding of sockeye salmon biocomplexity and its importance for providing resilience to climatic change.

Theme 3: Marine-Derived Nutrient Feedbacks to Local Productivity of Stock Components

Long-term Perspectives on Salmon Population Dynamics Using Paleolimnology

We have initiated a paleolimnological component to our program that aims to place our contemporary research in a longer temporal context. This component involves analysis of the sedimentary records from lake bottoms to reconstruct a variety of environmental time series, including sockeye population density, lake productivity, and some climatic signals. Thus far, we have used (1) nitrogen isotope characteristics to reconstruct historical salmon population dynamics, and (2) fossil algal pigments to reconstruct historical patterns of lake productivity. Our work has been focused mostly on the last 5 centuries of lake history, but we have initiated new collaborations that have the potential to push back our historical reconstructions to several thousand years before the present. Highlights of our most substantial results to date follow.

Spatial Variability in Sedimentary Records in Lakes

We intensively studied the spatial variation in the nitrogen stable isotope characteristics and fossil pigment characteristics of surface sediments throughout several lakes to assess how well a single sediment core represents ecosystem-wide dynamics in these parameters (Brock et al. 2006). This study was carried out in Lake Nerka, Little Togiak Lake, Hidden Lake, and Lynx Lake (see maps, p. 39), and the intensity of sampling was scaled roughly with lake size (e.g., Nerka was sampled at 74 sites, Hidden was sampled at 10). This work showed that sedimentary isotope characteristics had remarkably little spatial variation (coefficient of variation <15%) and that single cores were very likely to be representative of ecosystem-wide effects. This result suggests that nitrogen in these lakes is relatively well-mixed before it accumulates in sedimentary records. Fossil algal pigments showed more spatial variation than the isotope signatures and were correlated with water column depth at coring sites, suggesting an effect of decomposition during the sedimentation process.

Effects of Salmon Fisheries on the Role of Marine-Derived Nutrients in Lake Nutrient Cycles: Implications for Salmon Production from Nursery Ecosystems

A popular hypothesis linking marine-derived nutrients to salmon populations posits that nutrients provided by post-spawning mortality of salmon are critical for salmon population dynamics because they enhance prey populations in the freshwater ecosystems used as nursery habitats. We tested this hypothesis by reconstructing historical sockeye salmon populations for the last 300 years in the Wood River of Bristol Bay, Alaska (Schindler et al. 2005b). Stable nitrogen isotope chronologies in lake sediments and sockeye catch and escapement histories show that commercial fisheries have intercepted about two-thirds of marine-derived nutrients bound for freshwater spawning grounds since 1958. Reconstruction of lake algal production using sedimentary fossil pigments shows that this loss of nutrients has reduced lake algal productivity to about one-third of its level before the advent of commercial fishing in the late 1800s. However, contrary to expectation, recent sockeye population sizes (sum of spawning escapement and fishery catch) in the last half-century are equivalent to those before large-scale commercial fishing (Fig. 5.7). These results demonstrate that the marine-derived nutrient subsidy is important for the productivity of coastal lakes but that some sockeye salmon populations are limited by other features of ecosystems such as the amount of suitable spawning habitat. In fact, our paleolimnological estimates of historical carrying capacity for Lake Nerka in the Wood River System was within 10% of the carrying capacity estimated by Burgner et al. (1969) based on quality and spatial extent of spawning habitat.

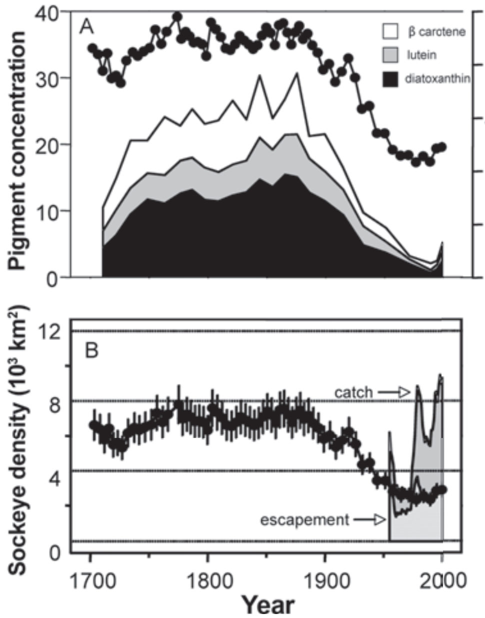


Figure 5.7. (A) Reconstucted sockeye salmon escapement to Lake Nerka for the last 300 years (●) and the associated changes in three dominant sedimentary fossil pigments (shaded regions). Pigment concentrations are expressed as nmol pigment per g of dry sediments. (B) Comparison of historical escapements to Lake Nerka (●) with contemporary estimates of catch and escapement (shaded region). From Schindler et al. (2005).

Comparison of the relative importance of marine-derived nutrients on lake primary production among lakes was investigated by comparing the strength of the correlation between our proxy of marine-derived nutrients in lakes and the concentration of fossil algal pigments (Brock et al. in press). This analysis showed that algal production was strongly correlated to marine-derived nutrients in lakes with high salmon densities, but that the strength of this correlation declined linearly with decreases in salmon escapement densities (Brock et al. in press). Thus, even at modest escapement densities such as those in Lake Nerka, temporal variation in algal production is strongly linked to escapement levels.

The Recent Boom of Alagnak River Sockeye: a New Regime or an Expression of Natural Variation in this Population?

During the last 3 years, returns of sockeye salmon to the Alagnak River, a tributary of the Kvichak River, have been unprecedented with respect to the last 5 decades. Enumerated run sizes averaged about 1 million fish from 1956 to 2002 but surged unexpectedly to average 5.4 million fish during 2003–2005. The reasons for these huge returns remain a mystery because it is unclear whether the recent surge in production is a new phenomenon or is due to interdecadal population variability of the Alagnak River populations. To answer this question, we used changes in lake sedimentary δ^{15}N coupled with an isotope-mixing model to reconstruct sockeye salmon populations in this ecosystem for the last 5 centuries. Our analyses show periods of high salmon production approximately every 100 years since about 1500 AD, interspersed by periods of substantially lower production (Fig. 5.8). Given the variability inferred from the paleo-reconstructions, we suggest that the recent high production rates will be a relatively transient phenomenon. For reasons we do not yet understand, this population appears to be especially variable and is characterized by century-long population cycles (Schindler et al. 2006).

Theme 4: Harvest Policy, Catch Stability, and Economic Resilience

C Costello (principal investigator, UC Santa Barbara), R Hilborn (principal investigator)

Biocomplexity theme 4 focuses on the policy and management of Alaskan salmon fisheries under uncertainty. The original proposal text challenged the traditional notion of "maximum sustainable yield" along biological and economic grounds. The traditional theory suggests

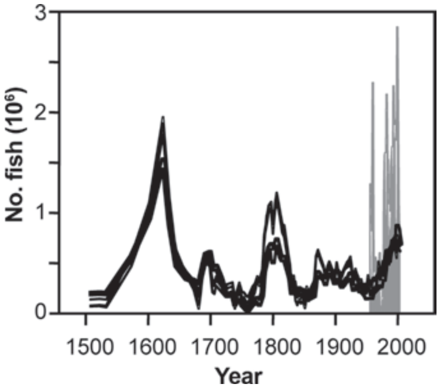


Figure 5.8. Reconstructed population dynamics of Alagnak River sockeye populations, 1500–2005. Solid lines represent different model scenarios to translate variation in sediment isotope characteristics to sockeye population sizes. The thick line is the reconstruction from the model with the best fit. The shaded regions show the enumerated run sizes since 1960. Peaks in production for this system have occurred about every 100 hundred years, centering on the turn of each century. Thus, the recent boom in Alagnak sockeye appears to be an expression of the inherent interdecadal variation in this population (Schindler et al. in press).

that a constant escapement policy maximizes sustainable yield—even in the presence of environmental variability. The escapement should be held constant regardless of whether the fishery had a "good" year or a "bad" year with respect to environmental shocks.

The Bristol Bay salmon fisheries have a number of important characteristics that may ultimately suggest this mantra is inefficient—both biologically and economically. The first, and most obvious, is extreme environmental variability. In accordance with existing theory, this would suggest a constant escapement rule, though large fluctuations may destroy this result. But these fisheries have a number of additional features—such as large market share, lower price in years of high harvest, and increasing harvest costs with large runs—that depart from this standard theory. Therefore, whether a constant escapement policy will lead to optimized sustainable economic returns is an open question.

We have narrowed our focus to four specific research projects. Briefly, they address the following issues:

- Focus 1—Optimal fisheries management with costs and price dependent upon volume of catch: The literature on fisheries management under uncertainty assumes (a) prices are constant, (b) marginal harvest cost is independent of harvest, and (c) fishermen are risk neutral. None of these are realistic. We have solved the more general problem where (a') prices are reflected by a downward-sloping demand function, (b') marginal harvest costs may be increasing in harvest, and (c') fishermen may exhibit risk aversion. The result makes two contributions. First it can be applied to real-world fisheries in Alaska, and suggests a more efficient way to set harvest quotas. Second, the result provides new theory that can guide the management of any renewable resource under uncertainty.
- Focus 2—Value of information: A recurring question in the Alaskan salmon fisheries is "What is the value of additional information?" For example, one way to improve management would be to have an improved smolt count (e.g., with ADFG in-river traps). Another would be to develop better preseason models of adult abundance. Value-of-information models would answer the question of which of these approaches would most improve management of the fishery. The papers we plan to publish on this work will primarily be empirical in nature.
- Focus 3—Optimal harvesting of multiple substocks: The interaction of substocks occurs in the economics through the demand curve. What is the downside to managing as if multiple substocks were one stock? Should different quotas/escapements be derived for each sub-stock? If so, how?
- Focus 4—Cooperative approach to fishery management: When is it optimal to form a cooperative? What is the optimal size/participation for the coop? These questions have arisen empirically in Chignik, and are likely to arise elsewhere in Alaska as the efficiency gains from cooperatives become widely acknowledged. The specific design of the Chignik cooperative allocated a share of the quota to the cooperative in accordance with the number of members. We are examining the efficiency and outcome of this design property, and whether alternative mechanisms are desirable.

Theme 5: Fleet Composition, Fisherman Behavior, and Resilience to Natural and Anthropogenic Stresses

Agent-Based Modeling of the Bristol Bay Drift Gillnet Salmon Fishery

G Knapp, B Chasco, R Hilborn

Alaska's Bristol Bay sockeye salmon fishery is the world's largest fishery for this species. Between 1980 and 2005, annual catches averaged 24 million fish, with an annual average ex-vessel value of US$165 million. Historically, the Bristol Bay sockeye salmon fishery has accounted for 20-40% of the total value of Alaska salmon fisheries.

Similar to most other Alaska salmon fisheries, Bristol Bay fisheries are managed to achieve escapement goals for several major river systems flowing into Bristol Bay. Fishing is allowed during period "openings" over the season to catch returning salmon surplus to escapement goals. In general, the current management system is reasonably successful from a biological point of view, in the sense that managers are usually able to control fishing effort to achieve escapement goals.

The Bristol Bay salmon fishery has been under limited entry management since 1975. Approximately 1,900 fishermen hold limited entry permits to participate in the Bristol Bay drift gillnet fishery. Permit holders must (with certain exceptions) be onboard vessels while they are fishing. Permits, which were originally issued for free to historical participants in the fishery, are transferable.

After increasing for most of the 1980s, the ex-vessel value of Bristol Bay sockeye salmon harvests declined dramatically from $307 million in 1989 to just $34 million in 2002 (Fig. 5.9). The fall in value was the combined result of lower harvest volumes and a dramatic decline in prices caused by competition from farmed salmon (Knapp 2004, Bjørndal et al. 2003). Ex-vessel value increased to $89 million in 2006, but remained far below the level of the late 1980s and early 1990s.

The decline in value of the Bristol Bay sockeye salmon led to an economic crisis in the fishery. Unable to cover their costs, many permit holders quit fishing. The percentage of entry permits fished, which had never previously been <96%, was 83% in 2001, 63% in 2002, and 76% in 2003 and 2004. Entry permit prices—historically closely correlated with ex-vessel value—also plummeted, causing permit holders significant losses in asset value (Fig. 5.10).

The economic crisis has led to calls to "restructure" the management of the Bristol Bay fishery to increase its profitability. Potential management changes discussed include permit buybacks, fishing co-ops, and individual fishing quotas (Link et al 2003, Commercial Fisheries Entry Commission (CFEC) 2004).

None of these proposals has yet generated significant political support, in part because the fishery value has increased since 2002, but also because of various other concerns about potential effects of restructuring: For example, might restructuring lead to further erosion in the share of permits held by local residents, which fell from 35% in 1980 to 24% in 1996, but has since held relatively steady (Fig. 5.11)? Also, might potential economic gains from restructuring be dissipated over time as permit holders invest in more expensive vessels and gear in an ultimately and collectively futile effort to gain a larger share of the total catch (Link et al. 2003)? One indicator of this phenomenon, known as "capital stuffing" by economists, was an increase in the average horsepower of Bristol Bay fishing boats from 205 in 1980 to 366 by 2004 (calculated from vessel data available at *http://www.cfec.state.ak.us*).

Changes to the management of the Bristol Bay fishery could have dynamic short-run and long-run implications for who participates in and benefits from the fishery over

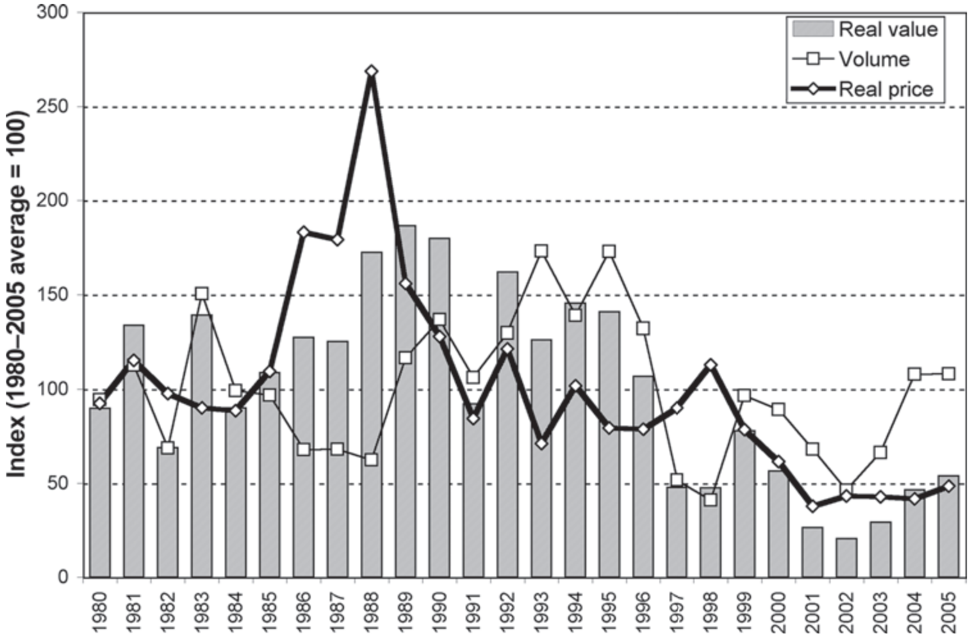


Figure 5.9. Ex-vessel value of Bristol Bay sockeye salmon harvest and indexes of harvest volume and ex-vessel price (1980–2005 averages = 100). Value and price are adjusted for inflation.

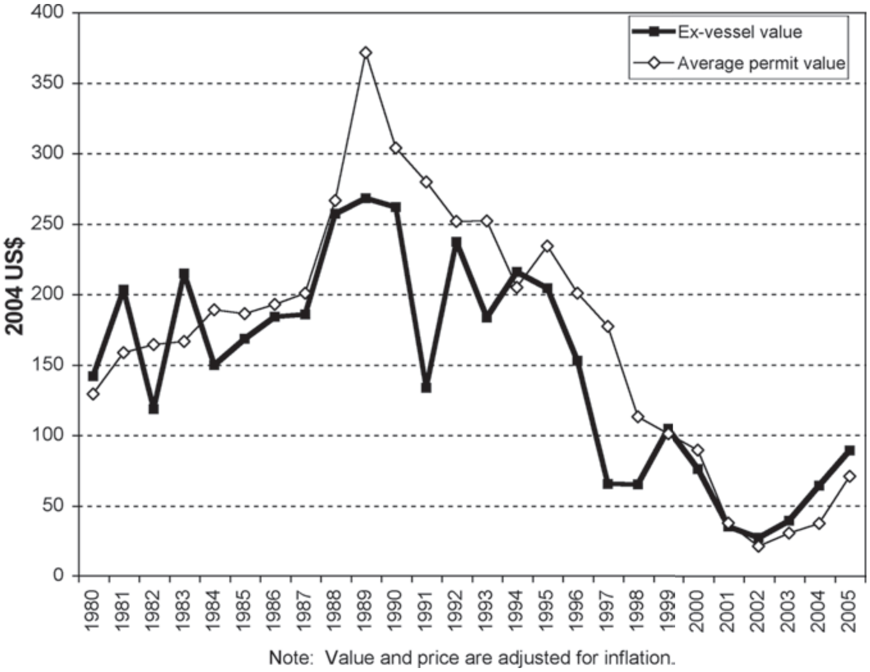


Figure 5.10. Ex-vessel value of Bristol Bay sockeye salmon harvest and average driftnet permit price. Value and price are adjusted for inflation. Price ranges (US$) are as follows: permit prices = thousands; ex-vessel value = millions.

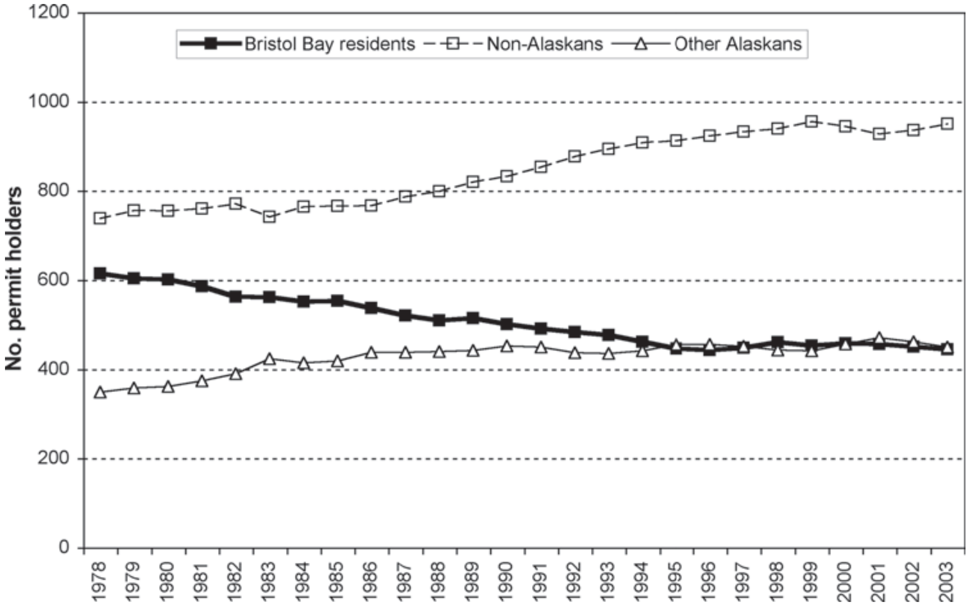


Figure 5.11. Number of Bristol Bay drift gillnet permit holders by residency.

time. We have begun an effort to model economic relationships in the fishery to understand how changes in fish returns, markets, and management have combined to affect this complex system in the past, and how potential management changes might affect it in the future.

We are using an agent-based modeling approach. Agent-based models use the behavior of agents (individuals) to predict population responses based on attributes and decision rules for agents, effects of agent decisions on other individuals and populations, and effects of population responses on agents.

In our model, agents are individual permit holders or potential permit buyers (Fig. 5.12). Each period is a year. Prior to the fishing season, permit holders make three sets of decisions based on their past experience and their expectations for future catches and prices: (1) whether to sell their

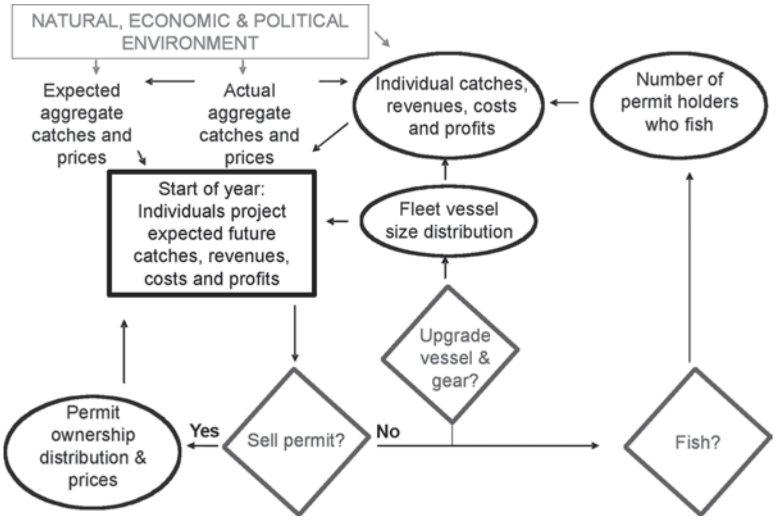


Figure 5.12. Agent-based model structure.

permit, (2) whether to upgrade their vessel and gear, and (3) whether to participate in the fishery. These decisions then affect their own and other permit holders' catches, revenues, costs, and profits during the fishing season, as well as the permit ownership distribution and permit prices.

In the first year of this study, we focused on collecting socioeconomic data for the Bristol Bay fishery, analyzing the data to formulate preliminary agent decision rules, programming the model, and testing whether the model can replicate historical trends in key model variables.

Detailed historical data for individual agents are available for some parts of our model. Databases maintained by Alaska's CFEC provide names and addresses of all permit holders for every year since 1975, as well as registration numbers and characteristics (e.g., horsepower, year of construction, hull type, etc.) of the vessels used by most of these permit holders. These data allow us to estimate some model relationships directly, such as permit transfer and vessel investment decision rules.

Data on individual permit holders' fishery participation and catches are confidential, limiting our ability to estimate formally how permit holder and vessel characteristics affect catches. However, analyses conducted by CFEC allow us to make reasonable assumptions about these relationships.

Our initial fishery data analysis supports key model relationships that we have hypothesized have important implications for how prices, runs, and management may affect the Bristol Bay fishery. For example, the higher the ex-vessel value of the fishery, the more rapid the rate of permit outmigration from the Bristol Bay region (Fig. 5.13). As can be seen in Figure 5.11, after declining rapidly when ex-vessel values were high, local permit ownership stabilized when ex-vessel value declined in the late 1990s. This is consistent with the hypothesis—also supported by data from other Alaska salmon fisheries—that local residents enjoy a relative cost advantage (lower travel and opportunity costs) that declines in importance as the value of a fishery increases. Thus, restructuring to increase the profitability of the Bristol Bay fishery could work against the social goal of maintaining local ownership of permits.

As another example of key model relationships, the rate of increase in vessel horsepower is positively correlated with ex-vessel value—supporting the hypothesis that the benefits of restructuring could be dissipated by further investment in boats.

We have programmed preliminary versions of the model in C++ and VisualBasic based on the critical assumption that a permit holder's share of the total catch is proportional to his share of aggregate horsepower. These preliminary model versions are able to replicate historical trends in fishery participation and permit prices. They also suggest that even simple, agent-based models can be instructive in understanding potential implications of management restructuring. For example, the simulated effects of a buyout depend on fishery participation, and profitability depends on which permit holders are bought out, as well as future runs and prices—all of which combine to affect the catches and revenues of the remaining permit holders.

Our current research is focused on the following:

- formal estimation and programming of agent decision rules for a full model incorporating all agent attributes,
- formal testing of the model's ability to replicate historical aggregate indicators, and
- initial programming of how selected restructuring options would affect agent decision options and model relationships.

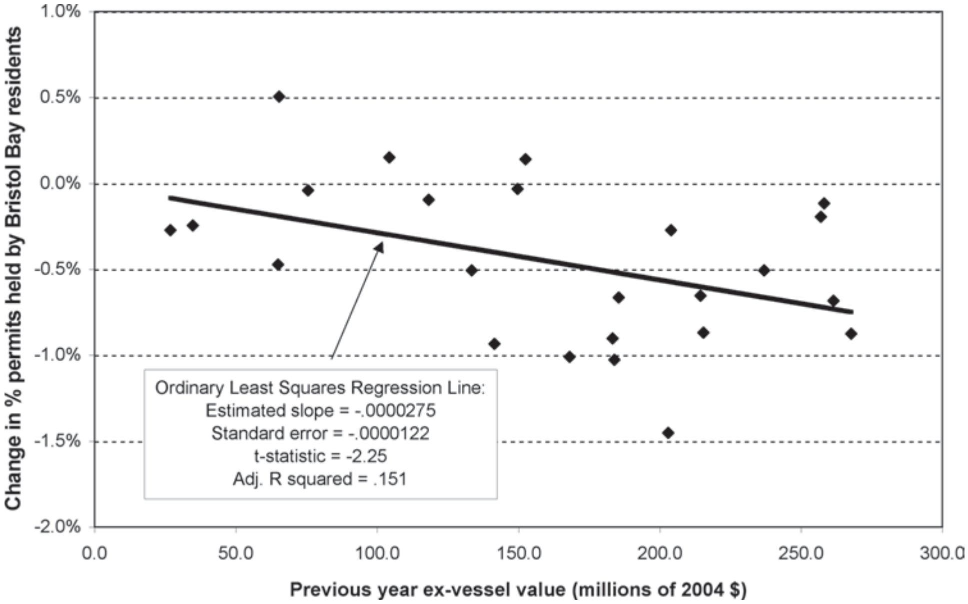


Figure 5.13. Bristol Bay ex-vessel value and change in local ownership share of permits.

6. Undergraduate Research

Since 1999, we have embedded an undergraduate research class, "Aquatic Ecological Research in Alaska (AERA)" within our field program of research. Each year, six students from the University of Washington spend about six and half weeks at the camps on lakes Aleknagik and Iliamna. They attend lectures by three of the faculty members—professors Hilborn, Schindler, and Quinn—and conduct a group project organized by each professor. These three projects, which are focused on limnology and lake ecosystems, population estimation, and evolutionary ecology, include data collection, analysis, preparation of a draft paper in scientific format, editorial comments by the professor, and a revision by the student.

In addition to these three major assignments, the students also help collect the long-term data that are the mainstay of the program, learning techniques such as zooplankton and insect sampling, beach seining, townetting, and otolith collection from adult salmon. Finally, each student designs and conducts an independent study during the summer; completes the sample processing, data analysis, report preparation; and gives a presentation for this project in the fall.

Topics chosen by students vary from year to year, but we have elected to present the abstracts as a discrete section, rather than distributing them throughout this report in the general topic areas into which they might be categorized, so that readers can view them as a group. Over the years, a number of these studies, either alone or combined with work by other undergraduate students or graduate students and faculty, have resulted in publications in peer-reviewed scientific journals, and have thus contributed to the careers of the students.

The Effects of Age and Length on Fecundity and Egg Weight of Sockeye Salmon in Hansen Creek, Lake Aleknagik, Alaska

E Holm

Sockeye salmon, like all other Pacific salmon, are semelparous fish and reproduce only once in their life, creating immense pressure on them to return to their natal spawning grounds and breed. Production and survival of the fry are critical for the reproductive success of the female, and by increasing fecundity and egg size there is a higher chance that some fry will survive to maturity. Female sockeye salmon usually spend 2 or 3 years at sea, and this variation in time spent feeding at sea can affect reproductive characteristics. Specifically, larger females can produce more numerous and larger eggs than smaller females, but there is also some evidence that older females have larger but less numerous eggs, for a given length, than younger females. The objective of this study was to test this hypothesis. Female sockeye salmon that had stranded and died at the mouth of Hansen Creek, Lake Aleknagik were measured for length, the otoliths were extracted for age determination, and fecundity and egg weight were estimated by weighing the total egg mass and then counting the eggs and weighing a subsample. The results indicated that larger fish, regardless of age, tended to have higher fecundity than smaller individuals. However, older fish tended to invest more into the size of the egg, which increases the fitness of the individual fry, rather than the number of eggs. In addition, a definite trade-off between egg weight and fecundity was seen in females that had spend 2 and 3 years at sea; individuals with high fecundity for their length tended to have smaller than average eggs, and vice-versa.

A First Look at the Population Structure of Wood River Pink Salmon

D Levin

Little is known about the pink salmon of Bristol Bay, Alaska, and even less is known about those of the Wood River system. Pink salmon are the most abundant Pacific salmon species and they have a unique 2-year life cycle. To begin to understand the population structure and dynamics in the Wood River system, we used three data sets: (1) ADFG commercial catch data, (2) University of Washington data on observations of pink salmon during foot surveys of small streams to count sockeye salmon, and (3) data on lengths of adult pink salmon collected in 2006 from 24 sites throughout the Wood River system.

The main results were as follows: (i) pink salmon are more abundant in Bristol Bay and the Wood River system in even-numbered years but the catch data do not appear to reliably reflect patterns of abundance; (ii) the stream surveys also showed this alternating pattern of abundance; (iii) the wider creeks of the Wood River system have been observed to contain pink salmon more often than narrower creeks, and some of these creeks may have self-sustaining populations but many seem to only contain strays; (iv) mean lengths of Wood River system pink salmon varied with the habitat (those in small creeks tended to arrive early and be small-bodied whereas those in larger rivers arrived later and were larger). There exists a myriad of possibilities for future research. Genetic tools coupled to higher and more consistent sampling effort will yield more definitive trends and quantitative characteristics of these populations.

Schistocephalus solidus: An Example of Parasitic Control over Its Host?

A Wallace

The evolutionary interactions of parasites with complex life cycles and their hosts represent some of the most perplexing processes in evolutionary biology. The parasitic cestode, *Schistocephalus solidus*, induces many abnormal behaviors in its second host, the threespine stickleback. These changes have been hypothesized to be a manipulation of the host by the parasite to increase the probability of the fish being eaten by a bird (a necessity if the parasite is to complete its life cycle). Alternatively, the changes may simply reflect the behavior of a fish in ill-health. To investigate this subject further, we investigated the effects of the parasite on vertical distribution of the stickleback in the lake and on the males' ability to develop nuptial coloration. A total of 248 sticklebacks were caught in Iliamna Lake, Alaska, and the parasite frequency, number, and percent of weight accounted for by the parasite (parasite intensity) were quantified. Normal behavior in the threespine stickleback is to migrate to the lake surface at night while remaining deeper during the day. Parasitism was more frequent in fish near the surface of the lake during daylight hours. Parasite number and intensity were also higher in this group. Males were also categorized by brilliance of their nuptial color. Males with some or bright nuptial color were significantly less frequently parasitized, as well as having fewer parasites per individual; and they were less intensely parasitized than males with no color. The fact that *Schistocephalus* can have effects on behavior as demonstrated in the diel vertical migration patterns and stickleback's ability to display secondary sexual characteristics raises questions as to how these infection symptoms evolved. Debate remains as to whether the physical and behavioral changes observed in infected threespine sticklebacks are the result of the parasite's manipulation of its host, the host attempting to protect itself from damage, or simply a side effect of the infection.

Determining Rates and Rationales for Scavenging of Salmon by Bears

T Hutton

The roles of salmon and bears in ecosystems are often intimately linked through interactions such as nutrient cycling and predation. As such, their management calls for integration because many aspects of the behavior, life history, and population biology of each species are affected by the other. Bears often kill salmon, including many that have yet to spawn, especially in small creeks. However, bears also scavenge dead salmon, and this obviously has no effect on the productivity of the salmon population. In addition to the role of scavenging in the foraging behavior and nutrition of bears, scavenging also constitutes a source of error when field personnel count salmon and quantify levels of predation because it can be difficult to distinguish fish that were killed from those that died of senescence and were subsequently scavenged. This study sought to investigate the prevalence of scavenging overall, as well as factors influencing the likelihood of an individual fish being scavenged. Carcasses were tagged at two study sites on Iliamna Lake in Bristol Bay and checked regularly for signs of scavenging. The results indicated that scavenging was very common: 79% of the fish were scavenged after three days, and 28% of fish were entirely removed from the study areas. Fish located on land were more likely to be scavenged than those in the water, and those with no previous bear consumption ("fresh" fish) were more likely to be removed from the sites than older carcasses that had already been bitten. The implications of these high rates of scavenging and removal are that bears likely facilitate large amounts of nutrient deposition in riparian and upland areas not directly in contact with the marine-derived nutrients brought back by spawning salmon. In addition, scavenging creates a potentially large source of bias and error in stream counts of spawning fish and estimates of predation rates.

Size Distribution of Sculpins Consuming Eggs of Beach Spawning Sockeye Salmon in Iliamna Lake

A Odle

Sculpins are benthic fishes that abound in lakes and streams. Their food items include a variety of organisms such as insects, mollusks, and (when available) salmon eggs. Sculpins apparently migrate to the spawning sites of sockeye salmon on island beaches in Iliamna Lake to feed on the readily available and highly nutritious salmon eggs. A study done in 1998 in Iliamna Lake was carried out to characterize the ecological relationship between sculpin and the beach-spawning sockeye salmon. While the study did use various laboratory and field tests to analyze the dynamics of sockeye salmon egg consumption by sculpins, it did not directly sample sculpins for egg consumption in the field in natural conditions. Thus, the objective of the present investigation was to better quantify the dynamics of egg predation by sculpins through field observations. Sculpins were sampled for abundance, length, weight, and diet in a known spawning site and nearby non-spawning site at Woody Island, Iliamna Lake. Larger sculpins tended to eat eggs and the larger sculpins were also found in the spawning sites. However, some small sculpins that had eaten eggs were found in the non-spawning site, suggesting that the small sculpins might have gained access into the spawning site to eat eggs, but might not be able to obtain full access because they are out-competed by the larger sculpins.

Opportunistic Feeding by Northern Pike

A Johnsen

The northern pike is well known as a top piscivore, capable of catching large fish with their sharp teeth and large powerful mouths. Pike are also very hardy and can live in habitats where few or no prey fish can survive. In these situations pike must eat the available prey, typically insects, which they would normally only eat as juveniles. The purpose of this study was to determine if pike employ an opportunistic feeding strategy, consuming what is available even if it is not a fish. Our approach was to examine the diets of pike from different habitats, including a large lake (Aleknagik) known to support populations of prey fish, and two small ponds (Eastwind and Stonehouse) that might have very limited populations of prey fish. Samples were taken from these lakes during August of 2006, with the pike ranging in size from 42 mm to 532 mm. Amphipods constituted the majority of the diet, and fish were only consumed at the Lake Aleknagik sample sites. The size of the pike did not appear to play any role in the size of the prey that was consumed: large pike ate small prey, as did small pike. The results suggest an opportunistic feeding strategy. The results may also be explained by habitat differences between the three lakes as no fish were found in the stomachs from two of the sites. It was noticed that the teeth of fish from these two sites were much smaller and duller than those found in the lake with prey fish. Future studies will involve determining whether an opportunistic feeding lifestyle may have implications on the ability of the pike to adapt to habitats completely devoid of prey fish.

7. Data and Web Development

Data

The Alaska Salmon Program has been collecting ecological data on Bristol Bay salmon populations and the lakes and streams they spawn in since 1946. These data are used by the program to complete numerous projects each year, to provide the best possible scientific information and advice on the ecological relationships between salmon and their environment, management and conservation objectives, forecast abundance, sustainable harvest strategies, and the understanding of the biological basis for productivity. These data are summarized yearly and made available in our annual report. These data are also analyzed and published in theses, dissertations, and peer-reviewed publications.

With recent funding from the Gordon and Betty Moore Foundation, the Alaska Salmon Program is now focusing on modernizing, validating, and compiling all our datasets into a single relational database. Because of the quantity of data we hold, we are processing and incorporating individual datasets into one comprehensive Alaska Salmon Program Database (ASPD). The ASPD has grown rapidly over the last year; we are on track to complete processing of archived hard-copy datasets by March 2008. As datasets are added to the ASPD, they are concurrently shared online with the larger scientific community. In this way our database development facilitates not only our own research but also the research of other scientists working to further our collective understanding of salmon ecosystems, ecology, and management.

Previously, all 60 years of data collected by the Alaska Salmon Program were archived as paper records in data books. Much of our data existed only in these data books when we began to develop the ASPD. Every dataset currently archived is being modernized for inclusion. Each dataset is error checked and verified against field and data books prior to its inclusion. When datasets have been entered, error checked, and verified, we provide (*http://fish.washington.edu/research/alaska/data.html*) the following for each data set on our website: (1) a summary graphic showing an example time-series trend for each dataset, (2) summary data available for download, (3) metadata, and (4) an opportunity to request data beyond the summary data using our online data request form.

We made significant progress toward integrating all of our data into the ASPD during 2006. Activities during 2006 included data processing of our remaining fish datasets, which are large, complicated, and valuable. These datasets are close to completely processed and will soon be incorporated into the ASPD. These nearly completed datasets are shown in Table 7.1 as year spans in black; the current contents of the ASPD are shown as year spans in gray. Once we complete the fish datasets, we will then process the smaller and simpler environmental and biological datasets that support our core fish datasets.

All current and future data collected by the Alaska Salmon Program is entered directly into custom relational databases in the field and subsequently reviewed for quality assurance and integrated into the ASPD upon return to Seattle at the end of each field season. Once we have completed incorporation of historical datasets into the ASPD, we will add ensuing years of data to each dataset and make the updated files available within 9 months of the end of the field season.

Website

The Alaska Salmon Program has maintained a website, hosted by the UW School of Aquatic & Fishery Sciences, since 1999. The original site primarily provided general information about the program, including a history of the research from program inception in 1946, a list of select publications with links to full-text pdfs of technical reports, facility descriptions, a photo gallery, and personnel directory. Data were limited to a table of the annual Bristol Bay salmon run forecast and links to the full report. Site content was primarily a function of the program's principal funding source and research impetus—the Bristol Bay commercial salmon fisheries.

A condition of recent program funding was to develop web-based resources for obtaining ASP datasets and associated information (e.g., publications). Funding is also supporting a dedicated web content developer to assist not only in developing online data resources, but to redesign

Table 7.1. Summary of data through 2006.

	Aleknagik	**Nerka**	**Beverley**	**Kulik**	**Little Togiak**	**Iliamna**	**Chignik**	**Black**
				Adult salmon data				
Spawning ground surveys	1946–2006	1946–2006	1947–2006	1946–2006	1950–2006			
Age structure of spawning ground populations	1947–2006	1947–2006	1947–2006	1950–1995 1997–2006	1950–1995 1997–1998 2000–2006	1965–1967 1973–2006		
				Adult and juvenile salmon and resident fish data				
Townet sampling of juvenile salmon and resident fishes	1958–2006	1957–2006	1958–1988	1958–1987	1958–2006	1961–1989 1999–2006	1961–2006	1961–2006
Beach seine sampling of salmon and resident fishes	1962–2006	1960–1970	1969	1969			1956–2006	1956–2006
				Supporting data				
Zooplankton abundance data	1967–2006	1967–2006	1967–2006	1967–2006	1967–1978 1983–2006			
Wind speed and direction	1966–2006							
Solar radiation and sky condition	1966–2006							
Water clarity	1973–2006							

and expand the scope and breadth of web content and provide timely updates and maintenance of that content.

Accomplishments for 2006, Goals for 2007

1. Publications

The list of publications by faculty, staff, and students conducting Alaska salmon research was expanded. Citations of peer-review and technical report citations range from 1959 to present.

For 2007, we will continue to improve access to publications, including the scanning of many reports and peer-review publications to PDF files that will be made available online through our the webpage publication list.

2. Data

In 2006, the data component of the website was made fully operational, and development of this resource is ongoing. Developments included online data support requests for Alaska Salmon Program personnel, as well as an online bulletin board where support requests and their answers are posted for Alaska Salmon Program personnel to search through when they need database help.

In 2006, we again provided daily online postings of the inseason run analysis for the Bristol Bay fishery. A restricted site was provided for salmon processors to access to obtain information on Port Moller test fishing results.

3. Photo Gallery

A dynamic, searchable photo gallery, including photos and descriptive information on various program components—biology, environment, socio-economics, infrastructure—was installed in 2006. It remains in an early state of development, with significant addition of content anticipated for 2007.

8. Facilities

In 2006 we continued to upgrade and renovate the field facilities. Projects undertaken in 2006 were as follows:

1. We completed a renovation of the Panabode structure at the Chignik camp, with an addition to the structure that doubles the interior floor space. This project has now shifted what is the "main house" at the Chignik camp to this Panabode structure, which gives our Chignik facility the capability to house five people in the main house with a washer/dryer and a shower in the building. We have also initated the process of dismantling and salvaging the structure that had previously served as the main living space at Chignik.
2. A project that concluded with a new, pile-supported dock was completed at the Aleknagik camp. The "Scow," which was approaching 100 years old and was plagued with extensive structural rot, was demolished and removed. In its place, a 25- x 60-ft pile-supported dock structure was installed. We will complete this project in 2007 with the addition of a 16- x 40-ft dock house.
3. A 20-ft all-weld aluminum boat equipped with a boom and 150-hp motor was added to our boat inventory in the Kvichak system.

9. Publications

2006

Branch, TA., R Hilborn, AC Haynie, G Fay, L Flynn, J Griffiths, KN Marshall, JK Randall, JM Scheuerell, EJ Ward, M Young. 2006. Fleet dynamics and fishermen behavior: lessons for fisheries managers. Can. J. Fish. Aquat. Sci. 63:1647-1668.

Brock, CS, PR Leavitt, DE Schindler, SP Johnson, JW Moore, PD Quay. 2006. Spatial variability of stable isotopes and fossil pigments in surface sediments of Alaskan coastal lakes: constraints on quantitative estimates of past salmon abundance. Limnol. Oceanogr. 51:1637-1647.

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11. Glossary

Acronyms

ADFG	Alaska Department of Fish & Game
ASP	Alaska Salmon Program
BBSRI	Bristol Bay Science and Research Institute
FRI	Fisheries Research Institute, the former University of Washington department through which Alaska salmon research was conducted; also still used to refer to the Alaska Salmon Program at the UW School of Aquatic & Fishery Sciences
NSF	National Science Foundation
UW	University of Washington

Common Names, Genus and Species

Arctic char	*Salvelinus alpinus*
Arctic grayling	*Thymallus arcticus*
Brown bear	*Ursus arctos*
Dolly Varden	*Salvelinus malma*
Ninespine stickleback	*Pungitius pungitius*
Pacific halibut	*Hippoglossus stenolepis*
Pacific salmon	*Oncorhynchus* spp.
Sockeye	*O. nerka*
Chinook	*O. tshawytscha*
Chum	*O. keta*
Pink	*O. gorbuscha*
Silver	*O. kisutch*
Steelhead/rainbow trout	*O. mykiss*
Pond smelt	*Hypomesus olidus*
Threespine stickleback	*Gasterosteus aculeatus*

12. Appendices

Appendix A. Summary of ground-based spawning ground surveys of adult sockeye salmon in Wood River streams, 2006. *Jacks are included in the live and dead counts. Average jack counts are from 2003-2006. Counts prior to these years are sporadic and unreliable. ** Total does not include the estimate off the mouth.

	Date		Live		Dead		Jacks*		Total**		Estimate off mouth	
Site	2006	Average	2006	Average	2006	Average	2006	Average	2006	Average	2006	Average
Lake Aleknagik												
Big Whitefish	8/20/2006	1950-2006	2778	730	323	144	44	41	3101	874	1500	186
Yako	8/16/2006	1946-2006	5662	1772	4489	637	30	38	10151	2409	2000	702
Bear	8/1/2006	1946-2006	2885	2586	1881	947	1	5	4766	3533	2000	432
Ice	8/5/2006	1946-2006	12205	4806	1725	3069	4	5	13930	7875	200	206
Sunshine	8/4/2006	1982-2006	1976	1075	28	524	1	1	2004	1599		140
Happy	8/8/2006	1946-2006	16683	2631	13105	2821	14	8	29788	5452	3000	503
Hansen	8/6/2006	1947-2006	7320	2487	5811	1744	26	113	13131	4231		305
Eagle	8/17/2006	1970-2006	601	948	224	166	13	15	825	1114		287
Mission	8/18/2006	1954-2006	2411	1019	1053	426	5	11	3464	1445	200	69
Lake Nerka												
Allah	8/6/2006		4380		3407		26		7787	0	2000	
Berm	7/30/2006		359		474		20		833	0	160	
Fenno	8/10/2006	1946-2006	4341	1808	2514	2387	36	28	6855	4195	500	32
Pick	8/13/2006	1946-2006	7275	6588	946	2584	3	8	8221	9172		263
Lynx	8/26/2006	1946-2006	244	2191	244	815	20	29	488	3006	10	386
N-4	8/6/2006		11		12				23	0		
Hidden Lake Cr	8/22/2006	1946-2006	825	1431	841	1105	19	12	1666	2536	30	104
Hidden Lake	8/22/2006	2000-2006	493	603	68	200			561	803	35	
Elva	8/24/2006	1946-2006	62	140	57	51	3	1	119	191	35	223
Sam	8/8/2006	1946-2006	1419	838	1389	900	19	8	2808	1738	250	690
Joe	8/9/2006	1983-2006	1060	999	785	1245	11	8	1845	2244	200	201
Stovall	8/27/2006	1954-2006	3461	936	2579	688	31	13	6040	1624	100	3
Pike	8/23/2006	1970-2006	1555	886	1613	713	40	26	3168	1599		0
Teal	8/16/2006	1970-2006	948	285	187	835	67	22	1135	1120	25	9
Kema	8/11/2006	1955-2006	4409	883	145	993		3	4554	1876		0
Little Togiak R	8/28/2006	1947-2006	3957	6340	23	161			3980	6501		1670

Appendix A–cont.

	Date		Live		Dead		Jacks*		Total**		Estimate off mouth	
Site	2006	Average	2006	Average	2006	Average	2006	Average	2006	Average	2006	Average
Little Togiak Lake												
A Creek	8/11/2006	1947-2006	183	36	215	90	0		398	126		98
C Creek	8/21/2006	1947-2006	13	140	91	180	0		104	320		242
Beverley												
Moose	8/16/2006	1955-2006	7140	1442	2174	1059	0	8	9314	2501		36
Kulik												
Grant River	8/21/2006	1946-2006	21023	4982	941	1641	1	2	21964	6623	1500	77

Appendix B1. Age composition of adult sockeye salmon determined by otolith sampling in Wood River spawning sites, 2006.

Lake	Location	Males						No. of fish	Females						No. of fish	Combined						No. of fish
		1.1	2.1	1.2	2.2	1.3	2.3		1.1	2.1	1.2	2.2	1.3	2.3		1.1	2.1	1.2	2.2	1.3	2.3	
Aleknagik	Agulowak River	0.00	0.00	0.05	0.00	0.95	0.00	110	0.00	0.00	0.11	0.00	0.88	0.01	106	0.00	0.00	0.08	0.00	0.92	0.01	216
	Bear Creek	0.02	0.00	0.35	0.00	0.64	0.00	110	0.00	0.00	0.76	0.00	0.24	0.00	106	0.01	0.00	0.55	0.00	0.44	0.00	216
	Eagle Creek	0.04	0.00	0.79	0.00	0.17	0.00	109	0.00	0.00	0.88	0.01	0.11	0.00	112	0.02	0.00	0.84	0.01	0.14	0.00	221
	Hansen Creek	0.06	0.00	0.91	0.00	0.04	0.00	109	0.00	0.00	0.98	0.00	0.02	0.00	105	0.03	0.00	0.94	0.00	0.03	0.00	214
	Happy Creek	0.01	0.00	0.37	0.00	0.61	0.01	107	0.00	0.00	0.49	0.00	0.51	0.00	107	0.01	0.00	0.43	0.00	0.56	0.01	214
	Ice Creek	0.00	0.00	0.15	0.00	0.84	0.00	104	0.00	0.00	0.13	0.00	0.86	0.01	106	0.00	0.00	0.14	0.00	0.85	0.00	210
	Midnight Creek	0.03	0.00	0.85	0.00	0.13	0.00	110	0.00	0.00	0.78	0.00	0.22	0.00	112	0.01	0.00	0.81	0.00	0.18	0.00	222
	Mission Creek	0.00	0.00	0.95	0.00	0.05	0.00	107	0.00	0.00	0.93	0.00	0.07	0.00	104	0.00	0.00	0.94	0.00	0.06	0.00	211
	Sunshine Creek	0.00	0.06	0.06	0.00	0.88	0.00	34	0.00	0.00	0.33	0.00	0.67	0.00	102	0.00	0.01	0.26	0.00	0.72	0.00	136
	Whitefish Creek (Big)	0.04	0.00	0.83	0.00	0.13	0.00	92	0.00	0.00	0.89	0.01	0.10	0.00	107	0.02	0.00	0.86	0.01	0.12	0.00	199
	Whitefish Creek (Little)	0.00	0.00	1.00	0.00	0.00	0.00	106	0.00	0.00	0.99	0.00	0.01	0.00	95	0.00	0.00	1.00	0.00	0.01	0.00	201
	Wood River	0.00	0.00	0.84	0.02	0.14	0.00	108	0.00	0.00	0.85	0.00	0.15	0.00	111	0.00	0.00	0.84	0.01	0.15	0.00	219
	Yako Creek	0.01	0.00	0.56	0.00	0.43	0.00	109	0.00	0.00	0.63	0.00	0.37	0.00	110	0.01	0.00	0.59	0.00	0.40	0.00	219
Nerka	Agulukpak River	0.00	0.00	0.09	0.01	0.88	0.02	106	0.00	0.00	0.16	0.00	0.83	0.01	106	0.00	0.00	0.13	0.01	0.85	0.01	212
	Anvil Bay Beaches	0.00	0.00	0.57	0.00	0.43	0.00	103	0.00	0.00	0.74	0.02	0.22	0.02	108	0.00	0.00	0.66	0.00	0.32	0.00	211
	Elva Creek	0.05	0.00	0.62	0.00	0.33	0.00	2	0.00	0.00	0.62	0.00	0.38	0.00	34	0.00	0.00	0.62	0.00	0.38	0.00	36
	Fenno Creek	0.03	0.00	0.69	0.00	0.28	0.00	108	0.00	0.00	0.86	0.00	0.13	0.00	104	0.01	0.00	0.77	0.00	0.21	0.01	212
	Hidden Lake Creek	0.13	0.02	0.61	0.03	0.21	0.01	127	0.00	0.00	0.71	0.03	0.25	0.01	151	0.06	0.01	0.66	0.03	0.23	0.01	278
	Joe Creek	0.06	0.00	0.79	0.00	0.15	0.00	108	0.00	0.00	0.83	0.00	0.15	0.00	104	0.03	0.00	0.81	0.01	0.15	0.01	212
	Kema Creek	0.11	0.00	0.72	0.03	0.14	0.01	110	0.00	0.00	0.88	0.04	0.08	0.01	112	0.05	0.00	0.80	0.03	0.11	0.01	222
	Lynx Creek	0.36	0.00	0.34	0.00	0.30	0.00	67	0.00	0.00	0.58	0.00	0.41	0.01	153	0.11	0.00	0.51	0.00	0.37	0.01	220
	N4-N6 Beach	0.00	0.00	0.42	0.00	0.54	0.03	92	0.00	0.00	0.73	0.00	0.21	0.05	98	0.00	0.00	0.58	0.00	0.37	0.04	190
	Pick Creek	0.03	0.00	0.62	0.00	0.36	0.00	107	0.00	0.00	0.71	0.00	0.28	0.00	104	0.01	0.00	0.66	0.01	0.32	0.00	211
	Pike Creek	0.14	0.00	0.83	0.00	0.04	0.00	109	0.00	0.00	0.92	0.00	0.08	0.00	109	0.07	0.00	0.87	0.00	0.06	0.00	218
	Sam Creek	0.07	0.00	0.67	0.02	0.22	0.02	99	0.00	0.00	0.68	0.04	0.27	0.02	108	0.03	0.00	0.67	0.03	0.25	0.02	207
	Stovall Creek	0.01	0.00	0.88	0.00	0.02	0.00	104	0.00	0.00	0.99	0.00	0.01	0.00	107	0.05	0.00	0.94	0.00	0.01	0.00	211
	Teal Creek	0.63	0.00	0.37	0.00	0.00	0.00	123	0.00	0.00	0.98	0.00	0.03	0.00	120	0.32	0.00	0.67	0.00	0.01	0.00	243

Appendix B1–cont.

Lake	Location	Males						No. of fish	Females						No. of fish	Combined						No. of fish
		1.1	2.1	1.2	2.2	1.3	2.3		1.1	2.1	1.2	2.2	1.3	2.3		1.1	2.1	1.2	2.2	1.3	2.3	
Little Togiak	A Creek	0.00	0.00	0.91	0.00	0.09	0.00	22	0.00	0.00	0.93	0.00	0.07	0.00	70	0.00	0.00	0.92	0.00	0.08	0.00	92
	C Creek	0.00	0.00	0.85	0.00	0.14	0.00	14	0.00	0.00	0.89	0.00	0.11	0.00	19	0.00	0.00	0.88	0.00	0.12	0.00	33
	Little Togiak River	0.00	0.00	0.30	0.00	0.68	0.02	103	0.00	0.00	0.40	0.02	0.52	0.06	108	0.00	0.00	0.35	0.01	0.60	0.04	211
Beverley	B-12 Beaches	0.00	0.01	0.74	0.06	0.18	0.00	98	0.00	0.00	0.90	0.04	0.04	0.02	101	0.00	0.01	0.82	0.05	0.11	0.01	199
	Hardluck Bay Beach	0.02	0.00	0.83	0.02	0.14	0.00	64	0.00	0.00	0.90	0.05	0.04	0.00	93	0.01	0.00	0.87	0.04	0.08	0.00	157
	Silver Horn Beaches	0.00	0.01	0.80	0.04	0.15	0.01	109	0.00	0.00	0.94	0.05	0.00	0.01	113	0.00	0.01	0.87	0.05	0.07	0.01	222
	Moose Creek	0.03	0.01	0.81	0.02	0.13	0.00	107	0.00	0.00	0.86	0.04	0.10	0.00	98	0.01	0.01	0.83	0.03	0.12	0.00	205
Kulik	Grant River	0.00	0.00	0.83	0.00	0.15	0.02	112	0.00	0.00	0.90	0.00	0.10	0.00	115	0.00	0.00	0.86	0.00	0.13	0.01	227
	Unweighted mean	0.06	0.00	0.63	0.01	0.30	0.00		0.00	0.00	0.74	0.01	0.24	0.01		0.02	0.00	0.69	0.01	0.27	0.01	

Appendix B2. Age composition of adult sockeye salmon determined by otolith sampling in Kvichak River spawning sites, 2006.

	COUNTS																				
		Males						No. of	Females						No. of	Combined						No. of
Lake	Location	1.1	2.1	1.2	2.2	1.3	2.3	fish	1.1	2.1	1.2	2.2	1.3	2.3	fish	1.1	2.1	1.2	2.2	1.3	2.3	fish
Iliamna	Chinkelyes Creek	0	0	39	22	38	1	100	0	0	28	13	51	8	100	0	0	67	35	89	9	200
	Copper River	0	0	10	13	61	14	98	0	0	6	22	61	9	98	0	0	16	35	122	23	196
	Fuel Dump Island	3	0	43	1	2	0	49	0	0	45	0	1	1	47	3	0	88	1	3	1	96
	Gibraltar Creek	0	0	11	0	36	51	98	0	0	1	4	21	18	44	0	0	12	4	57	69	142
	Knutson Bay Beach	0	0	17	1	1	1	20	0	0	10	0	1	0	11	0	0	27	1	2	1	31
	Knutson Bay Beach (October)	1	0	6	0	0	0	7	0	0	34	0	0	0	34	1	0	40	0	0	0	41
	Knutson Bay Creek	0	0	1	3	2	1	7	0	0	2	0	3	0	5	0	0	3	3	5	1	12
	Knutson Bay Slough	0	0	4	2	1	0	7	0	0	1	0	0	0	1	0	0	5	2	1	0	8
	Pedro Ponds- Grasss Pond	0	0	30	0	1	0	31	0	0	49	0	0	0	49	0	0	79	0	1	0	80
	Pedro Ponds- 1_2	0	0	5	0	0	0	5	0	0	6	0	0	0	6	0	0	11	0	0	0	11
	Pedro Ponds- Trail Pond	0	0	59	0	2	0	61	0	0	49	0	2	0	51	0	0	108	0	4	0	112
	Woody Island	3	0	40	0	1	1	45	0	0	46	0	2	1	49	3	0	86	0	3	2	94

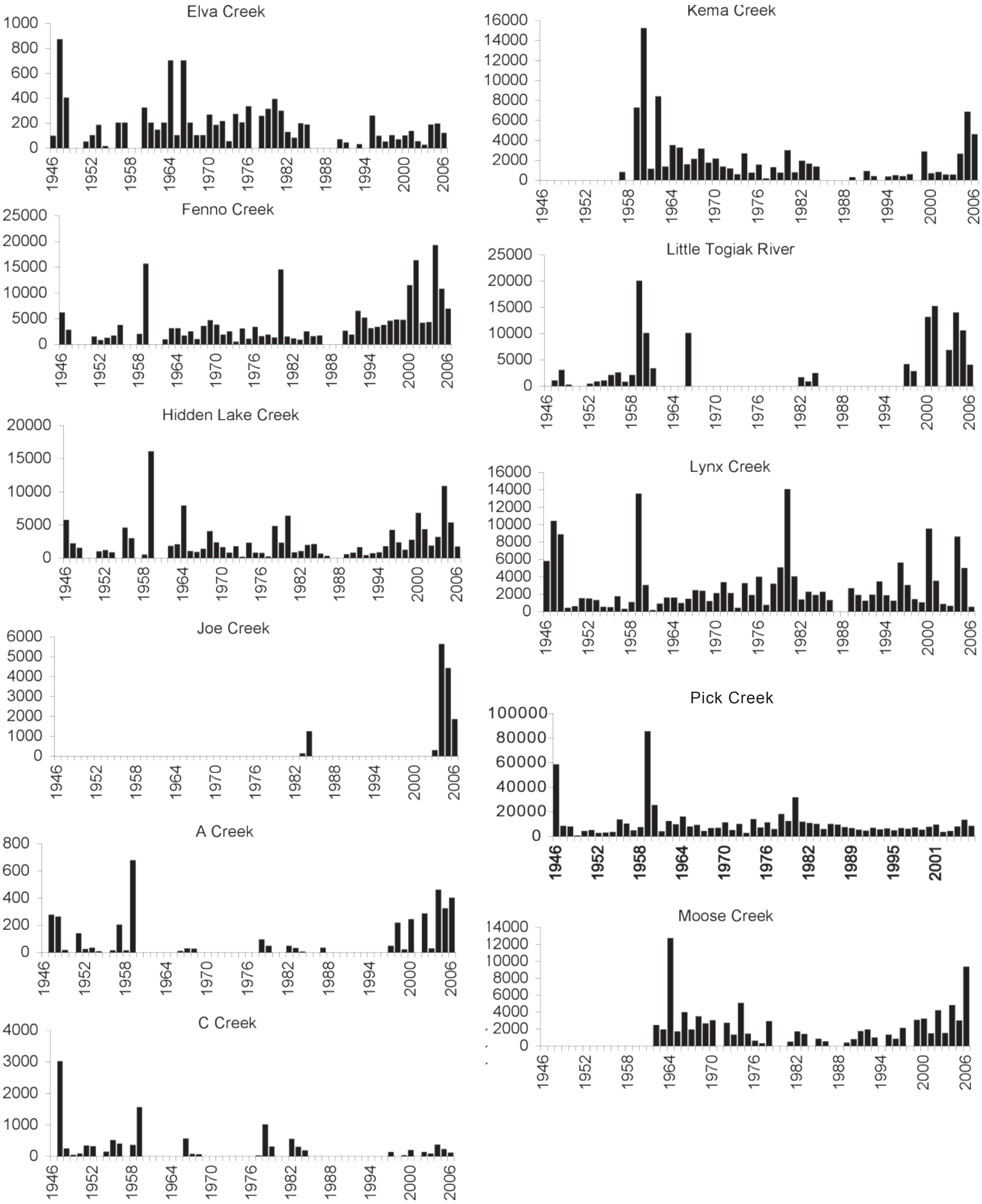
	PROPORTIONS																				
		Males						No. of	Females						No. of	Combined						No. of
Lake	Location	1.1	2.1	1.2	2.2	1.3	2.3	fish	1.1	2.1	1.2	2.2	1.3	2.3	fish	1.1	2.1	1.2	2.2	1.3	2.3	fish
Iliamna	Chinkelyes Creek	0.00	0.00	0.39	0.22	0.38	0.01	100	0.00	0.00	0.28	0.13	0.51	0.08	100	0.00	0.00	0.34	0.18	0.45	0.05	200
	Copper River	0.00	0.00	0.10	0.13	0.62	0.14	98	0.00	0.00	0.06	0.22	0.62	0.09	98	0.00	0.00	0.08	0.18	0.62	0.12	196
	Fuel Dump Island	0.06	0.00	0.88	0.02	0.04	0.00	49	0.00	0.00	0.96	0.00	0.02	0.02	47	0.03	0.00	0.92	0.01	0.03	0.01	96
	Gibraltar Creek	0.00	0.00	0.11	0.00	0.37	0.52	98	0.00	0.00	0.02	0.09	0.48	0.41	44	0.00	0.00	0.08	0.03	0.40	0.49	142
	Knutson Bay*	0.02	0.00	0.68	0.15	0.01	0.05	41	0.00	0.00	0.92	0.00	0.08	0.00	51	0.01	0.00	0.82	0.07	0.09	0.02	92
	Pedro Ponds*	0.00	0.00	0.97	0.00	0.03	0.00	97	0.00	0.00	0.98	0.00	0.02	0.00	106	0.00	0.00	0.98	0.00	0.02	0.00	203
	Woody Island	0.07	0.00	0.89	0.00	0.02	0.02	45	0.00	0.00	0.94	0.00	0.04	0.02	49	0.03	0.00	0.91	0.00	0.03	0.02	94
	Unweighted mean	0.02	0.00	0.57	0.07	0.22	0.11		0.00	0.00	0.59	0.06	0.25	0.09		0.01	0.00	0.59	0.07	0.23	0.10	

*Proportions calculated from totals of all sub locations

Appendix C. Five-day averages of catches of emergent midges and water temperatures at three stations at Lake Aleknagik in 2006.

	Days	Avg. catch per day			Avg. temp (°C)		
Date range	6/3 ice out	W	H	Mean	W	H	Mean
June							
6-10	5	0	11	6	6	6	6
11-15	10	3	8	5	7	6	7
16-20	15	21	4	12	7	8	8
21-25	20	12	2	7	11	11	11
26-30	25	7	2	5	7	12	10
July							
1-5	30	7	2	4	11	15	13
6-10	35	0	3	1	13	15	14
11-15	40	0	1	1			
16-20	45	0	8	4	10	13	11
21-25	50	3	10	6	12	13	12
26-30	55	6	0	3	13	13	13
31-4	60	11		11	13		13
August							
5-9	65						
10-14	70						
15-19	75	14		14	13		13
20-24	80	4		4	15		15
25-29	85	4		4	15		15
30-3	90						
September							
4-9	95	4		4			

Appendix D. Historical total peak sockeye counts for streams of lakes Nerka, Little Togiak, Beverley, and Kulik, 1946–2006.



Appendix D—cont.