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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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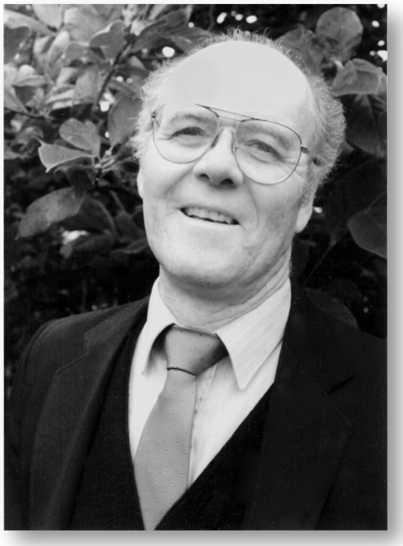
Acknowledgments

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.

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.



Donald E. Rogers, 1932-2004

Professor Emeritus Donald E. Rogers spent his career at UW Fisheries, first as a student starting in 1959, and ending with his retirement from the faculty in 1997. Despite retirement, he continued to assist with data analysis and forecasting the sockeye salmon runs into Bristol Bay, Alaska. He was passionate about his work and was highly regarded as a salmon biologist. His long-term association with the Alaska Salmon Program, through the School's Fisheries Research Institute, which he effectively led from the mid-1980s until retirement, earned him the nickname of "Emperor of the North" in a newspaper write-up.

On learning of Don's passing, School alumnus and longstanding faculty member Tom Quinn sent the following letter to the School of Aquatic & Fishery Sciences faculty:

I compose this letter, looking out the window of my cabin at our field camp on Iliamna Lake, in the Bristol Bay region of Alaska. This seems fitting, as the sockeye salmon of Bristol Bay were the focus of Don's professional and personal life. He starting working in Bristol Bay in 1959, the year that Alaska became a state, and he stopped coming here only in recent years when his pulmonary condition made the physical exertion too difficult. Even when he was restricted to Seattle, his mind was always in Alaska.

Don's work in Bristol Bay, and especially at the Wood River lake system, was characterized by much more than longevity. He was a true naturalist, with a keen eye and an equally keen interest in the insects, songbirds, vegetation, and geology of the region. Indeed, the Fisheries Research Institute's entire program on Bristol Bay sockeye salmon was remarkably foresighted. Before such terms as climate change, biocomplexity, ecosystem management, and marine-derived nutrients were coined, the program that Don joined and later directed was doing these kinds of research. Men such as W. F. Thompson, Bud Burgner, Ole Mathisen, and others came into largely unexplored areas and were challenged to determine the processes controlling the abundance of one commercially important species, sockeye salmon. Given the difficulties in doing any field work in these remote areas, most of us would have simply counted the sockeye salmon and called that good enough. However, these scientists took careful measurements of physical factors hypothesized to affect the salmon and their ecosystem (lake level, date of freezing and ice out, solar radiation, temperature), and the biotic factors including primary production, aquatic insects and zooplankton, and a variety of other fishes in these lakes. They chose the important variables to measure, and had the persistence to maintain consistent sampling regimes through flush and lean years of funding, through generations of students and technicians, and through the periods when certain hypotheses came in and out of favor. We now have the extraordinary opportunity to see the long-term patterns in these largely pristine ecosystems, because Don Rogers and the scientists and students working with him had the vision to build and the dedication to maintain a truly unique, ecosystem-based, long-term research program.

In addition to Don's legacy of research, he had an exceptional record of training graduate and undergraduate students over the decades. In an era when many faculty members dictated the project that each student undertook, Don Rogers always encouraged graduate students to design their own projects, and he gave undergraduates unparalleled research experience. Countless fisheries scientists have worked at the Bristol Bay camps, and many consider those to have been their most memorable years.

I had the opportunity to come to Bristol Bay to help Don supervise a graduate student, Greg Blair, in 1987 and I have been coming back ever since. This program is the focus of my research, and a part of my teaching duties, and it is truly an honor to help carry on the tradition that Don represented. He welcomed me into the program, encouraged me to increase my involvement, and stood by me when I needed his help. He was our leader, teacher, and friend, and he will be long remembered, and greatly missed.

Introduction

The year 2005 marked the 60th year of field work in Bristol Bay for our program and saw a significant expansion of both our field program and analytic work conducted at University of Washington. In the summer of 2005, we had a record number of people in our field camps (2,700 person days), had a full field season at Chignik for the first time in many years, and taught a new course on salmon management at the Aleknagik camp. The core of our program research remains focused on the biology and management of the salmon of western Alaska, but we have expanded the breadth of the program considerably with the addition 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 Chignik. 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://safs.washington.edu/alaska*. In addition, reference maps for the general research areas and specific study sites are provided on pages 37-41.

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.

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 concerned only with 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.

2005 Preseason Review

Given the 2005 forecast, which was 32.7 million, and the number of returns, 39.3 million fish, we underforecast the run by 17%. Notable differences between observed and forecasted returns (Table 1) were apparent for 1.3 fish returning to the Naknek, Alagnak, Nushagak, and Igushik systems, which all had higher numbers than forecasted. Aggregated across ages, the observed returns for the Naknek, Nushagak, Igushik, and Kvichak were all higher than forecasted; however, most of the under-prediction resulted from the large number of 1.3 fish. The forecast for 1.2 fish across all systems was accurate, although these fish represent only 12% of the total return. The magnitude of the error for the 2.2 and 2.3 fish was equal but opposite in sign. Our forecast of the total harvest was 138 million lb; the actual harvest was 153 million lb.

2006 Preseason Forecast

The 2006 Bristol Bay preseason forecast is for 38.8 million fish (Table 2), with a total catch of 31.6 million and an estimated weight of 164.6 million lb. We produced forecasts for all nine major rivers (Kvichak, Alagnak, Naknek, Egegik, Ugashik, Wood, Igushik, Nushagak–Mulchatna, and Togiak). We used 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 2005

Much of our effort recently has been devoted to increasing the accuracy of the inseason forecast model. We have recently improved upon the model developed by Hyun et al. (2005) to include the estimation of migration timing as well as run size. Every year, uncertainty in the timing has precluded us from making robust inferences about the total run size. The model framework we have developed allows us to estimate the timing and abundance simultaneously, thus enabling us to make inferences about which combination of size (i.e., small or large) and timing (i.e., late or early) attributes the run may exhibit.

Table 1. Difference in millions between the 2005 preseason forecast and the observed number of sockeye salmon (*Oncorhynchus nerka*) returning to Bristol Bay, Alaska, by river system and age class. A negative means the preseason forecast was lower than the observed returns, and vice-versa.

District River	1.2	1.3	2.2	2.3	Total
Naknek\Kvichak	0.76	-5.51	-0.70	-0.84	-6.65
Kvichak	-0.23	-0.86	-0.84	-0.17	-2.10
Naknek	0.12	-3.37	0.14	-0.60	-3.73
Alagnak	0.87	-1.28	-0.04	-0.07	-0.52
Egegik	0.22	0.07	-3.00	3.94	1.32
Ugashik	0.36	-0.87	0.83	-0.14	0.23
Nushagak	-0.54	-1.87	-0.08	-0.22	-3.00
Wood	-0.46	0.85	-0.04	-0.06	0.29
Nushagak	-0.18	-1.76	0.00	0.00	-1.92
Igushik	0.00	-0.96	-0.04	-0.18	-1.18
Togiak	0.00	0.04	-0.13	-0.01	-0.09
Totals	0.68	-8.09	-2.32	2.71	-7.00

Table 2. The 2006 preseason forecast of the number of sockeye salmon (*Oncorhynchus nerka*) in millions returning to the Bristol Bay, Alaska, by river system and age class.

		Ages						
District	River	1.2	1.3	2.2	2.3	Total	Escape-ment	Harvest
Naknek\Kvichak		5.6	4.0	2.5	1.3	13.4	3.3	7.4[a]
	Kvichak	2.0	0.9	1.4	0.3	4.6	2.0	2.6
	Naknek	2.5	1.7	0.8	0.9	5.9	1.1	4.8
	Alagnak	1.1	1.4	0.3	0.1	2.9	0.2	0.0
Egegik		3.5	1.0	5.4	3.5	13.4	1.1	12.3
Ugashik		1.5	0.8	0.9	0.3	3.5	0.9	2.6
Nushagak		2.1	4.1	0.2	0.2	6.6	1.9	4.7
	Wood	1.7	2.0	0.1	0.1	3.9	1.1	2.7
	Nushagak	0.2	1.4	0.0	0.0	1.7	0.2	1.5
	Igushik	0.2	0.6	0.0	0.1	0.8	0.6	0.3
Togiak		0.1	0.3	0.0	0.1	0.5	0.2	0.3
Totals		12.8	10.2	9.0	5.4	37.4	7.4	27.3[a]

[a] The forecast for total harvest includes 0.00 harvest from the Alagnak; thus, the 'HARVEST' estimates for the 'Naknek\Kvichak' district and the 'Totals' catergory cannot be summed horizontally.

The current model uses the following sources of information: catch and escapement for each day to each district, age composition of catch and escapement by district, Pt. Moller test fish index, and age composition at Pt. Moller. For 2006, we plan to incorporate the genetics sampling data from Pt. Moller and the inriver test-fishing indices into our model. If the district catch is genetically sampled, we will use that data as well.

Using the 2005 data, we developed a retrospective analysis (Fig. 1), which uses only the information available up to the day the forecast was made. The model's ability to predict the run size for the various districts is promising, as our estimates are near the observed run size throughout much of the forecasting period. Currently, we are focusing on reducing the uncertainty surrounding the run size estimates by incorporating environmental data to provide information on run timing and distribution.

Escapement Goal Analysis

One of the primary management decisions made in Bristol Bay each year is the escapement goal for each river system. This goal guides the inseason management of each system, with the daily opening and closing patterns being adjusted to ensure the final escapement falls within the target range that was set preseason. The escapement goals and management plans are set by the Alaska Board of Fisheries, with the primary scientific advice coming from the research staff of ADFG. UW faculty and staff have routinely been involved with ADFG staff in evaluating alternative goals by participating in workshops on Bristol Bay escapement goals, and in developing and implementing computer software for escapement goal analysis.

Escapement goals have been identified as a high priority research topic by Bristol Bay processors; they are an important part of our NSF biocomplexity project and a key part of the funding from the Gordon and Betty Moore Foundation. Bristol Bay escapement goals will be reviewed at the Alaska Board of Fisheries meeting in 2006.

The traditional approach to setting escapement goals is to calculate the spawning stock size that produces the highest average catch. In our current work, we are exploring several issues, including the following:

1. maximizing the economic value of the catch rather than the pounds landed to account for the lower price received by fishermen at higher catch levels;
2. maximizing the economic profit to the harvesting and processing industry by considering the costs, and looking at the inseason consequences of different harvest strategies;
3. considering the evolutionary consequences of different harvest strategies—for instance high escapement goals tend to lead to differential fishing pressure on early- and late-run fish;
4. considering the consequences of stock structure within a river system on impacts of harvest strategies;
5. considering how environmental conditions at different life-history stages can be used to evaluate alternative escapement goals;
6. considering the impact of marine-derived nutrients on the lake ecosystems and how the level of the escapement goal would affect lake productivity; and
7. evaluating how climate change and uncertainty in future productivity should be accounted for in setting escapement goals.

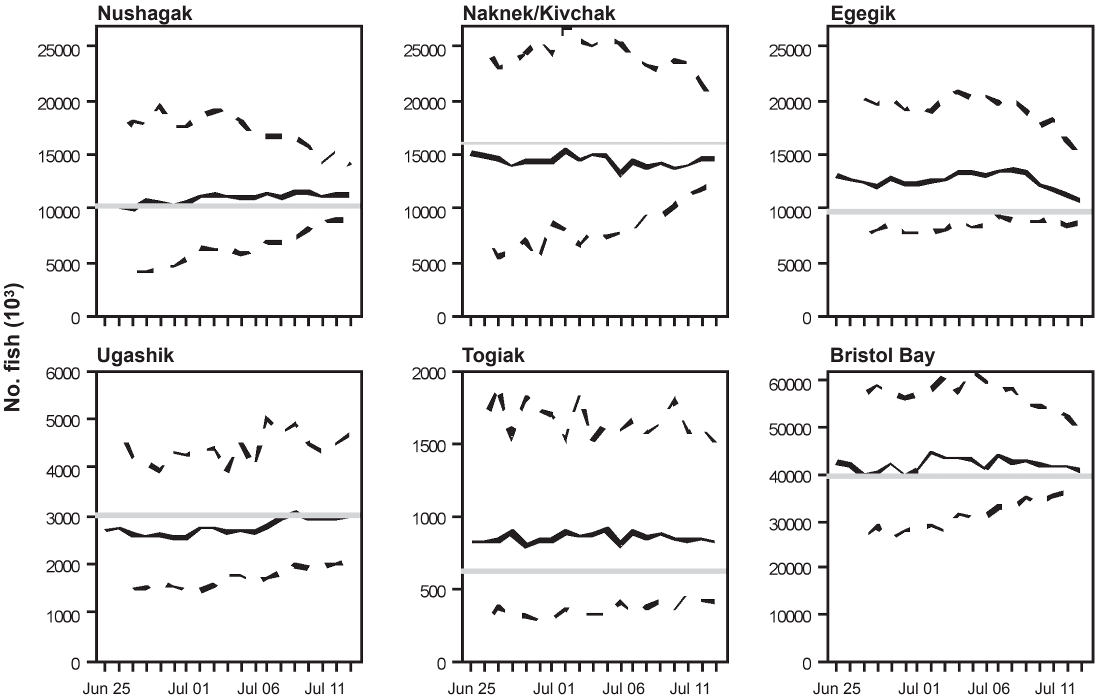


Figure 1. 95% probability intervals (dashed lines), best estimate (solid black line), and actual run size (gray line) for the Bristol Bay fishing districts for each day of the season.

The Kvichak is of particular interest as it has had very poor returns in recent years and all concerned parties want to know what can be done by management to improve its total returns.

During 2005, we began work on all of these topics, and now have computer software that can be used to examine the optimal harvest strategy when considering price and costs, and also software that considers the explicit life history of the stock. In a project done in conjunction with Bristol Bay Science and Research Institute and Brian Bue (fisheries consultant, Anchorage, Alaska), we have provided an analysis of policies to maximize economic returns.

ADFG has formed an external advisory committee to work with their staff in formulation of advice for the next round of escapement goals. Ray Hilborn is a member of this committee and he, Bob Lessard (research associate, UW Aquatic & Fishery Sciences, Seattle) and Chris Costello (faculty, UC Santa Barbara) attended the initial meeting of this committee on 4 July 2005 at King Salmon.

Consequences of Gillnet Scarring on Sockeye Salmon Escaped to Natal Streams

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

Most sockeye in Bristol Bay are caught in gillnets (76% drift gillnet; 24% set gillnet). Gillnets hang in mid-water, allowing fish to move partially through before becoming entangled at the gills or midsection. Although most of these fish are landed by the gillnet boat, some drop out of the nets or successfully fight their way through the net and escape to continue their migration to spawning areas, often with some degree of scarring. No estimates exist on the incidence of entangled fish that escape nets, successfully migrate to natal streams, or successfully spawn. While the impact of including mortality of gillnet-scarred fish in escapement numbers is addressed implicitly in spawner–recruitment predictions, it has not been explicitly considered or investigated. If scarring incidence varies from year to year, it could be relevant to establishing escapement targets; whether the scarring has size- or sex-selective bias is also an important management consideration.

This study sought to (1) estimate the incidence of scarred fish among those spawning adults that successfully migrated from the fishery to natal streams, and (2) determine the severity of scarring and its relative effect on spawning success.

Methods

During July and August 2005, beach seines were conducted at Pick, Elva, and Hidden creeks to estimate incidence of scarring, and a more intensive tagging study was conducted at Pick Creek to monitor the mortality rate of scarred fish over time and their presence and longevity in the stream as a proxy for spawning success. We chose Pick Creek owing to relatively shallow water and steady flows (which allowed good visibility for sighting fish), the broad and rocky beach at its mouth (which was suited to beach seining and tagging), and its close proximity to the camp. Sampling occurred on three consecutive days in mid-July, including nine beach seines; we sampled roughly 2,000 fish to record incidence of scarring in the population as a whole. Fish from a subset of these samples—100 scarred and 100 un-scarred (control)—were tagged with individually coded 3-cm Peterson disk tags. Each fish was anaesthetized, photographed, and measured for body length (mid-eye to end of hypural plate), body depth (anterior of dorsal fin to bottom of abdomen), and nose length (tip of upper jaw to mid-eye). Observations were conducted by four people walking the entire length of Pick Creek during the first five consecutive days following tagging, and then every other day throughout the lifespan of the fish (July 17–August 25).

Results

Incidence of scarring was found to be roughly 10% of those fish schooling at the mouth of Pick Creek. This percentage was also supported by evidence from Hidden and Elva creeks. Degree of scarring was categorized according to three ratings (minor, moderate, severe). The number of fish observed in each category was unevenly distributed, with 45%, 35%, and 20% minor, moderate, and severe scarring, respectively. In both males and females, the average length and depth of fish was slightly greater among scarred fish relative to un-scarred fish. In males, the depth (relative to length) and nose length (relative to length) was reduced in severely scarred fish, indicating inhibition of the development of secondary sexual characteristics in males (Fig. 2).

In terms of the stream life of scarred fish (proxy for spawning success), virtually all un-scarred fish (98%) were observed at least once over the sampling period. Most fish with minor scarring were observed, but they entered the stream at a later date, possibly because of delayed sexual maturity. Scarred fish generally demonstrated delayed morphological changes related to sexual maturity, possibly as a result of scar-related stress. Less than half (47%) of fish with moderate scarring were ever sighted again and very few (5%) severely scarred fish were sighted again after release (Fig. 3). The frequency of post-release sighting followed a similar trend (Fig. 4).

The most interesting finding was that fungus appears to be the main driver of mortality, explaining 68% of the variation in whether a given fish was resighted. In fact, whether a fish was infected with fungus was a better predictor of probability of resighting than the degree of scarring (Fig. 5). The fungus responsible for these infections, *Saprolegnia* spp., is the main genus of water molds responsible for fungal infections in the freshwater environment (Noga 1996). While present in almost all freshwater systems in Alaska, *Saprolegnia* spp. generally causes infections in adult salmon only when the fish are severely stressed or have a compromised epidermis, as in the case

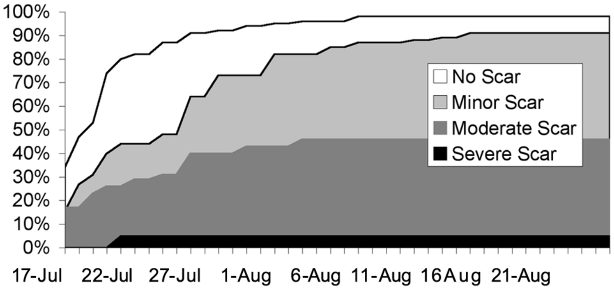


Figure 3. Percentage of fish resighted after release (overlay of each category of scarring).

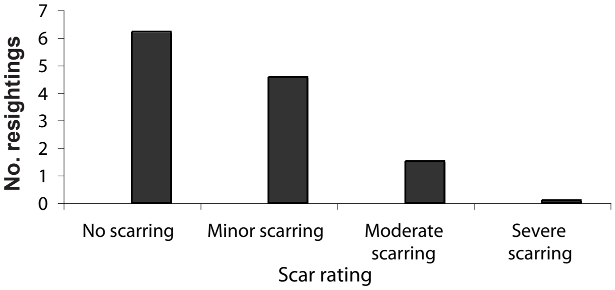


Figure 4. Frequency of resighting by scar rating.

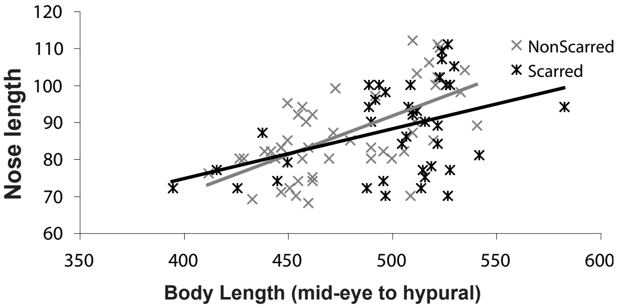


Figure 2. Development of male sexual characteristics.

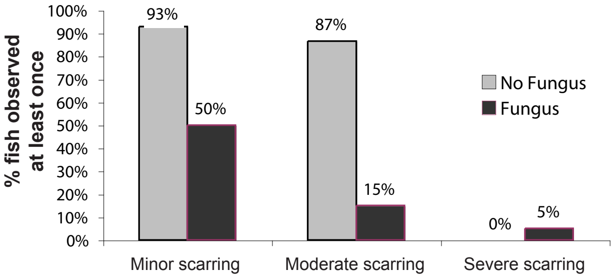


Figure 5. Impact of fungus on mortality of scarred fish.

of fish subject to gillnet scarring (Snieszko 1974, Neish 1977, Pickering 1994, Bruno and Wood 1999).

Future research in this area will include the following activities:

- repeat sampling over multiple years to determine whether incidence of scarring is constant or varies with run size throughout a range of creeks in the Wood River system,
- analysis of whether the morphology of scarred fish represents the morphological trends of individual creeks, and
- analysis of dropout rates in the fishery to provide estimates of the percentage of fish scarred by the fishery and the percentage that reach natal streams.

Fishery Selection on Length and Age at Maturity for Sockeye Salmon in the Wood River Lakes System, Bristol Bay, Alaska

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

Fishing gear, specifically gillnets, selectively removes certain individuals within a population and can affect life-history traits such as both size and age at maturity due to size- and age-specific exploitation. A commercially valuable sockeye salmon gillnet fishery has operated in the Wood River system of Bristol Bay, southwest Alaska, for over 100 years. This fishery is selective for size and age of sockeye based on mesh size and the timing of the fishery. In addition, fishing pressure and effort has varied greatly year-to-year owing to run-size fluctuations and evolving fishing techniques and technology. In this research, we are investigating whether and how the gillnet fishery gear selectivity has affected length and age at maturity of the Wood River sockeye salmon populations.

The life-history patterns—age and size at maturity, and size at age of sockeye—will be investigated in the lake system as a whole as well as in individual spawning populations within the system. This work entails two components:

1. review size- and age-selective fishing of Wood River system sockeye based upon over 50 years of data collected by the University of Washington and the Alaska Department of Fish and Game, and
2. assess population-specific fishery exploitation and model the effects of fishing on different life-history traits shown by the different spawning populations.

Bristol Bay has the greatest abundance and diversity of sockeye salmon in the world. The Wood River system is home to dozens of genetically and ecologically different sockeye spawning 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.

Because of mesh size and fishery timing, gillnets are highly selective on larger, 3-ocean sockeye of both sexes (Burgner 1964). Smaller fish are subject to lower fishing pressure as they can slip through the gillnet openings (Bue 1986, Hamon et al. 2000). As a result, certain fish passing through the fishery are more heavily selected than are others. Wood River system sockeye passing through the fishery are bound for different spawning localities, including streams, rivers, and beaches. Despite year-to-year fluctuations in fish size and age composition within populations, most still exhibit consistent composition differences from other populations (Burgner 1964). Because of these differences in the various spawning populations, fishing pressure is not uniform on individual runs destined for the different spawning localities. Certain populations may be more or less affected by the fishery, having more or fewer members removed.

While researchers have examined life-history traits of the Wood River system sockeye in other studies, a system-wide assessment is lacking and the effects of the fishery on the system as a whole have not been evaluated. We will compare fishery catch and escapement length and age data with similar data collected on the sockeye spawning grounds within the Wood River system. Long-term patterns of sockeye size and age at maturity and size at age will be examined. Also, trends between fishery harvest rate and spawning population numbers will be explored. This research aims to assess if and how fishery selectivity affects biocomplexity within the Wood River sockeye salmon populations. Finally, fishing technology and management tools and techniques, including fishery opening schedules and gillnet regulations, will be evaluated for their effects on fishery selectivity and thus on life-history traits and sustainable fishery yields. By applying this analysis, greater understanding of fishery selectivity and its past and potential future effects on Wood River system spawning populations can be accomplished.

Using Otolith Microchemistry to Determine Origins, Movement Patterns, and Habitat Preference of Sockeye Salmon Fry in Lakes Clark and Iliamna, Bristol Bay, Alaska

Scientists and fishery managers seek to better understand life-history traits and factors influencing the movement, rearing conditions, and survival of sockeye salmon fry in streams and lakes. Properties of freshwater lakes where sockeye fry rear are directly related to and affect survival at sea. Despite the importance of the fry stage, little information about salmon fry movements in rearing lakes and habitat preference is available for some watersheds, including lakes Clark and Iliamna in the Kvichak watershed of Bristol Bay, southwest Alaska. This project will use otolith microchemistry to better understand the environmental life history and movements of sockeye salmon of these two lakes.

Sockeye salmon fry rear in freshwater lakes, and different habitats may be more conducive to fry survival. The fry may move between lakes during their freshwater residence or remain in one lake until commencing with their migration to the ocean. Understanding salmon fry movement patterns and differentiating among individual fish has been limited by the availability of consistent, informative assessment tools. Otolith microchemistry can facilitate better understanding of habitats and movements of many fishes, including salmon. Otolith strontium isotope ratios ($^{87}Sr/^{86}Sr$) are influenced by the underlying geology surrounding the water in which the fish live and are analyzed by laser ablation–ion-coupled plasma mass spectrometry (LA–ICPMS).

In the Kvichak watershed, Lake Clark lies to the north and drains into Lake Iliamna (Fig. 6). The two lakes have vastly contrasting geology, suggesting that they have different Sr isotope signals. Sockeye salmon spawn throughout both lakes, and those who spawn in Lake Clark must migrate through Lake Iliamna as fry and adults. Scientists have been unable to discriminate Clark versus Iliamna sockeye using genetic information. In addition, whether sockeye that spawned in Lake Clark tributaries rear there or in Lake Iliamna is unclear. Clark sockeye could also rear in both lakes, spending differing amounts of time in each. Finally, we lack a method to know if a returning adult sockeye caught before it reaches its spawning ground is headed for Lake Clark or Iliamna. Our research seeks to answer these questions.

In this study, we examined the microchemistry of adult sockeye salmon otoliths. $^{87}Sr/^{86}Sr$ ratios of otoliths from five fish spawning in four populations, two each in Lakes Iliamna and Clark, were determined. The otoliths were laser ablated along the diameter of their interior freshwater regions to determine the Sr isotope ratios at different time periods in the fry life-history stage (Fig. 7). The interior core of the otolith corresponds with the embryonic phase, and outwards of this the otolith Sr isotope ratio is influenced by that of its surrounding lake water (Fig. 8). Lab results are being analyzed to understand how to best differentiate fish from the different populations.

Lake water samples from these spawning populations show significantly different Sr isotope ratios (Table 3). The Lake Clark sample differs from the Woody Island

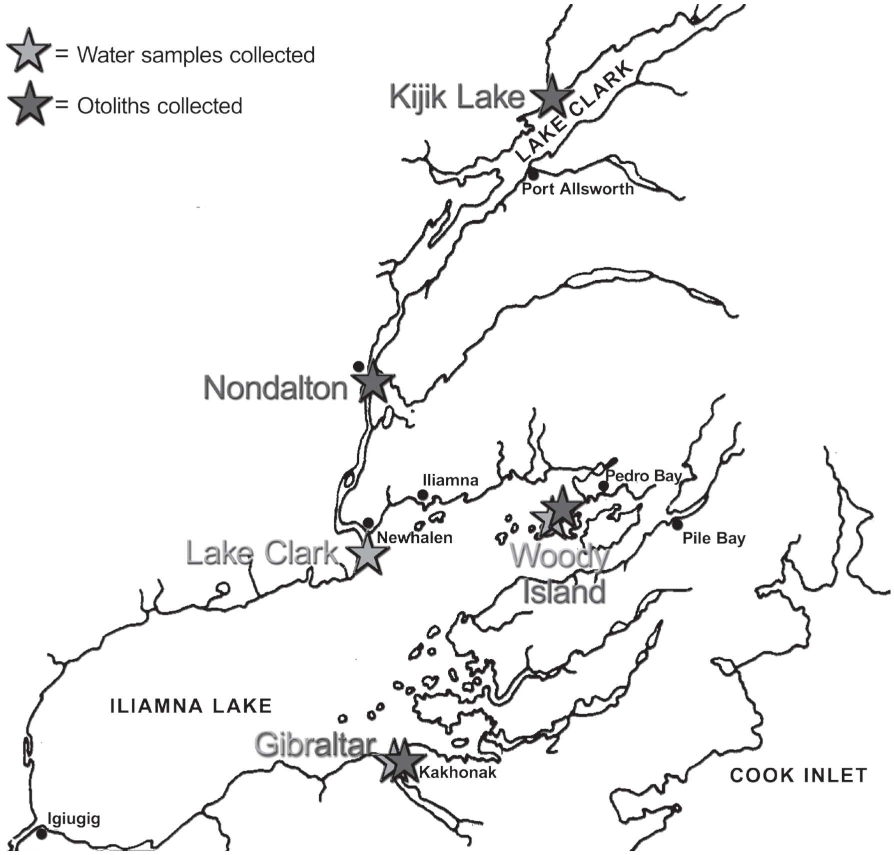


Figure 6. Map of lakes Clark and Iliamna and the four populations from which sockeye salmon otoliths were analyzed.

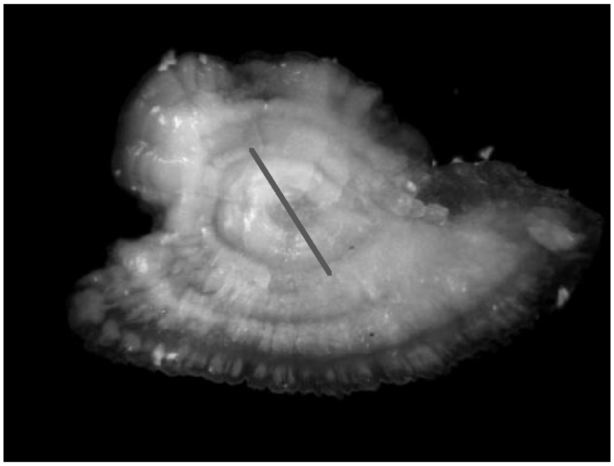


Figure 7. Otolith from a sockeye salmon that spent 1 year in freshwater and 3 years in the ocean. Each dark band indicates a year in the fish's life. The gray line indicates the path of the laser ablation where the otolith material was analyzed for its $^{87}Sr/^{86}Sr$ ratio.

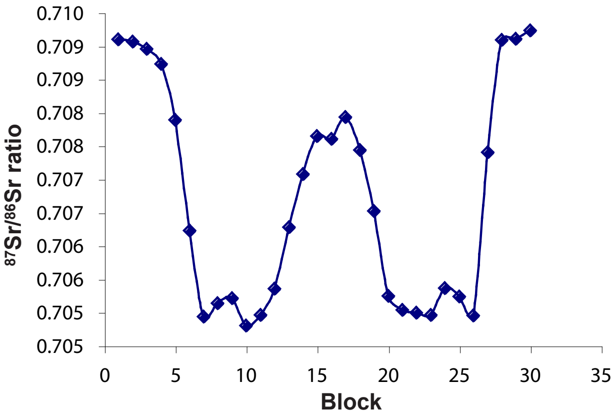


Figure 8. Graph showing the $^{87}Sr/^{86}Sr$ ratio of the freshwater region of a sockeye salmon otolith, corresponding with the line in Figure 2. The fish spawned at Gibraltar River, a tributary of Lake Iliamna. The $^{87}Sr/^{86}Sr$ ratio of saltwater is 0.7092 while that of freshwater is significantly less and is more variable, depending on the geology surrounding the water. The increased Sr ratio around block 15 corresponds with the embryonic period of the salmon fry. Blocks correspond with time periods in the life of the fish. Because the speed of ablation varies, each block corresponds to a different time period.

sample by four times the analytical error while the Gibraltar sample is very differvent from the other two samples. This suggests that Lake Gibraltar drains a watershed with different bedrock than Lake Clark and other parts of Lake Iliamna. We have not yet been able to differentiate Gibraltar otoliths, but the lake water results suggest that they may show different Sr ratios, at least in the most interior freshwater region.

Analysis will yield information that can help scientists understand what habitat attributes are important for salmon fry survival, and differentiate between Lake Clark and Iliamna adult sockeye, which will help to focus conservation goals and improve ecosystem and fishery management.

Table 3. Lake water Sr isotope results. Sr isotope compositions normalized to $^{86}Sr/^{88}Sr=0.1194$. NBS 987 average $^{87}Sr/^{86}Sr = 0.71023$. External 2σ reproducibility for $^{87}Sr/^{86}Sr$ is ±25 ppm.

Sample	$^{87}Sr/^{86}Sr$
Lake Clark	0.704586
Lake Iliamna—Woody Island	0.704505
Lake Iliamna—Gibraltar	0.704231

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 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. Further research is planned to investigate the possible variation in timing among populations within a given system (i.e., Wood River), and study other salmon fisheries that are selective on timing.

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. 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. Efforts to study processes on the spawning grounds have 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.

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. in press). 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 2005, we also studied the ecology of juvenile sockeye salmon in lakes Aleknagik (Schindler et al. 2005a), Iliamna, 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 both 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, 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 (Appendix A). Historically, these surveys were integrated across all small stream habitat and were sub-sampled with index reaches on the larger streams. 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.

With few notable exceptions, between 2003-2005, creek surveys showed no remarkable departures from the patterns observed over the last few decades within the Wood River system. Creeks along the north shore of the north arm of Lake Nerka (Sam and Joe creeks; see Wood River maps, pp. 38-39) had particularly strong returns in 2004–05 (i.e., >5X the long-term mean). Fenno Creek was also particularly strong the last 2 years (>3X the long-term mean). These three creeks have run timings that are relatively early compared with the run timing of other populations throughout Lake Nerka. Similarly, several of the "early" Lake Aleknagik populations were especially abundant in 2004–05, with Happy, Yako, and Ice creeks all showing very strong runs.

In the Nerka system, old beaver dams on Teal Creek and Kema Creek were washed out in 2005, allowing access to substantial amounts of spawning habitat (several kilometers) in each of these systems that had been unused during most of the last decade.

The age composition of spawners in the Wood River system was dominated by 1.2 fish, followed by 1.3 fish in 2003–2005, as in previous years (Appendix B). In general, 1.2 fish returned to smaller creeks and 1.3 fish to larger creeks, rivers, and beaches as expected. In 2004, the return was especially rich in 1.2 fish across the entire system.

Proportions of males that were jacks (i.e., 1.1 age fish) in Wood River spawning sites have been highly variable in the last 3 years, with some exceptional contributions in particular sites and years. For instance, in Lynx Creek in 2003, 46% of the males were jacks. Similarly, 9% of the males were jacks in Fenno Creek in 2003. In 2004, there were very large returns of 1.2 fish to these two creeks. In 2005, many creeks in the Wood River system had exceptionally high proportions of jacks. In particular, >10% of the males in Eagle, Mission, Hansen, and Whitefish creeks of Lake Aleknagik were jacks in 2005. In the Nerka system, >5% of the males were jacks in Elva, Pike, Stovall, and Teal creeks in 2005. These high jack proportions suggest that there should be strong 1.2 returns to these creeks in 2006 (Appendix B).

In 2005, in collaboration with ADFG, we resumed aerial surveys of the Wood River system (conducted between August 15 and 18) to enumerate spawning populations on beaches and in rivers. They were last done in 1998 by ADFG. Using the aerial survey data and the foot survey data of smaller streams (described previously), we counted a total of 247,748 sockeye salmon, which is 17% of the total Wood River system escapement estimated at the Wood River counting towers by ADFG. The 2005 survey dates were early for some spawning areas, including some large rivers (e.g., Agulukpak) and many of the beaches in the system. Thus, for 2006 we are hesitant to expand the survey numbers to project the total adult sockeye estimate by spawning site for the entire system, as has been done in the past. We intend to generate estimates of adult spawners by spawning site for the Wood River system in 2006 by using the aerial survey data mixed with the ground survey data.

This coming season we will, in conjunction with ADFG, again conduct aerial surveys that take counts by spawning site in mid to late August. In addition, we will conduct an abbreviated set of aerial surveys to verify original estimates of major spawning sites (e.g., larger rivers connecting the lakes) and to get better estimates for some of the spawning sites that have later spawning populations. The major rivers in the system serve not only as major spawning sites, but as migratory pathways for adult salmon that spawn higher up in the watershed.

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 2005; therefore, our observations on the distribution of the escapement of 2.3 million fish in 2005 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. In addition to these sites, we also obtained samples from Dream Creek, and because of the low number of island beach spawners, we expanded our surveys to include Cottonwood Point and Porcupine Island to round out this year's sampling. 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. Additionally we were able to obtain a sample of late-spawning beach fish from Knutson Bay in October. Interestingly, this sample revealed a large proportion of age 1.1 males, or "jacks" (Appendix B).

In general, the salmon were predominately 3-ocean fish as can be seen notably in Dream Creek, Gibraltar Creek, the Pedro ponds and throughout the island beach populations. Copper River and Dream and Gibraltar creeks also had moderate proportions of age 2.2 fish present (Appendix B). Also, most fish continue to be 1-freshwater age individuals, reflecting the dominance of 1-check individuals in the smolt migration in the last decade.

Hansen Creek Daily Runs and Bear Predation

H Rich (graduate student), T Quinn (adviser)

Hansen Creek is a small tributary to Lake Aleknagik. In 2005, we completed the 16th year of the ongoing study of bear and spawning sockeye salmon interactions (Table 4). In 2005, the run to Hansen Creek of 3,928 was similar to the 3,467 spawners seen in the 2-km creek in 2004, but both years were markedly less than the 2003 peak year of 11,162. This creek now shows a clear, 4-yr cycle, having had large peak runs in 1987, 1991, 1995, 1999, and 2003. Additionally, larger than average returns of jacks to Hansen Creek occurred in 1998 and 2002 ("pre-peak" years in the cycle), constituting 3.5% and 2.8% of the males, respectively. The long-term average of males that are jacks is 1.7% in Hansen Creek. The record number of jacks that returned in 2005 was unusual in that they made up such a large percentage of the males (33.8%), and this was not a pre-peak cycle year, so the high prevalence was unexpected. The exceedingly high density of jacks in Hansen Creek was paralleled by high levels of jacks throughout the Wood River system for 2005, presumably reflecting improved growth conditions in the marine environment.

Predation rate is density-dependent on an interannual basis, and the rate in 2005 was about 35% (run size of 3,900), consistent with the trend (Fig. 9). 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. These 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 (Figs. 10 and 11).

Larger rivers have more 3-ocean fish and fewer jacks. The fish are more deep-bodied for their size than the

Table 4. Salmon killed by bears, by sex and section in Hansen Creek 2005. Note: jacks are excluded.

Section	Status	Female	Male
Mouth	Bear	28	26
	Other	217	201
Lower	Bear	257	140
	Other	371	102
Middle	Bear	188	105
	Other	144	101
Pond	Bear	1	3
	Other	75	51
Upper	Bear	223	164
	Other	482	391
	Total Bear:	697	438
	Total Other:	1,289	846
	Total:	1,986	1,284

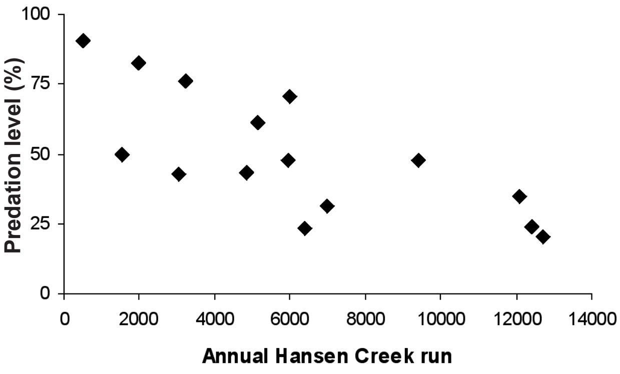


Figure 9. Effect of spawning run size on the kill rate by bears in Hansen Creek. From Rogers et al. 2003.

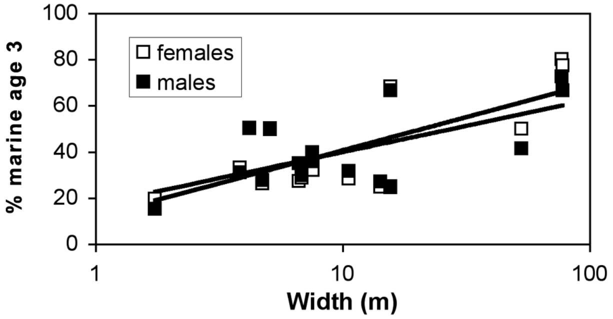


Figure 10. Relationship between the natural log of stream width (ln(stream width)) and the percentage of adult sockeye salmon that spent 3 years at sea for 16 populations in the Wood River system (males, $r^2 = 0.38$; females, $r^2 = 0.45$). From Quinn et al. 2001.

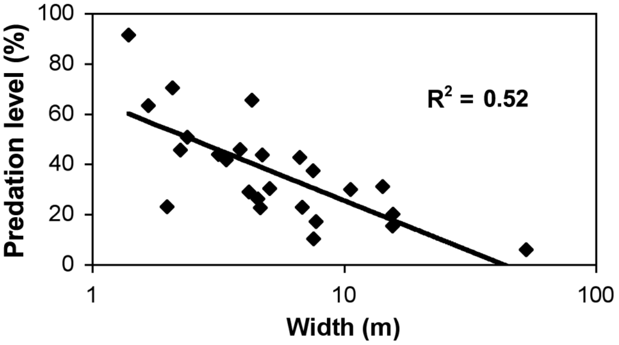


Figure 11. Relationship between the natural log of stream width (ln(stream width)) and the level of predation by bears on sockeye salmon. From Quinn et al. 2001.

fish in smaller creeks and there are higher levels of size-selective predation. The level of predation among creeks is thus related to fish density. Higher levels of escapement are associated with smaller percentages of the fish being killed as the absolute number killed reaches an asymptote. Not only does the level of predation vary among creeks as a function of size but also the proportion killed before they reproduce also varies. Hansen Creek sockeye are not only more vulnerable to bears than those in Pick Creek but they are killed earlier in their stream lives (Quinn et al. 2001b, Gende et al. 2004), and this fact determines the influence of predation on actual population dynamics.

The daily counts on Hansen Creek are not only important for predation studies; they also provide percentage estimates of the total number of spawners counted on a single “peak survey” date. This provides a means of adjusting annual survey counts to equal the true number of spawners, which comprises the cumulative dead plus live fish on the last day of the run. Hansen Creek has been surveyed most often on August 6 in past years, but in 20% of the years, the survey was done on August 1 or earlier. The Hansen Creek sockeye are among the earliest spawners in the lake system: fish usually enter the creek around July 20th and the run dwindles by mid to late August. On the basis of the daily counts, we can determine that if the surveys had all been conducted on August 6, the counts would have been 67% to 93% of the total; if all surveys were done on August 1, the counts would have been 38% to 78% of the actual number of spawners.

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

T Quinn, D Eggers (ADFG), J Clark (ADFG), H Rich, Jr. (graduate student)

In 2004 and 2005, exceptionally large runs of sockeye salmon to the Alagnak River system in Bristol Bay, Alaska coincided with weak runs to the nearby Kvichak River system. Protection of the Kvichak populations necessitated severe restrictions on fishing, resulting in densities on the Alagnak River system’s spawning grounds that were 6 to 7.6-fold above the long-term average. We examined carcasses of female salmon from four populations in this system to determine the extent to which egg retention might contribute to density dependent reduction in per capita production. We also collected comparable data on seven populations from the Kvichak River system and nine from the Wood River, where the runs did not appreciably exceed the escapement goals. We estimated that 23% and 44% of the potential egg deposition was lost to pre-spawning mortality or incomplete spawning in 2004 and 2005, respectively, in the Alagnak populations. These levels of egg retentions were much higher than observed in spawning populations in the Kvichak and Wood River Systems, where spawning densities were near normal. In 2005 significantly higher levels of egg retentions were observed in the Alagnak River system under lower escapement densities than occurred in 2004 indicating the occurrence of environmental and, likely, density-independent variation in pre-spawning mortality in these sockeye salmon populations.

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. 44), and Stephanie Carlson has been using the data in her analysis of senescence rates (this page). A major 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 to calculate several factors that are 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 the complete genetic sampling in 2004 and 2005. The offspring from 2003 spawning will return in 2007 and 2008.

While 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—bear predation was practically non-existent for the first 3 weeks of the run in 2005, providing excellent data on life-span of the fish in the absence of predation. Prior to 2004, there was a beaver dam on C Creek about 200 m from the lake. This dam broke down prior to the 2004 season and, in 2004 and 2005, we saw fish colonize the area above the dam, providing excellent data on how quickly new habitats are colonized. Figure 12 shows the number of fish entering, and the number of fish still alive in A and C creeks for 2005.

Effects of Bear Predation on the Evolution of Sockeye Salmon

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

Phenotypic diversity among populations may evolve as a result of population-specific differences in natural selection or sexual selection—which affect survival and reproductive success, respectively—or a compromise between the two selective pressures. One focus in our salmon behavior and ecology research involves exploring the importance of bear predation as a selective force leading to the diversification of salmon populations. Specifically, we are using a combination of modeling and field studies to better understand the role of bear predation as an agent of selection. For the field component, data were collected to estimate the factors influencing the breeding lifespan, breeding opportunities, size, and shape of sockeye salmon that spawn in different habitats subject to varying predation pressure by brown bears. These traits were measured in a suite of populations in the Wood River Lakes system that experience dissimilar predation intensities but other-

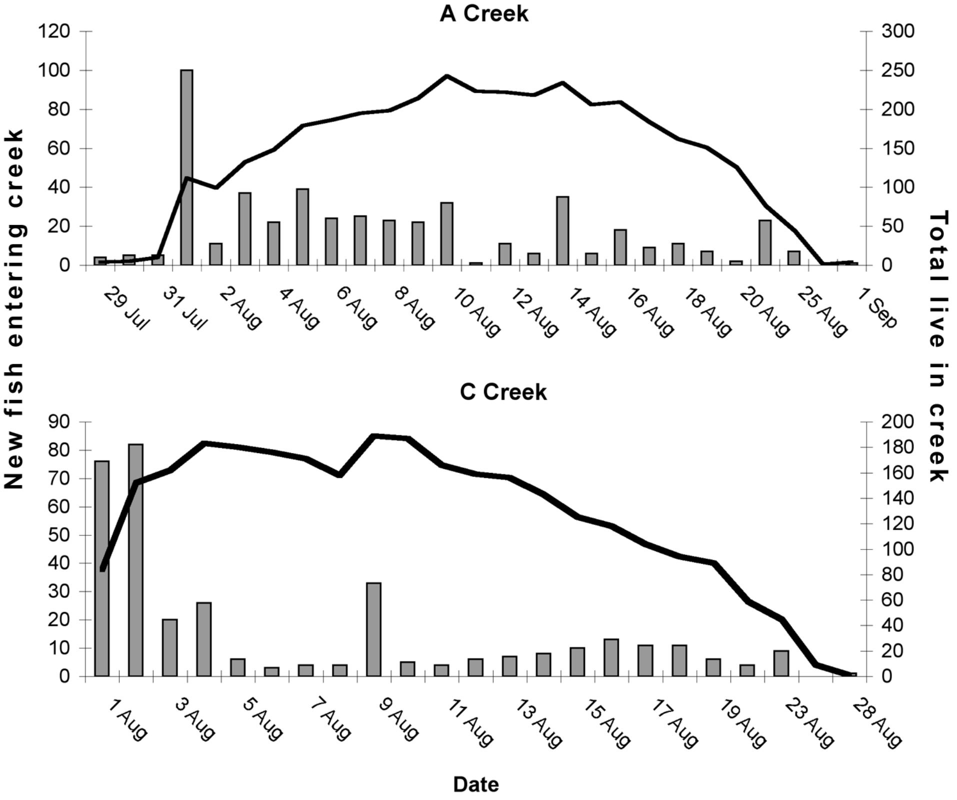


Figure 12. Number of fish entering (vertical bars) and still alive (line) in A and C creeks, Little Togiak Lake, for 2005.

wise experience similar conditions (e.g., climate, migration timing, and migration distance).

Evolutionary theory posits that populations experiencing different rates of extrinsic mortality should evolve different rates of senescence. In particular, populations experiencing higher rates of extrinsic mortality should senesce more rapidly. The generality of this prediction has been recently questioned because condition-dependent susceptibility to extrinsic mortality may favor slower senescence. We specifically assessed the relative importance of predation rate per se versus the magnitude of condition-dependence in this mortality. Results demonstrated that the evolution of senescence in this system is driven by condition-dependent mortality (the extent to which bears kill newly arrived, energy-rich salmon that show little senescence) rather than the overall rate of extrinsic mortality (percent of salmon killed by bears). The study therefore demonstrates the importance of covariance between individual condition and susceptibility to extrinsic mortality in the evolution of senescence rates in natural populations. We have prepared a manuscript focusing on this work, which we plan to publish in a peer-reviewed scientific journal.

The evolutionary effect of the bear predation on size and shape of salmon populations depends on the extent to which breeding opportunities are curtailed and the relationship between lost opportunities and heritable, phenotypic traits. Whether predation and sexual selection actually oppose each other in salmon populations remains unknown. Sampling multiple populations subject to a range of predation pressures made it possible to examine the balance between natural selection (in the form of bear predation) and sexual selection (in the form of female choice, or male–male competition, or both) as a function of local breeding environment. Our results suggest that predation substantially reduces the breeding opportunities of the salmon killed by bears (i.e., bears are not simply scavenging senescent carcasses, but recently arrived fish, too). Moreover, the population experiencing the highest level of predation was also the population with the strongest selection acting against large size and deep bodies (sexually selected traits). Preliminary analysis of the data is underway, and a manuscript will be submitted for peer-review publication.

Recently, work has involved exploring the evolution of body size using a theoretical model developed by Dr. Ray Hilborn. The basic model relies on standard quantitative genetic equations to predict evolutionary change in a trait based on the heritability of the trait and the selection differential. Our first assumption is that breeding salmon are subject to two sequential episodes of selection: first in the form of bear predation and second in the form of mate choice. The selection differential is then calculated as the difference between the average trait value after the two episodes of selection and the average trait value before selection. A sensitivity analysis is being conducted to determine which of the parameters describing the two episodes of selection is having the strongest impact on the evolution of length. For six populations in the Wood River Lakes system, we have established the relationship between the probability of being killed by bears and body length based on information collected on tagged fish. This information, combined with the current length distribution data, will allow us to back-calculate the relationship between reproductive success and body size in these six populations.

This study is important because it brings together fundamental principles of evolutionary ecology and the biodiversity of Pacific salmon. It also provides support for the emerging perspective that the stability of population-complexes and species depends on having many populations that are adapted to different physical habitats. Moreover, the various project components all highlight the importance of bears as a selective force in shaping salmon life history and morphology.

Correlations Between Pink and Chum Salmon Occurrence, Physical Habitat Characteristics, and Sockeye Salmon Densities in the Wood River Watershed, Alaska

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

Salmonids can quickly colonize new habitats and establish populations (Milner and York 1989, Hendry et al. 2003). But the key factors that determine salmonid colonization and recolonization rates after blockages are removed are not well understood. One hypothesis suggests that straying and the establishment of a salmonid population is related to the compatibility between specific life-history adaptations and 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 long-term spatio–temporal correlations between adult pink and chum salmon occurrence, physical habitat characteristics, and adult sockeye densities in the Wood River watershed, 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 nearest.

Our objective is to conduct descriptive (e.g., scatter-plots) and statistical analyses (e.g., analysis of variance and linear regression) using existing, long-term Wood River spawning ground survey data to determine where and what variables correlate with pink and chum salmon occurrence in streams of the Wood River system. Results interpretation will be based on the outcome of the statistical results and comparison with the literature on geomorphology and salmon behavior and preferences. Our goal is to further our understanding of how pink and chum habitat preferences and competition with numerous sockeye affect their success to colonize new habitats. This analysis will have implications for the more applied questions of what, where, and why salmon will colonize newly opened habitats when artificial barriers are removed.

We propose to examine pink and chum salmon occurrence as a potential indicator of salmon colonists because their 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 40 years by the Alaska Salmon Program. Sockeye salmon densities will be investigated in relation to pink and chum as an indicator of competition because they have the largest distribution and abundance in these streams. 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 which influence salmon populations, such as climate variability (Hilborn et al. 2003). Last, the Wood River has a diversity of stream and habitat types that lend well to the comparison of salmon occurrence among streams (T. Quinn, Univ. Washington, Seattle, pers. comm.).

This analysis will allow us to gain a preliminary understanding of the relative importance and interaction of variables such as habitat condition, competition, and population source, that lead to natural salmon colonization in a pristine setting. The combination of multiple reference-habitat locations and relatively unaltered salmon populations to answer questions related to salmon colonization, and salmon issues in general, is unique. The only other similar studies were conducted in southeast Alaska (Milner and York 1989). In addition, no other study has the combination of pristine conditions and a long-term fish dataset. Thus, the analysis will allow us to understand how natural salmon colonization occurs over time and in multiple settings. 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 summer of 2005, we collected habitat data on 20 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 20 streams had three to four sections measured that ranged in length between 50 and 300 m. The data will be (1) compared with other habitat surveys completed in the 1950s and 1960s to identify how the streams have changed, and (2) used to identify what characteristics correspond with the occurrence of other species besides sockeye, including pink and chum salmon. Data will also be collected for an additional 10 streams in 2006.

Preliminary results indicate that a wide range of stream habitat characteristics exist for salmonids in the Wood River system (Table 5). Bankfull width (m), a surrogate for stream power, ranges between 2.5 and 25 m, while stream channel gradients range 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 reveal that drainage area (km^2) may be an important factor in developing suitable habitat for species besides sockeye (Fig. 13). Pink and chum 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. Future research will involve both a more in-depth analysis of these preliminary results, and investigations of other hypotheses related to competition and population source

Temporal Coherence and Fine-Scale Biocomplexity in the Sockeye Salmon Stock Complex of Bristol Bay, Alaska

L Rogers (graduate student), 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 booming sockeye salmon populations during positive phases of the PDO, and diminished sockeye productivity during negative phases. However, at finer spatial scales, the response of sockeye to climate change has not been uniform across rivers, or even among neighboring creeks within watersheds (Hilborn et al. 2003, Rogers and Schindler 2005). 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. However,

Table 5. Habitat characteristics of streams entering (a) Lake Aleknagik and (b) Lake Nerka.

Creek	Bankfull width (m)	Bankfull depth (m)	Slope (%)	Wetted width (m)	Wetted depth (m)	% pool area	Cover type	Channel type
				A. Lake Aleknagik				
Eagle	2.9	0.5	1 to 2.0	1.2	0.2	27%	Grasses–cutbank	Pool–riffle
Hansen	5.5	0.5	<1.0	2.9	0.1	30%	Grasses	Pool–riffle
Ice	25.4	0.8	<1.0	10.8	0.4	51%	Veg–willow	Pool–riffle
Whitefish	5.2	0.5	1 to 2.0	3.4	0.3	30%	Grasses	Pool–riffle
Bear	6.0	0.5	< 1.0	3.0	0.3	38%	Grasses	Pool–riffle
Yako	6.1	0.7	1.5	3.3	0.3	21%	Gravel bar	Forced pool–riffle
Mission	3.0	0.4	< 1.0	1.7	0.1	50%	Grasses	Pool–riffle
Happy	10.1	0.5	1 to 2.0	4.2	0.3	34%	Grasses–cutbank	Forced pool–riffle
Sunshine	22.2	1.4	0.4	10.5	0.9	44%	Gravel bar	Pool–riffle
Youth	26.4	1.7	0.5	12.4	0.7	34%	Veg–mixed	Pool–riffle
				B. Lake Nerka				
Pick	11.2	0.7	0.6	6.4	0.5	34%	Veg–tundra	Pool–riffle
Little Togiak	17.3	1.3	0.5	7.1	0.7	37%	Veg–willow	Pool–riffle
A	2.5	0.5	1.8	1.3	0.1	13%	Veg–mixed	Plane–bed
C	5.0	0.7	1.1	1.6	0.1	29%	Veg–grasses	Pool–riffle
Little Togiak River	35.9	1.5	0.4	17.9	0.3	20%	Gravel bar	Pool–riffle
Elva	12.5	1.2	1.8	6.7	0.4	12%	Veg–wood	Step–pool/pool–riffle
Lynx	14.2	0.9	0.8	6.7	0.4	16%	Veg–mixed	Pool–riffle
N-4	6.0	0.4	4.2	4.1	0.1	50%	Veg–mixed	Step-pool
Kema	16.3	0.7	0.7	4.7	0.5	54%	Veg–mixed	Pool–riffle
Hidden Lake	6.3	0.7	0.7	4.1	0.2	50%	Veg–grasses	Forced pool–riffle

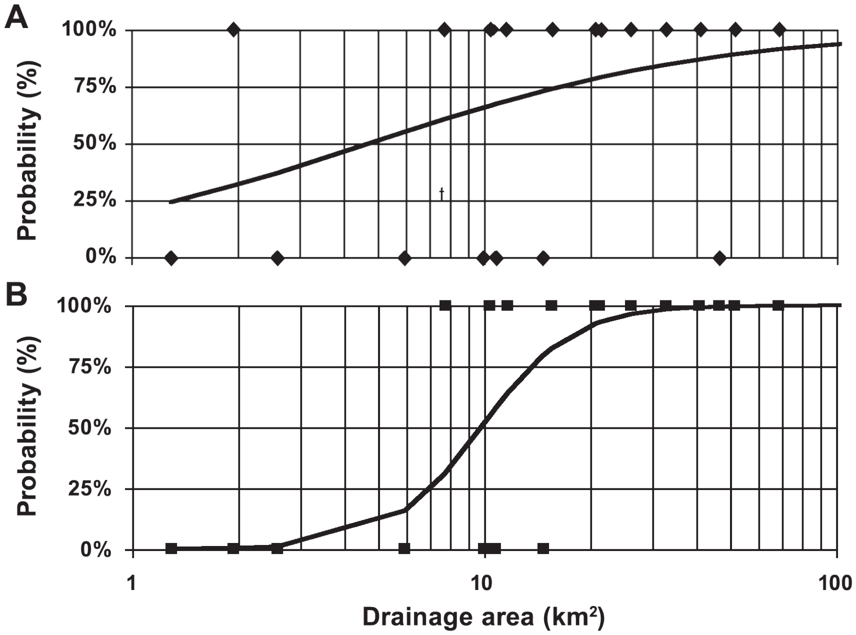


Figure 13. Logistic regression of probability of occurrence: (a) for pink salmon in streams entering lakes Aleknagik and Nerka; (b) for chum salmon in streams entering lakes Aleknagik and Nerka. ◆ and ■ = presence or absence for each stream for (a) and (b), respectively.

we do not understand the underlying drivers of these asynchronous population fluctuations. In this ongoing research, we are investigating how climatic variation affects sockeye salmon at different spatial and temporal scales, and we will explore whether geomorphic differences in the habitats used for spawning and rearing by sockeye result in asynchronous responses to climate among populations.

Patterns of covariation in productivity among fish populations have been used to investigate scales of common environmental or climatic forcing (Myers et al. 1997, Peterman et al. 1998, Meuter et al. 2002). Implicit in these studies is the idea that populations in close proximity to one another will be more synchronous than populations at greater distance because they experience similar environmental conditions. We have quantified patterns of covariation among populations at a fine scale—among creeks that are less than 50 km apart, feeding two lakes within the Wood River System of Bristol Bay, Alaska. We addressed the following questions: At the finest scale, how closely correlated are populations in terms of productivity? Is there spatial organization to trends in productivity? What is the role of common environmental effects (i.e., ocean conditions) versus processes occurring on a more local (lake, creek) scale? What can this tell us about processes affecting the survival and productivity of sockeye salmon?

To explore the patterns of productivity among populations of sockeye salmon, we analyzed 50 years of spawner survey data for nine creek populations within the Wood River System. The creeks included in this analysis were Bear, Happy, Hansen and Ice, which drain into Lake Aleknagik; and Fenno, Hidden Lake, Kema, Lynx and Pick, which drain into Lake Nerka (see maps, pp. 37-39). We calculated indices of productivity for each population based on reconstructed brood tables, and then computed correlations among populations. In addition, to look at the relationship between fine-scale and coarser-scale patterns in productivity, we calculated productivity indices for each of the nine major river systems that drain to Bristol Bay.

Results indicate that populations at a fine spatial scale are no more correlated in their productivity than populations aggregated at a course scale (Fig. 14). This is counter to expectations based on previous work suggesting that populations in closer proximity should be more coherent due to exposure to common climatic conditions (Meuter et al. 2002). Instead, even at these very fine scales, productivity is considerably incoherent in time, with correlations much less than 1.0. Further, populations in creeks within a single watershed have patterns of coherence that are organized by common nursery lake (Fig. 15). Correlations among creek populations that rear in the same lake are higher than among those that rear in different lakes.

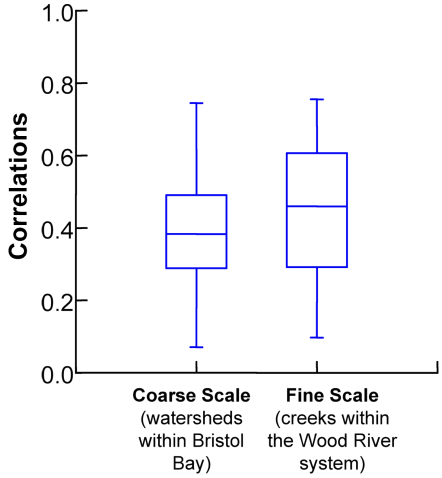


Figure 14. Boxplot showing the distribution of pairwise correlations among productivity indices of coarse-scale salmon populations within Bristol Bay (i.e. stocks from the Alagnak, Egegik, Igushik, Kvichak, Naknek, Nushagak, Togiak, Ugashik, and Wood River watersheds), and fine-scale creek populations within the Wood River System.

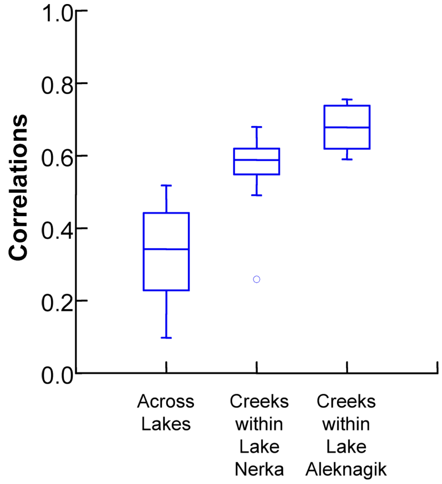


Figure 15. Boxplot showing the distribution of pairwise correlations among productivity indices of creek-scale salmon populations in the Wood River system, plotted by rearing lake.

These results suggest that populations spawning in different creeks within the same lake system are subject to common large-scale environmental conditions, such as ocean and lake conditions, but they do not respond uniformly to these common conditions. Local factors—such as stream morphology, habitat quality and availability—as well as diverse life-history strategies—such as different timing of migrations and age at maturity—are likely responsible for the variation in productivity between creek populations. This fine-scale variation may be important for the sustainability of the larger stock complex. Findings in this study emphasize the importance of maintaining diverse populations to ensure long-term fishery sustainability through environmental change.

Future research will build on these findings by expanding the analyses to include additional populations, and by incorporating habitat metrics to investigate patterns across habitat types. Statistical models will be used to determine whether habitat characteristics can explain variation in the responses of different populations to climatic conditions, thereby improving our understanding of sockeye salmon biocomplexity and the response of ecosystems to climatic change.

A Metapopulation Perspective for Pacific Salmon

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Funding: Belgian National Fund for Scientific Research

This study has been focused on conceptual research of a metapopulation perspective for anadromous salmonids. Sockeye salmon in Bristol Bay, a nearly unperturbed system, were used as a practical illustration of metapopulation concepts. A manuscript based on this work, and which elaborates on this report, is in progress.

The term "metapopulation" was coined more than three decades ago by Levins (1970) who defined it as a "population of populations which go extinct locally and recolonize." A new development in population dynamics research pertains to long-term persistence of a metapopulation, which cannot be explained only by the persistence of the local populations it comprises, but depends also on regional processes of (re)colonization and extinction. In other words, metapopulation dynamics depend on immigrations and emigrations, as population dynamics do on births and deaths: individuals (local populations) die but are replaced by new ones, and the population (metapopulation) persists far longer than any of its individual (local population). Currently, a metapopulation is broadly defined as a collection of local populations inhabiting discrete patches of suitable habitat, interacting through dispersal and persisting in a balance between stochastic extinctions and recolonizations. Studying metapopulations has been helpful in improving our understanding of the consequences of habitat fragmentation, as well as for designing conservation guidelines for species whose habitat is naturally or artificially fragmented (Hanski and Gilpin 1997, Hanski 1999 and references therein).

At first glance, the essence of the metapopulation concept seems to be particularly relevant to many species of salmonid fish. And yet, only a tiny fraction of the papers on conservation of salmonids list the keyword "metapopulation." To my best knowledge, few careful assessments exist on the existence of metapopulation dynamics in salmonids (e.g., Rieman and Dunham 2000), and nearly none on anadromous salmonids. Therefore, a conceptual summary of the processes leading to metapopulation dynamics, and an assessment of how they apply to anadromous salmonids, was warranted.

To satisfy to the concept of metapopulation, a network of habitat patches must meet three conditions (Fig. 16):

1. The local populations inhabit discrete habitat patches, well separated from the rest of the landscape, the latter being unsuitable for the species; otherwise, the delineation of habitat patches and populations is unclear and metapopulation theory is not applicable.
2. Some asynchrony in the dynamics across local populations occurs, making simultaneous stochastic extinction of all local populations very unlikely. With perfectly synchronized populations, metapopulation persistence is not higher than the persistence of any one of the local populations.
3. There is some amount of dispersal among habitat patches, allowing for (re)colonization of vacant suitable habitat patches.

The different life stages of anadromous salmonids occupy totally distinct biotopes. Reproduction is the key for defining the population concept (or local population or deme, depending on the context)—that is, a set of potentially interbreeding individuals (Berryman 2002). Therefore, the habitat associated directly with the delineation of anadromous salmonid populations is the spawning ground. Spawning habitat is clearly discrete: only some streams and lake beaches are suitable as spawning grounds.

Few studies have addressed the question of correlation of local population dynamics of anadromous salmonids. Local population dynamics of sockeye tend to be positively and uniformly correlated at the local and regional scales (a few hundreds of kilometers), but much less correlated at a larger scale (>1,000 km) (Peterman et al. 1998). Altogether, populations seem to fluctuate with enough asynchrony at each spatial scale to allow for metapopulation dynamics and to prevent the simultaneous extinction of a large number of populations.

The critical determinant of metapopulation dynamics is the existence and the magnitude of dispersal among local populations. Homing has been shown to be very strong and very precise in anadromous salmonids in general (Quinn 2005). Nevertheless, some individuals stray and spawn in another population. The frequency of such dispersal events is not well known, especially for wild populations, yet it does vary considerably between species, regions, and spatial scales (Quinn 1993, McElhany 2000). Nonetheless, given the large runs of many salmonid populations, even a tiny fraction of individuals straying

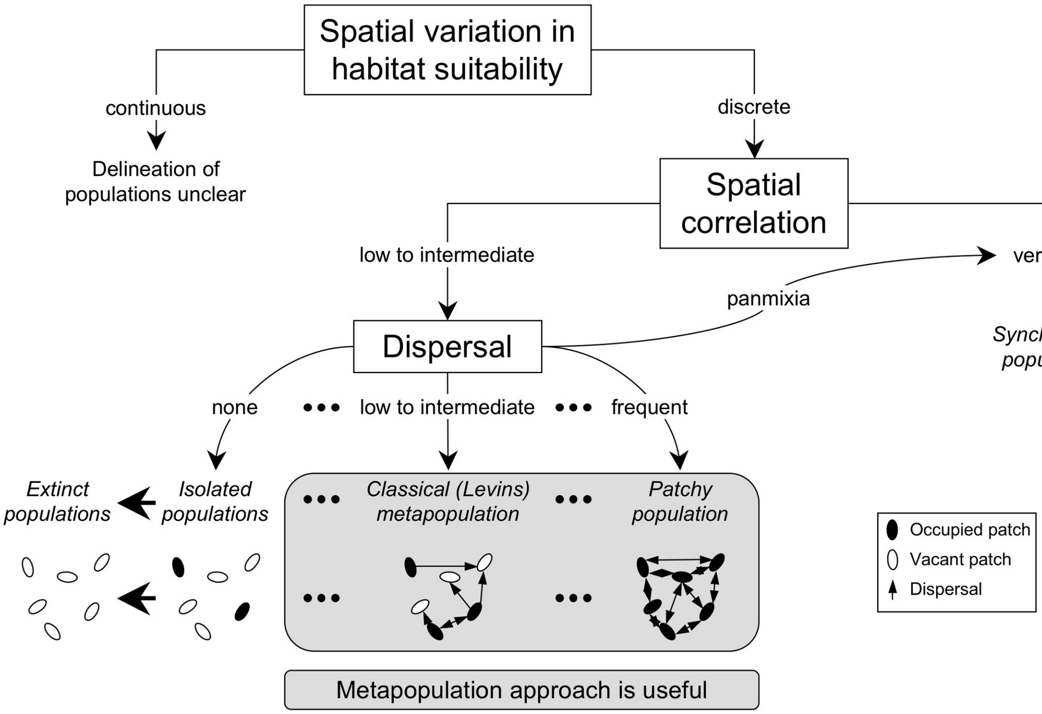


Figure 16. Schematic representation of the main conditions necessary for metapopulation theory to apply to a network of populations.

to adjacent rivers could be sufficient to recolonize suitable vacant habitats. Numerous examples of rapid natural recolonizations by salmonids have been observed in several species—for example, after glacial recession in southeast Alaska (Quinn 1993, Milner et al. 2000).

Anadromous salmonids seem to present life-history traits that are completely in agreement with the conditions for metapopulations to form and persist: a habitat fragmented into discrete patches, some asynchrony among the dynamics of the local populations, and dispersal events connecting populations (i.e., individuals returning to spawn in a population different from the one they hatched in). However, there will be large differences in this agreement to the metapopulation model between species, regions, and so forth. Specifically, human activities are likely to affect many aspects of salmon metapopulation dynamics.

In the near future, we will be addressing two questions regarding salmonids' likelihood to exhibit metapopulation dynamics:

- What are the main domains where a metapopulation perspective could improve a practical understanding of salmonid dynamics and the design of conservation guidelines?
- What main parameters/processes must be estimated in finer detail to allow the development of quantitative models of metapopulation dynamics and viability?

Lake Ecosystems and Nutrients

Introduction

We have continued monitoring environmental and limnological conditions in several lakes of the Wood River system and in Lake Iliamna. 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 major 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 diversity 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 addition to maintaining our routine environmental and limnological monitoring, we have initiated new paleolimnological research to reconstruct historical sockeye salmon escapement densities over the last several centuries. This research will enable 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 continues to experience warming climatic conditions and these changes are noticeable in our long-term records for the spawning and nursery lakes of the Wood River system and Lake Iliamna. Climate warming has been especially pronounced during the spring months. The springs of 2002–2005 were substantially milder than average as is reflected by the timing of spring ice break up 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. Statistical time-series analyses of the long-term changes in spring breakup date on Lake Aleknagik (Fig. 17) show that the Pacific Decadal Oscillation and a long-term warming trend associated with global warming have contributed about equally to the earlier ice breakup dates (Schindler et al. 2005a). In parallel to the earlier spring ice breakup dates are considerably warmer spring water temperatures in Lake Aleknagik (Fig. 17). During the last 5 years, late June water temperatures have averaged about 2.5°C warmer than the long-term average since 1962. 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 (Table 6).

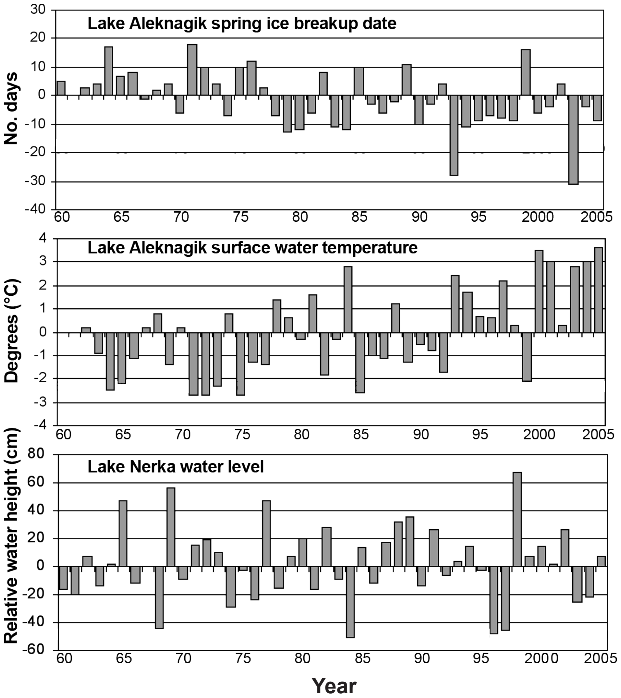


Figure 17. Time series of spring environmental indicators from the Wood River System. Ice breakup date is given as the number of days before/after May 28. Spring (June 22–25) water temperatures are given as the anomaly from the long-term mean (6.4°C). Water level at Lake Nerka is given as the anomaly from the long-term spring (June 6–30) mean (151 cm).

Table 6. Summary of environmental condition in the Wood River System in 2003–2005 compared with the long-term average conditions.

	Year	Date								
1. Date of ice breakup 1949-	2003	28-April								
	2004	25-May								
	2005	20-May								
	Average (1949-2003)									
	Range (1949-2005)									
		25-June	14-July	2-August	31-August					
2. Water surface temp. 0-20 m 1958-	2003	9.2	12.3	13.5	12.7					
	2004	10	12	14.2	13.4					
	2005	8	11.4	13.9	13.1					
	Average (1958-2005)	6.3	11.6	13.2	12.3					
	Range (1958-2005)	3.8-13.7	8.1-18.0	9.4-18.8	9.7-16.0					
3. Water transparency Secchi depth (m) 1962-	2003	5.2	12.3	10.5	6.8					
	2004	5.5	9.4	8.2	8.8					
	2005	5.6	7.8	8.7	6.4					
	Average (1962-2005)	7.5	8.1	9.1	9					
	Range (1962-2005)	4.8-10.5	5.0-12.3	6.3-10.9	5.8-12.1					
4. Water conductivity (micromhos/ cm) 1968-	2003									
	2004	39.7	39.6	39.3	39.5					
	2005	39.8	38.9	40	39.9					
	Average (1968-2005)	38	37.2	36.9	37.9					
	Range (1968-2005)	31.1-52.1	32.0-42.6	32.5-40.5	32.2-47.9					
		Jun 1-15	Jun 16-30	Jul 1-15	Jul 16-31	Aug 1-15	Aug 16-31	Sep 1-15	Sep 16-30	
5. Average daily solar radiation (gm cal cm^{-1}) 1963-	2003	394	205	356	260	256	221	203		
	2004		309	212						
	2005		351	419	279	326	142			
	Average (1963-2005)	403	375	357	327	271	247	204		
	Range (1963-2005)	272-588	205-572	212-543	192-485	195-402	142-421	114-282		
6.Water level (cm), Lake Nerka 1952-	2003	127	125	107	85	76	88	80		
	2004	144	121	88	71	69	53	37		
	2005	178	141	104	76	60	55	56	76	
	Average (1952-2005)	145	150	129	103	85	80	80	76	
	Range (1952-2005)	84-227	97-218	74-199	52-172	34-173	30-184	29-161	76	
		Jun 11	Jun 25	Jul 5	Jul 14	Jul 24	Aug 2	Aug 11	Aug 21	Aug 31
7. Chlorophyll "a", 0-20 m (mg/m^2) 1963-	2003		22	27	10	16				
	2004					9	5	8	11	17
	2005	26	19	29	9	1	8	18		34
	Average (1963-2005)		27		25		20			23
	Range (1963-2005)		10-45		10-43		6-37			5-38
		June		July		August		Sept.		
8. Total zooplankton count, 0–60 m (no. m^2) 1967-	2003	227		191		470		414		
	2004	307		487		434		247		
	2005	368		272		364		287		
	Average (1967-2005)	162		196		249		270		
	Range (1967-2005)	66-337		101-487		100-470		125 - 435		

Thermal conditions in Lake Iliamna have also been showing a steady warming trend over the last 5 decades that parallel the observed increases in spring air temperatures (Fig. 18). Since 1962, average spring air temperatures have warmed over 2°C and water temperatures have warmed about 3°C.

Between 2003 and 2005, 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 6).

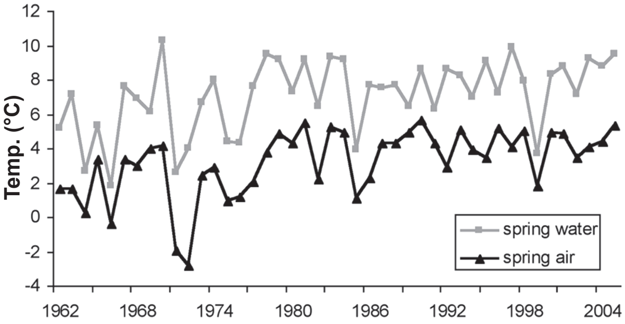


Figure 18. Average spring air temperatures (March–June) recorded at Intricate Bay, Iliamna Lake, and average spring water temperatures (June 1–15) recorded at outlet of Iliamna Lake at Igiugig. Water temperature data were collected by ADFG as part of their annual smolt enumeration project.

Water 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 6). 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.

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. 19). In 2003 and 2004, 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 *Bosmina* and *Daphnia*, which are important prey for sockeye throughout their range (Fig. 19; Schindler et al. 2005a). These taxa are found at relatively low densities in the spring and reach peak densities in August and September (Fig. 19). In 2003, *Bosmina* and *Daphnia* densities were approximately double the long-term means for August and September. In 2004, both taxa were above the long-term mean but this increase was not as pronounced as in 2003. 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. 19). At time of writing, the 2005 Lake Alekagnik zooplankton data were not yet available for analysis.

Sockeye Fry Abundance and Size

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 break up dates and in water temperatures have enhanced growing conditions for juvenile sockeye from 1962 to 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 since 1958, 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. 20). 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 this time period. 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 (Table 7).

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 8). Catch rates of

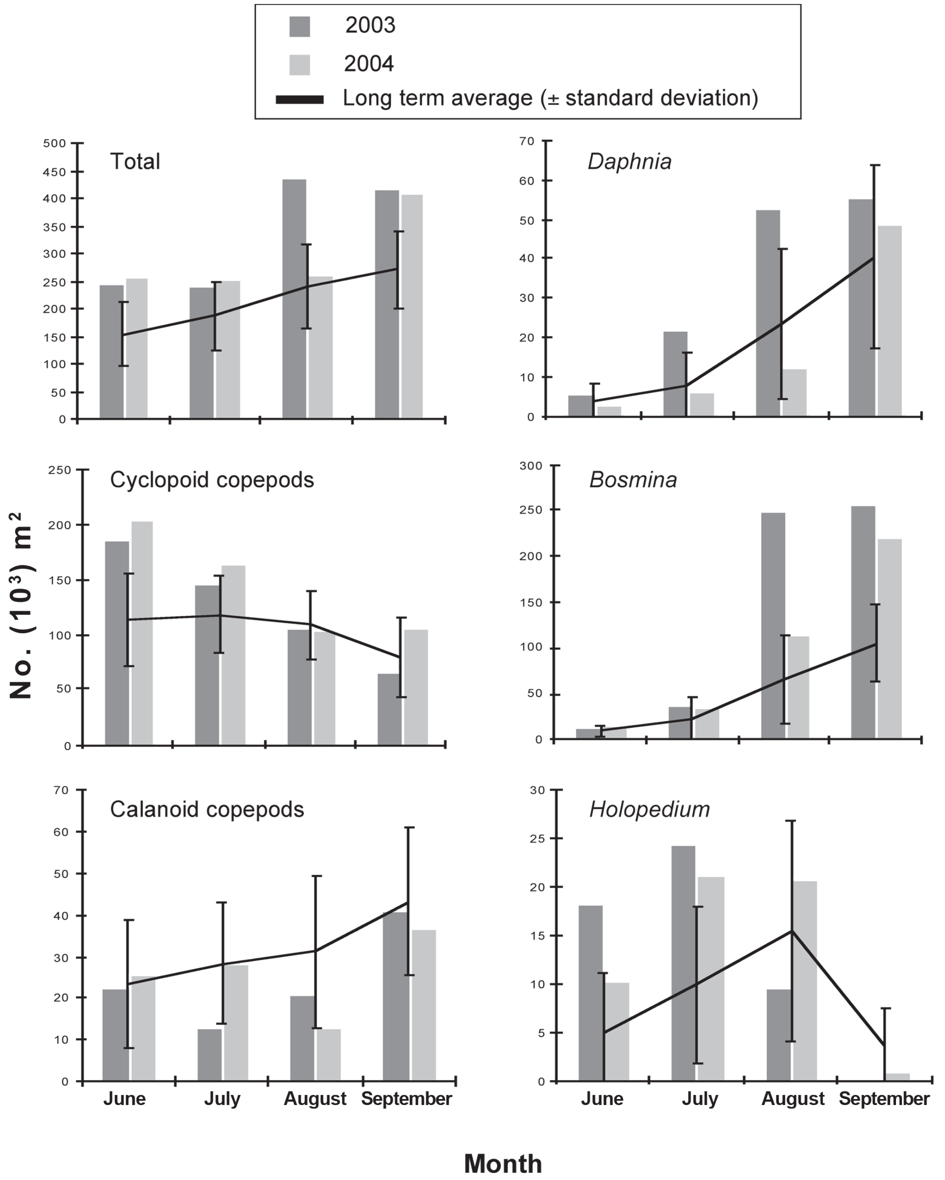


Figure 19. Monthly zooplankton densities in Lake Aleknagik from 1967 to the present (lines with standard deviations) compared with densities observed in 2003 and 2004.

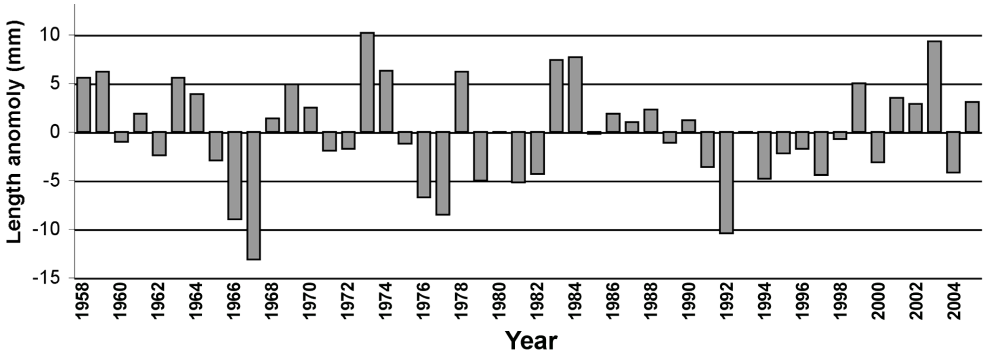


Figure 20. Size of sockeye salmon fry on September 1, 1958–2005, in Lake Aleknagik. All fish were sampled with night townet surveys. Annual length (measured as fork length) anomalies are based on the long-term average (56.5 mm).

Table 7. Townet catches and mean lengths in 2002–2005 compared with averages from 1958–2001.

Category									
LAKE ALEKNAGIK					1962–2001	1962–2005			
Sockeye salmon fry (age 0)	2002	2003	2004	2005	Mean	Min	Year	Max	Year
Mean beach seine catch	31				131	16	1988	549	1965
Mean length on 6/23 (mm)	33.5				31.5	29	1973	36.2	1984
Mean townet catch	20	6	61	5	46	1	1985	394	1976
Mean length on 9/1 (mm)	59.4	65.8	52.3	59.6	55.9	43.4	1967	66.7	1973
Growth rate (mm/d)	0.4				0.4	0.2	1967	0.54	1973
Escapement in yr-1 in 1,000s	677				341	31	1964	1230	1980
Threespine stickleback									
Mean beach seine catch	19				122	12	83, 01	426	1967
Mean length (age 1) on 6/23 (mm)	30.9				31.2	27.1	1966	35.9	1984
Mean townet catch	31	38	38	124	74	2	1985	272	1964
Mean length (age 1) on 9/1 (mm)	45.8	46.0	40.4	44.1	44.5	39.4	1966	50.1	1974
Growth rate (mm/d)	0.2				0.2	0.1	1985	0.29	1973
Age 0 townet catch	6	66.9	112.2	295.9	20	0	many	295.9	2005
LAKE NERKA					1958–2001	1958–2005			
Sockeye salmon fry (age 0)	2002	2003	2004	2005	Mean	Min	Year	Max	Year
Mean townet catch									
South arm	280	4	2	9	13	1	many	280	2002
Central	139	3	2	19	18	2	85, 88, 97, 04	139	2005
North arm	16	2	17	11	39	2	1984	197	1971
Mean length (mm) on 9/1									
South arm	56.4	72.1	59.5	57.6	60	50	1986	72	1984
Central	58.1	64.4	53.2	55.4	57	49	1976	65	1970
North arm	58.1	65.0	56.1	53.9	57	45	1976	65	68,03
Escapement in year-1 in 1,000s									
South arm					116	19	1974	564	1960
Central					127	29	1974	332	1960
North arm					246	52	1958	566	1981
Threespine stickleback									
Mean Nerka townet catch	25	32	15	55	17	<1	2000	107	1974
Mean length (age 1) on 9/1 (mm)	48.0	51.2	46.2	44.5	45	40	1976	51.2	2003
LITTLE TOGIAK LAKE					2002–2005	2002–2005			
Sockeye salmon fry (age 0)	2002	2003	2004	2005	Mean	Min	Year	Max	Year
Mean townet catch	180	24	6	138	87	6	2004	180	2002
Mean length (mm)	53.4	62.7	59.5	51.1	56.7	51.1	2005	62.7	2003
Escapement in year-1 in 1,000s									
Threespine stickleback									
Mean townet catch	27	18	37	109	48	18	2003	109	2005
Mean length (age 1) on 9/1 (mm)	43.9	48.3	46.0	38.4	44.1	38.4	2005	48.3	2003

Table 8. Mean townet catches and lengths on September 1 (mm) of sockeye salmon fry in lakes Iliamna and Clark (geometric mean of 20-min tows), 1961–2004.

		Iliamna Lake (tows in areas 7 and 8 only)		Lake Clark	
Brood year	Kvichak escapement (millions)	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				

sockeye fry in August townetting surveys have been consistently lower than average since 1991, coincident with the lower escapements to the Kvichak River during this time period (Fig. 21). The relatively large fry body sizes seen during this time period indicate good growth conditions due to warmer temperatures and relatively low fish densities. The two main exceptions to this trend were for fish from the 1998 and 1999 brood years, which were substantially smaller than average. 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. Fry sizes in the last 3 years (broods from 2002–2004) were substantially larger than average, apparently benefiting from the warm water temperatures and their own low densities. Harry Rich, Jr., is performing an extensive analysis of these long-term data to explore the effects of inter- and intra-brood competition, and changing thermal regimes, on growth of sockeye fry in Lake Iliamna for his Master's thesis. Some of his results are presented in a subsequent section of this report.

Our analyses of the long-term smolt data collected by ADFG show that there has been 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 on an opportunistic basis to monitor long-term trends in predation rates.

Since 1990 there has been a general increase in the average length of char in the Little Togiak River, and during 2002–2005 average lengths of char were substantially larger than the long-term average of 436 mm TL (Table 9).

Since 2000, we have sampled char diets non-lethally and have tagged and released all 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

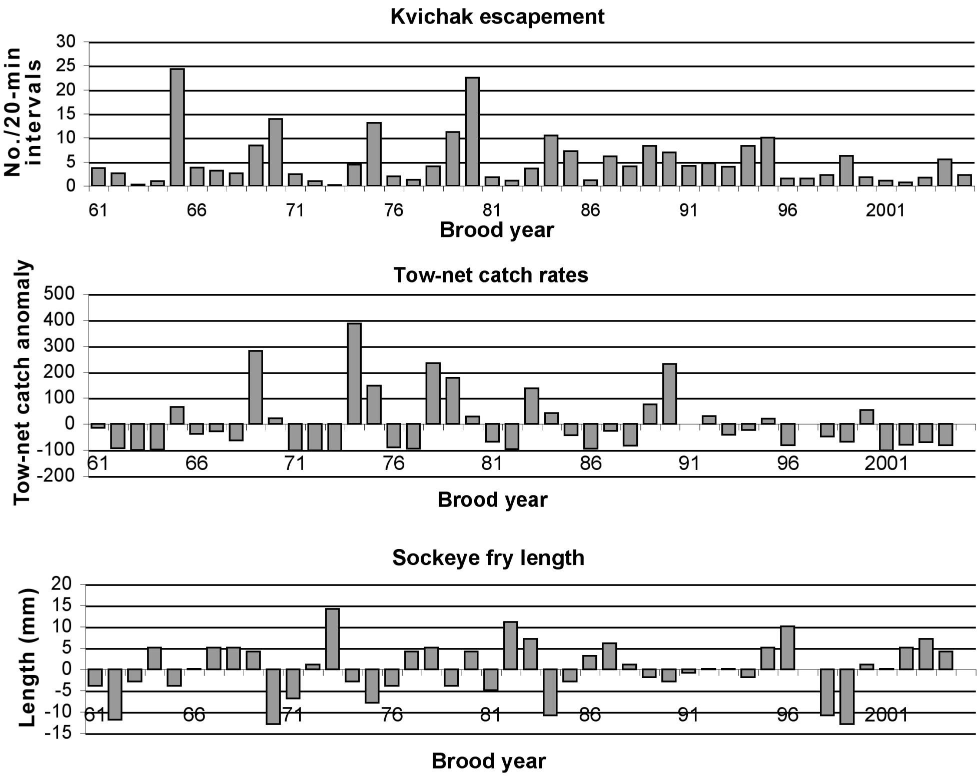


Figure 21. Sockeye salmon escapements to the Kvichak River, associated variation in townet catch rates for sockeye salmon fry and their average lengths in Iliamna Lake.

individuals migrate throughout the larger lake system. In 2002-2005, 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.

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 both arctic grayling and rainbow trout increases over fourfold once sockeye have entered streams and initiated spawning activities (Fig. 22). 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. 22). 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. After salmon entry to streams, rainbow trout diets become heavily dominated (>80%) by sockeye resources (eggs, flesh, and maggots) as invertebrates become rare in their diets (Fig. 22). 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

Table 9. 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: Fry	% char with: Smolt	Mean no. Per char Fry	Mean no. Per char Smolt	Mean no. Sockeye 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
Means	3-Jun		88	436	15	40	1.1	2	31

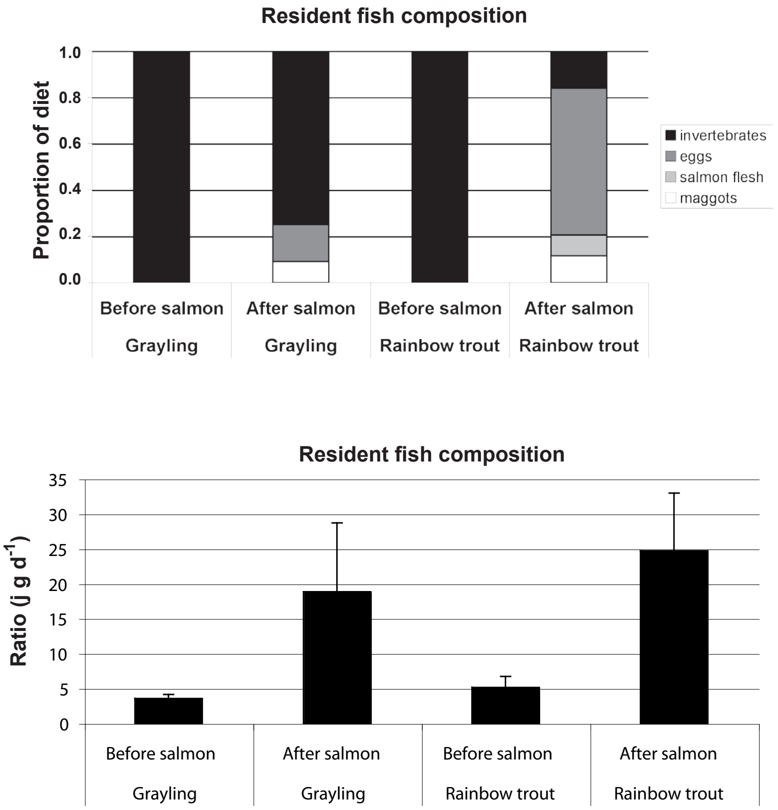


Figure 22. (A) Diet composition and (B) feeding rate for Arctic grayling (*Thymallus arcticus*) and rainbow trout (*Oncorhynchus mykiss*) before and after the entry of sockeye salmon into small streams on Lake Nerka. From MD Scheuerell, JW Moore, DE Schindler, CJ Harvey. Varying effects of anadromous salmon on the trophic ecology of resident stream fishes in Alaska, unpubl. ms.

years with variable sockeye escapement densities demonstrates that the foraging subsidy by sockeye is scaled by their density (Fig. 23). 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 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 prep.). These results demonstrate the importance of sockeye escapement for providing marine-derived prey subsidies to freshwater fish communities.

Lake Thermal Responses to Climate Change Mediated by Landscape Position

J Griffiths (post-baccalaureate student), D Schindler (adviser)

Understanding the responses of aquatic ecosystems to climate change is a critical goal of current ecological research. Do lakes need to be studied individually to predict their responses to climate change or can results from well-studied systems be extrapolated across lake districts? Thermal characteristics of aquatic ecosystems are a fundamental component of the mechanisms controlling nutrient cycling and biotic growth in lakes, and these characteristics have been shown to be sensitive to climate change. Geographic position has been shown to influence the response of lake and river freeze and thaw dates to climate change at the scale of the Northern Hemisphere (Magnuson et al. 2000). We sought to determine whether landscape position contributed, on a finer spatial scale, to thermal responses to climate change of four interconnected lakes in the Wood River System.

Groups of ecosystems in a geographic region can exhibit three types of responses: independent, coherent, or those dependent on a structuring feature such as landscape organization. An independent unique response indicates a strong effect of local topography where each lake behaves independently, while a coherent response suggests no effect of local topography. A response influenced by landscape organization shows the effects of local topography within a larger landscape context.

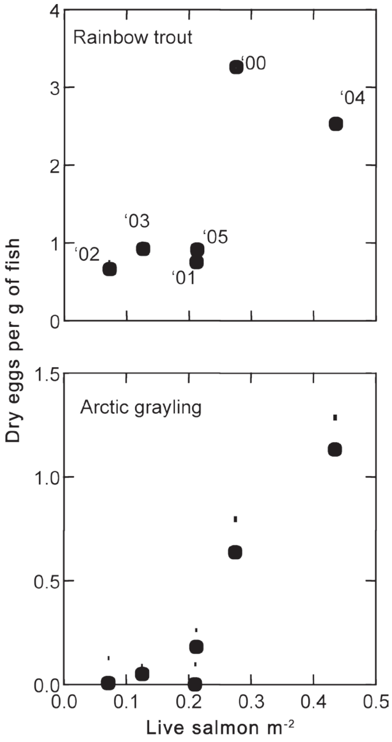


Figure 23. Feeding rate of rainbow trout and arctic grayling on sockeye salmon eggs in Hidden Creek, Alaska, 2000–2005. Consumption rates are standardized for the body mass of predators. Samples are based on at least 25 individuals in each year. From Moore et al., in prep.

Since 1998, temperature data have been collected twice daily and continuously in lakes Kulik, Beverly, Nerka, and Aleknagik using Hobo thermisters held at depth (7 m) with floats and held stationary by weights resting on the lake bottoms. All lakes showed a short-term warming trend in peak temperature.

We used a variety of metrics to integrate the temperature data and characterize lake thermal regimes. Thermal response variables important to lake characteristics include the timing of spring thaw and fall turnover, average monthly temperature, maximum temperature, length of summer (growing season), and degree-days (thermal capacity). The lakes were designated a number according to their landscape position: Lake 1 (Kulik) is the closest to the headwaters of the system. The lakes are numbered sequentially (Beverly = 2, Nerka = 3, Aleknagik = 4) because they receive the water and perhaps the nutrients and thermal signal of the lakes above them in the river system.

Maximum yearly temperature showed a coherent response among lakes. The date of spring thaw (when the lake warms to 4ºC) and date of fall turnover (when the lake cools to 4ºC) showed no clear trend among years. Overall, however, these data do not indicate a landscape-influenced trend. The length of the growing season was measured in two ways:

1. number of days between spring thaw and spring turnover, and
2. number of days ≥10ºC.

For both measurements, no landscape trend was indicated. However, these analyses relied on data from summer months that were incomplete for several years in several lakes.

Degree-days is obtained by summing the average daily temperature for the time period of interest. Degree-days by month showed a response mediated by landscape position for June and October (Fig. 24). Other months showed unique responses for each lake; however the key summer months of July, August, and September had several years of data missing for one or more lakes. The degree-day trends indicate a response that integrates not only air temperature fluctuations but the influence of upstream conditions.

Lakes high in the landscape have less thermal capacity than lakes lower in the landscape. This could have many implications for the biology of lake and river systems: for example, landscape organization of growth potential, and land organization of thermal stratification that controls the cycling of essential nutrients in the water column.

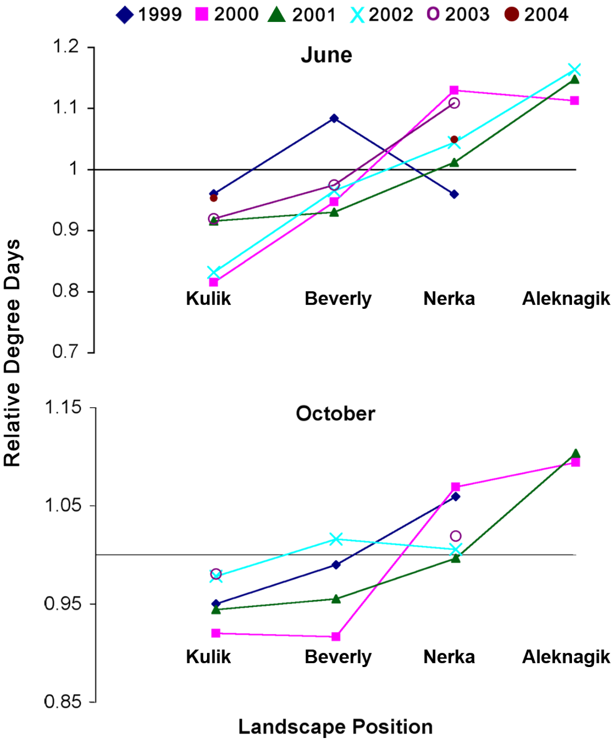


Figure 24. Relative degree-days for June and October plotted by landscape position (1 = mean). Lakes are arranged on the x-axis from highest in the landscape (Lake 1) on the left to lowest in the landscape (Lake 4) on the right.

As climate change continues, ecologists must develop means to predict ecosystem responses. Our results suggest that not every individual system must be studied to make predications; instead, spatial relationships can be used to generalize across landscape gradient. However, the biological significance of landscape gradients has yet to be explored.

Fish Out of Water: The Importance of Salmon and Bears for Productivity of Riparian Ecosystems

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

The importance of salmon in linking marine and freshwater/riparian ecosystems has recently received increased attention by ecologists and fisheries managers. Many species across multiple trophic levels depend on salmon for food resources, and their life-history patterns for feeding, reproduction, and migration are based on the annual return of salmon to their natal streams. Salmon are also rich in nitrogen and phosphorus, nutrients important to the productivity of freshwater and terrestrial ecosystems. Because salmon accumulate most of their biomass while at sea, the return of salmon to freshwater streams represents a large and important flux of resources that, if eliminated, may have broad implications for the healthy functioning of coastal ecosystems.

The goal of our research is to examine linkages between terrestrial and freshwater ecosystems, focusing on the role of sockeye salmon and brown bears in providing a source and vector of nutrients to riparian areas. To measure the effects of these "marine-derived nutrients" on nutrient availability to plants, we have monitored areas where bears concentrate their feeding activity—"bear kitchens"—for three summers and compared these sites with nearby reference areas not heavily used by bears. In the second year, we added an experimental component by excluding bears from two active kitchens with electric fences so that we could quantify changes in nutrient cycling upon removing the bears from the system. We have been careful to ensure that these fences do not endanger bears or other large animals but simply act as a deterrent by delivering a startling, low-power shock. The study sites are located on seven creeks and beaches around Lake Nerka, Alaska, in the Wood River System: C, Pick, Alder, N4, Lynx, Joe, and Hidden creeks (see maps, pp. 37–39).

We have been investigating changes in biologically important soil nutrients before and after salmon return to natal streams for spawning. More specifically, we are monitoring inorganic nitrogen pools; rates of nitrogen transformations, which are strong indicators of nutrient availability to plants; and the loss of nitrogen and carbon trace gases (nitrous oxide, N_2O; carbon dioxide, CO_2; and methane, CH_4) from soils as indicators of soil microbial activity. Our results indicate that bears feeding on salmon significantly increase soil microbial activity as demonstrated by an increase in the loss of N_2O and CO_2 from the soils (Fig. 25). Similarly, if bears are removed from an area, this rate of gas loss appears to decline quickly (≤1 yr) back to levels similar to reference areas with background bear activity (Fig. 26). However, soil nutrient pools appear relatively unaffected by the presence of salmon and bears, possibly because riparian sites are normally rich in nitrogen.

Results from this study have potentially broad implications for ecologists and resource managers. Riparian areas and other terrestrial–aquatic transition zones can serve as "control points" in regulating the movement and forms of nutrient flux, yet there is much to be learned about how these processes are controlled at the ecosystem scale. A detailed understanding of how such processes affect ecosystems is critical for determining appropriate land uses within watersheds, guiding restoration efforts, and protecting biodiversity. The results of our work will contrib-

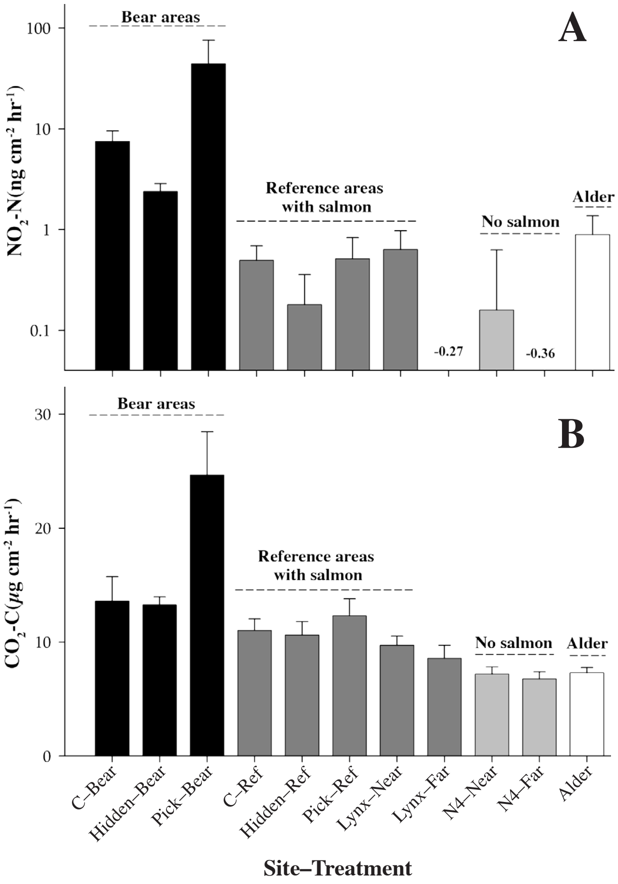


Figure 25. Nitrous oxide (A) and carbon dioxide (B) flux from riparian soils in areas with bears feeding on salmon, salmon only, no salmon, and alder.

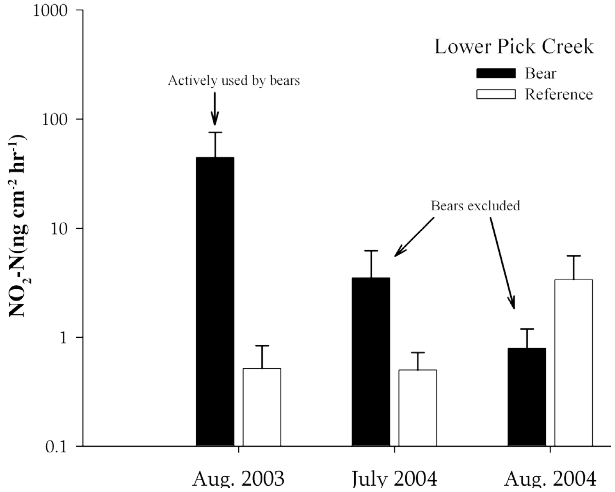


Figure 26. Nitrous oxide flux from soils at the Pick Creek bear exclusions site.

ute directly to the growing body of literature concerning the role of mobile organisms in ecosystem functioning.

Impacts of Salmon Nest-Digging on Stream Ecosystems

JW Moore (graduate student), 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. A female Pacific salmon digs at least one nest (redd) in which she lays and buries her eggs (Fig. 27). 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). 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.

Figure 27. A female sockeye salmon (*O. nerka*) 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 that is drifting downstream of the female. Photo by D. Schindler.

Experimental Approach

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 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.

Fluxes of Fine Sediments

During nest-digging, salmon dislodge fine sediments into the water column where they subsequently drift to downstream lakes (Fig. 27). The concentration of suspended particulate matter in stream water drastically increases as soon as salmon enter streams and start to dig their nests (Fig. 28). 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

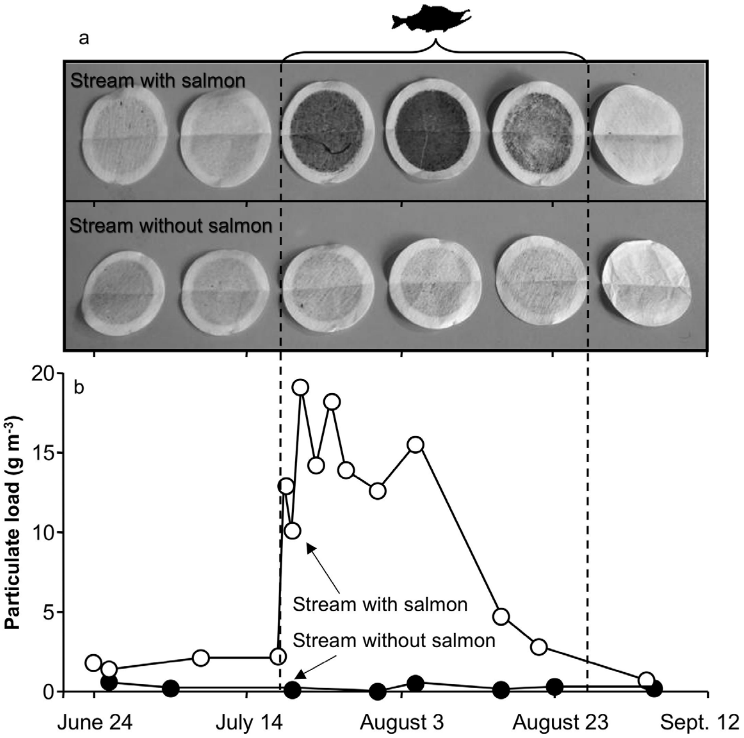


Figure 28. The impact of bioturbation by spawning salmon on the concentrations of total suspended particulate matter in the outflows of two Alaskan creeks. The dashed vertical lines indicate spawning period in the stream with salmon. (a) Seasonal progression of particulate load: Pictured are GF/F filters (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.

stream ecosystems. Fine sediments have been observed to negatively affect early life stages of salmon (Tappell and Bjornn 1983), suggesting that nest-digging might lead to feedback loops across generations of salmon.

Fluxes of Nutrients

Salmon also increase the export of nutrients such as nitrogen and phosphorus from streams when they dig their nests to spawn. 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, nest-digging exports large quantities of nutrients. In fact, in some streams and in some years, salmon export as much phosphorus as they contribute through their carcasses. A bioassay experiment suggested that the exported nutrients are used by primary producers and fuel primary productivity of downstream lakes.

Algae

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 m^{-2} or more, algal biomass plummets to about 10-20% of pre-salmon abundance (Fig. 29). While previous studies have suggested that salmon carcasses can fuel periphyton growth (Naiman et al. 2002), we have observed that any possible fertilization by salmon is overwhelmed by the disturbance caused by their nest-digging.

Benthic Invertebrates

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, some of our data

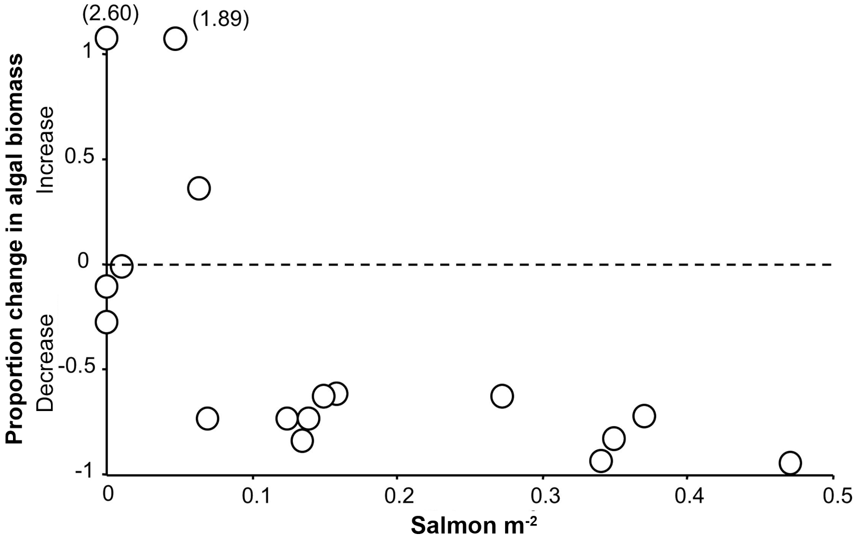


Figure 29. The impact of spawning salmon on periphyton abundance. Each point represents the proportion change in biomass of algae from before to during salmon spawning for a given stream year. Thus, any point above the dashed line represents a stream and year where algal biomass increased during the 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.

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.

Through physically modifying stream habitats during nest-digging, salmon are acting as ecosystem engineers. 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.

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

H Rich, Jr. (graduate student), 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, Alaska. Recently, we reconstructed the townet database from FRI archived records and entered it into a modern electronic format (MS Access). The data include records of sets made, number and species of fishes caught, lengths, and weights. Length and weight data are primarily for juvenile sockeye salmon of two age classes (age 0 and age 1) and threespine sticklebacks. Calculated catch indices—for all lake areas and for the long-term east-end sites—generated from our recently entered data match previous FRI catch indices (Fig. 30), suggesting that data recovery efforts were successful.

During 1962–1976, towing was conducted over the entire lake area, while in the subsequent years, 1977–2005, towing effort was concentrated in the eastern portion of Iliamna Lake, where the density of adult salmon spawning has been the greatest. For the years in which all lake sections were sampled, we will characterize patterns of density, age composition (age 0 and age 1), and size-at-age throughout Iliamna Lake. Additionally, we hope these data will allow us to estimate spatially specific growth rates from areas with multiple sampling events. Density, age composition, size-at-age, and growth rates will be tested for uniformity throughout the lake. We predict that densities will be higher in the east end where the ratio of adult spawners to lake area is higher, and growth there will be slower. Further, in their second year of life, juveniles should leave the eastern end and spread out towards the western end, where densities should be lower.

After the lake-wide patterns of juvenile rearing have been characterized, the production and growth of juvenile sockeye salmon will be analyzed using the longer time series of data collected in the eastern end of the lake (1962–2005). We calculated indices of relative abundance

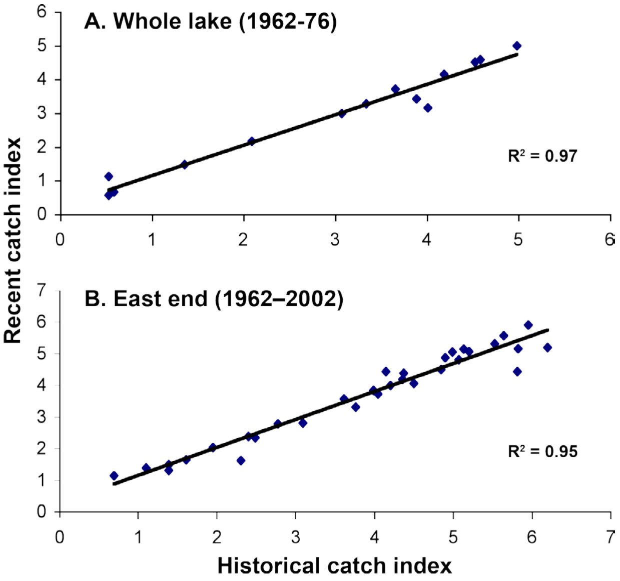


Figure 30. Relationship between historical Fisheries Research Institute catch index and recently calculated catch index using the updated Alaska Salmon Program database: (A) whole lake; (B) long-term east-end sites.

and production for juvenile fish in this reference area of the lake (Fig. 31–32). Juvenile fish growth has been shown to be affected by both biotic (density, competition, and food availability) and abiotic (climate, temperature, ice phenology, and nutrient concentrations) factors. We will fit time-series models to this long-term dataset to quantify the relative contributions of climate, density, and inter-brood-year competition in determining juvenile salmon growth in Iliamna Lake. We predict that years with warmer temperatures, lower densities of fry, and decreased levels of competition with older-aged juveniles will lead to improved growth in fry. Size of fry at the end of the growing season can affect the age at which juveniles undertake seaward migration. We expect to see higher proportions of a juvenile cohort leaving the lake after 1 year if they are larger at the end of the first year. Size and age of seaward migration can affect early marine survival, and thus, adult productivity and year class run strength.

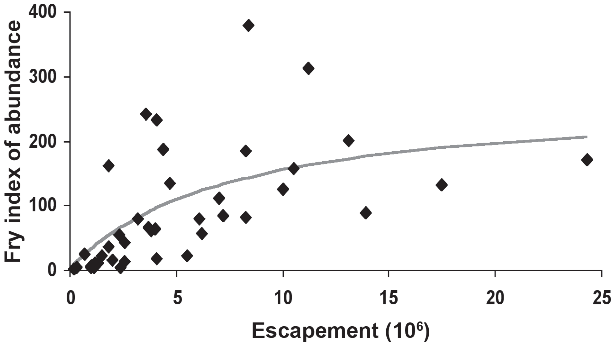


Figure 31. Annual index of abundance of sockeye fry from tow net operations in the eastern end of Iliamna Lake, Alaska as a function of parent escapement from 1962–2005. (The line is calculated using a Beverton–Holt spawner–recruit model).

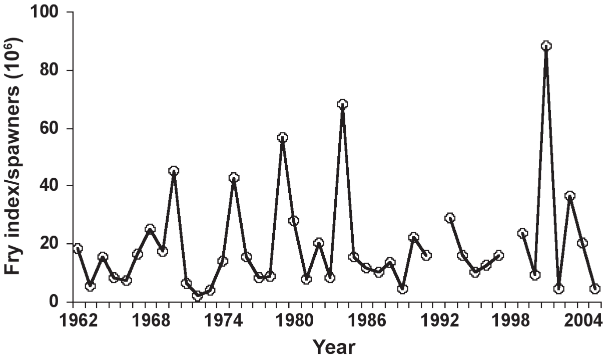


Figure 32. Annual production of sockeye fry from Iliamna Lake calculated using tow net index and parent escapement from 1962–2005.

Rapid Biotic Response to Natural Habitat Alteration in the Chignik Lake System, Alaska: Implications for Productivity and Fisheries Sustainability

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

This research addresses a fundamental ecological question concerning the response of biotic communities to rapid habitat evolution. The research focuses on the Chignik Lake system (see maps, p. 37, 41), which is situated on the south side of the Alaska Peninsula (56°16'N Lat., 158°50'W) and which produces the vast majority of the sockeye salmon in the region. The system comprises two interconnected lakes draining into the Gulf of Alaska. 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).

Within moments of arriving at any of the three Chignik communities (Lake, Lagoon, or Bay) it is clear, even to the first time visitor, that fishing dominates the economy and culture of the area. The Alaska Department of Commerce, Community, and Economic Development verifies this observation, and reports that fishing is indeed the mainstay for Chignik residents (State of Alaska 2005). The small community of Chignik Bay, in which a large cannery operates, becomes a bustling scene of activity during the summer fishing season. Besides the large commercial fishery operating in Chignik, many residents rely directly on subsistence use of salmon, halibut, and large mammals. Natural changes in the rearing habitat of Black Lake have apparently altered the productivity of the system, which has direct bearing on the livelihoods of residents in the region.

About half of the suitable spawning and nursery habitat for sockeye in the Chignik system is located within Black Lake and, within the past 50 years, natural changes to the geomorphology and the hydrology of the system have resulted in the lake volume being reduced by approximately 50%. In addition, the dominant inflowing tributary (the Alec River) is shifting to join the outflow river directly, thereby disconnecting the major spawning habitat for Black Lake sockeye from the nursery habitat. It is plausible that within the foreseeable future, all Black Lake sockeye will be forced to rear in downstream Chignik Lake, thereby substantially increasing competition for resources among juvenile sockeye in that system (Ruggerone 2003).

Biotic communities exploiting these two unique habitats have evolved local adaptations, which has likely contributed to the sustained high historical productivity of the system. For example, threespine stickleback, ninespine sticklebacks, and pond smelt exhibit unique inter-lake movements for spawning and rearing, and sockeye salmon return to spawn at distinct times, grow at dramatically different rates, rear for varying amounts of time in freshwater, and differ in preferred spawning habitat. However, how life histories of the resident and anadromous fishes of the system have adapted or changed as a response to rapid habitat alteration is unclear. Furthermore, it is unclear how management objectives and goals should themselves be adapted in response to change.

Much of this research will incorporate a unique long-term dataset collected in the Chignik system to answer the following general questions:

1. Have patterns of emigration of young-of-the-year sockeye from Black Lake changed significantly through time?
2. Have migration patterns of sticklebacks and pond smelt been altered through time?

To answer these questions, we will test three hypotheses:

1. Sockeye emigration has become more pronounced earlier in the season, presumably in response to reduced volume and increased demand for prey resources.
2. Migration of sticklebacks and pond smelt from Chignik Lake to Black Lake and subsequent emigration of their young-of-the-year represents a new phenomenon in the system.
3. Emigration of sockeye is induced by thermal stress, reduced growth rates, or environmental variables like high-water events.

During the summer of 2005, we quantified emigration of sockeye and other fishes out of Black Lake and attempted to correlate these movements with environmental variables. Black River was fished using three winged fyke nets for a combined total of 1,034 h between June 9 and September 4. Over 90% of the total fish captured comprised three- and ninespine sticklebacks and only 0.3% of the total catch constituted sockeye. Although total emigration of sockeye out of Black Lake was not estimated, the low catch rates did not indicate a massive exodus or migration. Furthermore, emigration was not correlated with temperature or high-flow events during the summer season.

Failing to catch fish may result from a lack of fish to catch (i.e., they are absent), or they are present to catch but exhibit behavior that makes capture difficult (i.e., net avoidance). Catch rates of sockeye were highest early in the season—which loosely correlated with high water—and may represent the tail end of a large emigration that occurred before sampling began. The spring of 2005 was unusually warm according to local residents, and may have stimulated early emigration. For our upcoming sampling in 2006, we will try to capture the emigration dynamics earlier in the season. However, contrary to expectations emigration out of Black Lake was not correlated with period for extreme temperatures (Fig. 33). Ultimately the mechanism triggering the emigration of young-of-the-year sockeye salmon from Black Lake remains unclear.

In 2005, a massive emigration of post-spawn sticklebacks and pond smelt and subsequent emigration of their young-of-the-year was quantified. Preliminary comparisons between catch rates from 2005, 1993, 1992, and 1971 indicate dramatic differences. Catch rates of sticklebacks in 2005 peaked at nearly 1,800 fish per h (Fig. 34), which is greater than most catches during a 24-h period in 1992 and 1993 (Ruggerone 1994). Interestingly, no large emigration of stickleback young-of-the-year was documented in 1971. Whether these discrepancies in catches are an artifact of sampling or indeed represent a dramatic change in life-history strategy (migration between lakes) warrants much more investigation.

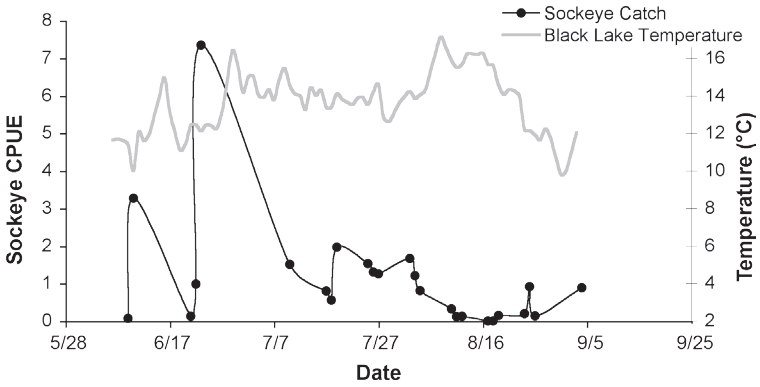


Figure 33. Catches of emigrating sockeye salmon (solid circles) and water temperatures in Black Lake (gray line) during the 2005 summer season

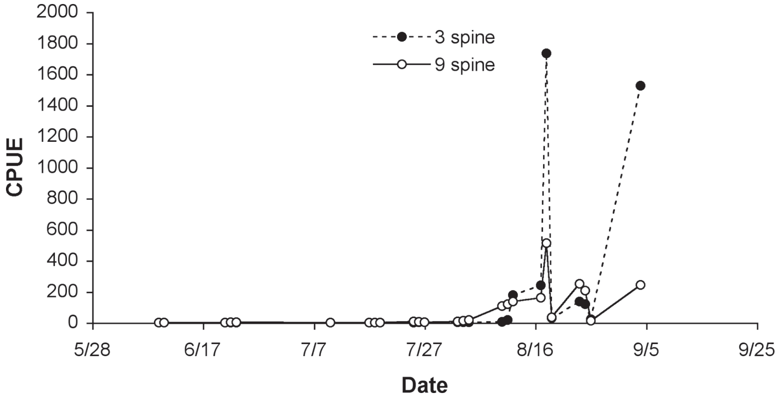
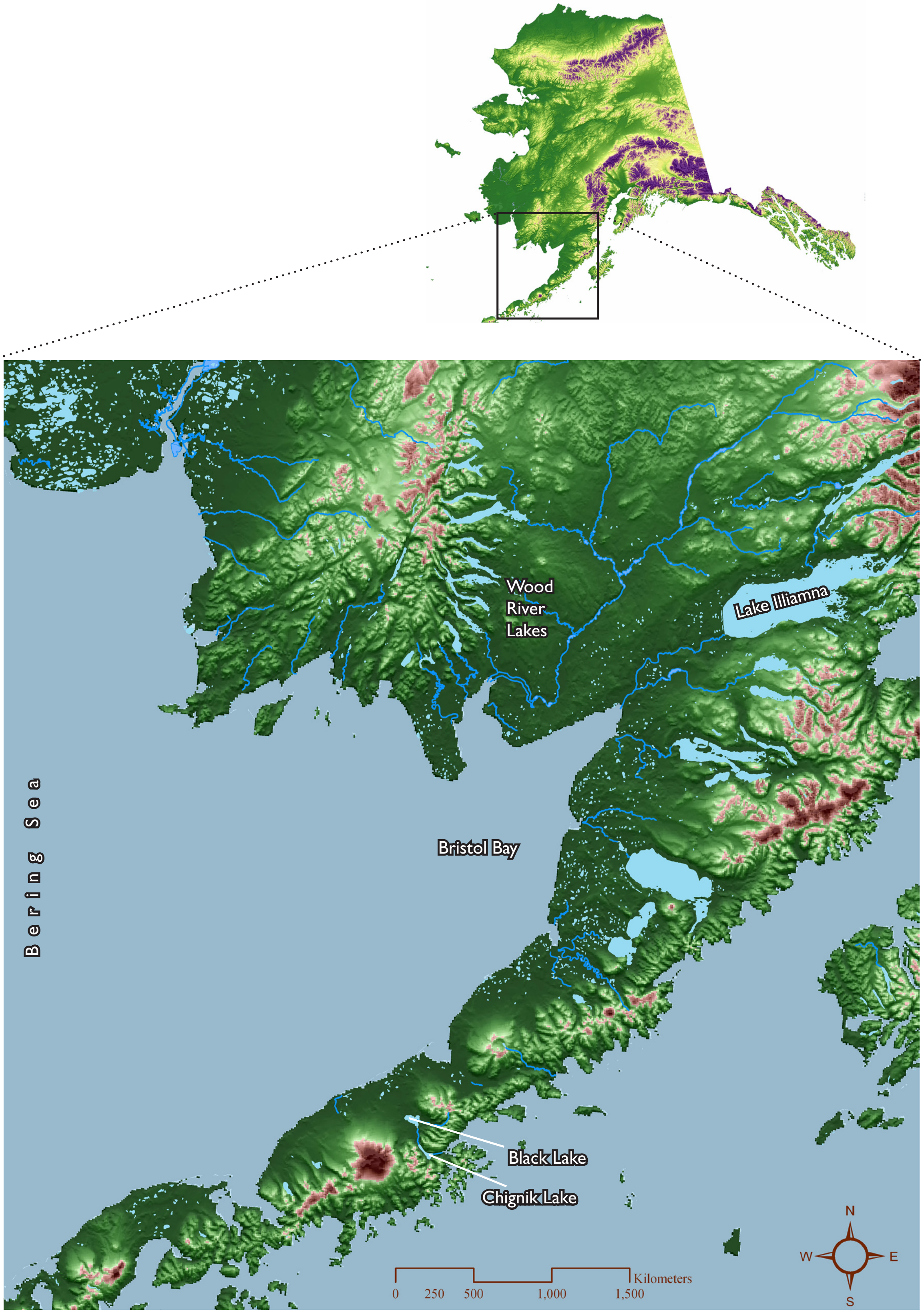


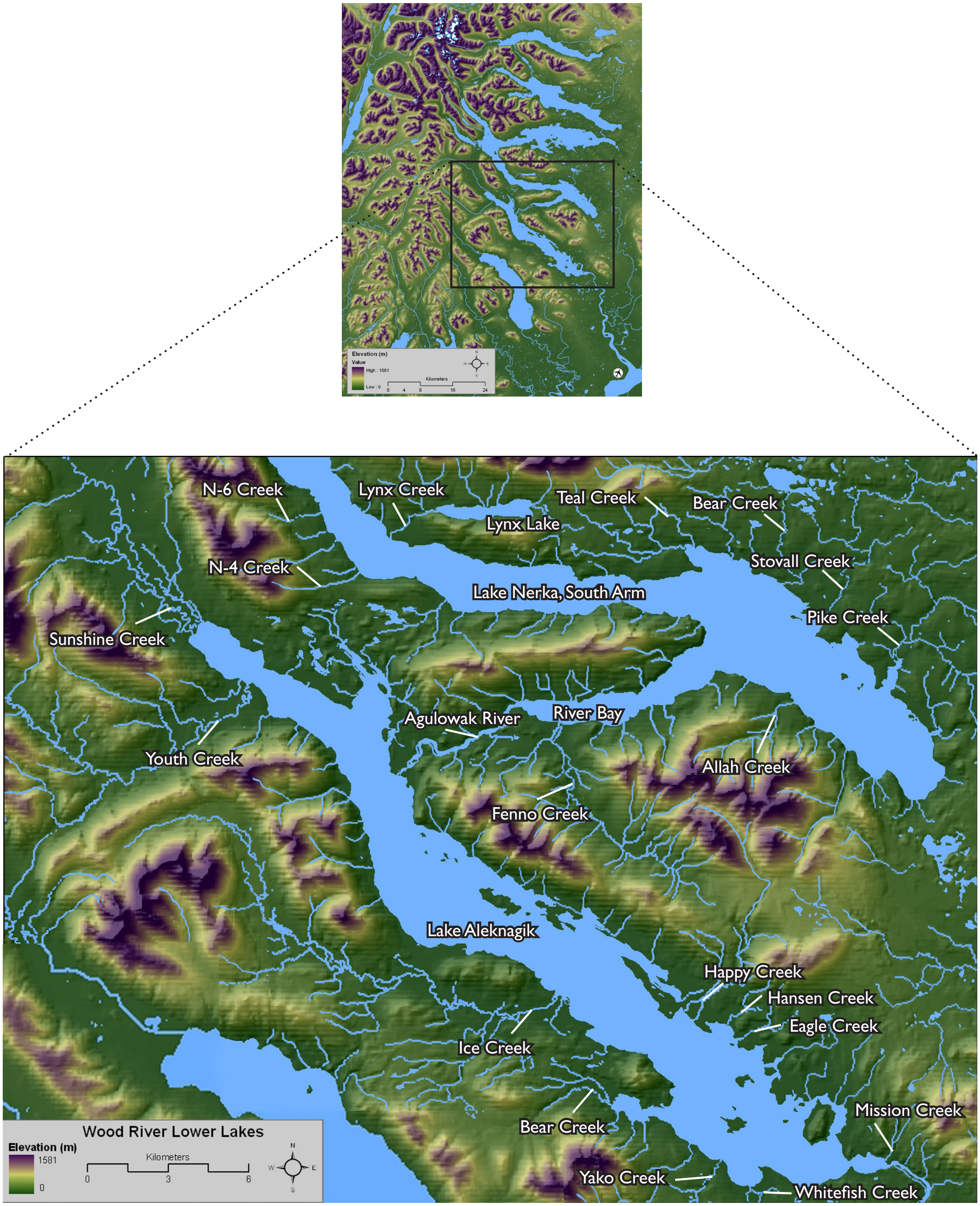
Figure 34. Catch rates of threespine (solid circles) and ninespine (open circles) sticklebacks caught via fyke net in the Black River, Alaska during 2005.

Text continues p. 43

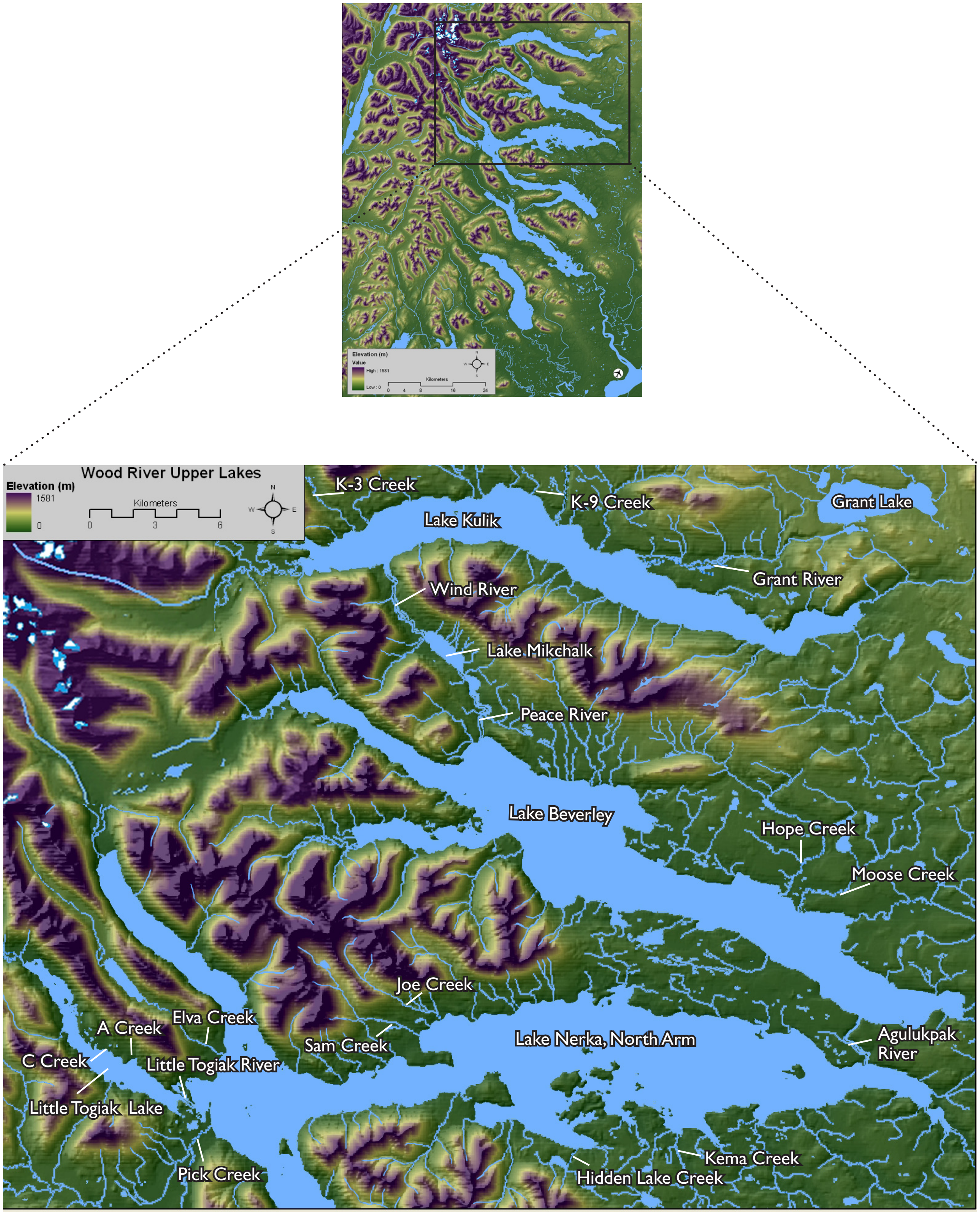
Maps



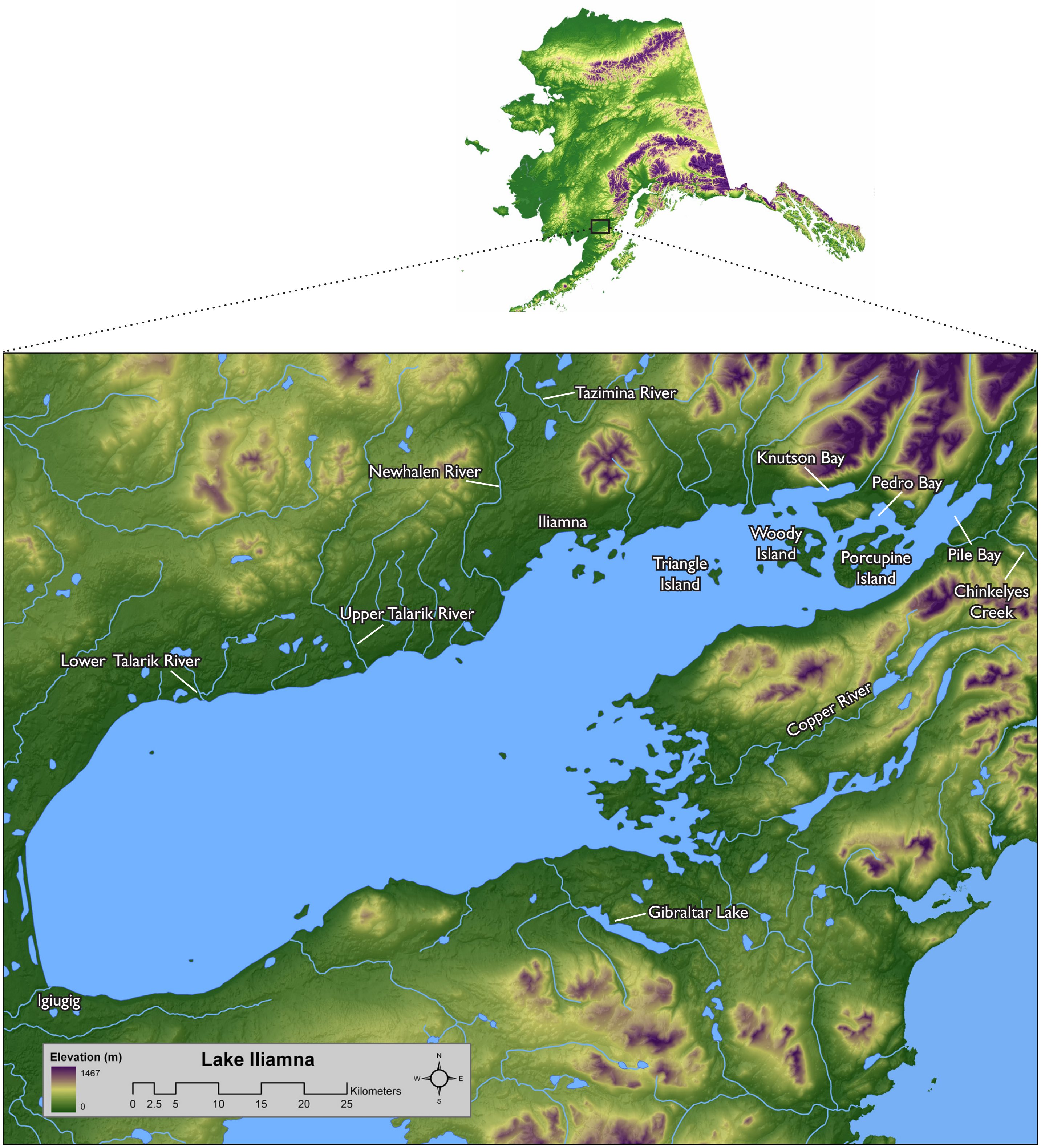
Map of the Alaska Salmon Program's three major research areas: Wood River lakes, Lake Iliamna, and the Chignik lake system.



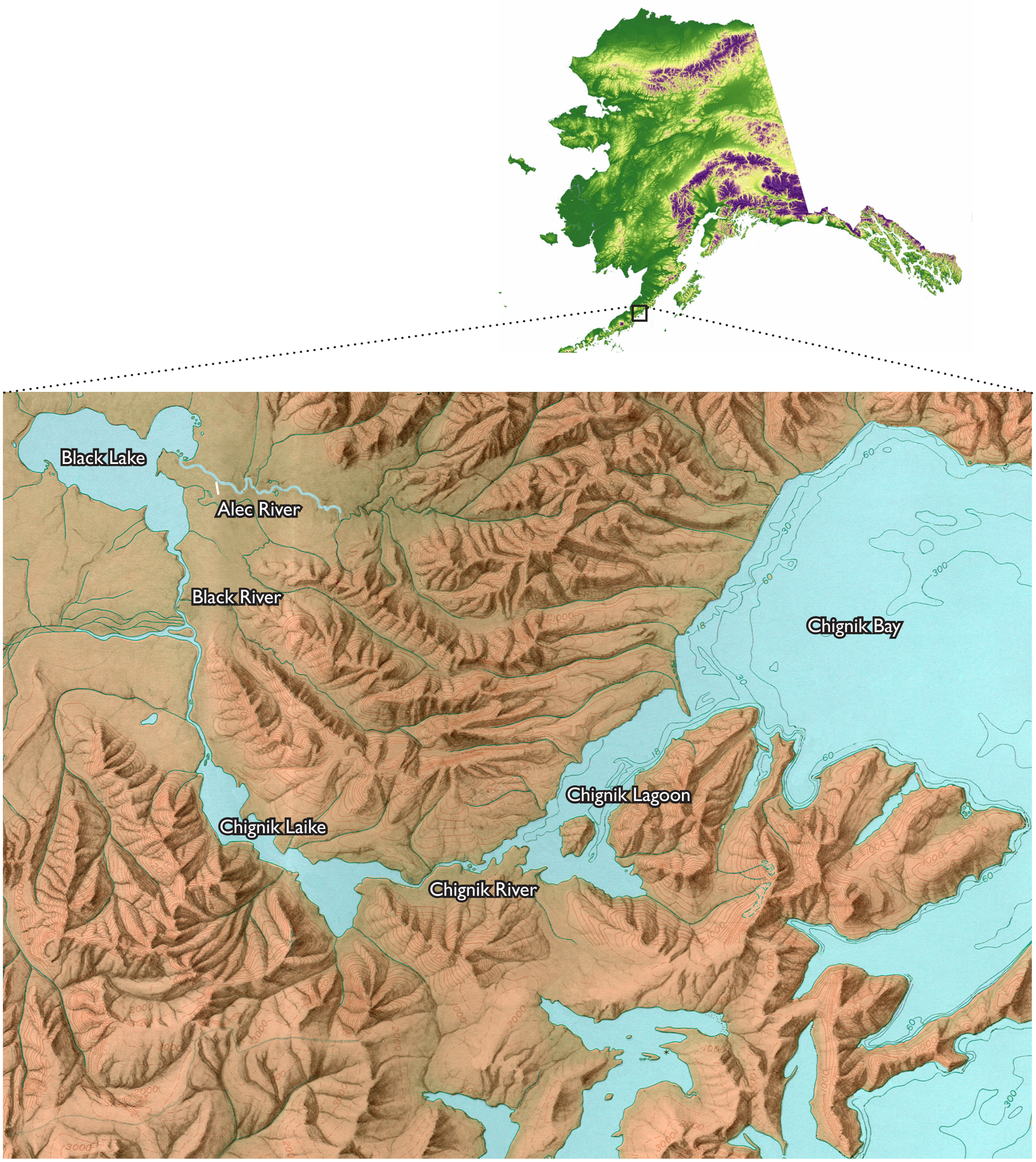
Detail map of lower Wood River lakes.



Detail map of upper Wood River lakes.



Detail map of Lake Iliamna.



Detail map of Chignik and Black lakes.

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. 2004), 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 data sets 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 three small streams, in close proximation, in a single bay of Lake Aleknagik: Happy, Hansen, and Eagle creeks (see map, p. 38). 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 Hansen and Eagle creek fish 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, thus suggesting the presence of strong selection pressures maintaining phenotypic differentiation (Ziegler et al., this volume).

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 (and 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. 2001a), we are collecting data on size and shape in 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 and samples from creek and beach spawners in Lynx Creek, in Lake Nerka, Yako Creek in Lake Aleknagik, and Knutson Creek in Iliamna Lake (see maps, 37-40). These samples will be examined 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 the 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 do 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, 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), 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 10) but analysis was performed primarily on those from Little Togiak Lake. The lake is the smallest in the system and has two creeks supporting consistent sockeye salmon runs: A Creek

Table 10. 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
A Beach	Wood River	B	34	4	64	21
A Creek	Wood River	S	34	32	496	444
C Beach	Wood River	B	33	31	54	18
C Creek	Wood River	S	26	28	383	280
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
N4 Creek	Wood River	S	---	---	52	51
Yako Beach	Wood River	B	---	---	51	100
Yako Creek	Wood River	S	---	---	229	
Knutson Bay Beach	Iliamna Lake	B	---	---	100	---
Knutson Creek	Iliamna Lake	S	---	---	98	---
Anvil Bay Beach	Wood River	B	---	---	---	100

and C Creek. Beach spawners spawn off the mouths of A and C 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 Creek, C Creek; see map, p. 39) and four beaches (A, C, North, South) in Little Togiak Lake were collected for three consecutive years (2002–04). Genetic variability was higher in beach spawners (H_E=0.789) than in creek spawners (H_E =0.730). To assess genetic differentiation, we calculated F_{ST} values and Cavalli-Sforza genetic distances, visualizing the latter in a multidimensional scaling plot (MDS; Fig. 35). 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), and A Creek spawners appeared to be more differentiated from beach spawners than were C Creek spawners (Fig. 35). Moreover, samples of beach spawners showed low but significant differentiation (F_{ST} =0.007), whereas stream spawners showed higher differentiation (F_{ST}=0.0382). Therefore, ecotypes do appear differentiated.

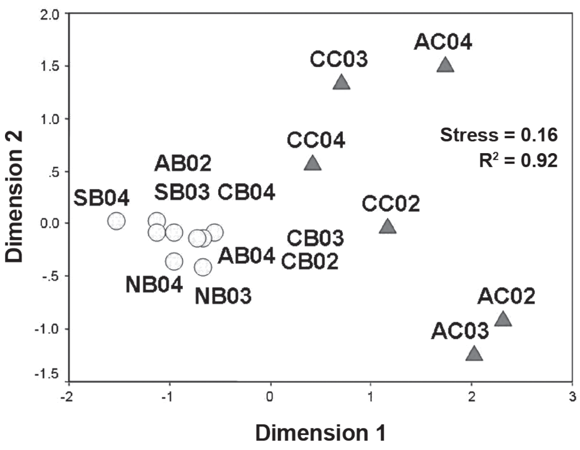


Figure 35. Multidimensional scaling plot of Cavalli-Sforza genetic distances for all analyzed samples. Samples are represented by location, ecotype, and year (e.g., AC02 = A Creek 2002); see Table 10 for location and ecotype abbreviations. Sample location abbreviations are as follows: AB = A Beach; AC = A Creek; CB = C Beach; CC = C Creek; NB = Little Togiak, north end; SB = Little Togiak, south end.

Clustering analyses by the likelihood program Structure (Pritchard et al. 2000) supported the notion of high migrant exchange among beach populations and relative reproductive isolation in the creeks (Fig. 36). In addition, C Creek appeared to have a higher proportion of immigrants than A Creek. A Creek also showed more temporal variation than C Creek, with the A Creek 2004 sample being significantly different from the 2002 and 2003 samples (Fig. 36). Thus, genetic patterns differed for each ecotype, and straying patterns differed by sample area.

The low differentiation among beach spawning populations compared with creek spawners may be due to higher straying rate, differences in population sizes, or more recent time since divergence. The beaches used by beach spawners generally receive oxygen via groundwater or wind-generated currents (Stewart et al. 2003). Beach spawning sites within a lake probably share many chemical and physical characteristics, and thus straying among sites may be common. Beach sites are also separated by few physical barriers, which may facilitate straying. Finally, the beach spawners may have been more recently separated, thus not allowing sufficient time for genetic differentiation to accumulate among populations. This scenario is possible if creek spawners represent more

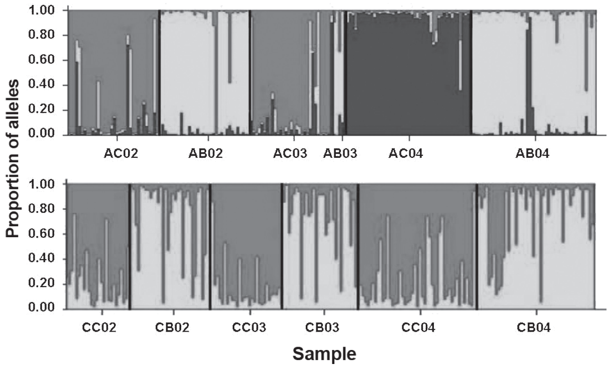


Figure 36. Population contribution to each genotype estimated by the multilocus clustering program Structure. Sample areas are separated by black lines (see Fig. 35 for sample legend), and different colors represent different populations as determined by the program. Each bar represents an individual fish, and the grayscale values in the bar show the inferred mixed population ancestry of that fish. Thus a hybrid individual will appear as a multicolored bar, and a migrant individual will differ in color 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, CC02–CC04). Note also the difference between AC02/AC03 and AC04, represented by different grayscale values. In contrast, beach spawners appear to be a mixture of several populations.

specialized descendants of generalized river spawners (Gustafson and Winans 1999) than beach spawners. To conclusively resolve these uncertainties, we need to survey more populations.

The dissimilarity in genetic patterns for A and C creeks indicated that the demographic dynamics in the two creek populations may be different. In 2004, C Creek (Fig. 36) appeared to receive many immigrants, whereas A Creek sockeye were genetically relatively homogenous. Temporal differentiation among years was also much higher at A Creek than at C Creek. We thus hypothesize that creek populations are subjected to temporally variable immigration 'waves' (C Creek, Fig. 36), which leave their genetic signature in temporal differentiation among subsequent years if these immigrants were reproductively successful (A Creek, Fig. 36). Measurable differences in environmental parameters among streams, such as gradient, pool area, and prevalence of cut banks, may affect the reproductive success of immigrants and explain differences between streams in extant and historical immigration rates.

Research results support the notion that both beach and creek spawning sockeye salmon behave as discrete metapopulations (Hanski 1996), with subpopulations that are connected by varying rates of migration and which may go extinct and be recolonized. In contrast to a standard metapopulation model, however, our data suggest that immigration among populations may occur in addition to recolonization. Furthermore, beach and creek spawners show very different rates of migration, or different stability (time since divergence), or both. Thus, the existence of ecotypes in geographically separated habitats may contribute to the biocomplexity of the Wood River sockeye salmon stock complex. 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.

Capstone Project–Genetic Differentiation among Phenotypically Differentiated Populations of Sockeye Salmon

E Ziegler (undergraduate student), J Lin (graduate 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, whether selection pressures in different habitats suffice to maintain the genetic basis of heritable adaptive traits despite gene flow reducing genetic differentiation is uncertain. 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 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, Alaska (Happy, Hansen and Eagle creeks, Fig. 37). 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 Creek, 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.

Genetic diversity was high and comparable among the five samples, with expected heterozygosities per locus ex-

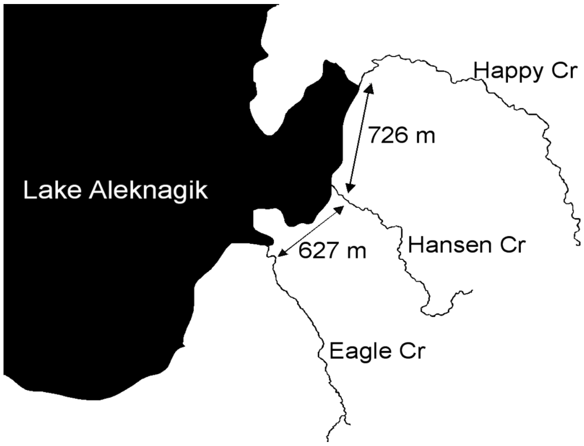


Figure 37. Map of Happy, Hansen and Eagle creeks and the distances between them.

ceeding 85% and more than 15 alleles per locus in each sample (Table 11). Most loci fulfilled population genetic expectations of randomly mating populations (Hardy–Weinberg equilibrium), although some significant deviations also occurred (Table 11). Despite this high variability and comparatively large sample sizes, measures of genetic differentiation among all samples were small and not significant (F_{ST} over all samples = 0.001). Pairwise F_{ST} estimates between samples ranged between -0.0008 and 0.0039, with no values significantly different from zero.

The lack of genetic differentiation among the three creek populations may be due to an inadequate number of loci surveyed, high rates of straying, or recent divergence of populations. Because of logistical constraints, only 4 loci were surveyed, whereas commonly over 10 loci have been used. Such a small number of loci clearly reduces the power of detecting significant differentiation. However, the same four loci showed significant differentiation between A and C creek in Little Togiak Lake (J Lin et al., Univ. Washington, Seattle, unpubl. data), suggesting that the differentiation between Hansen, Happy and Eagle creeks is considerably lower than that between A and C creeks. Nevertheless, the small number of loci precludes any analysis of multilocus genotyping using Bayesian or clustering approaches, which may be more powerful in detecting low-level population differentiation.

Given the dataset, distinguishing between high straying rate and recent divergence of populations is difficult. If even only a few fish stray between these creeks and are successful in reproducing, the resulting gene flow would be sufficient to prevent genetic differentiation to accumulate at neutral loci like microsatellites (Waples 1998), so the only force acting on those allele frequencies is genetic drift. As a result, only a small amount of gene flow is required to homogenize these allele frequencies. However, phenotypic traits such as spawning date, body size, and shape are probably under strong selective pressure, which counteracts gene flow, and these traits may therefore show differentiation despite some level of straying between populations.

Future work will include screening additional loci for these samples, allowing us to apply more powerful and sensitive statistical approaches to our dataset, and integrate the genetic data with information on life-history traits of these populations. These data will be used to provide further insight into selection pressures acting on salmon populations in different habitats, and to resolve fine-scale population structure. Such data will be crucial for a more specific assessment of biocomplexity at small spatial and temporal scales.

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). Other obvi-

Table 11. Sample sizes (N), number of alleles (A), heterozygosity (H_e), and p-values for the Hardy-Weinberg test (P-val) for five sockeye sample groups.

Locus		Hansen Early	Happy Early	Eagle	Happy Late	Hansen Late
One 100	N	58	58	49	52	55
	A	18	19	19	17	17
	H_E	0.902	0.915	0.914	0.920	0.900
	P-val	0.335	0.412	0.050*	0.109	0.125
One 101	N	50	57	51	51	54
	A	29	29	28	27	30
	H_E	0.961	0.956	0.957	0.962	0.957
	P-val	0.092	0.863	0.710	0.446	0.049*
One 108	N	57	56	52	52	56
	A	15	16	14	15	15
	H_E	0.888	0.902	0.899	0.877	0.900
	P-val	0.301	0.505	0.049*	0.187	0.835
One 112	N	48	54	54	49	56
	A	21	24	21	19	23
	H_E	0.880	0.897	0.862	0.875	0.864
	P-val	0.000*	0.735	0.146	0.679	0.258

*Instances where the Hardy–Weinberg probability test indicated a p-value of ≤0.05.

ous 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) 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. Thus, 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.

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 (see Salmon Ecology, p. 15) 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 (this page) 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 (see Biocomplexity Theme 3, page 44) 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.

Sockeye Salmon Responses to Climate Regime Shifts Based on Stable Isotopes in Salmon Scales

S Johnson (graduate student), D Schindler (adviser), L Fair (ADFG), F West (ADFG)

Widespread ecological changes related to variation in climate have been observed in the North Pacific Ocean (e.g., Pearcy and Schoener 1987, Anderson and Piatt 1999). One of these notable changes is a shift in the production of salmon (Hare and Francis 1995, Mantua et al. 1997) associated with the interdecadal regimes of the Pacific Decadal Oscillation (PDO). Mantua et al. (1997) showed that salmon production changes in response climatic conditions and demonstrated two important aspects of climate effects on salmon. First, climate forcing, as captured by PDO dynamics, is correlated with salmon production such that small changes in the physical environment translate into substantial changes in fisheries production. Second, there is geographic organization in salmon production responses to climate change. Areas such as Alaska show greater than average catches during positive PDO whereas, Washington and Oregon coastal populations and the Columbia River populations show a lower than average catch during the positive phases of the PDO. It remains unknown what mechanism drives these responses.

In western Alaska, which is dominated by Bristol Bay, salmon populations as a whole are responsive to the PDO (Mantua et al. 1997). Data from historical returns to area rivers can be used to examine how these individual river system populations respond to climatic variation. Returns to Bristol Bay rivers vary over time and are not synchronous with one another (Hilborn et al. 2003). Variation in returns may occur because individual populations respond to changes in the environment differently.

Hilborn et al. (2003) described freshwater adaptations and differences in life-history strategies among different populations of Bristol Bay sockeye salmon and referred to the suite of this variation as biocomplexity. The differences in life-history strategies likely have allowed the stock complex to sustain productivity despite environmental variation due to climate. Much is known about the freshwater phases of the salmon life cycle (cf. Quinn 2005). However, whether components of biocomplexity also occur in the marine phase of the life cycle is unknown. An untested assumption is that the ocean is a homogenous environment and that salmon stocks experience relatively similar conditions in the ocean.

One expression of marine biocomplexity may include variation in the trophic ecology of different salmon populations. For example, marine biocomplexity may be expressed as populations partitioning space or prey resources differently in the ocean. Kaeriyama et al. (2004) hypothesized that salmon feeding in the ocean adapt to changes in prey resources induced by climate by switching their diets between or within trophic levels. Welch and Parsons (1993) showed that different populations of sockeye salmon from British Columbia and Bristol Bay show different trophic ecologies based on stable isotope analysis. They hypothesized that these differences were due to spatial separation in ocean feeding.

Oceanic biocomplexity is one mechanism that would drive variability in the response of individual river populations to climate variability. Ongoing tagging studies and genetics can tell us about spatial partitioning in the marine phase of different populations (Myers et al. 1996), but they do not reveal trophic partitioning. If trophic partitioning is occurring in these different populations, perhaps the variation in salmon return response to climate is a result of differing foraging ecologies in the ocean.

This project uses stable isotope analysis to determine whether trophic shifts over time correlate with changes in PDO phase and associated population responses. Specifically, we will examine whether different populations exhibit differing foraging strategies over time and see if this correlates with environmental change as measured by the PDO.

Approach

Scales archived for more than 40 years (1962–2003) for different populations of Bristol Bay sockeye salmon (Wood River, Naknek, Kvichak, Egegik, Ugashik, Igushik, and Togiak) were obtained from the ADFG. The archived scales were used for ^{15}N stable isotope analysis, to reconstruct time series of the trophic position of salmon from each of the Bristol Bay rivers. All salmon sampled were the same age (2-ocean fish). The δ^{15}N and returns of individual populations were compared with the positive and negative phases of the PDO. In addition, recruits-per-spawner for each river system will be compared with PDO and δ^{15}N to determine if patterns emerge. Finally, we will use ADFG age, weight, and length data to determine whether changes in δ^{15}N track with changes in growth for each river system.

Results to Date

Annual returns of Bristol Bay populations responded differently to PDO. Some responded positively to the climate driver while some showed no response (Fig. 38). δ^{15}N varied over time in all populations. Interestingly, the same rivers that showed a positive correlation between returns and the PDO also showed a positive correlation between the PDO and δ^{15}N over time (Fig. 39). The positive correlation between PDO and δ^{15}N might be interpreted as a shift in trophic position in these populations that is synchronous with the change in the climate driver. This result suggests that change in trophic position is one mechanism through which PDO is expressed in salmon populations. Examination of the age, length, and weight data will reveal whether this change in trophic ecology translates to faster growth.

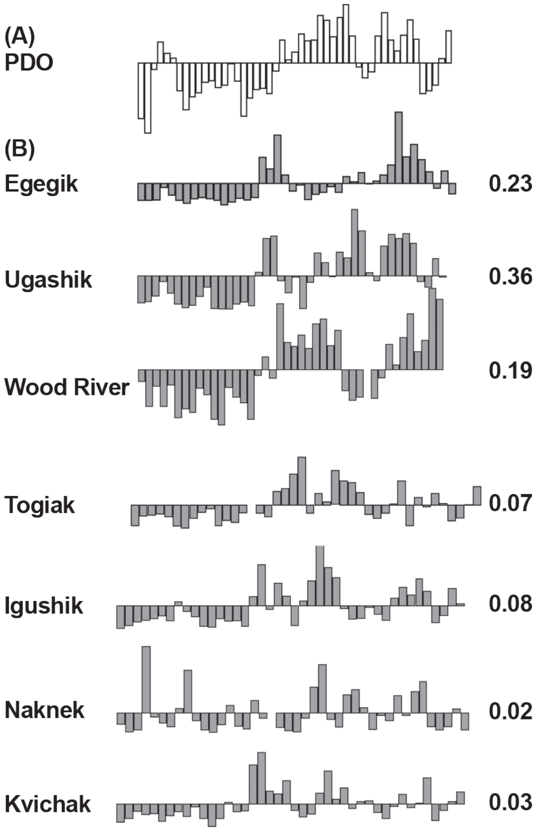


Figure 38. (A) PDO in its positive and negative phases over time; (B) standardized returns (catch + escapement standardized for the long-term mean and SD) for the rivers with correlation coefficients (right).

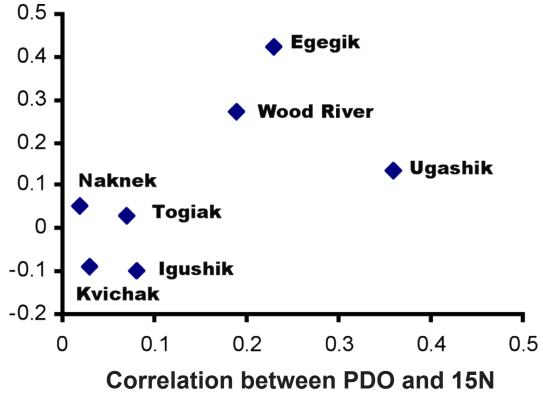


Figure 39. The correlation between (1) the strength of the relationship between PDO and annual return and (2) the strength of the relationship between PDO and trophic position of adult sockeye as inferred from 15N in the seven major Bristol Bay rivers (r=0.6, p<0.05).

However, while some salmon populations track PDO by feeding at different trophic levels, some do not respond. In the same river systems where returns are not strongly correlated with the PDO, there are weak correlations between $\delta^{15}N$ and PDO (Fig. 39). In these rivers, there apparently is no synchrony between trophic position and the climate driver; when there is a positive PDO phase, there is no relationship between trophic position and PDO.

Biocomplexity is a characteristic of stock complexes that is expressed as individual populations showing different responses to environmental variability (Hilborn et al. 2003). Studies in freshwater systems have shown how different populations are adapted to local conditions (Quinn et al. 2001), but there have been no studies to determine if or how individual populations are adapted to the ocean environment. The ocean has been considered as a homogeneous environment to salmon populations. However, results to date show that individual populations display distinct variation in trophic positions that appear to be population-specific response to changes in marine prey resources, which are driven by climate variability.

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 BP. 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 map, pp. 38-39), 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. 40).

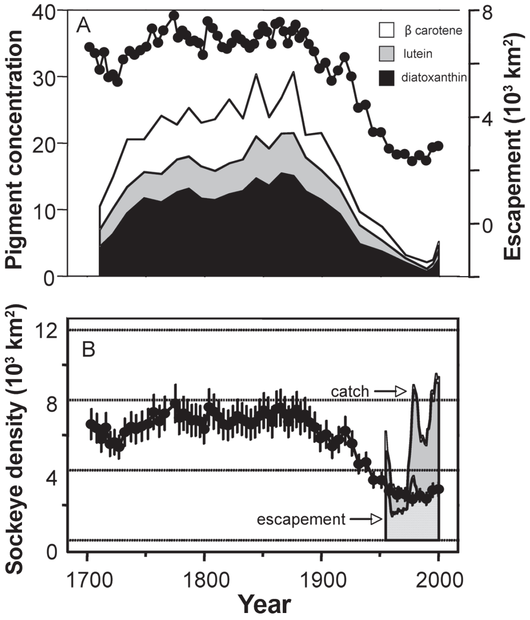


Figure 40. (A) Reconstucted sockeye salmon escapement to Lake Nerka for the last 300 years (●) and the associated changes in three dominant sedimentary fossil pigments (shaded regions). Pigment concentrations are expressed as nmol pigment per g of dry sediments. (B) Comparison of historical escapements to Lake Nerka (ϕ) with contemporary estimates of catch and escapement (shaded region). From Schindler et al. (2005).

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.

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 in the last 5 decades. Enumerated run sizes averaged about 1 million fish from 1956–2002 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 every ~100 years since ~1500 AD, interspersed by periods of substantially lower production (Fig. 41). Given the variability inferred from the paleoreconstructions, 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., in review).

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 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. The first, and most obvious, is extreme environmental variability. In accordance with existing theory, this would suggest a constant escapement

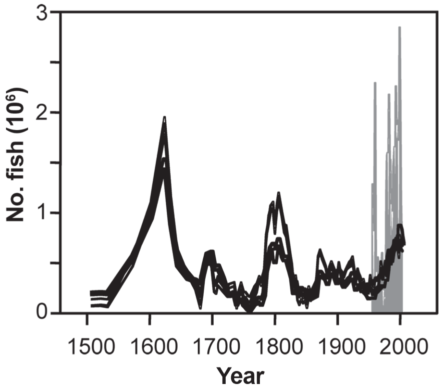


Figure 41. Reconstructed population dynamics of Alagnak River sockeye populations, 1500–2005. Solid lines represent different model scenarios to translate variation in sediment isotope characteristics to sockeye population sizes. The thick line is the reconstruction from the model with the best fit. 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).

rule. 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.

In this first year we have narrowed our theme 4 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.
- 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 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?

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. 42). 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. 43).

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. 44)? 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

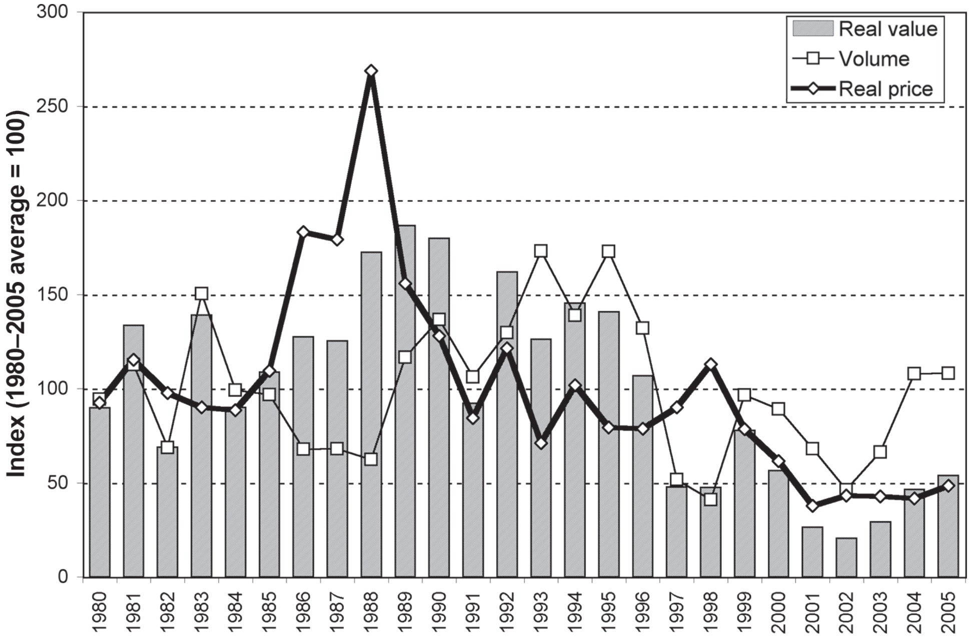


Figure 42. Ex-vessel value of Bristol Bay sockeye salmon harvest and indexes of harvest volume and ex-vessel price (1980–2005 averages = 100). Value and price are adjusted for inflation.

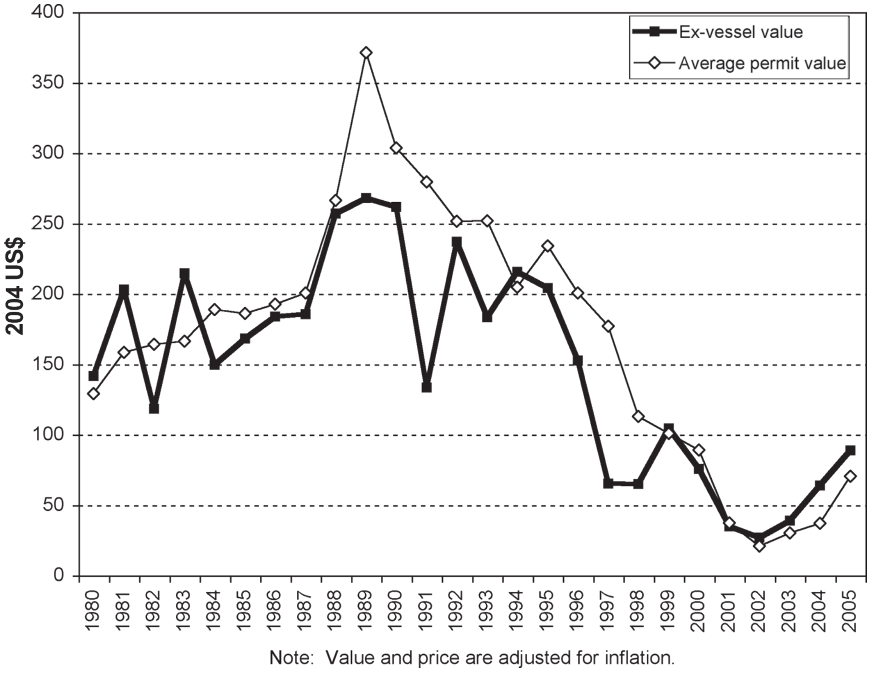


Figure 43. Ex-vessel value of Bristol Bay sockeye salmon harvest and average driftnet permit price. Value and price are adjusted for inflation. Price ranges (US$) are as follows: permit prices = thousands; ex-vessel value = millions.

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 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-

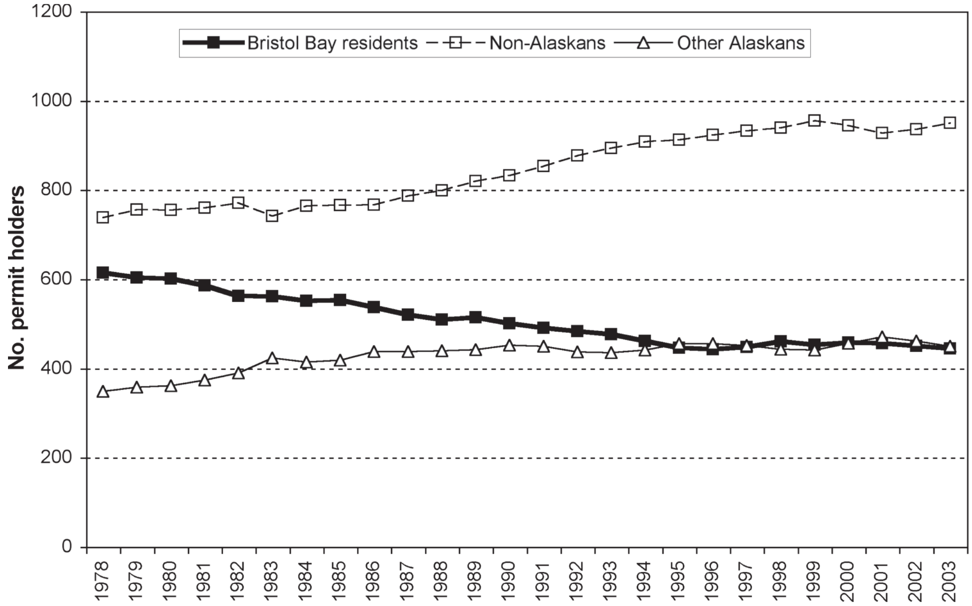


Figure 44. Number of Bristol Bay drift gillnet permit holders by residency.

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. 45). 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 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

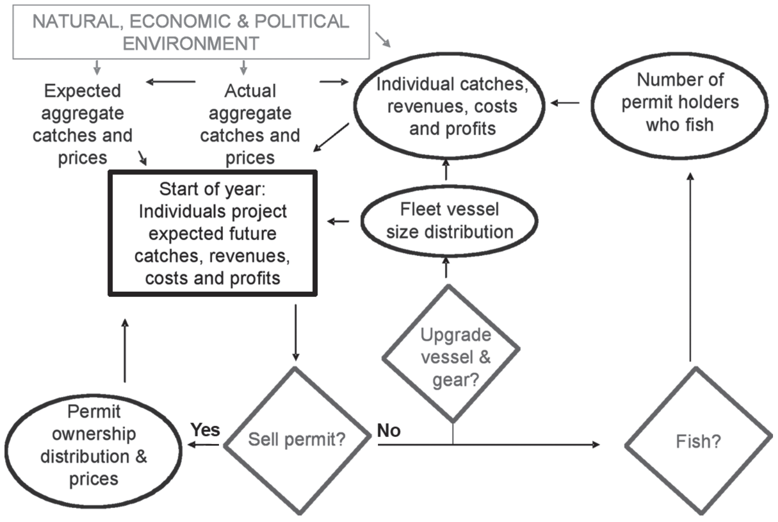


Figure 45. Agent-based model structure.

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. 46). As can be seen in Figure 44, 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.

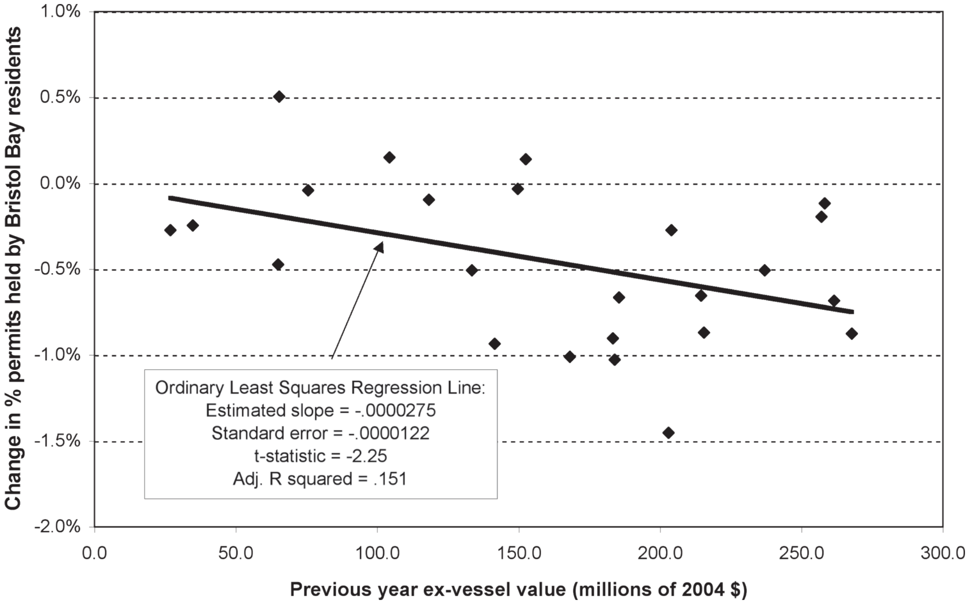


Figure 46. Bristol Bay ex-vessel value and change in local ownership share of permits.

Undergraduate Research

Since 1999 we have embedded an undergraduate class, “Aquatic Ecological Research in Alaska” within our field program of research. Each year, six students from the University of Washington spend about six and a 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, 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, and otolith collection from adult salmon. Finally, each student designs and conducts an independent study during the summer, and completes the sample processing, data analysis, and report preparation for this study in the fall.

The topics chosen by students vary from year to year, but we have elected to present the project report 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, graduate students and faculty, have been published in peer-reviewed scientific journals, and have thus contributed to the published literature and to the careers of the students.

The Spatial Distribution and Growth of the Parasite *Schistocephalus solidus* in Threespined Sticklebacks *Gasterosteus aculeatus* in Southwest Alaska

A Elliott-Buettner

Parasites are a common occurrence in the biological world. Some parasites cause deleterious effects on their host for the completion of their life cycle. *Schistocephalus solidus* is a hermaphroditic cestode that uses three intermediate hosts to complete its life cycle: copepods, threespine sticklebacks, and piscivorous birds. This study sought to ascertain the levels of parasitism of sticklebacks by *S. solidis* in different habitats of the Iliamna and Aleknagik lake systems in southwest Alaska. Parasite prevalence levels were higher in littoral areas despite the fact that the first intermediary host, copepods, live primarily in pelagic areas. In addition, bigger fish had higher prevalence of parasites than smaller fish. The question of why the littoral areas were more parasitized was not answered and awaits further investigation.

Egg Retention and Comparisons of Spawning Success of Female Sockeye Salmon (*Oncorhynchus nerka*) Between Two Lake Systems in Alaska

T Kleisborg

This study compared the relationship between egg retention and body length as well as how egg retention is affected by salmon population density. Seven female sockeye salmon populations were examined in two lakes in Alaska: Iliamna and Aleknagik. The purpose of this study was to determine whether (i) egg retention is greater among females in Iliamna Lake, (ii) larger females retain more eggs, and (iii) a high fish density causes a higher proportion of females to retain eggs. On the basis of the collection of 897 senescent female sockeye salmon, egg retention rates were higher in 2005 among females in Iliamna Lake than in Lake Aleknagik: 29% percent of the females in Iliamna Lake retained eggs whereas only 11% of the females in Lake Aleknagik retained eggs. The number of eggs retained ranged from zero to complete spawning failure, where none of the females eggs were spawned. For both lake systems, only 10% of the variation in number of eggs retained could be explained by a positive correlation with body length. There was no relationship between the density of sockeye salmon present and the percent of females retaining eggs.

Abundance and Age Composition of Coho Salmon in Whitefish Creek, Southwestern Alaska

D Luck

To aid the prioritization of habitat targets in stream conservation efforts and to help assess the degree to which salmonid habitats may overlap, we recorded the relative abundance and age composition of juvenile coho salmon in different habitats within a small creek—Whitefish Creek—in southwestern Alaska. Stick seines were used to sample fish from randomly selected sites along the entire stream. Each site was classified by habitat type, depth and velocity were measured, and coho caught there were enumerated and measured (fork length). Coho ≤75 mm were assumed to be young-of-the-year (YOY, age 0+) while fish >75 mm were assumed to be parr (age 1+). For comparisons between habitats, catch-per-unit-effort (CPUE) was used to estimate relative abundance, and the proportions of fish from each cohort were used to determine age composition. Both CPUE and age composition differed significantly between habitat types, but large values in a beaver-dam pool skewed these analyses: CPUE was >20 times greater there than in any other habitat, and the proportion of age 1^+ coho was 31% higher than the proportion for all other habitats combined. While differences in relative abundance between other habitat types were not significant, the proportion of age 1+ coho was greater in deep pools/riffles than in edge pools/glides. All coho caught in edge pools were YOY and edge pools had the second highest CPUE.

These results support previous work showing that beaver dams provide critical habitat for coho of all ages while edge pools may be important for YOY. Furthermore, these findings highlight the importance of maintaining habitats critical to various salmonid life-history stages and will help advance our understanding of how juvenile coho interact with other sympatric species.

Impacts of Salmon Spawning on Density and Assemblage of Benthic Insects in Alaska

K Shipe

Anadromous salmon act as ecosystem engineers when spawning by regulating the availability of resources to stream organisms including aquatic insects. A study by Moore et al. (2004) showed that salmon spawning can impact stream invertebrates directly and indirectly, as insect density decreased in areas where salmon actively spawned and also in areas from which salmon were excluded. My study was designed as a follow-up to test the hypotheses that insects in Bristol Bay, Alaska, are directly disturbed by salmon spawning activities and may also have evolved a seasonal emergence pattern either independent of or adapted to annual salmon spawning. Changes in insect density and assemblage were compared over time (before and after salmon entry into streams) in directly disturbed areas to less suitable spawning habitats: backwaters, where salmon create little to no annual spawning disturbance. A relative increase of insect density in backwater habitats suggested a direct disturbance and displacement effect, while a tendency for seasonal decrease in density across all streams and habitat types seemed to indicate a seasonal emergence pattern. A 3-way ANOVA resulted in significant creek by time and habitat by time interactions. Variable levels of change in density between creeks and habitat types in response to salmon spawning demonstrate the need for further comprehensive research in this area and others. No significant changes over time in the representation of the different insect orders in either habitat were discovered.

Intrapopulation Ontogenetic Habitat Segregation in Dolly Varden Char (*Salvelinus malma*)

J Thompson

Freshwater fish often use different habitats types during different developmental stages. Total fitness costs and benefits among the age groups drive this habitat segregation. We used mark–recapture data to define age groups, estimate abundance, and determine if ontogenetic habitat segregation was taking place among an isolated spring pond population of Dolly Varden char in southwest Alaska. The population was estimated by using the Chapman-Petersen equation. The small, shallow, open creek habitat had twice the total estimated population than the larger, deeper, more covered pond habitats. The creek also contained almost exclusively (94%) YOY, while the pond habitats had a more even distribution of the age groups (i.e., 1+, 2+, 3+). Density of fish in the creek was much higher than in the ponds, while biomass in the creek was less, indicating greater abundance, but much smaller-sized fish. Fish size correlated strongly with both average depth and area of each sample site. Ontogenetic habitat segregation is taking place among this population of Dolly Varden. Hypothetical fitness costs and benefits are proposed as the driving forces behind this segregation.

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, and are 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 of 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 will continue to grow rapidly over the next 2 years as we complete processing of archived hard-copy datasets. 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 at our website (*http://fish.washington.edu/research/alaska/data.html*) the following for each data set: (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 besides the summary data using our online data request form.

We made significant progress toward integrating all of our data into the ASPD during 2005. Activities during 2005 include the initial creation of the ASPD, development of the data section of our website, and the completion of processing seven multi-decadal datasets into the ASPD. The current contents of the ASPD are given in Table 12. In 2005 we also entered 285,000 records from data books for datasets that will be incorporated into the fatabase during 2006.

All future data collected by the Alaska Salmon Program will be 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 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.

Accomplishments for 2005, Goals for 2006

http://fish.washington.edu/alaska

A condition of recent program funding was to develop web-based resources for obtaining ASP datasets and as-

Table 12a. Summary of comprehensive datasets of the Alaska Salmon Program, collected from 1946 through 2005: Wood River, Kvichak and Chignik lakes data.

	Wood River						Kvichak		Chignik	
Data Type	Aleknagik	Nerka	Little Togiak	Beverley	Mikchalk	Kulik	Iliamna	Clark	Chignik	Black
Spawning ground surveys	1946–2005	1946–2005	1947–2005	1946–2005	1946–1980	1946–2005	1946–1984	1946–1984	1966–1972	1973–1980
Age data	1947–2005	1947–2005	1950–2005	1947–2005	1952–1980	1950–2005	2000–2005			
Townet sampling of juvenile sockeye and resident fishes	1958–2005	1957–2005	1958–2005	1958–1988		1958–1987	1961–2005	1962–1989	1961–2005	1961–2005
Beach seine sampling of sockeye and resident fish	1962–2005	1960–1970	1966–1983	1969–1969	1970–1970	1969–1969	1962–1983		1956–2005	1956–2005
Primary productivity	1961–2005	1961–2005	1961–2005	1961–2005		1961–2005	1961–2005		1961–2005	1961–2005
Water Clarity	1961–2005	1961–2005	1961–2005	1961–2005		1961–2005	1961–2005		1960–2005	1961–2005
Temperature- Depth profiles	1962–2005	1962–2005	1953–2005	1962–2005		1962–2005	1961–2005		2001–2005	2001–2005
Temperature- Year round	1998–2005	1998–2005	1998–2005	1998–2005		1998–2005	1990–2005			
Water Chemistry	1961–1967	1961–1967	1961–1967	1961–1967		1961–1967	1961–1965		1960–1963	1961–1963
Lake level	1952–2005	1952–2005					1961–2005		1960–2005	2001–2002
Weather	1946–2005	1946–2005					1946–2005		1955–2005	1955–2005
Zooplankton composition	1957–2005	1961–2005	1961–2005	1961–2005		1961–2005	1961–2005	1961	1961–2005	1961–2005
Solar Radiation	1961–2005						*		*	*
Spawning gravel measurements	1993–2002	1993					1993–2002			
Ice out date	1949–2005	1955								
Ice out & freeze dates							1969–2005			
Insect sampling	1969–2005									
Sockeye fry emergence									2000	

*Holdings being verified

Table 12b. Summary of comprehensive datasets of the Alaska Salmon Program, collected from 1946 through 2005: Egegik, Igushik Tikchik, Nunavagaluk, Naknet, Togiak and Ugashik lakes.

Data type	Egegik lakes	Igushik lakes	Tikchik lakes	Nunavagaluk	Naknek	Togiak lakes	Ugashik
Spawning ground surveys	1946–1959	1946–1959	1946–1967	1946–1954		1947–1967	1946–1949
Age data							
Townet sampling of juvenile sockeye and resident fishes		1974					
Beach seine sampling of sockeye and resident fish		1965–1981		1965–1965			
Primary productivity							
Water Clarity							
Temperature- Depth profiles							
Temperature- Year round							
Water Chemistry							
Lake level							
Weather							
Zooplankton composition							
Solar Radiation							
Spawning gravel measurements							
Ice out date							
Ice out & freeze dates	1975–1999				1972–2001		1976–1999
Insect sampling							
Sockeye fry emergence							

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

1. Research

We published overviews of the four major research areas:

- Salmon processors (industry)
- Biocomplexity and fisheries sustainability (NSF)
- Wild salmon ecosystems (Moore)
- Chignik Lakes (NOAA Fisheries)

Our goal is to publish further and more specific information—including research activities and results—to the respective research sections when appropriate.

2. 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.

In 2006, we have two objectives:

a. a searchable publication citation database
b. hyperlibrary expansion: we will be scanning many of the reports and peer-review publications to PDF files, and the webpage publication list citations will link to these as they become available.

3. Data

This component of the website was largely under development in 2005. A greatly expanded web-based data resource—including data collected from the program inception in the mid-1940s—was completed in April 2006. See previous page for further information.

In 2005, we provided daily online postings of the in-season 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.

4. Photo Gallery

A searchable photo gallery, including photos and descriptive information on various program components—biology, environment, socio-economics, infrastructure—was initiated. It remains in beta-testing, and we anticipate making this resource available in late 2006.

Facilities

We continued to upgrade and renovate the field facilities. Major projects undertaken in 2005 were as follows:

1. new foundations on the older Panabode at the Aleknagik camp and the small Panabode sleeping cabin at Porcupine Island;
2. installation of satellite internet with wireless at the Aleknagik, Nerka, and Porcupine camps and an internet connection at Chignik;
3. construction of a new 2-bedroom Panabode at the Nerka camp;
4. construction of a new lab/shop/storage building at the Chignik station;
5. replacement of many of our boat motors; and
6. construction of a new high-capacity septic system at the Aleknagik camp.

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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

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*

Appendices

Appendix A. Summary of ground-based spawning ground surveys of adult sockeye salmon in Wood River streams, 2003-2005. Note: stream temperature is for temperature at the bottom of the spawning reach unless noted otherwise. Live, natural, and bearkills include jacks for 2005.

Lake	Stream	Count	2003	2004	2005	Long-term average
Aleknagik	Big Whitefish	Date	8/15/03	8/13/04	8/27/05	1946-2002
		Estimated off mouth	0	400	150	198
		Live	1608	125	641	610
		Dead	330	71	352	87
		Natural	40	0	216	79
		Bear Kill	290	71	136	103
		Jacks	4	2	114	
		Total	1938	196	993	886
		Water temp	13	14	8	
	Yako	Date	8/5/03	8/4/04	8/6/05	1946-2002
		Estimated off mouth	2500	2000	1500	465
		Live	8503	3804	3487	1236
		Dead	1773	1838	4464	260
		Natural	866	1026	3132	288
		Bear Kill	907	812	1332	318
		Jacks	4	3	115	6
		Total	10276	5642	7951	1566
		Water temp		11	7	
	Bear	Date	8/9/03	8/8/04	8/9/05	1946-2002
		Estimated off mouth	500	1000	700	566
		Live	1811	606	3057	2041
		Dead	1613	2848	2765	554
		Natural	996	2414	2044	358
		Bear Kill	617	434	721	309
		Jacks	2	1	14	
		Total	3424	3454	5822	2741
		Water temp	11	9	7	
	Ice	Date	8/7/03	8/11/04	8/7/05	1946-2002
		98145	0	300		212
		Live	1878	3707	9935	4639
		Dead	5323	3915	9370	2843
		Natural	1206	1840	5108	2416
		Bear Kill	4117	2075	4262	627
		Jacks	2	4	11	
		Total	7201	7622	19305	7229
		Water temp	13	17	11	
	Sunshine	Date		8/19/04	8/16/05	1946-1982
		Estimated off mouth			200	1790
		Live		460	1836	29
		Dead		132	1923	124
		Natural		61	311	
		Bear Kill		71	1612	
		Jacks		0	0	
		Total		592	3759	950
		Water temp		11	10	
	Happy	Date	8/6/03	8/7/04	8/3/05	1946-2002
		Estimated off mouth	1200	900	500	451
		Live	6349	3723	4723	1922
		Dead	6915	7750	17595	713
		Natural	6020	6890	15487	2893
		Bear Kill	895	860	2108	1033
		Jacks	8	1	10	
		Total	13264	11473	22318	3719
		Water temp		9	9	

Appendix A—cont.

Lake	Stream	Count	2003	2004	2005	Long-term average
Aleknagik	Hansen	Date	8/5/03	8/6/04	8/6/05	1947-2002
		Estimated off mouth				529
		Live	1865	605	544	1689
		Dead	6955	2519	2365	649
		Natural	3833	823	1317	3231
		Bear Kill	3122	1696	1048	2275
		Jacks	25	22	378	31
		Total	8820	3124	2909	2990
		Water temp				
	Eagle	Date	8/11/03	8/10/04	8/20/05	1957-2002
		Estimated off mouth	1500	700	150	210
		Live	146	62	499	1001
		Dead	996	337	367	49
		Natural	105	26	244	38
		Bear Kill	891	311	123	147
		Jacks	2		29	
		Total	1142	399	866	1277
		Water temp	8	14	11	
	Mission	Date	8/13/03	8/14/04	8/18/05	1954-2002
		Estimated off mouth	0	100	0	96
		Live	1609	561	296	893
		Dead	753	80	270	35
		Natural	730	65	226	358
		Bear Kill	23	15	44	140
		Jacks	2	2	35	
		Total	2362	641	566	856
		Water temp	10	6	6	
Nerka	Fenno	Date	8/9/03	8/9/04	8/9/05	1946-2002
		Estimated off mouth	20	0	400	7
		Live	411	8064	3600	1608
		Dead	3819	11153	7123	1615
		Natural	1412	10515	6478	2545
		Bear Kill	2407	638	645	531
		Jacks	63	0	15	13
		Total	4230	19217	10723	3629
		Water temp	17	17	13	
	Pick	Date	8/12/03	8/16/04	8/16/05	1946-2002
		Estimated off mouth	200	700	500	237
		Live	2542	4894	6326	6625
		Dead	1459	2608	6731	2790
		Natural	253	1599	5527	1127
		Bear Kill	1206	1009	1204	888
		Jacks	1	0	28	6
		Total	4001	7502	13057	10391
		Water temp	10	9	9	
	Lynx	Date	8/22/03	8/22/04	8/22/05	1946-2002
		Estimated off mouth	2	1000	1500	360
		Live	520	5636	4219	2150
		Dead	69	2935	771	769
		Natural	33	1993	356	612
		Bear Kill	36	942	355	239
		Jacks	94	0	1	3
		Total	589	8571	4990	2936
		Water temp	15	16	12	

Appendix A—cont.

Lake	Stream	Count	2003	2004	2005	Long-term average
Nerka	Hidden Lake Cr	Date	8/19/03	8/18/04	8/18/05	1946-2002
		Estimated off mouth	0	1000	500	74
		Live	1795	5096	2546	1338
		Dead	1302	5711	2728	910
		Natural	201	4266	1831	638
		Bear Kill	1101	1445	897	497
		Jacks	25	0	5	9
		Total	3097	10797	5274	2373
		Water temp	12	15	15	
	Hidden Lake	Date	9/5/03	8/18/04	8/18/05	2000-2002
		Estimated off mouth				Hidden Lake Beach
		Live		978	426	574
		Dead		312	219	
		Natural				69
		Bear Kill				61
		Jacks				
		Total	176	1290	645	499
		Water temp				
	Elva	Date	8/24/03	8/21/04	8/21/05	1946-2002
		Estimated off mouth	250		230	231
		Live	9	73	62	151
		Dead	13	112	130	53
		Natural	3	85	89	20
		Bear Kill	10	27	41	18
		Jacks	0	0	1	
		Total	22	185	192	295
		Water temp	13		15	
	Sam	Date	8/10/03	8/2/04	8/8/05	1946-2002
		Estimated off mouth	200	2800		100
		Live	93	5590	1585	76
		Dead	558	1295	4122	140
		Natural	2	1197	2634	260
		Bear Kill	556	98	1488	1439
		Jacks	8	0	4	
		Total	651	6885	5707	1117
		Water temp	14	12	11	
	Joe	Date	8/10/03	8/10/04	8/7/05	1983-1984
		Estimated off mouth	0	500	325	90
		Live	68	2928	1784	78
		Dead	208	2688	2612	587
		Natural	7	2283	1818	
		Bear Kill	201	405	794	
		Jacks	17	0	5	
		Total	276	5616	4396	665
		Water temp	12		9	
	Stovall	Date	8/23/03	8/26/04	8/25/05	1954-2002
		Estimated off mouth	0	0	0	0
		Live	1281	1721	1889	814
		Dead	574	1377	606	714
		Natural	313	647	459	165
		Bear Kill	261	730	147	241
		Jacks	7	0	15	2
		Total	887	2024	1065	1531
		Water temp	14	17	13	

Appendix A—cont.

Lake	Stream	Count	2003	2004	2005	Long-term average
Nerka	Pike	Date	8/20/03	8/19/04	8/15/05	1970-2002
		Estimated off mouth	0	0	0	0
		Live	1403	1667	1437	654
		Dead	650	1356	990	206
		Natural	147	728	760	437
		Bear Kill	503	628	230	409
		Jacks	1	0	63	
		Total	2053	3023	2427	1260
		Water temp	13	14	14	
	Teal	Date	8/23/03	8/26/04	8/15/05	1970-2002
		98145	0	0	0	10
		Live	2	63	23	295
		Dead	2741	561	242	791
		Natural	16	199	28	240
		Bear Kill	2725	362	214	560
		Jacks	0	2	19	
		Total	2743	624	265	1090
		Water temp		15	17	
	Kema	Date	8/24/03	8/28/04	8/24/05	1955-2002
		Estimated off mouth	0	0		0
		Live	277	1068	2584	753
		Dead	239	1524	4212	1125
		Natural	30	1389	2837	251
		Bear Kill	209	135	1375	233
		Jacks	2	0	7	9
		Total	516	2592	6796	2043
		Water temp	14	12	13	
	Little Togiak River	Date	8/26/03	8/27/04	8/30/05	1947-2001
		Estimated off mouth	0	5000	2650	350
		Live	6718	13916	10485	5125
		Dead	41			229
		Natural	37			110
		Bear Kill	4			49
		Jacks				
		Total	6759	13916	10485	4485
		Water temp			14	
Little Togiak	A Creek	Date	8/14/03	8/16/04	8/18/05	1947-2002
		Estimated off mouth	200			91
		Live	0	137	162	16
		Dead	26	320	160	59
		Natural	0			16
		Bear Kill	26			80
		Jacks	0			
		Total	26	457	322	106
		Water temp	6			
	C Creek	Date	8/14/03	8/14/04	8/14/05	1947-2002
		Estimated off mouth				189
		Live	0	163	143	155
		Dead	71	193	66	224
		Natural	0			22
		Bear Kill	71			115
		Jacks	0			
		Total	71	356	209	342
		Water temp	8			

Appendix A—cont.

Lake	Stream	Count	2003	2004	2005	Long-term average
Beverly	Moose	Date	8/15/03	8/17/04	8/14/05	1955-2002
		Estimated off mouth	0	0	0	40
		Live	1145	2921	1521	1232
		Dead	334	1828	1431	1303
		Natural	49	494	1046	255
		Bear Kill	285	1334	385	312
		Jacks		0	23	2
		Total	1479	4749	2952	2254
		Water temp	14	17	18	
Kulik	Grant River	Date	8/22/03	8/21/04	8/31/05	98145
		Estimated off mouth	0	50		15
		Live	1905	4500	834	4585
		Dead	108	6/6/06	2812	1551
		Natural	26	1441	1584	1297
		Bear Kill	82	908	1228	580
		Jacks	0	1	8	1
		Total	2013	6849	3646	6410
		Water temp	13	1/15/1900		

Appendix B. Age composition of adult sockeye salmon determined by otolith sampling in Wood River and Kvichak River spawning sites, 2003–2004.

Lake	Location	Males						No. fish	Females						No. fish	Combined					
		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	0.03	0.00	0.96	0.01	113	0.00	0.00	0.05	0.00	0.95	0.00	100	0.00	0.00	0.04	0.00	0.96	0.01
	Bear Creek	0.00	0.00	0.54	0.00	0.46	0.00	97	0.00	0.00	0.47	0.00	0.53	0.00	98	0.00	0.00	0.50	0.00	0.50	0.00
	Hansen Creek	0.00	0.00	0.97	0.00	0.03	0.00	97	0.00	0.00	0.94	0.00	0.06	0.00	98	0.00	0.00	0.95	0.00	0.05	0.00
	Happy Creek	0.02	0.02	0.68	0.01	0.27	0.00	99	0.00	0.01	0.66	0.00	0.33	0.00	108	0.00	0.01	0.67	0.01	0.30	0.00
	Ice Creek	0.00	0.00	0.76	0.00	0.24	0.00	92	0.00	0.00	0.59	0.00	0.41	0.00	104	0.00	0.00	0.67	0.00	0.33	0.00
	Wood River	0.00	0.01	0.65	0.00	0.35	0.00	113	0.00	0.00	0.66	0.03	0.31	0.00	112	0.00	0.00	0.65	0.01	0.33	0.00
	Yako Creek	0.00	0.02	0.89	0.00	0.09	0.00	98	0.00	0.00	0.96	0.00	0.04	0.00	99	0.00	0.01	0.92	0.00	0.07	0.00
Nerka	Agulukpak River	0.00	0.00	0.02	0.04	0.93	0.01	107	0.00	0.00	0.02	0.04	0.93	0.01	100	0.00	0.00	0.02	0.04	0.93	0.00
	Anvil Bay	0.00	0.01	0.49	0.00	0.48	0.03	80	0.00	0.00	0.68	0.00	0.32	0.00	96	0.00	0.01	0.59	0.00	0.39	0.01
	Fenno Creek	0.09	0.00	0.65	0.00	0.26	0.00	103	0.00	0.00	0.83	0.00	0.17	0.00	103	0.05	0.00	0.74	0.00	0.21	0.00
	Hidden Lake Ck	0.06	0.01	0.79	0.00	0.13	0.00	97	0.00	0.00	0.88	0.01	0.11	0.00	107	0.03	0.01	0.84	0.01	0.12	0.00
	Kema Creek	0.00	0.02	0.85	0.00	0.13	0.00	54	0.00	0.00	0.95	0.01	0.03	0.01	96	0.00	0.01	0.91	0.01	0.07	0.01
	Lynx Creek	0.46	0.00	0.46	0.00	0.08	0.00	26	0.00	0.00	0.80	0.00	0.20	0.00	69	0.13	0.00	0.71	0.00	0.17	0.00
	N4 Beach	0.00	0.00	0.18	0.00	0.82	0.00	38	0.00	0.00	0.30	0.03	0.67	0.00	109	0.00	0.00	0.27	0.02	0.71	0.00
	N6 Beach	0.00	0.00	0.15	0.08	0.77	0.00	13	0.00	0.00	0.16	0.02	0.83	0.00	58	0.00	0.00	0.15	0.03	0.82	0.00
	Pick Creek	0.00	0.00	0.42	0.00	0.58	0.00	93	0.00	0.00	0.23	0.00	0.77	0.00	101	0.00	0.00	0.32	0.00	0.68	0.00
	Pike Creek	0.01	0.00	0.93	0.00	0.06	0.00	71	0.00	0.00	0.98	0.00	0.02	0.00	92	0.01	0.00	0.96	0.00	0.04	0.00
	Stovall Creek	0.05	0.00	0.79	0.00	0.16	0.00	96	0.00	0.00	0.83	0.01	0.15	0.01	100	0.03	0.00	0.81	0.01	0.15	0.01
Little Togiak	A Creek	0.00	0.00	0.75	0.00	0.25	0.00	4	0.00	0.00	0.50	0.17	0.33	0.00	6	0.00	0.00	0.60	0.10	0.30	0.00
	C Creek	0.00	0.00	0.53	0.29	0.18	0.00		0.00	0.03	0.53	0.19	0.25	0.00	32	0.00	0.02	0.53	0.22	0.22	0.00
	Little Togiak River	0.02	0.00	0.18	0.02	0.78	0.00	96	0.00	0.00	0.13	0.00	0.87	0.00	102	0.01	0.00	0.15	0.01	0.83	0.00
Beverley	Moose Creek	0.00	0.00	0.65	0.00	0.35	0.00	46	0.00	0.00	0.88	0.01	0.10	0.00	77	0.00	0.00	0.80	0.01	0.20	0.00
Kulik	Grant River	0.13	0.13	0.50	0.00	0.25	0.00	8	0.00	0.00	0.63	0.10	0.27	0.00	49	0.02	0.02	0.61	0.09	0.26	0.00
	Unweighted mean	0.04	0.01	0.56	0.02	0.37	0.00		0.00	0.00	0.59	0.03	0.38	0.00		0.01	0.00	0.58	0.02	0.38	0.00

Appendix B—cont. Kvichak River otoliths, 2003.

		Males						**No.**	**Females**						**No.**	**Combined**					
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
Iliamna	Chinkelyes Creek	0.00	0.16	0.45	0.22	0.14	0.04	102	0.00	0.00	0.30	0.46	0.19	0.05	100	0.00	0.08	0.38	0.34	0.16	0.04
	Copper River	0.00	0.01	0.06	0.38	0.32	0.23	98	0.00	0.00	0.05	0.23	0.33	0.38	99	0.00	0.01	0.06	0.30	0.32	0.31
	Finger Beach	0.00	0.04	0.65	0.10	0.10	0.10	49	0.00	0.00	0.25	0.50	0.25	0.00	4	0.00	0.04	0.62	0.13	0.11	0.09
	Fuel Dump	0.00	0.00	0.85	0.13	0.02	0.00	54	0.00	0.00	0.75	0.15	0.01	0.00	52	0.00	0.00	0.80	0.14	0.06	0.00
	Gibraltar Creek	0.00	0.03	0.40	0.16	0.38	0.03	98	0.00	0.00	0.29	0.16	0.52	0.03	94	0.00	0.02	0.34	0.16	0.45	0.03
	Knutson Bay	0.00	0.05	0.53	0.15	0.25	0.02	99	0.00	0.00	0.42	0.26	0.32	0.00	31	0.00	0.04	0.50	0.18	0.27	0.02
	Pedro Ponds	0.00	0.05	0.64	0.21	0.08	0.01	73	0.00	0.00	0.51	0.27	0.21	0.01	99	0.00	0.02	0.56	0.24	0.16	0.01
	Triangle Island	0.00	0.08	0.92	0.00	0.00	0.00	51	0.00	0.00	0.98	0.02	0.00	0.00	47	0.00	0.04	0.95	0.01	0.00	0.00
	Woody Island	0.00	0.05	0.81	0.05	0.09	0.00	57	0.00	0.00	0.88	0.04	0.08	0.00	51	0.00	0.03	0.84	0.05	0.08	0.00

Appendix B—cont. Wood River otoliths, 2004.

		Males						No.	Females						No.	Combined					
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
Aleknagik	Agulowak River	0.00	0.00	0.14	0.02	0.84	0.00	108	0.00	0.00	0.22	0.01	0.77	0.00	93	0.00	0.00	0.17	0.01	0.81	0.00
	Bear Creek	0.00	0.00	0.37	0.04	0.60	0.00	109	0.00	0.00	0.43	0.07	0.50	0.00	104	0.00	0.00	0.40	0.05	0.55	0.00
	Hansen Creek	0.00	0.00	0.64	0.14	0.22	0.00	252	0.00	0.00	0.71	0.11	0.17	0.00	381	0.00	0.00	0.68	0.12	0.19	0.00
	Happy Creek	0.00	0.00	0.38	0.06	0.55	0.00	110	0.00	0.00	0.60	0.15	0.25	0.00	107	0.00	0.00	0.49	0.11	0.41	0.00
	Ice Creek	0.00	0.00	0.22	0.03	0.76	0.00	111	0.00	0.00	0.48	0.05	0.48	0.00	105	0.00	0.00	0.34	0.04	0.62	0.00
	Wood River	0.00	0.00	0.41	0.04	0.54	0.00	68	0.00	0.00	0.69	0.08	0.24	0.00	119	0.00	0.00	0.59	0.06	0.35	0.00
	Yako Creek	0.01	0.00	0.47	0.16	0.35	0.01	110	0.00	0.00	0.49	0.16	0.35	0.00	108	0.01	0.00	0.48	0.16	0.35	0.01
Nerka	Agulukpak River	0.00	0.00	0.27	0.03	0.69	0.00	102	0.00	0.00	0.53	0.05	0.42	0.01	106	0.00	0.00	0.40	0.04	0.55	0.00
	Anvil Bay	0.00	0.00	0.76	0.02	0.22	0.00	108	0.00	0.00	0.89	0.02	0.09	0.00	103	0.00	0.00	0.82	0.02	0.16	0.00
	Fenno Creek	0.00	0.00	0.91	0.01	0.08	0.00	109	0.00	0.00	0.99	0.00	0.01	0.00	106	0.00	0.00	0.95	0.01	0.05	0.00
	Hidden Lake Creek	0.00	0.00	0.95	0.00	0.05	0.00	103	0.00	0.00	0.97	0.02	0.00	0.00	102	0.00	0.00	0.96	0.00	0.03	0.00
	Joe Creek	0.00	0.00	0.89	0.00	0.11	0.00	110	0.00	0.00	0.95	0.00	0.04	0.01	107	0.00	0.00	0.92	0.00	0.07	0.01
	Kema Creek	0.00	0.00	0.72	0.05	0.23	0.00	108	0.00	0.00	0.81	0.13	0.06	0.00	108	0.00	0.00	0.77	0.09	0.14	0.00
	Lynx Creek	0.00	0.00	0.95	0.00	0.05	0.00	112	0.00	0.00	0.99	0.00	0.00	0.00	102	0.00	0.00	0.97	0.00	0.03	0.00
	N4 Creek	0.02	0.00	0.96	0.00	0.02	0.00	56	0.00	0.00	1.00	0.00	0.00	0.00	43	0.01	0.00	0.98	0.00	0.01	0.00
	N4-N6 Beaches	0.01	0.00	0.86	0.00	0.01	0.03	72	0.00	0.00	0.94	0.00	0.05	0.00	104	0.01	0.00	0.91	0.01	0.07	0.01
	Pick Creek	0.00	0.00	0.58	0.00	0.42	0.00	97	0.00	0.00	0.84	0.00	0.16	0.00	103	0.00	0.00	0.72	0.00	0.29	0.00
	Pike Creek	0.00	0.00	0.85	0.00	0.15	0.00	108	0.00	0.00	0.95	0.02	0.03	0.00	98	0.00	0.00	0.90	0.00	0.09	0.00
	Sam Creek	0.00	0.00	0.81	0.00	0.19	0.00	101	0.00	0.00	0.93	0.01	0.06	0.00	100	0.00	0.00	0.87	0.01	0.12	0.00
	Stovall Creek	0.00	0.00	0.77	0.00	0.23	0.00	108	0.00	0.00	0.94	0.00	0.06	0.00	113	0.00	0.00	0.86	0.00	0.14	0.00
Little Togiak	A Creek	0.00	0.00	0.95	0.00	0.05	0.00	43	0.00	0.00	0.99	0.00	0.01	0.00	123	0.00	0.00	0.98	0.00	0.02	0.00
	C Creek	0.00	0.00	0.92	0.00	0.08	0.00	92	0.00	0.00	0.88	0.06	0.06	0.00	68	0.00	0.00	0.89	0.04	0.07	0.00
	Little Togiak Beaches	0.00	0.00	0.33	0.00	0.67	0.00	6	0.00	0.00	0.94	0.06	0.00	0.00	18	0.00	0.00	0.79	0.04	0.17	0.00
	Little Togiak River	0.00	0.00	0.82	0.00	0.18	0.00	103	0.00	0.00	0.97	0.02	0.00	0.00	102	0.00	0.00	0.89	0.00	0.01	0.00
Beverley	Moose Creek	0.00	0.00	0.75	0.02	0.23	0.00	101	0.00	0.00	0.95	0.00	0.05	0.00	102	0.00	0.00	0.85	0.00	0.14	0.00
Kulik	Grant River	0.00	0.00	0.87	0.00	0.13	0.00	113	0.00	0.00	0.98	0.00	0.01	0.01	107	0.00	0.00	0.92	0.00	0.07	0.01
	Unweighted mean	0.00	0.00	0.71	0.02	0.26	0.00		0.00	0.00	0.85	0.04	0.11	0.00		0.00	0.00	0.79	0.03	0.18	0.00

Appendix B—cont. Kvichak River otoliths, 2004.

		Males						No.	Females						No.	Combined					
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
Iliamna	Chinkelyes Creek	0.00	0.00	0.32	0.66	0.01	0.01	97	0.00	0.00	0.28	0.69	0.03	0.00	98	0.00	0.00	0.30	0.68	0.02	0.01
	Copper River	0.00	0.00	0.21	0.64	0.04	0.10	98	0.00	0.00	0.19	0.65	0.05	0.10	98	0.00	0.00	0.20	0.65	0.05	0.10
	Dream Creek	0.00	0.00	0.53	0.35	0.11	0.01	74	0.00	0.00	0.57	0.36	0.08	0.00	76	0.00	0.00	0.55	0.35	0.09	0.01
	Finger Beach	0.00	0.00	0.46	0.54	0.00	0.00	13	0.00	0.00	0.18	0.73	0.09	0.00	11	0.00	0.00	0.33	0.63	0.04	0.00
	Fuel Dump Island	0.00	0.00	0.02	0.96	0.02	0.00	50	0.00	0.00	0.02	0.96	0.02	0.00	50	0.00	0.00	0.02	0.96	0.02	0.00
	Gibraltar Creek	0.00	0.00	0.08	0.77	0.10	0.05	99	0.00	0.00	0.16	0.76	0.05	0.03	100	0.00	0.00	0.12	0.76	0.08	0.04
	Knutson Bay	0.00	0.00	0.05	0.87	0.08	0.00	97	0.00	0.00	0.02	0.93	0.05	0.00	98	0.00	0.00	0.04	0.90	0.07	0.00
	Pedro Ponds	0.00	0.00	0.26	0.69	0.04	0.01	98	0.00	0.00	0.18	0.71	0.11	0.00	99	0.00	0.00	0.22	0.70	0.08	0.01
	Tommy River	0.00	0.00	0.15	0.85	0.00	0.00	54	0.00	0.00	0.12	0.88	0.00	0.00	100	0.00	0.00	0.13	0.87	0.00	0.00
	Triangle Island	0.00	0.00	0.00	1.00	0.00	0.00	50	0.00	0.00	0.00	0.96	0.04	0.00	51	0.00	0.00	0.00	0.98	0.02	0.00
	Upper Talarik Creek	0.00	0.01	0.48	0.45	0.04	0.01	99	0.00	0.00	0.44	0.55	0.01	0.00	100	0.00	0.01	0.46	0.50	0.03	0.01
	Woody Island	0.00	0.00	0.04	0.92	0.04	0.00	50	0.00	0.00	0.02	0.94	0.04	0.00	51	0.00	0.00	0.03	0.93	0.04	0.00

Appendix B—cont. Wood River otoliths, 2005.

Lake	Location	Males						No. fish	Females						No. fish	Combined					
		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	0.18	0.00	0.78	0.03	109	0.00	0.00	0.26	0.00	0.73	0.01	93	0.00	0.00	0.22	0.00	0.76	0.02
	Bear Creek	0.01	0.00	0.37	0.01	0.58	0.03	158	0.00	0.00	0.57	0.00	0.40	0.03	159	0.01	0.00	0.47	0.00	0.49	0.03
	Eagle Creek	0.11	0.00	0.66	0.00	0.23	0.00	103	0.00	0.00	0.79	0.00	0.18	0.02	103	0.05	0.00	0.72	0.01	0.21	0.00
	Hansen Creek	0.14	0.00	0.74	0.00	0.12	0.00	126	0.00	0.00	0.88	0.00	0.12	0.00	123	0.07	0.00	0.81	0.00	0.12	0.00
	Happy Creek	0.01	0.00	0.22	0.00	0.75	0.02	134	0.00	0.00	0.33	0.00	0.64	0.04	137	0.00	0.00	0.28	0.00	0.69	0.03
	Ice Creek	0.00	0.00	0.22	0.00	0.75	0.02	105	0.00	0.00	0.34	0.00	0.61	0.06	107	0.01	0.00	0.28	0.00	0.68	0.04
	Mission Creek	0.12	0.00	0.80	0.00	0.08	0.00	109	0.00	0.00	0.94	0.00	0.06	0.01	108	0.06	0.00	0.87	0.00	0.07	0.01
	Sunshine Creek	0.00	0.00	0.17	0.00	0.79	0.04	48	0.00	0.00	0.29	0.00	0.70	0.01	109	0.00	0.00	0.25	0.00	0.73	0.02
	Whitefish Creek	0.17	0.00	0.52	0.00	0.30	0.01	111	0.00	0.00	0.76	0.00	0.23	0.01	106	0.09	0.00	0.64	0.00	0.26	0.01
	Wood River	0.03	0.00	0.74	0.01	0.21	0.01	97	0.00	0.00	0.78	0.00	0.22	0.01	116	0.01	0.00	0.76	0.01	0.21	0.01
	Yako Creek	0.02	0.00	0.43	0.00	0.53	0.02	101	0.00	0.00	0.49	0.01	0.46	0.04	108	0.00	0.00	0.46	0.01	0.50	0.03
Nerka	Agulukpak River	0.00	0.00	0.23	0.00	0.76	0.01	115	0.00	0.00	0.24	0.00	0.75	0.02	110	0.00	0.00	0.24	0.00	0.75	0.01
	Anvil Bay Beaches	0.00	0.00	0.31	0.01	0.64	0.04	97	0.00	0.00	0.54	0.03	0.42	0.01	118	0.00	0.00	0.44	0.02	0.52	0.02
	Elva Creek	0.08	0.00	0.38	0.00	0.54	0.00	13	0.00	0.00	0.62	0.02	0.36	0.00	42	0.02	0.00	0.56	0.02	0.40	0.00
	Fenno Creek	0.00	0.00	0.40	0.01	0.58	0.00	109	0.00	0.00	0.67	0.00	0.33	0.00	104	0.00	0.00	0.54	0.01	0.46	0.00
	Hidden Lake Creek	0.00	0.00	0.51	0.02	0.47	0.00	107	0.00	0.00	0.72	0.00	0.28	0.00	103	0.00	0.00	0.61	0.00	0.38	0.00
	Joe Creek	0.01	0.00	0.28	0.00	0.71	0.00	106	0.00	0.00	0.59	0.00	0.41	0.00	105	0.01	0.00	0.44	0.00	0.56	0.00
	Kema Creek	0.00	0.00	0.44	0.00	0.56	0.00	57	0.00	0.00	0.72	0.03	0.24	0.00	58	0.00	0.00	0.58	0.02	0.40	0.00
	Lynx Creek	0.00	0.00	0.29	0.00	0.71	0.00	21	0.00	0.00	0.56	0.00	0.44	0.00	34	0.00	0.00	0.45	0.00	0.55	0.00
	N4-N6 Beach	0.02	0.00	0.47	0.00	0.51	0.00	55	0.00	0.00	0.52	0.02	0.44	0.02	54	0.01	0.00	0.50	0.01	0.48	0.01
	Pike Creek	0.07	0.00	0.31	0.00	0.63	0.00	59	0.00	0.00	0.58	0.00	0.42	0.00	59	0.03	0.00	0.44	0.00	0.53	0.00
	Sam Creek	0.02	0.00	0.57	0.00	0.40	0.00	103	0.00	0.00	0.56	0.00	0.42	0.00	105	0.00	0.00	0.57	0.01	0.41	0.00
	Stovall Creek	0.05	0.00	0.29	0.00	0.66	0.00	62	0.00	0.00	0.38	0.00	0.62	0.00	58	0.03	0.00	0.33	0.00	0.64	0.00
	Teal Creek	0.36	0.00	0.36	0.00	0.29	0.00	14	0.00	0.00	0.86	0.00	0.14	0.00	14	0.18	0.00	0.61	0.00	0.21	0.00
Little Togiak	A Beach	0.00	0.00	1.00	0.00	0.00	0.00	1	0.00	0.00	1.00	0.00	0.00	0.00	4	0.00	0.00	1.00	0.00	0.00	0.00
	A Creek	0.00	0.00	0.55	0.00	0.45	0.00	98	0.00	0.00	0.68	0.01	0.31	0.00	201	0.00	0.00	0.64	0.01	0.35	0.00
	C Beach	0.00	0.00	0.00	0.00	0.00	0.00	0	0.00	0.00	1.00	0.00	0.00	0.00	1	0.00	0.00	1.00	0.00	0.00	0.00
	C Creek	0.01	0.00	0.43	0.03	0.53	0.01	80	0.00	0.00	0.56	0.00	0.43	0.00	102	0.01	0.00	0.50	0.02	0.47	0.01
	Little Togiak River	0.00	0.00	0.27	0.00	0.73	0.00	113	0.00	0.00	0.46	0.01	0.53	0.00	120	0.00	0.00	0.37	0.00	0.63	0.00
Beverley	Moose Creek	0.02	0.00	0.27	0.00	0.71	0.00	98	0.00	0.00	0.64	0.00	0.36	0.00	103	0.01	0.00	0.46	0.00	0.53	0.00
Kulik	Grant River	0.02	0.00	0.70	0.00	0.27	0.00	102	0.00	0.00	0.92	0.01	0.07	0.00	106	0.00	0.00	0.81	0.01	0.17	0.01
	Unweighted mean	0.04	0.00	0.42	0.00	0.49	0.01		0.00	0.00	0.60	0.01	0.35	0.01		0.02	0.00	0.54	0.00	0.42	0.01

Appendix B—cont. Kvichak River otoliths, 2005.

		Males						**No. of**	**Females**						**No. of**	**Combined**					
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
Iliamna	Chinkelyes Creek	0.01	0.00	0.49	0.12	0.27	0.10	99	0.00	0.00	0.36	0.14	0.43	0.07	98	0.01	0.00	0.43	0.13	0.35	0.09
	Copper River	0.00	0.00	0.30	0.26	0.39	0.06	98	0.00	0.00	0.21	0.32	0.35	0.12	98	0.00	0.00	0.26	0.29	0.37	0.09
	Dream Creek	0.00	0.00	0.17	0.27	0.49	0.06	95	0.00	0.00	0.10	0.34	0.52	0.04	98	0.00	0.00	0.13	0.31	0.51	0.05
	Gibraltar Creek	0.00	0.00	0.09	0.28	0.44	0.19	98	0.00	0.00	0.07	0.38	0.37	0.18	100	0.00	0.00	0.08	0.33	0.40	0.19
	Cottonwood Point	0.00	0.00	0.00	0.00	0.00	0.00	0	0.00	0.00	0.00	0.13	0.38	0.50	8	0.00	0.00	0.00	0.13	0.38	0.50
	Fuel Dump Island	0.00	0.00	0.00	0.29	0.29	0.43	21	0.00	0.00	0.00	0.15	0.48	0.37	27	0.00	0.00	0.00	0.21	0.40	0.40
	Porcupine Island	0.00	0.00	0.06	0.27	0.31	0.37	52	0.00	0.00	0.00	0.25	0.25	0.50	12	0.00	0.00	0.05	0.27	0.30	0.39
	Woody Island	0.00	0.00	0.06	0.32	0.26	0.35	31	0.00	0.00	0.06	0.15	0.36	0.43	53	0.00	0.00	0.06	0.21	0.32	0.40
	Knutson Bay Beach (October sample)	0.64	0.00	0.14	0.14	0.08	0.00	36	0.03	0.00	0.39	0.18	0.36	0.03	92	0.20	0.00	0.32	0.17	0.28	0.02
	Knutson Bay Beach	0.14	0.00	0.14	0.14	0.43	0.14	7	0.00	0.00	0.33	0.00	0.67	0.00	3	0.10	0.00	0.20	0.10	0.50	0.10
	Knutson Bay Creek	0.00	0.00	0.26	0.19	0.48	0.07	27	0.00	0.00	0.29	0.34	0.31	0.06	35	0.00	0.00	0.27	0.27	0.39	0.06
	Knutson Bay Slough	0.07	0.00	0.43	0.14	0.21	0.14	14	0.00	0.00	0.44	0.25	0.06	0.25	16	0.03	0.00	0.43	0.20	0.13	0.20
	Pedro Ponds- Berg's Pond	0.00	0.00	0.00	0.00	0.00	0.00	0	0.00	0.00	0.00	1.00	0.00	0.00	1	0.00	0.00	0.00	1.00	0.00	0.00
	Pedro Ponds- Big Pond	0.00	0.00	0.00	0.10	0.65	0.25	48	0.00	0.00	0.02	0.12	0.62	0.24	42	0.00	0.00	0.01	0.11	0.63	0.24
	Pedro Ponds- Trail Pond	0.43	0.00	0.21	0.29	0.00	0.07	14	0.00	0.00	0.42	0.17	0.00	0.42	12	0.23	0.00	0.31	0.23	0.00	0.23

Appendix C. Five-day averages of catches of emergent midges and water temperatures at 3 stations at Lake Aleknagik in 2003, 2004, and 2005.

2003

	Days	Catch per day				Temperature (°C)			
	4/28	B	H	W	Mean	B	H	W	Mean
June									
16-20	49	4	5	5	5	13.0	12.5	9.5	11.7
21-25	54	53	4	6	21	13.5	12.0	11.5	12.3
26-30	59	36	5	13	18	14.0	13.5	11.3	12.9
July									
1-5	64	54	7	7	23	13.5	13.5	13.5	13.5
6-10	69	17	24	9	17	16.0	15.3	15.3	15.6
11-15	74	6	3	16	8	17.0	14.0	13.5	14.8
16-20	79	4	11	41	19	18.0	15.2	14.3	15.8
21-25	84	2	12	139	51	18.0	15.8	11.5	15.1
26-30	89	7	11	42	20	16.5	16.0	16.0	16.2
31-4	94	2	10	5	5	17.8	16.5	17.0	17.1
August									
5-9	99	4	11	8	8	21.0	19.7	19.2	19.9
10-14	104								
15-19	109	1	1	15	6	14.3	14.5	15.3	14.7

2004

	Days	Catch per day				Temperature (°C)			
	ice out	B	H	W	Mean	B	H	W	Mean
June									
21-25		3	1	4	2	13.0	11.5	8.5	11.0
26-30		1	0	1	1	15.3	11.8	12.8	13.3
July									
1-5		2	0	0	1	17.0	15.3	13.5	15.3
6-10		6	6	0	4	20.5	17.8	20.0	19.4
11-15		38	53	1	31	20.0	18.8	14.5	17.8
16-20		26	6	2	12	17.0	15.7	13.2	15.3
21-25		3	7	10	6	18.5	17.3	13.8	16.5
26-30		6	4	6	6	16.0	14.8	13.5	14.8
31-4		13	5	8	9	18.0	16.0	16.8	16.9
August									
5-9		3	2	4	3	18.0	16.8	17.0	17.3
10-14		5	6	14	8	18.3	17.0	18.0	17.8
15-19		1	2	9	4	20.0	15.3	19.7	18.3
20-24			1	9	5	18.3	17.3	15.8	17.1
25-29		1	0	1	1	16.3	16.5	16.3	16.4
30-3		0	1	0	0	15.5	15.5	15.5	15.5

Appendix C—cont.

2005									
	Days	Catch per day				Temperature (°C)			
	ice out	B	H	W	Mean	B	H	W	Mean
June									
11-15		0	0	16	5	11.8	10.3	11.8	11.3
16-20		1	1	29	10	12.7	13.8	9.3	11.9
21-25		0	1	14	5	13.3	12.5	9.8	11.8
26-30		0	7	20	9	15.7	12.2	14.3	14.1
July									
1-5		9	0	1	3	16.0	18.0	13.0	15.7
6-10		2	14	54	23	16.3	16.3	15.0	15.9
11-15		165	13	165	114	15.5	17.0	15.5	16.0
16-20		35	5	63	34	14.5	15.0	12.0	13.8
21-25		20	2	16	13	16.0	15.5	13.5	15.0
26-30		13	10	10	11	16.0	16.0	15.0	15.7
31-4		15	10	10	11	17.5	17.0	14.0	16.2
August									
5-9		9	13	12	11	17.7	17.5	16.2	17.1
10-14		4	4	4	4	20.5	19.5	18.3	19.4
15-19		0	1	2	1	19.8	18.5	17.0	18.4
20-24		1	2	4	2	17.0	17.0	17.0	17.0
25-29		1	1	2	1	14.2	14.3	14.8	14.4
30-3		0	0	1	0	13.5	14.0	14.5	14.0
September									
4-9		0	0	0	0	13.5	14.0	13.0	13.5