Effects of climate and density on the distribution, growth, and life history of juvenile sockeye salmon (*Oncorhynchus nerka*) in Iliamna Lake, Alaska.

Harry B. Rich, Jr.

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Harry B. Rich, Jr.

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Committee Members:

Thomas P. Quinn

Daniel E. Schindler

Timothy E. Essington

Date: ____

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Abstract

Effects of climate and density on the distribution, growth, and life history of juvenile sockeye salmon (*Oncorhynchus nerka*) in Iliamna Lake, Alaska.

Harry B. Rich, Jr.

Chair of the Supervisory Committee:
Professor Thomas P. Quinn
School of Aquatic and Fishery Sciences

Physical features of lakes control the critical variables for the biotic community: temperature, light penetration, circulation, and chemistry, including nutrient inputs and outputs. Lakes not only vary greatly in these aspects but they may also have considerable internal heterogeneity that affects the abundance and distribution of organisms within them. Lakes with sockeye salmon span a wide range of latitudes, distances from the coast, altitudes and diverse physical attributes, but they share some key common features such as generally being oligotrophic and having relatively simple fish communities. Iliamna Lake in southwestern Alaska has a suite of characteristics that make it an interesting site for examination of lake processes and the ecology of juvenile sockeye salmon. In Chapter 1 we set out to 1.) characterize the trends in physical and biological characteristics pertaining to lake ecology and juvenile sockeye growth throughout Iliamna Lake, using data from 1962-1976, 2) determine whether the distributions (i.e., overall abundance) and density of sockeye fry, yearlings, and threespine sticklebacks are uniform throughout the major regions of the lake, 3) determine whether the sizes of

juvenile sockeye (fry and yearling) are similar in all regions or, if they differ, whether the differences are linked to spatial patterns of food availability, fish density, and temperature. We found significant trends across a west to east gradient in Iliamna Lake with regards to several physical characteristics such as water temperature ($p < 0 .001$), ice break up ($p = 0.070$), zooplankton density ($p = 0.022$) , spawning density, fish distribution and density, and juvenile sockeye sizes for 2 age classes across regions ($p < 0.001$for both ages). We believe these trends in distribution, density, and size are closely related to the ecological processes found within Iliamna Lake across these gradients.

The effects of density on growth and other aspects of performance have long been recognized by ecologists but evidence is mounting that global-scale changes in climate are also having significant effects on plant and animal populations. These effects are of particular interest when the species have commercial, recreational, and social values. Sockeye salmon (*O. nerka*) are of central importance to commercial and subsistence fisheries in Russia, Canada and Alaska, and as such are one of the best studied of the Pacific salmon. In Chapter 2 we used long term data (1962-2005) on juvenile sockeye salmon growth in Iliamna Lake in the Bristol Bay region of southwestern Alaska to determine the relative roles of climate and density in controlling growth and life history transitions in this species. We predicted that warmer conditions would be positively correlated with fry size at the end of the first summer and that high density of juvenile sockeye salmon (within and between brood years) was predicted to reduce body size. We used a class of Bayesian time series models known as dynamic linear models (DLM) to assess the relative contribution of important predictor variables in explaining the variation in sockeye fry length at the end of the first growing season. In all cases we found the best models included both estimates of temperature and density, however spring air temperature explained more variation in fry length than density of either age class of juvenile sockeye. Size of sockeye salmon fry at the end of their first growing season has implications on later life performance by influencing the size and age of smolts and the timing of their seaward migration.

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GENERAL INTRODUCTION

The University of Washington’s Fisheries Research Institute (FRI) began examining juvenile sockeye salmon (*Oncorhynchus nerka*) ecology in Iliamna Lake in the early 1960’s as part of their overall program on adult sockeye salmon ecology and management in Bristol Bay, Alaska. Iliamna Lake is the largest lake in Alaska and the largest sockeye producing lake in the world (2,622 km^2 surface area). Given its large size and physical setting, on the interface between tundra and mountains, Iliamna Lake provides a highly heterogeneous rearing environment for juvenile sockeye salmon. Iliamna Lake drains into the Kvichak River at its southwestern end, which has low-lying hills, an open tundra landscape, and few tributaries flowing into the lake. The western end of Iliamna Lake is wide and the shoreline contour is simple, and the lake is of uniform, shallow depth throughout this end. As you move across the lake to its northeastern end, Iliamna becomes progressively narrower and more confined as the landscape becomes mountainous; it becomes deeper with a very complex shoreline consisting of many protected bays and islands within the eastern end of the lake. Many tributaries flow into the lake at this end and the majority of the spawning habitat for adult salmon is found among the island beaches, mainland beaches and the tributaries flowing into the lake in the central and eastern end.

In addition to the spatial variation in physical features across Iliamna Lake, there are also two temporal components of variation in this system, one related to climate and one related to density. Regional climate indexes have shown that a significant regime shift to warmer conditions occurred around 1977. There is also growing evidence that general climate warming, which is experienced more dramatically at higher latitudes, has led to differences in climatic features around Iliamna Lake such as air and water temperature, and the timing of ice cover in the winter and of ice breakup in the spring. In addition to these climate-related temporal changes, Iliamna Lake is also noted for its highly variable levels of sockeye salmon abundance, from lows of a few hundred thousand adult salmon to over 40 million in a given year.

Iliamna Lake thus provides an interesting location to examine the interplay of significant changes in density and physical characteristics over both space and time. The overall objectives of this thesis project were to 1) summarize lake-wide processes affecting juvenile sockeye growth and distribution by examining temperature, zooplankton density, density of sockeye salmon and threespine sticklebacks, and growth of juvenile sockeye salmon in the west, central, and east regions of the lake, and 2) quantify the relative contributions of climate and density on juvenile sockeye growth over a long time series of data collected in the eastern region of Iliamna Lake (1962-2005).

CHAPTER 1

Physical and biological characteristics affecting the distribution and growth of juvenile sockeye salmon in Iliamna Lake, Alaska.

INTRODUCTION

Lake systems are important integrators of ecological processes, and the physical features of the lake strongly affect its productivity and community structure. Some of the key lake specific characteristics are its location (latitude, altitude, proximity to the coast, etc.), how it was formed, the size and shape (area, depth, shoreline complexity) of the basin, and the size, topography, geology and chemistry of its watershed (Horne and Goldman 1994). These physical features of the lake control the critical variables for the biotic community: temperature, light penetration, circulation, and chemistry, including nutrient inputs and outputs, pH, and other attributes. Lakes not only vary greatly in these aspects but they may also have considerable internal heterogeneity that affects the abundance and distribution of organisms within them. In addition, there are daily, seasonal, annual, and inter-annual cycles in many of these physical attributes that may vary among regions of the lake, and the biological consequences of this variation may be important for the population structure, life history, and diversity of fish populations.

In many coastal lakes draining into the North Pacific Ocean from Washington State north through British Columbia and Alaska, west to Russia, and south to Japan, juvenile sockeye salmon, *Oncorhynchus nerka,* are among the numerically dominant planktivores. Adult sockeye salmon characteristically spawn in the late summer and fall in streams associated with lakes, the fry emerge and migrate to the lake to feed in spring, and spend one or two years rearing in the lake prior to seaward migration (Burgner 1991).

In warmer and more productive lakes, especially at the southern end of their range, sockeye spend just one year rearing in the lake whereas in more northern, colder and less productive lakes a larger fraction of a given cohort may stay in the lake for a second year of growth. The percent of a given cohort that migrates to sea as age-1 or age-2 smolts among years in a given lake is also correlated with factors affecting growth (chiefly temperature and density; Burgner 1987). Although the lakes with sockeye salmon span a wide range of latitudes, distances from the coast, altitudes and diverse physical attributes, they are generally oligotrophic and have relatively simple fish communities. Juvenile sockeye salmon are often the most abundant planktivore, commonly competing with threespine sticklebacks (*Gasterosteus aculeatus*), a species that spawns in spring in the littoral zone. Both species feed in littoral habitats but the sockeye salmon typically shift to the limnetic zone later in their first summer (Rogers 1973, Burgner 1991, Abrey 2004). While in the near shore areas, sockeye fry feed primarily on aquatic insects, shifting to crustacean zooplankton as they move to offshore areas later in the summer. Sockeye growth is mediated primarily by temperature and food availability with lake characteristics such as location, morphology, and nutrient loads playing a critical role in addition to density and competition (Quinn 2005). Intraspecific competition for food can depress growth in many lakes (Burgner 1991). Diet overlap and competition for food between sockeye and threespine sticklebacks has also been shown in experimental enclosures (O'Neill and Hyatt 1987) but the importance of interspecific competition in natural systems is not always evident (Jaenicke et al. 1987). Sockeye salmon fry are preyed upon by resident salmonids such as Arctic charr (*Salvelinus alpinus*), Dolly

Varden (*S. malma*), coastal cutthroat (*O. clarki clarki*) and rainbow trout (*O. mykiss*), as well as birds, mammals, and some other fishes.

Iliamna Lake in southwestern Alaska is the largest lake in Alaska, and with a surface area of 2,622 km^2 is by far the largest sockeye salmon-producing lake in the world (Burgner 1991). In addition to its large size, Iliamna Lake has a suite of characteristics that make it an interesting site for examination of lake processes and the ecology of juvenile sockeye salmon. First, there is a marked west to east cline in many important physical and biotic attributes. The outlet of the lake is in the west, and the large western region is wide (ca. 30 km), shallow with uniform depth (avg ~ 38 m), has few islands, low shoreline complexity, and the surrounding watershed area is low-lying tundra with few streams flowing into the lake. Towards the east the lake becomes more confined as it is surrounded by mountains of both the Alaskan and Aleutian ranges, there are many islands and bays making for a complex shoreline, and the lake becomes progressively deeper (avg ~ 84 m) and achieves a maximum depth of 301 m.

Iliamna Lake is also characterized by large and variable abundance of sockeye salmon, with counts of adults escaping the fisheries ranging from 250,000 to over 24 million. For many years the abundance showed a cyclic pattern with peaks every 4-5 years (Eggers and Rogers 1987). As with the physical features, the use of the lake by sockeye salmon shows a west-east gradient. Of 93 documented spawning locations, 46 are found in the eastern region of the lake, which comprises just 12% of the total surface area (Demory et al. 1964).

The Fisheries Research Institute (FRI) of the University of Washington began studying the ecology of Iliamna Lake with an emphasis on juvenile sockeye salmon in

1961. Studies examined patterns of primary and secondary production, temperature and climatological conditions, and the abundance, distribution, and size of juvenile sockeye salmon and resident fishes. Results of some of the early FRI work were summarized by Burgner (1964), Burgner et al. (1969) and Mathisen (1969) and details were archived in FRI circulars, annual reports and other in-house publications. Data collection has continued, with varying levels of intensity and geographic scope, to the present. The purpose of this chapter is to synthesize this large body of work, providing a coherent picture of the ways in which the geographical features of the lake affect the distribution and growth of the juvenile sockeye salmon. The specific objectives of this study were to: 1) summarize the trends in physical and biological characteristics pertaining to lake ecology and juvenile sockeye growth throughout Iliamna Lake, using data from 1962-1976, 2) determine whether the distributions (i.e., overall abundance) and density of sockeye fry, yearlings, and threespine sticklebacks are uniform throughout the major regions of the lake, 3) determine whether the sizes of juvenile sockeye (fry and yearlings) are similar in all regions or, if they differ, whether the differences are linked to spatial patterns of food availability, fish density, and temperature. We expected to see higher densities of fry in the eastern end of the lake, where spawning densities are higher, and we expected to see yearling sockeye salmon move into the central and western areas of the lake where densities are lower.

METHODS

Water temperature:

Surface water temperature was measured at night in association with tow net operations to catch sockeye salmon and other limnetic fishes (see details below). Monthly averages were calculated for August and September between 1962 and 1976 when the majority of the towing operations were conducted. Surface temperature data were pooled across years and combined into three regions of the lake (west, central, and east). Average monthly temperatures from each region were compared using analysis of variance. Temperature at depth data were collected from discrete sites in Iliamna Lake between 1968 and 1976 using bathythermograph casts from the surface to water as deep as 130 m. Data from one station/site within each region, collected in July and August, were plotted for comparison between regions.

Ice cover:

The day when ice left the lake ("ice-off") was recorded annually from all three regions (west, central, and east) of Iliamna Lake between 1962 and 1976, based on the first day of the spring when the lake was clear enough of ice to navigate a boat safely from one side or end of the lake to the other. This date is somewhat subject to personal judgment and the motivation of the observer to cross the lake. Nevertheless, the loss of ice cover is a very fundamental component of the seasonal changes in lake ecology, as the ice greatly reduces light penetration and prevents water column mixing and the subsequent increases in primary and secondary production that follow in the long days of early summer at this latitude (Iliamna Lake- 59° 46'N). Data were collected by local residents, pilots, and ADF&G personnel, and compiled by FRI researchers. Average ice off day by region was compared using an analysis of variance.

Zooplankton:

Zooplankton were collected from 1963-1976 by FRI researchers using a 243 um mesh conical net with a 0.5 m opening. Vertical hauls were made from 100 m at approximately 1m/sec (or from near the bottom at stations shallower than 100 m). Zooplankton densities were calculated as geometric mean # organisms/m^3. We used total zooplankton abundance collected from sites located in four lake regions (in a west to east cline such that Region I was western most and Region IV was the eastern most) in June, July, and August. June data was thought to give the best estimate of standing crop prior to heavy grazing effects from emerging sockeye salmon fry. Any predation effects on zooplankton at this time should arise from yearling sockeye salmon. Some caution must be exercised in interpreting data on standing crop as a measure of food supply as it does not take into account rates of production, and sampling variance can be large. Nonetheless, average zooplankton densities were pooled across years and regional averages (I – IV) were compared using an analysis of variance for each month.

Tow Net Sampling:

Juvenile sockeye have been sampled by FRI staff each summer since 1962 using tow-nets. The 3 x 3 m opening net is towed at the lake's surface behind and between two boats for 20 minutes at approximately 3 km/hr. Towing began approximately an hour after nightfall, to allow juvenile sockeye to undergo their diel vertical migration to surface waters to feed (Scheuerell and Schindler 2002). The tow netting was conducted in the top 10 m of the water column, and would certainly have missed fish distributed deeper, and as such is only an index of abundance and density. Catches were identified to species, measured for fork length, and a subsample was weighed. Large catches were randomly sub sampled, and fish not kept for later measurement were returned to the lake.

Sampling took place throughout the lake from 1962-1976, and FRI subdivided the lake into 11 lake sections, numbered from west to east (Figure 1.1). The section classifications were used to aid repeat sampling, data collection, and organization. We have also divided the lake into three larger regions to facilitate regional comparisons, combining lake sections 1-3 into the west region, lake sections 4, 5, 10, and 11 into the central region, and lake sections 6-9 into the east region.

The two age classes of juvenile sockeye in Iliamna Lake, age-0 (fry) and age-1 (yearlings) were distinguished by inspection of length frequency histograms and length-weight relationships (Figure 1.2). Within each year the two age classes were readily distinguished, however, some size overlap did occur.

Index of abundance and density:

The tow net catches provided a relative measure of abundance across years for the limnetic fishes. An annual weighted index of relative abundance was calculated for sockeye salmon fry and yearlings, and threespine sticklebacks. These three fish types comprised over 95% of all fish caught during tow net operations. Ninespine sticklebacks (*Pungitius pungitius*) comprised about 4% of the tow net catch, with the remainder being least cisco (*Coregonus sardinella*), lamprey (Petromyzontidae spp.), sculpins (*Cottus* spp.), and pond smelt (*Hypomesus olidus*), in descending order of abundance. The index was calculated using the geometric mean of catch +1 for all tows conducted within a lake section, multiplied by the percent lake area of that sampling section (Table 1). As catch data were highly variable, the geometric mean was used so that extreme catch values were not over influential, and catch +1 was used as zeroes appear in the catch values. The section specific indexes were then summed to obtain the whole lake estimate of abundance by fish type (fry, yearling, and threespine stickleback) for that year. To provide an estimate of distribution throughout the lake (i.e., in what section of the lake are most of the fish found?), the annual index values for each lake section (as calculated above) were summed for each year from 1962-1976. Catch data used to calculate the index were restricted to towing conducted in August and September, to allow for offshore movement to the limnetic zone by fry, where they would be available for tow-net sampling. Additionally, the percent of each fish type caught by section was calculated using the cumulative weighted geometric mean catch +1 index (1962-76). The cumulative index for each lake section (1-11) was used, such that a section specific percent composition by fish type (fry, yearling, threespine stickleback) of the catch could be determined.

Estimates of relative fish densities were calculated using the geometric mean of catch +1 (by fish type) for all tows conducted within a lake section. The weighting factor used in the relative abundance index was not applied because the purpose was to estimate local density, not abundance in a broader region of the lake. Year specific densities were then calculated using the geometric mean of each fish type caught per tow in all sections. The cumulative density estimates were calculated by taking the average of the average annual values (1962-1976).

Fish size by region:

To determine if sockeye salmon fry and yearlings were uniform in size among the lake regions, we used the data (over 55,000 fish measured) collected from all lake areas between 1962 and 1976. Within each year, we subtracted the year specific ice off day from the date caught to get an estimate of number of growing days each fish had experienced. As only marginally significant differences between regions for ice off day were shown, we used the annual ice off day in the east region to calculate the number of growing days for all fish in all regions. Fish were binned into region of capture (west, central, or east) corresponding to the lake section scheme described above. The average length of fry caught from each region on each specific growing day was calculated. Because of the highly variable sample sizes and the wide variation around each mean, we employed a weighted least square (WLS) regression technique to compare slopes and intercepts (Neter et al. 1983).

We removed the confounding effect of growing day on average length by using Analysis of Covariance (ANCOVA) and used average length as our dependent variable, growing days as our independent variable, and region (west, central, and east) as our fixed grouping factor. Our weighting factor (w_i) was calculated as the inverse of the standard error of the mean of each daily average from each region.

Differences in elevations of these regression lines reflect differences in average length for a common growing day, whereas differences in slope would indicate that the relationship between length and growing days differed between the three regions. We first tested for differences in the slopes of the lines relating average length to growing days, (i.e. the interaction term from the ANCOVA). If this term was not significant, it was removed, and the model run again revealing the effect of the grouping term (region) and allowing comparisons of average length at a common growing day (adjusted mean lengths). For each age class of juvenile sockeye (fry or yearling) the reported means and associated confidence intervals were calculated at the grand mean of the independent variable (i.e. growing day). These are standard procedures for removing the effects of a covariate (Huitema 1980).

RESULTS

Water temperature:

An analysis of variance of the mean surface water temperatures in August (west, n = 226; central, n = 206; east, n = 226) revealed a significant difference between regions ($p < 0.001$). The temperatures in the west (10.94°C) and central (10.97°C) regions were not significantly different from each other ($p = 0.979$) but both were significantly warmer than the east region (9.81°C, $p < 0.001$; Tukey's post-hoc test). A similar pattern was seen in September (west, n = 43; central, n = 150; east, n = 226). The eastern region (mean = 9.22°C) was significantly cooler than the west (mean = 10.63°C; $p < 0.001$) and central regions (mean = 10.43°C), but the temperatures in the west and central regions were not significantly different from each other ($p = 0.752$).

Temperature at depth data collected from bathythermograph casts made at a discrete, consistent location in each of the three regions were pooled across the years 1968-76, and monthly averages were calculated for July and August (Figure 1.3). Consistent with the surface temperature data, the western and central regions were warmer than in the eastern region of Iliamna Lake. There was a greater difference between the three regions in the August temperatures over the first 40 m of depth, but both central and east converged in temperature at approximately 40 m. The temperature differences between regions were less pronounced in July, although the temperatures from the east and central sections converged about 10 m deeper in July. Temperatures in the west region were taken at a much shallower location, so only reveal temperatures through the first 30 m of the water column, but were warmer than the east and central areas in both months.

Ice off:

Analysis of variance of the mean ice off dates across this time series gave some evidence of a difference between regions (p = 0.070; west = day 153, central = day 146, and east = day 139; Figure 1.4). Tukey's post-hoc test revealed a marginally significant difference between west and east (p = 0.056), but no difference between west and central regions (p = 0.456) or central and east regions (p= 0.467). In general, ice appears to leave the eastern end about seven days earlier than in the central region, and about 14 days earlier than the west region, but the average dates vary considerably among years, reducing the power to detect regional differences.

Zooplankton:

Data on zooplankton standing crop were collected in June, July, and August each year from 1963-1976 from four regions (I-IV, from west to east) in Iliamna Lake. We tested mean values of zooplankton densities in June, at the beginning of the summer season, as our metric of food availability (data were not collected in June from Regions I – III in 1973-75, from Region IV in 1974-75, and from Region I in 1976; Figure 1.5). ANOVA revealed a significant difference between regions with a strong west-east gradient (p = 0.022; I. west = 5720.3/m^3 , II. central = 4967.3/m^3 , III. central 2 = 4251.7/m^3 , IV. east = 3335.0/m^3). Tukey's post-hoc test revealed significant differences between the western and the eastern regions (I – IV, p = 0.017), but not between the west and the 2 central regions (I – II, p = 0.768; I – III, p = 0.250). There was no significant differences between the two central-most regions (II – III, p = 0.782), nor between either of these two regions and the eastern region (II – IV, p = 0.142; III – IV, p = 0.610). The decreasing west to east gradient in zooplankton standing crop was observed in July and

August as well (Figure 1.5), along with a marked increase in zooplankton densities from June to August.

Fish distribution:

The weighted (by percent surface area) tow net catch index was an attempt to estimate the distribution of fish over large geographical areas. The west region, which is large (60% of surface area), comprised only16% of the total cumulative index. The central region is 29% of the surface area and contained an estimated 53% of the fish. The east region is only 12% of the surface area and contained 31% of the fish. The cumulative weighted geometric mean index of abundance showed that sockeye fry were the predominant fish type in the eastern region (sections 6-9; Figure 1.6). Fry were also abundant in the central region of the lake and their abundance diminished towards the west. Sockeye yearlings were most abundant in the central region (sections 4 and 5), followed by the western areas (sections 2 and 3). Threespine sticklebacks were most prevalent in lake sections with complex shorelines and protected bays, such as sections 10, 11, 4, and 8. Examination of the data by percent caught revealed an even stronger pattern of fry predominance in the eastern region (sections 6-9) of Iliamna Lake, where fry were 44 to 57% of the total catch (Figure 1.7). Yearling sockeye salmon were most prevalent as a percent of the catch in the central and western regions, but primarily in the open water sections (2, 3, 4, and 5). Threespine sticklebacks showed the most uniform distribution, with the exception of section 11, a shallow, complex, and protected bay, where they comprised over 75% of the catch.

The catch data were also examined without using the surface area weighting factor, to estimate relative fish densities. All three fish types (fry, yearling, and threespine sticklebacks) generally increased in density from west to east (Figure 1.8). The sockeye fry density estimates showed a striking, 15-fold west to east increase (west average = 4.5 per tow; central average = 34.8 per tow; east = 69.6 per tow). The highest densities of yearling sockeye salmon were also in the eastern sections (average 14.9 per tow), with 12.6 per tow in the central and 3.4 per tow in the western regions. Densities of threespine sticklebacks were also generally higher in the eastern region of the lake, except in the relatively shallow and complex habitat of section 11 (> 205 per tow). As a percentage of the catch within each area, sockeye salmon fry predominated in the eastern region, yearling sockeye were predominant in the western region, and sticklebacks were the majority of the catch in the central region (Figure 1.7).

Fish size by region:

We examined the lengths of age-0 and age-1 sockeye salmon across the growing season for 15 years (1962 -1976), from the west, central and east regions of Iliamna Lake. First, we investigated whether the average length of sockeye fry differed between regions (west, n = 2,599; central, n = 11,958; east, n = 40,402) after standardizing for date after ice off ("growing days" of the season). There was no interaction between growing days and region ($p = 0.256$), and a direct comparison of mean length at a common number of days in the growing season (Figure 1.9) revealed a significant difference between regions ($p < 0.001$). The adjusted mean lengths at a common growing day (day 104.5 grand mean of growing days) were similar in the west (lower confidence interval < mean < upper confidence interval; 53.4 mm < 56.2 mm < 59.0) and central (55.2 mm < 56.6 mm < 58.0 mm) but smaller in the east (51.0 mm < 51.7 mm < 52.5 mm) for fry. The lower and upper 95% confidence intervals for the east region did not overlap with the 95%

confidence intervals from the central and the west; however the 95% confidence intervals for the west and central regions overlapped.

Yearling sockeye salmon showed a similar pattern of size among regions. There was no interaction between growing days and region ($p = 0 .357$), and a direct comparison of mean length at a common number of days in the growing season (Figure 1.10) detected a significant difference between regions ($p < 0.001$). With day 79.6 set as the common growing day (grand mean of growing days), the fish were largest in the west (lower confidence interval < mean < upper confidence interval; 86.2 mm < 87.8 mm < 89.4 mm), intermediate in the central region (83.6 mm < 85.1 mm < 86.6 mm), and smallest in the east (76.8 mm < 77.9 mm < 79.0 mm). The lower and upper 95% confidence intervals for the east region do not overlap with those from the west and central regions, while the 95% confidence intervals from the west and central did overlap with each other (albeit only slightly).

DISCUSSION

We found clear and consistent trends in both physical and biotic features of Iliamna Lake across a west to east gradient. As the lake flows towards its outlet in the west it becomes progressively wider, less confined by mountains, and shallower. The average surface temperatures in the eastern region were about a 1.1°C cooler in August and about 1.3°C cooler in September than the western region. Qualitative examination of temperature at depth profiles showed the same general trend in the epilimnion for both July and August, cooler temperatures are seen in the eastern region. Paradoxically, ice has been leaving the lake earlier in the east end of the lake, averaging about 14 days earlier than the west end and about 7 days earlier than the central region, though there is considerable variation among years in all regions. The geographical layout and structure of how Iliamna Lake is situated likely influences these differences in temperature and ice patterns.

Despite the later date of ice-off, June zooplankton densities (geometric mean number/m^3) were also higher in the western region of the lake, decreasing towards the east. Production rates might also be higher in the shallower and warmer regions (west and central) of the lake, although zooplankton production is not solely temperature driven (Shuter and Ing 1997). We reported standing crop densities in June to minimize the grazing effects that planktivorous juvenile sockeye were likely to have. At this time in the season, most of the zooplankters are comprised of over-wintered adults and/or later stage copepodids (Gunnerod 1971, Carlson 1973). Additionally, we would primarily expect to see age-1 juvenile sockeye salmon in the limnetic zone at this time of year rather than fry, so any grazing effects would be expected to be higher in the western and central regions of the lake where these older juveniles were numerous. Our data revealed that zooplankton densities nonetheless were higher in the western and central regions and lower in the eastern region. Both Gunnerod (1971) and Carlson (1973) reported maximum mortality rates for zooplankton in mid to late July, corresponding with juvenile fry migration to limnetic habitats. The west-east gradient in zooplankton densities was maintained all summer as overall densities increased (Figure 1.5). Thus the prey resources available to limnetic fishes seemed to be greater in the western end of the lake, where warmed temperatures would also facilitate faster growth (Brett 1971).

Fish distribution:

In contrast to the favorable growing conditions in the western part of the lake, most spawning grounds for sockeye salmon are in the eastern region. Demory et al. (1964) listed about 50% of the documented spawning grounds in the east region, which accounts for only 12 % of the lake's surface area. Alaska Department of Fish and Game (ADF&G) reported that for this period (1962-76), on average of 40% of the salmon counted in aerial surveys of spawning grounds were in the eastern region (range: 4% to 66%).

We found significant regional differences in distribution of the two age classes of sockeye salmon (fry and yearling) and threespine sticklebacks. The weighted index revealed patterns of an extrapolated overall distribution of the fish types by lake section across this 15 year time series. In general, most of the fish were in the central region of the lake (sections 4, 5, 10, 11). The east region, which is smallest, contained the next largest number, and the large western are contained the fewest fish overall. The western end of the lake is shallow and the eastern end is very deep, so if anything the surface tow net catches might underestimate the relative abundance of fish in the eastern end because the fish would have more water in which to distribute themselves beyond the reach of our sampling.

Sockeye salmon fry were comparably abundant in both the east and central regions (101.7 and 105.1 cumulative index respectively) but markedly lower in the west region (39.3 cumulative index). Sockeye fry dominated both the density and percent caught in the east region (sections 6-9). The geometric mean number of sockeye fry per tow was about 2x greater in the east than in the central region, and over 10x greater than that in the west region. Given that spawning density is higher in the east end, with about 50% of the Iliamna Lake spawning grounds located in this small area, and the large proportion of the active spawning composition accounted for by this area (as counted from aerial surveys), this was not unexpected. Other physical features such as increased depth and more complex habitat along the network of islands, island beaches, and bays in the east end may also provide beneficial rearing habitat earlier in the growing season and deeper water refuge from predators for sockeye fry once they move into limnetic waters. These concentrations of fry may have multiple effects on fry growth and survival. As fry density increases, competition for food becomes more acute, especially as zooplankton densities and temperatures are lowest in this region. With higher density and lower food availability, the number of zooplankton per fish would be markedly lower in the east, along with colder temperatures at which to digest the food. Many studies have shown reduced capacity for growth when densities and thus intraspecific competition are high (Koening and Burkett 1987, Burgner 1987, Mazumder and Edmundson 2002, Schindler et al. 2005). Conversely, high densities may be advantageous to sockeye fry in terms of predator avoidance. Sockeye fry school during the day below the thermocline to reduce exposure to predators and optimize digestion efficiency (Levy 1990, Quinn 2005). Sockeye fry undertake diel vertical migrations (DVM), ascending to surface waters to feed during crepuscular periods (Levy 1987). Sockeye fry are visual predators, and so are their predators (Eggers 1977, Clark and Levy 1988). The DVM phenomena has likely developed as sockeye juveniles try to balance their need to see prey items while simultaneously avoid predators (Clark and Levy 1988, Scheuerell and Schindler 2002). With the cover of darkness the schooling behavior is likely relaxed and fry are free to spread out to forage for patchily distributed zooplankton prey items in the surface water areas (Eggers 1978).

Once fry leave littoral habitats and enter the limnetic zone, little is known of their migration within lakes. Burgner et al. (1969) cited several examples of inter-lake movement of juvenile sockeye in systems with more than one lake, such as the Naknek and Chignik lake systems. Interestingly, in the Wood River Lakes system, with several interconnected lakes, no evidence of inter-lake migration was found (between Little Togiak Lake, Lake Nerka, and Lake Aleknagik) however evidence of within lake movements of juvenile sockeye between regions of Lake Aleknagik were found (Pella 1968, Burgner et al. 1969). In Iliamna Lake, our catches indicated that while some down lake movement may occur, the majority of the fry congregate in the lake sections where they were spawned. Mathisen (1966) speculated that the open waters and exposure to high winds in the western and central regions were disincentives to fry moving westward in the first year of growth in Iliamna Lake. However, there must be down lake movements by sockeye fry at some point, as a percentage of each smolt migration will be comprised of age-1 smolts that would only spend one summer rearing in the lake. It is likely that the down lake movements by fry (east to west) would be undertaken by larger individuals. Larger fry are more likely to emigrate as age-1 smolts than smaller fry, and this outmigration occurs soon after ice breaks up the following spring (Burgner 1962, Burgner 1987, Quinn 2005).

Using the weighted index to extrapolate the overall distribution, yearling sockeye were found primarily in the central region, followed by the west region, suggesting westward movement as the fish grow and age. As a percent of fish the yearlings were most numerous in the west, followed by the central region. However, the number of sockeye yearlings caught per tow in the east region was high (Figure 1.8). Presumably, given their larger size and swimming performance, and the length of time they have been in the lake, they could have distributed themselves anywhere in the lake but many were in the less productive region (and more crowded) eastern end. It would be very interesting to know how far individuals move from the spawning grounds where they entered the lake, if movement varies among populations, and if it shows any response to density.

Yearlings, as a percent of the catch, increased from the east towards the outlet of the lake, comprising the majority of the catch in the west (Figure 1.7). Yearling distribution may be governed by better feeding conditions in the central and western regions, which are shallower, warmer, and have higher densities of zooplankton. They may move to west and central regions where zooplankton densities are greater and fish densities are lower, and thus have a better zooplankton per fish ratio. Certainly their larger size will require more food per capita to continue growth, and this may be more readily accomplished in these regions. Hoag (1968) showed that diet differed; yearlings fed primarily on *Cyclops scutifer* and fry primarily *Bosmina coregoni*. The yearlings may also be better able to elude predation in these areas given their larger size.

Yearlings also may favor distribution in this very large area as a precursor to smolt migration. The over-wintering age-1 juveniles leave the lake shortly after the ice breaks up the following spring as age-2 smolts (Burgner et al. 1969), and will have needed to complete any down lake movements by this time. They are least numerous as a proportion of the catch in the far eastern section of the lake (section 9) and in the shallow intricate bays of sections 10 and 11, which likely represents a balance between habitat and migratory needs. It is unknown when the different age class of juveniles will complete their down lake migration prior to outmigrating as smolts.

Threespine sticklebacks were most numerous in the central region, especially in areas with many islands, complex shorelines, protected bays and shallow areas. Threespine sticklebacks make use of littoral areas for spawning, where males construct and defend nests to attract female mates (Wootton 1984), so the association between abundance and shoreline complexity is not unexpected. Densities of stickleback were also high in the east region where the shoreline is long, relative to the area. Competition and diet overlap between threespine sticklebacks and sockeye fry has long been reported (Rogers 1973, Burgner 1987, O'Neill and Hyatt 1987). However, sockeye fry usually outnumber threespine sticklebacks (in Iliamna Lake this is true) and Burgner (1987) reported sockeye growth was likely more affected by sockeye density than that of sticklebacks, although there is certainly some competition for food resources.

Fish size by region:

Sockeye fry from the east region were consistently smaller than those from the west and central regions. This pattern of differential sockeye fry size by regions or areas within a lake has been reported by FRI researchers in both the Wood River system (Pella 1968, Burgner et al. 1969) and also in the Kvichak system (Burgner et al. 1969). These differences are thought to be caused by any or a combination of plausible factors, including: differences in growth rates, differences in emergence timing and therefore actual time growing in the lake, differences in fry size at time of hatching, and/or differences in rates of dispersion of larger or smaller individuals (Burgner et al. 1969). In Iliamna Lake, fry in the colder, more crowded, and less rich feeding grounds were smaller for a given day in the season, despite the fact that the ice left the eastern region earlier. Fry in the eastern region are competing for food with their own cohort, threespine sticklebacks, and also considerable densities of larger yearling sockeye.

Additional analysis of the data showed significant variation in fry length ranges, particularly towards the end of the growing season. Sockeye fry are generally about 28 mm upon emergence (Ruggerone 1989). In the east region in particular, we caught many fish that were 35 mm or less well into August and even September, which is quite late in the growing season (Table 2). This pattern was not seen to such a degree in either the west or central regions, and poses some interesting questions. Were these simply fish that emerged with normal timing and grew very slowly, as might occur in cold water and high densities of competitors and low densities of food, or did they emerge later in the season?

Yearling sockeye showed similar patterns of non-uniform size distribution; larger fish were caught in the west region, followed by the central region, and the smallest yearlings were caught in the east end. This general finding matches earlier trends reported in Iliamna Lake for this age class of juvenile sockeye (Kerns and Mathisen 1963, Kerns 1966, Mathisen 1966, Burgner et al. 1969). As surmised from the distribution pattern of yearlings, there may be benefits associated with increased growth opportunities in the less crowded, less confined, and larger areas associated with the west and central regions. It is likely that the same general processes governing growth for sockeye fry also affect yearling sockeye growth: water temperature, food availability, and density of competitors. The fish that move to this area could grow faster and therefore be larger for a given day in the season. They may be more able to elude predators due to increased swimming performance, especially important in the less complex and shallower bathymetry of the western area. Size distribution across this regional gradient could also be a function of differential movement patterns by larger fish. Older fish from a given system migrate to sea earlier (Burgner 1987), but larger fish of the same age also migrate earlier than smaller members of their cohort from Iliamna Lake (Quinn 2005). This size difference in migration timing may be related in part to the differences in size among yearlings from the west to east in the lake.

Summary:

Iliamna Lake is a large, heterogeneous lake producing great numbers of sockeye salmon, and it varies physically and biologically across spatial gradients, but also varies temporally with respect to biological factors such as density. As such, we see differential patterns of distribution and density by both anadromous sockeye salmon juveniles (fry and yearling) and resident threespine sticklebacks that are related to the spawning grounds of these fishes. Sockeye growth and life history are reflected in Iliamna Lake's variation in abiotic (temperature, depth, and ice phenology) and biotic (primary and secondary production, density of spawning adults and rearing juveniles) factors. Next we examine the characteristics of climate and density over a longer time series, focused on the eastern region in Iliamna Lake where we have shown the greatest use by sockeye salmon.

Table 1.1: Lake morphology from 11 lake sections in Iliamna Lake. The percent of the lake's surface area for each section was used in the weighted catch index.

Lake section	surface area (km^2)	% lake area	mean depth (m)
1	558.18	21.29	28.48
2	481.61	18.37	39.89
3	507.24	19.35	37.25
4	348.81	13.30	29.16
5	250.5	9.55	75.96
6	179.2	6.83	74.44
7	29.3	1.12	81.09
8	21.9	0.84	42.65
9	95.1	3.63	136.82
10	86	3.28	24.14
11	64.2	2.45	28.66
TOTAL	2622.04	100	54.41

Table 1.2: Counts and percentages of sockeye salmon fry caught in the west, central and east regions of Iliamna Lake 1962-1976 that were less than or equal to 35 mm fork length.

Catch 35 mm	west	central	east
August	4	72	976
September	4	12	240
Total	8	84	1216
Total Catch			
August	1720	3317	16481
September	865	8599	19663
TOTAL	2585	11916	36144
% Catch< 35mm			
% Aug	0.23	2.17	5.92
% Sept	0.46	0.14	1.22
% TOTAL	0.31	0.70	3.36

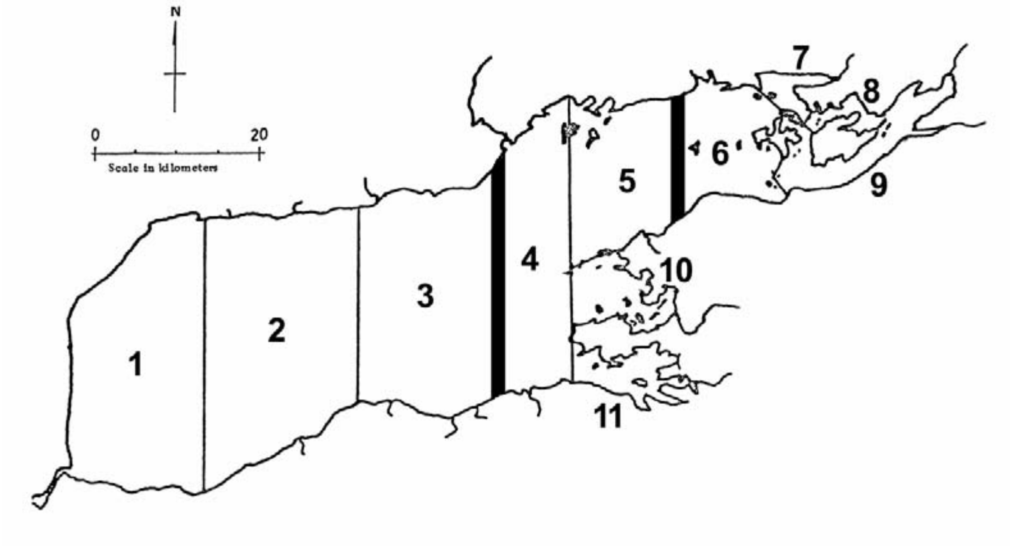
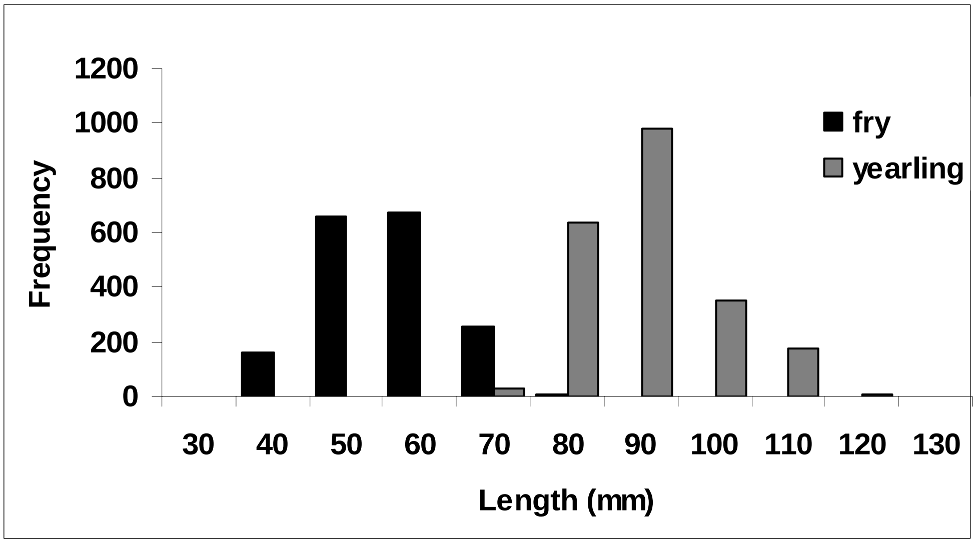


Figure 1.1: Iliamna Lake tow net and sampling subdivisions as delineated by FRI 1962-76. Lake sections are numbered 1-11, with bold black lines marking regions as west (sections 1-3), central (sections 4, 5, 10, 11), and east (sections 6-9).

(a)



(b)

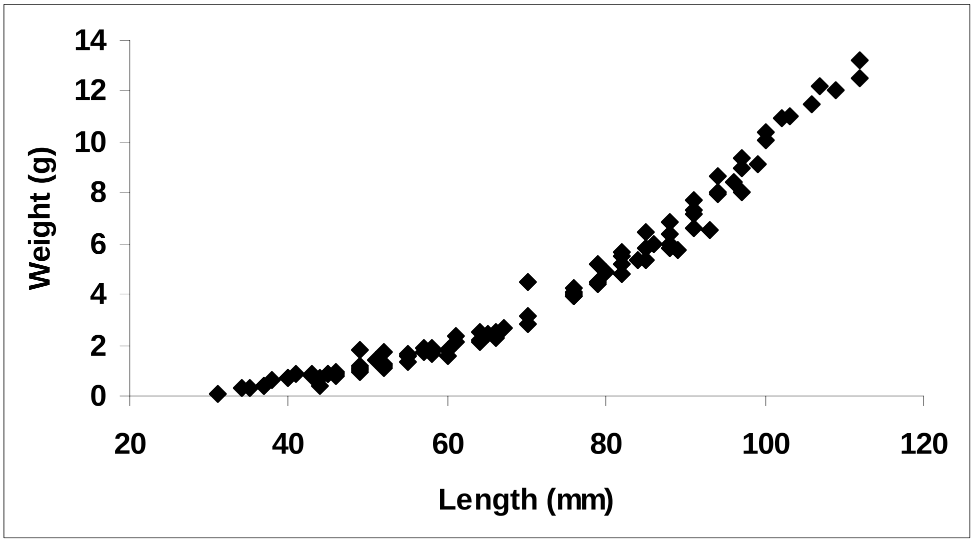
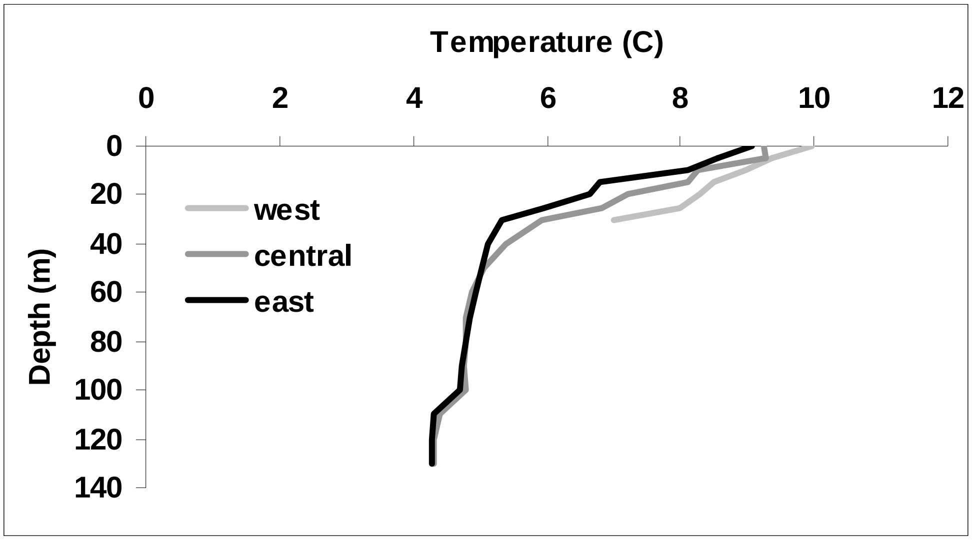


Figure 1.2: Histogram (a) and length-weight curve (b) for a representative year (1962) to demonstrate age-class differentiation between sockeye fry and yearlings.

(a)



(b)

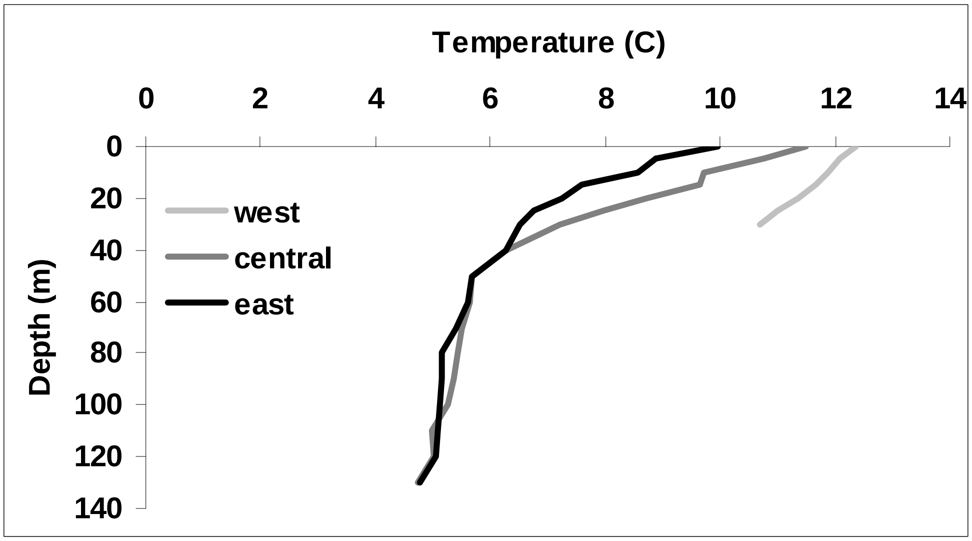


Figure 1.3: Temperature at depth profiles for three regions in Iliamna Lake, Alaska from bathythermograph casts made in July (a) and August (b) 1968-1976. Temperatures are averages at discrete depths from all years.

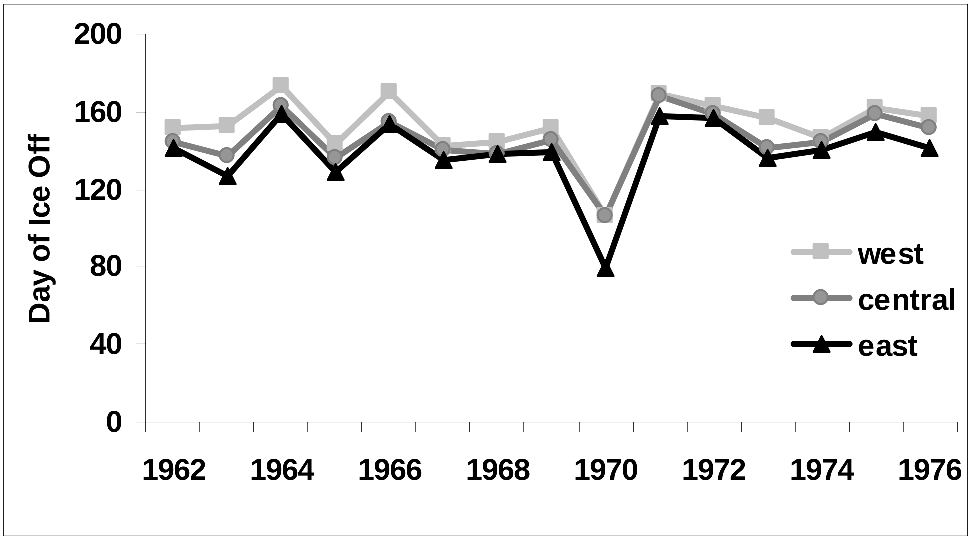


Figure 1.4: Annual ice off day for three regions in Iliamna Lake, Alaska compiled by FRI researchers 1962-1976. Average values were used for analysis of differences by region.

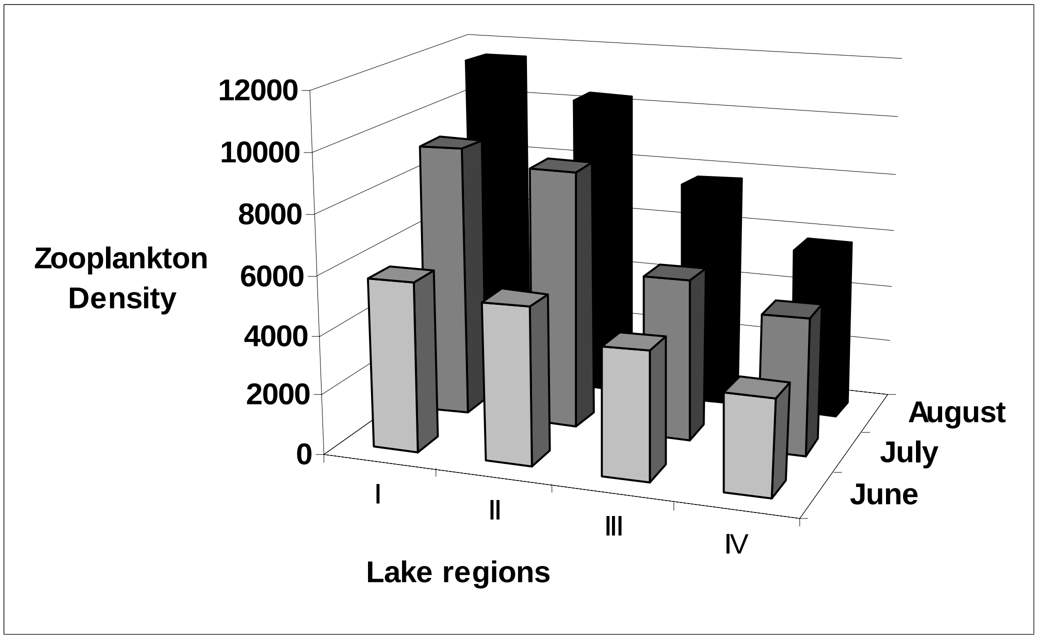


Figure 1.5: Standing crop of total zooplankton (geometric mean number/m^3) in four regions (Region I –western most; Region IV- eastern most) in Iliamna Lake, 1963-1976. Average values for each region were used for analysis of differences in density by region. (Modified from UW-FRI-7716).

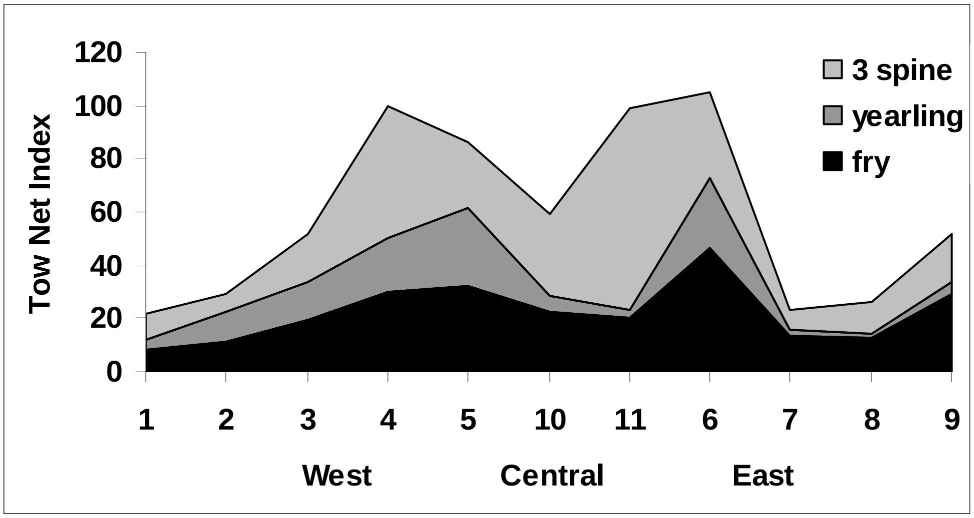


Figure 1.6: Weighted geometric mean catch index showing distribution of 2 age classes of sockeye salmon (fry and yearling) and threespine sticklebacks across 11 lake sections in Iliamna Lake from 1962-1976. Y-axis is the sum of the geometric mean index for all years.

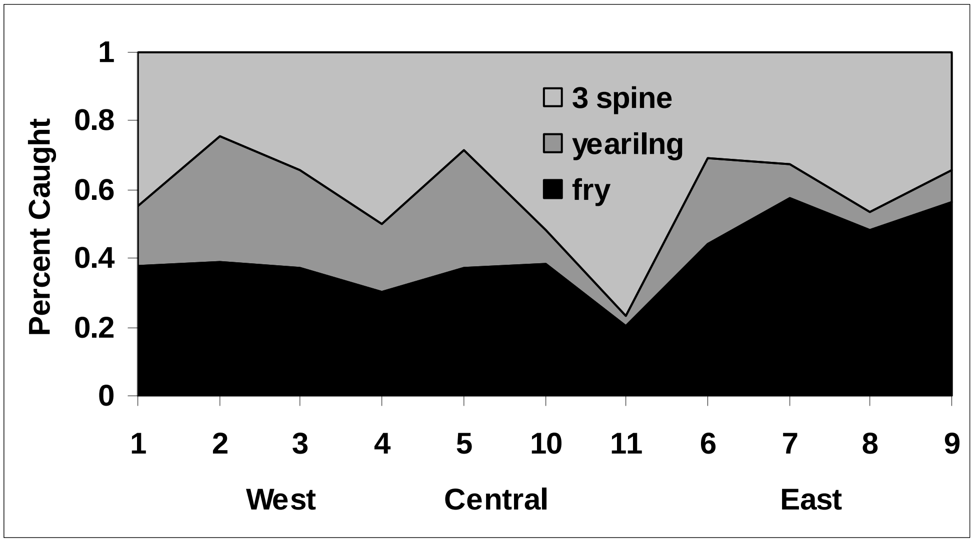


Figure 1.7: Relative abundance as a percent caught of two age classes of sockeye salmon (fry and yearling) and threespine sticklebacks from tow net catches in 11 sections in Iliamna Lake from 1962-1976.

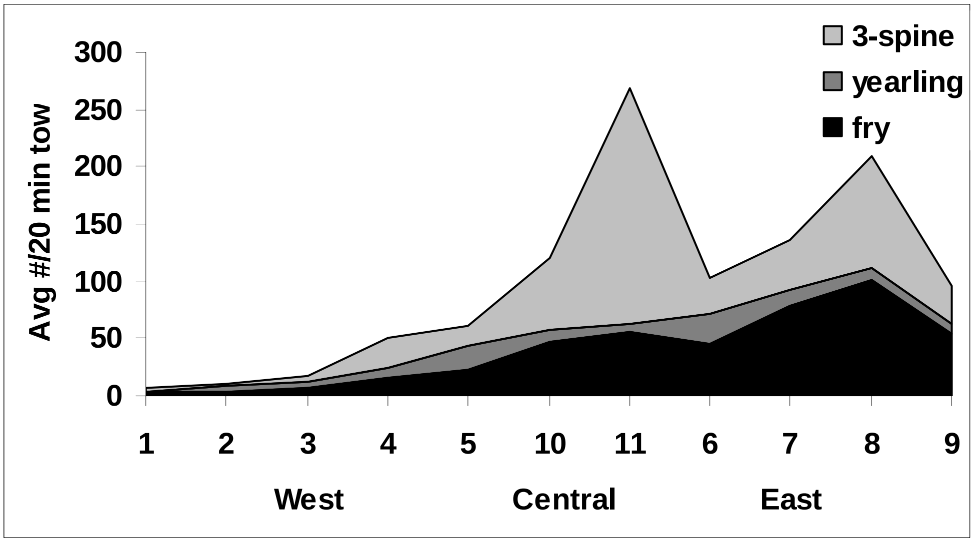


Figure 1.8: Density estimates for two age classes of sockeye salmon (fry and yearling) and threespine sticklebacks across 11 regions in Iliamna Lake from1962-1976. (Averages of annual geometric mean #/ 20 minute tow).

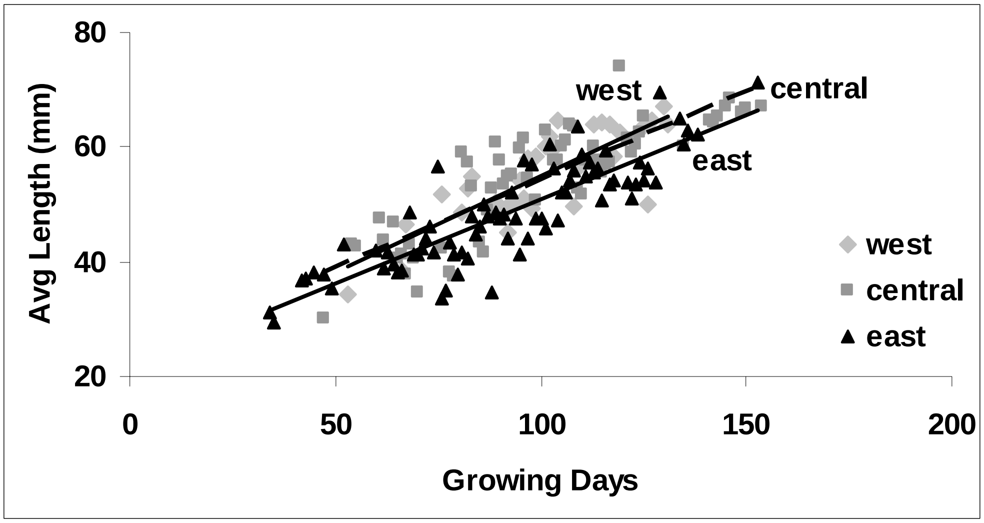


Figure 1.9: Average sockeye salmon fry length by growing day (day caught – ice off day) from three regions in Iliamna Lake (1962-1976).

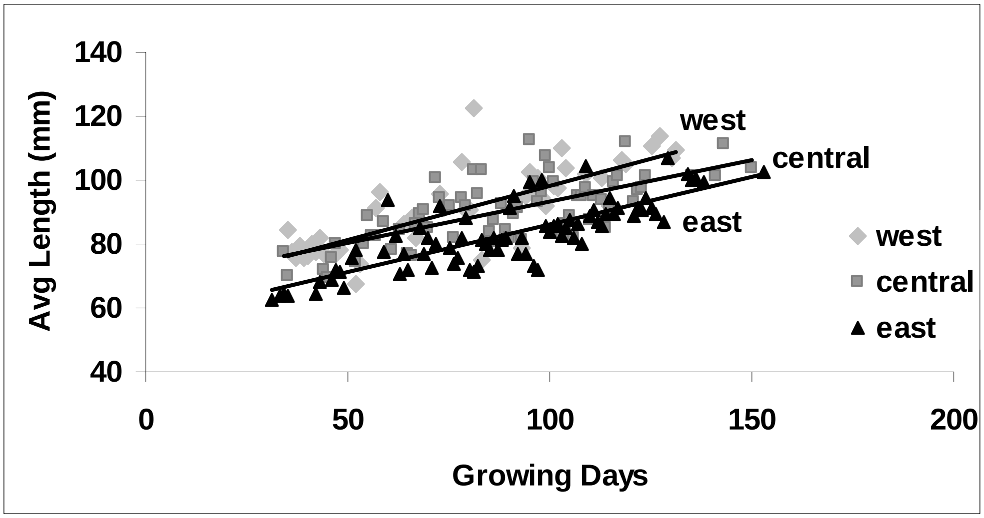


Figure1.10: Average sockeye salmon yearling length by growing day (day caught – ice off day) from three regions in Iliamna Lake (1962-1976).

CHAPTER 2

Climate and density dependent controls over growth and life history of juvenile sockeye salmon in Iliamna Lake, Alaska.

INTRODUCTION

Recent studies show the earth's climate has warmed by approximately 0.6° C over the past 100 years (IPCC 2001). In addition to large scale effects of general climate change as a result of warming, climate variability shown in multidecadal oscillatory dynamics such as those caused by the North Atlantic Oscillation (NAO) (Hurrel 1995) and Pacific Decadal Oscillation (PDO) (Mantua and Hare 2002) also affect climatological processes, as do cycles such as El Niño Southern Oscillation (ENSO) (Wang et al. 1999). Evidence is mounting that global-scale changes in climate are having significant ecological impacts on plant and animal populations (McCarty 2001, Walther et al 2002, Parmesan and Yohe 2003), and this is a critical challenge for basic and applied ecology.

Climate change has affected organisms in many ways, including northward shifts in the distributions of birds (Thomas and Lennon 1999), mammals (Hersteinsson and MacDonald 1992), butterflies (Parmesan et al. 1999), and plants (Sturm et al. 2001). Changes in precipitation and temperature have altered community structure, e.g. changing arid grasslands to woodier shrublands, with an associated loss of formerly prevalent species and increases in previously rare species (Brown et al. 1997). Sagarin et al. (1999) documented changes in community composition of inter-tidal invertebrates related to climate induced temperature changes; northern species declined in abundance whereas southern species increased. Perhaps the most well documented changes related to climate shifts are changes in phenologies. Crick et al. (1997) documented earlier breeding of birds in 78% of 65 species examined. Dunn and Winkler (1999) showed earlier shift in breeding date by 5-9 days across the range of tree swallows (*Tachycineta bicolor*). Changes in phenologies to earlier arrival and flight patterns, earlier breeding, and advances in blooming dates are also known in insects (Sparks and Carey 1995, Fleming and Tatchell 1995), in amphibians (Beebe 1995), and in plants (Bradley et al. 1999) respectively. Additionally, life history characteristics such as sex determination induced by temperature, seen in reptiles (e.g., the painted turtle, *Chrysemys picta*: Janzen 1994), have been affected by warming trends in climate.

The effects of climate change and variability on fishes are of particular interest as they have important commercial, recreational, and social values. Variations in landings of herring (*Clupea harengus*) off the Swedish coast and variations in abundance and range overlap between herring and sardines (*Sardina pilchardus*) off the southwestern English coast fluctuated with prevailing climate conditions in European waters (Alheit and Hagen 1997). Arctic and North Sea cod (*Gadus morhua*) growth rates were positively correlated with warm phases of the NAO (Ottersen et al. 1994, Brander 1995). Changes in the sizes of thermal habitats available to Atlantic salmon (*Salmo salar*) have fluctuated in synchrony with phase changes in the NAO (Friedland et al. 1998, Dickson and Turrell 1999). Climate effects can manifest them selves in freshwater as well as marine systems, and can affect larval and juvenile fishes as well as adults. For example, Jonnson et al. (2005) found an early developmental affect on parr size and age at seaward migration for Atlantic salmon linked to water temperatures experienced as embryos, and that temperatures experienced were directly linked to NAO. Similarly, Schindler et al.

(2005a) showed that growth rates of juvenile sockeye salmon (*Oncorhynchus nerka*) increased in response to regional warming since 1960 in southwest Alaska. However, the effects may not be simple. Some studies have predicted expansion of range and growth opportunities for some warm and cool-water species (Shuter and Post 1990, Magnuson et al. 1990), while others suggest that growth and habitat will be compromised for other, primarily cold-water species (Schindler 1990, McDonald et al. 1996, Melack et al. 1997).

High latitude lake systems are characterized by pronounced, seasonally influenced cycles of resource availability and scarcity, and evidence for warming and the ecological impacts of climate variability are most pronounced in higher latitudes (Magnuson et al. 2000, Bertaux et al.2004). Lake systems in the northern hemisphere have experienced significant changes in ice cover and phenology, air and water temperatures , evaporation, thermal stratification, and other important limnological events reflecting trends in warmer winters and earlier springs (Schindler et al. 1990, Magnuson et al. 2000, Winder and Schindler 2004).

Fishes of the family Salmonidae (Charr, trout, salmon, whitefishes) are often numerically and ecologically important in northern lake systems, and their complex life cycles offer insights into the effects of changing climate on life history and ecology. Anadromous Pacific salmon (genus *Oncorhynchus*) may be particularly sensitive to changes in climate as they rely on both freshwater and marine ecosystems to complete their life cycle. Salmon catch records showed a positive correlation with climate indices across the North Pacific (Beamish and Bouillion 1993) and fit particularly well with phases of the PDO for Alaskan stocks of salmon (Mantua et al. 1997). Studies using paleolimnology have revealed that fluctuations in Pacific salmon populations correlated with changes in climate regimes over several centuries (Finney et al. 2000, Schindler et al. 2005b).

Sockeye salmon (*O. nerka*) are of central importance to commercial and subsistence fisheries in Russia, Canada and Alaska, and as such are one of the best studied of the Pacific salmon. They often spawn at high densities in the late summer and fall, and the fry emerge the following spring. The juveniles rear in lakes for one or two years, then migrate to the ocean to grow for and additional 1 -3 years before returning to spawn (Burgner 1991). The lacustrine phase makes them particularly amenable for studies on the effects of changing climate because growth affects the length of time spent prior to seaward migration, and size can affect survival at sea (Quinn 2005).

Growth of juvenile sockeye salmon in lakes is positively related to temperature, nutrient concentrations, zooplankton quantity and quality, and negatively related to their own density (Hyatt and Stockner 1985, Eggers and Rogers 1987, Edmundson and Mazumder 2001, Schindler et al. 2005a). Burgner (1987) showed for some lake systems that at spawner densities above 20/ha, density effects could be determined, whereas in other lakes with much higher spawner densities (>200/ha) density did not seem to affect growth. In some systems, the age at which juvenile sockeye migrate to sea is not fixed (Burgner 1991). For such systems with multiple age classes of juveniles in the rearing lake at the same time, the stage is set for competition between year classes in addition to competition within a given year class. Less is known about the intensity of these inter-brood interactions and at what densities they may occur. Density effects may become more apparent within systems with multiple age classes of juveniles and subsequent years of high abundances (Selifonov 1970, Burgner 1987).

Climate and density affect growth and thus size at the end of the first growing season in sockeye salmon (Schindler et al. 2005a). Temperature has direct effects on rates of development and metabolic processes in fishes (Woottton 1998, Randall et al. 2002). Increases in air temperatures will lead to corresponding increases in ground and surface waters, resulting in elevated stream and lake temperatures on a local level. Increases in temperatures experienced by developing salmonids incubating in gravel nests and newly emerged fry residing in interstitial spaces in streambed gravel will increase their developmental rates and lead to earlier hatching and emergence (Quinn 2005). After emergence, warmer water increases the physiological scope for growth of sockeye salmon up to about 15° C (Brett 1995). At temperatures below this, food is digested too slowly to maximize growth and at temperatures above this, metabolic rates are so high that increased food intake is used for maintenance rather than growth. In addition to the direct effects of temperature on the date of emergence by fry in the spring and their scope for growth over the summer, changes in temperature can profoundly affect complex limnological processes such as ice breakup, absorption of solar radiation, and thermal stratification which influence the timing and rate of production and abundance of phytoplankton and zooplankton (Straile 2000, Scheffer et al. 2001, Winder and Schindler 2004, Schindler et al. 2005a).

Size at the end of the first growing season affects the age at seaward migration of sockeye salmon. Within lake populations, larger members of a year class tend to migrate a year earlier than smaller members, and larger individuals within a season tend to migrate earlier in the spring (Foerster 1968, Burgner 1987). Therefore, size at the end of the first growing season plays a role in both age and timing of seaward migration. Size and timing of seaward migration influence marine survival and thus play important role in overall population productivity (Henderson and Cass 1991, Koenings et al. 1993).

In this study we used long term data (1962-2005) on juvenile sockeye salmon growth in Iliamna Lake in the Bristol Bay region of southwestern Alaska to determine the relative roles of climate and density in controlling growth and life history transitions in this species. The Iliamna Lake populations of sockeye salmon include fish that migrate to sea after either one or two full growing seasons in the lake, allowing us to study competitive interactions between these two year classes. Iliamna Lake and its tributaries have had not only remarkably large runs of sockeye salmon during this period but also showed cycles of abundance (Eggers and Rogers 1987), and in recent years the runs have been very low. These changes in density, unrelated to degradation in habitat quality or access, have taken place during a period of dramatic shifts in climate (Mantua et al. 1997, Hilborn et al. 2003), making this an ideal system in which to study the interplay between these processes. Accordingly, the objectives of this study were to quantify the relative effects of climate and density on the size of juvenile sockeye salmon at the end of their first growing season in Iliamna Lake, Alaska. We predicted that warmer conditions would be positively correlated with fry size at the end of the first summer whereas density of juvenile sockeye salmon (within and between brood years) was predicted to correlate negatively with size.

METHODS

Study Site:

Iliamna Lake is the largest lake in Alaska, with a surface area of approximately 2,622 km^2. It drains into the 90 km long Kvichak River, flowing into the eastern portion of Bristol Bay. The southwestern end of the lake is relatively wide, open, and shallow (average depth: 35 m) with few islands and a simple shoreline whereas the northeastern end is narrow and deep (average depth: 80m, max depth: ~ 300 m), with a complex shoreline and many islands (Figure 2.1).

Sampling:

Juvenile sockeye have been sampled by University of Washington staff each summer using tow-nets since 1962. The 3 x 3 m opening net is towed at the lake's surface behind and between two boats for 20 min at approximately 3 km/hr. Towing began approximately an hour after nightfall, to allow juvenile sockeye to undergo their diel vertical migration, rising to surface areas to feed (Scheuerell and Schindler 2003). Catches were later identified to species, measured for fork length, and a subsample was weighed.

Sampling has taken place throughout the lake (Chapter 1) but spawning adults and juveniles are concentrated in the eastern end of the lake and so in recent years sampling has been most regular in two index areas (Knutson and Pedro Bays, Figure 2.1). All tow-net stations have been identified with GPS as to latitudinal and longitudinal coordinates.

Juvenile Growth:

Average sockeye salmon length in a given year was calculated as the weighted arithmetic mean length of each tow sample from within each index section. For example, multiple tows (i) were made in each index section (s), so the weighted mean from each tow section (Ls) was calculated as:

$$L_s = {\sum L_i * N_i} \Big/ {\sum N_i}$$

where *Ni* is the number of fish caught in tow *i*.

The two age classes of juvenile sockeye in Iliamna Lake, age-0 (fry) and age-1 (yearlings) were distinguished by inspection of length frequency histograms and length-weight relationships to determine age-specific estimates of length at the end of the growing season (see Chapter 1). Within each year, clear differentiation of age classes was evident and typically fry were < 75 mm and yearlings were ≥ 75 mm; the long-term average fry length was approximately 57 mm and the long-term average yearling length was 91 mm.

Lengths of juvenile sockeye fry were then standardized to length on September 1 because the actual sampling dates varied among years and often sampling also took place on more than one night each year. Lengths were adjusted by taking the product of the number of days between the sampling date and September 1 times the annual growth rate, and adding or subtracting this from the weighted mean length. The annual growth rate was calculated based on multiple sampling events in the same area that year. If sampling only took place at the end of the season we used a value of 0.33 mm/day (the long-term average growth rate for juvenile sockeye in this area of the lake; D.E. Rogers, FRI unpublished records). September 1 was used as the standard date because it is near the end of the growing season for Bristol Bay sockeye nursery lakes and in most years the final sampling was conducted shortly before or after this date (Schindler et al. 2005).

In calculating growth rate and catch rate, we also adjusted for the differences in surface area of the two index areas in the eastern part of the lake. To do so, the adjusted mean lengths from each index section were multiplied by the weighted geometric mean catch for each index section and summed. The weighted geometric mean catch of each area was calculated as:

Geometric mean (catch +1) * weighted surface area of index section (0.43 for Knutson Bay and 0.57 for Pedro Bay)

The adjusted mean length was then divided by the overall geometric mean catch of the two areas to give the overall adjusted mean size of fry in each year.

We initially used simple linear regressions to explore potential factors affecting fry growth and identified our predictor variables. Our first factor was fry density. There were no absolute estimates of fry abundance so we used data collected each year by Alaska Department of Fish and Game (ADF&G) on the size of the parent escapement that entered Iliamna Lake to spawn as our index of juvenile fry density. These counts were offset by one year because the offspring from Brood Year 1985, for example, were rearing in the lake as fry in 1986. We recognized that the production of fry is likely to be related to the number of spawning adults in a non-linear manner owing to density-dependent mortality (e.g., Essington et al. 2000). Therefore, we used ln(escapement) as our metric of fry density.

Our second factor was the density of yearling sockeye salmon. We estimated their abundance from the ln(estimated number of age-2 smolts) leaving Iliamna Lake (as reported by ADF&G) in the following spring. The number of smolts includes fish rearing in Lake Clark, which would not compete with the fry in Iliamna Lake. Moreover, not all fish that were alive in the summer would have survived to the following spring. Nevertheless, the smolt count provided an index of competition between brood years.

The third factor hypothesized to affect growth was water temperature, and we used data collected by ADF&G during smolt trapping operations conducted at Igiugig, at the outlet of Iliamna Lake. We used the daily average water temperature from June 1 to June 15 as an index of spring water temperatures. We also used the mean monthly air temperature from Intricate Bay, Alaska, located on the south side of Iliamna Lake from March-June as an index of climate experienced by juveniles each year. Intricate Bay (the Kakhonak village airfield) provided the most complete air temperature records over the period of this study (1962-2005), but in 10 instances, there were no records collected at Intricate Bay for a given month in a given year, and we used air temperatures collected at nearby Iliamna airport to complete the temperature record. Linear regression revealed a very strong correlation between the Intricate Bay and Iliamna airport records ($r^2 = 0.99$) and therefore we assumed that the temperatures used reasonably reflect local conditions. Data were collected from: http://cdo.ncdc.noaa.gov/CDO/cdo.

Time-series analysis:

We used a class of Bayesian time-series models known as dynamic linear models (DLM) (Pole et al. 1994), to quantify the relative effects of different factors on the growth of juvenile sockeye in their first year of life: the density of their parents (and so, presumably, the abundance of fry), the density of older conspecifics from the previous year's cohort, and temperatures the sockeye experienced as newly emerged fry. In ecological systems the events in one year are often linked to those in previous and succeeding years by various processes and DLM's account for the time ordered nature of the data. DLM's are now being applied regularly for use with ecological data (Lamon et al 1998, Scheuerell et al. 2002, Winder and Schindler 2004, Schindler et al. 2005a, Scheuerell and Williams 2005, Bunnell et al. 2006). The methodology has been described in detail elsewhere (e.g. Cottingham and Carpenter 1998, Lamon et al. 1998, Scheuerell et al. 2002) so we only describe it briefly here.

The observed response variable (Y_t) is sequentially fit at each time step *t*, to a 1 x *m* vector of the predictor variables ($\mathbf{X}_t$), with the *m* x 1 vector of model regression parameters ($\boldsymbol{\theta}_t$) and a normally distributed error term (v_t) to form what is known as the the observation equation:

$$Y_t = \mathbf{X}_t \boldsymbol{\theta}_t + v_t \qquad v_t \sim \mathrm{N}[0, V_t]$$

The observation errors (v_t) have a time dependent variance (V_t) that is estimated from all of the prior data and weighted by use of a discounting scheme as the analysis proceeds through time. (The discounting scheme described below also applies to (V_t)). The value of *m* equals the total number of regression parameters used in a particular model and includes predictor variables as well as any level or slope parameters.

A second equation known as the system equation allows the model regression parameters ($\boldsymbol{\theta}_t$) to change through time. The *m* x 1 vector of regression parameters uses prior information from Bayesian learning to change according to a first-order Markov process:

$$\boldsymbol{\theta}_\mathbf{t} = \boldsymbol{\theta}_\mathbf{t-1} + \boldsymbol{\omega}_\mathbf{t} \qquad \boldsymbol{\omega}_t \sim N[0, \mathbf{W}_t]$$

where ω_t is an m x 1 variance vector that accounts for stochastic change in each of the parameter estimates ($\boldsymbol{\theta}_t$) through time. $\mathbf{W_t}$ is the system variance matrix and is determined by the component discount factors applied to the posterior covariance matrix from the previous time step (Pole et al. 1994).

The parameters are updated as new information is included into the model and one-year ahead forecasts are made at each time step. Priors are calculated through the use of discounts (δ), such that $\delta \in (0\text{-}1]$. At time step t, the variance component for the process error W_t equals the posterior variance from the previous time step C_{t-1} plus some uncertainty owing to the passage of time, so that:

$$W_t = \left(\frac{1}{\delta} - 1 \right) C_{t-1}.$$

When $m > 1$, the m x m variance matrix $\mathbf{W}_t$ has the variance for each of the regression parameters down the diagonal and separate discount factors apply for the trend and regression. Discounting the observation variance is similar, but is done in terms of the precision $\phi_t = V_t^{-1}$. For a variance discount δ_V, the prior information on the scale at time t is given by:

$$\phi_t \mid D_{t-1} \sim G[\delta_V n_{t-1}/2, \delta_V d_{t-1}/2]$$

where the two parameters in the gamma distribution are the degrees of freedom (n_{t-1}) and the sum of squared errors (d_{t-1}). This has the convenient property of having no effect on the mean of the gamma distribution (i.e. the ratio of the two parameters) while inflating the variance by δ^{-1}. In practice, discounts are set systematically between 0.8 and 1 by choosing the values that minimize the negative log-likelihood of the overall forecast model (Pole et al. 1994).

We compared alternative models through the use of cumulative Bayes factors (H), which represent the odds in favor of one model relative to another while accounting for model complexity (Berger and Pericchi 1996). We were interested in two different comparisons among the competing models in our candidate set. For the first, we compared each model with predictor variables to a random-walk reference model, which contained only an intercept plus an error term. Because we used the marginal negative log-likelihood (NLL), the log Bayes factor for the first comparison becomes the difference in negative log-likelihood between the reference model (L_{ref}) and any other model (L_i):

$$H_{ref,i} = L_{ref} - L_i$$

For the second comparison, we selected the model with predictor variables that had the lowest marginal NLL as the "best" of the group (L_{min}) and calculated the log Bayes factor for each of the other predictor models (L_j) relative to it, such that:

$$H_{\min,j} = L_{\min} - L_j$$

Kass and Raftery (1995) suggest that when 2 $H_{ref,i}$ is 0-2, the evidence favoring model *i* over its' reference model is 'not worth more than a bare mention'; 2-6 indicates 'positive' support; 6-10 offers 'strong' support; and >10 offers 'very strong' support in favoring one model over its reference. The criteria are the same for 2 $H_{min,i}$, but with opposite signs, essentially indicating the 'weight of the evidence' against the lower ranked model compared to the best fit model.

To compare the magnitude of the effect of each regressor on the dependent variable of each model, we calculated effect sizes as the product of the regression coefficient and the value of the independent variable in each year of the time series. Effect sizes were expressed in the units of the dependent variable, providing a simple indication of the magnitude of each explanatory variable on the response variable in each model.

RESULTS

Spring air temperatures have shown a significant warming trend in the Iliamna Lake area from 1962 to the present (Figure 2.2). A simple linear trend model indicated that average spring temperatures are about 3.5° C warmer now than they were four decades ago. Spring water temperatures are strongly positively correlated with spring air temperatures ($p < 0.0001$, $r^2 = 0.63$) and day of ice break up is strongly negatively correlated with spring air temperatures ($p < 0.0001$, $r^2 = 0.44$).

We tested several other combinations of months before our temperature index was selected for analysis of fry length, including winter (Nov-Feb, Jan-Apr, Dec-Feb), summer (June-Aug, July-Sept), entire sequences of first year life (Nov-Oct, Sep-Oct), and even in other variations of spring temperature (Apr-Jun, Mar-May, Feb-May, Feb-June). However, spring air temperature had the highest correlation coefficient (positive) with fry length (0.64), followed by fry density (ln(escapement)), and yearling density (ln(age-2 smolts)), both of which correlations were negative (-0.41 and -0.35 respectively).

The DLM for the 44 year time series (1962-2005) that included both spring air temperature and fry density as predictors in explaining variation in sockeye fry length provided the best fit to the observed data for this model group (Bayes Factor = 27.2; Table 2.1). This forecast model fit the observed data fairly well, with the observed data falling within the prediction intervals in most instances and the forecast values matching the trends in the observed data (Figure 2.3., $r^2 = 0.32$, but does increase to 0.47 if one outlier is removed). The model including only spring air temperature performed much better (Bayes Factor = 15.8) than the model including only sockeye density (Bayes Factor = 3.3), and both performed better than the reference random-walk model (Table 2.1). The positive effect of air temperature was about three times as large as the negative effect of fry density (mean effects: 7.15 mm for temperature and -2.40 mm for density; Figure 2.3).

For the 39 year time series (1962-2000), for which estimates of yearling density were also available, the best models had both spring air temperature and density estimates from both age classes of sockeye juveniles as predictors (Table 2.1). The best fit model included spring air temperature and the combination of fry density and yearling density (Bayes Factor = 30.5). Models including only spring air temperature performed better than models containing only density of fry, only density of yearlings or the combination of juvenile density (fry density and yearling density) as predictor variables. Again, the forecast model fit the observed data fairly well, with the observed data falling outside the prediction intervals in only two instances (Figure 2.4., $r^2 = 0.33$). The positive effect size of temperature was the largest (mean 5.18 mm), followed by the negative effect of yearling density (-3.71 mm), and finally by the negative effect of fry density (-1.99 mm). The positive effect size of temperature had the largest magnitude of any predictor variable and was about 40% greater than yearling density and about two and half times greater than for fry density (Figure 2.4).

DISCUSSION

Spring air temperatures in the Iliamna Lake region of southwestern Alaska have warmed by about 3.5° C since 1962, in association with warmer spring water temperatures at the outlet of Iliamna Lake (Figure 2.5), and earlier date of ice breakup from the lake (Fig 2.6). The warming trend has had a strong positive effect on juvenile sockeye salmon growth in this system, combined with a weaker but also significant effect of density. The density effect resulted more from competition with yearlings from the previous year's brood than the present brood's fry density, at least as indexed by the values we used. The positive effect of spring air temperature was about three times as large as the negative effect of fry density. These results were consistent with previous work on this system that used much more limited periods of record (Rogers and Poe 1984, Burgner 1987). Rogers (1973) also found that much of the annual variation in fry size in the littoral zone of Lake Aleknagik, Alaska at the beginning of summer was attributable to surface water temperatures.

Increased spring air temperatures can affect growing conditions in a number of ways. Increased temperatures can reduce duration of ice cover, which will increase the length of the growing season. Schindler et al. (2005) showed that in nearby Lake Aleknagik, Alaska, spring ice breakup has become about seven days earlier over a similar period (1962-2002). They attributed the earlier breakup to longer term shifting in baseline climatic conditions as well as an effect from the warmer phase of the PDO during this time period. Longer growing seasons should improve productivity in the lake, both primary and secondary, leading to increased food supply and quality. Schindler et al. (2005) found that earlier ice breakup led to increased densities of summer zooplankton, the major food source for planktivorous juvenile sockeye. Interestingly, in Lake Aleknagik, the effects of fry density were more pronounced than climatic effects on fry growth (Schindler et al. 2005a), and the number of yearling sockeye salmon in the lake is negligible so the density effect is limited to a single age class. The mechanisms for the difference between the relative importance of climate and density on juvenile sockeye growth in these two nearby lakes remains unknown but may be related to lake size as Lake Aleknagik is over an order of magnitude smaller than Lake Iliamna.

Increased spring temperatures may also accelerate development of salmon embryos in the gravel, leading to earlier emergence of fry and enabling them to forage for a longer period of time before the onset of fall. Studies on the effects of reduced riparian zone vegetation (from experimental logging) revealed that milder temperatures led to earlier fry emergence in the spring, a longer growing season and faster growth in the summer, and a greater tendency to migrate to sea at age 1 rather than 2 in British Columbia coho salmon, *O. kisutch* (Holtby 1988, Holtby and Scrivener 1989). Atlantic salmon (*Salmo salar*) responded positively to warmer springs as well, with larger parr resulting at the end of the first growing season (Jonnson et al. 2005). Warmer temperatures may also improve egg-fry survival, which may be good for an individual, but perhaps increase negative density-dependent effects for the cohort. However, this effect would not be easy to detect, given the imprecision in assessment of survival in this system.

Early life stage influences affect later life performance such as growth, survival, and reproductive success in many taxa (Lindstrom 1999, Beckerman et al. 2003). Jonsson et al. (2005) found that climate (i.e., the NAO index), influenced water temperature and stream flow during egg incubation, producing a significant effect on mean length of Atlantic salmon fry at the end of their first growth season and on the proportion of the cohort smolting at age-1. They also found that temperatures during the main growing season (June-August) did not explain variation in fry size at the end of the first growing season. This is consistent with our results; summer temperatures (June-August) were less important than spring time temperatures (March-June) as an explanatory variable for sockeye fry length. This suggests that temperatures experienced in early development may be one important driver on size at the end of the first year for sockeye salmon fry in this system, and will also have important consequences for later life performance. Additionally, an alternative explanation of a growing season length effect that is correlated with spring temperature is also plausible.

However, Jonsson et al. (2005) acknowledged that factors other than climate, notably density, also affect fry growth. We found stronger effects of climate than density in Iliamna Lake. As has been shown elsewhere, sockeye fry growth was negatively affected by their cohort's density (Burgner 1987, Koenings and Burkett 1987, Kyle et al. 1988, Mazumder and Edmundson 2002, Schindler et al. 2005a). Interestingly, accounting for both year classes provided better model performance than by looking at density effects individually (fry density, yearling density), and the effects of yearling density (i.e., inter-brood competition) were almost twice as strong as competition within a cohort. Certainly, the biomass of some number of yearlings will be greater than that for an equivalent number of fry (average weight of fry is 1.7 g vs. 7.0 g for yearlings). We interpret this result as support of previous suggestions that in systems with multiple age-classes of juveniles, the yearlings produced by large escapements can reduce growth of the following year class (Selifonov 1970, Burgner 1987). The Kvichak system was known for its cyclical run dynamics, with many instances of large (> 6 million) escapements in two consecutive years (1969-70, 1974-75*, 1979-80, 1984-85, 1989-90, 1994-95; *the 1974-75 cycles were 4.4 and 13.9 million respectively) and the models were able to detect the negative effects of intraspecific competition, caused by both intra-brood and inter-brood year effects.

Schindler et al. (2005a) conducted a parallel analysis of sockeye fry growth in Lake Alekangik, on the west side of Bristol Bay, and found that density had a stronger influence on fry growth than temperature. Sockeye salmon from the Wood River system differ from those in the Iliamna system by having almost entirely one age class of juveniles in the lake in a given year. Additionally, while the densities of spawning adults for all the Wood River lakes combined are similar to the Iliamna system (~ 20/ha) (Burgner et al. 1987), Lake Alekangik itself has much higher spawner densities (~ 42/ha; FRI data). This may explain the fact that the negative effect of density on fry growth was about twice that of the positive effect of earlier spring breakup of ice.

In the past decade the Kvichak/Iliamna system has seen the combined effects of mild temperatures and reduced intraspecific competition. From 1960-1995 there were about 21 spawning adults/ha but from 1996-2005 the average has been only 8.5 adults/ha, an almost 60% reduction in spawning density. We have not seen consecutive large escapements since 1994-1995, and even the two ‘peak’ year returns since 1995 (6.2 million in 1999 and 5.5 million in 2004) were small in comparison the the peak years in the past. Concurrent with this reduction in spawner densities, environmental conditions have warmed considerably. Both of these factors are influencing size at the end of the first growing season, with larger than average fry found in six of the last nine summers, one year with average size and only 2 years with smaller than average fry.

Fry size affects the proportion of a cohort that migrates to sea as 1 year olds (Burgner 1987; Figure 2.X., $r^2 = 0.48$), so we have seen increasing proportions of age-1 smolts leaving this system, due to both increases in temperature and relaxation of density effects. Indeed, over the smolt migration years from 1993-2000 approximately 72% of outmigrants were age-1, compared to the average of 48% age-1 smolts from the 1963-1992 smolt years. This may have considerable consequences on population dynamics for the Kvichak system and it will obviously reduce inter-brood competition for food in the lake. As this inter-brood competition was more significant than intra-brood competition, the effect will be to increase growth of fry.

Smolt size affects the timing of seaward migration; older, larger smolts migrate earlier within a season than smaller, younger counterparts (Foerster 1968, Burgner 1987). Additionally, larger individuals of the same age tend to leave earlier within the migration season in this system (Quinn 2005). If fry continue to be large at the end of their first growing season in this system, it appears that large proportions will continue to migrate at age-1. Implications for this are complex, as younger, smaller age-1 smolts have typically migrated later in a season and warmer water and earlier ice breakup may disrupt this long-term pattern. Interestingly, there have been instances in recent years when the lake did not freeze over (2000, 2003). Burgner (1962) reported that smolts migrated earlier after or during a mild spring, and data presented in Quinn (2005) show this trend for Iliamna Lake smolts as well. Continuing trends of warmer and earlier springs, may affect long term trends in timing of seaward migration.

Additionally, as more fry reach a larger size, they may grow large enough to smolt the next spring, but still be substantially smaller than they would be as age-2 smolts. Data collected from this system (1962-2000 by ADF&G) indicate that age-1 smolts are 18% shorter and 43% lighter than age-2 smolts. Smolt size can have a positive effect on marine survival (Henderson and Cass 1991, Koenings et al. 1993). So, systems with historically high proportions of age-1 smolts may see beneficial effects of increases in temperature. However, systems experiencing a shift to earlier age at migration may see lower survival (Quinn 2005). Smolt age and marine age are linked; age-2 smolts tend to spend two years at sea rather than three to a greater extent that age-1 smolts. Thus the age-1 smolts may have reduced survival at sea in part because they are small when they enter the ocean and partly because they stay there longer and so have more exposure to predators and other mortality agents. Consistent with this scenario, improved survival (as evidenced by increased adult returns and higher recruit per spawner indexes) for Wood River system sockeye salmon have been occurring over the same time span as reduced returns and productivity in the Kvichak system (Hilborn et al. 2003). Both the similarities and differences found in the dynamics of fry growth between Iliamna Lake and Lake Aleknagik add support that complex ecological responses to climate change may not be uniform across systems, and that the interplay between climate and other ecological factors such as density and competition must be recognized.

Table 2.1 Summary statistics from dynamic linear models (DLM) to explain historical variation in juvenile sockeye length on September 1 from Iliamna Lake, Alaska. Within each group models are ranked in order of increasing predictive performance (i.e., lowest marginal negative log-likelihood (L)). The value of $2H_{ref,i}$ provides evidence in favor of a model compared to its reference model, and $2H_{min,i}$ provides evidence against any model i, relative to the best overall model, L_{min} . Values of 2H equal to 2 (-2), 6 (-6), and 10 (-10) represent 'positive' evidence for (against), 'strong' evidence for (against) and 'very strong' evidence for (against) any model i, respectively. See Methods for full details.

	Rank	Model	L	$2H_{ref}$	$2H_{min}$
(A) 2 Regressors	1	fry density-spring air	130.0	27.2	0.0
1962-2005	2	spring air	135.6	15.8	-11.4
44 years	3	fry density	141.9	3.3	-23.8
	4	reference	143.5	0.0	-27.2
(B) 4 Regressors	1	fry density-yearling density-spring air	113.3	30.5	0.0
1962-2000	2	yearling density-spring air	116.7	23.5	-7.0
39 years	3	fry density-spring air	117.1	22.8	-7.7
	4	spring air	121.8	13.4	-17.1
	5	fry density-yearling density	123.1	10.8	-19.7
	6	yearling density	127.4	2.3	-28.2
	7	fry density	127.5	2.0	-28.5
	8	reference	128.5	0.0	-30.5

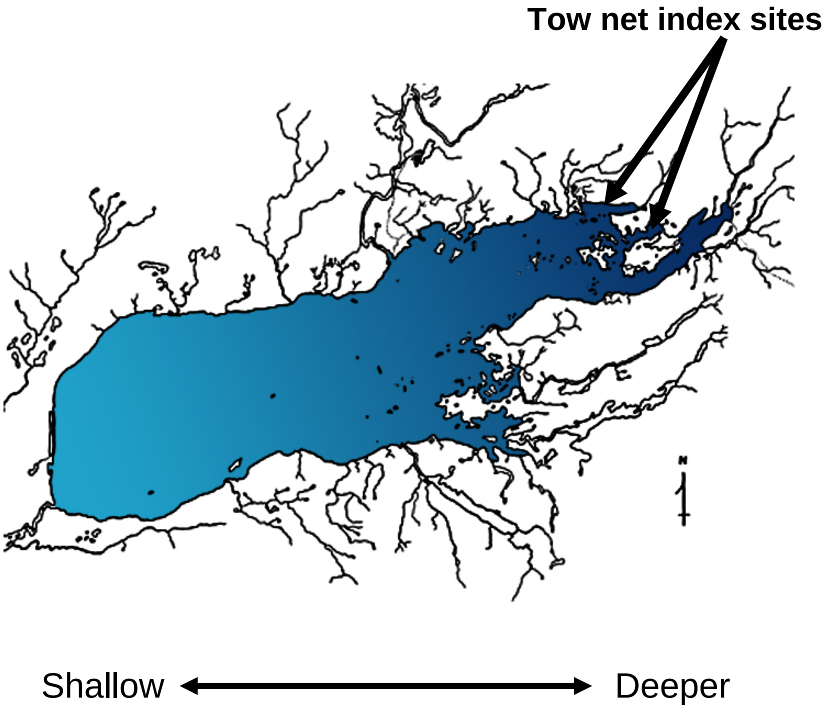


Figure 2.1 Iliamna Lake and index tow net sites used for long term data collection

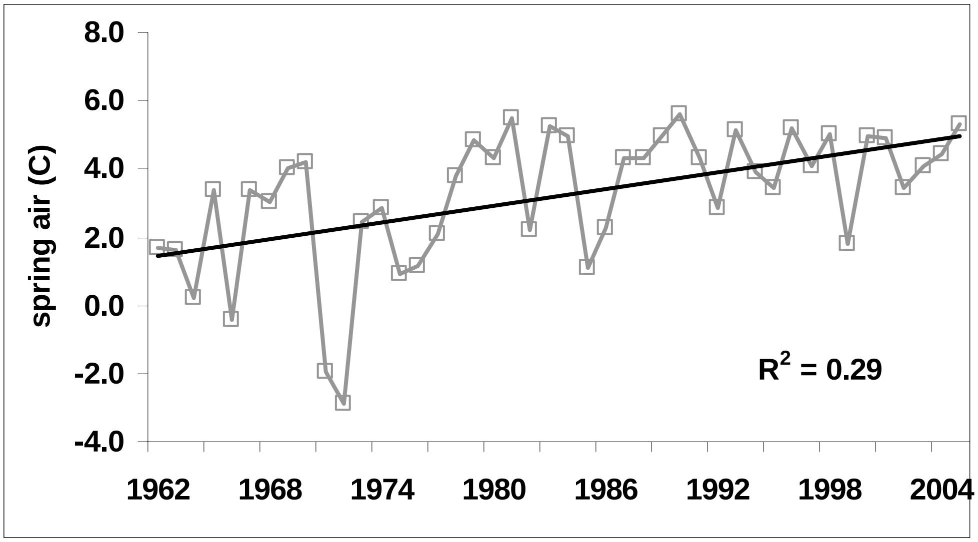


Figure 2.2. Time series of spring air temperature (monthly average of March-June) from Intricate Bay, Iliamna Lake, Alaska 1962-2005.

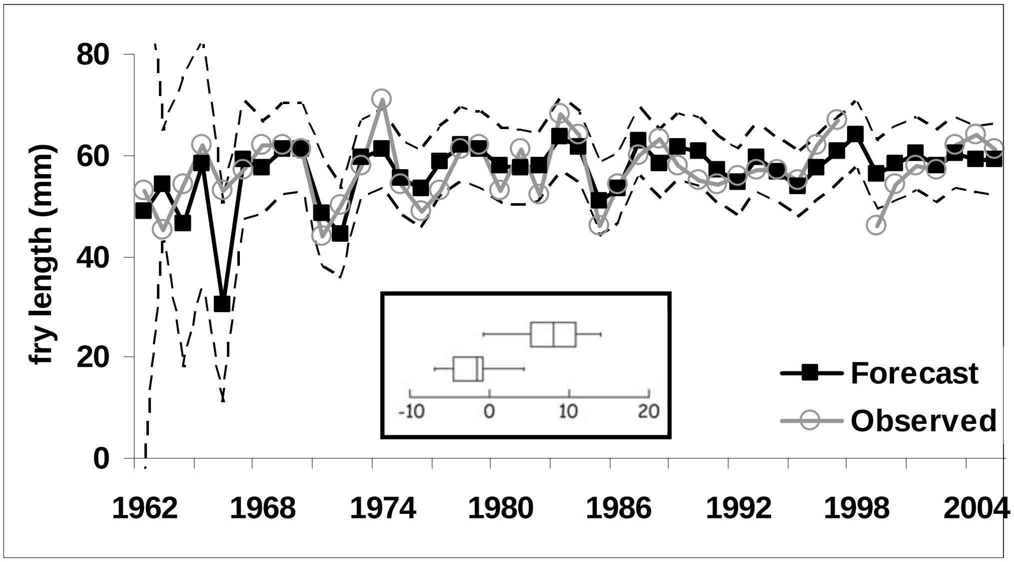


Figure 2.3 Model out put showing model forecast fit to observed data and the 90% prediction intervals for the fry density-spring air model. Effect size plot inset shows mean effect size over the time series for spring air temp (top plot) and fry density (lower plot). Model forecast to observed fit has $r^2 = 0.32$ (increases to 0.47 if outlier is removed).

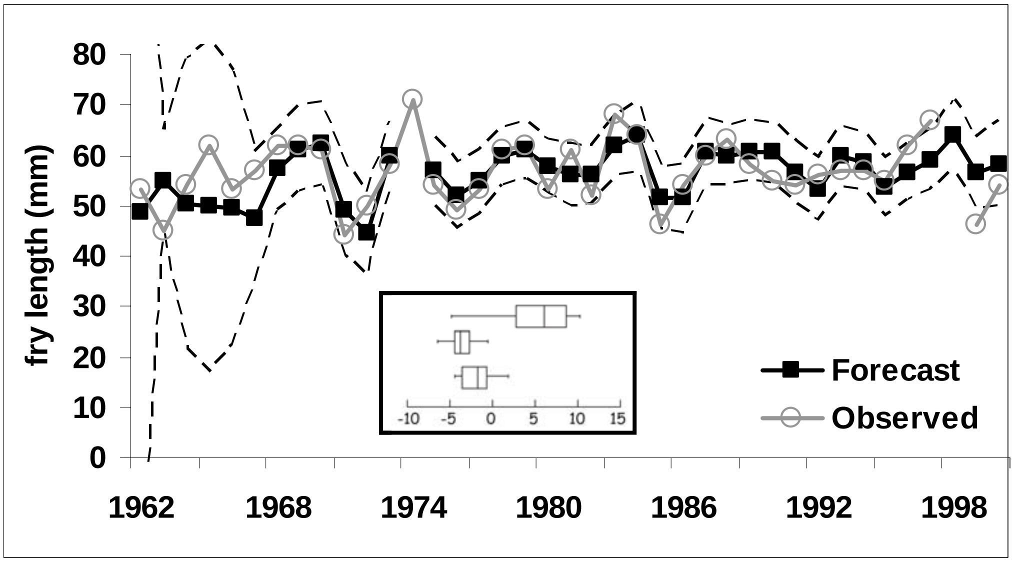


Figure 2.4 Model out put showing model forecast fit to observed data and the 90% prediction intervals for the fry density-yearling density-spring air model. Effect size plot inset shows mean effect size over the time series for spring air temp (top plot), yearling density (middle plot), and fry density (lower plot). Model forecast to observed fit $r^2 = 0.33$.

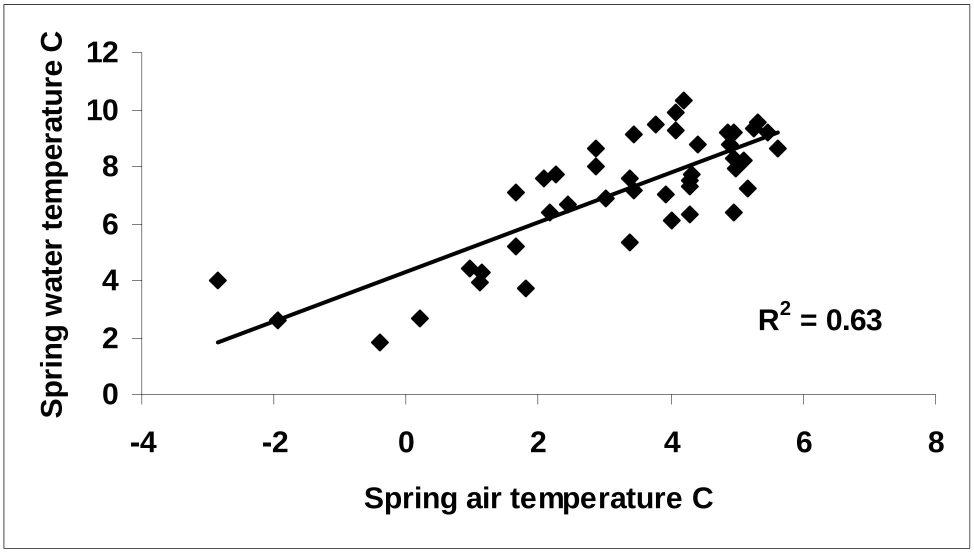


Figure 2.5 Relationship between spring air temperature (monthly average of March-June) in Intricate Bay, Iliamna Lake and spring water temperatures (daily averages June 1-15) at Igiugig, the outlet of Iliamna Lake, 1962-2005.

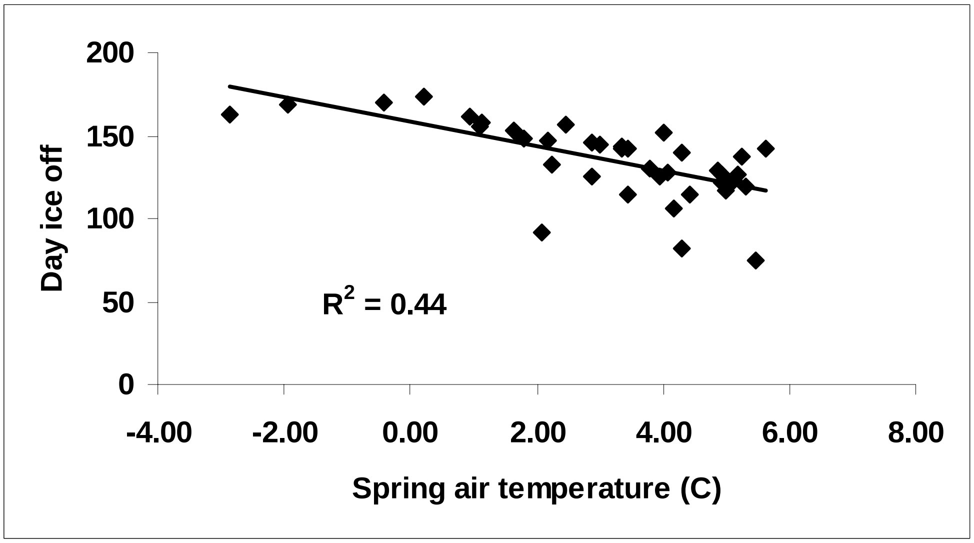


Figure 2.6 Relationship between spring air temperature (monthly average of March-June) in Intricate Bay, Iliamna Lake and day of ice breakup in Iliamna Lake, 1962-2005.

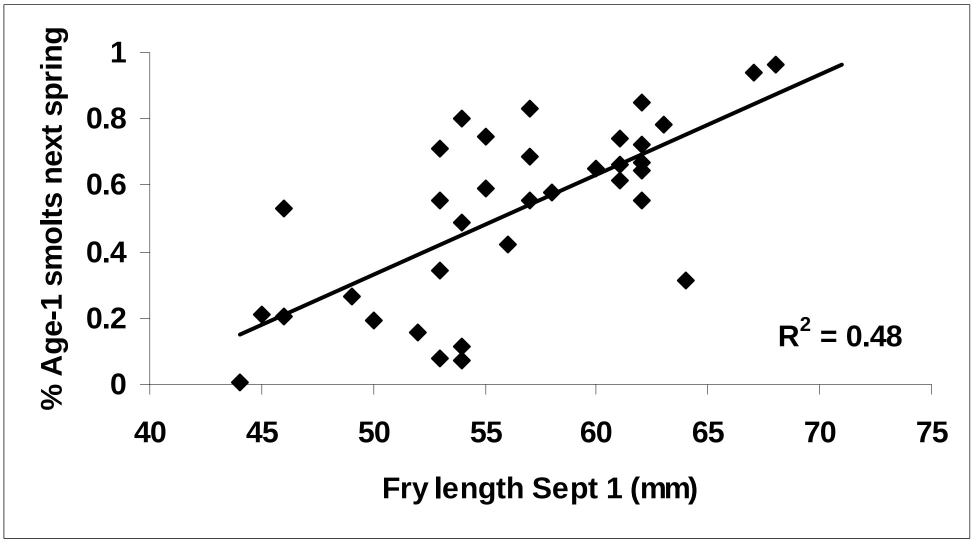


Figure 2.7 Iliamna Lake fry size on September 1 and the percent of cohort that smolt at age-1 the following spring, 1962-2000.

REFERENCES

Abrey, C.A. 2005. Variation in the early life history of sockeye salmon (*Oncorhynchus nerka*): emergence timing, an ontogenetic shift, and population productivity. Ph.D. dissertation. University of Washington, Seattle. 94 p.

Alheit, J. and E. Hagen. 1997. Long-term climate forcing of European herring and sardine populations. Fish. Oceanogr. 6 (2): 130-139.

Beamish, R.J. and D.R. Bouillon. 1993. Pacific salmon production trends in relation to climate. Can J. Fish. Aquat. Sci. 50: 1002-1016.

Beckerman, A.P., T.G. Benton, C.T. Lapsley, and N. Koesters. 2003. Talkin' 'bout my generation: environmental variability and cohort effects. Amer. Nat. 162 (6): 754-767.

Beebe, T.J.C. 1995. Amphibian breeding and climate. Nature. 374: 219-220.

Berger, J.O. and L.R. Pericchi. 1996. The intrinsic Bayes factor for model selection and inference. J. Amer. Stat. Assoc. 91: 109-122.

Berteaux, D., D.Reale, A.G. McAdam, and S. Boutin. 2004. Keeping pace with fastclimate change: can arctic life count on evolution? Integr. Comp. Biol. 44: 140-151.

Bradley, N.L., A.C. Leopold, J. Ross, and W. Huffaker. 1999. Phenological changes reflect climate change in Wisconsin. Proc. Natl. Acad. Sci. U.S.A. 96: 9701-9704.

Brander, K.M. 1995. The effect of temperature on growth of Atlantic cod (*Gadus morhua*). ICES J. Mar. Sci. 52:1-10.

Brett, J.R. 1971. Energetic responses of salmon to temperature: a study of some thermal relations in physiology and freshwater ecology of sockeye salmon (Oncorhynchus nerka). Amer. Zool. 11: 99-113.

Brett, J. R. 1995. Energetics. p. 1-68. In C. Groot, L. Margolis, and W.C. Clarke [ed] Physiological ecology of Pacific salmon. UBC Press. Vancouver.

Brown, J.H., T. J. Valone, and C.G. Curtin. 1997. Reorganization of an arid ecosystem in response to recent climate change. Proc. Natl. Acad. Sci. U.S.A. 96: 9729-9733.

Bunnell, D.B., C.P. Madenjian, and T.E. Croley, II. 2006. Long-term trends of bloater (*Coregonus hoyi*) recruitment in Lake Michigan: evidence for the effect of sex ratio. Can. J. Fish. Aquat. Sci. 63: 832-844.

Burgner, R. L. 1962. Studies of red salmon smolts from the Wood River Lakes, Alaska. p. 247-314. *In* T.S.Y. Koo [ed] Studies of Alaska red salmon. Univ. Wash. Publ. Fish. New Ser. 1.

Burgner, R.L. 1964. Factors influencing production of sockeye salmon (*Oncorhynchus nerka*) in lakes of southwestern Alaska. Verh. Int. Verein. Limnol. 15: 504-513.

Burgner, R.L. 1987. Factors influencing age and growth of juvenile sockeye salmon (*Oncorhynchus nerka*) in lakes. *In* H.D. Smith, L. Margolis, and C.C. Wood [ed.] Sockeye salmon (*Oncorhynchus nerka*) population biology and future management. Can. Spec. Publ. Fish. Aquat. Sci. 96: 129-142.

Burgner, R.L. 1991. Life history sockeye salmon (*Oncorhynchus nerka*). Pages 1-117. *In* C. Groot and L. Margolis [ed.] Pacific salmon life histories. UBC Press, Vancouver, British Columbia, Canada.

Burgner, R.L., C.J. DiCostanzo, R.J. Ellis, G.Y. Harry Jr., W.L. Hartman, O.E. Kerns Jr., O.A. Mathisen, and W.F. Royce. 1969. Biological Studies and estimates of optimum escapements of sockeye salmon in the major river systems in southwestern Alaska. U.S. Fish Wildl. Serv. Fish. Bull. 67: 405- 459.

Carlson, T. J. 1974. The life history and population dynamics of Bosmina coregoni in Pedro Bay, Iliamna Lake, Alaska. Ph.D. dissertation. University of Washington, Seattle. 142 p.

Clark, C.W., and D.A. Levy. 1988. Diel vertical migrations by juvenile sockeye salmon and the antipredation window. Amer. Nat. 131: 271-290.

Cottingham, K.L. and S.R. Carpenter. 1998. Population, community, and ecosystem variates as ecological indicators: phytoplankton responses to whole-lake enrichment. Ecol. Appl. 8: 508-530.

Crick, H.Q.P., C. Dudley, D.E. Glue, and D.L. Thomson. 1997. UK burds are laying eggs earlier. Nature: 388: 526.

Demory, R.L., R.F. Orrell, and D.R. Heinle. 1964. Spawning ground catalog of the Kvichak River system, Bristol Bay, Alaska. U.S. Fish Wildl. Serv. Spec. Sci. Rep. Fish. 448. 292 p.

Dickson, R.R. and W.R. Turrell. 1999. The NAO: the dominant atmospheric process affecting oceanic variability in home, middle, and distant waters of European Atlantic salmon. p. 92-115. *In* D. mills [ed] The ocean life of Atlantic salmon. Blackwell Press. Oxford.

Dunn, P.O. and D.W. Winkler. 1999. Climate change has affected breeding date of Tree Swallows throughout North America. Proc. Royal Soc. London. 266: 2487-2490.

Edmundson, J.A. and A. Mazumder. 2001. Linking growth of juvenile sockeye salmon to habitat temperature in Alaskan lakes. Trans. Amer. Fish. Soc. 130: 644-662.

Eggers, D.M. 1977. The nature of prey selection by planktivorous fish. Ecology 58: 46-59.

Eggers, D.M. 1978. Limnetic feeding beahavior of juvenile sockeye salmon inLake Washington and predator avoidance. Limn. Ocean. 23: 1114-1125.

Eggers, D.M. and D.E. Rogers. 1987. The cycle of runs of sockeye salmon (*Oncorhynchus nerka*) to the Kvichak River, Bristol Bay, Alaska: Cyclic dominance or depensatory fishing? *In* H.D. Smith, L. Margolis, and C.C. Wood [ed.] Sockeye salmon (*Oncorhynchus nerka*) population biology and future management. Can. Spec. Publ. Fish. Aquat. Sci. 96: 343-366.

Finney, B.P., I. Gregory-Eaves, J.Sweetman, M.S.V. Douglas, and J.P. Smol. 2000. Impacts of climatic change on Pacific salmon abundance over the past 300 years. Science. 290: 795-99.

Fleming, R.A. and G.M. Tatchell. 1995. Shifts in flight period of British Aphids: a response to climate warming? *In* R. Harrington and N.E. Stork [ed.] Insects in a changing environment. Academic Press. New York.

Foerster, R.E. 1968. The sockeye salmon, *Onchorhynchus nerka*. Bull. Fish. Res. Board Can. 162: 422 p.

Friedland, K.D., L.P. Hansen, and D.A. Dunkley. 1998. Marine temperatures experienced by postsmolts and the survival of Atlantic salmon (*Salmo salar*) in the North Atlantic. Fish. Oceanogr. 7: 22-34.

Gunnerød, T.B. 1971. The life history and population dynamics of Cyclops scutifer Sars in Pedro Bay, Iliamna lake, Alasaka. Ph.D. dissertation. University of Washington, Seattle. 136 p.

Henderson, M. A. and Cass, A. J. 1991. Effect of smolt size on smolt-to-adult survival for Chilko Lake sockeye salmon *(Oncorhynchus nerka).* – Can. J. Fish. Aquat. Sci. 48: 988-994.

Hilborn, R., T.P. Quinn, D.E. Schindler, and D.E. Rogers. 2003. Biocomplexity and fisheries sustainability. Proc. Natl. Acad. Sci. U.S.A. 100: 6564-6568.

Hoag, S.H. 1968. The food of juvenile sockeye salmon, Oncorhynchus nerka, related to the zooplankton in Iliamna Lake, Bristol Bay, Alaska. M.S. thesis. University of Washington, Seattle. 72 p.

Holtby, L.B. 1988. Effects of logging on stream temperatures in Carnation Creek, British Columbia, and associated impacts on the coho salmon *(Oncorhynchus kisutch)*. Can. J. Fish. Aquat. Sci. 45: 502-515.

Holtby, L.B. and J.C. Scrivener. 1989. Observed and simulated effects of climatic variability, clear-cut logging, and fishing on the numbers of chum salmon (*Oncorhynchus keta*) and coho salmon (*O. kisutch*) returning to Carnation Creek, British Columbia. Can Specl Publ. Fish. Aquat. Sci. 105: 62-81

Horne, A.J., and C. R. Goldman. 1994. Limnology. McGraw-Hill. New York

Huitema, B.E. 1980. The Analysis of Covariance and Alternatives. John Wiley & Sons. New York.

Hurrell, J.W. 1995. Decadal trends in the North Atlantic oscillation: regional temperatures and precipitation. Science 269 (5224): 676-679.

Hyatt,K.D. and J.G. Stockner. 1985. Responses of sockeye salmon (*Oncorhynchus nerka*) to fertilization of British Columbia coastal lakes. Can j. Fish. Aquat. Sci. 42: 320-331.

IPCC 2001. Climate Change 2001: Third Assessment Report of the Intergovernemental Panel on Climate Change. Cambridge University Press. Cambridge, Massachusetts.

Jaenicke, H.W., M.S. Hoffman, and M.l. Dahlberg. 1987. Food habits of sockeye salmon (*Oncorhynchus nerka*) fry and threespine stickleback (*Gastersosteus aculeatus*) in Lake nunavaugaluk, Alaska, and a strategy to improve salmon survival and growth. *In* H.D. Smith, L. Margolis, and C.C. Wood [ed.] Sockeye salmon (*Oncorhynchus nerka*) population biology and future management. Can. Spec. Publ. Fish. Aquat. Sci. 96: 161-175.

Janzen, F.J. 1994. Climate change and temperature-dependent sex determination in reptiles. Proc. Natl. Acad. Sci. U.S.A. 91: 7487-7490.

Jonsson, N., B. Jonsson, and L.P. Hansen. 2005. Does climate during embryonic development influence parr growth and age of seaward migration in Atlantic salmon (*Salmo salar*)? Can. J. Fish. Aquat. Sci. 62: 2502- 2508.

Kass, R.E. and A.E. Raftery. 1995. Bayes factors. J. Amer. Stat. Assoc. 90: 773-795.

Kerns, O.E. 1966. Abundance and size of juvenile red salmon and major competitor species in Iliamna Lake and Lake Clark, 1964 and 1965. University of Washington, Fish. Res. Inst. Circ. 66-13. 35 p.

Kerns, O.E. and O.A. Mathisen. 1963. Kvichak red salmon studies. Research in Fisheries, University of Washington, Seattle. 147: 7-10.

Koenings, J.P. and R.D. Burkett. 1987. Population characteristics of sockeye salmon (*Oncorhynchus nerka*) smolts relative to temperature regimes, euphotic volume, fry density, and forage base within Alaskan lakes. *In* H.D. Smith, L. Margolis, and C.C. Wood [ed.] Sockeye salmon (*Oncorhynchus nerka*) population biology and future management. Can. Spec. Publ. Fish. Aquat. Sci. 96: 216- 234.

Koenings, J.P.,H.J. Geiger, and J.J. Hasbrouck. 1993. Smolt-to-adult survival patterns of sockeye salmon (*Oncorhynchus nerka*) – effects of smolt length and geographic latitude when entering the sea. Can. J. Fish. Aquat. Sci. 50: 600-611.

Kyle, G.B., J.P. Koenings, and B.M. Barrett. 1988. Density-dependent, trophic level responses to an introduced run of sockeye salmon (Oncorhynchus nerka) at Frazer Lake, Kodiak Island, Alaska. Can. J. Fish. Aquat. Sci. 45: 856-867.

Lamon, E.C., III, S.R. Carpenter, and C.A. Stow. 1998. Forecasting PCB concentrations in Lake Michigan salmonids: a dynamic linear model approach. Ecol. Appl. 8: 659-668.

Levy, D.A. 1987. Review of the ecological significance of diel vertical migrations by juvenile sockeye salmon (*Oncorhynchus nerka*). *In* H.D. Smith, L. Margolis, and C.C. Wood [ed.] Sockeye salmon (*Oncorhynchus nerka*) population biology and future management. Can. Spec. Publ. Fish. Aquat. Sci. 96: 44-52.

Levy, D.A. 1990. Sensory mechanism and selective advantage for diel vertical migration in juvenile sockeye salmon (*Oncorhynchus nerka)*. Can. J. Fish. Aquat. Sci. 47: 1796-1802.

Lindström, J. Early development and fitness in birds and mammals. Trend. Ecol. Evol. 14 (9): 343-347.

Magnuson, J.J., D.M. Robertson, B.J. Benson, R.H. Wynne, D.M. Livingstone, T. aria, R.A. Assel, R.G. Barry, V. card, E. Kuusisto, N. G. Granin, T.D. Prowse, K.M. Stewart, andV.S. Vuglinski. 2000. Historical trends in lake and river ice cover in the Northern Hemisphere. Science. 289: 1743-1746.

Mantua, N.J., S.R. hare, Y. Zhang, J.M. Wallace, and R.C. Francis. 1997. A Pacific interdecadal climate oscillation with impacts on salmon production. Bull. Amer. Meteor. Soc. 78: 1069-1079.

Mantua, N.J. and S.R. Hare. 2002. The Pacific decadal oscillation. J. Ocean. 58: 35-44.

Mathisen, O.A. 1966. Some adaptations of sockeye salmon races to limnological features of Iliamna Lake, Alaska. Verh. Int. Verein. Limnol. 16: 1025-1035.

Mathisen, O.A. 1969. Growth of sockeye salmon in relation to abundance in the Kvichak District, Bristol Bay, Alaska. FiskDir. Skr. Ser. HavUnders. **15**: 172-185.

Mazumder, A. and J. A. Edmundson. 2002. Impact of fertilization and stocking on trophic interactions and growth of juvenile sockeye salmon (*Oncorhynchus nerka*). Can. J. Fish. Aquat. Sci. 59: 1361-1373.

McCarty, J.P. 2001. Ecological consequences of recent climate change. Conserv. Biol. 15 (2): 320-331.

McDonald, M.E., A.E. Hershey, and M.C. Miller. 1996. Global warming impacts lake on trout in arctic lakes. Limnol. Oceanogr. 41: 1102-1108.

Melack, J.M., J. Dozier, C.R. Goldman, D. Greenalnd, A.M. Milner, and R.J. Naiman. 1997. Effects of climate change on inland waters of the Pacific Coastal Mountains and Western Great Basin of North America. Hydrolog. Process. 11: 971-992.

Neter, J., M.H. Kutner, C.J. Nachtsheim, and W. Wasserman. 1983. Applied Linear Regression Models. McGraw-Hill. New York.

O'Neill, S.M. and K.D.Hyatt. 1987. An experimental study of competition for food between sockeye salmoin (*Oncorhhynchus nerka*) and threespine sticklebacks (*Gasterosteus aculeatus*) in a British Columbia coastal lake. *In* H.D. Smith, L. Margolis, and C.C. Wood [ed.] Sockeye salmon (*Oncorhynchus nerka*) population biology and future management. Can. Spec. Publ. Fish. Aquat. Sci. 96: 129-142.

Ottersen, G., H. Loeng, and A. Raknes. 1994. Influences of temperature variability on recruitments of cod in the Barents Sea. ICES Mar. Sci. Symp. 198: 471-481.

Parmesan, C. and G. Yohe. 2003. A globally coherent fingerprint of climate change impacts across natural systems. Nature. 421: 37-42.

Parmesan, C., N. Ryrholm, C. Stefanescus, J.K. Hill, C.D. Thomas, H. Descimon, B. Huntley, L. Kaila, J. Killberg, T. Tammaru, W.J. Tennet, J.A. Thomas, and m. Warren. 1999. Poleward shifts in geographical ranges of butterfly species associated with regional warming. Nature. 399: 579-583.

Pella, J.J. 1968. Distribution and growth of sockeye salmon fry in Lake Aleknagik, Alaska, during the summer of 1962. p. 45-111. *In* R.L. Burgner [ed.] Further studies of Alaska sockeye salmon. Univ. Wash. Publ. Fish. New Serv. 3.

Pole, A., M. West, and J. Harrison. 1994. Applied Bayesian Forecasting and Time Series Analysis. Chapman-Hall. New York.

Quinn, T.P**.** 2005. The Behavior and Ecology of Pacific Salmon and Trout. University of Washington Press. Seattle, Washington.

Randall, D.J., W.W. Burggren, K. French, and R. Eckert. 2002. Animal physiology: mechanisms and adaptations. W. H. Freeman and Co. New York.

Rogers, D.E. 1968. A comparison of the food of sockeye salmon fry and threespine sticklebacks in the Wood River Lakes. P. 1-43. *In* R.L. Burgner [ed.] Further studies of Alaska sockeye salmon. Univ. Wash. Publ. Fish. New Serv. 3.

Rogers, D.E. 1973. Abundance and size of juvenile sockeye salmon (*Oncorhynchus nerka*) and associated species in Lake Aleknagik, Alaska, in relation to their environment. U.S. Natl. Mar. Fish. Serv. Bull. 71-4: 1061-1075.

Rogers, D.E. and P.H. Poe. 1984. Escapement goals for the Kvichak River system. Univ. Washington Fish. Res. Inst. FRI-UW-8407: 66 p.

Ruggerone, G.T. 1989. Coho salmon predation on juvenile sockeye salmon in the Chignik Lakes, Alaska. Ph.D. dissertation. University of Washington, Seattle. 151 p.

Sagarin, R.D., J.P. Barry, S.E. Gilman, and C.H. Baxter. 1999. Climate related change in an intertidal community over short and long time scales. Ecol. Monogr. 69: 465-490.

Scheffer, M., D. Straile, E.H. van Nes, and H. Hosper. 2001. Climatic warming causes regime shifts in lake food webs. Limnol. Oceanogr. 46 (7): 1780-1783.

Scheuerell, M.D., D.E. Schindler, A.H. Litt, and W.T. Edmondson. 2002. Environmental and algal forcing of *Daphnia* production dynamics. Limnol. Oceanogr. 47: 1477-1485.

Scheuerell, M.D. and D.E. Schindler. 2003. Diel vertical migration by juvenile sockeye salmon: evidence for the antipredation window. Ecology 84: 1713-1720.

Scheuerell, M.D. and J.G. Williams. 2005. Forecasting climate-induced changes in the survival of Snake River spring/summer Chinook salmon (*Oncorhynchus tshawytscha*). Fish. Oceanogr. 14 (6): 448-457.

Schindler, D.E., M.D. Scheuerell, D.E. Rogers, and C.A. Abrey. 2005a. Effects of changing climate on zooplankton and growth of juvenile sockeye salmon in southwestern Alaska. Ecology 86(1): 198-209.

Schindler, D.E., P.R. Leavitt, C.S. Brock, S.P. Johnson, and P.D. Quay. 2005b. Marine-derived nutrients, commercial fisheries, and production of salmon and lake algae in Alaska. Ecology: 86(12): 3225-3231.

Schindler, D.W., K.G. Beaty, E.J. Fee, D.R. Cruikshank, E.R. DeBruyn, D.L. Findlay, G.a. Lindsey, J.A. Shearer, M.P. Stainton, and M.A. Turner. 1990. Effects of climatic warming on lakes of the central boreal forest. Science. 250: 967-970.

Selifonov, M.M. 1970. The growth of young sockeye salmon in Lake Kuril. Izv. Tikhookean. Nauchno-Issled. Inst. Rybn. Khoz. Okeanogr. 78: 33-41. (Transl. from Russian by Fish. Res. Board Can. Transl. Serv no. 2340).

Shuter, B. J. and J.R. Post. 1990. Climate, population viability, and the zoogeography of temperate fishes. Trans. Amer. Fish. Soc. 119: 314-336.

Shuter, B. J. and K.K. Ing. 1997. Factors affecting the production of zooplankton in lakes. Can. J. Fish. Aquat. Sci. 54: 359-377.

Sparks, T.H. and P.D. Carey. 1995. The responses of species to climate over two centuries: an analysis of the Marsham phonological record 1736-1947. J. Ecol. 83: 321-329.

Straile, D. 2000. Meteorological forcing of plankton dynamics in a large and deep continental European lake. Oecologia 122: 44-50.

Sturm, M.,C. Racine, and K. Tape. 2001. Increasing shrub abundance in the Arctic. Nature. 411: 546-547.

Thomas, C.D. and J.J. Lennon. 1999. Birds extend their ranges northward. Nature. 399: 213.

Walther, G.R., E. Post, P. Convey, A. Menzel, C. Parmesan, T. J. C. Beebe, J. Fromentin, O. Hoegh-Guldberg, and F. Bairlein. 2002. Ecological responses to recent climate change. Nature. 416: 389-395.

Wang, H., R. Zhang, J. Cole, and F. Chavez. 1999. El Niño and the related phenomenon Southern Oscillation (ENSO): the largest signal in interannual climate variation. Proc. Natl. Acad. Sci. U.S.A. 96: 11071-11072.

Wootton, R.J. 1984. A functional biology of sticklebacks. University of California Press. Berkeley, California.

Wootton, R.J. 1998. Ecology of Teleost Fishes. Kluwer Academic Press. Boston, Massachusetts.