Variation in the Early Life History of Sockeye Salmon (*Oncorhynchus nerka*): Emergence Timing, An Ontogenetic Shift, and Population Productivity

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This is to certify that I have examined this copy of a doctoral dissertation by

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Abstract

Variation in Early Life History Patterns of Sockeye Salmon (*Oncorhynchus nerka*): Emergence Timing, An Ontogenetic Shift, and Population Productivity

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Juvenile sockeye salmon (*Oncorhynchus nerka*) typically exhibit an extended period of lacustrine growth prior to their migration to salt water, and yet little is known about variation in the early life history traits among sympatric populations or the long-term implications of this period on growth and survival. In Lake Aleknagik, Alaska, neighboring sockeye salmon populations have evolved distinctly different peak dates of fry emergence. Among all populations, emergence extended over at least six weeks. This diversity may be a response to high interannual variation in environmental conditions, leading to the lack of a predictable optimal emergence period. In general, sockeye salmon fry emerged prior to peak prey abundance in the lake, suggesting a tendency to maximize the available growing period before the onset of winter.

During the first summer of growth, juveniles exhibited an ontogenetic niche shift from the littoral to the pelagic region of the lake and switched their primary prey from aquatic insects to zooplankton. The timing of this shift was driven by offshore habitat conditions (water temperature and zooplankton density), as indicated by path analysis models. This is distinctly different from the pattern of size-mediated ontogenetic shifts observed in more temperate species, suggesting that selective pressure to maximize growth may outweigh predation risk in this high-latitude system.

Populations characterized by later periods of emergence had greater proportions of offspring spending two years (rather than one) in fresh water. However, there was no difference in mean productivity among the populations and all exhibited highly significant interannual correlations. The date of the ontogenetic shift was strongly correlated with fish length at the end of the first summer of growth and with survival of the age-1 smolts to adulthood. Productivity was not correlated with the length of out-migrating smolts.

This study provides insight into the primary selective forces driving early life history patterns in a highly productive sockeye salmon system, and the impacts of this period on the long-term growth and survival of these populations. In addition, we gain perspective on the large-scale interactions among the biotic and abiotic components acting within an ecosystem largely unaffected by anthropogenic activities.

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Introduction

One of the primary challenges facing ecologists today is understanding the interactions among ecosystem processes that occur over different spatial and temporal scales. In recent years, increasing attention has been focused on such topics as the importance of biocomplexity in ecosystem stability and resilience to perturbation, the effect of ecosystem engineers on nutrient cycling and habitat condition, and the impact of climate on patterns of multi-trophic level productivity at large geographic scales. The results of all of these studies point to the importance of understanding the suite of key direct and indirect interactions present within complex ecosystems in order to be able to explain emergent ecological properties and predict how systems will respond to environmental change.

Theoretical ecologists have offered multiple conceptual models to explain how biotic and abiotic ecological processes might interact at the scale of the ecosystem. Of particular interest is the proposal by Maurer (1987), in which he states “the nature of the community is determined by an interaction between the biological processes operating within the community and the boundaries imposed upon those processes by the large-scale, abiotic forces operating in the environment.” From this ecological perspective, environmental conditions operating on broad spatial and temporal scales, such as climate, function as limiting factors on the possible states a ecosystem can achieve. Variation within these available state spaces is controlled by smaller-scale biological interactions such as competition, reproduction, predation, and prey availability. In this dissertation, I apply Maurer's theoretical perspective to ecological processes occurring in a natural lake ecosystem in southwest Alaska. Using field measurements collected from the 1940s through the present, I examined three components of the life history of sockeye salmon (*Oncorhynchus nerka*) occurring at different spatial and temporal scales, and quantified the effect of temperature (as a major environmental driver) on these processes.

Chapter One focuses on the emergence timing of neighboring sockeye salmon populations that all use the same lake (Lake Aleknagik) as a common rearing ground. The study addressed three questions. First, does emergence tend to occur early in the spring after the ice breakup on the lake, thereby maximizing the length of the growing season, or is emergence delayed until prey abundances have increased in the lake? Both possibilities have been argued in the literature, but not been explicitly tested. The second question addressed whether emergence in all of the neighboring populations occurred during a brief temporal period, which would indicate the presence of an "optimal window" providing maximum growth and survival of the juvenile fish. The third question compared the pattern of emergence timing among populations within the lake, estimating the length of the emergence period and the date of peak emergence for each. The data used to address all of these questions consisted of littoral sampling of juvenile sockeye salmon during their first summer of growth, analysis of age composition based on otolith microstructure patterns, and calculations of population-specific emergence dates based on spawn timing and incubation temperature. The answers provide insight into the life history strategies used by these populations in a northern region, which experience short growing seasons and harsh over-winter conditions.

Chapter Two examines the timing of an ontogenetic niche shift by the juvenile sockeye salmon. Midway through the first summer of freshwater growth, the salmon move from the littoral to the pelagic habitat of the lake, and concordantly switch their main prey item from aquatic insects to zooplankton. The date of this niche shift varied by up to 5 weeks among years, and the driving factors determining the timing of the shift were unknown. I tested a series of alternative hypotheses, measuring the effect of size, competition, emergence timing, and prey abundance and temperature in both the onshore and offshore habitats. In addition to testing the variables individually, I generated additive composite variables of the conditions in the two habitats to test the predictive ability of multiple variables simultaneously. The interactions among the independent and response variables were estimated using path analysis, a form of multivariate structural equation modeling which accounted for both direct and indirect effects among components within the system and tests the goodness-of-fit of the hypothesized model as a whole.

Chapter Three examines the effects of these two early life history patterns, emergence timing and date of ontogenetic shift, on the long-term productivity of the sockeye salmon populations within the Lake Aleknagik system. Based on annual surveys of adult abundance and age composition, I compared the emergence timing of five discrete populations with (1) the proportion of surviving offspring that spent one or two years in fresh water before migrating to sea, and (2) patterns of population-specific productivity based on a 20^{+}-year time series. The timing of the habitat shift was hypothesized to be correlated with lake-scale patterns of growth and productivity, specifically (1) juvenile size at the end of the first summer's growth, and (2) the proportion of individuals surviving to adulthood.

Patterns of Emergence Timing

Introduction

Juvenile fish experience strong selective pressure to optimize growth. Larger individuals swim faster and capture prey more efficiently (Miller et al. 1988), experience lower predation risk (Howick and O'Brien 1983, Christensen 1996, Lundvall 1999, Juanes 1994,), and store greater energy reserves for over-winter survival (Schultz et al. 1998). The benefits to maximizing early growth are particularly pronounced in high latitude systems, where growing seasons are short and harsh winter conditions tend to lead to high mortality rates (Conover 1990, Schultz et al. 1998, Schindler 1999).

Anadromous salmon (*Oncorhynchus* spp.) may experience additional pressure to maximize early growth opportunities, given their ontogenetic shift from fresh to salt water during early life history stages. For instance, juvenile sockeye salmon (*Oncorhynchus nerka*) typically rear in lakes for 1 or 2 years prior to migrating to sea as smolts (Burgner 1991), and their size at the time of migration is correlated to their early marine survival (Ricker 1962, Burgner 1991). The number of years spent in freshwater is also related to their relative growth rate; slow-growing individuals may spend an additional year in the lake and enter the marine environment at a greater absolute size than their faster-growing cohorts that outmigrated the previous year, but at the cost of an additional year of exposure to mortality in fresh water (Mathisen and Poe 1981, Burgner 1987, 1991). Thus, the ability of sockeye salmon fry to grow efficiently during their first summer not only has immediate implications for their freshwater survival but also for their success during the next life history stage, and consequently, their entire life cycle.

One of the primary life history characteristics driving growth opportunities is the date of fry emergence from sub-gravel incubation redds. Sockeye salmon embryos typically hatch in late winter / early spring and the fry emerge from the gravel in the spring or early summer when the majority of the yolk sac has been absorbed and they are ready to begin exogenous feeding (Burgner 1991). The timing and location of adult spawning the previous summer / fall has apparently evolved to optimize the resultant emergence date of their progeny (Olsen 1968, Beer and Anderson 2001, Hodgson and Quinn 2002, Connor et al. 2003). The incubation time to hatching and emergence in salmon is strongly controlled by water temperature, such that a predictable number of "degree days" (i.e., number of days multiplied by the temperature in ^{o}C) is required to reach each developmental stage (Brannon 1987, Beacham & Murray 1990). Unlike spring-spawning fishes that may optimize their date of egg deposition in response to proximate environmental conditions, fall-spawning salmon populations exhibit very consistent spawning dates among years (Brannon 1987). Salmonid egg deposition occurs months before the offspring emerge, making current habitat conditions an unreliable predictor of those that will be experienced by the offspring. Therefore, the date of reproduction appears to be driven by long-term average winter and spring temperatures; i.e., genetically determined rather than behaviorally plastic (Quinn and Adams 1996, Quinn et al. 2000). This constraint may be detrimental to fry survival in years when environmental conditions deviate significantly from the mean, particularly in systems exhibiting a high degree of uncertainty in spring conditions.

At present, the prevailing hypothesis holds that stabilizing selection moves the timing of emergence in salmonids towards some ‘optimal window’ for populations sharing a common rearing environment (Godin 1982, Brannon 1987; see also Einum and Fleming 2000). Individuals that emerge too early may encounter predators and a limited food supply, whereas later-arriving individuals may experience increased competition for resources and missed growing opportunities (Brännäs 1995). The average date of emergence into the lake or stream should have evolved to maximize the survival and growth potential of the fry, either by coinciding with peak prey abundance (Godin 1982) or earlier in the season to increase the amount of time available for growth (Bams 1969). Evidence regarding the synchrony of emergence timing in neighboring salmon populations, however, remains mixed. On one hand, eggs incubating in cold-water require a greater absolute period of time to develop than those in warm-water, and adults in cold systems tend to spawn earlier to compensate for this (Brannon 1987). In addition, eggs incubating at colder temperatures require fewer degree days to develop to hatching and emergence (i.e., develop at a relatively faster rate than those in warmer water; (Brannon 1987). Both of these factors tend to cause the emergence dates of populations incubating at different temperatures to converge. However, there are numerous examples of lakes where newly emerged sockeye salmon fry enter the lake over either a protracted period of several months or they enter in two distinct peaks, suggesting the lack of an optimal period during the growing season to begin freshwater residence (Hartman and Burgner 1972, Seiler and Kishimoto 1996, Boatright 2003). Despite the intuitive nature of the relationship between fry emergence and prey availability, there has been no explicit study of the temporal sequences of food, temperature, and emergence of sockeye salmon fry.

We addressed these conflicting patterns in the timing of emergence in juvenile sockeye salmon in a high latitude, cold water system where there is strong selective pressure to maximize growth by testing the following three predictions. First, the period of peak sockeye salmon fry emergence was not expected to coincide with maximum prey abundance, but rather occur earlier in the season and thus lengthen the amount of time available for growth. Second, we tested the null hypothesis that sockeye salmon fry in the lake would emerge within a short optimal time period each year against the alternative, that the highly variable spring environmental conditions in the study system might favor a broad period of emergence. Third, we predicted that, regardless of the length of the overall emergence period, the general pattern of appearance of newly emerged fry would not vary geographically among populations in the system, given that all individuals were exposed to equivalent post-emergence rearing conditions. Our analyses combined a long-term ecological dataset from a densely populated sockeye salmon nursery lake in southwest Alaska with detailed data from the same system in recent years, documenting emergence trends among specific populations based on otolith microstructure analysis of fry and recorded incubation temperatures on natural spawning sites.

Materials and Methods

Study site

Bristol Bay, Alaska has many large sockeye salmon populations, with as many as 60 million adults returning in any given year. The Wood River Lake system, a tributary of the Nushagak River on the west side of Bristol Bay, is comprised of a series of interconnected lakes and supports a minimum escapement of 1 million spawning sockeye salmon each summer. Lake Aleknagik (Figure 1) is the lowermost lake in the system, 83 km^2 in area with a mean depth of 43 m (Hartman and Burgner 1972). The lake is frozen 6-8 months each year (Hartman and Burgner 1972, Schindler et al. 2005); the date of spring ice break-up has been recorded in the village of Aleknagik each year since 1949.

The numerically dominant anadromous salmonid in Lake Aleknagik is sockeye salmon, with an average of 300,000 adults spawning on 14 major spawning grounds (creeks and beaches) throughout the lake. The vast majority ($\geq$90%) of the juvenile sockeye salmon in this system migrate to sea as smolts after one rather than two years in the lake (Rogers 1987), shortly after the ice breaks up, and therefore they achieve most of their freshwater mass during the summer immediately following their emergence. The primary resident fish species in the system include threespine sticklebacks (*Gasterosteus aculeatus*), and ninespine sticklebacks (*Pungitius pungitius*), both of which compete with juvenile sockeye salmon for food resources, and Arctic char (*Salvelinus alpinus*) and Dolly Varden (*S. malma*) which prey on sockeye salmon fry and smolts. The zooplankton community is dominated by calanoid and cyclopoid copepods (*Eudiaptomus gracilis, Eurytemora yukonensis, Leptodiaptomus pribilofensis, Cyclops columbianus, Acanthocyclops brevispinosus*), although *Eubosmina longispina, Daphnia longiremis* and *Holopedium gibberum* are also common.

Historical sampling

The University of Washington has maintained a research facility on Lake Aleknagik since 1947 and collected consistent measurements of the major ecological components of the system throughout much of that period. The primary focus of this facility is to monitor the adult and juvenile sockeye salmon populations. However, additional data are collected on the resident fish species, as well as on the biotic and abiotic limnological components of the lake.

Beach seining: Fish in the littoral habitat of the lake were sampled weekly to monitor the presence and growth rates of juvenile sockeye salmon in this habitat. Samples were collected at 10 standard locations between ~June 20 and ~August 1 from 1991 to 2003. The sampling sites were located around the perimeter of the lake, many situated near the outlets of tributaries where sockeye salmon spawn (Figure 1). Sampling was conducted with a 30 m beach seine deployed perpendicular to the beach from a skiff and pulled manually to shore. All of the fish (or a subset, if many were caught) were identified to species, enumerated, and measured for fork length. A surface water temperature measurement was taken at each sampling event.

Tow netting: The limnetic fish community was sampled on September 1 each year from 1996 – 2003 to monitor growth rates of juvenile sockeye late in their first growing season. Sockeye salmon fry in this system do not enter the limnetic area of the lake until the second half of the summer (Burgner 1962, Pella 1968, Chapter 2), and once there they exhibit strong diel vertical migration, approaching the surface only during the darkest parts of the night (Pella 1968, Scheuerell and Schindler 2003). Therefore, tow netting was only conducted at night in the latter part of the summer. Sampling on each date was conducted at 9 standard locations along the length of the lake (Figure 1). Surface tows were made using a 3 x 3 m double vertical beam tow-net pulled between two vessels at 3 km/h for 5 minutes at each sampling location. As with the beach seining, all fish were identified to species, counted, and measured for fork length.

Temperature and Zooplankton: Temperature and zooplankton samples were collected at six sites (Figure 1) every 10 days between late June and early September from 1967 to 2003. A vertical depth-temperature profile was taken to ~30 m at every other site, starting from the western end of the lake. Prior to 1999, temperatures were taken at 5 m depth intervals using a Van Dorn sampling bottle and a handheld thermometer. From 1999-2003, a Yellow Springs Inc. sonde measured depth and temperature at ~1 m increments to 30 m. Vertical zooplankton tows at all six sites were made using a 247 μm mesh conical net with 0.5 m opening and a width:length ratio of 1:3. Hauls were made from 60 m, except at the shallower Yako Creek site where tows were taken from 20 m. Zooplankton were identified and counted in a series of consecutive subsamples until approximately 500 individuals were counted. For purposes of this analysis, only *Daphnia* and calanoid and cyclopoid copepod species were considered, as they comprise the primary prey resources of juvenile sockeye salmon (Rogers 1968).

<u>Insects:</u> Traps for emerging terrestrial and aquatic insects were maintained in three bays of Lake Aleknagik (Figure 1) from 1969-2003 in order to monitor sockeye salmon prey dynamics . The conical plastic traps, 1 m high, consisted of a 1 m diameter opening at the base suspended 1 m above the substrate and a collection jar half-filled with air floating near the surface. Insects emerging from the substrate and ascending toward the surface were guided by the cone into the collection jar and trapped. Traps were checked every other day between 1800 and 2300 hours from early June through early September. All insects were identified to family and life stage (adult, pupal, larval), and counted.

Sockeye salmon fry emergence timing

Our estimate of emergence timing of sockeye salmon fry was based on the presence of ‘newly emerged’ fry (i.e., ≤ 30 mm) in the littoral habitat on a given date. Although the exact size of emerging fry varies among populations and individuals (largely a function of egg size), they are consistently less than 30 mm long (Beacham & Murray 1990). It was not feasible to intercept the sockeye salmon fry as they emerged from the gravel or migrated downstream due to ice cover on the lake and creeks early in the spring.

Because samples were not collected on exactly the same day of the year in all years, sampling dates were standardized on a weekly basis (e.g., fish caught between June 20 – 26 were assigned a standardized sampling date of June 23). Each of the 10 beach seine sites was considered separately to test for geographical variation in the synchrony of emergence timing. The proportion of the total number of newly emerged fish, based on the pooled data 1991 - 2003, was calculated for each site on each standardized sampling date. This resulted in one data point for each sampling location on each standardized sampling date. A chi-squared contingency table analysis was conducted to test for differences in the peak date of emergence among the different locations, and a post-hoc chi-squared partitioning test was used to determine which specific sites significantly differed from one another (Zar 1999).

In addition to the historical trends, the within year variation in emergence timing in Lake Aleknagik was examined for a subset of years using (1) an analysis of otolith microstructure in young-of-the-year sockeye salmon, and (2) an estimate of the predicted emergence timing of specific populations based on known spawning dates and incubation temperatures.

In 2002, 80 sockeye salmon fry were collected from two beach seining sites at opposite ends of the lake (7S and 2N, Figure 1) between June 19 and August 21. Both saggital otoliths were dissected from each fish, mounted to a microscope slide with ethyl acetate, and ground to a single plane using a progressive series of 13, 9, and 3 μ lapping film

(Stevenson and Campana 1992). The daily rings present since the emergence check (Wilson and Larkin 1980, Marshall and Parker 1982, Stevenson and Campana 1992) were counted from digital photographs taken through a compound microscope, and used to back-calculate the date of emergence of each fish. The range in emergence timing at the two sampling locations was compared based on the frequency distribution of estimated dates.

The identification of the emergence check and daily rings were validated based on known-age sockeye salmon fry raised in the lab. Gametes from a sockeye salmon population in Bear Lake, Alaska were fertilized and raised in incubators in the University of Washington hatchery (Boatright 2003). On the date of swim-up (corresponding to emergence timing under natural conditions), the fry were transferred to an aquarium and kept at constant conditions of 7^{o} C, 12-hour light/dark cycle, and fed once daily. Fry were sacrificed at 10, 27, or 40 days after emergence, and the otolith microstructure was analyzed blind to fish age or length. Post-emergence age estimates on the lab-reared fish were highly accurate (linear regression of measured age on actual age, $r^2 = 0.96$, $y = 0.94x-0.11$). There was a slight tendency to underestimate age (mean = -1.7 days, SE = 0.10), probably due to loss of material at the edge of the otoliths during preparation; however, this discrepancy was not significantly different from a 1:1 correlation.

Mathematical models are commonly used to compute the developmental rate of incubating Pacific salmon embryos (Brannon 1987, Beacham and Murray 1990, Beer and

Anderson 2001). Given information about spawning date and ambient water temperatures, the correlation between incubation temperature and rate of development can be used to predict the average date of emergence of a population. To this end, we determined the dates of peak spawning in four creeks on Lake Aleknagik and measured the incubation temperatures experienced by the embryos in these populations. During the spawning seasons of 2001 and 2002, Bear, Hansen, Happy, and Whitefish creeks (Figure 1) were each surveyed at least three times (daily on Hansen Creek) and the numbers of live and dead adult sockeye salmon were recorded. This information was used to estimate the date of peak spawning, defined as occurring when 75% of the estimated total number of females spawning in that year were alive in the creeks. To record incubation temperature, HOBO remote temperature loggers were buried 30 cm below the surface of the gravel on observed spawning sites in each of the creeks during the summers of 1997, 1998, 2001, and 2002, left over the winter, and retrieved the following June (except Bear Creek, where temperatures were only recorded in 2001 and 2002). The number of degree days required to reach emergence was based on the average water temperature in each creek (Brannon 1987). Only days with temperatures greater than or equal to 1.6 ^{o}C were included in the calculation of average incubation temperature, as developmental rates below this temperature have not been documented for sockeye salmon but are presumably negligible (Brannon 1987). The date of peak emergence for each population was calculated as the cumulative sum of the average daily temperature readings from each creek, beginning on the date of peak spawning and continuing until the designated number of degree days for that population was obtained (Table 1).

Results

Lake conditions

Lake Aleknagik experienced a period of peak productivity lasting approximately 15 weeks. Spring break-up of the ice cover, on average, occurred on June 1, although it was recorded as early as April 29 and as late as June 18. Spring ice break-up has occurred significantly earlier in recent years, apparently as a function of climate change and shifts in the Pacific Decadal Oscillation (Schindler et al. 2005).

The observed mean temperatures in the upper 20 m of the limnetic water column were consistent among all six sampling locations throughout the sampling period, ranging from approximately 5^{o} C on 24 June to 11^{o} C on 2 September (ANCOVA (1999-2002) site*date $p = 0.13$, site effect $p = 0.58$). A thermocline started to develop by the end of June, and was well established in August and September (Figure 2). Surface water temperatures at the 10 littoral beach seining sites generally increased from $6\text{-}8^{o}$ C in early June to $14\text{-}16^{o}$ C in early August. Although all sites experienced the same rate of increase over the course of the summer (ANCOVA $p = 0.64$), the mean temperatures differed significantly among the locations ($p<0.001$; we used Tukey's HS test for posthoc partitioning with $\alpha = 0.05$ (Day 1989). Sites 5N, 6N, and 8N tended to be warmer than the others, perhaps because they are located in shallow, protected bays (Figures 1 & 3a). Those sites with cooler average temperatures (1S, 2N, 2S, 4S, 7S, 8S) were generally more open to the main body of the lake (Figures 1 & 3a). These temperature differences may have implications for the optimal periods of emergence by sockeye salmon fry utilizing these regions.

The emerging insect community was dominated by Chironomidae, although other dipterans were also recorded. Insects were present in the littoral habitat immediately after ice break-up and densities fluctuated considerably throughout the summer; long-term averages indicated an apparently bimodal distribution with peaks in June and early August (Figure 3b). We found no evidence of consistent geographic differences in insect density among the sampling locations, based on detailed data from 1999 - 2002. Catch rates at the three sites were all significantly correlated with one another, although r^2 values were generally low (Figure 3b-inset). A Kruskal-Wallis test (used to due to the non-normality of the data) found no difference in the mean catch rates among the sites ($H = 1.8$, $p = 0.41$).

Zooplankton densities remained low in the period immediately following ice break-up, and peaked in mid-August at densities of 50-60 individuals / m^3 (Figure 3c). Large standard errors indicated a high degree of interannual variation in both the magnitude and timing of zooplankton production in the system. There were no consistent geographic differences in zooplankton densities among the six sampling locations (X^2 contingency table, $X^2 = 47.5$, $df = 25$, $p > 0.10$)

Emergence timing

Newly emerged sockeye salmon fry were present in littoral habitat of the lake on the first sampling date in June, 6 weeks before zooplankton production peaked in early August (Figures 3c & 4). Further, a length frequency histogram of the fish captured on that date between 1991 - 2003 showed a wide distribution of sizes, with some individuals larger than 40 mm in length (Figure 5). Given an average emergence length of 28 mm (Beacham and Murray 1990) and growth rate of 0.35 mm/day, as estimated from our otolith microstructure data (see also Schindler et al. 2005), the largest individuals were estimated to have been actively feeding on chironomids and perhaps zooplankton (Rogers 1968) for as many as 34 days.

The otolith microstructure analysis also indicated that sockeye salmon fry emergence period in the system occurred over as much as 2 months. In 2002, young-of-the-year sockeye (n = 80) from two beach seining sites (7S and 2N, both in the "middle" emergence timing group above) showed an approximately normal distribution of ages. Peak emergence of those fish sampled occurred around June 15 and individuals emerged as early as the beginning of May and as late as the beginning of July (Figure 6).

Catch patterns of newly emerged sockeye salmon fry around the perimeter of the lake suggested that synchronous emergence does not occur among the sympatric populations within Lake Aleknagik. At the 10 sampling locations, we found eight significantly different patterns of emergence (X^2 contingency table p<<0.001, Figure 4). Two sites in adjacent bays on the north shore of the lake (5N and 6N) exhibited similar emergence patterns dominated by a peak of newly emerged fry on or about 30 June. Two sites on opposite ends of the lake (1S and 8S) also had equivalent emergence patterns, with relatively constant levels of new fry between mid-June and mid-July. The remaining six sites exhibited varying catch patterns of newly emerged fry, differing in peak emergence date and length of emergence period. It is important to note that our catch records did not encompass any dates prior to 20 June, and thus overlooked the appearance of fry early in the season. Interestingly, however, the observed emergence patterns in each location at least qualitatively corresponded to the local water temperature patterns (Figure 3a & 4). For instance, sites 5N and 6N were warmest early in the season and were characterized by an early peak emergence date. Similarly, sites 1S and 8S had both the same pattern of emergence and equivalent mean water temperatures

Peak spawning in Happy, Hansen, Whitefish, and Bear creeks occurred between July 23 and August 22, with the date of peak spawning varying $\leq$ 8 days among years within populations (Table 1). All of the creeks experienced the same general pattern in seasonal incubation temperatures; summer water temperatures ranged from 11-14^{o} C and winter temperatures were near freezing (Figure 7a). However, some creeks experienced more pronounced fluctuations than others, consisting of greater maximum temperatures during summer months and colder winter temperatures (e.g., compare Whitefish and Bear creeks in Figure 7a). In three of the four years, the estimated emergence timing among the spawning locations ranged from late April to early August; intra-population variation in this peak date was no more than 7-15 days among years. However, in 2002-03, the mean incubation temperature in these four creeks was 0.1 – 3.2° C warmer than in previous years (Table 1), apparently due to warmer than normal winter temperatures (Figure 7b). The incubation model estimated that the change in thermal regime corresponded to an accelerated developmental rate, such that peak emergence in Hansen, Happy, and Whitefish creeks occurred $\geq$ 6 weeks earlier in 2003 than in previous years (Table 1). Bear Creek experienced the least difference in temperature regime during 2002-2003 and its estimated emergence timing was largely unchanged.

Discussion

Our documentation of the temporal patterns of temperature, food availability, and the emergence of sockeye salmon fry indicated that, in general, the appearance of fry occurred in close temporal proximity to the spring ice breakup on the lake in a single nursery lake in southwest Alaska. This supports the proposition by Bams (1969) that juvenile salmonids will maximize the length of their growing period rather than waiting for peak prey availability in the system (Godin 1982). In Lake Aleknagik, much of the sockeye salmon emergence occurred two months prior to maximum zooplankton abundance, despite the fact that zooplankton, when available, tend to be a primary prey resource in this and other populations (e.g., Rogers 1968, Beauchamp et al. 2004). This earlier emergence markedly extends the length of the growing season beyond what would be experienced if emergence coincided with maximum prey abundance; presumably a response to the strong selective pressure to maximize their growing opportunities prior to the onset of winter conditions (Conover 1990, Schultz et al. 1998, Schindler 1999). It should be noted, however, that sockeye salmon fry in this system (and most systems) use the littoral habitat early in the summer (Burgner 1962, Pella 1968) where water temperatures increase more rapidly and emerging insects are available as a food resource. The availability of this ecological niche, prior to beneficial growing conditions in the pelagic habitat, allows individuals to take advantage of this longer period of growth. Sockeye salmon populations in systems without suitable nearshore habitat may exhibit patterns of emergence timing more closely aligned with peak prey abundance.

The long-term ecological records suggest that the Lake Aleknagik ecosystem experiences high levels of interannual variability. The date of spring ice breakup fluctuated by 51 days during the last four decades, responding to regional winter temperatures, the climatic phase condition of the Pacific Decadal Oscillation (Francis and Hare 1994, Mantua et al. 1997, Schindler et al. 2005) and global warming trends (Magnuson et al. 2000, Schindler et al. 2005). Zooplankton abundance varied by a factor of two or more on any given sampling date among years, and much of this variation is attributable to the timing of spring breakup date and the concordant changes in summer water temperatures (Schindler et al. 2005). The density of spawning adult sockeye salmon, indicative of the density of their offspring competing for resources the following summer, ranged from 0.1 to 1.2 million between 1962 and 2002 (Schindler et al. 2005), and the variation would have been far greater had commercial fisheries not caught the great majority in years of high abundance. Nor is this high degree of variability unique to Lake Aleknagik. The date of ice break-up on Iliamna Lake, Alaska, for instance, has varied by as much as 85 days over the last 40 years; in some years, the lake remained ice-free for the entire winter (Univ. Washington, unpublished data).

Hilborn et al. (2003) demonstrated the importance of diversity in life history patterns on a more regional scale for Bristol Bay sockeye salmon, attributing variation in characteristics such as morphometrics, egg size, and freshwater residence to the sustained productivity of the system despite changes in local climate patterns. The variable nature of high-latitude lakes may prevent the evolutionary selection of a single life history strategy, and thereby enhance the long-term overall productivity of the systems.

Three lines of evidence support the hypothesis that diversity in emergence timing has been maintained in the sockeye salmon populations associated with Lake Aleknagik. (1) Multiple pulses of small, ‘newly emerged’ sockeye salmon appeared in the littoral habitat associated with different geographic regions of the lake over the course of the summer. (2) Otolith microstructure analysis from two locations in the lake indicated a minimum emergence window of eight weeks. (3) Predicted peak emergence date, based on incubation temperature, suggested a discrepancy of at least six weeks among discrete spawning populations within a given year. This variation in emergence dates could result from wide variation in spawning dates within all populations, but our records indicate that this is not the case. Observations of tagged fish (e.g., McPhee and Quinn 1998, Quinn et al. 2001) indicated that females begin spawning within a few days of entering a creek, and have completed spawning by about their fourth day in the creek. Adult salmon are only present in the small creeks for about 3-4 weeks, and our data indicated that the great majority of spawning in these creeks takes place within a 2-3 week window. The timing of spawning is somewhat more protracted in the larger creeks and rivers (e.g., the lake's outlet, the Wood River, and the Agulowak River, that drains the upper lakes into Lake Aleknagik (Figure 1). However, even these rivers have very regular dates of occupancy and the spawning does not extend over more than a few weeks. Variation in emergence could also result from synchronous spawning if the temperatures or levels of dissolved oxygen experienced by embryos among localized areas within each creek varied greatly. This is certainly possible, and our temperature records were not sufficient to characterize the full range of spatial variation in incubation conditions within creeks. This within-creek variation might result in broad emergence in the lake as a whole but does not explain the consistent variation among regions within the lake revealed by our beach seine surveys over many years. Finally, local, creek-specific conditions such as limited periods of access due to shifts in water level, may influence spawning dates, but these restrictions are insufficient to account for the observed level of variation in emergence timing within the lake.

Our analysis of the geographic patterns of emergence within the lake indicated the presence of eight distinct temporal entry patterns of the fry into the lake. Each of our beach seining sites presumably sampled fry from multiple spawning populations, rendering the observed emergence patterns indicative of both intra- and inter-population variability. For instance, site 6N (Figure 1) is adjacent to Happy, Happy, and Eagle Creeks. The appearance of newly emerged fry at this location would encompass the range of emergence dates of all three populations. In addition, our data suggested that lake conditions may also influence when the newly emerged fry enter the system. In general, the locations exhibiting the earliest appearance in the lake were within shallow, protected bays, which also tend to warm up earlier in the spring. Thus one possible explanation for this accelerated emergence may be the availability of suitable littoral habitat conditions prior to other locations in the lake (e.g., those creeks associated with shallow bays may develop an open moat prior to the ice leaving the whole lake). In contrast, those sites with later or more protracted periods of emergence tended to be associated with the open water of the lake and in close proximity to the two major rivers associated with the lake, and were typically colder early in the season. The non-synchronous nature of the emergence timing within this common nursery lake suggests inconsistent selection on the date of emergence as temperature and prey availability fluctuates among years, as well as localized thermal regimes within the nearshore habitat of the lake, results in alternative strategies among adjacent populations in the date of egg deposition and incubation temperatures.

In summary, the long-term average emergence timing of sockeye salmon fry in Lake Aleknagik appears to occur soon after spring ice breakup, and well before maximum prey abundance. This extends the length of the growing season by as much as two months, a factor which may be critical in high latitude systems characterized by short periods of productivity and high winter mortality. As long as there is sufficient food for growth at the thermal regime that prevails early in the season, the fish will benefit from the early growth opportunity, regardless of the fact that the food is more abundant later in the season. Second, the emergence of fry in the lake as a whole is not synchronized over a short period, but instead extends over one-third of the summer. We postulate that this is both a lack of convergence on a single life history strategy due to the high degree of interannual variation in the biotic and abiotic conditions in the lake, and also a consequence of the variation in temperatures experienced by embryos during the very protracted incubation period. Third, the populations in different regions of the lake do not all emerge synchronously. Certain areas of the lake show differences in emergence that persist over many years, suggesting some localized ecological adaptations that we do not as yet fully understand.

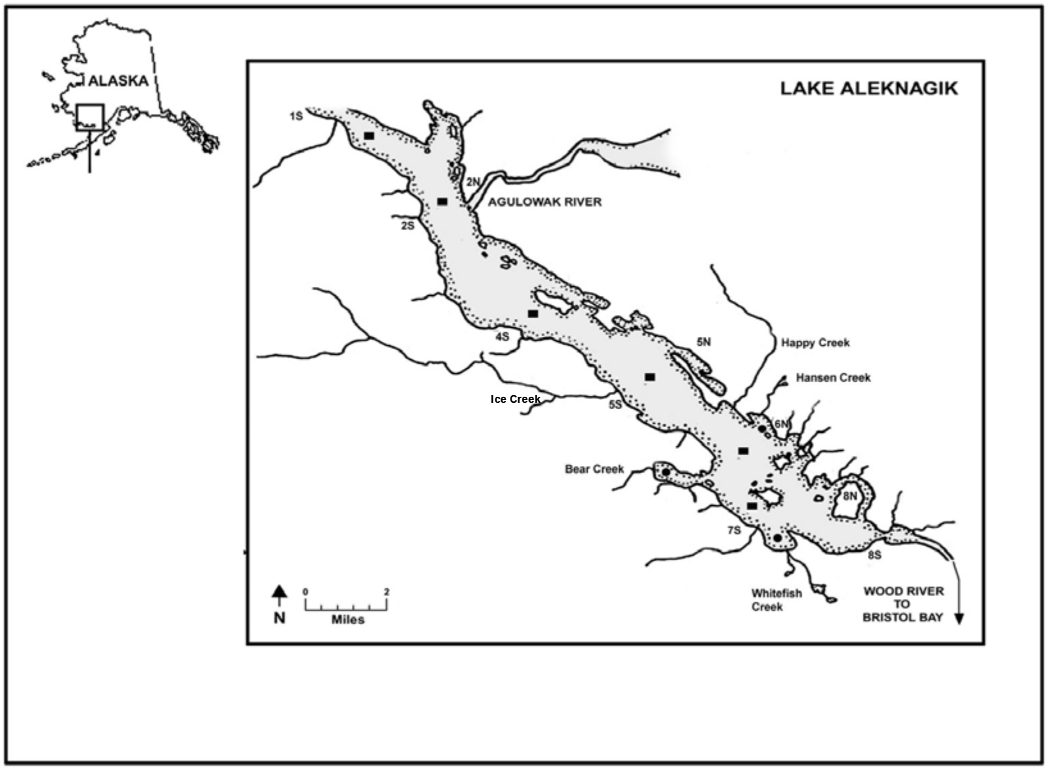


Figure 1: Study system and sampling locations. Beach seine sites are denoted by alphanumeric labels (e.g., 1S); ■ denotes limnology and townet locations; ● marks locations of insect traps.

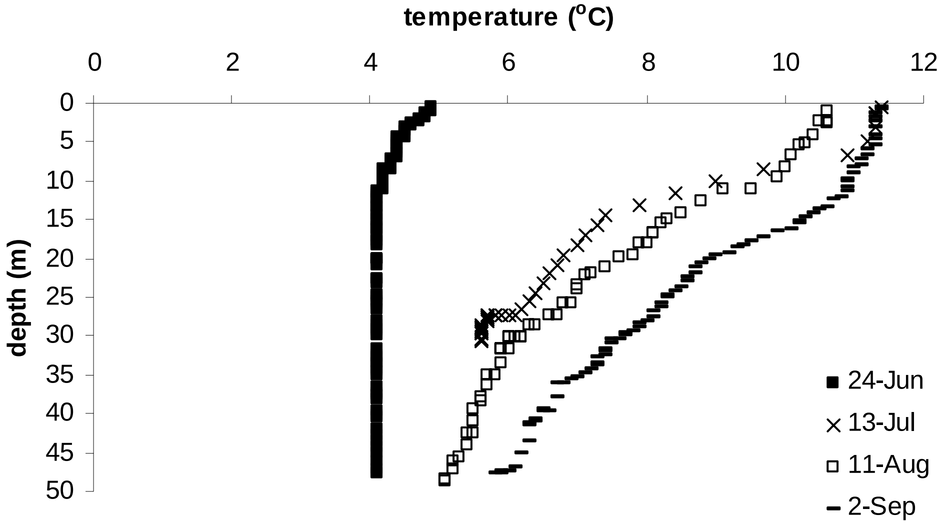
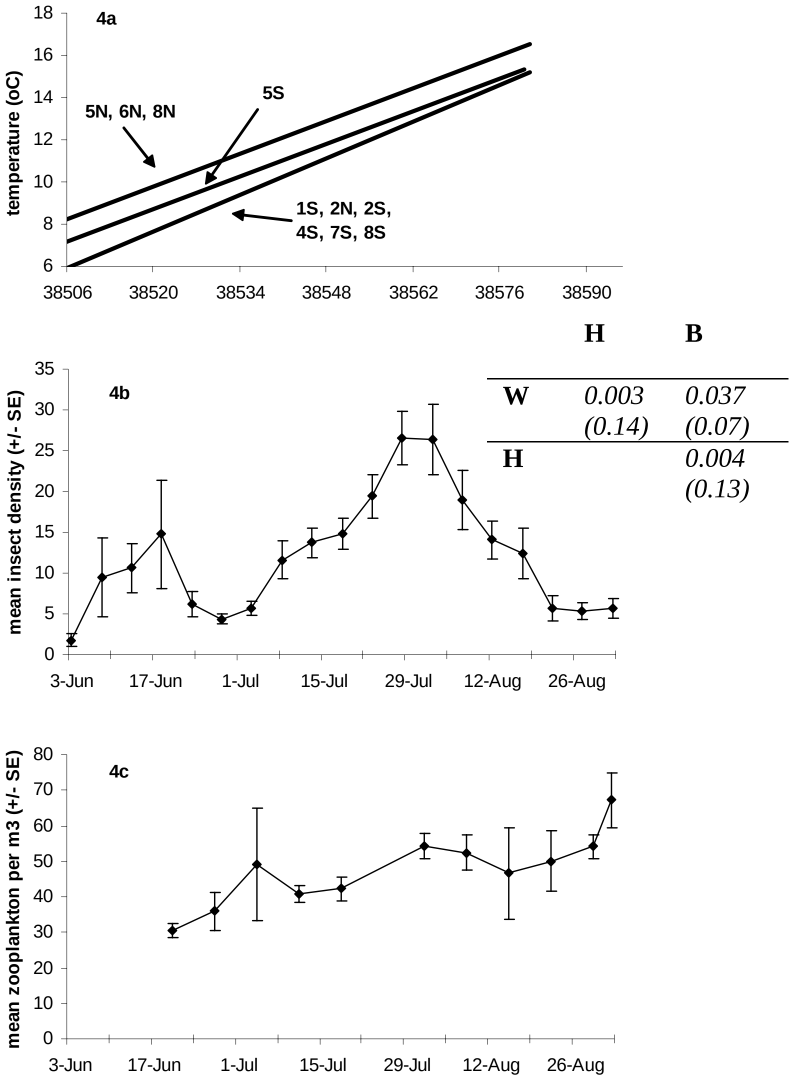


Figure 2: Temperature depth profile on four dates in a typical year (1999) at the Bear Point limnological sampling station.



	H	**B**
W	*0.003* *(0.14)*	*0.037* *(0.07)*
H		*0.004* *(0.13)*

Figure 3: (a) Seasonal trends in littoral water temperatures at the 10 beach seine sample locations, as indicated by ANCOVA (1964 – 2001). Slopes among all sites are equivalent (p = 0.64), but mean temperatures fell into these three significant groups (p<0.001). (b) Emerging insect trap abundances, as 5-day averages, from three bays, 1969-2003; inset shows p-values from correlation analysis among Whitefish (W), Hansen (H), and Bear (B) sites (r^2 in parentheses). (c) Zooplankton densities from the upper 60 m (except Yako site, 20m), 1967-2003.

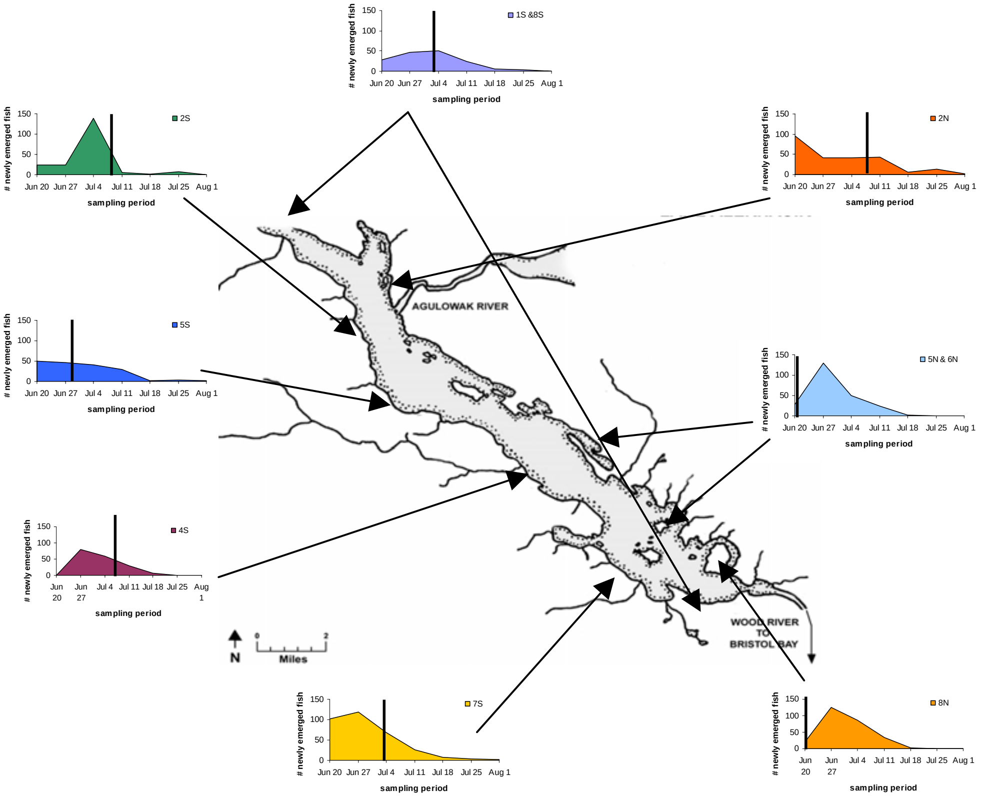


Figure 4: Patterns of emergence timing among geographic locations in Lake Aleknagik based on nearshore beach seine catches, 1991-2003. Y-axis on each graph represents the total number of newly emerged fish caught at that site on each sampling date. The vertical bars on each graph indicate the average date when nearshore water temperatures reach 10 ^{0}C at that site.

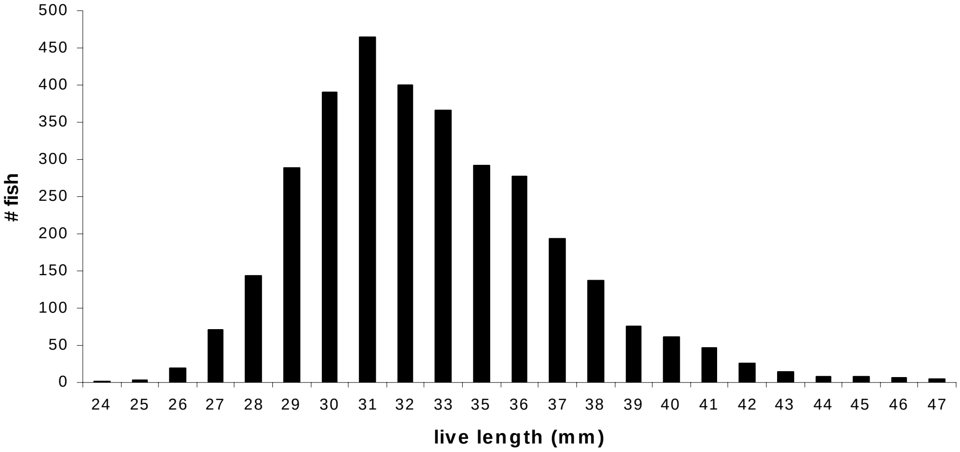


Figure 5: Length-frequency distribution of sockeye salmon fry caught on the first annual sampling date (~June 24), 1992-2003.

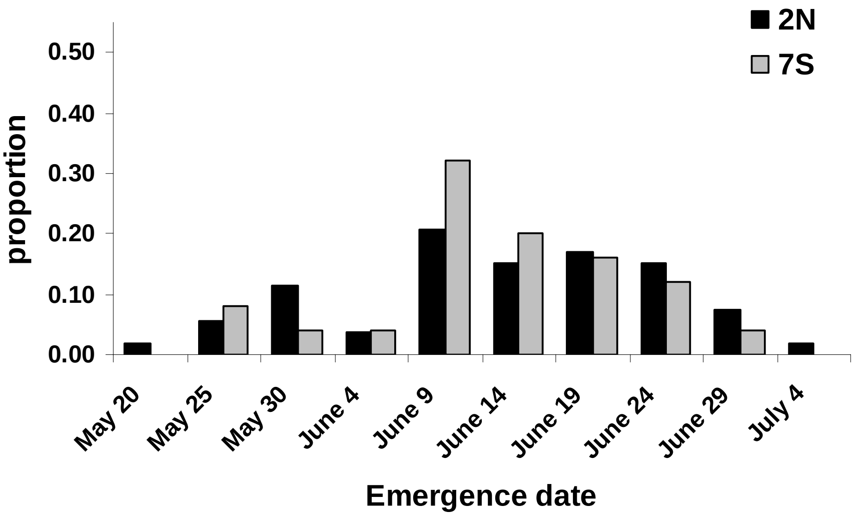


Figure 6: Estimated emergence timing of individual sockeye salmon fry collected at sites 2N and 7S in 2002, based on daily growth rings on otoliths.

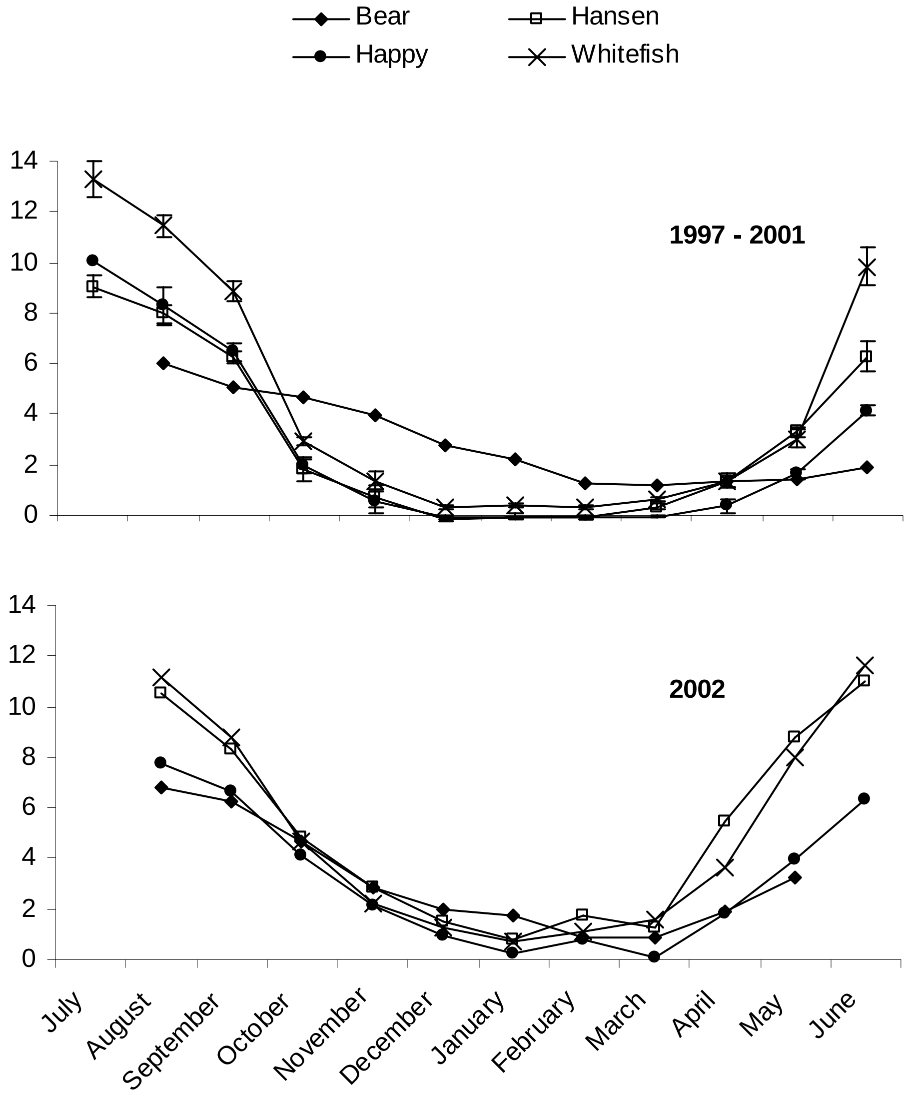


Figure 7a & b: Patterns of average monthly incubation temperatures (+/- SE) in Happy, Hansen, Bear, and Whitefish creeks during (a) 1997-1998, 1998-1999, 2001-2002, and (b) 2002-2003.

Table 1: Spawning dates, incubation temperatures, and estimated dates of emergence for four observed creeks in Lake Aleknagik.

			Mean Incubation Temperature		Estimated emergence date			
Creek	Peak spawning date	# degree days to emergence	(1997-2002)	(2003)	1998	1999	2002	2003
Bear	6-Aug	850	3.0	3.1	-	-	22-Apr	15-May
Happy	28-Jul	974	2.0	5.2	2-Aug	27-Jul	11-Aug	11-Jun
Hansen	23-Jul	980	2.7	3.2	12-Jul	10-Jul	2-Jul	2-Feb
Whitefish	19-Aug	999	3.9	5.0	27-Jun	4-Jul	27-Jun	15-May

Path Analysis of an Ontogenetic Shift

Introduction

Ecological factors within an ecosystem inherently tend to be highly interrelated, making it difficult to determine the causal relationships between physical features and biotic responses. Nevertheless, recent advances in ecological research have emphasized the importance of complex direct and indirect effects within a system. The role of climate patterns on population densities (Hare and Francis 1995, Mantua et al. 1997, Downton and Miller 1998), biodiversity on productivity (Loreau et al. 2001, Hilborn et al. 2003), and ecosystem engineers on nutrient exchange and hydrologic patterns (Pollock et al. 1995, Tardiff and Stanford 1998) are examples of complex interactions among biotic and abiotic factors. To date, however, little is known about how organisms specifically alter their behavior patterns in response to the direct and indirect effects of multiple environmental and ecological conditions (e.g., temperature, prey abundance, predation pressure) experienced over a range of temporal periods in natural systems. Traditional ethological studies tend to be either conducted under controlled conditions in which the number of variables are limited, or observational in nature but limited in the amount of quantitative information available about the strengths of the interactions. The use of long-term ecological records and more sophisticated analytical tools, however, may allow us to quantitatively assess the interactions occurring among different components within an ecosystem and discern which factors are driving the observed behavior of organisms within that environment.

The ontogenetic niche shift frequently exhibited by juvenile fish is an example of a behavior pattern that may be sensitive to multiple environmental cues. Typically, small individuals inhabit shallow and/or structurally-complex habitats while larger individuals are found in pelagic areas, and the timing of this shift appears to be size mediated in many populations (Werner and Gilliam 1984, Foster et al. 1988, Werner and Hall 1988, Dahlgren and Eggleston 2000, Sillett and Foster 2000). Werner and Gilliam (1984) found that this niche differentiation apparently balances growth potential (g) against predation risk (μ), with individuals minimizing the ratio of μ/g. Larger individuals are less vulnerable to predators and so are able to take advantage of the more productive open water environment. The level of 'acceptable predation risk' should vary in response to selective pressure from the environment to maximize growth (Schindler 1999); e.g., those individuals in systems with high over-winter mortality should take advantage of the more productive environment at a smaller size, trading an increased risk of predation for better growing opportunities. For those populations experiencing a significant risk of mortality other than predation, therefore, the timing of the ontogenetic shift may be less controlled by the size of the fish and more sensitive to environmental conditions. The same may hold true for populations inhabiting a system with variable temperatures and prey densities; the bioenergetic benefits of a given habitat may vary seasonally and interannually. The pelagic habitat may not always offer a more productive growing environment than the littoral region, and therefore the timing of the ontogenetic shift may wait until the presence of beneficial growing conditions, regardless of fish size.

In this study, we used path analysis to test specific factors hypothesized to control the ontogenetic shift in juvenile sockeye salmon (*Oncorhynchus nerka*) in a lake in southwest Alaska. The general pattern of the shift is similar to that described for other species; small individuals are found in shallow, littoral areas whereas larger fish inhabit the limnetic region of the lake. The majority of the cohort exhibits a coordinated habitat shift sometime during their first summer of life (Burgner 1962). However, the lake has long, cold winters and short periods of productivity in the summer, raising the possibility of high over-winter mortality and therefore strong selective pressure to maximize growth in the summer. The immediate objective of this study was to identify the proximate environmental cues associated with the ontogenetic habitat shift in juvenile sockeye salmon in this lake. From a broader perspective, however, we sought to understand interactions occurring between multiple ecological components at an ecosystem scale, and the ability of path analysis to differentiate the strengths of those interactions.

Based on a long-term ecological record in Lake Aleknagik, Alaska, we measured the interannual variability of the date on which the sockeye salmon fry in this system moved from the littoral to the pelagic habitat in the lake. We then tested a series of alternative hypotheses to account for the variation in the timing of this habitat shift. The first two hypotheses were single-variable analyses, proposing that the offshore shift occurred at (1) a consistent size, as might be expected from previous studies, or (2) on a consistent number of days after spring ice break-up on the lake. The remaining three hypotheses each examined integrated predictor variables functioning as indices of the suite of environmental conditions experienced by the fish: (3) emergence timing of the fry in the spring, (4) nearshore conditions, including thermal regime, prey abundance, and competition, and (5) limnetic conditions of temperature and prey abundance. Onshore conditions could have either a positive or negative effect on the timing of the movement; beneficial conditions might lead to increased growth and earlier movement to the open water habitat, or poor onshore conditions might result in an earlier migration in search of improved feeding sites. Alternatively, the fish may respond to improving offshore conditions, migrating into the pelagic habitat as soon as optimal temperature regimes and prey densities are available. We hypothesized that the behavior of the fish may be determined by the additive effects of multiple variables in the environment in a manner that would not be predicted by considering each condition independently. The path analysis of the three more complex hypotheses identified which model best explained the observed variation in the date of the habitat shift, and in addition, estimated the relative strength of each of the integrated model parameters.

Materials and Methods

Path Analysis

Path analysis is a form of structural equation modeling used to estimate the predictive value of multiple variables simultaneously and provide a mechanism for directly comparing alternative hypothetical models (Wright 1921, Shipley 1999, 2000, Mitchell 2001). Until recently, path analysis has received little attention in ecology (e.g., Wright 1921, Shipley 1999, Sih et al. 2002, Cariveau et al. 2004) but it offers a unique method to analyze complex ecosystems and processes occurring on different spatial and temporal scales. The multivariate models consist of hypothesized relationships among the variables of interest (e.g., $X \rightarrow Y \rightarrow Z$, see also Figure 9), where the "paths" (i.e., arrows) represent the direction and strength of the relationships among the components of the system. Both direct (e.g., $Y \rightarrow Z$) and indirect pathways (e.g., $X \rightarrow Z$) can be estimated, providing information about the cumulative effect of all linked components on a response variable. Although these path diagrams can be developed *post hoc* based on the regression analyses, it is generally accepted that a series of alternative models should be tested based on hypotheses generated from known ecological relationships (e.g., Mitchell 2001). The calculations associated with path analysis occur in two parts. First, the path coefficients between each pair of variables are estimated by a series of linear regression equations equivalent to a multiple regression analysis. The output is in the form of standardized regression coefficients (i.e., the number of standard deviation changes in Y in response to a unit change in X, all other factors being held constant). Therefore, the path coefficients indicate the strength of the direct relationship between two variables; the indirect effect can be calculated by multiplying the coefficients along a pathway. In addition, an r^2 value is calculated for the terminal response variable, indicating the total amount of variation explained by the model.

The second component of the path analysis tests the goodness-of-fit of the model as a whole, using a maximum likelihood X^2 distribution. In this case, a non-significant result ($p>0.05$) indicates a positive outcome, as it suggests that the relationships proposed in the hypothetical model do not differ significantly from the observed data. Alternative models are ranked based on the outcome of this goodness-of-fit test, using ascending relative scores of the Akaike Information Criteria (AIC) (Burnham and Anderson 2002, Wagenmakers and Farrell 2004). The ranks are calculated using

$$\Delta_i = AIC_i - AIC_{min}$$

where AIC_{min} is the model with the lowest AIC value. (E.g., the model with the lowest AIC score will have a Δ_i value of 0.) Models with Δ_i values from 4 – 7 have "considerably less" support compared to model generating the minimum AIC score, and a score greater than 10 indicates "essentially no" support for the alternate model (Burnham and Anderson 2002).

In summary, the output of path analysis provides two valuable pieces of information. First, it identifies which variables have the strongest effects on other components of the system, given the set of relationships assumed by the model. Second, it allows the direct, quantitative comparison of alternative models outlining the configuration of causal relationships within complex, multivariate ecosystems.

Study Site

The Wood River system is series of five large, interconnected lakes forming a major tributary to Bristol Bay in southwest Alaska. Lake Aleknagik is the southernmost lake in this system and, since 1970, has experienced a mean annual escapement of 428,000 (219,000 st. dev.) adult sockeye salmon. The adult salmon spawn in the lake and its tributaries between July and September. Their offspring hatch and emerge the following spring, and the fry generally rear for one or, less often, two years in the lake prior to migrating to the ocean (Rogers 1987). Lake Aleknagik is an oligotrophic lake, with a brief period of productivity between June and September, followed by 6-9 months of ice cover (Hartman and Burgner 1972). Juvenile sockeye salmon compete with threespine sticklebacks (*Gasterosteus aculeatus*) for prey resources, primarily aquatic insects and zooplankton (Rogers 1968). Both species show depressed growth in years with high sockeye salmon densities (Burgner 1964, Rogers 1968, Burgner 1991, Schindler et al. 2005). Here, we present data collected by the University of Washington's Fisheries Research Institute on the niche shift by young-of-the-year sockeye salmon and its relationship to prey density, temperature patterns, and competition in the littoral and limnetic habitats, as well as the day-of-the-year and mean length of the sockeye salmon cohort.

Field sampling

Beach seine sampling of the fish community was conducted at 10 nearshore sampling sites around the circumference of the lake. Samples occurred weekly between June 23 and August 5, 1964 - 2003. Fishes were collected during the day using a 30 m beach seine with lead lines and floats, deployed from a skiff and hauled to shore manually. All individuals were identified to species and measured for fork length.

Emerging aquatic insects in the littoral habitat were sampled using three conical traps suspended 1 m above the substrate, with an opening radius of 0.5 m. Traps were stationed in three bays and emptied every 48 hours between June 10 and September 1, 1970-2003. Nearshore surface water temperatures were also recorded every two days at the insect trap locations, using a handheld thermometer in the top 20 cm of the water column.

The date of spring ice break-up on the lake was recorded annually at the outlet of the lake since 1964. This date was used as a composite indicator of spring temperatures and the beginning of the annual period of primary and secondary productivity in the lake, as well as a relative index of the timing of emergence of the incubating sockeye salmon fry (Chapter 1).

Zooplankton samples were collected at 6 stations, once every 10 days between June 25 and September 1, 1970-2003. Zooplankton were collected using a 247 μm net with a 0.5

m opening. Vertical hauls were made from 60 m (except one site near Yako Creek, which was sampled from 20 m) with a retrieval rate of ~0.5 m/s. All samples were preserved using either 5% formalin or 50% ethanol. Subsamples of zooplankton were counted and identified to species, until approximately 500 individuals were recorded. Total crustacean density was calculated as the mean from all 6 stations. Limnetic temperature profiles were recorded at 3 locations in conjunction with each set of zooplankton samples. Prior to 1999, water was collected at 5 m depth intervals using a Van Dorn sampling bottle, and the temperature was recorded at the surface. From 1999-2003, a Yellow Springs Inc. sonde measured depth and temperature at ~1 m increments. In all years, water temperatures were averaged over 0-20 m, depths which encompassed the region of the water column inhabited by juvenile sockeye salmon during crepuscular feeding periods (Scheuerell and Schindler 2003).

Estimation of ontogenetic shift timing

Burgner (1962) demonstrated that sockeye salmon fry in Lake Aleknagik move from the structured littoral zone to the open-water pelagic habitat during their first summer of growth, and the majority of the cohort appears to make the shift on or about the same date. In this study, we used the disappearance of the sockeye salmon fry from the littoral habitat (i.e., absence from beach seine catches) as the indicator that the ontogenetic shift had occurred. To model this disappearance, the cumulative catch of sockeye salmon in the beach seine sampling was recorded for all sampling dates in each year. A logistic equation was fit to the points, calculating the date when 95% of that year's cumulative catch had been achieved (Figure 8). The 95% point most closely estimated the asymptote of the curve and thus provided the best indication of the date when the fish vacated the onshore habitat.

Alternative path models

We used path analysis to test a series of 6 alternative, nested models based on *a priori* hypotheses. The first was a base model that included all the individual variables hypothesized to affect the date of movement from the littoral habitat (Figure 9; Table 2). The range of annual sampling dates considered for each variable was optimized for the analysis to focus on the period of interest. For instance, the predictor variable characterizing littoral water temperatures only included measurements taken in June because the ontogenetic shift occurred as early as 3 July in some years, rendering temperature data from later in the season irrelevant or even misleading. In addition, all individual variables were standardized to have a mean of 0 and standard deviation of 1 to decrease the effects of collinearity (Mitchell-Olds and Shaw 1987).

Once the comprehensive baseline model was established, we then tested a series of 5 nested sub-models to examine the ability of different components of the ecosystem to predict the timing of the ontogenetic shift (Figure 10). In these models, related components were integrated into 3 composite predictor variables to function as indices of larger-scale ecological conditions (Table 2). “Onshore conditions” were represented by the thermal patterns, prey availability, and relative competitor density in the nearshore habitat. Temperature and prey abundance in the pelagic habitat were combined as an index of “offshore conditions.” “Emergence timing” was based on the mean length of the sockeye fry population on June 23, the earliest sampling date available in all years. If the fry were large at that date, we inferred that they had emerged earlier than in years when they were smaller. Variation in growth rate among years was assumed to contribute less to fry size than emergence date. In all cases, variables were combined additively in order to maintain the directionality of the conditions. Using the nested models, we tested each of these composite variables separately and then in combination with one another (Figure 10). Models were ranked based on their Δ_{AIC} values; those with equivalent scores were ranked based on r^2 values.

Results

The date of the ontogenetic shift from littoral to limnetic habitats did not occur on a fixed date but rather it varied by 34 days between 1964 and 2003 (Figure 11). The offshore shift by sockeye salmon fry occurred as early as 3 July, (i.e., 33 days after the average date of spring ice break-up) and as late as 6 August (i.e., 26 days before the estimated end of the primary growing season, Rogers, D.E. pers. comm.). The observed variation, then, encompassed a substantial portion of the available growing season.

The timing of the offshore migration did not occur at a fixed size, as has been suggested in other species (Werner and Gilliam 1984, Foster et al. 1988, Werner and Hall 1988, Dahlgren and Eggleston 2000, Sillett and Foster 2000). If this were the case, a length-frequency histogram of fish caught in the littoral habitat over all years would be expected to show a distribution truncated at the right side, indicating the emigration of fish once they reach the threshold size. Instead, we found a normal distribution of sizes, signifying the continued residence of large fish in the nearshore habitat (Figure12a). Further, a linear regression analysis (Figure 12b) showed a positive relationship between mean population length and estimated date of movement into the pelagic habitat. That is, in years when the fish moved offshore later, they did so at a larger size ($r^2 = 0.12$, $p = 0.04$). In addition, the timing of spring ice break-up alone was not a good predictor for when the ontogenetic shift would occur. Between 1964 and 2003, the date of the offshore migration ranged from 24 to 82 days after the disappearance of ice from the lake (Figure 13). These patterns of variation in the date of movement and size of the fish when they migrate suggested that more complex environmental factors triggered the habitat shift.

Path analysis results

The path analysis baseline model, considering all of the independent variables simultaneously (Figure 9), indicated that those parameters related to water temperature and pelagic zooplankton abundance had the highest standardized regression coefficients associated with ontogenetic shift date. However, the poor X^2 fit of the model as a whole ($p = .001$; i.e., rejecting the goodness-of-fit of the overall model) prevented a reliable assessment of the relationships among the variables. In contrast, the model considering only the parameter for offshore conditions accounted for 98% of the variation explained by the comprehensive baseline model, but with a highly non-significant $p = 0.36$ (i.e., supporting the overall goodness-of-fit of the model) and an AIC value more than 60 points smaller than the baseline (Table 3).

The path models considering emergence timing and onshore conditions as predictor variables (Figures 10a & b) performed substantially worse than the offshore conditions model. The emergence timing model had a similar AIC score to the offshore conditions model, but explained 30% less of the variation in the ontogenetic shift (Table 3). The onshore conditions model received an AIC score nearly 4 points higher and explained 59% less variation than the offshore conditions model. Furthermore, adding the indices for emergence timing and onshore conditions to the offshore conditions model (Figures 10d & e) did not improve its predictive ability or the AIC score (Table 3). Therefore, based on the ranking guidelines outlined by Burnham & Anderson (2002), we deemed the path analysis model based on offshore conditions to be the best predictor of when the ontogenetic shift from the littoral to the limnetic habitat would occur.

Discussion

Studies of ontogenetic shifts in juvenile fishes in temperate regions have consistently found that size and growth, as a mechanism for avoiding predation, determine the optimal time to move from one ecological niche to another (Werner and Gilliam 1984, Foster et al. 1988, Werner and Hall 1988, Dahlgren and Eggleston 2000, Sillett and Foster 2000). However, we found that environmental conditions were better predictors than size in determining when the ontogenetic shift would occur in a northern population of sockeye salmon. Specifically, water temperature and prey availability in the offshore region appeared to be the primary factors determining when salmon fry moved from the littoral to the limnetic habitat. We propose that this reliance on ecological cues, rather than a size threshold, is due to two factors specific to high latitude systems. First, fish inhabiting northern lakes experience strong selective pressure to maximize their growth in order to avoid over-winter mortality (West and Larkin 1987, Conover 1990, Schultz et al. 1998); this alternate selective pressure may decrease the expression of predation-mediated traits, such as habitat selection based on size. Second, the growing conditions of pelagic habitats in high latitude lakes exhibit marked seasonal variation. In the period closely following ice break-up, limnetic conditions may be too cold and/or offer insufficient prey resources to optimize growth rates. As such, even if a fish is large enough to avoid predators in open water, this habitat may not be beneficial until later in the productive season and thus delay the timing of the ontogenetic shift.

The pattern observed in Lake Aleknagik supports the conceptual construct outlined by Werner and Gilliam (1984). The movement into the alternative habitat when conditions become beneficial presumably still optimizes their growth while minimizing mortality. In this case, however, the primary mortality threat may derive from over-winter mortality or post-smolt mortality at sea (Henderson and Cass 1991) rather than predation. It should be noted that it was not feasible to measure predation rates on sockeye salmon fry in this system, preventing us from directly considering the predation rates in the two habitats. However, although several species of piscivores are present in the lake (e.g., Arctic char, northern pike, rainbow trout), there are some indications that the greatest predation intensity may occur during the sockeye salmon smolt out-migration (Ruggerone and Rogers 1984).

If the fish are timing their offshore migration based on environmental conditions in a remote habitat, rather than on changes in their own physiology or immediate surroundings, the question then becomes “how do they know when to go?” We propose three plausible hypotheses here, although do not presume to answer the question. First, they may in fact be responding to changes in the littoral habitat which are indicative of offshore conditions. Although zooplankton are found in greater densities in the pelagic region of the lake, they are also present in shallow areas. An increase in zooplankton density nearshore may trigger the migration by indicating abundance in the limnetic zone. Second, the fish may conduct periodic lateral migrations between the two habitats of the lake and simply remain in the limnetic region when conditions there are optimal. However, previous sampling in Lake Aleknagik found no evidence of repeated onshore-offshore commutes (Burgner 1962, UW Alaska Salmon Program unpublished data), and this would be an energetically taxing strategy. Third, it is possible that olfactory cues from increasing zooplankton densities offshore are detectable by juvenile sockeye salmon. As far as we know, a behavioral response to chemical cues from zooplankers has not been demonstrated in this (or any other) species. However, olfaction determines a wide variety of other behavior patterns in salmonids, including homing to natal streams by adults (Dittman and Quinn 1996), orienting toward lake water by juveniles (Brannon 1972), and recognition of siblings (Quinn and Busack 1985). Thus the olfactory systems of salmonids are very sensitive and responses to prey odors are not implausible. Regardless of the mechanism, behavioral plasticity in the timing of the ontogenetic shift in response to existing habitat conditions may provide important selective benefits in a system where the date of ice break-up varies by up to 6 weeks among years and peak zooplankton densities range by a factor of 2 (Schindler 2005, Chapter 1).

The timing of the ontogenetic shift into the pelagic habitat may have implications for the survival of the sockeye salmon fry over multiple temporal scales. Survival of harsh over-winter conditions has been directly linked to size and energy stores in fishes (Conover 1990, Schultz et al. 1998). Schindler et al. (2005) found strong correlations between limnetic habitat conditions (i.e., zooplankton abundance and conspecific density) and the size of young-of-the-year sockeye salmon in September. As such, years with earlier migration into the offshore habitat may allow the fish to attain a greater size during the first growing season, and thereby increase their probability of surviving until spring. In addition to over-winter survival, fish migrating to sea as smolts at a larger size also experience greater marine survival (Henderson and Cass 1991). In Lake Aleknagik, the majority of the population migrates from the lake one year after emerging from incubation (i.e., after only one summer of growth), and grow very little in the spring prior to their out-migration (Rogers 1987). Therefore, their summer growth rates in the previous year may also have substantial implications for early marine survival in this population.

Previous studies have emphasized the importance of considering multiple ecosystem parameters over a range of spatial and temporal scales when attempting to explain processes occurring within complex ecosystems (Hare and Francis 1995, Tardiff and Stanford 1998, Logerwell et al. 2003, Lawson et al. 2004). In this study, we demonstrated the use of path analysis as a tool for evaluating questions about behavioral ecology within the context of ecosystem-scale processes. Specifically, this analytical procedure provides a mechanism for (1) identifying significant predictive parameters to explain observed behavioral patterns, (2) quantifying the magnitude and direction of the interactions among components within the system, and (3) testing alternative hypotheses regarding ecological interactions. Finally, we propose that integrated parameters, such as those used for onshore and offshore conditions in this model, may provide insight into ecological patterns that may not be apparent if each of the related variables is considered independently.

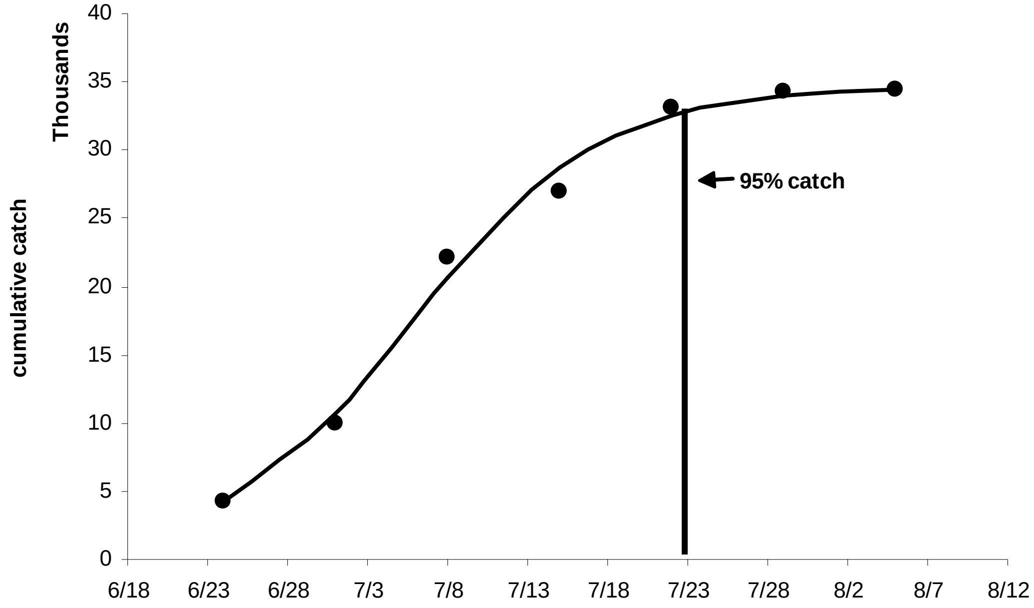


Figure 8: Example (2002) of logistic model identifying the 95% cumulative catch as an index of the date of the ontogenetic shift in sockeye salmon fry.

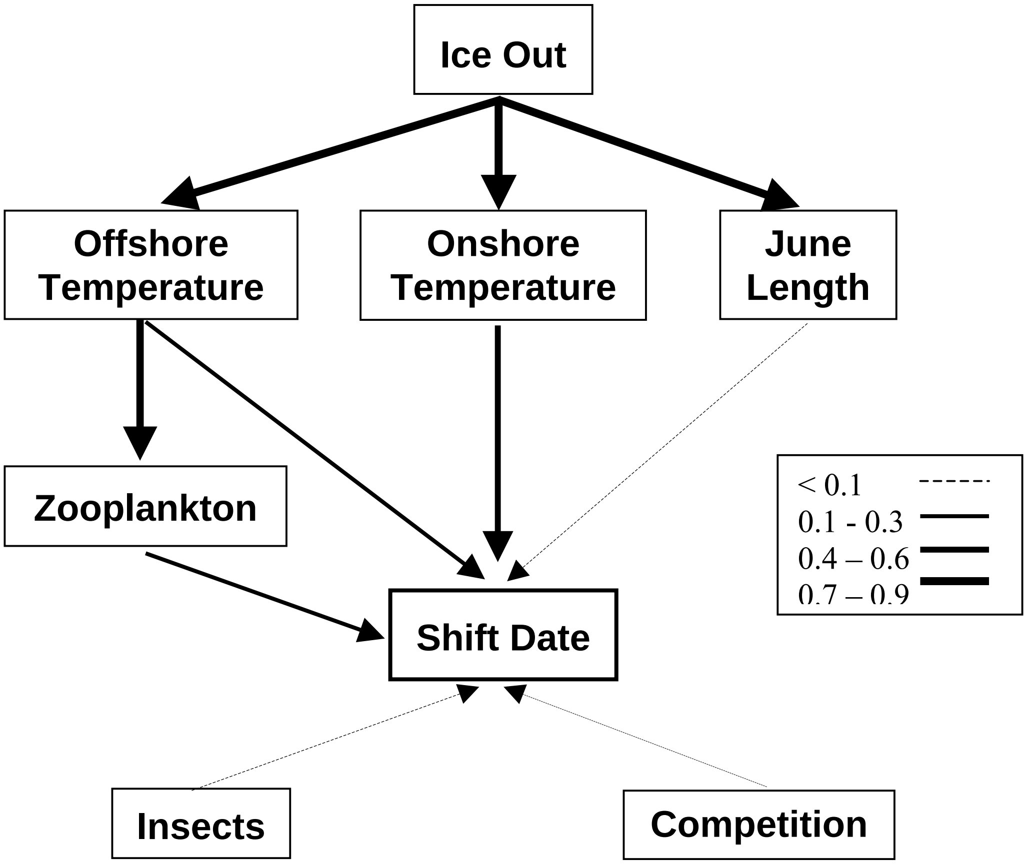


Figure 9: Baseline path analysis model indicating all of included parameters. Thickness of the arrows between variables indicates the estimated strength of the relationships (i.e., standardized regression coefficients), as denoted in the legend

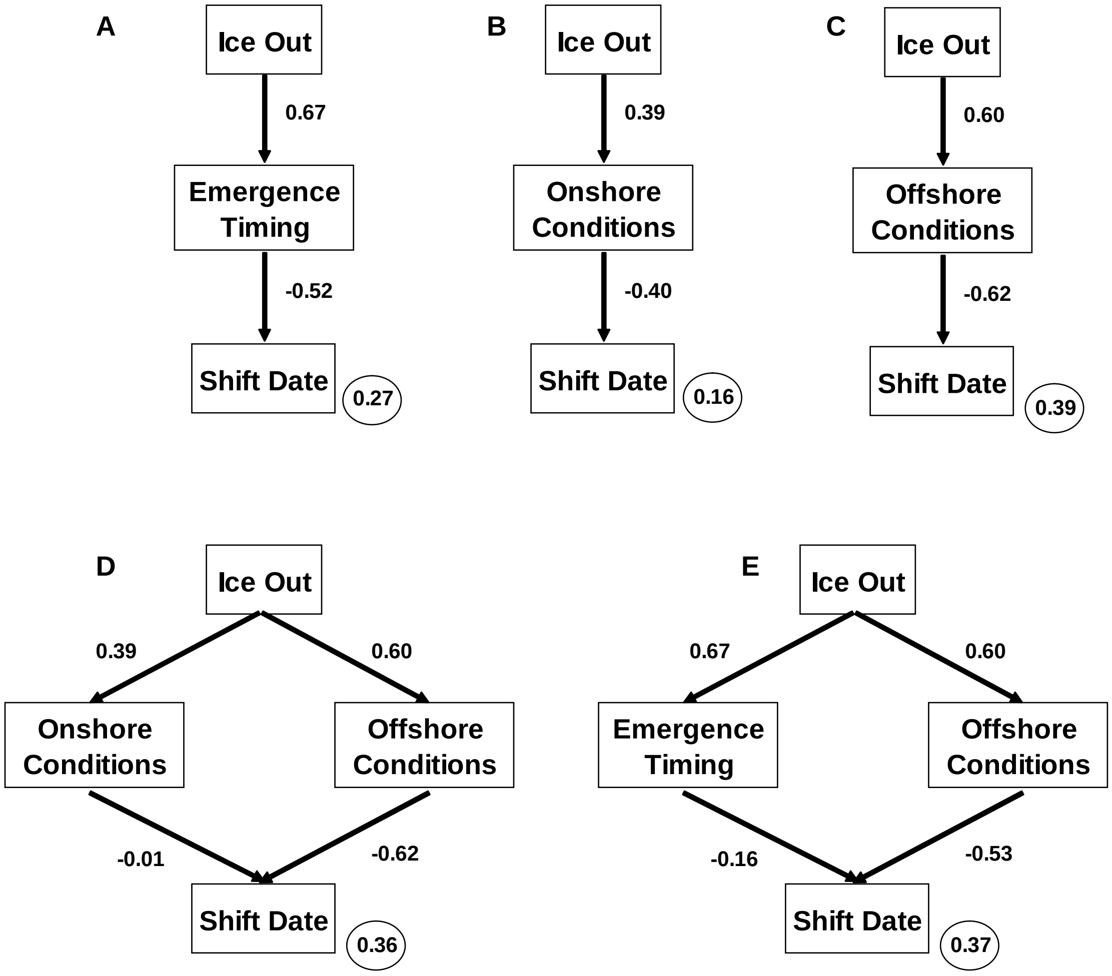


Figure 10: Five alternative nested path analysis models, comparing the integrated parameters for onshore and offshore conditions, and emergence timing. Values next to the arrows are the standardized regression coefficients. The numbers in circles are the r^2 values for the response variable, indicating the total amount of variation in the timing of the ontogenetic shift explained by the model.

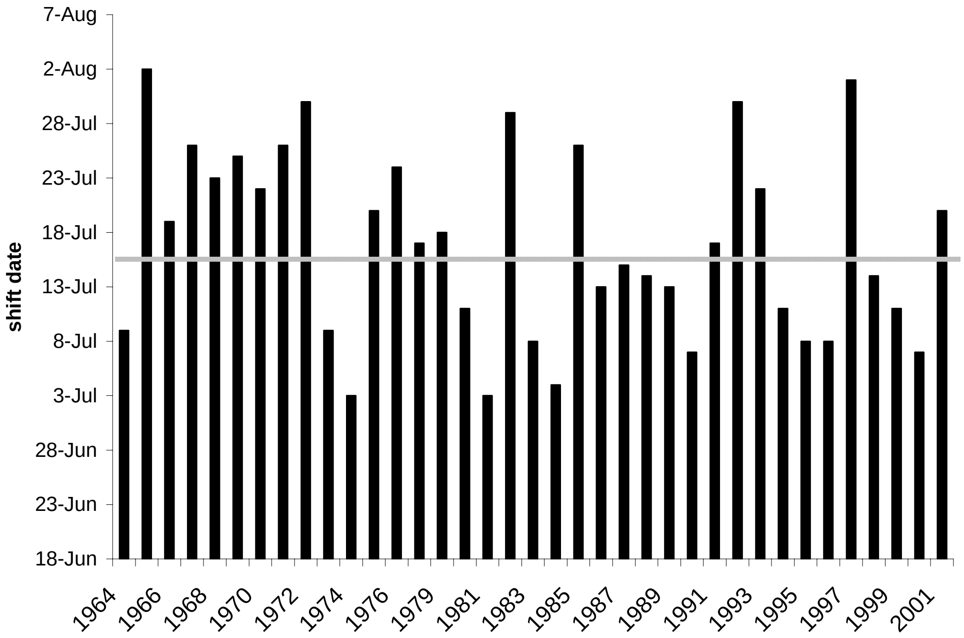


Figure 11: Time series of the estimated dates of the ontogenetic shift from littoral to limnetic habitats. Horizontal line denotes the mean date over all years.

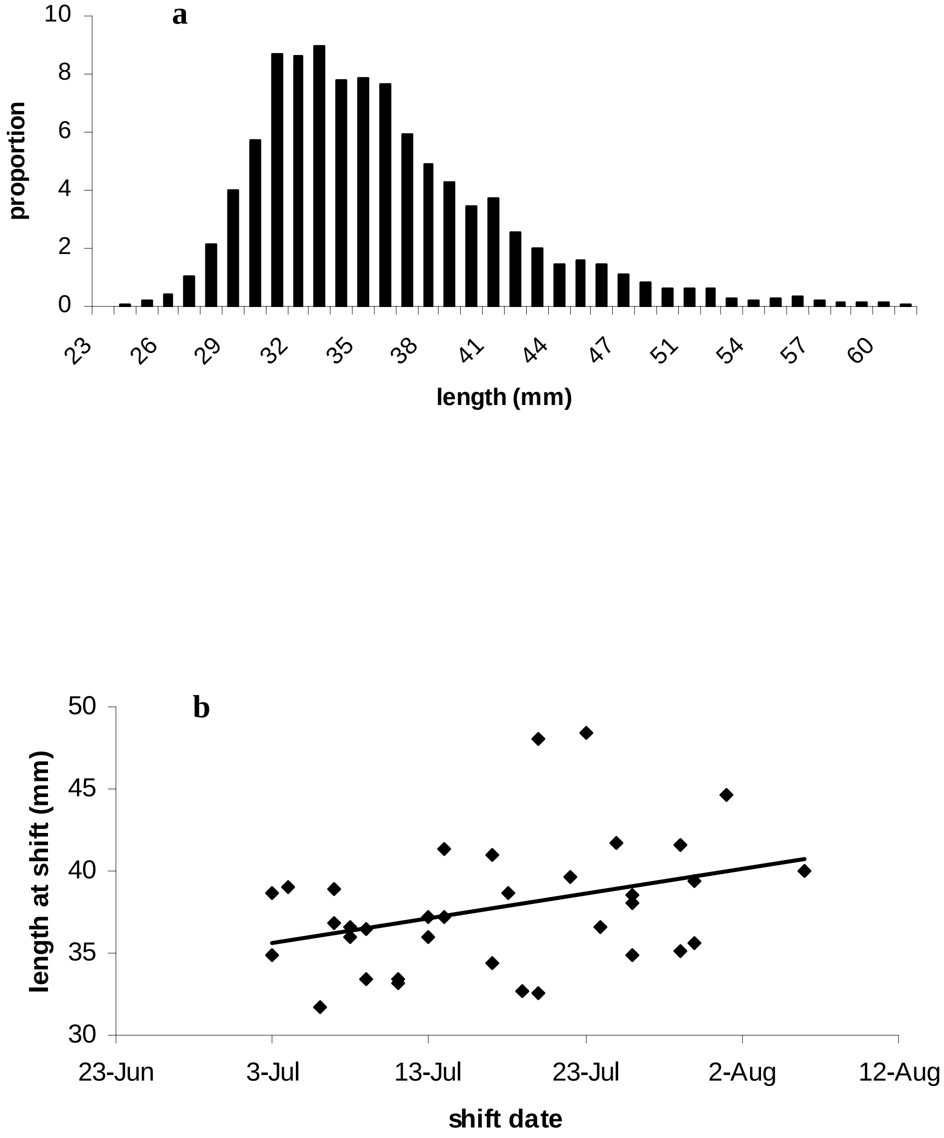


Figure 12 (a – b): Patterns of fish size in the littoral habitat; (a) the length-frequency of all fish sampled in the littoral habitat, as a proportion of the total catch; (b) the mean length of sockeye salmon caught in the littoral habitat on the estimated date of the ontogenetic shift ($r^2 = 0.12$, $p = 0.04$).

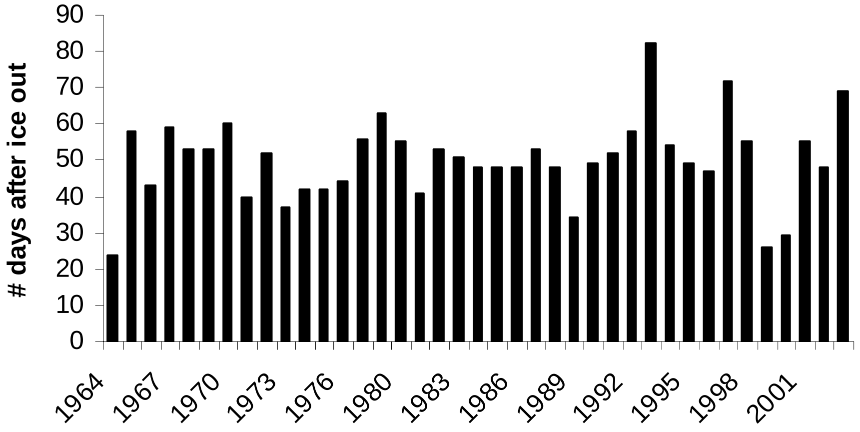


Figure 13: Time series of the date of the ontogenetic shift, displayed as the number of days it occurred after the spring ice break-up in that year.

Table 2: Summary of the variables included in the models, the dates and methods used to calculate them, and their groupings into the integrated parameters.

Composite variable	Variable Name	Calculation
	Ice Out	date of spring ice break-up at the outlet of lake
Emergence timing		
	Length on June 23	mean length of fry caught at all sites on ~June 23
Onshore Conditions		
	Onshore Temperature	mean water temperature at the 3 insect traps, June 2-28
	Insects	mean insect density in all 3 traps, June 18-28
	Competition	mean catch of threespine sticklebacks & arctic char fry in all beach seine sites, June 23-30; plus number of spawning adult sockeye salmon in previous year as index of sockeye salmon fry density
Offshore Conditions		
	Offshore Temperature	mean water temperature, 0-20 m, at 3 locations; July 10-19
	Zooplankton	mean zooplankton density (#/m^3) at 6 locations; July 1-31

Table 3: Summary of the path analysis model results, showing the offshore conditions model as the most parsimonious fit with the lowest AIC score and highest r^2 of the nested models.

Model	parameters	X^2	p	r^2	AIC	Δ_{AIC}
baseline	all individual factors	37.2	0.005	0.40	73.2	62.4
2a	emergence	1.3	0.26	0.27	11.3	0.5
2b	onshore (temp, insects & competition)	4.6	0.03	0.16	14.6	3.8
2c	**offshore (temp & zoop)**	**0.8**	**0.36**	**0.39**	**10.8**	**0**
2d	onshore + offshore	8	0.02	0.37	24	13.2
2e	offshore + emergence	9.2	0.01	0.37	25.2	14.4

Long-term Implications of Early Life History Patterns

Introduction

Early life history patterns apparently evolve to maximize immediate and long-term survival (Cushing 1969, Price et al. 1988, Rutherford et al. 1997, Cowan et al. 1999, Einum and Fleming 2000, Mortensen et al. 2000). In this regard, numerous taxa exhibit distinct spatial and temporal variation in the timing of reproduction (Cushing 1969, Price et al. 1988, Beer and Anderson 2001, Hodgson and Quinn 2002), date of offspring emergence (Brannas 1995, Einum and Fleming 2000, Chapter 1), habitat utilization (Werner and Gilliam 1984, Clark and Levy 1988, Werner and Hall 1988, Levy 1990, Dahlgren and Eggleston 2000, Scheuerell and Schindler 2003), diet composition (Scheuerell et al. in press, Henderson and Northcote 1985, Stockwell 1997), and growth rate of juveniles (Brandt et al. 1992, Skulason et al. 1996). Many of these traits clearly optimize the immediate growth and survival of the offspring, whether through avoiding predators, gaining access to profitable prey resources, or experiencing beneficial temperature regimes e.g. (Werner and Gilliam 1984, Clark and Levy 1988, Brannas 1995, Scheuerell and Schindler 2003). There is also substantial evidence that early life history events have important implications for the long-term survival of the individual as well as the overall productivity of the population e.g., (Crouse et al. 1987, Rutherford et al. 1997, Cowan et al. 1999, Mortensen et al. 2000). However, we know very little about the ways in which these early life history traits fluctuate under varying environmental conditions, or whether sympatric populations exhibiting alternative strategies are able to achieve equivalent long-term success rates.

Regional environmental factors exert selective pressure on the early life history characteristics of a population (see Roff 1992 for review). Constant or predictable habitat conditions are expected to move population traits toward some optimal window or state, whether through a consistent timing of reproduction, an optimal egg size, etc. However, in systems experiencing high temporal variability in climate conditions or prey densities, selection may favor plasticity or maintain variation rather than fixed behavioral patterns, thereby maintaining the ability to respond to changing habitat conditions (e.g., Brannas 1995, Jones et al. 2003, Halkett et al. 2004, Moore et al. 2004). Similarly, alternative life history patterns may develop in sympatric populations as a form of niche partitioning, and thereby increase their respective success.

Pacific salmonids (*Oncorhynchus* spp.) offer an ideal system to examine variation in early life history strategies, and then estimate the resulting correlations with long-term population productivity. Generation times are reasonably short (2-7 years; Groot and Margolis 1991), members of the genus are characterized by semelparous reproduction (adults reproduce only once), and most adults home to their natal freshwater breeding sites to spawn. These characteristics present an opportunity to feasibly examine productivity over multiple generations, as well as comparing productivity levels among similar species, clearly defined populations, and within distinct year classes. We conducted this study on sockeye salmon (*O. nerka)* in Lake Aleknagik, a densely populated sockeye salmon spawning region in southwest Alaska. Adults spawn in streams, rivers, and beaches associated with the lake, which is then used as a common rearing area for their progeny. The sockeye salmon fry in this system remain in fresh water for 1, or less commonly 2, years before migrating to salt water as smolts (Rogers 1987, Burgner 1991). The philopatry (natal homing) of adults (Quinn et al. 1999, Stewart et al. 2003) causes the offspring from multiple, genetically-isolated spawning populations to use the same common rearing lake during their freshwater phase, allowing us to examine the evolutionary responses of discrete populations to similar conditions. In addition, the lake experiences considerable interannual variability in temperature and prey availability (Schindler et al. 2005), and therefore we were able to observe the effectiveness of alternative strategies under a range of environmental conditions.

We selected two distinct aspects of the early life history of sockeye salmon as being of potential importance to the ultimate productivity of the population. The first is the emergence timing of the salmon fry in the spring. Adults lay their eggs in the gravel during the summer, and the embryos and hatchlings (“alevins”) incubate in the interstitial gravel habitat in stream or lake bottoms over the winter, and then emerge to begin exogenous feeding the following spring (Burgner 1991). Abrey et al. (chap 1) demonstrated that the fry in Lake Aleknagik emerge over a protracted period, encompassing approximately 62% of the available growing season. Further, the populations in the lake exhibited consistent differences in emergence timing; certain populations regularly emerged earlier or later than others in each year. This timing of fry emergence determines the length of their growing period during the first year, and therefore affects the size achieved by the end of the season. Fish size is important for both avoiding over-winter mortality (Conover 1990, Quinn and Peterson 1996, Schultz et al. 1998, Biro et al. 2004) as well as improving early marine survival (Burgner 1991, Koenings et al. 1993, Mortensen et al. 2000). In addition, smaller fish are more apt to delay seaward migration and spend an extra year growing in fresh water (Burgner 1962b). The fitness of spending one or two years in fresh water depends on the balance between the level of mortality experienced during the second year in the lake, and the survival advantage at sea associated with the larger size that resulted from that second year in fresh water.

The second life history trait that we examined was the timing of an ontogenetic shift during the first (and primary) summer of fry growth. In Lake Aleknagik, juvenile sockeye salmon spend the first several weeks after emergence distributed in the littoral area of the lake, but the cohort subsequently migrates into the pelagic habitat and remains there until they leave for the ocean (Burgner 1962a, Chapter 2). The growth achieved in the open-water region of the lake appears to be another strong determinant of fry size at the end of the season (Schindler et al. 2005), suggesting that the timing of the movement offshore may be important for their long-term survival. Previous work in this system (Chapter 2) has shown that the date of the ontogenetic shift varies by as much as 5 weeks, (i.e., 38% of the ~ 13 week growing season) among years.

In this study, we asked two simple questions about the effects of early life history traits on patterns of growth and productivity in sockeye salmon. (1) Do populations sharing a common rearing environment show similar patterns of freshwater age composition and productivity? Comparing five discrete populations spawning in tributaries to Lake Aleknagik, we examined (a) the proportion of successful offspring from each population that spent 2 years in freshwater and, where possible, compared this to estimated emergence date, (b) the relative productivity (i.e., the number of returning adults per spawner) of each population over a 38-year time period, and (c) the interannual correlation in age composition and productivity among each of the populations. (2) Is the date of the ontogenetic shift from the nearshore to the offshore habitat correlated with patterns of freshwater growth and levels of productivity in the lake as a whole? We tested the ability of the shift date to predict (a) the length of the sockeye salmon fry at the end of the first growing season, and (b) the productivity of each year class, as measured by the relative number of returning adults to freshwater prior to interception by the Bristol Bay fishery.

Materials and Methods

The study system

The Wood River system is series of five large, interconnected lakes forming a major tributary to Bristol Bay in southwest Alaska. Lake Aleknagik is the southernmost lake in this system and, since 1957, had a mean annual escapement of 351,000 (229,000 st. dev.)

adult sockeye salmon. The adult salmon spawn in the lake and its tributaries between July and September. The age composition of the returning adults is dominated by those having spent 1 year in freshwater and 2 or 3 years in the ocean (denoted as 1,2 and 1.3, respectively), but 1.1, 2.1, 2.2 and 2.3 individuals also occur (Rogers 1987). The only major anthropogenic influences on the system are the commercial and subsistence fisheries in Bristol Bay that intercept adult sockeye salmon returning to freshwater to spawn. Accounting for those fish intercepted by the fishery, the mean total annual run size to Lake Aleknagik was 848,000 (st.dev. 604,000). The fisheries are managed by the Alaska Department of Fish & Game (ADF&G), which maintains detailed records regarding the number and age composition of the annual sockeye salmon catches.

Lake Aleknagik is an oligotrophic lake, and most phytoplankton production occurs between June and September, interspersed by 6-9 months of ice cover (Hartman and Burgner 1972). The juvenile sockeye salmon prey primarily on aquatic insects and zooplankton (Rogers 1968), and exhibit depressed growth in years with high conspecific densities (Burgner 1964, Rogers 1980, Burgner 1991, Schindler et al. 2005). Here, we present data collected by the University of Washington’s Fisheries Research Institute between 1957 and 2003.

Population surveys

Total spawner densities in Lake Aleknagik were based on daily escapement estimates measured from counting towers on the Wood River (1960 – 2003). Population-specific density estimates were based on annual spawning surveys conducted on a consistent date for five tributaries of the lake, during which the number of male and female adult sockeye salmon present (alive and dead) were counted: Agulowak River, Bear Creek, Hansen Creek, Happy Creek, and Ice Creek (Figure 1). The population estimates for the Agulowak River were conducted via aerial surveys. At the other four locations, spawning surveys were conducted on foot over an established section of the available spawning habitat (Ice Creek and Happy Creek), or the entire length of the creek used by sockeye salmon (Hansen Creek and Bear Creek). Population densities were expanded to include those fish intercepted by the Bristol Bay fishery, based on age-specific catch rate estimates calculated by ADF&G (e.g., # age 1.1 on spawning site / proportion of 1.1 escapement in fishery). Age-specific fishing pressure was assumed to be equal among all populations. These expansion factors are essential because the proportion of the total run that gets caught varies greatly among years. Otoliths from approximately 100 male and 100 female salmon were collected annually from each of the populations to estimate the age composition of the spawning adults. The otoliths were read, without grinding or burning, under a dissecting microscope and the number of fresh water and marine annuli recorded for all individuals.

Mean productivity for each of the populations, as well as for the lake as a whole, was estimated using a modification of Kareiva et al. (2000):

$$\sum_{t=1}^{n}(R_t / N_t)/n \qquad \text{where} \qquad R_t = \sum_{2}^{5} N_{x,\,t+x}$$

is the number of recruits of a particular brood year, t, $N_{x,t+x}$ is the total number of adults (catch + escapement) of age *x* returning to freshwater *x* years after the brood year, N_t is the number of spawners (males + females) on the spawning ground in a given brood year, and *n* is the number of data years.

Lake surveys

The size of juvenile sockeye salmon at the end of the summer growing season was estimated based on the average fork length of individuals collected on about 1 September each year since 1957. Samples were collected at night with tow nets at 9-12 standard locations along the midline of the lake. The sampling procedure consisted of towing 3 m x 3 m vertical beam net at the surface between two boats at ~3 km/h for 5 min. at each station. The lengths presented here are the arithmetic mean fork lengths of all individuals sampled in each year (annual sample sizes: 200 – $1{,}000^{+}$ fry). Previous work on this system has shown a significant, negative conspecific density-dependent effect on September length for the sockeye salmon juveniles (Burgner 1964, Rogers 1980, Burgner 1991, Schindler et al. 2005). To account for this potentially confounding factor, we conducted a multiple regression analysis using the ontogenetic shift date and spawner density in the previous year (i.e., an index of conspecific density; Schindler et al. 2005) as independent variables, and juvenile length on 1 September as the response variable. The age composition of the sockeye salmon smolts in Lake Aleknagik was estimated based on samples of fish out-migrating down the Wood River to Bristol Bay from 1954 – 1966 and 1975 - 1990. Fish were collected by the University of Washington's Fisheries

Research Institute and ADF&G with fyke-nets in the river, and scale samples were analyzed to determine the number of freshwater annuli present (Burgner 1962b). Only fish collected during the first 20 days after spring ice break-up were included in our analysis in order to avoid including smolts originating from lakes farther up in the system (Burgner 1962b, D. Rogers, pers. comm.).

Results

Population comparisons

Among the five populations, the number of returning adults that spent 2 years in freshwater ranged from 7.5% to 16.6%, and differed significantly among four of the populations (Table 4; X^2 contingency table $p<<0.001$); only Bear Creek and the Agulowak River did not differ from one another. Furthermore, the proportion of 2-check fish was positively correlated to the estimated date of emergence in the three populations where these data were available; i.e., the latest emerging population (Happy Creek; Abrey Chap 1) produced the greatest proportion of 2-check fish, while the earliest emerging population (Bear Creek) produced less (Table 4).

The average productivity did not significantly vary among the 5 populations, despite the observed differences in age composition (Table 4; Kruskal Wallis, $X^2 = 1.8$, $p = 0.77$). Between 1957 and 1995, all but one of the populations experienced an average of 3 – 4 returning adult sockeye salmon per spawner and therefore were more than replacing themselves. (Productivity of 1.0 would indicate simple replacement.) The mean productivity for Ice Creek was notably higher than all of the other populations (7.1); however, this value was inflated by one year with very high productivity. Excluding the outlier from the analysis decreased the mean value to 3.6, suggesting a similar overall level of productivity as the other populations. However, we retained this data point in the overall analysis because the spawner and return estimates all appear to be valid in that year; furthermore, its inclusion did not change the statistical results.

All five populations exhibited high interannual variability in productivity, and the patterns tended to be synchronous (i.e., years of high productivity in one population were also highly productive in the others, etc.; Figure 14). Correlations among the populations over all years ranged between 0.40 and 0.88, and all were significant at the 0.05 level (Figure 14). It is notable, however, that the highest correlations did not occur between the populations that were either in closest proximity to one another or most similar in physical characteristics. For instance, the outlets to Hansen Creek and Happy Creek lie less than 0.5 km from one another (Figure 1) and empty into the same cove, presumably resulting in very similar environmental conditions for the newly emerged fry. However, the correlation between these two populations, 0.49, was near the low end of the observed range of values. In contrast, Hansen Creek and Ice Creek showed the highest correlation among all the populations (0.88). These sites lie on opposite sides of the lake many km from each other (Figure 1), and Hansen Creek outflows into a protected cove whereas Ice Creek flows directly into the lake.

Lake patterns

The date of movement from littoral to pelagic habitat was negatively correlated with the mean length on 1 September (multiple regression B = -0.59, p = 0.001; Figure 15). That is, in years when the fry moved offshore later, they were smaller at the end of the growing season. Furthermore, the shift date was a stronger predictor of fry length than the previously established relationship (Burgner 1964, Rogers 1980, Burgner 1991, Schindler et al. 2005) with conspecific densities in the lake (B = -0.38, p = 0.02; Figure 15). Fry length on 1 September was a strong predictor for age 1 smolt length the following spring (Figure 16; $r^2 = 0.73$, $p << 0.001$), and the length in September averaged 71% (SD 3%) of the smolt length in the following year.

The date of the ontogenetic shift was also a significant predictor for the overall productivity of the 1-check year classes (Figure 17; $r^2 = 0.23$, $p = 0.006$, Y variable log-transformed to correct for heterscedasticity). Years in which the cohort of juvenile sockeye salmon moved into the open-water habitat later, the productivity from ahe-1 smolts was lower. However, we did not find an interannual correlation between smolt length and productivity (Figure 18, Henderson and Cass 1991). Shift date was not as good a predictor for the returns per spawner of the sockeye salmon spending 2 years in freshwater ($r^2 = 0.10$, $p = 0.08$).

Discussion

Biodiversity is gaining increasing attention from ecologists as a component of ecosystem processes that lends stability and resilience to a system (Hector et al. 1999, Loreau et al. 2001, Hilborn et al. 2003). Here, we present evidence for intraspecific biodiversity in the early life history patterns among several sympatric sockeye salmon populations, despite the fact that they share a common rearing ground and presumably experience similar selective pressures during the juvenile portion of the life cycle. These populations are characterized by relatively broad, consistent variation in their emergence timing (Chapter 1), despite a very short summer growing season and apparently strong selective pressure to maximize growth in order to avoid over-winter mortality (Conover 1990, Quinn and Peterson 1996, Schultz et al. 1998, Biro et al. 2004). In our examination of the long-term effects of emergence timing, we (1) found significant differences in the freshwater age composition among populations within the lake, and furthermore, (2) evidence that this variation corresponded with the average emergence timing of the population. Although more than 50% (and often more than 90%) of the sockeye salmon fry in Lake Aleknagik migrate to sea as smolts after 1 year of growth, those populations that emerged later had significantly higher proportions of 2-check smolts. This suggests that fry from those populations are less likely to achieve sufficient size during the first summer to trigger their transformation into smolts the following spring.

Despite the observed variation in emergence timing and age composition, we found no evidence of differential productivity among the populations. All five of the populations we examined produced, on average, equivalent numbers of returning adults per spawner and were more than replacing themselves. This suggests that none of the observed early life history patterns were consistently less successful than the others and therefore were not selected against by environmental conditions. Furthermore, all of the populations appeared to respond similarly to interannual variation in conditions, such that they displayed synchronous periods of high and low productivity. If the populations showed a pattern of alternating productivity (i.e., some high when other were low), it would suggest a form of system-wide stability in response to unpredictable habitat conditions. Instead, the high correlation in productivity indicates that all populations are experiencing similar within-year survival in marine and fresh water, raising the possibility that the observed variation in emergence timing and age composition is a form of niche partitioning within the available rearing habitat. Those populations whose fry are more apt to spend two years in the lake may bypass some of the competition for food resources during the first summer of growth and make-up missed growing opportunities during the second year before going out to sea. Estimates of marine survival based on the proportion of 2-check fish in the smolt counts and in the returning adults suggest little or no improvement in marine survival resulting from spending an extra year in fresh water (see also Quinn 2004). We do not know the mortality rates experienced by the fry while in the lake, although delayed emergence and decreased growth during the first summer would be expected to increase the risk of mortality during the winter months. However, the small percentage of fish spending two years in the lake (even in those populations with the highest proportion of 2-check individuals) may not markedly lower population productivity in those years when over-winter survival is low.

The second objective of this study was to provide a quantitative link between the behavioral patterns occurring during the freshwater juvenile life stage of sockeye salmon and the ultimate productivity of the year class. In years when the young-of-the-year sockeye salmon moved into the pelagic habitat of the lake early in the summer, the number of returning adult salmon from that year class was higher than in years when the ontogenetic shift occurred later in the summer. This relationship is highly significant, and is clearly independent of other critical factors to sockeye salmon productivity, such as density dependent survival of embryos (Essington et al. 2000), ocean conditions (Hare and Francis 1995, Gargett 1997), and the level of intra-specific and inter-specific competition at sea (Rogers and Ruggerone 1993, Ruggerone et al. 2003). It is important to note that the timing of the ontogenetic shift is not independent of general growing conditions in the lake; i.e., years in which the habitat shift occurred early also tended to be characterized by early spring ice breakup, warm offshore water temperatures, and high zooplankton productivity (Chapter 2, Schindler et al. 2005) Interestingly, smolt length was not related to the productivity of the cohort (see also Henderson and Cass 1991), although the timing of the habitat shift was a strong indicator of fry length at the end of the first growing season. This suggests that the mechanism behind the increased productivity was not simply improved early marine survival due to a larger size. The date of the ontogenetic shift may affect survival in the lake, although the specific mechanism is not known.

One of the primary challenges facing ecologists is identifying the connections among biotic and abiotic processes occurring at different spatial and temporal scales (e.g.,Maurer 1987, Jones and Lawton 1995). The ontogenetic shift exhibited by juvenile sockeye salmon in Lake Aleknagik allows us to begin to quantify the links between climate conditions in the region, biotic conditions in the lake, and immediate and prolonged responses in sockeye salmon populations. Chapter 2 demonstrated that the date of the movement of the sockeye salmon fry from the nearshore to the limnetic habitat was determined by zooplankton densities and water temperatures in the open water region of the lake. These limnetic conditions are driven by local air temperatures, the date of spring ice break-up on the lake, and patterns of solar radiation. With this study, we provide evidence that the date of the ontogenetic shift influences the growth achieved by the sockeye salmon fry during their first summer of growth, supporting the findings of Schindler et al. (2005) linking zooplankton density to sockeye salmon growth in this system. Furthermore, clear relationships have been demonstrated between early life history patterns and the long-term survival of other organisms, whether through identifying critical life stages through population projection matrices (e.g., Crouse et al. 1987, Rutherford et al. 1997, Cowan et al. 1999) or explaining observed variation in population fluctuations based on changes in biotic and abiotic environmental conditions experienced by juveniles (Logerwell et al. 2003, Lawson et al. 2004). The apparent connection between environmental conditions, the behavior patterns associated with early life history traits, and the long-term productivity of this species reinforces the importance of our ability to explain processes occurring within complex ecosystems.

	Agulowak	Bear	Hansen	Happy	Ice
Agulowak	1.00	**0.69**	**0.60**	**0.47**	**0.53**
Bear		1.00	**0.46**	**0.84**	**0.40**
Hansen			1.00	**0.49**	**0.88**
Happy				1.00	**0.41**
Ice					1.00

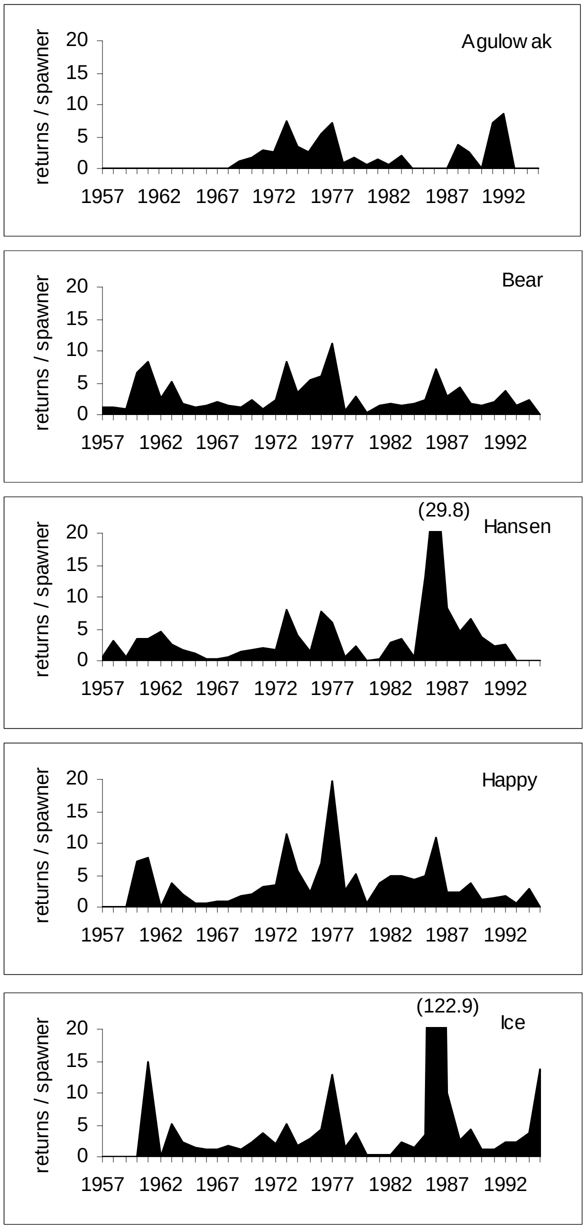


Figure 14**:** Interannual patterns of the number of returning adults per spawner in each of the 5 study populations. The inset table is a correlation matrix indicating the degree of correlation in productivity among the populations. All were significant at the 0.05 level.

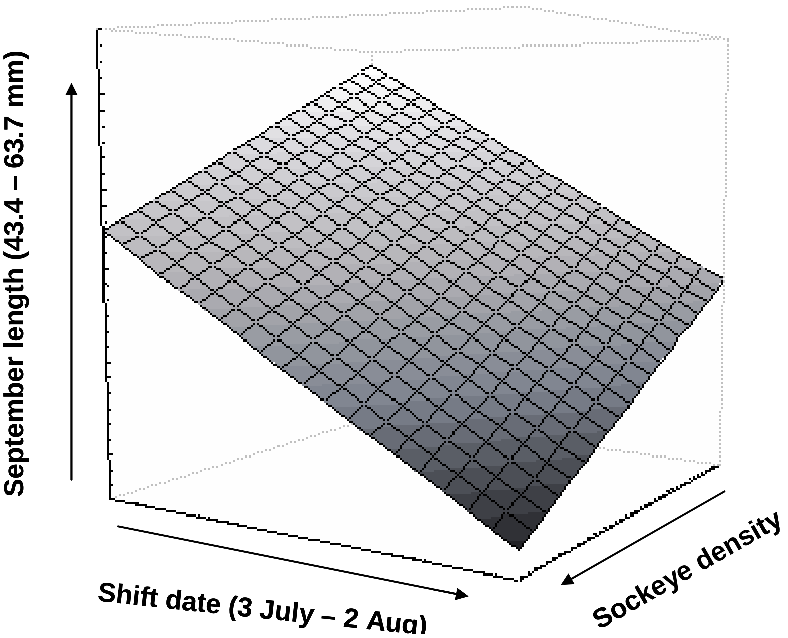


Figure 15**:** Multiple regression analysis of the length of sockeye salmon fry on September 1st against (1) the date of the ontogenetic shift and (2) the conspecific density of juvenile sockeye in Lake Aleknagik. Note that sockeye density values are shown in reverse order, as indicated by the arrow. Both density and shift date were significant predictors of length (density $p = 0.02$, $B = -0.38$; shift date $p = 0.001$, $B = -0.59$)

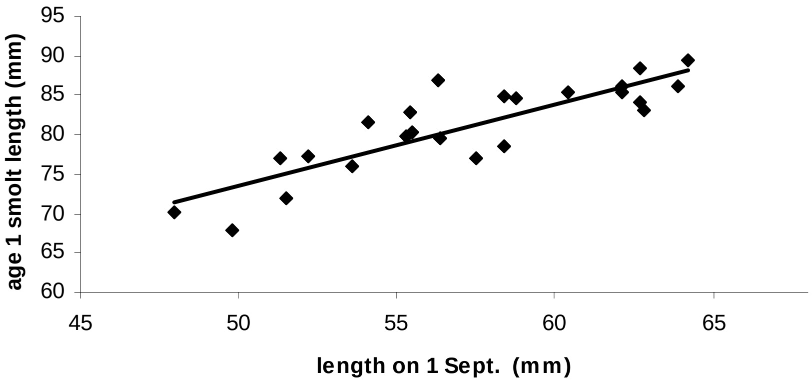


Figure 16: Correlation between the mean length of juvenile sockeye salmon on September 1st and the mean length of age 1 smolts leaving Lake Aleknagik the following spring.

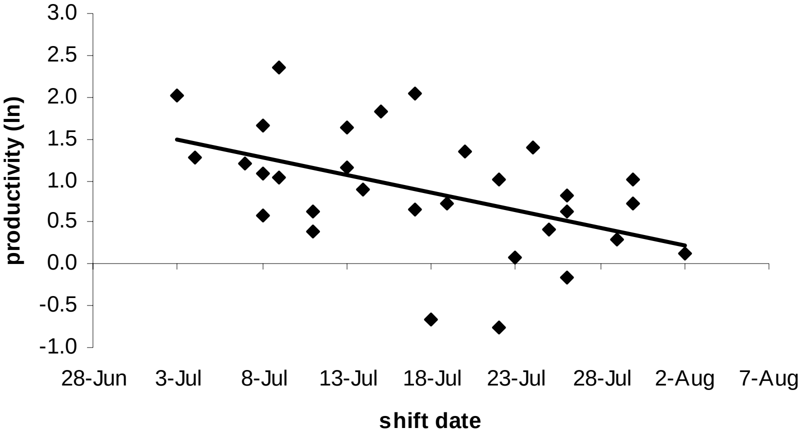


Figure 17: Correlation between the date of the ontogenetic shift by juvenile sockeye salmon and the number of returning age 1.* adults per spawner from each cohort. The productivity has been ln-transformed to correct for non-constant variance ($r^2 = 0.23$, $p = 0.006$).

Figure 18: Relationship (NS) between mean length of age 1 sockeye salmon smolts from Lake Aleknagik and the number of returning adults per spawner for that freshwater age class.

Table 4**:** Summary of the 5 study populations in Lake Aleknagik, listing the mean percentage of the returning adults that spent 2 years in freshwater (and standard error), the estimated mean emergence dates, and the mean number of returning adults per spawner (and standard error). Stars (*) denote significant differences (p<0.05) among the populations.

Population	Mean % 2-checks (SE)	Emergence date	Mean productivity (SE)
Ice	7.5 (2.2)*	unknown	7.1 (3.6)
Agulowak	12.4 (4.3)	unknown	3.3 (0.6)
Bear	11.4 (2.8)	22-Apr	3.0 (0.4)
Hansen	13.8 (3.1)*	8-Jul	3.8 (0.9)
Happy	16.6 (3.7)*	3-Aug	4.0 (0.7)

Conclusion

Life history strategies evolve in response to selective pressure from the biotic and abiotic environment. However, the type and strength of selection tends to vary throughout the life cycle – making it difficult to identify which factors are driving observed patterns and which life history stages are most critical. By examining three distinct periods of the sockeye salmon life cycle, operating over different spatial and temporal scales, we gain insight into the large-scale patterns of the interactions with the biotic and abiotic components of the ecosystem and the primary selective forces acting on the populations.

The incubation and emergence period is strongly controlled by annual temperature patterns. My results indicate that the sockeye salmon fry emerged relatively early in the spring, soon after spring ice breakup on the lake and prior to peak prey abundance. This suggests a tendency to maximize the length of the available growing period. However, despite their reliance on the same nursery lake, I found evidence of a high degree in inter-population variation in the date of peak emergence. This indicates the lack of strong selection for any one life history strategy, perhaps due to strong year-to-year variation in temperature and date of spring ice breakup.

The timing of the ontogenetic niche shift during the first summer of growth appeared to be driven largely by pelagic habitat conditions. The juvenile sockeye salmon vacated the littoral regions of the lake when water temperatures and zooplankton densities offshore were beneficial. The habitat shift was apparently not controlled by a size threshold, unlike patterns observed in other fish species. In this northern system, I propose that selective pressure to maximize growth outweighs the advantage of avoiding predation risk, and habitat selection occurs based on available growing conditions. Furthermore, the date of the habitat shift was best predicted by a composite variable indicative of offshore conditions, rather than zooplankton density or water temperature considered independently. This indicates that the fish may be responding to multiple indicators of habitat condition simultaneously.

Both emergence timing and the date of the ontogenetic shift had long-term implications for the annual sockeye salmon cohort. Emergence timing appeared to be negatively correlated to freshwater residence time, such that populations that emerged later tended to have a higher proportion of 2-check smolts. However, there was no evidence that emergence timing led to differential productivity success among the populations in a given year. The date of the offshore migration within the lake, and therefore the associated environmental conditions (e.g., temperature and zooplankton abundance), was strongly correlated with fish size at the end of the first summer and the survival of the cohort to adulthood. The increased survival was not attributable to smolt length at the time of outmigration to the ocean, indicating that freshwater survival may be a key component in year-class productivity.

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- Examination of the behavioral responses of tropical marine fish to changes in community structure.
- Experimental measurement of the establishment of dominance hierarchies in a simultaneous hermaphrodite, using controlled laboratory conditions

Publications (peer-reviewed)

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

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Abrey, C.A., Quinn, T.P., Rogers, D.E. (in prep) Diversity in early life history patterns: emergence timing of sockeye salmon fry.

Abrey, C.A., Quinn, T.P. (in prep) Path analysis of an ontogenetic shift in juvenile sockeye salmon: Is it all about size?

Abrey, C.A., Quinn, T.P. (in prep) The effect of early life history on population productivity of sockeye salmon in southwest Alaska.