AGE, GROWTH AND PRODUCTIVITY OF JUVENILE SOCKEYE SALMON IN TWO HIGH LATITUDE LAKES, ALASKA

By
Lorna I. Wilson

RECOMMENDED:

Milo D. Adkison

Christian E. Zimmerman

Eric C. Volk

W.W. Smoker
William W. Smoker, Advisory Committee Chair

S. Atkinson
Shannon K. Atkinson, Interim Director, Fisheries Division

APPROVED:

Denis A. Wiesenburg
Dean, School of Fisheries and Ocean Sciences

Lawrence K Duffy
Lawrence K. Duffy, Dean of the Graduate School

Dec 7, 2009
Date

AGE GROWTH AND PRODUCTIVITY OF JUVENILE SOCKEYE SALMON IN TWO HIGH LATITUDE LAKES, ALASKA

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Lorna I. Wilson, B.A.

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Abstract

The growth of Seward Peninsula sockeye salmon (*Oncorhynchus nerka*) from Salmon and Glacial lakes is related to their physical environment. Dermal scales collected over many years were measured to document the annual age specific growth of smolts and adults. The effect of fertilization on fry growth was examined using the first year of growth. The growth histories of Salmon Lake sockeye salmon were compared to Glacial Lake sockeye salmon through smolting and in the marine environment. Annual age specific fry growth had no direct relationship to fertilization; however, there were interactions between biomass of salmon prey and fertilization, and between prey biomass and age of smolting. Glacial Lake age-1 smolts are the same size as Salmon Lake age-1 smolts, but age-1.3 Salmon Lake juveniles after their first year in the ocean are smaller than age-1.3 Glacial Lake juveniles suggesting lower size based mortality. The differences in growth histories show each population’s response to lake production and mortality experienced by smolt between the rearing lake and the ocean.

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General Introduction

Sockeye Salmon Ecology

Sockeye salmon rear in lakes for one to three years before becoming smolt to increase their marine survival (Burgner 1991; Burgner 1987; Koenings and Burkett 1987). The number of years fry spend in lakes depends on lake rearing conditions; better conditions means less time is necessary to achieve minimum smolt size, generally around 60 mm (Koenings et al. 1993; Koenings and Burkett 1987). Better rearing conditions are characterized by lower fry to forage base ratio (Koenings and Burkett 1987; Mazumder and Edmundson 2002), an optimum temperature (Iwama and Tautz 1981; Mazumder and Edmundson 2002; Schindler et al. 2005a), deep euphotic zone depth (Burgner 1987; Koenings and Burkett 1987) and a longer growing season (Koenings and Burkett 1987). Also, temperature interacts with food availability to control fish growth (Brett 1983). Therefore, when season length, temperature and euphotic zone depth are favorable, fry growth should be limited only by zooplankton availability.

There are dynamic interactions between nutrients, zooplankton and sockeye salmon in rearing lakes (Koenings et al. 1989; Stockner 1987). Cladoceran clutch size is determined by food availability, egg production is determined by temperature (Wetzel 1975). In times of high nutrient content and high primary production, herbivorous cladocerans like *Bosmina* and *Daphnia* are the dominant zooplankton species. In times of low nutrient content copepods become the dominant species present because they digest their prey items more efficiently than the herbivorous cladocerans (Kyle et al. 1988). Also, sockeye salmon fry prefer herbivorous cladocerans like *Daphnia* and *Bosmina* in sizes ranging from 0.40 to 1.0 mm (Kyle et al. 1988) and avoid large evasive copepods like *Cyclops* (Koenings and Burkett 1987). Predation by sockeye salmon fry reduces *Bosmina* and *Daphnia* size (Kyle et al. 1988) and can even decimate the cladoceran populations (Koenings and Kyle 1997a).

Cladoceran production typically coincides with peak phytoplankton production. Under the “match mismatch” theory, in which matching of the secondary productivity bloom with larval abundance provides good survival, the mechanism of larval mortality is starvation, that is a mismatch of fish larvae and their principal prey will result in high mortality due to starvation . For example in Karluk Lake, Alaska, sockeye fry, peak temperature and peak zooplankton abundance are in September, therefore fry are not able to grow enough by the end of their first summer for successful smoltification, consequently smolt from Karluk Lake are all age 2.0 and 3.0 (Koenings and Burkett 1987).

Climate warming could enhance rearing conditions for sockeye salmon fry in large lakes of Alaska and increase smolt production. The annual timing of lake ice break up in Lake Aleknagik in the Wood River system in southwest Alaska (800 km south of the Seward Peninsula) has been related to an index of high latitude climate, the Pacific Decadal Oscillation (PDO)—earlier ice break up in warm phase years. Earlier break up was associated with increased *Daphnia* density (Schindler et al. 2005a). Even though fry density is thought to have a strong effect on zooplankton density, an association was not detected in annual records, demonstrating the importance of climate to zooplankton production (Schindler et al. 2005a) Sockeye salmon fry growth, however, was positively related to zooplankton abundance which increased with earlier spring break up, and was negatively related to fry density (Schindler et al. 2005a).

Salmon carcasses contribute marine derived nutrients (MDN) to lakes (Brock et al. 2007; Kline et al. 1993; Schindler et al. 2005b), and since nutrients typically limit phytoplankton and zooplankton production in sockeye rearing lakes, (Koenings et al. 1979; Koenings and Kyle 1997a), salmon carcasses can make rearing conditions for sockeye salmon fry better. For example, in Karluk Lake, nutrient loading from sockeye salmon carcasses is the only consistent explanation of long and short term trends in counts of adult sockeye salmon (Schmidt et al. 1998). It follows that variations in salmon returns due to climate or harvesting can have strong impacts on sockeye salmon nursery lake productivity in systems where adult salmon carcasses are important nutrient sources (Finney et al. 2000). Factors that determined MDN availability to juvenile salmon were the magnitude of escapement and water residence time for 23 Alaskan sockeye salmon rearing lakes (Uchiyama et al. 2008). Also, lakes with high MDN input have long water residency times, low terrestrial nutrient input, low precipitation and periods of high historical escapements (Finney et al. 2000). There have been periods of weak effects of MDN on algal production in Bristol Bay sockeye salmon nursery lakes even in lakes with abundant salmon (Brock et al. 2007). In addition, MDN input and stock-recruitment data are not directly related, perhaps due to the multitude of factors that affect smolt production (Uchiyama et al. 2008)

Physical conditions can limit the number of trophic levels in high latitude oligotrophic lakes. Arctic lakes have less complex trophic interactions compared to temperate lakes with similar species compositions (Kling et al. 1992). High latitudes experience shorter summer growing seasons and cooler temperatures, both limit plankton production in arctic lakes even in the presence of sufficient nutrients (McCoy 1983). Salmon fry growth can be predicted by temperature when zooplankton availability is late in the season (Peltz and Koenings 1989). These considerations suggest that high latitude lakes would be less productive of sockeye salmon. However, smolt to adult survival at sea generally increases from south to north, and some of the variability in smolt survival is explained by latitude (21%) and length (30%) (Koenings et al. 1993).

Sockeye salmon typically spend little time in estuaries but ocean-type juveniles (those that go to sea in their first year of life), may use estuaries more extensively (Birtwell et al. 1987), and advantages offered by estuaries could enhance sockeye salmon population production. Estuaries offer salmonids three primary advantages: productive foraging, relative refuge from predators, and a physically intermediate environment for transition from freshwater to marine physiological control systems (Thorpe 1994).

The length of estuarine residence by salmonids that typically use available estuaries (chum salmon (*O. keta*) and Chinoook salmon (*O. tshawytscha*) depends on the estuary's size, shape, and productivity, water flow patterns and velocities, salinity and temperature, and on the species and size of the salmon (Thorpe 1994). Also, the proportion of the estuary that is in pristine condition is significantly related to marine survival of Chinook salmon in Washington, Oregon and California populations (Magnusson and Hilborn 2003). Juvenile Chinook salmon rear in the northern region of Puget Sound, and chum salmon in the southern region which suggests that rearing habitats are species specific (Duffy et al. 2005).

Climate warming at sea could also positively influence salmon population's production since population productivity regimes are related to climate trends (Beamish et al. 1997). Basin wide conditions of the North Pacific are known to have been related to regional salmon population abundances (Mantua et al. 1997). For example, the Lake Nerka sockeye salmon abundance, reconstructed from lake sediment cores over the past 300 years, was positively correlated with the Gulf of Alaska sea surface temperatures, reconstructed from tree rings (Finney et al. 2000). Analysis of late 20th century Bristol Bay and Chignik sockeye salmon scales show that abundance was positively related to the growth of salmon in the first two years in the marine environment, the seasonal mean sea surface temperature in the North Pacific Ocean, and negatively related to the pink salmon (*O. gorbuscha*) index (Ruggerone et al. 2007). Sockeye salmon survival is related to both conditions in the marine environment, like all salmon, in addition to lake rearing conditions.

Lake Fertilization

Lakes with sockeye salmon fry are typically nutrient poor (Stockner 1987) therefore lake fertilization was designed to increase the rate of nutrient transfer through existing trophic levels to sockeye salmon fry (Koenings et al. 1979). Fertilization with phosphorus enhances phytoplankton production in sockeye salmon rearing lakes, since phosphorus and nitrogen limit phytoplankton production (Koenings et al. 1979). Increased food availability increases cladoceran survivorship, size and fecundity (the number of eggs per brood) (Wetzel 1975) and sockeye salmon fry prefer herbivorous cladocerans like *Bosmina* and *Daphnia* that are between 0.40 to 1.00 mm for their prey (Koenings and Burkett 1987).

Fertilization has been successfully implemented in sockeye rearing lakes in Alaska and British Columbia. In three coastal Alaskan lakes, fertilization increased primary production (chlorophyll-*a*) and zooplankton biomass (Kyle 1994). In Packers Lake, Alaska, fertilization and fry stocking experiment, the highest observed smolt biomass occurred with fertilization and in the absence of stocking, showing that a high ratio of forage base to fry leads to high smolt production (Stockner 1987). Fertilization was correlated with large sized zooplankton prey species *Daphnia* (Mazumder and Edmundson 2002). Large sized *Daphnia* lead to enhanced juvenile sockeye salmon fry growth (Mazumder and Edmundson 2002) and comparisons between an unfertilized period and the fertilized period show that smolt weights increased by 100% and the smolt to adult survival (SAS) rate increased by 43% (Kyle 1994).

Fertilization is not successful in lakes with inefficient energy transfer from lower trophic levels to sockeye salmon fry, or when fertilization enhances the production of unfavorable phytoplankton species. The length of the food chain present in coastal lakes causes less efficient energy transfer to sockeye salmon fry than inland more oligotrophic lakes in British Columbia (Hyatt and Stockner 1985). The production of unfavorable phytoplankton species can be enhanced in two ways. First, the presence of non-grazable phytoplankton can limit the production of preferred zooplankton species by sockeye salmon fry. The fertilization of Kennedy Lake, British Columbia, increased the biomass of *Rhizoselenia eriensis* (a non grazable diatom) to such an extent that the light penetration to the upper hypolimnion was reduced producing a net loss of algal biomass available to grazers (Stockner and Shortreed 1988). However, when fertilization was applied to the lake later in the summer, after *R. eriensis* was found only in the deep epilimnion, fertilization had a net positive effect on algal biomass available to grazers. The second way the production of unfavorable phytoplankton species can be enhanced is when the ratio of nitrogen to phosphorus is below 20:1, since this ratio favors the production of blue-green algae, which are inedible to zooplankton (Smith 1983).

In addition to the biotic factors that determine the effectiveness of fertilization, the water economy of a rearing lake can favor the success of fertilization. The lakes chosen to study historical MDN input are also good candidates for fertilization. These lakes are oligotrophic, have low nutrient input from erosion, low to moderate precipitation, long water residence time (> 1.0 year), and periods of high escapement (Holtham et al. 2004). Linear models were developed to predict smolt abundance and long term adult sockeye population from euphotic volume, and to differentiate between degrees of glacial input to lakes and between volumes of lakes (Koenings and Burkett 1987).

Seward Peninsula Sockeye Salmon

Sockeye salmon rear mainly in two lakes on the Seward Peninsula: Salmon Lake and Glacial Lake. Salmon and Glacial lakes have similar water residency times (1.6 and 1.5 years respectively) (Todd and Kyle 1997). Salmon Lake has a maximum depth of 35 m, volume of 111.5 x $10^6 m^3$. Glacial Lake has a maximum depth at 22 mm, much smaller volume, 23 x $10^6 m^3$ and very little estuary is available. However, the environment available to Salmon Lake sockeye salmon between Pilgrim River and the ocean is extensive (including Imuruk Basin, over 70 km long by air) and is complex. Tuksuk Channel and Imuruk Basin are pristine with respect to industrial development.

The Salmon Lake environment was judged to have a high potential for increased smolt production, indicated by small smolts (age 1 averaged 3.5 g; age 2 averaged 5.6 g), indicating a low forage base to fry ratio (Todd and Kyle 1997). Salmon Lake was fertilized in 1997-2001, 2004, 2007 and 2008 to increase smolt production. Glacial Lake smolts were found to be robust (age 1 averaged over 5 g; age 2 over 7 g) indicating a high forage base to fry ratio and no need for fertilization. Fertilization increased phytoplankton concentration, but zooplankton and age 1 smolt weight and length did not increase, suggesting limited success (Wilson et al. in press).

Annual age specific growth can be used to assess the fertilization of Salmon Lake, and to compare Glacial Lake sockeye salmon growth histories to Salmon Lake growth histories in relation to their physical environments. Because scale circuli are laid down progressively over time, the pattern of circuli widths represented on a scale can be used as a proxy for somatic growth rate (Farley et al. 2007; Fukuwaka and Kaeriyama 1997; Moss et al. 2005). Annual growth can be identified based on the distance between annuli, regions where circulus widths are narrow representing winter slowing of growth, a ‘check’ (Clutter and Whitsel 1956).

The goals of this study were to determine if fertilization affected sockeye salmon fry growth, to determine what factors are important to sockeye salmon fry growth, to compare the growth of sockeye salmon from Salmon and Glacial lakes in the freshwater and ocean environments. The alternative hypotheses explored were 1) relationships between lower trophic levels can be predicted by lower trophic levels in Salmon Lake, 2) annual age specific fry growth was effected by fertilization in Salmon Lake, 3) the age specific smolt sizes were not equal in Salmon and Glacial lakes, and 4) the age specific growth by Salmon Lake sockeye salmon in the first year in the ocean were not equal to Glacial Lake sockeye salmon in the first year in the ocean.

Objectives

This study explored the hypothesis that the growth of sockeye salmon was affected by their biotic and physical environments. The sockeye salmon populations of interest were from Salmon Lake, which was fertilized and has an extensive estuary, and nearby Glacial Lake, which was not fertilized and empties into the Bering Sea without an extensive estuary. The method involved studying growth during different life cycle phases by measuring scale radii at different annuli, summarizing the growth measurements, and analyzing historical variation of growth in the context of environmental variation. The study attempted to answer the following specific questions:

1. Do limnological factors affect the first year of sockeye salmon fry growth in Salmon Lake and is the first year of fry growth important to adult return?
2. Did artificial fertilization of Salmon Lake enhance sockeye salmon fry growth?
3. Is smolt size or the first year of marine growth greater for the Salmon Lake sockeye salmon population than for the Glacial Lake sockeye salmon population?

Literature Cited

Beamish, R., C. Neville, and A. Cass. 1997. Production of Fraser River sockeye salmon (*Oncorhynchus nerka*) in relation to decadal-scale changes in the climate and the ocean. Canadian Journal of Fisheries and Aquatic Sciences 54(3):543-554.

Birtwell, I., M. Nassichuk, and H. Buene. 1987. Underyearling sockeye salmon (*Oncorhynchus nerka*) in the estuary of the Fraser River. Canadian Special Publication of Fisheries and Aquatic Sciences 96:25-35.

Brett, J. 1983. Life energetics of sockeye salmon, *Oncorhynchus nerka*. Pages 29-63 [*in*] Behavioral energetics: the cost of survival in vertebrates

Brock, C., P. Leavitt, D. Schindler, and P. Quay. 2007. Variable effects of marine-derived nutrients on algal production in salmon nursery lakes of Alaska during the past 300 years. Limnology and Oceanography 52(4):1588.

Burgner, R. 1991. Life history of sockeye salmon (*Oncorhynchus nerka*). Pages 1-118 [*in*] C. Groot, and L. Margolis, Editors. Pacific Salmon Life Histories. UBC Press, Vancouver, BC.

Burgner, R. L. 1987. Factors influencing age and growth of juvenile sockeye salmon (*Oncorhynchus nerka*) in lakes. Pages 129–142 [*in*] H. D. Smith, L. Margolis, and C. C. Wood, Editors. Sockeye salmon (*Oncorhynchus nerka*) population biology and future management, Volume 96. Canadian Special Publication of Fisheries and Aquatic Sciences

Clutter, R., and L. Whitsel. 1956. Collection and interpretation of sockeye salmon scales. New Westminster, Canada, International Pacific Salmon Fisheries Commission

Duffy, E., D. Beauchamp, and R. Buckley. 2005. Early marine life history of juvenile Pacific salmon in two regions of Puget Sound. Estuarine, Coastal and Shelf Science 64(1):94-107.

Farley, E., J. Murphy, M. Adkison, L. Eisner, J. Helle, J. Moss, and J. Nielsen. 2007. Early marine growth in relation to marine-stage survival rates for Alaska sockeye salmon (*Oncorhynchus nerka*). Fishery Bulletin 105(1):121.

Finney, B., I. Gregory-Eaves, J. Sweetman, M. Douglas, and J. Smol. 2000. Impacts of climatic change and fishing on Pacific salmon abundance over the past 300 years. Science 290(5492):795-799.

Fukuwaka, M., and M. Kaeriyama. 1997. Scale analyses to estimate somatic growth in sockeye salmon, *Oncorhynchus nerka*. Canadian Journal of Fisheries and Aquatic Sciences 54(3):631-636.

Holtham, A., I. Gregory-Eaves, M. Pellatt, D. Selbie, L. Stewart, B. Finney, and J. Smol. 2004. The influence of flushing rates, terrestrial input and low salmon escapement densities on paleolimnological reconstructions of sockeye salmon (*Oncorhynchus nerka*) nutrient dynamics in Alaska and British Columbia. Journal of Paleolimnology 32(3):255-271.

Hyatt, K., and J. Stockner. 1985. Responses of sockeye salmon (*Oncorhynchus nerka*) to fertilization of British Columbia coastal lakes. Canadian Journal of Fisheries and Aquatic Sciences 42(2):320-331.

Iwama, G., and A. Tautz. 1981. A simple growth model for salmonids in hatcheries. Canadian Journal of Fisheries and Aquatic Sciences 38:649-656.

Kline, T., J. Goering, O. Mathiesen, P. Poe, P. Parker, and R. Scalan. 1993. Recycling of elements transported upstream by runs of Pacific salmon. II: d15N and d13C evidence in the Kvichak River watershed, Bristol Bay, Southwestern Alaska. Canadian Journal of Fisheries and Aquatic Sciences 50(11):2350-2365.

Kling, G., B. Fry, and W. O'Brien. 1992. Stable isotopes and planktonic trophic structure in arctic lakes. Ecology:561-566.

Koenings, J., R. Burkett, M. Haddix, G. Kyle, and D. Barto. 1989. Experimental manipulation of lakes for sockeye salmon (*Oncorhynchus nerka*) rehabilitation and enhancement. Alaska Department of Fish and Game, Division of Fisheries Rehabilitation, Enhancement and Development

Koenings, J., H. Geiger, and J. Hasbrouck. 1993. Smolt-to-adult survival patterns of sockeye salmon (*Oncorhynchus nerka*): effects of smolt length and geographic latitude when entering the sea. Canadian Journal of Fisheries and Aquatic Sciences 50(3):600-611.

Koenings, J., M. Kaill, M. Haddix, P. Novak, J. Clark, and L. Engel. 1979. Policy and Guidelines for Lake Fertilization. Alaska Department of Fish and Game Lake Fertilization Team

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

Koenings, J., and G. Kyle. 1997. Consequences to juvenile sockeye salmon and the zooplankton community resulting from intense predation. Alaska Fishery Research Bulletin 4(2):120-135.

Kyle, G., J. Koenings, and B. Barrett. 1988. Density-dependent, trophic level responses to an introduced run of sockeye salmon (*Oncorhynchus nerka*) at Frazer Lake, Kodiak Island, Alaska. Canadian Journal of Fishishereis Aquatic Sciences 45(5):856-867.

Kyle, G. 1994. Nutrient treatment of 3 coastal Alaskan lakes: trophic level responses and sockeye salmon production trends. Alaska Fishery Research Bulletin 1(2):153-167.

Magnusson, A., and R. Hilborn. 2003. Estuarine influence on survival rates of coho (*Oncorhynchus kisutch*) and chinook salmon (*Oncorhynchus tshawytscha*) released from hatcheries on the US Pacific coast. Estuaries and Coasts 26(4):1094-1103.

Mantua, N., S. Hare, Y. Zhang, J. Wallace, and R. Francis. 1997. A Pacific interdecadal climate oscillation with impacts on salmon production. Bulletin of the American Meteorological Society 78(6):1069-1079.

Mazumder, A., and J. A. Edmundson. 2002. Impact of fertilization and stocking on trophic interactions and growth of juvenile sockeye salmon (*Oncorhynchus nerka*). Canadian Journal of Fisheries and Aquatic Sciences 59(8):1361-1373.

McCoy, G. 1983. Nutrient limitation in two arctic Lakes, Alaska. Canadian Journal of Fisheries and Aquatic Sciences 40(8):1195–1202.

Moss, J., D. Beauchamp, A. Cross, K. Myers, J. Farley, E, J. Murphy, and J. Helle. 2005. Evidence for size-selective mortality after the first summer of ocean growth by pink salmon. Transactions of the American Fisheries Society 134(5):1313-1322.

Peltz, L., and J. P. Koenings. 1989. Evidence for temperature limitation of juvenile sockeye salmon, *Oncorhynchus nerka*, growth in Hugh Smith Lake, Alaska. Alaska Department of Fish and Game, Fisheries Rehabilitation, Enhancement, and Development Division Report 90.

Ruggerone, G., J. Nielsen, and J. Bumgarner. 2007. Linkages between Alaskan sockeye salmon abundance, growth at sea, and climate, 1955–2002. Deep-Sea Research Part II 54(23-26):2776-2793.

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

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

Schmidt, D., S. Carlson, G. Kyle, and B. Finney. 1998. Influence of carcass-derived nutrients on sockeye salmon productivity of Karluk Lake, Alaska: importance in the assessment of an escapement goal. North American Journal of Fisheries Management 18(4):743-763.

Smith, V. H. 1983. Low nitrogen to phosphorus ratios favor dominance by blue-green algae in lake phytoplankton. Science 221(4611):669-671.

Stockner, J., and K. Shortreed. 1988. Response of *Anabaena* and *Synechococcus* to manipulation of nitrogen : phosphorus ratios in a lake fertilization experiment. Limnology and Oceanography 33(6, part 1):1348-1361.

Stockner, J. 1987. Lake fertilization: the enrichment cycle and lake sockeye salmon (*Oncorhynchus nerka*) production. Pages 198–215 [*in*] H. D. Smith, L. Margolis, and C. C. Wood, Editors. Sockeye salmon (*Oncorhynchus nerka*) Population Biology and Future Management,volume 96. Candian Special Publication of Fisheries and Aquatic Sciences

Thorpe, J. 1994. Salmonid fishes and the estuarine environment. Estuaries and Coasts 17(1):76-93.

Todd, G., and G. Kyle. 1997. Limnological and sockeye salmon productivity investigations in Salmon and Glacial lakes: project completion report. Alaska Department of Fish and Game, Division of Commercial Fisheries, Regional Information Report 5J97-05, Juneau.

Uchiyama, T., B. Finney, and M. Adkison. 2008. Effects of marine-derived nutrients on population dynamics of sockeye salmon (*Oncorhynchus nerka*). Canadian Journal of Fisheries and Aquatic Sciences 65(8):1635-1648.

Wetzel, R. 1975. Limnology. Saunders Philadelphia

Wilson, L., G. Todd, and T. Hamazaki. in press. Sockeye salmon studies in Salmon Lake, Alaska: limnology and fishery investigations relative to a nutrient addition program, 1994-2008. Alaska Department of Fish and Game. Fishery Data Series No. 09-XX, Anchorage.

Chapter 1: Lower trophic relationships and the effect of fertilization on the growth of sockeye salmon fry in a high latitude lake[1]

Abstract

I hypothesized that annual age specific first year of growth of Seward Peninsula sockeye salmon (*Oncorhynchus nerka*) from Salmon Lakes were related to zooplankton biomass and increased due to the bottom up effects of fertilization. Dermal scales collected over many years were measured to document the annual age specific growth of smolts. Linear models were explored and phytoplankton concentration was related to phosphorus concentration, and zooplankton biomass was not related to phytoplankton concentration. Annual age specific first year of fry growth was not related to fertilization. The effectiveness of fertilization could be further evaluated using annual estimates of age specific fry density.

Introduction

Sockeye salmon (*Oncorhynchus nerka*) fry typically rear in oligotrophic lakes, suggesting that smolt production is also rearing limited (Bradford et al. 2000; Koenings and Burkett 1987; Mazumder and Edmundson 2002). In oligotrophic lakes, phytoplankton production is limited by phosphorus in freshwater (Koenings et al. 1987; Stockner 1987; Wetzel 1975). Survivorship and fecundity (the number of eggs per brood) of herbivorous cladoceran zooplankton species, such as *Bosmina* and *Daphnia*, increases with increased phytoplankton availability and a favorable temperatures (Wetzel 1975). Herbivorous cladocerans are the preferred zooplankton prey for sockeye salmon fry (Koenings and Burkett 1987). Fry growth is ultimately controlled by zooplankton prey

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[1] Wilson, L., G. Todd, C. Zimmerman, W. Smoker and E. Volk. 2009. Lower trophic relationships and the effect of fertilization on the growth of sockeye salmon fry in a high latitude lake. Prepared for submission in the North American Journal of Fisheries Management.

species production when temperature is not limiting (Hume et al. 1996; Koenings et al. 1989; Schindler et al. 2005b). Consequently, smolt length and the proportion of age 1 smolt increase with available forage base in lakes (Burgner 1987; Koenings and Burkett 1987). When nutrient concentration, phytoplankton and zooplankton production increase, smolt survival increases since larger smolts have higher survival rates than smaller smolts (Henderson and Cass 1991; Koenings et al. 1993; Koenings and Burkett 1987).

Lake fertilization has been used to increase sockeye salmon population production in many lakes throughout British Columbia and Alaska (Bradford et al. 2000; Koenings and Kyle 1997b; Mazumder and Edmundson 2002). Fertilization is designed to increase returns by increasing the rate of nutrient transfer through the existing trophic levels in sockeye salmon rearing lakes and increase fry growth (Koenings et al. 1979). Sockeye salmon rearing lakes are forage limited when there is a to low forage base to fry ratio (Koenings and Burkett 1987). Fertilization is successful when the lake is rearing limited, has a long water residency time (Stockner and Shortreed 1985), edible phytoplankton (Stockner and Shortreed 1988) and preferred zooplankton species. For example, lake fertilization decreased rearing limitation when the forage base to fry ratio increased and the smolt biomass increased three- to four- fold (Stockner 1987).

Aspects of lake ecosystems can limit the success of fertilization. For example, lakes with longer food chains are less successful at increasing smolt production than lakes with short food chains because of inefficient energy transfer through the trophic levels to smolt production (Hyatt and Stockner 1985). Also, fertilizer choice and timing determines the effectiveness of fertilization in decreasing rearing limitation. Fertilizer with a N:P ratio < 20:1 that was applied to water temperatures below 8° C increased rearing limitation since those conditions favored the production of blue-green algae which are inedible to zooplankton (Smith 1983). In some cases, the timing of fertilization can be altered to prevent the production non-grazable phytoplankton (e.g. *Rhizoselenia eriensias*), so that fertilization can increase grazable phytoplankton and decrease rearing limitation(Stockner and Shortreed 1988). Physical factors that promote the effectiveness of fertilization include long water residency time and low nutrient input from fluvial sources (Finney et al. 2000).

Salmon Lake, on the Seward Peninsula, Alaska, and was fertilized because it was considered limited in its capacity to produce sockeye salmon (*Oncorhynchus nerka*) smolts (< 85% above threshold size age 1 smolts) (Todd and Kyle 1997). The age 1 smolt production did not increase with fertilization, however the effects of fertilization on the lake ecosystem in Salmon Lake are unknown, since fry density was not estimated and the bottom up effects of fertilization cannot be distinguished from the top down effects of fry predation (Wilson et al. in press).

In the presence of top down effects of predation by fry, in Salmon Lake, the effects of fertilization is likely to be most evident in *Bosmina* biomass. The top down effects of sockeye salmon fry predation reduces prey size and structures the zooplankton community composition (Kyle et al. 1988). Sockeye salmon fry prefer cladocerans *Bosmina longirostris* and *Daphnia longiremis* within the size range 0.4 to 1.0 mm (Kyle et al. 1988). In Salmon Lake, the mean *Daphnia* size was 0.63 mm, within the preferred zooplankton size range, and the mean *Bosmina* size was 0.35 mm (Wilson et al. in press), smaller than the preferred zooplankton size. Since *Bosmina* are smaller than the preferred zooplankton size, they are more resistant to intense predation by sockeye fry than larger *Daphnia* (Koenings and Kyle 1997b).

Also, since fry sometimes spend more than one summer in the lake, age 1 smolt size is a biased indicator of overall fry growth. All ages of fry in the lake should increase their growth, and the first year of smolt age specific growth of fry should represent the rearing conditions in the lake with less bias. The first year of fry growth can be measured on dermal scales; circuli are laid down progressively over time and circuli spacing can be used as a proxy for somatic growth (Clutter and Whitsel 1956; Farley et al. 2007; Fisher and Pearcy 1990; Fukuwaka and Kaeriyama 1997; Moss et al. 2005; Ricker 1992; Ward et al. 1989). The sum of circuli measurements from the focus to the first annulus is directly related to growth achieved by fry in their first summer.

The goals of this study are to 1) determine the relationships between lower trophic levels, and 2) determine if the annual age specific fry growth was affected by fertilization.

Methods

Study site description

Salmon Lake is located on the Seward Peninsula (64°54'N, 165°00'W) approximately 55 km northeast of Nome, and is accessible via the Kougarok Road. The lake is at an elevation of 135 m, drains a watershed area of 209 km^2, and is the headwater of the Pilgrim River which drains into the Kuzitrin River, Imuruk Basin, Port Clarence and finally the Bering Sea (Todd and Kyle 1997).

Salmon Lake has a volume of 111.5 x 10^6 m^3, surface area of 7.49 km^2 (1,851 acres), mean depth of 14.9 m, and maximum depth of 40 m. Water residence time was estimated to be 1.6 years. It is ultra-oligotrophic since it has low nutrient and chlorophyll *a* concentrations.

Smolt age and length

Sockeye salmon smolts were collected using an incline plane trap in the Pilgrim River (Wilson et al. in press). Age and length (mm) samples were taken from approximately 10% of the smolts caught in the trap in 1995, 1996, 1998-2000 and 2002-2008 by ADF&G, Nome personnel (Wilson et al. in press). Smolt scale samples were scraped from smolt from the preferred area (Clutter and Whitsel 1956) with a scalpel then spread on a glass slide. Smolt age was determined from scale samples in 1995, 1996, 1999, 2000, and 2002-2008. Smolt length (tip of snout to fork in tail) was measured the nearest 1 mm.

Scale Measurements

Sample size

The necessary number of scale measurements for a relative error, ignoring the finite population correction since the sample size is small compared to the number of possible samples, was calculated as (Thompson 1992):

$$n = \frac{z^2\delta^2}{r^2} \tag{1}$$

where z is the upper $\alpha/2$ point of the normal distribution and

$$\delta = \frac{\sigma}{\mu} \text{ and } r < \frac{\hat{\mu} - \mu}{\mu} \tag{2}$$

where σ is the standard error of the mean μ. The μ and σ were calculated for each combination of lake and age from smolt samples. Then a chronological stratified sample was taken from samples each group of size *n*.

Image capture

Standard methods used at the ADFG Mark Tag Age Laboratory were used to generate images of scales selected to be measured (Hagen et al. 2001). The scale was scanned with

Screenscan, a high resolution line camera attached to an Indus 4601 microfiche reader with a magnification lens (42x). Scales were visually assessed for edge resorption, tears, holes, and asymmetry. Asymmetric scales suggest that the sample was not from the preferred area (from the left side of the salmon approximately two rows above the lateral line on the diagonal row that extends down from the posterior insertion of the dorsal fin to the anterior insertion of the anal fin (Koo 1955)). Each scale sample was oriented so that a diagonal line from the focus to the farthest edge of the scale was in the positive quadrant centered on the focus (0 to 90 degrees).

Measurement

Scale images were measured using the software program Optimate and the macro CIRCCHUM READER V.2 used by the ADF&G Mark Tag and Age (MTA) Lab in Juneau, Alaska (Hagen et al. 2001). First, a reference line was created from the focus to the farthest edge of the scale. Then annuli were marked after the first full circulus beyond each winter check (regions were circuli widths are narrow from slow somatic growth in the winter) by the reader starting from the focus and ending at the edge of the scale. Freshwater plus growth (growth in freshwater after the last annulus in freshwater before marine growth), was also marked with a marker. Then circuli were marked on their exterior edge first automatically by the macro then edited by the reader. An extra circulus was marked after the last annulus when the scale did not end in a circulus after the last annulus mark, at the edge of the scale. Measurement errors were indicated by the comment “EIA” for the extra circulus or “FWPL” for an annulus marker that indicates freshwater plus growth with the annulus number (e.g. FWPL-3). Scale measurements, the date, reader’s initials, and comments were saved in a text file.

Organization

The data from the text file was reshaped into a list of annuli and circuli measurements for each fish using the software program R (www.r-project.org). Then script files were written to correct the errors generated in the measurement process and to sum the circulus measurements for the first freshwater annulus for each fish. From these scale measurements, the mean annual age specific scale radii from the focus to the first freshwater annulus were measured.

Fertilizer application

There were two different fertilizers added to Salmon Lake, a blended nitrogen (N) and phosphorus (P) fertilizer, 20-5-0 (N-P-Potash or N:P 18-20:1 (by atoms) and a nitrogen fertilizer, 32-0-0. In 1997 through 2001, 40 tons of blended N and P fertilizer was applied to the deeper basin of Salmon Lake (Figure 1.1) throughout the growing season, recommended by Todd and Kyle (1997). Also, in 1997, six barrels of N fertilizer were applied late in the season. In 2004, 2007 and 2008, 27, 16 and 8 tons of the blended N and P fertilizer were applied, respectively.

Lake nutrient and plankton content

Annual mean total nitrogen (N) and phosphorus (P) concentrations ($\mu g\ L^{-1}$), chlorophyll-*a* biomass ($\mu g\ L^{-1}$), and zooplankton length (mm), density (no m^{-2}) and biomass (mg m^{-2}) were estimated from water samples taken from Salmon Lake approximately every 3-4 weeks analyzed according to standard ADF&G methods (Koenings et al. 1987).

Seasonal mean total nitrogen (TN, $\mu g\ L^{-1}$) and total phosphorus (TP, $\mu g\ L^{-1}$) concentrations (Table 1.1) were calculated from water samples taken from the fertilized lake basin, station 1, (Figure 1.1) at 1 m depth approximately every 30 days in years 1995-2008 (Wilson et al. in press).

The seasonal mean chlorophyll *a* biomass (µg L^{-1}) (Table 1.1) was estimated from water samples taken at station 1 (Figure 1.1) at 1 m by ADF&G, Nome personnel, and were analyzed by the ADF&G Limnology Laboratories in Soldotna (1995-2004) and Kodiak (2005-2008) (Wilson et al. in press).

Seasonal mean *Daphnia longiremis*, *Bosmina longirostris* and *Cyclops columbianus* and total cladoceran (*Bosmina* and *Daphnia*) biomass (mg m^{-2}) (Table 1.1) were estimated from zooplankton tows from the lake bottom at stations 1 and 2 (Figure 1.1) performed by ADF&G Nome office personnel, and were analyzed by the ADF&G Limnology Laboratories in Soldotna (1995-2004) and Kodiak (2005-2008) (Wilson et al. in press).

Temperature and season length

Daily Nome temperatures taken near the airport were obtained from the National Weather Service. Temperature anomalies were the sum of deviances of the average temperature (°C) for the months July, August and September from the average for that month from 1995-2008 (Table 1.1). Season length is the number of days that the average of the next 10 days' temperatures were above 1°C in Nome, also calculated from daily Nome temperatures taken near airport (Table 1.1).

Adult Escapement and Return

Salmon Lake sockeye salmon age, sex and length (ASL) samples were taken in 2001-2008. Aerial surveys (1994-2002) and counts of sockeye salmon from a floating weir on the Pilgrim River (2003-2008) were used to estimate Pilgrim River sockeye salmon escapement and brood year return (Table 1.2). Escapements were calculated by subtracting the harvest that occurred above the Pilgrim River weir from the weir count (2003-2008) and from escapement estimated from the linear regression through the origin between successful escapement and weir counts to aerial surveys (1994-2002) (ADF&G, *unpublished data*). Annual harvests were estimated from subsistence surveys performed by ADF&G (1994-2002) and from subsistence permits that specify above or below the weir or in Salmon Lake (2003-2008). Annual return per spawner (RS) were estimated by dividing the estimated return appropriated to brood year (calculated from adult age samples collected through the season) by the estimated escapement.

Data analysis

Phytoplankton model

Normality assumptions of variables.-The variables total phosphorus concentration (µg L^{-1}), euphotic zone depth (m), season length (days), and temperature anomaly (°C) were normally distributed. The variables *Bosmina*, *Daphnia, Cyclops* and total cladoceran (*Bosmina* and *Daphnia*) biomass (mg m^{-2}) and phytoplankton biomass (µg L^{-1}) were transformed by natural logarithm to achieve a normal distribution. The variables *Bosmina*, *Cyclops*, *Daphnia* and total cladoceran biomasses were significantly correlated (Table 1.3), so only *Bosmina* biomass was included.

Full linear model.-The full model for response variable chlorophyll-*a* biomass (Chl) had predictor variables temperature anomaly (°C), season length (SeasonL), *Bosmina* biomass, total phosphorus concentration (TotalP) and euphotic zone depth (EZD):

$$\text{Chl} = \beta_0 + \beta_1\text{Temp} + \beta_2\text{SeasonL} + \beta_4\text{TotalP} + \beta_5\text{EZD} \tag{3}$$

where β are variable coefficients and intercept β_0.

Zooplankton model

Normality and correlation of data.-The potential dependent variables *Bosmina* biomass (mg m^{-2}) was transformed by natural logarithm to achieve a normal distribution. The predictor variables temperature anomaly (°C), season length (days), scale measurement to first freshwater annulus (mm), euphotic zone depth (m), and chlorophyll *a* biomass (mg m^{-2}) were normally distributed.

Full linear model.- The full model for the response variable cladoceran zooplankton biomass (*Bosmina* and *Daphnia*) had predictor variables temperature anomaly (Temp), season length (SeasL), euphotic zone depth (EZD), and chlorophyll *a* biomass (Chl). The full model form is:

$$\text{ZB} = \beta_0 + \beta_1 \text{Temp} + \beta_2 \text{SeasonL} + \beta_4 \text{EZD} + \beta_5 \text{Chl} \tag{4}$$

where β were variable coefficients with intercept β_0.

First year freshwater growth model

Normality correlation and auto-correlation of data.-The dependent variable radius at the first freshwater annulus for each age was normally distributed. The predictor variable *Bosmina* biomass (mg m^{-2}) was transformed by natural logarithm to achieve a normal distribution. Fertilization treatment was unbalanced because the number of years in each fertilization treatment, unfertilized (1995, 1996, 2002, 2003, 2005, 2006) and fertilized (40 tons: 1997-2001, 27 tons: 2004, 16 tons: 2007, 8 tons: 2008), were not equal.

Full linear model.-A linear model was used to explore the relationship between the first year of freshwater growth at age and *Bosmina* biomass ($\mu g\ L^{-1}$), amount of fertilizer applied (tons), and smolt age, as well as their interactions. The model form was:

$$\begin{aligned} Fw1 = \beta_0 + \beta_1 \text{Bosmina} + \beta_2 \text{Fertilizer} + \beta_3 \text{Age} + \beta_4 \text{Bosmina} \cdot \text{Fertilizer} + \\ \beta_5 \text{Bosmina} \cdot \text{Age} + \beta_6 \text{Fertilizer} \cdot \text{Age} \end{aligned} \tag{5}$$

where β were variable coefficients with intercept β_0.

Ricker spawner-recruit models

Four Ricker spawner-recruit models were compared: no covariate (null), with covariate *Bosmina* biomass, with covariate average first year freshwater growth, and with both covariates *Bosmina* biomass and average first year freshwater growth. Each model was assumed to have lognormal residual errors.

1. Ricker spawner-recruit model

$$R = \alpha S e^{-\beta S} e^{\sigma Z} \tag{6}$$

where R are the recruits (the number of adults that return to the lake plus harvested fish), S are the spawners (the number of adults that return to the lake and are not harvested), a and b are parameters that define the shape of the relationship between R and S, Z are the error terms that are log normally distributed with standard error σ.

2. Ricker with covariate *Bosmina* biomass

$$R = \alpha S e^{-(\beta S)} e^{(\gamma Bosmina + \sigma Z)} \tag{7}$$

where R, S, a, b, Z and σ are described above, and γ is the variability explained by the variable *Bosmina* biomass.

3. Ricker with covariate freshwater growth:

$$R = \alpha S e^{-(\beta S)} e^{(\gamma Fw1 + \sigma Z)} \tag{8}$$

where R, S, a, b, Z and σ are described above, and γ is the variability explained by the variable scale radius to the first freshwater annulus, Fw1.

4. Ricker with covariates *Bosmina* biomass and freshwater growth from smolt scales:

$$R = \alpha S e^{-(\beta S)} e^{(\gamma_1 Bosmina + \gamma_2 Fw1 + \sigma Z)} \tag{9}$$

Where R, S, a, b, Z, σ, γ_1 and γ_2 are described above.

Model selection and analysis

The Akaike information criterion (AIC) for model selection is (Burnham and Anderson 2002):

$$AIC = n \ln\left(\frac{RSS}{n}\right) + 2k \tag{10}$$

where n is the number of observations, k is the number of parameters, and RSS is the residual sum of squared errors in the model. The AIC corrected to reflect small sample sizes (AIC_c) was used to select the best linear models:

$$AIC_c = AIC + \frac{2k(k+1)}{(n-k-1)} \tag{11}$$

Stepwise selection was performed using the “step” functions in R. The “step” function removed each variable from the full model individually then selected the model with the lowest AIC value to use as the full model in the next iteration. This procedure uses the AIC statistic; selected models were examined to ensure that they would also have been selected using AIC_c.

The Type III sum of squares, marginal or orthogonal significance of parameters were presented for unbalanced models. In this approach, the effect of each variable is evaluated after all other factors have been accounted for, which is robust to unbalanced designs.

Model residuals were examined for normality numerically using the Shapiro-Wilk normality test and by visually assessing histograms, boxplots and QQ plots of model residuals. Autocorrelation and partial autocorrelation of the residuals was examined visually using the output from the functions "acf" and "pacf" in R (Venables and Ripley 2002).

Results

Lower trophic relationships

Phytoplankton.-Variations in chlorophyll *a* biomass were best explained by the linear model with variables season length (Season, $P = 0.118$), total phosphorus concentration (TP, $P = 0.017$) and euphotic zone depth (EZD, $P = 0.169$), (Table 1.4). The model was:

$$\mathrm{Chl} = 2.74 - 0.02\mathrm{Season} + 0.15\mathrm{TP} - 0.07\mathrm{EZD} \tag{12}$$

($n = 13$; $R^2 = 0.56$; $P = 0.052$)

Model residuals were normally distributed with no correlation or autocorrelation.

Zooplankton.-Variations in *Bosmina* biomass (mg m^{-2}) were best explained by the linear models with variables season length (Season, $P = 0.118$), total phosphorus concentration (TP, $P = 0.017$) and euphotic zone depth (EZD, $P = 0.169$), (Table 1.4). The linear model was:

$$\mathrm{Bosmina} = 7.86 - 0.18EZD \tag{13}$$

($n = 13$; $R^2 = 0.94$; $P = 0.081$)

Model residuals were normally distributed with no correlation or autocorrelation.

Scale analysis

Body-scale radius relationship.-The following linear model was developed to back calculate fork length (*FL, mm*) from scale radius *Scale* (mm) using Salmon Lake smolt scales (Figure 1.2):

$$FL = 51.804 + 102.278 Scale \tag{14}$$

$(n = 749;\ R^2 = 0.505;\ P < 0.001)$

Inter-annual variability of scale growth.-There was inter-annual variability of the relationship between fish length and scale radius (Figure 1.3, Table 1.6). In some years (1995, 2003, 2006 and 2008), scale radius did not appear to be closely related to fish length for age 1 smolts, but in other years (e.g. 2004, 2007), scale radius was closely related to fish length.

First freshwater annulus model.-Variations in the scale radius to the first freshwater annulus (Fw1, Figure 1.4, Table 1.5) were best explained by smolt age (marginal ANOVA significance P = 0.015), and year (marginal ANOVA significance P = 0.001) (Tables 1.7 and 1.8). Scale radius decreased with smolt age, and was variably related to year.

Model residuals were normally distributed with no apparent correlation or autocorrelation, or relationship to years of fertilization (Figure 5).

Ricker spawner-recruit models

The best Ricker model selected by AIC_c scores was the null model with no covariates, $AIC_c = 5.03$ (Figure 1.6, Table 1.9). AIC_c values indicated no other model should be considered. The Ricker models with fry growth and *Bosmina* biomass as a covariates had similar AIC_c values, 8.58 and 9.26 respectively. The model that included covariates fry growth and *Bosmina* biomass had the worst AIC_c value, 19.84.

Discussion

The relationships between lower trophic levels and analysis of annual age specific growth of sockeye salmon fry suggest that fertilization did not affect fry growth. The lack of relationship between the first year of fry growth and fertilization could be due to a number of reasons. The first reason could be the uncertainty in the relationship between scale measurements and fry length. Dermal scales do not form immediately after emergence, e.g. juvenile kokanee sockeye salmon from Lake Shikotsu, Japan, had a mean fork length of fish that had not yet formed the first scale circulus of 41.2 ±1.42 mm (Fukuwaka and Kaeriyama 1997). Sockeye salmon smolt fork length was significantly related to scale radius in this study, however there were years the relationship was not as strong (Figure 3). Scale circulus formation was correlated with food consumption (Bilton and Robins 1971), suggesting that some of the variability in the relationship between scale formation and fork length for Salmon Lake sockeye salmon could be due to low food availability. The second reason could be that fertilization had no effect on fry growth because of the top down effects of fry predation on fish growth, as discussed in Wilson et al. (in press).

The relationships between lower trophic levels and fertilization were not always as expected. Phytoplankton concentration was significantly related to phosphorus concentration, suggesting that fertilization is an effective way of increasing phytoplankton production, however, zooplankton biomass was not related to phytoplankton concentration, suggesting that zooplankton biomass was not explained by the bottom up effects of fertilization.

Further research is needed to understand the effects of fertilization on the zooplankton production in Salmon Lake. Phytoplankton production in Salmon Lake is related to phosphorus concentrations, however, factors that limit zooplankton production are unknown. Zooplankton biomass was affected by bottom up effects of phytoplankton availability (Koenings and Burkett 1987; Stockner 1987), which was estimated, however, zooplankton biomass is also affected by top down effects of fry predation (Koenings and Kyle 1997b), which was not estimated. The forage base to fry ratio explains much of the variability in fry growth (Bradford et al. 2000a; Koenings and Burkett 1987), and should be included in future analyses.

Based on annual age specific measurements of the first year of freshwater growth of sockeye salmon fry in Salmon Lake, fertilization alone is not a reasonable approach to increasing fry growth in Salmon Lake. Additionally, since the first year of fry growth does not explain the variability of return well, efficacy of increasing adult returns with fertilization is limited. Fry growth and smolt production need to be monitored in addition to nutrient content and phytoplankton and zooplankton species' biomass to evaluate lake fertilization.

Acknowledgements

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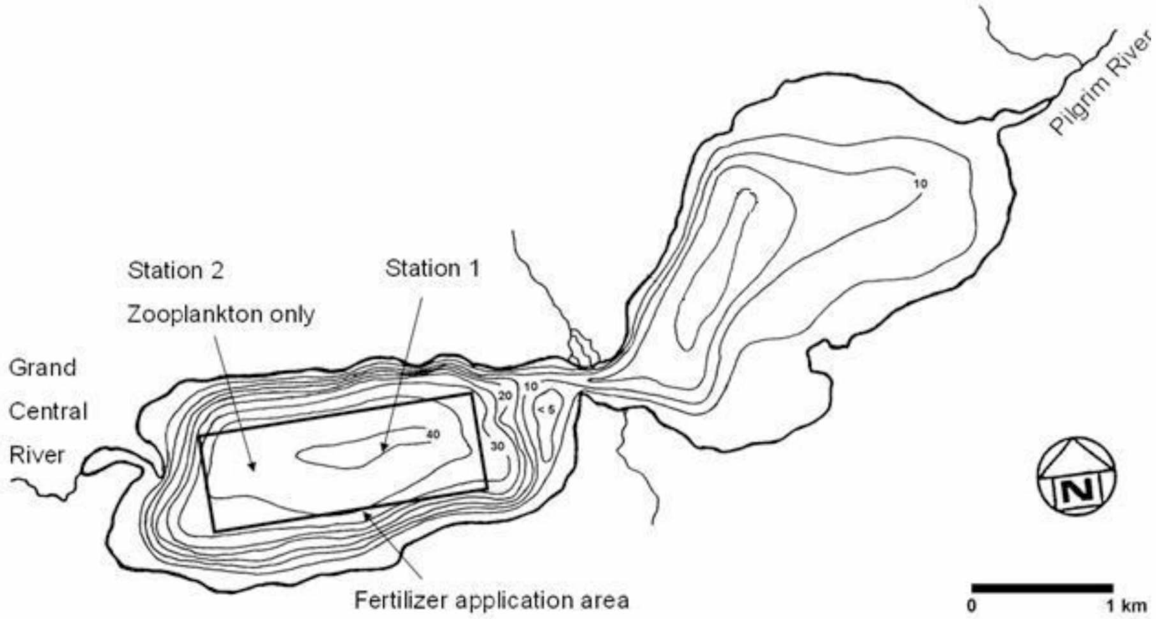

Figure 1.1.- Sampling stations and fertilizer application area, Salmon Lake (Todd and Kyle 1997).

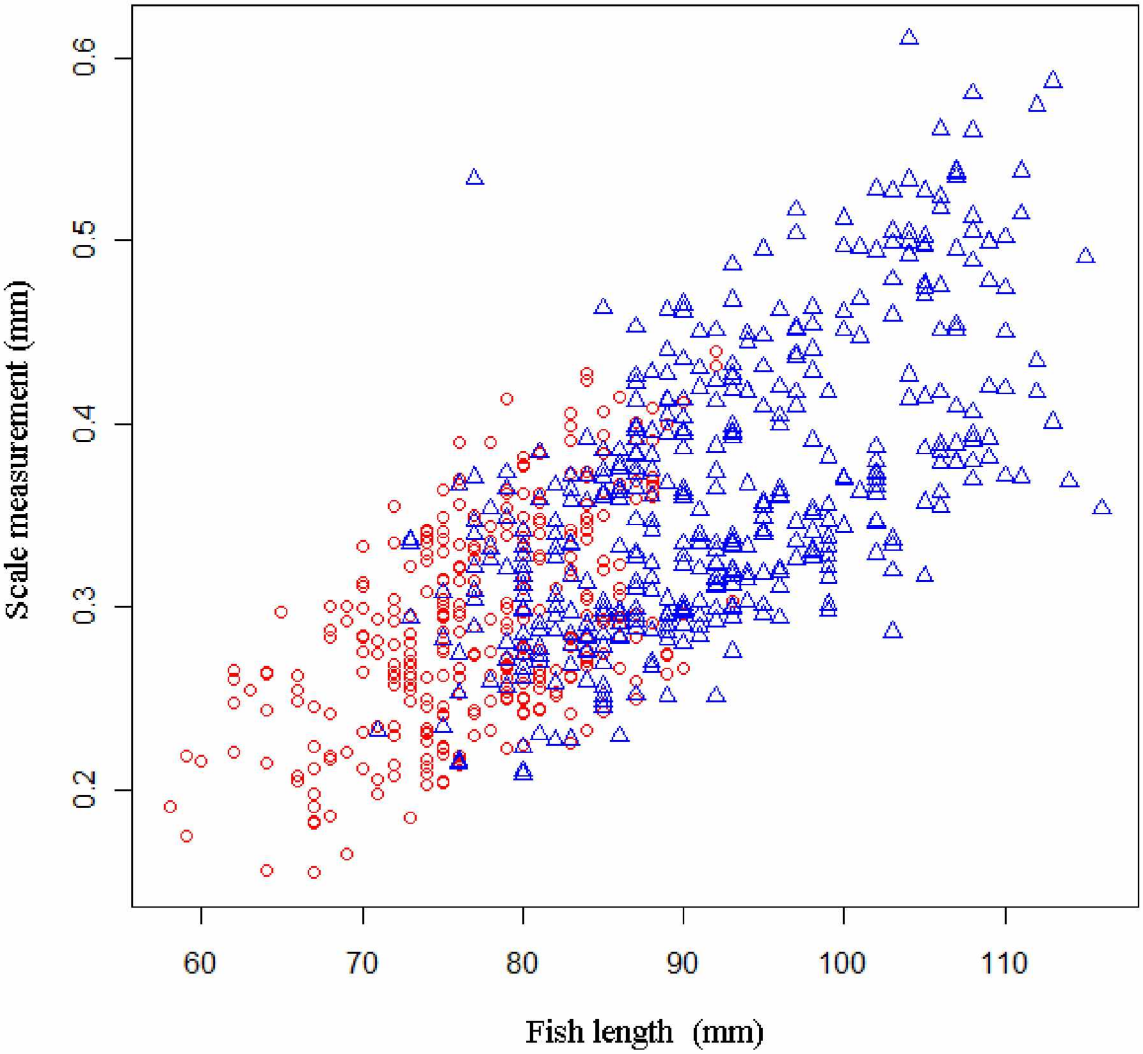

Figure 1.2.- Total scale radius (mm) plotted against fork length (mm) for age 1 (open circles) age 2 (triangles) from Salmon Lake smolt scales.

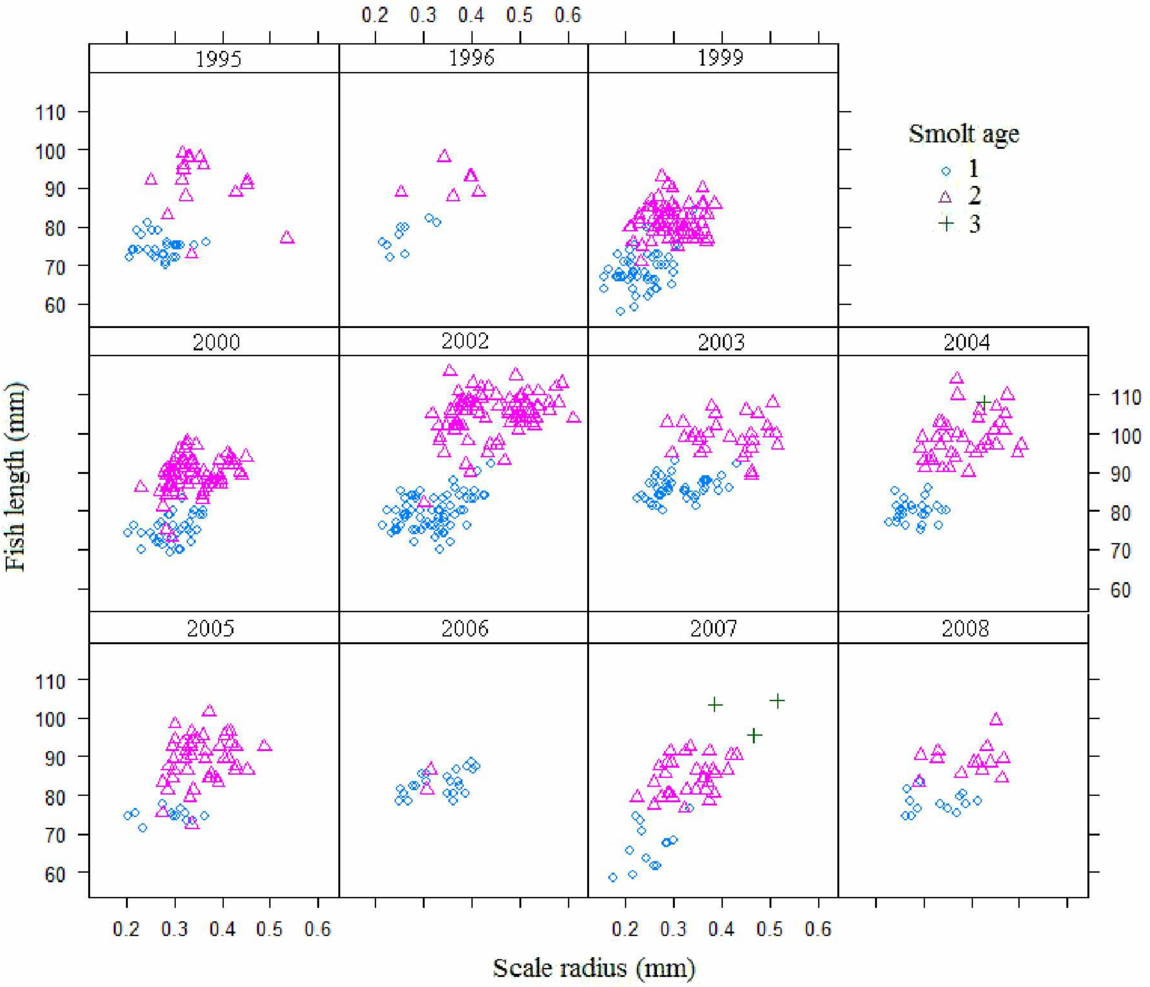

Figure 1.3.- Total smolt scale radius (mm) against fork length (mm) by year and age (age 1 (open circles) age 2 (triangles) and age 3 (plus signs), 1995, 1996, 1999, 2000, 2002-2008.

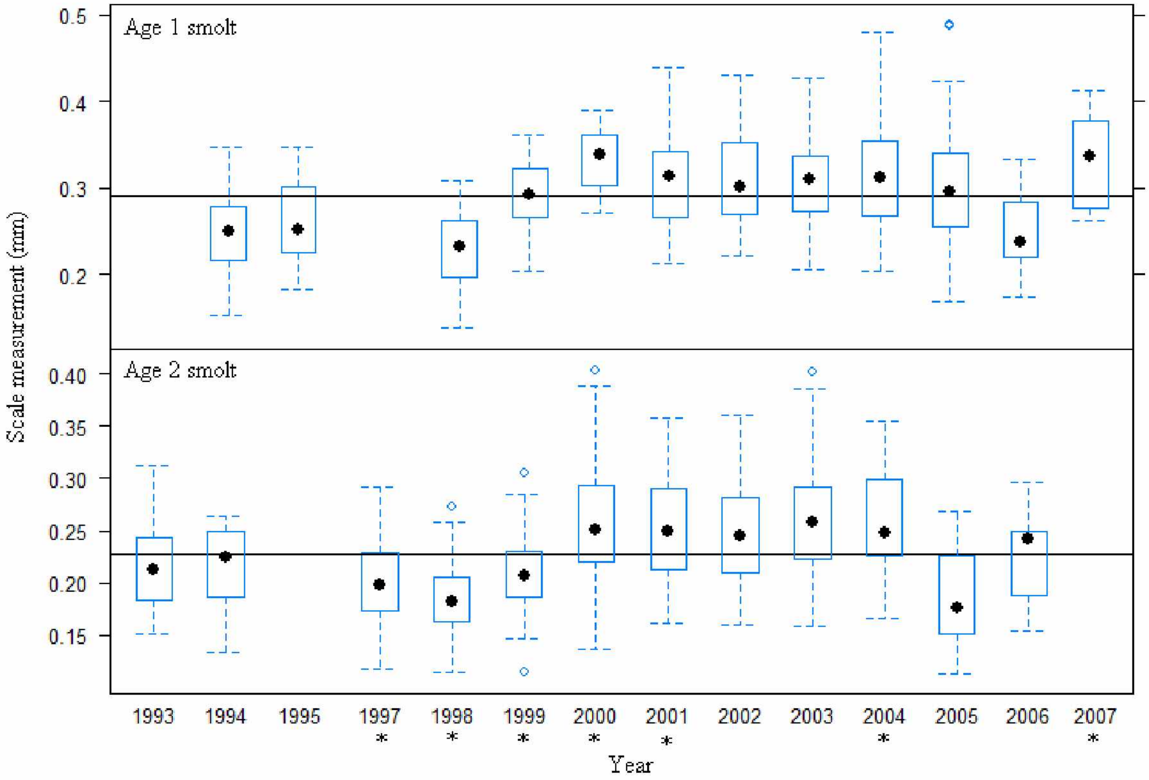

Figure 1.4.- Scale radius to the first freshwater annulus in lake rearing year from Salmon Lake age 1 (left panel) and age 2 (right panel) smolt scales, 1993-2007. Asterisks indicate years of fertilization (40 tons: 1997-2001, 27 tons: 2004 and 19 tons: 2007).

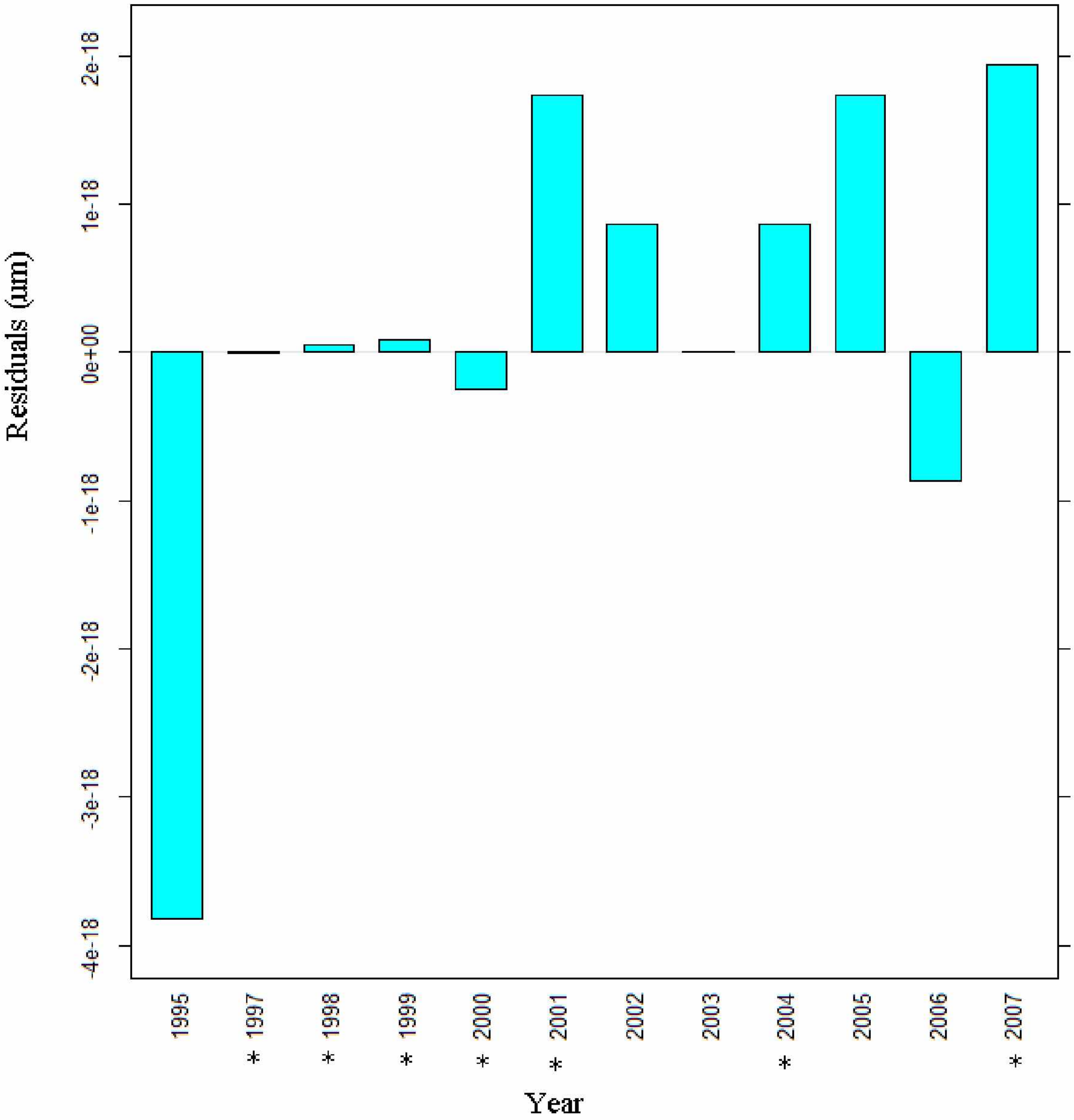

Figure 1.5.- First freshwater annulus model residuals from year and smolt age. Asterisks indicate years of fertilization (40 tons in 1997-2001, 27 tons in 2004 and 19 tons in 2007).

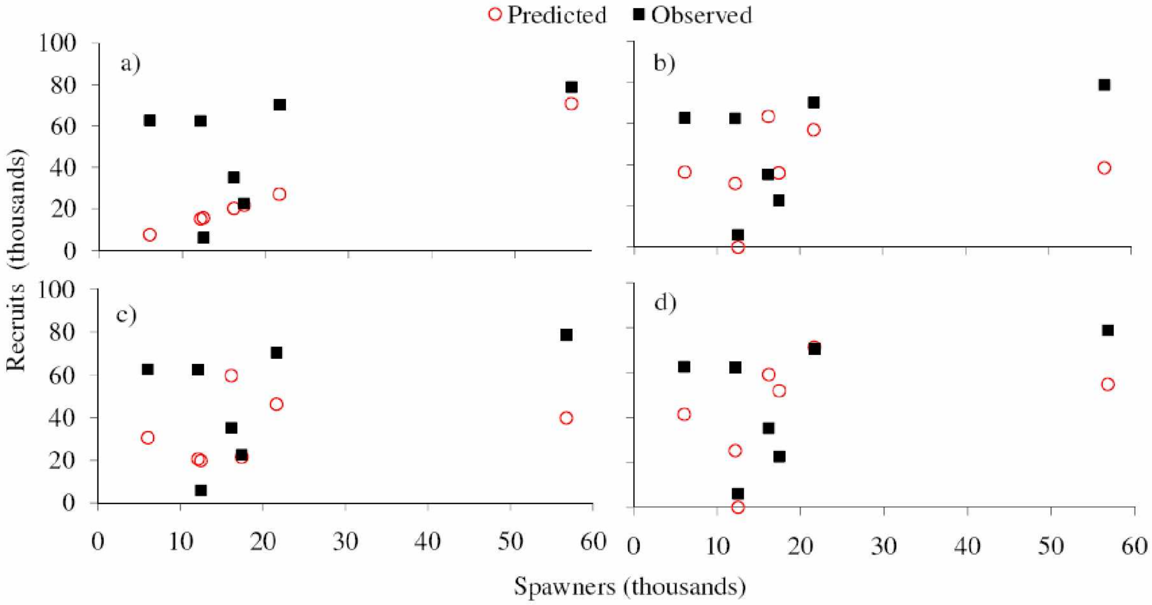

Figure 1.6.- Observed and predicted Ricker spawner-recruit relationships with covariates none (a), with covariate *Bosmina* biomass (b), with fry growth (c), and with both *Bosmina* biomass and fry growth (d).

Table 1.1.- Seasonal mean explanatory variables: temperature anomaly (ºC), season length (days), total nitrogen (μg L^{-1}), total phosphorus (μg L^{-1}), chlorophyll a biomass (μg L^{-1}), *Daphnia*, *Bosmina,* total cladoceran (*Daphnia* and *Bosmina*) and *Cyclops* biomass (mg m^{-2}).

Year	1995	1996	1997	1998	1999	2000	2001	2002	2003	2004	2005	2006	2007	2008
Temp. anomaly	-8.2	-2.5	3.7	-1.5	-1.3	-3.3	-2.9	-0.9	-1.7	5.2	3.6	0.3	8.9	0.7
Season length	158	141	164	148	143	132	128	150	166	177	161	151	147	147
Total N	46	81	130	133	100	128	91	70	68	73	103	127	79	
Total P	1.7	3.2	9.8	9.1	5.3	8.9	6.1	3.6	4.3	8.8	4.7	3.1	3.9	
Chl *a*	0.9	0.9	2.0	0.8	0.5	2.5	2.9	0.6	0.5	1.1	0.9	0.7	0.8	
Daphnia biomass	35	30	38	28	27	140	84	297	147	69	14	20	203	
Bosmina biomass	43	23	17	27	51	93	270	312	101	191	19	14	314	
Cladoc. biomass	78	53	55	55	78	233	354	609	247	260	34	34	517	
Cyclops biomass	223	620	165	92	102	286	365	379	473	537	258	105	395	

Table 1.2.- Salmon Lake sockeye salmon brood year escapement and return, 1996-2002.

Year	Escapement	Return
1996 [a]	12,298 [b]	5,906
1997	17,131 [b]	22,623
1998	11,976 [b]	62,440
1999	55,825 [b]	78,756
2000	21,283 [b]	70,407
2001	15,923 [b]	35,178
2002	5,984 [b]	62,265 [c]

[a] Does not include 4-year old fish (age 1.2 and 2.1), historically a small proportion (2001-2008 average 6.5%).

[b] Estimated from aerial survey data.

[c] Estimate does not include 7-year old fish (age 2.4), historically a small proportion (2001-2008 average 0.4%).

Table 1.3.- Explanatory variables' Pearson's correlation coefficients below the diagonal, and significance probabilities above the diagonal between the variables temperature anomaly (Temp), season length (Season), adult escapement (Escap.), *Cyclops*, *Bosmina*, *Daphnia*, and total cladoceran (*Bosmina* and *Daphnia*) biomass (mg m^{-2}), total nitrogen concentration (µg L^{-1}, N), total phosphorus concentration (µg L^{-1}, P), mean scale measurement to first freshwater annulus (mm, Scale), euphotic zone depth (m, EZD) and mean seasonal chlorophyll-*a* biomass (µg L^{-1}, Chl) with significant correlations ($\alpha < 0.05$) with borders and in bold and marginally significant correlations in bold.

Variable	Temp	Season	Escap.	*Cyclops*	*Bosmina*	*Daphnia*	Cladoc.	N	P	Scale	EZD	Chl-*a*
Temp	-	0.212	0.099	0.652	0.596	0.711	0.612	0.569	0.389	0.680	0.872	0.85661
Season	0.371	-	**0.050**	0.741	0.604	0.664	0.622	0.394	0.819	0.292	0.734	0.210
Escap.	0.501	**0.553**	-	0.771	0.832	0.506	0.905	0.861	0.473	0.820	0.516	0.599
Cyclops	0.139	0.102	0.090	-	**0.043**	**0.049**	**0.036**	**0.019**	0.532	0.120	0.354	0.615
Bosmina	0.162	-0.159	0.065	**0.567**	-	**0.000**	**0.000**	0.076	0.943	**0.002**	0.124	0.732
Daphnia	0.114	-0.133	-0.203	**0.555**	**0.861**	-	**0.000**	0.219	0.964	**0.031**	**0.051**	0.764
Cladoc.	0.156	-0.151	-0.037	**0.583**	**0.976**	**0.949**	-	0.120	0.957	**0.006**	0.081	0.669
N	0.174	-0.259	-0.054	-0.636	-0.508	-0.366	-0.316	-	**0.025**	**0.040**	0.212	0.273
P	0.261	0.070	0.219	-0.191	-0.022	0.014	0.165	**0.617**	-	0.157	0.155	0.062
Scale	0.127	-0.317	0.070	0.453	**0.772**	**0.597**	**0.451**	**-0.574**	-0.416	-	0.081	0.733
EZD	0.050	0.105	0.198	-0.280	-0.449	**-0.551**	-0.282	0.371	0.418	-0.501	-	0.724
Chl-a	-0.056	-0.373	-0.161	0.154	0.105	0.092	-0.055	0.328	0.530	-0.105	-0.109	-

Note: Correlation coefficients are in the lower triangle, their significance is in the upper triangle

Note: Significant correlations ($P < 0.05$) are bold and have borders; nearly significant correlations ($P < 0.06$) are bold.

Table 1.4.- Phytoplankton and *Bosmina* linear models. Significant (P value < 0.05) variables are bold.

Dependent variable	Independent variable	Coef.	S.E.	T value	P value
Phytoplankton biomass	Intercept	2.735	1.495	1.829	0.101
	Season length	-0.016	0.009	-1.728	0.118
	Total phosphorus	**0.149**	**0.051**	**2.916**	**0.017**
	Euphotic zone depth	-0.072	0.048	-1.496	0.169
Bosmina biomass	Intercept	-0.565	1.594	-0.354	0.730
	EZD	**20.825**	**6.099**	**3.414**	**0.006**

Table 1.5.- Summary of scale radius to the first freshwater annulus: annual mean (mm), coefficient of variation (CV) and sample size (N) from age 1 and age 2 smolts, shown in first year of freshwater growth, 1995-2008.

	Age 1 Smolt			Age 2 Smolt			Age 3 Smolt		
Year	Mean	CV	N	Mean	CV	N	Mean	CV	N
1993	-	-	0	0.216	21.7%	16	-	-	0
1994	0.248	16.9%	66	0.218	19.5%	9	-	-	0
1995	0.262	17.5%	43	-	-	0	-	-	0
1996	-	-	0	-	-	0	-	-	0
1997	-	-	0	0.205	18.3%	74	-	-	0
1998	0.229	18.1%	49	0.183	15.9%	78	-	-	0
1999	0.291	13.7%	39	-	-	0	-	-	0
2000	-	-	0	0.264	20.7%	86	-	-	0
2001	0.308	17.4%	71	0.237	19.0%	30	0.137	NA	1
2002	0.306	16.6%	46	0.252	19.1%	38	-	-	0
2003	0.277	12.4%	26	0.247	15.6%	45	-	-	0
2004	0.284	18.7%	13	0.253	16.8%	9	0.243	28.3%	3
2005	0.266	20.4%	28	0.186	24.7%	31	-	-	0
2006	0.247	17.5%	14	0.229	20.3%	13	-	-	0
2007	0.330	16.5%	13	-	-	0	-	-	0
Overall	0.277		408	0.226		429	0.190		4

Note: A dash indicates no scales were measured.

Table 1.6.- Analysis of variance table for scale radius to MEF length linear model showing marginal significance.

Factor	Df	SSQ	Mean Sq	F value	P (> F)
Smolt length	1	2.360	2.360	807.1	< 0.001
Year	10	0.156	0.016	5.3	< 0.001
Residuals	737	2.155	0.003		

Table 1.7.- Scale radius to the first freshwater annulus linear model. Significant (P value < 0.05) variables are bold.

Response	Predictor	Coef.	S.E.	T value	P value
Scale radius	**Intercept**	**0.262**	**0.262**	**16.377**	**0.000**
	1997	-0.047	-0.010	-0.398	0.705
	1998	-0.010	-0.032	-1.602	0.160
	1999	-0.032	0.030	1.313	0.237
	2000	0.030	0.049	2.032	0.088
	2001	0.049	0.034	1.705	0.139
	2002	0.034	0.041	2.052	0.086
	2003	0.041	0.024	1.184	0.281
	2004	0.024	0.031	1.529	0.177
	2005	0.031	-0.012	-0.600	0.571
	2006	-0.012	0.000	0.005	0.996
	2007	**0.000**	**0.068**	**3.007**	**0.024**
	Smolt age 2	**0.068**	**-0.047**	**-5.517**	**0.001**

Table 1.8.- Analysis of variance table for scale radius to the first freshwater annulus linear model showing marginal significance. Significant (P value < 0.05) variables are bold.

Factor	Degrees of freedom	SSQ	MSQ	F value	P value
Year	**11**	**0.019**	**0.002**	**6.687**	**0.015**
Smolt age	**1**	**0.008**	**0.008**	**30.437**	**0.001**
Residuals	6	0.002	0.000		

Table 1.9.- Ricker Spawner recruit models with covariates *Bosmina* biomass (*Bosmina*), scale radius to the first freshwater annulus (Fw1), and *Bosmina* plus Fw1, with parameter coefficients, residual sum of squares (RSS), and AIC$_c$ scores.

Model	n	α	β	γ_1	γ_2	RSS	AIC$_c$
Ricker	8	1.25	3.8E-10	-	-	9.63	3.08
Ricker, *Bosmina*	8	0.66	2.5E-05	0.38	-	5.68	9.26
Ricker, Fw1	7	1.00	4.4E-05	7.31	-	3.23	8.58
Ricker, *Bosmina* + Fw1	7	0.03	9.8E-05	50.17	-1.414	2.18	19.84

Literature Cited

Bilton, H., and G. Robins. 1971. Effects of feeding level on circulus formation on scales of young sockeye salmon (*Oncorhynchus nerka*). Journal of the Fisheries Research Board of Canada 28:861-868.

Bradford, M., B. Pyper, and K. Shortreed. 2000. Biological responses of sockeye salmon to the fertilization of Chilko Lake, a large lake in the interior of British Columbia. North American Journal of Fisheries Management 20(3):661-671.

Burgner, R. 1987. Factors influencing age and growth of juvenile sockeye salmon (*Oncorhynchus nerka*) in lakes. Pages 129–142 [*in*] H. D. Smith, L. Margolis, and C. C. Wood, Editors. Sockeye salmon (*Oncorhynchus nerka*) population biology and future management,volume 96. Canadian Special Publication of Fisheries and Aquatic Sciences

Burnham, K., and D. Anderson. 2002. Model selection and multimodel inference: A practical information-theoretic approach. Springer

Clutter, R., and L. Whitsel. 1956. Collection and interpretation of sockeye salmon scales. New Westminster, Canada, International Pacific Salmon Fisheries Commission

Farley, E., J. Murphy, M. Adkison, L. Eisner, J. Helle, J. Moss, and J. Nielsen. 2007. Early marine growth in relation to marine-stage survival rates for Alaska sockeye salmon (*Oncorhynchus nerka*). Fishery Bulletin 105(1):121.

Finney, B., I. Gregory-Eaves, J. Sweetman, M. Douglas, and J. Smol. 2000. Impacts of climatic change and fishing on Pacific salmon abundance over the past 300 years. Science 290(5492):795-799.

Fisher, J., and W. Pearcy. 1990. Spacing of scale circuli versus growth rate in young coho salmon. Fishery Bulletin 88(4):637-643.

Fukuwaka, M., and M. Kaeriyama. 1997. Scale analyses to estimate somatic growth in sockeye salmon, *Oncorhynchus nerka*. Canadian Journal of Fisheries and Aquatic Sciences 54(3):631-636.

Hagen, P., D. Oxman, and B. Agler 2001. Developing and deploying a high-resolution imaging approach for scale analysis. Alaska Department of Fish and Game Mark, Tag, and Age Lab, Juneau NPAFC Doc. No. 567.

Henderson, M., and A. Cass. 1991. Effect of smolt size on smolt-to-adult survival for Chilko Lake Sockeye Salmon (*Oncorhynchus nerka*). Canadian Journal of Fisheries and Aquatic Sciences 48(6):988-994.

Hume, J., K. Shortreed, and K. Morton. 1996. Juvenile sockeye rearing capacity of three lakes in the Fraser River system. Canadian Journal of Fisheries and Aquatic Sciences 53(4):719-733.

Hyatt, K. D., and J. G. Stockner. 1985. Responses of sockeye salmon (*Oncorhynchus nerka*) to fertilization of British Columbia coastal lakes. Canadian Journal of Fisheries and Aquatic Sciences 42(2):320-331.

Koenings, J., R. Burkett, M. Haddix, G. Kyle, and D. Barto. 1989. Experimental manipulation of lakes for sockeye salmon (*Oncorhynchus nerka*) rehabilitation and enhancement. Alaska Department of Fish and Game, Division of Fisheries Rehabilitation, Enhancement and Development

Koenings, J., H. Geiger, and J. Hasbrouck. 1993. Smolt-to-adult survival patterns of sockeye salmon (*Oncorhynchus nerka*): effects of smolt length and geographic latitude when entering the sea. Canadian Journal of Fisheries and Aquatic Sciences 50(3):600-611.

Koenings, J., M. Kaill, M. Haddix, P. Novak, J. Clark, and L. Engel. 1979. Policy and guidelines for lake fertilization. Alaska Department of Fish and Game Lake Fertilization Team

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

Koenings, J., and G. Kyle. 1997. Consequences to juvenile sockeye salmon and the zooplankton community resulting from intense predation. Alaska Fishery Research Bulletin 4(2):120-135.

Koenings, J., G. Kyle, J. Edmundson, and J. Edmundson. 1987. Limnology field and laboratory manual: methods for assessing aquatic production. Alaska Department of Fish and Game, Division of Fisheries Rehabilitation, Enhancement, and Development, Report No. 71, Juneau.

Koo, T. 1955. Biology of the red salmon, *Oncorhynchus nerka* (Walkbaum) of Bristol Bay, Alaska, as revealed by a study of their scales. University of Washington

Kyle, G., J. Koenings, and B. Barrett. 1988. Density-dependent, trophic level responses to an introduced run of sockeye salmon (*Oncorhynchus nerka*) at Frazer Lake, Kodiak Island, Alaska. Canadian Journal of Fisheries Aquatic Sciences 45(5):856-867.

Mazumder, A., and J. Edmundson. 2002. Impact of fertilization and stocking on trophic interactions and growth of juvenile sockeye salmon (*Oncorhynchus nerka*). Canadian Journal of Fisheries and Aquatic Sciences 59(8):1361-1373.

Moss, J., D. Beauchamp, A. Cross, K. Myers, J. Farley, EV, J. Murphy, and J. Helle. 2005. Evidence for Size-Selective Mortality after the First Summer of Ocean Growth by Pink Salmon. Transactions of the American Fisheries Society 134(5):1313-1322.

Ricker, W. 1992. Back-calculation of fish lengths based on proportionality between scale and length increments. Canadian Journal of Fisheries and Aquatic Sciences 49(5):1018-1026.

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

Smith, V. H. 1983. Low nitrogen to phosphorus ratios favor dominance by blue-green algae in lake phytoplankton. Science 221(4611):669-671.

Stockner, J., and K. Shortreed. 1985. Whole-lake fertilization experiments in coastal British Columbia lakes: empirical relationships between nutrient inputs and phytoplankton biomass and production. Canadian Journal of Fisheries and Aquatic Sciences 42(4):649-658.

Stockner, J., and K. Shortreed. 1988. Response of *Anabaena* and *Synechococcus* to manipulation of nitrogen : phosphorus ratios in a lake fertilization experiment. Limnology and Oceanography 33(6, part 1):1348-1361.

Stockner, J. G. 1987. Lake fertilization: the enrichment cycle and lake sockeye salmon (*Oncorhynchus nerka*) production. Pages 198–215 [*in*] H. D. Smith, L. Margolis, and C. C. Wood, Editors. Sockeye salmon (*Oncorhynchus nerka*) Population Biology and Future Management,volume 96. Canadian Special Publication of Fisheries and Aquatic Sciences

Thompson, S. 1992. Sampling. John Wiley & Sons New York

Todd, G., and G. Kyle. 1997. Limnological and sockeye salmon productivity investigations in Salmon and Glacial lakes: project completion report. Alaska Department of Fish and Game, Division of Commercial Fisheries, Regional Information Report 5J97-05, Juneau.

Venables, W., and B. Ripley. 2002. Modern applied statistics with S. Springer

Ward, B., P. Slaney, A. Facchin, and R. Land. 1989. Size-biased survival in steelhead trout (*Oncorhynchus mykiss*): Back-calculated lengths from adults' scales compared to migrating smolts at the Keogh River, British Columbia. Canadian Journal of Fisheries and Aquatic Sciences 46(11):1853-1858.

Wetzel, R. 1975. Limnology. Saunders Philadelphia

Wilson, L., G. Todd, and T. Hamazaki. in press. Sockeye salmon studies in Salmon Lake, Alaska: limnology and fishery investigations relative to a nutrient addition program, 1994-2008. Alaska Department of Fish and Game. Fishery Data Series No. 09-XX, Anchorage.

Chapter 2: Juvenile sockeye salmon (*Oncorhynchus nerka*) growth histories on the Seward Peninsula, Alaska[2]

Abstract

We hypothesize the age specific sockeye salmon (*Oncorhynchus nerka*) smolt sizes are not equal in Salmon and Glacial lakes, and that the age specific growth in the first year in the ocean are not equal in Salmon Lake. Dermal scales collected over many years were measured to document the annual age specific growth of Salmon and Glacial lakes sockeye salmon. Linear models were explored the scale radius to the last freshwater annulus was related to age at smoltification, life stage (smolt or adult) and year. The scale radius from the edge of freshwater growth to the first marine annulus was related to age at smoltification, ocean age, and year. Glacial Lake age 2 smolts were larger than Salmon Lake age 2 smolts, and the scale radius in the first ocean year from Salmon Lake age 1.3 adults were smaller than for Glacial Lake age 1.3 adults. These results suggest the minimum smolt size at Glacial Lake is larger, and lower size based mortality of Salmon Lake juveniles, possibly due to the extended rearing area between the river and ocean environments available to Salmon Lake and not to Glacial Lake sockeye salmon.

Introduction

Sockeye salmon (*Oncorhynchus nerka*) behaviors in freshwater are genetic adaptations to local environmental conditions with plastic responses to annual variability (Crozier et al. 2008). A notable example is that as juveniles, the rheotaxis of fry is specific to lake location relative to spawning location (Burgner 1991). Another is that "river type" sockeye salmon emigrate to the ocean in their first year and take advantage of estuaries. As adults, female sockeye salmon that spawn in rivers tend to be larger at age and older

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[2] Wilson, L.I. 2009. Juvenile sockeye salmon (*Oncorhynchus nerka*) growth histories on the Seward Peninsula, Alaska. Prepared for submission in the Transactions of the American Fisheries Society.

than those that spawn in lakes, an adaptation to spawning and incubation habitat (Quinn 2005).

Smolt size is related to the carrying capacity of the rearing lake and the mortality rate of juvenile sockeye salmon in their first year after leaving the lake. The lake carrying capacity varies with prey availability, which has been related to euphotic zone depth (EZD) in many sockeye rearing lakes (Burgner 1987; Koenings and Burkett 1987), though factors like temperature (McCoy 1983), water residency (Finney et al. 2000; Uchiyama et al. 2008) and trophic structure (Stockner 1987) can limit smolt production.

Smolt size upon entry into the marine environment is also affected by sources of mortality in their first year after leaving the lake. After sockeye leave the lake, stream discharge can affect survival of smolt, with low discharge correlated with low survival (Henderson and Cass 1991). Also, early marine growth has been positively related to marine survival after the first summer at sea (Farley et al. 2007; Moss et al. 2005; Ward et al. 1989). There is size dependent mortality at the end of the first marine summer (Beamish and Mahnken 2001; Mantua et al. 1997). If a lake is highly productive and morality sources are minimal once the smolt leaves then lake, smolt production is high (Burgner 1987).

An extended estuarine protected rearing environment could ameliorate mortality experienced by sockeye after the leaving the lake. Some chum salmon (*O. keta*) and Chinook salmon (*O. tshawytscha*) populations depend on estuaries for increased survival (Beamish et al. 2004; Farley et al. 2007). Estuaries offer salmonids three primary advantages: productive foraging, relative refuge from predators, and a physically intermediate environment for transition from fresh water to marine physiological control systems (Thorpe 1994).

Salmon and Glacial lakes are located in the interior of the Seward Peninsula in northwest Alaska, and both support sockeye salmon populations. The lakes are at approximately the same latitude and in close proximity; therefore latitude dependent survival and seasonal variations in their lake rearing environments are similar. However, Salmon Lake has a much larger volume than Glacial Lake and therefore has much higher potential smolt production. Also, Salmon Lake sockeye salmon have approximately 80 km of estuarine fresh and brackish water between the Pilgrim River and the ocean, while Glacial Lake sockeye salmon have little estuary at the mouth of the Sinuk River.

The alternative hypotheses explored in this study are 1) the age specific smolt sizes are not equal in Salmon and Glacial lake, and 2) the age specific growth in the first year in the ocean are not equal in salmon lake.

Methods

Study Site Description.-Salmon and Glacial lakes are located in the interior of the Seward Peninsula in northwest Alaska. Salmon Lake (64°54'N, 165°00'W) elevation 134 m, drains a watershed of 209 km^2. The lake is the headwaters of Pilgrim River, which enters the Kuzitrin River then empties into Imuruk Basin estuary. Grand Central River is the largest river flowing into Salmon Lake. Glacial Lake (64^o 52' N, 165^o 42' W), is west of Salmon Lake similar elevation, 120 m. Drains a smaller watershed, 49 km^2, and flows into the Sinuk River and then into northern Norton Sound (Todd and Kyle 1997).

Salmon Lake has a volume of $111.5 \times 10^6 m^3$, surface area is 7.49 km^2 (1,851 acres), mean depth is 14.9 m, and maximum depth is 40 m. Glacial Lake has a smaller volume, $23 \times 10^6 m^3$, surface area of 3.99 km^2 (986 acres), mean depth of 5.8 m, and maximum depth of 22 m. Estimated water residence time for Salmon Lake is 1.6 years, and mean summer discharge is 14.3 $m^3 s^{-1}$ (Todd and Kyle 1996, 1997). Estimated water residence time for Glacial Lake is 1.5 years and summer discharge at the outlet averaged 4.4 m^3

sec^{-1} in 1995 and 1996. Both Salmon Lake and Glacial lakes are ultra-oligotrophic (Todd and Kyle 1997).

Smolt age and length.-Pilgrim River sockeye salmon smolt age and length (mm) samples were measured in 1995, 1996, 1998-2000 and 2002-2008 by ADF&G, Nome and NSEDC personnel. Glacial Lake smolt age and length (mm) samples were taken in 1995, 1996, 2003 to 2005 and 2008 by the U.S. Bureau of Land Management (BLM), and NSEDC with cooperation from ADF&G. The scales were taken from smolt from the preferred area (Clutter and Whitsel 1956) using a scalpel then spread on a glass slide. Smolt age was determined visually by counting annuli on scale samples and smolt length (tip of snout to fork in tail) was measured the nearest 1 mm (Wilson et al. in press).

Adult age, sex, and length.-Salmon Lake sockeye salmon age, sex and mid eye to fork in tail (MEF) length (mm) (ASL) data are available for 2001-2008 sampled from Salmon Lake carcasses 2001-2002 and at a floating weir installed on Pilgrim River in 2003-2008 (Burkhart and Dunmall 2006; Dunmall 2004a, b, 2008; Kohler and Knuefer 2001; Kroeker and Dunmall 2006; Rob 1998, 1999; Todd and Kyle 1996, 1997; Waitman and Dunmall 2003). Glacial Lake scales were collected at a weir at the outlet of Glacial Lake from 2000-2008 (Parker 2008; Soong et al. 2008) Adult scales were placed on a gummed card, heat and pressure were applied to the gummed card to make impressions on acetate cards which were visually examined for annuli to determine each fish's age.

Scale measurements

Sample size.-To estimate the necessary number of scale measurements for a relative error, ignoring the finite population correction since the sample size is small compared to the number of possible samples, the formula is (Thompson 1992):

$$n = \frac{z^2\delta^2}{r^2} \tag{15}$$

where z is the upper $\alpha/2$ point of the normal distribution and

$$\delta = \frac{\sigma}{\mu} \quad \text{and} \quad r < \frac{\hat{\mu} - \mu}{\mu} \qquad (16),\ (17)$$

where σ is the standard error of the mean μ and r was 3. The μ and σ were calculated for each combination of lake and age from smolt samples, and for each combination of lake, smolt and saltwater age, and sex from adult fish samples. Then a chronological stratified sample was taken from samples each group of size *n*.

Image capture.-Standard methods used at the ADFG Mark Tag Age Laboratory were used to generate images of scales selected to be measured (Hagen et al. 2001). The scale was scanned with Screenscan, a high resolution line camera attached to an Indus 4601 microfiche reader with a magnification lens (42x). Scales were visually assessed for edge resorption, tears, holes, and asymmetry. Asymmetric scales suggest that the sample was not from the preferred area (from the left side of the salmon approximately two rows above the lateral line on the diagonal row that extends down from the posterior insertion of the dorsal fin to the anterior insertion of the anal fin (Koo 1955)). Each scale sample was oriented so that diagonal from the focus to the farthest edge of the scale was in the positive quadrant centered on the focus (0 to 90 degrees).

Measurement.-Scale images were measured using the software program Optimate and the macro CIRCCHUM READER V.2 used by the ADF&G Mark Tag and Age (MTA) Lab in Juneau, Alaska (Hagen et al. 2001). First, a reference line was created from the focus to the farthest edge of the scale. Then annuli were marked after the first full circulus beyond each winter check (regions were circuli widths are narrow from slow somatic growth in the winter) by the reader starting from the focus and ending at the edge of the scale. Freshwater plus growth (growth in freshwater after the last annulus in freshwater before ocean growth), was also marked with an annulus marker. Then circuli were marked on their exterior edge first automatically by the macro then edited by the reader.

An extra circulus was marked after the last annulus when the scale did not end in a circulus after the last annulus mark, at the edge of the scale. Measurement errors were indicated by the comment "EIA" for the extra circulus or "FWPL" for an annulus marker that indicates freshwater plus growth with the annulus number (e.g. FWPL-3). Scale measurements, the date, reader's initials, and comments were saved in a text file.

Organization

The data from the text file was reshaped into a list of annuli and circuli measurements for each fish using the software program R (www.r-project.org). Then script files were written to correct the errors generated in the measurement process and to sum the circulus measurements for the from the focus to the last freshwater annulus and from the last freshwater annulus to the end of the first ocean annulus. Then the mean of these age specific annual measurements were calculated.

Data Analysis

Smolt length.-The full model for response variable scale radius from the focus to the last freshwater annulus included lake origin (Lake, Salmon and Glacial lakes), smolt age (fw.age), life stage sampled (stage, smolt or adult) year, and their two way interactions. The full model form was:

$$\begin{aligned} SmoltSize = \beta_0 + \beta_1(lake) + \beta_2(fw.age) + \beta_3(stage) + \beta_4(year) + \beta_5(lake)(fw.age) \\ + \beta_6(lake)(stage) + \beta_7(fw.age)(stage) + \varepsilon_i \end{aligned} \tag{18}$$

where β are variable coefficients, intercept β_0 and error terms ε_i.

Length after the first ocean winter.-The full model for the response variable scale radius from the last freshwater annulus to the end of the first ocean annulus included lake origin (Salmon and Glacial lakes), smolt age (fw.age), the number of years spent in salt water (sw.age), year, and their two way interactions. The full model form was:

$$\begin{aligned} OceanSize = \beta_0 + \beta_1(lake) + \beta_2(fw.age) + \beta_3(sw.age) + \beta_4(year) \\ + \beta_5(lake)(fw.age) + \beta_6(lake)(sw.age) + \beta_7(fw.age)(sw.age) + \varepsilon_i \end{aligned} \quad (19)$$

where β are variable coefficients, intercept β_0 and error terms ε_i.

Model selection and analysis.-The Akaike information criterion (AIC) for model selection is (Burnham and Anderson 2002):

$$AIC = n\ln\left(\frac{RSS}{n}\right) + 2k \quad (20)$$

where n is the number of observations, k is the number of parameters, and RSS is the residual sum of squared errors in the model. The AIC corrected to reflect small sample sizes (AIC$_c$) was used to select the best linear models:

$$AIC_c = AIC + \frac{2k(k+1)}{(n-k-1)} \quad (21)$$

Stepwise selection was performed using the “step” functions in R. The “step” function removed each variable from the full model individually then selected the model with the lowest AIC value to use as the full model in the next iteration. This procedure uses the AIC statistic; selected models were examined to ensure that they would also have been selected using AIC$_c$.

Also, the Type III sum of squares, marginal or orthogonal significance of parameters were presented for unbalanced models. In this approach, the effect of each variable is evaluated after all other factors have been accounted for, which is robust to unbalanced designs.

Model residuals were examined for normality numerically using the Shapiro-Wilk normality test and by visually assessing histograms, boxplots and QQ plots of model residuals. Autocorrelation and partial autocorrelation of the residuals was examined visually using the output from the functions “acf” and “pacf” in R (Venables and Ripley 2002).

Intra-lake comparisons.-The proportion of age 1 smolt was calculated for each year of scale samples $\hat{p}$ = n $_{\text{age } 1}$ / n $_{\text{age } 1+2+3}$ with variance from Thompson (1992):

$$\operatorname{var}(\hat{p}) = \frac{\hat{p}(1-\hat{p})}{n-1} \tag{22}$$

where n is the total number of samples.

Frequency distributions of smolt size and size at the end of the first year in the ocean were compared at each age at return with two-sample Kolmorgorov-Smirnov tests (Conover 1980).

Results

Proportion of age 1 smolt.-The proportion of age 1 smolt leaving Salmon Lake was variable, ranging from 0.05 and 0.95 and averaged 0.64 (Table 2.1). Annual proportions of age 1 smolt from Salmon Lake adult samples in the year they returned ranged from 0.03 to 0.80, and averaged 0.12 (Table 2.1). Annual proportions of age 1 smolts from smolts leaving Glacial Lake ranged from 0.01 to 0.55 (Table 2.1). The proportion of age 1 Glacial Lake smolts from adult samples in ranged from 0.00 to 0.40 and averaged 0.08 (Table 2.1).

Scale analysis

Body-scale radius relationship.-The following linear model was developed to back calculate mid-eye to fork length (MEF, mm) from scale radius *Scale* (mm) using Salmon Lake and Glacial Lake smolt scales (Figure 2.1):

$$MEF = 474.304 + 30.590\,Scale \tag{23}$$

(n = 1307; $R^2 = 0.509$; $P < 0.001$)

Smolt length.-Annual mean age specific Lake and Glacial Lake smolts (Figure 2.1) and adults (Figure 2.2) scale radius to the first freshwater annulus showed no temporal pattern.

Smolt length model.-The best model for response variable scale radius from the focus to the last freshwater annulus (samples from Salmon Lake smolt: Table 2.2, Glacial Lake smolt: Table 2.3, smolts from both lakes: Figure 2.3, Salmon Lake adult: Table 2.4, Glacial Lake adult: Table 2.5, adults from both lakes: Figure 2.4) included the variables smolt age (1, 2 or 3; marginal ANOVA $P < 0.001$; Figure 2.3), life stage (smolt or adult; marginal ANOVA $P < 0.001$), and year (marginal ANOVA $P < 0.001$), selected stepwise by AIC_c values (Tables 2.6 and 2.7). The model significantly explained variations in scale radius from the focus to the last freshwater annulus ($n = 129$; $R^2 = 0.69$; $P < 0.001$). In general, the length frequencies of smolt scale radii were smaller than the length frequency distribution of adult scale radii (Figure 2.5). Model residuals were normally distributed, had no temporal pattern, and did not appear to be related by lake (Figure 2.6).

Length after the first ocean winter.-Annual mean age scale radius from the edge of freshwater growth to the first ocean annulus (samples from Salmon Lake: Table 2.8, Glacial Lake Table 2.9) had no temporal pattern (Figure 2.7). Variations in for the response variable scale radius from the last freshwater annulus to the end of the first ocean annulus were best explained by smolt age (marginal ANOVA $P < 0.001$) and ocean age (marginal ANOVA $P < 0.001$) and year (marginal ANOVA $P < 0.001$), selected stepwise by AIC_c values (Tables 2.10 and 2.11). The linear model significantly explained variations in scale radius from the edge of the freshwater portion of the scale to the fist ocean annulus ($n = 129$, $R^2 = 0.65$, $P < 0.001$). Model residuals were normally distributed, had no temporal pattern, and did not appear to be related to lake (Figure 2.8).

Intra-lake comparisons.-There was no difference in the length frequency distribution of the freshwater portion of smolt scale radius from distribution of Salmon or Glacial lake age 1 smolts (Table 2.12). However, the length frequency distribution of the freshwater portion of smolt scale radius from age 2 smolts differed between the two lakes (D = 0.145mm, $P < 0.001$. The mean age 2 smolt scale radius was greater for Glacial Lake sockeye salmon (0.290 mm) than for Salmon Lake sockeye salmon (0.275 mm).

Differences in the distribution of ocean growth were also age specific and lake specific (Table 2.12). The frequency distribution of scale radius during the first year of ocean growth significantly differed for age 1.3 Salmon and Glacial lake populations (D = 0.121mm, $P = 0.023$). The mean scale radius during the first year of ocean growth from age 1.3 sockeye salmon was greater for Glacial Lake sockeye salmon (1.35 mm) than for Salmon Lake sockeye salmon (1.29 mm). There were no significant differences in the length frequency distributions of Salmon versus Glacial Lake age 2.2 sockeye salmon or in the length frequency distributions of Salmon versus Glacial Lake age 2.3 sockeye salmon.

Discussion

The Seward Peninsula sockeye salmon populations both show evidence of smolt size based mortality. Measurements of smolt and adult scales show that the scale radius from the focus to the last freshwater annulus was smaller for smolts than adults in both the Salmon Lake and Glacial Lake sockeye salmon populations (Figure 2.5, Tables 2.8 and 2.9). This is not surprising since salmon typically experience high size based mortality in the initial entry into the marine environment (Beamish and Mahnken 2001; Moss et al. 2005; Ward et al. 1989) including sockeye salmon populations, since smolt size has been found to be positively related to survival (Henderson and Cass 1991; Koenings et al. 1993).

The Salmon and Glacial lake sockeye salmon populations showed population and age specific growth histories. Age-2 Salmon Lake sockeye smolts were smaller than age-2 Glacial Lake sockeye smolts (Salmon Lake means, Table 2.2; Glacial Lake means, Table

2.3; tests of length frequencies, Table 2.12), though the proportions of age 2 smolts in both the adult and smolt scales were generally lower in Salmon Lake samples than in Glacial Lake (Table 2.1). Age-1 Salmon Lake sockeye smolts were not different than age-1 Glacial Lake sockeye smolts (Salmon Lake means, Table 2.2; Glacial Lake means, Table 2.3; tests of length frequencies, Table 2.12), though the proportions of age-1 smolts in both the adult and smolt scales were lower (Table 2.1). Also, the Age 1.3 sockeye salmon from Salmon Lake were smaller than age 1.3 sockeye salmon from Glacial Lake, though the proportions of age 1.3 sockeye salmon was lower in Glacial Lake than in Salmon Lake (Table 1.3).

These results suggest that the Salmon Lake sockeye salmon population experience lower size based marine mortality than Glacial Lake sockeye salmon. Glacial Lake age 1 smolt experience higher size based mortality than Salmon Lake age 1 smolt since the Salmon Lake sockeye salmon age 1 smolts are the same size as the Glacial Lake age 1 smolts, but are a lower proportion of the smolt and adult samples. Further evidence that Salmon Lake sockeye salmon marine survival for age 1 smolts is higher than Glacial Lake age 2 smolts is shown in the significantly different length distribution marine growth. The length distributions of age 1.3 sockeye salmon are significantly different in Salmon Lake than in Glacial Lake samples, and the mean Salmon Lake scale radius to the first ocean annulus is less than the mean Glacial Lake radius to the same region.

The mechanism for increased survival of Salmon Lake sockeye salmon could be the estuary at the outlet of the Pilgrim River. Estuaries are known to provide the same things larger size provides, enhanced resistance to starvation, decreased vulnerability to predators, and better tolerance of environmental extremes (estuaries: Thorpe (1994); “bigger is better” theory: Sogard (1997), however, these qualities have not been measured in Imuruk Basin, Tuksuk channel, Grantley Harbor or Port Clarence. Alternatively, smaller size could be related to delayed entrance into the marine environment and a mismatch of fish presence and food availability.

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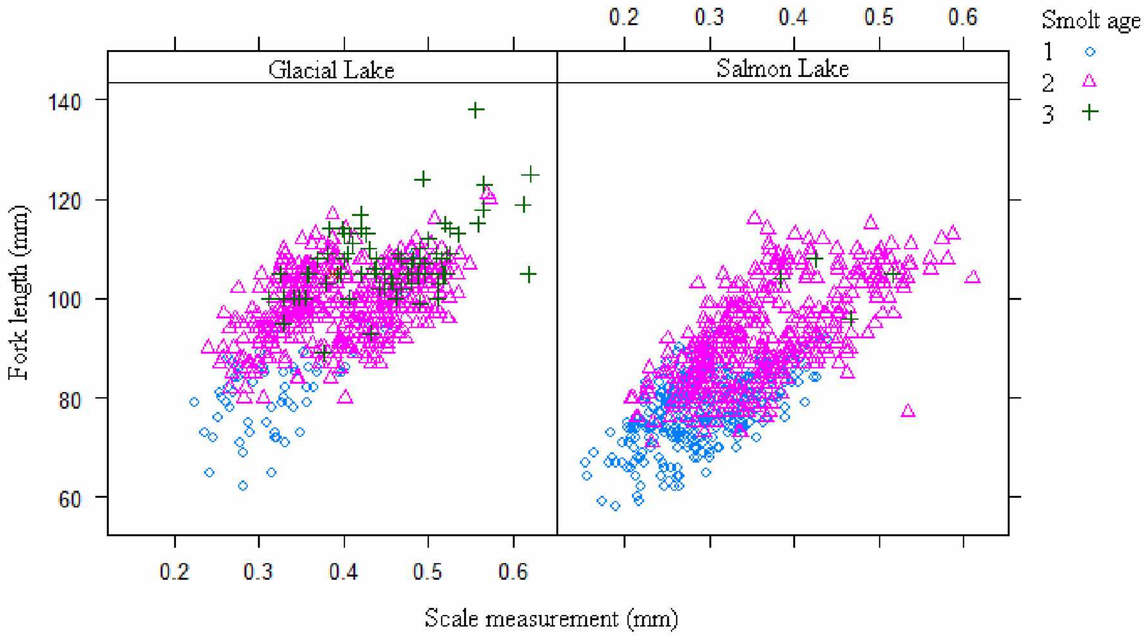

Figure 2.1- Smolt scale radius (mm) against fork length (mm) by lake, smolt age (Glacial Lake left panel, Salmon Lake right panel smolt age 1 (open circles) smolt age 2 (triangles) and smolt age 3 (plus signs) scale samples).

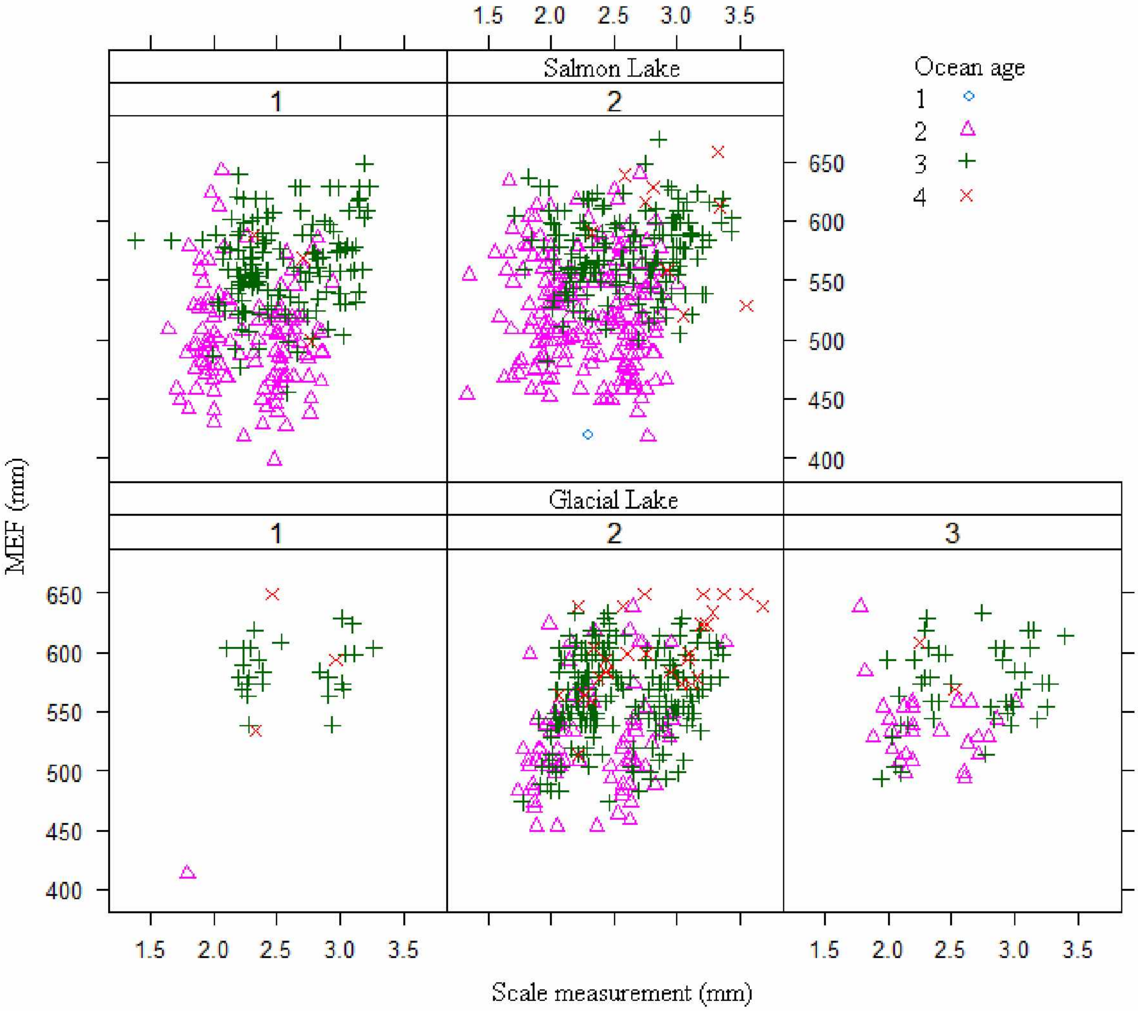

Figure 2.2- Adult scale radius (mm) against MEF length (mm) by lake and smolt age, (Salmon Lake top panel, Glacial Lake bottom panel, smolt age 1 left panel, smolt age 2 middle panel, smolt age 3 right panel with ocean age 1 (open circles) ocean age 2 (triangles) ocean age 3 (plus signs) and ocean age 4 (exes).

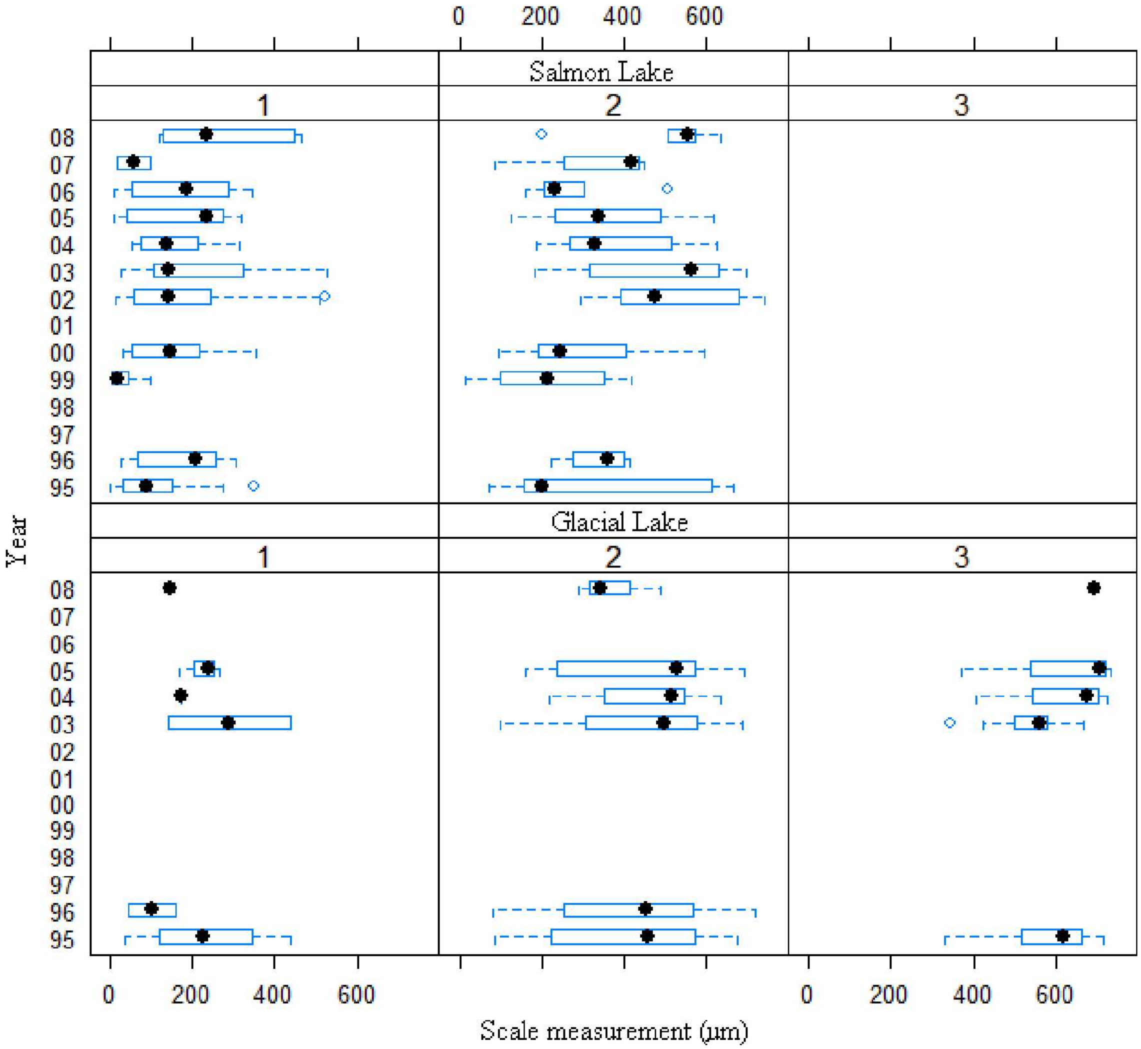

Figure 2.3- Smolt scale radius to the last freshwater annulus in smolting year by lake and year (Salmon Lake (top panel) and Glacial Lake (bottom panel), age 1 (left panel), age 2 (middle panel) and age 3 (right panel), 1995-2008).

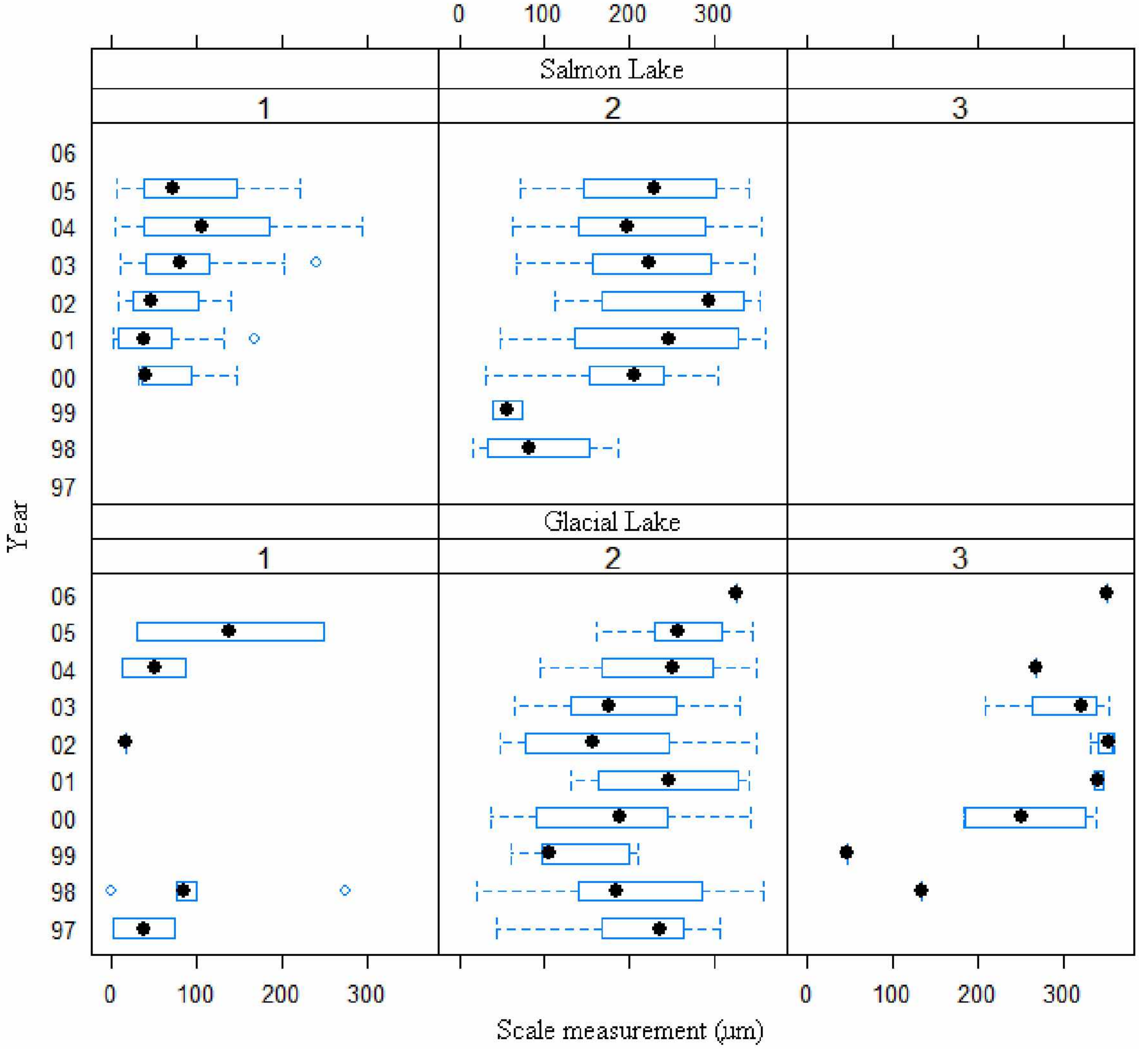

Figure 2.4- Adult scale radius to the last freshwater annulus in smolting year by lake and year (Salmon Lake (top panel) and Glacial Lake (bottom panel) age 1 (left panel), age 2 (middle panel) and age 3 (right panel), 1997-2006).

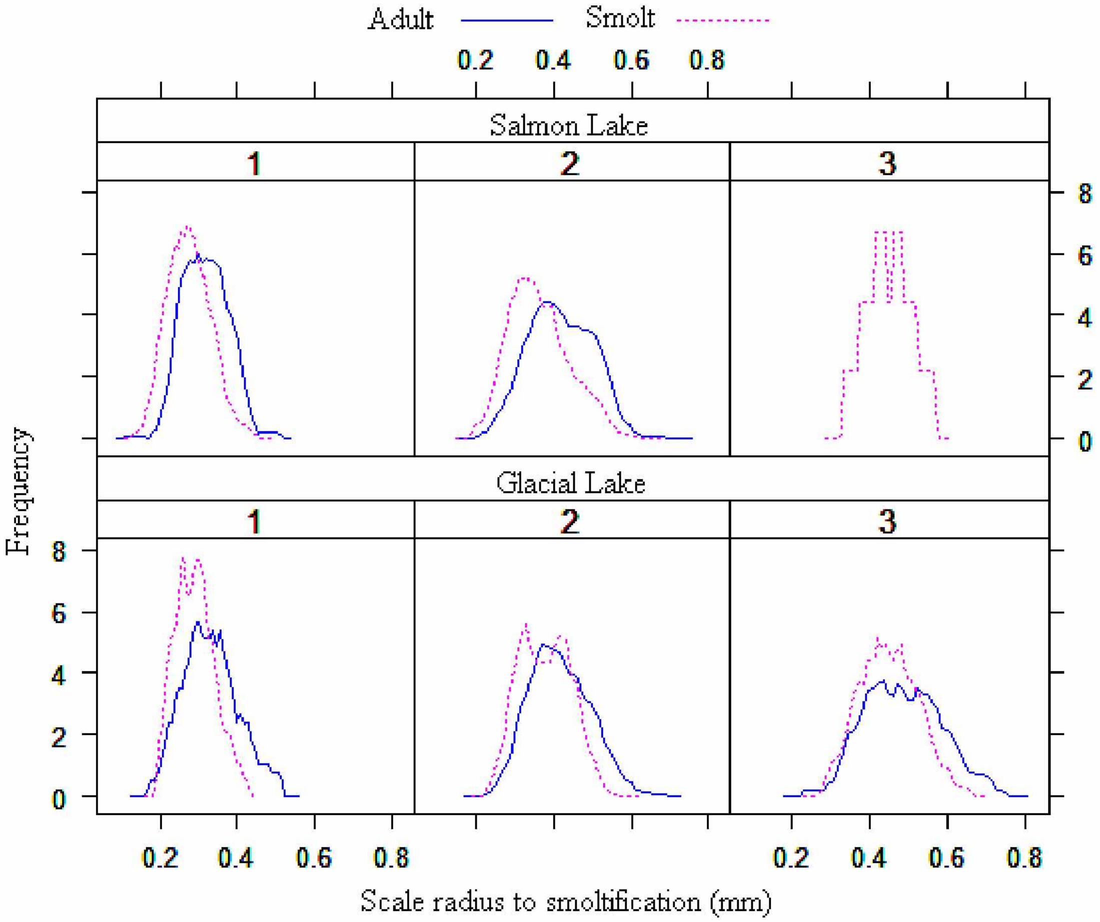

Figure 2.5- Scale radii to the last freshwater annulus by lake, age and life stage (Salmon Lake (top panel) and Glacial Lake (bottom panel) from smolting age 1 (left panel), age 2 (middle panel) and age 3 (right panel), smolt (dotted line) and adult (solid line)1995-2008).

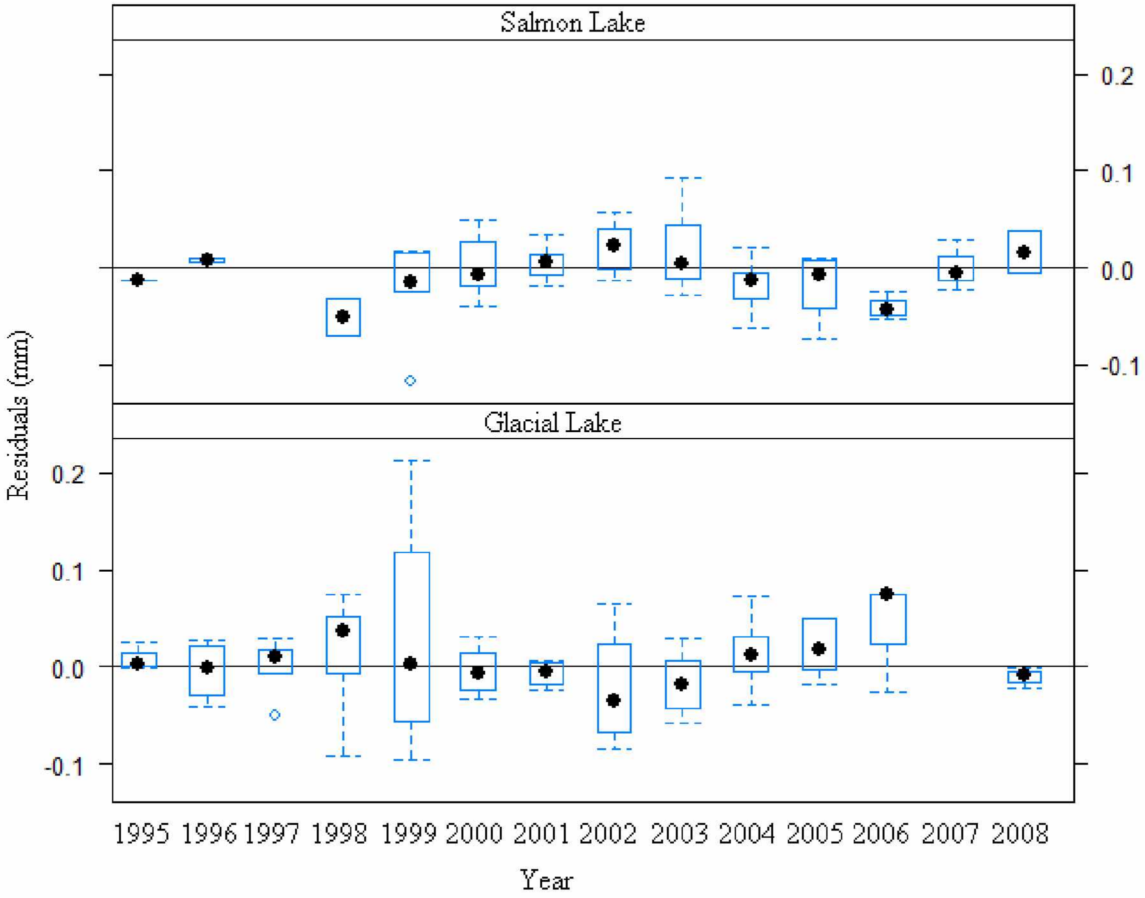

Figure 2.6- Smolt size model residuals by year and lake (Salmon Lake, top panel and Glacial Lake, bottom panel, 1995-2008)

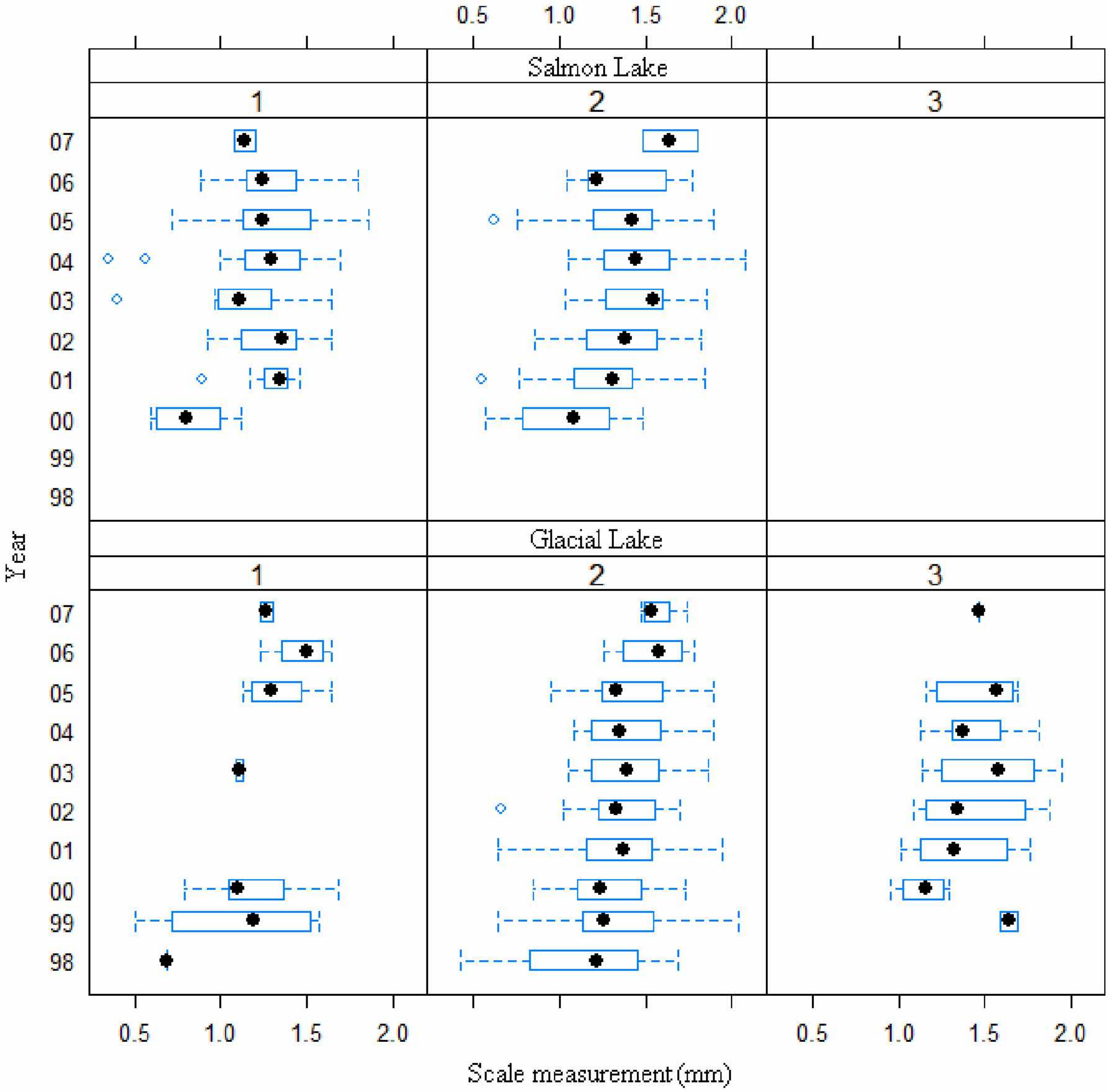

Figure 2.7- Annual mean first ocean scale radius by smolt age and lake (smolting age 1 (left panel), age 2 (middle panel) and age 3 (right panel), Salmon Lake (top panel) and Glacial Lake (bottom panel) shown in first year of ocean growth, 1998-2007).

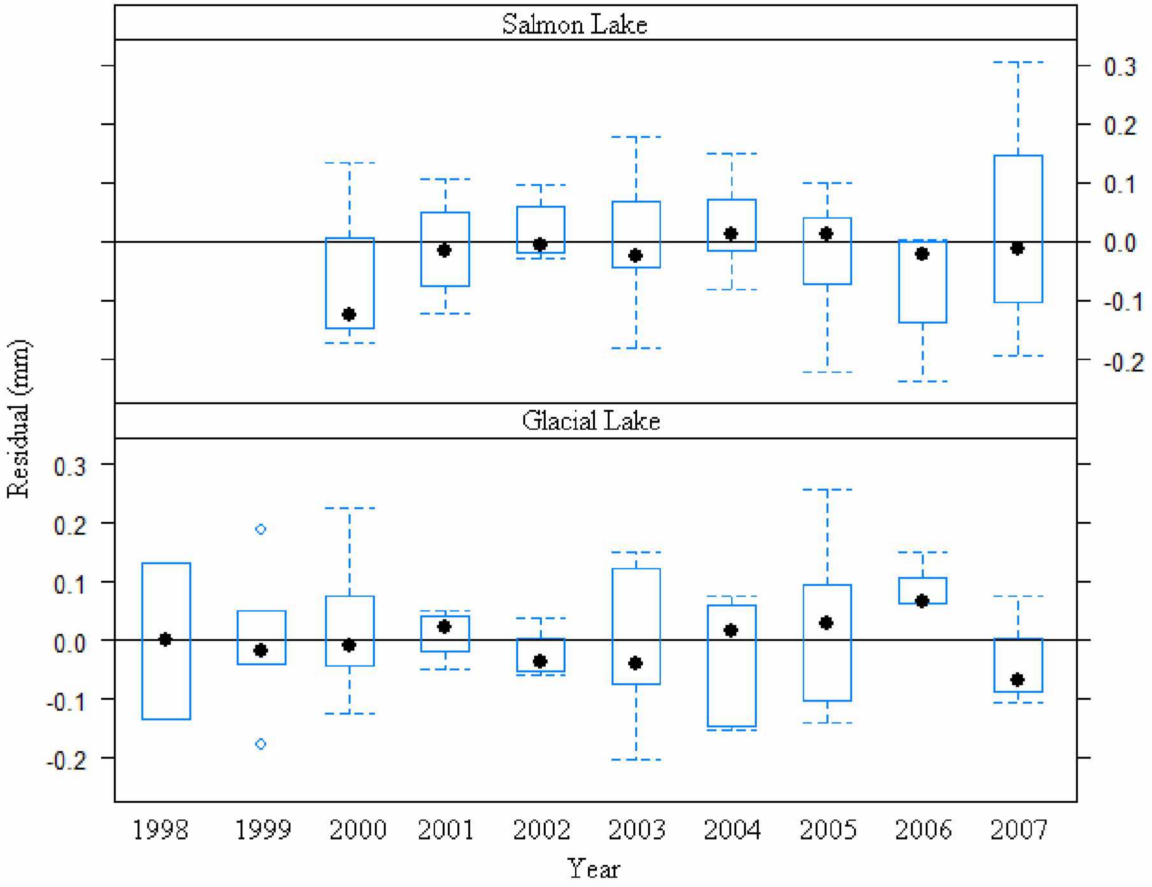

Figure 2.8- Ocean growth model residuals by year and lake (Salmon Lake, top panel, and Glacial Lake, bottom panel, 1998-2007)

Table 2.1- Annual proportion of age 1 smolt from smolt and adult scale samples from Salmon and Glacial lake sockeye salmon from 1995-2008, a dash indicates no samples were taken.

	Salmon Lake				Glacial Lake			
Year	Smolts	Variance	Adults	Variance	Smolts	Variance	Adults	Variance
1995	0.80	0.0018	-	-	0.55	0.0003	-	-
1996	0.95	0.0002	-	-	0.01	0.0000	-	-
1997		-	-	-	-	-	-	-
1998	0.60	0.0004	-	-	-	-	-	-
1999	0.15	0.0003	-	-	-	-	-	-
2000	0.63	0.0005	-	-	-	-	0.06	0.0003
2001	-	-	0.16	0.0005	-	-	0.19	0.0015
2002	0.30	0.0003	0.03	0.0002	-	-	0.00	0.0000
2003	0.60	0.0029	0.18	0.0002	0.01	0.0000	0.00	0.0000
2004	0.92	0.0001	0.22	0.0003	0.01	0.0000	0.00	0.0000
2005	0.75	0.0004	0.19	0.0002	0.01	0.0000	0.00	0.0000
2006	0.78	0.0009	0.43	0.0003	-	-	0.00	0.0000
2007	0.05	0.0002	0.80	0.0004	-	-	0.07	0.0005
2008	0.90	0.0003	0.49	0.0008	0.16	0.0012	0.40	0.0016
Avg.	0.62		0.31		0.12		0.08	

Table 2.2.- Summary of Salmon Lake smolt scale radii to the last freshwater annulus: annual mean (mm), variation (Var) and sample size (N), shown in sample year, 1995-2008.

	Age 1 smolts			Age 2 smolts		
Year	Mean	Var	N	Mean	Var	N
1995	0.248	0.002	39	0.351	0.005	16
1996	0.261	0.003	71	0.360	0.003	9
1999	0.228	0.003	46	0.292	0.002	74
2000	0.292	0.001	26	0.333	0.003	78
2002	0.308	0.003	13	0.438	0.006	86
2003	0.307	0.003	28	0.411	0.005	30
2004	0.277	0.002	14	0.385	0.004	38
2005	0.284	0.003	13	0.358	0.003	45
2006	0.266	0.002	66	0.341	0.003	9
2007	0.247	0.002	43	0.332	0.003	31
2008	0.330	0.002	49	0.389	0.004	13
Overall	0.277		408	0.363		429

Table 2.3- Summary of Glacial Lake smolt scale radii to the last freshwater annulus: annual mean (mm), variance (Var) and sample size (N), shown in sample year, 1995, 1996, 2003-2005, 2008.

	Age 1 smolts			Age 2 smolts		
Year	Mean	Var	N	Mean	Var	N
1995	0.286	0.002	22	0.364	0.005	42
1996	0.283	0.002	3	0.373	0.004	181
2003	0.325	0.005	4	0.381	0.004	130
2004	0.280	0.004	8	0.405	0.004	32
2005	0.293	0.001	4	0.382	0.005	34
2008	0.292	0.002	18	0.388	0.004	8
Overall	0.293		59	0.382		427

Note: A dash indicates no scales were measured.

Table 2.4.- Summary of Salmon Lake adult scale radii to the last freshwater annulus: annual mean (mm), variance (Var) and sample size (N), shown in sample year 1997-2006.

	Age 1.3			Age 2.2			Age 2.3		
Year	Mean	Var	N	Mean	Var	N	Mean	Var	N
1997	0.325	0.002	2	-	-	-	-	-	-
1998	0.311	0.006	26	-	-	-	0.300	0.003	17
1999	-	-	-	0.240	NA	1	0.343	0.004	6
2000	0.341	0.001	9	0.355	0.004	34	0.387	0.004	29
2001	0.306	0.003	21	0.450	0.007	53	0.422	0.005	26
2002	0.307	0.003	18	0.475	0.006	19	0.447	0.006	19
2003	0.326	0.002	58	0.443	0.006	29	0.440	0.005	40
2004	0.336	0.004	25	0.420	0.004	62	0.454	0.006	19
2005	0.349	0.007	19	0.451	0.008	14	0.369	0.003	15
2006	-	-	-	0.39	NA	1	-	-	-
Overall	0.325		178	0.403		213	0.395		171

Note: A dash indicates no scales were measured.

Table 2.5- Summary of Glacial Lake adult scale radii to the last freshwater annulus: annual mean (mm), variance (Var) and sample size (N), shown in sample year 1997-2006.

	Age 1.3			Age 2.2			Age 2.3		
Year	Mean	Var	N	Mean	Var	N	Mean	Var	N
1997	0.325	0.002	2	-	-	-	0.415	0.006	63
1998	0.340	0.004	19	0.415	0.002	6	0.421	0.008	41
1999				0.570	NA	1	0.384	0.002	13
2000				0.381	0.004	8	0.395	0.006	21
2001				0.392	0.003	5	0.417	0.006	25
2002	0.290	NA	1	0.414	0.005	19	0.359	0.003	17
2003	0.305	0.004	4	0.386	0.003	17	0.443	0.002	14
2004	0.393	0.007	4	0.470	0.006	19	0.428	0.006	13
2005				0.493	0.006	6	0.458	0.006	10
2006	-	-	-	0.51	0.0019	4	-	-	-
Overall	0.331		30	0.440		81	0.413		217

Note: A dash indicates no scales were measured.

Table 2.6.- Smolt size model parameter coefficients (Coef.), standard error (SE), and t-values.

Variable	Estimate	SE	t-value	P-value
(Intercept)	0.291	0.015	19.036	< 0.001
Smolt age 2	0.103	0.009	11.169	< 0.001
Smolt age 3	0.175	0.012	14.207	< 0.001
Smolt age 4	0.097	0.047	2.058	0.042
Stage: smolt	-0.043	0.011	-4.037	< 0.001
1995	0.013	0.026	0.518	0.605
1996	0.004	0.024	0.187	0.852
1997	0.027	0.025	1.093	0.277
1998	-0.026	0.021	-1.226	0.223
1999	-0.034	0.020	-1.680	0.096
2001	0.021	0.020	1.027	0.307
2002	0.029	0.018	1.615	0.109
2003	0.050	0.018	2.815	0.006
2004	0.038	0.017	2.205	0.029
2005	0.049	0.019	2.564	0.012
2006	0.043	0.023	1.878	0.063
2007	0.004	0.031	0.129	0.898
2008	0.044	0.026	1.692	0.093

Table 2.7- Analysis of variance table for the smolt size model with marginal significance shown.

Independent variables	Df	SSQ	Mean Sq	F-value	P-value
Smolt age	3	0.49268	0.16423	80.3461	< 0.001
Ocean Age	1	0.03837	0.03837	18.7729	< 0.001
Year	13	0.0856	0.00658	3.2213	< 0.001
Residuals	111	0.22688	0.00204		

Table 2.8- Summary of Salmon Lake adult scale radii of the first saltwater annulus: annual mean (mm), variance (Var) and sample size (N), shown in sample year 2000-2007.

	Age 1.3			Age 2.2			Age 2.3		
Year	Mean	Var	N	Mean	Var	N	Mean	Var	N
2000	0.822	0.049	7	-	-	-	1.040	0.079	25
2001	1.281	0.037	7	1.204	0.057	32	1.251	0.056	62
2002	1.297	0.052	17	1.374	0.054	56	1.369	0.055	86
2003	1.163	0.031	12	1.517	0.030	18	1.456	0.043	38
2004	1.209	0.058	33	1.466	0.049	28	1.450	0.052	68
2005	1.322	0.045	54	1.364	0.057	64	1.376	0.053	86
2006	1.280	0.061	16	1.474	0.063	14	1.356	0.057	28
2007	1.142	0.007	2	1.478	NA	1	1.638	0.051	2
Overall	1.189		148	1.411		213	1.367		395

Note: A dash indicates no scales were measured.

Table 2.9- Summary of Glacial Lake adult scale radii of the first ocean annulus: annual mean (mm), variance (Var) and sample size (N), shown in sample year 2000-2007.

	Age 1.3			Age 2.2			Age 2.3		
Year	Mean	Var	N	Mean	Var	N	Mean	Var	N
1998	-	-	-	-	-	-	0.935	0.446	3
1999	1.038	0.571	2	-	-	-	1.3287	0.086	54
2000	1.218	0.063	19	1.146	0.007	7	1.247	0.055	61
2001	-	-	-	1.347	0.058	6	1.297	0.085	32
2002	-	-	-	1.396	0.150	2	1.352	0.085	26
2003	1.090	NA	1	1.471	0.062	18	1.398	0.067	33
2004	-	-	-	1.327	0.029	20	1.411	0.047	35
2005	1.312	0.052	4	1.508	0.067	12	1.390	0.058	39
2006	1.469	0.030	4	1.548	0.048	3	1.484	0.044	9
2007	-	-	-	1.459	0.009	5	1.459	0.009	5
Overall	1.225		30	1.400		73	1.374		294

Note: A dash indicates no scales were measured.

Table 2.10- Linear model for response variable first year of ocean growth showing coefficients smolt age and ocean age, standard error (SE), t-values, and P-values.

Variable	Estimate	SE	t-value	P-value
(Intercept)	1.345	0.137	9.832	< 0.001
Smolt age 2	0.155	0.031	4.925	< 0.001
Smolt age 3	0.234	0.042	5.556	< 0.001
Ocean age 2	-0.354	0.129	-2.735	0.008
Ocean age 3	-0.351	0.129	-2.719	0.008
Ocean age 4	-0.424	0.131	-3.244	0.002
1998	-0.098	0.098	-1.004	0.319
1999	0.223	0.067	3.323	0.001
2001	0.181	0.058	3.103	0.003
2002	0.243	0.055	4.429	< 0.001
2003	0.194	0.053	3.669	< 0.001
2004	0.296	0.055	5.387	< 0.001
2005	0.289	0.052	5.586	< 0.001
2006	0.326	0.062	5.221	< 0.001
2007	0.344	0.065	5.283	< 0.001

Table 2.11.- Analysis of variance table for scale radius to the first ocean annulus showing marginal significance.

Independent variables	Df	SSQ	Mean Sq	F-value	P-value
Smolt age	2	0.51315	0.25657	17.3686	< 0.001
Ocean Age	3	0.48526	0.16175	10.9498	< 0.001
Year	9	0.91305	0.10145	6.8676	< 0.001
Residuals	69	1.01929	0.01477		

Table 2.12- Koglomorov-Smirnov tests of smolt scales' length frequency distribution from age 1 and age 2 smolt for Salmon and Glacial lakes.

Smolt age	D	P-value	N (Salmon)	N (Glacial)
1	0.115	0.215	408	59
2	0.145	< 0.001	429	427

Table 2.13.- Koglomorov-Smirnov tests of adult scales' length frequency distribution from age 1.3, 2.2 and 2.3 Salmon and Glacial lake sockeye salmon.

Adult age	D	P-value	N (Salmon)	N (Glacial)
1.3	0.121	0.023	319	291
2.2	0.094	0.652	213	85
2.3	0.075	0.651	171	217

Literature Cited

Beamish, R., and C. Mahnken. 2001. A critical size and period hypothesis to explain natural regulation of salmon abundance and the linkage to climate and climate change. Progress in Oceanography 49(1-4):423-437.

Beamish, R., C. Mahnken, and C. Neville. 2004. Evidence that reduced early marine growth is associated with lower marine survival of coho salmon. Transactions of the American Fisheries Society 133(1):26-33.

Burgner, R. 1987. Factors influencing age and growth of juvenile sockeye salmon (*Oncorhynchus nerka*) in lakes. Pages 129–142 [*in*] H. D. Smith, L. Margolis, and C. C. Wood, Editors. Sockeye salmon (*Oncorhynchus nerka*) population biology and future management, volume 96. Canadian Special Publication of Fisheries and Aquatic Sciences

Burgner, R. 1991. Life history of sockeye salmon (*Oncorhynchus nerka*). Pages 1-118 [*in*] C. Groot, and L. Margolis, Editors. Pacific Salmon Life Histories. UBC Press, Vancouver, BC.

Burkhart, K., and K. Dunmall. 2006. The Snake River, Eldorado River and Pilgrim River Salmon Escapement, Enumeration and Sampling Project Summary Report, 2005. Kawerak, Inc. Fisheries Department

Burnham, K., and D. Anderson. 2002. Model selection and multimodel inference: A practical information-theoretic approach. Springer

Clutter, R., and L. Whitsel. 1956. Collection and interpretation of sockeye salmon scales. New Westminster, Canada, International Pacific Salmon Fisheries Commission

Conover, W. 1980. Statistics of the Kolmogorov-Smirnov type. Practical nonparametric statistics:344–384.

Crozier, L., A. Hendry, P. Lawson, T. Quinn, N. Mantua, J. Battin, R. Shaw, and R. Huey. 2008. Potential responses to climate change in organisms with complex life histories: evolution and plasticity in Pacific salmon. Evolutionary Applications 1(2):252-270.

Dunmall, K. 2004a. The Snake River, Eldorado River and Pilgrim River Salmon Escapement Enumeration and Sampling Project Summary Report 2004 and Summary of the Conversion of Towers to Weirs Project at the Snake and Eldorado Rivers Kawerak, Inc. Fisheries Department

Dunmall, K. 2004b. The Snake River, Eldorado River and Pilgrim River Salmon Escapement Enumeration and Sampling Project Summary: A report prepared for the Norton Sound Salmon Research and Restoration Steering Committee Report, 2003. Kawerak, Inc. Fisheries Department

Dunmall, K. 2008. Norton Sound Salmon Escapement Projects: Summary of: Snake River 1995-2007, Eldorado River 1997-2007, Pilgrim River 2003-2007. Kawerak, Inc. Fisheries Department

Farley, E., J. Murphy, M. Adkison, L. Eisner, J. Helle, J. Moss, and J. Nielsen. 2007. Early marine growth in relation to marine-stage survival rates for Alaska sockeye salmon (*Oncorhynchus nerka*). Fishery Bulletin 105(1):121.

Finney, B., I. Gregory-Eaves, J. Sweetman, M. Douglas, and J. Smol. 2000. Impacts of climatic change and fishing on Pacific salmon abundance over the past 300 years. Science 290(5492):795-799.

Hagen, P., D. Oxman, and B. Agler 2001. Developing and deploying a high-resolution imaging approach for scale analysis. Alaska Department of Fish and Game Mark, Tag, and Age Lab, Juneau NPAFC Doc. No. 567.

Henderson, M., and A. Cass. 1991. Effect of smolt size on smolt-to-adult survival for Chilko Lake Sockeye Salmon (*Oncorhynchus nerka*). Canadian Journal of Fisheries and Aquatic Sciences 48(6):988-994.

Koenings, J., H. Geiger, and J. Hasbrouck. 1993. Smolt-to-adult survival patterns of sockeye salmon (*Oncorhynchus nerka*): effects of smolt length and geographic latitude when entering the sea. Canadian Journal of Fisheries and Aquatic Sciences 50(3):600-611.

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

Kohler, T., and G. Knuefer. 2001. Pilgrim River salmon counting tower project summary report, 2000. Alaska Department of Fish and Game, Division of Commercial Fisheries, Regional Information Report 3A01-23, Anchorage.

Koo, T. 1955. Biology of the red salmon, *Oncorhynchus nerka* (Walkbaum) of Bristol Bay, Alaska, as revealed by a study of their scales. University of Washington

Kroeker, T., and K. Dunmall. 2006. Snake River, Eldorado River and Pilgrim River Salmon Escapement Enumeration and Sampling Project Summary Report, 2005. Kawerak, Inc. Fisheries Department

Mantua, N., S. Hare, Y. Zhang, J. Wallace, and R. Francis. 1997. A Pacific interdecadal climate oscillation with impacts on salmon production. Bulletin of the American Meteorological Society 78(6):1069-1079.

McCoy, G. 1983. Nutrient limitation in two arctic lakes, Alaska. Canadian Journal of Fisheries and Aquatic Sciences 40(8):1195–1202.

Moss, J., D. Beauchamp, A. Cross, K. Myers, E. Farley, J. Murphy, and J. Helle. 2005. Evidence for Size-Selective Mortality after the First Summer of Ocean Growth by Pink Salmon. Transactions of the American Fisheries Society 134(5):1313-1322.

Parker, D. 2008. Glacial Lake sockeye salmon restoration project, 2000 to 2005. US Bureau of Land Management Open File Report 110, Anchorage, AK.

Quinn, T. 2005. The behavior and ecology of pacific salmon and trout. American Fisheries Society

Rob, P. 1998. Pilgrim River salmon counting tower project summary report, 1997. Alaska Department of Fish and Game, Division of Commercial Fisheries, Regional Information Report 3A98-10, Anchorage.

Rob, P. 1999. Pilgrim River salmon counting tower project summary report, 1998. Alaska Department of Fish and Game, Division of Commercial Fisheries, Regional Information Report 3A99-07, Anchorage.

Sogard, S. 1997. Size-selective mortality in the juvenile stage of teleost fishes: a review. Bulletin of Marine Science 60(3):1129-1157.

Soong, J., A. Banducci, S. Kent, and J. Menard. 2008. 2007 annual management report Norton Sound, Port Clarence, and Kotzebue. Alaska Department of Fish and Game, Fishery Management Report No. 08-39, Anchorage.

Stockner, J. 1987. Lake fertilization: the enrichment cycle and lake sockeye salmon (*Oncorhynchus nerka*) production. Pages 198–215 [*in*] H. D. Smith, L. Margolis, and C. C. Wood, Editors. Sockeye salmon (*Oncorhynchus nerka*) Population Biology and Future Management, volume 96. Canadian Special Publication of Fisheries and Aquatic Sciences

Thompson, S. 1992. Sampling. John Wiley & Sons New York

Thorpe, J. 1994. Salmonid fishes and the estuarine environment. Estuaries and Coasts 17(1):76-93.

Todd, G. L., and G. B. Kyle. 1996. Limnological and sockeye salmon productivity investigations in Salmon and Glacial lakes: 1994-1995 project report. Alaska Department of Fish and Game, Division of Commercial Fisheries, Regional Information Report 5J96-02, Juneau.

Todd, G. L., and G. B. Kyle. 1997. Limnological and sockeye salmon productivity investigations in Salmon and Glacial lakes: project completion report. Alaska Department of Fish and Game, Division of Commercial Fisheries, Regional Information Report 5J97-05, Juneau.

Uchiyama, T., B. Finney, and M. Adkison. 2008. Effects of marine-derived nutrients on population dynamics of sockeye salmon (*Oncorhynchus nerka*). Canadian Journal of Fisheries and Aquatic Sciences 65(8):1635-1648.

Venables, W., and B. Ripley. 2002. Modern applied statistics with S. Springer

Waitman, S., and K. Dunmall. 2003. Snake River, Eldorado River and Pilgrim River Salmon Escapement Enumeration and Sampling Project Summary, 2002. Kawerak, Inc. Fisheries Department:1-18.

Ward, B., P. Slaney, A. Facchin, and R. Land. 1989. Size-biased survival in steelhead trout (*Oncorhynchus mykiss*): Back-calculated lengths from adults' scales compared to migrating smolts at the Keogh River, British Columbia. Canadian Journal of Fisheries and Aquatic Sciences 46(11):1853-1858.

Wilson, L., G. Todd, and T. Hamazaki. in press. Sockeye salmon studies in Salmon Lake, Alaska: limnology and fishery investigations relative to a nutrient addition program, 1994-2008. Alaska Department of Fish and Game. Fishery Data Series No. 09-XX, Anchorage.

General Discussion

Factors that affect the growth and survival of specific sockeye salmon populations as fry in their rearing lake and in their first year in the marine environment are key to understanding population return. These results suggest that the first year of fry growth did not explain much of the variability in adult return, but that a productive lake environment and the availability of an estuary affects juvenile salmon growth and population production.

Climate change could possibly have positive effects on the rearing conditions for both Seward Peninsula populations of sockeye salmon. If both season length and temperature increase, smolt production in both Salmon and Glacial lakes are expected to increase, suggested by the relationship between early break up, the Pacific Decadal Oscillation (PDO) and *Daphnia* density in Lake Aleknagik (Schindler et al. 2005), the only predictor variable included in a time series model was spring break up timing (Schindler et al. 2005) even though fry density is thought to have a strong effect on zooplankton density. Sockeye salmon fry growth was positively related to zooplankton abundance and negatively affected by fry density (Schindler et al. 2005).

Climate change could have positive effects on the marine survival of Seward Peninsula sockeye salmon by enhancing conditions in the marine environment. Sockeye salmon abundance has been positively correlated with ocean temperature (Beamish et al. 1997), however, the production of stocks at latitudes of the Seward Peninsula sockeye salmon stocks have not been correlated with temperature. The possible positive trend in the scale radius to the first ocean annulus suggests that annual mean growth of sockeye salmon in their first summer in the ocean is increasing, though this trend needs to be examined further.

Literature Cited

Beamish, R., C. Neville, and A. Cass. 1997. Production of Fraser River sockeye salmon (*Oncorhynchus nerka*) in relation to decadal-scale changes in the climate and the ocean. Canadian Journal of Fisheries and Aquatic Sciences 54(3):543-554.

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