GROWTH OF JUVENILE CHINOOK SALMON (*ONCORHYNCHUS TSHAWYTSCHA*) AS AN INDICATOR OF DENSITY-DEPENDENCE IN THE CHENA RIVER

By

Megan T. Perry

RECOMMENDED: Matthew

Amanda Rosenberger

Advisory Committee Chair

Chair, Department of Biology and Wildlife

APPROVED: Paul W. Layer

Dean, College of Natural Science and Mathematics

Lawrence K Duffy

Dean of the Graduate School

July 27, 2012

Date

GROWTH OF JUVENILE CHINOOK SALMON (*ONCORHYNCHUS TSHAWYTSCHA*) AS AN INDICATOR OF DENSITY-DEPENDENCE IN THE CHENA RIVER

A

THESIS

Presented to the Faculty

of the University of Alaska Fairbanks

in Partial Fulfillment of the Requirements

for the Degree of

MASTER OF SCIENCE

By

Megan T. Perry, B.A.

Fairbanks, Alaska

August 2012

Abstract

In management of Pacific salmon, it is often assumed that density-dependent factors, mediated by the physical environment during freshwater residency, regulate population size prior to smolting and outmigration. However, in years following low escapement, temperature may be setting the upper limit on growth of juvenile Chinook salmon *Oncorhynchus tshawytscha* during the summer rearing period. Given the importance of juvenile salmon survival for the eventual adult population size, we require a greater understanding of how density-dependent and independent factors affect juvenile demography through time. In this study we tested the hypotheses that (1) juvenile Chinook salmon in the Chena River are food limited, and (2) that freshwater growth of juvenile Chinook salmon is positively related with marine survival. We tested the first hypotheses using an *in-situ* supplemental feeding experiment, and the second hypothesis by conducting a retrospective analysis on juvenile growth estimated using a bioenergetics model related to return per spawner estimates from a stock-recruit analysis. We did not find evidence of food limitation, nor evidence that marine survival is correlated with freshwater growth. However, we did find some evidence suggesting that growth during the freshwater rearing period may be limited by food availability following years when adult escapement is high.

Table of Contents

List of Figures

Page

Chapter 1

Chapter 2

Appendix

List of Tables

Page

Chapter 1

Chapter 2

Appendix

Acknowledgements

There are many people who helped to make this project possible, and to whom I am extremely grateful; I was fortunate to have the wonderful opportunity to work with so many who were enthusiastic about this project, who helped encourage and challenge me to become a better ecologist. Foremost, thank you to my thesis adviser, Dr. Mark Wipfli, for his guidance, encouragement, and support during this project, as well as fresh vegetables from the garden, amazingly fun lab potlucks and trips, and beautiful art; your joie de vivre inspires. And to the late Dr. Nicholas Hughes, for his insight, enthusiasm, and love for ecology; he was inspiring, a great friend and mentor, and is missed. Thank you to my committee members, Dr. Amanda Rosenberger and Mr. Matthew Evenson, for help in the planning of the project, support throughout, and editorial comments. Thank you also to my lab mate, Jason Neuswanger, who provided much assistance in field technologies and statistical analysis

A very sincere thank you to field technicians, Lorena Edenfield, Mel Durrett, Katie Skogen, James Reidman, T.J. Fayton, and Kyle Schumann, for your help sampling, with boat malfunctions, and thoughtful input; it was an adventure! Thank you especially to Bessie Green for help in the field, trouble shooting with abundance estimate methods and feeders, for help understanding R, and constant encouragement. Thank you to all the members of the Wipfli Aquatics Lab, and other students working under this grant, especially Emily Benson, Laura Gutierrez, Bessie Green and Jason Neuswanger. Thank you to James Saveride at the Alaska Department of Fish and Game for logistical help and field assistance during the planning stages and pilot season of this project, and thank you to Larry DuBois for help with scale data collection and interpretation. Thank you to Dr. Mike Bradford, Dr. Eva Enders, Dr. Christine Hunter, Dr. Franz Mueter, Dr. Terry Quinn, and Mr. Chris Stark for advice on sampling designs and data analysis.

My family and friends were also involved in helping this project succeed. Thank you to my father, James Perry, for helping design field equipment, and for coming up at the beginning of both of my field seasons to install fish feeders, and thank you to my mother, Sheila Perry, and sisters, Rachel and Anna, for assistance in installing field equipment. Finally, thank you to all of the friends and volunteers who came out to help sample a day in the field, and for encouragement. I miss those days on the river; you all made it so fun and enjoyable.

This study was supported in part by a generous grant from the Arctic Yukon Kuskokwim Sustainable Salmon Initiative, as well as logistical support from the Alaska Department of Fish and Game. The sampling method was approved by the University of Alaska Fairbanks Institutional Animal Care and Use Committee (IACUC # 07-21) and by the Alaska Department of Fish and Game (Fish Resource Permits: SF2008-133 and SF2009-141). Any use of trade firm names in this publication is for descriptive purposes only and does not imply endorsement by the U.S. Government.

General Introduction

Growth of organisms can be regulated by density-independent and density-dependent factors. Density-independent factors are those unrelated to population density and affect everyone in the population regardless of density. For stream salmonids, examples of density-independent factors are stream flow, water temperature, and flooding. Density-dependent factors are those influenced by the density of a population, with increasing pressure at higher densities. They are predominantly caused by competition for resources among a cohort. Typically, density-dependent effects are most significant at high populations densities (Keeley 2001). Effects of density-dependence can appear as reduced growth, poor condition of organisms, and mortality (Mason 1976, Cada et al. 1987, Nislow et al. 1998).

Research on salmonids suggest that density-dependent interactions that regulate population size may occur in freshwater, rather than in the marine environment: coho salmon *Oncorhynchus kisutch* (Holtby and Scrivener 1989; Hartman and Scrivener 1990); steelhead trout *O. mykiss*, (Ward and Slaney 1993); brown trout *Salmo trutta*, (Elliott 1989, 1993, 1994); and Atlantic salmon *S. salar*, (Gibson 1993; Jonsson et al. 1998). Data on Chinook salmon *O. tshawytscha* is lacking; this is probably a consequence of their preferences for rearing in large to medium sized rivers, which makes the necessary research difficult (Healey 1991; Bradford and Taylor 1997; Red Weller and Ed Jones, Alaska Department of Fish and Game, pers. comm.). Furthermore, Chinook salmon may undergo long-distance migrations shortly after emergence (Daum and Flannery 2009).

Our research took place in the Chena River, an important spawning and rearing tributary of the Yukon River located in Interior (central) Alaska. Extensive sampling of the Tanana River, a tributary of the Yukon River, and into which the Chena River flows, has not yielded evidence of juvenile Chinook rearing in the river (Mecum 1984; Ott et al. 1998; Hemming and Morris 1999; Durst 2001; Ken Alt, ADF&G, pers. comm.), and it is believed that juveniles that emerge in the Chena River tend to rear there.

In a pilot study conducted in 2007, we[1] identified areas of the Chena River that provided suitable habitat for juvenile Chinook salmon rearing in both early and late summer. The results of this initial study indicated that the majority of juveniles reared in a 75 km section of the middle reach of the river. We also found that juvenile Chinook salmon concentrate in areas of large woody debris (LWD), which provides protection from predators (Grand and Dill 1997), favorable flow regimes (Fausch and Northcote 1992), and increased foraging opportunities (Crowder and Cooper 1982).

While the growth rate of fish is strongly controlled by temperature (Wooton 1990, Elliott et al. 1995, Elliott and Hurley 1999), food availability is clearly important for stream salmonids, and past research shows positive correlations between food supply and fish abundance, biomass, and growth rates, (coho salmon: Mason 1976; rainbow trout *O. mykiss*: Keeley 2001; cutthroat trout *O. clarki*: Boss and Richardson 2002; Wilzbach et al. 1986; cutthroat trout and brown trout: Ensign et al. 1990). The amount of food

---

[1] Throughout this document, ”we” refers to primary author Megan T. Perry as well as co-authors listed in the footnote for each chapter.

necessary is partly a function of metabolism: fish experiencing higher water temperatures require more food intake (Ursin 1979).

Our study aimed to examine the interaction of food availability and water temperature on the growth of juvenile Chinook salmon: at the individual level, by measuring mass at length; at the sub-population level, by estimating abundance and monitoring sub-population metrics of condition; and on a population size level, by investigating the relationship between average size attained during freshwater and the number of recruits per spawner.

This project was a component of a larger project, Ecology and Demographics of Chinook Salmon in the Chena River, Interior Alaska, funded by the Arctic Yukon Kuskokwim Sustainable Salmon Initiative (AYKSSI). The goal of this project was to improve our understanding of the way ecological processes regulate population size and generate annual variability in the abundance of adult Chinook salmon returning to the Chena River. The specific objectives of my project were: 1) determine whether food or temperature limits juvenile Chinook salmon growth, 2) investigate if seasonal patterns of fish growth or changes in fish abundance give evidence of competitive bottlenecks that lead to density-dependent mortality, 3) develop a model capable of predicting the effect of stream temperature on juvenile growth, 4) test whether the growth model can be used to predict annual growth and annual variation in smolt size, and 5) determine whether there is a positive correlation between smolt size and the productivity of a brood year in terms of recruits per spawner.

To achieve these objectives, we monitored growth of juvenile Chinook salmon over two summer rearing periods, choosing sites within a section of the river identified in 2007 as a high abundance area, with sites that provided complex habitat in the form of large woody debris. In 2009, we conducted a supplemental food experiment to test the hypothesis that juvenile Chinook salmon are food-limited in the Chena River by comparing condition of fish in supplemental and control sites. We also monitored growth throughout the summer rearing season to identify times when density-dependent regulation was occurring. We then used a bioenergetics model (Rasmussen and From 1991) to estimate end of season length of Chena River Chinook salmon, based on temperature, food rations, and length of growing season from 1981-2009. We compared predicted length to observed length for juvenile Chinook length collected during our study period, and length data of juvenile and smolting Chinook from the Chena River found in the literature, and regressed those data on estimates of recruits per spawner.

References

Boss, S. M., and J. S. Richardson, 2002. Effects of food and cover on the growth, survival, and movement of cutthroat trout (*Oncoryhnchus clarki*) in coastal streams. Canadian Journal of Fisheries and Aquatic Sciences 89:1044-1053.

Bradford, M. J., and G. C. Taylor. 1997. Individual variation in dispersal behaviour of newly emerged Chinook salmon (*Oncorhynchus tshawytscha*) from the Upper Fraser River, British Columbia. Canadian Journal of Fisheries and Aquatic Sciences. 54:1585-1592.

Cada, G. F., J. M. Loar, and M. J. Sale. 1987. Evidence of food limitation of rainbow and brown trout in southern Appalachian soft-water streams. Transactions of the American Fisheries Society 116:692-702.

Crowder, L. B., and W. E. Cooper. 1982. Habitat structural complexity and the interaction between bluegills and their prey. Ecology 43:96-102.

Daum, D. W., and B. G. Flannery. 2009. Canadian-origin Chinook salmon rearing in non-natal U.S. tributary streams of the Yukon River, Alaska, 2006-2007. Alaska Fisheries Technical Report Number 102.

Durst, J. D. 2001. Fish habitat use in the Tanana River floodplain near Big Delta, Alaska, 1999-2000. Alaska Department of Fish and Game, Habitat and Restoration Division. Technical Report No. 01-5.

Elliott, J. M. 1989. Mechanisms responsible for population regulation in young migratory trout, *Salmo trutta*. I. The critical time for survival. Journal of Animal Ecology 58:987-1002.

Elliott, J. M. 1993. The pattern of natural mortality throughout the life cycle in contrasting populations of brown trout, *Salmo trutta* L. Fisheries Research 17:123-136.

Elliott, J. M. 1994. Quantitative ecology and the brown trout. Oxford University Press, Oxford.

Elliott, J. M., and M. A. Hurley. 1999. A new energetics model for brown trout, *Salmo trutta*. Freshwater Biology 45:235-246.

Elliott, J. M., M. A. Hurley, and R. J. Fryer. 1995. A new, improved growth model for brown trout, *Salmo trutta*. Functional Ecology 9:290-298.

Ensign W. E., R. J. Strange, and S. E. Moore. 1990. Summer food limitation reduces brook and rainbow trout biomass in a southern Appalachian stream. Transactions of the American Fisheries Society 119:894-901.

Fausch, K. D., and T. G. Northcote. 1992. Large wood debris and salmonid habitat in a small coastal British Columbia Stream. Canadian Journal of Fisheries and Aquatic Sciences 49:682-693.

Gibson, R. J. 1993. The Atlantic salmon in fresh water: spawning, rearing, and production. Reviews in Fish Biology and Fisheries 3:39-73.

Grand, T. C., and L. M. Dill. 1997. The energetic equivalence of cover to coho salmon (*Oncorhynchus kisutch*): ideal free distribution applied. Behavioural Ecology 8:437-447.

Hartman, G. F., and J. C. Scrivener. 1990. Impacts of forestry practices on a coastal stream ecosystem, Carnation Creek, British Columbia [Canada]. Canadian Bulletin of Fisheries and Aquatic Sciences No. 223.

Healey, M. C. 1991. Life history of Chinook salmon (*Oncorhynchus tshawytscha*). Pages 311-393 *in* C. Groot and L. Margolis, editors. Pacific salmon life histories. UBC Press, Vancouver.

Hemming, C. R., and W.A. Morris. 1999. Fish habitat investigations in the Tanana River watershed, 1997. Alaska Department of Fish and Game, Habitat and Restoration Division. Technical Report No. 99-1.

Holtby, L. B., and J. C. Scrivener. 1989. Observed and simulated effects of climatic variability, clear-cut logging, and fishing on the numbers of chum salmon (*Oncorhynchus keta*) and coho salmon (*O. kisutch*) returning to Carnation Creek, British Columbia, Pages 62-81 *in* C. D. Levings, L. B. Holtby, and M. A. Anderson, editors. Proceedings of the national workshop on effects of habitat alteration on salmon stocks. Canadian Special Publication of Fisheries and Aquatic Sciences 105.

Jonsson, N., B. Jonsson, and L. P. Hansen. 1998. The relative role of density-dependent and density-independent survival in the life cycle of Atlantic salmon *Salmo salar*. Journal of Animal Ecology 67:751-762.

Keeley, E. R. 2001. Demographic responses to food and space competition by juvenile steelhead trout. Ecology 82:1247-1259.

Mason, J. C. 1976. Response of underyearling coho salmon to supplemental feeding in a natural stream. Journal of Wildlife Management 40:775-788.

Mecum, R. D. 1984. Habitat utilization by fishes in the Tanana River near Fairbanks, Alaska. MS thesis. University of Alaska Fairbanks.

Nislow K. H., C. Folt, and M. Seandel. 1998. Food and foraging behavior in relation to microhabitat use and survival of age-0 Atlantic salmon. Canadian Journal of Fisheries and Aquatic Science 55:16-127.

Ott, A. G., J. F. Winters, and A. H. Townsend. 1998. Juvenile fish use of selected habitat in the Tanana River near Fairbanks (preliminary report). Alaska Department of Fish and Game, Habitat and Restoration Division. Technical Report No. 97-1.

Rasmussen, G., and J. From. 1991. Improved estimates of a growth model and body composition of rainbow trout, *Oncorhynchus mykiss* (Walbaum, 1792) as function of feeding level, temperature and body size. Dana 9:15-30.

Ursin, E. 1979. Principles of growth in fishes. Symposium of the Zoological Society of London 44:63-87.

Ward, B. R., and P. A. Slaney. 1993. Egg-to-smolt survival and fry-to-smolt density dependence of Keogh River steelhead. Pages 209-217 *in* R. J. Gibson and R. E. Cutting, editors. Production of juvenile Atlantic salmon, *Salmo salar*, in natural waters. Canadian Special Publication of Fisheries and Aquatic Sciences 118.

Wilzbach, M. A., K. W. Cummins, and J. D. Hall. 1986. Influence of habitat manipulations on interactions between cutthroat trout and invertebrate drift. Ecology 67:898–911.

Wooton, R. J. 1990. Ecology of teleost fishes. Chapman and Hall, London, U.K

Chapter 1

Responses to *in-situ* supplemental feeding of juvenile Chinook salmon (*Oncorhynchus tshawytscha)* in the Chena River, Alaska[2]

Abstract

In management of Pacific salmon, it is often assumed that density-dependent factors, mediated by the physical environment during freshwater residency, regulate population size prior to smolting and outmigration. Given the importance of juvenile salmon survival for eventual adult population size, we require an understanding of the nature of these density-dependent factors and their constancy through time. In this study, we tested the hypothesis that juvenile Chinook salmon *Oncorhynchus tshawytscha* in the Chena River are food-limited with an experiment that compared condition and abundance of juvenile fish in control reaches to reaches supplemented with food. We measured the effects of food supplementation on age 0+ fish in two 15-km reaches within a 100-km section of the Chena River, interior Alaska, with two control and two supplemented sites in each reach. Fish were sampled using baited minnow traps during three 3-day sampling events during summer 2009. The results of this study suggest that juvenile Chinook salmon were not food limited during the summer 2009 study period. However, while anecdotal, during a pilot study of our supplemental feeding

---

[2] Perry, M. T., M. S. Wipfli, N. F. Hughes, J. R. Neuswanger, A. E. Rosenberger, and M. J. Evenson. 2012. Responses to *in-situ* supplemental feeding of juvenile Chinook salmon (*Oncorhynchus tshawytscha)* in the Chena River, Alaska. Prepared for submission to Transactions of the American Fisheries Society.

methods, we observed greater fish retention at supplemented sites compared to control sites, which suggest that food limitation may have caused density-dependent effects during summer 2008. Interannual variation in aquatic and terrestrial invertebrate drift as well as spawner density likely plays an important role influencing population dynamics.

Introduction

Food availability, water temperature and fish size are the three most important variables affecting fish growth. In salmonids, competition for food can affect growth rates and survival (Brodeur et al. 2000) and regulate population size (Chapman 1966). When fish occur in high population densities and food becomes restricted, individual growth rate decreases, lowering productivity and biomass (Fryer and Iles 1972). Research on anadromous salmonids suggests that the density-dependence that regulates population size may act in freshwater rather than the marine environment (Holtby and Scrivener 1989). This mortality is the consequence of competition for food or space during the summer months juveniles spend rearing in fresh water (Elliott 1994). During the summer rearing period, competition for food increases as fish biomass increases (Steingrimsson and Grant 1999). Seasonal fluctuations in both the supply of food and the availability of space for feeding during the first summer interact to determine the productivity of stream reaches (Nislow et al. 2000).

Density-dependent effects occur when the number of organisms in an area exceed that allowable by resource availability. Density-dependence effects are predominantly caused by competition for resources among a cohort and are most significant at high population densities. Effects of density-dependence can appear as reduced growth, poor condition, increased rates of mortality, and lower fish densities.

Where individuals compete for feeding territories, density-dependent competition is thought to occur whenever a habitat becomes saturated with territories of a given size (Chapman 1966; Grant and Kramer 1990). Keeley (2001) investigated how density-dependence operates through mortality, growth or migration and how unequal resource partitioning influences the variance in success of individuals in a population of juvenile steelhead trout *Oncorhynchus mykiss*. If a population is limited by food and space, a reduction in competition for those resources should lead to a decrease in density-dependent effects on the population (Lomnicki 1988). If populations are limited by food only, an increase in food abundance should support higher salmonid density (Marchall and Crowder 1995).

Data demonstrating competition in juvenile Chinook salmon (*O. tshawytscha*) is lacking, likely a consequence of their life history. Chinook salmon in interior Alaska have a stream-type life history (Healey 1991). Adults spawn in July and August, fry emerge from gravel the following spring, juveniles rear in fresh water for the summer, over-winter, and migrate to the ocean the following spring. Available evidence suggests that juvenile Chinook salmon that hatch in the Chena River tend to rear there, rather than dropping downstream into larger rivers (Walker 1983), making it feasible to conduct research on competition.

We hypothesized that density-dependent interactions due to food limitation are occurring in juvenile Chinook salmon populations in the Chena River. To test our hypothesis, we designed a food supplement experiment for juvenile Chinook salmon. We predicted supplemental feeding would eliminate correlates of density-dependence, therefore leading to fish with a greater mass at length, or condition, than fish at control sites, indicating density-dependent interactions occurring at unsupplemented sites. In addition, we were interested in site-level sub-population effects. We hypothesized that abundance and changes in abundance would differ between supplemented and unsupplemented sites and that the distribution of mass frequencies at unsupplemented sites would show more inequality, as measured by Gini coefficients, indicating density-dependent effects (Mason 1976; Keeley 2001). We expected periods of density-dependent mortality to be marked by more rapid declines of abundance as fish grow in size (Hughes and Griffiths 1998) in control sections than in experimentally fed sections.

Methods

Study Area

This research was conducted in the Chena River, Interior Alaska (Figure 1). The Chena River is near the northernmost range of the Chinook salmon spawning distribution and is an important spawning stream in the middle Yukon drainage (Eiler et al. 2004). A pilot study conducted in 2007 indicated that the majority of juvenile Chinook salmon reared between river kilometers 95 and 160 upstream from its confluence with the

Tanana River. Surveys on spawning adults indicated that the majority of spawning occurs in the lower 150 km of the river (Decker 2010).

We selected research sites in the middle reach of the Chena River because this reach included areas of highest spawner density and areas of juvenile presence both late and early season, as determined from our 2007 pilot season. Eight research sites were chosen using a randomized plot design. Four upstream sites (US1-4) were located between 64.864021N, -146.782157W, and 64.892929N, -146.648643W and four downstream sites (DS1-4) were located between, 64.790316N, -147.162720W and 64.822348N, -147.074728W.

We identified suitable sites in early May 2009, based on the presence of large woody debris accumulation throughout the water column. These sites were typically located on the cut banks of the river and were considered edge habitats, with complex cover composed of rootwads and debris. Sites were between 10-20 m long. All sites were velocity shelters; a boundary between the site and the main river was visible as a current shear line (Beechie et al. 2005). Rootwads and debris jams were the most abundant cover at all sites, but some also had undercut banks, live forbs and grasses, and mats of floating detritus. Site substrates were composed of sand and gravel or cobble. Water temperature was recorded hourly using HOBO® data loggers (Onset Corporation, Bourne, MA, USA) suspended from instream large woody debris and weighted to the stream bed. The uppermost site was randomly chosen to either be control or supplemental food. The remaining sites alternated between control and fed sites, to ensure that appropriate distances between fed sites were such that migration to fed sites from control would be unlikely.

Fish diversity was similar across all sites. Juvenile Chinook salmon were the most common. Occasionally, we would capture other species, such as slimy sculpin *Cottus cognatus,* juvenile Arctic grayling *Thymallus arcticus,* Arctic lamprey *Lampetra japonica,* and juvenile longnose sucker *Catostomus catostomus.* In addition to those caught with the minnow traps, we noted congregations of Arctic grayling, adult long nose sucker, and round whitefish *Prosopium cylindraceum*, immediately downstream of supplemental sites.

Supplemental Feeding

For supplemental feeding, custom designed feeders from TEC Industrial Inc. (Rochester, MN, USA), were installed at the upstream end of selected sites in early June 2009. Feeders continuously added food (Silver Cup Fish Feed, Murray, UT, USA) to each site, at the rate of ~750g/day, 10 times the maximum rations that 75 fish with mean mass of 7g and mean length of 80mm would require at ideal temperatures for growth (Sagar and Glova 1988), providing a super-abundance of food available to fish at each site. During our pilot study of supplemental feeding in 2008, we observed that juvenile Chinook salmon readily consumed the supplemental food. Feeders were continually powered through a deep cell battery kept charged by solar panels, and refilled on a weekly basis.

Mark-Recapture, Fish Condition, and Mass Frequency Distribution

To estimate local fish abundance and fish condition at our research sites, and plot sub-population mass frequency distribution, we conducted a series of independent mark-recapture experiments. Sampling was designed to estimate abundance at each site during three periods (July, August, and September 2009). Each experiment consisted of three capture events conducted over three consecutive days. Ten Gee-type minnow traps (23 x 45 cm, 0.6 cm wire mesh, 2.5 cm diameter opening) baited with salmon roe were set out at each of the sites, and soaked for 2-5 hours. Captured fish were placed in a bucket of river water, anesthetized with tricaine methanesulphonate (MS-222®) until loss of equilibrium. Fork length was measured to the nearest mm and mass was measured to the nearest 0.01 g using a Pescola® spring scale. Event and site specific marks were then implanted on each fish using visible implant elastomer (Northwest Marine Technology, Shaw Island, Washington). Marks consisting of up to three colors were placed on their anal fins, caudal fin, adipose fin, or on their bodies, using one or two color combinations for each capture. After marking, fish were returned to a bucket of river water until they recovered and released back into the same site. Marks were made on the first and second day of each experiment. On the third day, fish length and mass were taken, and the fish were inspected for previous marks.

Data Analysis

Fish Condition

To investigate indicators of competition, we explored the effects of supplemental feeding on individual mass at length. To meet assumptions of normality, we log-transformed our data. Linear mixed effects models (Pinheiro et al. 2008) were used in the ‘nlme’ package version 3.1-89 in the R programming environment (R Development Core Team 2008), with fixed treatment effects, and random site effects to evaluate the effects of supplemental feeding on individual fish condition:

$$\log_{10}(M) = \alpha_t + \beta_t * \log_{10}(L) + a_s + b_s * \log_{10}(L) + \varepsilon_{ts},$$

where M is the fish response, mass of juvenile Chinook salmon at length, L. α_t and β_t are the slopes and intercepts for the treatment (fixed) effect, a_s and b_s are the slopes and intercepts for the site (random) effect, and ε are errors.

Indices of Competition

We plotted mass-frequency distributions for all sampled fish at each site during each sampling event, except at the farthest downstream site (DS4), due to low sample size. Plots were made using the ‘lattice’ program in the R programming environment (Sarkar 2008) on a scale from 0 to 10 grams, using 50 bins to distribute proportions of the population. Distributions were examined for skew to investigate potential density-dependence. We also calculated the Gini coefficient, a measure of inequality, for each site and event (Weiner and Solbrig 1984; Keeley 2001). The Gini coefficient is a number between 0 and 1, with higher numbers indicating more inequality in the data. Coefficients were calculated using the 'reldist' package version 1.595 of the R programming environment (Handcock and Morris 1999). We used a repeated measures analysis of variance (rm ANOVA) with sampling event as the repeated measure to test for significant differences in the Gini coefficients between treatments and through time. The rm ANOVA was done using IBM SPSS Statistics 19 (SPSS Inc. 2010).

Abundance Estimates

In addition to visualizing local subpopulation effects of mass distribution, we gathered abundance and count data at each of the sites. For the mark-recapture experiment study design and analysis, specific conditions are needed to meet model estimate assumptions (Seber 1982). For each site during each 3-day experiment, we assumed that each animal was equally likely to be caught, that marking did not effect capture probability, and that sampling each day was instantaneous. We assumed that animals retained their tags throughout the 3-day experiment and all tags were read properly. We also assumed that survival rates were the same for marked and unmarked animals and between each sampling occasion. Finally, we assumed that the study area was closed to immigration and emigration during the course of each 3-day experiment. An experiment on juvenile Chinook salmon from the Fraser River found mortality for tagged fish to be low (1.6%), and retention of elastomer tags to be 100% after 3 months (Bradford et al. 2001).

Abundance estimates for each of the sampling events were conducted in the program MARK (White and Burnham 1999) for closed population capture-recapture models (Otis et al. 1978). The closed capture model is based on the full-likelihood parameterization with three types of parameters; p_i is the probability of first capture, c_i is the probability of recapture, and N is abundance. Three models were run for each of the study sites to estimate abundance.

$$N, p(.) = c(.)$$

$$N, p(t) = c(t)$$

$$N, p(.) = c(.)$$

Where (.) = a constant parameter, and (t) = a time varying parameter. Models were ranked using Akaike's Information Criterion (AIC_c), and we selected our most likely model based on the lowest AIC_c score; $\Delta AIC_c > 2$ for all other models (Burnham and Anderson 2002). For all sampling events, AIC_c preferred N, p(t) = c(t) over the other models, and we used that model to estimate abundance (N) and standard errors.

We estimated catch per unit effort (CPUE) for each of our trapping days, where catch was the total number of fish caught at each sampling event, and effort was the number of minnow traps multiplied by the number of minutes fished. We used Spearman's rank correlation *rho* to investigate the correlation between abundance estimates and total CPUE.

Results

During the 2009 study season, we did not find a significant effect of supplemental feeding on individual growth, condition, or subpopulation level abundance. The linear mixed effects model used to test the effects of supplemental feeding on individual fish condition found no significant difference in fish condition between fed and unfed treatment sites ($p = 0.30$) (Table 1), and the plots of log-transformed mass (g) on length (mm) regressions suggested no difference between treatments (Figure 2). Mass frequency distributions showed similar size inequalities for all treatment sites across all dates, between both upstream and downstream reaches (Figures 3 and 4). Gini coefficients were not significantly different between treatments (rm ANOVA, $F_{1,6} = 1.778$, $p = 0.23$), but did lessen through time (rm ANOVA, $F_{1,6} = 12.000$, $p = 0.013$).

Due to low recapture at upstream sites, estimates of juvenile Chinook population abundance could only be calculated at sites DS1-3 (Table 2). After the first sampling event, DS4 had insufficient captures to calculate an abundance estimate. Abundance estimates for DS1 were similar for both events (Figure 5). We observed a significant increase in abundance from July to August at DS2, but not between August and September. DS3 abundance was nearly identical for July and August, but was slightly larger in September. CPUE (Table 2) and abundance were strongly correlated ($S = 4$, $p = 0.0005$, $rho = 0.95$, correlation coefficient = 0.97). Because they were strongly correlated, we used CPUE as a proxy for abundance at our sites where we were unable to estimate abundance because of low numbers of recaptured fish.

Discussion

Fish mass at length at sites that received supplemental food were not significantly different from control sites in this study. This did not support our hypothesis that fish at supplemental sites would have improved condition. In addition, juvenile Chinook salmon did not display evidence of density-dependent interactions as indicated by mass frequency distributions or measured by Gini coefficients. Additionally, site-specific estimates of abundance/CPUE that would explain the null effect on individual growth or mass frequency distributions were not observed.

The homogeneity we observed in individual growth did not suggest density-dependent interactions. Alternatively, we may have been able to infer density-dependent interactions if population abundance at control sites decreased throughout the summer (self-thinning) but remained stable at supplemental food sites. However, our ability to make such an inference was compromised by our inability to estimate abundance at many of the sites. Over the course of the summer, many of our sites likely experienced recruitment (Table 2), but we were unable to estimate abundance at our upstream sites due to low capture and recapture numbers, which, in addition to low population size, may have occurred because of inefficient closure of the site over the 3-day sampling event. At our downstream sites, population abundance was similar across all months, except for substantial recruitment at the DS2 site between July and August.

We assumed closure at our sites over the 3-day period in order to estimate abundance, however, there was evidence of an open population over a longer time period. We had evidence of site fidelity in 2.1 – 7.2% of captured fish in all sites between two sampling events, and evidence of site fidelity by 0.4 - 4.2% of captured fish in 4 sites across all three sampling events. The percentages of fish exhibiting site fidelity were similar in both supplemented and unsupplemented sites. Conversely, we documented 6 unique instances of an individual Chinook salmon migrating between sites in both upstream and downstream directions. However, because we did not sample outside of research sites, we have no data regarding the scale or frequency of movements.

Seasonal fluctuations in both the supply of food and the availability of space for feeding during the first summer interact to determine the productivity of stream reaches (Nislow et al. 2000). The DS2 site, which had a relatively high density of juvenile Chinook salmon and experienced significant recruitment between June and July, was located at the outside edge of a meander bend. It had apparent low velocity and large amounts of birch woody debris buildup throughout its depths. A study by Beechie et al. (2005) looked at habitat types and their use by juvenile salmonids in large rivers and found that Chinook and coho salmon were most abundant in channel margins, where velocities were low and cover more abundant. We had a site with similar characteristics as DS2 during the 2008 field season, with lower velocities and substantial woody debris, just off the main channel. Both of these sites proved to be particularly productive, with the highest fish presence of all sites throughout the season. However, during a large flooding event in 2008, the debris jam was reorganized, and flows appeared to be modified at the site. We monitored this site throughout the 2009 season again. Though the habitat structure was still similar, flows were visually different, though this was never quantified. The site no longer supported large aggregations of juvenile salmon. We captured and observed between 13 and 17 fish during sampling events in June, July, in August (Site US2, Table 1) during 2009. During our 2008 season, we consistently saw large numbers of fish at this site, and on one occasion where we attempted enumerations, visually observed over 120 fish. In addition to considering food availability in the abundance and growth of juvenile Chinook salmon, the important of habitat configurations may prove an interesting area for further research.

The mass frequency distributions of fish at all sites and sampling events were nearly normally distributed and did not indicate inequalities. This method of detecting competition has proved effective in other studies (Mason 1976; Keeley 2001). Mason tested whether food or space set the limitation on juvenile coho production in streams, especially in the summer months. The results of Mason's study indicated that food was the limiting factor of juvenile coho salmon productivity. By increasing food availability, Mason was able to increase fish densities to 6 -7 times above naturally occurring densities. Supplemental food also normalized the length frequency distributions of the fish. Skew in the distributions suggests inequitable distribution of food through interference competition. Considering Figures 3 and 4, most of our data shows a slight right skew or a normal distribution, however, analysis of the Gini coefficient suggests similar inequalities in all sites, and the skew is not isolated to one treatment type. The relative normality of our distributions is likely because the fish were not experiencing competition for food.

Keeley (2001) demonstrated how density-dependence can regulate population size in steelhead trout through mortality, growth and emigration by experimentally manipulating food availability, density, and the possibility of emigration as well. Density-dependence operated by reducing growth and increasing mortality as a population reached carrying capacity. The results of Keeley's work found that, while both food and space are important factors in shaping the demography of stream salmonid populations, neither appeared to limit salmonid abundance exclusively. Within our experiment, had competition for food been occurring to the level to cause density-dependent effects, we believe this would have been detected.

While anecdotal, we observed different trends during summer 2009 than in summer 2008. During the 2008 field season, we observed a greater abundance of fish that appeared to remain at food-supplemented sites during some of our trial feeding runs, where declines were observed at unsupplemented sites. Also, the number of fish at all sites was higher. However, during our 2007 pilot and 2008 season, we tested fish enumeration methods that required no fish handling (snorkel surveys, grid point sampling and line transects utilizing underwater videography, and visual counts), but were unable to get estimates of abundance that could be used to compare between the two years.

In addition to the appearance of lower numbers of juveniles in 2009, the salmon run of 2008 was lower than the previous year (Brase 2011), and a 40-yr flood two weeks after the peak spawning caused major scouring of the river bed, both of which could have contributed to lower numbers of juveniles rearing in the Chena River in 2009 than 2008 (Lapointe et al. 1999) and a reduction of potential density-dependent effects. If the number of fish rearing in the Chena River is low, resource limitation is less likely to have a measurable effect on their growth.

Besides a lower number of recruits due to a smaller parent stock, there may have been increased amount of food available to the rearing juveniles over the previous summer (Gutierrez 2011). Using study sites within the same upstream and downstream reaches as our study, Gutierrez measured invertebrate infall (adult aquatic and terrestrial invertebrates), prey sources for juvenile salmon, using floating pan traps, and also measured drift. Gutierrez (2011) found a suggestion of greater infall in 2009 than in 2008, but slightly greater drift in 2008 than in 2009; however, neither of these results were significant. The combination of lower spawner abundance, leading to fewer recruits, and perhaps a slight increases in food availability from terrestrial infall are both factors that may have contributed to not observing density-dependent interactions during the 2009 field season.

The synthesis of our results lead us to reject the hypotheses that Chinook salmon in the Chena River exhibited density-dependent interactions due to competition for food resources in 2009. However, this pattern may not be a consistent one for this system. Interannual variability of many factors, including habitat, spawner abundance, and food availability may explain our results and are topics which deserves further observation and study, as evidence of limitation was present, but not substantiated during the 2008 field season.

References

Beechie, T. J., M. Liermann, E.M. Beamer, and R. Henderson. 2005. A classification of habitat types in a large river and their use by juvenile salmonids. Transactions of the American Fisheries Society 134:717-729.

Bradford M. J., J. A. Grout, and S. Moodie. 2001. Ecology of juvenile chinook salmon in a small non-natal stream of the Yukon River drainage and the role of ice condition on their distribution and survival. Canadian Journal of Zoology 79:2043-2054.

Brase, A. 2011. Fish count database search for Chinook salmon in the Chena River 2007 and 2008. Alaska Department of Fish and Game. http://www.adfg.alaska.gov/index.cfm?adfg=fishingSportFishingInfo.displayResults&speciesid=410&countlocationid=37&year=2007 & http://www.adfg.alaska.gov/index.cfm?adfg=fishingSportFishingInfo.displayResults&speciesid=410&countlocationid=37&year=2008 (accessed 10 March 2011)

Brase, A. L. J., and M. Doxey. 2006. Salmon studies in the Chena, Chatanika, Delta Clearwater, and Salcha Rivers, 2004 and 2005. Alaska Department of Fish and Game, Divisions of Sport Fish and Commercial Fisheries. Fishery Data Series No. 06-61,

Brodeur R. D., W. T. Peterson, G. W. Boehlert, E. Casillas, M. H. Schiewe, M. B. Eldridge, S. T. Lindley, J. H. Helle and W. R. Heard. 2000. A coordinated research plan for estuarine and ocean research on pacific salmon. Transactions of the American Fisheries Society 26:7-16.

Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference: a practical information-theoretic approach, 2nd edition. Spring-Velag, New York.

Chapman D. W. 1966. Food and space as regulators of salmonid populations in streams. The American Naturalist 100:345-357.

Decker, S. K. S. 2010. Thermal limitations on Chinook salmon spawning habitat in the northern extend of their range. MS thesis. University of Alaska Fairbanks.

Eiler, J. H., T. R. Spencer, J. J. Pella, M. M. Masuda, and R. R. Holder. 2004. Distribution and movement patterns of Chinook salmon returning to the Yukon River basin in 2002- 2002. U.S. Department of Commerce, NOAA Technical Memo. NMFS-AFSC-148.

Elliott, J. M. 1994. Quantitative ecology and the brown trout. Oxford, UK, Oxford University Press.

Fryer, G., and T. D. Iles. 1972. The Cichlid Fishes of the Great Lakes of Africa. Olive & Boyd, Edinburgh, Scotland.

Fulton, T. W. 1904. The rate of growth of fishes. Annual Report Fisheries Board of Scotland 22:141-241.

Grant, J. W. A., and D. L. Kramer. 1990. Territory size as a predictor of the upper limit to population density of juvenile salmonids in streams. Canadian Journal of Fisheries and Aquatic Sciences 47:1724-1737.

Gutierrez, L. 2011. Terrestrial invertebrate prey for juvenile Chinook salmon; Abundance and environmental controls in an interior Alaska river. MS thesis, University of Alaska Fairbanks.

Handcock, M. S., and M. Morris. 1999. Relative distribution methods in the social sciences. Springer, New York.

Healey, M. C. 1991. Life history of Chinook salmon (On*corhynchus tshawytscha).* Pages 311-394 *in* C. Groot and L. Margolis, editors. Pacific salmon life histories. University of British Columbia Press, Vancouver.

Holtby, L. B., and J. C. Scrivener. 1989. Observed and simulated effects of climatic variability, clear-cut logging, and fishing on the numbers of chum salmon (*Oncorhynchus keta*) and coho salmon (*O. kisutch*) returning to Carnation Creek, British Columbia, Pages 62-81 *in* C. D. Levings, L. B. Holtby, and M. A. Anderson, editors. Proceedings of the national workshop on effects of habitat alteration on salmon stocks. Canadian Special Publication of Fisheries and Aquatic Sciences 105.

Hughes, R. N., and C. L. Griffiths. 1998. Self-thinning in barnacles and mussels: the geometry of packing. American Naturalist 132:484-491.

Keeley, E. R. 2001. Demographic responses to food and space competition by juvenile steelhead trout. Ecology 82:1247-1259.

Lapointe, M., B. Eaton, S. Driscoll, and C. Latulippe. 1999. Modeling the probability of salmon egg pocket scour due to floods. Canadian Journal of Fisheries and Aquatic Science 27:1120-1130.

Lomnicki, A. 1988. Population ecology of individuals. Princeton University Press, Princeton.

Marschall, E. A., and L. B. Crowder. 1995. Density-dependent survival as a function of Sciences 52: 136-140. Erratum: volume 52:2304.

Mason, J. C. 1976. Response of underyearling coho salmon to supplemental feeding in a natural stream. Journal of Wildlife Management 40:775-788.

Nislow, K. H., C. L. Folt, and D. L Parrish. 2000. Spatially explicitly bionenergetic analysis of habitat quality for Age-0 Atlantic salmon. Transactions of the American Fisheries Society 129:1067-1081.

Nislow, K. H., C. L. Folt, and D. L. Parrish. 1999. Favorable foraging locations for young atlanic salmon: application to habitat and population restoration. Ecological Applications 9:1085-1099.

Nislow, K. H., C. Folt, and M. Seandel. 1998. Food and foraging behavior in relation to microhabitat use and survival of age-0 Atlantic salmon. Canadian Journal of Fisheries and Aquatic Science 55:16-127.

Otis, D. L., K. P. Burnham, G. C. White, and D. R. Anderson. 1978. Statistical inference from capture data on closed animal populations. Wildlife Monographs 62.

Pinheiro, J., D. Bates, S. Debroy, D. Sarkar, and the R Development Core team. 2008. nlme: Linear and nonlinear mixed effects models. R package version 3.1-89.

R Development Core Team (2008). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL http://www.R-project.org.

Sagar, P. M., and G. J. Glova. 1988. Diel feeding periodicity, daily ration and prey selection of a riverine population of juvenile Chinook salmon, *Oncorhynchus tshawytscha* (Walbaum). Journal of Fish Biology 33:643-653.

Sarkar, D. 2008. Lattice. Lattice Graphics. R package version 0.17-13.

Seber, G. A. F. 1982. The estimation of animal abundance and related parameters. 2nd edition. Charles Criffin and Co. Ltd. London.

SPSS Inc. 2010. IBM SPSS statistics 19. Chicago, IL, USA.

Steingrimsson, S. O., and J. W. A. Grant. 1999. Allometry of territory size and metabolic rate as predictors of self-thinning in young-of-the-year Atlantic salmon. Journal of Animal Ecology 68:17-26.

Walker, R. J. 1983. Growth of young-of-the-year salmonids in the Chena River, Alaska. MS Thesis. University of Alaska Fairbanks.

Weiner, J., and O. T. Solbrig. 1984. The meaning and measurement of size hierarchies in plant populations. Oecologia 61:334-335.

White, G. C., and K. P. Burnham. 1999. Program MARK: survival estimation from populations of marked animals. Bird Study 46: Supplement 120-138.

Figures

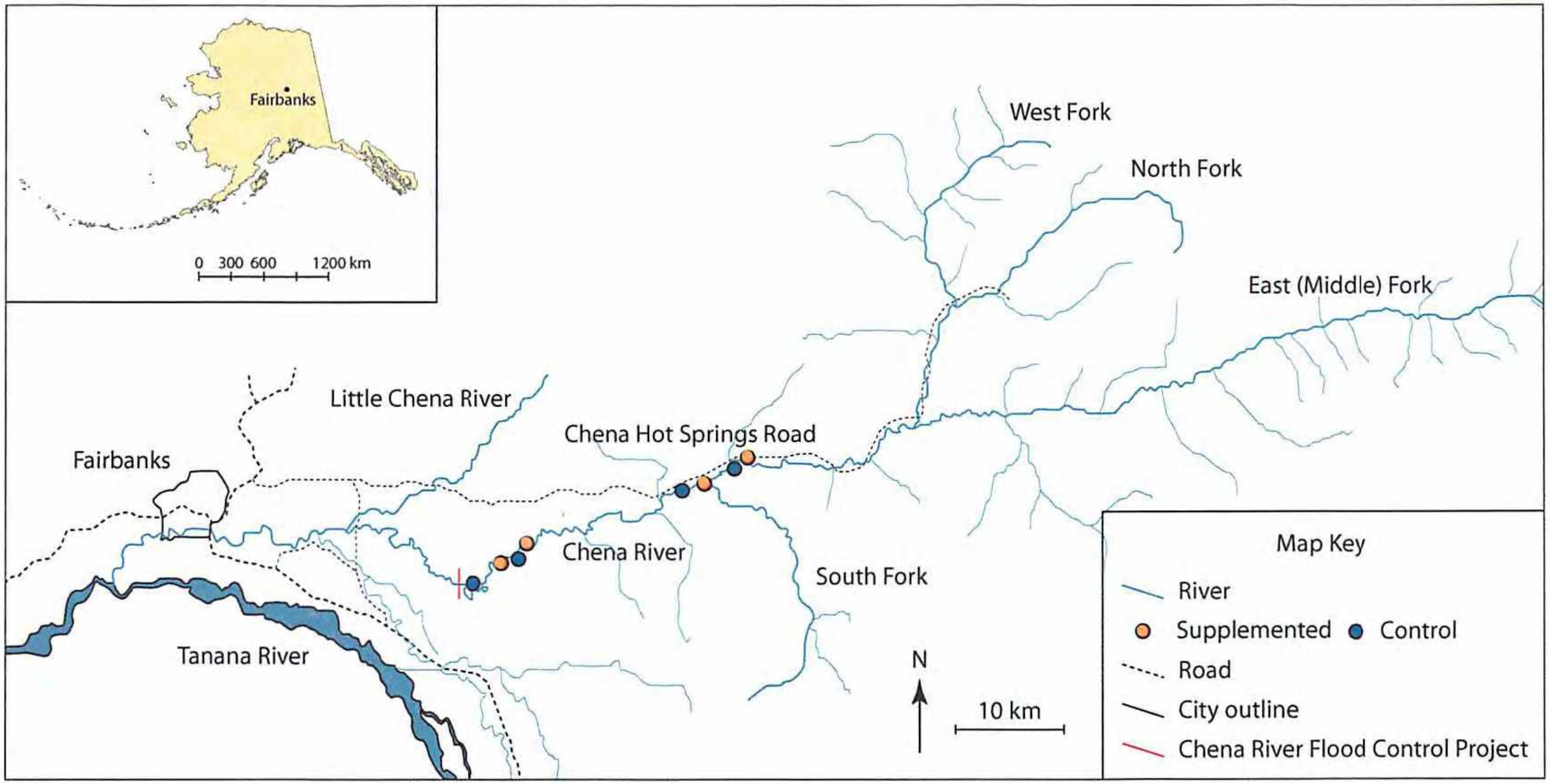

Figure 1. Map of the Chena River demarcating upper and lower study reaches and control and supplemented sites within each reach (modified from: Brase and Doxey 2006).

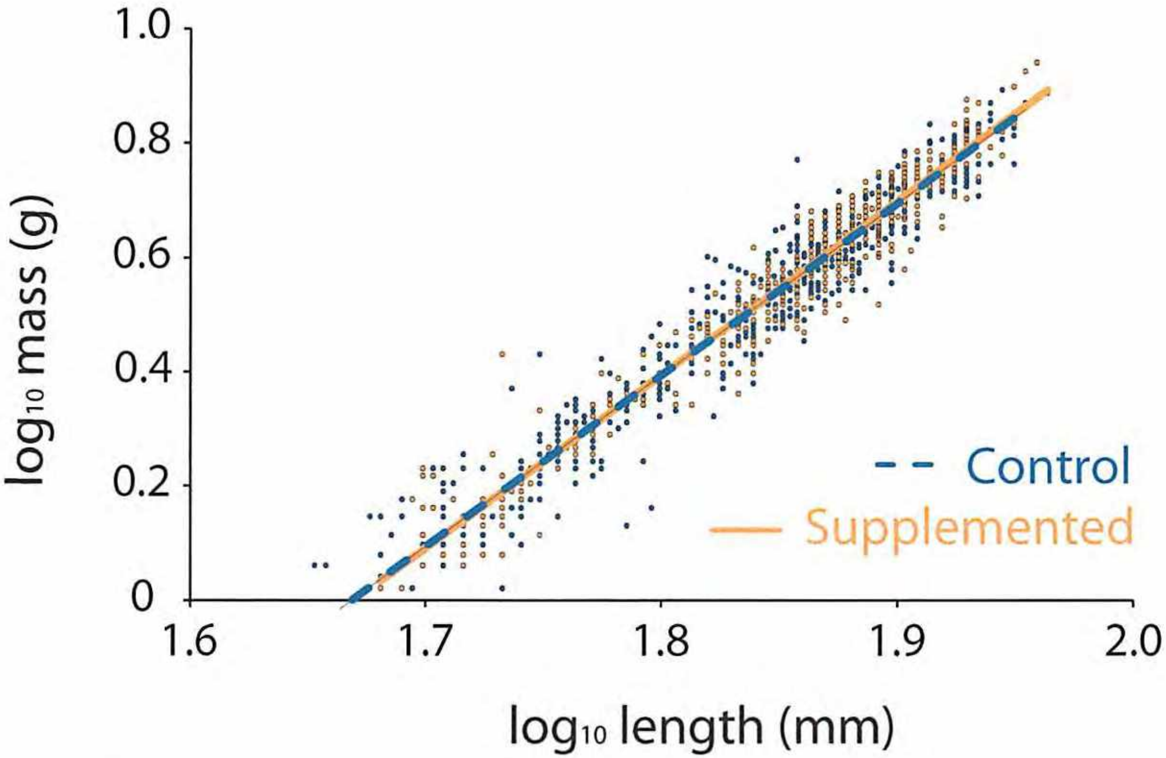

Figure 2. Regression of log-transformed mass and length for all juvenile Chinook salmon collected from upstream and downstream reaches in both control and supplemented food sites of the Chena River, Alaska.

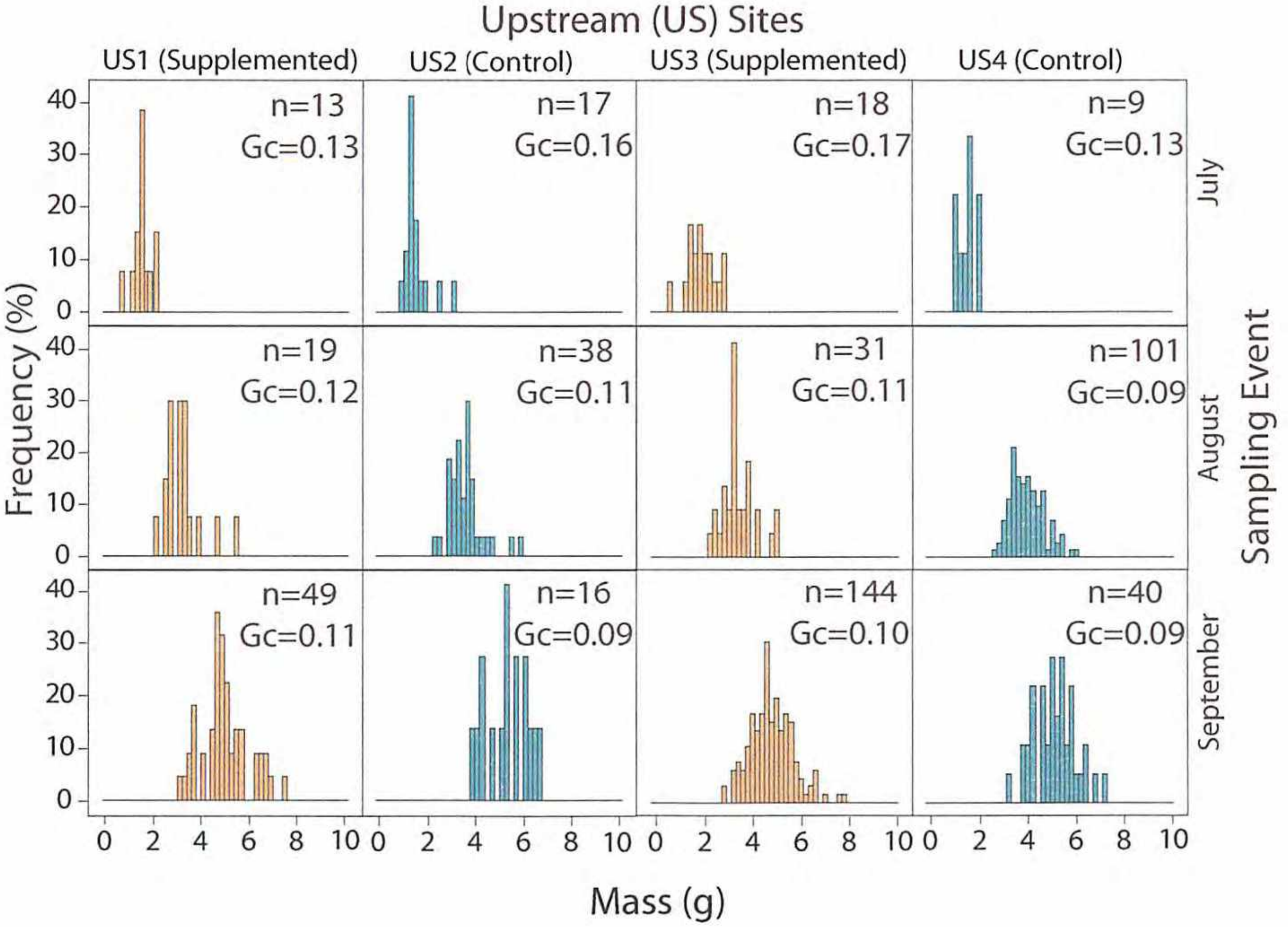

Figure 3. Mass frequency distributions of juvenile Chinook salmon at upstream sites of the Chena River, AK, 2009. In the upper right hand of each plot is the sample size used to make the plot, as well as the Gini coefficient (Gc) for the sampling event.

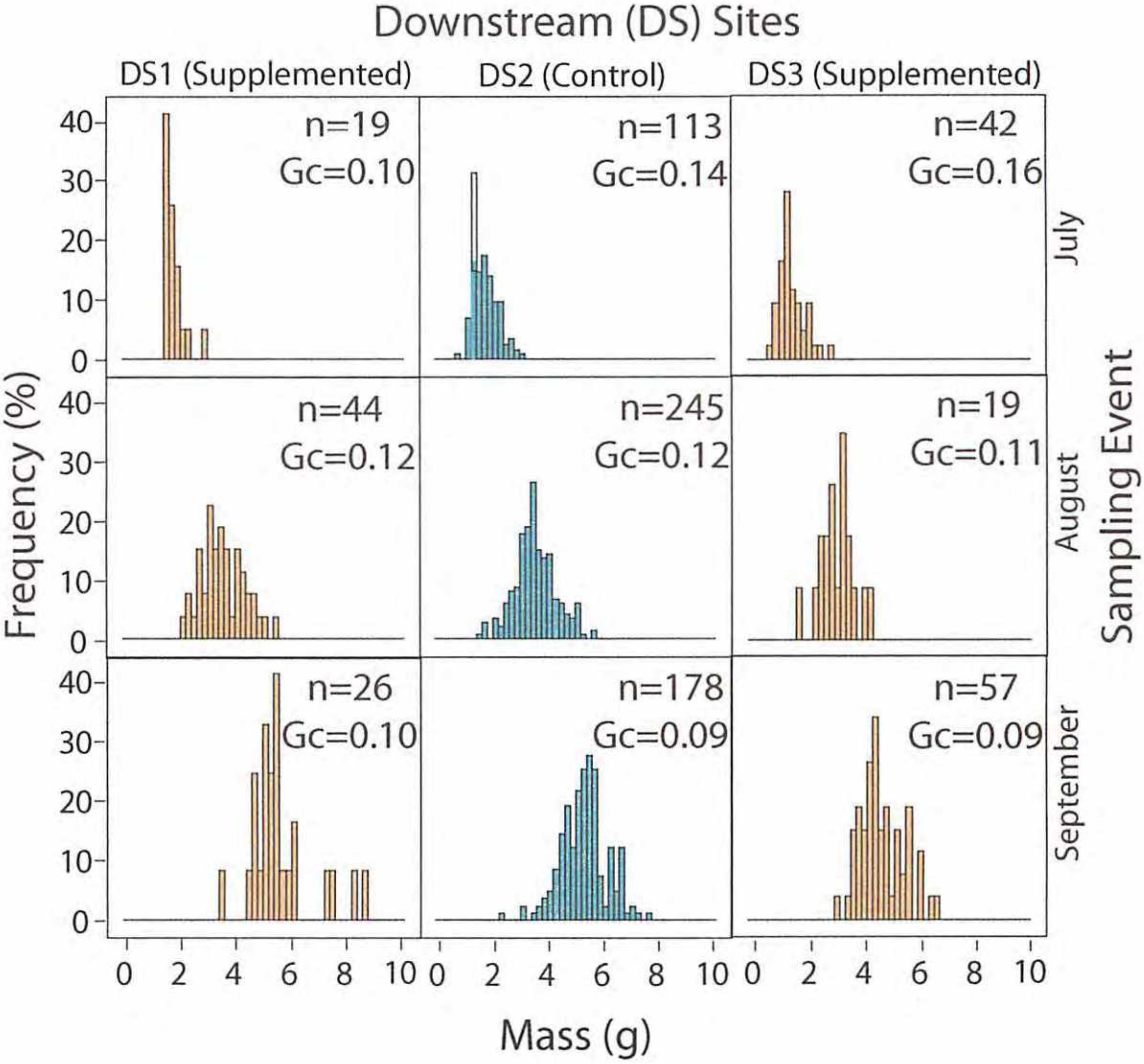

Figure 4. Mass frequency distributions of Chinook salmon at downstream sites of the Chena River, AK, 2009. In the upper right hand of each plot is the sample size used to make the plot, as well as the Gini coefficient (Gc) for the sampling event.

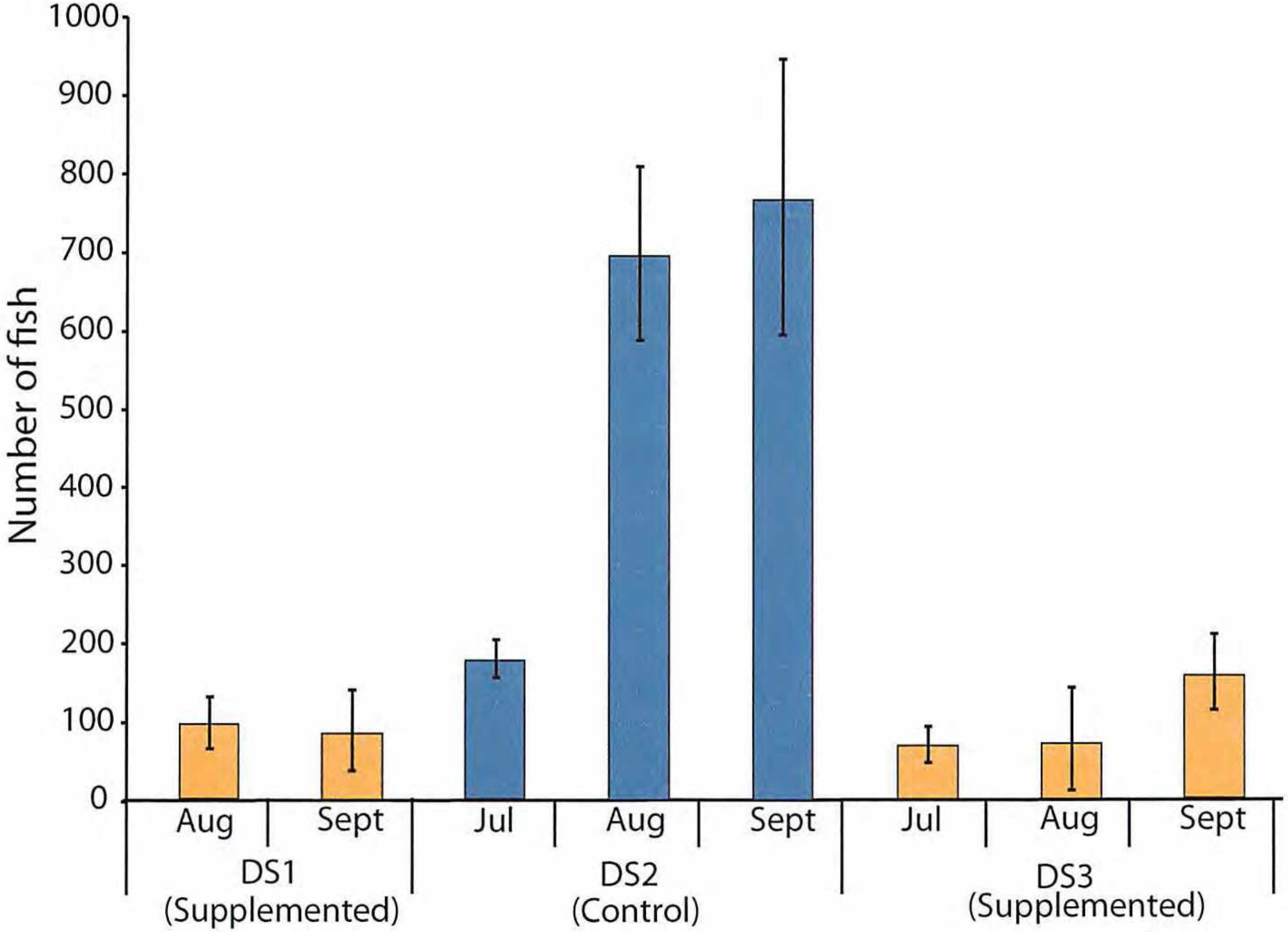

Figure 5. Abundance estimates (± standard error) of juvenile Chinook salmon at three sites in the downstream reach of the Chena River, AK, 2009.

Tables

Table 1. Sample statistics of juvenile Chinook salmon for length and mass analyses from the Chena River, AK, 2009.

	Sampling		Fork length (mm)	Mass (g)	Fulton's K
Site	Event	n	Mean (SE)	Mean (SE)	Mean (SE)
US1	Jul	13	53.3 (1.1)	1.5 (0.1)	1.00 (0.02)
	Aug	44	70.9 (0.7)	3.5 (0.1)	0.97 (0.02)
	Sept	48	77.8 (0.7)	5.0 (0.1)	1.05 (0.01)
US2	Jul	17	53.6 (1.1)	1.6 (0.1)	0.99 (0.03)
	Aug	13	71.8 (1.6)	3.7 (0.3)	0.98 (0.02)
	Sept	16	81.5 (1.0)	5.4 (0.2)	0.99 (0.03)
US3	Jul	7	56.0 (2.8)	1.9 (0.3)	1.00 (0.04)
	Aug	31	72.2 (0.7)	3.5 (0.1)	0.93 (0.02)
	Sept	63	78.8 (0.5)	4.7 (0.1)	0.96 (0.01)
US4	Jul	20	56.6 (1.0)	1.9 (0.1)	1.00 (0.02)
	Aug	101	75.0 (0.4)	4.1 (0.1)	0.97 (0.01)
	Sept	121	79.7 (0.5)	5.2 (0.1)	1.01 (0.01)
DS1	Jul	19	55.2 (1.0)	1.8 (0.1)	1.04 (0.03)
	Aug	44	70.6 (0.7)	3.6 (0.1)	1.01 (0.02)
	Sept	26	81.7 (0.9)	5.7 (0.2)	1.03 (0.02)
DS2	Jul	113	56.2 (0.4)	1.8 (0.0)	1.00 (0.01)
	Aug	245	71.4 (0.3)	3.7 (0.2)	1.02 (0.04)
	Sept	178	80.7 (0.3)	5.4 (0.1)	1.02 (0.01)
DS3	Jul	42	54.1 (0.7)	1.5 (0.1)	0.94 (0.01)
	Aug	19	67.1 (1.1)	3.1 (0.2)	1.01 (0.02)
	Sept	57	77.5 (0.6)	4.8 (0.1)	1.02 (0.01)

Table 2. Sample size (n), Abundance estimates ± standard error (SE), and Total CPUE for each sampling event of juvenile Chinook salmon at upstream (US) and downstream (DS) sites of the Chena River, AK, 2009.

Site	Sampling Event	n	Abundance	(SE)	Total CPUE
US1	Jul	13	-	-	6.9
	Aug	44	-	-	9.3
	Sept	48	-	-	9.7
US2	Jul	17	-	-	5.0
	Aug	13	-	-	2.3
	Sept	16	-	-	3.5
US3	Jul	7	-	-	0.3
	Aug	31	-	-	4.8
	Sept	63	-	-	42.9
US4	Jul	20	-	-	3.0
	Aug	101	-	-	27.8
	Sept	121	-	-	11.7
DS1	Jul	19	-	-	1.2
	Aug	44	100	(30)	4.6
	Sept	26	86	(50)	3.9
DS2	Jul	113	175	(24)	8.2
	Aug	245	693	(110)	52.0
	Sept	178	756	(175)	39.8
DS3	Jul	42	80	(22)	3.2
	Aug	19	74	(65)	2.7
	Sept	57	159	(48)	12.1

Chapter 2

Retrospective analysis of juvenile Chinook salmon growth in an Interior Alaska River: Insight into marine survival and density dependence[3]

Abstract

Water temperature is an important density-independent variable that influences growth of juvenile salmonids rearing in fresh water. In the Chena River, a tributary of the Yukon River in Interior Alaska, temperature may be the most important factor regulating growth of rearing juveniles. In this study we tested the hypothesis that freshwater growth of juvenile Chinook salmon *Oncorhynchus tshawytscha* is positively correlated with marine survival, as measured by recruits per spawner. We used Generalized Additive Models (GAM) to investigate the growth in length of juveniles rearing at eight sites along the Chena River in 2009. Using a non-linear regression approach, we estimated water temperature from the Hunts Creek gauging station on the Chena River back to 1967. We used a simple individual based bioenergetics approach to estimate size of juvenile Chinook at the end of their first summer residency using actual and hindcasted water temperature data to estimate fish length from the 1981 brood year forward. We used data from a stock recruit analysis conducted by the Alaska Department of Fish and Game to determine whether a relationship between water temperature, freshwater growth, and marine survival exists in the Chena River. We did not find

---

[3] Perry, M. T., M. S. Wipfli, N. F. Hughes, J. R. Neuswanger, A. E. Rosenberger and M. J. Evenson. 2012. Retrospective analysis of juvenile Chinook salmon growth in an Interior Alaska River: Insight into marine survival and density dependence. Prepared for submission to Transactions of the American Fisheries Society.

evidence that marine survival is correlated with freshwater growth; however, we did find evidence suggesting that growth during the freshwater rearing period may be related to food availability following years when adult escapement is high.

Introduction

Temperature influences a number of physiological process that determine growth in fish, including metabolic rate and oxygen supply (Elliott 1994), thereby affecting survival, growth rates, distribution and the development of juvenile salmonids. At high latitudes, warmer water tends to produce bigger fish (Dion and Hughes 2004). During the summer rearing season, temperature may be the most important factor regulating juvenile Chinook salmon *Oncorhynchus tshawytscha* growth in the Chena River. On maximum rations, juvenile Chinook salmon growth is optimized at 19°C (Brett et al. 1982), however, their thermal preference is between 11 and 12°C (Brett 1952). During the summer, the Chena River is near optimal temperatures of growth for juvenile Chinook salmon, but high fish densities may increase the potential for food limitation.

Growth of juvenile salmonids may affect survival to maturity, with greater growth in freshwater correlated with greater marine survival (Henderson and Cass 1991; Koenings et al. 1993). The development of seawater tolerance (smoltification) in Chinook salmon is partially a function of size (Clarke and Shelbourn 1985), with larger smolt having higher marine survival rates (Ward et al. 1989; Zabel and Achord 2004), indicating that large fish may have a competitive advantage when they enter the marine environment (Zabel and Williams 2002). Faster growing fish may be more effective at prey capture earlier, increasing their growth and survival rates (Mortensen et al. 2000; Quinn 2005), and larger fish may have better winter survival in the marine environment, when prey are less available (Beamish and Mahnken 2001).

If temperature and food abundance regulate the growth of salmonids, these factors may impact the number of recruits per spawner. This leads to the prediction that, at high latitudes, warmer water temperatures and longer growing seasons should be correlated with higher survival and more recruits per spawner. We investigated growth during the first summer rearing season for juvenile Chinook salmon, to see if it is a factor influencing survival of salmon in the marine environment.

We hypothesized that the density-independent factor, temperature, regulates growth of juvenile Chinook salmon rearing in the Chena River and that growth achieved during the freshwater residency may help explain variability in abundance of adult Chinook salmon returning to the river to spawn. To test this hypothesis, we measured water temperature and juvenile Chinook salmon growth in the river over 3 years. We then used a bioenergetics model to predict end of summer length of juvenile salmon back through 1981 to compare estimated growth to the number of recruits per spawner returning to the river.

Methods

Study Area

Our study took place in the Chena River, Alaska, a tributary in the middle Yukon drainage supporting a large spawning population of Chinook salmon. The Chena River drains a watershed of 5,130 km^2 and has five major tributaries; the North Fork, West Fork, South Fork, East (Middle) Fork, and Little Chena River. It originates in the Tanana Uplands and it flows approximately 241 km from the uppermost reach of the East Fork to its confluence with the Tanana River at Fairbanks. It is one of the largest clearwater streams in the Tanana drainage. A pilot study conducted in 2007 indicated that the majority of juvenile Chinook salmon reared between river kilometers 95 and 160 upstream from its confluence with the Tanana River (Wipfli, unpubl. data). Surveys on spawning adults indicate that the majority of spawning occurs in the lower 150 km of the river (Decker 2010). Adults migrate to the Chena River in July and August to spawn. Eggs incubate during the fall and winter, and the juvenile salmon emerge from the gravel the following spring. Juveniles spend one complete year in freshwater after emerging, and then migrate out to the ocean the following spring, where most will spend 3 or 4 years before returning to spawn. Juvenile Chinook salmon that emerge in the Chena River also rear there, rather than moving downstream and out to other rearing areas (Walker 1983).

Length Data

We gathered juvenile Chinook salmon length data over the summer in 2009 via underwater videography at eight sites; four upstream sites (US1-4) were located between 64.864021N, -146.782157W, and 64.892929N, -146.648643W and four downstream sites (DS1-4) were located between, 64.790316N, -147.162720W and 64.822348N, -147.074728W. The video recording system consisted of two Sony 480 Exview Microcrams mounted to a lightweight aluminum rod; underwater footage was recorded using two Sony HC32 digital recorders. When we first arrived at a site, we visually identified where fish were located within the site before introducing the camera into the water to record video of fish and of the calibration object (a 3-D grid of dots on a clear polycarbonate cube) for 3-D measurements. Approximately 10 minutes of video were recorded at each site, for each session. Once video was recorded, we used the freely available software program VidSync 1.2 (vidsync.sourceforge.net; Neuswanger, pers. comm.) to estimate fish length from the video. Video from the cameras was uploaded into the VidSync program and footage from paired cameras was synchronized. Using video of the calibration object, the software calculated 2D-to-2D projective transformations from the screen coordinates of both videos to two surfaces of the cube. For each measurement of a fish's head or tail, we clicked the object and the software calculated a line through two surfaces to represent the line-of-sight from the camera. It then intersected the lines from both cameras to triangulate the position of a fish's head or tail in 3-D, and calculated the length of a fish based on the 3-D distances between its head and tail. We tested the accuracy of measurements by measuring the length of known objects in our videos; additionally, the mean and variance in the length distributions collected by video methods were not significantly different from those collected by minnow traps during the same period of time ($t = 0.0476$, d.f. = 29.689, $p = 0.9624$).

We also recorded fish lengths while conducting mark-recapture abundance estimates (Chapter 1). Sampling was designed to estimate abundance at each site during three periods (July, August, and September 2009). Each experiment consisted of three capture events conducted over three consecutive days. Ten Gee-type minnow traps (23 x

45 cm, 0.6 cm wire mesh, 2.5 cm diameter opening) baited with salmon roe were set out at each of the sites and allowed to soak for 2-5 hours. Captured fish were placed in a bucket of river water and anesthetized with tricaine methanesulphonate (MS-222®) until they lost equilibrium. Then we measured fork length to the nearest mm, and mass was measured to the nearest 0.01 g using a Pescola® spring scale.

A concurrent study provided information on fish diet (Gutierrez 2011). Fish in this study were sampled in four sites, two sites in the upstream reach, and two sites in the downstream reach. Juvenile Chinook salmon stomach contents were sampled approximately every other week from 6 June to 25 September 2008 and from 12 May to 15 September 2009, for a total of eight sampling events each summer. Fish were captured using dip nets and seines in early summer (May-mid July) because minnow traps were not effective in the beginning of the season; from mid-July through September, baited minnow traps were used to capture fish. Sampled fish were measured for length (nearest mm), and fish mass (nearest 0.1 g) was also measured.

We found historical length data from 1981, 1982, 1995 and 1996 from two theses. The length data for years 1981 and 1982 were from juvenile Chinook salmon sampled during the summer rearing period and were collected using standard minnow traps and common sense minnow seines at 8 sites, located upstream from the mouth of the Chena River at river kms 9.6, 35, 42, 71, 124, 134, 148, and 188 (Walker 1983). For the purpose of our study, we excluded the Badger Slough (35 km) and Nordale Road (42 km) sites because of skew in the data caused by capturing age 1+ juvenile Chinook salmon. The 1995 and 1996 data came from spring sampling efforts on outmigrating smolt, primarily sampled by a rotary screw trap, but also with minnow traps, beach seines, and a modified incline plane trap (Daigenault 1997). Three sampling sites (upper, middle, and lower) were located near the Moose Creek Dam, which is 71 km from the mouth of the Chena River. Although the 1995 and 1996 data were collected from outmigrating salmon we considered using it to compare our model prediction of end of first growing season length because it is typically strongly correlated with early smolt lengths; Bradford et al. (2001) showed that growth slowed considerably over winter for juvenile Chinook salmon, and winter growth for Arctic grayling is <10% that of summer growth (Roguski and Schallock 1967). However, Bradford et al. (2001) also found that early season growth in May and June before smoltification was significant, with mass of the fish doubling, and mean length increasing 18mm before outmigration. After further investigation of the historical data, we decided to exclude the 1995 smolt data, because of small sample size and because observed length was much greater (10-20 mm) than any other years' actual or predicted length. We believe this is because the sampling was conducted later in the 1995 study season in order to increase sample size, and the fish likely experienced rapid growth in length in the short open water period before the sampling occurred. We used only length data from 1996 for comparisons of observed to predicted length, because of earlier sampling dates, consistent sampling techniques and higher sample size in that year.

Temperature Data

During 2009, average daily water temperature was calculated from hourly measurements made at each site using HOBO® data loggers (Onset Corporation, Bourne, MA, USA) suspended from instream woody debris and weighted to the streambed. We obtained additional water temperature data collected by the United States Geological Survey (USGS) at the Hunts Creek gauging station near Two Rivers, 64.860006°N, -146.803319°W, (USGS 14593400). Hourly water temperature data were available from 11 September 2006 forward. Air temperature data were collected from the Fairbanks International Airport, 64.815°N 147.85639°W, by the Alaska Climate Research Center, part of the Geophysical Institute at the University of Alaska Fairbanks. The USGS has been collecting stream discharge data since 1967 from the Chena River, near Two Rivers gauging station, 64.902758°N, -146.356972°W, (USGS 15493000).

For years when instream water temperature data were not available, we used a model for predicting water temperature based on air temperature and discharge (van Vliet et al. 2011)

$$Tw = \mu + \frac{\alpha - \mu}{(1 + e^{\gamma(\beta - Tair)})} + \frac{\eta}{Q} + \varepsilon .$$

$$\text{with } \gamma = \frac{4\tan\theta}{\alpha - \mu}$$

where μ = lower bound of water temperature (°C); α = upper bound of water temperature (°C); γ = measure of the slope at inflection point (steepest slope) of the S-shaped relation (°C^{-1}); β = air temperature at inflection point (°C); η = fitting parameter

(°C m^3s^{-1}); Tw = water temperature(°C); $Tair$ = air temperature (°C); Q = river discharge (m^3s^{-1}); ε = error term (°C); and $tan\ \theta$ = slope at inflection point (-).

To apply this equation, we used Mathematica (Wolfram Research, Inc. 2008) to use a long time series of daily air temperature data available from the Fairbanks International Airport and daily discharge data from the USGS gauging station on the Chena River near Two Rivers, AK (USGS 15493000), available since October 1, 1967, and water temperature from the USGS gauging station at Hunts Creek since September 2006. During the period that all data series overlapped (2006-2011), we calculated a regression to estimate water temperature based on air temperature at the airport and discharge and used that regression to generate a complete water temperature time series.

Water temperatures tend to lag behind air temperature (Erickson and Stefan 2000; Jeppesen and Iversen 1987; Webb et al. 2003), and, because of this, a lag effect was incorporated into the regression analysis (van Vliet et al. 2011). For the Chena River we found that water temperature was most correlated with air temperature from the previous day. We ran linear and non-linear models to predict water temperature, in addition to models with air temperature and discharge alone (both variables squared, or with just one squared). Using ANOVA and ranking the models using Akaike's Information Criterion (AIC) (Burnham and Anderson 2002), the model with air temperature squared alone was best. Discharge was relevant, but barely; it accounted for very little of the variance, and the discharge parameter was not significant ($p = 0.25$).

Growth Modeling

We investigated growth over time using Generalized Additive Models (GAM) (Wood 2006) in the 'mgcv' package version 3.1-89 in the R programming environment (R Development Core Team 2008). For all models we investigated the growth patterns, measured in terms of length, by date. We estimated each model on two levels; by reach (upstream vs. downstream) and with full models fit with all sites. Our first model type was relatively simple, and examined the growth by site or reach. This model assumed the same growth pattern at each site, but a fixed difference in length between sites (i.e., a growth curve shifted up or down). We also fit a model that allowed for different growth patterns by site and reach, and ranked the models using AIC. ΔAIC suggested that the more complex model with different growth curves for each site was the best fit for the data. To compare differences between sites, we refit the GAM using a polynomial with 5 d.f., which was roughly equivalent to our estimated degrees of freedom in our 'best' GAM model and ran pairwise comparisons between all sites.

Bioenergetics

To test the hypothesis that temperature regulates growth of juvenile Chinook salmon rearing in the Chena River, we used a simple individual based model from Rasmussen and From's (1991) rainbow trout bioenergetics model to predict the growth of a single rainbow trout through different temperature histories. Bioenergetics models are useful tools; one way they can be used is to detect poor growth by comparing measured length to predicted length under optimal conditions (maximum rations) and they can be used to identify factors that limit growth (e.g., food, space, and predation). We used the Rasmussen and From model because the required parameters have not yet been established for Chinook salmon, because it is parameterized to a more closely related stream salmonid in the same genus (*Oncorhynchus*) than other available bioenergetics models (e.g., genus *Salmo*, Elliott et al. 1995), and because it was parameterized for fish in a similar size range experiencing similar temperatures. This model was derived for rainbow trout on pellets, however, it showed no significant difference in parameters between dry and wet pellets (From and Rasmussen 1984), suggesting that the parameters are not overly sensitive to food type. Larsson and Berglund (1998) found in Arctic charr *Salvelinus alpinus* that the relationship between growth and temperature was not significantly different between food pellets and live *Neomysis* food. The main difference between food sources is that the maximum ration (i.e. the maximum amount of food a fish is able to consume) on wild food is much smaller, around 0.3x the maximum pellet ration, averaged over all fish of all sizes in one productive stream studied (Rasmussen, pers comm.). We suspect this is caused by both the lower energy density of wild food and the practical limitations of drift-feeding. The model we used takes this pellet-to-wild-food multiplier as an adjustable parameter for determining the maximum daily ration.

We input mean daily water temperature data into the model for the period of the summer growing season when mean water temperature was above 4°C. For our first application of the model, we averaged daily mean water temperature data collected *in situ* at each of our sites in 2009, to get a daily mean temperature for upstream and downstream reaches. For brood years 2007-2009, we also ran the model using temperature data collected by the USGS at Hunts Creek. For brood years 1981-2006, we input hindcasted temperature data into the model.

We compared the model output length and weight with observed fish length and weight data collected during 2009 to determine how well it predicted growth throughout the freshwater rearing season at upstream and downstream sites. The model did not predict end of season Chinook weight accurately, which may be due to species differences for which the model was parameterized; however, the model did accurately predict length. Using actual and hindcasted temperature data from Hunts Creek, we predicted the length of juveniles at the end of the freshwater rearing season given maximum wild rations, approximately where the first annulus would be deposited on their scales for brood years 1981-2009. We compared predicted to actual length of juveniles at the end of their first summer using data we collected during our 3-year study, as well as fish length data from Chena River salmon found in the literature for years 1981, 1982, and 1996.

Survival

To examine the relationships between smolt size, temperature, and survival of salmon, and to determine whether there is a positive correlation between smolt size and the productivity of a brood year (in terms of recruits per spawner), we used estimates of recruits per spawner for years 1986-2002 from the Alaska Department of Fish and Game stock recruitment analysis (Matthew Evenson, ADF&G, pers. comm.) and regressed these on predicted smolt size estimated using the Rasmussen and From (1991) bioenergetics model.

Results

Considering the growth in length at each site by date using a polynomial, the trend in length was highly significant ($r^2 = 0.91$, $F_{8,304} = 391.8$, $p < 0.001$). Using pairwise comparisons, all upstream and downstream sites were significantly different from each other ($p < 0.001$). In the upstream reach, the furthest upstream site was significantly less than all other sites ($p < 0.001$), the rest were not significantly different ($p > 0.168$). In the downstream reach, DS1 was not significantly different from any of the other sites ($p > 0.187$). DS3 was significantly less than DS2 ($p < 0.001$), and DS4 was significantly greater than DS3 ($p < 0.001$), but DS2 and DS4 were not significantly different ($p = 0.658$).

Using temperature data collected *in-situ*, Rasmussen and From's (1991) bioenergetic model worked well to predict length of juvenile Chinook salmon based on maximum wild rations during the 2009 summer growing season. There was a strong correlation between predicted and observed growth in both upstream and downstream reaches ($r^2 = 0.95$ and 0.93, respectively) (Figure 1).

Using temperature data from Hunts Creek, we were able to predict fish length at the end of the summer rearing season for years 1981-2009. Of 18 observations of fish length from 6 years of data, the predicted length was encompassed by the confidence interval of observed length in 4 observations. From 2007-2008, using actual water data from the Hunts Creek USGS gauging station, our predicted length was within 2 standard errors of observed length at the end of the summer growing season, and, in 2009 predicted length was within 2 standard errors of observed length for 1 of our 4 comparisons (Table 1). Using the hindcasted temperature data from Hunts Creek, predicted growth was 1.1 – 3.1 mm less than observed growth of smolt during 1996 (Daignault 1997). In 1981 and 1982, predicted growth was greater than observed for all sites by as much as 17 mm (Walker 1983).

Estimated smolt length was not correlated with recruits per spawner ($r^2 = 0.049$, $p = 0.39$) (Figure 2). The relationship between recruits per spawner and growing degree-days and mean summer temperature were also not significant ($r^2 = 0.047$ and 0.0005 respectively, and $p = 0.39$ and 0.93, respectively).

Discussion

Our primary goal in this study was to investigate if temperature or food availability was the primary factor limiting growth of juvenile Chinook salmon in the Chena River. Density-dependence is often assumed the most important biological mechanism for both individual fish condition and overall production of fish populations; a thermal limitation to growth would instead imply that food and space were readily available to juvenile fish and other, density-independent factors may be more important in limiting juvenile production. A bioenergetics model (Rasmussen and From 1991) assuming maximum wild rations worked well to predict growth of juvenile Chinook salmon in 2009 (Figure 1). Only in 1980 and 1981 (Walker 1983) were observed lengths less than predicted by the bioenergetics model (Table 1); for all other years of data, the predicted length was greater (i.e. 1996, 2009) or within 2 standard errors of observed length (i.e. 2007, 2008). Walker (1983) noted in his thesis that the 1980 and 1981 escapements of Chinook salmon in the Chena River were the highest in recent years (Fred Anderson, ADF&G, pers. comm.) and stated that those high escapements probably resulted in high densities of juvenile Chinook salmon the following year. Unfortunately, mark-recapture and counting tower estimates of escapements of adult salmon on the Chena River were not initiated until 1986, so we do not have a metric to compare the runs in 1980 and 1981. Conversely, the runs in 2006-2008 were three of the lowest seven escapements since run estimates have been made, and, in the rearing years following the 2006-2008 escapements (2007-2009), the bioenergetics model effectively predicted growth (i.e. 2007-2008) or underestimated growth (i.e. 2009) on maximum wild rations, which suggests that density-dependent interactions were not occurring. In 1981 and 1982, our bioenergetics model predicted growth only when reduced rather than maximum rations were assumed (Table 2). This implies potential for food limitation in the Chena River, but only during high-escapement periods, though it does not preclude the importance of other density-dependent factors such as space and feeding territory. Our results imply temporal dynamics in the importance of density-dependent processes; in years when Chinook salmon runs were average or low, density-independent factors (e.g., floods during spawning or scouring spring flows) may have overwhelmed the potential for density-dependence, and juvenile Chinook salmon growth was limited only by river temperature.

Observed growth of individual fish along the Chena River was not uniform due to spatial variability in thermal regimes along the Chena River, both at the reach scale (e.g., upstream versus downstream reaches) and at the site scale (e.g., sites within an upstream or downstream reach). Because of this, temperature influences on average length of a cohort at outmigration may be better predicted and inferred at whole-reach scales (Walker 1983; Gutierrez 2011). Further, interannual variability in temperatures and density-dependent processes implies predictions are most valid if made on a cohort-by-cohort basis, factoring in run size, thermal conditions, and the length of the growing season. However, if investigating spatial variability in growth potential within a single cohort is the focus of the study, a full thermal profile of the river will be required; very subtle differences in thermal regimes resulted in differential observed growth among river locations.

Our secondary goal in this study was to examine if there was a positive relationship between predicted growth of juvenile Chinook salmon during their freshwater period and the productivity of a brood year in terms of recruits per spawner. Our study did not detect such a relationship; however, this may be due to our assumption of maximum potential growth (i.e., no food limitation) for estimating fish length. A limitation in testing our bioenergetics model is its low sample size – data for actual end of season lengths were available for only 5 years. Further, our ability to validate our model was only for those years of low escapement (n= 3), when food limitation was unlikely. A bioenergetics model that modifies ration based on escapement size would be possible if additional data were available; we recommend sampling juvenile Chinook salmon at the end of the first summer rearing season to determine average cohort length. A long-term data set of this kind would be relatively inexpensive to obtain and would allow for an effective test of whether juvenile length at the end of the first growing season significantly affects overall marine survival on a cohort-by cohort basis. This is certainly not a given; some years of high escapement in the Chena River have been followed by high returns, which indicates that, even if density-dependent interactions are negatively affecting overall growth of juvenile Chinook salmon in freshwater, this does not, in turn, negatively affect their marine survival. Research suggests that it is in the marine life stage that population-level controls take place, which limits our potential to make marine survival predictions based on individual traits during their freshwater phase (Beamish and Mahnken 2001).

In a dynamic system like the Chena River, we anticipate but do not always account for variability in ecological processes that regulate the demographic characteristics and abundance of juvenile salmon. Numerous and highly dynamic processes over a large area (i.e., oceanic conditions, weather, flooding, adult returns, habitat quality, and food availability) make this task difficult. This is certainly the case for our study; we were unable to observe consistent evidence of either density-independent or density-dependent processes on freshwater growth of juveniles. However, our bioenergetics model showed potential for testing the assumption of density-dependence on a cohort-by-cohort basis, a powerful tool for predicting and understanding demographic processes within the Chena River population and beyond.

References

Beamish, R. J., 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 49:423-437.

Bradford, M. J., J. A. Grout, and S. Moodie. 2001. Ecology of juvenile Chinook salmon in a small non-natal stream of the Yukon River drainage and the role of ice condition on their distribution and survival. Canadian Journal of Zoology 79:2043-2054

Brett, J. R., 1952. Temperature tolerance in young Pacific salmon, genus *Oncorhynchus*. Journal of the Fisheries Research Board of Canada 9:265-323.

Brett, J. R., W. C. Clarke, and J. E. Shelbourn. 1982. Experiments on thermal requirements for growth and food conversion efficiency of juvenile Chinook salmon. Nanaimo, B.C.: Department of Fisheries and Oceans, Fisheries Research Branch. Canadian Technical Report of Fisheries and Aquatic Sciences No. 1127.

Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference: a practical information-theoretic approach, 2nd edition. Spring-Velag, New York.

Clarke, W. C., and J. E. Shelbourn. 1985. Growth and development of seawater adaptability by juvenile fall Chinook salmon (*Oncorhynchus tshawytscha*) in relation to temperature. Aquaculture 45:21-31.

Daigneault, M. J. 1997. Health and condition of juvenile Chinook and chum salmon near the Chena River Dam, Alaska. MS thesis, University of Alaska Fairbanks.

Decker, S. K. S. 2010. Thermal limitations on Chinook salmon spawning habitat in the northern extend of their range. MS thesis. University of Alaska Fairbanks.

Dion, C. A., and N. F. Hughes. 2004. Assessing the ability of a temperature-based growth model to predict growth of age-0 Arctic Grayling. Transactions of the American Fisheries Society 133:1047-1050.

Elliott, J. M. 1994. Quantitative ecology and the brown trout. Oxford University Press, Oxford.

Elliott, J. M., M. A. Hurley, and R. J. Fryer. 1995. A new, improved growth model for brown trout, *Salmo trutta*. Functional Ecology 9:290-298.

Erickson, T. R., and H. G. Stefan. 2000. Linear air/water temperature correlations for streams during open water periods. Journal of Hydrological Engineering 5:317-322.

From, J., and G. Rasmussen. 1984. A growth model, gastric evacuation, and body composition in rainbow trout, *Salmo gairdneri* Richardson, 1836. Dana 3:61-139.

Gutierrez, L. 2011. Terrestrial invertebrate prey for juvenile Chinook salmon; Abundance and environmental controls in an interior Alaska river. MS thesis, University of Alaska Fairbanks.

Henderson, M. A., and A. J. Cass. 1991. Effects of smolt size on smolt-to-adult survival for Chilko Lake sockeye salmon. Canadian Journal of Fisheries and Aquatic Sciences 48:988-994.

Jeppesen, E., and T. M. Iversen. 1987. Two simple models for estimating daily mean water temperatures and diel variations in a Danish low gradient stream. Oikos 49:149-155.

Koenings, J. P., H. J. Geiger, and J. J. Hasbrouck. 1993. Smolt-to-adult survival patterns of sockeye salmon: effects of smolt length and geographic latitude when entering the sea. Canadian Journal of Fisheries and Aquatic Sciences 49:600-611.

Larsson, S., and I. Berglund. 1998. Growth and food consumption of age 0+ Arctic charr fed pelleted or natural food at six different temperatures. Journal of Fish Biology 52:230-242.

Mortensen, D., J. Ito, S. Ito, and H. Godfrey. 2000. The relation between early marine growth of pink salmon, *Oncorhynchus gorbuscha*, and marine temperature, secondary production and survival to adulthood. Fishery Bulletin 98:319-335.

Quinn, T. P. 2005. The behavior and ecology of pacific salmon and trout. University of Washington Press, Seattle, Washington.

R Development Core Team. 2008. R: A language and environment for statistical compusion. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL http://www.R-project.org.

Rasmussen, G., and J. From. 1991. Improved estimates of a growth model and body composition of rainbow trout, *Oncorhynchus mykiss* (Walbaum, 1792) as function of feeding level, temperature and body size. Dana 9:15-30.

Roguski, E. A., and E. W. Schallock. 1967. Investigations of the Tanana River and Tangle Lakes grayling fisheries: migratory and population study. Alaska Department of Fish and Game. Federal Aid in Fish Restoration, Annual Report of Progress, 1966-1967, Project F-5-R-8, 8(16-b).

van Vliet, M. T. H., F. Ludwig, J. J. G. Zwolsman, G. P. Weedon, and P. Kabat. 2011. Global river temperatures and sensitivity to atmospheric warming and changes in river flow. Water Resources Research 47 W02544.

Walker, R. J. 1983. Growth of young-of-the-year salmonids in the Chena River, Alaska. MS thesis, University of Alaska Fairbanks.

Ward, B. R., P. A. Slaney, A. R. Facchin, and R. W. Land. 1989. Size-biased survival in steelhead trout: back-calculated lengths from adults' scales compared to migrating smolts at the Keogh River, B.C. Canadian Journal of Fisheries and Aquatic Sciences 46:1853-1858.

Webb, B. W., P. D. Clack, and D. E. Walling. 2003. Water-air temperature relationships in a Devon river system and the role of flow, Hydrological Processes 17:3069-3084.

Weiner, J., and O. T. Solbrig. 1984. The meaning and measurement of size hierarchies in plant populations. Oecologia 61:334-335.

Wood, S. N. 2006. Generalized additive models: An introduction with R. Chapman and Hall/CRC, Boca Raton, FL.

Zabel, R, W., and S. Achord. 2004. Relating size of juveniles to survival within and among populations of Chinook salmon. Ecology 85:795-806.

Zabel, R. W., and J. G. Williams. 2002. Selective mortality in Chinook salmon: what is the role of human disturbance? Ecological Applications 12:173-183.

Figures

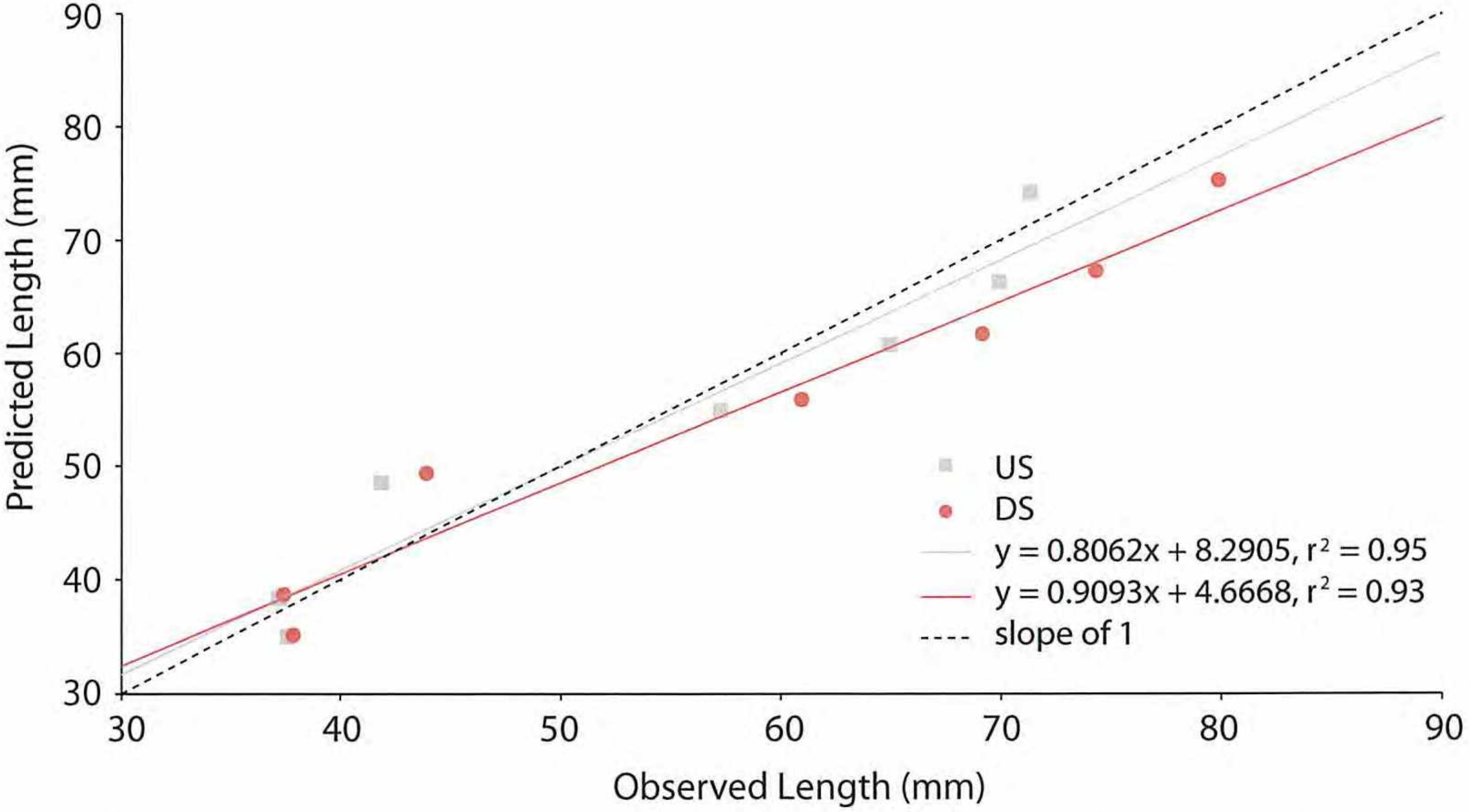

Figure 1. Mean observed length for fish in upstream and downstream reaches of the Chena River, Interior Alaska summer 2009, versus bioenergetics model (Rasmussen and From 1991) predicted lengths, based on temperature and maximum wild rations. The solid lines represent the relationships between observed and predicted growth. The dashed line represents a line with a slope of 1.

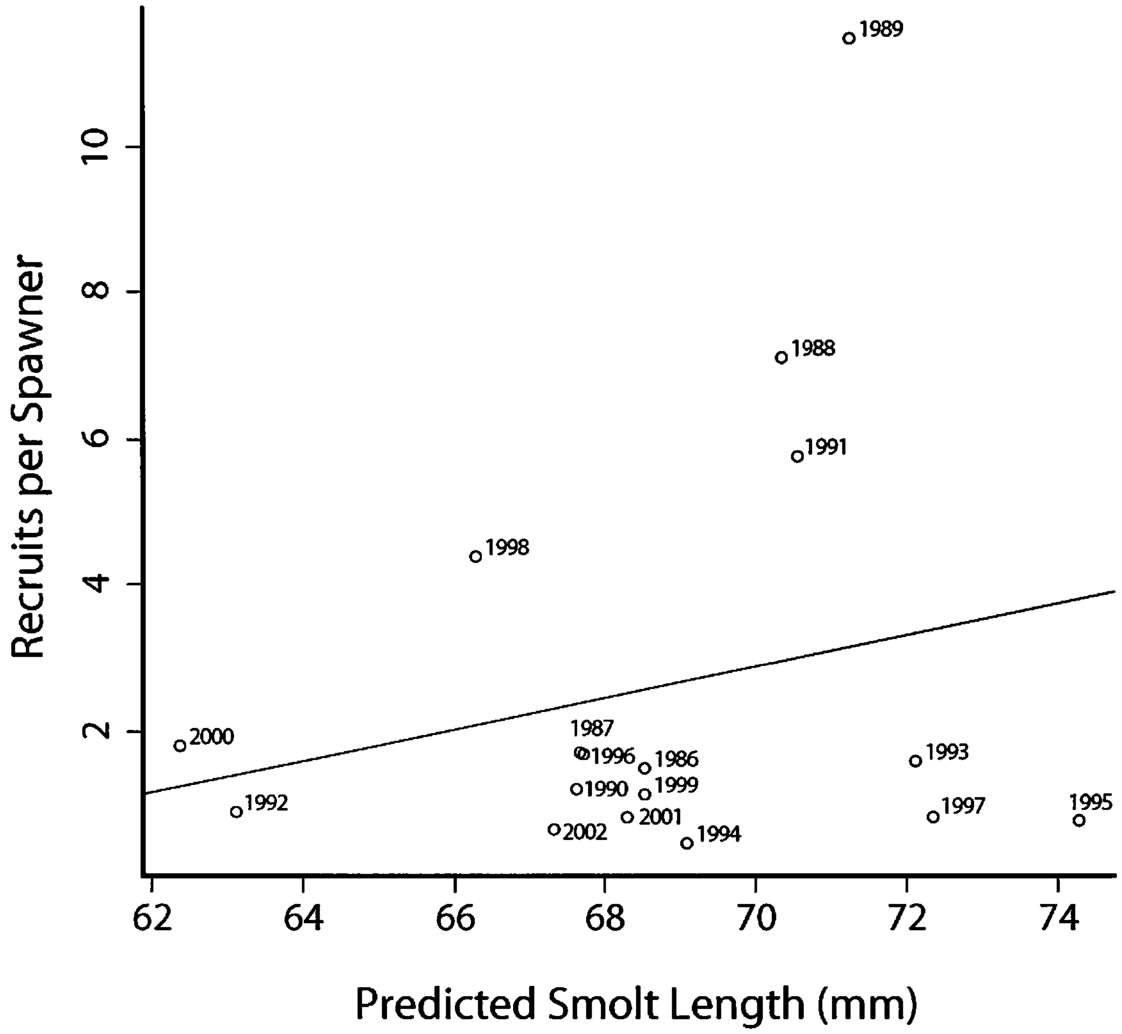

Figure 2. Recruits per spawner from an Alaska Department of Fish and Game stock recruitment analysis (1986-2002) from the Chena River, AK (Matthew Evenson, ADF&G, pers. comm.) regressed on smolt length predicted from a bioenergetics model ($r^2 = 0.049$).

Tables

Table 1. Predicted length of juvenile Chinook salmon at the end of the first freshwater rearing season compared to observed measurements of juvenile Chinook salmon from the Chena River, AK. * = Predicted measurement within two standard errors of observed mean. Location names from data source where applicable. US indicates upstream reach, DS indicated downstream reach.

Year	Length (mm)		Location	Date	N	Source
	Predicted	Actual (SE)				
2009	73.5	80.1 (0.5)	US	9/15/09-9/17/09	250	This study
		79.9 (2.2)	DS	9/9/09-9/11/09	261	This study
		79.9 (0.7)	US	9/17/09	12	Gutierrez 2011
		71.2 (5.1) *	DS	9/17/09	4	Gutierrez 2011
2008	71.6	72.6 (1.8) *	US	9/11/08	37	Gutierrez 2011
		72.1 (1.5) *	DS	9/12/08	29	Gutierrez 2011
2007	71.8	71.1 (0.7) *	Entire River	8/22/07-8/24/07	170	Wipfli, unpubl data
1996	67.9	70 (0.5)	Upper (near 71 km)	5/6/96-6/10/96	1111	Daigneault 1997
		71 (0.5)	Middle (near 71 km)	5/6/96-6/10/96	1093	Daigneault 1997
		69 (0.3)	Lower (near 71 km)	5/6/96-6/10/96	2126	Daigneault 1997
1982	67.9	50.9 (1.0)	Colorado Creek Wayside (134 km)	9/20/82	45	Walker 1983
		57.5 (1.7)	First Bridge (148 km)	9/20/82	32	Walker 1983
		59.7 (1.4)	West Fork (188 km)	9/10/82	3	Walker 1983
		53.6 (1.6)	Mile 28 CHSR (124 km)	9/20/82	36	Walker 1983
1981	68.7	62.2 (4.1)	University Avenue (9.6 km)	8/27/81	9	Walker 1983
		57.0 (1.0)	Moose Creek Dam (71 km)	9/2/81	73	Walker 1983
		51.5 (0.9)	Colorado Creek Wayside (134 km)	8/28/81	103	Walker 1983
		57.9 (1.3)	First Bridge (148 km)	8/28/81	47	Walker 1983

Table 2. Model predicted lengths of juvenile Chinook salmon at the end of the first freshwater rearing season on reduced rations for brood years 1981 and 1982. Actual observed mean lengths were between 50.9 and 62.2 mm respectively. Ration level is a proportion of maximum daily rations, 1.0.

	Predicted Length (mm)	
Ration Level	1981	1982
0.2	49.1	49.6
0.225	53.8	54.4
0.25	58.4	59.1
0.275	62.9	63.7
0.3 (max wild)	67.2	68.2

General Conclusion

The results of these experimental studies and retrospective analyses indicate that temperature plays a major role in the growth of juvenile Chinook salmon *Oncorhynchus tshawytscha* in the Chena River, and in brood years following low escapement, may be the major factor limiting growth. However, in years following high escapement, density-dependent interactions, such as competition for food or space, may be affecting fish growth. During the course of the study, we had 3 of the lowest years of escapement on record, limiting our ability to study density-dependent growth; however, we were able to find some data in the literature of growth achieved during years following high escapement. During 2009, using a supplemental food experiment, we found that food was not limiting growth during the summer growing season for juvenile Chinook salmon; rather temperature was likely setting the limit on fish growth. Further, we were able to predict the growth of juveniles during 2009, and our predicted growth of fish on maximum rations matched our observed growth on maximum rations. The same was true for years 2007 and 2008, also years following low escapement. In two years of data from 1981 and 1982 (Walker 1983) following high escapement, observed length deviated negatively from our model predicted length, which is an indicator of competition.

In a 15-yr analysis of juvenile Chinook salmon in the Salmon River Basin, Idaho, researchers found that there was strong evidence for a negative interaction between mean summer temperature and density (Crozier et al. 2010). Growth was positively correlated with temperature at lower densities, but the correlation was negative at the highest densities (Crozier et al. 2010). While the daily mean temperature of the Chena River, as measured from the Hunts Creek Station, is within the preferred zone of temperature (11-12°C) for Chinook salmon, daily temperature peaked at 13.2°C. Decker (2010) recorded hourly temperature at 21 sites along the Chena River during 2005 and 2006, from km 11-km 232 and found that mean daily temperature at some sites along the Chena could be as high as 18.8°C. For sockeye salmon, Brett et al. (1969) found that on reduced rations, a reduced range of temperatures allow for positive growth and reduced rations decreased optimum temperatures for growth. Some circumstantial evidence exists for density-dependent interactions and potential resource limitation restricting growth during the 1981 and 1982 brood years in the Chena. In years where fish densities are high, fish may be competing for limiting resources of food and/or space, decreasing their growth.

Results from this project are contributing to a project focused on improving upon stock-recruitment analysis for the Chena River that incorporates environmental processes, especially those that may drive population effects during freshwater (i.e., temperature, flow, and food availability). The results of these analyses will potentially allow biologists and managers to predict optimal escapements and forecast future returns, by improving our understanding of the importance of the freshwater period of the Chinook salmon lifecycle, and the potential relationship between freshwater growth and marine survival.

References

Brett, J. R., J. E. Shelbourn, and C. T. Shoop, 1969. Growth rate and body composition of fingerling sockeye salmon, *Oncorhynchus nerka,* in relation to temperature and ration size. Journal of the Fisheries Research Board of Canada 30:2363–2394.

Crozier, L. G., R. W. Zabel, E. E. Hockersmith, and S. Achord, 2010. Interacting effects of density and temperature on body size in multiple populations of Chinook salmon. Journal of Animal Ecology 79:342-249.

Decker, S. K. S. 2010. Thermal limitations on Chinook salmon spawning habitat in the northern extend of their range. MS thesis. University of Alaska Fairbanks.

Walker, R. J. 1983. Growth of young-of-the-year salmonids in the Chena River, Alaska. MS thesis, University of Alaska-Fairbanks.

Appendix

Scale data analysis of archived scales of returned spawners.

Scale Data

We performed scale data analysis from archived scales of returned spawners to identify links between growth in freshwater residency and subsequent life stages. Our purpose in doing this was to use the estimates of back-calculated fish length to compare with predicted lengths from our bioenergetics model (Chapter 2).

Methods

To examine the effects of temperature on growth, we acquired existing scale collections measurements from the Alaska Department of Fish and Game's (ADF&G) Age, Sex, Length sampling program for Chena River Chinook salmon *Oncorhynchus tshawytscha*. Each year when adult salmon returned to spawn on the Chena River, fish were identified by sex, fish length (mid-eye to tail fork, L_{ETF}) taken, and a scale sample was removed from the preferred zone for aging (Maher and Larkin 1954). Scale measurements followed procedures described by Hagen et al. (2001). Plastic impressions of scales were read by a microfiche reader and stored as a high-resolution digital file. Scales collected from years 1995-2000 (n = 817) were analyzed by hand by ADF&G employees. Because of changes in available technology, scales from 2001-2003 (n = 448) were analyzed by ADF&G using Optimas 6.5 (www.mediacy.com) image processing software. Circuli distances were measured between each growth zone.

Measurements were taken beginning at the focus, and the distance in µm between each circulus to the freshwater 1 (FW1) annulus were measured. Circulus distance was measured for each circulus in the freshwater plus (FWPL) zone. For age 1.3 fish (1 year in freshwater, 3 winters in ocean), distance between each circulus were measured for the saltwater 1 (SW1) zone, and total annulus distance was measured for the saltwater 2 (SW2) zone. For 1.4 (1 year in freshwater, 4 winters in ocean) fish, each circulus distance was measured for the SW1 and SW2 zones, and total annulus distance was measured for the saltwater 3 (SW3) zone. The last saltwater zone and saltwater plus zone was not measured for each fish. All scale data were read by the ADF&G Scale Lab in Anchorage, AK.

We reformatted the ADF&G data into a text file to combine all circuli lengths for each year for every fish. When combining files, occasionally an error would result from the transformation, and those fish were excluded from calculations (n = 10). Once files were reformatted, Microsoft® Excel was used to combine all circuli lengths into total annulus length for each zone (FW1, FWP, SW1, SW2). Sample sizes for each year and age class (1.3 and 1.4) were between 18 and 135.

Dubois (ADF&G, pers comm.) had cautioned of differences in readers and methodology for this data set, and stated that scales measured using the same methods should be relatively comparable between years, but certainly comparable within the same age class and return year. Following the work of Ruggerone et al. (2009), linear regressions were performed to determine whether scale growth during each life stage could be explained by growth during the previous stage for years 1995-2003.

Regressions were performed for each age group, 1.3 and 1.4. Correlation coefficients were calculated between FW1 and FW1+FWPL with L_{ETF}. Linear regressions were also performed with mean FW1 length and estimated water temperature from the freshwater growing season for years 1995-2000. For age 1.3 and 1.4 fish returning in 1995, the FW1 mean distance was 54μm longer than the mean distance in years 1992-2000, indicating potential reader error, so we ran temperature regressions with and without that year. We were able to compare fish growth by brood year during the years 1992-1999, except for 1997, which had to be excluded because of methodological changes in scale reading that caused a gap in comparable data. We compared FW1 growth between age 1.3 and 1.4 fish for each brood year using analysis of variance. All regressions were performed using the R programming environment (R Development Core Team 2008).

Results

We ran 99 regressions to evaluate the relationship between annual scale growth and the previous zone of scale growth for age 1.3 and 1.4 fish returning as adults during an 8-yr period from 1996-2003. The majority of all growth zones were positively correlated with the previous zone, however, the majority of the correlations were not significant (Table 2). Annual growth between the SW1 and FWPL, was the only relationship in which the majority of the years were negatively correlated; again, the majority of the relationships were not significant.

Linear regressions of FW1 annulus distance with estimated summer growing season temperatures were positive for both age 1.3 and 1.4 fish; they were significant for age 1.3 fish ($p = 0.013$), but not for age 1.4 fish ($p = 0.33$). Annulus distance for the

FW1 zone for age 1.3 and 1.4 fish from the same brood year, were significantly different ($F_{(2,5)} = 11.32, p = 0.014$) (Figure 4). Age 1.3 fish FW1 radius was on average longer than 1.4 FW1 radius by 11.8 ± 21.7µm. However, the 1992 brood year had that largest difference, with age 1.3 fish having achieved 60µm greater distance than 1.4. Excluding that brood year, average FW1 growth for 1.3 fish was 5.0 ± 10.5µm greater than 1.4 growth. In 1996, 1.4 fish achieved a longer FW1 zone growth than age 1.3 fish.

Discussion

Ruggerone et al. (2009) conducted extensive scale data analysis with nearly 40 years of data on Yukon and Kuskoswim Chinook salmon scale growth. Their work found that annual growth of individuals was related to growth during the previous year. They also found that adult length (L_{ETF}) was weakly correlated to growth that occurred during the summer freshwater rearing period. We too found that annual growth of individuals was positively related to growth during the previous year; however, the majority of years were not significant in our study, which may be partially due to small sample size (n = 8 versus n = 40); also, the methods employed to take scale measurements were slightly different than those Ruggerone et al. (2009) used and did not provide as much data. Scale radius, the last ocean annulus, and salt water plus growth were not measured in our data sets.

Investigating scale data is an interesting prospect for future research. It provides a long time series of potentially useful information to investigate many questions. ADF&G has collected scales on the Chena River as far back as 1986; however, years 1991-1994 are missing, a method shift occurred in 2000, and scales haven't been digitized or analyzed since 2003. There is also some evidence of potential reader error. The adult fish from 1995 had considerably longer FW1 annulus distance readings than any other year using that method. Adults that returned in 1999 and 2000 were captured using two techniques, a mark recapture study as well as carcass sampling, and the mean FW1 growth between fish returning that year and of the same age was different, indicating possible reader error. While acknowledging this source of bias, errors are probably relative (DuBois pers comm.) and should not be an issue when comparing growth within a year class, as they have a consistent bias in each year, but may potentially lead to problems when comparing across years, which makes problematic any interpretation of our results because of that potential error and low sample size.

Regression of mean FW1 length on mean growing season temperature was positive and significant for age 1.3 fish ($F_{(1,6)} = 45.61, p = 0.013$), and positive for age 1.4 fish, but not significant ($F_{(1,6)} = 0.085, p = 0.780$). We also saw that age 1.4 fish were smaller than 1.3 fish from the same brood year (Figure 4). In a study examining at size-based survival in steelhead trout (*O. mykiss*) using back-calculated smolt (BSL) lengths from adult scales, Ward et al. (1989) found that, on average, the BSL was lowest for fish that spent more time in salt water. Previous research for many salmonids indicate that years spent in freshwater is inversely related to years spent in salt water; this is the case for Chinook salmon (Scheuerell 2005), coho salmon (*O. kisutch*) (Bilton et al. 1982), steelhead trout, (Ward and Slaney 1993), sockeye salmon, (*O. nerka*) (Peterman 1982), and Atlantic salmon (*Salmo salar*) (Nicieza and Brana 1993). These data suggest that larger smolt are the first to mature. Zabel and Achord (2004) modeled data on over 54,000 juvenile Chinook from the Snake River and found that larger stream-type juvenile Chinook salmon 10 mm greater than the mean length of their cohort after the first summer rearing period had two times higher survival rates than fish 10 mm below the mean length. While our study was smaller, and the scale data used had potential sources of bias, it lends support to this same hypothesis. One possible explanation of (larger) fish having a better correlation with temperature, versus the 1.4 (smaller) fish, is that age 1.4 were fish that were experiencing reduced growth as a result of competition, perhaps for food or space during their brood season.

References

Bilton, H. T., D. F. Alderdice, and J. T. Schnute. 1982. Influence of time and size at release of juvenile coho salmon (*Oncorhynchus kisutch*) on returns at maturity. Canadian Journal of Fisheries and Aquatic Sciences 39:426-447.

Hagen, P. T., D. S. Oxman, and B. A. Agler. 2001. Developing and deploying a high resolution imaging approach for scale analysis. NPFAC Doc. 567. Alaska Department of Fish and Game, Juneau.

Maher, F. P., and P. A. Larkin. 1954. Life history of the steelhead trout of the Chilliwack River, B.C. Transactions of the American Fisheries Society 84:27-38.

Nicieza, A. G., and F. Brana. 1993. Relationships among smolt size, marine growth, and sea age at maturity of Atlantic salmon (*Salmo salar*) in northern Spain. Canadian Journal of Fisheries and Aquatic Sciences 50:1632-1640.

Peterman, R. M.1982. Nonlinear relation between smolts and adults in Babine Lake sockeye salmon (*Oncorhynchus nerka*) and implications for other salmon populations. Canadian Journal of Fisheries and Aquatic Sciences 39:904-913.

Ruggerone, G. T., J. L. Nielsen, and B. A. Agler. 2009. Linking marine and freshwater growth in western Alaska Chinook salmon *Oncorhynchus tshawytscha*. Journal of Fish Biology 75:1287-1301.

Scheuerell, M. D. 2005. Influence of juvenile size on the age at maturity of individually marked wild Chinook salmon. Transactions of the American Fisheries Society 134:999-1004.

Ward, B. R., and P. A. Slaney. 1993. Egg-to-smolt survival and fry-to-smolt density dependence of Keogh River steelhead, p.209-217. In R.J. Gibson and R.E. Cutting [ed.] Production of juvenile Atlantic salmon, *Salmo salar*, in natural waters. Canadian Special Publications in Fisheries and Aquatic Sciences 118.

Ward, B. R., P. A. Slaney, A. R. Facchin, and R. W. Land. 1989. Size-biased survival in steelhead trout: back-calculated lengths from adults' scales compared to migrating smolts at the Keogh River, B.C. Canadian Journal of Fisheries and Aquatic Sciences 46:1853-1858.

Zabel, R, W., and S. Achord. 2004. Relating size of juveniles to survival within and among populations of Chinook salmon. Ecology 85:795-806.

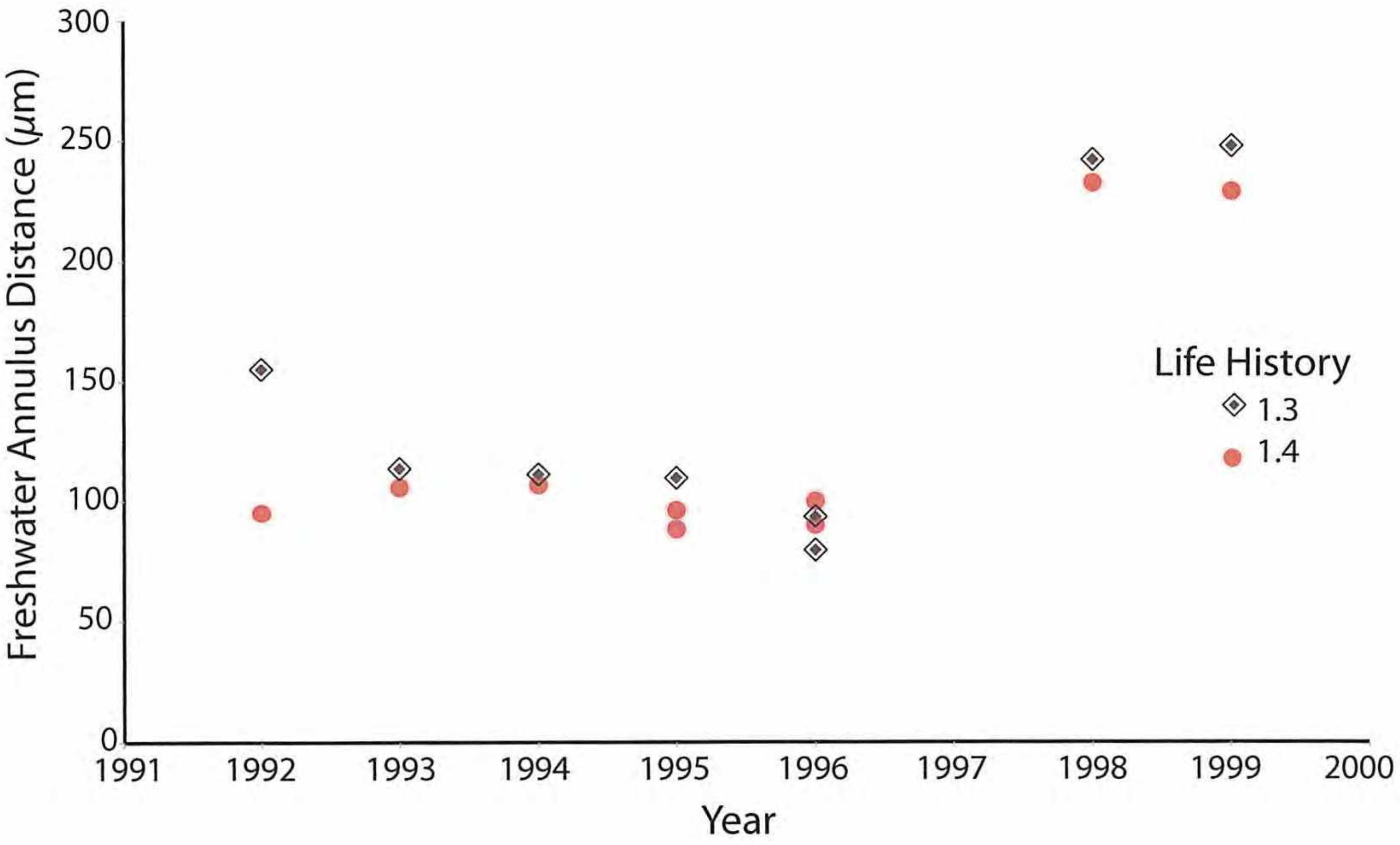

Figure 1. Freshwater annulus distance for age 1.3 and 1.4 fish of the Chena River, AK from the same brood year. Annulus distance for brood years 1998 and 1999 were measured using new methodology, differences indicate method-based bias.

Table 1. Percent of positive regressions for scale circuli distance regressions between the proceeding zone; scales were collected from adults salmon returning to the Chena River, AK. % Pos = Percentage of total regressions that were positively correlated. %Sig[4] = Percentage of regressions that were significant ($p < 0.05$). Each percentage in the table is based on regressions from 11 data sets.

Age	Number of Data Sets	FWPL on FW1		SW1 on FW1		SW1 on FWPL		SW2 on SW1		SW3 on SW2	
		% Pos	% Sig	% Pos	% Sig	% Pos	% Sig	% Pos	% Sig	% Pos	% Sig
1.3	11	82	18	64	9	36	0	55	45		
1.4	11	91	18	64	18	27	18	55	27	91	45
Mean ± s.d. coefficient of determination (r^2)		0.058 ± 0.083		0.043 ± 0.063		0.027 ± 0.028		0.069 ± 0.072		0.063 ± 0.050	
Maximum coefficient of determination (r^2)		0.34		0.29		0.1		0.21		0.13	

---

[4] We expected 5% of regressions to be significant by chance alone.