

VARIATION IN AGE AND SIZE AT MATURITY OF LAKE CLARK,
ALASKA SOCKEYE SALMON

By

Elizabeth B. Benolkin

RECOMMENDED:




Dr. Milo Adkison



Dr. Carol Ann Woody



Dr. Joseph Margraf, Advisory Committee Chair



Dr. Shannon Atkinson
Interim Director, Fisheries Division

APPROVED:



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



Dr. Lawrence Duffy, Dean of the Graduate School



Date

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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

Elizabeth B. Benolkin, B.A.

Fairbanks, Alaska

December 2009

Abstract

Salmon returning to Lake Clark, Alaska are a valuable subsistence, commercial and ecological resource, and are an important component of the larger Kvichak River escapement. Average escapement to the Kvichak River declined sharply during 1996-2005, prompting studies to investigate age and size at maturity, key life history traits of salmon linked to reproductive success and survival. We examined potential factors which may influence sockeye salmon *Oncorhynchus nerka* age and size at maturity: spawning habitat and ocean environment, and examined variation in both traits over time. Sockeye salmon age and length at maturity differed among spawning locations and between brood years, but no consistent patterns were observed among habitat types. Age and length at maturity differed over time; the proportion of older marine age 3 fish was larger in recent brood years, while fish were smaller during 1997-2001 compared to 1976-1980. Sea surface temperatures and coastal upwelling appeared to be important indicators of fish length, highlighting the importance of the ocean environment in salmon growth. These results demonstrate the complexity and importance of both the freshwater and ocean ecosystems in variation in age and size at maturity, and indicate that trends may not necessarily be similar among systems or years.

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Acknowledgements

This project was a collaborative effort between the United States Geological Survey, Alaska Science Center (USGS ASC) and Lake Clark National Park and Preserve, National Park Service (NPS). Funding was provided by the U.S. Fish and Wildlife Service (USFWS), the National Park Service, and the USGS ASC. Carol Ann Woody, Kristina Ramstad and others helped secure funding and designed sampling protocols. I thank my advisor, Joe Margraf of the University of Alaska Fairbanks, School of Fisheries and Ocean Sciences (UAF-SFOS) and my committee members Milo Adkison (UAF-SFOS) and Carol Ann Woody (Fisheries Research and Consulting) for their support, guidance, and critical reviews of this project. I thank Vanessa von Biela (USGS) and Chris Zimmerman (USGS) for helpful discussions, editorial advice, and reviews of drafts. Chris Boatright, Pat Poe, and others at University of Washington, Alaska Salmon Program shared historical sockeye salmon age and size data. Greg Ruggerone (Natural Resource Consultants) compiled and shared North Pacific and Gulf of Alaska sea surface temperature data. Many people helped collect samples in the field and provided logistical support including Leon Alsworth, Kristy Balluta, Tara Balluta, Mike Booz, Iris Bowers, Jared Irvine, Ryan Kreiner, Buck Mangipane, Pat Poe, Laura Sorenson, Carol Ann Woody, Julia Vinciguerra, Dan Young, and many more. Joel Reynolds (USFWS) provided valuable statistical advice. Dan Young created and shared maps of Lake Clark study sites. I thank Gabrielle Hazelton, Madeline Scholl, and the administrative staff at UAF SFOS for helping navigate graduate school. I thank Carol Ann Woody for all she has taught me, and for her encouragement, patience, and belief in my potential. I also would like to thank my family and friends for all of their support and encouragement: my mom and dad, Patrick, Louie, Katie, Elaine, Pat, Dale, Ellie, Vanessa, and lastly my husband Aaron for his limitless patience, love, perspective, and inspiration.

Introduction

This thesis describes findings from a sockeye salmon life history study conducted in Lake Clark, Alaska from 2001 to 2007, and from historical sockeye salmon age and size data collected from the upper Newhalen River from 1979 to 1985. The objectives of this research were to 1) compare sockeye salmon age composition and size at maturity among tributary and beach spawning locations and to 2) examine age and size at maturity over 2 time periods (brood years 1976-1980 and 1997-2001), and test relationships between size at age and environmental variables including the Aleutian Low pressure system, the Pacific Decadal Oscillation, seasonal sea surface temperatures, and coastal upwelling.

Poor returns of sockeye salmon to Lake Clark/Newhalen River and the larger Kvichak River watershed were observed from 1996 to 2005 (ADFG 2006), prompting studies of variation in age and size at maturity, key life history traits in salmon. The Kvichak River system has historically been the largest contributor to the Bristol Bay fishery, the largest producer of sockeye salmon in the world (Fair 2000). All harvests (subsistence, sport, and commercial) were impacted by these declines and minimum escapement goals for the Kvichak River (2 million fish) were not met in 6 of 10 years from 1996 to 2005 (ADFG 2006). Salmon returning to Lake Clark comprise between 7 and 30% of the total Kvichak River escapement (Poe and Rogers 1984; Woody 2004). Sockeye salmon are a valuable cultural, subsistence, economic, and ecological resource, and play an important link in food chains by providing a critical food resource for over 40 species of birds, mammals, and fish, and by delivering marine derived nutrients into freshwater ecosystems, which helps sustain productivity in those ecosystems (Kline et al. 1993; Wilson and Halupka 1995).

Age and size at maturity vary within and among populations (Foerster 1968; Healey 1986; Burgner 1991), and may be influenced by genetics and by a number of environmental factors generally associated with growth, including water temperature, food availability, or fish density. This study examined potential factors which may

influence sockeye salmon age and size at maturity: spawning habitat and ocean environment.

At least some of the variation in age and size at maturity has been shown to reflect adaptations to differences in spawning environment (Ricker 1972; Healey 1987; Rogers 1987; Bishop 1990; Taylor 1991; Blair et al. 1993; Wood 1995; Hendry and Quinn 1997; Quinn et al. 2001). Blair et al. (1993) found that sockeye salmon from tributaries of nearby Iliamna Lake were both older and larger compared to Iliamna beach-spawning salmon, and other researchers have documented variation in other phenotypic traits (body depth, egg weight) associated with Lake Clark spawning habitats (beach, tributary, and glacial habitats; Ramstad 2006, Ramstad et al. in press). To determine if similar patterns in age and size at maturity would be observed among salmon from the Lake Clark portion of the Kvichak watershed sockeye salmon, we hypothesized that marine age and size at maturity would be greater for tributary spawning sockeye salmon compared to beach spawning sockeye salmon.

Changes in abundance and in age and size at maturity of Pacific salmon have been documented by numerous researchers over the past decades (Bigler et al. 1996; Helle and Hoffman 1995, 1998). Several hypotheses have been proposed to explain changes in age and size of salmon (Ricker 1980; Quinn 2005), including changes in the ocean environment (temperature, upwelling, salinity, competition for food). Numerous studies have found correlations between salmon size and trends in the ocean environment (Rogers 1980, 1984; Nickelson 1986; Fisher and Pearcy 1988; Beamish and Bouillon 1993; Rogers and Ruggerone 1993; Bigler and Helle 1994; Cox and Hinch 1997). This study tested for changes in age and size over two time periods, and investigated relationships between several environmental variables and size at maturity of sockeye salmon collected from the Lake Clark region of the Kvichak River watershed, Alaska.

Understanding the causes of variation and patterns in age and size at maturity of sockeye salmon is important because age and size at maturity are closely linked to fecundity, growth and survival (Healey 1986). Changes in age or size at maturity

have the potential to change the weight of the commercial catch or alter egg production or fitness. A complex interaction of factors may influence age and size at maturity of salmon, but research exploring the mechanisms underlying the relationships between salmon growth and ocean conditions is important for management of these stocks.

Chapter 1: Variation in age and size at maturity among Lake Clark, Alaska sockeye salmon spawning locations¹

Abstract

Age and size at maturity are key life history traits in sockeye salmon *Oncorhynchus nerka* closely linked to fecundity, growth, and survival, and vary within and among populations. Salmon returning to Lake Clark are a valuable subsistence, commercial, and ecological resource, and are an important component of the larger Kvichak River escapement. Consistent patterns of variation observed in age and size at maturity among salmon spawning in river and beach habitats are considered to be evidence of local adaptations to spawning environment. Age composition and size at maturity were compared among nine Lake Clark sockeye salmon spawning locations from brood years 1998 and 1999 (capture years 2002-2005) to test the hypothesis that age and size at maturity would be greater for river spawning sockeye salmon compared to beach spawning sockeye salmon. Lake Clark sockeye salmon displayed significant variation in age composition and length at maturity among spawning locations by location and brood year, but no consistent patterns were observed among habitat types. These differences in age and size at maturity may be related to differences in migration distance, growing conditions, or genetic factors. While spawning habitat did not influence age and size at maturity, a relationship between habitat type and other life history traits has been documented in Lake Clark. These findings indicate that trends in age and size at maturity across beach and tributary habitats are not necessarily consistent among systems or years. Understanding the causes of variation in age and size at maturity is important because these traits have potentially adaptive value, and the potential to influence reproductive success and survival of sockeye salmon.

¹Benolkin, E. B., C. A. Woody, J. H. Reynolds, and M. D. Adkison. Variation in age and size at maturity among Lake Clark, Alaska sockeye salmon spawning locations. Prepared for submission in Transactions of the American Fisheries Society.

Introduction

Poor returns of sockeye salmon to the Kvichak River watershed (Figure 1.1) were observed during 1996-2005 (ADFG 2006), and this decline has been a priority concern for subsistence fishers and resource managers. The Kvichak River system has historically been the largest contributor to the Bristol Bay fishery, the largest producer of sockeye salmon in the world (Fair 2000). All harvests (subsistence, commercial, and sport) were impacted by these declines and minimum escapement goals for the Kvichak River (2 million fish) were not met in 6 of 10 years from 1996 to 2005 (ADFG 2006). Salmon returning to Lake Clark comprise between 7 and 30% of the total Kvichak River escapement (Poe and Rogers 1984; Woody 2004).

Sockeye salmon exhibit wide variation in life history patterns (Burgner 1991). Anadromous juvenile sockeye salmon typically rear in lakes for one to two years after emerging from the gravel. They spend from one to four years in the ocean before returning to spawn in their natal habitats, which may include spring fed streams, tributary creeks, or lake beach areas (Burgner 1991). Sockeye salmon exhibit precise homing behavior associated with genetic isolation, leading to wide variation in life history traits (Beacham and Murray 1987; Fleming and Gross 1989), and to distinct locally adapted populations (Taylor 1991). The wide variety of life history traits is associated with the diverse habitats in which sockeye salmon spawn and rear (Wood 1995).

Age and size at maturity are key life history traits in sockeye salmon, and vary within and among populations (Foerster 1968; Healey 1986; Burgner 1991). Age and size at maturity may be influenced by genetics and by a number of environmental factors generally associated with growth, including water temperature, food availability, or fish density. The number of years spent in the ocean is positively correlated with size at maturity because most growth occurs in the marine environment. In females, larger size at maturity results in higher fecundity and egg

size (Bilton 1971; Burgner 1991), which can improve reproductive success and survival (Healey 1986).

At least some of the variation in age and size at maturity has been shown to reflect adaptations to differences in spawning environment (Ricker 1972; Healey 1987; Rogers 1987; Bishop 1990; Taylor 1991; Blair et al. 1993; Wood 1995; Hendry and Quinn 1997; Quinn et al. 2001). Blair et al. (1993) provided evidence that phenotypic variation in age and size at maturity among sockeye salmon populations of Iliamna Lake within the Kvichak River system, Alaska, reflects adaptations to beach and tributary habitats, where fish spawning along beaches were smaller and younger at age of maturity compared to tributary spawning fish.

In the Lake Clark region of the Kvichak watershed, sockeye salmon use at least 33 discrete spawning locations (Young 2004; Young and Woody 2007; Young and Woody 2009a, 2009b), and display variation in other heritable phenotypic traits associated with spawning habitats (beach and tributary; Ramstad 2006; glacial; Ramstad et al. in press). Ramstad (2006) found that sockeye salmon from Lake Clark are adapted to habitat by body depth, snout length, and egg weight, with beach spawning fish having deeper bodies, longer snouts and larger eggs than tributary spawning fish (Ramstad 2006; Ramstad et al. in press). These patterns are consistent with patterns observed among sockeye salmon from other systems (Blair et al. 1993; Quinn et al. 1995; Hamon et al. 2000; Hendry et al. 2000; Quinn et al. 2001). For example, body depth of male sockeye salmon was positively correlated with water depth of spawning habitat in the Kvichak River watershed (Blair et al. 1993) and Tustumena Lake, Alaska (Woody 1998).

Here we test whether patterns between spawning habitat and age and size at maturity of sockeye salmon in the Lake Clark portion of the watershed are similar to those documented in Iliamna Lake. Juvenile sockeye salmon use the same nursery lake for rearing (Schlenger 1996), smolts migrate downstream to sea jointly (Orrell 1963; Woolington et al. 1990), and adults share a common ocean distribution (French et al. 1976), and migratory route to spawning grounds (Jensen and Mathisen 1987).

Although a number of factors influence the diverse life history characteristics of sockeye salmon, Lake Clark sockeye salmon share similar environments for most of their lives, allowing the influence of spawning location on age and size at maturity to be assessed. The objectives of this research were to estimate sockeye salmon age composition and size at maturity among nine Lake Clark spawning locations, and to test the hypothesis that age and size at maturity would be greater for tributary spawning sockeye salmon compared to beach sockeye salmon.

Methods

Study Area

Lake Clark is part of the Kvichak River watershed, located in northeast Bristol Bay in Southwest Alaska (Figure 1.1). It is connected to Iliamna Lake by the Newhalen River and is one of two main lake systems in which sockeye salmon spawn and rear (Mathisen and Poe 1969; Burgner 1991). Lake Clark is the second largest lake (267 km³) within the Kvichak River system (Anderson 1969), and the largest lake within Lake Clark National Park and Preserve. It is a glacial lake approximately 74 km long, with a mean depth of 103 m (Anderson 1969). Six major tributaries feed Lake Clark, five of which are glacially influenced resulting in very cold and turbid waters, especially in the upper portion of the lake (Brabets 2002). A number of smaller glacier-fed and clearwater streams also flow into Lake Clark (Brabets 2002; Figure 1.1).

Lake Clark spawning salmon begin their upstream migration in Bristol Bay, swim up the Kvichak River, through Iliamna Lake, up the Newhalen River, and through Sixmile Lake before segregating to spawn in beaches and tributaries of Lake Clark (Figure 1.1). The Kvichak River system has historically been the largest contributor to the Bristol Bay fishery, the largest producer of sockeye salmon in the world (Fair 2000). Salmon returning to Lake Clark comprise between 7 and 30% of the total Kvichak River escapement (Poe and Rogers 1984; Woody 2004; Young and Woody 2009a, 2009b), but poor returns of sockeye salmon to Lake Clark and the

Kvichak River watershed were observed from 1996 to 2005 (ADFG 2006), leading to studies to examine age and size at maturity of sockeye salmon within this system.

Salmon were sampled from four main lake beaches (MLB) on Lake Clark, from two beaches in tributary lakes (TRIB) of Lake Clark, and from three tributary rivers (RIV) of Lake Clark during the peak of spawning, which generally occurs from mid September through mid October (Figure 1.1; Table 1.1; Young and Woody 2007). Main lake beach spawning areas included clear water beaches Chi Point Beach (CHI) and Chulitna Lodge (CHU), and turbid beaches Hatchet Point Beach (HBP) and Little Lake Clark (LLC). The tributary lake beaches, Kijik Lake South Beach (KLSB) and Sucker Bay Lake (SBL), are clear water beaches located above inlet tributaries of Lake Clark (Figure 1.1; Table 1.1). The Tazimina River (TAZ) is lake-fed and drains approximately 829 km² into Sixmile Lake (Table 1.1; Figure 1.1; Woody 2004). The Little Kijik River (LKR) is a small (1.6 km long; Demory et al. 1964), shallow (0.47 m) outlet stream (Ramstad 2006) which flows out of Kijik Lake into the main stem of the Kijik River (Table 1.1; Figure 1.1). The Tlikakila River (TLIK) is a large (1613 km²) glacially-fed river with large seasonal variation in flow (1-340 m³/sec), high summer turbidity, and drains approximately 21 percent of the Lake Clark basin (Figure 1.1; Table 1.1; Brabets 2002).

Data Collection

Sockeye salmon age and size data were collected from beaches and tributaries of Lake Clark from August 30th to October 26th during 2002 to 2005 (Figure 1.1). Spawning fish were captured with beach seines or tangle nets on spawning grounds. Sex was identified and fish were measured with calipers from mid-eye to hypural plate (MEH) and recorded in millimeters (mm). Otoliths were extracted from approximately 100 fish (50 per sex) at each location. Age was determined from annuli on the otoliths at the University of Washington (B. Rogers), using European notation (freshwater age.marine age).

Age

Binary logistic regression was used to evaluate the effects of spawning location, sex, and brood year (1998 and 1999) on marine age for fish captured during 2002-2005 (MINITAB, version 15, State College, PA). The response variable was marine age (2 or 3). Freshwater age was not considered in the analysis because size at maturity is primarily influenced by marine age (Burgner 1991), and freshwater age remained relatively consistent (freshwater age was 1 year in 74% of samples; n = 1818; Figure 1.2). The logit link function was used to generate estimates of the probability (MINITAB, version 15) that a fish from a given spawning location will be marine age-3. The relationship is given by:

$$\hat{p} = e^{\text{logit}} / (1 + e^{\text{logit}}).$$

Using log likelihood ratio tests, a full model (all factors) was compared to each of three reduced models, which removed one factor of interest at a time (spawning location, sex, or brood year) to determine the importance of the factors.

To better evaluate the effects of spawning location on marine age, sex was removed as a factor, data were grouped by individual brood year, and an additional logistic regression model was evaluated for each brood year (marine age versus spawning location). Spawning locations were grouped by three habitat types likely to describe marine age (MLB, TRIB, and RIV; Table 1.1). The Tlikakila River (RIV TLIK), the largest river in this study and a major tributary flowing into Lake Clark, was used as the reference spawning location in all analyses since it was expected to have the highest proportion of older (marine age-3) fish. A chi-square goodness of fit test (Hosmer and Lemeshow 1989) was used to assess the adequacy of the logistic regression function. Statistical limits of significance were < 0.05 for all tests.

Size

Differences in size at maturity among spawning locations, sexes, brood years, and marine age were examined with a four-way analysis of variance (ANOVA, fixed effects, with all interaction terms; $\alpha = 0.05$) to determine which factors were correlated to length. To examine location and brood year more closely, data were grouped by sex and marine age in four two-way ANOVA's (length versus spawning location and brood year). Tukey's multiple comparison post hoc tests were applied to test for differences among spawning locations (Zar 1999). Spawning locations were arranged by the three habitat types described above (MLB, TRIB, and RIV) to evaluate differences in mean length among habitat types.

Results

Age

The full parameter model (marine age versus spawning location, sex, and brood year) indicated that marine age was dependent on spawning location and brood year, but not sex (Figure 1.2A). Across all spawning locations, salmon spawned at younger ages (higher proportion of ocean age-2 fish) in 1999 with 41% of fish being marine age-3 in brood year 1998 and only 30% of fish being marine age-3 in brood year 1999 ($\chi^2 = 11.66$; DF = 1; $P = 0.001$; Figure 1.2A). Sex did not impact marine age, with 37% of female and 36% of male sockeye salmon spending three years in the ocean ($\chi^2 = 0.45$; DF = 1; $P = 0.502$; Figure 1.2B). Spawning location had a significant effect on marine age ($\chi^2 = 96.85$; DF = 8; $P < 0.001$; Figure 1.2C). Salmon from four spawning locations (MLB CHI, MLB HPB, TRIB SBL, and RIV TAZ) were likely to be younger (marine age 2) than fish from the reference spawning location (RIV TLIK), while fish from TRIB KLSB were likely to be older (marine age 3; $P < 0.05$; Figure 1.2C) than fish from RIV TLIK. A Hosmer and Lemeshow goodness of fit test on the full parameter model indicated that the model adequately described the data ($\chi^2 = 3.75$; DF = 7; $P = 0.808$).

When marine age was examined by spawning location within individual brood years, significant differences in marine age among spawning locations were found in brood year 1998, but not in brood year 1999, where the probability of being marine age-3 was equally likely among all spawning locations compared to RIV TLIK ($P > 0.05$; Table 1.2; Figure 1.3). Within brood year 1998, salmon from four spawning locations (MLB CHI, MLB HPB, TRIB SBL, and RIV TAZ) were likely to be younger than fish RIV TLIK (odds ratios < 1.0 ; P values < 0.021 ; Table 1.2; Figure 1.3), while fish from TRIB KLSB were 3 times likely to be older than fish from RIV TLIK (odds ratio = 3.09; $P = 0.000$; Table 1.2; Figure 1.3). The probability of being marine age-3 was 49% at RIV TLIK in brood year 1998 (Figure 1.3). Probabilities of being marine age-3 were 30 and 31% at the two MLB sites (CHI and HPB, respectively), 15% at TRIB SBL, and 18% at RIV TAZ (Figure 1.3). In contrast, the probability of being marine age-3 was 75% at TRIB KLSB (Figure 1.3).

Size

Spawning location, sex, brood year, and marine age significantly influenced mean length (four-way ANOVA; $P < 0.05$; $N = 1818$). Marine age had the strongest effect on length ($F = 2032.0$; $P = 0.000$), followed by sex ($F = 191.5$; $P = 0.000$), brood year ($F = 65.5$ $P = 0.000$), and finally spawning location ($F = 17.7$; $P = 0.000$). Sockeye salmon that spent three years in the ocean were significantly larger than fish that spent two years in the ocean (526 ± 1.02 versus 469 ± 0.75 mm), male salmon were significantly larger than female salmon (506 ± 0.84 versus 489 ± 0.94 mm), and salmon from brood year 1998 were larger than those from 1999 (502 ± 0.77 versus 492 ± 1.00 mm). Fish from MLB CHI (508 ± 1.75 mm) were significantly larger than fish from all locations except two other MLB, CHU (504 ± 1.6 mm) and HPB (502 ± 1.8 mm), which were not different in size. Fish from RIV TAZ (485 ± 1.6 mm) were significantly smaller than fish from all other locations except those from MLB LLC (489 ± 1.9 mm) and those from TRIB KLSB (493 ± 2.6 mm), which were similarly small.

Among marine age-2 female sockeye salmon ($N=548$), mean length differed by spawning location ($F = 4.8$; $P = 0.000$), and at one spawning location by brood year (TRIB SBL; location*brood year interaction; $F = 4.19$; $P = 0.000$; Figure 1.4). Overall (brood years 1998 and 1999), fish from MLB CHI (466 ± 2.3 mm), MLB CHU (466 ± 2.9 mm) and RIVER TLIK (465 ± 3.3 mm) were significantly larger than fish from RIVER TAZ (449 ± 2.4 mm; Table 1.3; Figure 1.4). At TRIB SBL, brood year significantly impacted mean length, with brood year 1999 fish being larger than brood year 1998 fish (467 ± 3.1 versus 445 ± 3.7 mm; Table 1.3; Figure 1.4)

Among marine age-3 female sockeye salmon ($N = 325$), mean length differed by spawning location ($F = 4.9$; $P = 0.000$), brood year ($F = 44.2$; $P = 0.000$; Figure 1.5), and at two spawning locations by brood year (RIV TAZ and RIV TLIK; location*brood year interaction; $F = 2.0$; $P = 0.044$; Figure 1.5). Similar to marine age-2 females, fish from MLB CHI (527 ± 4.2 mm), CHU (528 ± 3.1 mm), and RIV TLIK (521 ± 4.3 mm) were significantly larger than fish from RIV TAZ (503 ± 3.6 mm), which had the smallest fish (Table 1.3; Figure 1.5). In contrast to marine age-2 females which were not significantly different across brood years, marine age-3 females from brood year 1998 were significantly larger (528 ± 1.8 mm) than marine age-3 fish from brood year 1999 (507 ± 2.6 mm; Table 1.3; Figure 1.5). Fish from two river sites (TAZ and TLIK) were larger in 1998 (519 ± 4.3 and 540 ± 3.6 mm, respectively) compared to 1999 (486 ± 5.7 mm and 501 ± 7.8 mm; Table 1.3; Figure 1.5).

Among marine age-2 male sockeye salmon ($N = 607$), mean length differed by spawning location ($F = 11.95$; $P = 0.000$), brood year ($F = 6.9$; $P = 0.009$; Table 1.3; Figure 1.6), and at one spawning location by brood year (TRIB SBL; location*brood year interaction; $F = 3.8$; $P = 0.000$; Table 1.3; Figure 1.6). Similar to marine age-2 female sockeye salmon, marine age-2 males from MLB CHI (488 ± 2.5 mm) were largest, and fish from all but one spawning location (MLB LLC, 469 ± 3.2 mm) were significantly larger than fish from RIV TAZ (463 ± 1.9 mm; Figure 1.6),

which were smallest. Marine age-2 male sockeye salmon from brood year 1998 (475 ± 1.3 mm) were significantly smaller than marine age-2 males from brood year 1999 (481 ± 1.5 mm; Table 1.3; Figure 1.6). At TRIB SBL, brood year influenced mean length, where brood year 1998 marine age-2 males (464 ± 3.4 mm) were significantly smaller brood year 1999 fish (493 ± 3.1 mm; Table 1.3; Figure 1.6).

Among marine age-3 male sockeye salmon ($N = 338$), mean length differed by spawning location ($F = 6.5$ $P = 0.000$), brood year ($F = 82.6$; $P = 0.000$; Table 1.3; Figure 1.7), and at three spawning locations by brood year (MLB LLC, TRIB KLSB, and RIV TLIK; location*brood year interaction; $F = 4.1$; $P < 0.05$; Table 1.3; Figure 1.7). Fish from MLB LLC (516 ± 3.8 mm) were significantly smaller than fish from four other spawning locations (MLB CHI, 551 ± 4.9 ; MLB CHU, 543 ± 4 ; MLB HPB, 545 ± 4.3 ; and RIV LKR, 537 ± 4.8 ; Figure 1.7). Marine age-3 males from brood year 1998 (548 ± 3.9) were significantly larger than fish from brood year 1999 (520 ± 2.4 ; Table 1.3; Figure 1.7). Marine age-3 males from brood year 1998 were larger than fish from brood year 1999 at three spawning locations: MLB LLC (540 ± 4.4 in 1998 versus 493 ± 6.2 mm in 1999), TRIB KLSB (552 ± 4.4 versus 502 ± 7.2 mm), and RIV TLIK (554 ± 4.6 versus 506 ± 7.5 mm; Table 1.3; Figure 1.7).

Discussion

Age composition and length at maturity varied among spawning locations in Lake Clark, although no consistent patterns were observed in either trait by spawning habitat type. Although sockeye salmon from the largest tributary (TLIK) were among the oldest and largest fish compared to other locations as anticipated, tributary spawners were not, in general, older or larger than beach spawning salmon. These findings contrast with Blair et al. (1993) who found that sockeye salmon spawning in tributaries in a nearby section of the Kvichak River watershed (Iliamna Lake) were both older and larger than beach spawning sockeye salmon.

Our study differed from Blair et al. (1993) in several aspects, including the number of capture years, and population status. Blair et al. (1993) combined ten years of data collected between 1965 and 1990 (1965, 1978, 1981, 1983-1985, and 1987-1990), while our study spanned five consecutive years beginning in 2002. A ocean regime shift (warm phase) occurred in 1977, which was associated with an increase in salmon abundance in Alaska (Mantua et al. 1997; Helle and Hoffman 1998), a decrease in average size at maturity of most populations of salmon in North America, and an increase in age at maturity (Bigler et al. 1996; Helle and Hoffman 1995, 1998). It is believed that the warm phase lasted through at least the late 1990's (Helle and Hoffman 1995). Data used in Blair et al.'s (1993) study spanned two regimes, but were collected during predominately strong salmon production years, while sample collection for this study occurred during warmer temperatures in the North Pacific Ocean, and was during a sharp decline in salmon abundance to Lake Clark and the larger Kvichak River watershed. A decline in abundance is usually associated with changes in age structure or size of returning salmon through density dependent effects on growth (Rogers 1980; Peterman 1984; Ishida et al. 1993; Helle and Hoffman 1995, 1998; Bigler et al. 1996).

Rivers

Sockeye salmon from the RIV TAZ were among the youngest and smallest fish captured in this study, and this may be related to differences in migration distance, growing conditions, or genetic factors. In contrast to our results, Blair et al. (1993) found that fish from the Tazimina River matured later and were larger than fish from island beaches in Iliamna Lake, which was not included in this study. Sockeye salmon spawning in RIV TAZ migrated the shortest distance from sea compared to other sites in our study, while this site was the furthest distance from sea in Blair et al.'s study (1993; Table 1.1; Figure 1.1). Age and size at maturity of salmonids have been correlated with migration distance or difficulty, with shorter migrations correlating to smaller fish (Schaffer and Elson 1975; Scarnecchia 1983; L'Abée-Lund 1991). In both studies, this relationship between age and size at

maturity and migration distance supports the hypothesis that the relationship between fish length is an adaptation to arduousness or distance of migration.

Genetics may play a role in controlling age and size at maturity among fish from RIV TAZ. Ramstad et al. (2004) found that the fish from the Tazimina River were genetically divergent from Lake Clark fish, and were genetically similar to Iliamna Lake sockeye salmon populations, which tend to be younger and smaller, compared to Lake Clark fish (Blair et al. 1993). Iliamna sockeye salmon had a higher proportion of younger (marine age-2) fish compared to Lake Clark sockeye salmon (80 vs. 64%), and were, on average 4% smaller than Lake Clark sockeye salmon. Since age and size at maturity are genetically controlled to some extent, it is plausible that the differences observed in both traits among Tazimina River fish are a result of genetic differences.

The differences in age and size at maturity among RIV TAZ salmon may also have arisen if they used different rearing locations than fish from other spawning locations. The Tazimina River is fed by Tazimina Lake and flows into Sixmile Lake (Figure 1.1). Although the Tazimina River is lake fed, a steep waterfall blocks salmon from migrating to the lake, so it is presumed that juveniles rear in Sixmile Lake, Lake Clark, or Iliamna Lake (Orrell 1963). If juvenile salmon use Iliamna Lake for rearing they may experience better growing conditions than those in Lake Clark, since Iliamna Lake is warmer and more productive than Lake Clark (Mathisen and Poe 1969). Smolt size may affect age at maturity; larger smolts may experience rapid growth in the ocean and mature at earlier ages (Quinn 2005).

Tributary Beaches

Sockeye salmon from the two tributary beach spawning locations (TRIB KLSB and TRIB SBL) displayed wide variation in both age and size at maturity compared to fish from other spawning locations (Figures 1.2-1.6). The Kijik River basin, which includes Kijik Lake and Little Kijik River (Figure 1.1), is an important sockeye salmon producing tributary within Lake Clark (Brabets and Ourso 2006). Recent evidence indicates genetic divergence of Kijik River basin and Sucker Bay

Lake populations compared to other populations within Lake Clark (Ramstad et al. 2004), and precise spawning migration (in speed and direction) to these locations (Young 2004). The genetic isolation which is associated with precise homing behavior and the variability in age and size at maturity at these locations may suggest an adaptive response to local conditions. Sucker Bay Lake is believed to have a persistent low effective population size (Ramstad et al. 2007), which may also contribute to the wide variation in age and size at maturity at this site.

The variation in age and size at maturity among the tributary beach (KLSB and SBL) spawners may be related to differences in growing conditions they experience. It is not clear whether Kijik Lake and Sucker Bay Lake are used for rearing, or whether juveniles migrate to Lake Clark for rearing. Numerous factors may affect freshwater growth, such as water temperature, abundance and distribution of food supply, competition, fish density, or species composition (Burgner 1991). Rearing conditions likely differ among the tributary beach locations (KLSB, and SBL) and Lake Clark, and may differ between years. If juvenile salmon do remain in KLSB or SBL to rear, differences in any of these factors may affect annual growth and length of residence in freshwater, which in turn may affect age and length at maturity.

Main Lake Beaches

Sockeye salmon from the four main lake beaches were not consistently younger or smaller than fish from the three tributary rivers sampled, which contrasts to Blair et al. (1993), who found that Iliamna Lake beach spawners were both younger and smaller than river spawners. Interestingly, fish from one location (CHI) were likely to be younger than fish from RIV TLIK, but were largest in both brood years among males of either age. Chi Point fish were not highly genetically divergent from other Lake Clark populations, except those from TRIB KLSB and TRIB SBL (Ramstad et al. 2004). It is not clear why sockeye salmon spawning at MLB CHI are young but large, since the fastest growing members of a population typically mature earlier and at smaller sizes compared to fish that grow more slowly (Parker and

Larkin 1959). However, the large size of beach spawning fish may have arisen if marine feeding distribution varied between this population and others.

Brood Years

No consistent patterns in age or size at maturity among habitats were observed over brood years, but overall fish were older and larger in brood year 1998 than in 1999. Fish from different broods likely experienced different growing conditions in the ocean, which may be related to varying abundance of other salmon stocks or species. For example, interaction with Asian pink salmon *Oncorhynchus gorbuscha* in odd years, when they are most abundant, has been shown to influence Bristol Bay sockeye salmon growth and survival in the ocean, with female salmon attaining smaller size at age of maturity in years when Asian pink salmon abundance is high (Ruggerone et al. 2003; Ruggerone et al. 2007). It is possible that competition between Asian pink salmon and Bristol Bay sockeye salmon affected marine growth of Lake Clark salmon during this study (Rogers and Ruggerone 1993), through density dependent effects.

Results from this study revealed significant variation in age composition and length at maturity among sockeye salmon spawning locations, but variability was observed among habitat types, within habitat types, and between brood years. Evidence of local adaptation in other heritable phenotypic traits, such as body depth or egg size, however, has been found among beach and tributary spawners in Lake Clark (Ramstad 2006). Although clear patterns in age and size by spawning habitat were not observed within Lake Clark, the variation in phenotypes (or biocomplexity, Hilborn et al. 2003) among and within the component populations of the Kvichak River watershed (including those in Lake Clark) likely influences the stability and sustainability of the larger Bristol Bay sockeye salmon fishery because a combination of life history strategies and local adaptations would allow buffers to large-scale environmental changes in freshwater or the ocean (Giesel 1974; Altukov 1981; Hilborn et al. 2003). Understanding the causes of variation in age and size at maturity is important because these traits have potentially adaptive value, and the

potential to influence reproductive success and survival (Healey 1986). These results demonstrate the complexity of the system, and indicate that trends in age and size at maturity across beach and tributary habitats are not necessarily similar among systems or years.

Acknowledgements

This project was a collaborative effort between the United States Geological Survey, Alaska Science Center (USGS ASC), and Lake Clark National Park and Preserve, National Park Service (NPS). Funding was provided by the U.S. Fish and Wildlife Service (USFWS), the National Park Service, and the USGS ASC. Kristina Ramstad and others helped secure funding and designed sampling protocols. I am grateful to Vanessa von Biela (USGS) and Chris Zimmerman (USGS) for helpful discussions, editorial advice, and reviews of drafts. Many people helped with field collections and logistics including Leon Alsworth, Kristy Balluta, Tara Balluta, Nate Blewett, Mike Booz, Jeff Caulfield, Jared Irvine, Ryan Kreiner, Kimberly Lohnas, Buck Mangipane, Darren Mayers, Ele McKay, Judy Putera, Michelle Ravenmoon, Jaclyn Reamy, Dan Ruggirello, Heather Ruggirello, Ryan Reynolds, John Staley, Terina Trefon, and Dan Young. Dan Young created and shared maps of Lake Clark study sites. I thank Chris Zimmerman (USGS) and the Alaska Science Center for continued support of this project.

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Table 1.1. Physical characteristics of Lake Clark spawning locations. From Young (2004), Ramstad et al. (2004), and Ramstad (2006). The estimated mean peak of spawning is in parentheses. Distance was calculated by adding the distance from sea (203 km; Burgner 1991) to the distance from the outlet of Lake Clark.

Study Site Description			Water	Depth (m)	Spawning Activity	Distance from sea (km)	Percent Substrate		
					(mean peak)		Fine	Moderate	Course
Main Lake Beach	CHI	Chi Point	Clear		9/1-9/30 (9/24)	215	-	-	-
Main Lake Beach	CHU	Chulitna Lodge	Clear		-	240	-	-	-
Main Lake Beach	HPB	Hatchet Point Beach	Turbid		9/15-10/15 (10/12)	262	-	-	-
Main Lake Beach	LLC	Little Lake Clark	Turbid	0.90	9/15-10/15 (10/7)	275	2	32	66
Tributary Beach	KLSB	Kijik Lake South Beach	Clear	0.48	9/15-10/31 (9/25)	252	16	80	4
Tributary Beach	SBL	Sucker Bay Lake	Clear	0.72	8/25-9/15 (8/30)	210	11	41	49
River	TAZ	Tazimina River	Clear	0.63	(8/25)	200	11	75	14
River	LKR	Little Kijik River	Clear	0.47	9/15-10/15 (9/18)	248	-	-	-
River	TLIK	Tlikakila River	Turbid	0.38	9/15-10/15 (10/7)	290	24	56	20

Table 1.2. Logistic regression results for spawning location on marine age. Lake Clark sockeye salmon spawning locations are grouped by brood year (1998 and 1999) and habitat type, Main Lake Beaches (MLB), Tributary Beaches (TRIB), and Rivers (RIV). Spawning locations which differed significantly in marine age from the reference spawning location (RIV TLIK) in 1998 are indicated in bold. Marine age did not differ by spawning location in brood year 1999.

Year	Habitat	Variable	Parameter		Z	P value	Odds Ratio	95% CI	
			Estimate	SE				Lower	Upper
1998		Constant	-0.044	0.171	-0.26	0.798			
		Location							
	MLB	CHI	-0.787	0.249	-3.17	0.002	0.46	0.28	0.74
	MLB	CHU	0.087	0.241	0.36	0.718	1.09	0.68	1.75
	MLB	HPB	-0.774	0.242	-3.20	0.001	0.46	0.29	0.74
	MLB	LLC	-0.350	0.239	-1.47	0.142	0.70	0.44	1.13
	TRIB	KLSB	1.128	0.296	3.81	0.000	3.09	1.73	5.51
	TRIB	SBL	-1.705	0.356	-4.78	0.000	0.18	0.09	0.37
	RIV	TAZ	-0.589	0.255	-2.32	0.021	0.55	0.34	0.91
	RIV	LKR	-0.036	0.287	-0.13	0.900	0.96	0.55	1.69
1999		Constant	-0.840	0.275	-3.06	0.002			
		Location							
	MLB	CHI	-0.293	0.381	-0.77	0.441	0.75	0.35	1.57
	MLB	CHU	0.653	0.359	1.82	0.069	1.92	0.95	3.88
	MLB	HPB	0.339	0.395	0.86	0.390	1.40	0.65	3.04
	MLB	LLC	0.530	0.393	1.35	0.177	1.70	0.79	3.67
	TRIB	KLSB	0.603	0.441	1.37	0.171	1.83	0.77	4.34
	TRIB	SBL	-0.194	0.343	-0.57	0.571	0.82	0.42	1.61
	RIV	TAZ	-0.648	0.345	-1.88	0.060	0.52	0.27	1.03
	RIV	LKR	-0.141	0.364	-0.39	0.698	0.87	0.43	1.77

Table 1.3. Mean length (ML) of salmon from Lake Clark spawning locations. Mean length, standard error (SE), and sample size (N) are grouped by marine age (2 or 3), sex, habitat type (main lake beaches (MLB), tributary beaches (TRIB), and rivers (RIV)), and are summarized by brood years 1998 and 1999.

Marine Age	Sex	Habitat	Loc	Brood Year								
				1998			1999			1998 & 1999		
				ML	SE	N	ML	SE	N	ML	SE	N
2	F	MLB	CHI	472	3.0	49	461	3.6	34	466	2.3	83
		MLB	CHU	463	3.3	40	469	4.8	19	466	2.9	59
		MLB	HPB	460	2.8	55	459	5.7	13	459	3.2	68
		MLB	LLC	455	3.2	43	458	5.2	16	457	3.0	59
		TRIB	KLSB	468	5.7	13	456	7.8	7	461	4.9	20
		TRIB	SBL	445	3.7	32	467	3.1	45	456	2.4	77
		RIV	TAZ	450	4.1	26	449	2.7	58	449	2.4	84
		RIV	LKR	450	4.5	21	464	3.4	37	456	2.8	58
		RIV	TLIK	464	4.6	20	466	4.6	20	465	3.3	40
			All	458	1.3	299	461	1.6	249	460	1.0	548
3	F	MLB	CHI	534	4.7	22	519	7.0	10	527	4.2	32
		MLB	CHU	532	3.7	36	525	5.1	19	528	3.1	55
		MLB	HPB	528	4.9	20	514	7.8	8	521	4.6	28
		MLB	LLC	519	4.3	27	510	9.0	6	514	5.0	33
		TRIB	KLSB	518	3.7	35	490	12.8	3	504	6.6	38
		TRIB	SBL	538	9.9	5	508	5.4	17	523	5.6	22
		RIV	TAZ	520	4.3	27	487	5.7	15	503	3.6	42
		RIV	LKR	522	5.7	15	508	5.9	14	515	4.1	29
		RIV	TLIK	540	3.6	38	502	7.8	8	521	4.3	46
			All	528	1.8	225	507	2.6	100	517	1.6	325
2	M	MLB	CHI	484	2.9	52	493	4.2	25	488	2.5	77
		MLB	CHU	479	3.9	28	476	4.4	22	477	3.0	50
		MLB	HPB	481	2.8	56	484	4.6	20	482	2.7	76
		MLB	LLC	467	3.1	46	471	5.6	14	469	3.2	60
		TRIB	KLSB	481	6.6	10	481	6.0	12	481	4.4	22
		TRIB	SBL	464	3.4	37	493	3.1	45	479	2.3	82
		RIV	TAZ	460	2.8	55	466	2.6	66	463	1.9	121
		RIV	LKR	483	4.9	18	478	4.0	27	481	3.2	45
		RIV	TLIK	480	2.9	50	484	4.2	24	482	2.6	74
			All	475	1.3	352	481	1.5	255	478	1.0	607
3	M	MLB	CHI	555	5.3	22	547	8.3	9	551	4.9	31
		MLB	CHU	549	4.2	35	538	6.5	15	543	3.9	50
		MLB	HPB	549	4.6	29	540	7.2	12	545	4.3	41
		MLB	LLC	540	4.4	33	493	6.2	16	516	3.8	49
		TRIB	KLSB	552	4.4	33	502	7.2	12	527	4.2	45
		TRIB	SBL	544	9.4	7	519	6.5	15	531	5.7	22
		RIV	TAZ	541	6.2	16	512	6.9	13	527	4.7	29
		RIV	LKR	547	5.5	21	527	7.9	10	537	4.8	31
		RIV	TLIK	554	4.6	29	506	7.5	11	530	4.4	40
			All	548	1.9	225	520	2.4	113	534	1.5	338

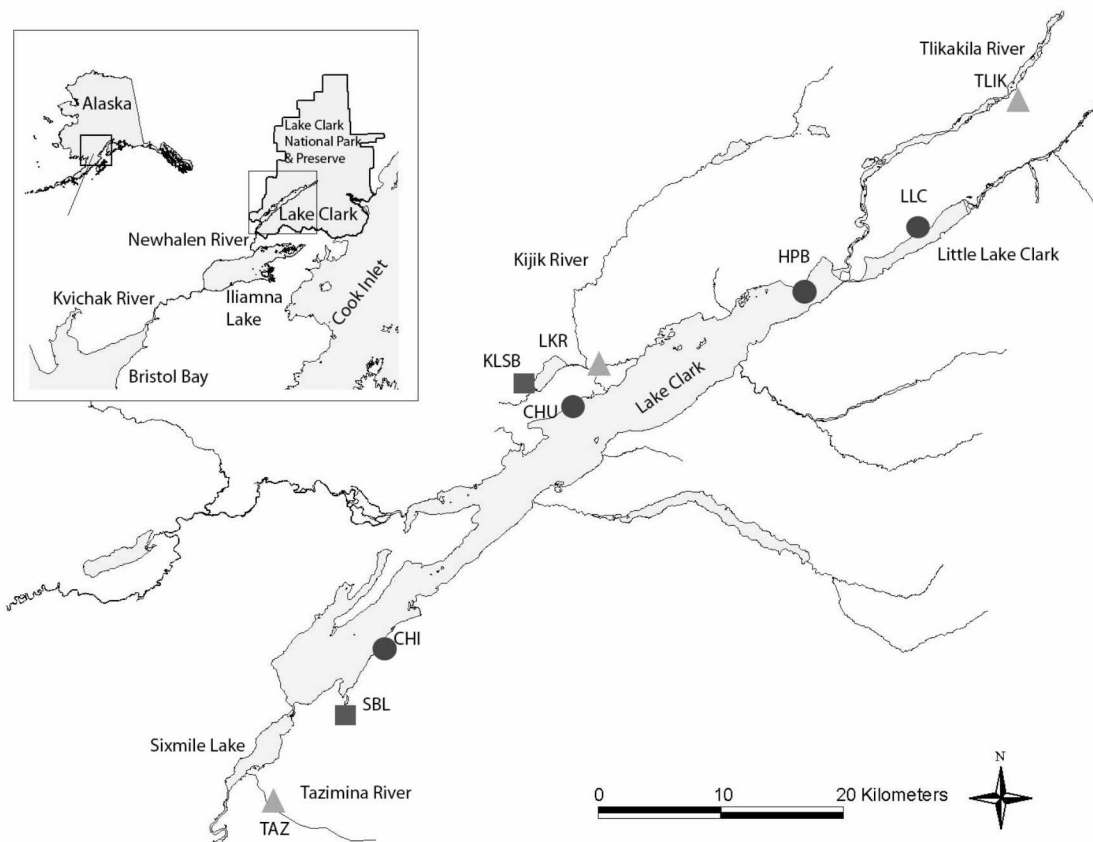


Figure 1.1. Lake Clark spawning locations relative to Bristol Bay, Alaska. Nine beach and tributary spawning locations were sampled from 2002-2005. Main lake beach (MLB) sites are indicated by circles, tributary beaches (TRIB) are indicated by squares, and rivers (RIV) are indicated by triangles.

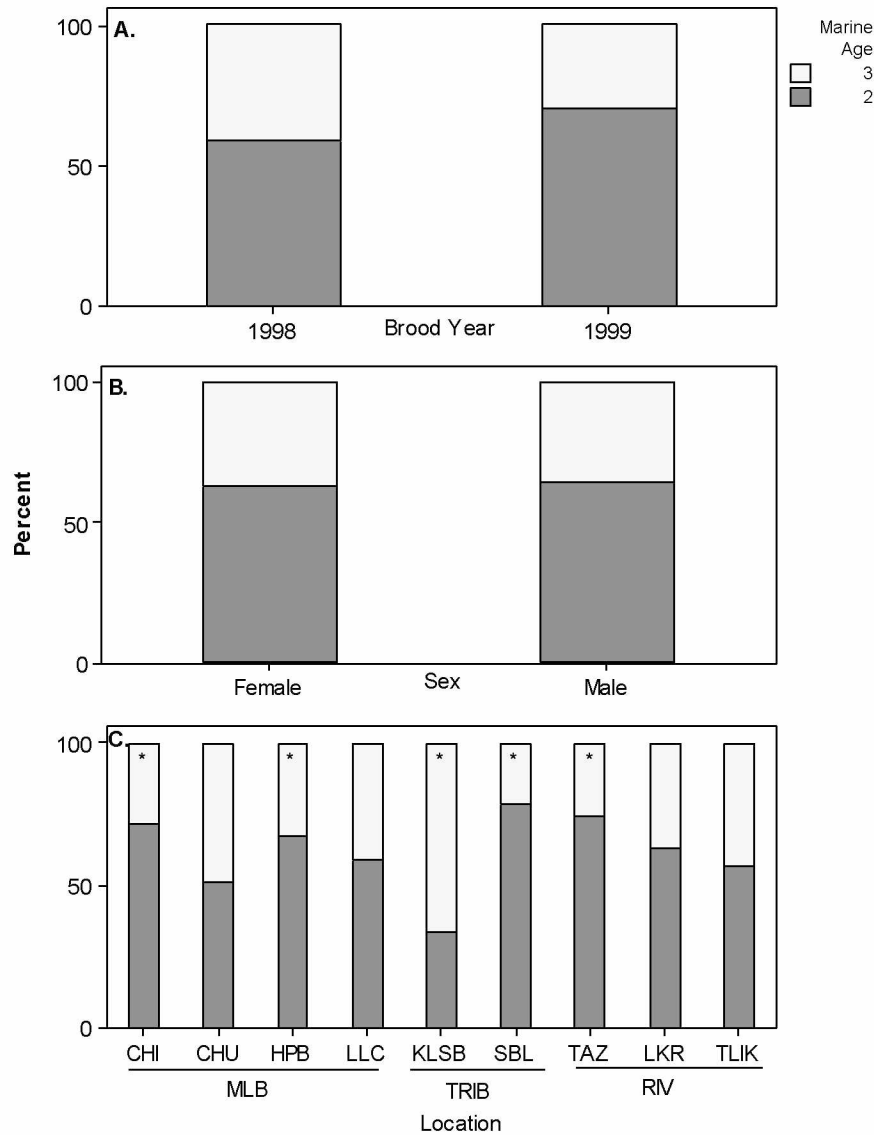


Figure 1.2. Marine age composition of Lake Clark sockeye salmon. Percent marine age composition is grouped by brood year (top panel A), sex (middle panel B) and spawning location (bottom panel C). Marine age differed by spawning location and brood year, but not by sex. Spawning locations that differed significantly in marine age from the reference location (RIV TLIK) are indicated by asterisks.

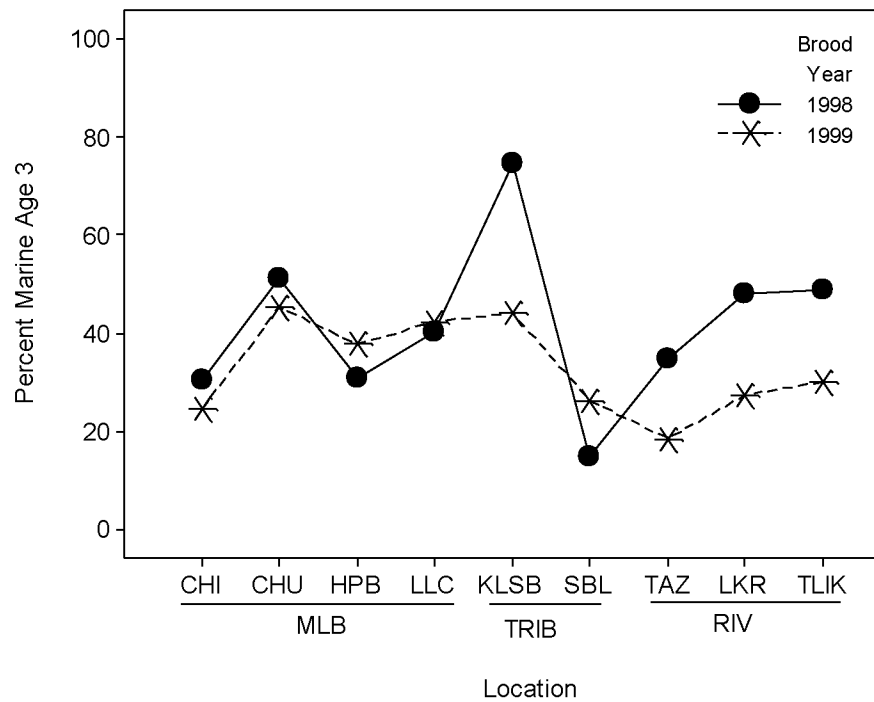


Figure 1.3. Marine age of Lake Clark sockeye salmon within each brood year. The probability (%) of being marine age-3 was examined within each individual brood year (1998 and 1999) using binary logistic regression. Spawning locations are along the x axis and are grouped by habitat types, characterized as main lake beaches (MLB), tributary beaches (TRIB), and rivers (RIV). The RIV TLIK was the reference spawning location in all analyses. The probability of being marine age-3 differed by spawning location in brood year 1998, but not in 1999.

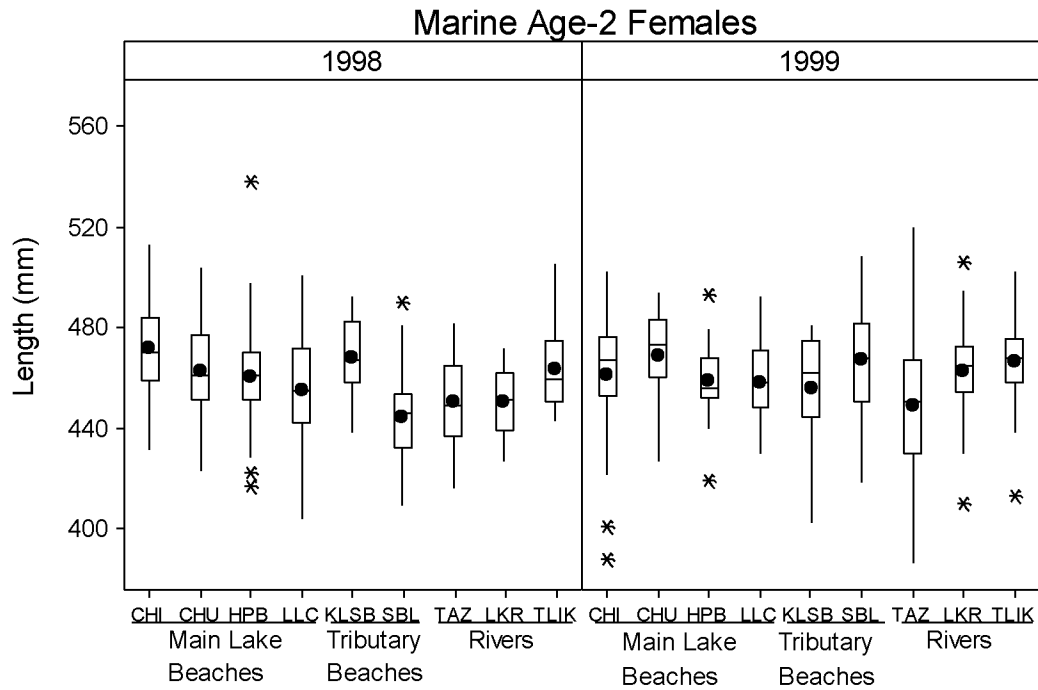


Figure 1.4. Mean length of marine age-2 female fish by year and location. Lake Clark sockeye salmon mean lengths were analyzed within each brood year (1998 in left panel and 1999 in right panel), and compared among spawning locations grouped by main lake beach, tributary beach, and river habitat types. Boxes represent the interquartile range, where the middle line is the median. Circles are mean length, whiskers extend to minimum and maximum data points, and asterisks are suspected outliers. Overall, mean length did not differ by brood year, but did differ among spawning locations, where fish from three locations (CHI, CHU, and TLIK) were larger than fish from TAZ. Length differed across years at SBL, where brood year 1999 fish were larger than brood year 1998 fish ($P < 0.05$).

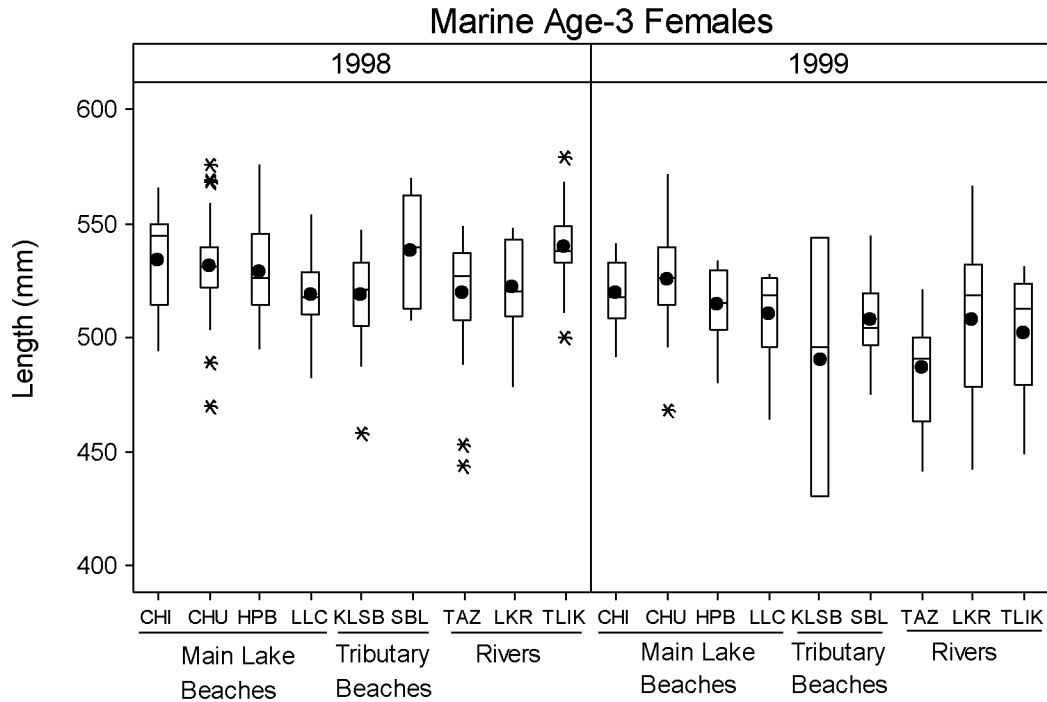


Figure 1.5. Mean length of marine age-3 female fish by year and location. Lake Clark sockeye salmon mean lengths were analyzed within each brood year (1998 in left panel and 1999 in right panel), and compared among spawning locations grouped by main lake beach, tributary beach, and river habitat types. Boxes represent the interquartile range, where the middle line is the median. Circles are mean length, whiskers extend to minimum and maximum data points, and asterisks are suspected outliers. Overall, marine age-3 females from brood year 1998 were larger than fish from brood year 1999, and fish from three spawning locations (CHI, CHU, and TLIK) were larger overall than fish from TAZ. Length differed across years at two river locations (TAZ and TLIK), where brood year 1998 fish were larger than brood year 1999 fish ($P < 0.05$).

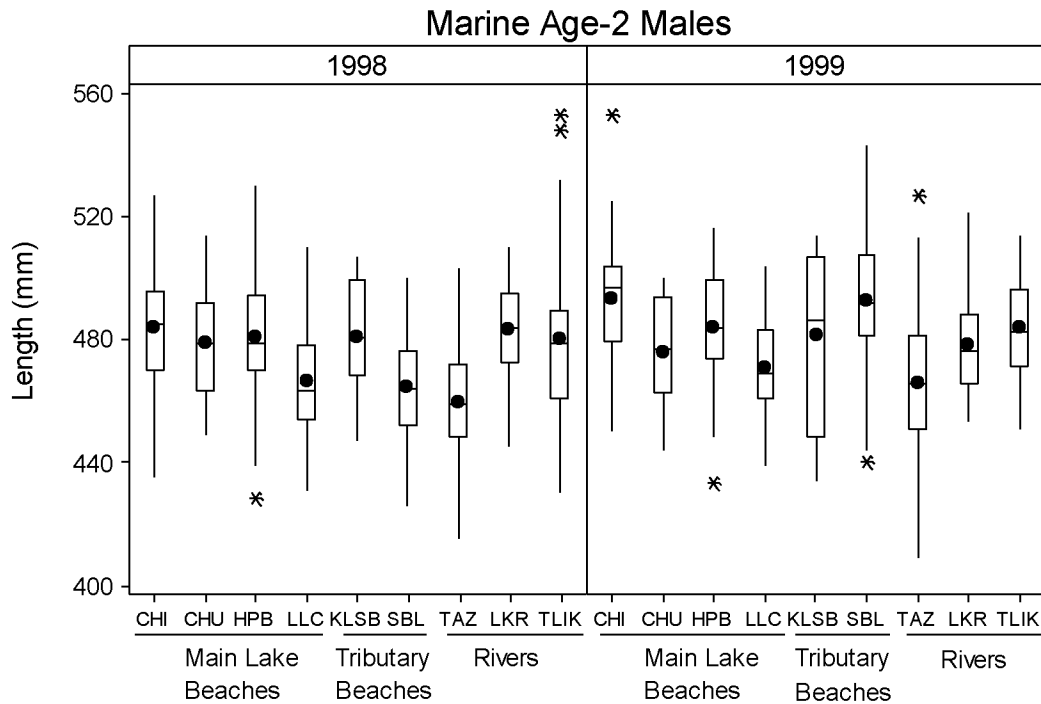


Figure 1.6. Mean length of marine age-2 male fish by year and location. Lake Clark sockeye salmon mean lengths were analyzed within each brood year (1998 in left panel and 1999 in right panel), and compared among spawning locations grouped by main lake beach, tributary beach, and river habitat types. Boxes represent the interquartile range, where the middle line is the median. Circles are mean length, whiskers extend to minimum and maximum data points, and asterisks are suspected outliers. Overall, marine age-2 males from brood year 1999 were larger than males from brood year 1998, and fish from TAZ were smaller overall than fish from all other locations except LLC, which were similarly small. Length differed across years at one location (SBL), where brood year 1999 fish were larger than 1998 fish ($P < 0.05$).

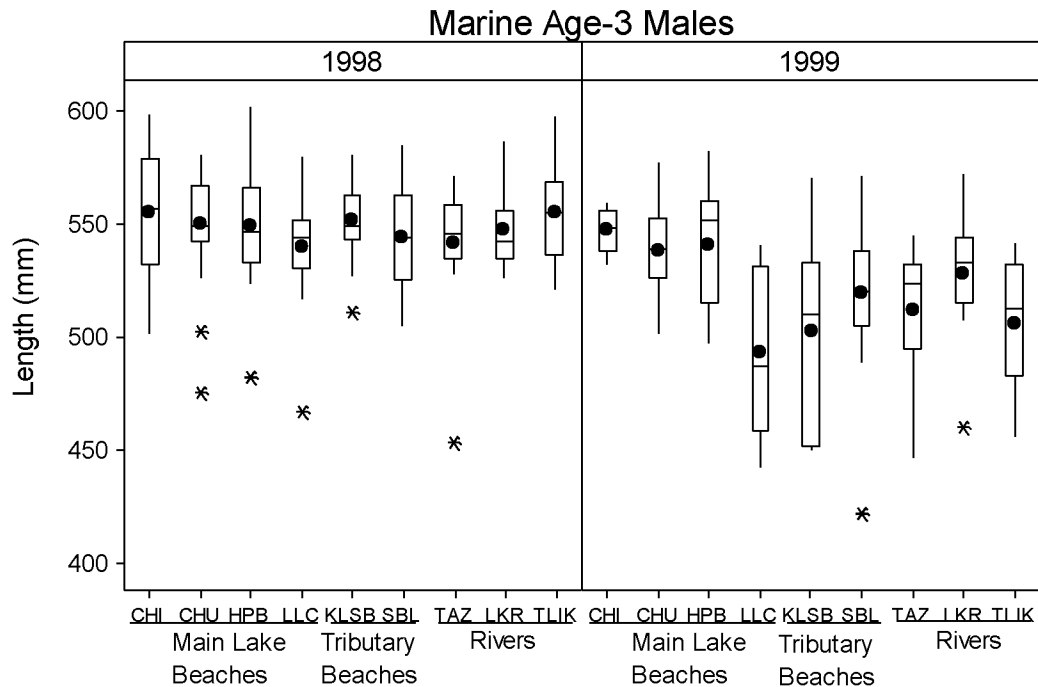


Figure 1.7. Mean length of marine age-3 male fish by year and location. Lake Clark sockeye salmon mean lengths were analyzed within each brood year (1998 in left panel and 1999 in right panel), and compared among spawning locations grouped by main lake beach, tributary beach, and river habitat types. Boxes represent the interquartile range, where the middle line is the median. Circles are mean length, whiskers extend to minimum and maximum data points, and asterisks are suspected outliers. Overall, marine age-3 males from brood year 1998 were larger than males from brood year 1999, and fish from LLC were smaller overall than fish from four locations (CHI, CHU, HPB, and LKR). Males from 1998 were larger than those in 1999 at three locations (LLC, KLSB, and TLIK; $P < 0.05$).

Chapter 2: Temporal variation in age and size at maturity, and oceanic influences on size at maturity among Lake Clark, Alaska sockeye salmon¹

Abstract

Sockeye salmon *Oncorhynchus nerka* originating from Lake Clark and the upper Newhalen River are an important subsistence, commercial, and ecological resource, and are an important component of the larger Kvichak River escapement. Average escapement to the Kvichak River declined sharply during 1996-2005, prompting the listing of the Kvichak originating salmon as a “stock of concern” in 2003. To determine if demographic changes occurred during this period, we investigated age and size at maturity, key life history traits of salmon. We examined trends in age and size at maturity of Lake Clark and upper Newhalen River sockeye salmon from two time periods (brood years 1976-1980 and 1997-2001) and tested relationships between size at maturity and environmental variables including the Aleutian Low pressure system, the Pacific Decadal Oscillation, sea surface temperatures, and coastal upwelling. Age composition and size at maturity of Newhalen River sockeye salmon differed between time periods; the proportion of older marine age 3 fish was greater in recent brood years, while fish size at maturity was significantly smaller during 1997-2001 compared to 1976-1980. Broad-scale environmental indices (Aleutian Low and Pacific Decadal Oscillation) were not correlated with sockeye salmon length in either sex or in any age group. Sea surface temperatures were negatively correlated with fish length, and coastal upwelling was positively correlated with fish length. Changes in sea surface temperatures and coastal upwelling may be related to changes in food availability for salmon, leading to differential growth. Our study may provide managers with a better understanding of how environmental processes affect size at maturity of sockeye salmon originating from Lake Clark and the upper Newhalen River.

¹ Benolkin, E. B., C. A. Woody, V. R. von Biela, and M. D. Adkison. Temporal variation in age and size at maturity, and oceanic influences on size at maturity among Lake Clark, Alaska sockeye salmon. Prepared for submission in Transactions of the American Fisheries Society

Introduction

Sockeye salmon are a valuable subsistence, commercial, and ecological resource, and comprise over 50% of the total subsistence harvest in nearly all of the Kvichak River watershed communities of southwest Alaska (Fall et al. 2001). Salmon returning to Lake Clark and the upper Newhalen River comprise between 7 and 30% of the total Kvichak River (Poe and Rogers 1984; Woody 2004), which has historically been the largest contributor to the Bristol Bay fishery. The Bristol Bay fishery has been the largest producer of sockeye salmon in the world (Fair 2000), with a commercial harvest averaging US\$122.4 million since 1998 (ADFG 2009). Sockeye salmon provide a critical food source for over 40 bird, mammal, and fish species, and adult salmon deliver marine derived nutrients into freshwater, which sustains productivity in those ecosystems (Kline et al. 1993; Wilson and Halupka 1995).

Poor returns of sockeye salmon to Lake Clark, the upper Newhalen River, and the larger Kvichak River watershed (Figure 2.1) were observed between 1996 and 2005 (ADFG 2006), and understanding the potential causes for this decline is a priority concern of resource managers. Changes in abundance and age and size at maturity of Pacific salmon were documented by numerous researchers over the past decades (Bigler et al. 1996; Helle and Hoffman 1995, 1998). Several hypotheses have been proposed to explain changes in age and size of salmon (Ricker 1980; Quinn 2005), including changes in the ocean environment (temperature, upwelling, salinity, competition for food), genetics (through selective fisheries on larger fish or delayed maturation), increases in hatchery production which may lead to increased competition for food, or statistical artifacts. Correlations between salmon abundance, size, and environmental trends (Rogers 1980, 1984; Nickelson 1986; Fisher and Pearcy 1988; Beamish and Bouillon 1993; Rogers and Ruggerone 1993; Bigler and Helle 1994; Cox and Hinch 1997) have been documented. Here we examine the potential influence of several indices of ocean environment on the length at age of maturity of Lake Clark/Newhalen River: the Aleutian Low Pressure index (ALPI), the

North Pacific Index-National Center for Atmospheric Research (NPI-NCAR), the Pacific Decadal Oscillation (PDO), seasonal sea surface temperatures (SST), and coastal upwelling.

The Aleutian Low pressure system has been positively correlated with salmon abundance (Beamish and Bouillon 1993), and increased salmon abundance has been negatively correlated with marine growth of salmon (Davidson and Vaughan 1941; Peterman 1978; Helle and Hoffman 1995, 1998; Bigler et al. 1996; Pyper and Peterman 1999). The Aleutian Low pressure system is a winter weather pattern that settles over much of the North Pacific Ocean in autumn, intensifies in winter, and weakens the following spring (Beamish and Bouillon 1993; Beamish et al. 1999). The intensity of the Aleutian Low can influence the strength of winter storms, depth of mixed-layer, wind stress, and ocean productivity, including Alaska salmon production (Venrick et al. 1987; Beamish and Bouillon 1993; Gargett 1997; Beamish et al. 1999). A strong Aleutian Low is characterized by a more intense low pressure system, warmer conditions, and increased primary production, which can lead to increased salmon abundance and decreased growth due to density dependence or increased metabolic costs that would be associated with warmer temperatures (Davidson and Vaughan 1941; Peterman 1978; Venrick et al. 1987; Beamish and Bouillon 1993; Helle and Hoffman 1995, 1998; Hinch et al. 1995a; Jobling 1994; Noakes et al. 1998; Gargett 1997; Beamish et al. 1999; Wells et al. 2006). The ALPI measures the geographic area of low pressure in the North Pacific Ocean (Beamish et al. 1997). Positive values indicate strong or intense Aleutian Low and negative values indicate a weaker or less intense Aleutian Low. The NPI-NCAR is another index of the Aleutian Low which measures area-weighted mean sea level pressure (Trenberth and Hurrell 1994).

The warm phase of the PDO is characterized by of warm sea surface temperatures along the west coast of North America coupled with cool SSTs in the central North Pacific Ocean, while the cool phase produces an opposite pattern of cool SSTs along the west coast and warm SSTs in the central North Pacific Ocean.

Changes in these alternating patterns (regime shifts) occurred during 1925, 1947, and 1976/1977 (Mantua et al. 1997). During the regime shift of 1976/1977 (to a warm phase), the Aleutian Low deepened, causing an increase in storm intensity in the North Pacific, and was accompanied by a reorganization of the North Pacific biota (Miller et al. 1994; Francis et al. 1998; Kaeriyama et al. 2004), and this pattern lasted through at least the late 1990's (Helle and Hoffman 1995). Warm phases of the PDO have been associated with an increase in salmon abundance in Alaska and a decrease in salmon abundance along the west coast of North America (Mantua et al. 1997; Helle and Hoffman 1998), and links between salmon abundance and the PDO have been identified on both regional and large scales (Beamish and Bouillon 1993; Francis and Hare 1994; Hare and Francis 1995; Adkison et al. 1996; Beamish et al. 1997; Mantua et al. 1997; Beamish et al. 1999). A decrease in average size at maturity of most populations of salmon in North America was observed after the 1976/1977 regime shift, and was coupled with an increase in age at maturity (Bigler et al. 1996; Helle and Hoffman 1995, 1998).

Ocean temperatures may affect age and size at maturity in sockeye salmon because food availability and growth are influenced by temperature (Nikolsky 1963; Rogers 1980; Burgner 1987; Rogers 1987; Rogers and Ruggerone 1993; Pyper and Peterman 1999). Temperature may affect growth directly through changes in metabolic costs or indirectly through changes in food availability (Nikolsky 1963; Ricker 1982; Laevastu 1984; Furnell and Brett 1986; Blackbourn 1987; Hsieh et al. 1991; Jobling 1994; Hinch et al. 1995a, 1995b; Ishida et al. 1995; Welch et al. 1995). Changes in SST have been associated with variation in adult body size of Bristol Bay and British Columbia salmon (Rogers 1980, 1984, 1987; Peterman 1984; Rogers and Ruggerone 1993; Hinch et al. 1995a, 1995b; Cox and Hinch 1997). Average size at maturity of 10 Fraser River sockeye salmon stocks was smaller during years of relatively warm sea surface temperatures (Cox and Hinch 1997). Warmer sea surface temperatures and lower food availability were associated with reduced size of Fraser River sockeye salmon (Hinch et al. 1995a, 1995b). A change in size at maturity has

the potential to alter egg production or fitness (Forbes and Peterman 1994), because egg size and egg number decline with body size (Quinn et al. 1995).

Coastal upwelling may also influence salmon survival and growth (Nickelson 1986; Fisher and Pearcy 1988; Scheuerell and Williams 2005; Wells et al. 2006). Several studies show positive relationships between salmon survival or growth and upwelling (Nickelson 1986; Fisher and Pearcy 1988; Wells et al. 2007; Black et al. 2008). Upwelling occurs when winds transport surface waters away from land masses. The surface layer is replaced by upwelled water from the deeper ocean, which stimulates primary productivity (Ware 1992) and can impact all trophic levels including salmon (Percy 1996). Downwelling, or negative values of upwelling, occurs as a result of onshore wind forcing and inputs from freshwater and can relocate prey to nearshore areas used by juvenile salmon (Royer 1981; Ware and McFarlane 1989; Percy 1996). The Coastal Downwelling Domain, located along the west coast of Alaska and northern British Columbia, is an area of high primary productivity (Sambrotto and Lorenzen 1987) and a migratory and feeding area for many stocks of juvenile salmon (Hartt and Dell 1986; Percy 1996). Large freshwater discharge and downwelling are believed to be important drivers of coastal circulation in the Gulf of Alaska (Schumacher and Reed 1980; Royer 1981; Royer 1998). Downwelling areas are typically not areas associated with high productivity, but the GOA is highly productive (Sambrotto and Lorenzen 1987), and numerous mechanisms which may supply nutrients to the area have been investigated (Weingartner et al. 2002; Stabeno et al. 2004; Ladd et al. 2005; Hermann et al. 2009). Hermann et al. (2009) report substantial upwelling of nutrients over large portions of the shelf, driven by local wind-stress curl- the effects of which were large enough to overcome the downwelling flux. Hermann et al. (2009) believe three sources of nitrate (upwelling, horizontal advection, and tides) likely contribute to high primary production in the coastal Gulf of Alaska. Ladd et al. (2005) provide evidence of 3 other mechanisms which may influence nutrient availability in the GOA: relaxed downwelling (or episodic upwelling), eddies, and tidal mixing. It is possible that

episodic upwelling influences potential ocean productivity which in turn might affect salmon growth.

We examined age and size at maturity of sockeye salmon originating from Lake Clark and the upper Newhalen River, Alaska (Figure 2.1) to detect potential trends over time (brood years 1976-1980 and 1997-2001), and to test relationships between size at age and environmental variables including the Aleutian Low pressure system the Pacific Decadal Oscillation, seasonal sea surface temperatures, and coastal upwelling. We expected negative correlations between ALPI, NPI-NCAR, SST and salmon length, poorer growth associated with warm index values of the PDO, and positive relationships between upwelling and length.

Methods

Study Area

The Newhalen River is part of the Kvichak River watershed, which is located in northeast Bristol Bay in Southwest Alaska (Figure 2.1). It connects two main lake systems, Lake Clark and Iliamna Lake, in which sockeye salmon spawn and rear (Mathisen and Poe 1969; Burgner 1991). Salmon originating from Lake Clark begin their upstream migration in Bristol Bay, swim up the Kvichak River through Iliamna Lake, and finally pass through the Newhalen River before segregating to spawn in beaches and tributaries of Lake Clark (Figure 2.1). Sockeye salmon age and size samples were collected from 13 subsistence fish camps on Sixmile Lake near the village of Nondalton and from the upper Newhalen River (Figure 2.1).

Data Collection

Sockeye salmon age, sex, and size data were collected from Nondalton and Newhalen River subsistence gill nets from 2001 to 2007 between 30 June and 27 July. Comparable data for years 1979 to 1985 were provided by the University of Washington, Fisheries Research Institute for individuals sampled between 4 July and 2 August. Sex was identified and fish were measured with calipers from mid-eye to

the hypural plate (MEH) or from mid-eye to the tail fork (MEF) and recorded to the nearest millimeter (mm). To make measurements comparable, MEF measurements were converted to MEH using regression equations derived from 1,005 paired measurements of Lake Clark sockeye salmon MEH and MEF lengths collected in 2000 (Woody 2004; $r^2 = 0.96$). Otoliths were used to determine age by the Alaska Department of Fish and Game Laboratory in Juneau (2001 collections) or the University of Washington (all other years), and recorded using European notation.

Age

The proportion of fish in each age class was calculated and arranged by brood year (1976-1980 and 1997-2001). Chi square tests were used to test whether proportions of fish in four major age groups (1.2, 2.2, 1.3, and 2.3) differed between the two time periods, and multiple comparison tests based on Tukey's honest significant difference test were used to identify significant differences (Zar 1999). Female and male sockeye salmon were analyzed separately; only fish sampled for both age and size were used in the analyses (N= 4,014).

Size

A two-way analysis of variance with interactions (fixed-effects ANOVA; general linear model) was used to examine variation in mean length at maturity among major age groups (1.2, 2.2, 1.3, and 2.3) and time periods (1976-1980 and 1997-2001) of Newhalen River sockeye salmon. Female and male sockeye salmon were analyzed separately. Tukey's honest significant difference multiple comparison tests were used to identify significant differences in length among age groups.

Environmental variables

Environmental variables included the ALPI, NPI-NCAR, winter PDO index, seasonal SST indices from the North Pacific Ocean (NPO) and Gulf of Alaska (GOA), and seasonal coastal upwelling indices. The ALPI (provided by Fisheries and Ocean's Canada; Beamish et al. 1997) and NPI-NCAR (provided by NOAA at

<http://www.beringclimate.noaa.gov/data/index.php>; Trenberth and Hurrell 1994; Kalnay et al. 1996) provide measures of the relative intensity of the mean wintertime Aleutian Low pressure system. The ALPI winter index is the mean from December through March, and the NPI-NCAR winter index is mean from November through March, where the year refers to January in the monthly series. Both are expressed as anomalies from long term means, where positive values reflect a strong or intense Aleutian Low. The PDO index (provided by NOAA/JISAO; Mantua et al. 1997) is the leading principal component of North Pacific monthly sea surface temperature variability poleward of 20° N for 1900-1993 (Mantua et al. 1997). We used yearly values of the ALPI, NPI-NCAR, and PDO indices that corresponded to the first winter that fish were at sea.

Seasonal indices for SST and upwelling were calculated for the first and second summers that salmon are at sea (s1 and s2; Jun-Aug), and the intervening or first winter at sea (w1; Dec-Feb), with the year referring to January of the three month series. Monthly sea surface temperatures (ICOADS 2.4; Worley et al. 2005) were compiled for the Gulf of Alaska (averaged over the region bounded by 140-160°W and 52-56°N) and the North Pacific Ocean (170°E-140°W and 48-54°N), which reflect the general area inhabited by Bristol Bay sockeye salmon (French et al. 1976) during their ocean residency. A mean monthly coastal upwelling index, provided by the Pacific Fisheries Environmental Laboratory, measures the strength of wind forcing in the ocean (cubic meters per second per 100 meters of coastline; Bakun 1990), and was used as a measure of summer upwelling (and winter downwelling) and potential ocean productivity that might affect salmon growth. The upwelling station was located off the Kenai Peninsula at 60°N, 149°W (NMFS 2003). Because the GOA is a downwelling system, where negative index values indicate strong downwelling, we removed the negative signs in the “winter upwelling” index and renamed them “winter downwelling”.

Linear regression weighted by sample size was used to assess associations between mean length at maturity of Newhalen River sockeye salmon and a given

environmental parameter within a sex and age class (1.2, 2.2, and 1.3) across brood years (six regressions for each (12) environmental variable; $n = 10$). Age 2.3 fish were not included in the environmental analyses because this age class comprised less than 5% of samples in most years when sex-specific mean lengths were summarized.

Results

Age

More female and male sockeye salmon spent three years in the ocean in recent brood years compared to earlier brood years (chi square, $P < 0.05$; Table 2.1; Figure 2.2). The proportion of age 1.3 female fish increased (13 to 42%), while the proportion of age 1.2 and 2.2 female fish decreased over time (58 to 37% and 22 to 16%, respectively; Table 2.1; Figure 2.2). Similarly, the proportion of age 1.3 male fish increased (11 to 43%) and the proportion of age 1.2 male fish decreased (62 to 36%; Table 2.1; Figure 2.2). The proportion of age 2.3 male fish decreased over time (from 8 to 4 %; Table 2.1; Figure 2.2).

Size

Female sockeye salmon ($N = 2,117$) were smaller during 1997-2001 than during 1976-1980 ($F = 975.69$, $P < 0.001$; two-way ANOVA; Table 2.1; Figure 2.3), and female sockeye salmon that spent three years in the ocean (1.3 and 2.3) were significantly larger than fish that spent two years in the ocean (1.2 and 2.2; $F = 863.69$, $P < 0.001$; two-way ANOVA; Table 2.1; Figure 2.3). Differences in female mean length among age groups were not the same over time periods in all but three comparisons (time*age interaction; $F = 2.47$; $P = 0.060$). Within every age class, female fish were significantly smaller during 1997-2001 than during 1976-1980 (Tukey's post hoc tests; $P < 0.01$; Table 2.1; Figure 2.3).

Male sockeye salmon ($N = 1,897$) were also smaller during 1997-2001 than during 1976-1980 ($F = 616.3$; $P < 0.001$; two-way ANOVA; Table 2.1; Figure 2.3).

Male sockeye salmon that spent three years in the ocean (1.3 and 2.3) were significantly larger than fish that spent two years in the ocean (1.2 and 2.2; $F = 686.5$, $P < 0.001$; two-way ANOVA; Table 2.1; Figure 2.3). Differences in male mean length among age groups were not the same over time periods (time*age interaction; $F = 4.77$; $P = 0.003$). Within every age class, male fish were significantly smaller during 1997-2001 than during 1976-1980 (Tukey's post hoc tests; $P < 0.01$; Table 2.1; Figure 2.3).

Environmental variables

The ALPI, NPI-NCAR, and PDO indices were not correlated with Newhalen River sockeye salmon length in either sex or in any age group ($P > 0.05$; Table 2.3). Winter SST (NPOw1 and GOAw1) was negatively correlated with length in female and male age 2.2 sockeye salmon (Table 2.3; Figures 2.4 and 2.5). North Pacific Ocean SST was negatively correlated with age 1.3 female and male sockeye salmon length during the second summer at sea (NPOs2; $r^2 = 0.48$ and 0.50 ; Table 2.3; Figure 2.6). Coastal upwelling was positively correlated with age 1.2 female and male length during the first summer at sea (UPs1; $r^2 = 0.59$ and 0.59 ; Table 2.3; Figure 2.7). Coastal upwelling was positively correlated with length in female fish age 1.2 and males age 1.2 and 2.2 during the second summer at sea (UPs2; $r^2 = 0.53$ and 0.63 ; Table 2.3; Figure 2.8). Winter coastal upwelling was negatively correlated with length in females age 1.2, 1.3, and 2.2, and in males age 1.2 (UPw1; Table 2.3; Figure 2.9).

Discussion

Age composition and length at maturity of Newhalen River sockeye salmon differed over time; both female and male fish more likely to spend an extra year at sea and were smaller during 1997-2001 as compared to 1976-1980. Broad-scale environmental variables (the ALPI, NPI-NCAR, and PDO) were not correlated with

salmon length, but SST and coastal upwelling appeared to be important indicators of fish length.

An increase in age and decrease in size is consistent with past research which has shown declines in size at maturity for many stocks of Pacific salmon over the past several decades (Ricker 1981, 1982, 1995; Bigler and Helle 1994; Helle and Hoffman 1995; Ishida et al. 1995; Bigler et al. 1996). Several hypotheses have been proposed to explain changes in average size and age of salmon (Ricker 1980; Quinn 2005). The first examines the possibility that declines in fish size are a result of statistical artifacts (biased data) and not actual changes in salmon. The second hypothesis suggests that changes are genetic, resulting from selection against populations with large individuals or selection against delayed maturation. The third potential cause of change in age or size involves effects of hatchery propagation due to larger smolt size of hatchery-reared fish, genetic differences which result from selective breeding, or increased competition in the ocean. Lastly, changes in age and size may be related to the ocean environment (temperature, upwelling, salinity, and competition for food) which could affect growth.

Helle and Hoffman (1995) found that adult size of two North American populations of chum salmon *Oncorhynchus keta* decreased from the 1970s to the 1990s, and attributed this decline to changes in the ocean environment, most likely increased population density. They also observed an increase in average age at maturity in both populations over time (Helle and Hoffman 1995). Bigler and Helle (1994) found a trend of decreased average body size of five species of Pacific salmon coincident with increases in population abundance of North Pacific salmon, and attributed the pattern to density dependent pressures. Increased population density may lead to reduced per capita food availability, which contributes to reduced growth, causing delays in spawning migrations, and may result in older age and smaller size at maturity (Bigler and Helle 1994). Abundance of North Pacific salmon (as estimated from commercial catches of all Pacific salmon species; Eggers et al. 2005) has increased since the 1970's. Although returns to the Kvichak River declined in

recent study years, intra or inter-species population density in the North Pacific Ocean could be a factor in the decreases in size at maturity observed among Lake Clark and the upper Newhalen River spawners through density dependent competition for food.

Sex and age-specific Newhalen River sockeye salmon length at maturity was correlated with SST. Winter (NPOw1 and GOAw1) and summer (NPOs2) SST was negatively correlated with length of Newhalen River female and male age 2.2 and 1.3 sockeye salmon over brood years. These findings are consistent with past research that showed associations between increased SST and reduced body size in Alaskan and Canadian sockeye salmon (Cox and Hinch 1997; Pyper and Peterman 1999). This relationship between length and SST may be related to increased metabolic costs that would be associated with warmer SST (Jobling 1994; Hinch et al. 1995a), or may be a result of increased density dependence due to decreases in foraging area as warmer SST shift salmon distributions north (Welch et al. 1995). Salmon length and wintertime SST relationships (in both the GOA and NPO) displayed different patterning within each group of early and late brood years, which may indicate that other factors specific to those time periods could be driving the variation observed, and may warrant further investigation. Sea surface temperatures in summer (NPO) appear to better explain the differences between time periods. Weak, but negative relationships were found among other age groups, and similar negative relationships were observed within each group of early and later brood years. Significant trends may have been observed among the older (1.3) fish because growth in the later life stages in the ocean is important in determining final size at maturity (Rogers and Ruggerone 1993; Brett 1995).

Length was positively associated with both winter downwelling and summer upwelling, indicating that growth may be enhanced by conditions that are conducive to increased nutrient availability. The Southeast Alaska coast is a downwelling system and deep water mixing and input from freshwater are believed to be important in nutrient supply (Favorite et al. 1976; Peterson et al. 2005). Other mechanisms

which may provide nutrients to support the productive ecosystem have been proposed including relaxed winter downwelling or episodic summer upwelling (Stabeno et al. 2004; Ladd et al. 2005; Hermann et al. 2009). Ladd et al. (2005) showed increasing saline (nutrient-rich) waters on the GOA shelf occurring about a week after downwelling winds had weakened in winter 2001/2002 (but which coincided with periods of strong downwelling winds). As downwelling winds increased, waters responded with decreasing salinity (Ladd et al. 2005). Winter downwelling relaxation events do not appear to be unusual in other years (Ladd et al. 2005). Wells et al. (2008) also found a relationship between increased growth of Chinook salmon from the Situk River and decreased winter upwelling (November through March; onshore transport along the GOA coast). It is possible that although growth appeared to be related to increased downwelling, salmon growth may actually be impacted by increases in nutrient-rich water resulting from relaxed winter downwelling events.

Summer upwelling was stronger during years when salmon were larger (early brood years 1976-1980), compared to later years when fish were smaller and upwelling was weaker, which is consistent with previous research showing similarly positive relationships between coastal upwelling and salmon growth (Nickelson 1986; Fisher and Pearcy 1988; Wells et al. 2007; Black et al. 2008). Upwelling occurs throughout the year in the GOA, but is more common in summer when strong winter winds weaken (Ladd et al. 2005). Upwelling events are associated with increased salinity and nutrient availability (Stabeno et al. 2004; Ladd et al. 2005), high levels of primary production ($300 \text{ g} \cdot \text{cm}^{-2} \cdot \text{yr}^{-1}$; Ware and McFarlane 1989) and secondary production, or zooplankton prey (Cooney 1986), and have been related to increased salmon growth (Nickelson 1986; Fisher and Pearcy 1988; Wells et al. 2007; Black et al. 2008). Although we found positive relationships between upwelling and fish length, it is possible that fish did not respond independently to upwelling in early versus later brood years, as is observed in the relationships between first summer upwelling and fish length. We also observed similar patterns among upwelling in summer 2 and length among all age groups and sexes, but these patterns may be

misleading if strongly driven by one year. Further analyses of these potential effects may help improve our understanding of these relationships.

The ALPI, NPI-NCAR, and PDO indices were not correlated with Newhalen River sockeye salmon length in either sex or in any age group. Past studies have found both similar and contrasting results to these (Wells et al. 2006; Black et al. 2008). For example, Wells et al. (2006) did not find a relationship between Alaska coho salmon *Oncorhynchus kisutch* length and the ALPI and PDO (Wells et al. 2006), and suggested density dependence may have influenced the lack of relationship, or suggested that size may be better modeled using biological rather than physical parameters. Other research showed positive correlations between an intense Aleutian Low and increased abundance, which was believed to be related to reduced salmon growth in early marine life (Peterman 1978; Venrick et al. 1987; Beamish and Bouillon 1993; Helle and Hoffman 1995, 1998; Noakes et al. 1998; Gargett 1997; Beamish et al. 1999). It is unclear why similar patterns between the Aleutian Low pressure system, PDO and growth were not observed among Newhalen River sockeye salmon. Broad-scale climatic patterns (PDO, APLI, and NPI-NCAR) may affect salmon growth on scales not detected during this study. Analyses which incorporate multiple cycles of these indices may be necessary to better detect patterns. Although the relationships between environment and fish length were quantified as if direct, complex interactions in the ecosystem probably complicate these relationships, and may be better modeled with additional variables.

Changes in the age and size of Newhalen sockeye salmon over time could be related to selection of larger individuals by gillnets, which have been used in the Bristol Bay fishery since 1883 to target larger (male) fish (Ricker 1981; Rogers 1987; Trippel 1995; Hutchings 2004). Gillnets select for different sized fish (Todd and Larkin 1971), and in general the degree of selectivity is determined by the size of the mesh used in the gillnet, where smaller fish are captured with smaller mesh size (Fried et al. 1984). Ricker (1981) reported decreases in age and size of all species of Pacific salmon from British Columbia catch and escapement, and suggested that gear

selectivity, among other factors, affected these traits. Kendall (2009, in press) found the Nushagak District of Bristol Bay fishery exploited older and larger sockeye salmon in most of the 60 years studied (from 1940s to 2000s), but reported that vulnerability of sockeye salmon to the gillnet fishery varied over time. Specifically, she found that the magnitude of fishery selection has decreased, and has not been as consistent in recent years (since the 1970's). Kendall (2009, in press) concluded that the Nushagak District fishery may not be strongly size selective, but found differential patterns of selection for different sexes and ocean ages. It is possible that size of Newhalen River sockeye salmon was affected by fishery selection, but long term research quantifying selection and genetic variability would be needed to determine if selection led to the changes. Newhalen River sockeye salmon are likely exposed to a combination of factors, including changes in the ocean environment, density dependent responses to changes in abundance, and the size-selective fishery, which may influence age and size at maturity.

Across age groups and sexes, we found an increase in the proportion of older (marine age 3) fish, and a decrease in fish length over two time periods which appears to be influenced by increased SST, strengthened summer upwelling, and strengthened winter downwelling. Our results highlight the importance of the ocean environment in salmon production and growth as others have noted. A complex interaction of factors may influence age and size at maturity of salmon. A better understanding of the mechanisms underlying the relationships between salmon growth and ocean conditions is important for management of these stocks.

Acknowledgements

This project was a collaborative effort between the United States Geological Survey – Alaska Science Center (USGS ASC) and Lake Clark National Park and Preserve – National Park Service (NPS). Funding support was provided by the U.S. Fish and Wildlife Service (USFWS), the National Park Service, and the USGS ASC. The generosity and kindness of the Balluta and Tracey families of Nondalton helped make field seasons a success. I thank the many people who helped collect samples in the field including Gerald Anelon, Tatiana Askoak, Kristy Balluta, Tara Balluta, Nate Blewett, Iris Bowers, Mike Donnelly, Max Hensley, Janell Kakaruk, Jared Irvine, Kevyn Jalone, Kathryn Leifeste, Pat Poe, Laura Sorenson, Heather Sowalla, Danielle Stickman, Shavela Stickman, Julia Vinciguerra, Ann Williams, and Dan Young. Greg Ruggerone (Natural Resource Consultants) compiled and shared North Pacific and Gulf of Alaska sea surface temperature data. Chris Boatright, Pat Poe, and others at University of Washington, Fisheries Research Institute generously shared historic sockeye salmon age and size data. Dan Young assisted with logistics, sampling, and created and shared maps of study sites. I thank Chris Zimmerman (USGS) and the Alaska Science Center for continued support of this project.

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Table 2.1. Summary statistics from two-way ANOVA of salmon length, location, and time. Lake Clark sockeye salmon mean length (ML, in mm), standard error (SE), sample size (N), and percent age class composition (%) are grouped by sex and early (1976-1980) and late (1997-2001) brood years. Mean length differed significantly among age groups, sexes, and time periods (brood years 1976-1980 and 1997-2001).

Sex	Brood Years	Age 1.2				Age 2.2				Age 1.3				Age 2.3				All Ages		
		ML	SE	N	%	ML	SE	N	%	ML	SE	N	%	ML	SE	N	%	ML	SE	N
F	1976-1980	503	0.81	577	58	517	1.60	218	22	561	1.81	124	13	558	3.23	71	7	517	0.96	990
F	1997-2001	468	0.93	418	37	476	1.44	181	16	525	0.94	477	42	517	2.42	51	5	495	0.99	1127
F	All	488	0.82	995	47	498	1.49	399	19	532	1.03	601	28	541	2.82	122	6	506	0.73	2117
M	1976-1980	513	0.88	564	62	529	2.01	181	20	579	2.71	97	11	578	3.50	70	8	528	1.13	912
M	1997-2001	483	1.16	353	36	498	1.65	169	17	541	1.09	420	43	533	3.57	43	4	512	1.11	985
M	All	502	0.86	917	48	514	1.55	350	18	548	1.21	517	27	561	3.30	113	6	520	0.81	1897

Table 2.2. Summary statistics for sockeye salmon from individual brood years. Lake Clark sockeye salmon mean length (ML), standard deviation (SD), sample size (N), and percent age composition are grouped by sex and individual brood year for each major age group (1.2, 2.2, 1.3, and 2.3).

Sex	Brood Year	Age 1.2				Age 2.2				Age 1.3				Age 2.3				Total
		ML	SD	N	%	ML	SD	N	%	ML	SD	N	%	ML	SD	N	%	
Female	1976	505	18	5	3	523	19	84	46	564	23	36	20	559	27	56	31	181
	1977	517	15	11	11	519	37	37	37	559	19	51	51	571	*	1	1	100
	1978	502	21	272	89	509	19	27	9	551	11	4	1	585	*	1	0	304
	1979	504	17	284	80	509	20	44	12	558	22	20	6	567	17	9	3	357
	1980	523	48	5	10	515	17	26	54	565	13	13	27	514	5	4	8	48
	1997	464	24	59	38	477	24	35	22	528	20	61	39	535	7	2	1	157
	1998	465	18	151	63	494	12	13	5	536	23	73	31	531	*	1	0	238
	1999	472	14	104	35	472	18	103	35	525	21	46	16	516	17	42	14	295
	2000	464	18	31	10	482	16	25	8	522	19	252	81	512	16	5	2	313
	2001	473	20	73	59	480	18	5	4	514	20	45	36	538	*	1	1	124
Male	1976	483	30	8	6	535	16	74	51	584	20	24	17	580	25	38	26	144
	1977	519	20	12	13	550	43	26	28	575	30	55	59	*	*	0	0	93
	1978	515	22	280	90	524	21	24	8	576	10	5	2	607	10	2	1	311
	1979	512	18	259	78	512	24	47	14	584	21	7	2	590	27	21	6	334
	1980	516	18	5	17	528	14	10	33	599	32	6	20	539	17	9	30	30
	1997	480	25	54	34	507	17	37	23	545	21	70	43	*	*	0	0	161
	1998	480	19	103	53	505	23	11	6	552	23	80	41	524	39	2	1	196
	1999	489	21	90	33	494	21	109	40	534	21	44	16	536	20	28	10	271
	2000	479	25	50	21	515	17	7	3	541	20	172	74	546	20	4	2	233
	2001	484	20	56	45	479	18	5	4	529	22	54	44	520	29	9	7	124

Table 2.3. Linear regression results for length on environmental variables. Each variable is listed on the left, followed by the season tested. Coefficient of determination (r^2) values are shown for female (left panel) and male (right panel) Lake Clark sockeye salmon in each of the three major age groups (1.2, 2.2, and 1.3). Plus or minus sign indicates slope direction; blank cells indicate non-significance ($P > 0.05$).

Variable	Season	r^2			r^2		
		Female			Male		
		1.2	2.2	1.3	1.2	2.2	1.3
Aleutian Low							
ALPI	Winter 1						
NPI-NCAR	Winter 1						
Pacific Decadal Oscillation	Winter 1						
North Pacific Ocean SST	Summer 1						
North Pacific Ocean SST	Winter 1		- 0.55			- 0.63	
North Pacific Ocean SST	Summer 2			- 0.48			- 0.50
Gulf of Alaska SST	Summer 1						
Gulf of Alaska SST	Winter 1		- 0.59			- 0.56	
Gulf of Alaska SST	Summer 2						
Upwelling	Summer 1	+ 0.59			+ 0.59		
	Summer 2	+ 0.53			+ 0.63	+ 0.42	
Downwelling	Winter 1	+ 0.78	+0.41	+0.49	+ 0.64		

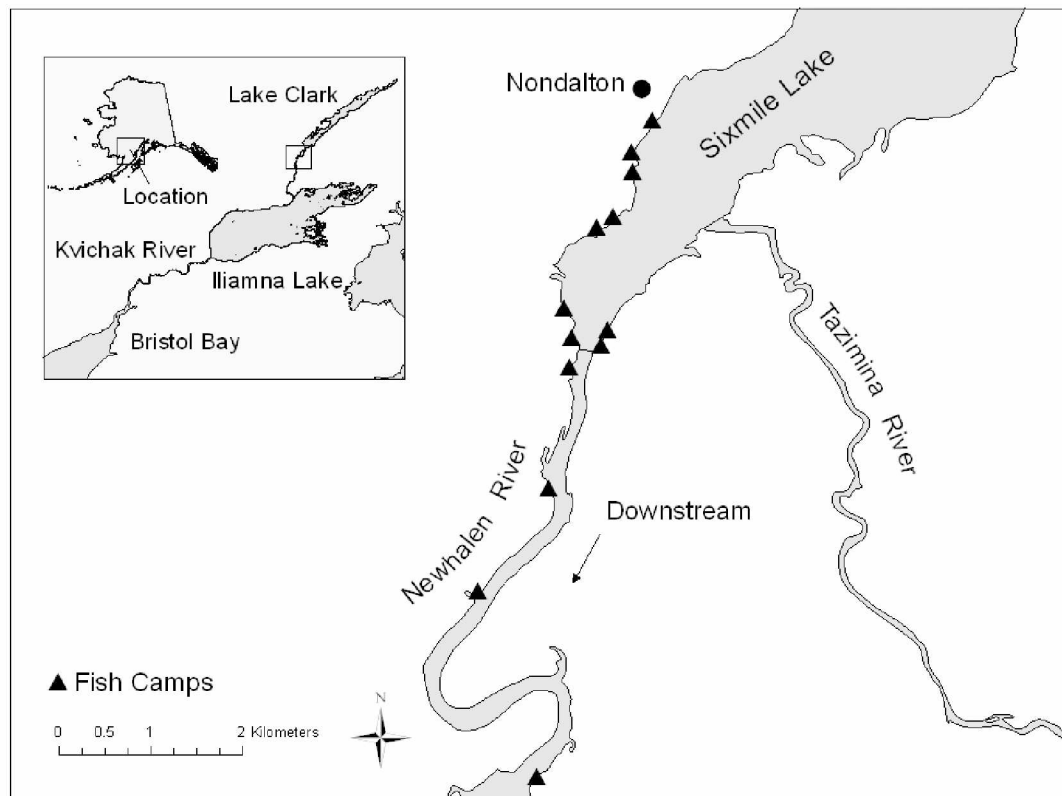


Figure 2.1. Sampling locations on Sixmile Lake and the upper Newhalen River. Age and size samples were collected from subsistence fish camps (indicated by triangles) just below the outlet of Lake Clark, Alaska.

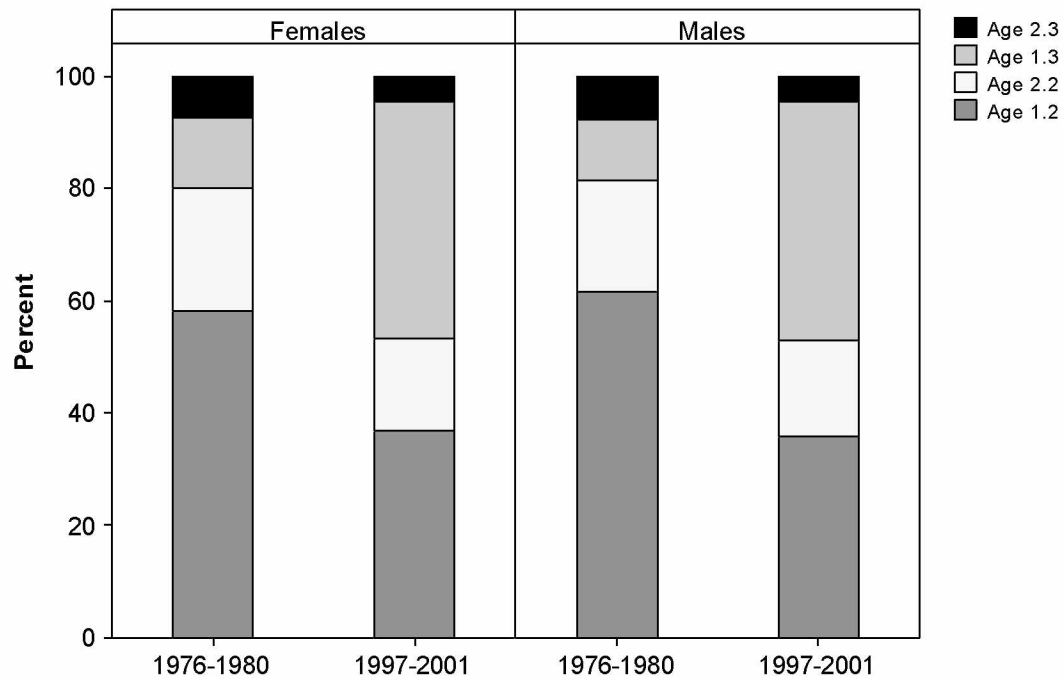


Figure 2.2. Percent age composition Lake Clark sockeye salmon. Bar graphs show the results of the chi square analysis of age composition over the two time periods for female salmon (on the left panel) and male salmon (on the right panel). Time (grouped by early and late brood years) is on the X axis, and percent age in each of the four major age groups is on the Y axis. Among both sexes, the proportion of older age 1.3 fish increased, and the proportion of younger age 1.2 fish decreased over time periods ($P < 0.05$).

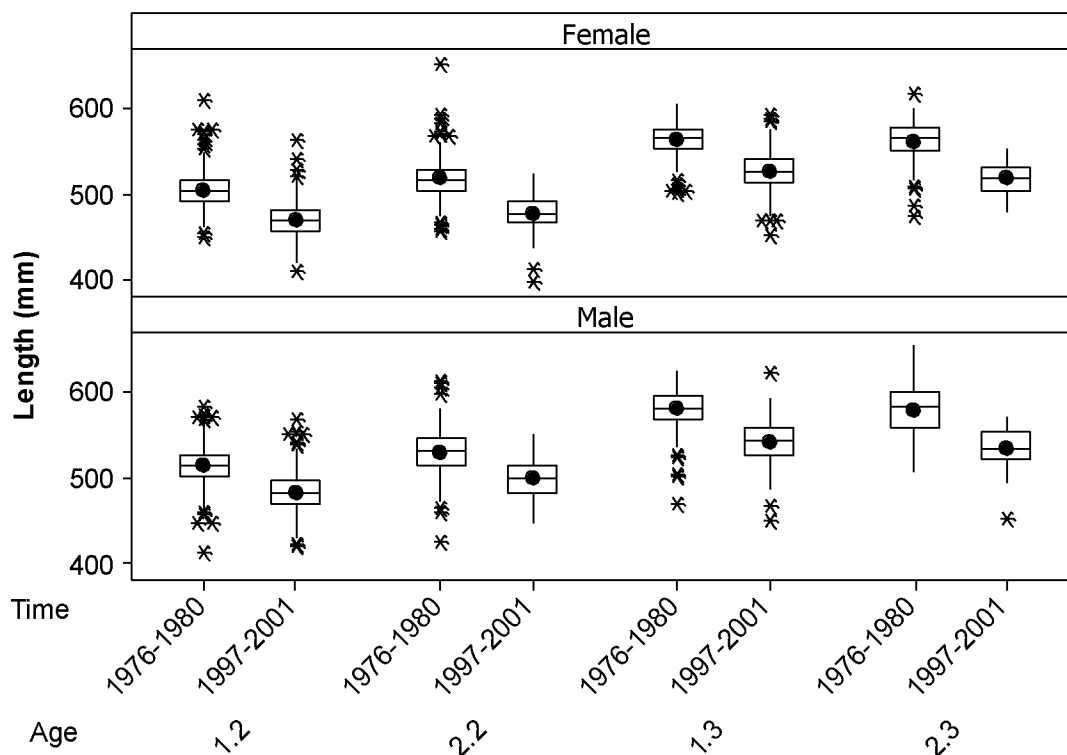


Figure 2.3. Mean length of sockeye salmon from four major age groups. Lake Clark sockeye salmon mean lengths were analyzed separately for each sex using a two-way ANOVA of mean length versus age group and time period (early and late brood years). Within all age groups and sexes, salmon were significantly larger during 1976-1980 than during 1997-2001 brood years ($P < 0.05$). Boxes represent the interquartile range where the middle line is the second quartile or median. The lower and upper whiskers extend to minimum and maximum data points, circles are means, and asterisks represent outliers.

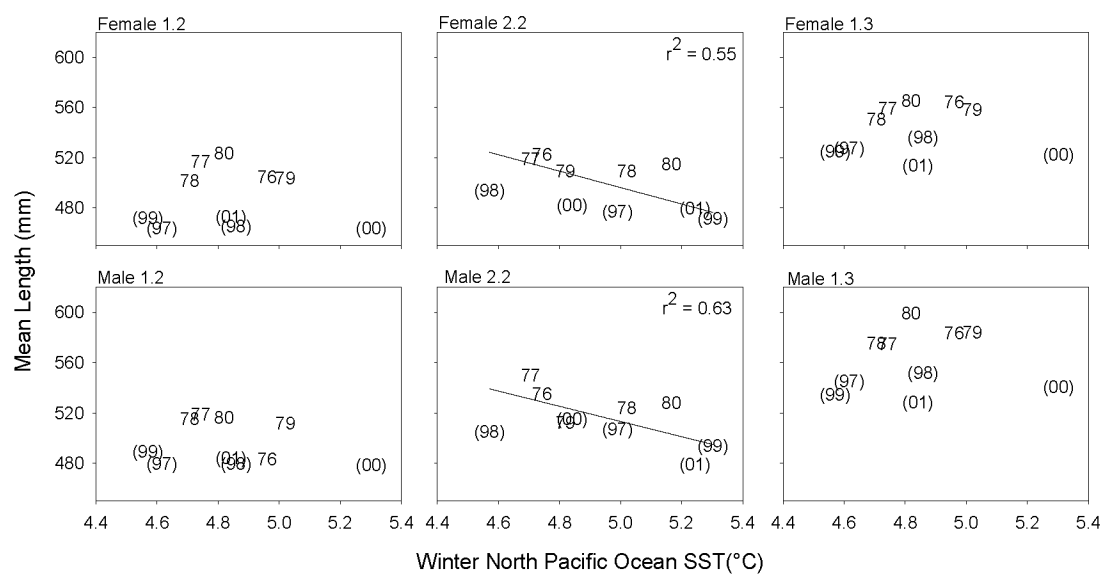


Figure 2.4. Length and North Pacific Ocean winter sea surface temperature. Lake Clark sockeye salmon lengths were regressed (weighted linear regression) on sea surface temperatures for female (top panels) and males (bottom panels) within each age group. Winter SST in the North Pacific Ocean was negatively correlated with age 2.2 fish length ($P = 0.013$ and 0.006 for female and male sockeye salmon). Recent brood years (1997-2001) are displayed in parentheses to distinguish them from earlier brood years.

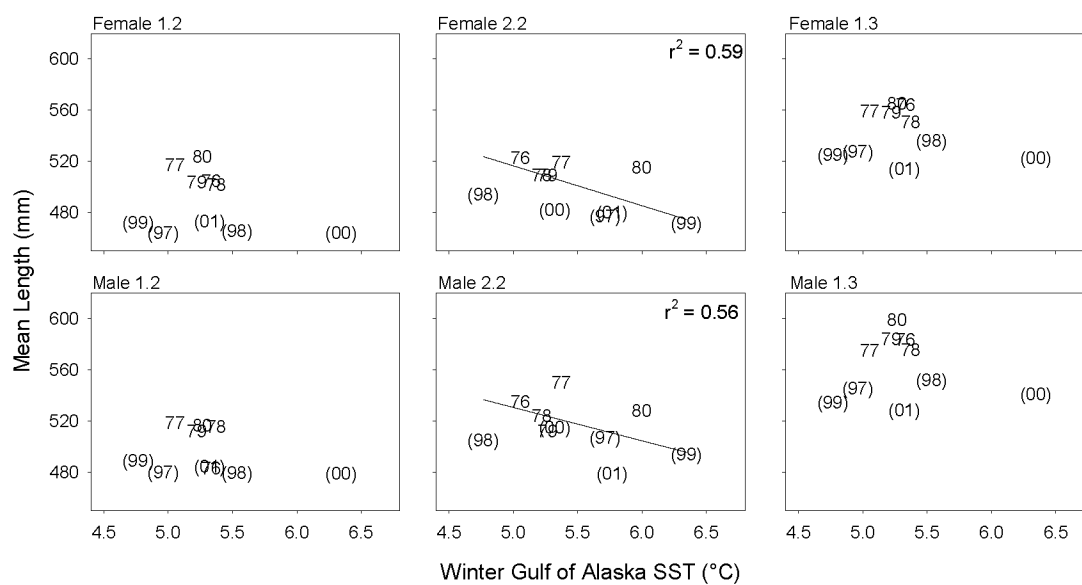


Figure 2.5. Length and Gulf of Alaska winter sea surface temperature. Lake Clark sockeye salmon lengths were regressed (weighted linear regression) on sea surface temperatures for female (top panels) and males (bottom panels) within each age group. Winter SST in the Gulf of Alaska was negatively correlated with age 2.2 fish length ($P = 0.010$ for female and 0.012 for male sockeye salmon). Recent brood years (1997-2001) are displayed in parentheses to distinguish from earlier brood years.

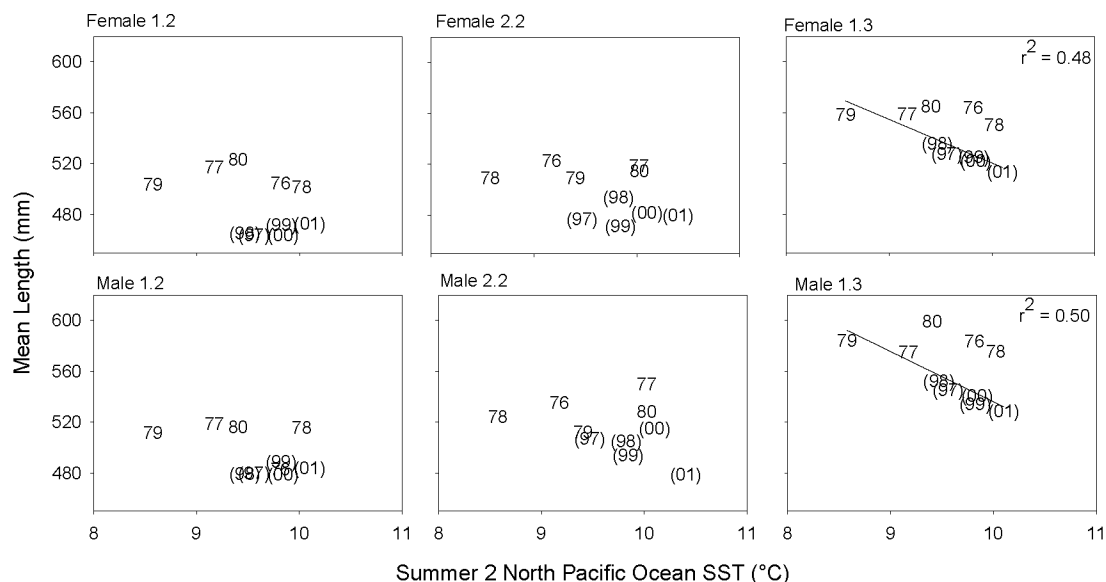


Figure 2.6. Length and North Pacific Ocean summer 2 sea surface temperature. Lake Clark sockeye salmon lengths were regressed (weighted linear regression) on sea surface temperatures for female (top panels) and males (bottom panels) within each age group. Summer 2 SST in the North Pacific Ocean was negatively correlated with age 1.3 fish length ($P = 0.028$ female and 0.023 for male sockeye salmon). Recent brood years (1997-2001) are displayed in parentheses to distinguish them from earlier brood years.

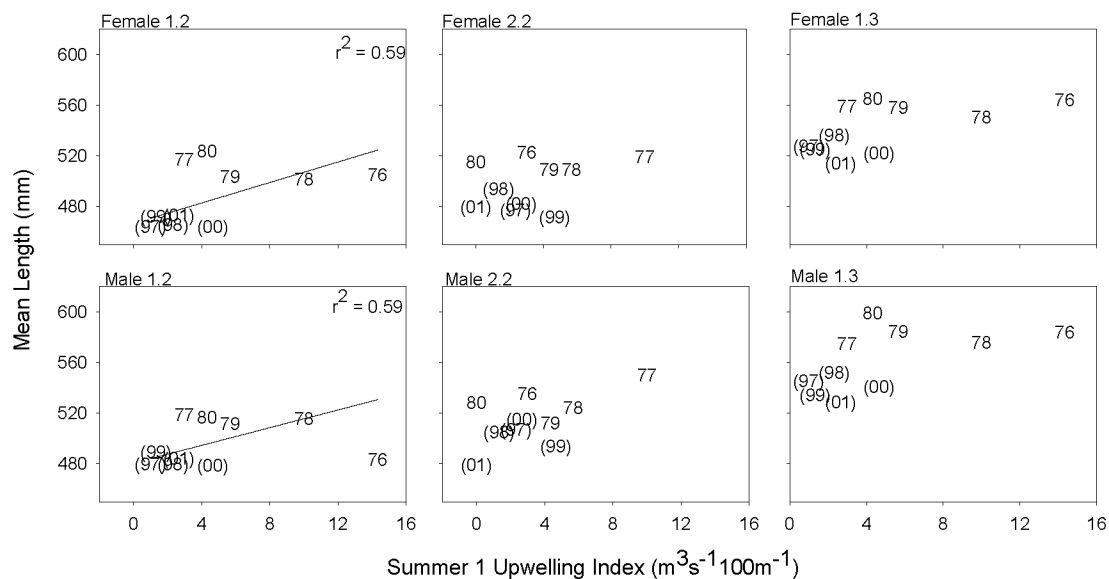


Figure 2.7. Length and summer 1 coastal upwelling. Lake Clark sockeye salmon lengths were regressed (weighted linear regression) on coastal upwelling for female (top panels) and males (bottom panels) within each age group. Summer 1 upwelling was positively correlated with age 1.2 fish length ($P = 0.009$ female and 0.010 for male sockeye salmon). Recent brood years (1997-2001) are displayed in parentheses to distinguish them from earlier brood years.

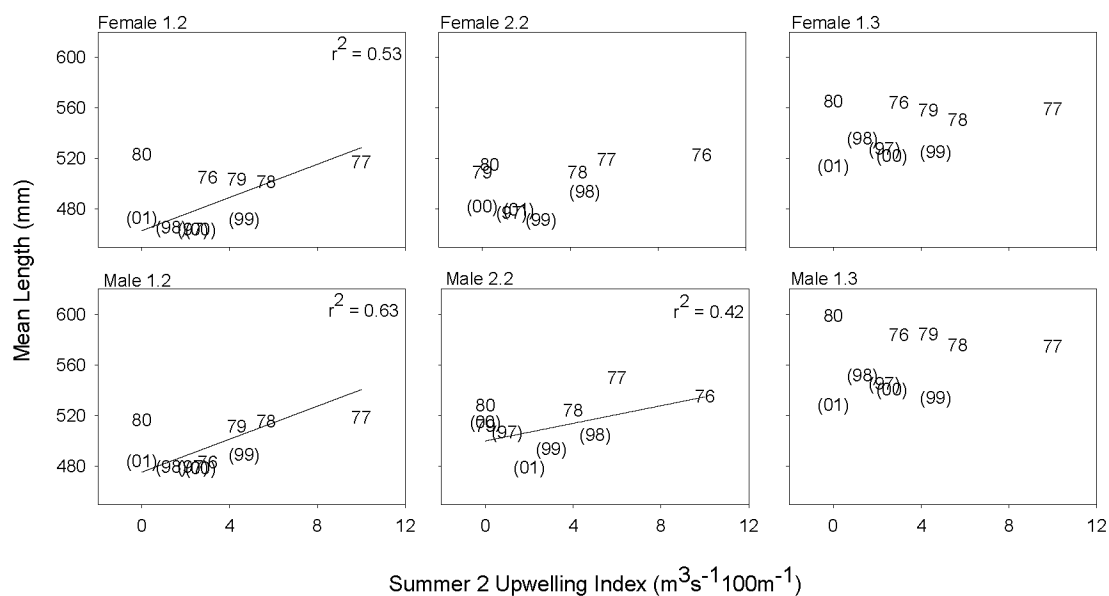


Figure 2.8. Length and summer 2 coastal upwelling. Lake Clark sockeye salmon lengths were regressed (weighted linear regression) on coastal upwelling for female (top panels) and males (bottom panels) within each age group. Summer 2 upwelling was positively correlated with age 1.2 fish length ($P = 0.018$ female and 0.006 for male sockeye salmon) and male age 2.2 fish length ($P = 0.044$). Recent brood years (1997-2001) are displayed in parentheses to distinguish them from earlier brood years.

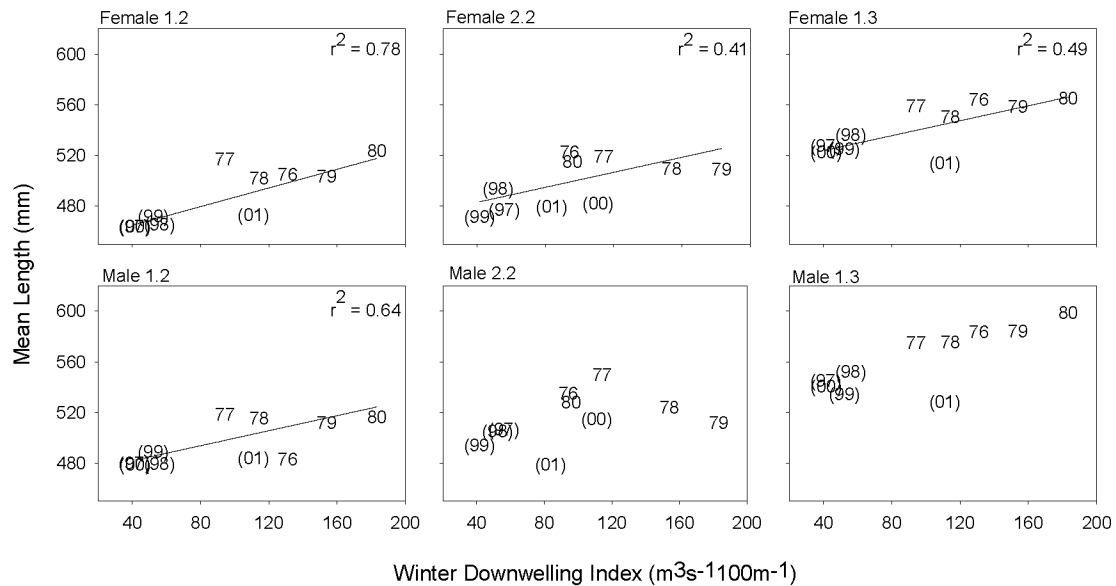


Figure 2.9. Length and winter coastal downwelling. Lake Clark sockeye salmon lengths were regressed (weighted linear regression) on coastal downwelling for female (top panels) and males (bottom panels) within each age group. Winter downwelling was positively correlated with age 1.2 fish length ($P = 0.001$ female and 0.005 for male sockeye salmon), female age 2.2 fish length ($P = 0.023$), and female age 1.3 fish length ($P = 0.047$). Recent brood years (1997-2001) are displayed in parentheses to distinguish them from earlier brood years.

Conclusions

Results from this study revealed significant variation in age composition and length at maturity among Lake Clark and upper Newhalen River sockeye salmon by spawning location and over time. Differences did not appear to be related to beach or tributary spawning habitat, but the ocean environment (SST and upwelling) appeared to be an important indicator of length at age of maturity. Although clear patterns in age and size by spawning habitat were not observed within Lake Clark, the variation in phenotypes (or biocomplexity, Hilborn et al. 2003) among and within the component populations of the Kvichak River watershed (including those in Lake Clark) likely influences the stability and sustainability of the larger Bristol Bay sockeye salmon fishery because a combination of life history strategies and local adaptations would allow buffers to large-scale environmental changes in freshwater or the ocean (Giesel 1974; Altukov 1981; Hilborn et al. 2003).

Female and male sockeye salmon were more likely to spend an extra year at sea and were smaller in recent brood years (1997-2001) compared to past brood years (1976-1980). These patterns are consistent with past research which has shown increases in age and declines in size at maturity of many stocks of Pacific salmon over past decades (Ricker 1981, 1982, 1995; Bigler and Helle 1994; Helle and Hoffman 1995; Ishida et al. 1995; Bigler et al. 1996), and may be related to changes in the ocean environment, increased salmon abundance, or selection of larger fish by gillnets over time. Sea surface temperature was negatively correlated with fish length, which is consistent with previous research (Cox and Hinch 1997; Pyper and Peterman 1999). These relationships could be related to increased metabolic costs that would be associated with warmer temperatures (Jobling 1994; Hinch et al. 1995) or a result of density dependent competition for food if foraging areas shifted to smaller areas with warmer temperatures (Welch et al. 1995). Summer upwelling was also an important indicator of Lake Clark sockeye salmon length. Lake Clark sockeye salmon were larger in years when upwelling was stronger (1976-1980)

compared to recent years when fish were smaller (1997-2001), consistent with previous work showing similar positive relationships between upwelling and salmon growth (Nickelson 1986; Fisher and Pearcy 1988; Wells et al. 2007; Black et al. 2008). Upwelling events are associated with increased nutrient availability, and high primary and secondary productivity (Cooney 1986; Ware and McFarlane 1989; Stabenot et al. 2004; Ladd et al. 2005), which can affect higher trophic levels including salmon (Brodeur 1988).

Sockeye salmon originating from Lake Clark and the upper Newhalen River are an important commercial, ecological, and subsistence resource, and are an important component of the larger Kvichak River escapement. Average escapement to the Kvichak River declined sharply during 1996-2005, prompting the listing of the Kvichak originating salmon as a “stock of concern” in 2003. Although returns to the Kvichak River declined in recent study years, North Pacific salmon abundance has increased since the 1970s (Eggers et al. 2005), which could be related to favorable environmental factors or increased hatchery propagation, and has the potential to influence age and size at maturity. Understanding freshwater or oceanic factors which influence variation in age and size at maturity is important because these traits have potentially adaptive value, and the potential to influence reproductive success and survival (Healey 1986). These results demonstrate the complexity of both the freshwater and ocean ecosystems, and indicate that trends in age and size at maturity across beach and tributary habitats are not necessarily similar among systems or years. Our results highlight the importance of the both spawning location and ocean environment in salmon age and size at maturity. A complex interaction of factors likely influence age and size at maturity of salmon, but further research exploring the mechanisms underlying the relationships between salmon growth and ocean conditions will be important for effective management of these stocks.

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