

**2011 Arctic-Yukon-Kuskokwim Sustainable Salmon Initiative  
Project Final Product<sup>1</sup>**

**AYK – Historical Analyses of AYK & Asian Chum, Phase 1 & 2**

by:

Beverly A. Agler<sup>2</sup>, Gregory T. Ruggerone<sup>3</sup>, Lorna I. Wilson<sup>2</sup>

<sup>2</sup> Alaska Department of Fish and Game, Mark, Tag, and Age Laboratory, 10107 Bentwood Place, Juneau, Alaska 99801

<sup>3</sup> Natural Resources Consultants, Inc., 4039 21<sup>st</sup> Avenue West, Suite 404, Seattle, Washington 98199

June 2012

<sup>1</sup> Final products of AYK Sustainable Salmon Initiative-sponsored research are made available to the Initiatives Partners and the public in the interest of rapid dissemination of information that may be useful in salmon management, research, or administration. Sponsorship of the project by the AYK SSI does not necessarily imply that the findings or conclusions are endorsed by the AYK SSI.

## Growth of Western Alaska and Asian Chum Salmon

(*Oncorhynchus keta*) in Relationship to Climatic factors and Inter- and Intraspecific Competition

### Abstract

Ocean climate shifts and interspecific interactions with Russian pink salmon and Asian chum salmon are all believed to influence the growth of chum salmon in the North Pacific Ocean. Stepwise generalized least squares regression and Mantel's tests were used to examine factors influencing mean annual growth from adult scales collected from 6 watersheds during 1962-2008. First-year scale growth was affected by warmer regional temperatures, the North Pacific Index (NPI), and reduced ice cover. Significant negative effects of Asian chum salmon abundance were found on third-year growth of five of six age 0.3 populations and three of four age 0.4 populations examined, indicating intraspecific competition. Third-year growth of chum salmon was negatively correlated with North Pacific annual sea surface temperature (SST) and the NPI, an index of the intensity of the Aleutian Low. Effects of interspecific interactions on third-year growth due to Russian pink salmon abundance were smaller than effects of Asian chum salmon abundance and SST. Warmer large-scale SSTs associated with reduced third-year growth contradicted the original hypothesis and suggested that the abundance of Asian chum salmon created a masking effect overwhelming other factors promoting growth. Strong correlations among third-year growth of the sampled populations suggested that chum salmon experienced similar environmental conditions in the North Pacific and had overlapping distributions. More synchronous growth was observed among populations from close rivers than distant ones, indicating the importance of regional scale versus oceanwide factors. In the first year, intercircular distance declined then rapidly increased at circuli 5-9. Intercircular distance was similar by gender until the third year at sea when male growth exceeded female growth for all populations except Japan. Back-calculated lengths indicated that fish reach ~494 mm fork length, on average, by the third year before returning as age 0.3 adults. Overall, these results suggested possible effects on chum salmon growth due to abundance of Asian chum salmon, and this effect led to a reduction in western Alaska chum length of approximately 42 mm, potentially affecting fecundity by 3%. These results contribute to growing evidence of competition among conspecific salmon.

## Table of Contents

	Page
Title Page .....	i
Abstract .....	ii
Table of Contents .....	iii
List of Figures .....	vii
List of Tables .....	x
Acknowledgments .....	xiii
General Introduction .....	1
Climate – Ocean Conditions .....	1
Density Dependence .....	4
Other issues .....	6
Multicollinearity .....	6
Auto-correlation .....	7
Objectives and research question .....	7
Chapter 1 Historical Analyses of Seasonal Growth of western Alaska and Asian Chum Salmon Estimated from Scale Samples.....	9
Abstract .....	9
Introduction.....	10
Methods.....	12
Study Area.....	12
Scale Sampling.....	13
Scale Measurements .....	14
Scale Growth Analyses .....	15
Length Correction .....	15
Back-calculation of Growth .....	15
Seasonal Growth .....	16
Annual Growth Trends by Life Stage .....	16
Chum and Pink Salmon Relationships .....	17
Comparisons Across Geographic Distance .....	17
Figures.....	18
Results.....	18

Scale Growth .....	18
Back-calculations of Total Fish Length Based on Scale Size .....	19
Seasonal Growth .....	20
Male-female comparisons .....	20
Odd-even year comparisons .....	20
Temporal Trends by Growth Zone.....	21
Comparisons Across Geographic Distance .....	23
Discussion .....	23
Chum Salmon Migrations within the North Pacific Ocean.....	23
Seasonal Growth Among Populations.....	24
Basin-scale or Regional Effects?.....	26
Comparison of Back-calculations with Actual Measurements .....	27
Climate Change Effects on Growth.....	28
Interactions with Pink Salmon .....	29
Interactions with Asian Chum Salmon.....	29
Comparisons Across Geographic Distance .....	30
How Do These Results Compare with Previous Studies?.....	31
Acknowledgments.....	33
References .....	34
Tables and Figures .....	46
Appendix 1A.....	64
Appendix 1B .....	87
Chapter 2 Historical Growth of Bristol Bay and Yukon River, Alaska Chum Salmon ( <i>Oncorhynchus keta</i> ) in Relationship to Climate and Inter- and Intraspecific Competition.....	93
Abstract .....	93
Introduction.....	94
Methods.....	96
Study Area.....	96
Scale Sampling .....	96
Explanatory Variables .....	98
Analyses and Models .....	100
SW1 Model.....	101

SW3 Model.....	101
Other Analyses .....	102
Results.....	102
Gender .....	103
Yukon River .....	103
SW1 growth.....	103
SW3 growth.....	103
Bristol Bay .....	104
SW1 growth.....	104
SW3 growth.....	105
Regime shift effects.....	105
Regime shift effects on Yukon River chum salmon.....	105
Regime shift effects on Bristol Bay chum salmon .....	106
Discussion .....	107
Acknowledgments.....	112
References .....	112
Tables and Figures .....	117
Appendix 2A.....	138
Chapter 3 Historical Growth of western Alaska and Asian Chum Salmon ( <i>Oncorhynchus keta</i> ) in Relationship to Climate and Inter- and Intraspecific Competition .....	141
Abstract .....	141
Introduction.....	142
Methods.....	144
Study Area.....	144
Scale Sampling.....	144
Explanatory Variables .....	146
Analyses .....	149
SW1 Models .....	150
SW3 Models .....	150
Outliers .....	151
Results.....	151
Gender .....	152

Norton Sound .....	152
SW1 growth .....	152
SW3 growth .....	153
Kuskokwim River .....	153
SW1 growth .....	153
SW3 growth .....	154
Anadyr River .....	155
SW1 growth .....	155
SW3 growth .....	155
Chitose River .....	155
SW1 growth .....	155
SW3 growth .....	156
Comparison across the North Pacific Ocean .....	156
SW1 growth .....	156
SW3 growth .....	157
Acknowledgments .....	166
References .....	166
Tables and Figures .....	173
Appendix 3A .....	196
General Conclusions .....	199
Comparisons across geographic distance .....	199
Seasonal growth among populations .....	199
Climate change effects on growth .....	200
Interactions with pink salmon .....	200
Interactions with Asian chum salmon .....	200
Effects of SST on chum salmon .....	201
Conclusions .....	201
References .....	202

## List of Figures

	Page
Figure 1.1 Map of the study area .....	47
Figure 1.2 Example of a chum salmon scale .....	48
Figure 1.3 Yukon River, Alaska (Big Eddy) age 0.3 chum salmon linear regression comparing mean adult fish length (mm, mid-eye to fork of tail) to mean scale radius (mm) . .....	49
Figure 1.4 Scale radius measurements by zone, total scale radius and adult length (+ 1 SD) of age 0.3 from Big Eddy, Yukon River, Alaska. ....	50
Figure 1.5 Mean seasonal scale growth (mm) of male and female age 0.4 western Alaska chum salmon from Big Eddy and age 0.3 from Anadyr River, Russia and Chitose River, Japan .....	51
Figure 1.6 Mean seasonal scale growth of age 0.4 (mm) western Alaska chum salmon from Unalakleet River and Big Eddy and age 0.3 Asian chum salmon from Anadyr River, Russia and Chitose River, Japan in odd and even years. ....	52
Figure 1.7 Mean annual growth of age 0.4 Big Eddy, Yukon River, Alaska chum salmon. ....	53
Figure 1.8 Percent change in scale growth for age 0.3 Big Eddy, Alaska and Anadyr River, Russia chum salmon .....	54
Figure 1.9 Percent change in scale growth between age 0.3 Unalakleet River, Alaska and Chitose River, Japan chum salmon. ....	55
Figure 1.10 Scale measurement distance (mm) and geographic distances (km) for age 0.3 western Alaska and Asian chum salmon. ....	56
Figure 2.1 Map of the study area .....	118
Figure 2.2 Example of a chum salmon scale. ....	119
Figure 2.3 Mean adult fish length (mm, mid-eye to fork of tail) compared to mean scale growth (mm) for chum salmon from Big Eddy, Yukon River and Nushagak River, Bristol Bay .....	120
Figure 2.4 Mean annual growth of age 0.3 and 0.4 Nushagak River, Bristol Bay, Alaska chum salmon .....	121
Figure 2.5. Mean annual growth of age 0.3 and 0.4 Big Eddy, Yukon River, Alaska chum salmon .....	122

Figure 2.6. Model coefficients from generalized least squares regressions (GLS) comparing SW1 growth of chum salmon .....	123
Figure 2.7. Model coefficients from generalized least squares regressions (GLS) comparing SW3 growth of chum salmon .....	124
Figure 2.8. Model coefficients from generalized least squares regressions (GLS) comparing SW3 growth of chum salmon .....	125
Figure 3.1. Map of the study area. ....	174
Figure 3.2. Example of a chum salmon scale. ....	175
Figure 3.3. Mean adult fish length (mm, mid-eye to fork of tail) compared with mean scale growth (mm) for chum salmon from Unalakleet River, Norton Sound, Alaska and Quinhagak, Kuskokwim River, Alaska .....	176
Figure 3.4. Mean adult fish length (mm, mid-eye to fork of tail) compared with mean scale growth (mm) for chum salmon from Chitose River, Japan and Anadyr River, Russia. .	177
Figure 3.5. Mean annual growth of age 0.3 (1977-2008) and 0.4 (1975-2008) Unalakleet River, Norton Sound, Alaska chum salmon.....	178
Figure 3.6. Mean annual growth of age 0.3 and 0.4 Quinhagak, Kuskokwim River, Alaska chum salmon .....	179
Figure 3.7. Mean annual growth of age 0.3 Anadyr River, Russia and Chitose River, Japan chum salmon .....	180
Figure 3.8. Model coefficients from generalized least squares regressions (GLS) comparing SW1 growth of chum salmon. ....	181
Figure 3.9. Model coefficients from the final generalized least squares regression (GLS) models comparing SW1 growth of chum salmon. ....	182
Figure 3.10. Model coefficients from generalized least squares regressions (GLS) comparing SW3 growth of chum salmon. ....	183
Figure 3.11. Model coefficients from generalized least squares models (GLS) comparing SW3 growth of chum salmon. ....	184
Appendix 1A-1. Mean adult fish length (mm, mid-eye to fork of tail) to mean scale radius (mm) relationship for age 0.3 western Alaska. ....	65
Appendix 1A-2. Mean adult fish length (mm, mid-eye to fork of tail) to mean scale radius relationship for age 0.4 western Alaska. ....	66



Appendix 1A-3. Mean adult fish length (mm, mid-eye to fork of tail) to mean scale radius relationship for age 0.3 Asian chum salmon.....	67
Appendix 1A-4. Scale radius measurements by zone, total scale radius and fish length (+ 1 SD) of Unalakleet River chum salmon .....	68
Appendix 1A-5. Scale radius measurements by zone, total scale radius and fish length (+ 1 SD) for Quinhagak chum salmon. ....	69
Appendix 1A-6. Scale radius measurements by zone, total scale radius and fish length (+ 1 SD) for Nushagak River chum salmon. ....	70
Appendix 1A-7. Scale radius measurements by zone, total scale radius and fish length (+ 1 SD) for age 0.3 chum salmon from Russia and Japan. ....	71
Appendix 1A-8. Mean seasonal scale growth (mm) of age 0.3 western Alaska chum salmon ...	72
Appendix 1A-9. Mean seasonal scale growth (mm) of age 0.4 western Alaska chum salmon ...	73
Appendix 1A-10. Mean seasonal scale growth (mm) of age 0.3 western Alaska chum salmon ..	74
Appendix 1A-11. Mean annual growth of age 0.3 Unalakleet River, Alaska chum salmon. ....	75
Appendix 1A-12. Mean annual growth of age 0.4 Unalakleet River, Alaska chum salmon .....	76
Appendix 1A-13. Mean annual growth of age 0.3 Big Eddy, Alaska chum salmon .....	77
Appendix 1A-14. Mean annual growth of age 0.3 Quinhagak, Alaska chum salmon.....	78
Appendix 1A-15. Mean annual growth of age 0.4 Quinhagak, Alaska chum salmon. ....	79
Appendix 1A-16. Mean annual growth of age 0.3 Nushagak River, Alaska chum salmon .....	80
Appendix 1A-17. Mean annual growth of age 0.4 Nushagak River, Alaska chum salmon .....	81
Appendix 1A-18. Mean annual growth of age 0.3 Anadyr River, Russia chum salmon .....	82
Appendix 1A-19. Mean annual growth of age 0.3 Chitose River, Japan chum salmon .....	83
Appendix 1A-20. Percent change in scale growth between age 0.3 western Alaska chum salmon. ....	84
Appendix 1A-21. Percent change in scale growth between age 0.4 western Alaska chum salmon. ....	85
Appendix 1A-22. Percent change in scale growth between age 0.4 Unalakleet River, Alaska chum salmon. ....	86

## List of Tables

	Page
Table 1.1. Populations sampled for chum salmon scales .....	57
Table 1.2. Pearson's correlation coefficients and significance between scale zones for age 0.3 chum salmon from western Alaska and Asia.....	58
Table 1.3. Pearson's correlation coefficients and significance between scale zones for age 0.4 chum salmon from western Alaska.....	59
Table 1.4. Pearson's correlation and significance between scale growth zones for age 0.3 and 0.4 chum salmon from western Alaska.....	60
Table 1.5. Pearson's correlation coefficients and significance comparing populations of age 0.3 chum salmon by scale zone, total scale radius, and fish length .....	61
Table 1.6. Back-calculated lengths of chum salmon .....	62
Table 1.7. Mantel tests comparing total scale measurement (mm) and geographic (km) distances for age 0.3 and 0.4 chum salmon in western Alaska and Asia.....	63
Table 2.1. Pairwise Pearson's correlation coefficients and corresponding <i>P</i> values between environmental variables potentially affecting growth of age 0.3 and 0.4 chum salmon in Bristol Bay and Yukon River Alaska .....	126
Table 2.2. Pearson's correlations and corresponding <i>P</i> values comparing marine scale growth of Yukon River, Alaska .....	127
Table 2.3. Pearson's correlations and corresponding <i>P</i> values comparing marine scale growth of Bristol Bay, Alaska.....	128
Table 2.4. Student's two-sample <i>t</i> -tests comparing mean growth of chum salmon between odd and even years.....	129
Table 2.5. Generalized least squares models (GLS) of growth during the first (SW1) and third year at sea (SW3) for Big Eddy, Yukon River.....	130
Table 2.6. Generalized least squares models (GLS) of growth during the first (SW1) year at sea for Yukon River, Alaska .....	131
Table 2.7. Generalized least squares models (GLS) of growth during the third year at sea (SW3) for Yukon River, Alaska .....	132
Table 2.8. Generalized least squares models (GLS) of growth during the first (SW1) and third year at sea (SW3) for nNushagak River, Alaska.....	133

Table 2.9. Generalized least squares models (GLS) comparing growth during the third year at sea (SW3) prior to the regime shift (pre-1977) for Yukon River, Alaska .....	134
Table 2.10. Generalized least squares models (GLS) comparing growth during the third year at sea (SW3) after the regime shift (post-1976) for Yukon River, Alaska .....	135
Table 2.11. Generalized least squares models (GLS) comparing growth during the third year at sea (SW3) prior to the regime shift (pre-1977) for Bristol Bay .....	136
Table 2.12. Generalized least squares models (GLS) comparing growth during the third year at sea (SW3) after the regime shift (post-1976) for Bristol Bay, Alaska .....	137
Table 3.1. Populations within the North Pacific Ocean sampled for chum salmon scales. ....	185
Table 3.2. Pearson's correlations and corresponding <i>P</i> values comparing marine scale growth of Unalakleet River, Norton Sound, Alaska .....	186
Table 3.3. Pearson's correlations and corresponding <i>P</i> values comparing marine scale growth of Quinhagak, Kuskokwim River, Alaska. ....	187
Table 3.4. Pearson's correlations and corresponding <i>P</i> values comparing marine scale growth of Anadyr River, Russia and Chitose River, Japan age 0.3 chum salmon.....	188
Table 3.5. Student's two-sample <i>t</i> -tests comparing mean growth of chum salmon between odd and even years.....	189
Table 3.6. Generalized least squares regressions (GLS) of growth during the first (SW1) and third year at sea (SW3) for Unalakleet River.....	190
Table 3.7. Generalized least squares models (GLS) comparing SW1 growth of chum salmon .	191
Table 3.8. Generalized least squares models (GLS) comparing SW3 growth of age 0.3 chum salmon.....	192
Table 3.9. Generalized least squares models (GLS) comparing SW3 growth for age 0.4 chum salmon .....	193
Table 3.10. Generalized least squares regressions (GLS) of growth during the first (SW1) and third year at sea (SW3) for Quinhagak chum salmon .....	194
Table 3.11. Generalized least squares regressions (GLS) of growth during the first (SW1) and third year at sea (SW3) for Anadyr River, Russia and Chitose River, Japan.....	195
Appendix 1B-1. Mean ( $\mu$ ) widths by scale growth zone, total scale radius, and mean total fish length .....	88
Appendix 1B-2. Mean ( $\mu$ ) circuli counts by scale growth zone and total scale radius .....	89
Appendix 1B-3. Analysis of variances (ANOVA) comparing scale zones, radius and length.....	90

Appendix 1B-4. Analysis of variances (ANOVA) comparing chum salmon scale zones .....	91
Appendix 1B-5. Multiple comparisons for factor “Population” from the analysis of variances. ....	92
Appendix 2A-1. Explanatory variables used in generalized least squares regressions.....	138
Appendix 3A-1. Explanatory variables used in generalized least squares regressions.....	196

## **Acknowledgments**

This project report is the combination of three projects: AYK – Historical Analyses of AYK and Asian chum, Phase 1 and 2, and a Basin-wide Retrospective Analysis of Growth and Survival Patterns in Pink and Chum Salmon. The first two projects were supported by AYK-SSI funding and the latter project was funded by North Pacific Marine Research Program.

This study was part of Dr. Agler's Ph.D. research at the University of Alaska Fairbanks (UAF). Many individuals contributed to the completion of that work, including her advisor, Dr. William Smoker, and graduate committee, Drs. Gordon Kruse, Peter Hagen and Franz Mueter. Dr. Milo Adkison was a committee member until his move to Fairbanks.

Many staff at the Mark, Tag, and Age Laboratory, Alaska Department of Fish and Game (ADF&G) participated in and supported this project, including Dr. Peter Hagen, Ron Josephson and Cathy Robinson, Tim Frawley, William Rosky, William Johnson, Ben Gregg, and Kevin Trick, Megan Lovejoy, Dion Oxman, Wendy Whelan, Jim Chesmore, Joe Cashen, John Baker, Scott Hinton, Abby Norman, and Jen Chahanovich. Multiple unknown ADF&G staff collected, measured and aged scales, as well as Central Region staff: Tim Baker, Lowell Fair, Fred West, and Terry Tobias; Arctic-Yukon-Kuskokwim staff, Larry Dubois, Dave Folletti, Linda Brannian, Dani Evenson, Doug Molyneaux, and Holly Krenz; Southeast Region staff, Iris Frank, and Mark Olsen. Elizabeth Siddon and Jon Richar developed the SST program as part of an UAF graduate class.

Dr. Alexander Zavolokin, Pacific Research Fisheries Center (TINRO-Centre), Vladivostok, Russia, provided the Anadyr River acetate scale impressions, and Dr. Toshihiko Saito, Fisheries Research Agency, Hokkaido National Fisheries Research Institute, Sapporo, Japan, provided the Chitose River acetate scale impressions. Several individuals assisted with obtaining acetate scale impressions from other countries: Dr. Nancy Davis, Dr. Kate Myers, Dr. Shigehiko Urawa, Vladimir Sviridov, Wakako Morris, Eric Volk, Dr. Olga Temnykh, and Dr. Masahide Kaeriyama.

## General Introduction

Pacific salmon (*Oncorhynchus* spp.) are an important part of the ecosystem of the North Pacific Ocean. Poor productivity of some western Alaska salmon stocks in the late 1990s and early 2000s prompted disaster declarations by the Governor of Alaska and federal agencies for the Arctic-Yukon-Kuskokwim (AYK) region (AYK-SSI 2006). This led to restrictions on commercial and some subsistence fisheries and significant hardship on the people depending on these fisheries (AYK-SSI 2006). Stock-recruitment analyses indicated that declining productivity of AYK chum salmon was synchronous and indicative of a region-wide factor that has yet to be identified but was likely tied to changes in the ocean (Hilborn et al. 2007). Little is known about the oceanic phase of these salmon. Are growth and survival determined by ocean conditions near the estuaries or are they determined later when these fish intermingle with fish from Russia, Japan and other Alaska stocks? Do abundant odd-year Asian pink salmon (*O. gorbuscha*) populations inhibit growth? Has hatchery production resulted in competitive limitations in growth of western Alaska chum salmon (*O. keta*)? I addressed these questions by comparing scale growth patterns at different life stages from four western Alaska chum salmon stocks with one stock from Japan and one from Russia. These questions forced me to address two major issues related to chum salmon: climate or ocean conditions and density-dependence, which are introduced below.

### Climate – Ocean Conditions

The probable biological mechanisms by which climate and ocean conditions affect salmon growth include the direct physiological determination of growth by temperature and food supply (reviewed by Weatherly and Gill 1995), the indirect positive ecological effect of temperature on prey availability, and the enhancing effect of rapid growth on survival during critical life stages (review for chum salmon by Salo 1991). The study of scale growth offers an opportunity to study relationships between growth at different life stages in different places and varying climate. Salmonid scales, used for aging fish, have been collected and archived by Alaska Department of Fish and Game (ADF&G) since the early 1960s and provide a tool for examining growth over time.

Several studies (Beamish et al. 1998; Mueter et al. 2002a; Ruggerone et al. 2000; 2005) have shown that sea surface temperature (SST) affects the growth of salmon species (i.e. -- sockeye *O. nerka* and Chinook *O. tshawytscha*). The internal body temperature of salmon

changes with the surrounding temperature, thus, their metabolism and growth is affected by SST. Bioenergetics modeling has shown that at low temperatures growth efficiency increases as temperature increases (Moyle and Cech 1982). At some point increasing temperature leads to reduced growth efficiency and death. Welch et al. (1998) suggested that changing SSTs may affect salmon because they would reach an upper “thermal limit.” Fish grow faster in warmer water only if the supply of food is great enough to overcome the increased caloric demand of a higher metabolism. Thus, as SSTs warm, the habitat suitable for salmon would decrease, possibly leading to greater density dependent interactions (Welch et al. 1998).

In the Bering Sea, the timing of sea ice break-up is important to the development of the pelagic food web each spring (Hunt and Stabeno 2002). Sea ice has melted relatively early since the mid-1970s and exceptionally early during 2000-2004 (Overland and Stabeno 2004). Unusual climatic events in the Bering Sea led Overland and Stabeno (2004) to conclude that significant changes in the composition of marine species could occur if the warming continues. Farley and Moss (2009) found that during cold years, juvenile chum salmon south of the Kuskokwim River were similar in size among years and their relative abundance dropped dramatically suggesting that smaller, slower growing individuals experienced higher size-selective mortality early in marine residency. This was not the case further north; however, it was possible that size-selective mortality occurred later during the first winter at sea. It has been suggested that ice cover in Norton Sound may protect small salmon from piscivorous birds (predation) while promoting food production for salmon (C. Lean, Norton Sound Economic Development Council, 2007, personal communication).

Sea surface temperature also affects prey productivity, which affects salmon growth. Prolonged changes in SST likely influence prey productivity in the Gulf of Alaska and the Bering Sea, and this ultimately affects chum salmon growth. SSTs, in conjunction with sea level pressure (SLP), affect prey productivity by altering wind patterns and upwelling intensity, which influence plankton movements and limit distributions, ultimately affecting fish distributions. For example, one well-known environmental index in the North Pacific Ocean is the Pacific Decadal Oscillation (PDO), which is defined as the leading principal component of North Pacific Ocean monthly SST variability. During the 1976-77 winter, the atmosphere-ocean climate system over the North Pacific Ocean shifted abruptly (Miller et al. 1994). The Aleutian Low pressure system deepened shifting storm tracks southward. From 1976 to 1978, an intensification of the Aleutian

Low resulted in warmer SSTs along the northern North American west coast and cooler SSTs offshore (Beamish 1993; McLain 1984). These changes were associated with strong year classes of many marine and anadromous fishes and increased productivity of salmon stocks north of British Columbia (Francis and Sibley 1991; Mantua et al. 1997; Pearcy 1992). Accompanying changes in primary productivity in the Pacific basin also occurred (Hallowed et al. 2001). Although the causes of the PDO are still largely unknown (Mantua and Hare 2002), Hare et al. (1999) found an inverse production regime for salmon from 1977 to the early 1990s and suggested that ocean conditions from 1977-1990 favored Alaska stocks. Their results supported the hypothesis that Pacific salmon production in Alaska is temperature- or climate-driven.

Changes in large scale climate, such as the PDO, caused “regime shifts” in 1976-77 (Mantua et al. 1997), and in 1989, another shift occurred (Hare and Mantua 2000). Instead of returning to previous conditions, the North Pacific Ocean shifted to a new state. In 1997-1998, an El Niño (a 6-18 month weather pattern) affected western Alaska Chinook (*O. tshawytscha*, Ruggerone et al. 2007a) and sockeye salmon (*O. nerka*, Kruse 1998). Thus, although salmon are extremely adaptable when attempting to ascertain how ocean conditions affect salmon, fisheries researchers must distinguish between the influences of 6-18 month weather patterns (El Niño), 10-30 year regimes (PDO), and longer-term climate change on salmon populations (Chittenden et al. 2009; Seo et al. 2011).

In addition to large basin-scale climate shifts, such as the PDO, Pyper et al. (2001; 2002) demonstrated the need to examine regional conditions. Although basin-scale shifts in ocean productivity can affect salmon across broad regions (Beamish and Mahnken 2001), Pyper et al. (2002) found that salmon stocks in adjacent regions tended to be more correlated than those of distant regions, indicating the importance of understanding regional conditions (Mueter et al. 2002a; 2002b; Peterman et al. 1998; Pyper et al. 2001; 2002). For example, Mueter et al. (2002b) found regional measures of SST to be useful predictors of salmon survival rates and future recruitment. Although advances have been made to understand the effects of climate change and species interaction on growth, survival, and abundance of Pacific salmon, interactions among and within species, short-term climate patterns, decadal regimes, and long-term climate-change trends are complex, and the causes of the declines in western Alaska chum salmon remain unclear.



## Density Dependence

Salmon growth may be one key to unraveling how survival and abundance link to climate change (Farley et al. 2004; Farley and Moss 2009; Martinson et al. 2008; 2009; Ruggerone et al. 2005; Ruggerone et al. 2007b). Seasonal and annual scale growth of salmon has been correlated with salmon body length (Fisher and Pearcy 2005; Fukuwaka and Kaeriyama 1997). Somatic growth inferred from scale pattern analyses was related to increased Bristol Bay sockeye abundance after the mid-1970s regime shift with a significant increase in growth during the first and second years at sea (Ruggerone et al. 2005; 2007b). Recent evidence suggested that the 1989 regime shift also affected Bristol Bay sockeye salmon. Size-at-age of adult Bristol Bay sockeye salmon following the 1989 shift was low and may have influenced the decline of Bristol Bay sockeye salmon (Ruggerone and Link 2006). Since 1975, Bigler et al. (1996) observed a decrease in body size of 45 of 47 (96%) salmon stocks from five salmon species in North America and Asia. Helle and Hoffman (1995, 1998) found declines in body size of chum salmon from two locations in North America between 1972 and 1992, although from 1993-1996 body size began to increase. Helle et al. (2007) found that from 1995-2006 although salmon abundance remained high, body weight increased. Thus, these studies added to increasing evidence that western Alaska stocks of salmon may be food-limited during their offshore migrations in the North Pacific Ocean and Bering Sea, but also demonstrated the difficulty in examining density dependence. High seas salmon research has suggested that inter- and intraspecific competition for food and density-dependent growth effects were apparent among older ages of salmon, when stocks originating from around the Pacific intermingled and fed in offshore waters (Fukuwaka et al. 2007; Myers et al. 2004). Helle et al. (2007) concluded that carrying capacity of salmon within the North Pacific Ocean was not a constant value and varied with changing environmental and biological factors making this a difficult and tricky issue to investigate. There is likely no one answer.

Ruggerone and Nielsen (2004) suggested that there might be possible interspecific competition due to pink salmon (*O. gorbuscha*) being competitively dominant over other salmon because they are abundant, grow rapidly, and consume prey preferred by other species. Asian pink salmon have alternating years of abundance, and this was used to examine interactions between pink salmon and other species. Asian pink salmon abundance inhibited the growth and survival of sockeye and chum salmon during odd-numbered years (Ruggerone and Nielsen 2004;

Ruggerone et al. 2005). For example, when sockeye salmon distributions overlapped with abundant odd-year Asian pink salmon, Bristol Bay salmon experienced reduced growth (scale and adult length-at-age), leading to a 26% - 45% reduction in smolt to adult survival (depending on smolt age; Ruggerone et al. 2003). Asian pink salmon may affect the feeding and distribution of chum salmon on the high seas; the abundance of Asian chum salmon was inversely related to the abundance of pink salmon (Azumaya and Ishida 2000). In the Pacific Northwest, pink and chum salmon fry compete for similar prey in marine waters, and as a result, researchers hypothesized that chum salmon had a genetic trait influencing age composition and reducing competition with abundant odd-year pink salmon (Smoker 1984). It has been suggested that there is biennial selection in chum salmon against offspring that compete with cyclically dominant Asian pink salmon (Ishida et al. 1993).

On the other hand, releases of Asian hatchery chum salmon increased rapidly in the 1970s, so they are now the most abundant chum salmon stock in the North Pacific Ocean (Ruggerone et al. 2010). Distribution of Japanese chum salmon overlap those of western Alaska salmon during part of their life history (Myers et al. 2007). Holt et al. (2008) raised the question: how much does large-scale hatchery production affect growth and survival of wild salmon? Ruggerone et al. (2011) found smaller adult length-at-age, delayed age-at-maturation, and reduced productivity and abundance of Norton Sound Kwiniuk River chum salmon population, which was associated with greater production of Asian hatchery chum salmon.

Discussion of density dependence has ebbed and flowed in the literature, and other hypotheses have been developed. For example, Strong (1986) suggested the concept of density vagueness. In density vagueness, emphasis is on the variance around the relationship rather than on the change in the growth rate of the population or often the lack of change in growth rate at medium densities. Shepherd et al. (1990) argued that the variability should be studied. They suggested that variability might be a more important part of regulation. The role of density-dependent processes may be primarily local, and they may act mainly to modulate variability, and only indirectly affect total recruitment.

Density-dependent effects on growth of salmon are not clearly understood (Peterman 1984; Ricker 1962), although evidence for density-dependent population effects on growth of salmon in the ocean has accumulated in recent years (e.g.—Bigler et al. 1996; Helle and Hoffman 1995, 1998; Ishida et al. 1993; Kaeriyama 1996). A fundamental assumption of hatchery

production has been that salmon use a fraction of the available forage, but Cooney and Brodeur (1998) estimated that wild and hatchery production in the North Pacific Ocean has probably placed substantial forage demands on both coastal and oceanic feeding domains. Under these conditions, it would seem surprising if density-dependent growth limitations were not evident in some populations (Cooney and Brodeur 1998). There is, however, no consensus on density-dependence in fish (e.g. - Myers and Cadigan 1993; Ricker 1962; Shepherd et al. 1990). Shepherd et al. (1990) suggested that most fish biologists believe in regulation even though they have been unable to find little direct evidence. Deterministic density-dependent processes may be very weak, and stochastic processes may provide a rather effective mechanism for regulation of population size in practice.

This represents the problem with studying density-dependent growth. Much of the literature examined density-dependent survival. Fish leave the rivers and return. Numbers may be measured. But the effects of increased population size on growth are difficult to detect. If a fish returns at a smaller size, what does that do to the population? Does it affect long-term population trends? Does an individual lay fewer eggs? Does it affect the population as a whole? One concern is that the size of the parents may influence the survival of their offspring (Forbes and Peterman 1994; Helle 1989). Beacham and Murray (Beacham and Murray 1987) found that small eggs produce small alevins and fry with diminished probability of survival. Thus, if competition for forage resources, driven by increasing numbers of salmon in the North Pacific Ocean results in decreased body size, diminished overall survival may result. For wild salmon, decreased body size and reproductive potential resulting from forage deprivation (increased competition or decreased ocean production) may provide important population regulation under conditions of declining marine food reserves. Overall, the effects of density dependence are difficult to detect. The trends, if any, are small, thus most statistical models have little power to detect them.

## **Other issues**

### *Multicollinearity*

Many of the environmental variables in this study that were compared with chum salmon growth from the North Pacific Ocean (i.e. - North Pacific Index, Aleutian Low Pressure Index, and the Pacific Decadal Oscillation) were based on similar measurements, such as sea surface temperature or sea level pressure. Thus, they were highly correlated. If the explanatory variables

were highly correlated, it may be difficult to determine which explanatory variable was affecting the response variable. The key is to find the balance of “enough” but “not too many” terms. Extreme multicollinearity does not necessarily violate the assumptions of ordinary least squares (OLS) regressions. OLS estimates are still unbiased and best linear unbiased estimators. Nevertheless, the greater the multicollinearity, the greater the standard errors. When multicollinearity is present, confidence intervals for coefficients tend to be wide and t-statistics tend to be small.

#### *Auto-correlation*

Because I am using time series data or annual observations, the data may be “auto-” or “serially-correlated.” Because of the auto-correlation present in some of the data, I used a generalized least squares (GLS) model rather than an ordinary least squares regression model in Chapters 2 and 3, which allows for dependent errors and unequal variances. Dependent (correlated) errors produce standard errors that are too small and have fewer degrees of freedom than expected but have no effect on bias. The GLS model allows one to specify a correlation structure of the errors and account for dependence. As long as the variance-covariance matrix has a certain structure (something found in time series data), GLS will result in the “best linear unbiased estimates.” Overall, the GLS minimizes the generalized sum of squares. F-tests and t-tests are still valid.

#### **Objectives and research question**

Does marine growth of western Alaska chum salmon vary in response to climate change and density-dependent processes of competition among salmon species?

In this investigation, I tested the following hypotheses:

- Marine growth of western Alaska chum salmon varied in response to climate change and density-dependent processes of competition among salmon species.
- Climate change, as shown through a variety of indices, influenced growth of Norton Sound, Yukon River, Kuskokwim River, and Bristol Bay chum salmon. More specifically, increasing sea surface temperature promoted faster growth.
- Interactions with pink salmon altered growth of Norton Sound, Yukon River, Kuskokwim River, and Bristol Bay chum salmon.

- Interactions with Asian chum salmon (mostly hatchery fish) altered growth of Norton Sound, Yukon River, Kuskokwim River, and Bristol Bay chum salmon.
- Annual growth patterns of chum stocks originating from Norton Sound, Yukon River, Kuskokwim River, Bristol Bay, Japan, and Russia were correlated indicating the importance of large-scale ocean-climate effects versus regional effects.

I tested these hypotheses by reconstructing seasonal and annual growth patterns of chum salmon. This project created chum salmon growth indices from 1975-2008 for Norton Sound (Unalakleet River – ages 0.3 and 0.4), 1965-2006 for Yukon River (Big Eddy – ages 0.3 and 0.4), 1967-2007 for Kuskokwim River (Quinhagak – ages 0.3 and 0.4), 1965-2006 for Bristol Bay (Nushagak River – ages 0.3 and 0.4), 1962-2007 for Russia (Anadyr River – age 0.3), and 1976-2008 for Japan (Chitose River – age 0.3). Seasonal and annual growth of salmon was based on scale patterns, which are known to be correlated with salmon body length (Fisher and Pearcy 2005; Fukuwaka and Kaeriyama 1997).

Chapter One presents an overview of the data and examines the seasonal growth of the six populations. In addition in Chapter One, I include a latitudinal comparison of scale growth. Chapter Two focuses on two populations: Bristol Bay and Yukon River. In that chapter, I present the GLS models by comparing first and third years of growth with SST and other environmental variables. Third-year growth is also compared with Asian pink and chum salmon abundance. In Chapter Two, the models are developed and explained, and I examined differences between the two populations before and after the 1976-77 regime shift. In Chapter Three, the results of the GLS models for Norton Sound, Kuskokwim River, Japan and Russia are presented and compared with the results from Chapter Two for Bristol Bay and Yukon River. Chapter Three synthesizes all chapters.

## Chapter 1

# HISTORICAL ANALYSES OF SEASONAL GROWTH OF WESTERN ALASKA AND ASIAN CHUM SALMON ESTIMATED FROM SCALE SAMPLES<sup>1</sup>

## Abstract

We examined factors influencing scale growth of western Alaska chum salmon (*Oncorhynchus keta*, Norton Sound, Yukon River, Kuskokwim River, and Bristol Bay; age 0.3 and 0.4 fish) and Asian chum salmon (Chitose River, Japan and Anadyr River, Russia; age 0.3 fish). We found strong correlations among all six populations in third-year growth, suggesting these populations experienced similar environmental variation. We found a weak relationship between Asian pink salmon (*O. gorbuscha*) and scale growth of Asian and western Alaskan chum salmon. More synchronous growth was observed among populations from close rivers than from distant ones. Adult length was correlated with third-year growth. For first-year growth of all populations, intercirculus distance initially declined then rapidly increased for both genders at circuli 5-9. Intercirculus distance was similar by gender until the third year when growth of males exceeded females for all populations except Japan. Japanese females' growth was greater than males during the third year and homeward migration. Back-calculated lengths indicated that fish must reach 494 mm by the third year to return as age 0.3 fish, or they remained and returned as age 0.4 fish. Most smolts that entered the ocean during an odd year had greater distance between adjacent circuli during the next year, suggesting reduced growth in the first year and compensatory growth during the second and third years. Most populations showed long-term growth patterns coinciding with major climate or environmental events in the North Pacific (i.e. - the 1976-77 regime shift, the second regime shift in 1989, or the 1997-98 El Niño). In western Alaska, there was little difference in long-term growth patterns between age 0.3 and 0.4 fish. Adult length from western Alaska and Russia was above average until the late-1980s to early-1990s then was below the long-term average.

---

<sup>1</sup> Agler, B.A., G.T. Ruggerone, and L.I. Wilson. Historical growth of western Alaskan and Asian chum salmon estimated from scale samples. Prepared for Transactions of the American Fisheries Society.

## Introduction

Pacific salmon (*Oncorhynchus* spp.) are an important part of the ecosystem of the North Pacific Ocean. In western Alaska, low numbers of salmon returned to many rivers in the late 1990s and early 2000s. Low returns and harvests prompted disaster declarations for the Arctic-Yukon-Kuskokwim (AYK) region (AYK-SSI 2006; Linderman and Bergstrom 2009; Menard et al. 2009).

Salmon growth and survival has been shown to covary with climate (Farley et al. 2005; 2007a,b; Ruggerone et al. 2005; 2007a,b), and the North Pacific Ocean has experienced significant climate shifts (Hare and Mantua 2000; Mantua et al. 1997). Large scale climate or regime shifts occurred in 1976-77 and 1989, leading to increases in salmon abundance in the North Pacific Ocean and Bering Sea (Anderson and Piatt 1999; Hare and Francis 1995; Hare and Mantua 2000; Mantua et al. 1997; Rogers 1984). Abrupt transitions in climate may trigger detectable changes in life-history traits and other biological indicators, such as changes in marine survival, recruitment, growth and age distribution. These abrupt transitions have been correlated with changes in abiotic factors, such as sea surface temperature (Hinch et al. 1995; Ishida et al. 1995; Mueter et al. 2002; Pyper and Peterman 1999; Ruggerone et al. 2005), climate indices (Beamish and Bouillion 1993; Fukuwaka et al. 2011; Ishida et al. 2001; Kaeriyama et al. 2009; Ruggerone and Nielsen 2009), and sea surface salinity (Morita et al. 2001). Features of the 1976-77 regime shift, which correlated with major increases in salmon abundance in northern regions and declines in abundance in the south, included cooler sea surface temperatures and a deeper winter-spring mixed layer depth in the central North Pacific, a shallower mixed-layer depth in the Gulf of Alaska, and warmer surface temperatures in the extreme eastern North Pacific Ocean (Francis and Hare 1994; Mantua et al. 1997; Walker et al. 1998). Although advances have been made in unraveling the effects of climate on salmon, the causes of the AYK chum salmon (*O. keta*) population declines in the late 1990s and early 2000s remain unclear.

Growth histories of salmon have been used to examine the changes in Alaska salmon populations (Farley et al. 2004, 2007a; Martinson et al. 2008, 2009; Ruggerone et al. 2005, 2007b). Scale pattern analyses demonstrated that the growth of Japanese chum salmon declined since the 1980s (Kaeriyama et al. 2007b), and the growth of Russian chum salmon declined during the second, third and fourth years at sea from the 1960s through the mid 2000s (Zavolokin et al. 2009). Indices of body growth from 1955-2002 of Bristol Bay and Chignik, Alaska sockeye

salmon (*O. nerka*) scales showed that growth during the first and second years at sea was higher after the 1976-1977 regime shifts; whereas, growth during the third year and homeward migration was below average (Ruggerone et al. 2009). Helle et al. (2007) found that although the abundance of salmon remained high during the 1995-2006 period, the body size of salmon was not necessarily related to population density. The 1995-2006 time period was favorable for salmon in that ocean resources supported salmon of large body size and large population numbers. Helle et al. (2007) suggested that the carrying capacity of the North Pacific Ocean for salmon was not constant but varied with changing environmental and biological factors.

Since the mid-1980s, abundances of many species of Pacific salmon, including sockeye, chum and pink (*O. gorbuscha*), increased in the North Pacific concurrent with favorable ocean conditions and large enhancement programs (Kaeriyama and Edpalina 2008). Corresponding changes in age at maturity and adult body size have been observed (Bigler et al. 1996; Helle et al. 2007; Ishida et al. 1993, 1998), and these effects have been attributed to competition. Interspecific competition among Pacific salmon may lead to reduced growth (Ruggerone and Nielsen 2004; Ruggerone et al. 2005). For example, the biennially-cycling abundance of Asian pink salmon possibly altered the diet of Asian chum salmon and indirectly influenced their growth by changing their distribution during odd years (years of high abundance), leading to higher densities of chum salmon in the Gulf of Alaska and possible density dependent growth (Azumaya and Ishida 2000).

Intraspecific competition may lead to density-dependent growth within Pacific salmon (Ishida et al. 1993; Peterman et al. 1998; Ruggerone et al. 2003). Salmon are migratory, and competition among conspecifics originating from distant locations may occur when stocks intermingle in a central location (Pyper and Peterman 1999). Since 1980, approximately 3.1 billion hatchery chum salmon have been released annually from hatcheries (Ruggerone et al. 2010). A significant reduction in growth of Asian chum salmon (hatchery and wild) and delay in age-at-maturation was associated with increased hatchery production (Ishida et al. 1993; Kaeriyama et al. 2007a; Zavolokin et al. 2009). Overlap of Asian hatchery chum abundance with western Alaska chum salmon led Myers et al. (2004) to hypothesize that Asian hatchery chum salmon compete with western Alaska chum salmon for food (Myers et al. 2007; Seeb et al. 2004; Urawa et al. 2009). Hatchery chum salmon from North America may also compete with western Alaska chum salmon, but they are less abundant and do not overlap as much with western Alaska



salmon (Beacham et al. 2009; Myers et al. 2007; Urawa et al. 1999, 2009).

Spatial and temporal synchrony in growth and abundance is typical for many animal populations (Fox et al. 2011; Ranta et al. 1997; Ripa and Ranta 2007). Such synchrony often arises from exogenous factors, such as temperature, rainfall, or other meteorological elements (Moran 1953). Many fish species exhibit synchrony in population sizes and recruitment (Friedland et al. 1998; Niemelä et al. 2004; Nunn et al. 2007; Pyper et al. 2002; Tedesco et al. 2004). Peterman et al. (1998) examined spatial patterns among survival rate indices of sockeye salmon in the northeast Pacific Ocean and found positive correlations at regional scales but not at a larger, ocean-basin scale. Similar results were found for pink (Pyper et al. 2001) and chum salmon (Pyper et al. 2002). Jensen et al. (2011) observed synchronous scale growth among close populations but not among more distantly separated ones in Atlantic salmon in Norway, supporting the importance of regional scale versus basinwide studies.

We examined the scale growth of six chum salmon populations: four from western Alaska (Unalakleet River, Norton Sound; Big Eddy, Yukon River; Quinhagak, Kuskokwim River; and Nushagak River, Bristol Bay) and two from Asia (Chitose River, Japan and Anadyr River, Russia). We examined whether climate change influenced the scale growth of western Alaska chum salmon, whether interactions with pink salmon abundance inhibited growth of western Alaska chum, and whether interactions with Asian chum abundance affected the growth of western Alaska chum salmon. We hypothesized that uncorrelated growth indicated the importance of regional effects on growth and implied less overlap at sea. We also hypothesized that more similar marine patterns would be found in salmon populations from adjacent rivers than in more distant populations. We tested these hypotheses by reconstructing seasonal and annual growth patterns of western Alaska and Asian chum salmon based on scale pattern analyses over a 32-42 year period.

## **Methods**

### *Study Area*

We examined six chum salmon populations originating from four rivers in western Alaska, one river in Russia and one river in Japan. Samples represented chum salmon from rivers entering marginal seas of the subarctic North Pacific Ocean, except the Chitose River, which

flows into the Sea of Japan, between 42°N and 65°N latitude and 158°W and 141°E longitude (Table 1.1, Figure 1.1).

### *Scale Sampling*

Acetate impressions of the western Alaska scales were obtained from the Alaska Department of Fish and Game (ADF&G) in Anchorage, Alaska; impressions of Japanese scales were obtained from the Hokkaido National Fisheries Research Institute, Sapporo, Japan; and impressions of Russian scales were obtained from the Chukotka Branch of the Pacific Research Fisheries Center, Anadyr, Russian Federation. Scales were sampled over the years by different personnel following established protocols.

Scales were sampled from the “preferred area” of adult chum salmon, located between the posterior insertion of the dorsal fin and the adipose fin close to the lateral line. Age was designated using European notation. Thus, the number of winters spent in freshwater before going to sea, “0” for a chum salmon, would be 0.X, followed by the number of winters spent at sea. Thus, three winters at sea would be designated by X.3. A four-year old fish, which spent a year in the gravel, would be aged as 0.3. Growth zones corresponding to seasonal and annual scale growth were measured. Growth zone SW1 was the area between the scale focus and the outer edge of the first saltwater annulus, growth zones SW2, SW3, and SW4 represented annual ocean growth, and growth zone SWPlus represented growth after the last ocean annulus and capture (Figure 1.2).

Scales have been collected annually in most of the western Alaska sites (Table 1.1). We attempted to measure acetate impressions of 25 male and 25 female chum salmon scales each year from both age 0.3 and 0.4 fish, which were the dominant age groups in Alaska. In western Alaska, scales were primarily collected from 15 June to 15 July, but in some years, dates were expanded to obtain the sample size. Due to limited samples from Japan and Russia, all possible scales were used. All Russian scales were collected in August, and 87% of Japanese scales, which are a fall run, were collected in October. We were unable to restrict scales by net mesh size due to lack of data for most populations. We obtained the sample size for both genders for all years only in the Quinhagak and Big Eddy populations. For the other populations, we were unable to obtain the sample size in some years, usually 1960s or mid-1970s, due to limited sampling.

We only measured age 0.3 salmon for the Chitose River, Japan and the Anadyr River, Russia. Scales were only available to us from Japan for 1976 to 2008. In all years but one, we measured  $\geq 23$  samples. Scales were collected annually in Russia since 1962 (Table 1.1). In most years we were unable to measure 25 scales per gender, and in 28% of the years, numbers of scales measured by gender was  $\leq 10$  scales. We used annual mean values in most analyses and weighted by the number of samples to account for sample size when possible.

In the Unalakleet and Yukon rivers, scales were collected during commercial and test fisheries. Quinhagak samples came from a commercial fishery located near the village of Quinhagak, Alaska. Quinhagak represented the Kuskokwim River management area, because it is located in Kuskokwim Bay. Nushagak River scales were mostly collected during commercial fisheries, but in recent years the collection was supplemented by escapement samples to obtain enough scales. In the Anadyr River, wild fish were sampled from shore with beach seines. In the Chitose River, samples were collected using a fish wheel, approximately 70 km from the river mouth of the Ishikari River, at the Chitose Salmon Aquarium.

We observed resorption of the last annulus on some Asian scales (2.6% Japan; 1% Russia). Because we used growth zones (e.g. - SW1, Figure 1.2) for specific analyses, these scales were still useful and allowed us to keep the sample sizes for individual growth zones as large as possible.

### *Scale Measurements*

Scales were selected for measurement when: 1) the reader agreed with the age determination previously made by either ADF&G, Chukotka Branch of the Pacific Research Fisheries Center, Russia, or Hokkaido National Fisheries Research Institute, Japan; 2) the scale shape indicated the scale was collected from the preferred area (Bilton and Station 1975; Koo 1962); and 3) circuli and annuli were clearly defined and not affected by scale regeneration or resorption along the measurement axis (see above).

Scale measurements followed procedures described by Hagen et al. (2001). Scales were first scanned using a microfiche reader, then stored as a high resolution digital image (3352 x 4425 pixels). This image allowed the entire scale to be viewed and provided enough pixels between narrow circuli to ensure accurate measurements of spacing between circula (resolution  $\sim 0.0017$  mm/pixel). The digital image was viewed in Optimas 6.5 image processing software

where a customized program was used to measure the circulus spacing (mm) by growth zone (Figure 1.2). The scale measurement axis was defined as the longest axis extending from the scale focus. Data associated with the scale, such as date of collection, location, sex, length, and fishery type, were included in the dataset and stored in a Microsoft Access database.

### *Scale Growth Analyses*

Salmon length was plotted on scale radius by population. We hypothesized that uncorrelated growth among populations would indicate the importance of regional effects on growth and imply less overlap at sea. To determine whether common factors affected growth of western Alaska and Asian chum salmon, annual mean scale growth was compared using Pearson's correlation analysis to determine whether growth of one zone was correlated to growth in a previous zone within a population. Then populations were compared to determine whether growth zones among populations were correlated. For western Alaska, growth was compared using Pearson's correlation analysis by age. Growth was compared by first year at sea, and growth years were aligned so that comparisons were made across the years that fish were in the ocean.

### *Length Correction*

Lengths of western Alaskan fish were recorded as mid-eye to fork of tail, but the Japanese and Russian fish were measured from snout to fork of tail. We used Pahlke's (1989) "brite" correction factor for southeast Alaska chum salmon to equalize fish length:

$$MEF = 0.826 (SNF) + 63.502,$$

where *MEF* is mid-eye to fork of tail and *SNF* is snout to fork of tail.

### *Back-calculation of Growth*

Annual length increments were estimated by back-calculation, using the Dahl-Lea method (direct proportion formula through the origin) developed by Lea (1910) and described in detail in Francis (1990):

$$L_i = (S_i / S_c) L_c,$$

where  $L_c$  and  $S_c$  are body length and scale radius at capture, respectively, and  $L_i$  and  $S_i$  are the corresponding measurements at the time of formation of the  $i$ -th scale mark. Back-calculated

lengths were compared by population and age using analysis of variance (ANOVA, version 2.9.2, The R Development Core Team 2009).

### *Seasonal Growth*

To examine seasonal marine growth among populations, mean scale circuli increments (distance between adjacent circuli pairs) were calculated for each age group by growth zone and year. We compared the growth between genders and between odd- and even-numbered years at sea. To facilitate evaluation of trends by gender and by odd- and even-numbered years at sea, the scale circuli measurements were plotted by the year in which an individual salmon entered the ocean (first year at sea). For example, an age 0.3 Yukon River fish returning in 1990, an even-numbered year, entered the Bering Sea as a fry during 1987, an odd-numbered year. These salmon interacted with abundant odd-year Asian pink salmon during the latter part of their first year of growth (SW1), the less abundant even-year pink salmon during their second year of growth (SW2), and then highly abundant odd-year Asian pink salmon during their third year of growth (SW3), and the less abundant even-year Asian pink salmon during homeward migration (SWPlus). Because not all fish have the same circuli count in each growth zone, circuli measurements were only included if they were present in  $\geq 90\%$  of fish. Therefore, this approach places an upper limit on the number of circuli in a growth zone based on  $\geq 90\%$  of the fish.

### *Annual Growth Trends by Life Stage*

Unequal numbers of male and female scales were available for measurement in some years. Because male and female chum salmon grow at different rates, we developed growth indices to weight male and female scale growth by year:

$$Z = (n_M Z_M + n_F Z_F) / (n_M + n_F),$$

where  $Z$  is the annual mean growth,  $n_M$  and  $n_F$  are sample sizes of male and female salmon, and  $Z_M$  and  $Z_F$  represent the normalized mean growth of male and female salmon, respectively. To compare trends in annual scale growth by zone among populations, the scale measurements were normalized. Normalized values were the number of standard deviations above and below the long-term un-weighted mean and were calculated for each gender and population. Normalized growth of western Alaska age 0.3 fish was compared to age 0.4 fish using Pearson's product-moment correlation by population in R (version 2.9.2, The R Development Core Team 2009). Pearson's correlations were also used on all data to compare one growth zone to another within a

population for all populations by age. Growth zone widths and number of circuli within a growth zone were compared for all populations by sex and year using ANOVAs. Multiple comparisons (package *glht* in R; version 2.9.2, The R Development Core Team 2009) were used to determine the pairs of populations that contributed to the results.

### *Chum and Pink Salmon Relationships*

For each population, we plotted the normalized values by growth zone width and total fish length by odd and even year. We compared scale growth zone width by odd and even year using a two-factor ANOVA by population and age to examine whether there were differences among scale growth in odd and even years, possibly indicating effects from higher Russian pink salmon abundances in odd years.

To compare odd and even years before and after the 1976-77 regime shift, the percent difference of measurements by zone and circuli number was calculated:

$$P = (\mu_{e,p} - \mu_{o,p}) / \mu_{o,p}$$

$$A = (\mu_{e,a} - \mu_{o,a}) / \mu_{o,a},$$

where  $P$  is the percent difference prior to the 1976-77 regime shift and  $A$  is the percent difference after the 1976-77 regime shift. The mean during the even years prior to the 1976-77 regime shift is represented by  $\mu_{e,p}$ , the mean during the even years after the regime shift is represented by  $\mu_{e,a}$ , the mean during the odd years prior to the regime shift is represented by  $\mu_{o,p}$ , and the mean during the odd years after the regime shift is represented by  $\mu_{o,a}$ .

For Unalakleet and Japan, whose time series began in 1975 and 1976 respectively, we used 1988 and 1989 as the pre- and post-time periods. The late 1980s represented the dates of the second regime shift that occurred in the North Pacific (Hare and Mantua 2000).

### *Comparisons Across Geographic Distance*

Growth zone widths were compared among populations by sex and year using analysis of variance (The R Development Core Team 2009). We then used multiple comparisons to pinpoint pairs of populations that did not show differences in growth. To compare differences in growth zones among populations by geographical distance, we used a Mantel test (Mantel 1967; function *Mantel* from package *Ade4* in R; version 2.9.2; The R Development Core Team 2009). This test compared two matrices for a correlation among scale growth measurements (mm) and geographic

distances (km). We determined the latitude and longitude of the mouth of each river system and used that to calculate geographic distances (km) from the other river systems.

### *Figures*

We chose Big Eddy as a representative population to reduce the number of figures. This population had one of the longest, most complete time series of data, and the figures were representative of most of the populations.

## **Results**

### *Scale Growth*

Chum salmon scale radius was a good indicator of adult salmon length (Figure 1.3, Appendices A1-A3). All populations and ages showed a significant relationship between scale radius and adult length, except Unalakleet age 0.3 fish. Scale growth differed by sex and population for all zones, except the first growth zone for most populations (ANOVAs,  $P < 0.05$ , Figure 1.4, Appendices A4-A6, B1-B2). Japan and the Unalakleet River showed a different pattern. The SW1 growth zone differed significantly by gender only for Unalakleet River age 0.4 fish (ANOVA,  $F = 4.14$ ,  $P = 0.05$ ), and the SW2 growth zone did not differ significantly for either age in Unalakleet River (Appendix A4). There was no significant difference by zone, sex, total radius, or length for Japan (Appendix A6).

Correlations between scale growth zones were examined within each population for all six river systems (Tables 1.2-1.5). Most (85%) of the significant correlations were positive. All negative correlations were observed within western Alaska, and 62% of these involved SW1 growth (Tables 1.2-1.3). For age 0.3 fish, the mean SW1 growth zone was correlated with the mean SW2 growth zone for only 50% of the populations (Table 1.2). The SW2 growth zone was correlated with the SW3 growth zone for five of the six populations. For age 0.4 fish, the mean SW1 growth zone was correlated with the SW2 growth zone, and the SW2 growth zone was correlated with the SW3 growth zone for three of the four populations (Table 1.3). The SW4 growth zone was correlated with the SW3 growth zone in all western Alaska populations, except Nushagak. The SWPlus growth zone was correlated with the SW3 growth zone in all age 0.4 populations, except Unalakleet.

Mean adult length was positively correlated with several growth zones in most populations, notably the third year of growth (SW3) in all except two populations (Tables 1.2-

1.3). For age 0.4 fish, length was correlated with the SW4 growth zones and scale radius in 75% of the populations (Table 1.3). Nushagak age 0.4 fish showed no correlation among fish length and any growth zone (Table 1.3), although the age 0.3 fish were positively correlated with the SW3 growth zone and scale radius (Table 1.2).

Growth of western Alaska age 0.3 was compared to age 0.4 fish by population (Table 1.4). Adult length was positively correlated by first year at sea (Table 1.4). For Unalakleet, only the SW2 and SW3 growth zones were correlated; whereas, in Big Eddy, all growth zones were correlated. In Quinhagak, all growth zones, except total scale radius, were correlated by age, and in Nushagak, only SW1 through SW3 were correlated by age (Table 1.4).

When growth zones were compared among populations, 11 of 15 (73%) possible correlations were positively correlated in the SW3 growth zone, and 10 of 15 (67%) possible correlations were positively correlated in the SW2 growth zone (Table 1.5). Although Russian fish were correlated with western Alaskan fish in the SW3 growth zone and in length and with Big Eddy in the SW2 growth zone, there were no significant correlations between the Japanese and Russian measurements in any zone, total radius, or fish length (Table 1.5).

#### *Back-calculations of Total Fish Length Based on Scale Size*

The back-calculated lengths were similar to measurements from three Russian rivers (given in Salo's 1991 review) and immature fish caught in the North Pacific Ocean (Ishida et al. 1998, Table 1.6). There were no significant differences in back-calculated lengths in any zones among populations when age 0.3 or 0.4 fish were analyzed separately (Table 1.6). ANOVAs comparing the SW1 and SWPlus growth zones indicated that these zones were not significantly different between ages. The mean growth increment for the SW1 growth zone ranged from 248-268 mm in western Alaska (Table 1.6); whereas, Russia was quite a bit smaller at the end of the first year (230 mm). The SW2 growth zone was not significantly different among populations. Although the Japanese fish were larger after SW1 growth (302 mm), Unalakleet age 0.3 fish were larger at the end of both the SW2 (442 mm) and SW3 (532 mm) growth zones. The Japanese (615 mm) and Russian (602 mm) fish grew larger during the SWPlus growth zone, but they returned to the natal site later. Annual growth of western Alaskan fish at age 0.3 was significantly greater than that of age 0.4 chum salmon for all zones except SWPlus (two-sample t-test,  $P < 0.001$ ).



### *Seasonal Growth*

*Male-female comparisons.*--Growth (distance between adjacent circuli or intercirculi distance) in the first year initially declined likely corresponding with downstream migration from the natal site (Figure 1.5), then once the fish reached the ocean, intercirculi distance rapidly increased for both genders (SW1). Intercirculi distances were similar by gender in the second growth zone (SW2, Figure 1.5, Appendices A7-A8).

Intercirculi distances of males exceeded that of females in the SW3 growth zone for both ages of western Alaska and age 0.3 Russian fish (Figure 1.5). The females from Japan had slightly larger intercirculi distances than males in the SW3 growth zone (Figure 1.5). Throughout the SW4 growth zone, age 0.4 western Alaska males had consistently larger intercirculi distances than females (Figure 1.5).

For all populations and ages, except Japan, male intercirculus growth was greater than female intercirculus growth during the homeward migration (SWPlus, Figure 1.5). Most populations showed substantially larger growth. Japanese female chum salmon had larger intercirculi distances than males (Figure 1.5).

*Odd-even year comparisons.*--ANOVAs comparing scale growth zones and body length between odd- and even-numbered years by population (Appendices B3-B4) indicated that scale growth by zone was significantly larger during odd years only for Unalakleet age 0.3 and 0.4 fish in the SW3 growth zone (age 0.3,  $F = 4.621$ ,  $P = 0.040$ ; age 0.4,  $F = 4.985$ ,  $P = 0.033$ ).

In all populations, intercirculus growth initially declined until circuli 7-10 (Russia, circuli 2-3). After circuli 7-10 (Russia, circuli 2-3), intercirculus distance increased rapidly, reaching peak growth near circuli 15-19 for age 0.3 western Alaskan fish. Age 0.4 fish appeared to reach maximum growth at a higher circulus number (circuli 17-21, Figure 1.6). Japanese and Russian fish had lower overall distances than western Alaskan fish. Russia had fewer circuli (22.4) than western Alaska (28.1) or Japan (31.4, Figure 1.6, Appendices A9-A10).

For three of the four western Alaska populations and Russia, there was a slight difference in circuli distances between smolts that entered the ocean during even years and those that entered the ocean during odd years when Asian pink salmon were highly abundant, although the distribution of western Alaskan fish would probably not overlap with that of Asian pink salmon until late in the first growth year. Unalakleet showed an opposite trend, but there was a strong

even-year local pink salmon population in Norton Sound (S. Kent, Alaska Department of Fish and Game, personal communication). In Japan and Big Eddy, smolts entering the ocean during odd- and even-numbered years showed similar intercirculi distances between the odd- and even-years in the SW1 growth zone.

Overall, smolts that entered the ocean during an odd year had greater distances between adjacent circuli during the next (even-numbered) year, suggesting the possibility of compensatory or “catch-up” growth during the second and third growth years (Figure 1.6). Big Eddy and Nushagak showed a rapid increase in spacing between circuli 1-5 in the SW2 growth zones. Other populations started with very high growth, which diminished throughout the zone. The same pattern was observed in SW3 and SW4.

All western Alaska populations showed similar intercirculi distances in SWPlus. If a smolt entered the ocean in an odd year and returned as an age 0.3 fish in an even year, SWPlus growth was slightly better than that of smolts entering the ocean during an even year and returning during an odd year. If these fish returned as an age 0.4 fish, they did not grow as well in homeward migration during an odd-numbered year. If migrating during an odd-numbered year, they would be competing with abundant Asian pink salmon. That would not have been the case if the fish had returned the previous year as age 0.3 fish. Japanese and Russian fish exhibited a different pattern, because both populations showed larger intercirculi distances in this zone.

#### *Temporal Trends by Growth Zone*

Most of the long-term growth patterns, visible in all six populations, could be divided into two to three periods, and these usually coincided with climatic or environmental events in the North Pacific, such as the 1976-77 regime shift, the 1989 regime shift, or the 1997-98 El Niño (Figure 1.7, Appendices A11-A19). For example, SW2 in Big Eddy age 0.4 fish show growth mostly above the long-term mean until 1988 then poor growth after until the end of the study.

In western Alaska, there was little difference in long-term growth patterns between ages. SW1 growth of Nushagak fish (both ages) exhibited similar poor growth in the early years, which improved in the late 1970s; whereas, Russian chum growth, poor in the 1960s, did not improve until approximately 1989. The SW1 growth in other populations (Unalakleet, Big Eddy, Quinhagak, and Japan) was variable.

In the second year of growth (SW2), all populations' mean growth (e.g. - Figure 1.7), except Russia, was above the long-term mean for both ages until 1986-1989, then the growth fell below the mean for most populations and remained low. Age 0.3 fish from Unalakleet showed a different pattern (Appendix A11).

In the third year of growth (SW3), we observed relatively similar growth patterns in all six populations (e.g. - Big Eddy, Figure 1.7). Scale growth in all populations was above the mean for both ages until 1976-79 or 1988-89 then scale growth fell below the mean. A few populations had some growth above the long-term mean after 1996-97. In the fourth year of growth (SW4), all western Alaska populations showed growth mostly above the long-term mean until 1985-1989, and then growth fell below the mean (Figure 1.7).

The growth during the homeward migration (SWPlus) was the most variable; however, most populations appeared to have three major sections. In western Alaska, there was a shift in the early to mid-1980s from below average growth to above average growth reverting to below average growth again in the 2000s (Figure 1.7).

Overall, adult length from three western Alaska populations (Nushagak, Quinhagak, and Big Eddy) was above the mean until the mid-1980s to early-1990s then fell below the long-term average (e.g. – Big Eddy, Figure 1.7). Adult length of fish from Russia was above the long-term mean until 1981-82 then mostly below the mean. On the other hand, length of fish from Japan was above the long-term mean until 1982-83, then mostly below the mean until 1996-97 when it was above the mean (Appendix A19). Length of Unalakleet age 0.3 and 0.4 fish was variable (Appendices A11-A12).

The percent change in scale growth plots for age 0.3 Big Eddy fish (Figure 1.8, Appendices A20-A22) showed that in the SW2 growth zone there was some difference between odd and even years before the regime shift (indicated by the dashed line representing the pre-1976 change being below 0). For all western Alaska age 0.3 populations SW2 growth, there was some difference in growth between odd and even years after the regime shift as indicated by the black line hovering around 0. For western Alaska age 0.3 fish, SWPlus growth between odd and even years differed before and after the regime shift. In Russia, SW1 growth differed more between odd and even years before the regime shift than any other growth zones. Japan and Unalakleet River, which had shorter time series, showed differences before and after the 1988-89

shift (Figure 1.9). Growth differed most between odd and even years before the regime shift in the second and third year of growth for Unalakleet and in the third year of growth for Japan.

#### *Comparisons Across Geographic Distance*

Each growth zone was significantly different among populations for all populations by sex and year (ANOVAs, Appendix B3-5), except the first growth zone. In the first growth zone, four pairs of populations (mostly the ones closest to one another) did not differ significantly. In the second growth zone, the only pair of populations not significantly different from one another was Nushagak – Big Eddy, and in the third growth zone, all population pairs were significantly different. In the SWPlus growth zone, Quinhagak was not significantly different from Big Eddy and Unalakleet, and Big Eddy and Unalakleet were also not significantly different. For total scale radius, the only non-significant pair was Quinhagak and Big Eddy, the closest rivers.

More similar (synchronous) variation among years in mean growth zone width was observed among populations from close rivers than from more distant ones (Mantel test, Figure 1.10, Table 1.7). We found no significant differences among western Alaska age 0.3 or age 0.4 fish, but when we included Russia and Japan, SW2, SW3 and SWPlus were significantly different (Figure 1.10, Table 1.7).

### **Discussion**

#### *Chum Salmon Migrations within the North Pacific Ocean*

Chum salmon have the widest natural geographic distribution of all Pacific salmon. Fry migrate to the sea soon after emergence. In western Alaska, most juvenile chum salmon remain close to their estuaries of origin until fall of the first year then move slowly southwest (Urawa et al. 2003, 2004, 2009). After the first year, western Alaskan fish migrate into the Gulf of Alaska where they remain until homeward migration. Questions remain about whether western Alaska chum salmon re-enter the Bering Sea prior to returning as mature fish (Myers et al. 2007; Seeb et al. 2004; Urawa et al. 2001).

In contrast, juvenile Japanese chum salmon distribute throughout the Okhotsk Sea in their first summer-fall, then move into the southwestern North Pacific Ocean during the first winter-spring (Urawa et al. 2004, 2007). During the first ocean year, juvenile Japanese and North American salmon rarely intermingle (Myers et al. 2000), although Russian and western Alaskan

stocks of juvenile salmon may mix during their first summer and fall in the northeastern Bering Sea (Farley et al. 2005). In the second summer-fall, Japanese chum salmon migrate into the Bering Sea and in late fall move south and east to spend the second winter in the Gulf of Alaska. In subsequent years, Japanese chum salmon migrate between summer-fall feeding areas in the Bering Sea and winter habitat in the Gulf of Alaska (Urawa et al. 2009). In their last summer and fall, maturing fish migrate back to Japan through the western Bering Sea and western North Pacific (Myers et al. 2007; Walker et al. 1998). Fish from northeastern Russia (e.g. – Anadyr River) may follow a similar pattern (Zavolokin 2009), migrating back and forth between wintering grounds in the Gulf of Alaska and summer grounds in the Bering Sea. Thus, most intermingling of North American and Asian chum salmon occurs when Asian fish extend their range into the Gulf of Alaska during their second and third winters at sea (Fukuwaka et al. 2007a,b; Myers et al. 2004; Urawa et al. 2003, 2004, 2009). Ishida et al. (1998) suggested that density dependent growth occurred most for chum salmon in the third year at sea (Ishida et al. 1993; Kaeriyama 1996). They hypothesized that growth rates during life stages when density dependent growth occurs are higher than those in other life stages, and that higher growth rates required greater demands for food intake, which led to density dependent growth during rapid growth seasons when prey resources were limited. Consequently, overlapping distributions of these six chum salmon populations at sea during these time periods could contribute to the similarities in growth observed in this comparison of chum salmon from the North Pacific.

#### *Seasonal Growth Among Populations*

Male chum salmon are larger than females at maturity, and the ANOVA results indicated that the zone measurements diverged by gender in the second year of growth, supporting Helle (1979). On the other hand, visual examination of the circuli increments of all populations, except Japan, indicated that growth was similar by gender until the third year. This difference could be due to the plots showing overall average of all included years; whereas, the ANOVA included year as a factor. Because our ANOVA results were similar to those found by Helle (1979), it is likely that the genders begin to diverge in size in the second growth year.

In all populations, the intercirculus distance during the first year initially declined in the first 1-9 circuli then increased markedly at circuli 2-3 for Russian and circuli 5-9 for western Alaskan and Japanese fish. This was very different than that observed in sockeye salmon (Ruggerone et al. 2005). Sockeye intercirculus distances showed no decline. Instead, they

increased sharply from circulus 1 to 4-5 before flattening and slowing declining. Sockeye salmon spend one to two years in freshwater; whereas, chum salmon migrate downstream upon emergence. In some of the larger rivers in Alaska, such as the Yukon that flows 3,190 km from its headwaters in British Columbia, Canada through the Yukon across Alaska, emigration may take 11-59 days (Hillgruber and Zimmerman 2009). These initial declines in growth suggested that chum salmon traversed lower quality freshwater or estuarine habitats, and when they reached the ocean, encountering increased warmer water, growth increased. Calculations from juveniles collected in the eastern Bering Sea in September showed that it takes approximately nine days for an individual circulus to form (J. Murphy, National Marine Fisheries Service, personal communication). Thus, our data indicated that it may take some western Alaskan fish 45 - 80 days to reach marine waters, confirming and possibly increasing previous time estimates.

Ishida et al. (1998) reported that salmon growth was greatest between June and July, a period apparently later than peak scale growth and peak zooplankton biomass. Hillgruber and Zimmerman (2009), in a review of estuarine ecology of juvenile western Alaska chum salmon, reported that peak numbers were caught in estuaries in June, and fish were 33-68 mm in length. By late August to mid-September, juvenile chum salmon collected on the southeastern Bering Sea shelf were an average of 173 mm in length (J. Murphy, National Marine Fisheries Service, personal communication), suggesting an increase of 2.5 times their size in two months during the first summer at sea. Japanese and Russian chum salmon showed lower overall scale growth in the first marine zone and did not reach as high a peak as western Alaskan fish, supporting the hypothesis that these fish feed in different locations during the first year. This indicated that the Okhotsk Sea and western Bering Sea were not as productive for chum salmon as the eastern Bering Sea. Of course, this study examined fish that survived to adulthood, and differing survival rates could bias the results if survival was a function of growth in the first year.

Big Eddy and Nushagak showed similar rapid increases in spacing among circuli 1-5 in the SW2 through SW4 growth zones. All other populations started with much higher growth, which diminished throughout the zone. This difference in growth suggested the possibility of different winter distributions for these two populations. Based on circuli seasonal growth patterns, Big Eddy and Nushagak fish may be feeding earlier in the spring and growing slower earlier than the other populations that put on a large amount of growth between the last winter circulus and the first spring circulus. This might also be due to annulus marker placement error

or differing scale formation among populations. Scale annuli were marked before the first complete circulus after the winter. Sometimes there were incomplete circuli between the annulus marker and the first complete circulus. These incomplete circuli may represent spring growth or growth in the next annulus and cause inaccurate placement of the annulus marker.

Some of the differences observed among the growth of Japanese fish and the other populations could be due to sampling dates. Japanese fish were collected in the fall (most in October). All western Alaskan fish were collected in early June to late July, and the Russian fish were collected in August, thus Japanese fish spent more time in saltwater, possibly increasing the size of the saltwater-plus zone, enhancing overall scale radius. On the other hand, it has been suggested that returning fish, influenced by the warm Oyashio Current, swim near the bottom in cooler waters where little food is available. Also, the Japanese fish had a different early marine life history. They were mostly artificially-enhanced fish, and the scales we examined were 137% larger at circulus five than other populations, suggesting a larger body size upon ocean entry in contrast to the wild fish from western Alaska and Russia. Also, fall run fish, such as these Japanese fish, may have some genetic adaptations for their unique conditions. Yukon River fall chum salmon are believed to have evolved to utilize distant upriver spawning areas and late migration timing requiring fat reserves (Bue et al. 2006), thus they carry a higher proportion of belly fat than summer run chum. Other fall chum salmon have similar characteristics, and the Japanese run is considered a “fall” run (Salo 1991), but none mention whether these Chitose River salmon have similar morphological or behavioral characteristics. The Chitose River, a tributary of the Ishikari River, is only 268 km in length, or 8% of the length of the Yukon River, so the Japanese fish may not need belly fat to sustain them during a long migration.

#### *Basin-scale or Regional Effects?*

We hypothesized that correlated growth among the six salmon stocks around the North Pacific Ocean would indicate basin scale effects. We found that for all populations, except Unalakleet age 0.3 fish and Nushagak age 0.4 fish, adult length was primarily correlated with growth that occurred during the last full year at sea but not during the homeward migration (SWPlus growth). For 60% of the populations, this included the last two years an individual fish spent at sea prior to the homeward migration. This corresponded with previous results from Kwiniuk River, Norton Sound, Alaska (Ruggerone and Agler 2008), supporting the hypothesis that salmon must reach a certain size prior to the homeward migration or they spend another year

in the ocean and return to the natal site as age 0.4 fish (Bigler et al. 1996; Fukuwaka et al. 2009; Helle and Hoffman 1995, 1998; Helle et al. 2007; Helle and Fukuwaka 2009; Ishida et al. 1993, 2001; Morita and Fukuwaka 2007). The average back-calculated length at the SW3 zone of an age 0.3 fish was 527 mm in length, and only 484 mm for the age 0.4 western Alaskan fish. Although the ranges overlapped, the lower range of the back-calculated length at the SW3 growth zone of age 0.3 fish was 494 mm, approximately 10 mm greater than the average length of a fish that returned at age 0.4. The homeward migration for western Alaska salmon includes cessation of feeding and a shift in energy allocation from growth to egg production, thus it is important that growth is achieved at sea, and western Alaska chum cannot rely on this time period to increase length-at-age (Quinn 2005).

We also found that although Russian fish were correlated with western Alaskan fish in the SW3 growth zone and fish length, there were no significant correlations between the measurements for Japanese and Russian fish for any zone, total scale radius, or fish length. Russian and Japanese fish supposedly occupy the Bering Sea during the summer, but then Russian fish migrate to the mid-North Pacific Ocean rather than in the Gulf of Alaska; whereas, the Japanese fish move into the Gulf of Alaska during the winter. Our results indicated that there was overlap among western Alaskan fish and both Russian and Japanese fish, but little overlap among Russian and Japanese fish. This emphasizes one of the interesting results from our data. We found slightly different results among these populations in seasonal growth and in these correlations. Thus, it appears possible that these stocks are partitioning the habitat of the North Pacific Ocean. They were all occupying this broad region at the same time, but they were probably not in the same exact places at the same time. The overlap likely occurred over a large scale.

#### *Comparison of Back-calculations with Actual Measurements*

Despite the fact that there are several back-calculation methods available (e.g. - Campana 1990; Francis 1990; Morita and Matsuishi 2001; Schirripa 2002), the merits and limitations of alternative approaches remain challenging. Fish growth and scale growth could be uncoupled (Morita and Matsuishi 2001) due to two primary causes: (1) the “growth effect” in which scales from slow-growing fish are larger than those of fast-growing fish of the same size (e.g. Campana 1990; Pierce et al. 1996; Reznick et al. 1989), and (2) the “age effect” in which the scale increases in size continuously, although the fish does not (Holmgren 1996; Secor and Dean



1992). Thus, traditional back-calculation methods may over-estimate fish growth rates for slow-growing fish at older ages.

We used the simplest back-calculation method: the Dahl-Lea method (Francis 1990; Jensen et al. 2011; Lea 1910). This method did not account for the fact that salmonid scales do not form until chum salmon smolt reach ~35-40 mm in length (Yamada 1971). Jensen et al. (2011) compared the Dahl-Lea and Fraser-Lee methods on Atlantic salmon in Norway and found that the bias associated with the extrapolation of the Dahl-Lea method did not affect overall trends in growth. We also tried the Fraser-Lee method (Francis 1990; Lee 1920) but found that it overestimated total length. The lengths of known age juveniles and immature chum salmon caught in the North Pacific on research cruises (Ishida et al. 1998) were similar to lengths found in this study. After converting the snout to fork lengths from Ishida et al. (1998) using Pahlke (1989), we found that the back-calculated lengths were similar to the lengths measured in situ. These back-calculated lengths provided an index to compare temporal variation among the populations. We encourage caution when using back-calculated body lengths and do not recommend using these values for comparisons with other studies (Campana 1990; Morita and Matsuishi 2001).

#### *Climate Change Effects on Growth*

The effects of major climate events were visible in the chum salmon scale growth trends. The salmon scales were acting as data loggers in the ocean recording the results of these events. In almost every population, growth during the second or third marine year was above normal until the regime shifts (1976-77 or 1988-89) that occurred in the North Pacific (Hare and Mantua 2000; Mantua et al. 1997; Rogers 1984) then the growth fell below normal for 10-30 years. A few populations appeared to recover (Unalakleet age 0.3 SW2 and Quinhagak both ages SW3), but most did not. Changes in growth coincided with or lagged behind the regime shifts by one to four years, indicating that chum salmon growth was influenced by these climate shifts, but the effects on growth lagged 2-5 years lagged behind the climate events. Ishida et al. (2002) suggested that climate changes affected sea surface temperature, which, in turn, influenced chum salmon distributions and densities and affected salmon growth through intraspecific competition. Thus, climate appears to be important to growth of chum salmon, although its effects may not be immediately apparent.

### *Interactions with Pink Salmon*

Our results indicated that chum salmon growth was weakly related to abundance of pink salmon during odd years. There were slight differences in circuli numbers among odd and even years, but the ANOVA results, except for Unalakleet, were not significant. Walker et al. (1998) examined scale growth of chum salmon collected south of the Aleutian Islands and concluded that chum growth during their third year at sea was inversely related to both Asian pink and chum salmon abundances. The inverse correlation between chum scale growth and Asian pink salmon abundance was observed before and after the 1976-77 regime shift. Competition with Asian pink salmon was not apparent during the first two years at sea. Consequently, we would not expect to see an effect in the seasonal growth plots until the third year, and we did not see these effects until the third growth year when it was evident in both males and females.

These results could be explained by the differences in diet between chum and pink salmon. In contrast to sockeye salmon, which are sympatric with Asian pink salmon and share similar prey, chum salmon are more omnivorous. Chum salmon have a different gut architecture than other salmon, which allows them to eat a more diverse diet than other salmon species. When pink salmon abundance increases, chum salmon are capable of “prey switching” and foraging on lower energy prey (i.e. - gelatinous zooplankton, Davis et al. 2000; Davis et al. 2004).

### *Interactions with Asian Chum Salmon*

We examined this question by determining whether growth among populations was correlated, indicating whether their distributions overlapped during that growth period. During the first year of growth, a few of the western Alaska populations may have overlapping distributions indicated by correlated growth. Farley et al. (2007a) found that western Alaskan fish intermingled with Russian fish during their first fall as they pass through the Bering Sea, and two western Alaska populations showed close correlations (Nushagak  $P = 0.065$  and Unalakleet  $P = 0.080$ ), indicating that these populations may overlap somewhat during this growth period. Japanese fish spend the first fall in the Okhotsk Sea, thus they do not overlap with western Alaskan fish (Myers et al. 2007; Sato et al. 2009; Urawa et al. 2000, 2009).

The second (SW2) and third years of growth (SW3) were correlated among most western Alaska populations and Japan, suggesting considerable overlap of their distributions during this period. Russia’s second year of growth was not correlated with most other populations,

suggesting that their distributions did not overlap. The migrations for Russian fish are not as clearly understood as those for Japanese fish, and Russian stocks tend to be “lumped” with Japanese fish as Asian fish in descriptions of migratory movements of chum salmon (Myers et al. 2007). Thus, our results suggested that perhaps these stocks should not be lumped, because their distributions were not the same during the second year of growth.

During the third year at sea, 11 of the 15 pair combinations were significantly correlated, suggesting considerable overlap of these fish during this growth stage or possibly a response to the same ocean conditions. This was the time when overlap was most likely to occur. Most stocks intermingled in the Gulf of Alaska during the winter (see previous discussion on migration). During the homeward migration (SWPlus growth), the western Alaska populations were correlated, indicative of overlapping distributions as they headed north through the Aleutian Islands and eastern Bering Sea.

Overall, Unalakleet River fish often showed a different pattern compared with the western Alaska populations. Unalakleet, representing Norton Sound, was the furthest north Alaskan population examined. The Unalakleet River is shorter (only 145 km) than the Yukon River (3,190 km) and drains into a large bay or sound, which is often covered by ice late into the spring. Thus, we were unclear whether some of the differences in Unalakleet fish were due to the fact that this was a shorter time series (years) or was due to some environmental variable, such as ice cover, that affected this population and not the others. In addition, Norton Sound had a strong local even-year pink salmon population that possibly inhibited growth of Kwiniuk River chum salmon, another river in the area (Ruggerone et al. 2011).

#### *Comparisons Across Geographic Distance*

Synchrony has been observed in population sizes and recruitment in many fish species (Friedland 1998; Pyper et al. 2002). Jensen et al. (2011) found synchronous growth among Atlantic salmon in Norway. Atlantic salmon growth was more synchronous among geographically close populations than distantly separate ones (Jensen et al. 2011), and our results were similar. The scale measurements among the western Alaska populations were synchronous among both ages. Circuli counts, zone measurements, and back-calculated lengths were similar when tested using the Mantel test. When we compared all populations (North Pacific), we found that the further the populations were apart, the less synchronicity was observed in scale growth. These results suggested that even though fish had overlapping distributions for part of their life

history, regional-scale effects on populations were important to population level growth and recruitment (Peterman et al. 1998; Pyper et al. 2001, 2002). Although climate occurred at a basin-wide level, regional-scale effects may be as or more important to the fish.

#### *How Do These Results Compare with Previous Studies?*

Zavolokin et al. (2009) examined the Anadyr River, Russia scales, and Seo et al. (2011) and Kaeriyama et al. (2007a,b) examined the Japanese scales using different measuring systems. We recreated the measurements, so that they were comparable with western Alaska. We used the same dataset as Zavolokin et al. (2009). Our time series from Japan was from 1976-2008; however, Seo et al. (2011) and Kaeriyama et al. (2007a) used different datasets, from 1943-2005 and 1970-2001, respectively.

Zavolokin et al. (2009) observed declines in body size and annual growth during the second, third, and fourth years at sea of Anadyr chum salmon from 1962 to 2007 and suggested that these declines were the result of the increase in the total abundance of Pacific salmon after the mid-1980s. They speculated that this was a density-dependent response by Anadyr River chum salmon resulting from a decreased food supply. We found that growth of Anadyr chum salmon began to decline in their second year at sea in 1976-77. Kaev (2000) observed reductions in body length and fecundity from Iturup Island, a more southern population of chum salmon. Kaev (2000) attributed the declines in growth to increased ocean mortality. Feeding conditions in the western Bering Sea where Anadyr chum salmon were believed to spend the first year of life did not change substantially during the study (Naydenko et al. 2007; Shuntov and Temnykh 2004; Zavolokina 2007).

Seo et al. (2011) examined the relationship of effects of regional and basin-wide spatial scales of climate and ocean conditions on the growth of Japanese chum salmon. Although the growth of Japanese chum salmon initially increased in the first year at sea, it declined overall after the 1980s (Seo et al. 2011). Seo et al. (2011) attributed increased growth in the first year at sea to higher sea surface temperatures in the Okhotsk Sea and increased survival rates but suggested that these increased survival rates led to increases in abundance and declines in growth due to density-dependent growth effects. Seo et al. (2009) compared the Japan fish with growth measurements from Namdae River, Korea and found that although the second, third and fourth years of scale growth were similar total length and body mass were significantly different. They suggested that growth of chum salmon was influenced more by effects of intra-population

competition than by inter- and intraspecific interactions in the Bering Sea. These results were similar to our findings on the interspecific interactions of pink salmon on chum. Although we only found weak effects, there were strong correlations among the growth of chum salmon populations, indicating overlap of all populations during the third year of marine life, which may have an effect on the growth of chum salmon if prey availability becomes reduced or the climate changes, altering the carrying capacity of the North Pacific.

Recent studies used cluster analysis and maximum likelihood estimation to separate stocks by number of circuli (Bugaev 2003; Bugaev and Myers 2009; Bugaev et al. 2009; Nitta and Ueno 1989). Although these studies separated stocks between Russia and Japan by circuli number successfully over a two- to seven-year period, our comparisons from longer time series indicated the need to exercise caution due to variability over time.

We examined whether marine growth of western Alaska chum salmon varied in response to climate change and possible competition among and within salmon. These are difficult-to-answer questions. Helle et al. (2007) concluded that the carrying capacity of the North Pacific Ocean for Pacific salmon was not a constant value but varied with changing environmental and biological factors. Density-dependence and its overall effects are difficult to detect because growth is influenced by highly variable ocean productivity. There are a number of factors that can mask the relationship between inter- and/or intraspecific factors, climate, and salmon growth (Morita et al. 2005, 2006; Ogura and Ito 1994). Artificial propagation of salmon stocks or hatcheries may be masking our ability to detect these relationships as clearly as was seen with sockeye salmon (Friedland et al. 2009; Fukuwaka et al. 2011). Most Japanese chum salmon stocks originated in hatcheries, and although the western Alaska stocks are “wild,” approximately 550-650 million chum salmon were released each year into the Gulf of Alaska by Prince William Sound and southeast Alaska hatcheries. Fukuwaka et al. (2011) suggested that because the numbers of fish released from hatcheries are controlled artificially, the adult – offspring relationship could be altered even if the survival rate after release were to be affected by climate. The results of the percent difference plots pre- and post-regime shift indicated that our ability to distinguish odd-even year patterns may be masked by some other factor, whether it was the addition of hatchery fish to the North Pacific Ocean in recent years or the various climate shifts that occurred. Those plots indicated that the possibility that the odd-even year patterns differed before the regime shift occurred; consequently, this could be an area of future research. We

examined long time series, but there were shorter patterns occurring within the time series that could be explored further. The relationships between climate and density dependent effects are dynamic and should not be assumed to remain the same.

Marine teleosts are believed to experience the highest mortality rates during their early life history, which may represent a “critical period” (Beamish and Mahnken 2001; Pearcy 1992). Hatchery fish are incubated and reared artificially, migrating to sea soon after release. A large percentage of the mortality of Pacific salmon occurs during early marine life, and chum salmon likely experience the first period of critical mortality immediately after seaward migration (Hillgruber and Zimmerman 2009). Chum salmon that survive this period were significantly larger and had larger circulus intervals on the scales (Healey 1982). Hatchery fish may already be at the size necessary for survival upon release (Japan fish were 137% larger at circulus five than other populations); however, further research would be necessary to validate this hypothesis. Beamish and Mahnken (2001) suggested that Pacific salmon have a second period of size-related mortality during the first ocean winter. Future research might include defining a “critical period” on the scales and using the individual circulus measurements to compare populations by this measure. Because the early marine period is often considered an important time period, we could examine the first five or ten circuli to examine early growth.

### **Acknowledgments**

This investigation was funded by the Arctic-Yukon-Kuskokwim (AYK) Sustainable Salmon Initiative (Projects 45677 and 45164) as Historical Analyses of AYK and Asian Chum Salmon, phase one and two, and by the North Pacific Marine Research Program (Project SFOS 99-188). We appreciate the efforts to gather, measure, and catalog scales by many unknown researchers, as well as: D. Folletti, J. Baker, J. Cashen, J. Chesmore, S. Hinton, M. Lovejoy, A. Norman, W. Rosky, and W. Whelan. We also received support from a number of ADF&G staff, including I. Frank, L. Brannian, D. Evenson, E. Volk, L. Dubois, D. Molyneaux, H. Krenz, T. Baker, F. West, L. Fair, M. Olsen, D. Oxman, T. Frawley, W. Johnson, and T. Tobias. Dr. O. Temnykh, Russia, and Dr. H. Urawa, Japan, assisted us with obtaining samples. Dr. T. Saito, Fisheries Research Agency, Hokkaido National Fisheries Research Institute, Sapporo, Japan, and Dr. A. Zavolokin, Pacific Research Fisheries Center (TINRO-Centre), Vladivostok, Russia provided scale samples. Constructive comments on the paper were provided by B. Agler’s graduate committee, Drs. W. Smoker, F. Mueter, P. Hagen, and G. Kruse.

## References

- Anderson, P. J., and J. F. Piatt. 1999. Community reorganization in the Gulf of Alaska following ocean climate regime shift. *Marine Ecology Progress Series* 189:117-123.
- AYK-SSI. 2006. Arctic-Yukon-Kuskokwim Salmon Research and Restoration Plan. Bering Sea Fishermen's Association, Anchorage, AK.
- Azumaya, T., and Y. Ishida. 2000. Density interactions between pink salmon (*Oncorhynchus gorbuscha*) and chum salmon (*O. keta*) and their possible effects on distribution and growth in the North Pacific Ocean and Bering Sea. *North Pacific Anadromous Fish Commission Bulletin* 2:165-174.
- Beacham, T. D., J. R. Candy, S. Sato, S. Urawa, K. D. Le, and M. Wetklo. 2009. Stock origins of chum salmon (*Oncorhynchus keta*) in the Gulf of Alaska during winter as estimated with microsatellites. *North Pacific Anadromous Fish Commission Bulletin* 5:15-23.
- Beamish, R. J., and D. R. Bouillon. 1993. Pacific salmon production trends in relation to climate. *Canadian Journal of Fisheries and Aquatic Sciences* 50(5):1002-1016.
- Beamish, R. J., and C. Mahnken. 2001. A critical size and period hypothesis to explain natural regulation of salmon abundance and the linkage to climate and climate change. *Progress in Oceanography* 49:423-437.
- Bigler, B. S., D. W. Welch, and J. H. Helle. 1996. A review of size trends among North Pacific salmon (*Oncorhynchus* spp.). *Canadian Journal of Fisheries and Aquatic Sciences* 53:455-465.
- Bilton, H. T., and P. B. Station. 1975. Factors influencing the formation of scale characters. *International North Pacific Fisheries Commission Bulletin* 32:102-108.
- Bue, F. J., B. M. Borba, and D. J. Bergstrom. 2006. Yukon River fall chum salmon stock status and fall season salmon fisheries; a report to the Alaska Board of Fisheries. Alaska Department of Fish and Game, Special Publication No. 06-36, Anchorage.
- Bugaev, A. 2003. Identification of local stocks of sockeye salmon (*Oncorhynchus nerka*) by scale pattern analysis in the Russian economic zone. *North Pacific Anadromous Fish Commission Technical Report* 5:58-64.
- Bugaev, A. V., and K. W. Myers. 2009. Stock-specific distribution and abundance of immature sockeye salmon in the Western Bering Sea in summer and fall 2002-2004. *North Pacific Anadromous Fish Commission Bulletin* 5:71-86.

- Bugaev, A. V., E. A. Zavolokina, L. O. Zavarina, A. O. Shubin, S. F. Zolotukhin, N. F. Kaplanova, M. V. Volobuev, I. N. Kireev, and K. W. Myers. 2009. Stock-specific distribution and abundance of immature chum salmon in the Western Bering Sea in summer and fall 2002–2003. *North Pacific Anadromous Fish Commission Bulletin* 5:105-120.
- Campana, S. E. 1990. How reliable are growth back-calculations based on otoliths? *Canadian Journal of Fisheries and Aquatic Sciences* 47:2219-2227.
- Davis, N., J. L. Armstrong, and K. Myers. 2004. Bering Sea salmon diet overlap in fall 2002 and potential for interactions among salmon. Final report to the Yukon River Drainage Fisheries Association. SAFS-UW-0311. Fisheries Research Institute, University of Washington, Seattle, .34 pp.
- Davis, N. D., K. Y. Aydin, and Y. Ishida. 2000. Diel catches and food habits of sockeye, pink, and chum salmon in the Central Bering Sea in summer. *North Pacific Anadromous Fish Commission Bulletin* 2:99-109.
- Engen, S., and B. E. Saether. 2005. Generalizations of the Moran effect explaining spatial synchrony in population fluctuations. *American Naturalist* 166:603-612.
- Farley, E. V., Jr., C. M. Kondzela, J. M. Murphy, and A. Middleton. 2004. Stock-specific distribution and migration of juvenile chum salmon along the Eastern Bering Sea shelf. *North Pacific Anadromous Fish Commission Technical Report* 5:27.
- Farley, E. V., Jr., J. H. Moss, and R. J. Beamish. 2007a. A review of the critical size, critical period hypothesis for juvenile Pacific salmon. *North Pacific Anadromous Fish Commission Bulletin* 4:311-317.
- Farley, E. V., Jr., J. M. Murphy, M. D. Adkison, L. B. Eisner, J. H. Helle, J. H. Moss, and J. Nielsen. 2007b. Early marine growth in relation to marine-stage survival rates for Alaska sockeye salmon (*Oncorhynchus nerka*). *Fishery Bulletin* 105(1):121-130.
- Farley, E. V., Jr., J. M. Murphy, B. W. Wing, J. H. Moss, and A. Middleton. 2005. Distribution, migration pathways, and size of western Alaska juvenile salmon along the Eastern Bering Sea shelf. *Alaska Fishery Research Bulletin* 11(1):15–26.
- Fox, J. W., D. A. Vasseur, S. Hausch, and J. Roberts. 2011. Phase locking, the Moran effect and distance decay of synchrony: experimental tests in a model ecosystem. *Ecology Letters* 14:163-168.
- Francis, R. C., and S. R. Hare. 1994. Decadal-scale regime shifts in the large marine ecosystems of the North-East Pacific: a case for historical science. *Fisheries Oceanography* 3:4:279-291.



- Francis, R. I. C. C. 1990. Back-calculation of fish length: a critical review. *Journal of Fish Biology* 36:883-902.
- Friedland, K. D. 1998. Ocean climate influences on critical Atlantic salmon (*Salmo salar*) life history events. *Canadian Journal of Fisheries and Aquatic Sciences* 55:119-130.
- Friedland, K. D., L. P. Hansen, and D. A. Dunkley. 1998. Marine temperatures experienced by postsmolts and the survival of Atlantic salmon, *Salmo salar* L., in the North Sea area. *Fisheries Oceanography* 7(1):22-34.
- Friedland, K. D., J. C. MacLean, L. P. Hansen, A. J. Peyronnet, L. Karlsson, and D. G. Reddin. 2009. The recruitment of Atlantic salmon in Europe. *ICES Journal of Marine Science* 66(2):289-304.
- Fromentin, J., J. Gjosaeter, O. N. Bjornstad, and N. C. Stenseth. 2000. Biological processes and environmental factors regulating the dynamics of the Norwegian *Skagerrak* cod populations since 1919. *ICES Journal of Marine Science* 57:330-338.
- Fukuwaka, M., T. Azumaya, T. Nagasawa, A. N. Starovoytov, J. H. Helle, T. Saito, and E. Hasegawa. 2007a. Trends in abundance and biological characteristics of chum salmon. *North Pacific Anadromous Fish Commission Bulletin* 4:35-43.
- Fukuwaka, M., N. D. Davis, T. Azumaya, and T. Nagasawa. 2009. Bias-corrected size trends in chum salmon in the Central Bering Sea and North Pacific Ocean. *North Pacific Anadromous Fish Commission Bulletin* 5:173-176.
- Fukuwaka, M., T. Kaga, and T. Azumaya. 2011. Regional differences in climate factors controlling chum and pink salmon abundance. *ICES Journal of Marine Science* 68:1131-1137.
- Fukuwaka, M., S. Sato, S. Takahashi, T. Onuma, O. Sakai, N. Tanimata, K. Makino, N. D. Davis, A. F. Volkov, and K. B. Seong. 2007b. Winter distribution of chum salmon related to environmental variables in the North Pacific. *North Pacific Anadromous Fish Commission Technical Report* 7:29-30.
- Hagen, P. T., D. S. Oxman, and B. A. Agler. 2001. Developing and deploying a high resolution imaging approach for scale analysis. *North Pacific Anadromous Fish Commission Document* 567:1-11.
- Hare, S. R., and R. C. Francis. 1995. Climate change and salmon production in the Northeast Pacific Ocean Pages 357-372 [in] R. J. Beamish, Editor. *Climate Change and Northern Fish Populations*, volume 121. Canadian Special Publication of Fisheries and Aquatic Sciences.

- Hare, S. R., and N. J. Mantua. 2000. Empirical evidence for North Pacific regime shifts in 1977 and 1989. *Progress in Oceanography* 47:103-145.
- Healey, M. C. 1982. Timing and relative intensity of size-selective mortality of juvenile chum salmon (*Oncorhynchus keta*) during early sea life. *Canadian Journal of Fisheries and Aquatic Sciences* 39:952-957.
- Heino, M., V. Kaitala, E. Ranta, and J. Lindström. 1997. Synchronous dynamics and rates of extinction in spatially structured populations. *Proceedings of the Royal Society of London. Series B* 264:481-486.
- Helle, J. H. 1979. Influence of marine environment on age and size at maturity, growth, and abundance of chum salmon, *Oncorhynchus keta* (Walbaum), from Olsen Creek, Prince William Sound, Alaska. PhD thesis. Oregon State University, Corvallis.
- Helle, J. H., and M. Fukuwaka. 2009. Body size of maturing chum salmon in relation to sea surface temperatures in the Eastern Bering Sea. *North Pacific Anadromous Fish Commission Bulletin* 5:303-319.
- Helle, J. H., and M. S. Hoffman. 1995. Size decline and older age at maturity of two chum salmon (*Oncorhynchus keta*) stocks in Western North America, 1972-92. *Canadian Journal of Fisheries and Aquatic Sciences* 121:245-260.
- Helle, J. H., and M. S. Hoffman. 1998. Changes in size and age at maturity of two North American stocks of chum salmon (*Oncorhynchus keta*) before and after a major regime shift in the North Pacific Ocean. *North Pacific Anadromous Fish Commission Bulletin* 1:81-89.
- Helle, J. H., E. C. Martinson, D. M. Eggers, and O. Gritsenko. 2007. Influence of salmon abundance and ocean conditions on body size of Pacific salmon. *North Pacific Anadromous Fish Commission Bulletin* 4:289-298.
- Hillgruber, N., and C. E. Zimmerman. 2009. Estuarine ecology of juvenile salmon in western Alaska: a review. Pages 183-199 [in] C. C. Krueger, and C. E. Zimmerman, Editors. *Pacific Salmon: Ecology and Management of Western Alaska's Populations*. American Fisheries Society, Symposium 70, Bethesda, MD.
- Hinch, S. G., M. C. Healey, R. E. Diewert, K. A. Thomson, R. Hourston, M. A. Henderson, and F. Juanes. 1995. Potential effects of climate change on marine growth and survival of Fraser River sockeye salmon. *Canadian Journal of Fisheries and Aquatic Sciences* 52:2651-2659.

- Holmgren, K. 1996. Otolith growth scaling of the eel, *Anguilla anguilla* (L.), and back-calculation errors revealed from alizarin labeled otoliths. *Nordic Journal Freshwater Research* 72:71-79.
- Ishida, Y., T. Azumaya, and M. Fukuwaka. 2001. Interannual variability in stock abundance and body size of Pacific salmon in the central Bering Sea. *North Pacific Anadromous Fish Commission Document* 549:1-12.
- Ishida, Y., T. Azumaya, M. Fukuwaka, and N. Davis. 2002. Interannual variability in stock abundance and body size of Pacific salmon in the central Bering Sea. *Progress in Oceanography* 55:223-234.
- Ishida, Y., S. Ito, M. Kaeriyama, S. McKinnell, and N. K. 1993. Recent changes in age and size of chum salmon (*Oncorhynchus keta*) in the North Pacific ocean and possible causes. *Canadian Journal of Fisheries and Aquatic Sciences* 50:290-295.
- Ishida, Y., I. Soto-o, Y. Ueno, and J. Sakai. 1998. Seasonal growth patterns of Pacific salmon (*Oncorhynchus spp*) in offshore waters of the North Pacific Ocean. *North Pacific Anadromous Fish Commission Bulletin* 1:66-80.
- Ishida, Y., D. W. Welch, and M. Ogura. 1995. Potential influence of North Pacific sea-surface temperatures on increased production of chum salmon (*Oncorhynchus keta*) from Japan. *Canadian Special Publication of Fisheries and Aquatic Sciences* 121:271-275.
- Jensen, A. J., P. Fiske, L. P. Hansen, B. O. Johnsen, K. A. Mork, and T. F. Næsje. 2011. Synchrony in marine growth among Atlantic salmon (*Salmo salar*) populations. *Canadian Journal of Fisheries and Aquatic Sciences* 68(3):444-457.
- Kaeriyama, M. 1996. Population dynamics and stock management of hatchery-reared salmon in Japan. *Bulletin of National Research Institute of Aquaculture, Supplement* 2:11-15.
- Kaeriyama, M., and R. R. Edpalina. 2008. Evaluation of the biological interaction between wild and hatchery population for sustainable fisheries management of Pacific salmon. Pages 245-259 [in] K. M. Leber, Kitada, S., Blankenship, H. L., Svåsand, T., Editor. *Stock Enhancement and Sea Ranching: Developments, Pitfalls and Opportunities, Second Edition, volume 2*. Blackwell Publishing Ltd., Oxford.
- Kaeriyama, M., H. Seo, and H. Kudo. 2009. Trends in run size and carrying capacity of Pacific salmon in the North Pacific Ocean. *North Pacific Anadromous Fish Commission Bulletin* 5:293-302.
- Kaeriyama, M., A. Yatsu, H. Kudo, and S. Saitoh. 2007a. Where, when, and how does mortality occur for juvenile chum salmon *Oncorhynchus keta* in their first ocean year? *North Pacific Anadromous Fish Commission Technical Report* 7:52-55.

- Kaeriyama, M., A. Yatsu, M. Noto, and S. Saitoh. 2007b. Spatial and temporal changes in the growth patterns and survival of Hokkaido chum salmon populations in 1970–2001. *North Pacific Anadromous Fish Commission Bulletin* 4:251-256.
- Kaev, A. M. 2000. Recent reduction in chum salmon (*Oncorhynchus keta*) growth and its consequences for reproduction. *North Pacific Anadromous Fish Commission Bulletin* 2:247-253.
- Kiessling, A., K. Lindahl-Kiessling, and K. H. Kiessling. 2004. Energy utilization and metabolism in spawning migratory Early Stuart sockeye salmon (*Oncorhynchus nerka*): the migratory paradox. *Canadian Journal of Fisheries and Aquatic Sciences* 61(3):452-465.
- Koo, T. S. Y. 1962. Age designation in salmon. *Studies of Alaska red salmon*. University of Washington Publications in Fisheries, New Series 1:37-48.
- Lea, E. 1910. On the methods used in the herring investigations. *Publications de Circonstance. Conseil Permanent International pour l'Exploration de la Mer* 53:7-174.
- Lee, R. M. 1920. A review of the methods of age and growth determination in fishes by means of scales. *Fisheries Investigations London, Series 2*. 4(2):1-32.
- Liebhold, A., W. D. Koenig, and O. N. Bjornstad. 2004. Spatial synchrony in population dynamics. *Annual Review of Ecology and Systematics* 35:467-90.
- Linderman, J., Jr., and D. J. Bergstrom. 2009. Kuskokwim management area: salmon escapement, harvest, and management. Pages 541-599 [in] C. C. Krueger, and C. E. Zimmerman, Editors. *Pacific salmon: ecology and management of western Alaska's populations*. American Fisheries Society, Symposium 70, Bethesda, MD.
- Mantel, N. 1967. The detection of disease clustering and a generalized regression approach. *Cancer research* 27(2):209.
- Mantua, N. J., S. R. Hare, Y. Zhang, J. M. Wallace, and R. C. Francis. 1997. A Pacific interdecadal climate oscillation with impacts on salmon production. *Bulletin of the American Meteorological Society* 78(6):1069-1079.
- Martinson, E. C., J. H. Helle, D. L. Scarnecchia, and H. H. Stokes. 2008. Density-dependent growth of Alaska sockeye salmon in relation to climate-oceanic regimes, population abundance, and body size, 1925 to 1998. *Marine Ecology Progress Series* 370:1-18.
- Martinson, E. C., J. H. Helle, D. L. Scarnecchia, and H. H. Stokes. 2009. Growth and survival of sockeye salmon (*Oncorhynchus nerka*) from Karluk Lake and River, Alaska, in relation

- to climatic and oceanic regimes and indices, 1922-2000. *Fishery Bulletin* 107(4):488-500.
- Menard, J., C. C. Krueger, and J. Hilsinger. 2009. Norton Sound salmon fisheries: history, stock abundance, and management. Pages 621-673 [in] C. C. Krueger, and C. E. Zimmerman, Editors. *Pacific salmon: ecology and management of western Alaska's populations*. American Fisheries Society, Symposium 70, Bethesda, MD.
- Moran, P. A. P. 1953. The statistical analysis of the Canadian lynx cycle: II. synchronization and meteorology. *Australian Journal of Zoology* 1(3):291-298.
- Morita, K., and M. Fukuwaka. 2007. Why age and size at maturity have changed in Pacific salmon. *Marine Ecology Progress Series* 335:289-294.
- Morita, K., and T. Matsuishi. 2001. A new model of growth back-calculation incorporating age effect based on otoliths. *Canadian Journal of Fisheries and Aquatic Sciences* 58(9):1805-1811.
- Morita, K., S. H. Morita, and M. Fukuwaka. 2006. Population dynamics of Japanese pink salmon (*Oncorhynchus gorbuscha*): are recent increases explained by hatchery programs or climatic variations? *Canadian Journal of Fisheries and Aquatic Sciences* 63(1):55-62.
- Morita, K., S. H. Morita, M. Fukuwaka, and H. Matsuda. 2005. Rule of age and size at maturity of chum salmon (*Oncorhynchus keta*): implications of recent trends among *Oncorhynchus spp.* *Canadian Journal of Fisheries and Aquatic Sciences* 62(12):2752-2759.
- Morita, S. H., K. Morita, and H. Sakano. 2001. Growth of chum salmon (*Oncorhynchus keta*) correlated with sea-surface salinity in the North Pacific. *ICES Journal of Marine Science: Journal du Conseil* 58(6):1335-1339.
- Mueter, F. J., R. M. Peterman, and B. J. Pyper. 2002. Opposite effects of ocean temperature on survival rates of 120 stocks of Pacific salmon (*Oncorhynchus spp.*) in northern and southern areas. *Canadian Journal of Fisheries and Aquatic Sciences* 59(3):456-463.
- Myers, K. W., N. V. Klovach, O. F. Gritsenko, S. Urawa, and T. C. Royer. 2007. Stock-specific distributions of Asian and North American salmon in the open ocean, interannual changes, and oceanographic conditions. *North Pacific Anadromous Fish Commission Bulletin* 4:159-177.
- Myers, K. W., R. V. Walker, H. R. Carlson, and J. H. Helle. 2000. Synthesis and review of US research on the physical and biological factors affecting ocean production of salmon. *North Pacific Anadromous Fish Commission Bulletin* 2:1-9.

- Myers, K. W., R. V. Walker, N. D. Davis, and J. L. Armstrong. 2004. Diet overlap and potential feeding competition between Yukon River chum salmon and hatchery salmon in the Gulf of Alaska in summer. High Seas Salmon Research Program, Fisheries Research Institute, School of Aquatic and Fishery Sciences, University of Washington, Seattle.
- Naydenko, S. V., A. Y. Efimkin, A. F. Volkov, N. A. Kuznetsova, and N. S. Kosenok. 2007. Trophic position of Pacific salmon juveniles in the Western Bering Sea epipelagic communities during autumn. North Pacific Anadromous Fish Commission Technical Report 7:40-41.
- Niemelä, E., J. Erkinaro, J. B. Dempson, M. Julkunen, A. Zubchenko, S. Prusov, M. A. Svenning, R. Ingvaldsen, M. Holm, and E. Hassinen. 2004. Temporal synchrony and variation in abundance of Atlantic salmon (*Salmo salar*) in two subarctic Barents Sea rivers: influence of oceanic conditions. Canadian Journal of Fisheries and Aquatic Sciences 61(12):2384-2391.
- Nitta, A., and Y. Ueno. 1989. Stock identification of chum salmon *Oncorhynchus keta* from their maturity and scale characters. North Pacific Anadromous Fish Commission Document 375:651-656.
- Nunn, A. D., J. P. Harvey, J. R. Britton, P. A. Frear, and I. G. Cowx. 2007. Fish, climate and the Gulf Stream: the influence of abiotic factors on the recruitment success of cyprinid fishes in lowland rivers. Freshwater Biology 52:1576-1586.
- Ogura, M., and S. Ito. 1994. Change in the known ocean distribution of Japanese chum salmon, *Oncorhynchus keta*, in relation to the progress of stock enhancement. Canadian Journal of Fisheries and Aquatic Sciences 51(3):501-505.
- Pahlke, K. A. 1989. Length conversion equations for sockeye, chinook, chum and coho salmon in southeast Alaska. Alaska Department of Fish and Game, Division of Commercial Fisheries. Fisheries Research Bulletin 89-02:1-14.
- Pearcy, W. 1992. Ocean Ecology of North Pacific Salmonids. Washington Sea Grant Program, Seattle.
- Peterman, R. M., B. J. Pyper, M. F. Lapointe, M. D. Adkison, and C. J. Walters. 1998. Patterns of covariation in survival rates of British Columbian and Alaskan sockeye salmon (*Oncorhynchus nerka*) stocks. Canadian Journal of Fisheries and Aquatic Sciences 55(11):2503-2517.
- Pierce, C. L., J. B. Rasmussen, and W. C. Leggett. 1996. Back-calculation of fish length from scales: empirical comparison of proportional methods. Transactions of the American Fisheries Society 125(6):889-898.

- Pyper, B. J., F. J. Mueter, R. J. Peterman, D. J. Blackbourn, and C. C. Wood. 2001. Spatial covariation in survival rates of Northeast Pacific pink salmon (*Oncorhynchus gorbuscha*). *Canadian Journal of Fisheries and Aquatic Sciences* 58:1501-1515.
- Pyper, B. J., F. J. Mueter, R. J. Peterman, D. J. Blackbourn, and C. C. Wood. 2002. Spatial covariation in survival rates of Northeast Pacific chum salmon. *Transactions of the American Fisheries Society* 131:343-363.
- Pyper, B. J., and R. M. Peterman. 1999. Relationship among adult body length, abundance, and ocean temperature for British Columbia and Alaska sockeye salmon (*Oncorhynchus nerka*), 1967-1997. *Canadian Journal of Fisheries and Aquatic Sciences* 56(10):1716-1720.
- Quinn, T. P. 2005. *The behavior and ecology of Pacific salmon and trout*. University of Washington Press.
- R Development Core Team. 2009. *A language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna.
- Ranta, E., V. Kaitala, J. Lindstrom, and E. Helle. 1997. The Moran effect and synchrony in population dynamics. *Oikos* 78(1):136-142.
- Reznick, D., E. Lindbeck, and H. Bryga. 1989. Slower growth results in larger otoliths: an experimental test with guppies (*Poecilia reticulata*). *Canadian Journal of Fisheries and Aquatic Sciences* 46(1):108-112.
- Ripa, J., and E. Ranta. 2007. Biological filtering of correlated environments: towards a generalised Moran theorem. *Oikos* 116:783-792.
- Rogers, D. 1984. Trends in abundance of Northeastern Pacific stocks of salmon. Pages 100-127 [in] W. Percy, Editor. *The influence of ocean conditions on the production of salmonids in the North Pacific*. Oregon State University Press, Corvallis, OR.
- Royama, T. 1977. Population persistence and density dependence. *Ecological Monographs* 47(1):1-35.
- Ruggerone, G. T., and B. A. Agler. 2008. Retrospective analyses of AYK chum and coho salmon - 2008 Arctic Yukon Kuskokwim Sustainable Salmon Initiative Project Product. Natural Resources Consultants, Inc, Seattle, WA and ADF&G Division of Commercial Fisheries, Mark, Tag, and Age Lab, Juneau, AK. 57 pp.

- Ruggerone, G. T., B. A. Agler, and J. L. Nielsen. 2011. Evidence for competition at sea between Norton Sound chum salmon and Asian hatchery chum salmon. *Environmental Biology of Fishes* 1-15.
- Ruggerone, G. T., E. Farley, J. Nielsen, and P. Hagen. 2005. Seasonal marine growth of Bristol Bay sockeye salmon (*Oncorhynchus nerka*) in relation to competition with Asian pink salmon (*O. gorbuscha*) and the 1977 ocean regime shift. *Fishery Bulletin* 103(2):355-370.
- Ruggerone, G. T., and J. L. Nielsen. 2004. Evidence for competitive dominance of pink salmon (*Oncorhynchus gorbuscha*) over other salmonids in the North Pacific Ocean. *Reviews in Fish Biology and Fisheries* 14:371-390.
- Ruggerone, G. T., and J. L. Nielsen. 2009. A review of growth and survival of salmon at sea in response to competition and climate change. *American Fisheries Society Symposium* 70:1-46.
- Ruggerone, G. T., J. L. Nielsen, and B. Agler. 2007a. Retrospective analysis of AYK chinook salmon growth. Prepared for the 2007 Arctic Yukon Kuskokwim Sustainable Salmon Initiative, Anchorage, AK. 44 pp.
- Ruggerone, G. T., J. L. Nielsen, and B. A. Agler. 2009. Climate, growth and population dynamics of Yukon River Chinook salmon. *North Pacific Anadromous Fish Commission Bulletin* 5:279-285.
- Ruggerone, G. T., J. L. Nielsen, and J. Bumgarner. 2007b. Linkages between Alaskan sockeye salmon abundance, growth at sea, and climate, 1955-2002. *Deep Sea Research Part II* 54(23-26):2776-2793.
- Ruggerone, G. T., R. M. Peterman, B. Dorner, and K. W. Myers. 2010. Magnitude and trends in abundance of hatchery and wild pink salmon, chum salmon, and sockeye salmon in the North Pacific Ocean. *Marine and Coastal Fisheries* 2:306-328.
- Ruggerone, G. T., M. Zimmermann, K. W. Myers, J. L. Nielsen, and D. E. Rogers. 2003. Competition between Asian pink salmon (*Oncorhynchus gorbuscha*) and Alaskan sockeye salmon (*O. nerka*) in the North Pacific Ocean. *Fisheries Oceanography* 12(3):209-219.
- Salo, E. O. 1991. Life history of chum salmon (*Oncorhynchus keta*). Pages 231-310 [in] C. Groot, and L. Margolis, Editors. *Pacific Salmon Life Histories*. UBC Press, Vancouver.
- Sato, S., S. Moriya, T. Azumaya, H. Nagoya, S. Abe, and S. Urawa. 2009. Stock distribution patterns of chum salmon in the Bering Sea and North Pacific Ocean during the summer and fall of 2002–2004. *North Pacific Anadromous Fish Commission Bulletin* 5:29-37.



- Schirripa, M. J. 2002. An evaluation of back-calculation methodology using simulated otolith data. *Fishery Bulletin* 100:789-799.
- Secor, D. H., and J. M. Dean. 1992. Comparison of otolith-based back-calculation methods to determine individual growth histories of larval striped bass, *Morone saxatilis*. *Canadian Journal of Fisheries and Aquatic Sciences* 49(7):1439-1454.
- Seeb, L. W., P. A. Crane, C. M. Kondzela, R. L. Wilmot, S. Urawa, N. V. Varnavskaya, and J. E. Seeb. 2004. Migration of Pacific Rim chum salmon on the high seas: insights from genetic data. *Environmental Biology of Fishes* 69(1):21-36.
- Seo, H., H. Kudo, and M. Kaeriyama. 2009. Spatiotemporal change in growth of two populations of Asian chum salmon in relation to intraspecific interaction. *Fisheries Science* 75(4):957-966.
- Seo, H., H. Kudo, and M. Kaeriyama. 2011. Long-term climate-related changes in somatic growth and population dynamics of Hokkaido chum salmon. *Environmental Biology of Fishes* 90:131-142.
- Shuntov, V. P., and O. S. Temnykh. 2004. North Pacific Ocean carrying capacity—is it really too low for highly abundant salmon stocks? myths and reality. *North Pacific Anadromous Fish Commission Technical Report* 6:3-7.
- Stenseth, N. C., A. Mysterud, G. Ottersen, J. W. Hurrell, K. S. Chan, and M. Lima. 2002. Ecological effects of climate fluctuations. *Science* 297:1292.
- Tedesco, P. A., B. Hugueny, D. Paugy, and Y. Fermon. 2004. Spatial synchrony in population dynamics of West African fishes: a demonstration of an intraspecific and interspecific Moran effect. *Journal of Animal Ecology* 73:693-705.
- Urawa, S. 2003. Stock identification studies of high seas salmon in Japan: a review and future plan. *North Pacific Anadromous Fish Commission Technical Report* 5:9-10.
- Urawa, S., T. Azumaya, P. A. Crane, and L. W. Seeb. 2004. Origins and distribution of chum salmon in the Central Bering Sea. *North Pacific Anadromous Fish Commission Technical Report* 6:67-70.
- Urawa, S., M. Kawana, G. Anma, Y. Kamei, T. Shoji, M. Fukuwaka, K. Munk, K. W. Myers, and E. V. Farley. 1999. Stock origin of chum salmon caught in offshore waters of the Gulf of Alaska during the summer of 1998. *North Pacific Anadromous Fish Commission Document* 420:1-16.

- Urawa, S., M. Kawana, G. Anma, Y. Kamei, T. Shoji, M. Fukuwaka, K. M. Munk, K. W. Myers, and J. Farley, E V. 2000. Geographic origin of high-seas chum salmon determined by genetic and thermal otolith markers. North Pacific Anadromous Fish Commission Bulletin 2:283-290.
- Urawa, S., S. Sato, P. A. Crane, B. Agler, R. Josephson, and T. Azumaya. 2009. Stock-specific ocean distribution and migration of chum salmon in the Bering Sea and North Pacific Ocean. North Pacific Anadromous Fish Commission Bulletin 5:131-146.
- Urawa, S., S. Sato, N. Varnavskaya, P. A. Crane, and T. D. Beacham. 2007. Genetic stock identification of juvenile chum salmon caught in the Okhotsk Sea during the fall of 2003. North Pacific Anadromous Fish Commission Technical Report 7:72-74.
- Urawa, S., J. Seki, M. Kawana, P. A. Crane, L. W. Seeb, K. Gorbatenko, and M. Fukuwaka. 2003. Juvenile chum salmon in the Okhotsk Sea: their origins estimated by genetic and otolith marks. North Pacific Anadromous Fish Commission Technical Report 5:87-88.
- Urawa, S., Y. Ueno, Y. Ishida, L. W. Seeb, P. A. Crane, S. Abe, and N. D. Davis. 2001. A migration model of Japanese chum salmon during early ocean life. North Pacific Anadromous Fish Commission Technical Report 2:1-2.
- Walker, R., K. Myers, and S. Ito. 1998. Growth studies from 1956-95 collections of pink and chum salmon scales in the central North Pacific Ocean. North Pacific Anadromous Fish Commission Bulletin 1:54-65.
- Yamada, J. 1971. A fine structural aspect of the development of scales in the chum salmon fry. Bulletin of the Japanese Society of Scientific Fisheries 37(1):18-29.
- Zavolokin, A. V. 2009. Forage base of Pacific salmon in the Western Bering Sea and adjacent Pacific waters in 2002-2006. North Pacific Anadromous Fish Commission Bulletin 5:165-172.
- Zavolokin, A. V., E. A. Zavolokina, and Y. N. Khokhlov. 2009. Changes in size and growth of Anadyr chum salmon (*Oncorhynchus keta*) from 1962-2007. North Pacific Anadromous Fish Commission Bulletin 5:157-163.
- Zavolokina, E. A. 2007. Spatial distribution and age composition of chum salmon in the Western Bering Sea in 2002 and 2003. North Pacific Anadromous Fish Commission Bulletin 4:189-192.

## **Tables and Figures**

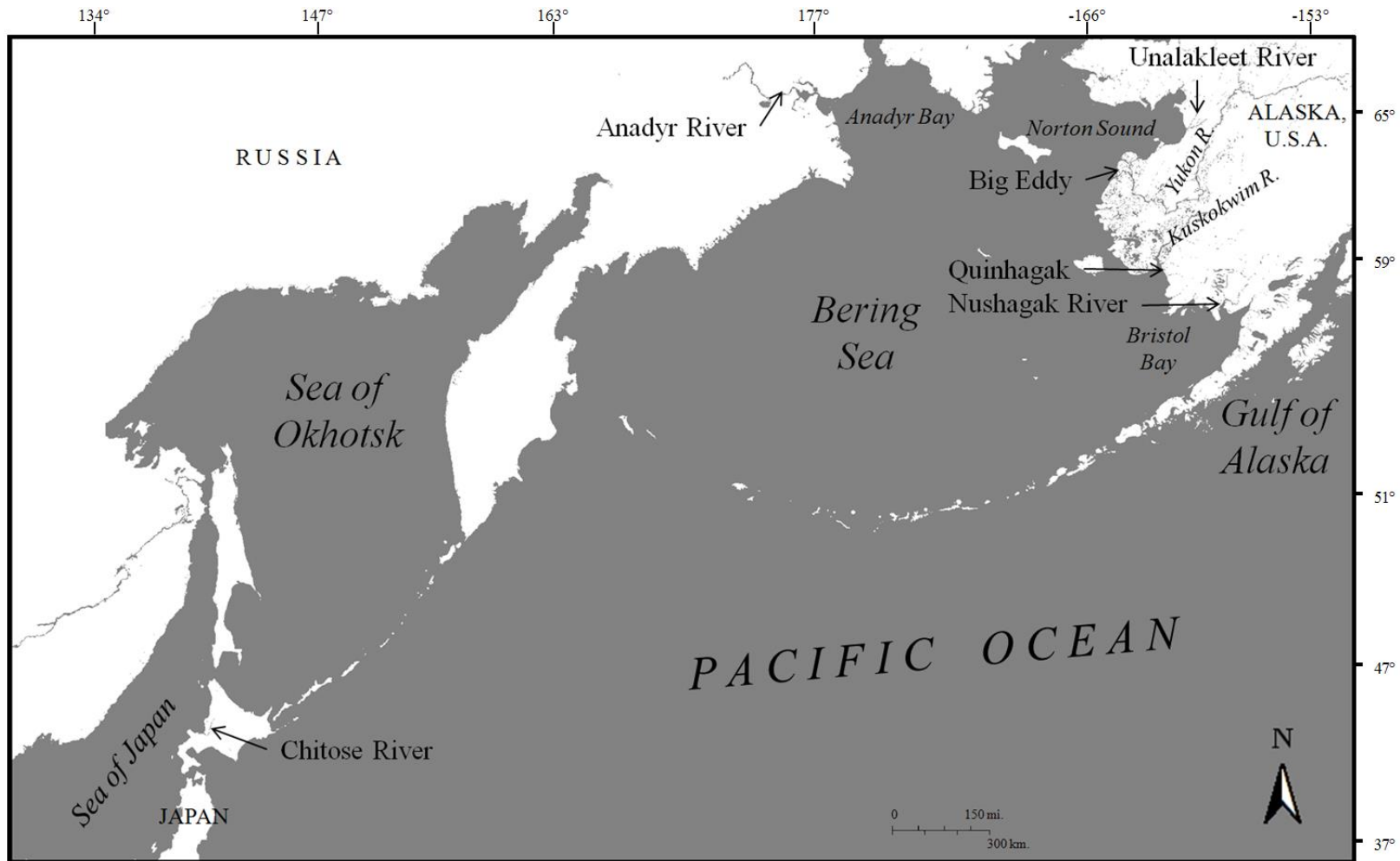


Figure 1.1. Map of the study area. The six chum salmon river systems included in this study were: four western Alaska populations (Unalakleet and Nushagak rivers, Quinhagak, and Big Eddy on the Yukon River) and two Asian populations (Anadyr River, Russia and Chitose River, Japan).

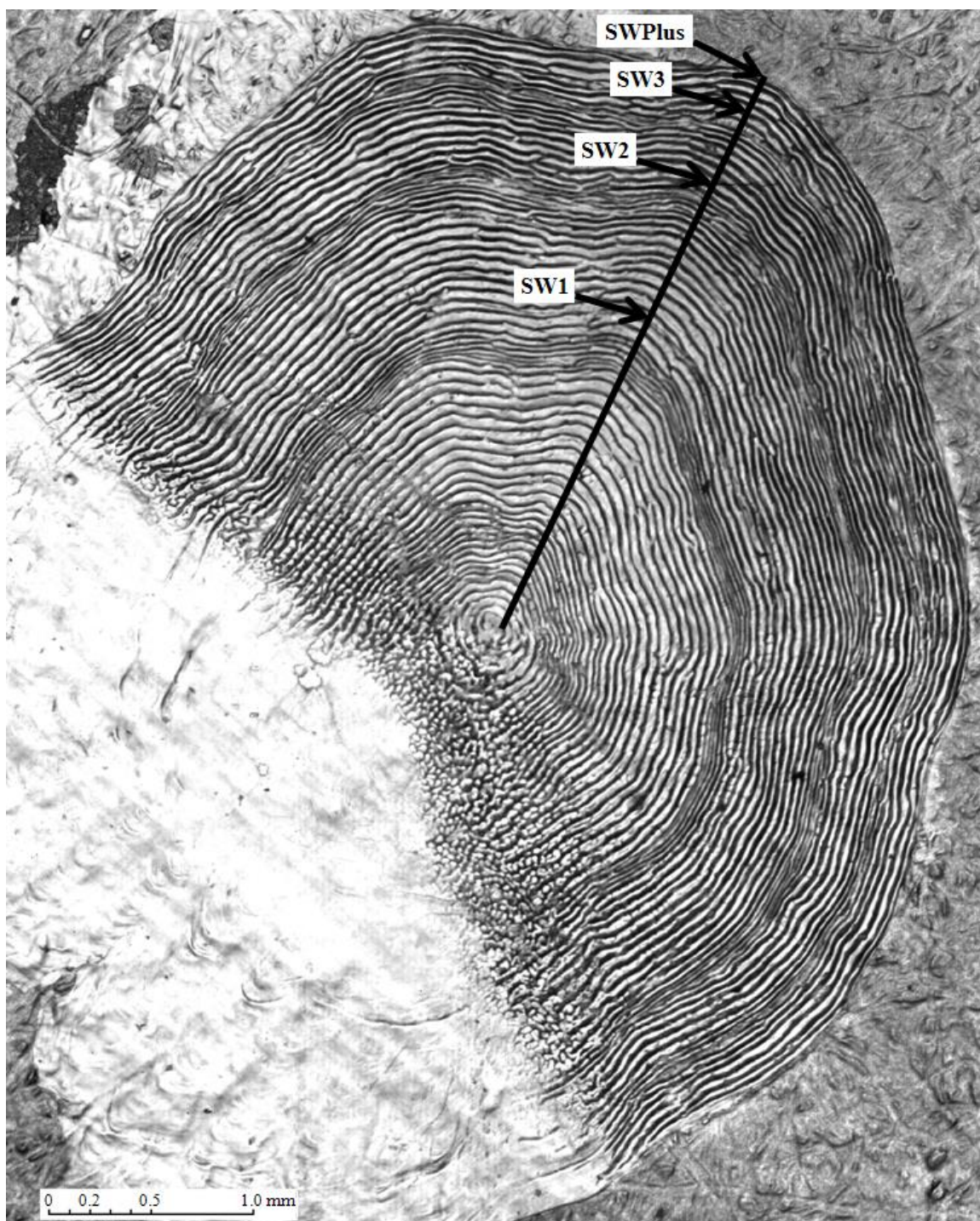


Figure 1.2. Example of a chum salmon scale. This is an age 0.4 chum salmon scale with the annuli marked by seasonal growth zones SW1, SW2, etc. SW is an abbreviation for saltwater, indicating the fish is in marine waters. The numbers 1, 2, etc. indicate the number of years at sea.

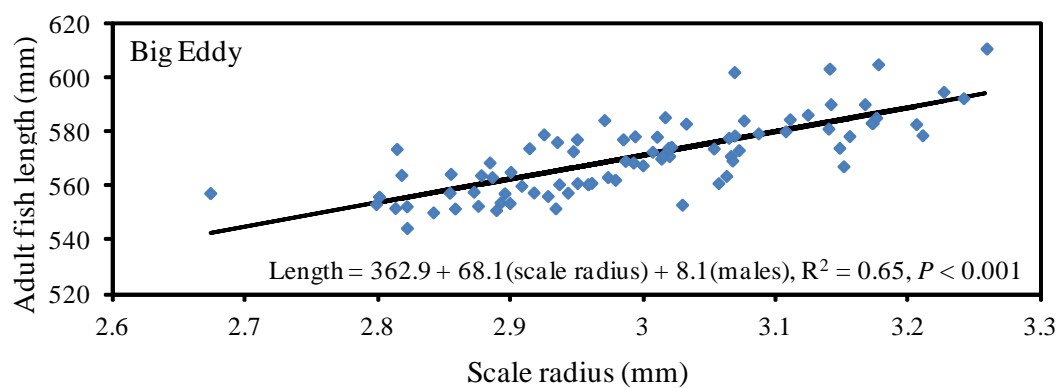


Figure 1.3. Yukon River, Alaska (Big Eddy) age 0.3 chum salmon linear regression comparing mean adult fish length (mm, mid-eye to fork of tail) to mean scale radius (mm).

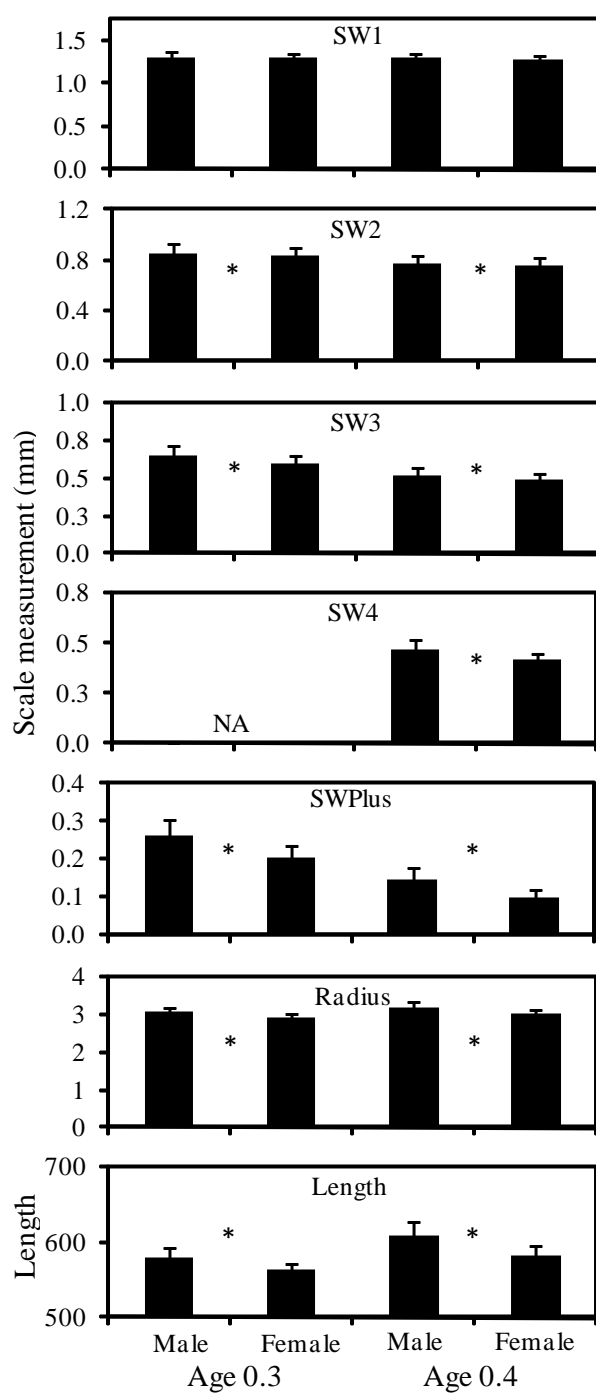


Figure 1.4. Scale radius measurements by zone, total scale radius and adult length ( $\pm 1$  SD) of age 0.3 western Alaska chum salmon from Big Eddy, Yukon River, Alaska by gender for return years 1965-2006 (Asterisk \* indicates  $P < 0.05$ ).

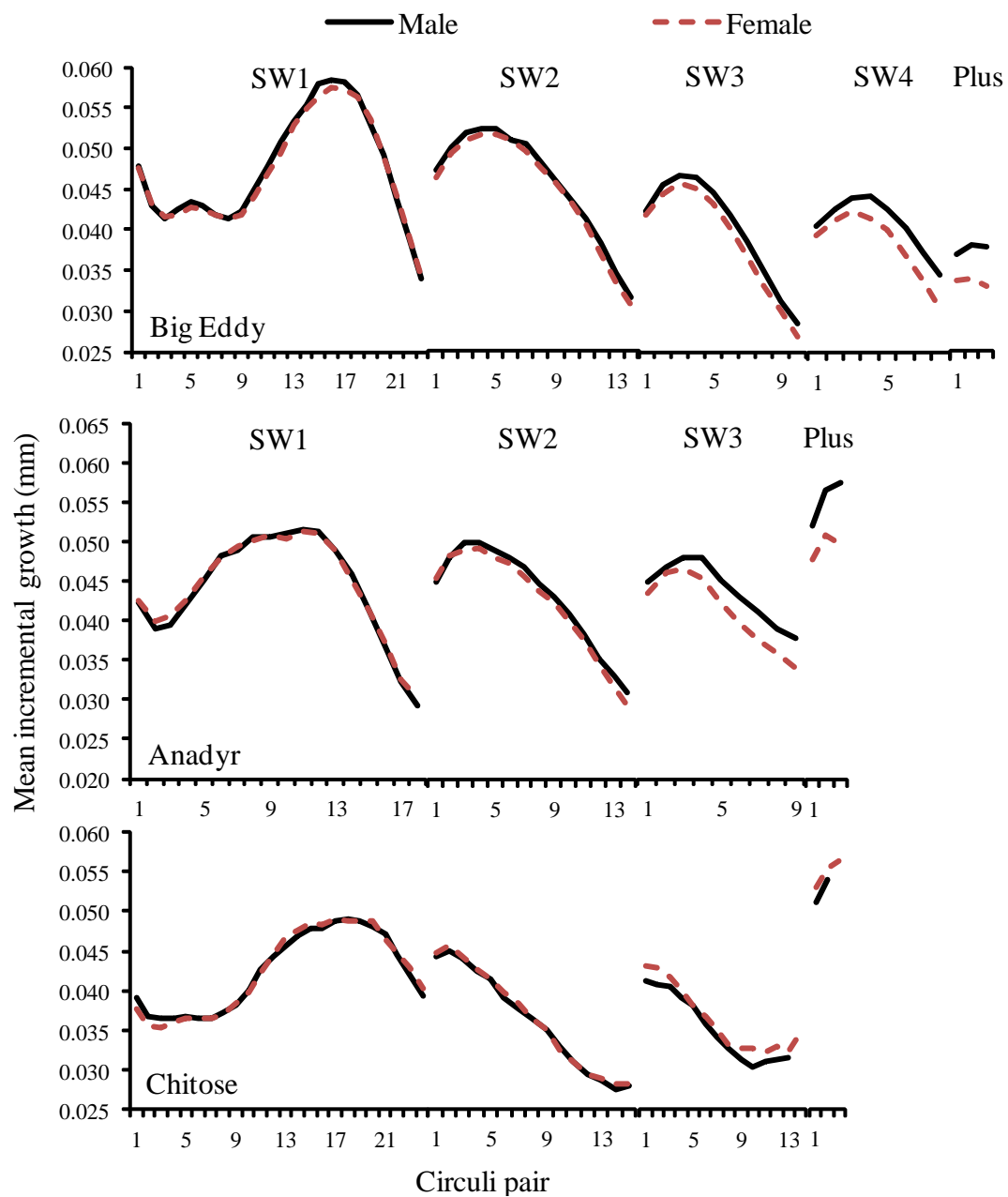


Figure 1.5. Mean seasonal scale growth (mm) of male and female age 0.4 western Alaska chum salmon from Big Eddy and age 0.3 Asian chum salmon from Anadyr River, Russia and Chitose River, Japan. Values are mean incremental scale growth.



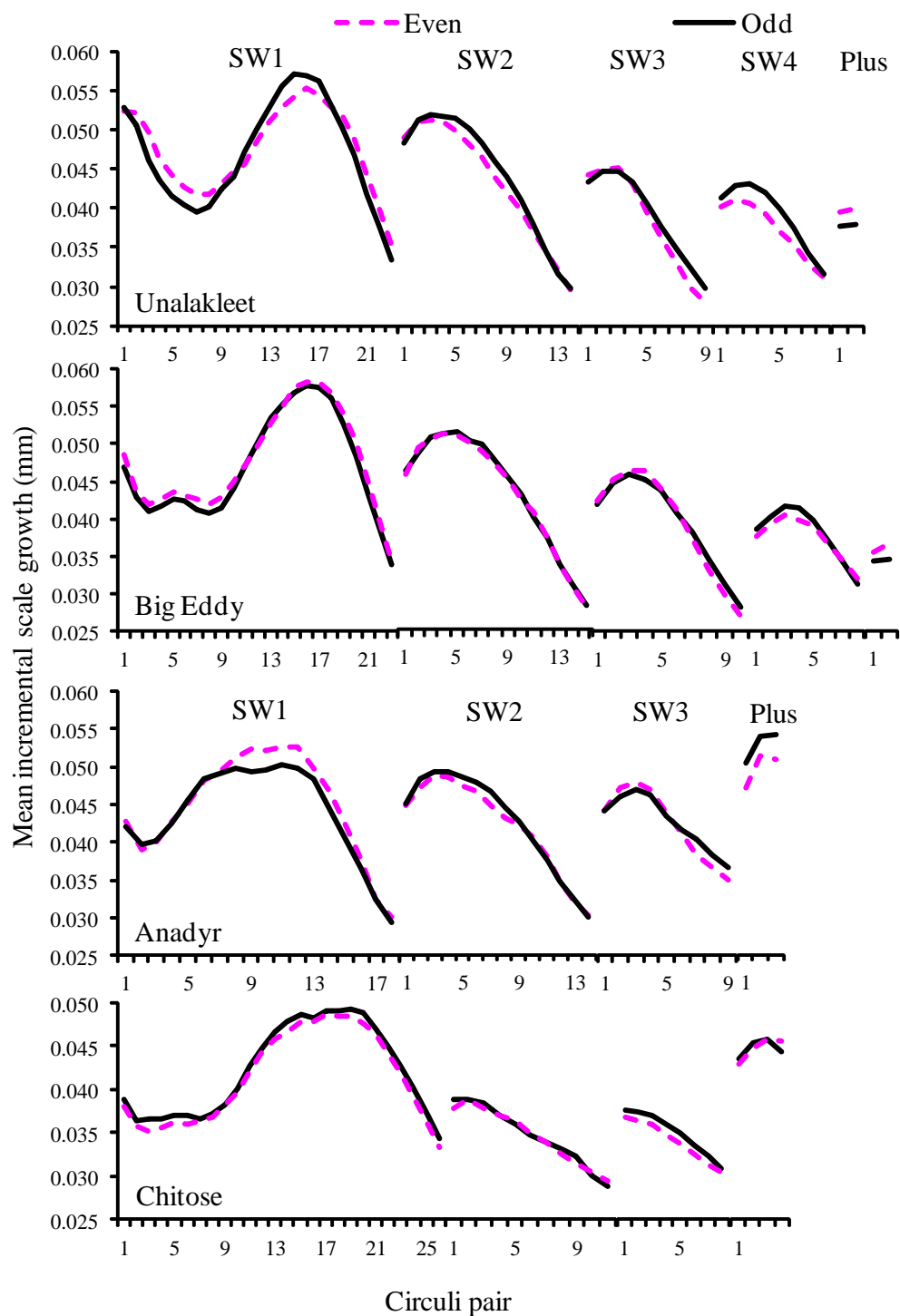


Figure 1.6. Mean seasonal scale growth (mm) of age 0.4 western Alaska chum salmon from Unalakleet River and Big Eddy and age 0.3 Asian chum salmon from Anadyr River, Russia and Chitose River, Japan in odd and even years. Values are mean incremental scale growth.

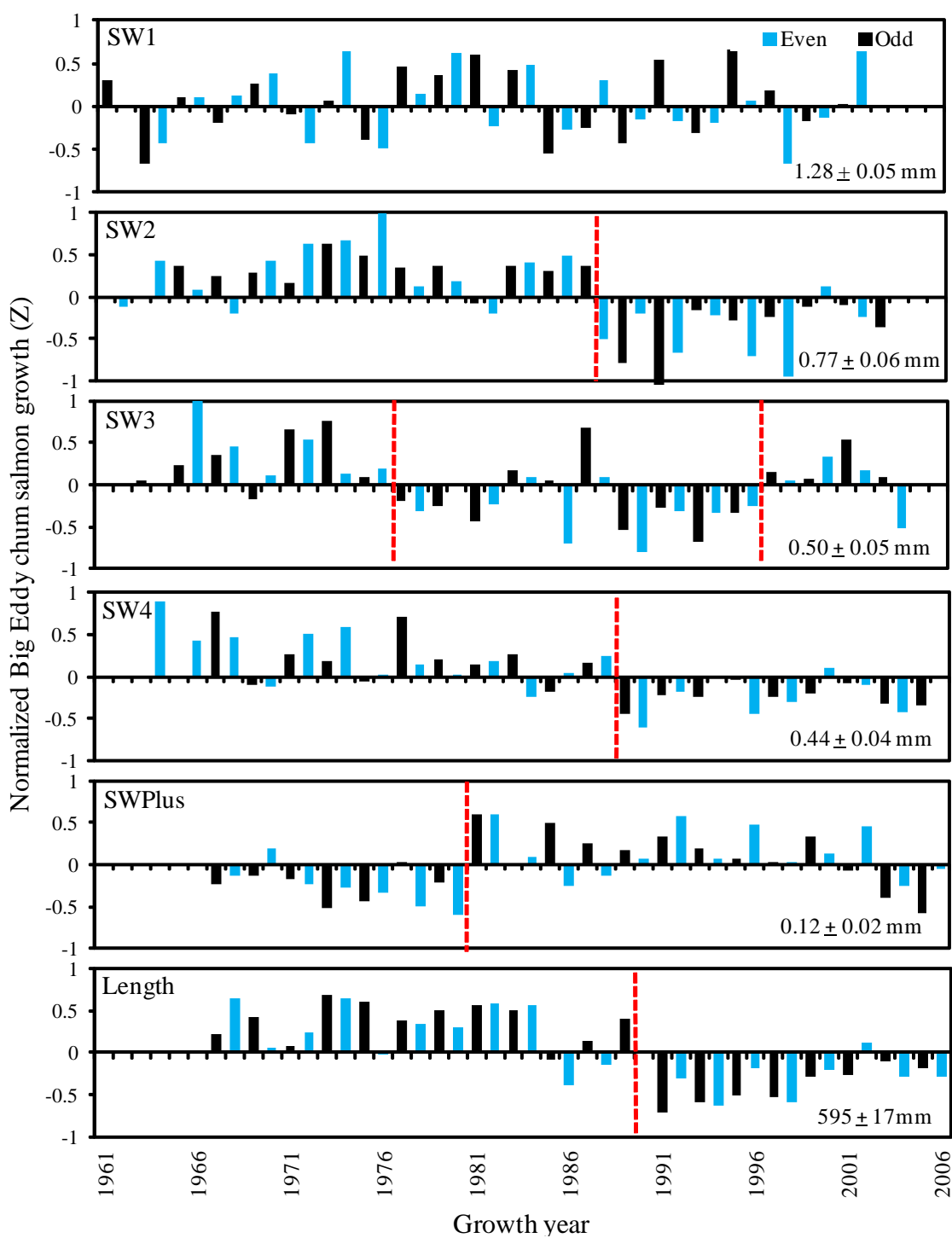


Figure 1.7. Mean annual growth of age 0.4 Big Eddy, Alaska chum salmon by life stage, growth years 1961-2006. Un-weighted mean  $\pm$  1 SD by life stage is shown. Red dashed lines highlight important climate shifts.

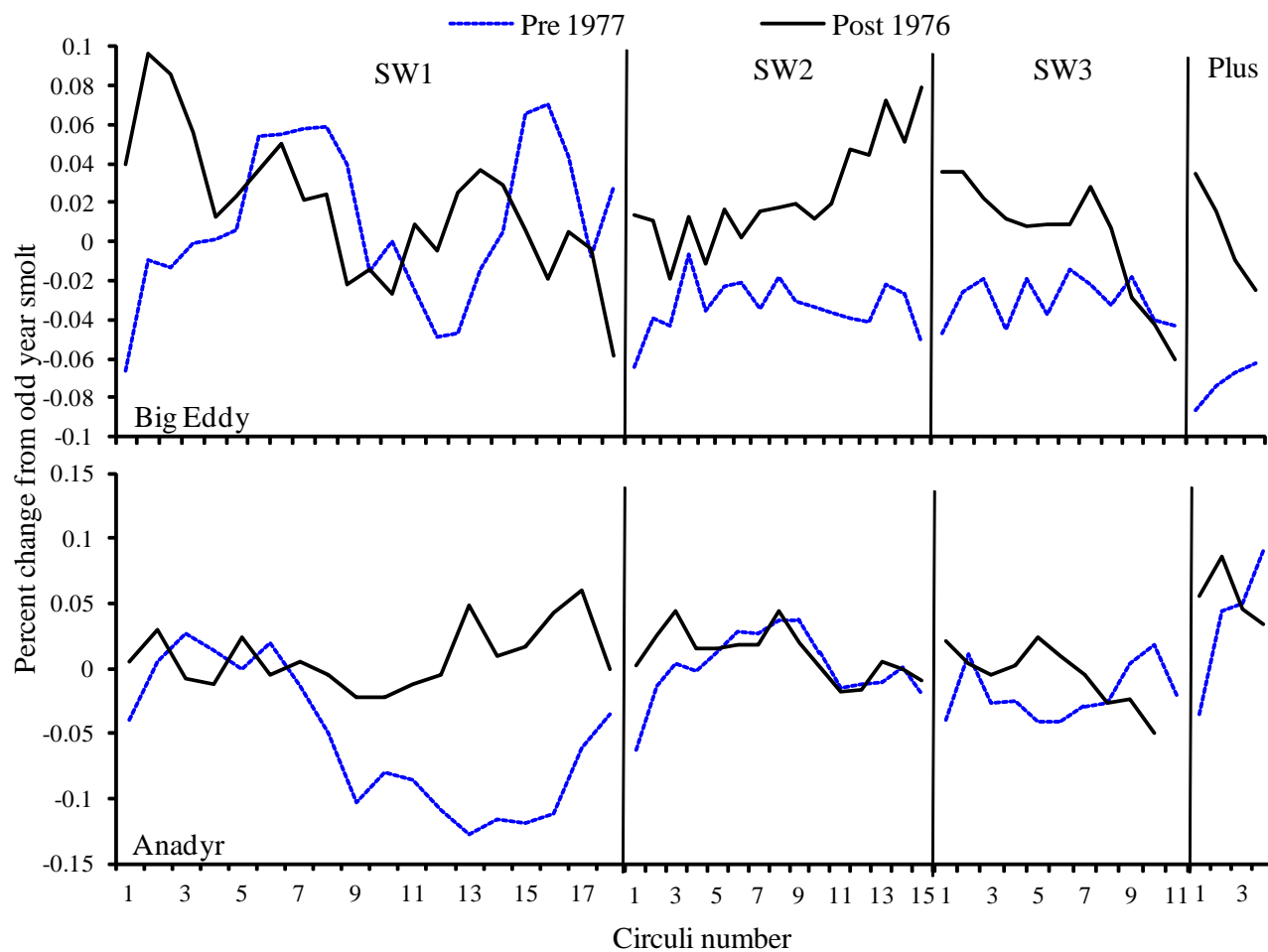


Figure 1.8. Percent change in scale growth for age 0.3 Big Eddy, Alaska and Anadyr River, Russia chum salmon entering the ocean during odd- and those entering during even years. Figures are grouped by pre-1977 and post-1976 years to reflect the regime shift in the North Pacific Ocean.

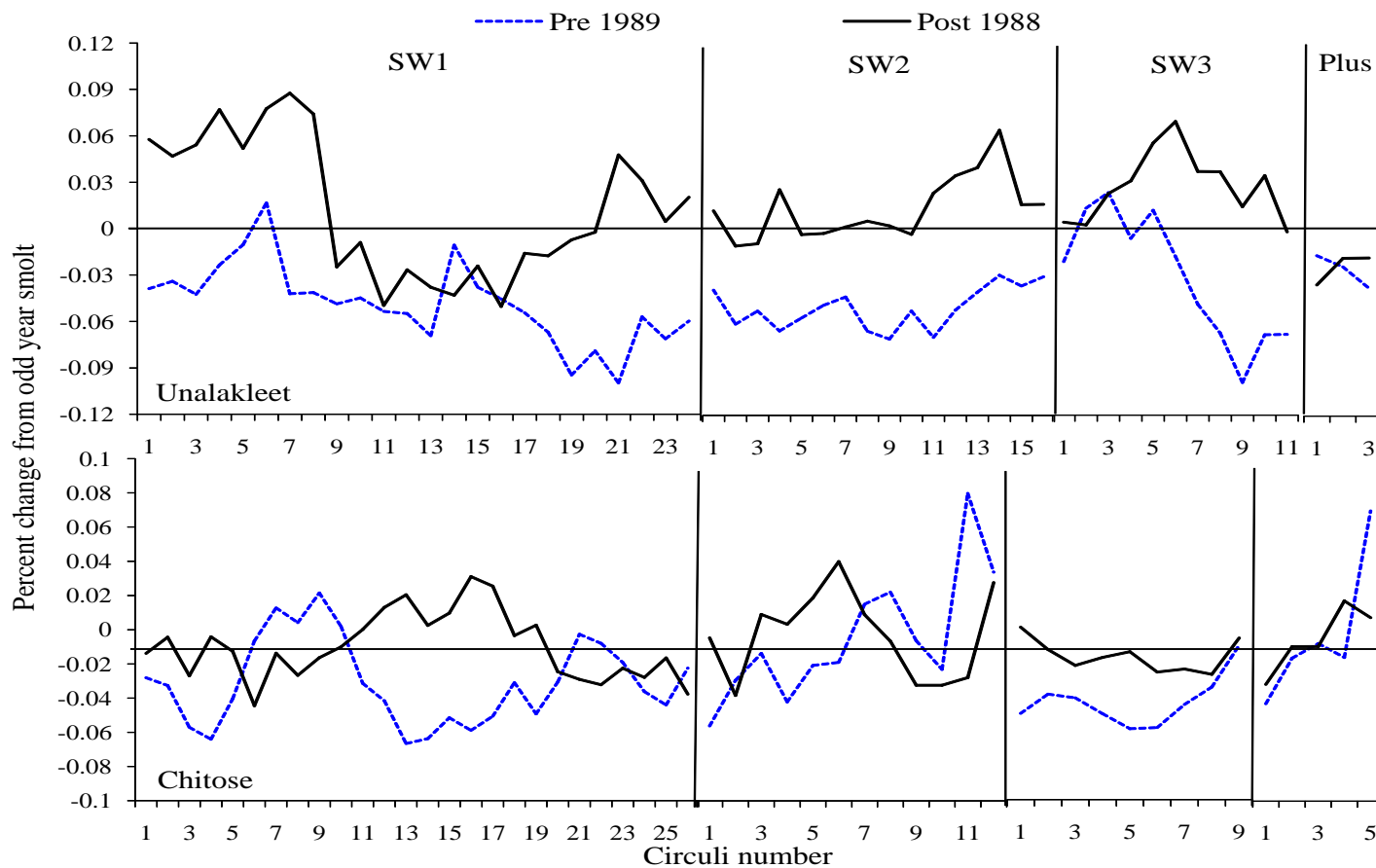


Figure 1.9. Percent change in scale growth between age 0.3 Unalakleet River, Alaska and Chitose River, Japan chum salmon entering the ocean during odd- and those entering during even years. Figures are grouped into pre-1989 and post-1988 years to reflect the secondary regime shift in 1989 in the North Pacific Ocean (Hare and Mantua 2000).

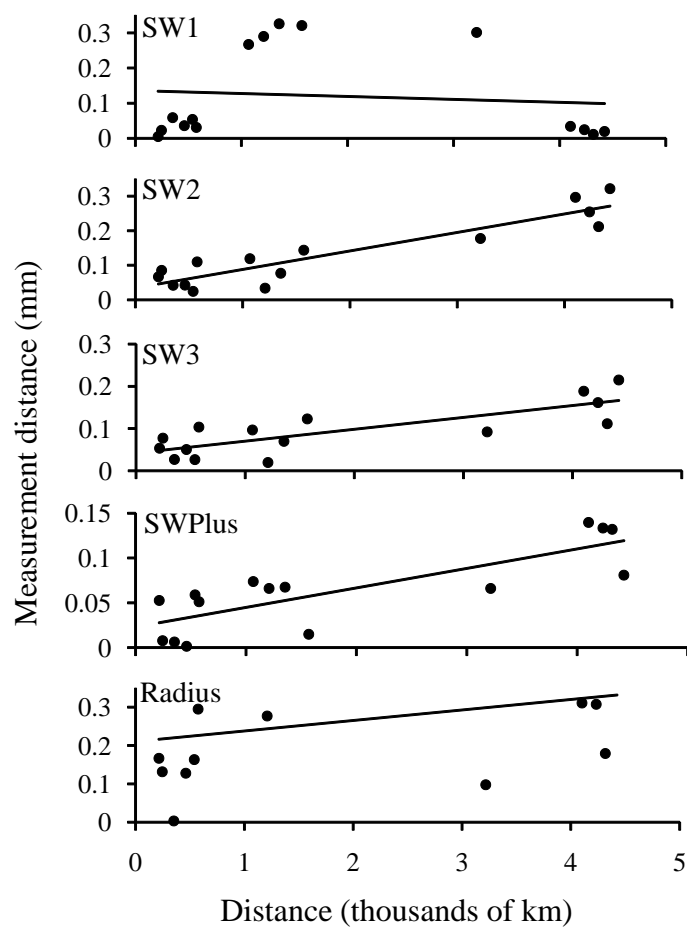


Figure 1.10. Scale measurement distance (mm) and geographic distances (km) for age 0.3 western Alaska and Asian chum salmon by zone and total scale radius.

Table 1.1. Populations sampled for chum salmon scales. General location, latitude and longitude of sampling locations, sampling period, age, sample size, and years missing from sample period are listed.

Populations	Location	Lat. (°N)	Long. (°E)	Age	Sampling period	Sample size	Years missing
Unalakleet	Norton Sound	63.869	-160.788	0.3	1977-2008	1,630	1979
				0.4	1975-2008	1,779	1979
Big Eddy	Yukon River	62.599	-164.800	0.3	1965-2006	2,060	1966
				0.4	1967-2006	2,221	
Quinhagak	Kuskokwim River	59.749	-161.931	0.3	1967-2007	1,910	1971-73
				0.4	1968-2007	1,732	1971-73
Nushagak	Bristol Bay	58.799	-158.630	0.3	1960-2006	2,417	1962, 1964, 1960 <sup>a</sup>
				0.4	1966-2006	2,172	-
Anadyr	Russia	64.849	174.023	0.3	1962-2007	1,112	1963, 1966, 1967, 1969, 1970, 1976, 1977, 2005
Chitose	Japan	42.852	141.659	0.3	1976-2008	1,554	1985, 1980 <sup>a</sup>

<sup>a</sup> Females only

Table 1.2. Pearson's correlation coefficients (lower left triangle) and significance ( $P$ , upper right triangle) between scale zones for age 0.3 chum salmon from western Alaska and Asia. Asterisk (\*) indicates  $P < 0.05$ .

Population	Zone	SW1	SW2	SW3	SWPlus	Radius	Length
Unalakleet	SW1		0.001*	0.275	0.434	< 0.001*	0.016*
	SW2	0.569		0.009*	0.222	< 0.001*	0.805
	SW3	0.196	0.449		0.889	0.001*	0.062
	Plus	0.141	-0.219	-0.025		0.155	0.257
	Radius	0.878	0.752	0.554	0.253		0.646
	Length	-0.416	0.045	0.328	0.203	-0.083	
Big Eddy	SW1		0.573	0.018*	0.614	0.133	0.103
	SW2	-0.091		0.006*	0.015*	< 0.001*	0.001*
	SW3	-0.367	0.424		0.050*	< 0.001*	0.009*
	Plus	-0.081	-0.377	-0.309		0.417	0.489
	Radius	0.239	0.784	0.587	-0.130		< 0.001*
	Length	0.258	0.494	0.405	-0.111	0.700	
Quinhagak	SW1		0.352	0.185	0.027*	< 0.001*	0.181
	SW2	-0.155		0.004*	0.120	0.001*	< 0.001*
	SW3	-0.220	0.455		0.568	0.002*	0.001*
	Plus	0.358	-0.256	-0.096		0.057	0.651
	Radius	0.634	0.518	0.488	0.312		0.033*
	Length	-0.222	0.545	0.510	0.076	0.347	
Nushagak	SW1		< 0.001*	0.002*	0.860	0.943	0.665
	SW2	-0.676		0.088	0.574	0.010*	0.172
	SW3	-0.447	0.258		0.891	< 0.001*	0.001*
	Plus	0.027	-0.086	0.021		< 0.001*	0.495
	Radius	0.011	0.378	0.537	0.529		< 0.001*
	Length	-0.066	0.207	0.483	0.104	0.513	
Anadyr	SW1		0.010*	0.545	0.385	< 0.001*	0.059
	SW2	0.411		< 0.001*	0.764	< 0.001*	0.049*
	SW3	0.101	0.700		0.084	< 0.001*	< 0.001*
	Plus	-0.145	0.050	0.284		0.057	0.009*
	Radius	0.693	0.815	0.725	0.312		0.060
	Length	-0.309	0.322	0.721	0.416	0.307	
Chitose	SW1		0.794	0.691	0.837	0.002*	0.775
	SW2	0.048		0.006*	0.772	< 0.001*	0.598
	SW3	-0.073	0.476		0.192	< 0.001*	< 0.001*
	Plus	-0.038	0.053	0.237		0.017*	0.144
	Radius	0.527	0.657	0.685	0.421		0.015*
	Length	0.053	0.097	0.599	0.264	0.428	

Table 1.3. Pearson's correlation coefficients (lower left triangle) and significance ( $P$ , upper right triangle) between scale zones for age 0.4 chum salmon from western Alaska (Unalakleet and Nushagak rivers, Quinhagak, and Big Eddy). Asterisk (\*) indicates  $P < 0.05$ .

Zone	SW1	SW2	SW3	SW4	SWPlus	Radius	Length
<b>Unalakleet</b>							
SW1		< 0.001*	0.065	0.136	0.108	0.710	0.268
SW2	-0.593		0.076	0.242	0.368	0.032*	0.059
SW3	-0.315	0.304		0.001*	0.176	< 0.001*	< 0.001*
SW4	-0.257	0.203	0.517		0.251	< 0.001*	< 0.001*
Plus	-0.276	-0.157	-0.234	-0.199		0.467	0.220
Radius	0.065	0.362	0.697	0.611	-0.127		< 0.001*
Length	-0.193	0.323	0.632	0.674	-0.212	0.669	
<b>Big Eddy</b>							
SW1		0.160	0.066	0.646	0.196	0.009*	0.458
SW2	-0.224		0.009*	0.003*	0.040*	< 0.001*	0.002*
SW3	-0.290	0.403		0.003*	0.032*	< 0.001*	0.008*
SW4	0.074	0.452	0.459		0.009*	< 0.001*	< 0.001*
Plus	0.206	-0.322	-0.336	-0.404		0.323	0.066
Radius	0.403	0.689	0.608	0.750	-0.158		< 0.001*
Length	0.119	0.476	0.408	0.826	-0.290	0.723	
<b>Quinhagak</b>							
SW1		0.011*	0.144	0.415	0.571	0.710	0.759
SW2	-0.412		0.002*	< 0.001*	0.512	< 0.001*	< 0.001*
SW3	-0.245	0.484		< 0.001*	0.011*	< 0.001*	0.004*
SW4	-0.138	0.596	0.676		0.695	< 0.001*	< 0.001*
Plus	-0.096	0.111	-0.412	-0.067		0.377	0.273
Radius	0.063	0.781	0.626	0.791	0.150		< 0.001*
Length	-0.052	0.642	0.459	0.700	0.185	0.784	
<b>Nushagak</b>							
SW1		< 0.001*	< 0.001*	0.029*	0.160	0.866	0.668
SW2	-0.651		0.021*	0.805	0.572	0.002*	0.527
SW3	-0.568	0.354		0.197	0.043*	0.030*	0.475
SW4	-0.337	0.039	0.203		0.576	0.076	0.383
Plus	0.221	-0.090	-0.313	0.089		0.003*	0.218
Radius	0.027	0.455	0.335	0.276	0.451		0.126
Length	-0.068	0.100	0.113	0.194	0.240	0.138	



Table 1.4. Pearson's correlation and significance between scale growth zones for age 0.3 and 0.4 chum salmon from western Alaska (Unalakleet and Nushagak rivers, Quinhagak, and Big Eddy). Asterisk (\*) indicates  $P < 0.05$ .

			<i>P</i>		<i>r</i>
Population		Age 03	SW1		
Unalakleet	Age 04	SW1	0.098		0.313
Big Eddy			< 0.001	*	0.618
Quinhagak			0.019	*	0.385
Nushagak			0.000	*	0.888
		Age 03	SW2		
Unalakleet	Age 04	SW2	0.045	*	0.374
Big Eddy			< 0.001	*	0.876
Quinhagak			0.019	*	0.722
Nushagak			< 0.001	*	0.789
		Age 03	SW3		
Unalakleet	Age 04	SW3	< 0.001	*	0.786
Big Eddy			< 0.001	*	0.894
Quinhagak			< 0.001	*	0.626
Nushagak			< 0.001	*	0.754
		Age 03	SWPlus		
Unalakleet	Age 04	SWPlus	0.459		0.143
Big Eddy			0.047	*	0.320
Quinhagak			0.001	*	0.519
Nushagak			0.142		0.231
		Age 03	Radius		
Unalakleet	Age 04	Radius	0.279		0.204
Big Eddy			< 0.001	*	0.597
Quinhagak			0.835		0.036
Nushagak			0.082		0.272
		Age 03	Length		
Unalakleet	Age 04	Length	0.001	*	0.589
Big Eddy			< 0.001	*	0.535
Quinhagak			< 0.001	*	0.556
Nushagak			0.452		-0.119

Table 1.5. Pearson's correlation coefficients (lower left triangle) and significance ( $P$ , right triangle) comparing populations of age 0.3 chum salmon by scale zone, total scale radius and fish length from four western Alaska populations (Unalakleet and Nushagak rivers, Quinhagak, and Big Eddy) and two Asian populations (Anadyr River, Russia and Chitose River, Japan). Asterisk (\*) indicates  $P < 0.05$ .

Zone	Population	Big Eddy	Nushagak	Quinhagak	Unalakleet	Anadyr	Chitose
SW1	Big Eddy		0.008*	0.001*	0.352	0.705	0.922
	Nushagak	0.408		< 0.001*	0.624	0.065	0.511
	Quinhagak	0.538	0.659		0.906	0.170	0.365
	Unalakleet	0.176	0.092	-0.022		0.080	0.829
	Anadyr	-0.066	0.315	0.249	-0.336		0.195
	Chitose	-0.019	0.125	0.168	0.041	0.319	
SW2	Big Eddy		< 0.001*	< 0.001*	0.003*	0.023*	0.003*
	Nushagak	0.868		< 0.001*	0.046*	0.091	0.009*
	Quinhagak	0.705	0.752		0.022*	0.489	0.025*
	Unalakleet	0.523	0.362	0.409		0.365	0.889
	Anadyr	0.384	0.290	0.127	0.178		0.142
	Chitose	0.525	0.471	0.403	-0.027	0.471	
SW3	Big Eddy		< 0.001*	< 0.001*	< 0.001*	< 0.001*	0.031*
	Nushagak	0.852		< 0.001*	0.009*	0.002*	0.088
	Quinhagak	0.629	0.651		< 0.001*	0.063	0.105
	Unalakleet	0.710	0.459	0.662		< 0.001*	0.007*
	Anadyr	0.652	0.509	0.333	0.711		0.535
	Chitose	0.395	0.317	0.297	0.485	0.003*	
SWPlus	Big Eddy		< 0.001*	< 0.001*	0.017*	0.105	0.216
	Nushagak	0.690		0.001*	0.090	0.096	0.284
	Quinhagak	0.624	0.528		< 0.001*	0.386	0.039*
	Unalakleet	0.433	0.310	0.603		0.601	0.420
	Anadyr	0.279	0.286	0.159	0.103		0.337
	Chitose	0.233	0.202	0.372	0.153	0.079	
Radius	Big Eddy		0.002*	0.849	0.823	0.501	0.054
	Nushagak	0.466		0.185	0.056	0.718	0.110
	Quinhagak	0.032	0.223		0.277	0.373	0.575
	Unalakleet	-0.043	-0.347	-0.201		0.862	0.805
	Anadyr	0.118	0.063	-0.163	0.035		-0.059
	Chitose	0.356	0.298	0.105	-0.047	0.764	
Length	Big Eddy		0.001*	0.069	0.111	0.012*	0.167
	Nushagak	0.512		0.128	0.017*	0.115	0.010*
	Quinhagak	0.302	0.255		0.093	0.007*	0.433
	Unalakleet	0.297	0.427	0.307		0.005*	0.007*
	Anadyr	0.421	0.271	0.470	0.516		0.495
	Chitose	0.259	0.463	0.146	0.481	0.007	

Table 1.6. Back-calculated lengths of chum salmon at each growth zone from four populations in western Alaska (Unalakleet and Nushagak rivers, Quinhagak, and Big Eddy) and two in Asia (Anadyr River, Russia and Chitose River, Japan). A dash (-) indicates no data, and SD = standard deviation of the mean.

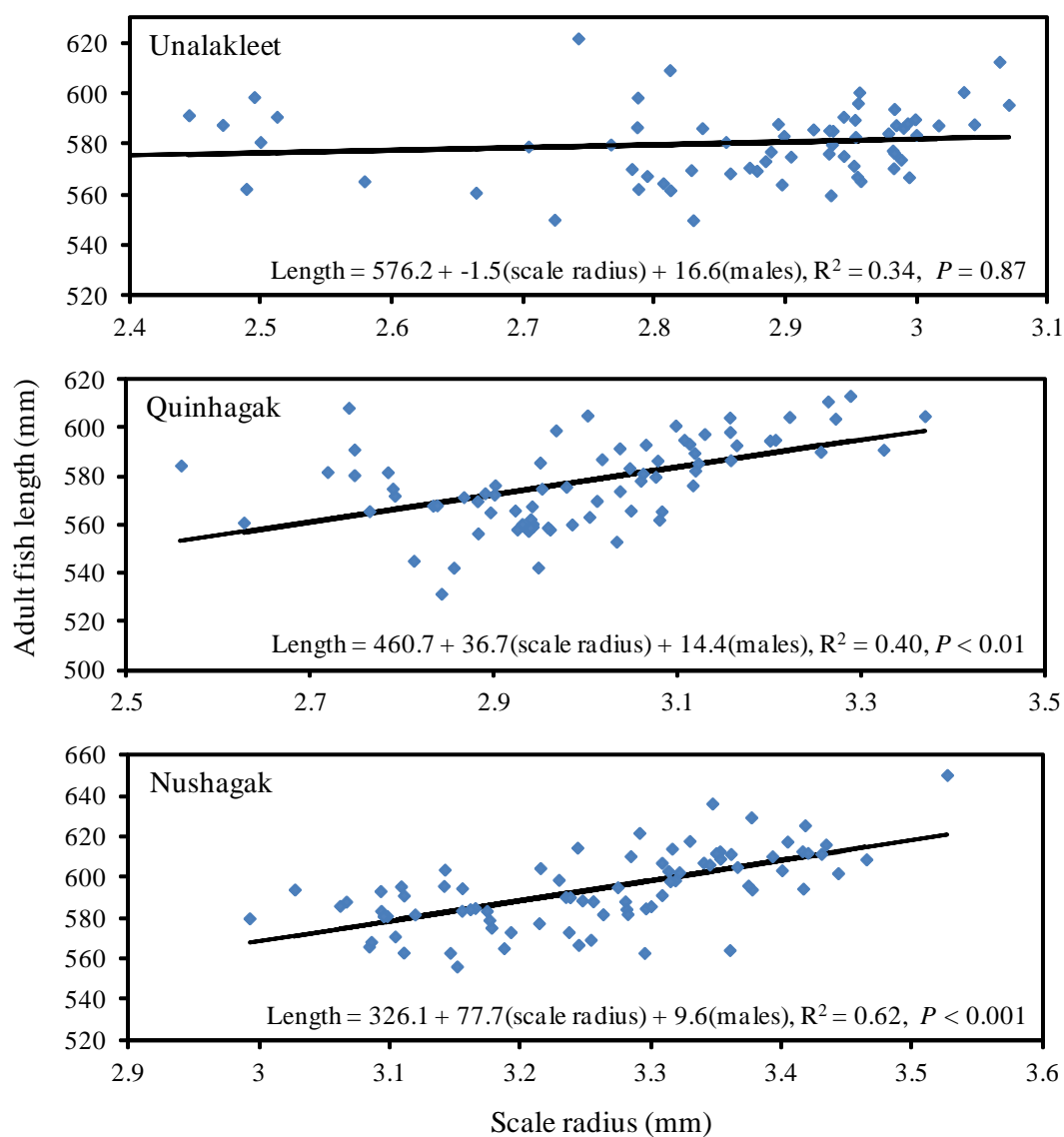
Population	Age	Length	SD	SW1	SD	SW2	SD	SW3	SD	SW4	SD	SWPlus	SD
Unalakleet	0.3	580.2	27.6	267.7	19.9	442.3	24.5	532.4	28.8	-	-	579.9	31.1
	0.4	602.3	32.7	253.1	23.3	396.7	24.1	487.7	28.5	570.6	34.7	587.8	97.0
Big Eddy	0.3	570.8	26.5	247.7	20.2	408.7	24.4	526.7	28.0	-	-	569.5	38.6
	0.4	592.0	33.0	245.0	20.6	391.3	23.9	485.8	27.5	569.1	33.3	573.1	109.1
Quinhagak	0.3	577.5	31.3	261.9	22.2	417.3	24.6	531.8	29.8	-	-	577.5	31.3
	0.4	579.6	35.4	249.6	23.2	392.1	24.5	484.0	29.3	564.8	34.9	580.3	106.0
Nushagak	0.3	577.4	33.2	248.5	23.4	406.7	27.1	525.4	32.5	-	-	576.4	40.6
	0.4	593.4	34.4	244.4	22.6	385.6	24.8	479.4	28.9	562.3	33.6	590.1	55.8
Anadyr <sup>a</sup>	0.3	592.1	39.8	230.3	23.1	398.0	26.8	521.0	38.7	-	-	602.1	42.5
Chitose <sup>a</sup>	0.3	606.9	41.0	301.7	26.1	425.9	30.0	523.4	38.0	-	-	615.1	42.9

<sup>a</sup> Length corrected from snout to fork of tail to mid-eye to fork of tail (Pahlke 1989).

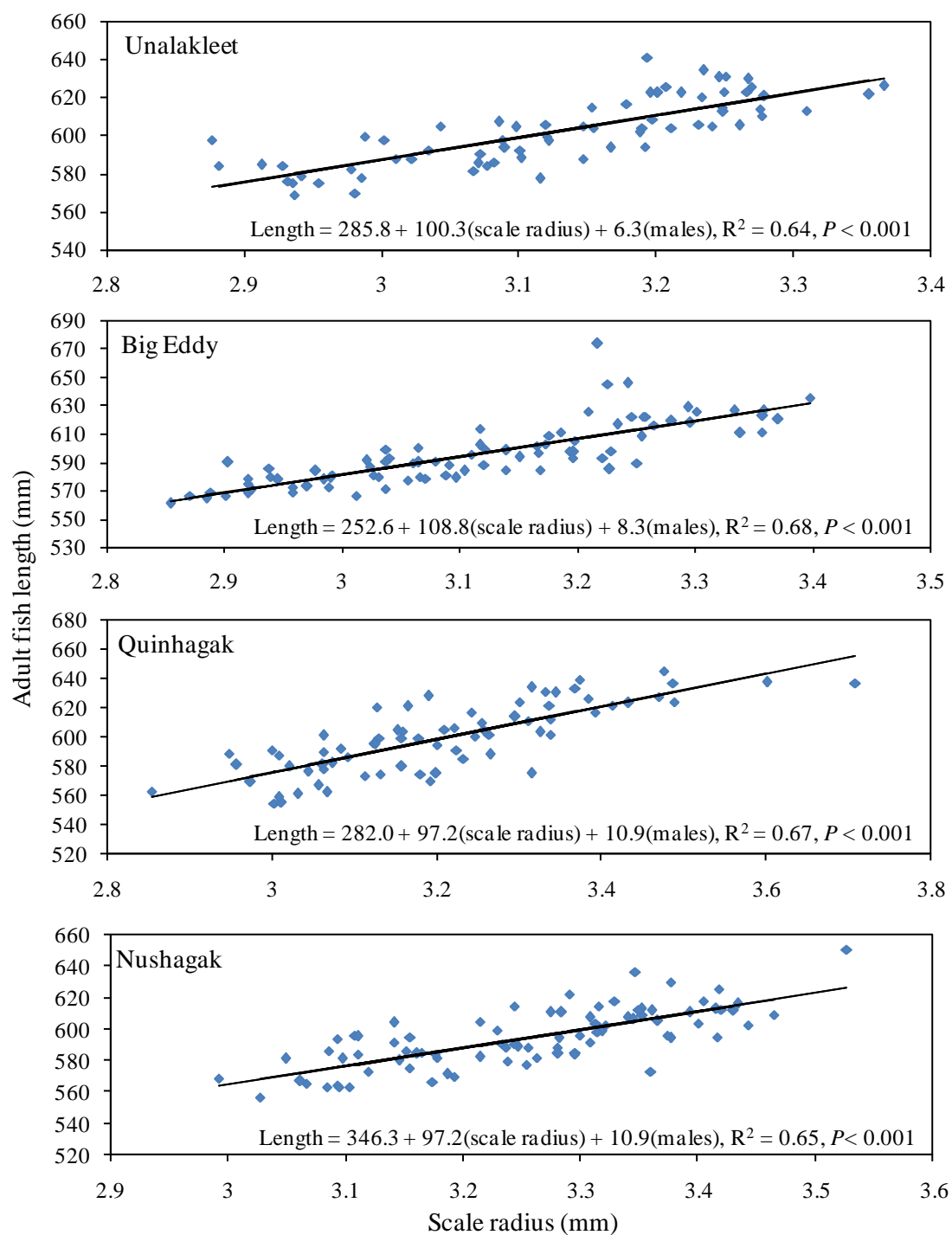
Table 1.7. Mantel tests comparing total scale measurement (mm) and geographic (km) distances for age 0.3 and 0.4 chum salmon in western Alaska and Asia. Shown by scale growth zone. Asterisk (\*) indicates  $P < 0.05$ , and a dash (-) indicates no data.

Populations	Age	Statistic	SW1	SW2	SW3	SW4	SWPlus	Radius
Alaskan	0.3	Correlation	0.549	-0.064	0.109	-	0.311	0.462
	0.3	$P$	0.250	0.455	0.334	-	0.165	0.124
	0.4	Correlation	0.104	0.555	0.579	0.388	0.120	0.887
	0.4	$P$	0.419	0.086	0.075	0.129	0.414	0.121
All	0.3	Correlation	-0.105	0.921	0.801	-	0.807	0.293
	0.3	$P$	0.289	0.011*	0.011*	-	0.032*	0.304

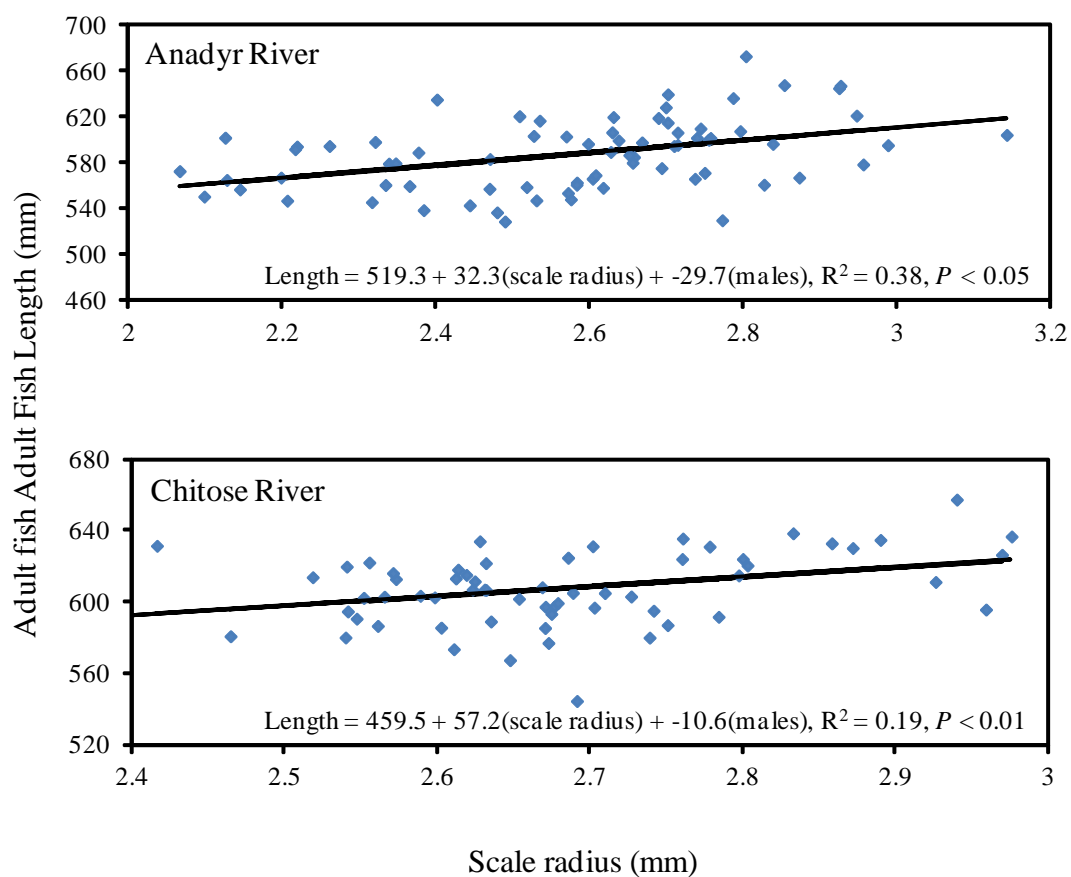
## **Appendix 1A**



Appendix 1A-1. Mean adult fish length (mm, mid-eye to fork of tail) to mean scale radius (mm) relationship for age 0.3 western Alaska (Unalakleet River, Quinhagak, and Nushagak River) chum salmon.

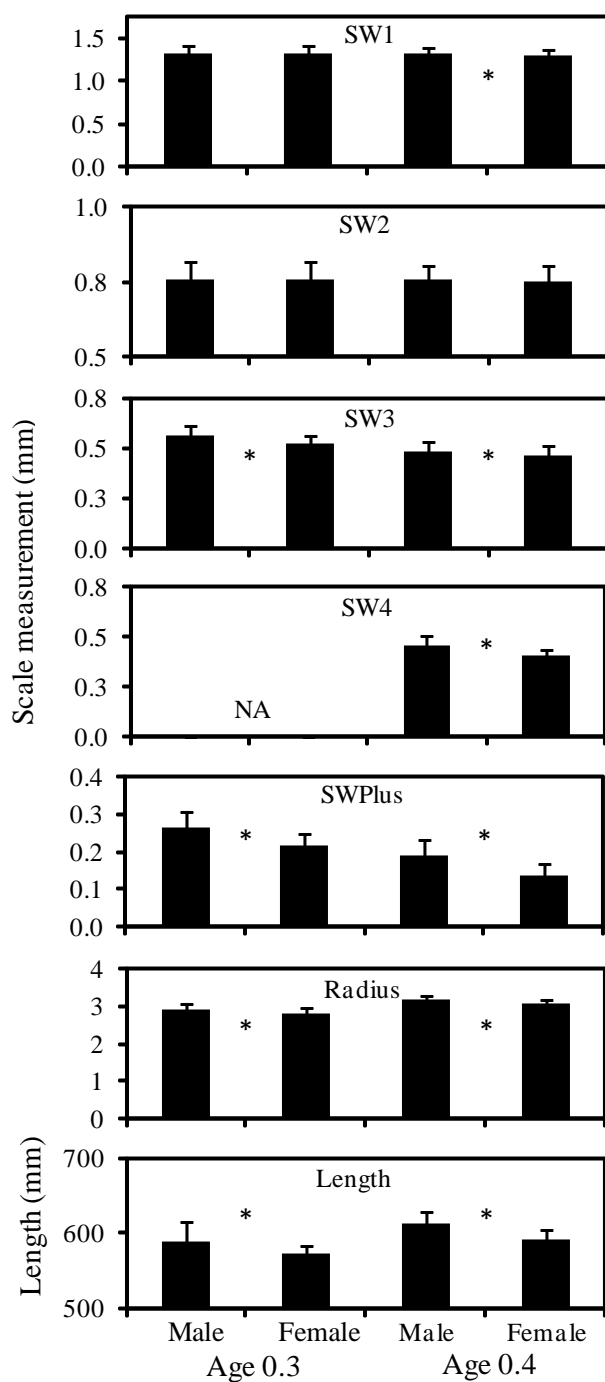


Appendix 1A-2. Mean adult fish length (mm, mid-eye to fork of tail) to mean scale radius (mm) relationship for age 0.4 western Alaska (Unalakleet River, Quinhagak, and Nushagak River) chum salmon.

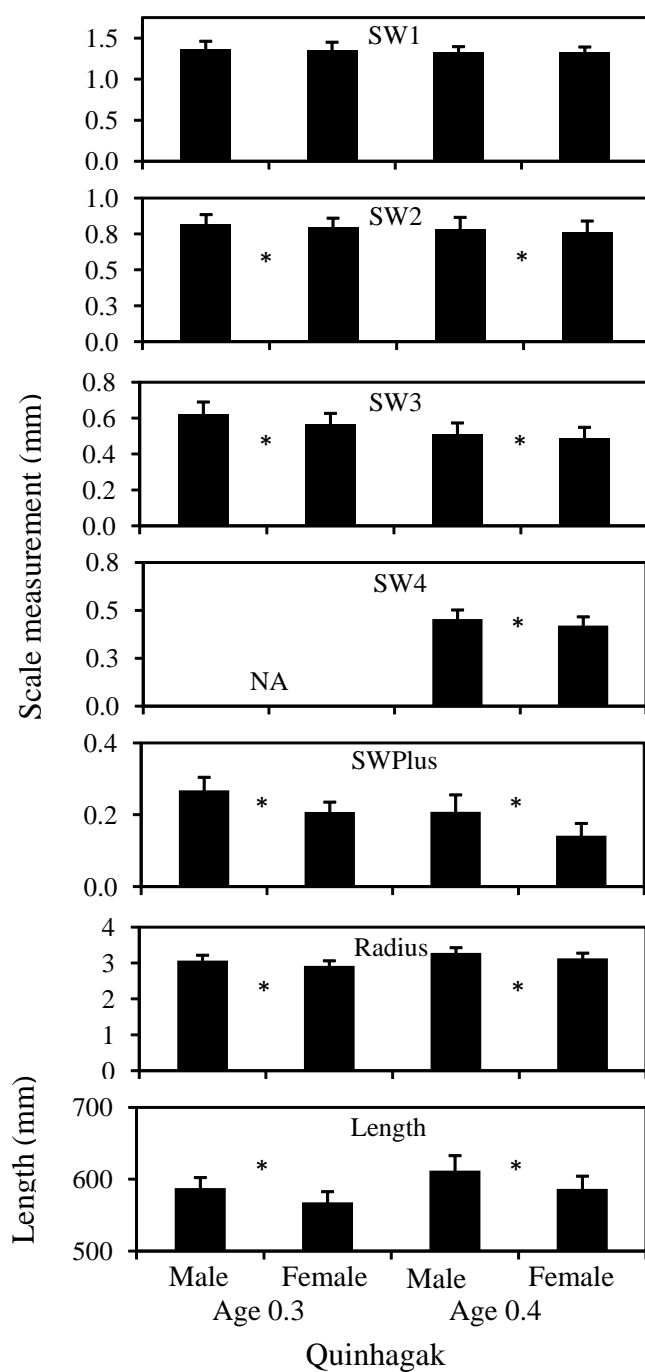


Appendix 1A-3. Mean adult fish length (mm, mid-eye to fork of tail) to mean scale radius (mm) relationship for age 0.3 Asian chum salmon.

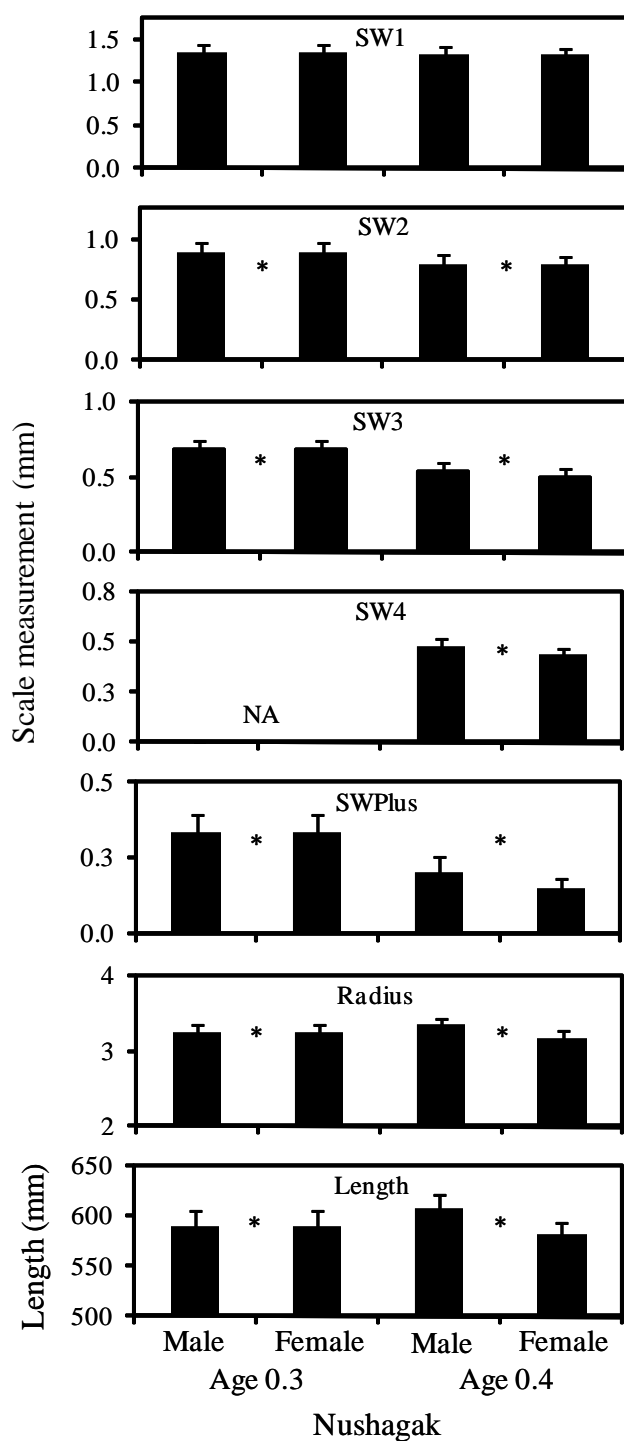




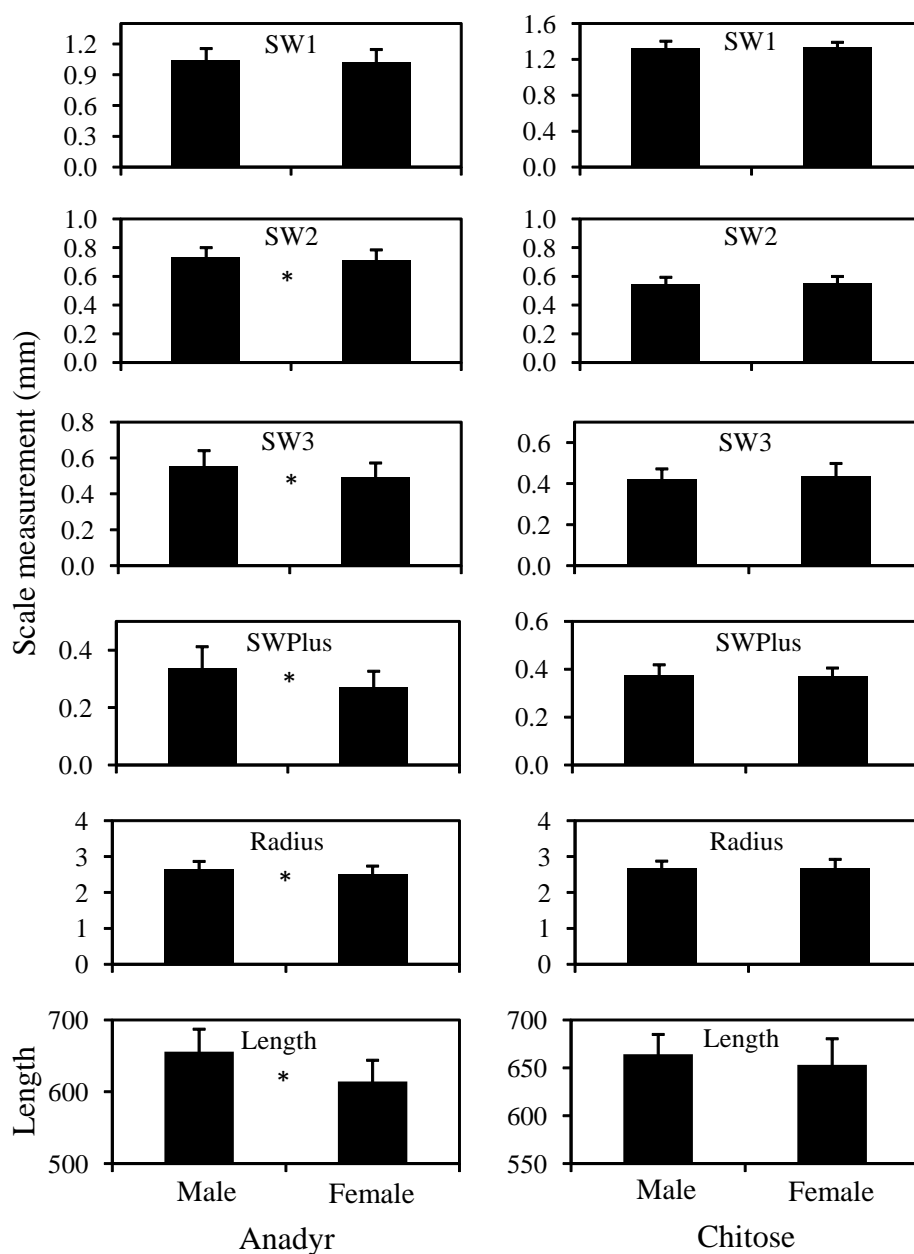
Appendix 1A-4. Scale radius measurements by zone, total scale radius and fish length ( $\pm 1$  SD) of Unalakleet River chum salmon by gender for age 0.3 return years 1977-2008 and age 0.4 return years 1975-2008 (\* indicates  $P < 0.05$ ).



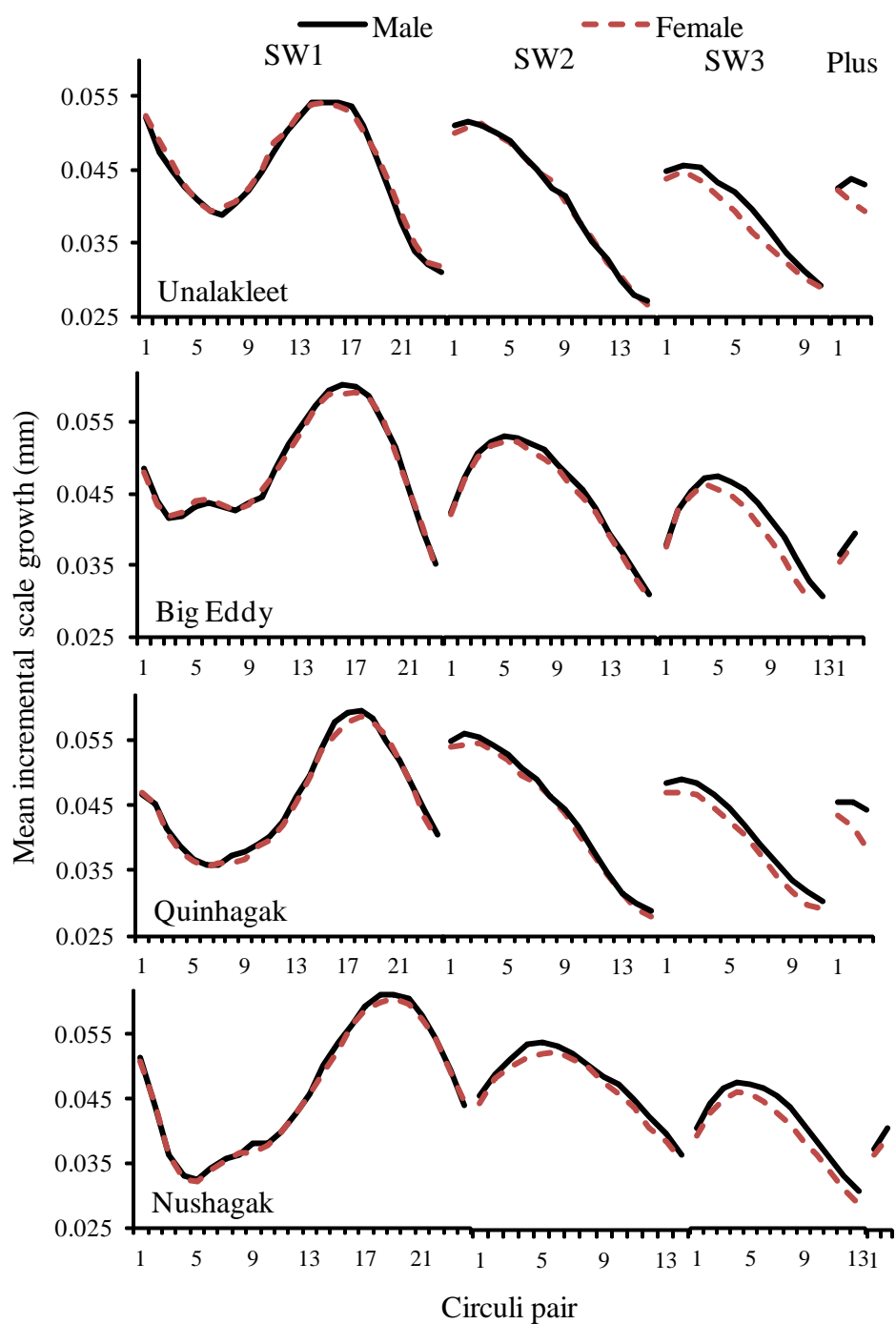
Appendix 1A-5. Scale radius measurements by zone, total scale radius and fish length ( $\pm 1$  SD) for Quinhagak chum salmon by gender for age 0.3 return years 1967-2007 and age 0.4 return years 1968-2007 (\* indicates  $P < 0.05$ ).



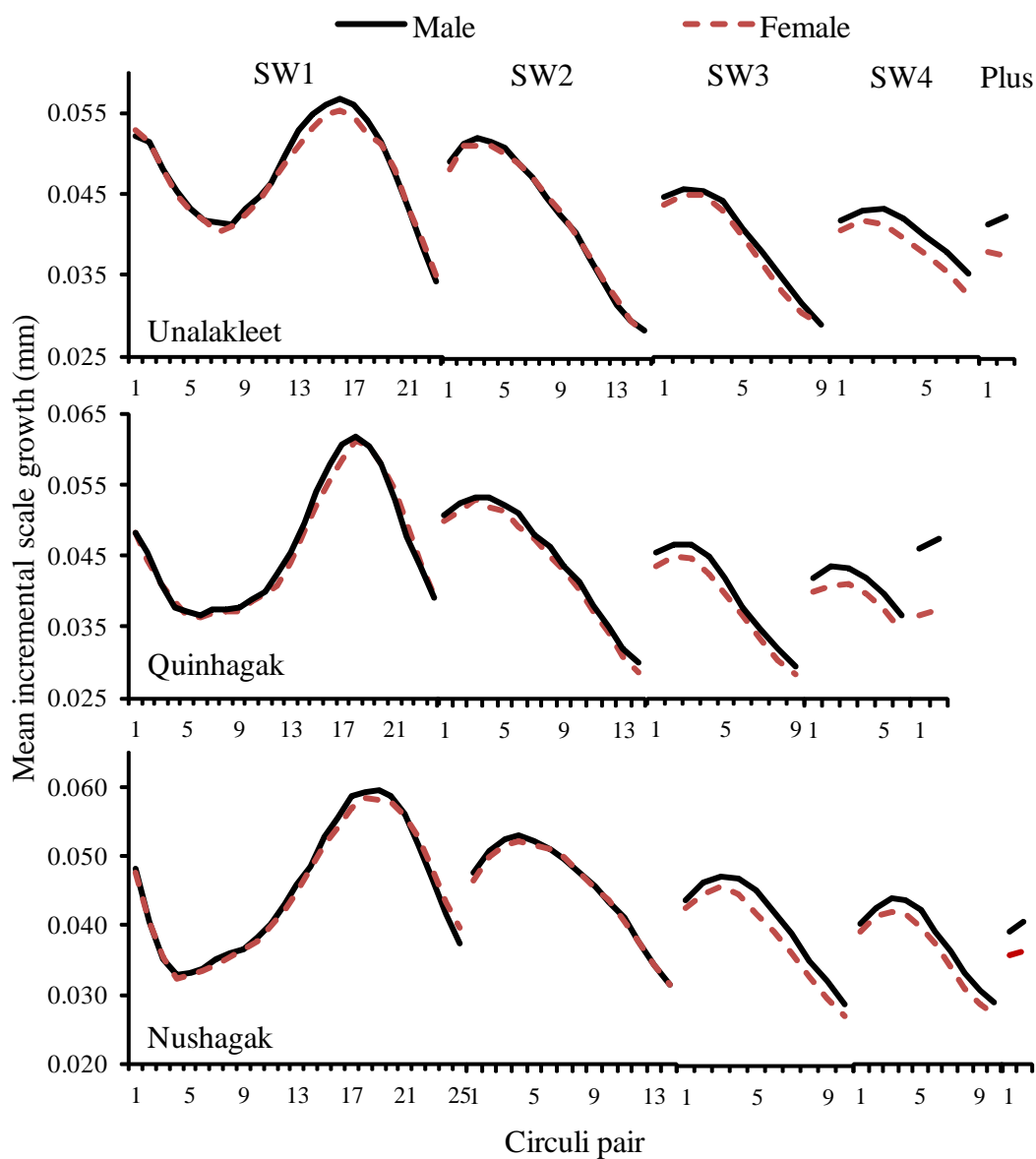
Appendix 1A-6. Scale radius measurements by zone, total scale radius and fish length ( $\pm 1$  SD) for Nushagak River chum salmon by gender for age 0.3 return years 1960-2006 and age 0.4 return years 1966-2006 (\* indicates  $P < 0.05$ ).



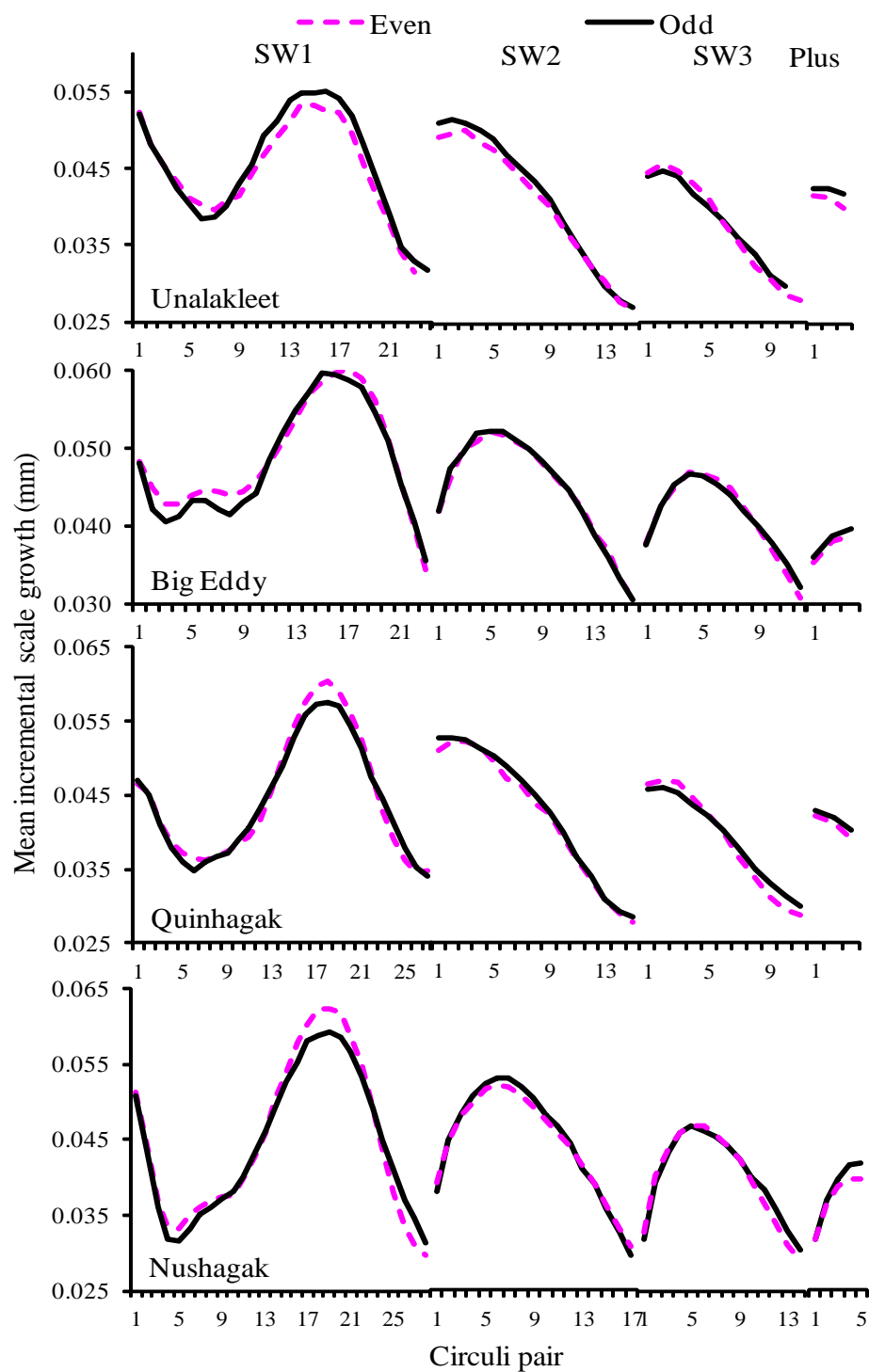
Appendix 1A-7. Scale radius measurements by zone, total scale radius and fish length ( $\pm 1$  SD) by gender for age 0.3 chum salmon from Russia and Japan. For the Anadyr River, Russia, return years were 1962-2007 and for the Chitose River, Japan, return years were 1976-2008 (\* indicates  $P < 0.05$ ).



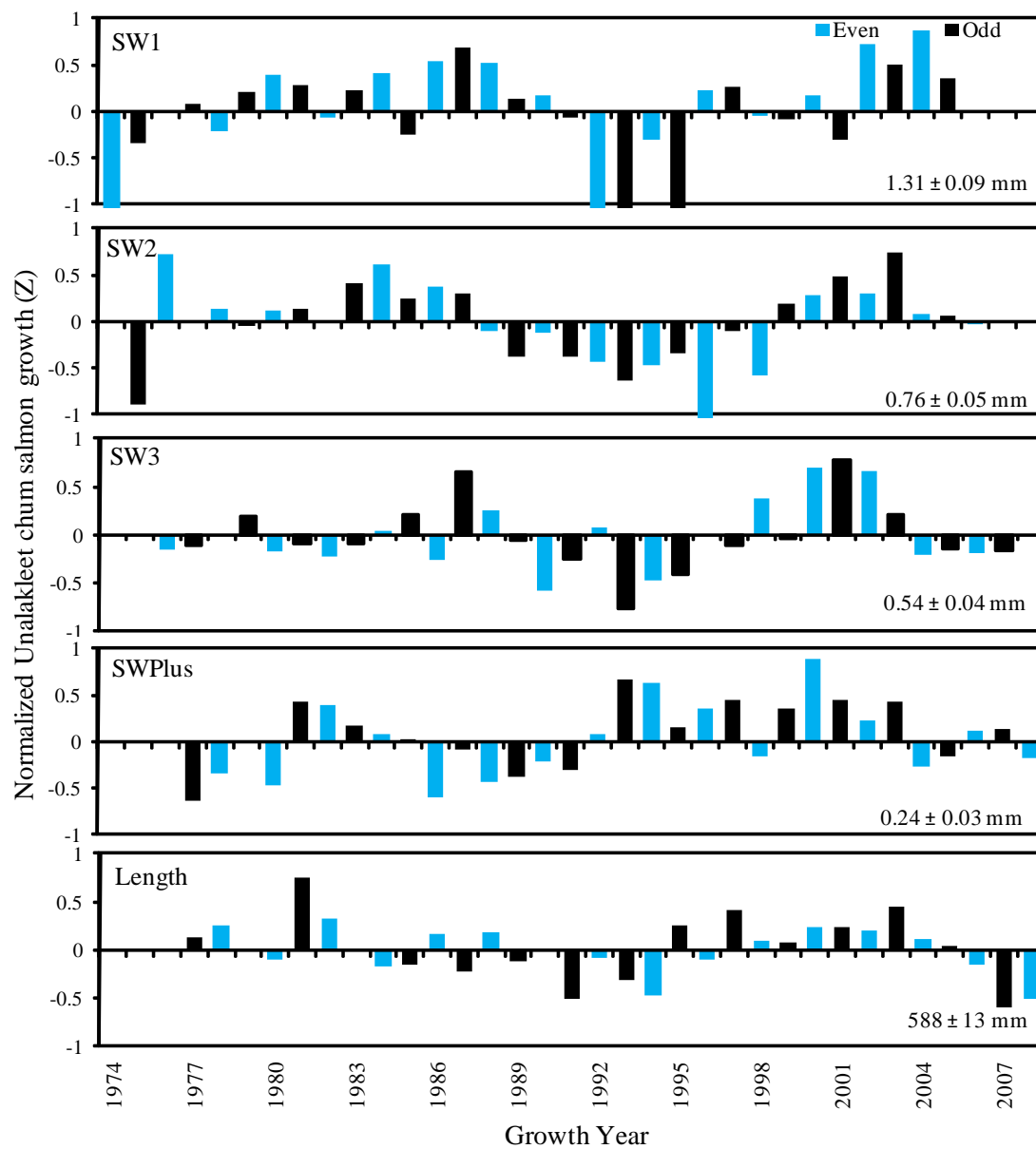
Appendix 1A-8. Mean seasonal scale growth (mm) of age 0.3 western Alaska chum salmon from Unalakleet River, Big Eddy, Quinhagak, and Nushagak River by gender. Values are mean incremental scale growth.



Appendix 1A-9. Mean seasonal scale growth (mm) of age 0.4 western Alaska chum salmon from Unalakleet River, Quinhagak, and Nushagak River by gender. Values are mean incremental scale growth.

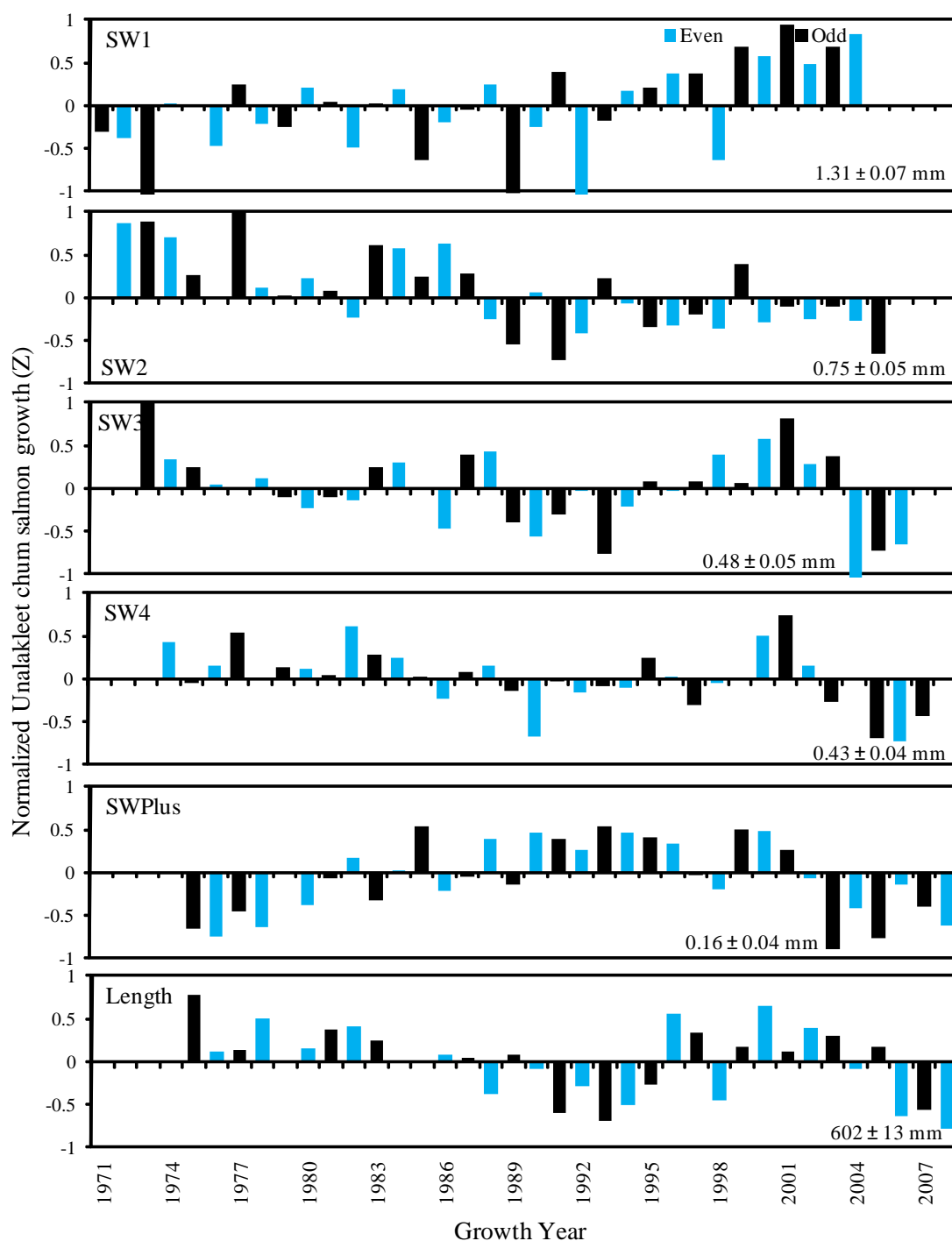


Appendix 1A-10. Mean seasonal scale growth (mm) of age 0.3 western Alaska chum salmon from Unalakleet River, Big Eddy, Quinhagak, and Nushagak River in odd and even years. Values are mean incremental scale growth.

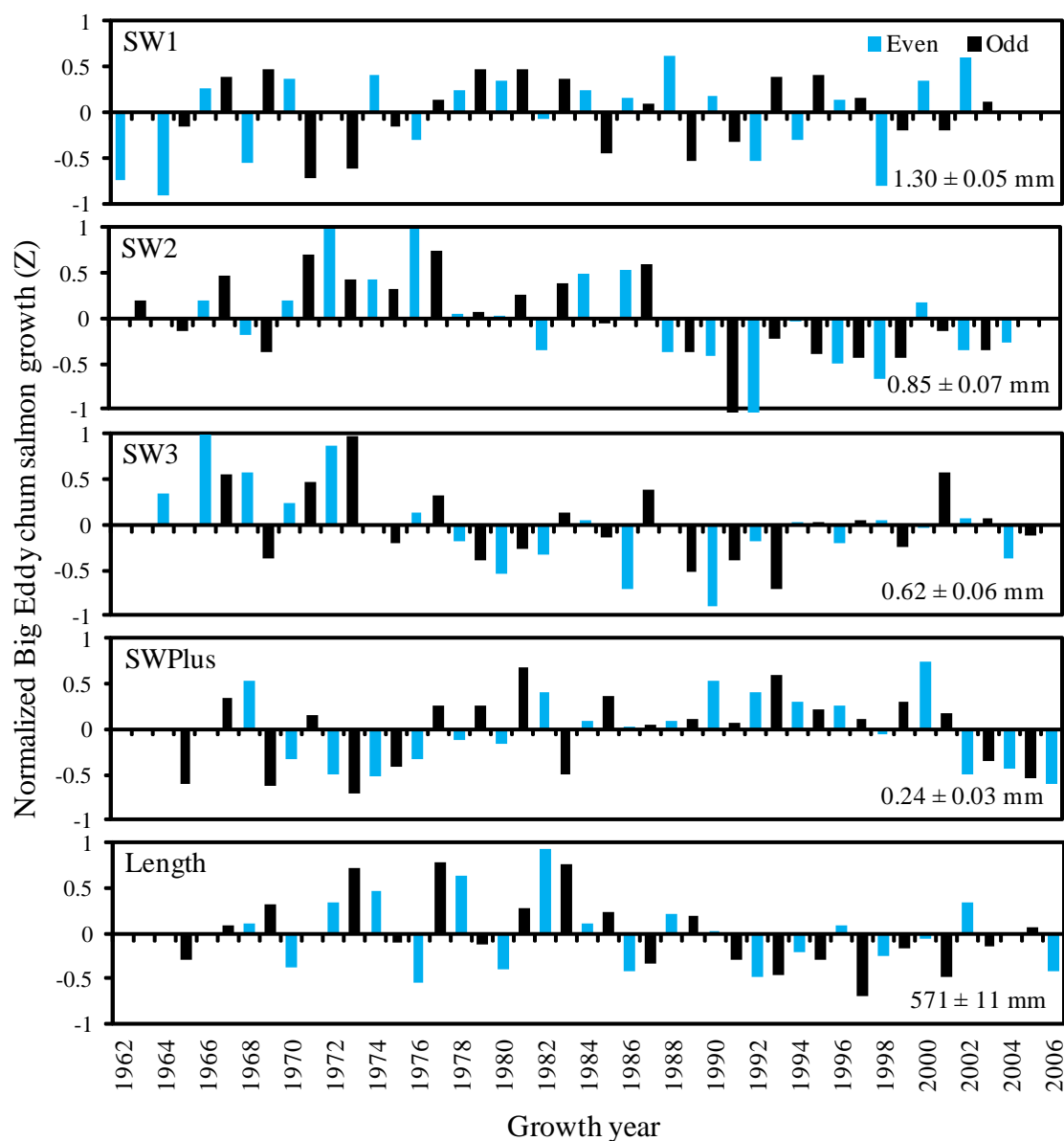


Appendix 1A-11. Mean annual growth of age 0.3 Unalakleet River, Alaska chum salmon by life stage, growth years 1974-2008. Un-weighted mean  $\pm$  1 SD by life stage shown.

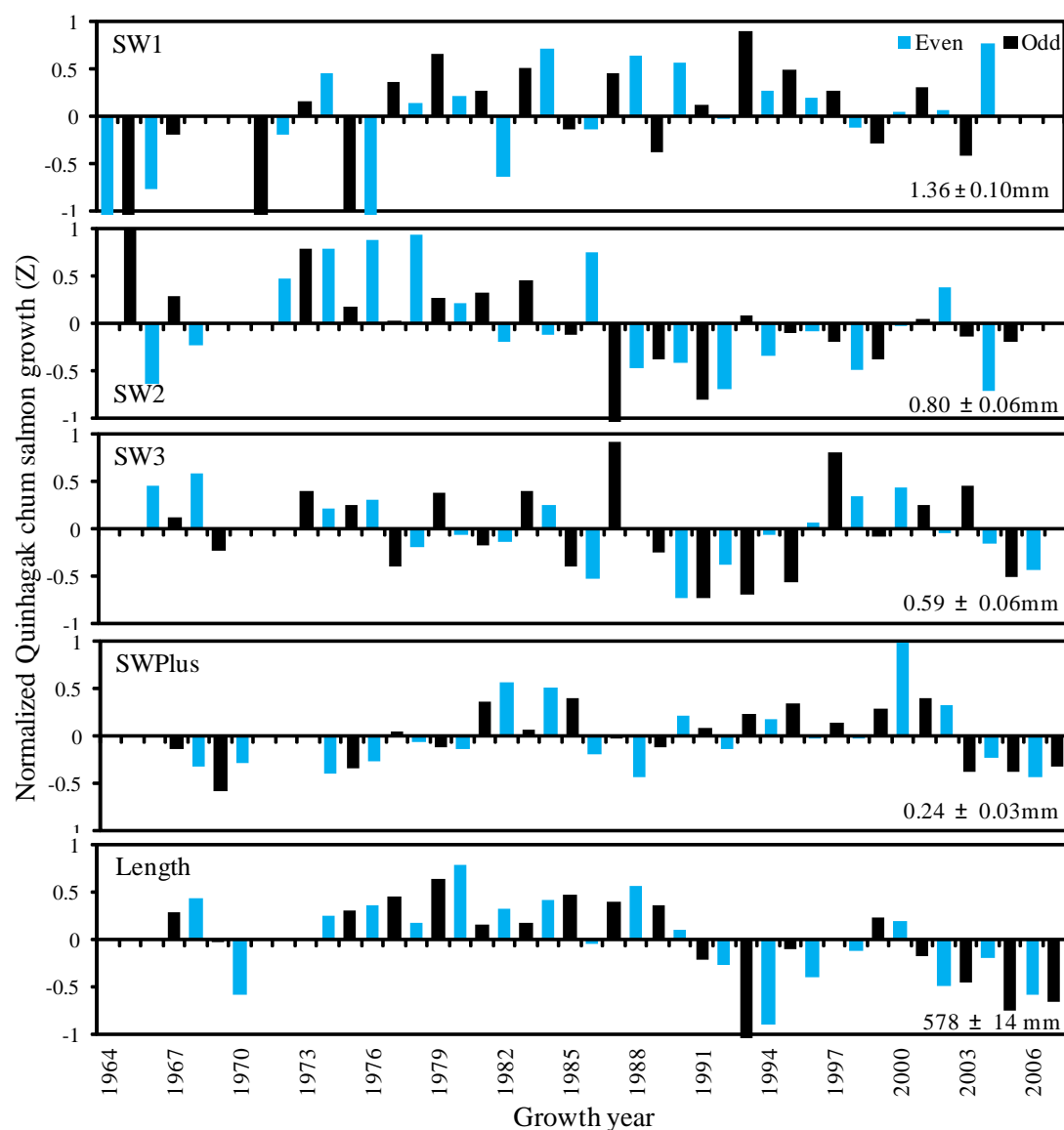




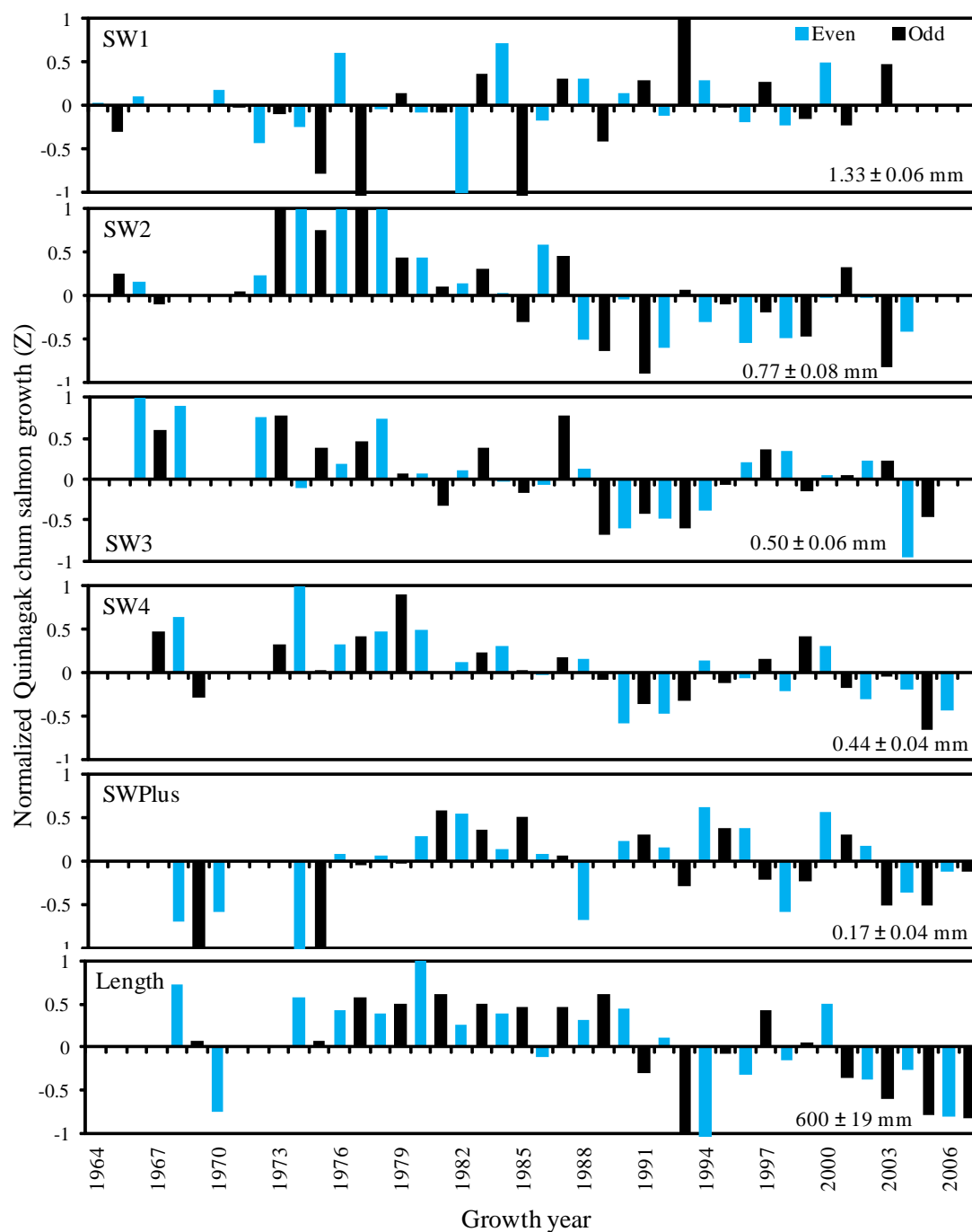
Appendix 1A-12. Mean annual growth of age 0.4 Unalakleet River, Alaska chum salmon by life stage, growth years 1971-2008. Un-weighted mean  $\pm$  1 SD by life stage shown.



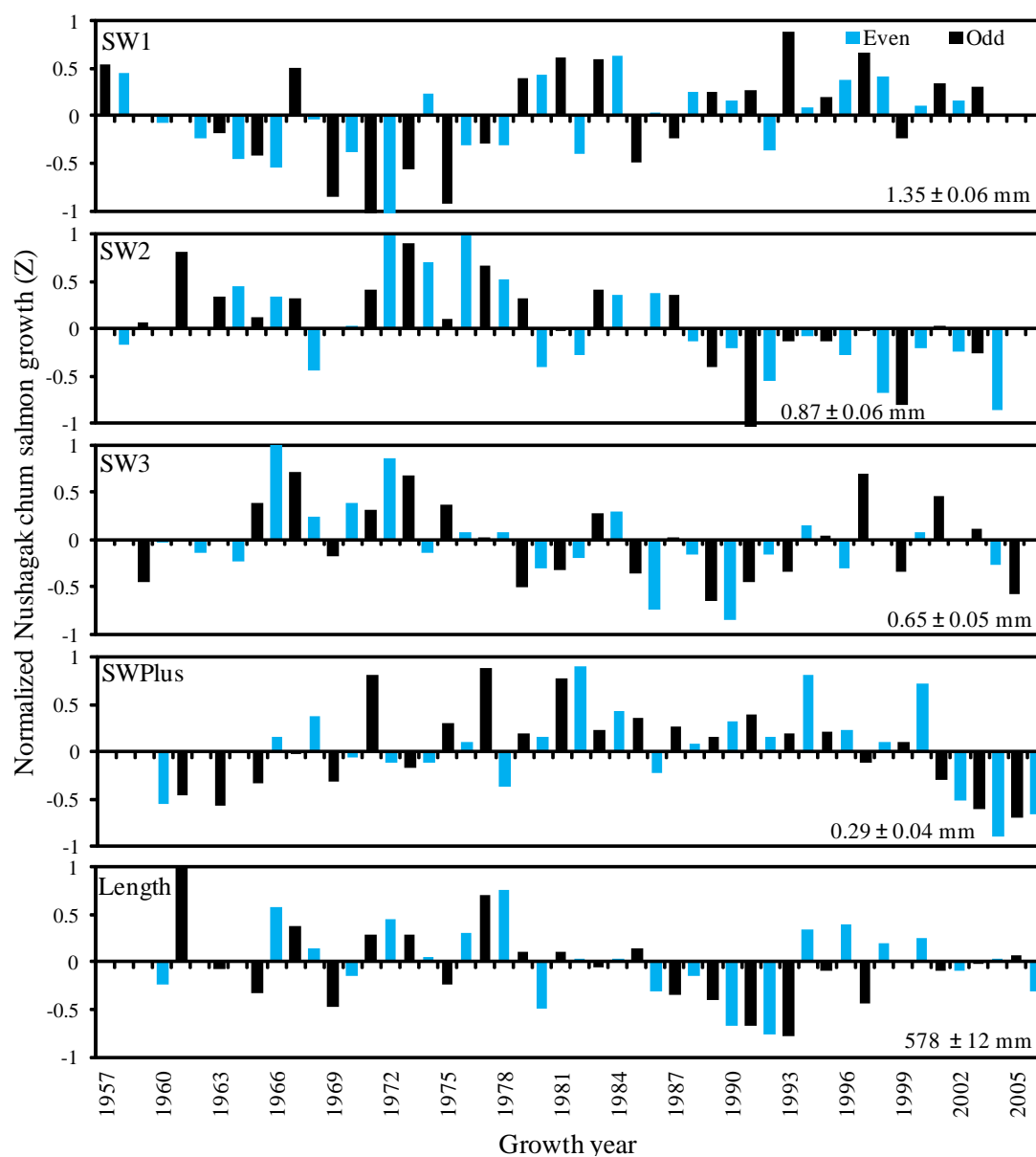
Appendix 1A-13. Mean annual growth of age 0.3 Big Eddy, Alaska chum salmon by life stage, growth years 1962-2006. Un-weighted mean  $\pm$  1 SD by life stage shown.



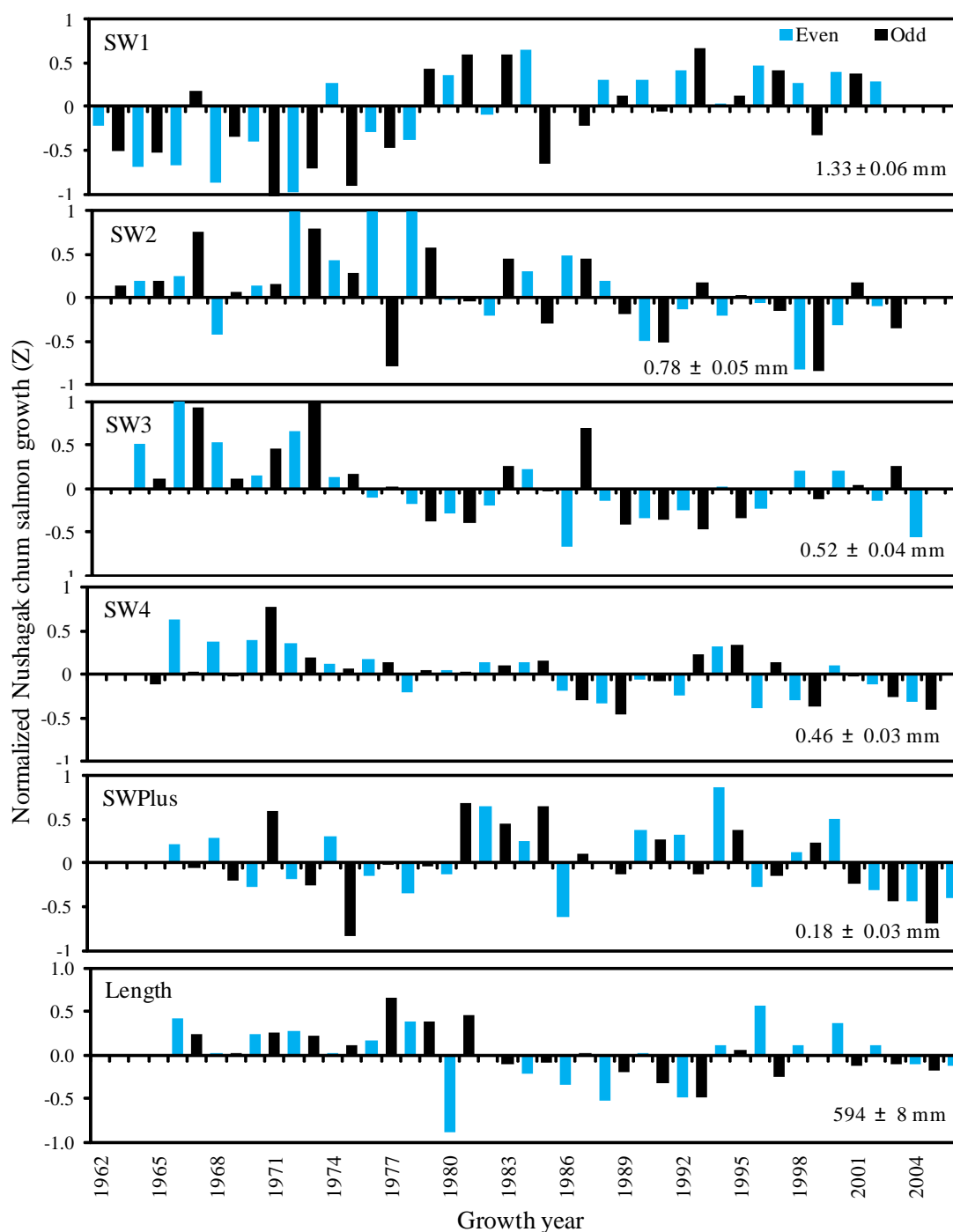
Appendix 1A-14. Mean annual growth of age 0.3 Quinhagak, Alaska chum salmon by life stage, growth years 1964-2007. Un-weighted mean  $\pm$  1 SD by life stage shown.



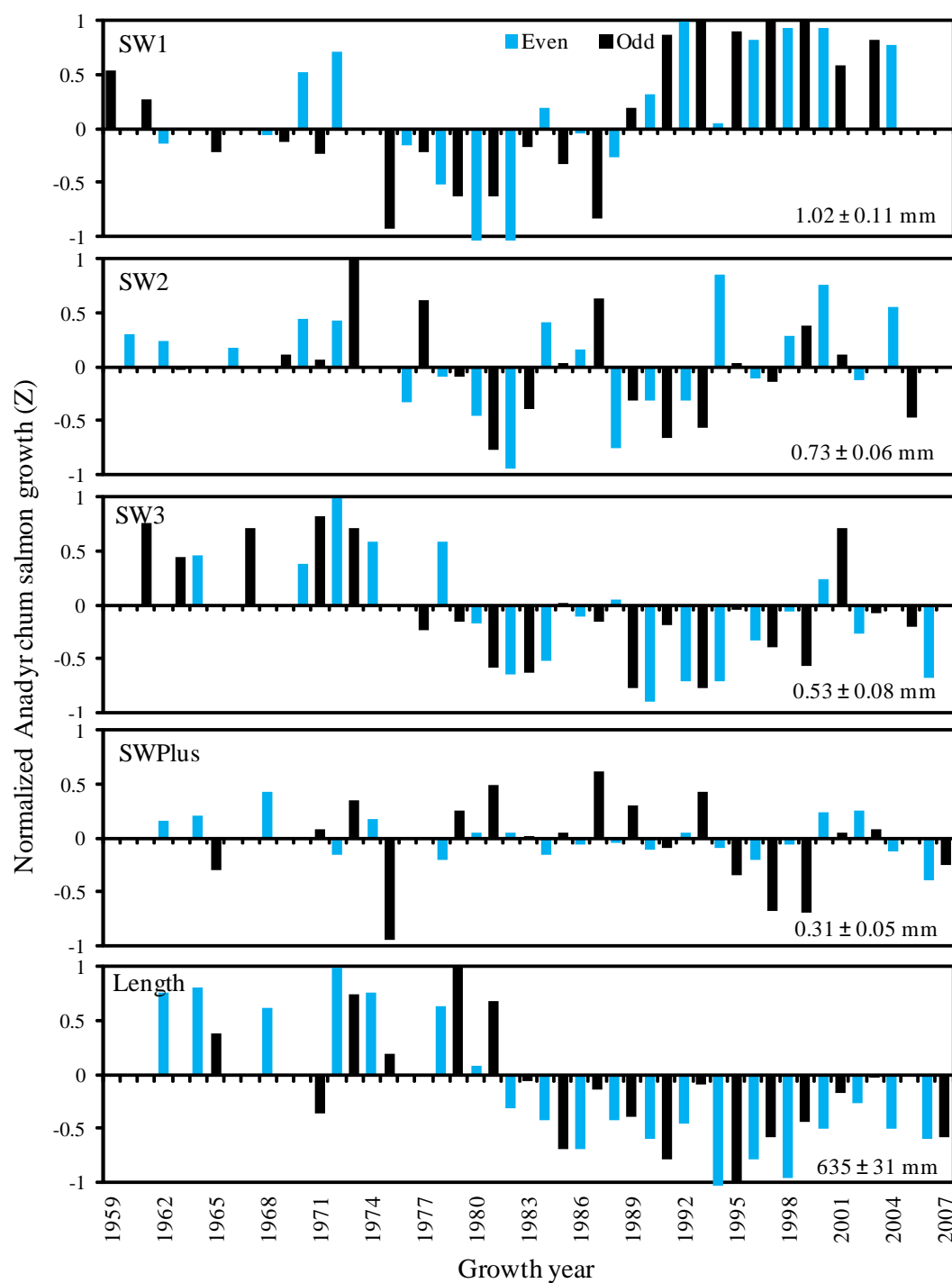
Appendix 1A-15. Mean annual growth of age 0.4 Quinhagak, Alaska chum salmon by life stage, growth years 1964-2007. Un-weighted mean  $\pm$  1 SD by life stage shown.



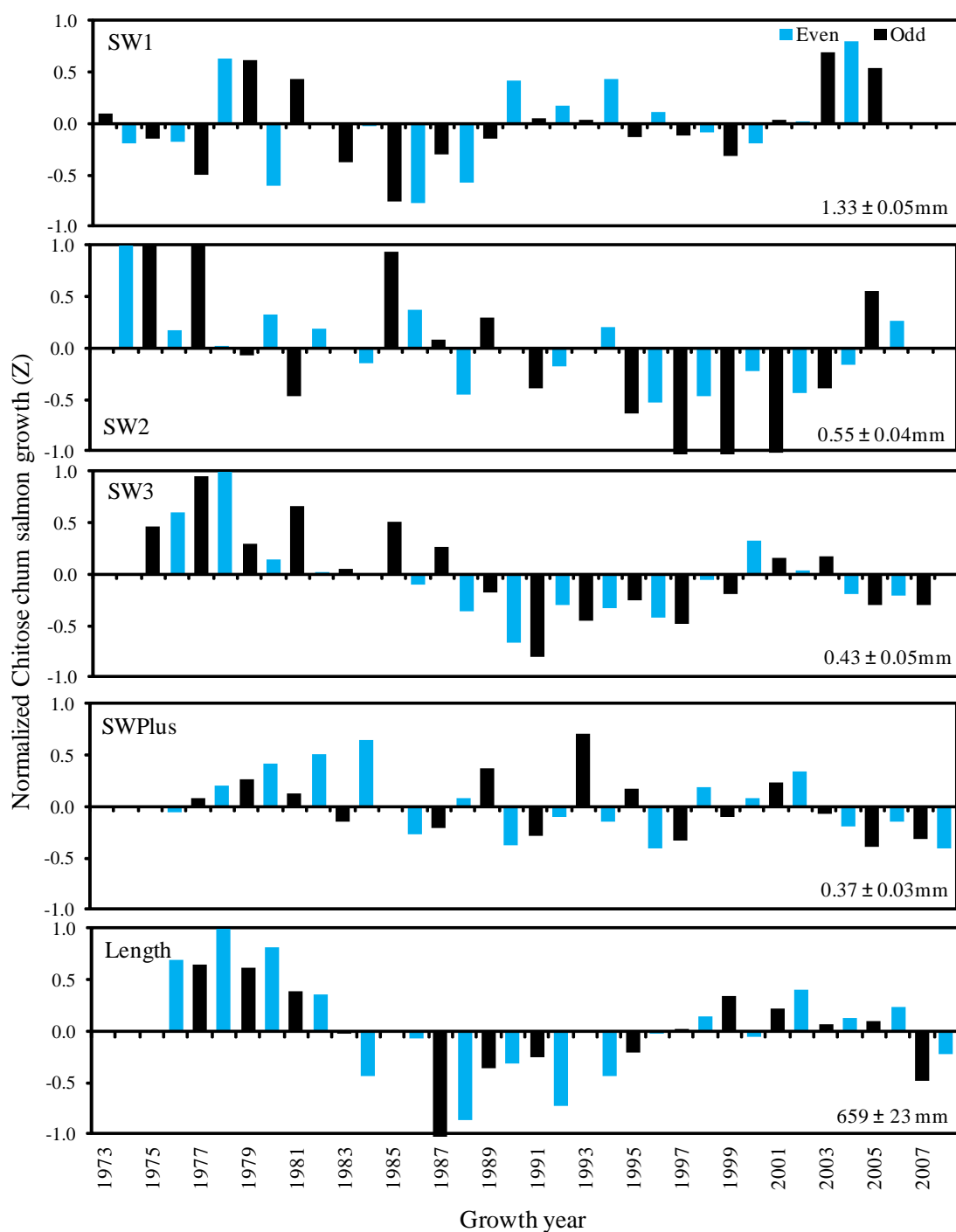
Appendix 1A-16. Mean annual growth of age 0.3 Nushagak River, Alaska chum salmon by life stage, growth years 1957-2006. Un-weighted mean  $\pm$  1 SD by life stage shown.



Appendix 1A-17. Mean annual growth of age 0.4 Nushagak River, Alaska chum salmon by life stage, growth years 1962-2006. Un-weighted mean  $\pm$  1 SD by life stage shown.

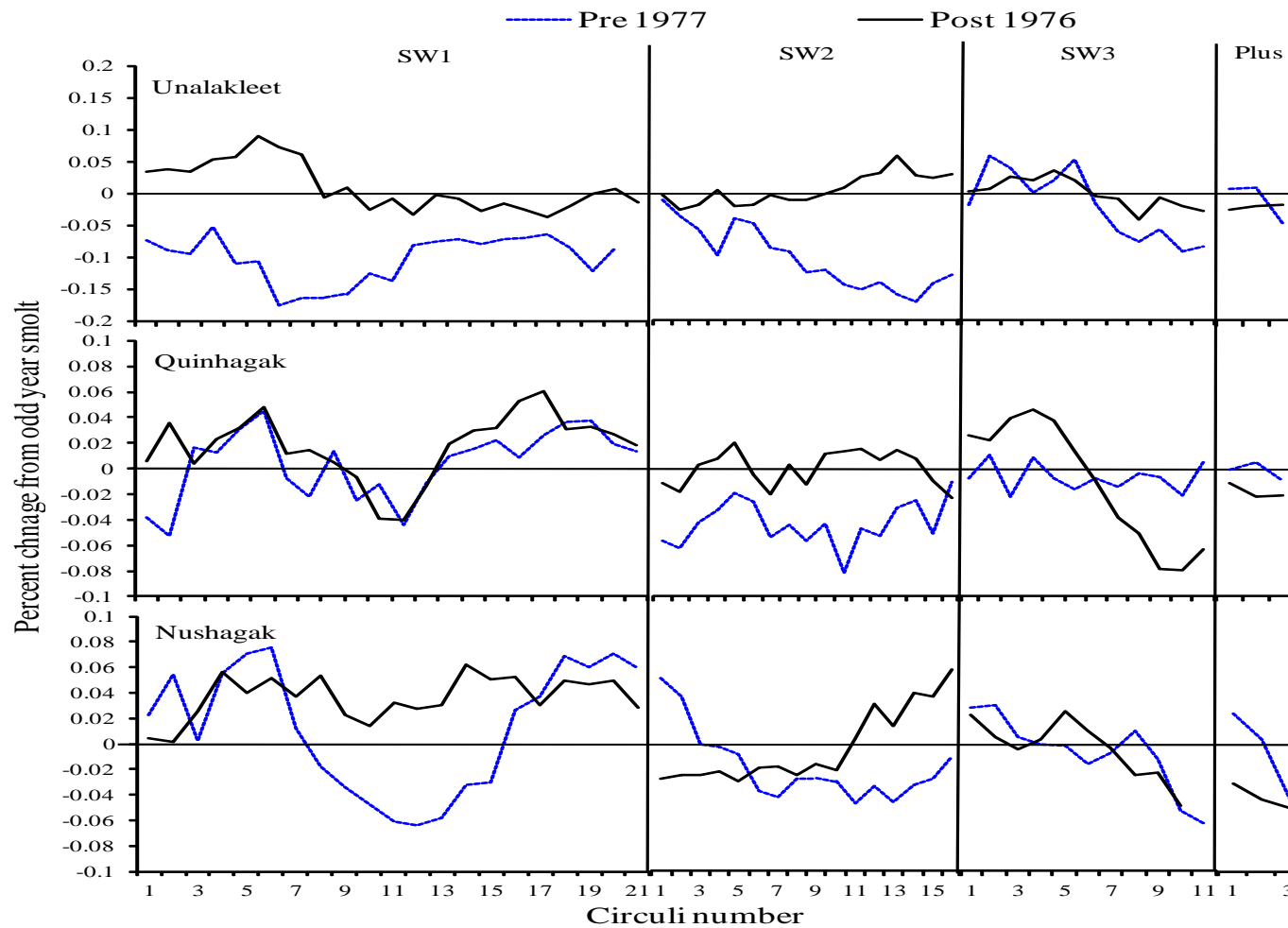


Appendix 1A-18. Mean annual growth of age 0.3 Anadyr River, Russia chum salmon by life stage, growth years 1959-2007. Un-weighted mean  $\pm$  1 SD by life stage shown.

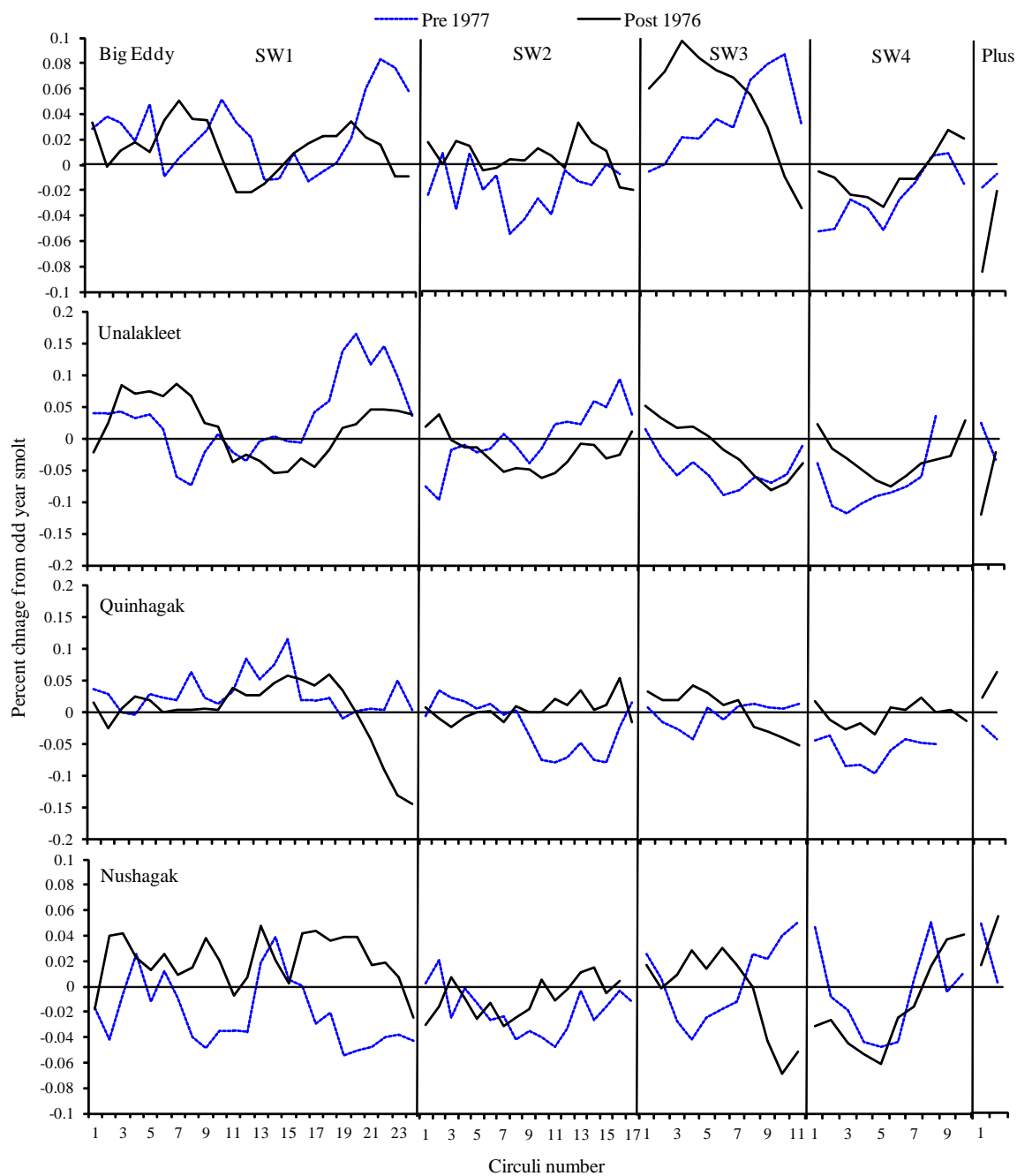


Appendix 1A-19. Mean annual growth of age 0.3 Chitose River, Japan chum salmon by life stage, growth years 1973-2008. Un-weighted mean  $\pm$  1 SD by life stage shown.

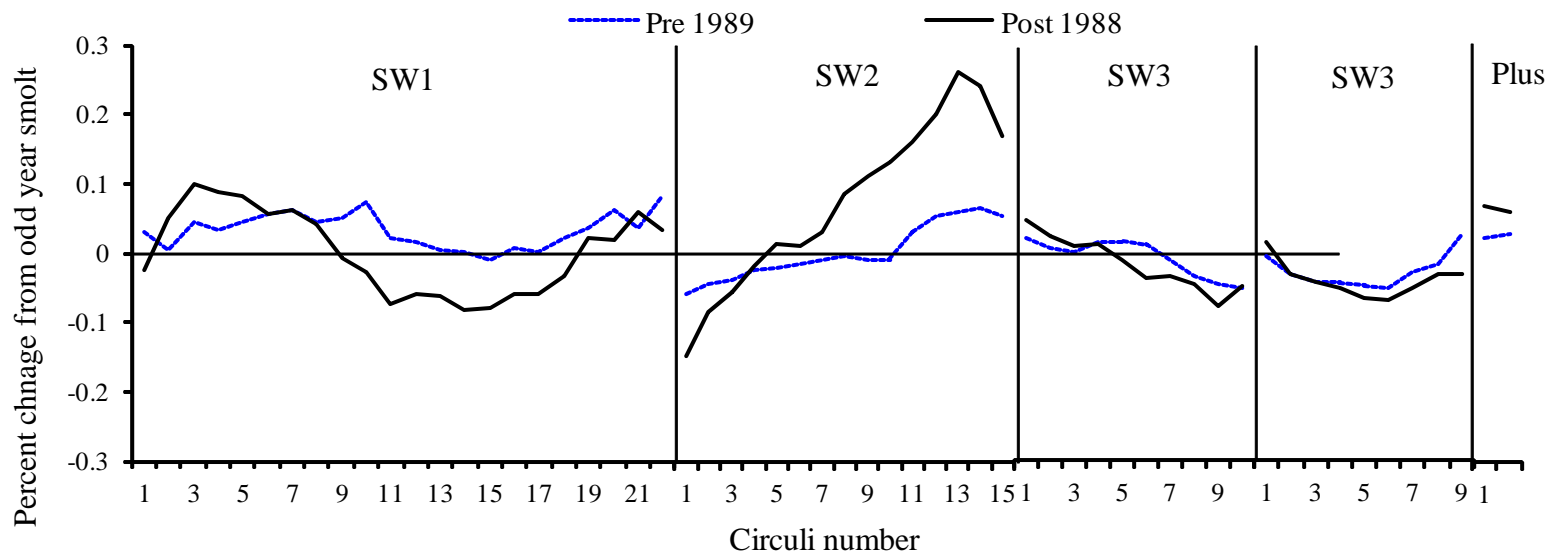




Appendix 1A-20. Percent change in scale growth between age 0.3 western Alaskan chum salmon entering the ocean during odd years, and those entering during even years grouped into pre-1977 and post-1976 years.



Appendix 1A-21. Percent change in scale growth between age 0.4 western Alaskan chum salmon entering the ocean during odd year, and those entering during even years grouped into pre-1977 and post-1976 years.



Appendix 1A-22. Percent change in scale growth between age 0.4 Unalakleet River, Alaska chum salmon entering the ocean during odd years, and those entering during even years grouped into pre-1989 and post-1988 years.

**Appendix 1B**

Appendix 1B-1. Mean ( $\mu$ ) widths (mm) by scale growth zone, total scale radius, and mean total fish length with standard deviations (SD) for chum salmon from four populations in western Alaska (Unalakleet and Nushagak Rivers, Quinhagak, and Big Eddy) and two in Asia (Anadyr River, Russia, and Chitose River, Japan). Dash (-) indicates no data.

Population	Age	Sex	SW1		SW2		SW3		SW4		SWPlus		Radius		Length	
			$\mu$	SD	$\mu$	SD	$\mu$	SD	$\mu$	SD	$\mu$	SD	$\mu$	SD	$\mu$	SD
Unalakleet	0.3	Male	1.31	0.16	0.76	0.13	0.56	0.12	-	-	0.26	0.10	2.90	0.30	588.1	27.7
		Female	1.32	0.14	0.76	0.12	0.52	0.11	-	-	0.21	0.09	2.82	0.28	572.0	24.9
	0.4	Male	1.32	0.13	0.75	0.11	0.49	0.11	0.46	0.11	0.19	0.09	3.20	0.24	612.6	32.7
		Female	1.30	0.13	0.74	0.11	0.47	0.10	0.41	0.09	0.14	0.08	3.05	0.24	591.3	28.8
Big Eddy	0.3	Male	1.30	0.12	0.85	0.13	0.65	0.13	-	-	0.26	0.09	3.07	0.25	579.9	26.9
		Female	1.29	0.12	0.84	0.13	0.59	0.12	-	-	0.20	0.08	2.92	0.24	562.2	23.2
	0.4	Male	1.29	0.13	0.78	0.12	0.51	0.11	0.47	0.11	0.15	0.07	3.18	0.29	605.0	34.7
		Female	1.28	0.13	0.76	0.11	0.48	0.10	0.41	0.09	0.10	0.06	3.01	0.27	579.3	25.4
Quinhagak	0.3	Male	1.36	0.17	0.81	0.14	0.62	0.14	-	-	0.27	0.09	3.07	0.35	587.5	31.1
		Female	1.35	0.17	0.79	0.13	0.57	0.13	-	-	0.21	0.07	2.92	0.32	567.8	28.4
	0.4	Male	1.33	0.14	0.78	0.13	0.51	0.12	0.46	0.10	0.21	0.10	3.27	0.29	610.5	36.1
		Female	1.32	0.14	0.76	0.12	0.49	0.11	0.42	0.09	0.14	0.08	3.11	0.28	584.9	29.8
Nushagak	0.3	Male	1.35	0.14	0.89	0.14	0.67	0.14	-	-	0.33	0.11	3.23	0.28	589.2	32.8
		Female	1.35	0.14	0.86	0.13	0.62	0.13	-	-	0.25	0.09	3.07	0.27	565.9	29.3
	0.4	Male	1.33	0.15	0.79	0.14	0.54	0.12	0.48	0.12	0.20	0.10	3.33	0.31	607.9	34.1
		Female	1.32	0.14	0.78	0.13	0.50	0.11	0.43	0.10	0.15	0.08	3.16	0.27	579.2	28.3
Russia	0.3	Male	1.04	0.17	0.74	0.13	0.55	0.14	-	-	0.34	0.11	2.65	0.38	609.3 <sup>a</sup>	37.9
		Female	1.02	0.18	0.71	0.13	0.49	0.13	-	-	0.27	0.10	2.48	0.36	575.0 <sup>a</sup>	33.8
Japan	0.3	Male	1.33	0.15	0.55	0.10	0.42	0.11	-	-	0.37	0.12	2.68	0.29	611.7 <sup>a</sup>	39.3
		Female	1.33	0.15	0.55	0.37	0.44	0.11	-	-	0.37	0.10	2.69	0.29	602.5 <sup>a</sup>	41.9

<sup>a</sup> Lengths converted from snout to fork of tail to mid-eye to fork of tail (Pahlke 1989).

Appendix 1B-2. Mean ( $\mu$ ) circuli counts by scale growth zone and total scale radius (mm) with standard deviations (SD) for chum salmon from four populations in western Alaska (Unalakleet and Nushagak rivers, Quinhagak, and Big Eddy) and two in Asia (Anadyr River, Russia and Chitose River, Japan). Dash (-) indicates no data.

Population	Age	Sex	SW1		SW2		SW3		SW4		SWPlus		Radius	
			$\mu$	SD	$\mu$	SD	$\mu$	SD	$\mu$	SD	$\mu$	SD	$\mu$	SD
Unalakleet	0.3	Male	27.7	0.16	19.6	0.13	15.5	0.12	-	-	6.5	0.10	69.3	5.46
		Female	27.8	0.14	19.6	0.12	14.6	0.11	-	-	5.5	0.09	67.5	5.56
	0.4	Male	27.2	0.13	18.5	0.11	13.3	0.11	12.4	0.11	4.7	0.09	76.3	6.51
		Female	27.2	0.13	18.4	0.11	12.9	0.10	11.3	0.09	3.7	0.08	73.6	6.19
Big Eddy	0.3	Male	26.7	0.12	21.0	0.13	17.3	0.13	-	-	7.0	0.09	71.9	5.44
		Female	26.6	0.12	20.7	0.13	16.1	0.12	-	-	5.7	0.08	69.2	5.20
	0.4	Male	26.8	0.13	19.1	0.12	14.1	0.11	12.8	0.11	4.1	0.07	76.7	6.31
		Female	26.8	0.13	18.8	0.11	13.5	0.10	11.8	0.09	3.1	0.06	73.6	5.80
Quinhagak	0.3	Male	29.2	0.17	19.9	0.14	16.5	0.14	-	-	6.5	0.09	72.1	5.72
		Female	29.2	0.17	19.7	0.13	15.5	0.13	-	-	5.5	0.07	69.9	5.40
	0.4	Male	28.0	0.14	18.7	0.13	13.8	0.12	12.4	0.10	5.3	0.10	78.2	6.41
		Female	28.2	0.14	18.6	0.12	13.6	0.11	12.0	0.09	4.0	0.08	76.0	6.17
Nushagak	0.3	Male	28.7	0.14	21.4	0.14	17.7	0.14	-	-	8.3	0.11	76.1	5.77
		Female	28.8	0.14	21.2	0.13	17.0	0.13	-	-	6.8	0.09	73.8	5.49
	0.4	Male	28.4	0.15	18.9	0.14	14.4	0.12	13.1	0.12	5.3	0.10	80.5	6.75
		Female	28.3	0.14	18.9	0.13	13.8	0.11	12.2	0.10	4.2	0.08	77.6	6.09
Russia	0.3	Male	22.7	0.17	18.7	0.13	14.0	0.14	-	-	6.6	0.11	62.3	5.96
		Female	22.6	0.18	18.2	0.13	12.8	0.13	-	-	6.0	0.10	59.6	5.57
Japan	0.3	Male	31.4	0.15	14.9	0.10	11.6	0.11	-	-	7.6	0.12	65.5	5.25
		Female	31.5	0.15	15.0	0.37	11.6	0.11	-	-	7.4	0.10	65.4	5.26

Appendix 1B-3. Analysis of variances (ANOVA) comparing scale zones, radius and length measurements from four populations in western Alaska (Unalakleet and Nushagak rivers, Quinhagak, and Big Eddy) and two in Asia (Anadyr River, Russia and Chitose River, Japan) age 0.3 and 0.4 chum salmon with odd first year at sea. Sample size ( $N$ ),  $F$ , and  $P$  shown. Dash (-) = no data. An asterisk (\*) indicates  $P < 0.05$ .

Population	Factor	Age 0.3				Age 0.4			
		$N$	$F$	$P$	Year	$N$	$F$	$P$	Year
Unalakleet	SW1	31	0.316	0.578		33	1.628	0.212	
	SW2	31	0.044	0.836		33	0.975	0.331	
	SW3	31	4.621	0.040*	Odd	33	4.985	0.033*	Odd
	SW4	-	-	-		33	0.975	0.331	
	SWPlus	31	0.002	0.962		33	0.044	0.835	
	Scale radius	31	1.010	0.323		33	0.170	0.683	
	Fish length	31	0.008	0.931		33	0.603	0.443	
Big Eddy	SW1	41	0.720	0.401		41	3.485	0.069	
	SW2	41	0.505	0.482		41	0.077	0.783	
	SW3	41	2.547	0.119		41	2.694	0.109	
	SW4	-	-	-		41	0.168	0.684	
	SWPlus	41	0.095	0.760		41	1.833	0.184	
	Scale radius	41	0.008	0.930		41	0.131	0.719	
	Fish length	41	0.004	0.951		41	0.547	0.464	
Quinhagak	SW1	38	0.000	0.989		37	0.018	0.893	
	SW2	38	0.043	0.837		37	0.018	0.893	
	SW3	38	3.017	0.091		37	0.520	0.476	
	SW4	-	-	-		37	0.003	0.956	
	SWPlus	38	0.000	0.996		37	0.361	0.552	
	Scale radius	38	0.721	0.402		37	0.043	0.837	
	Fish length	38	0.000	0.994		37	0.011	0.918	
Nushagak	SW1	45	0.504	0.482		42	0.009	0.925	
	SW2	45	0.245	0.623		42	0.200	0.658	
	SW3	45	1.835	0.835		42	1.473	0.232	
	SW4	-	-	-		42	1.201	0.280	
	SWPlus	45	0.363	0.550		42	1.793	0.188	
	Scale radius	45	0.068	0.796		42	0.006	0.939	
	Fish length	45	0.053	0.819		42	0.718	0.402	

Appendix 1B-3. continued.

Population	Factor	Age 0.3				Age 0.4			
		<i>N</i>	<i>F</i>	<i>P</i>	Year	<i>N</i>	<i>F</i>	<i>P</i>	Year
Anadyr	SW1	38	0.003	0.958		-	-	-	
	SW2	38	0.403	0.529		-	-	-	
	SW3	38	0.107	0.745		-	-	-	
	SWPlus	38	0.225	0.638		-	-	-	
	Scale radius	38	0.198	0.659		-	-	-	
	Fish length	38	1.286	0.264		-	-	-	
Chitose	SW1	32	0.009	0.924		-	-	-	
	SW2	32	0.000	0.998		-	-	-	
	SW3	32	0.070	0.794		-	-	-	
	SWPlus	32	0.013	0.910		-	-	-	
	Scale radius	32	0.008	0.930		-	-	-	
	Fish length	32	0.164	0.689		-	-	-	

Appendix 1B-4. Analysis of variances (ANOVA) comparing chum salmon scale zones from four populations in western Alaska (Unalakleet and Nushagak rivers, Quinhagak, and Big Eddy) and two in Asia (Anadyr River, Russia, and Chitose River, Japan) by sex, and year. Degrees of freedom (df), sum of squares (Sum Sq), mean-squared error (Mean Sq), *F*, and *P* shown.

Variable	Factor	df	Sum Sq	Mean Sq	<i>F</i>	<i>P</i>
SW1	Population	5	116.212	23.242	1169.09	< 0.001
	Sex	1	0.028	0.028	1.42	0.233
	Year	48	27.839	0.58	29.17	< 0.001
SW2	Population	5	58.619	11.724	480.87	< 0.001
	Sex	1	0.419	0.419	17.19	< 0.001
	Year	48	37.878	0.789	32.37	< 0.001
SW3	Population	5	55.254	11.051	805.35	< 0.001
	Sex	1	5.162	5.162	376.18	< 0.001
	Year	48	24.231	0.505	36.79	< 0.001
SWPlus	Population	5	25.097	5.019	593.94	< 0.001
	Sex	1	8.416	8.416	995.86	< 0.001
	Year	48	8.827	0.184	21.76	< 0.001
Scale radius	Population	5	381.43	76.29	901.30	< 0.001
	Sex	1	37.64	37.64	444.77	< 0.001
	Year	48	44.06	0.92	10.85	< 0.001



Appendix 1B-5. Multiple comparisons for factor “Population” from the analysis of variances (ANOVA) described in previous table. Data are from chum salmon scales collected from four populations in western Alaska (UR-Unalakleet River, BE-Big Eddy, Q-Quinhagak, and NR-Nushagak River) and two in Asia (AR-Anadyr River, Russia and CR-Chitose River, Japan).

Populations	SW1			SW2			SW3			Plus			Scale radius		
	Est.	<i>t</i>	<i>P</i>	Est.	<i>t</i>	<i>P</i>	Est.	<i>t</i>	<i>P</i>	Est.	<i>t</i>	<i>P</i>	Est.	<i>t</i>	<i>P</i>
CR - BE	0.01	2.4	0.17	-0.20	-37.2	<0.01	-0.17	-42.2	<0.01	0.14	43.8	<0.01	-0.30	-29.9	<0.01
NR - BE	0.05	12.1	<0.01	0.01	2.7	0.07	0.03	7.9	<0.01	0.06	20.9	<0.01	0.16	17.8	<0.01
Q - BE	0.05	11.9	<0.01	-0.04	-8.5	<0.01	-0.02	-5.1	<0.01	0.01	1.8	0.47	0.00	0.1	1
AR - BE	-0.30	-55.4	<0.01	-0.14	-22.4	<0.01	-0.09	-20.8	<0.01	0.07	19.7	<0.01	-0.46	-40.9	<0.01
UR - BE	0.00	0.8	0.96	-0.08	-15.7	<0.01	-0.06	-14.1	<0.01	0.01	1.8	0.45	-0.12	-11.9	<0.01
NR - CR	0.04	8.6	<0.01	0.21	40.7	<0.01	0.20	50.5	<0.01	-0.08	-25.9	<0.01	0.46	46.6	<0.01
Q - CR	0.04	8.7	<0.01	0.16	29.1	<0.01	0.15	37.2	<0.01	-0.13	-41.9	<0.01	0.30	29.8	<0.01
AR - CR	-0.31	-53.8	<0.01	0.06	9.8	<0.01	0.08	15.5	<0.01	-0.07	-17.9	<0.01	-0.16	-13.2	<0.01
UR - CR	-0.01	-1.5	0.68	0.12	20.7	<0.01	0.11	27.0	<0.01	-0.13	-40.4	<0.01	0.18	17.5	<0.01
Q - NR	0.00	0.4	0.99	-0.06	-11.3	<0.01	-0.05	-12.8	<0.01	-0.05	-18.5	<0.01	-0.16	-17.1	<0.01
AR - NR	-0.35	-65.6	<0.01	-0.15	-24.8	<0.01	-0.12	-27.3	<0.01	0.01	3.3	0.01	-0.62	-55.4	<0.01
UR - NR	-0.05	-10.2	<0.01	-0.10	-18.6	<0.01	-0.08	-21.6	<0.01	-0.05	-17.2	<0.01	-0.28	-28.3	<0.01
AR - Q	-0.36	-63.6	<0.01	-0.09	-15.0	<0.01	-0.08	-16.2	<0.01	0.06	17.7	<0.01	-0.46	-39.9	<0.01
UR - Q	-0.05	-10.2	<0.01	-0.04	-7.7	<0.01	-0.04	-9.3	<0.01	0.00	0.1	1	-0.12	-11.9	<0.01
UR - AR	0.31	52.5	<0.01	0.05	8.0	<0.01	0.04	7.8	<0.01	-0.06	-16.9	<0.01	0.34	28.4	<0.01

## Chapter 2

### **HISTORICAL GROWTH OF BRISTOL BAY AND YUKON RIVER, ALASKA CHUM SALMON (*ONCORHYNCHUS KETA*) IN RELATIONSHIP TO CLIMATE AND INTER- AND INTRASPECIFIC COMPETITION<sup>1</sup>**

#### **Abstract**

To determine whether climate variability, such as changes in sea surface temperature and other large climate indices, was related to chum salmon growth, and whether high pink and Asian chum salmon abundance reduced chum salmon growth, we examined the marine growth of Bristol Bay and Yukon River adult chum salmon from scale growth during 1965-2006 using correlations and generalized least squares regression models. Warmer regional temperatures, the North Pacific Index, the Aleutian Low Pressure Index, and less ice cover significantly affected the first-year growth of chum salmon in Bristol Bay and the Yukon River. Third-year growth was significantly affected by Asian chum salmon abundance for all but age 0.4 Bristol Bay fish. Warmer large-scale sea surface temperatures from the Gulf of Alaska were associated with reduced third-year growth. There was evidence of interspecific interactions due to the abundance of Russian pink salmon, but the effects were smaller than the effects of Asian chum salmon abundance and Gulf of Alaska sea surface temperature on third-year growth. It is possible that this may be due to the climate regime shift in 1976-1977, because pink salmon effects on growth of Yukon River fish switched from negative before the climate regime shift to positive after the climate shift. It is possible that the abundance of Asian chum salmon created a masking effect, overwhelming other effects on the growth of western Alaska chum salmon in the North Pacific Ocean.

*Keywords:* growth, salmon fisheries, climatic changes, surface temperature

---

<sup>1</sup> Agler, B.A., G.T. Ruggerone, L.I. Wilson, and F.J. Mueter. Historical growth of Bristol Bay and Yukon River, Alaska chum salmon (*Oncorhynchus keta*) in relationship to climate and inter- and intraspecific competition. Prepared for Deep-Sea Research II.

## 1. Introduction

Growth affects survival and age-at-maturation of Pacific salmon (*Oncorhynchus* spp.) in general and chum salmon (*O. keta*) in particular (e.g. -- Healey, 1986; Farley et al., 2007b; Ruggerone et al., 2007a; Ruggerone et al., 2007b; Martinson et al., 2008). Faster growing salmon may be better able to avoid predators, and larger body size may provide juvenile salmon with the lipid stores necessary to survive during the winter when prey availability is low (Beamish and Mahnken, 2001; Farley et al., 2007a; Farley et al., 2011). Salmon growth and survival have been shown to co-vary with climate during the period of this study from the mid-1960s to the mid-2000s (Ruggerone et al., 2005; Farley et al., 2007a; Ruggerone et al., 2007b), when the North Pacific Ocean experienced climate shifts (Mantua et al., 1997; Hare and Mantua, 2000). Climate change has resulted in regime shifts in 1976-77 and in 1989, leading to changes in abundances of salmon stocks from different parts of the Eastern North Pacific Ocean and Bering Sea (Mantua et al., 1997; Anderson and Piatt, 1999; Hare and Mantua, 2000).

Growth and productivity of North American salmon in the North Pacific Ocean may be affected by ecological interactions with Asian pink salmon (*O. gorbuscha*) populations, which are characterized by large differences in the abundance of odd and even year populations. Interspecific competition for food and density-dependent growth effects have been observed when abundant stocks originating from Asia and western Alaska intermingle and feed together in offshore waters (Myers et al., 2004; Ruggerone and Nielsen, 2004; Ruggerone et al., 2005). Ruggerone and Nielsen (2004) suggested that pink salmon may be competitively dominant over other salmon species in the North Pacific Ocean and Bering Sea because they are highly abundant, grow rapidly, and prefer high energy prey that is also consumed by other salmon species. It has been hypothesized that biennially-cycling pink salmon abundance inhibited growth and survival of sockeye (*O. nerka*), chum and Chinook (*O. tshawytscha*) salmon during odd-numbered years in the western Bering Sea (Ruggerone and Nielsen, 2004; Ruggerone et al., 2005). The growth and survival of chum salmon may be inhibited by pink salmon through competition for similar prey (Kaeriyama et al., 2004). A previous study on Norton Sound, western Alaska chum salmon found that growth during the third year at sea tended to be negatively correlated with Eastern Kamchatka pink salmon abundance, leading to reduced recruits per spawner (Ruggerone et al., 2011). Researchers have suggested that increased pink salmon abundance altered the feeding and distribution of chum salmon on the high seas (Azumaya and Ishida, 2000; Kaeriyama et al., 2004; Myers et al., 2004).

Intraspecific competition may lead to density-dependent growth within Pacific salmon (Ishida et al., 1993; Peterman et al., 1998; Ruggerone et al., 2003). Salmon are migratory, and competition may occur among conspecifics originating from distant locations (Pyper and Peterman, 1999). Since 1980, approximately 3.1 billion hatchery chum salmon have been released annually from Asian and North American hatcheries (Ruggerone et al., 2010). Increasing hatchery production of chum salmon since the 1970s has led to concerns about possible effects of hatchery populations on wild salmon in the marine environment (Cooney and Brodeur, 1998; Holt et al., 2008). Hatchery chum production has been associated with a significant reduction in the growth of Asian chum salmon (hatchery and wild) and in delayed age-at-maturation (Ishida et al., 1993; Kaeriyama et al., 2007a; Zavolokin et al., 2009). Wild salmon populations may compete for food with abundant hatchery populations. Asian chum abundance, mostly from Japan, and their distributional overlap with western Alaska chum salmon led Myers et al. (2004) to hypothesize that Asian chum salmon, including abundant hatchery stocks, compete with western Alaska chum salmon for food. Hatchery and wild chum salmon from North America (Gulf of Alaska stocks) may also compete with wild chum salmon from western Alaska, but they are less abundant than Asian fish and do not overlap with western Alaska salmon to the same extent (Myers et al., 2007; Beacham et al., 2009; Urawa et al., 2009). Thus, competition among chum salmon for food may lead to reduced growth and survival (Zaporozhets and Zaporozhets, 2004).

Previous studies have shown that the growth of salmon scales provides an index of annual and seasonal growth of salmon at sea (Fukuwaka and Kaeriyama, 1997; Fisher and Pearcy, 2005). Several recent studies have used scales to examine similar issues with salmon species (e.g.—sockeye, Chinook; Ruggerone et al., 2005; Kaeriyama et al., 2007b; Martinson et al., 2008; Ruggerone et al., 2009; Zavolokin et al., 2009; Ruggerone et al., 2011). This is part of a broad study to compare marine growth of several western Alaska chum salmon populations with two Asian chum salmon populations to determine whether growth within the North Pacific Ocean varied in response to climate change and inter- and intraspecific competition. This is the first part of this larger study. In this paper, we tested the following hypotheses: (1) climate variability (e.g. changes in sea surface temperature (SST), North Pacific Index, etc.) is related to the growth of Bristol Bay and Yukon River, Alaska chum salmon, and (2) high Russian pink and Asian chum salmon abundance reduces the growth of Bristol Bay and Yukon River chum salmon. We used historical chum salmon scale collections from Bristol Bay (age 0.3, 1965-2006; age 0.4 1966-

2006) and Yukon River (age 0.3, 1965-2006; age 0.4, 1967-2006) to reconstruct seasonal and annual scale growth of chum salmon. These data were compared with several environmental variables, large-scale climate indices, the abundance of Asian chum salmon, and the alternating year pattern of pink salmon abundance, which provided a natural experimental control.

## 2. Methods

### 2.1. Study Area

Scales were collected annually by various personnel from Alaska Department of Fish and Game (ADF&G) following established protocols. This study focused on two populations in western Alaska: Bristol Bay and the Yukon River. Bristol Bay scales were collected from a mixed stock commercial fishery located near the mouth of the Nushagak River where it flows into Bristol Bay (Fig. 2.1), and Yukon River scales were collected from commercial and test fisheries in the lower river. From 1965-1979, ADF&G sampled chum salmon at Flat Island in the Yukon River Delta, but after 1979, sampling was moved to Big Eddy; about 32 km upriver, after flooding removed Flat Island (L. Dubois, ADF&G, pers. comm.).

### 2.2. Scale Sampling

Age was designated using European notation. These fish spend minimal time in freshwater and spend three to four winters in marine waters before returning to the natal stream to spawn. Thus, a fish that spent 0 winters in freshwater followed by three winters at sea would be designated by 0.3. Including the winter spent as an embryo in gravel, this fish would be four years old (Fig. 2.2).

Acetate impressions of adult chum salmon scales were obtained from the ADF&G regional archive in Anchorage, Alaska. Only age 0.3 and 0.4 fish, the dominant age groups, were used in this study. In Bristol Bay, we obtained samples from 1965 – 2006 for age 0.3 fish and from 1966 – 2006 for age 0.4 fish, and in the Yukon River we obtained samples from 1965– 2006 for age 0.3 fish and from 1967 – 2006 for age 0.4 fish. Scales were collected from salmon captured by drift gillnets. Yukon River fish were captured with 14 cm (85%) and 22.6 cm (15%) mesh size nets; whereas, the mesh size of nets used in Bristol Bay was not recorded. Images of scales were selected for measurement only when: 1) the reader agreed with the age determination previously made by ADF&G; 2) the scale shape indicated the scale was collected from the preferred area of the body (Koo, 1962); 3) circuli and annuli were clearly defined and not affected by scale regeneration or significant resorption along the measurement axis; and, 4) the scale was

from a fish collected between 5 June and 26 July. We sampled scales across the run from 15 June to 15 July to capture timing-related differences in returning salmon, but in some years sample sizes were not sufficient; in which case, sampling extended beyond 15 July to achieve the minimum sample size.

Scale measurements were collected using procedures described by Hagen et al. (2001). Prior to measurement, quality of the acetate impression was examined, and only scales that met measurement selection criteria were included. A digital microfiche reader was used to scan the scale from the acetate impressions, and the image was stored as a high resolution digital image (3352 x 4425 pixels). This allowed the entire scale to be viewed and provided enough pixels between the narrow circuli for accurate measurements of circulus spacing. The scale image was displayed on a digital LCD flat panel monitor, and Optimas 6.5 image processing software was used to measure the scale with a customized program. Scales were measured from the focus to the edge along the longest axis. The distance (resolution ~0.0017 mm/pixel) between each pair of circuli was measured within each growth zone from the scale focus to the outer edge of the first ocean annulus (SW1) then from the outer edge of SW1 to the end of the second ocean annulus (SW2) and so on until the edge of the scale was reached (Fig. 2.2). Data were stored in a Microsoft Access database by growth zone and were linked to the age, sex, and length data by an identification number for each fish. In most years, 25 male and 25 female scales were measured. Previous scale studies indicated 40-50 scales were sufficient to provide an accurate estimate of the mean (Zimmerman, 1991; Briscoe, 2004).

This study focused on two growth zones: the first marine year (SW1) and the third marine year (SW3, Fig. 2.2). The SW1 zone was chosen because it has been hypothesized that growth in the early marine period was critical to the survival of an individual fish (Beamish and Mahnken, 2001). The SW3 zone was chosen because it has been hypothesized that if a fish did not reach a certain size by the end of that year, it remained in marine waters another year and returned the next summer as an age 0.4 fish (Beamish and Mahnken, 2001). If it reached this “critical” size, it returned to spawn as an age 0.3 fish.

Scales were collected from fish during the year of maturation. Growth data (SW1 and SW3) were paired with the corresponding years of environmental data. For example, an age 0.4 fish that returned in 2006 was conceived in 2001, emerged from gravel and spent its first year at

sea in 2002 and its third year at sea in 2004, hence environmental data for 2002 were compared with SW1 growth, and the data from 2004 were compared with SW3 growth.

### 2.3. *Explanatory Variables*

Pink salmon have a two-year life cycle that created an alternating-year pattern of abundance, and Russian pink salmon populations were dominated by odd-year adult pink salmon. We used population abundance of Russian pink salmon because they were the dominant pink salmon population in the western North Pacific Ocean and Bering Sea during this study. In addition, Russian pink salmon abundance was correlated with that of Alaska pink salmon populations ( $p < 0.001$ ), thus the effects would be similar. Total Russian pink ( $Pinks_t$ , 1952-2007) and Asian chum salmon abundances were obtained from Ruggerone et al. (2010) and were updated with North Pacific Anadromous Fish Commission data (Appendix C1). We calculated a four-year moving average of Asian chum salmon abundance ( $Asian\ chums_t$ ) to coincide with the four- to five-year life cycle pattern that dominates North Pacific chum salmon.

As recommended by Mantua (2001), we used a “winter index” of the Pacific Decadal Oscillation (PDO) or an average of the monthly PDO indices from November of the previous year through March of the current year, because year-to-year fluctuations are most apparent during winter. These months were chosen because conditions during this time likely determine the amount of pre-winter and winter mortality of salmon, and both western Alaska and Asian fish overwinter in the Gulf of Alaska and central North Pacific Ocean. We extracted SST data from global monthly temperatures on a 2-degree x 2-degree grid available from the National Oceanic and Atmospheric Administration’s (NOAA) Climate Data Center. To compare SSTs with SW1 growth, we averaged temperatures from areas corresponding with juvenile chum salmon distribution during the first summer ( $Local\ SST_t$ , Appendix C1). Growth in the SW3 zone was compared to average annual SSTs within the Gulf of Alaska, corresponding to the approximate distribution of chum salmon after the first winter until the homeward migration ( $GOA\ Annual\ SST_t$ ). We averaged SSTs within a 10-degree x 30-degree box (48°-58°N, 130°-160°W) over the Gulf of Alaska at year  $t$ .

The North Pacific Index ( $NPI_t$ ) at year  $t$  is the area-weighted sea level pressure over the region 30°N-65°N, 160°E-140°W. The dominant atmosphere-ocean relation in the North Pacific is one where atmospheric changes lead changes in SSTs by one to two months. The Aleutian Low Pressure Index ( $ALPI_t$ ) is the relative intensity of the Aleutian Low pressure system of the

North Pacific (December through March in year  $t$ ). It is calculated as the mean area ( $\text{km}^2$ ) with sea level pressure expressed as an anomaly from the 1950-1997 mean. A positive index value reflects a relatively strong or intense Aleutian Low. We used two wind mixing indices:  $MayMix_t$ , measured in  $\text{m}^3/\text{sec}^3$  at year  $t$  from the vicinity of St. Paul Island, Alaska collected from 1950-2010, and  $JJMixM2_t$ , measured at Mooring 2 ( $57^\circ\text{N}$ ,  $164^\circ\text{W}$ ) in  $\text{m}^3/\text{sec}^3$  from June-July 1950-2010. We used wind mixing indices because they provide an estimate of the rate of mixing at the base of the upper mixed layer, an area in the ocean important to juvenile salmon. The average ice concentration in the Bering Sea at year  $t$  was represented by  $Ice\ Cover_t$ . The index was developed from a  $2^\circ \times 2^\circ$  box ( $56^\circ\text{-}58^\circ\text{N}$ ,  $163^\circ\text{-}165^\circ\text{W}$ ) from 1 January – 31 May. The amount of ice cover has been shown to affect the spring plankton bloom and be important to juvenile salmon (Hunt et al., 2002; Moss et al., 2009). The effect of the El Niño - Southern Oscillation ( $ENSO_t$ ) on the northern hemisphere reaches its maximum during the boreal winter, and we used the mean December-January values of the multivariate ENSO index from the NOAA Earth System Research Laboratory Physical Science Division. El Niño episodes occur every four to five years and can last up to 12 to 18 months. The ENSO index is based on six observed variables over the tropical Pacific: sea-level pressure, zonal and meridional components of surface wind, SST, surface air temperature and total cloudiness fraction of the sky (Wolter and Timlin, 1998). The Arctic Oscillation Index ( $AO_t$ ) examines how atmospheric pressure fluctuates between positive and negative phases. The negative phase brings higher-than-normal pressure over the polar region and lower-than-normal pressure at  $45^\circ\text{N}$  latitude. Thus, in this phase cold air plunges into the Midwestern United States and Western Europe and storms bring rain to the Mediterranean. The positive phase brings opposite conditions, steering ocean storms farther north and bringing wetter weather to Alaska, Scotland and Scandinavia. The AO was most variable during the winter, thus, it captured characteristics when fish may not have enough fat reserves to survive. The Bering Sea Level Pressure winter index ( $BSLPw_t$ ) represents deviations from the mean value of sea level pressure average over the Bering Sea ( $55^\circ - 65^\circ\text{N}$ ,  $170^\circ\text{E} - 160^\circ\text{W}$ ) December through March.

Air temperatures (*Local Air Temp<sub>t</sub>*) from the nearest city to the population (Nome, Alaska for the Yukon River and King Salmon, Alaska for the Nushagak River) were used as a proxy for SST and river temperatures. We obtained air temperatures from western Alaska from the Weather Underground website (Appendix C1). Air temperatures were averaged for winter (November – March), summer (May – September), and annually and were compared with only



first-year growth. All explanatory variables were normalized or “scaled” using the ‘base’ package in R version 2.9.2 (R Development Core Team, 2009), allowing us to directly compare the magnitudes of the estimated effects.

#### 2.4. *Analyses and Models*

We examined relationships between chum salmon growth and potential explanatory variables using correlation analysis followed by multiple linear regression. First, we computed Pearson’s correlations among environmental variables (Table 2.1) to assess potential multi-collinearity. We also computed Pearson’s correlations between growth and environmental variables to identify important variables (Tables 2.2-2.3). Results were used to select a subset of variables for the regression models. We modelled chum salmon growth as a function of the selected variables using a general regression approach:

$$y = \mathbf{X}\boldsymbol{\beta} + \varepsilon \quad (1)$$

where  $y$  was observed growth (SW1 or SW3),  $\mathbf{X}$  was a matrix of explanatory variables, and  $\varepsilon$  were the residuals. Because the time series nature of the data and preliminary analyses suggested the residuals were autocorrelated, we used generalized least squares (GLS) regression to allow for autocorrelation in the residuals. Generalized least squares regression is a technique for estimating unknown parameters in a linear regression model, and GLS is often applied when the variances of the observations are unequal (heteroscedastic) or when there is correlation among observations.

We first used GLS regression to examine the individual hypotheses (i.e. - Asian chum salmon abundance inhibited growth of western Alaska chum salmon). To attempt to explain the processes occurring in the ocean, we created full models based on the results of the simple models and the correlation analyses. We fit each full model assuming that residuals are independent and used a backward stepwise approach, choosing the model with the lowest Akaike Information Criterion (AIC) to select the best submodel. To account for time-series dependence in the residuals, we used a generalized variance-covariance structure that modeled the dependence as an auto-regressive process of order  $p$ , where  $p$  was assumed to be between 1 and 6 to span the generation time of chum salmon. If it existed, we chose the model with the lowest AIC by at least four points (Burnham and Anderson, 2004). We chose the most parsimonious model, if differences in AIC were smaller or whenever the larger model was deemed biologically unrealistic. Plots of the residuals of the reduced final model were examined for normality and influence of outliers. The model was weighted by the number of scales measured per year to

account for unequal sample sizes among years. In the Yukon River, we measured >25 scales per gender per age each year, but in Bristol Bay, there were not enough samples for age 0.3 fish in 1966, and for age 0.4, we had reduced sample sizes in 1969, 1970, 1975, 1977, 1980, and 2000. All model parameters were estimated via restricted maximum likelihood estimation using the 'nlme' package (Pinheiro and Bates, 2000) in R version 2.9.2 (R Development Core Team, 2009).

#### 2.4.1. *SW1 Model*

The SW1 models focused on environmental variables that might influence early marine growth in chum salmon, such as wind mixing and local SST; whereas, the SW3 models focused on comparison of growth with density dependence, competition, SST, and gender differences. Because there were no differences by gender in SW1 growth, we combined the data for SW1, giving us larger samples sizes ( $\geq 50$  in most years). Based on Pearson's correlations and simple linear regressions (Tables 2.1-2.3), we developed a full model that we applied to both populations:

$$SW1_t = \alpha + \beta_1(local\ SST_t) + \beta_2(ALPI_t) + \beta_3(NPI_t) + \beta_4(MayMix_t) + \beta_5(IceCover_t) + \beta_6(local\ Air\ Temp_t) + \varepsilon_t \quad (2)$$

where the terms are defined in Appendix C1.

#### 2.4.2. *SW3 Model*

To test for interactions between pink or Asian chum salmon abundance and third-year growth, we compared SW3 growth with pink and Asian chum salmon abundances. To examine effects of SST on growth, we also included the Gulf of Alaska SST, and at least one environmental index, in this case, the NPI. From our exploratory data analysis, there appeared to be an interaction between pink salmon and Asian chum salmon abundance. In addition, it was suggested that pink salmon abundance altered the feeding and distribution of chum salmon on the high seas (Azumaya and Ishida, 2000; Kaeriyama et al., 2004; Myers et al., 2004). Because of uncertainty about this interaction, we chose to examine the model with and without the interaction. We also included separate intercepts by gender in these models to account for the observed larger mean size of males. The Nushagak female SW3 growth zone had an outlier (1975). Removal of the outlier did not have a strong effect on the results, thus it was retained for further analyses.

$$SW3_t = \alpha + \beta_1(Pinks_t) + \beta_2(Asian\ Chums_t) + \beta_3(GOA\ Annual\ SST_t) + \beta_4(NPI_t) + \beta_5(Pinks_t * Asian\ Chums_t) + Gender_k + \varepsilon_t \quad (3)$$

where the terms are defined in Appendix C1.

#### 2.4.3. Other Analyses

We examined whether total mean scale radius was a good predictor of average adult fish length (mm) using the following linear model:

$$L_t = \alpha + \beta_1(R_t) \quad (4)$$

where  $L_t$  was mean adult length at year  $t$ , and  $R_t$  was mean scale radius a year  $t$ .

All response variables (SW1 and SW3) were plotted and examined for normality and outliers. Shapiro-Wilk tests for normality were used to assess the normality of the response variables. The response variables were plotted by odd and even year of growth to determine whether there was an odd-even year effect due to pink salmon abundance. We compared mean annual growth between odd and even years using Student's  $t$ -test. Differences in growth by gender were examined by comparing annual mean male and female growth using a Welch Two Sample  $t$ -test.

Because preliminary analyses revealed potential non-stationarity in some of the observed relationships for SW3 growth, we examined relationships between marine growth (SW3) and the environment more closely by repeating the analyses for the period before (pre-1977) and after (post-1976) the regime shift (Hare and Mantua, 2000; Mantua and Hare, 2002). There were fewer years prior to the regime shift available.

### 3. Results

Adult fish length was positively related to total scale growth for both ages in both populations (Fig. 2.3; Yukon River: age 0.3,  $R^2 = 0.65$ ; age 0.4,  $R^2 = 0.68$ ; Bristol Bay: age 0.3,  $R^2 = 0.62$ ; age 0.4,  $R^2 = 0.65$ ). Scale growth explained 62-68% of the variability in fish length depending on stock and age.

Normalized time series plots of SW1 and SW3 growth showed no apparent pattern related to the odd-even year abundance of Asian pink salmon (Figs. 2.4-2.5). All plots showed changes in growth around the 1976-77 regime shift. For example, Nushagak River age 0.3 SW1 growth increased and SW3 growth decreased in the mid-1970s, corresponding to the PDO (Fig.

2.4). Only first-year growth of Yukon River age 0.4 males was significantly different in odd versus even years ( $t = 2.088$ ;  $p = 0.044$ ), and Yukon River age 0.3 females third-year growth was marginally significantly more negative in odd years versus even years ( $t = -1.863$ ;  $p = 0.070$ ; Student  $t$ -test; Table 2.4). Third-year growth, scale radius, and fish length was significantly larger for males (Welch Two-Sample  $t$ -test,  $p < 0.005$ ) for both age classes (age 0.3 and 0.4 fish) and populations. In contrast, first-year growth did not differ significantly between males and females ( $p > 0.4$  in all cases). Therefore, differences by gender were included in all models of SW3 growth.

### 3.1. *Gender*

We found that for most populations and ages the growth of females was significantly less than that of males during SW3, as indicated by negative model coefficients (Tables 2.5-2.12). For age 0.4 fish from Bristol Bay, some of the values were positive. This contradicted previous work examining seasonal growth using different methods, indicating females grew faster than males during the third year of growth (Chapter 1).

### 3.2. *Yukon River*

#### 3.2.1. *SW1 growth*

For age 0.3 fish, simple linear regressions indicated that Nome annual air temperature, PDO, and local SST had significant positive effects, and NPI, BSLP winter index, and ice cover had significant negative effects on the first year of growth of Yukon River chum salmon (Table 2.5). The ALPI had a marginally significant positive effect on first-year growth of age 0.3 fish (Fig. 2.6). For age 0.4 fish, we found that ALPI, Nome annual air temperature, and local SST had significant positive effects; however, NPI had significant negative effects on the first year of growth of Yukon River chum salmon (Table 2.5).

The best overall model for first-year growth of age 0.3 fish included a negative effect of the May mixing index and a positive relationship with Nome annual air temperature (Table 2.6). For age 0.4 fish, the best model suggested positive effects of local sea surface temperature, ALPI, and the May mixing index on first-year growth (Table 2.6).

#### 3.2.2. *SW3 growth*

Correlations and simple linear regressions indicated that total Russian pink salmon and Asian chum salmon abundance, and Gulf of Alaska SST had significant negative effects on the

third year of marine growth for both ages for Yukon River chum salmon (Table 2.7 and Fig. 2.7). Males grew faster than females in the SW3 growth zone, and the gender difference was more pronounced for age 0.3 than for age 0.4 salmon. The best multiple regression for age 0.3 Yukon River fish suggested a positive effect of pink salmon and a negative effect of GOA SST on third-year growth and included the interaction term (AIC = -246.9). When the interaction term was removed, the model included Russian pink and Asian chum salmon abundance, but it was difficult to determine whether or not to include GOA SST. The AIC values with and without GOA SST were very similar ( $\Delta\text{AIC} = 1.1$ ). In all three models, the model coefficient for pink salmon abundance, although very small, was significantly positive, contradicting our hypothesis. Asian chum salmon abundance had significant negative relationship with third-year growth ( $p \leq 0.051$ ).

For age 0.4 fish, the final model with the interaction term indicated that pink and Asian chum salmon abundance, Gulf of Alaska SST had significant negative effects on third-year growth. Russian pink salmon abundance and the interaction term of pink and Asian chum salmon abundance had significant positive correlation with SW3 growth (Table 2.7). Without the interaction term, the model reduced to indicate that Gulf of Alaska SST had a significant negative effect on SW3 growth. For age 0.4 fish, we found that overall females grew slower than males.

For both ages, the AIC values of the full model, including the interaction term, were lower than AIC values from reduced models without the interaction term, indicating that the more complex model was a better representation of what was occurring in the ocean.

### 3.3. *Bristol Bay*

#### 3.3.1. *SW1 growth*

For both ages, the results of the simple linear regression models indicated that the ALPI, PDO, King Salmon annual air temperature, and local SST had significant positive effects, and NPI, and a second wind mixing index (JMMixM2) had significant negative effects on the first year of marine growth of Bristol Bay chum salmon (Fig. 2.6 and Table 2.8). The May wind mixing index, ice cover, and BSLP winter index all showed marginally significant negative effects on first-year growth. For age 0.3 fish, the full model reduced to show that local SST and the ice cover index had significantly positive effects on SW1 growth (Table 2.6). For age 0.4 fish, the full model reduced by one term to include local SST, ALPI, NPI, May wind mixing, and the ice cover index as factors affecting first-year growth. Local SST and ice cover had a significant

positive relationship, but the other explanatory variables (ALPI, May wind mixing and NPI) showed a detectable negative relationship with first-year growth (Table 2.6).

### 3.3.2. *SW3 growth*

The results of the simple linear regression models (Table 2.8) indicated that for age 0.3 Bristol Bay chum salmon Asian chum salmon abundance and the Gulf of Alaska SST had significant negative effects on the third year of marine growth; while pink salmon abundance had significant positive effects on SW3 growth when gender was removed from the model (Fig. 2.7). We also found a significant positive relationship of the ENSO with SW3 growth and age 0.3 chum salmon. For age 0.4 fish, pink salmon abundance, and ENSO had significant positive effects and Gulf of Alaska SST showed significant negative effects on third-year growth. Asian chum salmon abundance showed no significant effect ( $p = 0.910$ ) on third-year growth. The ALPI showed marginally significant negative effects on SW3 growth.

The best model for age 0.3 Bristol Bay fish (Table 2.7) indicated that Asian chum salmon abundance had negatively significant effects on third-year growth. Pink salmon abundance and the interaction term (Pinks\*Asian chums) had a significant positive relationship with SW3 growth. Females showed significantly less SW3 growth than males. When the initial model did not include the interaction term, the reduced model indicated that Asian chum salmon abundance had significant negative effects on SW3 growth of age 0.3 chum salmon from Bristol Bay. For age 0.4 fish, the reduced model indicated that GOA SST had significant negative effects and pink salmon abundance had significant positive effects on third-year growth (Table 2.7).

## 3.4. *Regime shift effects*

### 3.4.1. *Regime shift effects on Yukon River chum salmon*

For age 0.3 fish, the simple linear regressions of the pre-1977 growth indicated that NPI and PDO had negative effects on third-year growth before and after the regime shift; whereas, ENSO, ALPI and Asian chum had positive effects on third-year growth pre- and post- regime shift (Fig. 2.8). These were not always significant (i.e., Asian chums,  $p = 0.176$ ). Gulf of Alaska SST had a marginally positive effect pre-regime shift and a negative effect post-regime shift on SW3 growth. Pink salmon abundance showed marginally negative significant effect on SW3 growth prior to the regime shift then significant positive effects on SW3 growth after the regime shift (Table 2.9). As expected, growth of females was slower during the SW3 zone than growth

of males. For age 0.4 fish, we found that GOA SST had negative effects on SW3 growth before and after the regime shift; whereas, ENSO had positive effects on SW3 growth pre- and post-regime shift (Fig. 2.8). Otherwise, pink salmon abundance, Asian chums, ALPI, and PDO all had mixed effects on SW3 growth. All variables, except Asian chums, had a negative relationship with SW3 growth prior to the regime shift and a positive relationship with SW3 growth after the shift. Most of the pre-regime shift relationships with SW3 growth were significant, while the post-regime relationships with third-year growth were not (Table 2.10).

The best pre-regime model for age 0.3 fish indicated that pink salmon abundance, Gulf of Alaska SST, and NPI had significant negative effects on SW3 growth; however, the best model for age 0.4 fish indicated a significantly positive relationship with SW3 growth, GOA SST, and Asian chum salmon abundance prior to the regime shift (Table 2.9). One alternative model for both ages, which seemed biologically plausible, included an additive term combining pink and Asian chum salmon abundance. These two explanatory variables were highly correlated (Table 2.10). The best post-regime model indicated for both ages that pink abundance had significant positive effects, while Gulf of Alaska SST and NPI had negative effects on third-year growth (Table 2.10).

#### 3.4.2. *Regime shift effects on Bristol Bay chum salmon*

For age 0.3 fish, the simple linear regressions indicated that pinks and Asian chum salmon abundance, ENSO, and PDO had positive effects on third-year growth pre- and post-regime shift (Fig. 2.6). NPI, Gulf of Alaska SST, and ALPI had different pre- and post-regime effects on SW3 growth (Tables 2.11-2.12). For age 0.4 fish, we found that Asian chum salmon abundance showed negative effects on SW3 growth before and after the regime shift; whereas, pink salmon abundance and ENSO had positive effects on SW3 growth pre- and post-regime shift (Fig. 2.8). Otherwise, NPI, GOA SST, ALPI, and PDO all showed mixed effects on SW3 growth. NPI, GOA SST, and ENSO had a positive relationship with SW3 growth prior to the regime shift and a negative relationship with SW3 growth post-regime shift; however, ALPI and PDO had negative relationships with third-year growth prior to the 1976-77 regime shift (Fig. 2.8).

Prior to the regime shift, the best model for age 0.3 Bristol Bay salmon was the full model (AIC = -73.1). For age 0.4 fish, the model reduced to a simple linear regression or an additive term of pink + Asian chum abundance, which resulted in a significant positive

relationship with SW3 growth (Table 2.11). After the regime shift, the best model for age 0.3 fish indicated that Asian chum abundance and NPI significantly affected SW3 growth. For age 0.4 age fish, the best model included the interaction term. Without the pink\*chum interaction term the AICs indicated that there was a tie for either a model with a significant positive effect of Asian chum salmon abundance on SW3 growth or one with a significant positive effect of pink salmon abundance on SW3 growth, neither of which really makes biological sense (Table 2.12).

#### 4. Discussion

Overall, we found that warmer regional temperatures, NPI, and less ice cover significantly enhanced the first-year growth of chum salmon in Bristol Bay and Yukon River. We found that third-year growth was significantly affected by Asian chum salmon abundance for all except Bristol Bay age 0.4 fish. In contrast to our hypothesis that cooler temperatures in the Gulf of Alaska would inhibit growth, we found that warmer large-scale SSTs from the Gulf of Alaska were associated with reduced SW3 growth.

Although we found evidence of interspecific interactions due to the effect of the abundance of Russian pink salmon on third-year growth, the effects were much smaller than the effects of Asian chum salmon abundance and GOA SST on SW3 growth. It is possible that this may be due to the regime shift in 1976-1977 because in the Yukon River, we observed the pink salmon relationship with SW3 growth switch from negative before the regime shift to positive after the regime shift. Consequently, it appeared that although pink salmon abundance affected chum salmon growth, it was not as disruptive to growth as expected (Fig. 2.7). It is possible that the abundance of Asian chum salmon has created a masking effect, overwhelming other effects on the growth of western Alaska chum salmon in the North Pacific Ocean.

Enhanced first-year growth was associated with either local SST and/or regional air temperature in both populations. After the 1976-77 regime shift, SSTs in coastal areas warmed (Mantua et al., 1997; Hare et al., 1999), and likely this has contributed to the positive correlation between SW1 growth and SST. Overall, first-year growth was negatively correlated with the NPI and positively correlated with the ALPI. Including the NPI improved the fit of the full models, thus this might be a useful component to add when trying to improve salmon forecasting models. Ice cover showed negative effects on first-year growth in the simple regressions (Fig. 2.6) and was part of the full model for Bristol Bay. The varying ice cover in recent years has possibly had significant effects on juvenile salmon growth and consequently salmon abundance. Farley and



Moss (2009) reported that the relative abundance of juvenile chum salmon in the southern region (southeastern Bering Sea – Kuskokwim River south to the Alaska Peninsula) was less during cold years or years with greater ice cover.

The only environmental indices that had a significant effect on the growth of Bristol Bay and Yukon River were ENSO and PDO. Both are correlated with the GOA SSTs. We hypothesized that cooler temperatures in the Gulf of Alaska would inhibit the marine growth of western Alaska chum salmon, and Gulf of Alaska temperatures significantly affected marine growth of both ages of Bristol Bay and Yukon River chum salmon, but the model coefficients were negative. Thus, this contradicts our hypothesis. We found that warmer SSTs, which are generally believed to promote salmon growth, coincided with reduced chum salmon growth in western Alaska. Although this appears counterintuitive, Ruggerone et al. (2011) found that adult length-at-age was negatively correlated with SST, rather than positively correlated as hypothesized (Mueter et al., 2002a; Mueter et al., 2002b; Ruggerone et al., 2007b). They suggested that this was due to density-dependent effects involving abundance of hatchery chum salmon. Perhaps the abundance of hatchery chum salmon overwhelmed the favorable growing conditions associated with warm SSTs. Our results support this suggestion. We found strong negative relationships with the abundance of Asian chum salmon, which were mostly hatchery salmon, and the growth of three out of four populations/ages that we examined.

We hypothesized that Russian pink salmon abundance inhibited the growth of western Alaska chum salmon during the third year in the ocean. Studies of sockeye salmon also found a negative effect of the abundance of pink salmon during the second and third year at sea, and it began immediately after peak prey availability in spring and continued to the end of the growing season (Ruggerone and Nielsen, 2004; Ruggerone et al., 2005). In this study, Russian pink salmon abundance was shown to significantly affect third-year growth in most of the models, but the model coefficients for Russian pink salmon were extremely small. When compared to the coefficients calculated for Asian chum salmon abundance and SST, it appears likely that Russian pink salmon affect third-year growth less than other factors.

Because we found the model coefficients for pink salmon abundance oscillating between both positive and negative results, which did not make biological sense, we compared these models pre- and post-regime shift to determine if the regime shift affected the results. Prior to the regime shift, the abundance of Russian pink salmon affected the age 0.3 marine growth of the

Yukon River negatively, but there was a significant positive result for both populations and ages post-regime shift. After the regime shift, all simple linear regressions indicated significant positive results with pink salmon abundance. Considering how closely the growth of Yukon River and Bristol Bay chum salmon in the first and third year of growth were linked to SST, it is possible that the variability in SSTs after the regime shift altered ocean productivity, allowing pink and chum salmon abundance to increase concurrently. In addition, increased chum abundance was likely due to hatchery production. Approximately 3.1 billion hatchery chum salmon are released each year from Asian and North American hatcheries (Kaeriyama and Edpalina, 2008).

Researchers have suggested that Asian chum salmon shift their spatial distribution from the Bering Sea to the North Pacific Ocean in years when pink salmon abundance is high (Ogura and Ito, 1994; Azumaya and Ishida, 2000). Azumaya and Ishida (2000) found that there was no significant relationship between growth of chum salmon and abundance of pink salmon, suggesting that growth of chum salmon during their marine life was more affected by intraspecific interactions than interspecific interactions. If pink salmon showed increased productivity and abundance due to variability in SSTs, and this abundance forced chum salmon to move into the Gulf of Alaska where the SSTs were slowly increasing over time although were highly variable, it is possible that productivity or growing conditions were good for both species. Thus, variability in SSTs might explain the positive model coefficients for Russian pink salmon abundance. Both pink and chum salmon might show improved abundance due to the improved ocean conditions and variability in SST, which possibly increased prey production and salmon growth. In addition, the unique gut architecture of chum salmon allows them to eat a diverse diet. In comparison with sockeye salmon, which are sympatric with Asian pink salmon and share similar prey, chum salmon are omnivorous. When pink salmon abundance increased, chum salmon were capable of “prey switching” and foraged on lower quality prey, such as gelatinous zooplankton, including amphipods, euphausiids, pteropods, and copepods (Andrievskaya, 1966; Davis et al., 2000; Davis et al., 2004). Prey switching would permit chum salmon to survive and possibly increase in abundance when prey productivity was high, unlike sockeye salmon, whose growth has been reduced in odd years due to competition with abundant pink salmon (Ruggerone et al., 2003; Ruggerone et al., 2005).

The “best” model for SW3 growth included gender as a factor in all of the GLS models. Breeding males are larger than females, and this appeared to be when size differentiation occurred (Chapter 1).

Most intermingling of North American and Asian chum salmon occurs when Asian fish extend their range into the Gulf of Alaska during their second and third winters at sea (Urawa, 2003; Myers et al., 2004; Urawa et al., 2004; Fukuwaka et al., 2007a; Fukuwaka et al., 2007b; Urawa et al., 2009). We found that the abundance of Asian chum salmon was negatively correlated with the growth of both ages of Yukon River and age 0.3 Bristol Bay chum salmon. Asian chum salmon abundance had more of an effect on the growth of age 0.3 than age 0.4 fish. Age 0.3 is the predominant age group of Asian chum salmon (Kaeriyama, 1989), thus it is likely that the growth of these fish was affected first by increased abundance of Asian chum. Competition among conspecifics for prey items would likely be greater among those from the same age group. To return one year earlier, age 0.3 fish must grow faster to attain the length necessary to reproduce one year prior to age 0.4 fish, thus competition would affect them first. Age 0.4 fish have another year to feed in the ocean and “catch up” to reach the minimum size needed for reproduction.

These findings were consistent with results from a study of Norton Sound chum salmon (Kwiniuk River, G. Ruggerone, NRC, Inc., pers. comm.). Although we did not examine SW2 growth, they found that SW2 scale growth and length-at-age of chum salmon was negatively correlated with abundance of Asian chum salmon. Western Alaska chum salmon are believed to be in the Gulf of Alaska and North Pacific Ocean during the second and third years of growth and potentially are affected by similar growth conditions. We also found that the interaction with Asian chum salmon was stronger than the interspecific effects of pink salmon. Production of adult hatchery chum salmon from Asia increased rapidly beginning in 1970, and numbers of hatchery chum salmon have exceeded total production of wild adult salmon in the North Pacific Ocean. Asian chum salmon, at approximately two billion fish per year (Ruggerone et al., 2010), are currently the dominant chum salmon stock in the Bering Sea and North Pacific Ocean. It appears that it would be advisable to examine our SW2 data to see if we can determine when these interactions begin to occur. In addition, other factors, such as the regime shift, appeared to obscure the overall results.

The Gulf of Alaska is part of a dynamic ecosystem, and several of the explanatory variables used in the models overlap or have “autocorrelation.” In addition, we found that the dynamic nature of the ecosystem created additional problems, which is evident by the importance of the multiplicative effects in the full models. Some would suggest that these interactions led to spurious results, while others indicate that these were interactions among a complex ecosystem. Overall, it appeared that SST, abundance of pink salmon, the NPI, May wind mixing, ice cover, local air temperature, and the abundance of Asian chum salmon influenced scale growth of Bristol Bay and Yukon River chum salmon during the first and third year at sea depending upon population, fish age, and interactions among the explanatory variables.

Asian chum salmon are currently the dominant chum salmon stock in the Bering Sea and North Pacific Ocean (Ruggerone et al., 2010). Our results indicated that intraspecific interactions with conspecific chum salmon were stronger than interspecific interactions with abundant pink salmon. Because most of the Asian chum salmon were hatchery-raised, this has become a conundrum. There is a great deal of controversy around the issue of whether hatchery salmon affect wild salmon, but our results demonstrated significant negative effects on chum salmon growth due to the abundance of Asian chum salmon. Determination of how detrimental these effects are to the overall population is a future exercise.

In recent decades, researchers have raised serious concerns about density-dependent effects on salmon due to increased hatchery production, questioning whether there are limits to the carrying capacity of the North Pacific Ocean. Climate change may have altered the carrying capacity. Our results add to concerns about density dependence and the possible effects this may have on wild salmon. Salmon, originating from distant regions and adjacent continents, share a common food resource and due to distributional overlap in the North Pacific Ocean and Bering Sea, it appears that possible density-dependent effects occur. This paper was part of a study prompted by declining chum salmon abundance in the Yukon River and western Alaska. The effects on local communities, many of whom depend on these fish for subsistence, were devastating, and disaster declarations were enacted. We were unable to determine the mechanism causing the declines in abundance of western Alaska chum salmon, but our results contribute to growing evidence for density dependence and for competition for among conspecific salmon.

## Acknowledgments

This investigation was funded by the Arctic-Yukon-Kuskokwim (AYK) Sustainable Salmon Initiative (Projects 45677 and 45164) as Historical Analyses of AYK and Asian Chum Salmon, phase one and two, and by the North Pacific Marine Research Program (Project SFOS 99-188). We appreciate the efforts to gather, measure, and catalogue scales by many unknown ADF&G staff, as well as: D. Folletti, J. Baker, J. Cashen, J. Chesmore, S. Hinton, M. Lovejoy, A. Norman, W. Rosky, and W. Whelan. We also received support from a number of ADF&G staff, including: L. Brannian, D. Evenson, E. Volk, L. Dubois, H. Krenz, T. Baker, F. West, L. Fair, D. Oxman, T. Frawley, and W. Johnson. E. Siddon and J. Richar developed the SST program as part of a University of Alaska Fairbanks graduate class. Constructive comments on the paper were provided by Drs. W. Smoker, P. Hagen, G. Kruse., C. Robinson, and E. Volk. Two anonymous reviewers provided helpful suggestions.

## References

- Anderson, P.J., Piatt, J.F., 1999. Community reorganization in the Gulf of Alaska following ocean climate regime shift. *Marine Ecology Progress Series* 189, 117-123.
- Andrievskaya, L.D., 1966. Food relationships of the Pacific salmon in the sea. *Voprosy Ikhtiologii* 6 (1), 84-90.
- Azumaya, T., Ishida, Y., 2000. Density interactions between pink salmon (*Oncorhynchus gorbuscha*) and chum salmon (*O. keta*) and their possible effects on distribution and growth in the North Pacific Ocean and Bering Sea. *North Pacific Anadromous Fish Commission Bulletin* 2, 165-174.
- Beacham, T.D., Candy, J.R., Sato, S., Urawa, S., Le, K.D., Wetklo, M., 2009. Stock origins of chum salmon (*Oncorhynchus keta*) in the Gulf of Alaska during winter as estimated with microsatellites. *North Pacific Anadromous Fish Commission Bulletin* 5, 15-23.
- Beamish, R.J., Mahnken, C., 2001. A critical size and period hypothesis to explain natural regulation of salmon abundance and the linkage to climate and climate change. *Progress in Oceanography* 49, 423-437.
- Briscoe, R.J., 2004. Factors affecting marine growth and survival of Auke Creek, Alaska coho salmon (*Oncorhynchus kisutch*), MS thesis, University of Alaska, Fairbanks.
- Burnham, K.P., Anderson, D.R., 2004. Understanding AIC and BIC in model selection. *Sociological Methods and Research* 33, 261-304.
- Cooney, R., Brodeur, R.D., 1998. Carrying capacity and North Pacific salmon production: stock-enhancement implicatoin. *Bulletin of Marine Science* 62 (2), 443-464.
- Davis, N.D., Aydin, K.Y., Ishida, Y., 2000. Diel catches and food habits of sockeye, pink, and chum salmon in the Central Bering Sea in summer. *North Pacific Anadromous Fish Commission Bulletin* 2, 99-109.

- Davis, N.D., Fukuwaka, M., Armstrong, J.L., Myers, K.W., 2004. Salmon food habits studies in the Bering Sea, 1960 to present. North Pacific Anadromous Fish Commission Technical Report 6, 24-29.
- Farley, E.V., Jr., Moss, J.H., 2009. Growth rate potential of juvenile chum salmon on the Eastern Bering Sea Shelf: an assessment of salmon carrying capacity. North Pacific Anadromous Fish Commission Bulletin 5, 265-277.
- Farley, E.V., Jr., Moss, J.H., Beamish, R.J., 2007a. A review of the critical size, critical period hypothesis for juvenile Pacific salmon. North Pacific Anadromous Fish Commission Bulletin 4, 311-317.
- Farley, E.V., Jr., Murphy, J.M., Adkison, M.D., Eisner, L.B., Helle, J.H., Moss, J.H., Nielsen, J., 2007b. Early marine growth in relation to marine-stage survival rates for Alaska sockeye salmon (*Oncorhynchus nerka*). Fishery Bulletin 105 (1), 121-130.
- Farley, E.V., Jr., Starovoytov, A.N., Naydenko, S.V., Heintz, R., Trudel, M., Guthrie, C., Eisner, L., Guyon, J., 2011. Implications of a warming eastern Bering Sea for Bristol Bay sockeye salmon. ICES Journal of Marine Science 68 (6), 1138-1146.
- Fisher, J.P., Percy, W.G., 2005. Seasonal changes in growth of coho salmon (*Oncorhynchus kisutch*) off Oregon and Washington and concurrent changes in the spacing of scale circuli. Fishery Bulletin 103, 34-51.
- Fukuwaka, M., Azumaya, T., Nagasawa, T., Starovoytov, A.N., Helle, J.H., Saito, T., Hasegawa, E., 2007a. Trends in abundance and biological characteristics of chum salmon. North Pacific Anadromous Fish Commission Bulletin 4, 35-43.
- Fukuwaka, M., Kaeriyama, M., 1997. Scale analyses to estimate somatic growth in sockeye salmon, *Oncorhynchus nerka*. Canadian Journal of Fisheries and Aquatic Sciences 54 (3), 631-636.
- Fukuwaka, M., Sato, S., Takahashi, S., Onuma, T., Sakai, O., Tanimata, N., Makino, K., Davis, N.D., Volkov, A.F., Seong, K.B., 2007b. Winter distribution of chum salmon related to environmental variables in the North Pacific. North Pacific Anadromous Fish Commission Technical Report 7, 29-30.
- Hagen, P.T., Oxman, D.S., Agler, B.A., 2001. Developing and deploying a high resolution imaging approach for scale analysis. North Pacific Anadromous Fish Commission Document 567, 1-11.
- Hare, S.R., Mantua, N.J., 2000. Empirical evidence for North Pacific regime shifts in 1977 and 1989. Progress in Oceanography 47, 103-145.
- Hare, S.R., Mantua, N.J., Francis, R.C., 1999. Inverse production regimes: Alaska and west coast Pacific salmon. Fisheries 24 (1), 6-14.
- Healey, M.C., 1986. Optimum size and age at maturity in Pacific salmon and effects of size-selective fisheries. Canadian Special Publication of Fisheries and Aquatic Sciences 89, 39-52.
- Holt, C.A., Rutherford, M.B., Peterman, R.M., 2008. International cooperation among nation-states of the North Pacific Ocean on the problem of competition among salmon for a common pool of prey resources. Marine Policy 32 (4), 607-617.

- Hunt, G.L., Jr, Stabeno, P., Walter, G., Sinclair, E., Brodeur, R.D., Napp, J.M., Bond, N.A., 2002. The Eastern Bering Sea: evidence for change and a new hypothesis linking ecosystem control and climate. *Deep Sea Res. II: Topical Studies in Oceanography* 49, 5821-5853.
- Ishida, Y., Ito, S., Kaeriyama, M., McKinnell, S., Nagasawa, K., 1993. Recent changes in age and size of chum salmon (*Oncorhynchus keta*) in the North Pacific Ocean and possible causes. *Canadian Journal of Fisheries and Aquatic Sciences* 50 (2), 290-295
- Kaeriyama, M., 1989. Comparative morphology and scale formation in four species of *Oncorhynchus* during early life. *Ichthyological Research* 35 (4), 445-452
- Kaeriyama, M., Edpalina, R.R., 2008. Evaluation of the biological interaction between wild and hatchery population for sustainable fisheries management of Pacific salmon. In: Leber, K.M., Kitada, S., Blankenship, H. L., Svåsand, T. (Ed.), *Stock Enhancement and Sea Ranching: Developments, Pitfalls and Opportunities*, Second Edition. Blackwell Publishing Ltd., Oxford, pp. 245-259.
- Kaeriyama, M., Nakamura, M., Edpalina, R.R., Bower, J.R., Yamaguchi, H., Walker, R.V., Myers, K.W., 2004. Change in feeding ecology and trophic dynamics of Pacific salmon (*Oncorhynchus* spp.) in the central Gulf of Alaska in relation to climate events. *Fisheries Oceanography* 123, 197-207.
- Kaeriyama, M., Yatsu, A., Kudo, H., Saitoh, S., 2007a. Where, when, and how does mortality occur for juvenile chum salmon *Oncorhynchus keta* in their first ocean year? *North Pacific Anadromous Fish Commission Technical Report* 7, 52-55.
- Kaeriyama, M., Yatsu, A., Noto, M., Saitoh, S., 2007b. Spatial and temporal changes in the growth patterns and survival of Hokkaido chum salmon populations in 1970–2001. *North Pacific Anadromous Fish Commission Bulletin* 4, 251-256.
- Koo, T.S.Y., 1962. Age designation in salmon. *Studies of Alaska red salmon*. University of Washington Publications in Fisheries, New Series 1, 37-48.
- Mantua, N.J., 2001. The Pacific Decadal Oscillation. In: McCracken, M.C., Perry, J.S. (Eds.), *The Encyclopedia of Global Environmental Change, The Earth System: physical and chemical dimension of global environmental change*, pp. 592-594.
- Mantua, N.J., Hare, S.R., 2002. The Pacific decadal oscillation. *Journal of Oceanography* 58, 35-44.
- Mantua, N.J., Hare, S.R., Zhang, Y., Wallace, J.M., Francis, R.C., 1997. A Pacific interdecadal climate oscillation with impacts on salmon production. *Bulletin of the American Meteorological Society* 78 (6), 1069-1079.
- Martinson, E.C., Helle, J.H., Scarnecchia, D.L., Stokes, H.H., 2008. Density-dependent growth of Alaska sockeye salmon in relation to climate-oceanic regimes, population abundance, and body size, 1925 to 1998. *Marine Ecology Progress Series* 370, 1-18.
- Moss, J.H., Murphy, J.M., Farley, E.V., Jr., Eisner, L.B., Andrews, A.G., 2009. Juvenile pink and chum salmon distribution, diet, and growth in the Northern Bering and Chukchi Seas. *North Pacific Anadromous Fish Commission Bulletin* 5, 191-196.
- Mueter, F., Pyper, B.J., Peterman, R.M., Wood, C.C., Blackbourn, D.J., 2002a. Opposite effects of sea-surface temperature on survival rates of Pacific salmon from northern and southern areas. *North Pacific Anadromous Fish Commission Technical Report* 4, 22-23.

- Mueter, F.J., Peterman, R.M., Pyper, B.J., 2002b. Opposite effects of ocean temperature on survival rates of 120 stocks of Pacific salmon (*Oncorhynchus spp.*) in northern and southern areas. *Canadian Journal of Fisheries and Aquatic Sciences* 59 (3), 456-463.
- Myers, K.W., Klovach, N.V., Gritsenko, O.F., Urawa, S., Royer, T.C., 2007. Stock-specific distributions of Asian and North American salmon in the open ocean, interannual changes, and oceanographic conditions. *North Pacific Anadromous Fish Commission Bulletin* 4, 159-177.
- Myers, K.W., Walker, R.V., Davis, N.D., Armstrong, J.L., 2004. Diet overlap and potential feeding competition between Yukon River chum salmon and hatchery salmon in the Gulf of Alaska in summer. High Seas Salmon Research Program, Fisheries Research Institute, School of Aquatic and Fishery Sciences, University of Washington, Seattle.
- Ogura, M., Ito, S., 1994. Change in the known ocean distribution of Japanese chum salmon, *Oncorhynchus keta*, in relation to the progress of stock enhancement. *Canadian Journal of Fisheries and Aquatic Sciences* 51 (3), 501-505.
- Peterman, R.M., Pyper, B.J., Lapointe, M.F., Adkison, M.D., Walters, C.J., 1998. Patterns of covariation in survival rates of British Columbian and Alaskan sockeye salmon (*Oncorhynchus nerka*) stocks. *Canadian Journal of Fisheries and Aquatic Sciences* 55 (11), 2503-2517.
- Pinheiro, J., Bates, D., 2000. *Mixed-effects models in S and S-Plus*. 528 pp.
- Pyper, B.J., Peterman, R.M., 1999. Relationship among adult body length, abundance, and ocean temperature for British Columbia and Alaska sockeye salmon (*Oncorhynchus nerka*), 1967-1997. *Canadian Journal of Fisheries and Aquatic Sciences* 56 (10), 1716-1720.
- R Development Core Team, 2009. *A language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna.
- Ruggerone, G.T., Agler, B.A., Nielsen, J.L., 2011. Evidence for competition at sea between Norton Sound chum salmon and Asian hatchery chum salmon. *Environmental Biology of Fishes* 92, 1-15.
- Ruggerone, G.T., Farley, E., Nielsen, J., Hagen, P., 2005. Seasonal marine growth of Bristol Bay sockeye salmon (*Oncorhynchus nerka*) in relation to competition with Asian pink salmon (*O. gorbuscha*) and the 1977 ocean regime shift. *Fishery Bulletin* 103 (2), 355-370.
- Ruggerone, G.T., Nielsen, J.L., 2004. Evidence for competitive dominance of pink salmon (*Oncorhynchus gorbuscha*) over other salmonids in the North Pacific Ocean. *Reviews in Fish Biology and Fisheries* 14, 371-390.
- Ruggerone, G.T., Nielsen, J.L., Agler, B., 2007a. Retrospective analysis of AYK chinook salmon growth. Prepared for the 2007 Arctic Yukon Kuskokwim Sustainable Salmon Initiative, Anchorage, AK. 44 pp.
- Ruggerone, G.T., Nielsen, J.L., Agler, B.A., 2009. Linking marine and freshwater growth in western Alaska Chinook salmon *Oncorhynchus tshawytscha*. *Journal of Fish Biology* 75 (6), 1287-1301.
- Ruggerone, G.T., Nielsen, J.L., Bumgarner, J., 2007b. Linkages between Alaskan sockeye salmon abundance, growth at sea, and climate, 1955-2002. *Deep Sea Research Part II* 54 (23-26), 2776-2793.



- Ruggerone, G.T., Peterman, R.M., Dorner, B., Myers, K.W., 2010. Magnitude and trends in abundance of hatchery and wild pink salmon, chum salmon, and sockeye salmon in the North Pacific Ocean. *Marine and Coastal Fisheries* 2, 306-328.
- Ruggerone, G.T., Zimmermann, M., Myers, K.W., Nielsen, J.L., Rogers, D.E., 2003. Competition between Asian pink salmon (*Oncorhynchus gorbuscha*) and Alaskan sockeye salmon (*O. nerka*) in the North Pacific Ocean. *Fisheries Oceanography* 12 (3), 209-219.
- Urawa, S., 2003. Stock identification studies of high seas salmon in Japan: a review and future plan. *North Pacific Anadromous Fish Commission Technical Report* 5, 9-10.
- Urawa, S., Azumaya, T., Crane, P.A., Seeb, L.W., 2004. Origins and distribution of chum salmon in the Central Bering Sea. *North Pacific Anadromous Fish Commission Technical Report* 6, 67-70.
- Urawa, S., Sato, S., Crane, P.A., Agler, B., Josephson, R., Azumaya, T., 2009. Stock-specific ocean distribution and migration of chum salmon in the Bering Sea and North Pacific Ocean. *North Pacific Anadromous Fish Commission Bulletin* 5, 131-146.
- Wolter, K., Timlin, M.S., 1998. Measuring the strength of ENSO - how does 1997/98 rank? *Weather* 53, 315-324.
- Zaporozhets, O.M., Zaporozhets, G.V., 2004. Interaction between hatchery and wild Pacific salmon in the Far East of Russia: a review. *Reviews in Fish Biology and Fisheries* 14, 305-319.
- Zavolokin, A.V., Zavolokina, E.A., Khokhlov, Y.N., 2009. Changes in size and growth of Anadyr chum salmon (*Oncorhynchus keta*) from 1962-2007. *North Pacific Anadromous Fish Commission Bulletin* 5, 157-163.
- Zimmerman, M., 1991. Trends in freshwater growth of sockeye salmon (*Oncorhynchus nerka*) from the Wood River Lakes and Nushagak Bay, Alaska, University of Washington, Seattle.

## **Tables and Figures**

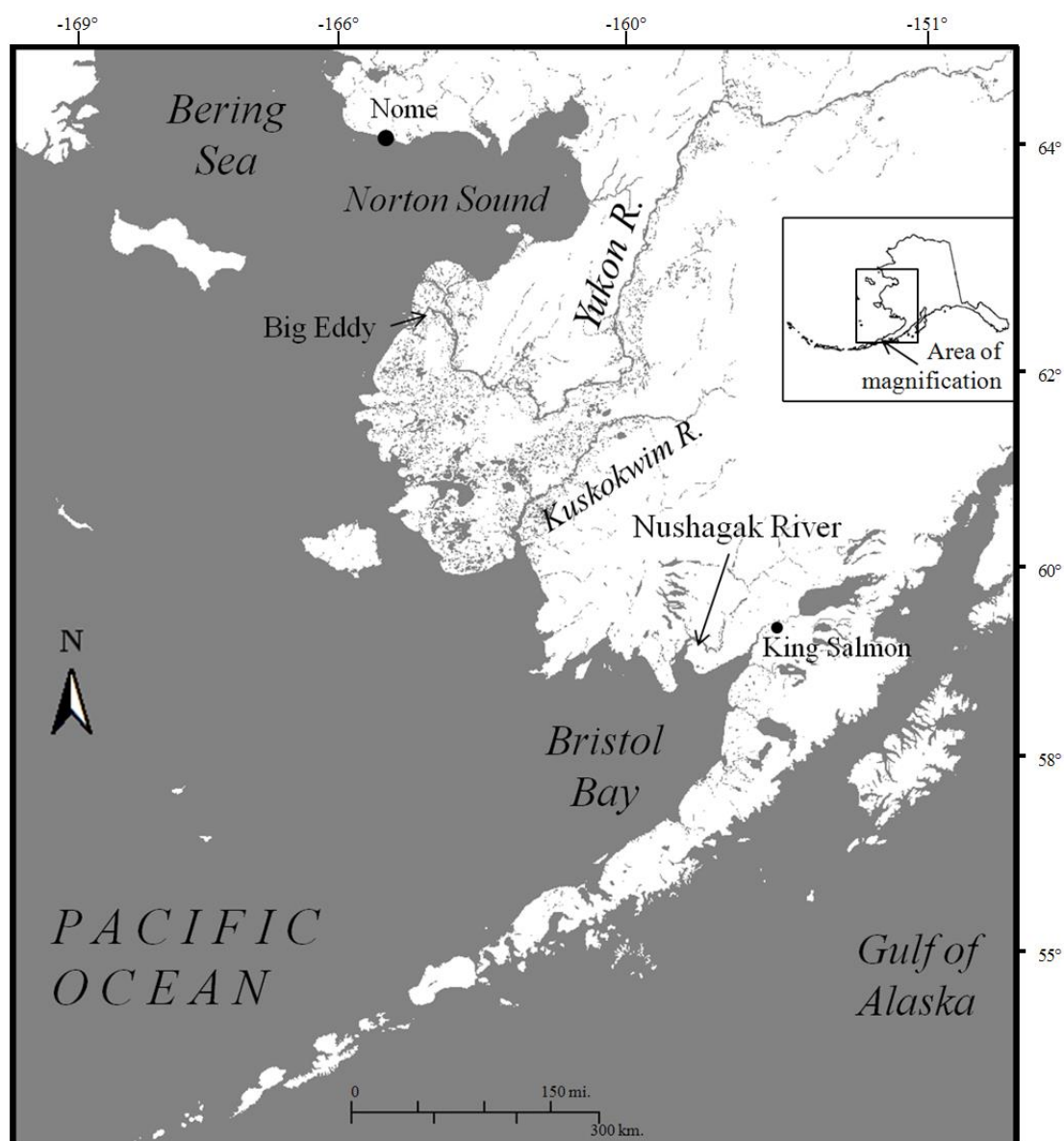


Figure 2.1. Map of the study area. Scales were collected annually during the commercial chum fisheries in the Nushagak District of Bristol Bay, Alaska. The Nushagak District is located at the mouth of the Nushagak River. Scales were also collected annually during commercial and test fisheries from Big Eddy at the mouth of the Yukon River, Alaska.

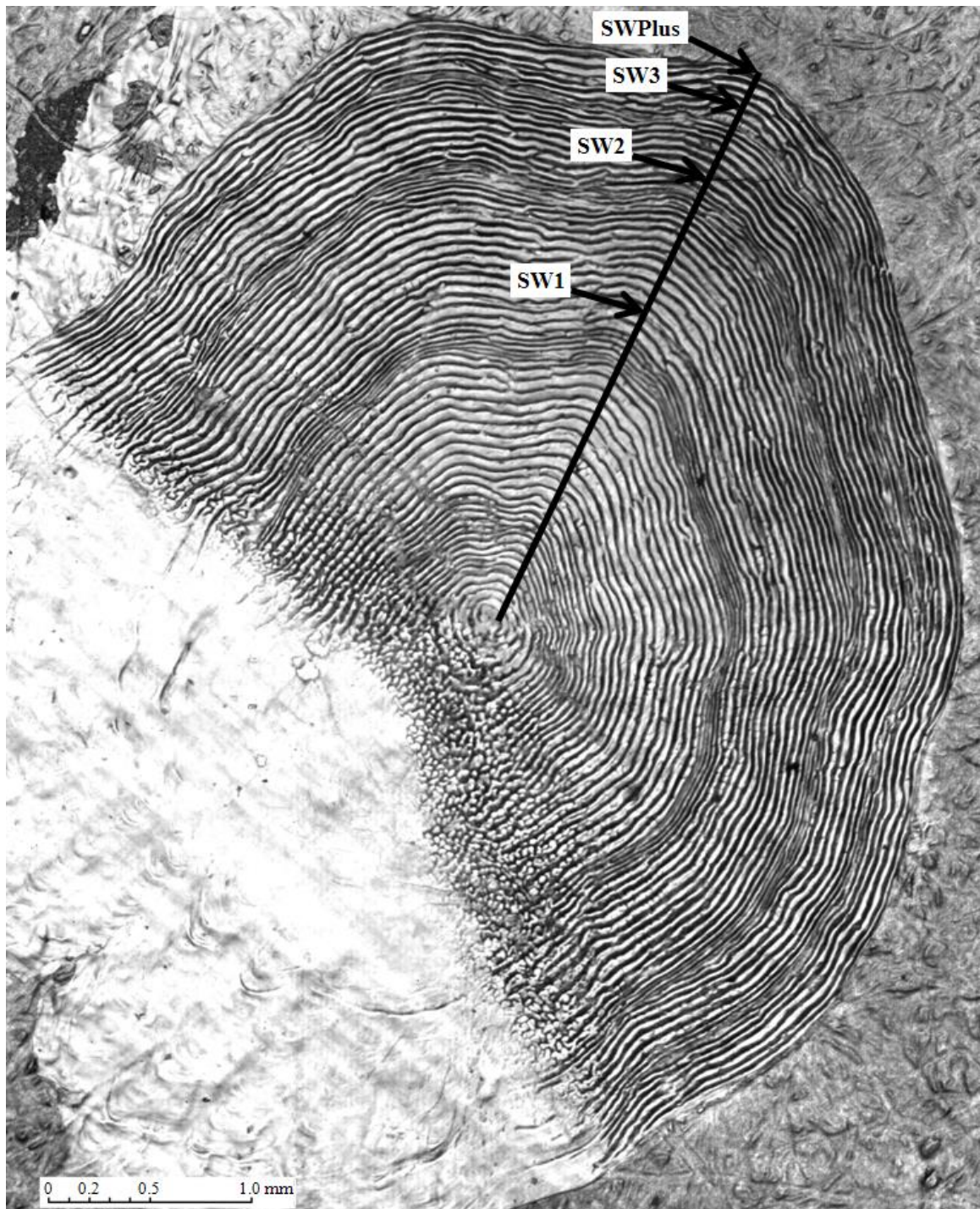


Figure 2.2. Example of a chum salmon scale. This is an age 0.3 chum salmon scale with the annuli marked by seasonal growth zones SW1, SW2, etc. SW is an abbreviation for saltwater, indicating the fish is in marine waters. The numbers 1, 2, etc. indicate the number of years at sea. We used the longest axis to measure scales.

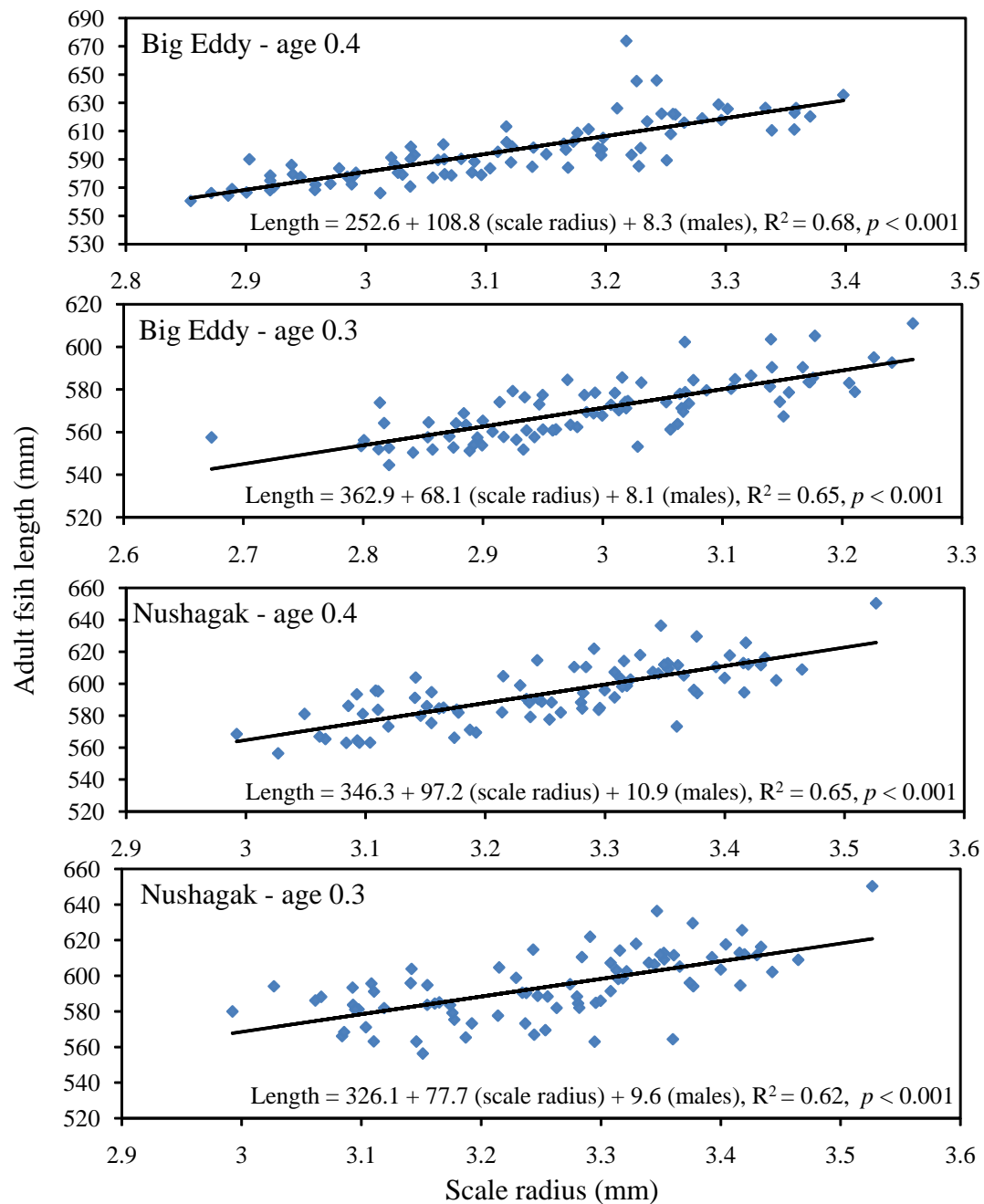


Figure 2.3. Mean adult fish length (mm, mid-eye to fork of tail) compared to mean scale growth (mm, radius) for chum salmon from Big Eddy, Yukon River and Nushagak River, Bristol Bay, Alaska.

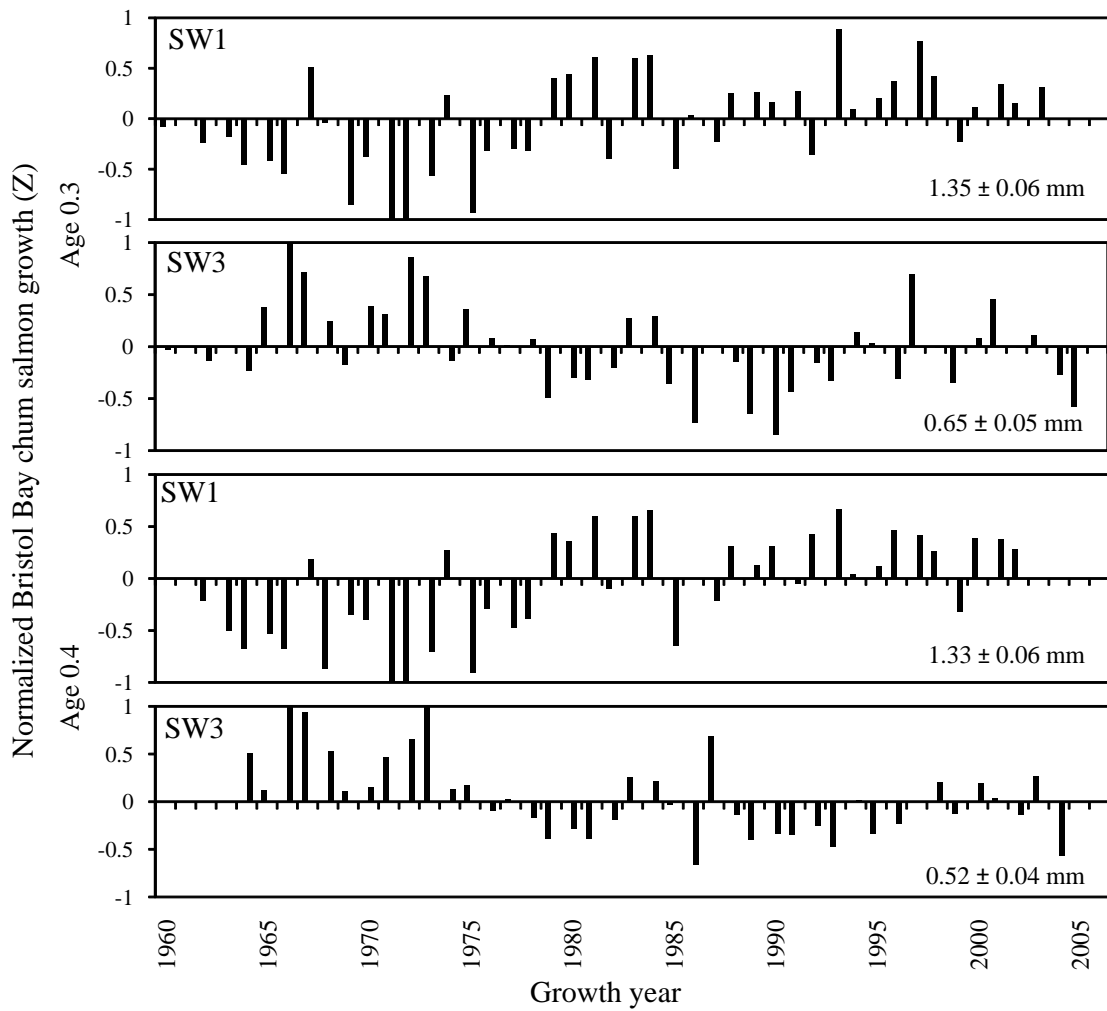


Figure 2.4. Mean annual growth of age 0.3 and 0.4 Nushagak River, Bristol Bay, Alaska chum salmon during first (SW1) and third (SW3) growth years 1961-2006. Un-weighted mean  $\pm$  1 SD during each life stage is shown.

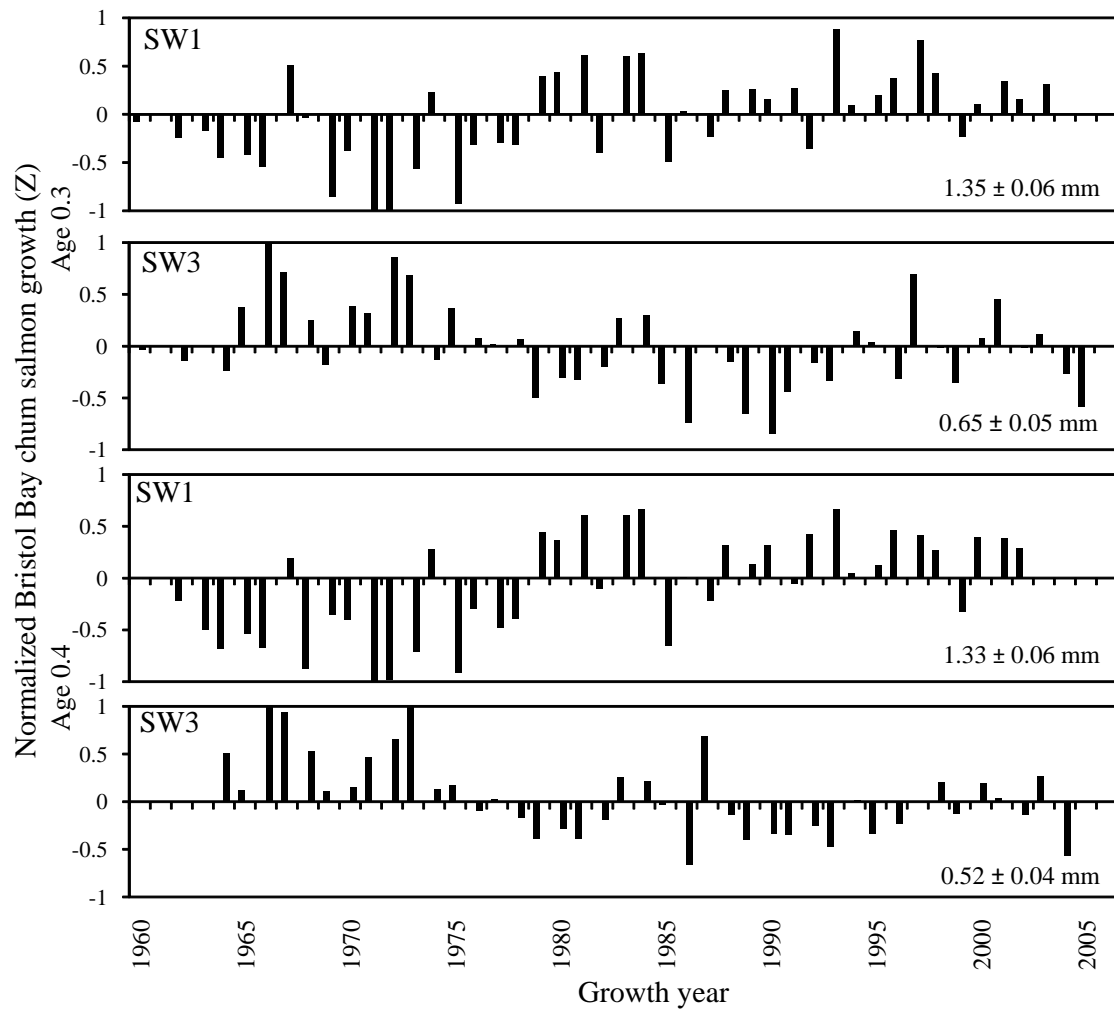


Figure 2.5. Mean annual growth of age 0.3 and 0.4 Big Eddy, Yukon River, Alaska chum salmon during first (SW1) and third (SW3) growth years 1961-2006. Un-weighted mean  $\pm$  1 SD during each life stage is shown.

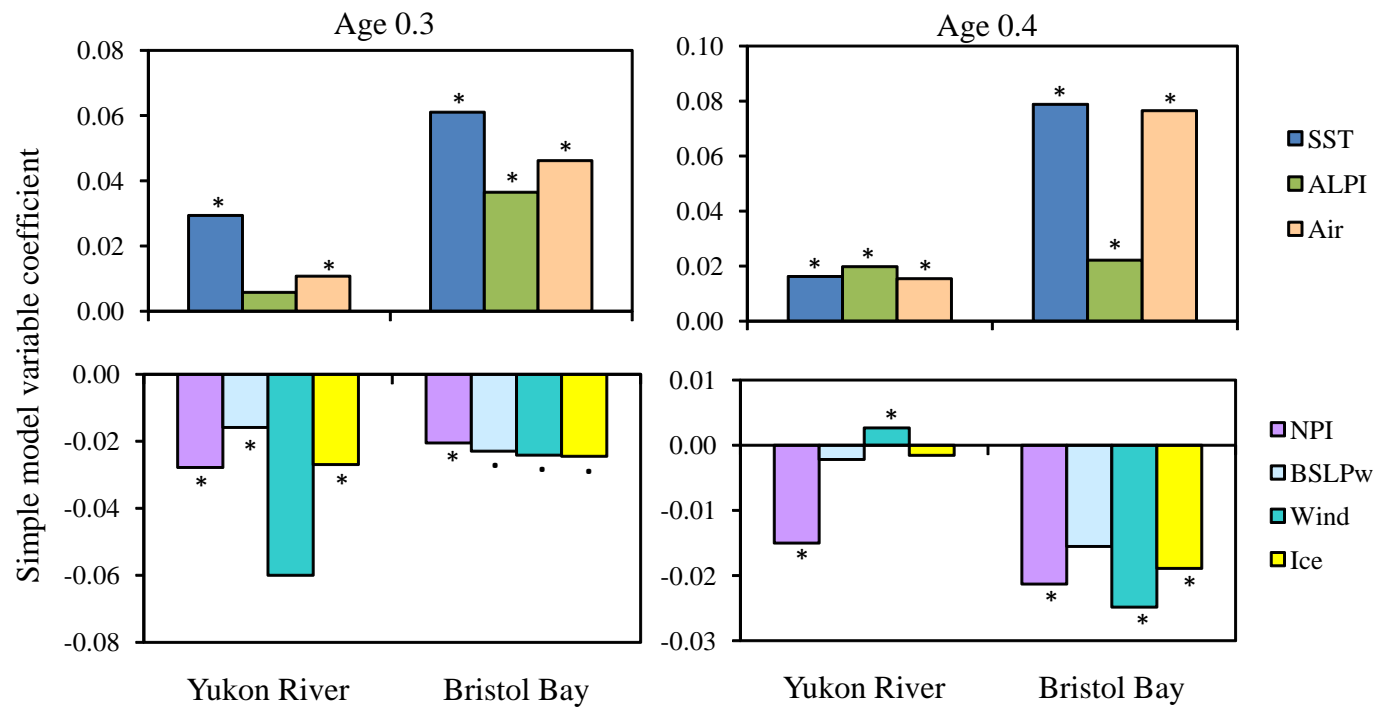


Figure 2.6. Model coefficients from generalized least squares regressions (GLS) comparing SW1 growth of chum salmon from Yukon River age 0.3 (1965-2006) and age 0.4 fish (1967-2006) and Bristol Bay age 0.3 (1960-2006) and age 0.4 fish (1966-2006) with environmental variables. An asterisk (\*) represents  $p \leq 0.05$ , and a dot (·) represents  $p \leq 0.1$ .



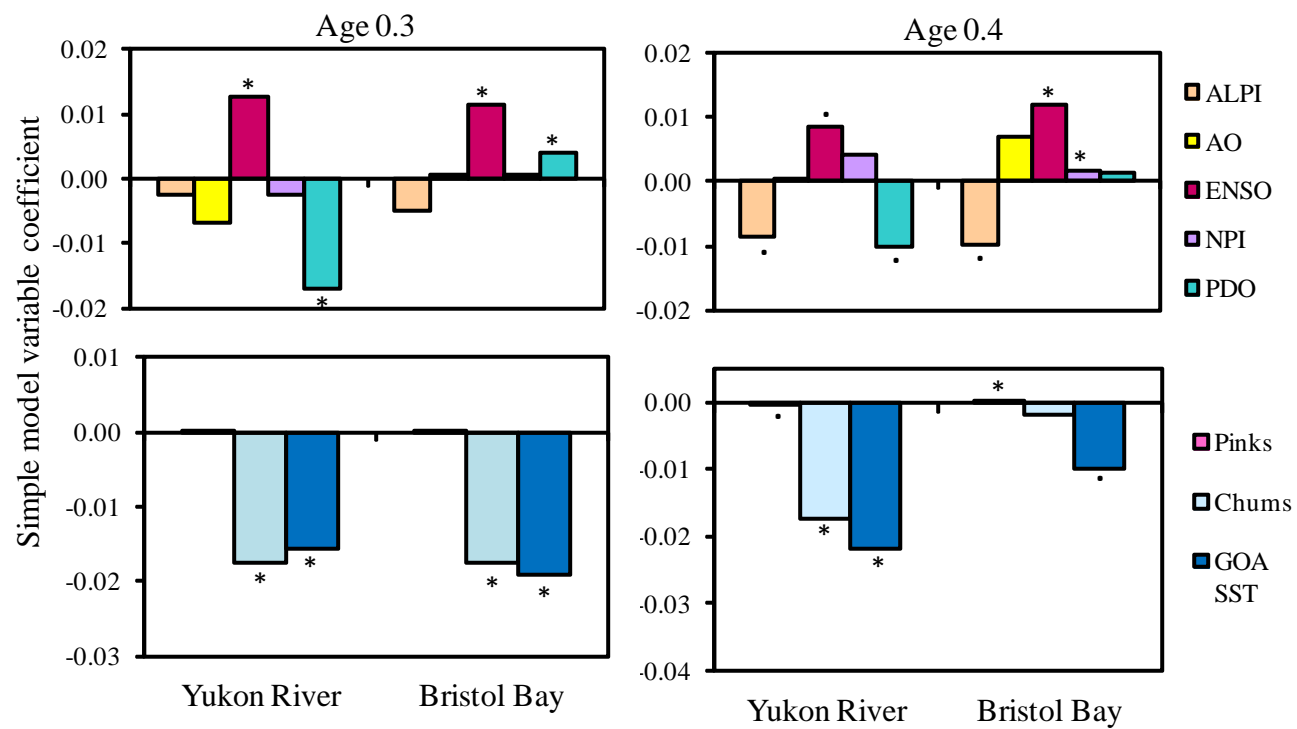


Figure 2.7. Model coefficients from generalized least squares regressions (GLS) comparing SW3 growth of chum salmon from Yukon River age 0.3 (1965-2006) and age 0.4 fish (1967-2006) and Bristol Bay age 0.3 (1960-2006) and age 0.4 fish (1966-2006) with environmental variables. An asterisk (\*) represents  $p \leq 0.05$ , and a dot (.) represents  $p \leq 0.1$ .

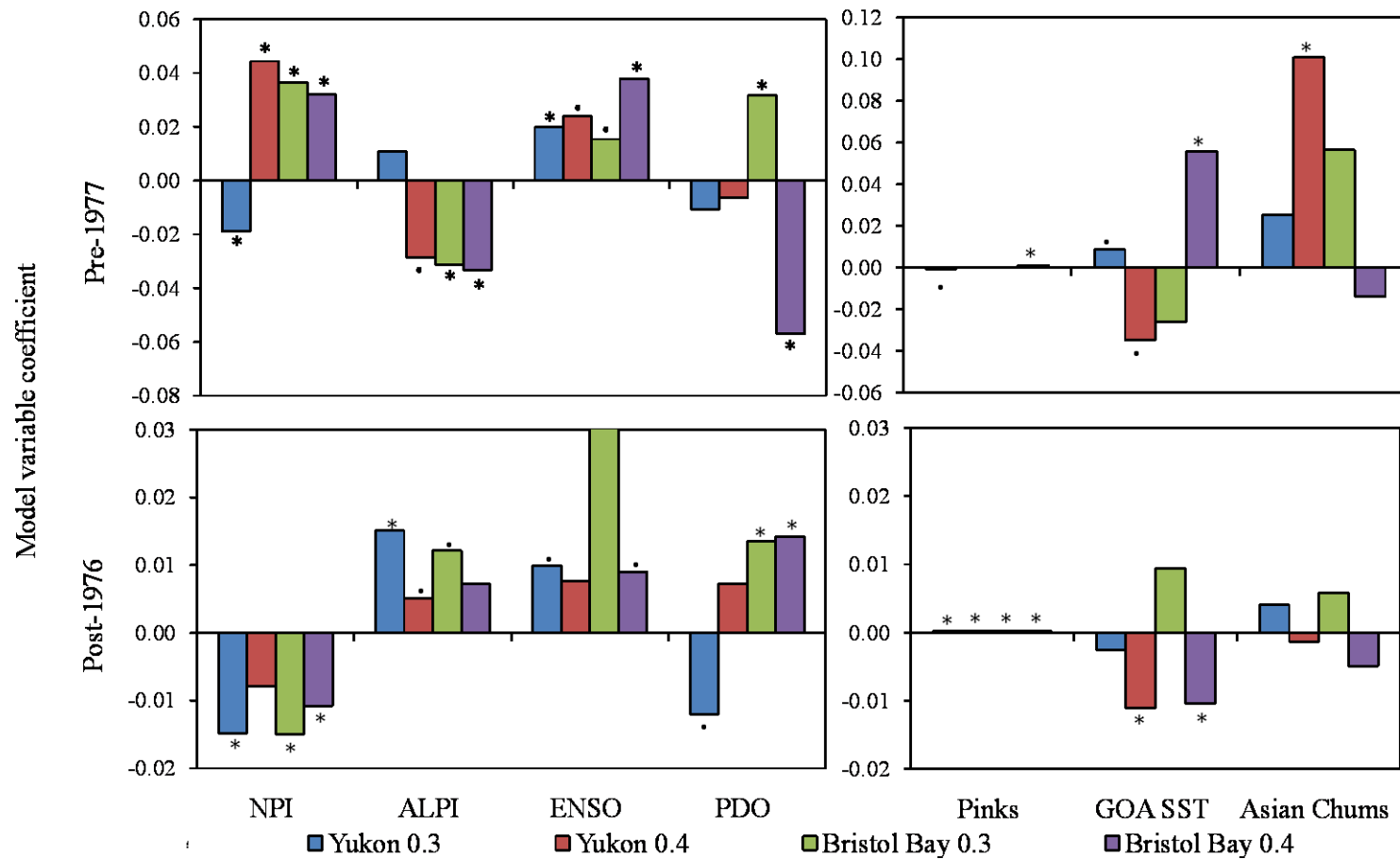


Figure 2.8. Model coefficients from generalized least squares regressions (GLS) comparing SW3 growth of chum salmon from Yukon River (Yukon) age 0.3 (1965-2006) and age 0.4 fish (1967-2006) and Bristol Bay (BB) age 0.3 (1960-2006) and age 0.4 fish (1966-2006) with environmental variables pre-regime shift (prior to 1977) and post regime shift (after 1976). An asterisk (\*) represents  $p \leq 0.05$ , and a dot (.) represents  $p \leq 0.1$ .

Table 2.1. Pairwise Pearson's correlation coefficients (below diagonal) and corresponding *P* values (above diagonal) between environmental variables potentially affecting growth of age 0.3 and 0.4 chum salmon in Bristol Bay and Yukon River, Alaska (see Appendix C1 for key).

	Pinks	ALPI	PDO	AsianChum	YR SST	BB SST	GOA SST	Ice Cover	AO	NPI	ENSO	May SST	Bering SLP	MayMix	K. Salmon	Nome
Pinks	-	0.009	0.001	0.000	0.000	0.000	0.000	0.150	0.030	0.036	0.081	0.799	0.024	0.932	0.000	0.000
ALPI	0.28	-	0.930	0.012	0.007	0.000	0.000	0.981	0.037	0.000	0.000	0.012	0.000	0.007	0.000	0.000
PDO	0.35	0.01	-	0.001	0.171	0.044	0.016	0.004	0.497	0.356	0.746	0.075	0.298	0.803	0.162	0.031
AsianChum	0.66	0.27	0.37	-	0.000	0.000	0.000	0.117	0.008	0.090	0.238	0.048	0.053	0.565	0.000	0.001
YR SST	0.45	0.29	0.15	0.48	-	0.000	0.000	0.000	0.670	0.152	0.280	0.000	0.061	0.791	0.000	0.000
BB SST	0.55	0.51	0.22	0.58	0.84	-	0.000	0.000	0.340	0.000	0.008	0.000	0.000	0.892	0.000	0.000
GOA SST	0.57	0.52	0.26	0.60	0.72	0.87	-	0.000	0.936	0.000	0.009	0.000	0.001	0.435	0.000	0.000
Ice Cover	-0.16	0.00	-0.31	-0.17	-0.54	-0.58	-0.39	-	0.013	0.323	0.388	0.000	0.049	0.921	0.001	0.000
AO	0.24	-0.23	0.08	0.29	0.05	-0.11	0.01	0.27	-	0.014	0.232	0.003	0.008	0.152	0.963	0.395
NPI	-0.23	-0.86	-0.10	-0.19	-0.16	-0.43	-0.44	0.11	0.27	-	0.000	0.021	0.000	0.004	0.000	0.001
ENSO	0.19	0.41	0.04	0.13	0.12	0.29	0.28	-0.10	-0.13	-0.42	-	0.029	0.000	0.379	0.001	0.001
May SST	-0.03	0.27	-0.20	-0.22	0.52	0.49	0.39	-0.49	-0.32	-0.25	0.24	-	0.006	0.232	0.000	0.000
Bering SLP	-0.25	-0.68	-0.12	-0.21	-0.21	-0.47	-0.36	0.22	0.29	0.67	-0.51	-0.30	-	0.022	0.000	0.001
MayMix	0.01	-0.29	0.03	0.06	-0.03	0.02	0.09	-0.01	-0.16	0.31	-0.10	-0.13	0.25	-	0.886	0.722
K. Salmon	0.49	0.50	0.15	0.48	0.68	0.79	0.73	-0.35	-0.01	-0.43	0.36	0.39	-0.45	-0.02	-	0.000
Nome	0.45	0.44	0.24	0.34	0.65	0.71	0.68	-0.42	-0.09	-0.36	0.34	0.48	-0.35	-0.04	0.88	-

Table 2.2. Pearson's correlations and corresponding *P* values comparing marine scale growth of Yukon River, Alaska age 0.3 (1965-2006) and age 0.4 (1967-2006) chum salmon during the first (SW1) and third (SW3) year at sea with several environmental variables (see Appendix C1 for key).

Variable	Age 0.3				Age 0.4			
	SW1		SW3		SW1		SW3	
	Cor.	<i>P</i>	Cor.	<i>P</i>	Cor.	<i>P</i>	Cor.	<i>P</i>
Pinks	0.087	0.429	-0.196	0.074	0.010	0.928	-0.222	0.048
ALPI	0.286	0.008	-0.126	0.252	0.342	0.002	-0.175	0.120
PDO	0.200	0.068	-0.274	0.012	0.066	0.563	-0.173	0.124
AsianChum3yr	0.128	0.245	-0.288	0.008	-0.021	0.851	-0.346	0.002
AsianChum4yr	0.128	0.245	-0.280	0.010	-0.011	0.922	-0.333	0.003
YR Sum SST	0.332	0.002	-0.232	0.034	0.368	0.001	-0.334	0.002
YR Ann SST	0.333	0.002	-0.272	0.012	0.271	0.015	-0.344	0.002
GOA Ann SST	-	-	-0.322	0.003	-	-	-0.432	0.000
GOA Sum SST	-	-	-0.245	0.025	-	-	-0.363	0.001
Ice Cover	-0.203	0.063	0.012	0.915	0.009	0.937	-0.006	0.958
AO	-0.081	0.467	-0.176	0.109	-0.133	0.240	-0.148	0.191
NPI	-0.207	0.058	0.079	0.472	-0.236	0.035	0.144	0.203
ENSO	0.096	0.384	0.084	0.445	0.153	0.176	0.035	0.759
BSLP winter	-0.240	0.028	0.066	0.550	-0.047	0.676	0.054	0.636
BSLP spring	-0.166	0.132	0.194	0.078	-0.078	0.493	0.100	0.379
MayMix	-0.223	0.041	-0.001	0.992	0.086	0.448	0.082	0.470
JJMixM2	-0.139	0.208	0.105	0.343	0.218	0.052	0.093	0.411
Nome Summer air	0.439	0.000	-0.415	0.000	0.332	0.003	-0.470	0.000
Nome Annual air	0.489	0.000	-0.319	0.003	0.242	0.030	-0.369	0.001
Nome winter air	0.250	0.022	-0.039	0.727	0.141	0.211	-0.088	0.438

Table 2.3. Pearson's correlations and corresponding *P* values comparing marine scale growth of Bristol Bay, Alaska age 0.3 (1965-2006) and age 0.4 (1966-2006) chum salmon during the first (SW1) and third (SW3) year at sea with environmental variables (see Appendix C1 for key.).

Variable	Age 03				Age 04			
	SW1		SW3		SW1		SW3	
	Cor.	<i>P</i>	Cor.	<i>P</i>	Cor.	<i>P</i>	Cor.	<i>P</i>
Pinks	0.424	0.000	-0.174	0.113	0.522	0.000	-0.254	0.021
ALPI	0.470	0.000	-0.163	0.140	0.432	0.000	-0.391	0.000
PDO	0.369	0.001	-0.129	0.243	0.367	0.001	-0.383	0.000
Asian Chum3yr	0.498	0.000	-0.277	0.011	0.547	0.000	-0.208	0.061
Asian Chum4yr	0.501	0.000	-0.273	0.012	0.546	0.000	-0.182	0.101
BB Sum SST	0.689	0.000	-0.166	0.131	0.708	0.000	-0.202	0.069
BB Ann SST	0.729	0.000	-0.244	0.025	0.774	0.000	-0.292	0.008
GOA Ann SST	-	-	-0.287	0.008	-	-	-0.370	0.001
GOA Sum SST	-	-	-0.184	0.094	-	-	-0.281	0.011
Ice Cover	-0.269	0.013	0.024	0.831	-0.268	0.015	0.042	0.708
AO	0.197	0.073	-0.122	0.269	0.264	0.017	-0.078	0.488
NPI	-0.391	0.000	0.098	0.376	-0.393	0.000	0.134	0.230
ENSO	0.141	0.201	0.086	0.439	0.180	0.105	0.141	0.205
BSLP winter	-0.311	0.004	0.136	0.218	-0.384	0.000	0.068	0.544
BSLP spring	-0.033	0.768	0.153	0.165	-0.080	0.476	0.177	0.111
MayMix	-0.274	0.012	-0.010	0.928	-0.354	0.001	-0.004	0.973
JJM <sub>ix</sub> M <sub>2</sub>	-0.319	0.003	0.154	0.162	-0.298	0.007	0.180	0.106
K. Salmon winter air	0.285	0.009	-0.290	0.008	0.357	0.001	-0.392	0.000
K. Salmon Annual air	0.554	0.000	-0.313	0.004	0.626	0.000	-0.376	0.000
K. Salmon Summer air	0.591	0.000	-0.248	0.023	0.605	0.000	-0.325	0.003

Table 2.4. Student's two-sample *t*-tests comparing mean growth of chum salmon between odd and even years by population, age, growth zone, and gender. Data are from chum salmon caught in commercial and test fisheries in Bristol Bay, Alaska age 0.3 (1965-2006) and age 0.4 (1966-2006) and Yukon River, Alaska age 0.3 (1965-2006) and age 0.4 (1967-2006).

Population	Age	Growth Zone	Males		Females	
			t	<i>P</i>	t	<i>P</i>
Yukon River	0.3	SW1	1.383	0.174	0.750	0.458
		SW3	-1.555	0.128	-1.863	0.070
	0.4	SW1	2.088	0.044	1.671	0.103
		SW3	-1.316	0.196	-1.669	0.103
Bristol Bay	0.3	SW1	0.325	0.747	1.012	0.318
		SW3	-1.412	0.166	-1.588	0.120
	0.4	SW1	0.242	0.810	0.080	0.937
		SW3	-1.012	0.318	-1.429	0.161

Table 2.5. Generalized least squares models (GLS) of growth during the first (SW1) and third year at sea (SW3) for Big Eddy, Yukon River, Alaska for age 0.3 (1965-2006) and age 0.4 chum (1967-2006) salmon. Only significant  $p$  values listed. AR = order of AIC-best auto-regressive model. Partial  $P$  values are listed below the coefficient.  $b$  = Intercept,  $p < 0.001$ .

Growth			Autoregressive Terms				AIC	AR	$b$	Model coefficients		Partial $P$	
Zone	Age	Variables	$\Phi 1$	$\Phi 2$	$\Phi 3$	$\Phi 4$				Variable	Gender	Variable	Gender
SW1	0.3	ALPI					-126.9	0	1.292	0.006		0.057	
		NPI	-0.16	-0.01	-0.24	-0.44	-123.0	4	1.296	-0.021		0.002	
		Nome Annual Air					-136.0	0	1.010	0.011		<0.001	
		YR SST					-128.9	0	1.211	0.029		0.030	
		Ice Cover	-0.40				-127.4	1	1.291	-0.027		<0.001	
		PDO	-0.21	0.07	-0.20	-0.30	-121.6	4	1.297	0.004		0.010	
		BSLPw	-0.11	0.13	-0.12		-121.6	3	1.295	-0.016		0.042	
SW1	0.4	ALPI					-126.4	0	1.286	0.020		0.012	
		NPI	0.04	-0.12	-0.15		-118.7	3	1.286	-0.015		0.045	
		Nome Annual Air	-0.13				-121.5	1	1.287	0.015		0.045	
		YR SST					-123.9	0	1.287	0.016		0.049	
		JJMixM2	-0.19	-0.17			-121.3	2	1.285	0.014		0.067	
SW3	0.3	GOA SST + Gender	0.23				-242.2	1	0.654	-0.016	-0.060	0.020	<0.001
		Asian Chums + Gender	0.28				-242.0	1	0.654	-0.017	-0.060	0.033	<0.001
		ENSO + Gender	0.42				-243.2	2	0.654	0.013	-0.058	0.017	0.005
		PDO + Gender	0.23	0.19	-0.26		-242.8	3	0.654	-0.017	-0.061	0.006	<0.001
		Pinks	0.61				-236.2	1	0.593	2.20E-04		0.017	
SW3	0.4	Pinks + Gender	0.13	0.16	-0.17	0.32	-251.0	4	0.545	-1.74E-04	-0.034	0.089	0.042
		GOA SST + Gender					-260.1	1	0.516	-0.022	-0.034	<0.001	0.002
		Asian Chums + Gender	0.18				-252.6	1	0.516	-0.017	-0.034	0.008	0.010
		ALPI + Gender	0.22	0.12	-0.14	0.35	-252.6	4	0.520	-0.009	-0.032	0.056	0.095
		PDO + Gender					-246.0	0	0.517	-0.010	-0.034	0.080	0.004
		ENSO	0.30	0.30			-250.6	2	0.501	0.010		0.032	

Table 2.6. Generalized least squares models (GLS) comparing growth during the first (SW1) year at sea for Yukon River, Alaska age 0.3 (1965-2006) and age 0.4 (1967-2006) and for Bristol Bay age 0.3 (1965-2006) and age 0.4 (1966-2006) chum salmon. The third and fourth autoregressive terms are below the first two values, and partial *P* values are listed below the coefficient. *b* = Intercept, *P* < 0.001.

Population	Age	Autoregressive terms				AIC	AR	<i>b</i>	Model coefficients					
		Φ1	Φ2	Φ3	Φ4				SST	ALPI	Ice	NPI	MayMix	Air temp
<b>Bristol Bay</b>	0.3	0.021	0.157	-0.294		-120.3	3	1.349	0.075		0.016			
									<0.001		0.070			
	0.4					-128.1	0	0.541	0.200	-0.017	0.024	-0.033	-0.770	
									<0.001	0.022	0.032	0.055	0.005	
<b>Yukon R</b>	0.3	-0.224	-0.061	-0.247	-0.209	-131.8	4	1.071					-1.131	0.010
													0.061	<0.001
	0.4	0.001	-0.057	-0.076	0.505	-126.8	4	1.289	0.021	0.016			0.014	
									0.002	0.022			0.053	

**Note:** Candidate models were:  $SW1 = \beta_0 + \beta_1 X_1 + \dots + \beta_n X_n + \epsilon$  where parameters  $X_n$  were explanatory variables, and  $\epsilon$  were residuals.



Table 2.7. Generalized least squares models (GLS) comparing growth during the third at sea (SW3) for Yukon River, Alaska age 0.3 (1965-2006) and age 0.4 (1967-2006) and for Bristol Bay age 0.3 (1965-2006) and age 0.4 (1966-2006) chum salmon. Partial *P* values are listed below the coefficient. *b* = Intercept, *p* < 0.001. Int. = Pink\*Asian chum interaction in the model.

Population	Age	Autoregressive terms				AIC	AR	<i>b</i>	Model coefficients				
		Φ1	Φ2	Φ3	Φ4				Pinks	Chums	SST	Int.	Gender
<b>Bristol Bay</b>	0.3	0.276				-236.4	1	0.629	2.3E-04	-0.071		2.7E-04	-0.050
<i>w/ interaction</i>									0.040	0.002		0.027	<0.001
<i>w/o interaction</i>		0.317	0.005	-0.044		-227.6	3	0.676		-0.017			-0.052
										0.045			0.003
<b>Bristol Bay</b>	0.4	0.443	0.096	0.216	0.224	-239.2	4	0.641	2.35E-04		-0.012		0.051
<i>w/ or w/o interaction</i>									0.024		0.037		0.028
<b>Yukon River</b>	0.3	0.261				-246.9	1	0.604	2.64E-04	-0.060	-0.015	2.49E-04	-0.060
<i>w/ interaction</i>									0.020	0.005	0.047	0.027	<0.001
<i>w/o interaction</i>		0.385				-243.2	1	0.623	2.08E-04	-0.027			-0.059
									0.044	0.012			0.002
		0.366				-244.3	1	0.617	2.55E-04	-0.021	-0.013		-0.059
									0.019	0.051	0.087		0.002
<i>w/ interaction</i>	0.4	0.229				-263.3	1	0.469	2.48E-04	-0.053	-0.019	2.40E-04	-0.034
									0.016	0.004	0.002	0.016	0.008
<i>w/o interaction</i>		0.244				-259.0	1	0.488	1.92E-04	-0.014	-0.019		-0.034
									0.059	0.081	0.003		0.012
		0.164				-260.1	0	0.516			-0.022		-0.034
											<0.001		0.002

**Note:** Candidate models were:  $SW3 = \beta_0 + \beta_1 X_1 + \dots + \beta_n X_n + \epsilon$  where parameters  $X_n$  were explanatory variables, and  $\epsilon$  were residuals.

Table 2.8. Generalized least squares models (GLS) comparing growth during the first (SW1) and third year at sea (SW3) for Nushagak River, Bristol Bay, Alaska for age 0.3 (1965-2006) and age 0.4 chum (1966-2006) salmon. Only significant *P* values are listed, and partial *P* values are listed below the coefficient. *b* = Intercept, *p* < 0.001.

Growth		Variables	AR Terms			AIC	AR	<i>b</i>	Model coefficients		Partial <i>P</i>	
Zone	Age		Φ1	Φ2	Φ3				Variable	Gender	Variable	Gender
SW1	0.3	ALPI				-96.0	0	1.346	0.036		0.003	
		NPI	0.330			-95.3	1	1.345	-0.028		0.012	
		King Salmon Annual										
		Air				-101.8	0	1.347	0.046		<0.001	
		May Mixing				-89.9	0	1.346	-0.024		0.065	
		SST				-121.7	0	1.348	0.061		<0.001	
		Ice Cover				-90.2	0	1.345	-0.024		0.054	
		PDO				-92.7	0	1.346	0.031		0.014	
		BSLPw				-90.0	0	1.347	-0.023		0.059	
		JJMIXM2				-90.8	0	1.348	-0.026		0.039	
SW1	0.4	ALPI	0.914			-80.4	1	1.128	0.022		0.035	
		NPI	0.504	0.454		-88.6	2	1.118	-0.021		0.039	
		King Salmon Annual										
		Air				-91.4	0	1.307	0.077		<0.001	
		May Mixing	0.506	0.454		-91.9	2	1.121	-0.025		0.007	
		SST				-118.4	0	1.315	0.079		<0.001	
		Ice Cover	0.405	0.558		-88.1	2	1.104	-0.019		0.044	
SW3	0.3	GOA SST + Gender				-225.9	0	0.677	-0.019	-0.051	0.006	<0.001
		Asian Chums + Gender	0.317	0.005	-0.044	-229.3	3	0.676	-0.017	-0.052	0.045	0.003
		ENSO + Gender	0.445			-234.5	1	0.678	0.011	-0.050	0.034	0.017
		Pinks	0.521	0.036	0.156	-227.2	3	0.633	2.03E-04		0.028	
SW3	0.4	Pinks + Gender	0.552	0.129	0.297	-235.9	3	0.655	2.26E-04	0.063	0.015	0.008
		GOA SST + Gender				-187.3	0	0.551	-0.043	-0.019	<0.001	0.196
		ENSO + Gender	0.568	0.394		-231.6	2	0.670	0.012	0.034	0.010	0.171

Table 2.9. Generalized least squares models (GLS) comparing growth during the third year at sea (SW3) prior to the regime shift (pre-1977) for Yukon River, Alaska age 0.3 (1965-2006) and age 0.4 chum (1967-2006) salmon. Partial *P* values are listed below the coefficient. *b* = Intercept, *p* < 0.001.

Age	Autoregressive Terms				AIC	AR	<i>b</i>	Model coefficients					
	Φ1	Φ2	Φ3	Φ4				Pinks	SST	Chums	NPI	ALPI	Gender
0.3	-0.02	-0.04	-0.83		-79.4	3	0.755	-0.001					-0.072
								0.054					<0.001
	-0.47	-0.29	-0.66	-0.75	-89.8	4	0.718		0.009				-0.072
									0.082				<0.001
	0.09	-0.15	-0.79		-82.3	3	0.722				-0.019		-0.073
											0.022		<0.001
0.4	0.02	0.04	-0.92		-85.4	3	0.787	-0.001	-0.026		-0.018		-0.072
								0.006	0.014		0.017		<0.001
	0.30				-56.5	1	0.515		-0.035				
									0.041				
	-0.40	-0.34	-0.49		-60.1	3	0.679			0.101			-0.043
										0.018			<0.001
0.4	-0.50				-62.6	1	0.536				0.044		-0.041
											0.002		0.005
	-0.30	-0.23			-56.6	2						-0.029	-0.041
												0.062	0.011
	-0.92	-0.89	-0.89	-0.84	-73.8	4	0.697		0.014	0.107			-0.042
									0.002	<0.001			<0.001

Table 2.10. Generalized least squares models (GLS) comparing growth during the third year at sea (SW3) after the regime shift (post-1976) for Yukon River, Alaska age 0.3 (1965-2006) and age 0.4 chum (1967-2006) salmon. Partial *P* values are listed below the coefficient. *b* = Intercept, *p* < 0.001.

Autoregressive Terms					Model coefficients									
Age	Φ1	Φ2	Φ3	Φ4	AIC	AR	<i>b</i>	Pinks	SST	NPI	PDO	Gender	ALPI	Pinks + Chums
0.3	-0.03	0.16	-0.24		-187.1	3	0.635				-0.012	-0.054		
										0.07	<0.001			
					-194.3	0	0.582	2.83E-04			-0.054			
								0.009			<0.001			
					-193.0	0	0.628		-0.015	-0.054				
								0.018	<0.001					
					-189.7	1	0.627			-0.055	0.015			
									<0.001	0.023				
					-206.6	0	0.556	4.48E-04	-0.024	-0.020	-0.054			
								<0.001	0.003	<0.001	<0.001			
0.4	0.15	0.05	-0.10	0.40	-206.6	0	0.556		-0.024	-0.020	-0.054		4.5E-04	
								0.003	<0.001	<0.001		<0.001		
					-207.3	1	0.461	2.25E-04		-0.030				
								0.022		0.014				
					-210.3	4	0.509		-0.011	-0.039				
									0.024	0.008				
					-210.8	0	0.501		-0.015	-0.013	-0.031			
									0.014	0.026	0.003			
					-221.1	0	0.446	3.35E-04	-0.023	-0.014	-0.031			
								<0.001	<0.001	0.008	0.001			
0.4	0.15	0.05	-0.10	0.40	-221.1	0	0.446		-0.023	-0.014	-0.031		3.3E-04	
								<0.001	<0.001	0.008	0.001		<0.001	

Table 2.11. Generalized least squares models (GLS) comparing growth during the third year at sea (SW3) prior to the regime shift (pre-1977) for Bristol Bay, Alaska age 0.3 (1965-2006) and age 0.4 chum (1966-2006) salmon. Partial *P* values are listed below the coefficient. *b* = Intercept, *p* < 0.001. Int. = Pink\*Asian chum interaction in the model.

Autoregressive Terms							Model coefficients										Pinks + Chums
Age	Φ1	Φ2	Φ3	Φ4	AIC	AR	<i>b</i>	Pinks	Chums	SST	NPI	PDO	Gender	Int.	ENS O		
0.3	0.32	-0.37			-62.7	2	0.709			-0.026			-0.062				
										0.068			0.009				
					-66.1	0	0.707				0.037		-0.058				
											0.039		0.015				
0.4	-1.00	-0.94	-0.90		-73.1	3	0.030	0.008	-0.776	-0.026	0.115		-0.053	0.011			
								<0.001	<0.001	0.008	<0.001		<0.001	<0.001			
					-47.6	0	0.516	0.001									
								0.010									
	0.15	0.25	0.40	0.17	-51.5	4	0.705				0.032						
											0.043						
					-50.6	0	0.603								0.038		
															0.002		
					-45.0	0	0.561					-0.057					
												0.036					
				-47.6	0	0.518										0.001	
																0.010	
	0.14	-0.11			-49.4	2	0.544	7.3E-04							0.031		
								0.047							0.005		

Table 2.12. Generalized least squares models (GLS) comparing growth during the third year at sea (SW3) after the regime shift (post-1976) for Bristol Bay, Alaska age 0.3 (1965-2006) and age 0.4 chum (1966-2006) salmon. Partial *P* values are listed below the coefficient. *b* = Intercept, *p* < 0.001. Int. = Pink\*Asian chum interaction in the model.

Age	Autoregressive Terms				AIC	AR	<i>b</i>	Model coefficients						
	Φ1	Φ2	Φ3	Φ4				Pinks	Chums	SST	NPI	PDO	Gender	Int.
0.3					-188.9	0	0.598	3.1E-04					-0.046	
								0.005					<0.001	
					-186.7	0	0.648				-0.015		-0.046	
											0.017		<0.001	
	0.04	0.07	-0.02	0.17	-178.0	4	0.646					0.014	-0.043	
												0.047	0.011	
0.4	-0.27	-0.21	-0.23		-191.0	3	0.594	2.8E-04	-0.052		-0.020		-0.048	3.0E-04
								0.032	0.035		<0.001		<0.001	0.032
	-0.27	-0.09			-191.9	2	0.582	3.8E-04			-0.021		-0.047	
								<0.001			<0.001		<0.001	
					-213.3	0	0.490	2.2E-04					-0.048	
								0.023					<0.001	
	-0.15	-0.05	-0.08	0.14	-205.7	4	0.527	-0.010					-0.046	
								0.035					<0.001	
	-0.22				-211.4	1	0.523				-0.011		-0.047	
											0.030		<0.001	
					-214.4	0	0.522					0.014	-0.048	
												0.013	<0.001	
	-0.48	-0.42	-0.09		-228.6	3	0.473	3.1E-04	0.039	-0.030	-0.023		-0.044	-1.8E-04
								0.001	0.039	<0.001	<0.001		<0.001	0.097
	-0.49	-0.26			-230.9	2	0.521		0.012	-0.024	-0.023		-0.045	
									0.005	<0.001	<0.001		<0.001	
					-231.4	0	0.462	3.8E-04		-0.023	-0.016		-0.045	
								<0.001		<0.001	0.001		<0.001	

**Appendix 2A**

Appendix 2A-1. Explanatory variables used in generalized least squares regressions (GLS) to compare with first and third-year growth of western Alaska and Asian chum salmon.

Variable	Name	Description	Source
$NPI_t$	North Pacific Index	area-weighted sea level pressure over the region 30°N-65°N, 160°E-140°W	<a href="http://www.cgd.ucar.edu/cas/jhurrell/npindex.html">http://www.cgd.ucar.edu/cas/jhurrell/npindex.html</a>
$ALPI_t$	Aleutian Low Pressure Index	The relative intensity of the Aleutian Low pressure system of the North Pacific (December through March). It is calculated as the mean area (km <sup>2</sup> ) with sea level pressure expressed as an anomaly from the 1950-1997 mean. A positive index value reflects a relatively strong or intense Aleutian Low.	
$Local\ Air\ Temp_t$	local air temperature	Temperatures were averaged as winter (November-March), summer (May-September), and annually.	
$Nome$	Yukon River	from the Nome, Alaska airport	<a href="http://www.wunderground.com/">http://www.wunderground.com/</a>
$K.Salmon$	Bristol Bay	from the King Salmon, Alaska airport	<a href="http://www.wunderground.com/">http://www.wunderground.com/</a>
$MayMix_t$	wind mixing index	measured in m <sup>3</sup> /sec <sup>3</sup> at year $t$ in the vicinity of St. Paul Island, Alaska from 1950-2010	<a href="http://www.beringclimate.noaa.gov/index.html">http://www.beringclimate.noaa.gov/index.html</a>
$Ice\ Cover_t$	average ice concentration	Average ice concentration in the Bering Sea in a 2-deg x 2-deg box (56°-58°N, 163°-165°W) from 1 January – 31 May. Ice Cover represented normalized anomalies by year, based on mean (7.15) and standard deviation (4.01) for the period 1981-2000.	<a href="http://www.beringclimate.noaa.gov/index.html">http://www.beringclimate.noaa.gov/index.html</a>
$Local\ SST_t$	local sea surface temperature	used a 2° x 2° grid available from the National Oceanic and Atmospheric Administration's Climate Data Center	NOAA Climate Data Center
$YR\ SST$	Yukon River	mean sea surface temperature 62°-66°N latitude & 160°-166°W longitude	
$BB\ SST$	Bristol Bay	mean sea surface temperature 56°-60°N latitude & 160°-180°W longitude	



Appendix 2A-1 continued.

Variable	Name	Description	Source
$GOA SST_t$	SST	Gulf of Alaska annual SSTs from a 10-degree x 30-degree box (48°-58°N, 130°-160°W) at year $t$ .	
$Pinks_t$	pink salmon abundance	represents the total abundance of Russian pink salmon at year $t$	Ruggerone et al. 2010
$Asian chums_t$	Asian chum salmon abundance	A three and four-year moving average of the Asian chum salmon abundance at year $t$ (catch and escapement in millions of fish). We used a four-year moving average because it corresponded with SW3 growth.	Ruggerone et al. 2010 <a href="http://www.npafc.org/new/index.html">http://www.npafc.org/new/index.html</a>
PDO	1960-2008	Winter index, mean of monthly PDO indices from Nov-March	<a href="http://jisao.washington.edu/pdo/PDO.latest">http://jisao.washington.edu/pdo/PDO.latest</a>
$AO_t$	Arctic Oscillation Index	Leading mode of Empirical Orthogonal Function analysis of monthly mean during the period 1979-2000. Largest variability during the cold season.	<a href="http://www.ncdc.noaa.gov/oa/ncdc.html">http://www.ncdc.noaa.gov/oa/ncdc.html</a>
$ENSO_t$	El Niño/So. Oscillation Index	Used the mean December-January values of the multivariate ENSO index.	<a href="http://www.ncdc.noaa.gov/oa/ncdc.html">http://www.ncdc.noaa.gov/oa/ncdc.html</a>
$JJM_{ix}M2_t$	wind mixing index	Wind mixing index at Mooring 2 (57°N, 164°W) in m <sup>3</sup> /sec <sup>3</sup> from June-July 1950-2010.	<a href="http://www.ncdc.noaa.gov/oa/ncdc.html">http://www.ncdc.noaa.gov/oa/ncdc.html</a>
$BSLP_{w_t}$	Bering Sea level pressure winter index	Deviations from the mean of sea level pressure average over the Bering Sea (55° - 65°N, 170°E - 160°W) December through March.	<a href="http://www.ncdc.noaa.gov/oa/ncdc.html">http://www.ncdc.noaa.gov/oa/ncdc.html</a>

### Chapter 3

## HISTORICAL GROWTH OF WESTERN ALASKA AND ASIAN CHUM SALMON (*ONCORHYNCHUS KETA*) IN RELATIONSHIP TO CLIMATE AND INTER- AND INTRASPECIFIC COMPETITION<sup>1</sup>

### Abstract

Declines in chum salmon abundance in western Alaska in the late 1990s prompted examination of factors affecting salmonid growth in the marine environment. Mean annual growth of western Alaska and Asian chum salmon was measured from adult scales collected 1962-2008. We found significant negative effects of Asian chum salmon abundance on five of six age 0.3 populations examined and three of four of age 0.4 populations examined, indicating possible intraspecific competition. Most Asian chum salmon are hatchery-produced; whereas, most western Alaska chum salmon are wild. Third-year growth of age 0.3 females was affected more than males, but the opposite was true for some age 0.4 fish. Third-year growth was negatively correlated with North Pacific annual sea surface temperature and the North Pacific Index. We found significant effects of Russian pink salmon abundance on third-year growth, but the model estimated effect size was small, indicating that although interspecific interactions may occur, intraspecific interaction with Asian chum salmon likely had a stronger influence on third-year growth. This estimated effect of Asian chum abundance, if applied to marine growth during and after the second year, suggests that the presence of abundant Asian chums was associated with a reduction in average length of as much as 42 mm among western Alaska chum salmon and a 3-5% reduction of fecundity. This would probably not account for the drastic decline in western Alaska chum salmon abundance in the 1990s. First-year growth was positively associated with sea surface temperature, Aleutian Low Pressure Index, and El Niño-Southern Oscillation Index, and negatively associated with wind mixing, North Pacific Index, Arctic Oscillation Index, and Bering Sea level pressure winter index.

---

<sup>1</sup>Agler, Beverly A., Gregory T. Ruggerone, and Lorna I. Wilson. Historical growth of western Alaskan and Asian chum salmon (*Oncorhynchus keta*) in relationship to climate and inter- and intraspecific competition. Prepared for Canadian Journal of Fisheries and Aquatic Sciences.

## Introduction

Chum salmon (*Oncorhynchus keta*) are the second most abundant salmon species in the North Pacific Ocean and are an integral part of the salmon biomass in the North Pacific Ocean, comprising 38% of the commercial catch in 2008 (Azumaya and Ishida 2000). In western Alaska, low numbers of salmon returned to many rivers in the late 1990s and early 2000s. This decline in productivity of western Alaska chum salmon was synchronous and indicative of a region-wide factor that has yet to be identified but was likely tied to changes in the ocean. Little is known about growth of chum salmon in the marine environment. Climate has been shown to covary with salmon growth and survival (Ruggerone et al. 2005, 2007, Farley et al. 2005, 2007a,b), and the climate shifts that have occurred in the North Pacific Ocean (Hare and Mantua 2000, Mantua et al. 1997) have been shown to affect the growth of Pacific salmon (*O. spp*; Fukuwaka and Ishida 2000, Kruse 1998, Martinson et al. 2008, Martinson et al. 2009, Ruggerone et al. 2002). The abundances of many fish species in the Bering Sea and North Pacific Ocean changed following the 1976 – 77 climate shift (Beamish and Bouillon 1993, Mantua et al. 1997). This climate shift was associated with increased storminess, which resulted in increased winter sea surface temperatures (SST) in some northern regions. Following this transition, the abundance of some species assemblages increased (zooplankton, Pacific salmon, and groundfish); while others declined (crustaceans, forage fishes, piscivorous birds, and pinnipeds; Alverson 1992, Anderson 2000, Anderson and Piatt 1999, Francis et al. 1998, Rogers 1984). Several hypotheses have been developed to explain the complex responses of species to shifts in oceanographic conditions in the North Pacific Ocean and the Bering Sea (Anderson and Piatt 1999, Francis et al. 1998, Gargett 1997, Hollowed et al. 2001, Ware and Thomson 2005). Hunt et al. (2002), as part of the Oscillating Control Hypothesis, suggested that salmon abundance in the southeastern Bering Sea may increase during warm regimes in response to greater prey abundance.

Interspecific interactions with Asian pink salmon (*O. gorbuscha*) may also affect the growth and productivity of chum salmon in the North Pacific Ocean. Asian pink salmon populations are characterized by large differences in abundance during odd and even years. When abundant salmon stocks originating from Asia and western Alaska mix in offshore waters, biennially-cycling pink salmon abundance may inhibit growth and survival of sockeye (*O. nerka*), chum and Chinook (*O. tshawytscha*) salmon during odd-numbered years in the western Bering

Sea (Myers et al. 2004, Ruggerone et al. 2005, Ruggerone and Nielsen 2004). Thus, it has been suggested that pink salmon can be competitively dominant over other salmon (Ruggerone and Nielsen 2004). Researchers have hypothesized that increased pink salmon abundance altered the feeding and distribution of chum salmon on the high seas (Azumaya and Ishida 2000, Kaeriyama et al. 2004, Myers et al. 2004). Walker et al. (1998) found that chum salmon scale-edge growth in the central North Pacific Ocean was negatively correlated with Asian pink and chum salmon abundance, and pink salmon abundance might influence the third-year growth of salmon in the North Pacific Ocean.

Intraspecific interactions may lead to increased density of chum salmon, and this may inhibit growth (Ishida et al. 1993, Peterman et al. 1998, Ruggerone et al. 2003). Competition has been observed to occur among conspecifics originating from distant locations (Pyper and Peterman 1999). Approximately 3.1 billion hatchery chum salmon were released annually from Asian and North American hatcheries since the mid-1980s (Ruggerone et al. 2010). Increased Asian chum salmon abundance in the North Pacific Ocean since the 1970s has led to concerns about possible effects of hatchery populations on wild salmon in the marine environment (Cooney and Brodeur 1998, Holt et al. 2008). Although this suggests that wild salmon populations may compete for food with abundant hatchery populations, it has also been suggested that Asian chum salmon are surviving due to ocean conditions encountered by fry in the first year in the Sea of Japan and the Okhotsk Sea. Myers et al. (2004) hypothesized that the distributional overlap of Asian chum salmon (mostly hatchery fish) with western Alaska chum salmon caused them to compete with western Alaska chum salmon for food (Myers et al. 2007, Seeb et al. 2004, Urawa et al. 2000, Urawa et al. 2009). Zaporozhets and Zaporozhets (2004) speculated that intraspecific competition among chum salmon for food may lead to reduced growth and survival.

This is part of a broad study designed to compare marine growth of western Alaska chum salmon with Asian chum salmon and determine whether growth within the North Pacific Ocean varied in response to climate change and inter- and intraspecific competition. In this paper, we tested the following hypotheses: (1) climate variability as reflected in large scale climate indices was related to the growth of western Alaska and Asian chum salmon, and (2) high pink and Asian chum salmon abundance reduced the growth of western Alaska and Asian chum salmon. We reconstructed seasonal and annual scale growth of chum salmon by measuring scale collections from Norton Sound (age 0.3, 1977-2008; age 0.4, 1975-2008) and Kuskokwim River (age 0.3,

1967-2007; age 0.4, 1968-2007) and compared these measurements with a previous study of Bristol Bay (age 0.3, 1965-2006; age 0.4 1966-2006) and the Yukon River (age 0.3, 1965-2006; age 0.4, 1967-2006) chum salmon (Chapter 1). In addition, we compared these measurements with Asian chum salmon from the Anadyr River, Russia (age 0.3, 1962-2007) and the Chitose River, Japan (age 0.3, 1976-2008). These data were compared with several environmental variables, large-scale climate indices, the abundance of Asian chum salmon, and the alternating year pattern of pink salmon abundance, which provided a natural experimental control.

## **Methods**

### **Study Area**

Scales were sampled from four chum salmon populations originating from two rivers in western Alaska, one river in Russia and one river in Japan then compared with two western Alaska rivers from a previous study (Chapter 1). Samples represented chum salmon from the North Pacific Ocean between 42°N and 65°N latitude and 158°W and 141°E longitude (Table 3.1, Fig. 3.1). Populations in western Alaska included: Unalakleet River representing Norton Sound, Big Eddy representing the Yukon River, Quinhagak representing the Kuskokwim River, and the Nushagak River representing Bristol Bay. Samples were also obtained from the Chitose River, a tributary of the Ishikari River, Hokkaido, Japan and the Anadyr River, Russia.

In the Unalakleet and Yukon rivers, scales were collected during commercial and test fisheries. Quinhagak samples came from a commercial fishery. Nushagak River scales were collected during commercial fisheries, but in recent years, the collection was supplemented by escapement samples to obtain enough scales. In the Anadyr River, wild fish were sampled from shore with beach seines, and in the Chitose River, samples were collected using a fish wheel, approximately 70 km from the river mouth of the Ishikari River, at the Chitose Salmon Aquarium.

### **Scale Sampling**

Acetate impressions of western Alaska salmon scales were obtained from the Alaska Department of Fish and Game (ADF&G) in Anchorage, Alaska; impressions of Japanese scales were obtained from the Hokkaido National Fisheries Research Institute, Sapporo, Japan; and impressions of Russian scales were obtained from the Chukotka Branch of the Pacific Research

Fisheries Center, Anadyr, Russian Federation. Scales were sampled over the years by different personnel following established protocols.

Scales were collected annually in most of the western Alaska sites (Table 3.1). We attempted to measure acetate impressions of 25 male and 25 female chum salmon scales each year from both age 0.3 and 0.4 fish, which were the dominant age groups in Alaska. Previous scale studies indicated 40-50 scales were sufficient to provide a measure of central tendency (Briscoe 2004, Zimmerman 1991). We previously demonstrated that overall chum salmon scale radius was a good predictor of average adult fish length (mm, Chapter 1).

In western Alaska, scales were primarily collected from 15 June to 15 July to sample fish throughout the main return period to capture timing-related differences in returning salmon. In some years, sample sizes were insufficient; in which case, sampling was extended beyond 15 July to achieve the minimum sample size. Due to limited samples from Japan and Russia, all possible scales were used. All Russian scales were collected in August, and 87% of Japanese scales were collected in October from a fall run. We were unable to restrict scales by net mesh size because it was often not recorded or possibly changed over time. We obtained the sample size for both genders for all years only in the Quinhagak and Big Eddy populations. For the other populations, we were unable to obtain the gender-specific sample size in some years, usually 1960s or mid-1970s, due to limited sampling. To account for unequal samples sizes in some years, the regression models were weighted by the number of scales measured per year.

Scales were selected for measurement when: 1) the reader agreed with the age determination previously made either by ADF&G, Chukotka Branch of the Pacific Research Fisheries Center, Russia, or Hokkaido National Fisheries Research Institute, Japan; 2) the scale shape indicated the scale was collected from the preferred area (Koo 1962); and 3) circuli and annuli were clearly defined and not affected by scale regeneration or significant resorption along the measurement axis.

Scale measurements were collected using procedures described by Hagen et al. (2001). Prior to measurement, quality of the scale impression was examined, and only scales that met measurement selection criteria were included. A digital microfiche reader was used to scan the scale from the acetate impressions, and the image was stored as a high resolution digital image (3352 x 4425 pixels). This allowed the entire scale to be viewed and provided enough pixels between the narrow circuli for accurate measurements of circulus spacing. The scale image was

displayed on a digital LCD flat panel monitor, and Optimas 6.5 image processing software was used to measure the scale with a customized program. Scales were measured from the focus to the edge along the longest axis. The distance (resolution  $\sim 0.0017$  mm/pixel) between each pair of circuli was measured within each growth zone from the scale focus to the outer edge of the first ocean annulus (SW1) then from the outer edge of SW1 to the end of the second ocean annulus (SW2) and so on until the edge of the scale was reached (Fig. 3.2). Data were stored in a Microsoft Access database by growth zone and were linked to the age, sex, and length data by an identification number for each fish.

For western Alaska both age 0.3 and 0.4 fish were measured for this study; however, for the Asian chum salmon only age 0.3 fish were measured. Chum salmon spend minimal time in freshwater (indicated by the leading 0) and then spend three or four winters in marine waters before returning to the natal stream to spawn (indicated by the second number of the age). This study focused on two growth zones: SW1, the first marine year and SW3, the third marine year (Fig. 3.2). The SW1 zone was chosen because it has been hypothesized that the first marine year is critical to the survival of an individual fish (Beamish and Mahnken 2001). The SW3 zone was chosen because it has been hypothesized that if a fish does not reach a certain size by the end of that year, it remains in marine waters another year and returns the next summer as an age 0.4 fish (Beamish and Mahnken 2001). If it reaches this “critical” size, it returns to spawn as an age 0.3 fish.

Scales were collected from fish in the return year. Growth data (SW1 and SW3) were paired with the corresponding years of environmental data. For example, an age 0.4 fish that returned in 2006 was conceived in 2001, emerged from gravel and spent its first year at sea in 2002 and its third year at sea in 2004, hence environmental data for 2002 were compared with SW1 growth, and data from 2004 were compared with SW3 growth.

### **Explanatory Variables**

Pink salmon have a two-year life cycle that can create an alternating-year pattern of abundance, and Russian pink salmon populations were dominated by odd-year adult pink salmon. We used Russian pink salmon because during most of the time period of this study, they were the dominant pink salmon stock in the North Pacific Ocean. In addition, Russian pink salmon were correlated with Alaska pink salmon populations ( $p < 0.001$ ), thus the effects would be similar. Total Russian pink (*Pinks*, 1952-2007) and Asian chum salmon abundances were obtained from

Ruggerone et al. 2010. We calculated a four-year moving average of Asian chum salmon abundance ( $\text{Asian chum}_{s,t}$ ) to coincide with the four- to five-year life cycle pattern that dominates chum salmon in the North Pacific Ocean and updated the data from North Pacific Anadromous Fish Commission data.

As recommended by Mantua (2001), we used a “winter index” of the Pacific Decadal Oscillation (PDO) or an average of the monthly PDO indices from November of the previous year through March of the current year, because year-to-year fluctuations are most apparent during winter. These months were chosen because conditions during this time likely determine the amount of pre-winter and winter mortality, and both western Alaska and Asian fish overwinter in the Gulf of Alaska and central North Pacific Ocean. We extracted SST data from global monthly temperatures on a 2-degree x 2-degree grid available from the National Oceanic and Atmospheric Administration’s (NOAA) Climate Data Center. To compare SSTs with SW1 growth, we averaged temperatures from small areas corresponding with juvenile chum salmon distribution during the first summer ( $\text{Local SST}_t$ , Appendix D1). Growth in the SW3 zone was compared to average annual SSTs within the North Pacific Ocean, corresponding to the approximate distribution of chum salmon after the first winter until the homeward migration ( $\text{NP Annual SST}_t$ ). We averaged SSTs within an 18-degree x 40-degree box ( $44^\circ\text{-}62^\circ\text{N}$ ,  $140^\circ\text{-}180^\circ\text{W}$ ) over the North Pacific Ocean at year  $t$ .

The North Pacific Index ( $\text{NPI}_t$ ) is the area-weighted sea level pressure over the region  $30^\circ\text{N}\text{-}65^\circ\text{N}$ ,  $160^\circ\text{E}\text{-}140^\circ\text{W}$  at year  $t$ . The NPI measures interannual to decadal variations in atmospheric circulation. The dominant atmosphere-ocean relation in the North Pacific is one where atmospheric changes lead changes in SSTs by one to two months. The Aleutian Low Pressure Index ( $\text{ALPI}_t$ ) is the relative intensity of the Aleutian Low pressure system of the North Pacific Ocean (December through March in year  $t$ ). It is calculated as the mean area ( $\text{km}^2$ ) with sea level pressure expressed as an anomaly from the 1950-1997 mean. A positive index value reflects a relatively strong or intense Aleutian Low. We used two wind mixing indices:  $\text{MayMix}_t$  measured in  $\text{m}^3/\text{sec}^3$  at year  $t$  from the vicinity of St. Paul Island, Alaska collected from 1950-2010, and  $\text{JJMixM2}_t$  measured at Mooring 2 ( $57^\circ\text{N}$ ,  $164^\circ\text{W}$ ) in  $\text{m}^3/\text{sec}^3$  from June-July 1950-2010. We used wind mixing indices because they provide an estimate of the rate of mixing at the base of the upper mixed layer, an area in the ocean important to juvenile salmon. The average ice concentration in the Bering Sea at year  $t$  was represented by  $\text{Ice Cover}_t$ . The index was



developed from a  $2^{\circ} \times 2^{\circ}$  box ( $56^{\circ}$ - $58^{\circ}$ N,  $163^{\circ}$ - $165^{\circ}$ W) from 1 January – 31 May. The amount of ice cover has been shown to affect the spring plankton bloom and be important to juvenile salmon (Hunt et al. 2002, Moss et al. 2009). The effect of the El Niño - Southern Oscillation ( $ENSO_t$ ) on the northern hemisphere reaches its maximum during the boreal winter, and we used the mean December-January values of the multivariate ENSO index from the NOAA Earth System Research Laboratory Physical Science Division. El Niño episodes occur every four to five years and can last up to 12 to 18 months. The ENSO index is based on six observed variables over the tropical Pacific: sea-level pressure, zonal and meridional components of surface wind, SST, surface air temperature and total cloudiness fraction of the sky (Wolter and Timlin 1998). The Arctic Oscillation Index ( $AO_t$ ) examines how atmospheric pressure fluctuated between positive and negative phases. The negative phase brings higher-than-normal pressure over the polar region and lower-than-normal pressure at  $45^{\circ}$ N latitude. Thus, in this phase cold air plunges into the Midwestern United States and Western Europe and storms bring rain to the Mediterranean. The positive phase brings opposite conditions, steering ocean storms farther north and bringing wetter weather to Alaska, Scotland and Scandinavia. The AO was most variable during the winter, thus, it captured characteristics when fish may not have enough fat reserves to survive. The Bering Sea Level Pressure winter index ( $BSLPw_t$ ) represents deviations from the mean value of sea level pressure average over the Bering Sea ( $55^{\circ}$  -  $65^{\circ}$ N,  $170^{\circ}$ E -  $160^{\circ}$ W) December through March.

Air temperatures (*Local Air Temp<sub>t</sub>*) from the nearest city to the river system (Nome, Alaska for Unalakleet and Yukon rivers; Bethel, Alaska for Quinhagak; King Salmon, Alaska for Nushagak River; Anadyr, Russia for Anadyr River; and Sapporo, Japan for Chitose River) were used as a proxy for nearshore SST and river temperatures. We obtained air temperatures from western Alaska from the Weather Underground website (Appendix D1). A. Zavolokin provided air temperatures for Anadyr, Russia (Pacific Research Fisheries Center, TINRO-Centre, Vladivostok, Russia, 2011), and the Japan Meteorological Agency website provided the Sapporo, Japan temperatures. Air temperatures were averaged for winter (November – March), summer (May – September) and annually and were compared with first-year growth only. All explanatory variables were normalized or “scaled” prior to analysis using the ‘base’ package in R version 2.9.2 (R Development Core Team 2009) allowing us to compare the magnitudes of the estimated effects directly.

## Analyses

We examined relationships between chum salmon growth and potential explanatory variables using correlation analysis followed by multiple linear regression. First, we computed Pearson's correlations among environmental variables to assess potential multi-collinearity. We also computed Pearson's correlations between growth variables and environmental variables to identify key variables (Tables 3.2-3.4, Chapter 1). Results were used to select a subset of variables for the regression models. We then modeled chum salmon growth as a function of the selected variables using a general regression approach:

$$(1) \quad y = X\beta + \varepsilon$$

where  $y$  was observed growth (SW1 or SW3),  $X$  was a matrix of explanatory variables, and  $\varepsilon$  were the residuals. Because of the time series nature of the data and because preliminary analyses suggested that the residuals were autocorrelated, we used Generalized Least Squares (GLS) regression to allow for autocorrelation in the residuals. Generalized least squares regression is a technique for estimating unknown parameters in a linear regression model, and GLS is often applied when the variances of the observations are unequal (heteroscedastic) or when there is correlation among observations.

We used simple linear regression models with autocorrelated errors to examine the individual hypotheses (i.e. - Asian chum salmon inhibit growth of western Alaska chum salmon). To account for the effects of multiple variables, we constructed multiple linear regression models (full models) based on results from simple linear regressions and correlation analyses. Because of strong multi-collinearity, we selected one SST, one large scale climate index, one wind mixing index, and one air temperature, which served as a proxy for local SST and freshwater temperature. We fit each full model assuming that residuals are independent and used a backward stepwise approach, choosing the model with the lowest Akaike Information Criterion (AIC) to select the best submodel. We examined the residuals for possible autocorrelation and, if we found significant autocorrelation, we re-fit the model with an autoregressive error structure using GLS. We used an autoregressive error structure up to order  $p = 6$  to account for the possibility of spawners affecting the growth of their offspring, then used AIC to choose the appropriate order, if deemed biologically reasonable. We chose the model with the lowest AIC by at least four points (Burnham and Anderson 2004). We chose the most parsimonious model, if differences in AIC were small or whenever the larger model was deemed biologically unrealistic

(e.g., usually when order  $p > 4$ ). Plots of the residuals of the reduced final model were examined for normality and influence of outliers. The model was weighted by the number of scales measured per year to account for unequal sample sizes among years. In the Yukon River, we measured >25 scales per gender per age each year, but in Bristol Bay, there were not enough samples for age 0.3 fish in 1966, and for age 0.4, we had reduced sample sizes in 1969, 1970, 1975, 1977, 1980, and 2000. All model parameters were estimated via restricted maximum likelihood estimation using the 'nlme' package (Pinheiro and Bates 2000) in R version 2.9.2 (R Development Core Team 2009).

### *SW1 Models*

The SW1 growth models were designed to compare growth with environmental variables that might influence early marine growth in chum salmon, such as wind mixing and local SST; whereas, the SW3 growth models focused on assessing potential effects of density dependence, competition, SST, and gender on growth. Because there were no differences by gender in SW1 growth, we combined the sexes for our analyses of SW1 growth, giving us larger samples sizes ( $\geq 50$  in most years). Based on the results of Chapter 1, the simple linear regressions, and Pearson's correlations for these chum salmon populations (Tables 3.2-3.4), we developed a full model that we applied to all populations:

$$(2) \quad SW1_t = \alpha + \beta_1(local\ SST_t) + \beta_2(ALPI_t) + \beta_3(NPI_t) + \beta_4(MayMix_t) + \beta_5(IceCover_t) + \beta_6(local\ Air\ Temp_t) + \varepsilon_t$$

where the terms are defined above and in Appendix D1. Based on results from the Pearson's correlations, it appeared that we could use the same model for all populations, but results were mixed. We found that we had to revise the model to fit specific populations.

### *SW3 Models*

To test for competition between our study populations and Russian pink or Asian chum salmon, we compared SW3 growth with pink and Asian chum salmon abundances. To examine effects of SST on growth, we also included the North Pacific SST, and one large-scale environmental index, the NPI. Exploratory data analysis suggested a possible interaction between pink salmon and Asian chum salmon abundance. It has been suggested that pink salmon abundance altered the feeding and distribution of chum salmon on the high seas (Azumaya and Ishida 2000, Kaeriyama et al. 2004, Myers et al. 2004). Because of uncertainty about this

interaction, we chose to examine the model with and without the interaction term. We also included separate intercepts by gender in these models to account for the observed larger mean size of males.

$$(3) \quad SW3_t = \alpha + \beta_1(Pinks_t) + \beta_2(Asian\ Chums_t) + \beta_3(GOA\ Annual\ SST_t) + \beta_4(NPI_t) + \beta_5(Pinks_t * Asian\ Chums_t) + Gender_k + \varepsilon_t$$

where the terms were defined above and in Appendix D1.

All response variables (SW1 and SW3) were plotted and examined for normality and outliers. Shapiro-Wilk tests for normality were used to assess the normality of the response variables. The response variables were also plotted by odd and even year of growth to determine whether there was an odd-even year effect due to pink salmon abundance. We compared mean annual growth between odd and even years with Student's *t*-tests. Differences in growth by gender were examined by comparing annual mean male and female growth with a Welch Two Sample *t*-test.

#### *Outliers*

The Unalakleet River age 0.3 SW1 data had an outlier (1977) that strongly affected the results and was removed. The Quinhagak age 0.3 SW1 data had an outlier (2006) that strongly affected the results and was removed, and the Quinhagak age 0.4 SW1 data had two outliers (1979 and 1980), which were removed.

#### **Results**

Adult fish length was positively related to total scale growth for both ages in western Alaska (Figs. 3.3-3.4; Norton Sound: age 0.3,  $R^2 = 0.34$ ; age 0.4,  $R^2 = 0.64$ ; Kuskokwim River: age 0.3,  $R^2 = 0.40$ ; age 0.4,  $R^2 = 0.67$ ) and for the age 0.3 fish examined in Asia (Russia,  $R^2 = 0.38$ ; Japan,  $R^2 = 0.19$ ). Thus, scale growth explained 19-67% of the variability depending on stock and age group.

Normalized time series plots of SW1 and SW3 growth showed no apparent pattern related to the odd-even year abundance of Asian pink salmon (Figs. 3.5-3.7). Most plots showed changes in growth around major climate events in the North Pacific Ocean. For example, Anadyr River age 0.3 SW3 growth decreased in the mid-1970s, corresponding to the well-known climate shift in 1976-77 (Fig. 3.7), and Quinhagak SW3 growth declined in the late 1980s corresponding

with a second climate shift around 1988-1989 (Fig. 3.6). On the other hand, results of the *t*-tests indicated some differences in growth in the SW3 zone of some populations between odd and even years. For example, growth of Norton Sound age 0.3 females ( $p = 0.015$ ) and age 0.4 (both sexes) was significantly greater in odd years (males,  $p = 0.049$ ; females,  $p = 0.043$ ), and growth of Yukon River age 0.3 females SW3 was marginally significantly lower in even years at sea ( $p = 0.070$ ; Student *t*-test; Table 3.5). There was no significant difference in growth between genders in the SW1 zone for all populations and ages. There was a significant difference, indicating that males were larger than females, in the SW3 growth zone, scale radius, and overall adult body length for all ages and populations, except Japan (SW3,  $p = 0.306$ ; radius,  $p = 0.647$ ; length,  $p = 0.066$ ). The difference in SW3 growth between Unalakleet River age 0.4 males and females was marginally significant (Welch two sample *t*-test;  $p = 0.064$ ).

## **Gender**

We found that growth of females was significantly less than that of males during SW3 for all age 0.3 fish, except Japan, as indicated by negative model coefficients (Tables 3.6-3.11). Growth of female age 0.3 fish from the Chitose River was significantly greater than growth of males during SW3. For age 0.4 fish from Bristol Bay and Kuskokwim River, the reverse was true. Growth of age 0.4 Norton Sound and Yukon River females was significantly less than growth of males in all models in which gender was significant.

## **Norton Sound**

### *SW1 growth*

For age 0.3 fish, simple linear regressions indicated that local SST had significant positive effects, and the ALPI and local air temperature in Nome had marginally significant positive effects on SW1 growth. There were no significant negative effects on SW1 growth of Norton Sound fish (Table 3.6). For age 0.4 fish, the results of the simple linear regressions indicated that the ALPI, Nome summer air temperature, and local SST had significant positive effects, and the May wind mixing index and BSLP winter index had significant negative effects on SW1 growth of Norton Sound chum salmon (Fig. 3.8, Table 3.6).

The best overall model included significant positive effects of local SST, ALPI and NPI on Norton Sound SW1 growth of age 0.3 fish (Fig. 3.9, Table 3.7). For age 0.4 fish, the best

model suggested positive effects of local sea surface temperature and ALPI on first-year growth (Fig. 3.9, Table 3.7).

#### *SW3 growth*

Correlations and simple linear regressions indicated that total Russian pink salmon abundance had significant negative effects on the SW3 growth of age 0.4 Norton Sound fish, but significant positive effects on the growth of age 0.3 fish. North Pacific SST had significant negative effects on SW3 growth for both ages of Norton Sound chum salmon (Table 3.6). Asian chum salmon abundance had marginally significant negative effects on the growth of age 0.4 Norton Sound fish (Table 3.6) but showed no effects on the growth of age 0.3 fish ( $p = 0.624$ ). The NPI showed positive effects on SW3 growth; whereas, the AO showed marginally significant negative effects on the growth of age 0.3 fish and positive effects on the SW3 growth of age 0.4 fish. The ENSO showed strong positive effects on SW3 growth of age 0.4 fish and no effects on growth of age 0.3 fish.

The best multiple regression for age 0.3 Norton Sound fish suggested a positive effect of pink salmon on third-year growth as well as slower growth of females in the third year (Table 3.8). For age 0.4 fish, the best model was one with pink salmon showing a significant positive effect on SW3 growth, and North Pacific SST and NPI and gender showed a significantly negative correlation with SW3 growth (Table 3.9). Age 0.4 females grew slower than males during the SW3 growth zone.

### **Kuskokwim River**

#### *SW1 growth*

For age 0.3 fish, the results of the simple linear regression models indicated that the ALPI, Bethel annual and summer air temperature, local SST, PDO, and ENSO had significant positive effects, and the NPI, ice cover, BSLP winter index had significant negative effects on the first year of marine growth of Kuskokwim River chum salmon (Table 3.10). The May wind mixing index had marginally significant negative effects on SW1 growth ( $p = 0.107$ ). For age 0.4 fish, the only significant result from the simple linear regression models indicated a positive relationship between SW1 growth and ENSO (Table 3.10).

For age 0.3 fish, the best model indicated that local SST, Bethel annual air temperature, and the ice cover index had significantly positive effects; whereas, BSLP winter index had

significant negative effects on SW1 growth (Table 3.7). For age 0.4 fish, the best model indicated that ENSO and AO had a significantly positive relationship with the SW1 growth of Kuskokwim River chum salmon (Table 3.7).

#### *SW3 growth*

The results of the simple linear regression models (Table 3.10) indicated that for age 0.3 Kuskokwim River chum salmon, NP SST, Asian chum abundance and NPI had significant negative effects on the third year of marine growth, while ENSO had a marginally significant positive relationship ( $p = 0.051$ ). Pink salmon abundance, ALPI, and AO showed no effects on SW3 growth of age 0.3 fish ( $p = 0.715$ ,  $0.799$ , and  $0.527$ , respectively). For age 0.4 fish, ENSO had significant positive effects, and NP SST showed significant negative effects on SW3 growth (Table 3.10). Pink and Asian chum salmon abundance, and ALPI all showed significant negative effects on SW3 growth when gender was removed from the regression model. AO and NPI showed no effects on third-year growth of Kuskokwim River chum salmon ( $p = 0.160$  and  $0.139$ , respectively).

The best model for age 0.3 Kuskokwim River fish (Table 3.8) was the full model with the interaction term (AIC = -212.0). Asian chum salmon abundance, NP annual SST, and NPI showed significant negative effects on SW3 growth. Russian pink salmon abundance and the interaction term (Pinks\*Asian chums) showed a significantly positive relationship with SW3 growth, but the model coefficients were very small (Fig. 3.11, Table 3.8). Females showed significantly less SW3 growth than males. When the initial model did not include an interaction term, the full model reduced to two models with close AICs values: one indicated that there were significant negative effects of Asian chum salmon abundance on SW3 growth and that females grew slower than males in SW3 (AIC = -209.4). The other model indicated that there was a strong negative influence of the NP annual SST, and NPI, and that females grew slower than males in SW3 (AIC = -205.5). For age 0.4 fish, the model (with and without interaction included) reduced to a negative relationship with NP annual SST and NPI and SW3 growth. In contrast to the other populations, females showed faster growth than males in the SW3 zone (Fig. 3.11, Table 3.9).

## **Anadyr River**

### *SW1 growth*

For age 0.3 fish, the results of the simple linear regression models indicated that the Anadyr summer air temperature had a significant positive relationship with SW1 growth (Table 3.11). The AO and Anadyr annual air temperature also had a marginally significant positive relationship with SW1 growth ( $p = 0.060$  and  $0.089$ , respectively). The best model indicated that the AO and Anadyr annual air temperature had significantly positive effects; whereas, NPI had a significant negative effect on SW1 growth of age 0.3 Anadyr River fish (Table 3.7).

### *SW3 growth*

The results of the simple linear regression models (Table 3.11) indicated that for age 0.3 Anadyr River chum salmon the abundance of Russian pink and Asian chum salmon abundance, and North Pacific annual SST had significant negative effects on the third year of marine growth. The AO showed a marginally significant negative relationship with SW3 growth ( $p = 0.090$ ). NPI, ALPI, and ENSO showed no effects on third-year growth of age 0.3 Anadyr River fish ( $p = 0.802$ ,  $0.714$ , and  $0.851$ , respectively). Gender was significantly negative for most variables tested, indicating that females grew slower than males in the SW3 zone. The best final model from the stepwise regression (with or without interaction term) for age 0.3 Anadyr River fish (Table 3.8) indicated that Asian chum salmon abundance had a significant negative relationship with SW3 growth (Figs. 3.10-3.11). Females grew significantly slower than males in the third year.

## **Chitose River**

### *SW1 growth*

The results of the simple linear regression models indicated that Japan annual air temperature and local SST had significant positive effects on age 0.3 Chitose River fish, and ice cover had significant negative effects on the first year of marine growth of Chitose River chum salmon (Table 3.11). The best full model indicated that local SST had significant positive effects; whereas, the BSLP winter index had significant negative effects on SW1 growth of Japanese chum salmon (Table 3.7).



### *SW3 growth*

The results of the simple linear regression models (Table 3.11) indicated that for age 0.3 Chitose River chum salmon the NPI, Gulf of Alaska annual SST, Asian chum salmon abundance and AO had significant negative effects on the third year of marine growth (Fig. 3.10). Russian pink salmon abundance had marginally significant negative effects on SW3 growth when gender was not included in the model ( $p = 0.104$ ). The North Pacific annual SST, ALPI, and ENSO showed no effects on SW3 growth of age 0 Chitose River fish ( $p = 0.421$ ,  $0.312$ , and  $0.846$ , respectively).

The best SW3 model for age 0.3 Chitose River fish was the only SW3 full model to not include gender in the model (Table 3.8). Russian pink salmon and Asian chum salmon abundance, and NPI showed significant negative effects on SW3 growth, while the pink and chum salmon interaction term (Pinks\*Asian chums) showed a significant positive relationship (AIC = -207.4, Fig. 3.11, Table 3.8). When the initial model did not include an interaction term, the model reduced to indicate a negative relationship of Asian chum salmon abundance and the NPI on SW3 growth (AIC = -206.1).

### **Comparison across the North Pacific Ocean**

#### *SW1 growth*

When we compared the simple linear regressions presented here with previous results from the Yukon River and Bristol Bay, Alaska (Chapter 1), we found two environmental variables that affected the SW1 growth of age 0.3 fish: local SST and local air temperature. Local SST showed positively significant effects on SW1 growth in five of six of the populations: Norton Sound, Yukon River, Kuskokwim River, Bristol Bay, and Chitose River. The only population in which we did not find a significant relationship between age 0.3 SW1 growth and SST was Anadyr River. Local air temperature showed significant or marginally significant positive effects on SW1 growth in five of the six populations. Local air temperature did not have a significant relationship with SW1 growth in the Yukon River. Consistent with a positive temperature effect, the ice cover index showed a significant negative relationship with four (67%) of the six populations: Yukon and Kuskokwim rivers, Bristol Bay and Japan. Within western Alaska only, the ALPI showed significant or marginally significant positive effects on the SW1 growth of all four western Alaska populations, and the PDO (positive) and BSLP winter index

(negative) had significant effects on the SW1 growth of three of the four western Alaska populations (Yukon and Kuskokwim rivers, and Bristol Bay).

Similar to age 0.3 fish, we found positive correlations with first-year growth of age 0.4 fish and local SST, local summer air temperature, and ALPI in western Alaska (Norton Sound, Yukon Rivers, and Bristol Bay). We also found that first-year growth of age 0.4 Kuskokwim River fish was significantly affected only by the ENSO (Table 3.10).

First-year growth of age 0.3 chum salmon had few predictor variables in common (Fig. 3.9). For example, Norton Sound, Bristol Bay, Kuskokwim and Chitose rivers had local SST as a significant positive component of the final model, while the other populations did not. The final models for the Kuskokwim and Chitose rivers were similar: both included local SST and BSLPw as factors affecting first-year growth of chum salmon, but the Kuskokwim River model also indicated that ice cover and local air temperature affected SW1 growth (Fig. 3.9; Table 3.7). There was an alternate model for SW1 growth in Chitose River with a slightly lower AIC (-99.9) that included the ice cover index and that model overlapped with growth of chum salmon from Kuskokwim and Anadyr rivers, showing significant negative effects of ice cover and NPI combined with significant positive effects of local air temperature on first-year growth. The model's AIC (-82.9) was higher, but this still indicated a need to choose models by region to improve our modeling.

When comparing the final models for age 0.4 fish from western Alaska, results were also unique by population. The model for Norton Sound was fairly similar to that for the Yukon River. Both included significant positive effects of local SST and ALPI on first-year growth, but the Yukon River SW1 model included May wind mixing as an important factor in SW1 growth (Fig. 3.9; Table 3.7). The model for Bristol Bay indicated that local SST and the ice cover index showed significant positive effects; whereas, ALPI, NPI, and May wind mixing showed significant negative effects on first-year growth. The first-year growth of age 0.4 fish in the Kuskokwim River was positively affected by the ENSO and the AO.

### *SW3 growth*

The results of the simple linear regression models indicated that all age 0.3 chum salmon populations, except Norton Sound, showed a significant negative relationship with the abundance of Asian chum salmon. In addition, the third-year growth of age 0.4 fish for all western Alaska

populations, except Bristol Bay, showed significant negative relationships with Asian chum salmon abundance (Figs. 3.10-3.11). We also found a detectable negative effect of NP SST on SW3 scale growth for all age 0.4 western Alaska chum salmon and for age 0.3 fish from Yukon, Kuskokwim, and Anadyr rivers. Third-year growth of age 0.3 fish from Norton Sound, Bristol Bay and Chitose River showed no detectable differences when compared with NP annual SST, indicating possible differential ocean distribution by age. Third-year growth was significantly affected by Russian pink salmon abundance from four of the age 0.3 populations (Yukon, Chitose, and Anadyr rivers, and Bristol Bay), and pink salmon was a significant factor for all age 0.4 western Alaska populations. The effects on saltwater growth in western Alaska (especially for age 0.3 fish) were sometimes positive. This result appeared anomalous, but overall compared with other results, the model coefficient for pink salmon was extremely small (Figs. 3.10-3.11).

We tested a number of environmental indices, but our results indicated that there was no index that had a significant effect on the SW3 growth of all populations. For example, the NPI showed significant negative effects on the SW3 growth of two of the age 0.3 populations (Kuskokwim and Chitose rivers), but NPI showed a significant positive relationship with the SW3 growth Norton Sound, and there was no detectable relationship with NPI and the SW3 growth of any western Alaska age 0.4 population. When comparing the ALPI and SW3 growth, we found that there was no relationship with the SW3 growth of the age 0.3 populations in this study and ALPI, but we found marginally significant results with the SW3 growth of two western Alaska age 0.4 populations (Yukon River and Bristol Bay) and ALPI. We also found significant correlations with ALPI and SW3 growth of Kuskokwim River age 0.4 chum salmon. We found a significant relationship with the AO and the SW3 growth of Japanese chum salmon, and a marginally significant relationship with the AO and SW3 growth of Anadyr River and Norton Sound (both ages) fish. There were no correlations with the AO and SW3 growth of other western Alaska populations. The PDO showed significant negative effects on SW3 growth of fish from the Yukon River (both ages) and Russia, but we found a significant positive correlation between the PDO and SW3 growth for Norton Sound (age 0.3 fish), Kuskokwim River (age 0.4 fish), and Japan (age 0.3 fish). We observed strong positive effects between ENSO and SW3 growth of all western Alaska populations of both ages. Asian chum salmon SW3 growth significantly was not significantly affected by ENSO.

The best models for age 0.3 fish indicated that Asian chum salmon abundance had a significant negative impact on SW3 growth of all populations, except Norton Sound, and females grew slower in all populations, except Japan (Fig. 3.11, Table 3.8). We found a significant negative relationship between NP annual SST and SW3 growth in the Yukon and Kuskokwim rivers, and NPI showed significant negative effects on third-year growth in the Yukon, Kuskokwim and Chitose rivers. Pink salmon abundance showed significant positive effects on SW3 growth in Bristol Bay, Kuskokwim River, and Norton Sound, but negative effects on third-year growth in the Yukon and Chitose Rivers. Overall, these model coefficients were extremely small when compared with other predictor variables in the models (Fig. 3.11), indicating that although pink salmon influenced chum salmon growth, the effect was likely small.

The best SW3 models for age 0.4 chum salmon yielded slightly different results. Asian chum salmon abundance had a significant negative impact only on the SW3 growth of the Yukon River, and age 0.4 females grew slower than males during the third year only in the Yukon River and Norton Sound. In Bristol Bay and the Kuskokwim River, we found that females grew faster than males during the SW3 growth zone (Fig. 3.11, Table 3.9). A significant negative relationship between NP annual SST and SW3 growth was found for three of the four age 0.4 populations (Yukon and Kuskokwim rivers and Norton Sound), and NPI showed significant negative effects on the SW3 growth of Norton Sound, Kuskokwim River and Bristol Bay fish. Pink salmon abundance showed positive significant effects on the SW3 growth of Bristol Bay, Yukon River, Norton Sound chum salmon. These model coefficients were extremely small when compared with other variables in the models (Fig. 3.11), indicating that although pink salmon were affecting chum salmon growth, the effect was likely small.

## Discussion

When we compared the growth data of six western Alaska and Asian chum salmon populations (age 0.3 fish), we found that Asian chum salmon abundance showed significant negative effects on third-year growth in five of six populations and three of four age 0.4 populations from western Alaska. In contrast to our hypothesis that cooler temperatures in the North Pacific Ocean inhibited growth, we found warmer large-scale SSTs in the North Pacific Ocean associated with reduced third-year chum salmon growth in most populations. Although we found evidence of interspecific interactions with the abundance of Russian pink salmon, these effects were inconsistent and smaller overall than the effects of Asian chum abundance and SST,

which may be due to changes associated with the regime shifts in 1976 – 1977 and 1989 (Chapter 1). Thus, although pink salmon abundance was an important factor affecting chum salmon growth, it did not affect growth as much as expected.

Across all populations and age examined in this study, enhanced first-year growth (SW1) was associated with warmer local and/or regional temperatures. Another factor that appeared to be important to several populations was the influence of ice cover, and it appears that less ice has enhanced first-year growth. After the 1976-77 regime shift, SSTs in coastal areas warmed (Hare et al. 1999, Mantua et al. 1997), and this may have contributed to the positive correlations observed among SW1 growth and SST and/or air temperature. Thus, our results corroborated the importance of temperature to first-year or juvenile chum salmon growth. Although we found similar negative effects on growth of both ages associated with NPI, BSLP winter index, and May wind mixing, results for other environmental variables were less consistent, and the AIC best models differed by ecosystems and by fish age.

It is important to remember that we used scale measurements as an index of fish growth over time, and although we had a fairly large sample size (25-50 scales per year), we only sampled a small number of the fish inhabiting the North Pacific Ocean. Total abundance of Pacific salmon in the North Pacific Ocean increased sharply from approximately 300 to 700 million adults per year following the 1976-1977 climate shift, largely as a result of increases in northern regions (Rogers 1984). Also, the fish we examined were ones that survived to adulthood; hence, they may not be representative of the whole population. In addition, the fish may have been sampled non-randomly (e.g.—oversampling of early- or late-returning fish and gear effects, which may result in our samples not being representative of the population). We examined six populations individually, which could introduce issues of multiple testing into our methodology. There are methods to compare the six populations directly, such as vector autoregression, which would examine the serial autocorrelation between and within the models. We considered these methods, but due to the costs associated with them, we chose to focus on the characteristics of the individual populations rather than the ecosystem as a whole.

When examining the third-year growth of chum salmon, several environmental indices affected the growth of some, but not all, populations. For example for age 0.3 fish, NPI was negatively correlated with third-year growth in the Kuskokwim and Chitose rivers but positively correlated with third-year growth in Norton Sound. This emphasizes the difficulty in examining

large-scale patterns, and the need to tailor the models by ecosystem (Mueter et al. 2002b, Mueter et al. 2002c, Peterman et al. 1998, Pyper et al. 2002). Using one model to encompass all six populations meant that sometimes the model failed, even though the initial Pearson's correlations and simple linear regressions indicated that the full model chosen was useful. It is possible that other indices exist which would improve the fit of the model for the Asian populations. We had difficulty fitting the models to those populations. This may also have been due to sample size. We received limited acetate impressions from the other countries. We used all measureable scales, but for Russia, in some years only ~10 scales per year per gender were measured. We weighted the GLS regressions by number of scales to account for this, but the variability in measurements could have affected population-wide comparisons.

During the third year at sea, western Alaska chum salmon and most Asian chum salmon were likely in the Gulf of Alaska encountering open water conditions and colder water temperatures associated with the positive phase of the PDO. From the mid-1960s through approximately 1980 (Farley et al. 2004, Urawa et al. 2009), growth increased. We hypothesized that cooler temperatures in the North Pacific Ocean would inhibit the marine growth of western Alaska and Asian chum salmon, and North Pacific Ocean temperatures appeared to affect marine growth of both ages of chum salmon from all populations. Our hypothesis implied that we would find positive coefficients, thus our results did not support our hypothesis. Firstly, we found overall SSTs in the North Pacific Ocean were warmer after the 1980s, and this should have promoted salmon growth, but we found that SSTs coincided with reduced chum salmon growth. Although this appears counterintuitive, Ruggerone et al. (2011) found that adult length-at-age was negatively correlated with SST, rather than positively correlated as expected based on other studies of salmon (Mueter et al. 2002a, Mueter et al. 2002b, Ruggerone et al. 2007). They suggested that this unexpected result was due to density-dependent effects involving abundance of hatchery chum salmon. Perhaps the abundance of hatchery chum salmon overwhelmed the favorable growing conditions associated with warm SSTs. Our results supported this suggestion. We found strong negative relationships between the abundance of Asian chum salmon, which were mostly hatchery salmon, and the growth of 90% of the populations/ages we examined indicating that these Asian chum salmon likely had an effect on the growth of other chum salmon in the North Pacific Ocean. It is also important to note that SST and chum salmon abundances have both shown long-term increasing trends. This could result in a spurious negative relationship with growth for both variables because growth generally showed a decreasing trend.

One other question would be why were we showing warmer overall SSTs in the Gulf of Alaska, although the PDO predictions indicated that SSTs in that area should be cooler? One reason might be that the box we used to capture SSTs for the North Pacific Ocean was fairly broad and may have included inshore temperatures, which increased during the study period. Perhaps we need to use a narrower box of SSTs to improve our comparisons. Farley and Moss (2009) found that juvenile chum salmon growth rates were higher in both regions during years with cold SSTs, agreeing with our results. Although fish in their study were younger, perhaps most chum salmon do not grow well in warm SSTs. Maybe they grow better in colder SSTs and the warmer SSTs in recent years have actually caused their growth to decline. One future analysis would be to subset the data by warm and cold years, similar to Farley and Moss (2009).

We hypothesized that Russian pink salmon abundance inhibited the growth of western Alaska chum salmon during the third year in the ocean. During this time period, the distribution of Russian pink salmon and western Alaska chum salmon would overlap in the North Pacific Ocean between 160°W longitude and 170°E longitude (Myers et al. 2007). Studies of sockeye salmon found a negative effect of the abundance of pink salmon on sockeye salmon growth during the third year at sea (Ruggerone et al. 2005, Ruggerone and Nielsen 2004). Although pink salmon was a significant part of most of our models, the coefficients for both the pink salmon effect and the pink-Asian chum interaction were very small, indicating that although significant, these effects on third-year growth of chum salmon were not as strong as those from SST and Asian chum salmon abundance. Because growth of chum salmon in the first and third year appears to be closely linked to SST, it is possible that the variability in SSTs after the regime shift altered ocean productivity, allowing pink and chum salmon abundances to increase concurrently.

Researchers have suggested that Asian chum salmon shift their spatial distribution from the Bering Sea to southern areas in years when pink salmon abundance is high (Azumaya and Ishida 2000, Ogura and Ito 1994). Azumaya and Ishida (2000) found that there was no significant relationship between growth of chum salmon and abundance of pink salmon, suggesting that growth of chum salmon was more affected by intraspecific interactions than interspecific interactions. Both pink and chum salmon may have increased in abundance due to improved ocean conditions and higher marine survival associated with warmer SST. Increasing temperatures also may have increased prey production and salmon growth, but this may be masked by the negative effects of competition with increasing numbers of Asian hatchery salmon.

Chum salmon are fairly omnivorous due to an unique gut architecture, permitting them to eat a more diverse diet than other salmon species. This may reduce competition with pink salmon. When pink salmon abundance increased, chum salmon were capable of “prey switching,” foraging on lower quality prey, such as gelatinous zooplankton (e.g., amphipods, euphausiids, pteropods, and copepods, Andrievskaya 1966, Davis et al. 2000, Davis et al. 2004). Switching food sources possibly allowed chum salmon to survive and increase in abundance when prey productivity was high, unlike sockeye salmon, whose growth has been reduced in odd years due to pink salmon abundance (Ruggerone et al. 2005, Ruggerone et al. 2003).

The best model for third-year growth included gender in all age 0.3 models, except Japan. This was to be expected from previous work (B. Agler, ADF&G, unpubl. data). For some reason, female Japanese fish are larger-at-age than males. The models for two populations, Norton Sound and the Yukon River, indicated that females tended to grow slower than males in the SW3 zone, but in Bristol Bay and the Kuskokwim River, we found the opposite, males grew slower than females. Breeding males are larger than females, and this appeared to be when size differentiation occurred (Chapter 2), so it is possible that in Bristol Bay and the Kuskokwim River, females were using compensatory growth in the SW3 growth zone to attain the size necessary to return to the natal site to breed. These females had already spent an “extra” year in the ocean by not returning to the natal site as 0.3 year-old fish.

Asian chum salmon abundance appeared effect third-year growth of age 0.3 fish more than growth of age 0.4 fish. It was a factor in both the simple linear regression results and the full models for five of the six age 0.3 populations; whereas, it was a significant negative factor in the simple linear regressions for the age 0.4 fish but not included in all of the best models. Age 0.3 is the predominant age group of Asian chum salmon (Kaeriyama 1989), thus it is likely that other age 0.3 fish would be affected first by the increased abundance of fish of a similar age. Competition among conspecifics for prey items would likely be greatest among those from the same age group, because they would be a similar size at each life stage. In addition, age 0.3 fish grow faster to be large enough to return to the natal site one year before age 0.4 fish. Competition would probably affect these fish first. Age 0.4 fish feed another season in the ocean and have more time to “catch up” to attain the minimum size needed for reproduction. Most intermingling of North American and Asian chum salmon occurs when Asian fish extend their



range into the Gulf of Alaska during their second and third winters at sea (Fukuwaka et al. 2007a, Fukuwaka et al. 2007b, Myers et al. 2004, Urawa 2003, Urawa et al. 2004, Urawa et al. 2009).

Ruggerone et al. (2011) and Ruggerone and Agler (2008) found that adult length-at-age and second-year growth of Kwiniuk chum salmon, a Norton Sound, Alaska population, was negatively correlated with the abundance of Asian chum salmon. Western Alaska chum salmon frequent the Gulf of Alaska and North Pacific Ocean during the second and subsequent years of growth and may be affected by similar environmental conditions in the North Pacific Ocean. Thus, a future goal is to examine second-year growth to determine when the effects of Asian chum salmon abundance began to affect the growth of western Alaska chum salmon. Although the results of our current study indicated that Asian chum salmon abundance had strong negative effects on growth of western Alaska chum salmon in the North Pacific Ocean, it is difficult to determine the effects of density dependence on the dynamics of a population. In an earlier paper, we used scale measurements to back-calculate fish length by scale zone (Chapter 2). Combining these lengths with the model coefficients from the regressions (approximately -0.05), we calculated potential effects of density dependence on length by applying the model coefficient to the back-calculated lengths for the SW2 through SWPlus growth zones. The effect of increasing Asian chum salmon abundance ( $\pm$  one SD) led to a reduction in mean length of approximately 42-43 mm. From our data, we calculated that mean length of age 0.3 fish prior to 1970, when Asian chum salmon abundance began to increase, was 630 mm, and mean length of age 0.4 fish was 650 mm. Thus, this could affect fecundity by 85-86 eggs depending on fish age, or approximately 3-5% (Salo 1991).

In addition, there may be other effects on the population of which we are unaware. For example, size may be important for building redds. Fish from Fish Creek, Alaska are some of the largest in the North Pacific, and this is believed to be due to the size of the substrate where they bury their eggs (J. Helle, pers. comm.). If these fish were not large enough, they could not build nests. Larger females tend to construct deeper redds than smaller females, and these deeper redds are presumably more resistant to disturbance by other females and less susceptible to scour and intrusion of fine sediment associated with floods (Quinn 2005). Fecundity tends to increase with length, although this relationship has been shown to be quite variable, and larger salmon tend to produce larger eggs as well as more numerous eggs (Quinn 2005). Larger eggs equate to larger fry size at emergence. These fry are believed to be more resistant to starvation if food is scarce

and have higher survival rates thus providing advantages to large females in both the number of offspring and their odds of survival (Quinn 2005). Helle (1989) found that production of Olsen Creek, Alaska chum was positively related to the size of females in the parental generation, even after accounting for higher fecundity of such large fish. It is believed that the early marine growth period is critical to marine survival (Beamish and Mahnken 2001), thus a small reduction in body size could have ripple effects throughout the population. Reduced growth at sea might be related to reduced marine survival as indicated in the Ruggerone et al. (2011) study but not evaluated here due to inadequate data.

The North Pacific Ocean and the Gulf of Alaska are dynamic ecosystems, and the need for separate models by population indicated the need to examine areas on a regional scale rather than on a basin-wide scale (Mueter et al. 2002b, Mueter et al. 2002c). Examination of these six populations allowed us to determine some commonalities among chum salmon within the North Pacific Ocean, but we must emphasize that there was no “one size fits all” model for first-year growth. This was likely due to the dynamic nature of the ecosystem; others would state that this was due to interactions among the various components of a complicated and complex ecosystem. Overall, it appeared that sea surface temperature, abundance of Asian chum salmon, the North Pacific Index, May wind mixing, ice cover, and local air temperature influenced the scale growth of western Alaska and Asian chum salmon during the first and third year at sea depending upon the population, fish age, and interactions among the explanatory variables.

Production of adult hatchery chum salmon from Asia increased rapidly beginning in 1970, and hatchery chum salmon eventually began to exceed total production of wild adult salmon. Asian chum salmon, at approximately two billion fish per year (Ruggerone et al. 2010), are currently the dominant chum salmon stock in the Bering Sea and North Pacific Ocean. Our results suggested that there were likely significant negative effects on chum salmon growth due to the high abundance of Asian chum salmon. In recent decades, researchers have raised concerns about density-dependent effects on salmon due to the sheer number of salmon in the ocean, and there has been increasing interest in the possible effects of the abundance of hatchery salmon on wild salmon. Salmon, originating from distant regions and adjacent continents, share a common food resource, and due to distributional overlap in the North Pacific Ocean and Bering Sea, it is likely that density-dependent effects are occurring across the region. This study was prompted by sharp declines in chum salmon abundance in western Alaska and affected local communities,

many of whom depend on these fish for subsistence. We were unable to determine the mechanism causing these declines in abundance of western Alaska chum salmon, but our results contribute to growing evidence for competition among conspecific salmon. We encourage international cooperation among nations to explore the possibility of managing numbers of salmon oceanwide (e.g. proposals by Heard 1998, Holt et al. 2008).

### **Acknowledgments**

This investigation was funded by the North Pacific Marine Research Board (Project SFOS 99-188), the Arctic-Yukon-Kuskokwim – Sustainable Salmon Initiative (Projects 45677 and 45164), and the Alaska Department of Fish and Game (ADF&G). We greatly appreciate efforts to gather, measure, and catalogue scales by multiple unknown ADF&G staff, as well as, W. Whelan, J. Baker, J. Chesmore, J. Cashen, S. Hinton, M. Lovejoy, A. Norman, and W. Rosky. E. Siddon and J. Richar developed the SST program as part of a class. We also received support from a number of ADF&G staff, including C. Robinson, R. Josephson, L. Brannian, D. Evenson, E. Volk, L. Dubois, H. Krenz, T. Baker, F. West, L. Fair, D. Oxman, T. Frawley, and W. Johnson. We are especially grateful to Dr. A. Zavolokin, Pacific Research Fisheries Center (TINRO-Centre), Vladivostok, Russia, who provided the Anadyr River scale impressions and to Dr. T. Saito, Fisheries Research Agency, Hokkaido National Fisheries Research Institute, Sapporo, Japan, who provided the Chitose River scale impressions. In the process of coordinating a multi-country study, several individuals assisted with translations, suggestions, and obtaining samples, including Dr. N. Davis, Dr. K. Myers, Dr. S. Urawa, V. Sviridov, Dr. O. Temnykh, and Dr. M. Kaeriyama. Constructive comments on this paper were provided by Agler's graduate committee from University of Alaska Fairbanks: Dr. W. Smoker, Dr. P. Hagen, Dr. G. Kruse, and Dr. F. Mueter. Two anonymous reviewers provided helpful suggestions.

### **References**

- Alverson, D. 1992. A review of commercial fisheries and the Steller sea lion (*Eumetopias jubatus*): the conflict arena. *Rev. Aquat. Sci.* **6**: 2-3-256.
- Anderson, P.J. 2000. Pandalid shrimp as indicators of ecosystem regime shift. *J. Northwest Atl. Fish. Sci.* **27**: 1-10.
- Anderson, P.J., and Piatt, J.F. 1999. Community reorganization in the Gulf of Alaska following ocean climate regime shift. *Mar. Ecol. Prog. Ser.* **189**: 117-123.

- Andrievskaya, L.D. 1966. Food relationships of the Pacific salmon in the sea. *Vopr. Ikhtiol.* **6**(1): 84-90.
- Azumaya, T., and Ishida, Y. 2000. Density interactions between pink salmon (*Oncorhynchus gorbuscha*) and chum salmon (*O. keta*) and their possible effects on distribution and growth in the North Pacific Ocean and Bering Sea. *NPAFC Bull.* **2**: 165-174.
- Beamish, R.J., and Bouillon, D.R. 1993. Pacific salmon production trends in relation to climate. *Can. J. Fish. Aquat. Sci.* **50**(5): 1002-1016.
- Beamish, R.J., and Mahnken, C. 2001. A critical size and period hypothesis to explain natural regulation of salmon abundance and the linkage to climate and climate change. *Prog. Oceanogr.* **49**: 423-437.
- Briscoe, R.J. 2004. Factors affecting marine growth and survival of Auke Creek, Alaska coho salmon (*Oncorhynchus kisutch*), MS thesis, Fisheries, University of Alaska, Fairbanks.
- Burnham, K.P., and Anderson, D.R. 2004. Understanding AIC and BIC in model selection. *Sociol. Method Res.* **33**: 261-304.
- Cooney, R., and Brodeur, R.D. 1998. Carrying capacity and North Pacific salmon production: stock-enhancement implications. *Bull. Mar. Sci.* **62**(2): 443-464.
- Davis, N.D., Aydin, K.Y., and Ishida, Y. 2000. Diel catches and food habits of sockeye, pink, and chum salmon in the Central Bering Sea in summer. *NPAFC Bull.* **2**: 99-109.
- Davis, N.D., Fukuwaka, M., Armstrong, J.L., and Myers, K.W. 2004. Salmon food habits studies in the Bering Sea, 1960 to present. *NPAFC Tech. Rep.* **6**: 24-29.
- Farley, E.V., Jr., Kondzela, C.M., Murphy, J.M., and Middleton, A. 2004. Stock-specific distribution and migration of juvenile chum salmon along the Eastern Bering Sea shelf. *NPAFC Tech. Rep.* **5**: 27.
- Farley, E.V., Jr., Murphy, J.M., Adkison, M.D., Eisner, L.B., Helle, J.H., Moss, J.H., and Nielsen, J. 2007a. Early marine growth in relation to marine-stage survival rates for Alaska sockeye salmon (*Oncorhynchus nerka*). *Fish. Bull.* **105**: 121-130.
- Farley, E.V., Jr., Murphy, J.M., Wing, B.W., Moss, J.H., and Middleton, A. 2005. Distribution, migration pathways, and size of western Alaska juvenile salmon along the Eastern Bering Sea shelf. *Alaska Fish. Res. Bull.* **11**: 15-26.
- Farley, E.V., Moss, J.H., and Beamish, R.J. 2007b. A review of the critical size, critical period hypothesis for juvenile Pacific salmon. *NPAFC Bull.* **4**: 311-317.

- Farley, E.V., Jr., and Moss, J.H. 2009. Growth rate potential of juvenile chum salmon on the Eastern Bering Sea Shelf: an assessment of salmon carrying capacity. NPAFC Bull. **5**: 265-277.
- Francis, R.C., Hare, S.R., Hollowed, A.B., and Wooster, W.S. 1998. Effects of interdecadal climate variability on the oceanic ecosystems of the NE Pacific. Fish. Oceanogr. **7**(1): 1-21.
- Fukuwaka, M., Azumaya, T., Nagasawa, T., Starovoytov, A.N., Helle, J.H., Saito, T., and Hasegawa, E. 2007a. Trends in abundance and biological characteristics of chum salmon. NPAFC Bull. **4**: 35-43.
- Fukuwaka, M., and Ishida, Y. 2000. Ocean condition and Pacific salmon stock assessment in the North Pacific Ocean, 2000. NPAFC Doc.( 481): 1-9.
- Fukuwaka, M., Sato, S., Takahashi, S., Onuma, T., Sakai, O., Tanimata, N., Makino, K., Davis, N.D., Volkov, A.F., and Seong, K.B. 2007b. Winter distribution of chum salmon related to environmental variables in the North Pacific. NPAFC Tech. Rep. **7**: 29-30.
- Gargett, A.E. 1997. The optimal stability 'window': a mechanism underlying decadal fluctuations in North Pacific salmon stocks? Fish. Oceanogr. **6**(2): 109-117.
- Hagen, P.T., Oxman, D.S., and Agler, B.A. 2001. Developing and deploying a high resolution imaging approach for scale analysis. NPAFC Doc. **567**: 1-11.
- Hare, S.R., and Mantua, N.J. 2000. Empirical evidence for North Pacific regime shifts in 1977 and 1989. Prog. Oceanogr. **47**: 103-145.
- Hare, S.R., Mantua, N.J., and Francis, R.C. 1999. Inverse production regimes: Alaska and west coast Pacific salmon. Fisheries **24**(1): 6-14.
- Heard, W.R. 1998. Do hatchery salmon affect the North Pacific Ocean ecosystem? NPAFC Bull. **1**: 405-411.
- Helle, J.H. 1989. Relation between size at maturity and survival of progeny in chum salmon, *Oncorhynchus keta* (Walbaum). J. Fish. Biol. **35**: 99-107.
- Hollowed, A.B., Hare, S.R., and Wooster, W.S. 2001. Pacific Basin climate variability and patterns of Northeast Pacific marine fish production. Prog. Oceanogr. **49**(1-4): 257-282.
- Holt, C.A., Rutherford, M.B., and Peterman, R.M. 2008. International cooperation among nation-states of the North Pacific Ocean on the problem of competition among salmon for a common pool of prey resources. Mar. Policy **32**(4): 607-617.

- Hunt, G.L., Jr, Stabeno, P., Walter, G., Sinclair, E., Brodeur, R.D., Napp, J.M., and Bond, N.A. 2002. The Eastern Bering Sea: evidence for change and a new hypothesis linking ecosystem control and climate. *Deep Sea Res. Part II* **49**: 5821-5853.
- Ishida, Y., Ito, S., Kaeriyama, M., McKinnell, S., and Nagasawa, K. 1993. Recent changes in age and size of chum salmon (*Oncorhynchus keta*) in the North Pacific Ocean and possible causes. *Can. J. Fish. Aquat. Sci.* **50**(2): 290-295.
- Kaeriyama, M. 1989. Comparative morphology and scale formation in four species of *Oncorhynchus* during early life. *Ichthyol. Res.* **35**(4): 445-452.
- Kaeriyama, M., Nakamura, M., Edpalina, R.R., Bower, J.R., Yamaguchi, H., Walker, R.V., and Myers, K.W. 2004. Change in feeding ecology and trophic dynamics of Pacific salmon (*Oncorhynchus* spp.) in the central Gulf of Alaska in relation to climate events. *Fish. Oceanogr.* **123**: 197-207.
- Koo, T.S.Y. 1962. Age designation in salmon. *Studies of Alaska red salmon*. University of Washington Publications in Fisheries, New Series **1**: 37-48.
- Kruse, G.H. 1998. Salmon run failures in 1997-1998: a link to anomalous ocean conditions? *Alaska Fish. Res. Bull.* **5**(1): 55-63.
- Mantua, N.J. 2001. The Pacific Decadal Oscillation. *In The Encyclopedia of Global Environmental Change. Edited by M.C. McCracken and J.S. Perry, The Earth System: physical and chemical dimension of global environmental change.* pp. 592-594.
- Mantua, N.J., Hare, S.R., Zhang, Y., Wallace, J.M., and Francis, R.C. 1997. A Pacific interdecadal climate oscillation with impacts on salmon production. *Bull. Am. Meteorol. Soc.* **78**(6): 1069-1079.
- Martinson, E.C., Helle, J.H., Scarnecchia, D.L., and Stokes, H.H. 2008. Density-dependent growth of Alaska sockeye salmon in relation to climate-oceanic regimes, population abundance, and body size, 1925 to 1998. *Mar. Ecol. Prog. Ser.* **370**: 1-18.
- Martinson, E.C., Helle, J.H., Scarnecchia, D.L., and Stokes, H.H. 2009. Alaska sockeye salmon scale patterns as indicators of climatic and oceanic shifts in the North Pacific Ocean, 1922–2000. *NPAFC Bull.* **5**: 177-182.
- Moss, J.H., Murphy, J.M., Farley, E.V., Jr., Eisner, L.B., and Andrews, A.G. 2009. Juvenile pink and chum salmon distribution, diet, and growth in the Northern Bering and Chukchi Seas. *NPAFC Bull.* **5**: 191-196.

- Mueter, F., Pyper, B.J., Peterman, R.M., Wood, C.C., and Blackbourn, D.J. 2002a. Opposite effects of sea-surface temperature on survival rates of Pacific salmon from northern and southern areas. NPAFC Tech. Rep. **4**: 22-23.
- Mueter, F.J., Peterman, R.M., and Pyper, B.J. 2002b. Opposite effects of ocean temperature on survival rates of 120 stocks of Pacific salmon (*Oncorhynchus spp.*) in northern and southern areas. Can. J. Fish. Aquat. Sci. **59**(3): 456-463.
- Mueter, F.J., Ware, D.M., and Peterman, R.M. 2002c. Spatial correlation patterns in coastal environmental variables and survival rates of salmon in the North-East Pacific Ocean. Fish. Oceanogr. **11**(4): 205-218.
- Myers, K.W., Klovach, N.V., Gritsenko, O.F., Urawa, S., and Royer, T.C. 2007. Stock-specific distributions of Asian and North American salmon in the open ocean, interannual changes, and oceanographic conditions. NPAFC Bull. **4**: 159-177.
- Myers, K.W., Walker, R.V., Davis, N.D., and Armstrong, J.L. 2004. Diet overlap and potential feeding competition between Yukon River chum salmon and hatchery salmon in the Gulf of Alaska in summer. High Seas Salmon Research Program, Fisheries Research Institute, School of Aquatic and Fishery Sciences, University of Washington, Seattle.
- Ogura, M., and Ito, S. 1994. Change in the known ocean distribution of Japanese chum salmon, *Oncorhynchus keta*, in relation to the progress of stock enhancement. Can. J. Fish. Aquat. Sci. **51**(3): 501-505.
- Peterman, R.M., Pyper, B.J., Lapointe, M.F., Adkison, M.D., and Walters, C.J. 1998. Patterns of covariation in survival rates of British Columbian and Alaskan sockeye salmon (*Oncorhynchus nerka*) stocks. Can. J. Fish. Aquat. Sci. **55**(11): 2503-2517.
- Pinheiro, J., and Bates, D. 2000. Mixed-effects models in S and S-Plus. 528 pp.
- Pyper, B.J., Mueter, F.J., Peterman, R.J., Blackbourn, D.J., and Wood, C.C. 2002. Spatial covariation in survival rates of Northeast Pacific chum salmon. Trans. Am. Fish. Soc. **131**: 343-363.
- Pyper, B.J., and Peterman, R.M. 1999. Relationship among adult body length, abundance, and ocean temperature for British Columbia and Alaska sockeye salmon (*Oncorhynchus nerka*), 1967-1997. Can. J. Fish. Aquat. Sci. **56**(10): 1716-1720.
- Quinn, T.P. 2005. The behavior and ecology of Pacific salmon and trout. University of Washington Press.

- R Development Core Team. 2009. A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna.
- Rogers, D. 1984. Trends in abundance of Northeastern Pacific stocks of salmon. *In* The influence of ocean conditions on the production of salmonids in the North Pacific. Edited by W. Pearcy. Oregon State University Press, Corvallis, OR. pp. 100-127.
- Ruggerone, G.T., and Agler, B.A. 2008. Retrospective analyses of AYK chum and coho salmon - 2008 Arctic Yukon Kuskokwim Sustainable Salmon Initiative Project Product. Natural Resources Consultants, Inc, Seattle, WA and ADF&G Division of Commercial Fisheries, Mark, Tag, and Age Lab, Juneau, AK. 57 pp.
- Ruggerone, G.T., Agler, B.A., and Nielsen, J.L. 2011. Evidence for competition at sea between Norton Sound chum salmon and Asian hatchery chum salmon. *Environ. Biol. Fish.* **92**: 1-15.
- Ruggerone, G.T., Farley, E., Nielsen, J., and Hagen, P. 2005. Seasonal marine growth of Bristol Bay sockeye salmon (*Oncorhynchus nerka*) in relation to competition with Asian pink salmon (*O. gorbuscha*) and the 1977 ocean regime shift. *Fish. Bull.* **103**(2): 355-370.
- Ruggerone, G.T., and Nielsen, J.L. 2004. Evidence for competitive dominance of pink salmon (*Oncorhynchus gorbuscha*) over other salmonids in the North Pacific Ocean. *Rev. Fish Biol. Fish.* **14**: 371-390.
- Ruggerone, G.T., Nielsen, J.L., and Bumgarner, J. 2007. Linkages between Alaskan sockeye salmon abundance, growth at sea, and climate, 1955-2002. *Deep Sea Res. Part II* **54**(23-26): 2776-2793.
- Ruggerone, G.T., Nielsen, J.L., Farley, E., Ignell, S., Hagen, P., Agler, B., Rogers, D., and Bumgarner, J. 2002. Long-term trends in annual Bristol Bay sockeye salmon scale growth at sea in relation to sockeye abundance and environmental trends, 1955–2000. *NPAFC Tech. Rep.* **4**: 56-58.
- Ruggerone, G.T., Peterman, R.M., Dorner, B., and Myers, K.W. 2010. Magnitude and trends in abundance of hatchery and wild pink salmon, chum salmon, and sockeye salmon in the North Pacific Ocean. *Mar. Coast. Fish.* **2**: 306-328.
- Ruggerone, G.T., Zimmermann, M., Myers, K.W., Nielsen, J.L., and Rogers, D.E. 2003. Competition between Asian pink salmon (*Oncorhynchus gorbuscha*) and Alaskan sockeye salmon (*O. nerka*) in the North Pacific Ocean. *Fish. Oceanogr.* **12**(3): 209-219.
- Seeb, L.W., Crane, P.A., Kondzela, C.M., Wilmot, R.L., Urawa, S., Varnavskaya, N.V., and Seeb, J.E. 2004. Migration of Pacific Rim chum salmon on the high seas: insights from genetic data. *Environ. Biol. Fish.* **69**(1): 21-36.



- Salo, E.O. 1991. Life history of chum salmon (*Oncorhynchus keta*). In Pacific Salmon Life Histories. Edited by C. Groot and L. Margolis. UBC Press, Vancouver. pp. 231-310.
- Urawa, S. 2003. Stock identification studies of high seas salmon in Japan: a review and future plan. NPAFC Tech. Rep. **5**: 9-10.
- Urawa, S., Azumaya, T., Crane, P.A., and Seeb, L.W. 2004. Origins and distribution of chum salmon in the Central Bering Sea. NPAFC Tech. Rep. **6**: 67-70.
- Urawa, S., Kawana, M., Anma, G., Kamei, Y., Shoji, T., Fukuwaka, M., Munk, K.M., Myers, K.W., and Farley, J., E V. 2000. Geographic origin of high-seas chum salmon determined by genetic and thermal otolith markers. NPAFC Bull. **2**: 283-290.
- Urawa, S., Sato, S., Crane, P.A., Agler, B., Josephson, R., and Azumaya, T. 2009. Stock-specific ocean distribution and migration of chum salmon in the Bering Sea and North Pacific Ocean. NPAFC Bull. **5**: 131-146.
- Walker, R., Myers, K., and Ito, S. 1998. Growth studies from 1956-95 collections of pink and chum salmon scales in the central North Pacific Ocean. NPAFC Bull. **1**: 54-65.
- Ware, D.M., and Thomson, R.E. 2005. Bottom-up ecosystem trophic dynamics determine fish production in the Northeast Pacific. Science **308**: 1280-1284.
- Wolter, K., and Timlin, M.S. 1998. Measuring the strength of ENSO - how does 1997/98 rank? Weather **53**: 315-324.
- Zaporozhets, O.M., and Zaporozhets, G.V. 2004. Interaction between hatchery and wild Pacific salmon in the Far East of Russia: a review. Rev. Fish Biol. Fish. **14**: 305-319.
- Zimmerman, M. 1991. Trends in freshwater growth of sockeye salmon (*Oncorhynchus nerka*) from the Wood River Lakes and Nushagak Bay, Alaska, School of Fisheries, University of Washington, Seattle.

## **Tables and Figures**

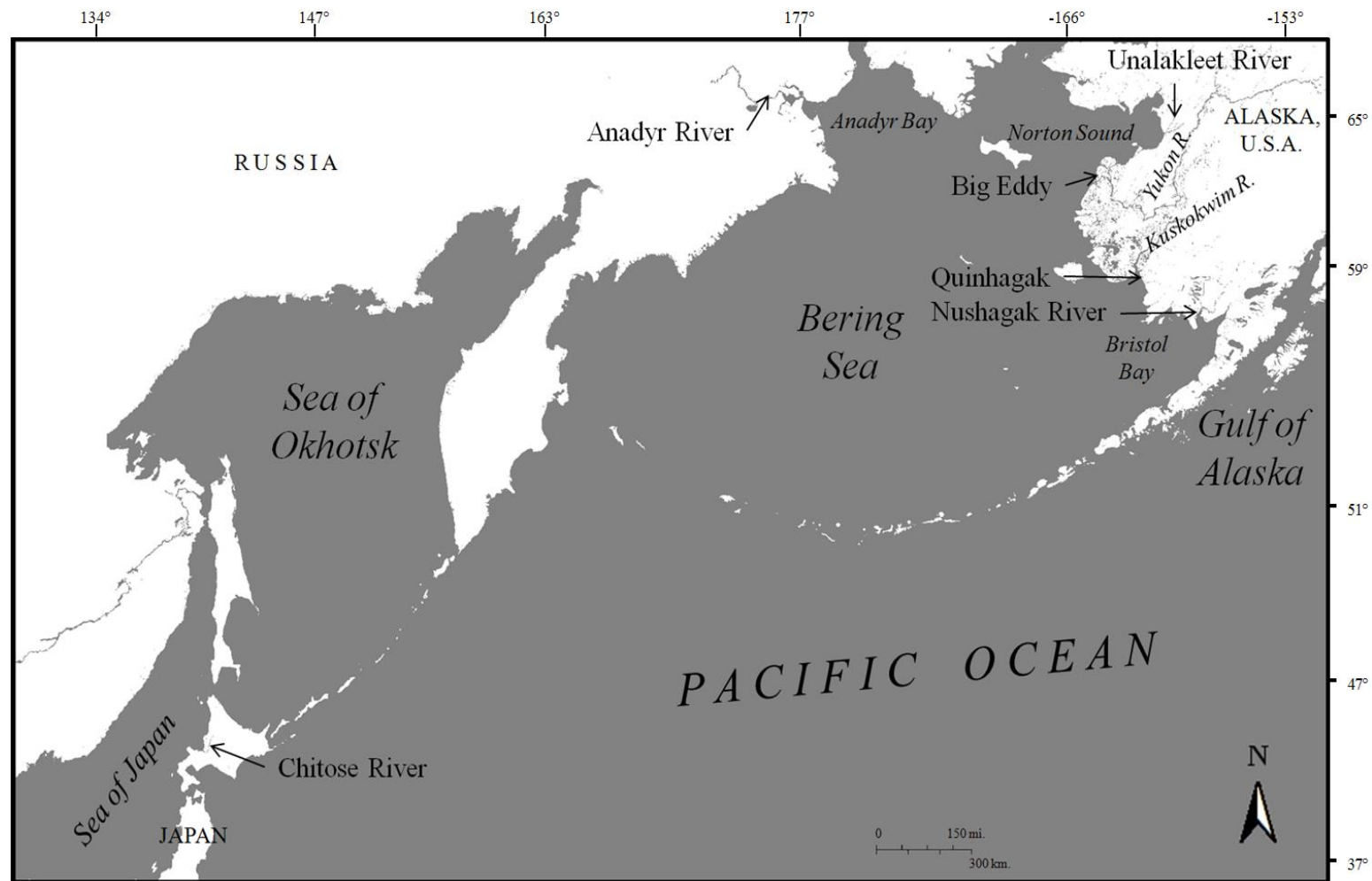


Figure 3.1. Map of the study area. The six chum salmon river systems included in this study were: four western Alaska populations (Unalakleet River, representing Norton Sound; Big Eddy, representing Yukon River, Quinhagak, representing Kuskokwim River, and Nushagak River, representing Bristol Bay) and two Asian populations (Anadyr River, Russia and Chitose River, Japan).

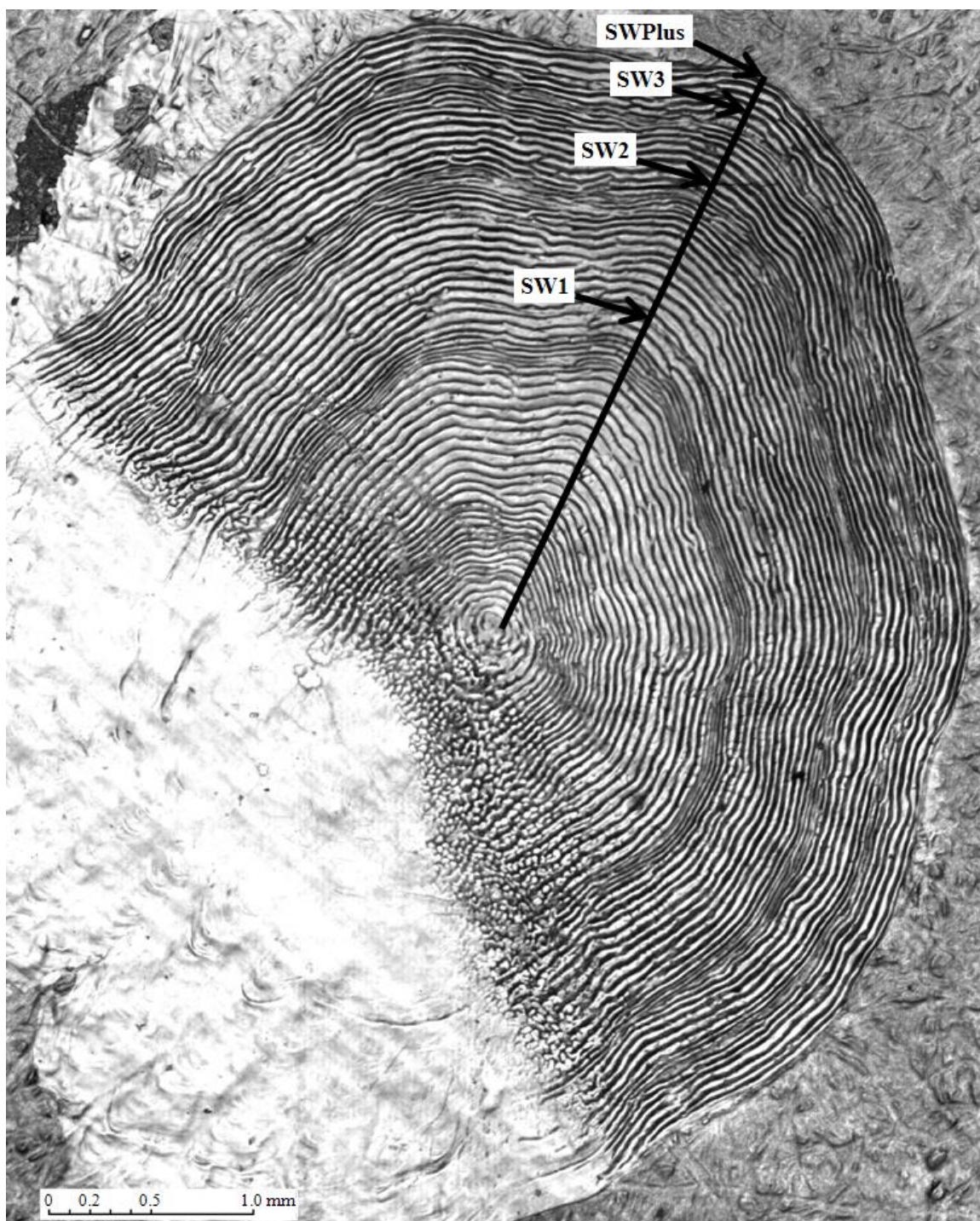


Figure 3.2. Example of a chum salmon scale. This is an age 0.3 chum salmon scale with the annuli marked by seasonal growth zones SW1, SW2, etc. SW is an abbreviation for saltwater, indicating the fish is in marine waters. The numbers 1, 2, etc. indicate the number of years at sea.

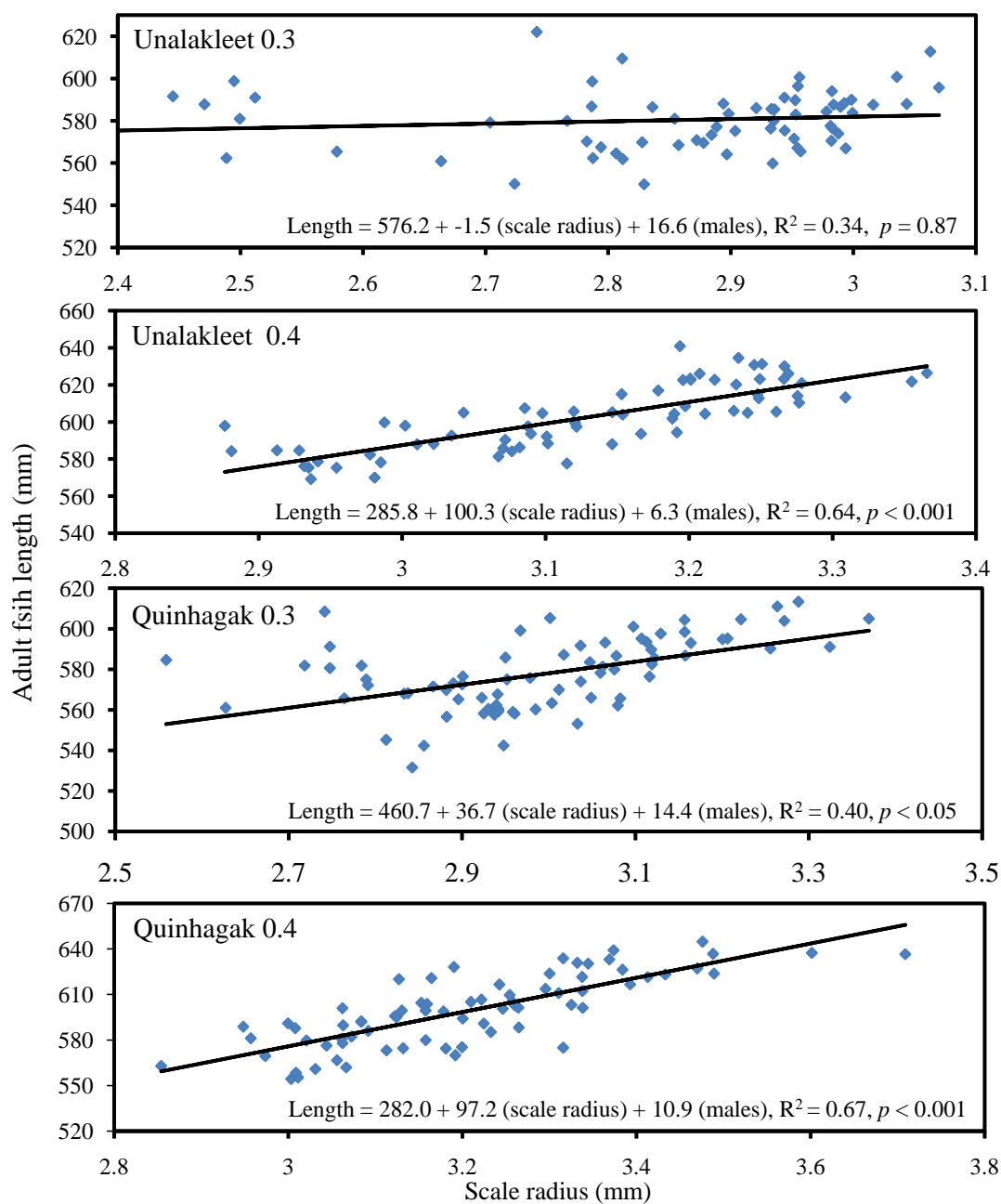


Figure 3.3. Mean adult fish length (mm, mid-eye to fork of tail) compared with mean scale growth (mm, radius) for chum salmon from Unalakleet River, Norton Sound, Alaska and Quinhagak, Kuskokwim River, Alaska.

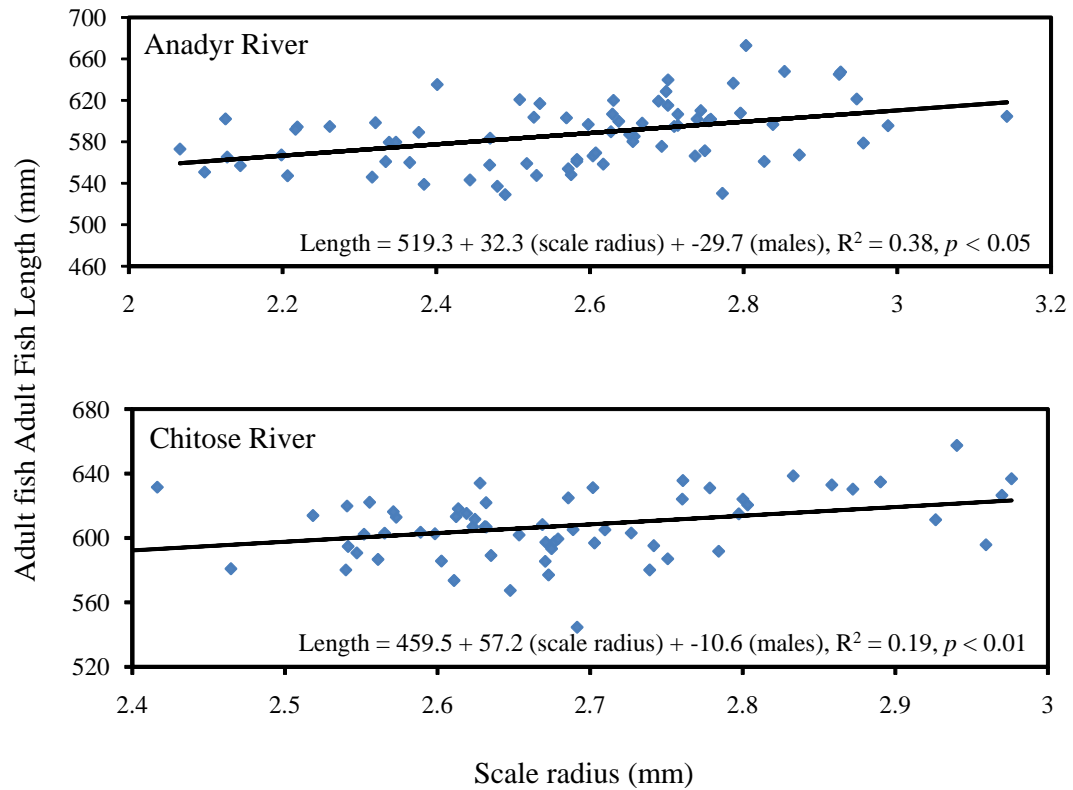


Figure 3.4. Mean adult fish length (mm, mid-eye to fork of tail) compared with mean scale growth (mm, radius) for age 0.3 chum salmon from Chitose River, Japan and Anadyr River, Russia.

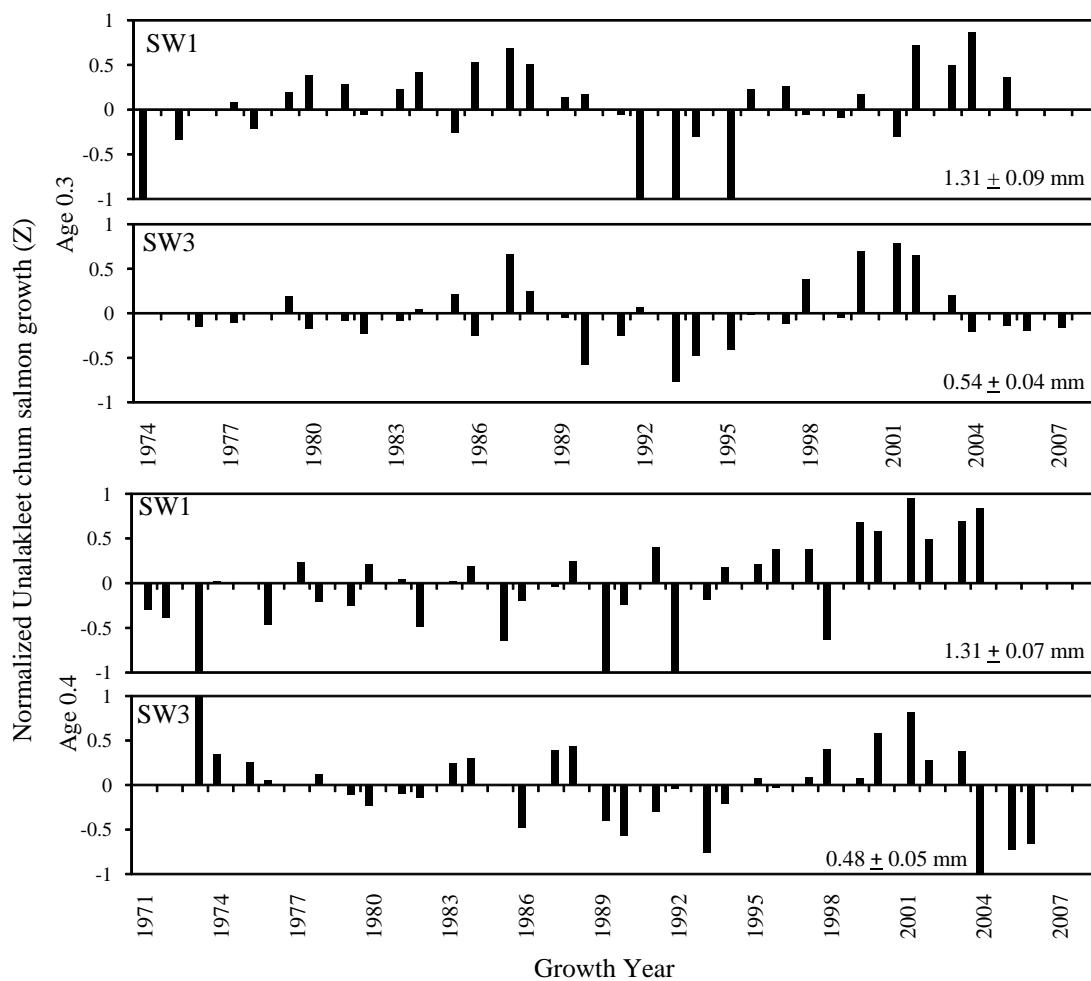


Figure 3.5. Mean annual growth of age 0.3 (1977-2008) and 0.4 (1975-2008) Unalakleet River, Norton Sound, Alaska chum salmon during first (SW1) and third (SW3) growth years. Un-weighted mean  $\pm 1$  SD during each life stage is shown.

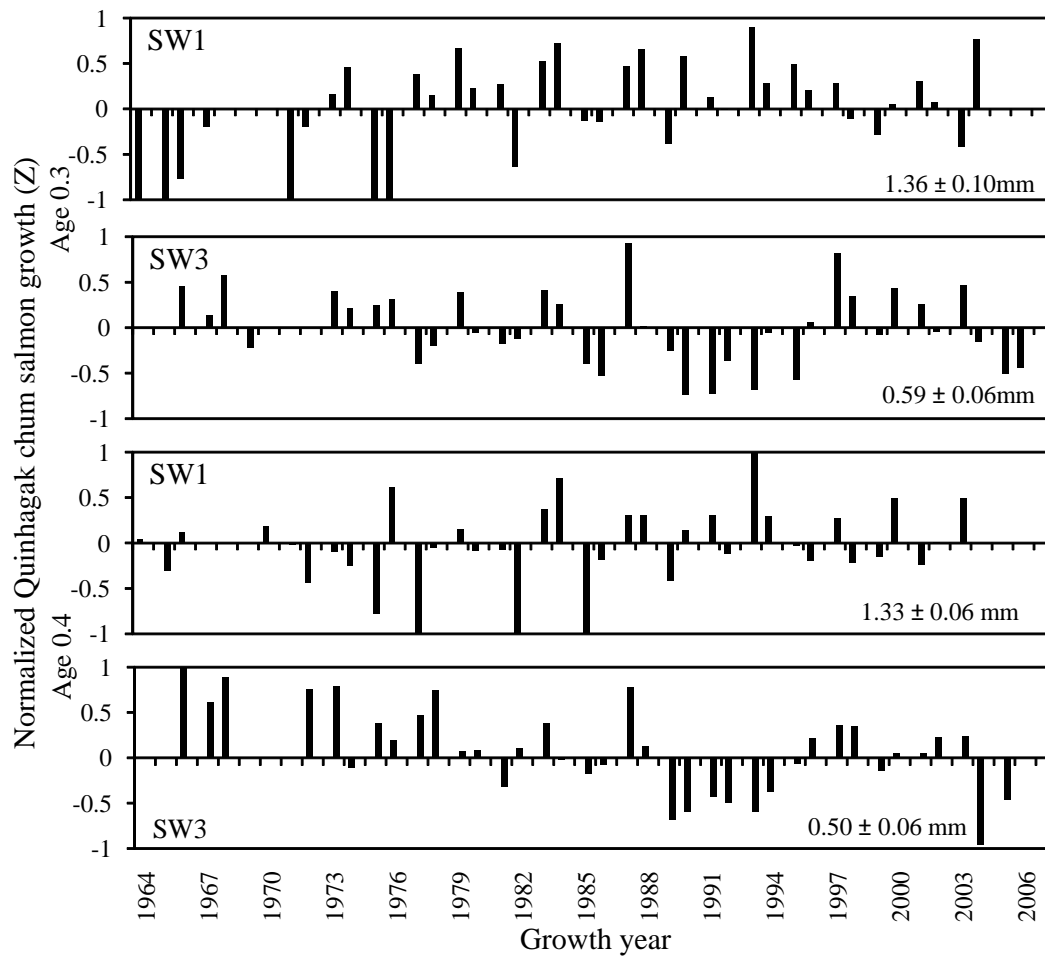


Figure 3.6. Mean annual growth of age 0.3 and 0.4 Quinhagak, Kuskokwim River, Alaska chum salmon during first (SW1) and third (SW3) growth years 1964-2006. Un-weighted mean  $\pm$  1 SD during each life stage is shown.



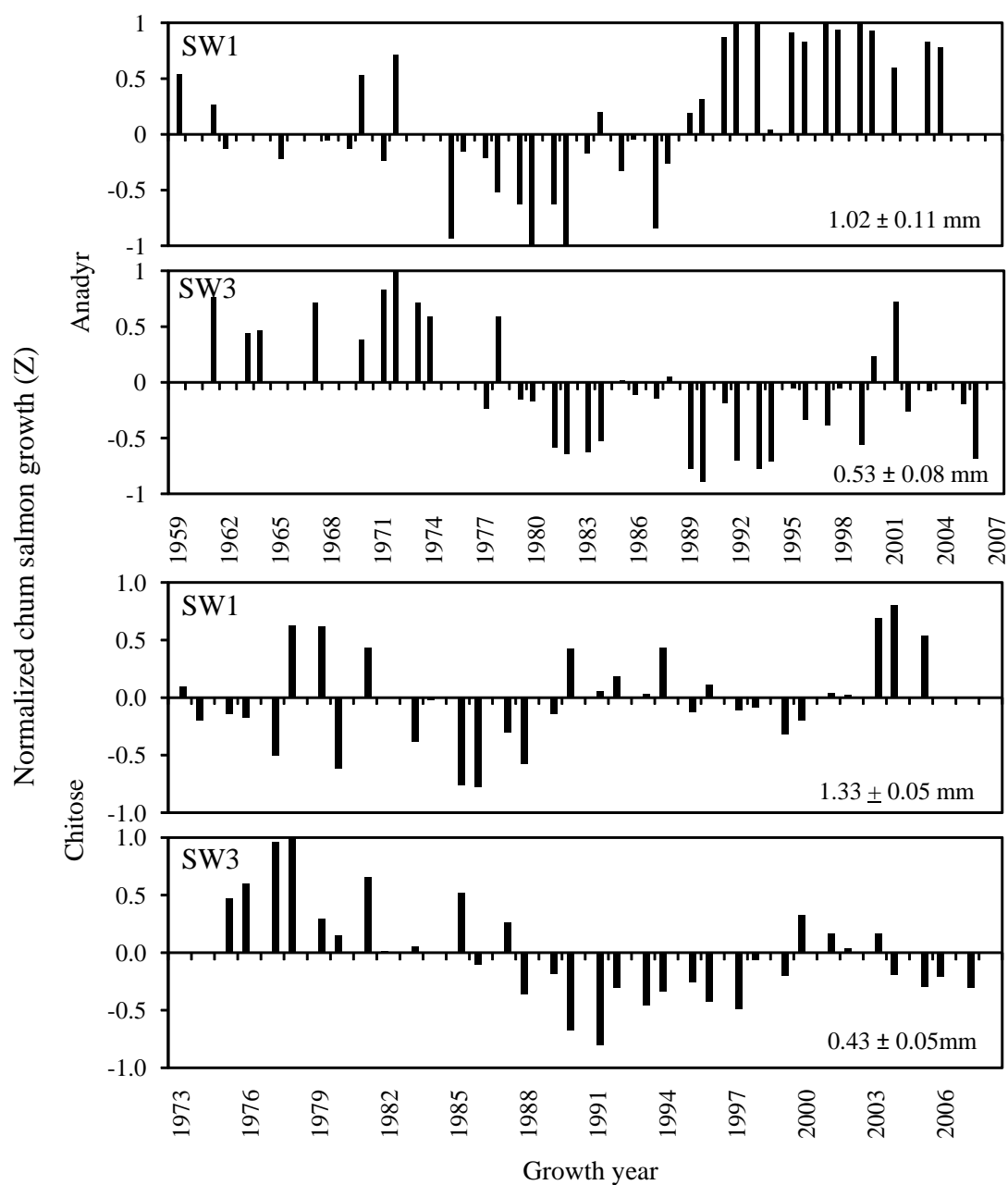


Figure 3.7. Mean annual growth of age 0.3 Anadyr River, Russia and Chitose River, Japan chum salmon during first (SW1) and third (SW3) growth years 1974-2007. Un-weighted mean  $\pm$  1 SD during each life stage is shown.

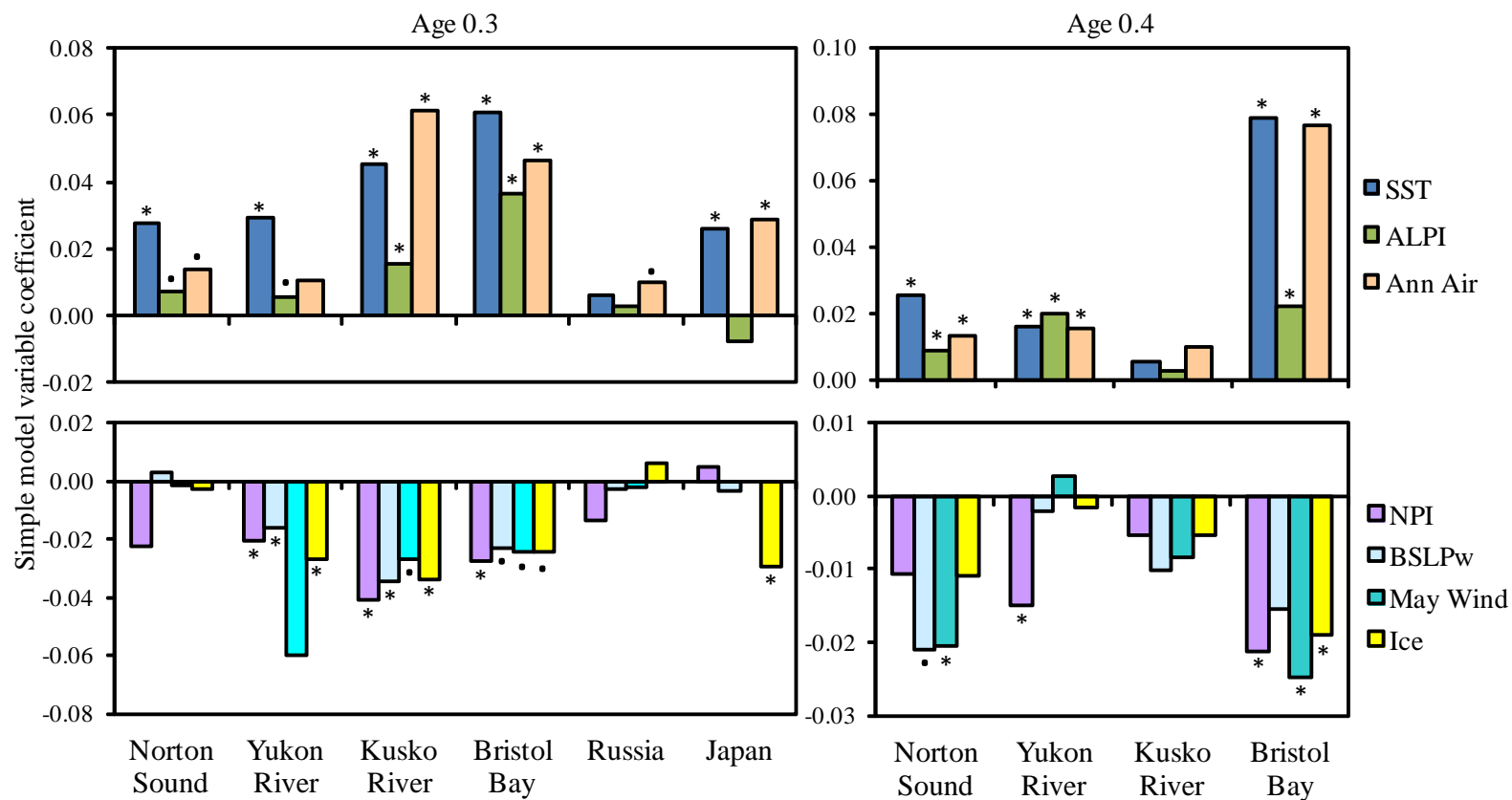


Figure 3.8. Model coefficients from generalized least squares regressions (GLS) comparing SW1 growth of chum salmon from Bristol Bay age 0.3 (1960-2006) and age 0.4 fish (1966-2006), Kuskokwim River age 0.3 (1967-2007) and age 0.4 fish (1968-2007), Yukon River age 0.3 (1965-2006) and age 0.4 fish (1967-2006), Norton Sound age 0.3 (1977-2008) and age 0.4 fish (1975-2008), Anadyr River, Russia age 0.3 fish (1962-2007), and Chitose River, Japan age 0.3 fish (1976-2008) with several environmental variables.

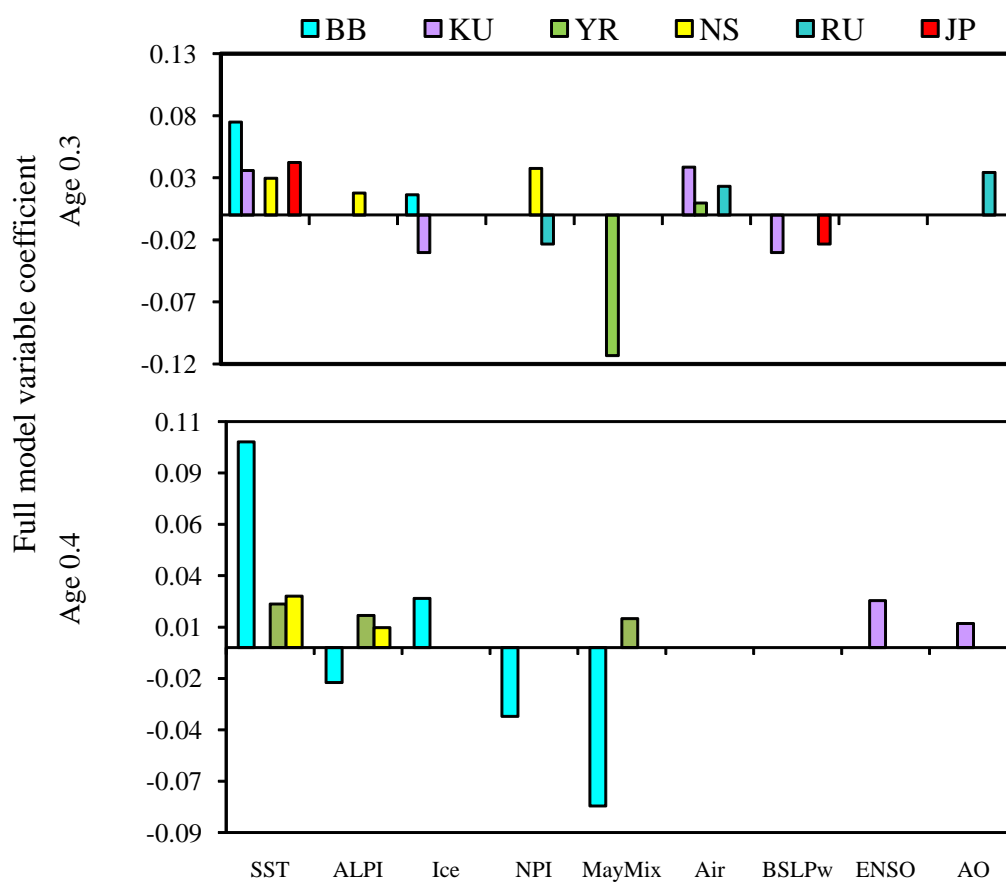


Figure 3.9. Model coefficients from the final generalized least squares regression (GLS) models comparing SW1 growth of chum salmon from Bristol Bay (BB) age 0.3 (1960-2006) and age 0.4 fish (1966-2006), Kuskokwim River (KR) age 0.3 (1967-2007) and age 0.4 fish (1968-2007), Yukon River (YR) age 0.3 (1965-2006) and age 0.4 fish (1967-2006), Norton Sound (NS) age 0.3 (1977-2008) and age 0.4 fish (1975-2008), Anadyr River, Russia (RU) age 0.3 fish (1962-2007), and Chitose River, Japan (JP) age 0.3 fish (1976-2008) with several environmental variables.

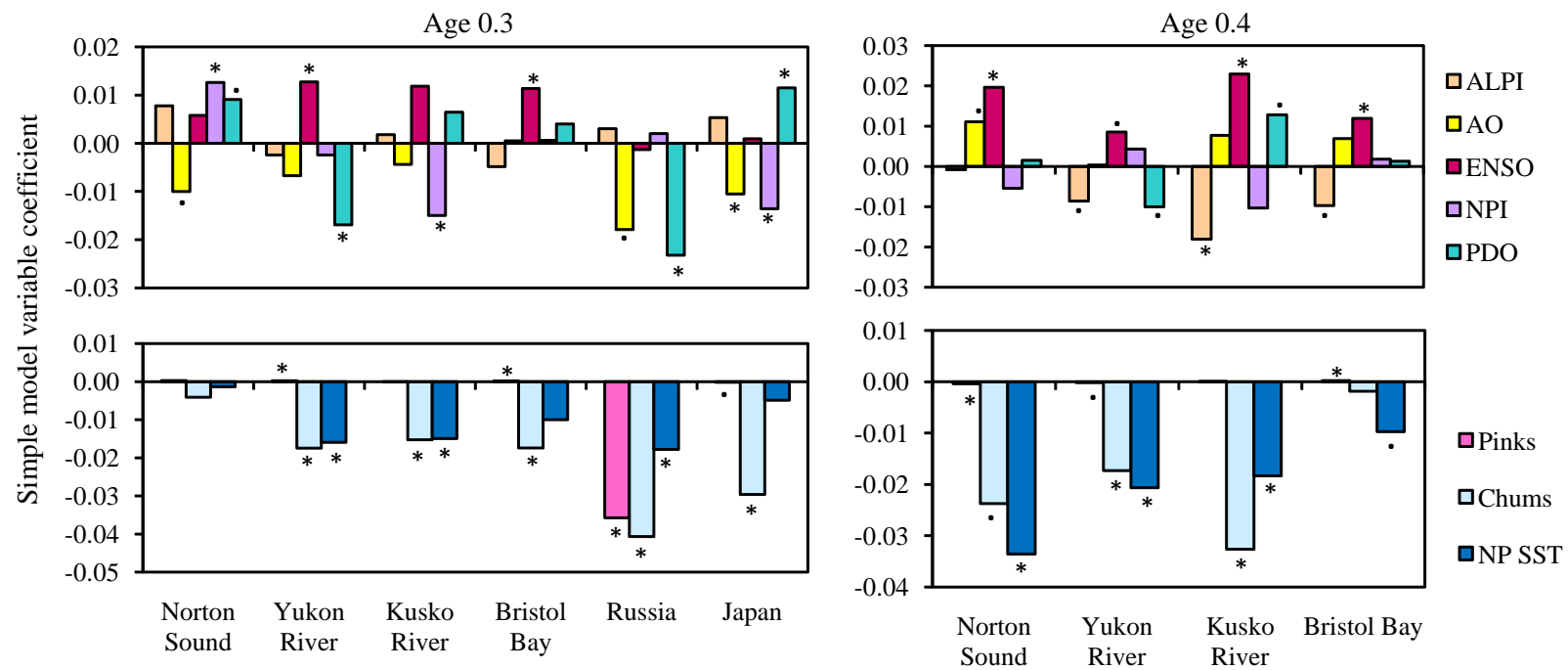


Figure 3.10. Model coefficients from generalized least squares regressions (GLS) comparing SW3 growth of chum salmon from Bristol Bay age 0.3 (1960-2006) and age 0.4 fish (1966-2006), Kuskokwim River age 0.3 (1967-2007) and age 0.4 fish (1968-2007), Yukon River age 0.3 (1965-2006) and age 0.4 fish (1967-2006), Norton Sound age 0.3 (1977-2008) and age 0.4 fish (1975-2008), Anadyr River, Russia age 0.3 fish (1962-2007), and Chitose River, Japan age 0.3 fish (1976-2008) with several environmental variables.

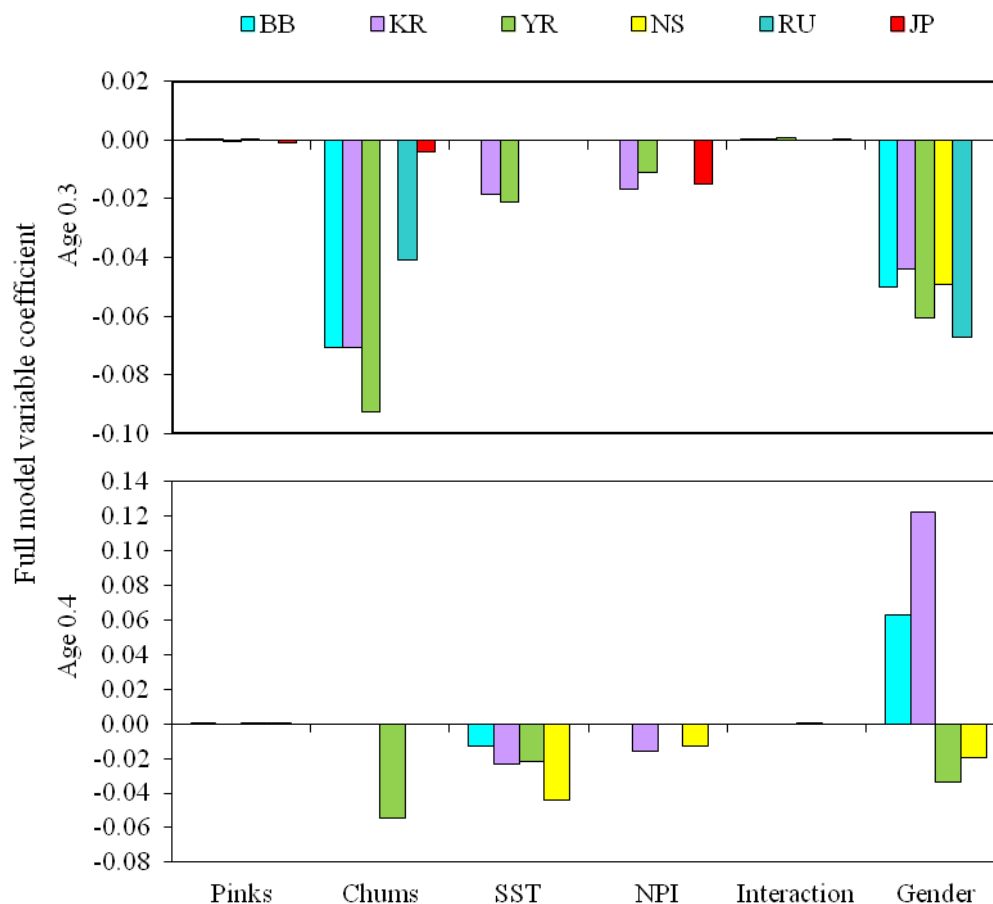


Figure 3.11. Model coefficients from the final generalized least squares models (GLS) comparing SW3 growth of chum salmon from Bristol Bay (BB) age 0.3 (1960-2006) and age 0.4 fish (1966-2006), Kuskokwim River (KR) age 0.3 (1967-2007) and age 0.4 fish (1968-2007), Yukon River (YR) age 0.3 (1965-2006) and age 0.4 fish (1967-2006), Norton Sound (NS) age 0.3 (1977-2008) and age 0.4 fish (1975-2008), Anadyr River, Russia (RU) age 0.3 fish (1962-2007), and Chitose River, Japan (JP) age 0.3 fish (1976-2008) with several environmental variables.

Table 3.1. Populations within the North Pacific Ocean sampled for chum salmon scales. General location, latitude and longitude of sampling location, sampling period, age, sample size, and years missing from sample period are listed.

Population	Location	Lat. (°N)	Long. (°E)	Age	Sampling period	Sample size	Years missing	
Unalakleet	Norton Sound	63.869	-160.788	0.3	1977-2008	1,630	1979	
				0.4	1975-2008	1,779	1979	
Big Eddy	Yukon River	62.599	-164.800	0.3	1965-2006	2,060	1966	
				0.4	1967-2006	2,221		
Quinhagak	Kuskokwim River	59.749	-161.931	0.3	1967-2007	1,910	1971-73	
				0.4	1968-2007	1,732	1971-73	
Nushagak	Bristol Bay	58.799	-158.630	0.3	1960-2006	2,417	1962, 1960 <sup>a</sup>	1964,
				0.4	1966-2006	2,172	-	
Anadyr	Russia	64.849	174.023	0.3	1962-2007	1,112	1963, 1967, 1970, 1977, 2005	1966, 1969, 1976,
Chitose	Japan	42.852	141.659	0.3	1976-2008	1,554	1985, 1980 <sup>a</sup>	

<sup>a</sup> Females only

Table 3.2. Pearson's correlations and corresponding *P* values comparing marine scale growth of Unalakleet River, Norton Sound, Alaska age 0.3 (1965-2006) and age 0.4 (1966-2006) chum salmon during the first (SW1) and third (SW3) year at sea with environmental variables.

Variable	Age 0.3				Age 0.4			
	SW1		SW3		SW1		SW3	
	Cor.	<i>P</i>	Cor.	<i>P</i>	Cor.	<i>P</i>	Cor.	<i>P</i>
Pinks	0.208	0.105	0.277	0.402	0.165	0.062	-0.032	0.715
ALPI	0.266	0.044	0.010	0.082	0.006	0.288	0.078	0.538
PDO	0.368	0.007	0.092	0.460	0.487	0.029	0.028	0.861
AsianChum3yr	0.050	0.856	-0.017	0.803	0.032	0.212	-0.179	0.239
AsianChum4yr	0.087	0.859	0.012	0.998	0.019	0.226	-0.164	0.159
Local Sum. SST	0.116	0.211	-0.205	0.075	0.013	0.187	-0.394	0.001
Local Ann. SST	0.202	0.160	-0.163	0.103	0.007	0.220	-0.378	0.001
NP Sum. SST	-	-	-0.007	0.957	-	-	-0.346	0.004
NP Ann. SST	-	-	-0.077	0.957	-	-	-0.346	0.001
Ice Cover	-0.329	0.013	-0.204	0.089	0.410	-0.046	0.067	0.606
AO	-0.171	0.049	-0.197	0.149	0.010	-0.331	0.020	0.879
NPI	-0.167	0.210	-0.248	0.072	0.116	-0.169	-0.208	0.087
ENSO	0.130	0.419	0.047	0.916	0.106	-0.230	0.145	0.237
BSLPw	-0.294	0.020	-0.402	0.000	0.069	-0.127	-0.155	0.277
BSLPsp	-0.242	0.093	-0.008	0.994	0.382	-0.076	-0.053	0.951
MayMixP	-0.055	0.123	0.048	0.841	0.115	-0.229	0.082	0.384
JJMIXM2	-0.182	0.005	-0.238	0.876	0.070	-0.194	0.227	0.878
Local air summer	0.276	0.023	-0.255	0.018	0.015	0.168	-0.431	0.000
Local air annual	0.366	0.001	0.091	0.482	0.035	0.208	-0.197	0.107
Local air winter	0.383	0.003	0.415	0.001	0.060	0.177	0.151	0.218

Table 3.3. Pearson's correlations and corresponding  $P$  values comparing marine scale growth of Quinhagak, Kuskokwim River, Alaska age 0.3 (1965-2006) and age 0.4 (1966-2006) chum salmon during the first (SW1) and third (SW3) year at sea with environmental variables.

Variable	Age 0.3				Age 0.4			
	SW1		SW3		SW1		SW3	
	Cor.	$P$	Cor.	$P$	Cor.	$P$	Cor.	$P$
Pinks	0.001	0.001	0.496	0.496	0.058	0.058	0.045	0.014
ALPI	0.001	0.001	0.516	0.516	0.055	0.055	0.098	0.045
PDO	0.000	0.000	0.490	0.490	0.373	0.373	0.000	0.098
AsianChum3yr	0.001	0.001	0.153	0.153	0.054	0.054	0.000	0.000
AsianChum4yr	0.001	0.001	0.198	0.198	0.057	0.057	0.046	0.000
Local Sum. SST	0.207	0.207	0.458	0.458	0.165	0.165	0.002	0.046
Local Ann. SST	0.001	0.001	0.312	0.312	0.053	0.053	0.005	0.002
NP Sum. SST	-	-	-0.146	0.208	-	-	-0.367	0.001
NP Ann. SST	-	-	-0.045	0.702	-	-	-0.318	0.006
Ice Cover	0.010	0.010	0.114	0.114	0.804	0.804	0.008	0.644
AO	0.948	0.948	0.470	0.470	0.063	0.063	0.617	0.008
NPI	0.002	0.002	0.181	0.181	0.100	0.100	0.057	0.617
ENSO	0.012	0.012	0.505	0.505	0.047	0.047	0.416	0.057
BSLPw	0.003	0.003	0.266	0.266	0.113	0.113	0.933	0.776
BSLPsp	0.137	0.137	0.370	0.370	0.156	0.156	0.923	0.933
MayMixP	0.038	0.038	0.607	0.607	0.013	0.013	0.932	0.923
JJMIXM2	0.072	0.072	0.251	0.251	0.159	0.159	0.039	0.038
Local air annual	0.000	0.000	0.246	0.246	0.008	0.008	0.070	0.075



Table 3.4. Pearson's correlations and corresponding *P* values comparing marine scale growth of Anadyr River, Russia and Chitose River, Japan age 0.3 chum salmon during the first (SW1) and third (SW3) year at sea with environmental variables.

Variable	Russia				Japan			
	SW1		SW3		SW1		SW3	
	Cor.	<i>P</i>	Cor.	<i>P</i>	Cor.	<i>P</i>	Cor.	<i>P</i>
Pinks	0.286	0.013	-0.342	0.000	0.290	0.021	-0.061	0.632
ALPI	0.068	0.561	-0.220	0.385	-0.065	0.615	-0.098	0.447
PDO	-0.090	0.441	-0.332	0.001	-0.003	0.979	-0.243	0.055
AsianChum3yr	0.555	0.000	-0.488	0.000	0.200	0.116	-0.568	0.000
AsianChum4yr	0.574	0.000	-0.479	0.000	0.196	0.124	-0.543	0.000
Local Sum. SST	0.181	0.120	-0.132	0.273	0.329	0.009	-0.303	0.016
Local Ann. SST	0.271	0.019	-0.396	0.002	0.367	0.003	-0.415	0.001
NP Sum. SST	-	-	-0.389	0.001	-	-	-0.337	0.007
NP Ann. SST	-	-	-0.267	0.021	-	-	-0.273	0.031
Ice Cover	0.121	0.302	0.235	0.002	-0.447	0.000	0.154	0.228
AO	0.323	0.005	-0.154	0.039	0.031	0.812	-0.105	0.411
NPI	-0.035	0.767	0.150	0.171	0.061	0.636	-0.001	0.993
ENSO	0.079	0.498	-0.266	0.035	0.154	0.228	-0.131	0.308
BSLPw	-0.008	0.945	0.300	0.240	0.021	0.869	-0.035	0.786
BSLPsp	0.169	0.148	0.123	0.003	0.045	0.725	-0.098	0.445
MayMixP	0.005	0.965	0.079	0.665	-0.172	0.178	-0.091	0.480
JJMIXM2	0.021	0.857	0.278	0.734	0.002	0.987	0.129	0.987
Local air annual	0.327	0.004	-0.180	0.121	0.394	0.001	-0.425	0.001

Table 3.5. Student's two-sample *t*-tests comparing mean growth of chum salmon between odd and even years by population, age, growth zone, and gender. Data are from chum salmon caught in commercial and test fisheries in Bristol Bay age 0.3 (1960-2006) and age 0.4 fish (1966-2006), Kuskokwim River age 0.3 (1967-2007) and age 0.4 fish (1968-2007), Yukon River age 0.3 (1965-2006) and age 0.4 fish (1967-2006), Norton Sound age 0.3 (1977-2008) and age 0.4 fish (1975-2008), Anadyr River, Russia age 0.3 fish (1962-2007), and Chitose River, Japan age 0.3 fish (1976-2008).

Population	Age	Zone	Males		Females	
			<i>t</i>	<i>P</i>	<i>t</i>	<i>P</i>
Norton Sound	0.3	SW1	-0.318	0.753	-0.778	0.443
		SW3	-1.453	0.157	-2.594	0.015
	0.4	SW1	1.337	0.191	1.129	0.268
		SW3	-2.048	0.049	-2.107	0.043
Yukon River	0.3	SW1	1.383	0.174	0.750	0.458
		SW3	-1.555	0.128	-1.863	0.070
	0.4	SW1	2.088	0.044	1.671	0.103
		SW3	-1.316	0.196	-1.669	0.103
Kuskokwim River	0.3	SW1	0.378	0.708	-0.345	0.732
		SW3	-1.779	0.084	-1.497	0.143
	0.4	SW1	-0.248	0.805	-0.096	0.924
		SW3	-1.268	0.213	-0.240	0.812
Bristol Bay	0.3	SW1	0.325	0.747	1.012	0.318
		SW3	-1.412	0.166	-1.588	0.120
	0.4	SW1	0.242	0.810	0.080	0.937
		SW3	-1.012	0.318	-1.429	0.161
Anadyr River	0.3	SW1	0.153	0.879	0.635	0.530
		SW3	-0.470	0.641	-0.095	0.925
Chitose River	0.3	SW1	-0.687	0.498	-0.607	0.548
		SW3	-0.724	0.475	-1.193	0.242

Table 3.6. Generalized least squares regressions (GLS) of growth during the first (SW1) and third year at sea (SW3) for Unalakleet River, Norton Sound, Alaska for age 0.3 (1977-2008) and age 0.4 chum (1975-2008) salmon. Only models with  $P \leq 0.10$  are listed. AR = order of AIC-best auto-regressive model.  $b$  = Intercept.

Model	Autoregressive Terms					AIC	AR	<i>b</i>	Model coefficients		Partial <i>P</i>	
	Φ1	Φ2	Φ3	Φ4	Φ5				Variable	Gender	Variable	Gender
SW1 - Age 0.3												
ALPI	0.49	-0.01	0.26	-0.43		-68.3	4	1.311	0.007		0.074	
Nome Annual Air	0.52	-0.03	0.28	-0.40		-67.6	4	1.320	0.014		0.117	
SST	0.56					-72.0	1	1.322	0.027		0.030	
SW1 - Age 0.4												
Pinks	-0.01	0.25				-76.8	2	1.247	3.9E-04		0.065	
Asian chums						-80.2	0	1.314	0.021		0.043	
ALPI						-80.9	0	1.304	0.009		0.030	
May Wind Mixing	-0.07	0.39	0.60			-86.4	3	1.280	-0.021		0.005	
SST						-80.7	0	1.313	0.025		0.032	
BSLPw						-79.7	0	1.313	-0.021		0.056	
SW3 - Age 0.3												
Pinks + Gender	0.42					-202.6	1	0.515	2.7E-04	-0.049	0.005	0.010
GOA SST + Gender	0.17	0.29				-208.4	2	0.565	-0.019	-0.052	0.003	0.005
NPI + Gender						-199.3	0	0.563	0.013	-0.046	0.040	<0.001
AO + Gender	0.19	0.34	-0.25			-203.5	3	0.565	-0.010	-0.049	0.065	0.001
PDO + Gender	0.27	0.30	-0.30	0.09		-201.0	4	0.5651	0.009	-0.050	0.108	0.003
SW3 - Age 0.4												
Pinks + Gender	0.39	0.34	-0.02	0.45	-0.27	-174.3	5	0.566	-3.7E-04	0.067	0.008	0.029
NP SST + Gender						-186.3	0	0.488	-0.034	-0.013	<0.001	0.323
Asian Chum + Gender	0.51	0.37				-172.2	2	0.515	-0.024	0.069	0.087	0.055
AO + Gender	0.44	0.23	0.01	0.28		-174.1	4	0.547	0.011	0.064	0.064	0.054
ENSO + Gender						-180.8	2	0.504	0.020	0.089	<0.001	0.007

Table 3.7. Generalized least squares models (GLS) comparing SW1 growth of chum salmon from Bristol Bay age 0.3 (1960-2006) and age 0.4 fish (1966-2006), Kuskokwim River age 0.3 (1967-2007) and age 0.4 fish (1968-2007), Yukon River age 0.3 (1965-2006) and age 0.4 fish (1967-2006), Norton Sound age 0.3 (1977-2008) and age 0.4 fish (1975-2008), Anadyr River, Russia age 0.3 fish (1962-2007), and Chitose River, Japan age 0.3 fish (1976-2008). AR = order of AIC-best auto-regressive model.  $b$  = Intercept. Partial  $P$  values are listed below corresponding coefficient.

Population	Age	AR terms		AIC	AR	$b$	Model coefficients								
		$\Phi 1$	$\Phi 2$				SST	ALPI	Ice	NPI	MayMix	Air temp	BSLPw	ENSO	AO
<b>Bristol Bay</b>	0.3	0.02	0.16	-120.3	3	1.349	0.075		0.016						
		(3) -0.29					<0.001		0.070						
	0.4			-128.1	0	0.541	0.200	-0.017	0.024	-0.033	-0.770				
							<0.001	0.022	0.032	0.055	0.005				
<b>Kusko River</b>	0.3			-84.4	0	1.358	0.036		-0.030			0.039	-0.030		
							0.013		0.029			0.010	0.029		
	0.4	-0.23	-0.39	-106.5	4	1.328								0.023	0.012
		(3) 0.07	(4) -0.14											0.001	0.060
<b>Yukon River</b>	0.3	-0.22	-0.06	-131.8	4	1.071					-1.131	0.010			
		(3) -0.25	(4) -0.21								0.061	<0.001			
	0.4	0.00	-0.06	-126.8	4	1.289	0.021	0.016			0.014				
		-0.08	0.50				0.002	0.022			0.053				
<b>Norton Sound</b>	0.3	0.65		-77.4	1	1.303	0.030	0.018		0.038					
							0.009	0.004		0.019					
	0.4			-78.1	0	1.300	0.025	0.010							
							0.047	0.028							
<b>Russia</b>	0.3	0.70		-75.9	1	1.086				-0.023		0.023			0.034
										0.045		0.035			0.008
<b>Japan</b>	0.3	0.25	0.49	-82.9	3	1.334	0.042						-0.023		
		(3) -0.17					0.002						0.024		

**Note:** Candidate models were:  $SW1 = \beta_0 + \beta_1 X_1 + \dots + \beta_n X_n + \epsilon$  where parameters  $X_n$  were explanatory variables, and  $\epsilon$  were residuals.

Table 3.8. Generalized least squares models (GLS) comparing SW3 growth for age 0.3 chum salmon from Bristol Bay (1960-2006), Kuskokwim River age 0.3 (1967-2007), Yukon River age 0.3 (1965-2006), Norton Sound age 0.3 (1977-2008), Anadyr River, Russia (1962-2007), and Chitose River, Japan (1976-2008). AR = order of AIC-best auto-regressive model. *b* = Intercept. Partial *P* values are listed below corresponding coefficient.

Population	Autoregressive terms			AIC	AR	<i>b</i>	Model coefficients					
	Φ1	Φ2	Φ3				Pinks	Chums	SST	NPI	Int.	Gender
<b>Bristol Bay</b>	0.276			-236.4	1	0.629	2.3E-04	-0.071			2.7E-04	-0.050
<i>w/ interaction</i>							0.040	0.002			0.027	0.003
<i>w/o interaction</i>	0.402	-0.031		-232.3	2	0.650	1.9E-04	-0.026				-0.053
							0.062	0.019				0.005
<b>Kuskokwim River</b>	0.024	-0.219		-212.0	2	0.548	3.2E-04	-0.071	-0.019	-0.017	3.3E-04	-0.044
<i>w/ interaction</i>							0.010	<0.001	0.018	0.013	0.004	<0.001
<i>w/o interaction</i>	0.024	0.003	0.130	-205.5	3	0.611			-0.016	-0.014		-0.043
									0.023	0.052		0.006
				-209.4	0	0.612		-0.015				-0.043
								0.025				0.002
<b>Yukon River</b>	0.047	-0.142	-0.628	-272.8	5	0.651	-1.7E-04	-0.093	-0.021	-0.011	5.9E-04	-0.061
<i>w/ interaction</i>	(4) 0.104	(5) -0.260					0.059	<0.001	<0.001	0.006	<0.001	<0.001
<i>w/o interaction</i>	0.419			-246.4	1	0.610	3.0E-04	-0.020	-0.018			-0.058
							0.005	0.081	0.027			0.003
<b>Norton Sound</b>	0.423			-202.6	1	0.515	2.7E-04					-0.049
<i>w/ or w/o interaction</i>							0.005					0.010
<b>Russia</b>	-0.049	0.224	0.331	-161.8	3	0.552		-0.041				-0.067
<i>w/ or w/o interaction</i>								0.002				0.010
<b>Japan</b>				-207.4	0	0.694	-9.8E-04	-0.004		-0.015	1.4E-05	
<i>w/ interaction</i>							0.027	0.001		0.016	0.027	
<i>w/o interaction</i>	0.010	0.250		-206.1	2	0.426		-0.027		-0.011		
								<0.001		0.048		

**Note:** Candidate models were:  $SW3 = \beta_0 + \beta_1 X_1 + \dots + \beta_n X_n + \epsilon$  where parameters  $X_n$  were explanatory variables, and  $\epsilon$  were residuals.

Table 3.9. Generalized least squares models (GLS) comparing SW3 growth for age 0.4 chum salmon from Bristol Bay (1966-2006), Kuskokwim River (1968-2007), Yukon River (1967-2006), and Norton Sound (1975-2008). AR = order of AIC-best auto-regressive model.  $b$  = Intercept. Partial  $P$  values are listed below corresponding coefficient.

Population	Autoregressive terms			AIC	AR	$b$	Model coefficients					
	$\Phi 1$	$\Phi 2$	$\Phi 3$				Pinks	Chums	SST	NPI	Int.	Gender
<b>Bristol Bay</b>	0.538	0.109	0.329	-238.9	3	0.627	2.90E-04		-0.013			0.063
<i>w/ or w/o interaction</i>							0.002		0.028			0.007
<b>Kuskokwim River</b>	0.459	0.423		-183.3	2	0.467			-0.023	-0.016		0.122
<i>w/ or w/o interaction</i>									0.002	0.026		<0.001
<b>Yukon River</b>	0.277			-265.0	1	0.465	2.76E-04	-0.054	-0.022		2.56E-04	-0.034
<i>w/ interaction</i>							0.006	0.003	<0.001		0.010	0.011
<i>w/o interaction</i>	0.164			-259.5	1	0.516			-0.021			-0.034
									<0.001			0.006
<b>Norton Sound</b>	0.055	-0.128	-0.283	-188.0	3	0.430	3.47E-04		-0.044	-0.013		-0.020
<i>w/ or w/o interaction</i>							0.013		<0.001	0.042		0.050

**Note:** Candidate models were:  $SW3 = \beta_0 + \beta_1 X_1 + \dots + \beta_n X_n + \epsilon$  where parameters  $X_n$  were explanatory variables, and  $\epsilon$  were residuals.

Table 3.10. Generalized least squares regressions (GLS) of growth during the first (SW1) and third year at sea (SW3) for Quinhagak chum salmon age 0.3 (1967-2007) and age 0.4 (1968-2007) aught near the mouth of the Kuskokwim River, Alaska. Only models with  $P \leq 0.10$  are listed. AR = order of AIC-best auto-regressive model.  $b$  = Intercept. Partial  $P$  values are listed below corresponding coefficient.

Model	AR Terms			AIC	AR	<i>b</i>	Model coefficients		Partial <i>P</i>	
	Φ1	Φ2	Φ3				Variable	Gender	Variable	Gender
SW1 - Age 0.3										
ALPI				-68.5	0	1.348	0.016		0.009	
NPI				-68.3	0	1.358	-0.041		0.010	
Bethel Annual Air				-79.3	0	1.358	0.061		<0.001	
May Mixing				-64.0	0	1.358	-0.027		0.107	
SST				-69.8	0	1.358	0.045		0.005	
Ice Cover				-65.8	0	1.358	-0.034		0.038	
PDO				-71.6	0	1.359	0.010		0.002	
BSLPw				-68.0	1	1.356	-0.035		0.024	
ENSO				-65.5	0	1.358	0.033		0.046	
SW1 - Age 0.4										
ENSO				-108.6	0	1.325	0.014		0.034	
SW3 - Age 0.3										
NPI + Gender				-209.2	0	0.612	-0.015	-0.043	0.027	0.002
NP Ann SST + Gender				-209.2	0	0.612	-0.015	-0.043	0.027	0.002
Asian Chums + Gender				-209.4	0	0.612	-0.015	-0.043	0.025	0.002
ENSO	0.21	0.15	0.22	-203.1	3	0.589	0.012		0.051	
SW3 - Age 0.4										
NP Ann SST + Gender	0.47	0.37		-180.3	2	0.479	-0.018	0.119	0.011	<0.001
ENSO + Gender	0.45	0.45		-200.0	2	0.493	0.023	0.105	<0.001	<0.001
PDO + Gender	0.38	0.27	0.28	-178.3	3	0.496	0.013	0.128	0.089	<0.001
Pinks				-157.8	0	0.564	-3.0E-04		0.006	
Asian Chums				-168.4	0	0.505	-0.033		<0.001	
ALPI				-153.9	0	0.527	-0.018		0.049	

Table 3.11. Generalized least squares regressions (GLS) of growth during the first (SW1) and third year at sea (SW3) for Anadyr River, Russia (age 0.3, 1962-2007) and Chitose River, Japan (age 0.3, 1976-2008) salmon. Only models with  $P \leq 0.10$  are listed. AR = order of AIC-best auto-regressive model.  $b$  = Intercept.

Model	Autoregressive Terms				AIC	AR	$b$	Model coefficients		Partial $P$	
	$\Phi 1$	$\Phi 2$	$\Phi 3$	$\Phi 4$				Variable	Gender	Variable	Gender
Russia - SW1											
Anadyr Annual Air	0.73				-70.1	1	1.197	0.010		0.060	
AO	0.45	0.42			-75.2	2	1.145	0.020		0.089	
Russia - SW3											
Pinks + Gender	-0.10	0.27	0.41		-165.1	3	0.547	-0.036	-0.070	<0.001	0.010
GOA SST + Gender	0.10	0.32			-152.1	2	0.537	-0.022	-0.067	0.015	0.009
NP Ann SST + Gender	0.10	0.28			-150.7	2	0.536	-0.018	-0.062	0.028	0.012
Asian Chums + Gender	-0.05	0.22	0.33		-161.8	3	0.552	-0.041	-0.067	0.002	0.010
AO+ Gender	0.21				-143.2	1	0.535	-0.018	-0.059	0.090	0.008
PDO + Gender	-0.02	0.32	0.43	-0.12	-163.5	4	0.527	-0.023	-0.043	0.001	0.094
Japan - SW1											
Japan Annual Air	0.11	0.33			-83.4	2	1.337	0.029		0.017	
SST	0.15	0.28			-82.6	2	1.335	0.026		0.031	
Ice Cover	0.36				-87.0	1	1.336	-0.030		0.004	
Japan - SW3											
NPI + Gender	0.40	0.55			-203.0	2	0.301	-0.014	0.103	0.008	0.007
GOA SST + Gender	0.27	0.36	0.34		-201.8	3	0.295	-0.014	0.089	0.015	0.014
Asian Chums + Gender					-204.2	0	0.419	-0.030	0.016	<0.001	0.171
AO + Gender	0.22	0.40	0.25	0.11	-198.2	4	0.274	-0.011	0.122	0.043	<0.001
PDO + Gender	0.43	0.53			-201.0	2	0.296	0.012	0.113	0.028	0.005
Pinks	0.20	0.39			-198.2	2	0.457	-1.7E-04		0.104	



**Appendix 3A**

Appendix 3A-1. Explanatory variables used in generalized least squares regressions (GLS) to compare with first and third-year growth of western Alaska and Asian chum salmon.

Variable	Name	Description	Source
$NPI_t$	North Pacific Index	area-weighted sea level pressure over the region 30°N-65°N, 160°E-140°W	<a href="http://www.cgd.ucar.edu/cas/jhurrell/npindex.html">http://www.cgd.ucar.edu/cas/jhurrell/npindex.html</a>
$ALPI_t$	Aleutian Low Pressure Index	relative intensity of the Aleutian Low pressure system of North Pacific (December - March). A positive index value reflects a relatively strong or intense Aleutian Low.	
$Local\ Air\ Temp_t$	local air temperature	temperatures averaged as winter (November-March), summer (May-September) and annually.	
	Yukon & Unalakleet rivers	Nome, AK airport, National Weather Service	<a href="http://www.wunderground.com/">http://www.wunderground.com/</a>
	Quinhagak	Bethel, AK airport, National Weather Service	<a href="http://www.wunderground.com/">http://www.wunderground.com/</a>
	Bristol Bay	King Salmon, AK airport, National Weather Service	<a href="http://www.wunderground.com/">http://www.wunderground.com/</a>
	Anadyr River	air temperatures for Anadyr, Russia	A. Zavolokin, Pacific Research Fisheries Center, TINRO-Centre, Vladivostok, Russia, 2011
	Chitose River	from Sapporo, Japan, used Japan Meteorological Agency	<a href="http://www.jma.go.jp/jma/indexe.html">http://www.jma.go.jp/jma/indexe.html</a>
$MayMix_t$	wind mixing index	measured in m <sup>3</sup> /sec <sup>3</sup> at year $t$ in the vicinity of St. Paul Island, Alaska from 1950-2010	<a href="http://www.beringclimate.noaa.gov/index.html">http://www.beringclimate.noaa.gov/index.html</a>
$Ice\ Cover_t$	average ice concentration	average ice concentration in the Bering Sea in a 2° x 2° box (56°-58°N, 163°-165°W) from 1 January – 31 May. Ice Cover represented normalized anomalies by year.	<a href="http://www.beringclimate.noaa.gov/index.html">http://www.beringclimate.noaa.gov/index.html</a>
PDO	1960-2008 Arctic Oscillation Index	Winter index, average of monthly PDO indices from Nov-March	<a href="http://jisao.washington.edu/pdo/PDO.latest">http://jisao.washington.edu/pdo/PDO.latest</a>
$AO_t$		leading mode of Empirical Orthogonal Function analysis of monthly mean during the period 1979-2000. Largest variability during cold season.	<a href="http://www.ncdc.noaa.gov/oa/ncdc.html">http://www.ncdc.noaa.gov/oa/ncdc.html</a>

Appendix 3A-1 continued.

Variable	Name	Description	Source
<i>Local SST<sub>t</sub></i>	local sea surface temperature	used a 2° x 2° grid	NOAA Climate Data Center
	Norton Sound	mean temperature 56°-60°N latitude & 160°-180°W longitude	
	Yukon River	mean temperature 62°-66°N latitude & 160°-166°W longitude	
	Kuskokwim River	mean temperature 58°-62°N latitude & 160°-166°W longitude	
	Bristol Bay	mean temperature 56°-60°N latitude & 160°-180°W longitude	
	Anadyr River	mean temperature 58°-64°N latitude & 172°-180°E longitude	
	Chitose River	mean temperature 42°-62°N latitude & 134°-162°E longitude	
<i>NP Annual SST<sub>t</sub></i>	SST	North Pacific annual SSTs from a 18° x 40° box (44°-62°N, 140°-180°W) at year t.	
<i>Pinks<sub>t</sub></i>	pink salmon abundance	represents the total abundance of Russian pink salmon at year t	Ruggerone et al. 2010
<i>Asian chums<sub>t</sub></i>	Asian chum salmon abundance	A four-year moving average of the Asian chum salmon abundance at year <i>t</i> (catch and escapement in millions of fish). Used 4-year moving average because it corresponded with chum salmon life cycle.	Ruggerone et al. 2010 <a href="http://www.npafc.org/new/index.html">http://www.npafc.org/new/index.html</a>
<i>ENSO<sub>t</sub></i>	El Niño/So. Oscillation Index	Used the mean December-January values of the multivariate ENSO index.	<a href="http://www.ncdc.noaa.gov/oa/ncdc.html">http://www.ncdc.noaa.gov/oa/ncdc.html</a>
<i>JJMixM2<sub>t</sub></i>	wind mixing index	wind mixing index at Mooring 2 (57°N, 164°W) in m3/sec3 from June-July 1950-2010.	<a href="http://www.ncdc.noaa.gov/oa/ncdc.html">http://www.ncdc.noaa.gov/oa/ncdc.html</a>
<i>BSLPw<sub>t</sub></i>	Bering Sea level pressure winter index	Deviations from the mean of sea level pressure average over the Bering Sea (55° - 65°N, 170°E - 160°W) December through March.	<a href="http://www.ncdc.noaa.gov/oa/ncdc.html">http://www.ncdc.noaa.gov/oa/ncdc.html</a>

## **General Conclusions**

We examined several hypotheses regarding growth of chum salmon in relationship to climate change and density-dependent processes, such as competition.

### **Comparisons across geographic distance**

Synchrony has been observed in population sizes and recruitment in many fish species (Friedland 1998; Pyper et al. 2002). We hypothesized that correlations among the six salmon stocks would indicate basin scale effects. We found that for all populations, except Unalakleet age 0.3 fish and Nushagak age 0.4 fish, adult length was primarily correlated with growth that occurred during the last full year at sea but not during homeward migration (SWPlus growth). For 60% of the populations, this included the previous two years at sea.

We found that the further the populations were apart, the less synchronicity was observed in scale growth. These results suggested that although fish distributions overlapped during part of their life histories, regional-scale effects on populations were important to population level growth and recruitment (Peterman et al. 1998; Pyper et al. 2001; Pyper et al. 2002). Although climate occurred at a basin-wide level, regional-scale effects were as or more important to fish.

### **Seasonal growth among populations**

During the first year, we found intercirculus distance initially declined then increased markedly at circuli 2-3 for Russian and circuli 5-9 for western Alaskan and Japanese chum salmon. This was very different than observed in sockeye salmon (Ruggerone et al. 2005). Sockeye intercirculus distances showed no decline. Sockeye salmon spend one to two years in freshwater; whereas, chum salmon migrate downstream upon emergence. These initial declines in growth suggested that chum salmon traversed lower quality freshwater or estuarine habitats, and when they reached the ocean, growth increased. These data indicated that some western Alaskan fish required 45 - 80 days to reach marine waters, confirming and possibly increasing previous time estimates (Hillgruber and Zimmerman 2009).

We found that Japanese and Russian chum salmon had lower overall scale growth in the first marine zone and did not reach as high a peak as western Alaskan fish, which supported the hypothesis that these fish feed in different locations during the first year. This suggested that the Okhotsk Sea and western Bering Sea were not as productive for chum salmon as the eastern Bering Sea.

### **Climate change effects on growth**

The effects of major climate events were visible in the chum salmon scale growth trends. In almost every population, growth during the second or third marine year was above normal until the regime shifts (1976-77 or 1988-89) that occurred in the North Pacific Ocean (Mantua et al. 1997; Rogers 1984) then the growth fell below normal for 10-30 years.

### **Interactions with pink salmon**

We hypothesized that Russian pink salmon abundance inhibited the growth of western Alaska chum salmon during the third year in the ocean. Our results indicated that chum salmon growth was weakly related to the abundance of pink salmon during odd years. From our multivariate regression analyses, we found evidence of interspecific interactions with the abundance of Russian pink salmon, but the effects of pink salmon abundance were inconsistent and smaller overall than the effects of Asian chum abundance and SST. This may indicate that although pink salmon abundance influenced chum salmon populations, it was not as important to their growth as expected.

### **Interactions with Asian chum salmon**

We found that most of the western Alaska and Asian chum salmon populations had correlated second and third-year growth, indicating that their distributions overlapped during this period. We found that Asian chum salmon abundance showed significant negative effects on SW3 growth in five of the six populations in the study and three of the four age 0.4 populations from western Alaska only. Asian chum salmon abundance appeared to have more of an effect on age 0.3 fish than on age 0.4 fish. Age 0.3 is the predominant age group of Asian chum salmon (Kaeriyama 1989), thus it is likely that other age 0.3 fish would be affected first by the increased abundance of fish of a similar age, such as Asian chum salmon. Competition among conspecifics for prey items would likely be greatest among those from the same age group, because they would likely be of similar size at a similar life stage. Although the results of our current study indicated that Asian chum salmon abundance had strong negative effects on growth of western Alaska chum salmon in the North Pacific Ocean, it is difficult to determine the effects of density dependence on the dynamics of a population. In an earlier paper, we used the scale measurements to back-calculate fish length by scale zone (Chapter 2). In this study, we examined potential effects of density dependence on length by applying the model coefficient to the back-

calculated lengths for the SW2 through SWPlus growth zones. The effect of increasing Asian chum salmon abundance led to a reduction in mean length of approximately 42-43 mm. This change in length could affect fecundity by 85-86 eggs, depending on fish age, or approximately 3-5% (Salo 1991).

### **Effects of SST on chum salmon**

Across all populations, enhanced first-year growth was associated with warmer local and/or regional temperatures: either local SSTs or regional air temperatures for both ages and all populations. Less ice cover also has enhanced growth in several populations. We found similar negative effects associated with NPI, BSLP winter index, May wind mixing and ice cover for both ages. After the 1976-77 regime shift, SSTs in coastal areas warmed (Hare et al. 1999; Mantua et al. 1997), and likely this has contributed to the positive correlations observed among SW1 growth and SST and/or air temperature.

In contrast to our hypothesis that cooler temperatures in the North Pacific Ocean would have inhibited growth, we found that warmer large-scale SSTs from the North Pacific Ocean were associated with reduced third year chum salmon growth in most populations. Although this appears counterintuitive, Ruggerone et al. (2011) found that adult length-at-age was negatively correlated with SST, rather than positively correlated as expected based on studies involved salmon in northern latitudes (Mueter et al. 2002b; Mueter et al. 2002a; Ruggerone et al. 2007b). They suggested that this unexpected result was due to density-dependent effects involving abundance of hatchery chum salmon.

### **Conclusions**

Examination of these six populations allowed us to determine commonalities among chum salmon in the North Pacific Ocean. Overall, it appeared that sea surface temperature, abundance of Asian chum salmon, the North Pacific Index, May wind mixing, ice cover, and local air temperature influenced scale growth of western Alaska and Asian chum salmon during the first and third year at sea by population and age.

Helle et al. (2007) suggested that carrying capacity in the North Pacific Ocean for Pacific salmon was not constant but varied with changing environmental and biological factors. Density-dependence effects are difficult to detect because growth is influenced by highly variable ocean productivity. A number of factors may mask the relationship between inter- and/or intraspecific

factors, climate, and salmon growth. One factor, which potentially interferes with our ability to detect density dependence, is human activity (Friedland et al. 2009). One human activity, contributing to this, is artificial propagation of salmon stocks (Fukuwaka et al. 2011). Most Japanese chum salmon stocks have been maintained by hatchery release, and although the western Alaska stocks are “wild,” approximately 550-650 million chum salmon were released each year into the Gulf of Alaska by Prince William Sound and southeast Alaska hatcheries. Researchers have raised concerns about density-dependent effects on salmon and the effects of hatchery salmon on wild salmon. Salmon, originating from distant regions and adjacent continents, share a common food resource and due to distributional overlap in the North Pacific Ocean and Bering Sea, it appears that possible density-dependent effects are occurring across the region. This study was prompted by declines in chum salmon abundance in western Alaska, and subsequent effects on local communities, many of whom depend on these fish for subsistence food resources. We were unable to determine the mechanism causing declines in abundance of western Alaska chum salmon, but our results contribute to growing evidence for competition for among conspecific salmon.

## References

- AYK-SSI. 2006. Arctic-Yukon-Kuskokwim Salmon Research and Restoration Plan. Bering Sea Fisherman's Association, Anchorage, AK.
- Azumaya, T., and Y. Ishida. 2000. Density interactions between pink salmon (*Oncorhynchus gorbuscha*) and chum salmon (*O. keta*) and their possible effects on distribution and growth in the North Pacific Ocean and Bering Sea. North Pacific Anadromous Fish Commission Bulletin 2:165-174.
- Beacham, T. D., and C. B. Murray. 1987. Adaptive variation in body size, age, morphology, egg size, and developmental biology of chum salmon (*Oncorhynchus keta*) in British Columbia. Canadian Journal of Fisheries and Aquatic Sciences 44(2):244-261.
- Beamish, R., D. Noakes, G. McFarlane, and J. King. 1998. The regime concept and recent changes in Pacific salmon abundance. North Pacific Anadromous Fish Commission Technical Report 1:1-3.
- Beamish, R. J. 1993. Climate and exceptional fish production off the west coast of North America. Canadian Journal of Fisheries and Aquatic Sciences 50(10):2270-2291.

- Beamish, R. J., and C. Mahnken. 2001. A critical size and period hypothesis to explain natural regulation of salmon abundance and the linkage to climate and climate change. *Progress in Oceanography* 49:423-437.
- Bigler, B. S., D. W. Welch, and J. H. Helle. 1996. A review of size trends among North Pacific salmon (*Oncorhynchus* spp.). *Canadian Journal of Fisheries and Aquatic Sciences* 53:455-465.
- Chittenden, C. M., R. J. Beamish, and R. S. McKinley. 2009. A critical review of Pacific salmon marine research relating to climate. *ICES Journal of Marine Science* 66(10):2195-2204.
- Cooney, R., and R. D. Brodeur. 1998. Carrying capacity and North Pacific salmon production: stock-enhancement implicatoin. *Bulletin of Marine Science* 62(2):443-464.
- Farley, E. V., Jr., and J. H. Moss. 2009. Growth rate potential of juvenile chum salmon on the Eastern Bering Sea Shelf: an assessment of salmon carrying capacity. *North Pacific Anadromous Fish Commission Bulletin* 5:265-277.
- Farley, E. V., Jr., J. M. Murphy, M. D. Adkison, L. B. Eisner, J. H. Helle, J. H. Moss, and J. L. Neilsen. 2004. Critical-size, critical-period hypothesis: an example of the relationship between early marine growth of juvenile Bristol Bay sockeye salmon, subsequent marine survival, and ocean conditions. *North Pacific Anadromous Fish Commission Technical Report* 6:46.
- Fisher, J. P., and W. G. Pearcy. 2005. Seasonal changes in growth of coho salmon (*Oncorhynchus kisutch*) off Oregon and Washington and concurrent changes in the spacing of scale circuli. *Fishery Bulletin* 103:34-51.
- Forbes, L., and R. Peterman. 1994. Simple size-structured models of recruitment and harvest in Pacific salmon (*Oncorhynchus* spp.). *Canadian Journal of Fisheries and Aquatic Sciences* 51:603-616.
- Francis, R. C., and T. H. Sibley. 1991. Climate change and fisheries: what are the real issues? *Northwest Environmental Journal* 7(2):295-307.
- Friedland, K. D. 1998. Ocean climate influences on critical Atlantic salmon (*Salmo salar*) life history events. *Canadian Journal of Fisheries and Aquatic Sciences* 55:119-130.
- Friedland, K. D., J. C. MacLean, L. P. Hansen, A. J. Peyronnet, L. Karlsson, and D. G. Reddin. 2009. The recruitment of Atlantic salmon in Europe. *ICES Journal of Marine Science* 66(2):289-304.



- Fukuwaka, M., and M. Kaeriyama. 1997. Scale analyses to estimate somatic growth in sockeye salmon, *Oncorhynchus nerka*. *Canadian Journal of Fisheries and Aquatic Sciences* 54(3):631-636.
- Fukuwaka, M., T. Kaga, and T. Azumaya. 2011. Regional differences in climate factors controlling chum and pink salmon abundance. *ICES Journal of Marine Science* 68:1131-1137.
- Fukuwaka, M., S. Sato, S. Takahashi, T. Onuma, O. Sakai, N. Tanimata, K. Makino, N. D. Davis, A. F. Volkov, and K. B. Seong. 2007. Winter distribution of chum salmon related to environmental variables in the North Pacific. *North Pacific Anadromous Fish Commission Technical Report* 7:29-30.
- Hallowed, A. B., S. R. Hare, and W. S. Wooster. 2001. Pacific-Basin climate variability and patterns of Northeast Pacific marine fish production. *Progress in Oceanography* 49(1-4):257-282.
- Hare, S. R., and N. J. Mantua. 2000. Empirical evidence for North Pacific regime shifts in 1977 and 1989. *Progress in Oceanography* 47:103-145.
- Hare, S. R., N. J. Mantua, and R. C. Francis. 1999. Inverse production regimes: Alaska and west coast Pacific salmon. *Fisheries* 24(1):6-14.
- Helle, J. H. 1989. Relation between size at maturity and survival of progeny in chum salmon, *Oncorhynchus keta* (Walbaum). *Journal of Fish Biology* 35:99-107.
- Helle, J. H., and M. S. Hoffman. 1995. Size decline and older age at maturity of two chum salmon (*Oncorhynchus keta*) stocks in Western North America, 1972-92. *Canadian Journal of Fisheries and Aquatic Sciences* 52:245-260.
- Helle, J. H., and M. S. Hoffman. 1998. Changes in size and age at maturity of two North American stocks of chum salmon (*Oncorhynchus keta*) before and after a major regime shift in the North Pacific Ocean. *North Pacific Anadromous Fish Commission Bulletin* 1:81-89.
- Helle, J. H., E. C. Martinson, D. M. Eggers, and O. Gritsenko. 2007. Influence of salmon abundance and ocean conditions on body size of Pacific salmon. *North Pacific Anadromous Fish Commission Bulletin* 4:289-298.
- Hilborn, R., R. Lessard, D. Goodman, B. Bue, M. Adkison, J. Stanford, D. Whited, and E. Knudsen. 2007. Alternative methods for setting escapement goals in AYK. Prepared for: 2007 Arctic Yukon Kuskokwim sustainable salmon initiative project final product. .

- Hillgruber, N., and C. E. Zimmerman. 2009. Estuarine ecology of juvenile salmon in western Alaska: a review. Pages 183-199 [in] C. C. Krueger, and C. E. Zimmerman, Editors. Pacific Salmon: Ecology and Management of Western Alaska's Populations. American Fisheries Society, Symposium 70, Bethesda, MD.
- Holt, C. A., M. B. Rutherford, and R. M. Peterman. 2008. International cooperation among nation-states of the North Pacific Ocean on the problem of competition among salmon for a common pool of prey resources. *Marine Policy* 32(4):607-617.
- Hunt, G. L., Jr, and P. Stabeno. 2002. Climate change and the control of energy flow in the southeastern Bering Sea. *Progress in Oceanography* 55:5-22.
- Ishida, Y., S. Ito, M. Kaeriyama, S. McKinnell, and N. K. 1993. Recent changes in age and size of chum salmon (*Oncorhynchus keta*) in the North Pacific ocean and possible causes. *Canadian Journal of Fisheries and Aquatic Sciences* 50:290-295.
- Kaeriyama, M. 1989. Comparative morphology and scale formation in four species of *Oncorhynchus* during early life. *Ichthyol. Res.* 35(4):445-452.
- Kaeriyama, M. 1996. Population dynamics and stock management of hatchery-reared salmon in Japan. *Bulletin of National Research Institute of Aquaculture, Supplement* 2:11-15.
- Kruse, G. H. 1998. Salmon run failures in 1997-1998: a link to anomalous ocean conditions? *Alaska Fishery Research Bulletin* 5(1):55-63.
- Mantua, N. J., and S. R. Hare. 2002. The Pacific decadal oscillation. *Journal of Oceanography* 58:35-44.
- Mantua, N. J., S. R. Hare, Y. Zhang, J. M. Wallace, and R. C. Francis. 1997. A Pacific interdecadal climate oscillation with impacts on salmon production. *Bull. Am. Meteorol. Soc.* 78(6):1069-1079.
- Martinson, E. C., J. H. Helle, D. L. Scarnecchia, and H. H. Stokes. 2008. Density-dependent growth of Alaska sockeye salmon in relation to climate-oceanic regimes, population abundance, and body size, 1925 to 1998. *Marine Ecology Progress Series* 370:1-18.
- Martinson, E. C., J. H. Helle, D. L. Scarnecchia, and H. H. Stokes. 2009. Growth and survival of sockeye salmon (*Oncorhynchus nerka*) from Karluk Lake and River, Alaska, in relation to climatic and oceanic regimes and indices, 1922-2000. *Fishery Bulletin* 107(4):488-500.
- McLain, D. R. 1984. Coastal ocean warming in the northeast Pacific, 1976-83. Pages 61 [in] Pacific Environmental Group. The Program, Monterey, California. .

- Miller, A. J., D. R. Cayan, T. P. Barnett, N. E. Graham, and J. M. Oberhuber. 1994. The 1976–1977 climate shift of the Pacific Ocean. *Oceanography* 7(1):21-26.
- Moyle, P., and J. Cech, JJ. 1982. *Fishes: an introduction to ichthyology*. Prentice-Hall, Inc, Englewood Cliffs, NJ.
- Mueter, F., B. J. Pyper, R. M. Peterman, C. C. Wood, and D. J. Blackbourn. 2002a. Opposite effects of sea-surface temperature on survival rates of Pacific salmon from northern and southern areas. *North Pacific Anadromous Fish Commission Technical Report* 4:22-23.
- Mueter, F. J., R. M. Peterman, and B. J. Pyper. 2002b. Opposite effects of ocean temperature on survival rates of 120 stocks of Pacific salmon (*Oncorhynchus spp.*) in northern and southern areas. *Canadian Journal of Fisheries and Aquatic Sciences* 59(3):456-463.
- Myers, K. W., N. V. Klovach, O. F. Gritsenko, S. Urawa, and T. C. Royer. 2007. Stock-specific distributions of Asian and North American salmon in the open ocean, interannual changes, and oceanographic conditions. *North Pacific Anadromous Fish Commission Bulletin* 4:159-177.
- Myers, K. W., R. V. Walker, N. D. Davis, and R. L. Burgner. 2004. A history of US high seas salmon and steelhead stock identification research. *North Pacific Anadromous Fish Commission Technical Report* 5:16-17.
- Myers, R. A., and N. G. Cadigan. 1993. Density-dependent juvenile mortality in marine demersal fish. *Canadian Journal of Fisheries and Aquatic Sciences* 50(8):1576-1590.
- Overland, J. E., and P. J. Stabeno. 2004. Is the climate of the Bering Sea warming and affecting the ecosystem? *Transactions of the American Geophysical Union* 85(33):309-316.
- Pearcy, W. 1992. *Ocean Ecology of North Pacific Salmonids*. Washington Sea Grant Program, Seattle.
- Peterman, R. 1984. Density-dependent growth in early ocean life of sockeye salmon (*Oncorhynchus nerka*). *Canadian Journal of Fisheries and Aquatic Sciences* 41:1825-1829.
- Peterman, R. M., B. J. Pyper, M. F. Lapointe, M. D. Adkison, and C. J. Walters. 1998. Patterns of covariation in survival rates of British Columbian and Alaskan sockeye salmon (*Oncorhynchus nerka*) stocks. *Canadian Journal of Fisheries and Aquatic Sciences* 55(11):2503-2517.

- Pyper, B. J., F. J. Mueter, R. J. Peterman, D. J. Blackbourn, and C. C. Wood. 2001. Spatial covariation in survival rates of Northeast Pacific pink salmon (*Oncorhynchus gorbuscha*). *Canadian Journal of Fisheries and Aquatic Sciences* 58:1501-1515.
- Pyper, B. J., F. J. Mueter, R. J. Peterman, D. J. Blackbourn, and C. C. Wood. 2002. Spatial covariation in survival rates of Northeast Pacific chum salmon. *Transactions of the American Fisheries Society* 131:343-363.
- Ricker, W. E. 1962. Comparison of ocean growth and mortality of sockeye salmon during their last two years. *Journal of the Fisheries Research Board of Canada* 19(4):531.
- Rogers, D. 1984. Trends in abundance of Northeastern Pacific stocks of salmon. Pages 100-127 [in] W. Percy, Editor. *The influence of ocean conditions on the production of salmonids in the North Pacific*. Oregon State University Press, Corvallis, OR.
- Ruggerone, G. T., B. A. Agler, and J. L. Nielsen. 2011. Evidence for competition at sea between Norton Sound chum salmon and Asian hatchery chum salmon. *Environmental Biology of Fishes* 92:1-15.
- Ruggerone, G. T., J. D. Bumgarner, M. Zimmermann, and D. E. Rogers. 2000. Annual marine growth of two Alaskan sockeye salmon (*Oncorhynchus nerka*) stocks in relation to salmon production and environmental trends. Pages 1-31 [in]. *School of Fisheries* Seattle, Washington.
- Ruggerone, G. T., E. Farley, J. Nielsen, and P. Hagen. 2005. Seasonal marine growth of Bristol Bay sockeye salmon (*Oncorhynchus nerka*) in relation to competition with Asian pink salmon (*O. gorbuscha*) and the 1977 ocean regime shift. *Fishery Bulletin* 103(2):355-370.
- Ruggerone, G. T., and M. R. Link. 2006. Collapse of Kvichak sockeye salmon production brood years 1991-1999: population characteristics, possible factors, and management implications. Report to North Pacific Research Board and the Bristol Bay Science and Research Institute, Anchorage, AK. 90 pp.
- Ruggerone, G. T., and J. L. Nielsen. 2004. Evidence for competitive dominance of pink salmon (*Oncorhynchus gorbuscha*) over other salmonids in the North Pacific Ocean. *Reviews in Fish Biology and Fisheries* 14:371-390.
- Ruggerone, G. T., J. L. Nielsen, and B. Agler. 2007a. Retrospective analysis of AYK chinook salmon growth. Prepared for the 2007 Arctic Yukon Kuskokwim Sustainable Salmon Initiative, Anchorage, AK. 44 pp.

- Ruggerone, G. T., J. L. Nielsen, and J. Bumgarner. 2007b. Linkages between Alaskan sockeye salmon abundance, growth at sea, and climate, 1955-2002. *Deep Sea Res. Part II* 54(23-26):2776-2793.
- Ruggerone, G. T., R. M. Peterman, B. Dorner, and K. W. Myers. 2010. Magnitude and trends in abundance of hatchery and wild pink salmon, chum salmon, and sockeye salmon in the North Pacific Ocean. *Marine and Coastal Fisheries* 2:306-328.
- Ruggerone, G. T., M. Zimmermann, K. W. Myers, J. L. Nielsen, and D. E. Rogers. 2003. Competition between Asian pink salmon and North American sockeye salmon in the North Pacific Ocean. *Fisheries and Oceanography* 12(3):209-219.
- Salo, E. O. 1991. Life history of chum salmon (*Oncorhynchus keta*). Pages 231-310 [in] C. Groot, and L. Margolis, Editors. *Pacific Salmon Life Histories*. UBC Press, Vancouver.
- Seo, H., H. Kudo, and M. Kaeriyama. 2011. Long-term climate-related changes in somatic growth and population dynamics of Hokkaido chum salmon. *Environmental Biology of Fishes* 90:131-142.
- Shepherd, J. G., D. H. Cushing, and R. J. H. Beverton. 1990. Regulation in fish populations: myth or mirage?[and discussion]. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences* 330(1257):151-164.
- Smoker, W. W. 1984. Genetic effect on the dynamics of a model of pink (*Oncorhynchus gorbuscha*) and chum (*O. keta*) salmon. *Canadian Journal of Fisheries and Aquatic Sciences* 41(10):1446-1453.
- Strong, D. R. 1986. Density-vague population change. *Trends in Ecology & Evolution* 1(2):39-42.
- Weatherly, A., and H. Gill. 1995. Growth. Pages 103-158 [in] C. Groot, L. Margolis, and W. Clarke, Editors. *Physiological ecology of Pacific salmon*. UBC Press, Vancouver.
- Welch, D. W., Y. Ishida, and K. Nagasawa. 1998. Thermal limits and ocean migrations of sockeye salmon (*Oncorhynchus nerka*): long-term consequences of global warming. *Canadian Journal of Fisheries and Aquatic Sciences* 55(4):937-948.