DETERMINANTS OF LIFE HISTORY VARIABILITY IN THE CHINOOK SALMON (*ONCORHYNCHUS TSHAWYTSCHA*) OF WESTERN ALASKAN

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Abstract

Chinook salmon from western Alaska have experienced recent declines in abundance, size, and age at maturity. Declines have led to hardships for the region's dependent subsistence and commercial users. Thus there is a managerial need to better understand factors effecting life history expression in these populations. I used retrospective scale analysis and run reconstructions to investigate the causes of declines in age at maturity and the effect of the marine environment on growth, maturation, and survival in two western Alaskan Chinook salmon populations subject to long-term monitoring: the East Fork of the Andreafsky River and the Kogrukluk River (tributaries of the Yukon River and Kuskokwim River respectively). Sex-specific responses in the expression of age at maturation to variability in growth were demonstrated. Additionally, thresholds for maturation, as described by a newly presented measure of maturation reaction norms that accounts for growth history, were found to have declined in both sexes. This can be interpreted as indirect evidence that observed declines in age at maturity represent an evolutionary response. Results also suggest that sea surface temperatures in the Bering Sea exert strong control on the expression of life history variability. Warmer sea surface temperatures appear to lead to a younger age at maturity, largely through the vector of augmented growth. However, result suggest that warmer sea surface temperatures additionally decrease the average age of male recruits by lowering growth thresholds for early male maturation. Despite the demonstrated relationship between Bering Sea surface temperatures and age at maturation, a lack of a temporal trend during the period of analysis (1977-2013) suggests that they cannot explain documented declines in average age. However, this result suggests that the average age at maturation of western Alaskan Chinook salmon will continue to decline with future predicted warming of the Bering Sea as a consequence of climate change.

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Introduction

The Chinook salmon of the Arctic-Yukon-Kuskokwim (A.Y.K.) region experienced sharp declines in abundance in the late 1990s (Schindler et al. 2013). Following a small recovery in the mid-2000s, returns in recent years have been historically low. Low returns have led to significant restrictions on subsistence and commercial harvests as managers aim to meet escapement goals. The Yukon-Kuskokwim delta region accounts for the majority of Chinook salmon subsistence harvests in Alaska (Fall et al. 2012). Harvest on the Yukon River, that averaged around 150,000 fish throughout the 1980's was reduced to just 2,724 fish in 2014 (JTC 2016). Harvest on the Kuskokwim River has been similarly restricted. The act of harvesting has cultural significance to many native Alaskans. Additionally, many residents are dependent on subsistence harvests for basic nutritional needs. With few wage paying jobs in rural communities, commercial fishing represents a unique source of non-government income. Rural residents depend on commercial earnings to purchase equipment and other inputs for subsistence fishing and some residents use the same gear and boats for both fisheries (Howe and Martin 2009). Consequently, harvest limitations have been highly detrimental, culminating in recent economic disaster declarations (Alaska Department of Fish and Game 2013). There is accordingly a strong need to understand the causes of declines to inform the management of this resource.

As returns have declined there have been concurrent region-wide decreases in the average size, age, and size-at-age of Chinook salmon (Lewis et al. 2015). Thus, the per-fish value in the fisheries has also decreased. Smaller returns may have contributed to declines in productivity as a consequence of decreased spawner quality (Schindler et al. 2013). There is concern that a younger age at maturation may be a response to selectivity in the terminal fisheries. The mesh-sizes of gill nets commonly used in the fisheries of the Yukon and Kuskokwim rivers have been shown to be size-selective (Howard and Evenson 2010), likely leading to age biased harvests. The potential for size-selective fishing to produce declines in average size and age at maturity has been increasingly recognized and theoretical modeling has suggested that selective fisheries potentially could cause declines in the average age of western Alaskan Chinook salmon (Bromaghin et al. 2011). However, environmental causes currently cannot be ruled out and thus further research is needed to determine the source of age and size declines.

Creating additional uncertainty regarding the future of A.Y.K Chinook salmon, the environments that these fish inhabit are likely to experience substantial changes in coming decades as a consequence of climate change. The Bering Sea, where A.Y.K. Chinook salmon spend their entire marine residency (Myers et al. 2010), is predicted to warm 3 C° during the 21st century (Wang et al. 2012). Increasing temperatures will directly influence rates of salmon physiological processes involved in survival, growth,

and maturation. Climate variability in the marine environment can have a profound impact on the food web that supports salmon (Aydin and Mueter 2007, Eisner et al. 2014, Hertz et al. 2016). Warming is likely to lead to significant reductions in sea ice (Wang et al. 2012), a major driver of ecosystem processes in the Bering Sea (Hunt Jr et al. 2002). Consequently, the ecosystem that supports Chinook salmon in the Bering Sea will experience significant changes. Thus there is also a need to understand the drivers of life history variability in these populations to predict how they will respond to future changes to the environment.

The assessment of the life history drivers in A.Y.K. Chinook salmon is difficult as a consequence of the complexity of the ecosystem (Schindler et al. 2013). The ecosystem which these fish inhabit is multifaceted, with dynamic interacting elements operating on various spatial and temporal scales. This makes the isolation of individual relationships difficult. Additionally, investigations are limited by the availability of complete and accurate stock information in the region which restricts the questions that researchers can investigate. A number of regional tributary populations have been monitored by long running escapement weirs. These projects provide an opportunity to analyze the population dynamics of A.Y.K. Chinook salmon at a finer resolution than is possible for the combined Yukon and Kuskokwim river populations (Bue et al. 2012, Bue and Hamazaki 2014). Monitoring weirs are used to produce estimates of the age and size distributions of the escapement (Williams and Shelden 2011, Mears 2013). Covariation of life history traits between multiple monitored populations may demonstrate representation of the larger region, as opposed to being unique to the individual populations. Thus the analysis and comparison of two or more tributary populations may be useful tool to demonstrate region wide trends.

This thesis investigates factors affecting the expression of life history characteristics in two regional populations subject to long term monitoring; the East Fork of the Andreafsky River (from here on referred to as the Andreafsky River) and the Kogrukluk River. The Andreafsky River is the lowest significant tributary in the Yukon River, draining the hills above the Yukon delta. The Kogrukluk River is a tributary of the Holitna River, which itself is a tributary of the mid-Kuskokwim River, the second largest system in the A.Y.K. region. Escapement weirs on the Andreafsky River and the Kogrukluk River began operations in 1994 and 1981 respectively. Genetic studies have determined that the lower Yukon River stock group is genetically similar to other coastal western Alaskan stocks, including those in Norton Sound, the Kuskokwim River drainage and Bristol Bay, while distinct from the mid and Canadian stock-groups in the Yukon (Templin et al. 2011). Thus these analyses may be more representative of the coastal western Alaskan populations than those of the mid and Canadian origin stock-groups of the Yukon River. Accordingly, this investigation will refer to western Alaskan Chinook salmon when referring to results in contrast to the larger A.Y.K. region.

This investigation focuses on the determinants of growth, maturation, and survival in the study populations, as well as the interaction between these population measures. Analyses were informed by information from two sources: run reconstructions for each population and retrospective scale analysis. In run reconstructions, which are provided in the Appendix, total returns in each of the study populations were estimated by combining information on the escapement with estimates of mature fish harvested in terminal fisheries. Information from run reconstructions was used to produce estimates of average age and productivity, and to weight average growth estimates and maturation models. Retrospective scale analysis from scales collected at escapement weirs was used to produce individual and population level growth estimates.

Chapter 1 explores the determinants of age at maturity to help illuminate the nature of declines in age. To achieve this goal, sex-specific relationship were modeled between annual growth increments from retrospective scale analysis and age at maturation by implementing the probabilistic maturation reaction norm methodology (PMRNs, see Heino et al. 2002). In Chinook salmon, males generally mature earlier than females and at a wider range of ages. While female spawning success is thought to be directly related to size, male spawning success is believed to be bimodal due to the expression of alternative reproductive strategies in smaller individuals. Thus males and females are expected to have distinct determinants of maturity. Accordingly, sex-specific population measures were accounted for throughout the study.

If declines in age are a consequence of size-selective fisheries, this would represent an adaptive (genetic) response. In contrast, changing age could be a consequence of environmental change leading to faster growth, and thus an earlier age of maturation as a plastic response. PMRNs have been proposed as a method to distinguish between adaptive and plastic responses in age at maturity in observational studies. PMRNs describe the probability of maturation of a population given size-at-age. Much of the plastic variability in the expression of age at maturity is accounted for by growth and thus trends in PMRNs suggest adaptive change (Heino et al. 2002). However, it has been recognized that there are residual environment effects in this method that could cause trends in PMRNs as a consequence of plasticity (Heino and Dieckmann 2008). In Chapter 1, a new measure of maturation reaction norms that accounts for growth history is presented, the "probability of maturation with average growth" (PMAG). PMAG is an expansion of the PMRN method that incorporates information on stage specific growth from retrospective scale analysis. It has been demonstrated that growth during important life history periods can have an outsized influence on the age at maturation (Morita and Fukuwaka 2006). Thus the route which size-at-age is achieved can lead to distinct probabilities of maturation. Accordingly, PMAG can be considered an improvement over the PMRN method that can be widely applied to distinguish between

adaptive and plastic changes in age at maturation in populations where information on growth history is available.

Chapter 2 examines the effect of the marine environment on growth, survival, and maturation. Sea surface temperature (SST) is used to describe variability in marine conditions due to the direct effect that temperature has on salmon physiological processes. Furthermore, climate conditions largely described by warm and cold periods have been shown to have a profound effect on the food web that support salmon in the Bering Sea (Aydin and Mueter 2007, Eisner et al. 2014, Hertz et al. 2016). Correlation matrices were used to explore the relationships between SST and measures of growth, maturation, and survival in the study population. Additionally, determinants of productivity were investigated using an extended Ricker stock-recruit modeling approach. In Chapter 2, PMAG is tested to determine if it is influenced by temperature. Temperature may have an effect on maturation beyond growth (Tobin and Wright 2011). Informed by the above analyses, a conceptual model describing the effect of sea surface temperatures on growth, survival, and maturation, and the interaction between these variables, is presented. Results of Chapter 2 are used to predict how western Alaskan Chinook salmon will respond to the predicted warming of the Bering Sea as a consequence of climate change.

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Chapter 1: Changes in sex-specific maturation reaction norms in western Alaskan Chinook salmon[1]

1.1 Abstract

In salmonids, larger fish tend to have higher reproductive success, but the relationship between size and fitness differs between the sexes. Accordingly, males and females are expected to express distinct responses of age at maturity to environmental variability and selection. In this study, we compared sex-specific growth patterns and maturation reaction norms in two populations of Chinook salmon *Oncorhynchus tshawytscha* in western Alaskan. We also present a new measure to assess changes in maturation reaction norms accounting for growth history that we believe has the potential to be widely applied, the "probability of maturation with average growth" (PMAG). Similar results were found in both populations. Males and females demonstrated distinct maturation reaction norms, with females maturing almost a year later on average. However, we found that the second year of marine growth best described age at maturity of both sexes. Males tended to grow more than females in length during this period, possibly due to females storing more energy in preparation for the high cost of female gonad development. Additionally, males were more likely than females to delay maturation in periods of low growth. Finally, we found that, in each population, growth thresholds for maturation have shown a long-term decline in both sexes as demonstrated by an increase in PMAG. This suggests that declines in the average age of western Alaskan Chinook salmon may have been caused in part by adaptation to environmental or fisheries-induced selection, although non-evolutionary mechanisms are also possible. Our results demonstrate the importance of accounting for sex-specific life-history imperatives when examining how populations respond to environmental variability and selection pressures.

[1]Jared E. Siegel, Milo D. Adkison, Megan V. McPhee. 2017. Manuscript submitted to Ecosphere.

1.2 Introduction

Age at maturity is an important fitness-related trait, particularly in species with indeterminate growth (Charnov 1993). Older individuals are generally larger, leading to greater reproductive success, but experience a higher probability of mortality before reproducing (Stearns 1992). While age at maturity in salmonids (Salmonidae) has a heritable component (Hankin et al. 1993, Berejikian et al. 2011), most species exhibit plasticity in the determination of age at maturity, allowing for individual responses to heterogeneity in environmental experience. The capacity to mature is constrained by the accrual of sufficient energy stores during critical life history periods, and maturation is delayed if energy stores are insufficient (Thorpe 1994). Somatic and gonadal growth are both constrained by energy consumption; thus faster growing individuals are more likely to mature at a younger age, but generally at a smaller final size than their later maturing counterparts. Accordingly, the determination of age at maturity in salmonids is often described as a conditional strategy where the heritable relationship with growth (hereafter referred to as the 'maturation reaction norm') evolves to optimize the tradeoff between increased reproductive success with size versus increased mortality risk before reproduction (Stearns 1992).

Populations demonstrate variability in maturation reaction norms (see Hutchings 2004) as a consequence of selection that maximizes the reproductive success of individuals under the constraints of the local environmental experience (e.g., Quinn et al. 2001). Diversity in genetically derived traits, such as maturation reaction norms, may be in part maintained in populations encountering a variable environment that leads to unevenness in the reproductive success of genotypes (Gillespie and Turelli 1989). Heritable diversity in maturation reaction norms within populations creates the potential for adaptive changes in age at maturity given consistent directional changes to selective pressures. Many salmonid populations have experienced declines in average size and changing age at maturity (Ricker 1981, Bigler et al. 1996, Lewis et al. 2015). There is consequently much interest in determining the origins of these trends. Environmental change (Otero et al. 2012), increased competition (Bigler et al. 1996), and fisheries selectivity (Ricker 1981) have all been implicated in changes in the average age at maturity of salmonid populations.

While larger spawners generally have higher reproductive success, the relative success of different life history tactics in salmonids is sex-specific. Female spawning success is primarily a function of the quantity and size of eggs and thus is largely proportional to body size (Fleming and Gross 1994, Fleming 1996). In high-density spawning events, competition further drives selection towards larger females, which can access more spawning territory by mobilizing larger gravel, dig deeper redds that are more likely to survive superimposition (van den Berghe and Gross 1984, Montgomery et al. 1996), and more successfully defend redds once established (van den Berghe and Gross 1989; but see McPhee and

Quinn 1998). The relationship between reproductive success and size in males is more complex and thought to be bimodal. Larger males dominate competition for direct access to spawning females, and selection favors expression of secondary sexual characteristics. However, smaller males can employ alternative mating tactics, such as mimicking females or hiding in order to achieve "sneak" fertilizations (Fleming and Gross 1994, Fleming 1996). The success of each male reproductive strategy is frequency dependent, increasing when that tactic is less represented in the spawning population (Berejikian et al. 2010). Due to the success of this alternative mating tactic, males are on average younger than females and demonstrate more variation in age at maturity (Healey 1991). Additionally, a younger average age of males leads to male-biased sex ratios in spawning populations due to lower risk of mortality before spawning (Quinn 2005).

As a result of differing selective pressures for male and female size in salmonids, age at maturity can be viewed as a sexually antagonistic trait, where selection for a trait in one sex (e.g., later maturity in females) can be maladaptive in the other sex. As a consequence, it is likely that males and females exhibit distinct maturation reaction norms and thus age at maturity in the sexes might change at different rates as a plastic response to a change in growth. When sexually antagonistic traits are present, sex-specific genetic control is expected (Rice 1984) and has been observed for age at maturity in Atlantic Salmon *Salmo salar* (Barson et al. 2015). Consequently, consistent changes in selection pressures could also cause distinct adaptive changes in males and females. It is therefore important to consider sex when examining population responses to environmental heterogeneity and changes to selection pressures.

Distinguishing between genetic and plastic responses in observational studies is challenging (see Law 2000, Morita and Fukuwaka 2006, Kraak 2007, Heino and Dieckmann 2008). Probabilistic maturation reaction norms (PMRNs) are a method proposed to help distinguish genetic and plastic responses in the expression of age at maturity in fish populations (Heino et al. 2002). PMRNs describe the probabilistic relationship between size-at-age and maturation using a logistic regression model with a binomial distribution. PMRNs help disentangle plastic effects from genetic effects on maturation because a major source of plasticity in the age of maturation is variation in growth conditions (Heino and Dieckmann 2008). Accordingly, temporal shifts in the midpoint of the model fit, or the size-at-age at which 50% of a cohort matures, have been used to suggest adaptive changes in maturation reaction norms, most commonly as a consequence of fisheries-induced evolution (e.g., Sharpe and Hendry 2009; Kendall et al. 2014).

A criticism of the PMRN midpoint method is its inability to account for growth history. A single size-at-age can be achieved by different growth trajectories, and growth during certain life history periods may have an outsized influence on the timing of maturity. Thorpe (1994) argued that size is a measure of past performance and that growth rate (a measure of current performance) may be more important for

inhibiting or allowing maturation. Thorpe et al. (1998) presented a model for plasticity in age at maturity in salmonids in which they suggested that maturation will occur if the rate of energy acquisition exceeds a genetically determined threshold during important life history periods. A fish that is unable to achieve sufficient condition during critical periods may delay maturation even if it has achieved a sufficient size-at-age because attempted maturation without sufficient energy stores would lead to reduced reproductive success, or even death before reproduction. Growth and condition are both constrained by energetic consumption. Additionally, endocrine factors associated with growth, including GH and IGF-1, have been associated with the onset of maturation in physiological studies (Chandrashekar et al. 2004). Consequently, Morita and Fukuwaka (2006) suggested that changes in the midpoint of the PMRN could occur as a plastic response to changes in growth potential during specific life history periods.

In this study, we examine the causes of declining age in two populations of western Alaskan Chinook salmon *Oncorhynchus tshawytscha* by investigating sex-specific growth patterns and maturation reaction norms. Previously, we identified the second year of marine growth as the best predictor of age at maturity in female Chinook salmon in these populations (McPhee et al. 2016). Here, we present a new method for investigating changes in maturation reaction norms in populations that accounts for growth history, the "probability of maturation with average growth", or PMAG. We use information on the annual growth of individual fish from retrospective scale analysis to predict PMAG in both sexes.

Chinook salmon exhibit substantial variation in life history tactics, including outmigration timing and size, the duration of marine residency, migration routes, age at maturity, size at maturity, and seasonal run timing (Healey 1991). Western Alaskan Chinook salmon represent the northern extent of the species' range, containing some of the oldest spawning runs, with historical modal ages of maturity of six years for females and five years for males. Return numbers, average size, and age at maturity have all declined in these populations since the late 1990s (Lewis et al. 2015). The majority of Alaska's subsistence harvest of Chinook salmon occurs in the Yukon-Kuskokwim delta region (Fall et al. 2012), and commercial fisheries provide a unique source of income in regional rural communities (Howe and Martin 2009). Declines have led to restrictions on commercial and subsistence harvests resulting in hardships for the region's rural residents, culminating in recent economic disaster declarations (Alaska Department of Fish and Game 2013). Accordingly, there is a managerial need to better understand the factors controlling the life history of western Alaskan Chinook salmon.

To better understand changing size and age of western Alaskan Chinook salmon, we addressed the following research questions:

1. Has age at maturity changed in our study populations?
2. Do the sexes exhibit distinct growth rates?
3. Do the sexes exhibit distinct maturation reaction norms?

4. Have maturation reaction norms for males and females changed over the study period?

1.3 Methods

1.3.1 Biological Sampling and Annual Growth Measurements

We focused our analysis on two western Alaskan Chinook salmon populations subject to long-term monitoring: the East Fork Andreafsky River (hereafter referred to as the Andreafsky River) and the Kogrukluk River (Figure 1.1; see also McPhee et al. 2016). We used retrospective scale analysis to estimate the growth of individual fish on an annual life-history basis. Retrospective scale analysis has a long history of use for aging and estimating growth of salmonids. Scale growth is proportional to somatic growth in length (Fukuwaka and Kaeriyama 1997, Walker and Sutton 2016) and accrues in a pattern of concentric ridges called circuli. Circuli spacing is wider during periods of faster growth (Fukuwaka and Kaeriyama 1997). Salmonid growth is reduced in the winter, thus annual growth increments can be identified from circuli spacing allowing for a fish to be aged and annual growth to be estimated throughout a fish's life.

Adult Chinook salmon were sampled at weirs on both rivers. Weir operations were designed to produce unbiased escapement estimates, as well as age, sex, and length distribution data as detailed by Mears (2013) for the Andreafsky River and Williams and Shelden (2011) for the Kogrukluk River. Acetate impressions of scales were provided by the Alaska Department of Fish and Game Mark, Tag, and Age Lab. While earlier years, which included years where scales were collected from carcass surveys, were included in analyses in McPhee et al. (2016), in this investigation we restricted our analysis to years with supporting age distribution data from weir operations (return years 1994-2012 and 1981-2013 on the Andreafsky River and Kogrukluk River respectively). Most female scales were already scanned and measured as described in McPhee et al. (2016). Female scales from return years 2011-2013 and all male scales were scanned and measured for this study following the same protocol. Sample size goals were 25 males and 25 females per return year for each of the commonly observed age classes (defined below), although this number of samples was not always available (Tables 1.S1 and 1.S2).

We used the European notation (Koo 1962) for age designation, where the first number is the number of winters spent post emergence in freshwater and the second number after the decimal is the number of winters spent in saltwater before maturation. Both populations were primarily composed of females maturing at ages 1.3, 1.4, and 1.5 and males maturing at ages 1.2, 1.3, and 1.4. These age/sex combinations represented an estimated 98.9% of the Kogrukluk River and 97.3% of the Andreafsky River escapement on average (Appendix). Most of the remaining fish in the Andreafsky River which were not

analyzed in this investigation were identified as 1.2 females (2.2% of the total escapement), many of which were likely misidentified males (Randy Brown, USFWS, personal communication).

Annual growth zone measurements were defined following the notation of Ruggerone et al. (2007), where *FW1* is first year freshwater growth, *SW1* is first year marine growth, *SW2* is second year marine growth, and so on. We were not confident in our ability to consistently distinguish freshwater growth accrued during the spring outmigration (spring or freshwater-plus growth, *FWPL* in Ruggerone et al. 2007) from subsequent saltwater growth during the year an individual underwent the parr-smolt transformation. Thus all scale growth accrued during the year following the last freshwater annulus was included in the first year marine growth increment (*SW1*).

1.3.2 Statistical analyses

1: Has age at maturity changed in our study populations?

In run reconstructions, total adult returns, including terminal fisheries harvest estimates, were indexed by brood year (Appendix). This allowed for the estimation of the mean age at maturity of the recruits in each cohort. Run reconstructions were based on escapement data from weirs and harvest data from the Alaska Department of Fish and Game. A full description of run reconstruction methods is provided in the Appendix. Changes in the mean age at maturity of all recruits, as well as males and females separately, were quantified for the Andreafsky River (brood years 1990-2005) and the Kogrukluk River (brood years 1977-2006) with ordinary least squares linear regression, using one-tailed significance test because we expected age at maturity to be declining in these populations (Lewis et al. 2015). This analysis, and all subsequent analyses, were performed using the statistical program R Version 3.1.2 (R Core Team 2014).

2. Do the sexes exhibit distinct growth rates?

We calculated mean scale growth of each annual increment for every combination of brood year, age at maturity, and sex in both populations. To determine if the difference in average growth between male and female fish maturing at the same age was significantly greater than zero, the differences in male and female mean cohort growth estimates across the time series were compared using one-sample t tests.

We hypothesized that females maturing at the same age as males would demonstrate greater growth in the aforementioned analysis because they represent a faster growing subset of the population. For example, 1.3 males were the central age class of males (i.e., representing the average growing male) while 1.3 females were the younger age class of females (representing fast growing females). Thus to determine if average cohort growth differed between the sexes, we estimated average growth for males

and females separately by weighting the estimates of average growth for each age at maturity by the proportional representation of each age at maturity in the return estimates from run reconstructions (Appendix). To determine if the difference in the average growth of males and females was significantly greater than zero, we again used one-sample t tests. To assess the biological significance of differences in scale growth, we fit a linear relationship between scale radius and mid-eye to fork length (mm) with data from both sexes and rivers to back-calculate scale growth into estimates of somatic growth. We fixed the intercept of this relationship at 40 mm, which represented a reasonable estimate of the size at first scale formation (Rich 1920): Length = 171.6*Radius + 40.0 (Appendix: Figure A.S1).

Because we used scales from mature fish, our average male and female growth estimates were representative only of fish that survived to return to the rivers. This technique likely overestimated the average cohort growth due both to size-selective mortality and the additional period of mortality for the slower growing fish, which tend to mature at older ages. Thus variation in the timing and magnitude of mortality across cohorts remains a source of noise in our estimates.

3. Do the sexes exhibit distinct maturation reaction norms?

To determine the relationship between stage-specific growth and age at maturity for each sex, we modeled the maturation reaction norms for male and female fish separately as binary responses (mature or not mature) using logistic regression. Each "decision point" during which a fish either matured or did not mature was modeled in each population at the level of individual fish. Since we analyzed three age classes for each sex (males: 1.2, 1.3, 1.4; females: 1.3, 1.4, 1.5), two models were created for each sex in each population, creating a total of eight models. Males faced maturity decisions at ages 1.2 and 1.3. Females similarly faced maturity decisions at ages 1.3 and 1.4. To determine if the sexes exhibit distinct maturation reaction norms, estimated reaction norms for the 1.3 maturity decision for each sex were compared.

Our scale samples were collected on a return-year basis, and thus were not proportional to brood year returns across multiple return years. Additionally, the target sample size was not proportional to the age composition of the return. To correct for disproportionate sampling, we considered our dataset to be a stratified random sample (Lumley 2010), with age at maturity/sex combinations for each brood year representing the strata. Each brood year was weighted evenly in the models and finite population corrections were added for each stratum using the R package Survey (Lumley 2010). Strata weights (Tables 1.S3 and 1.S4) were calculated using proportion-at-age estimates from run reconstructions (Appendix). There are a few cases where we had no scale samples for strata, mainly 1.5 females (Tables 1.S1 and 1.S2). In these cases, the mean growth value across the times series in each river for that age

and sex combination was applied in the models. Strata without samples were rare in the returns and thus this had a minimal effect on model fitting due to low weighting.

To make coefficients comparable within models, growth increments were converted to standard deviation anomalies from estimated mean growth values. We estimated population-level mean growth values by taking the average of the weighted mean cohort growth estimates, as calculated for each cohort in the above methods, for the entire time series. Population-level standard deviation values for each growth increment were similarly estimated by first estimating the standard deviation in growth of each cohort, and then calculating the mean value of all cohorts in the respective times series. Only cohorts with multiple scale samples in each stratum were used for standard deviation estimation (Tables 1.S1 and 1.S2). The following equation was used to estimate growth standard deviation values for each cohort in the respective populations:

$$\sqrt{\frac{1}{N-1}\sum_{h=1}^{k}\left(\sum_{i=1}^{n_h}(x_{ih}-\bar{x})^2\right)\frac{N_h}{n_h}}$$

where N is the population of the entire cohort, N_h is the population of stratum h (1 through k), n_h is the number of samples from stratum h (1 to n_h), x_{ih} is the growth value of fish i in stratum h, and $\bar{x}$ is the estimated population-level mean growth value.

For each maturity decision model, all growth increments up to the point of the maturity decision were included in analysis. Brood year was also included (as a fixed categorical variable) to estimate variability in the relationship between growth and maturity among cohorts. Accordingly, the 1.2 male maturity decision was modeled as:

$$\log\left(\frac{p}{1-p}\right)_{i,y} = \beta_0 + \beta_1 FW1_i + \beta_2 SW1_i + \beta_3 SW2_i + B_y + \varepsilon_{i,y}$$

where p is the probability of maturing at age 1.2 for fish i in brood year y, *FW1* is the freshwater growth increment, *SW1* and *SW2* are the first and second year marine growth increments respectively, and B is a coefficient estimated for each brood year y. Full models for 1.3 maturity decisions included an additional third year saltwater growth parameter and female 1.4 maturity decision models included additional third and fourth year saltwater growth parameters (*SW3* and *SW4*). Model parameters were estimated using maximum likelihood. All possible variable combinations were compared and final models were selected using the Akaike Information Criterion (AIC). We described PMRNs specific to each annual growth

increment predicted from selected models by holding other annual growth increments constant at the defined estimated population level mean growth values and by using the mean of estimated brood year coefficients.

We had scale and return data from return years 1981-2013 on the Kogrukluk River and 1994-2012 on the Andreafsky River. Due to the different age classes associated with each maturity decision, this allowed for analysis of a slightly different range of brood years for each modeled maturity decision. For the Andreafsky River, we analyzed brood years 1990-2006 for the male 1.2 maturity decision, brood years 1989-2006 for the male 1.3 maturity decision, brood years 1989-2005 for the female 1.3 maturity decision, and brood years 1988-2005 for the female 1.4 maturity decision. For the Kogrukluk River, we analyzed brood years 1977-2007 for the male 1.2 maturity decision, brood years 1976-2007 for the male 1.3 maturity decision, brood years 1976-2006 for the female 1.3 maturity decision, and brood years 1975-2006 for the female 1.4 maturity decision.

4. Have maturity reaction norms for males and females changed over the study period?

In order to better account for growth history, we developed a new method to describe changes in maturation reaction norms over time that accounts for annual growth rather than total size. For each maturity decision, we used our logistic models to predict, for each brood year, the probability of maturation for fish with "average" growth throughout its life history. We refer to this newly created variable as the "probability of maturation with average growth" (PMAG). While the size-at-age of 50% maturation is an inherent property of PMRNs, the "average" growth value used to estimate PMAG must be defined. To calculate PMAG, we defined "average" growth as the estimated population-level mean growth values across the respective study periods. Since growth was held constant, the only thing that varied in the prediction of PMAG in each model was B_y, the distinct coefficient estimated for each brood year in the factor variable. To determine whether PMAG for each maturity decision changed over the respective study periods in each population, we used ordinary least squares linear regression.

1.4 Results

1.4.1 Has age at maturity changed in our study populations?

All regression models estimated trends of decreasing mean age (Figure 1.2, Table 1.1), although the coefficients were not statistically significant ($P > 0.05$) in the Andreafsky River, possibly because of substantial interannual variability and the shorter time series. In the Andreafsky River, between brood years 1990-2005 the mean age of all recruits was estimated to have declined from 5.17 to 5.06 years, from

4.93 to 4.72 years for males, and from 5.62 to 5.51 years for females. Mean age declined significantly (Table 1.1) in the Kogrukluk River, at a rate similar to that observed in the Andreafsky River (Figure 1.2). In the Kogrukluk River, between brood years 1977-2006 mean age was estimated to have declined from 5.37 to 5.12 years for all recruits, from 5.07 to 4.82 years for males, and from 6.00 to 5.74 for females.

1.4.2 Do the sexes exhibit distinct growth rates?

Estimates of mean growth of males and females were similar for most increments (Table 1.2). The most prominent exception was that males grew more than females during *SW2* in both the Andreafsky River (one-sample *t* test, $t = 3.72$, df = 15, $P = 0.002$) and Kogrukluk River (one-sample *t* test, $t = 7.84$, df = 29, $P < 0.001$). Male SW2 growth averaged 6.9% (~ 12.8 mm) more than female growth in the Andreafsky River and 7.1% (~ 12.6 mm) more than female growth in the Kogrukluk River. Females were also estimated to have grown more than males during *SW1* in the Kogrukluk River, though this difference was a smaller (2.3% or ~5.4 mm) increase over male growth (one-sample *t* test, $t = -4.24$, df = 29, $P < 0.001$).

As we predicted, average marine growth (*SW1-SW4*) of females was higher than males that matured at the same age (Table 1.2), leading to larger female size-at-age estimates for the same age at maturity (Figure 1.3 and Figure 1.S2). This relationship held true for all comparisons in the Andreafsky River and the Kogrukluk River. In the Andreafsky River, 4 out of 7 of the differences were significantly larger than zero while 6 out of 7 of the differences were significantly larger than zero in Kogrukluk River. This result is consistent with the observation that females are larger than the males of the same age at maturity in these spawning populations (Hansen and Blain 2013, Mears 2013), and similar results had previously been documented by Ruggerone et al. (2007a) for the combined Yukon and Kuskokwim river populations.

1.4.3 Do the sexes exhibit distinct maturation reaction norms?

Distinct PMRNs for males and females in both of the study populations were apparent (Figure 1.4.). Due to the differences in the expressed ages at maturity of males and females, the 1.3 maturity decision was the only maturity decision measured for both sexes. Over all analyzed brood years, a male that achieved the estimated population-level mean growth up until this decision point (defined in methods) had an 85% probability of maturing in the Andreafsky River and a 79% probability of maturing in the Kogrukluk River, while females accruing the same growth had only 34% and 12% probabilities of maturing respectively.

However, while the sexes demonstrated distinct reaction norms for the same age at maturity, the 1.3 female and 1.2 male PMRNs were fairly analogous (Figure 1.4). While the selected 1.3 female maturity models included an effect of *SW3* growth (which occurs after the 1.2 male maturation decision), the effect of *SW2* was found to be strongest for both sexes in each population (Table 1.3). This suggests that the proportion of males in a cohort that mature early at age 1.2 is likely to covary with the proportion of females that mature early at age 1.3 the following year due to shared environmental influences. In contrast, PMRNs suggested that females were much less likely to mature late as 1.5s in comparison to males maturing at age 1.4, irrespective of growth. Thus, in cohorts experiencing lower than average growth, average age increased to a greater degree in males than in females (although males were still younger on average than females). While the Andreafsky River population demonstrated somewhat higher probabilities of maturing with mean growth compared to the Kogrukluk River population, both populations exhibited similar patterns in stage-specific PMRNs (Figure 1.4).

Model selection suggested that age at maturity in the study populations is primarily influenced by marine growth in both males and females; freshwater growth was only retained in two of the eight selected models (Table 1.3). All coefficients for growth increments in the selected models were positive, suggesting a ubiquitous relationship between faster growth and earlier maturation. The fixed effect for brood year was retained in each model, suggesting variability in the relationship between growth and maturity across cohorts. Final chosen logistic age at maturity models were generally not well distinguished from full models by the AIC criterion (Tables 1.S5 and 1.S6).

Models suggest that the second year in the marine environment is an important period in the determination of age at maturity for western Alaskan Chinook salmon. *SW2* was the only variable retained in all maturity decisions models, and was found to have the strongest relationship with age at maturity in each case (Table 1.3). Standard deviations of brood-year coefficients were relatively large for the female 1.4 models in each river in comparison to other maturity decision models, demonstrating high variability in reaction norms during this maturity decision. This may be a consequence of estimated 1.5 female returns being rare in some years, particularly in more recent years (e.g., Andreafsky brood year 1993 and Kogrukluk brood years 2004 and 2006). In those years, the predicted probability of females maturing at age 1.5 approached zero, irrespective of growth.

1.4.4. Have maturation reaction norms for males and females changed over the study period?

The predicted probability of maturation with average growth (PMAG) increased over the period of study for all maturity decisions analyzed in both sexes in the Andreafsky River and Kogrukluk River Chinook salmon populations (Figure 1.5). All linear models demonstrated positive slopes (Table 1.4).

These slopes were significantly different than zero for the Kogrukluk River male 1.3, female 1.3 and female 1.4 models ($P < 0.05$). In the Andreafsky River, PMAG for the 1.2 male maturity decision was estimated to have increased from 26.4% to 33.6% between brood years 1990-2006, from 77.4% to 87.0% between brood years 1989-2006 for the male 1.3 maturity decision, from 29.7% to 44.0% between brood years 1989-2005 for the female 1.3 maturity decision, and from 97.4% to essentially 100% between brood years 1988-2005 for the female 1.4 maturity decision. In the Kogrukluk River, PMAG for the 1.2 male maturity decision was estimated to have increased from 18.4% to 26.7% between brood years 1977-2007, from 63.5% to 88.2% between brood years 1976-2007 for the male 1.3 maturity decision, from 8.1% to 24.1% between brood years 1976-2006 for the female 1.3 maturity decision, and from 93.2% to 99.9% between brood years 1975-2006 for the female 1.4 maturity decision.

1.5 Discussion

Our results demonstrate distinct maturation reaction norms between the sexes in both the Andreafsky River and Kogrukluk River Chinook salmon populations. Males were more likely than females to mature at an earlier age for a given amount of growth for the 1.3 maturation decision (Figure 1.4). This result was expected given the average age of females is almost a year older than males in both populations. However, we found that the maturation reaction norms of the 1.2 maturity decision in males and the 1.3 maturity decision in females to be fairly analogous, despite the 1.3 female maturity decision occurring a year later (Figure 1.3). This suggests that the environmental influences for males maturing at age 1.2 and females maturing at age 1.3 are similar, and consequently the proportion of 1.2 males should predict the proportion of 1.3 females maturing from the same cohort the following year. In contrast, the later maturity responses (1.3 male and 1.4 female decisions) were distinct between the sexes. Females were much less likely to delay maturation to the later age of 1.5 compared to males delaying maturation to age 1.4 across all levels of commonly observed growth (Figure 1.4). Age 1.5 females are not numerous in these populations, averaging an estimated 2.1% of Andreafsky River and 6.6% of Kogrukluk River female brood returns (Appendix). Thus, while above-average growth will lead to a similar increase in the proportion of males and females maturing early (at ages 1.2 and 1.3 respectively), our results suggest that below-average growth will cause the average age of males to increase to a greater extent than the average age of females (though males will remain younger than females on average). These findings demonstrate the importance of taking sex into account when investigating growth and maturation responses to environmental variation. Similarities in the relationship between growth and age at maturity in the Kogrukluk River (a Kuskokwim River tributary) and Andreafsky River (a Yukon River tributary)

populations suggests that the patterns we describe here may be representative of Chinook salmon in the western Alaskan region.

Our results suggest that age at maturity in both males and females is largely determined during the same growth period (*SW2)* in western Alaskan Chinook salmon, despite females maturing on average nearly a year later than males. This suggests that the plastic effects of environmental experience on the age at maturity influence females further in advance of maturation. We also found evidence of sexually dimorphic growth during this important period of age determination, with lower average growth in females than males. Consistent with this result, past analysis of bycatch samples from the Bering Sea NOAA Fisheries Observer Program found that female Chinook salmon captured following their second year of marine growth were significantly smaller on average than their male counterparts by about one centimeter (Myers et al. 2010).

Maturation in salmonids has been described as a continuous process, with the potential for completion annually, which is inhibited during critical life history periods if lipid stores are insufficient (Thorpe 1994, Thorpe et al. 1998, Rikardsen et al. 2004). In accordance with this theory, Chinook salmon demonstrate the ability to mature annually after emergence with mature precocious parr occurring in some populations with high growth conditions (e.g., Beckman et al. 2007). Due to the energetic cost of maturation and the homing migration, attempted maturation without sufficient energy stores would likely lead to reduced spawning success or death before reproduction. In a model originally developed for Atlantic Salmon, Thorpe et al. (1998) described two important periods, one in the fall a year before spawning and one in the spring before spawning, where maturation is either continued or aborted through hormonal control. In alignment with this theory, Morita and Fukuwaka (2006) found that the last year of growth before the maturity decision had the strongest correlation with age at maturity in Chum Salmon *O. keta* in a similar retrospective scale analysis to ours. However, in contrast to Morita and Fukuwaka's (2006) findings, we identified a more complex and sex-specific relationship in the study populations of Chinook salmon. Only the 1.2 male maturity decision was most heavily influenced by growth occurring the year prior to maturation, while all other decisions were better correlated with growth occurring two or more years in advance of maturation. Assuming the presence of similarly timed hormonal maturation switches in Chinook salmon as described by Thorpe and colleagues, our results suggest that the accumulation of energy stores well in advance of these switches, particularly for females, has a considerable effect on the ability to surpass energetic thresholds for maturity. The development of eggs and ovaries requires relatively more energy than the development of sperm and testes. Accordingly, we hypothesize that sexual dimorphic growth during *SW2* may be a consequence of females allocating more energy to storage, in contrast to somatic growth, in advance of maturation in preparation for the higher energetic cost of gonad development. A comparison of energy content between immature males and

females sampled at sea, possibly from Bering Sea Walleye Pollock *Gadus chalcogrammus* fishery bycatch samples (Stram and Lanelli 2015), could address this hypothesis.

Past research has demonstrated a strong relationship between smolt size and condition and the age at maturity of Chinook salmon in hatchery (Silverstein et al. 1998, Vøllestad et al. 2004, Larsen et al. 2013, Spangenberg et al. 2014, 2015) and wild populations (Scheuerell 2005, Tattam et al. 2015). These results, particularly those from wild populations, are similar to our results in that they suggest that age at maturity in Chinook salmon can be influenced by growth conditions well in advance of maturation decisions. However, our results contrast with these past findings in that we found a minimal relationship between freshwater growth and age at maturity, suggesting that western Alaskan Chinook salmon age at maturity is primarily influenced by marine growth conditions (see also McPhee et al. 2016). The above cited studies were performed on populations in the contiguous United States, representing the southern portion of the species' range. Southern populations of Chinook salmon tend to have higher freshwater growth rates (Taylor 1990) and mature at an earlier average age in comparison to more northern populations in Canada and Alaska (Myers et al. 1998). Additionally, population-level differences in maturation reaction norms presumably have evolved as a consequence of selection that maximizes the reproductive success of individuals given the local environmental experience (Hutchings 2004). Accordingly, the later influence of growth on maturity timing in western Alaskan Chinook in comparison to other studied populations is likely a consequence of an interaction between genetic differences in maturation reaction norms and environmentally-based lower growth rates during early life history preventing individuals from surpassing thresholds earlier. A common-garden experiment comparing growth and maturation rates between western Alaskan Chinook salmon and southern populations reared under identical conditions (e.g., Spangenberg et al. 2015) would help determine the relative contribution of environmental and genetic sources of variation in age at maturation.

We presented evidence that fish with the same growth have become more likely to mature early in recent years in both the Andreafsky River and Kogrukluk River Chinook salmon populations. To achieve this result, we implemented a new measure of maturation reaction norms, the "probability of maturation with average growth" (PMAG). An increase in PMAG over time was found in all maturity decisions analyzed for both sexes in each population (Figure 1.5), suggesting that declines in age may have represent a genetic response to a change in selection pressures. This result is consistent with reports of declines in size-at-age of maturing Chinook salmon in western Alaska (Lewis et al. 2015). Measures of maturation reaction norms help disentangle plastic effects from genetic effects on maturation because a major source of plasticity in the determination of age of maturation is variation in environmental growth conditions (Heino and Dieckmann 2008). Changes over time in measures of maturation reaction norms can be interpreted as evolution to the extent that that they are determined by genetics. The commonly

used PMRN midpoint method does not account for variability in the growth experience leading to a single size-at-age and therefore might not account for other environmental sources of variation in maturation (Heino and Dieckmann 2008). It has clearly been shown in past studies (Morita and Fukuwaka 2006, McPhee et al. 2016) and in our investigation that growth during important life history periods can have a disproportionate influences on the age at maturation (e.g., SW2 in our study populations). Accordingly, in populations where information on stage-specific growth exists (generally from otoliths, scales, or repeated observations), we suggest that using PMAG is preferable to the PMRN midpoint method due to its ability to account for growth history.

Fisheries-induced evolution has been proposed as a possible driver of declines in the age at maturity of western Alaskan Chinook salmon and potentially could be the source of the described trends in PMAG. There is evidence that the terminal fisheries in the Yukon and Kuskokwim rivers has been size-selective due to net selectivity (Howard and Evenson 2010) leading to age biased harvests. The potential for size-selective fishing to produce declines in average size and age at maturity has been well discussed (Law 2000, Conover et al. 2005, Hard et al. 2008). Theoretical modeling has suggested that selective fisheries could be responsible for declines in average age of western Alaskan Chinook salmon (Bromaghin et al. 2011) and changes in the average age of nearby Bristol Bay Sockeye Salmon *O. nerka* have been attributed to size selective fishing (Kendall et al. 2014). While not the focus of this investigation, our run reconstructions allowed us to estimate age-specific exploitation in the terminal fisheries. We estimated that average exploitation in our study populations was greater on average for older fish in both populations, suggesting a possible source of trends (Calculations from Appendix: Andreafsky exploitation by age, 1.2s [8%], 1.3s [13%], 1.4s [28%], 1.5s [38%]; Kogrukluk average exploitation by age, 1.2s [32%], 1.3s [44%], 1.4s [45%], 1.5s [51%]). While exploitation was estimated to be higher on average in the Kogrukluk population, size selectivity appeared to be more consistent in the Andreafsky population (Figure 1.6).

Another possible source of our trends in PMAG could be environmental change altering selective pressures. Primary productivity in the Bering Sea is highly variable, largely driven by the seasonal extent of sea ice determining the timing of the spring phytoplankton bloom with cascading trophic effects on the ecosystem (Coyle et al. 2011, Hunt et al. 2011, Eisner et al. 2014). Climate change is expected to lead to substantial warming and declines in sea-ice extent in the Bering Sea (Wang et al. 2012) and may have already resulted in significant ecosystem-level changes. If the potential for marine growth of older fish has diminished, or the probability of mortality for these fish has increased, this could have selected for earlier maturing fish as the reproductive gain of remaining in the ocean to offset the added mortality risk would have become diminished. Additionally, increasing Russian Pink Salmon *O. gorbuscha* abundance in the Bering Sea (Ruggerone and Irvine 2015) has affected growth and maturation of other Pacific

salmon species through interspecific competition (Ruggerone et al. 2003, Ruggerone and Nielsen 2004, Kaga et al. 2013) and may also have had a detrimental effect on Chinook salmon growth and condition as a consequence of substantial diet overlap (Davis et al. 2004).

However, definitively distinguishing between genetic change and plastic responses remains beyond the scope of this study. It should first be noted that because our analysis was retrospective, we only analyzed information on individuals that survived to maturation. Thus we cannot consider our dataset an unbiased random sample of mature and immature individuals at the time of the maturity decision. While we weighted our models to represent the proportion of age/sex strata in the returns, variation in the mortality of fish that delay maturation remains a source of error in our estimates. Consequently, it is possible that the observed increases in PMAG are a result of an increase in the mortality of these older fish. We believe our trends in PMAG are more likely a consequence of declining maturation growth thresholds because this is consistent with trends towards smaller size-at-age (Lewis et al. 2015). However, we cannot definitively rule out changes in mortality patterns as a contributing factor to our results.

Additionally, while PMAG is an improvement over the PMRN method that we believe has potential to be widely applied, it still cannot be used to conclusively demonstrate genetic change (even assuming unbiased sampling of individuals at the time of the maturation decision) due to an inability to account for all environmental factors that could contribute to a plastic response in age at maturity beyond growth (Kraak 2007, Heino and Dieckmann 2008). For example, temperature may have an independent effect on the "decision" to mature (Tobin and Wright 2011). Furthermore, as described in the salmonid maturation model presented by Thorpe et al. (1998), higher condition could encourage earlier maturity due to the energetic cost of reproduction. While condition and growth are generally thought to correlate, there may be circumstances that cause decoupling. For example, higher lipid content feed in hatchery reared salmonids has been shown to increase early male maturity rates (Shearer and Swanson 2000, Jonsson et al. 2013), likely due to increased condition. Silverstein et al. (1998) tested the independent effects of size and "fatness" on early male maturity of hatchery reared Chinook salmon. They concluded that while size appeared to be the primary determinant of maturity, "fatness" caused a higher probability of maturity in smaller fish that would not otherwise mature. If changes to the environment led fish to achieve better condition through the increased availability of higher quality prey, or alternatively, experience higher temperatures during the early marine growth period, these un-modeled factors possibly could have led to the observed increase in PMAG via a plastic response. Further investigation into the interaction between the Bering Sea ecosystem and growth/condition, and the subsequent effects on maturation is warranted before strong conclusion on the sources of our trends in PMAG can be made.

1.6 Conclusions

We identified distinct maturation reaction norms between the sexes in wild spawning western Alaskan Chinook salmon. Males were found to mature nearly a year earlier on average than females and females were shown to be less likely to delay maturity with low growth. Additionally, females grew less than males during the second marine growth year when maturity timing is largely determined. We hypothesize that this sexually dimorphic growth may be a consequence of females prioritizing energy storage over somatic growth during the second year at sea in preparation for the higher energetic demands of female gonad development. Age at maturity is an important fitness trait in salmonids, representing a balance between increased risk of mortality before spawning and higher reproductive success with size. Males and females have distinct relationships between size and reproductive success and the reproductive potential of the escapement is largely determined by the abundance and size of spawning females. Our results suggest that the average age of males and females will respond distinctly to changes in growth potential as a consequence of plasticity. Additionally, consistent changes to selective pressures could cause distinct adaptive changes in males and females due to sex-specific genetic control of maturation reaction norms. It is therefore important to consider sex when examining how populations respond to pressures such as exploitation, inter-/intra-specific competition, and changing environmental conditions.

We also found evidence that the thresholds for maturation in western Alaskan Chinook have declined in recent years using a new method to characterize maturation reaction norms, the "probability of maturation with average growth", or PMAG. Declines in size and age are a common concern in fisheries management and understanding the causes and mechanisms of such trends remains a major focus of research. In the effort to disentangle genetic and plastic sources of phenotypic changes, PMAG improves the more commonly used midpoint of the PMRN method by accounting for growth history, rather than just total size. PMAG can be applied in populations where information on growth history is available, generally either through repeated observations or retrospectively from scales or otolith samples. However, we recognize that similar to the midpoint PMRN method, PMAG could also be affected by other factors that could cause a plastic response, including temperature and fish condition, and thus cannot be used to conclusively demonstrate adaptive change alone. We suggest examining the relationship between PMAG and other environmental variables when possible. The estimation methods of PMAG could easily be extended to include other variables that were found to influence the maturation process (e.g., Tobin and Wright 2011, Uusi-Heikkilä et al. 2011).

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1.8 References

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1.9 Tables

Table 1.1. Results of ordinary least squares linear regression for average brood recruit age over time in the Andreafsky River (Andr.) and the Kogrukluk River (Kog.) Chinook salmon populations. Model slope value (change in mean age per year), model R^2 values, and *P* values for one-tailed significant tests presented.

	Age Model	Slope	R^2	p
Andr.	All	-0.008	0.048	0.208
	Males	-0.014	0.082	0.141
	Females	-0.007	0.036	0.241
Kog.	All	-0.008	0.124	0.028
	Males	-0.009	0.112	0.035
	Females	-0.009	0.202	0.006

Table 1.2. Mean (standard deviation) back-calculated scale annual growth increment estimates (mm) for each sex and age at maturity combination of Chinook salmon from the Andreafsky River (return years 1994-2012) and the Kogrukluk River (return years 1981-2013). Growth estimates of males and females maturing at the same age, as well as estimated total cohort male and female average estimates, were statistically compared within each population. Early maturing males (1.2s) and late maturing females (1.5s), as well as the estimate for the total cohort growth, were not involved in direct statistical comparisons due to no analogous age class in the opposite sex. Mean differences between males and females that are significantly different from zero (one sample t tests) are demonstrated with asterisks: * ($P > 0.05$), **($P > 0.01$), ***($P > 0.005$).

	Age	Sex	FW1	SW1	SW2	SW3	SW4	SW5
Andreafsky	1.2	Male	101.6 (4.7)	248.7 (15.5)	215.6 (20.1)			
	1.3	Male	101.1 (5.6)	241.4*** (14.0)	193.0 (16.3)	189.4 (14.2)		
		Female	101.4 (4.5)	249.7*** (11.6)	200.4 (20.5)	192.1 (18.0)		
	1.4	Male	99.2 (3.6)	232.2*** (13.6)	171.7* (15.3)	169.0*** (9.7)	142.1 (9.7)	
		Female	99.6 (3.9)	240.4*** (12.3)	179.9* (12.5)	177.7*** (6.9)	143.4 (12.2)	
	1.5	Female	97.1 (3.4)	240.1 (14.5)	144.3 (15.8)	160.3 (16.4)	145.7 (11.7)	101.2 (14.1)
	Avg.	Male	101.2 (4.3)	243.5 (14.2)	197.8*** (17.2)	184.6 (12.9)	142.1 (9.7)	
		Female	99.9 (3.4)	243.6 (11.1)	185.0*** (12.9)	181.9 (8.5)	143.5 (12.1)	101.2 (14.1)
		Total	100.7 (3.7)	243.4 (12.5)	193.0 (14.0	183.1 (10.1)	143.4 (10.1)	101.2 (14.1)
Kogrukluk	1.2	Male	99.0 (4.1)	244.4 (14.0)	211.9 (20.8)			
	1.3	Male	97.3(4.9)	232.3*** (14.2)	188.1*** (14.9)	184.9* (15.7)		
		Female	97.8 (5.0)	248.0*** (14.0)	206.8*** (16.8)	193.8* (23.8)		
	1.4	Male	96.9 (5.2)	226.6*** (11.2)	164.5*** (19.0)	171.4*** (13.8)	150.6 (14.9)	
		Female	96.7 (5.2)	234.8*** (11.6)	172.8*** (15.9)	181.9*** (11.3)	150.9 (16.3)	
	1.5	Female	95.8 (7.9)	240.2 (21.3)	136.2 (28.2)	158.1 (26.5)	152.1 (19.3)	109.6 (21.3)
	Avg.	Male	97.6 (3.7)	234.8*** (12.1)	189.0*** (17.1)	180.6 (13.5)	150.6 (14.9)	
		Female	96.8 (4.7)	240.2*** (11.6)	176.4*** (16.0)	182.7 (11.8)	151.1 (15.8)	109.6 (21.3)
		Total	97.3 (3.6)	236.5 (11.4)	184.8 (16.2)	181.3 (11.3)	150.9 (12.1)	109.6 (21.3)

Table 1.3. Log-scale coefficients of chosen models for maturity decisions from AIC selection. Males and females from the Kogrukluk River and Andreafsky River were modeled separately. Standard deviations of calculated brood year coefficients are shown to demonstrate variability in reaction norms across the time series. Variable significant values shown by asterisks: * ($P > 0.05$), **($P > 0.01$), ***($P > 0.005$).

	Decision model	FW1	SW1	SW2	SW3	SW4	Brood year
Andreafsky	Male 1.2		0.29^{***}	0.88^{***}			0.98
	Male 1.3	0.13	0.32^{**}	0.68^{***}	0.63^{***}		0.89
	Female 1.3		0.25^{**}	0.68^{***}	0.26^{**}		0.68
	Female 1.4	0.36		1.32^{***}	0.87^{***}		3.90
Kogrukluk	Male 1.2		0.52^{***}	0.75^{***}			0.68
	Male 1.3		0.14^{*}	0.84^{***}	0.35^{***}		0.82
	Female 1.3		0.29^{***}	1.08^{***}	0.23^{**}		1.08
	Female 1.4			1.20^{***}	0.69^{***}	0.20^{*}	4.54

Table 1.4. Results from linear models for each modeled maturity decision of predicted probabilities of maturing by brood year for a fish with average growth (PMAG) in the Andreafsky River and the Kogrukluk River Chinook salmon populations. Model slope values (in units of percent change in probability of maturing per year), model R^2 values, and *P* values are presented.

	Decision Model	Slope	R^2	*P*
E.F.A.	Male 1.2	0.45	0.018	0.607
	Male1.3	0.56	0.071	0.285
	Female 1.3	1.13	0.136	0.144
	Female 1.4	0.18	0.145	0.119
Kogrukluk	Male 1.2	0.27	0.043	0.267
	Male1.3	0.80	0.292	0.001
	Female 1.3	0.53	0.190	0.014
	Female 1.4	0.22	0.161	0.023

1.10 Figures

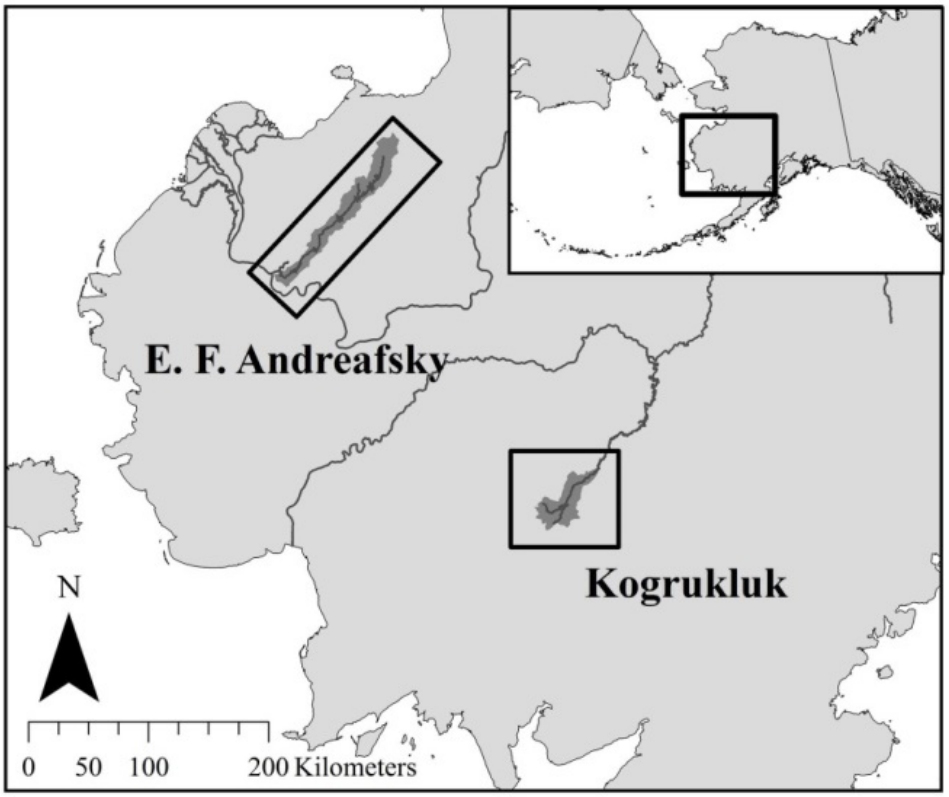

Figure 1.1. Map showing location of the two study watersheds: the East Fork of the Andreafsky River (Yukon River drainage) and Kogrukluk River (Kuskokwim River drainage).

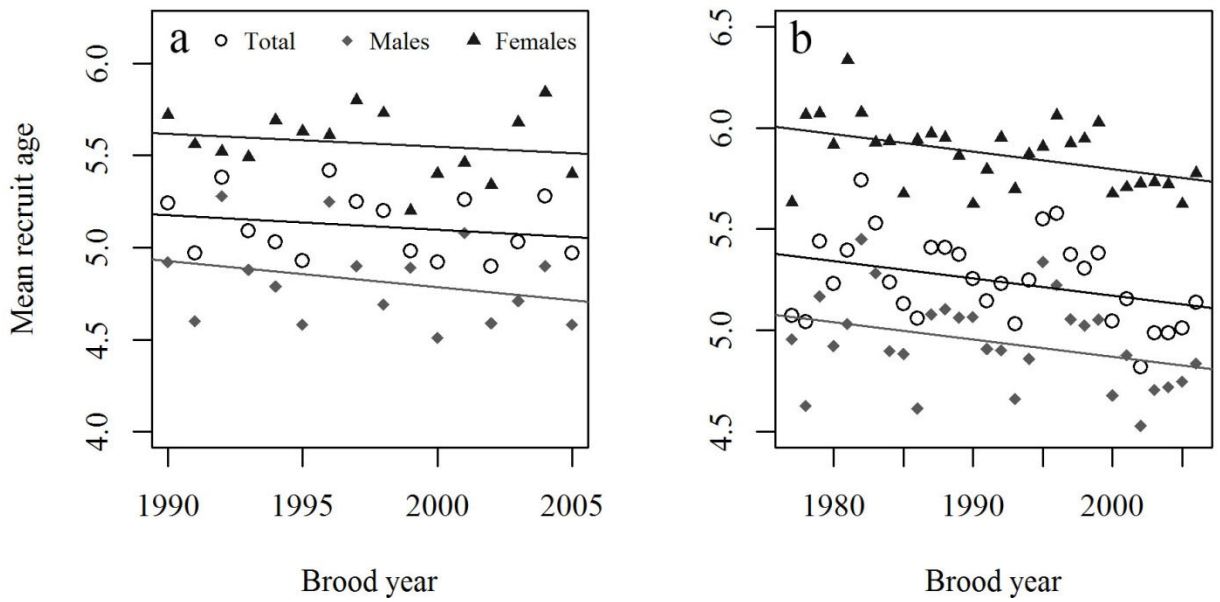

Figure 1.2. Estimated brood recruit average age by brood year for the Chinook salmon populations of the Andreafsky River (a) and the Kogrukluk River (b). Ordinary least squares linear regression fit lines are shown.

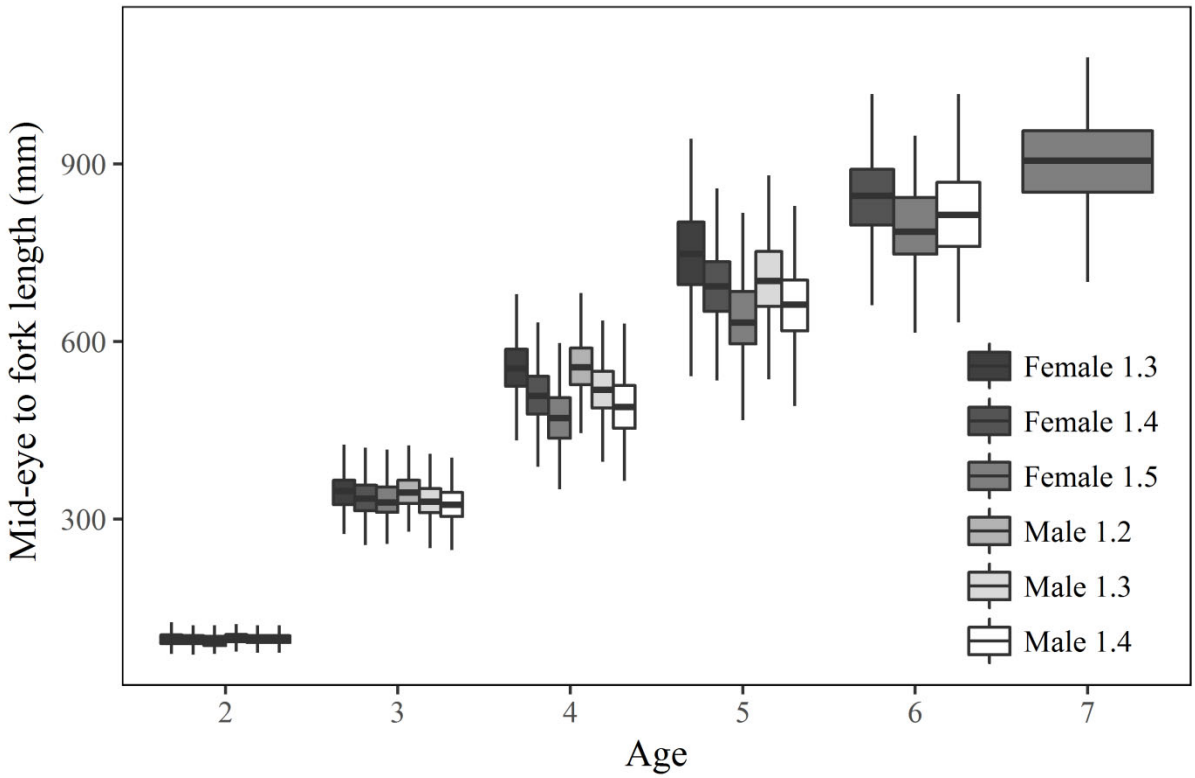

Figure 1.3. Boxplots of back-calculated size-at-age estimates (mid-eye to fork lengths) for all scale samples from the Kogrukluk River (return years 1981-2013). Samples are shown separated by sex and age at maturity combinations. Relationship between scale radius and fork length was estimated using ordinary least squares linear regression with a fixed intercept (mid-eye to fork length [mm] = 171.6*radius + 40.0).

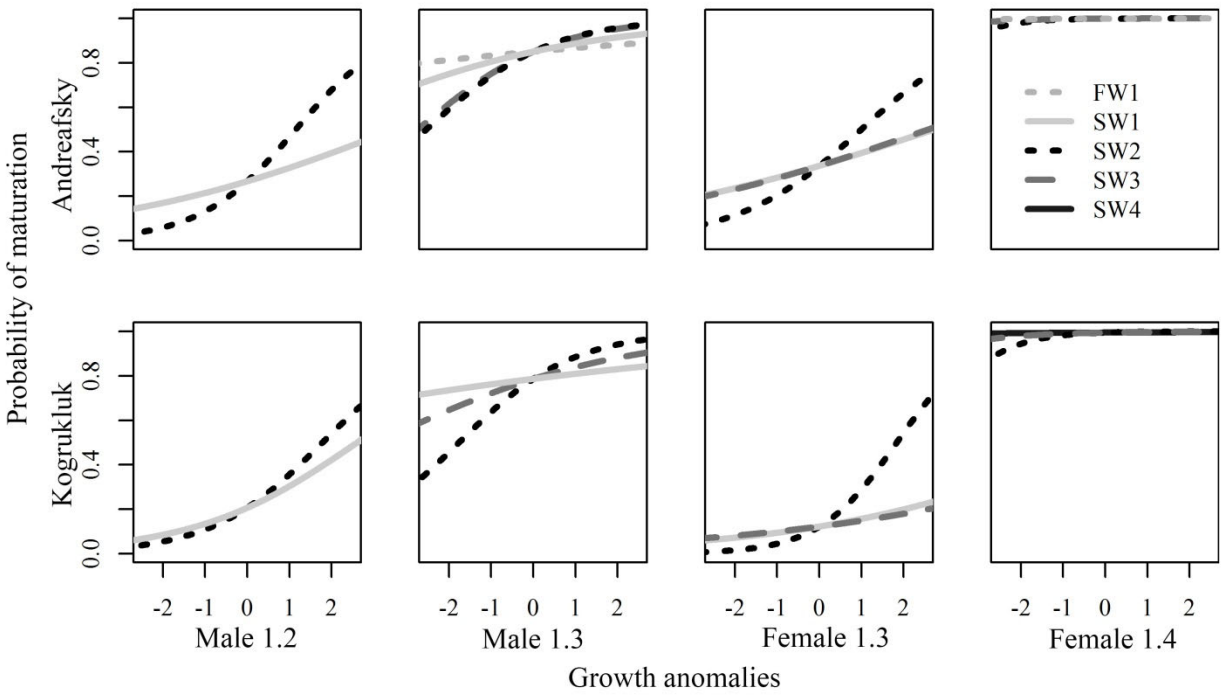

Figure 1.4. Sex-specific probabilistic maturation reaction norms isolated for the effects of annual growth for the Andreafsky River and Kogrukluk River Chinook salmon populations. Reaction norms for each annual growth increment are plotted by holding all other stages of growth at the defined mean value.

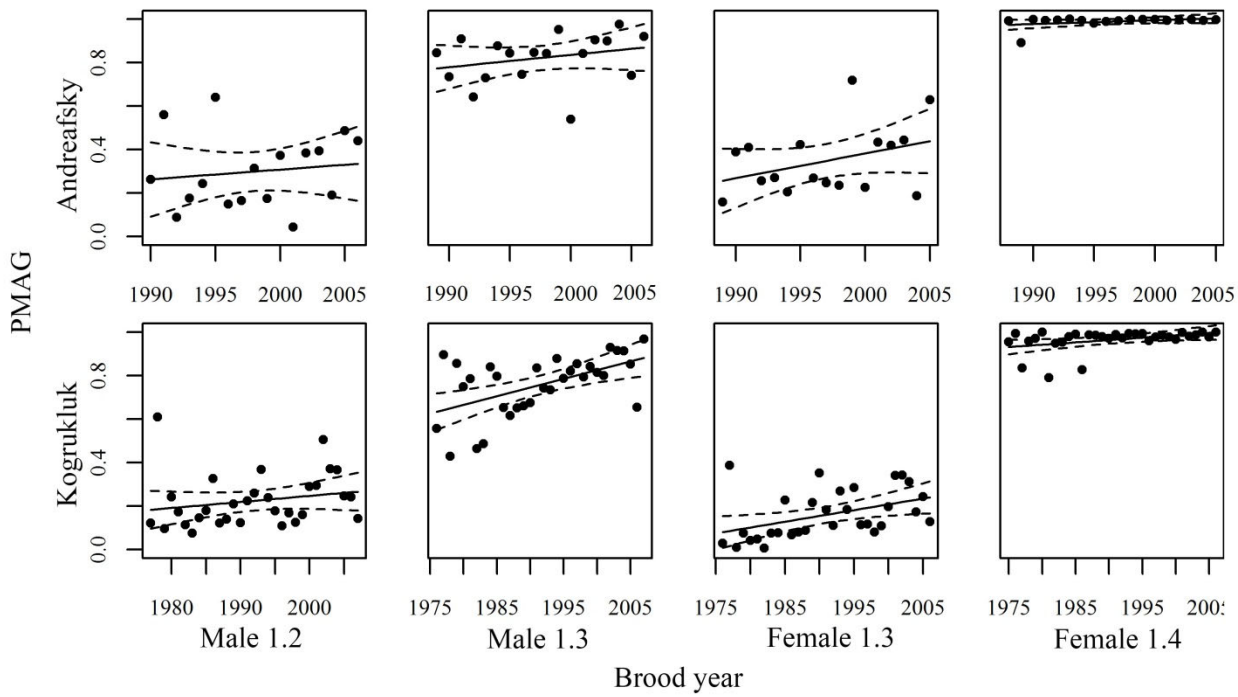

Figure 1.5. Predicted probabilities of maturation with average growth (PMAG) by brood year for each modeled maturity decision in the Andreafsky River and Kogrukluk River Chinook salmon populations. Linear regression model fits of PMAG over time are also shown with 95% confidence intervals.

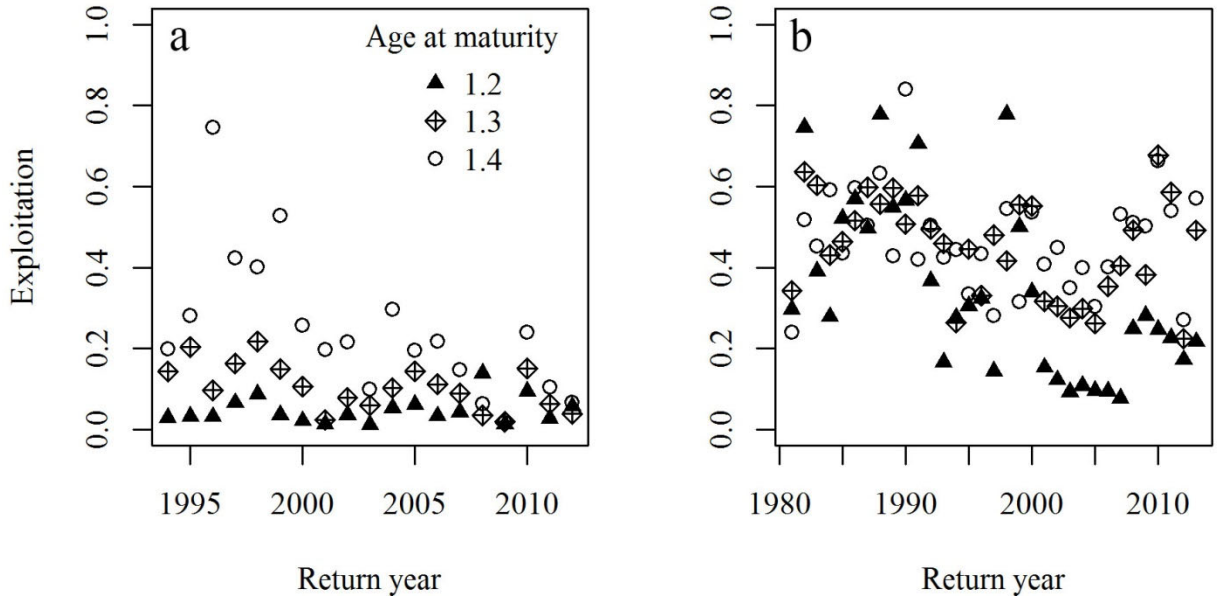

Figure 1.6. Estimated exploitation proportion by return year and age at maturity in the Yukon River and Kuskokwim River terminal fisheries for the Chinook salmon populations of the Andreafsky River (a) and the Kuskokwim River (b). Exploitation in the Kogrukluk River was assumed to be proportional to exploitation in the Kuskokwim River. Kuskokwim estimates calculated from unpublished data provided by the Alaska Department of Fish and Game.

1.11 Supplementary tables and figures in order of text reference

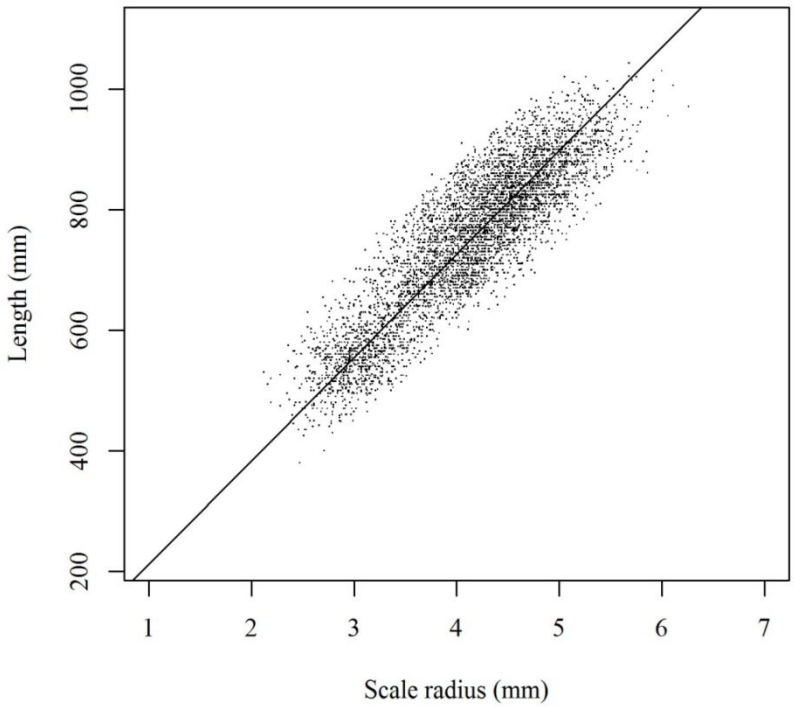

Figure 1.S1. Scatterplot showing the relationship between mid-eye to fork length (mm) and scale radius (mm) from samples taken from the Kogrukluk River escapement weir (1981-2013) and the Andreafsky River escapement weir (1994-2012). Solid line is the ordinary least squares linear fit used in back-calculations with a biologically reasonable intercept set at 40 mm (mid-eye to fork length [mm] = 171.6*radius + 40.0).

Table 1.S1. Numbers of measured scales by brood year, sex, and age at maturity for the Andreafsky River Chinook salmon population. F. represents females and M. represents males. Superscript *a* represents a stratum that was present in the population but from which there were no scales in good condition available to measure.

Brood Year	M. 1.2	M. 1.3	M. 1.4	M. Total	F. 1.3	F. 1.4	F. 1.5	F. total	Total
1988	-	-	25	25	-	26	5	31	56
1989	-	25	25	50	22	27	11	60	110
1990	14	19	11	44	3	25	0[a]	28	72
1991	26	25	23	74	19	26	4	49	123
1992	8	18	6	32	8	24	0[a]	32	64
1993	24	25	20	69	24	24	0	48	117
1994	24	20	10	54	13	25	2	40	94
1995	25	25	10	60	20	26	5	51	111
1996	8	8	19	35	2	23	5	30	65
1997	11	25	19	55	23	27	3	53	108
1998	25	24	10	59	21	24	1	46	105
1999	25	25	9	59	22	24	0[a]	46	105
2000	25	25	22	72	21	25	2	48	120
2001	13	25	12	50	24	20	6	50	100
2002	25	23	15	63	8	23	1	32	95
2003	23	25	25	73	18	22	3	43	116
2004	9	24	4	37	7	24	0[a]	31	68
2005	25	25	9	59	23	21	0[a]	44	103
2006	25	25	24	74	16	25	-	41	115
2007	25	24	-	49	20	-	-	20	69
Total	360	435	298	1093	314	461	48	823	1916

Table 1.S2. Numbers of measured scales by brood year, sex and age at maturity for the Kogrukluk River Chinook salmon population. F. represents females and M. represents males. Superscript *a* represents a stratum that was present in the population but from which there were no scales in good condition available to measure.

Brood Year	M. 1.2	M. 1.3	M. 1.4	M. Total	F. 1.3	F. 1.4	F. 1.5	F. total	Total
1975	-	-	25	25	-	25	15	40	65
1976	-	25	13	38	13	24	10	47	85
1977	16	21	25	62	3	23	24	50	112
1978	15	25	25	65	0[a]	21	13	34	99
1979	25	25	23	73	11	27	12	50	123
1980	25	25	25	75	5	23	0	28	103
1981	25	25	23	73	5	24	26	55	128
1982	25	20	21	66	0	24	1	25	91
1983	19	24	24	67	24	24	4	52	119
1984	25	25	8	58	2	24	5	31	89
1985	17	25	25	67	19	25	4	48	115
1986	25	24	20	69	21	25	5	51	120
1987	11	25	9	45	11	23	2	36	81
1988	23	15	12	50	6	22	2	30	80
1989	24	23	25	72	19	23	20	62	134
1990	12	22	20	54	13	22	3	38	92
1991	18	25	23	66	22	23	1	46	112
1992	24	24	8	56	5	19	6	30	86
1993	17	23	25	65	11	24	1	36	101
1994	0[a]	24	5	29	10	23	3	36	65
1995	2	22	22	46	7	21	4	32	78
1996	5	23	23	51	8	23	11	42	93
1997	15	25	14	54	12	23	5	40	94
1998	25	24	24	73	10	20	5	35	108
1999	17	25	25	67	16	22	13	51	118
2000	24	25	17	66	21	25	8	54	120
2001	25	23	14	62	23	17	2	42	104
2002	19	25	4	48	12	21	2	35	83
2003	25	25	7	57	18	24	3	45	102
2004	25	21	12	58	16	24	0	40	98
2005	24	25	11	60	16	17	0[a]	33	93
2006	24	25	7	56	7	15	0	22	78
2007	26	17	3	46	11	13	-	24	70
2008	0[a]	9	-	9	5	-	-	5	14
Total	611	759	567	1937	384	758	223	1365	3302

Table 1.S3. Model weights for the Andreafsky River Chinook salmon population. F. represents females and M. represents males.

Brood Year	M 1.2	M 1.3	M 1.4	F 1.3	F 1.4	F 1.5
1988	-	-	-	-	1.131	0.319
1989	-	1.678	0.322	0.409	1.447	1.086
1990	1.022	0.996	0.979	2.884	0.851	0.033
1991	1.410	1.202	0.317	0.920	1.153	0.386
1992	0.464	0.938	1.901	1.123	1.011	0.376
1993	0.817	1.535	0.551	0.722	1.278	0.000
1994	0.779	1.398	0.734	0.711	1.168	0.782
1995	1.309	0.830	0.652	0.832	1.157	0.857
1996	0.397	2.484	0.629	4.169	0.890	0.241
1997	1.088	1.468	0.333	0.436	1.507	0.765
1998	0.959	1.219	0.577	0.577	1.449	0.049
1999	0.385	1.850	0.347	1.437	0.682	0.019
2000	1.883	0.586	0.467	0.689	1.340	0.019
2001	0.294	1.560	0.598	1.080	1.166	0.125
2002	1.278	1.077	0.418	1.763	0.802	0.230
2003	1.317	1.338	0.370	0.786	1.287	0.177
2004	0.745	1.198	0.387	0.900	1.078	0.415
2005	1.270	0.841	0.692	1.208	0.859	0.089
2006	1.168	1.526	0.278	0.813	1.120	-
2007	0.957	1.044	-	-	-	-
Avg.	0.964	1.306	0.604	1.214	1.125	0.332

Table 1.S4. Model weights for the Kogrukluk River Chinook salmon population. F. represents females and M. represents males.

Brood Year	M. 1.2	M. 1.3	M. 1.4	F. 1.3	F. 1.4	F. 1.5
1975	-	-	-	-	1.451	0.248
1976	-	0.859	1.271	0.163	1.852	0.044
1977	0.630	2.190	0.238	7.744	0.886	0.266
1978	2.682	0.414	0.576	0.293	1.548	0.224
1979	0.289	1.947	0.743	0.269	1.503	0.539
1980	0.871	1.588	0.541	0.430	1.124	0.000
1981	0.639	1.656	0.680	0.580	1.281	0.821
1982	0.395	1.239	1.492	0.161	1.053	1.204
1983	0.383	1.376	1.113	0.317	1.691	0.952
1984	0.524	1.500	0.924	1.568	1.116	0.214
1985	1.077	1.562	0.386	0.885	1.216	0.199
1986	1.459	1.024	0.396	0.485	1.367	1.328
1987	0.660	0.955	1.542	0.263	1.356	0.956
1988	0.444	1.639	1.267	0.478	1.157	0.838
1989	0.705	1.509	0.815	0.638	1.997	0.198
1990	0.855	1.371	0.678	1.240	0.912	0.605
1991	1.027	1.467	0.471	0.342	1.653	0.723
1992	0.667	1.228	1.315	0.670	1.304	0.312
1993	1.866	1.023	0.390	1.044	1.031	0.393
1994	4.448	0.778	0.687	0.602	1.244	0.454
1995	2.246	1.032	0.855	0.648	1.233	0.392
1996	0.773	1.369	0.680	0.392	1.443	0.516
1997	0.486	1.459	0.730	0.364	1.472	0.354
1998	0.546	1.904	0.568	0.308	1.537	0.237
1999	0.662	1.722	0.507	0.308	1.811	0.480
2000	1.247	1.142	0.443	0.910	1.295	0.315
2001	0.870	1.165	0.960	0.541	1.709	0.255
2002	1.327	0.793	0.741	0.967	1.023	0.952
2003	0.861	1.215	0.728	0.765	1.238	0.510
2004	0.856	1.504	0.419	0.672	1.219	0.000
2005	0.886	1.293	0.581	0.698	1.313	0.752
2006	0.836	1.015	1.509	0.717	1.132	0.000
2007	0.542	1.835	0.238	1.180	0.847	-
2008	4.613	0.197	-	-	-	-
Avg.	1.137	1.302	0.765	0.833	1.330	0.485

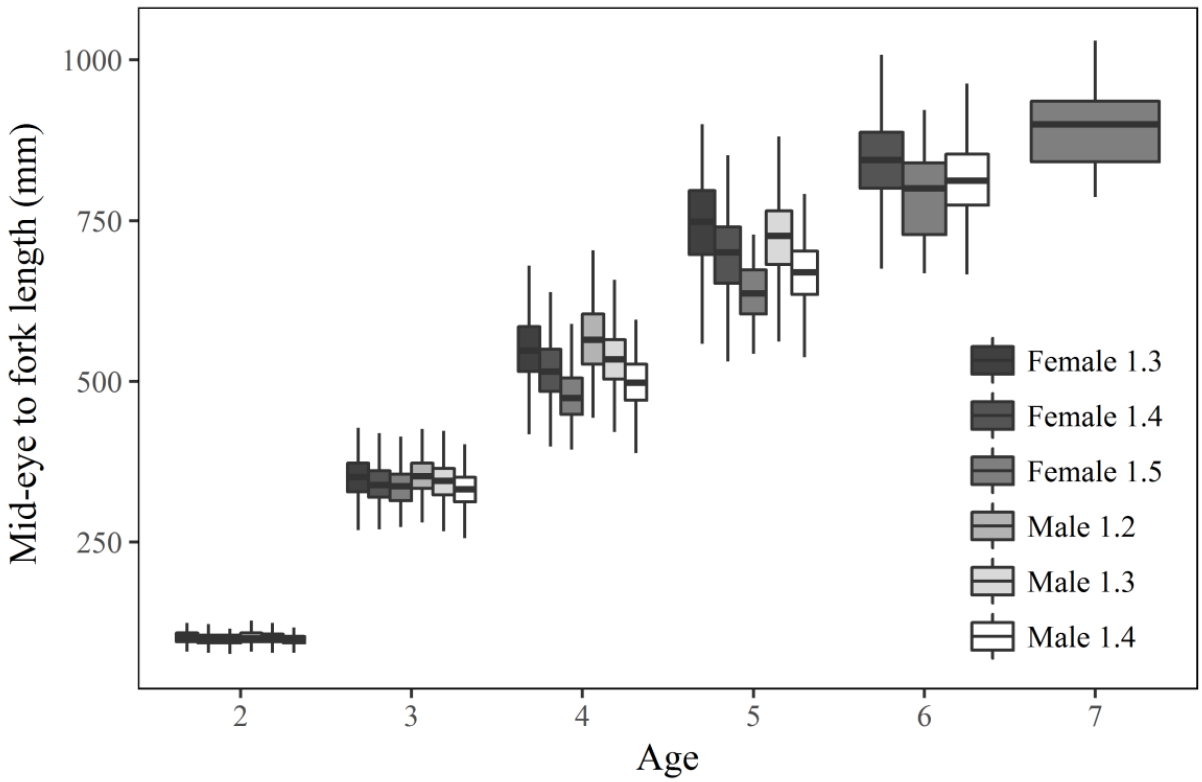

Figure 1.S2. Boxplots of back-calculated mean size-at-age (mid-eye to fork lengths) for all scale samples from the Andreafsky River (return years 1994-2012). Samples are shown separated by sex and age at maturity. Relationship between scale radius and fork length was estimated using ordinary least squares linear regression with a fixed intercept (mid-eye to fork length [mm] = 171.6*radius + 40.0).

Table 1.S5. AIC selection table for each modeled Andreafsky River Chinook salmon maturity decision. While every combination of variables was considered in model selection, only models within 10 AIC of selected models and null model are shown.

Decision	Model	AIC	ΔAIC
Male 1.2	SW1 + SW2 + BY	1015.0	0.0
	FW1 + SW1 + SW2 + BY	1017.0	2.0
	null	1273.5	258.5
Male 1.3	FW1 + SW1 + SW2 + SW3 + BY	581.0	0.0
	SW1 + SW2 + SW3 + BY	581.0	0.0
	FW1 + SW2 + SW3 + BY	588.7	7.7
	SW2 + SW3 + BY	589.6	8.6
	null	696.5	115.5
Female 1.3	SW1 + SW2 + SW3 + BY	806.4	0.0
	FW1 + SW1 + SW2 + SW3 + BY	808.0	1.6
	SW2 + SW3 + BY	813.6	7.2
	SW2 + SW3 + BY	813.8	7.4
	FW1 + SW2 + SW3 + BY	814.6	8.2
	FW1 + SW1 + SW2 + BY	815.5	9.1
	null	950.6	144.2
Female 1.4	FW1 + SW2 + SW3 + BY	141.9	0.0
	SW2 + SW3 + BY	142.1	0.2
	FW1 + SW1 + SW2 + SW3 + BY	142.6	0.7
	FW1 + SW2 + SW3 + SW4 + BY	143.2	1.3
	SW2 + SW3 + SW4 + BY	143.4	1.5
	SW1 + SW2 + SW3 + SW4 + BY	143.6	1.7
	FW1 + SW1 + SW2 + SW3 + SW4 + BY	143.9	2.0
	FW1 + SW2 + BY	149.5	7.6
	SW1 + SW2 + BY	149.9	8.0
	SW2 + SW4 + BY	150.7	8.8
	FW1 + SW2 + SW4 + BY	150.8	8.9
	SW1 + SW2 + SW4 + BY	151.1	9.2
	FW1 + SW1 + SW2 + SW4 + BY	151.7	9.8
	null	207.9	66.0

Table 1.S6. AIC selection table for each modeled Kogrukluk River Chinook salmon maturity decision. While every combination of variables was considered in model selection, only models within 10 AIC of selected models and null model are shown

Decision	Model	AIC	ΔAIC
Male 1.2	SW1 + SW2 + BY	1774.6	0.0
	FW1 + SW1 + SW2 + BY	1776.6	2.0
	null	2195.2	420.6
Male 1.3	SW1 + SW2 + SW3 + BY	1307.8	0.0
	FW1 + SW1 + SW2 + SW3 + BY	1308.9	1.1
	SW2 + SW3 + BY	1309.7	1.9
	FW1 + SW2 + SW3 + BY	1310.6	2.8
	null	1532.3	224.5
Female 1.3	SW1 + SW2 + SW3 + BY	920.3	0.0
	FW1 + SW1 + SW2 + SW3 + BY	922.4	2.1
	SW1 + SW2 + BY	925.3	5.0
	FW1 + SW1 + SW2 + BY	928.1	7.8
	SW2 + SW3 + BY	930.1	9.8
	null	1224.1	303.8
Female 1.4	SW2 + SW3 + SW4 + BY	403.1	0.0
	SW1 + SW2 + SW3 + SW4 + BY	403.2	0.1
	SW2 + SW3 + BY	404.0	0.9
	SW1 + SW2 + SW3 + BY	404.1	1.0
	FW1 + SW1 + SW2 + SW3 + SW4 + BY	404.3	1.2
	FW1 + SW2 + SW3 + SW4 + BY	404.3	1.2
	FW1 + SW1 + SW2 + SW3 + BY	405.2	2.1
	FW1 + SW2 + SW3 + BY	405.2	2.1
	null	562.7	159.6

Chapter 2: Marine temperatures control expression of life history traits in western Alaskan Chinook salmon[1]

2.1 Abstract

Chinook salmon from western Alaska have experienced recent declines in abundance, size, and age at maturity. Declines have led to hardships for the region's subsistence and commercial salmon harvesters, prompting calls to better understand factors effecting the life history of these populations. Western Alaskan Chinook salmon are thought to spend their entire marine residency in the Bering Sea. The Bering Sea ecosystem demonstrates high interannual variability, largely driven by the annual extent of sea ice. However, warming is expected to supersede interannual variability in the next couple of decades as a consequence of climate change. In this study we investigated the influence of sea surface temperatures on the life history of western Alaskan Chinook salmon using information from two regional populations subject to long-term monitoring. We found evidence that early marine growth is strongly regulated by sea surface temperatures. Warmer sea surface temperatures appear to lead to a younger age at maturity, largely through the vector of augmented growth. However, warmer sea surface temperatures were found to additionally decrease the average age of male recruits through reduced growth thresholds for early male maturation. Our results suggest that the anticipated warming of the Bering Sea will lead to higher early marine growth and a younger average age of maturation of western Alaskan Chinook salmon.

[1]Jared E. Siegel, Milo D Adkison, Megan V. McPhee. 2017. Prepared for submission to the Transaction of the American Fisheries Society.

2.2 Introduction

Chinook salmon *Oncorhynchus tshawytscha* populations in western Alaska have declined in abundance since the late 1990s. At the same time, decreases in the size and age of fish have also been observed (Lewis et al. 2015), causing concern that diminishing escapement quality might be contributing to low returns. Low returns have led to restrictions on commercial and subsistence harvests as managers aim to meet escapement goals. The Chinook salmon subsistence fisheries in the Yukon-Kuskokwim delta region are the largest in Alaska (Fall et al. 2012), and commercial fisheries provide a unique source of income in regional rural communities (Howe and Martin 2009). Thus restrictions have led to substantial hardships for the region's rural residents, culminating in recent disaster declarations (Alaska Department of Fish and Game 2013). There is accordingly considerable interest in better understanding the factors controlling the life history of western Alaskan Chinook salmon.

A changing marine environment has been proposed as a possible source of population declines (Schindler et al. 2013). The physical environment (e.g., sea surface temperature and salinity) can directly influence rates of salmon physiological processes involved in survival, growth, and maturation. Additionally, the marine environment can have a profound impact on the food web that supports salmon (Aydin and Mueter 2007, Eisner et al. 2014, Hertz et al. 2016). Western Alaskan Chinook salmon are thought to spend their entire marine residency in the Bering Sea (Myers et al. 2010). Climate patterns over the last century in the Bering Sea have demonstrated interannual and decadal scale variability, characterized by warm and cold periods. These periods represent substantial shifts in air temperatures, sea surface temperatures, and sea ice extent (Stabeno et al. 2012). The Bering Sea climate has been shown to have a profound impact on the survival and recruitment of zooplankton taxa (Eisner et al. 2014) with demonstrated cascading effects on higher taxa. Climate has been shown to affect Chinook salmon (Farley et al. 2009, Myers et al. 2010), Chinook salmon competitors such as Walleye Pollock *Gadus chalcogrammus* (Hunt et al. 2011) and juvenile Pink Salmon *O. gorbuscha* and Chum Salmon *O. keta* (Wechter et al. 2016), and Chinook salmon prey species such as capelin *Mallotus villosus* and Pacific herring *Clupea pallasii* (Andrews III et al. 2016). Accordingly, investigating how Chinook salmon have responded to this climate variability in the past may help illuminate the causes of recent population declines.

Understanding how western Alaskan Chinook salmon have responded to ecosystem variability in the past may also provide insights to how they will respond to future climate change. Major reductions in sea ice and increases in sea surface temperature (SST) are predicted in the Bering Sea during the 21st century by climate model projections (Wang et al. 2012). While considerable natural climatic variability in the Bering Sea makes distinguishing the effect of climate change difficult on a short timescale,

warming of the ocean surface is expected to supersede natural variability by mid-century (Wang et al. 2010). Consequently, Chinook salmon in the Bering Sea will experience an altered ecosystem with unprecedented conditions in coming decades.

There is accumulating evidence that Chinook salmon growth in the Bering Sea has been limited by temperature (Farley et al. 2009, Myers et al. 2010, McPhee et al. 2016). The Bering Sea represents the northern extent of the species' range and thus temperatures tend to be cooler than those in other important marine rearing areas, such as the Gulf of Alaska. Myers et al. (2010) found that first year marine growth of rearing Chinook salmon in the Bering Sea was positively correlated with warm El Niño events and that second year marine growth was positively correlated with the Pacific Decadal Oscillation (PDO) and direct measures of SSTs in the eastern Bering Sea. In ectotherms such as salmon, warmer temperatures increase both maintenance metabolic demands and growth potential. If prey is readily available to meet augmented energetic demands, warmer temperatures below detrimental levels will lead to higher growth. Conversely, if prey is limited, energetic demand may outweigh energy intake, and growth will diminish at higher temperatures (e.g., Daly and Brodeur 2015). The previously documented positive relationship between temperature and growth suggest that Chinook salmon in the Bering Sea have not been limited by the quantity and quality of available prey during warmer periods, and are thus have been able to capitalize on higher growth potentials as a consequence of warmer temperatures.

Growth-dependent survival during the first year at sea is thought to be a common driver of productivity in salmon populations (Beamish and Mahnken 2001). Larger fish are better able to avoid predators as a result of faster swimming speeds and outsizing of predator's mouth gape. Previous work in the Yukon River detected size-selective mortality in first summer of marine growth by comparing the distribution of marine caught juveniles to back-calculated juvenile lengths from surviving adults in the Canadian-origin population (Murphy et al. 2013). Thus warmer marine temperatures may lead to increased survival of western Alaskan Chinook salmon as a consequence of a decrease in size selective mortality with augmented growth (Farley et al. 2009).

The analysis of factors affecting the life history of western Alaskan Chinook salmon is limited by the lack of accurate stock information. Long running escapement monitoring weirs on tributary populations provide an opportunity to analyze population dynamics at a finer resolution than is possible for the combined Yukon and Kuskokwim river populations. Sampling at weirs is designed to produce unbiased estimates of the age and size distributions of the escapement (Williams and Shelden 2011, Mears 2013). Covariation of life history traits between monitored populations may be representative of the larger region. Thus the congruent analysis two or more populations may be a useful tool to demonstrate region wide trends and determinants of life history variability.

In this study we explore the interplay between the marine environment (as described by SST), population productivity (recruits/spawner), and sex-specific measures of growth, average age at maturation, and maturation reaction norms (as provided in Chapter 1) in two western Alaskan Chinook salmon populations subject to long-term monitoring: the East Fork of the Andreafsky River and the Kogrukluk River (tributaries of the Yukon River and Kuskokwim River respectively). Coastal populations of western Alaskan Chinook salmon, including the study populations, are genetically distinct from mid and Canadian stock-groups in the Yukon River (Templin et al. 2011). Thus the results of our investigation may best represent these coastal stocks of western Alaska. We previously completed run reconstructions estimating total returns in the study populations by combining escapement data from weirs with harvest data from the Alaska Department of Fish and Game (Appendix). In Chapter 1 we found that thresholds for maturation had decreased over time in these populations using a new measure of maturation reaction norms that accounts for growth history, the "probability of maturation with average growth" (PMAG). This result suggests that documented declines in the age at maturation in the populations may represent an adaptive response. However, it was noted that environmental factors, including temperature, could affect the probability of maturation beyond the effects of growth, and should therefore be accounted for before strong inferences can be made regarding the cause of changing age at maturity.

Here, we use correlation matrices and extended Ricker stock-recruit analysis to inform a conceptual model describing the effects of ocean temperatures on the above-described life history characteristics of the study populations. Specifically, we address the following predictions: (1) warmer temperatures will correlate with higher growth in our study populations, (2) warmer temperatures during the early marine period will lead to higher productivity through the vector of increased growth decreasing size selective mortality, and (3) as a consequence of faster growing individuals maturing earlier (McPhee et al. 2016;), warmer temperatures will lead to earlier maturation. Additionally, we test if maturation thresholds (PMAG) are independent of temperature, which may have an autonomous effect on maturation (Tobin and Wright 2011).

2.3 Methods

2.3.1 Study area

We analyzed populations from the East Fork of the Andreafsky River (hereafter referred to as the Andreafsky River) and the Kogrukluk River, tributaries of the lower Yukon and Kuskokwim basins respectively (Figure 2.1; see also McPhee et al. 2016). Both populations have been subject to long-term

monitoring with escapement weirs, starting in 1994 for the Andreafsky River and 1981 on the Kogrukluk River. Weir operations are designed to produce escapement estimates and to monitor escapement characteristics, including age, sex, and length distributions. Weir methods are described in more detail by Mears (2013) for the Andreafsky River and Williams and Shelden (2011) for the Kogrukluk River.

2.3.2 SST variable selection

We used the average April-December SST in the central Bering Sea (60.0 N – 54.3 N, 178.1 E – 170.6 W) to characterize annual Bering Sea surface temperature (Figure 2.2). Monthly averaged SST data from the National Oceanic and Atmospheric Administration's Earth System Research Laboratory Physical Science Division's reanalysis datasets (Kalnay et al. 1996) were downloaded on 10/21/2016 for the years 1975-2015 (https://www.esrl.noaa.gov/psd/cgi-bin/data/timeseries/timeseries1.pl). The mean of monthly averaged temperatures from April-December was taken to create a single annual metric for SST. SST during the first year of marine residency was notated as SST1, the second year of marine residency as SST2, and so on.

Our choice of the geographical extent of our SST polygon was supported by the existing information on migration patterns of western Alaskan Chinook salmon. While data on the marine residency of western Alaskan Chinook salmon are limited, Myers et al. (2010) developed a conceptual model of migration patterns by analyzing the existing scientific samples combined with opportunistic bycatch samples from the Bering Sea/Aleutian Island pollock fishery. They suggested that most western Alaskan Chinook salmon spend their entire marine residency in the Bering Sea. Following their outmigration, juveniles are believed to spend their first marine summer and fall in the waters of the eastern Bering Sea shelf (Murphy et al. 2009). During the first and subsequent winters, fish occupy areas along the shelf break beyond the edge of the sea ice extent. In the summer they appear to be primarily distributed in productive surface layers (epipelagic habitat) over the deep Aleutian Basin in the central and western Bering Sea. Our choice of location is centrally located along the Bering Sea shelf break and includes shelf habitat and open ocean. Tag recoveries and bycatch samples suggest that the chosen area is frequently occupied by Chinook salmon (Myers et al. 2010). Additionally, preliminary analyses (results not shown) found that temperatures in the central Bering Sea correlate fairly well ($r > 0.5$) with temperatures in other areas fish may inhabit in the eastern (52.4 N. – 65.7 N., 174.4 W. – 159.4 W.) and western (54.9 N. – 61.3 N., 163.1 E. – 176.3 E.) Bering Sea.

In addition to considerations based on current understanding of the marine distribution of Chinook salmon in the Bering Sea, we chose to focus on the central Bering Sea because it is less influenced by sea ice than the eastern and western Bering Sea. When sea ice is present, SST

measurements represent the surface of the ice, which is more influenced by atmospheric temperatures than ocean temperatures. Consequently, SST monthly averages from periods of time influenced by sea ice can be well below 0 C°, and are thus not representative of the temperatures that Chinook salmon would be experiencing. While sea ice is less influential in our chosen polygon in comparison to other areas, it commonly encroaches into the northeast region of our SST polygon during mid-winter, creating negative temperature readings. Accordingly, we removed January-March from our annual metric leaving us with the mean April-December SST (Figure 2.2a). Chinook salmon growth in the Bering Sea is seasonally controlled by ecosystem productivity and temperature, and thus generally limited in winter months in the Bering Sea when temperatures approach freezing. Accordingly, the exclusion of these months is likely to have a limited effect on our ability to relate annual growth to our annual SST metric.

2.3.3 Life history metrics

Growth

Retrospective scale analysis allows one to estimate age and growth for each year of a fish's life. Annual growth increments of individual recruits were estimated using retrospective scale analysis from samples collected at the Andreafsky River (return years 1994-2012) and the Kogrukluk River (return years 1981-2013) weirs, following methods detailed in McPhee et al. (2016). We use the European notation for age classes (Koo 1962), where the first number is the number of years spent in freshwater and the second number after the decimal is the number of years spent in saltwater. The Andreafsky River and the Kogrukluk River Chinook salmon populations are primarily composed of females maturing at ages 1.3, 1.4, and 1.5 and males maturing at ages 1.2, 1.3, and 1.4 (Appendix). We only analyzed scales from these age/sex combinations, which represented > 97% of each population on average. Annual growth zone measurements were defined using the notation presented by Ruggerone et al. (2007), where *FW1* is first year freshwater growth, *SW1* is first year marine growth, *SW2* is second year marine, and so on.

To produce a single estimate of mean cohort growth for each annual growth increment, the mean growth of each age/sex combination was weighted by its proportional representation in the returns (escapement plus harvest). Returns by age/sex combination were previously estimated in run reconstructions (Appendix). Estimates of growth for the total population, as well as those for males and females separately, were analyzed.

Average recruit maturation age

The average age of recruits by brood year was previously calculated by summing the multiples of each age at maturity and its proportional representation in the return (Appendix). Estimates of the

number of recruits include estimates of the escapement (fish that survive to make it past monitoring weirs) plus estimates of fish harvested in the terminal fisheries of both populations.

Reaction norms for age at maturity

For a measure of maturation reaction norms, we used the "probability of maturation with average growth", or PMAG, which was estimated for these populations in Chapter 1. PMAG was proposed as an improvement to the midpoint of the probabilistic maturation reaction norm method because it accounts for growth history. To estimate PMAG, in Chapter 1 we used logistic models informed by annual growth estimates from retrospective scale analysis. In the prediction of PMAG, growth at each annual stage was held constant at the population-level mean growth value in selected models, and thus PMAG allows for the estimation of how the probability of fish with equal growth maturing changes over time using an estimated fixed effect for each brood year. PMAG for two maturation decision points for each sex were estimated for every cohort in both populations, the male 1.2 and 1.3 maturity decisions and the female 1.3 and 1.4 maturity decisions.

2.3.4 Statistical analysis

Life history dynamics

We used Pearson's product-moment correlation matrices to examine the relationship between SSTs and the above-described life history metrics. The relationships among life-history metrics were also compared using correlation matrices. Because we previously found that males and females differed in their relationship between growth and age at maturity (Chapter 1), we investigated male and female specific life history metrics in addition to measures of the total population. This and all subsequent analyses were performed using the statistical program R Version 3.1.2 (R Core Team 2014).

Productivity modeling

We used Ricker stock-recruit model (Ricker 1954) residuals to investigate the relationship between life history metrics and population productivity, defined as the number of returning adult recruits per spawner. We defined the number of spawners as the number of fish in the escapement as measured by the escapement weirs. Recruits mature and return across a range of return years at different ages. Our estimate of recruitment was the sum of estimated escapement and the estimated number of fish harvested in the terminal fisheries (fisheries that catch mature fish returning to spawn within the river system), indexed by brood year. All methods and data used to produce productivity estimates come from run

reconstructions of the Kogrukluk River (brood years 1977-2006) and Andreafsky River (brood years 1990-2005) Chinook salmon populations (Appendix).

We used the linearized version of the extended Ricker stock-recruit model (Quinn II and Deriso 1999) to model the relationship between recruits and spawners:

$$\ln\left(\frac{R_y}{S_y}\right) = \ln(a) - bS_y + cE_y + \varepsilon_y$$

where *R* is the number of recruits from brood year *y*, *S* is the number of spawners that spawned in brood year *y*, *E* is an optional explanatory variable such as growth or temperature, *a* is the productivity parameter, *b* is the inverse capacity parameter, *c* is the magnitude of the effect of the explanatory variable, and ε is the error term. The *a* and *b* parameters were estimated by fitting the basic Ricker model (excluding *E*) to the stock/recruit data from the run reconstructions. Once *a* and *b* had been estimated, the yield producing maximum returns (*Smax, 1/b*), the equilibrium yield (*Seq, ln(a)/b*), the maximum predicted recruits ($Rmax, a/b*e^{-1}$), and the maximum sustainable yield (*Smsy, Seq*(0.5-0.07*ln(a))*) were calculated (Hilborn and Walters 1992).

Following the presentation of the results for the simple linear Ricker model, we extended the model to include additional growth and SST variables. Growth and SST variables were analyzed separately since we expected them to be correlated. We focused our analysis on the first two years of marine residency due to the hypothesized effects of early marine growth on survival and the demonstrated importance of SW2 on the age at maturity of individual fish in Chapter 1. Variables analyzed include SW1, SW2, and the sum of SW1 and SW2 as a single variable (SWsum). Analogous SST models including an effect of SST1, SST2, and the average of SST1 and SST2 as a single variable (SSTavg) were analyzed in separate models. Explanatory variables were standardized to units of standard deviations from the mean to make coefficients comparable. All analyzed models for each system are presented in an AICc model weighting table using the AICcmodavg package (Mazerolle 2016).

2.4 Results

2.4.1 Sea surface temperatures

The mean (± standard deviation) April-December central Bering Sea surface temperature (SST) from the period 1975-2015 was 5.40 C˚ ± 0.54 (Figure 2.2b). The maximum value during this period was 6.75 C˚ in 2014 and the minimum was 4.28 C˚ in 2010. Average SSTs were cool in the years 1975 and

1976 before oscillating around the mean value through the mid-1990s. Average SSTs were cool again in 1998 and 1999 before climbing to a peak in 2001, which was followed by a continual decline for six consecutive years. Relatively cool conditions persisted from 2007-2013 before becoming very warm again in 2014 and 2015.

2.4.2 Life history dynamics

All measures of growth in each sex in both populations and during the first two years of marine residency (SW1 and SW2) significantly increased with SST during the year growth occurred, as summarized by Table 2.1. Relationships were stronger in the Andreafsky River in comparison to the Kogrukluk River. SST was not significantly correlated with any measure of later growth in either population. The positive relationship between SST and SW1 and SW2 growth appears to be largely consistent across the time series of analysis in both populations except during the late 1980s in the Kogrukluk River (Figure 2.3). Additionally, growth estimates from the Andreafsky River and the Kogrukluk River populations were highly correlated, suggesting a shared environmental experience (Table 2.2; see also Chapter 1).

Warmer SST was generally associated with younger recruit age (Table 2.1). The ages of all recruits (r = -0.57, P = 0.021) and male recruits (r = -0.73, P = 0.002 [one outlier removed, discussed below]) were significantly correlated with SST1 in the Andreafsky River (Figure 2.4a). Female recruit age in the Andreafsky River was significantly correlated with SST3 (r = -0.59, P = 0.015). In the Kogrukluk River, the age of all recruits and male recruits (Figure 2.4b) were significantly correlated with SST2 (r = -0.45 and -0.53, P = 0.011 and 0.002, respectively). Female recruit age in the Kogrukluk River was not significantly correlated with SST during any growth year, although correlation coefficients were negative from SST1-SST3.

The relationships between marine growth and male recruit age were similar to those between SSTs and male recruit age, suggesting that much of the effect of SST on recruit age was through increased growth (Table 2.2). As with SST, the total age of all recruits and male recruits declined with increasing growth during SW1 in the Andreafsky River (r = -0.53 and -0.62, P = 0.033 and 0.001, respectively) and SW2 in the Kogrukluk River (r = -0.50 and -0.52, P = 0.005 and 0.004, respectively). SW2 growth was significantly correlated with earlier maturity of females in both the Andreafsky River (r = -0.55, P = 0.029) and the Kogrukluk River (r = -0.41, P = 0.025). In contrast, SW4 growth in the Kogrukluk River was found to be positively correlated with recruit age (r = 0.42, P = 0.020).

Warmer temperatures were associated with lower growth thresholds for early male maturity in both populations (Table 2.1, Figure 2.4). In the Kogrukluk River, PMAG for the male 1.2 maturity

decision was positively correlated with SST2 (r = 0.51, P = 0.003), and PMAG for the female 1.3 maturity decision was positively correlated with SST1 (r = 0.39, P = 0.027). In the Andreafsky River, brood year 2001 appeared as an outlier in the relationship between PMAG for the male 1.2 maturity decision and SST1 (Figure 4c). 2001 was an anomalous year for having the warmest SST1 but also seeing very low numbers of age 1.2 males returning in 2005 (Table A.4). This also led 2001 to be an outlier in the relationship between SST1 and male recruit age in the Andreafsky River as described above. When this outlier was not included, a significant positive correlation between PMAG for the male 1.2 maturity decision and SST1 was detected (r = 0.56, P = 0.027).

Productivity of the Andreafsky River population increased in brood years experiencing warmer SSTs during early marine residency (Table 2.1). Andreafsky River Ricker residuals were positively correlated with SST1 (r = 0.58, P = 0.047) and SST2 (r = 0.67, P = 0.017). Kogrukluk River Ricker residuals were not significantly related to SST during any year of marine growth (Table 2.1). We detected no significant correlations between Ricker residuals and any measure of growth (from FW1 to SW4) in either river, although the correlation coefficients were all positive in the Kogrukluk River (and variable sign in the Andreafsky River; Table 2.2). Ricker residuals tended to be greater in brood years with older recruit age in both populations; however, this relationship was only significant for female recruit age in the Kogrukluk River (Table 2.2).

2.4.3 Productivity modeling

Productivities of the two populations were significantly correlated during the overlapping years of analysis (brood years 1994-2005, r = 0.86, P = 0.0003). Both populations experienced three continuous brood years below replacement level from 1994-1996 and peaks of productivity in 2000 of 4.4 and 10.6 in the Andreafsky River and Kogrukluk River respectively (Figure 5a and b). The Kogrukluk River population experienced another spike in productivity in 1983 of 14.8.

In the Andreafsky River, extended Ricker model analysis supported the hypothesis that warmer SST and higher growth during the first two years of marine residency led to increased survival. A model including an effect of SSTavg was chosen as the best model for the Andreafsky River by AICc criteria (Table 2.4). Additionally, separate models including effects of SST1, SST2, and SWsum had more support than the basic Ricker model. Support for an effect of SSTs on productivity in the Kogrukluk River was minimal. In the Kogrukluk River, no extended models surpassed the basic Ricker model by AICc criteria (Table 2.4). However, separate models including an effect of SW1 growth and an effect of SWsum growth had nearly as much support as the basic Ricker model (ΔAICc = 0.23 and 0.61 respectively).

2.5 Discussion

Our results demonstrate that ocean temperatures exert strong control over the life history of western Alaskan Chinook salmon. We found evidence that (1) warmer ocean temperatures in the central Bering Sea led to higher growth during the first two years of marine residency, (2) warmer ocean temperatures during this period additionally led to higher productivity in the Andreafsky population though no effect was found in the Kogrukluk population, and (3) warmer temperatures led to earlier maturation, not only through the effect of temperature on growth, but also as a consequence of a decrease in early male maturation thresholds. We summarize our results in a conceptual model of the effect of SST on the life history and productivity of western Alaskan Chinook salmon (Figure 6). Growth and productivity were highly correlated between the two study populations during the years of overlapping analysis, suggesting that our results may be representative of Chinook salmon from the western Alaskan region. Although Bering Sea surface temperatures were found to strongly influence age at maturation of western Alaskan Chinook salmon, a lack of a temporal trend during the period of analysis (1977-2013) combined with the temperature independence of most measures of PMAG suggests that SST alone cannot explain documented age declines.

Our finding of greater growth during warmer seas during early marine residency suggest that Chinook salmon have not been limited by the availability of prey in the Bering Sea in their first two years of marine rearing and thus have been able to capitalize on higher growth potentials in warmer years. Chinook salmon prey consumption in the Bering Sea is variable and has been linked to climate conditions. In an analysis of juveniles on the eastern Bering Shelf, Farley et al. (2009) found that prey during the first marine year was dominated by fish and squid during the relatively warm years of 2002-2005, while euphausiids were primary in the relatively cold year of 2006. The cold year of 2006 was associated with distributional changes and generally poorer condition of juvenile Chinook salmon. Larger squid and fish prey in the Bering Sea are more calorically dense than alternative prey items (Davis et al. 1998), potentially stimulating greater growth of Chinook salmon beyond the direct effects of warmer temperatures

The relationship between SSTs and growth was found to break down after SW2. This result suggests that the drivers of growth in the marine environment shift as fish age. Growth of fish from consecutive brood years rearing at the same time in the marine environment was significantly correlated, while growth of fish separated by two or more years of age was not, in both populations (Table 2.5). This may be due to a combination of fish consuming different prey and/or occupying different habitats as they

increase in size and age. For example, younger Chinook salmon on the Bering shelf have been shown to eat more fish in comparison to higher proportions of squid consumed by generally older fish over the shelf break and in the Bering basin (Davis et al. 2003).

However, it also must be noted that our estimates of SW3 and SW4 are not completely independent measures because variable portions of the population mature before the third year of marine residency. While growth rate is largely determined by the environment, there is likely a genetic effect driven by differences in behavior and the allocation of energy (e.g. Berejikian et al. 2011). Thus if a larger number of faster growing fish mature earlier, this could have a negative effect on our estimates of later growth because the faster growing fish are removed from the population. This may explain the positive correlation between SW4 growth and recruit age observed in the Kogrukluk River (Table 2.2). Consequently, we cannot draw strong conclusions about the relationship between marine temperatures and SW3 and SW4 growth from our analysis alone.

We also found evidence that SSTs during the first two years of marine residency decreased growth thresholds for early male maturity in both populations. For the 1.2 male maturity decision, a significant positive correlation was found between PMAG and SST1 in the Andreafsky River and SST2 in the Kogrukluk River (Table 2.1). No other consistent relationship between SST and PMAG was found in both populations for the other maturation decisions. Because PMAG already accounts for growth, this suggests that any additional effects of temperature on maturation (beyond temperature's effect on growth) might be limited largely to the male early-maturity decision. Age 1.2 males are substantially smaller than older males (averaging about 550 mm mid-eye to fork length, compared to about 700 mm and over 800 mm for 1.3s and 1.4s respectively). Their size is similar to "jacks" in more southern populations that only spend one winter at sea (e.g. Vøllestad et al. 2004). As a consequence of their smaller size combined with male biased escapements, many of these smaller males are unlikely to be able to compete with larger males for direct access to females. This suggests that these fish may largely engage in the alternative male reproductive tactic of "sneak" spawning. Accordingly, our results suggest that warmer temperatures can lead to a higher proportion of males pursuing alternative mating tactics in two ways: by lowering growth thresholds for maturation while simultaneously leading to increased growth, and thus a higher proportion of fish surpassing these thresholds.

The observed disproportional effect of temperature on early male maturation may be a physiological consequence of the smaller size of early maturing males. Higher mass specific metabolic rates of smaller fish may lead to a disproportionate effect of temperature on physiological processes affecting maturation. Alternatively, this result could be a consequence of an evolved response to the lower energetic requirements for reproduction in sneak spawners. Each individual fish obtains a limited amount of energy from the environment which must be allocated amongst competing uses. Sneak

spawners generally mimic females or maintain satellite positions before darting in to achieve fertilizations at the moment the female exudes her eggs (Fleming and Gross 1994, Fleming 1996). While sneak spawners generally have larger testes proportional to their body size (Quinn 2005), and may spend more energy on spermatogenesis than older males (Young et al. 2013), their total energetic expenditure of reproduction is likely less than that of females and competing males. Female salmon spend substantially more energy towards the development of gonads in comparison to males (e.g. Hendry et al. 2000). Additionally, females excavate and protect redds once established (Quinn 2005). Larger males expend significant energy competing for access to females and on the development of secondary sexual characteristics, including large kypes in Chinook salmon and dorsal humps in other species (Quinn 2005). Additionally, smaller size may not be maladaptive to sneak spawners to the extent that it is with competing males. Thus maturation at smaller sizes as a consequence of temperature may not lead to a reduction in reproductive success. Consequently, maturation in early maturing males may have evolved to be more influenced by the control of temperature over physiological processes (e.g.Tobin and Wright 2011), while maturation in older males and females is more strongly regulated by growth and energetic status (see Thorpe 1994).

A younger recruit age was found to be related to higher productivity in both populations, though this relationship was only significant for females in the Kogrukluk River (Table 2.2). There are two competing mechanisms in which recruit age could be related to survival to maturation. If size selective mortality was a strong influence in a population, the disproportionate removal of slower growing individuals on a trajectory to mature at older ages could lead to a younger average age of surviving recruits in cohorts with lower survival as a consequence of low growth. In contrast, higher growth will lead individuals to mature at a younger age as a consequence of phenotypic plasticity (see Stearns 1992 for general theory and Chapter 1 for study populations). A younger recruit age could thus be associated with higher survival as a consequence of less size selective mortality with higher growth and less exposure to potential mortality with earlier maturation. The negative relationship observed between productivity and recruit age suggest the latter is the stronger influence on the relationship between recruit age and productivity, though the limited strength of this relationship may be a result of interaction between these two processes.

Extended Ricker model stock-recruit analysis found evidence supporting our hypothesis that warmer early marine SSTs lead to higher productivity in the Andreafsky River (Table 2.3). In the Andreafsky River, the average combined temperature during the first two years of marine residency (SSTavg) explained 53% of the remaining variation in productivity unexplained by spawner density in the basic Ricker model (R^2 increased from 0.81 to 0.91). The positive relationship between productivity and SSTs may be a consequence of higher growth during warmer years leading to reduced size-selective

mortality. Size-selective mortality was found to occur in the Canadian stock-group, which likely are occupying the same rearing areas on the shelf as Andreafsky River fish during the first year of marine rearing (Murphy et al. 2013). Earlier maturation as a consequence of higher growth at warmer temperatures, and thus less exposure to potential marine morality, is likely a contributing factor.

However, while the Andreafsky River and Kogrukluk River populations had similar relationships between marine growth and SSTs, we found no strong evidence for a relationship between SSTs and Kogrukluk River productivity. The inability to relate marine conditions to productivity in the Kogrukluk River may be a consequence of an inadequate resolution of our data. With 82% of the variability explained by the basic Ricker model, we may be limited in our ability to describe the remaining unexplained variance by the precision of our productivity estimates. However, the increased importance of SST for survival in the Andreafsky River in comparison to the Kogrukluk River could also be a consequence of the Yukon River's more northern location. There is some evidence that fish from the Yukon River may get entrained in the ice buildup reducing survival during colder years (Murphy et al. 2013) providing a possible source of additional mortality during colder years beyond reduced growth. Ice begins to build up on the northern shelf in rearing areas during November (Murphy et al. 2013) while the southeastern Bering Sea generally remains ice free for longer. Thus fish in the Kuskokwim River may be less likely to experience ice related mortality.

The effect of higher marine temperatures on productivity in the Kogrukluk River could also be obscured by a dominant driver of productivity during freshwater rearing. There are numerous freshwater processes that can affect egg-smolt mortality, which is generally substantial and can be highly variable. While there is limited published information on the freshwater ecology of western Alaskan Chinook, freshwater processes have been shown to be important in determining productivity in other Yukon River tributary populations (Neuswanger et al. 2015). We did not analyze the effect of the freshwater environment in our investigation because we were unable to find consistent and reliable direct measures of the environmental experience of these populations (e.g. water temperatures and water discharge). This highlights the need to develop quality environmental time series of data describing the freshwater environment in western Alaska in order to be able to better investigate freshwater drivers of productivity and life history traits.

2.6 Conclusion

Our results have substantial implications for the future of Chinook salmon in western Alaska as a consequence of climate change. Major reductions in sea ice and increases in SSTs of around 3 C° compared to 1980-1999 averages are predicted in the Bering Sea by 2050 (Wang et al. 2012).

Consequently, Chinook salmon in the Bering Sea will experience unprecedentedly warm conditions during the coming decades. Our results suggest that western Alaskan Chinook salmon will respond with higher growth and a younger average age at maturity, particularly in males. While these populations have historically represented some of the oldest maturing populations of Chinook salmon, they may become younger with age structures similar to more southern populations.

However, caution must be used when using retrospective correlations to predict future responses in complicated ecosystems. As the Bering Sea enters an unprecedented physical state, the food web that supports Chinook salmon is likely to change significantly as well. Thus past environmental relationships determining the expression of life history traits may break down and new ones may form as the species adapts. For example, the one outlier observed in our relationship between SST and male maturation in the Andreafsky River (brood year 2001) occurred during the warmest temperatures in the times series. Due to this only being one point, we can draw no strong conclusions on whether this is a data inaccuracy, or if it represents a change in ecosystem dynamics at anomalously high temperatures. However, this result demonstrates the need to monitor the relationships described in this study to determine if the drivers of growth, survival, and maturation change as these high temperatures become more common. Additionally, as a consequence of the uncertainty inherent in forecasting biological responses to unprecedented conditions, management should be responsive and adaptable to change (see Schindler et al. 2008).

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Tables 2.8

Tables 2.1. Pearson product-moment correlation coefficient matrix showing the relationship between April-December central average Bering Sea surface temperature (SST) and life history metrics of the Andreafsky River and Kogrukluk River Chinook salmon populations (Significance key: $p < 0.05$ = *, $p < 0.01$ = **, $p < 0.005$ = ***). SSTs were correlated with growth increments occurring accrued during the same year (SST1 with SW1, SST2 with SW2, etc.). Subscript o represents a correlation value where a single outlier was removed.

	Andreafsky				Kogrukluk			
	SST1	SST2	SST3	SST4	SST1	SST2	SST3	SST4
Total growth	0.69***	0.83***	0.35	-0.11	0.50**	0.48**	0.11	-0.20
Male growth	0.68***	0.80***	0.24	0.06	0.51***	0.50**	0.18	-0.12
Female growth	0.65**	0.65**	0.31	-0.14	0.45*	0.41*	-0.07	-0.19
Total age	-0.57*	-0.24	0.03		-0.24	-0.45*	-0.13	
Male age	-0.73***$_o$	-0.09	0.23		-0.16	-0.53***	-0.12	
Female age	-0.24	-0.33	-0.59*	-0.21	-0.22	-0.17	-0.08	0.25
PMAG 1.2 M	0.56*$_o$	-0.34$_o$			0.22	0.51***		
PMAG 1.3 M	0.24	-0.26	-0.25		0.19	-0.10	0.06	
PMAG 1.3 F	0.14	0.01	0.07		0.39*	0.08	0.07	
PMAG 1.4 F	-0.02	0.38	0.02	0.31	0.09	-0.04	-0.10	0.00
Ricker residual	0.58*	0.69*	0.27	0.14	0.11	-0.02	0.15	-0.21

Table 2.2. Pearson product-moment correlation coefficient matrix showing the relationship between life history metrics of the Andreafsky River and Kogrukluk River Chinook salmon populations (Significance key: $p < 0.05$ = *, $p < 0.01$ = **, $p < 0.005$ = ***). Sex-specific recruit ages were correlated with sex-specific growth estimates. River comparison column shows the correlation of analogous growth increments between the two populations.

	Andreafsky				Kogrukluk				
	Recruit age				Recruit age				
	Total	Male	Female	Ricker Resid.	Total	Male	Female	Ricker Resid.	River Comp.
FW1	-0.08	-0.01	0.14	-0.32	-0.10	-0.02	0.02	0.14	0.57*
SW1	-0.53*	-0.62***	-0.15	0.56	-0.25	-0.22	-0.28	0.31	0.70**
SW2	-0.14	-0.23	-0.55*	0.41	-0.50**	-0.52**	-0.41*	0.13	0.84***
SW3	0.33	0.20	-0.10	-0.51	0.18	0.20	0.13	0.12	0.47
SW4	-0.16	-0.07	0.21	-0.15	0.42*	0.33	0.35	0.00	0.78***
Ricker Resid.	-0.39	-0.36	-0.03		-0.26	-0.17	-0.46*		

Table 2.3. Ricker stock-recruit parameters for the Andreafsky River (brood years 1990-2005) and Kogrukluk River (brood years 1977-2006) Chinook salmon populations.

	Andreafsky	Kogrukluk
a	5.669	8.706
b	0.00039	0.00014
Smax	2590	6964
Rmax	5401	22303
Seq	4494	15070
Smsy	1701	5252

Table 2.4. Model weighting tables based on AICc values for Ricker and extended Ricker models including sea surface temperature (SST) and growth variables for the Andreafsky River and Kogrukluk River Chinook salmon populations. All explanatory variables were analyzed as SD anomalies to make coefficients comparable. SSTsum represent total growth and SSTavg represents the average SST during the first two years of marine residency.

River	Formula	R^2	logLik	ΔAICc	Weight
Andreafsky	-0.092 - 0.743 S + 0.327 SSTavg	0.91	-1.16	0.00	0.43
	-0.053 - 0.700 S + 0.253 SST2	0.90	-1.87	1.42	0.21
	-0.011 - 0.669 S + 0.235 SWsum	0.89	-2.50	2.67	0.11
	-0.093 - 0.774 S + 0.229 SST1	0.88	-2.84	3.35	0.08
	-0.009 - 0.726 S	0.81	-5.49	3.94	0.06
	-0.013 - 0.721 S + 0.227 SW1	0.87	-3.24	4.16	0.05
	-0.009 - 0.671 S + 0.162 SW2	0.85	-4.22	6.11	0.02
	-0.086 - 0.733 S + 0.121 SST1 + 0.185 SST2	0.91	-1.09	6.13	0.02
	-0.012 - 0.680 S + 0.197 SW1 + 0.122 SW2	0.89	-2.28	8.51	0.01
	-0.048 - 0.756 S + 0.129 SST1 + 0.212 SST2 - 0.078 SST1:SST2	0.92	-0.63	14.01	0.00
	-0.013 - 0.679 S + 0.200 SW1 + 0.117 SW2 + 0.006 SW1:SW2	0.89	-2.23	17.31	0.00
Kogrukluk	0.648 - 0.837 S	0.82	-12.22	0.00	0.24
	0.651 - 0.849 S + 0.125 SW1	0.84	-10.93	0.24	0.22
	0.649 - 0.810 S + 0.108 SWsum	0.84	-11.12	0.61	0.18
	0.647 - 0.813 S + 0.061 SW2	0.83	-11.97	2.31	0.08
	0.645 - 0.840 S + 0.052 SST1	0.83	-12.06	2.49	0.07
	0.647 - 0.834 S + 0.032 SSTavg	0.82	-12.18	2.74	0.06
	0.648 - 0.841 S - 0.012 SST2	0.82	-12.21	2.80	0.06
	0.650 - 0.823 S + 0.121 SW1 + 0.050 SW2	0.84	-10.75	2.97	0.06
	0.645 - 0.852 S + 0.068 SST1 - 0.040 SST2	0.83	-11.98	5.43	0.02
	0.649 - 0.834 S + 0.130 SW1 + 0.065 SW2 + 0.053 SW1:SW2	0.84	-10.61	6.12	0.01
	0.653 - 0.851 S + 0.073 SST1 - 0.028 SST2 - 0.035 SST1:SST2	0.83	-11.92	8.73	0.00

Table 2.5. Pearson's product-moment correlation values between average annual growth estimates from the same growth year (different aged cohorts growing at the same time) for the Chinook salmon populations of the Andreafsky River (Andy., brood years 1990-2005) and the Kogrukluk River (brood years 1977-2006). Significance key: $p < 0.05$ = *, $p < 0.01$ = **, $p < 0.005$ = ***.

		FW1	SW1	SW2	SW3
Andreafsky	SW1	-0.32			
	SW2	-0.41	0.60*		
	SW3	-0.44	0.45	0.56*	
	SW4	0.05	0.09	0.11	0.62*
Kogrukluk	SW1	0.33			
	SW2	0.09	0.40*		
	SW3	0.12	0.15	0.56***	
	SW4	0.06	-0.26	-0.05	0.48**

2.10 Figures

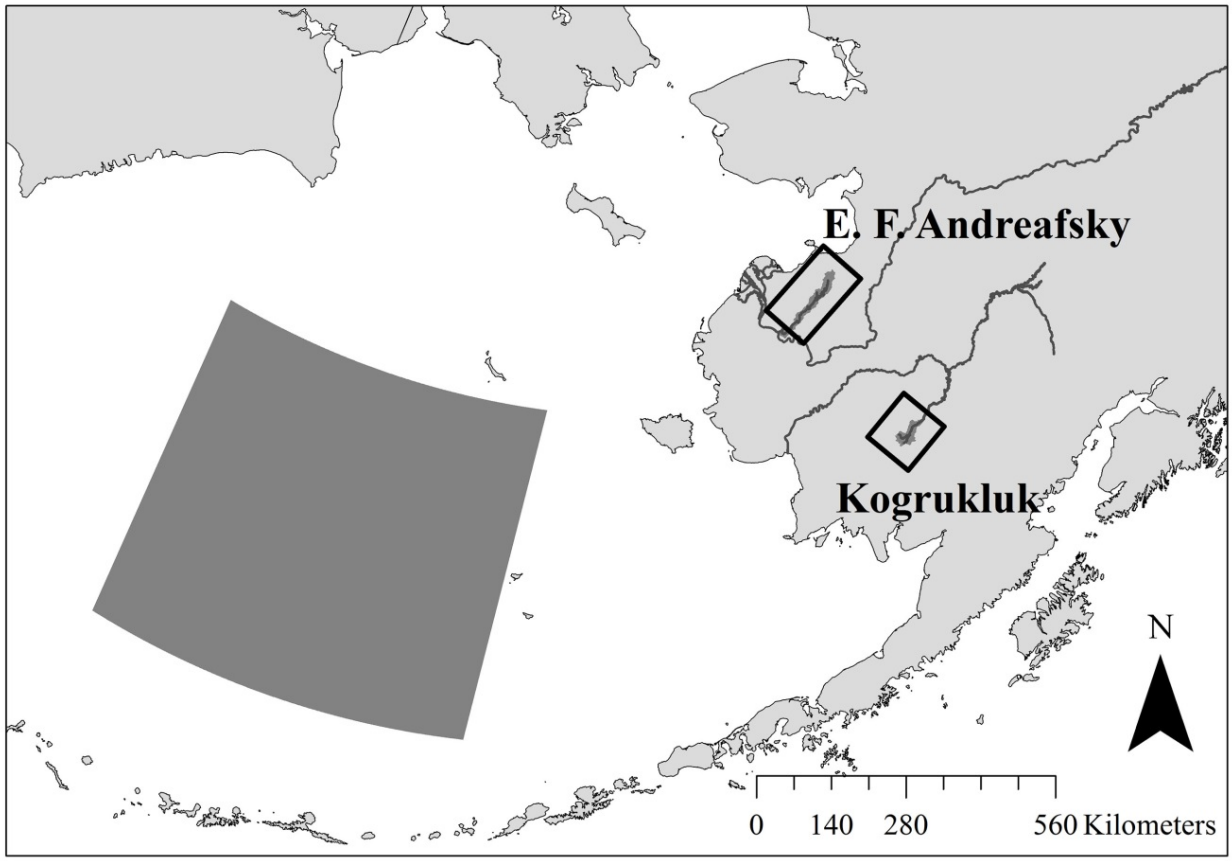

Figure 2.1. Map showing the locations of the study Chinook salmon populations, the East Fork of the Andreafsky River and the Kogrukluk River, and the area in the Bering Sea from which sea surface temperature data was extracted (54.3 N - 60.0 N, 178.1 E – 170.6 W).

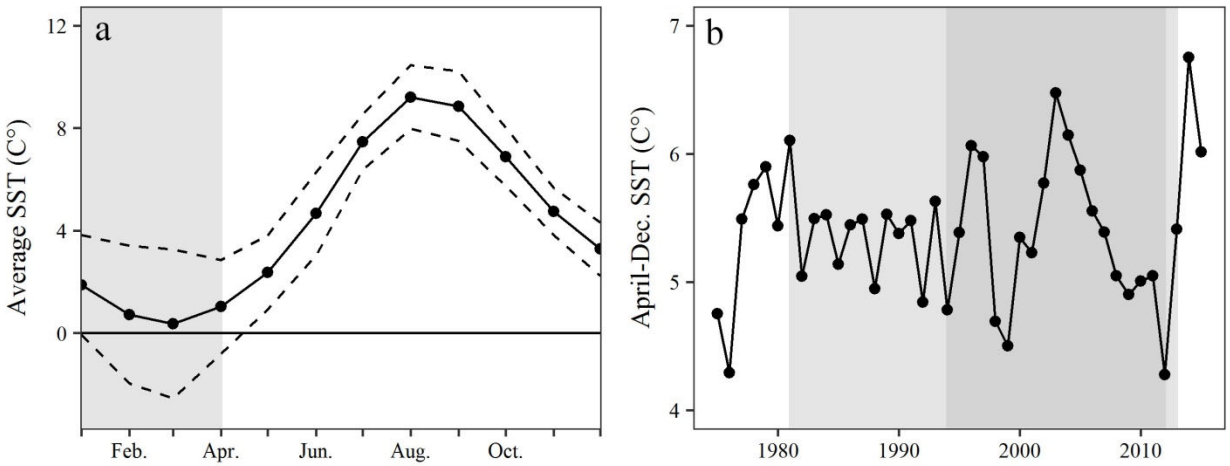

Fig 2.2. Monthly central Bering Sea surface temperature averaged from 1975-2015 (60.0 N - 54.3 N, 178.1 E - 170.6 E) with 2 standard deviation confidence intervals (a). Shaded area (January – March) represents time period effected by sea ice from which data were not used to produce annual temperature metric. Average April-December SST for years 1975-2015 (b). Dark shaded area (1994-2012) represents period of data for the Andreafsky River Chinook salmon returns. Light shaded area (1981-2013) represents period of data for the Kogrukluk River Chinook salmon returns.

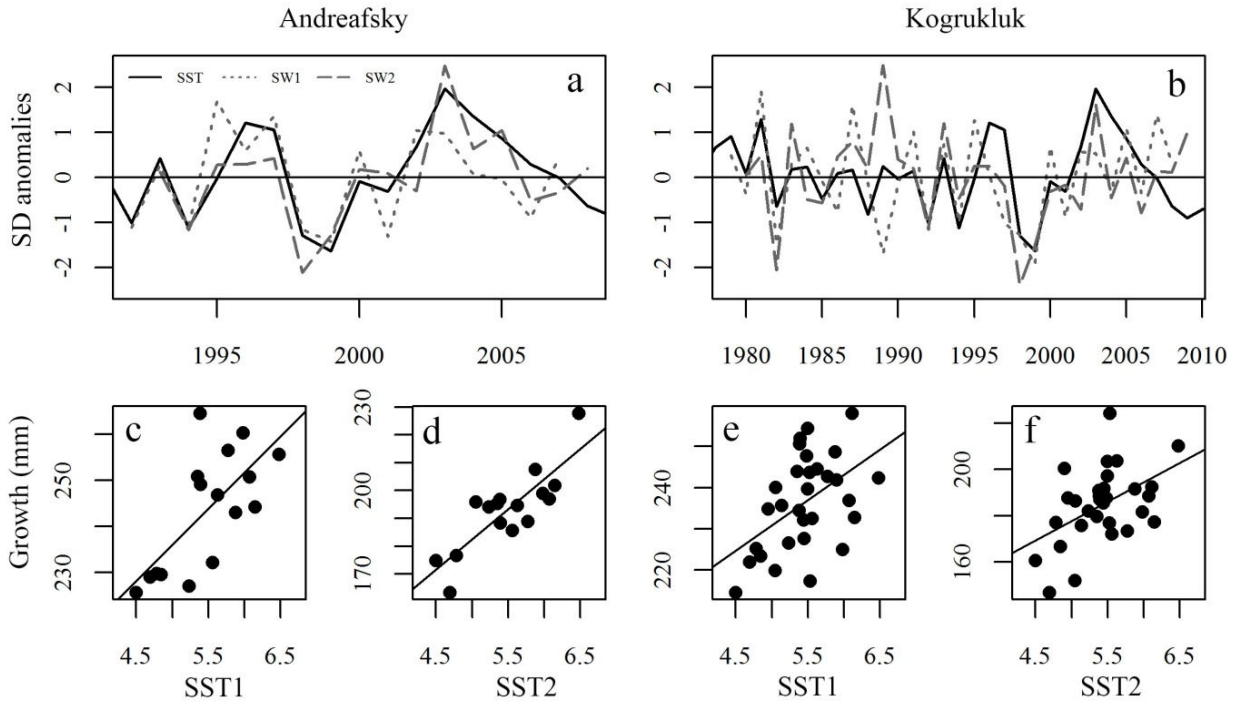

Figure 2.3. Line graphs demonstrating the variability of average April-December central Bering Sea surface temperatures (SSTs) over time and first and second year marine growth (SW1 and SW2) occurring during corresponding years in the Andreafsky River (a) and Kogrukluk River (b) Chinook salmon populations. Scatterplots with linear fit lines between first and second year growth and corresponding SSTs are also shown for the Andreafsky River (c and d) and the Kogrukluk River (e and f).

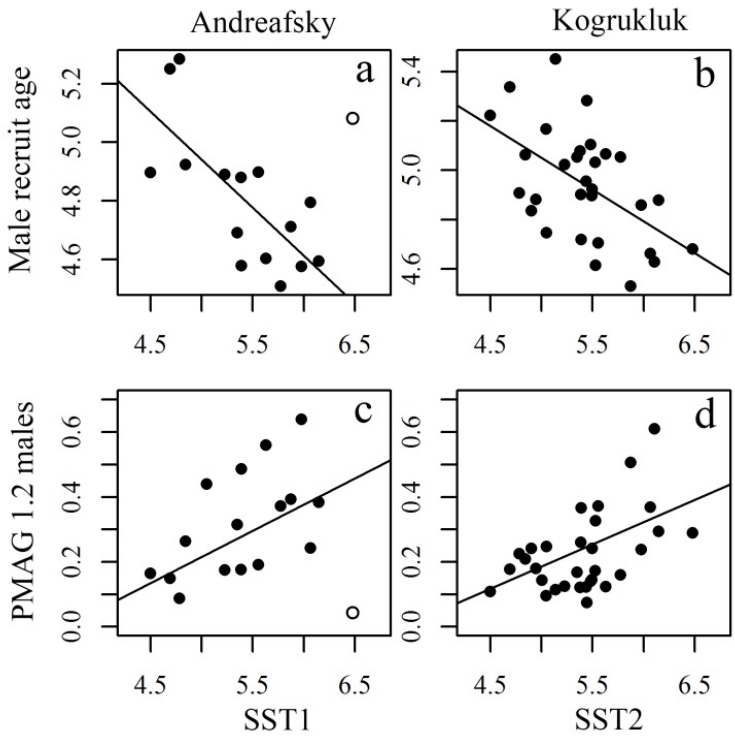

Figure 2.4. Scatter plots with linear fit lines showing the relationship between sea surface temperature and male recruit age as well as PMAG for the 1.2 male maturity decision in the Andreafsky (a and c) and Kogrukluk River (b and d) Chinook salmon populations. Outlier in the Andreafsky River graphs (brood year 2001, open circles) was excluded from presented linear fits.

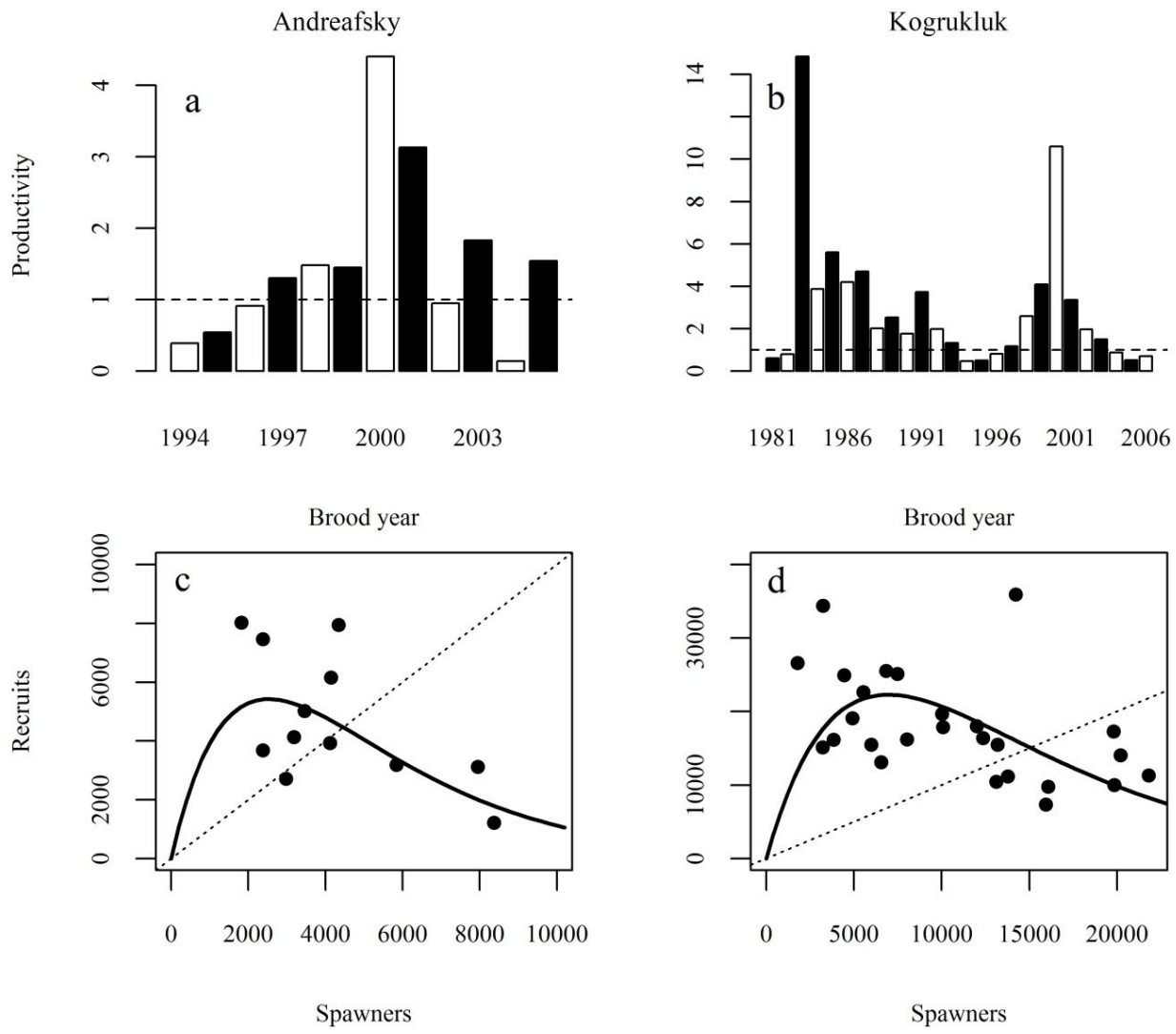

Figure 2.5. Bar plots of productivity by brood year (a and b) and scatterplots of spawners and recruits (c and d) with basic Ricker stock-recruit relationships fit lines (solid lines) in the Andreafsky River and the Kogrukluk River Chinook salmon populations. In bar plots, even years plotted in white and odd years in black. Replacement level is shown by the dotted line in all graphs.

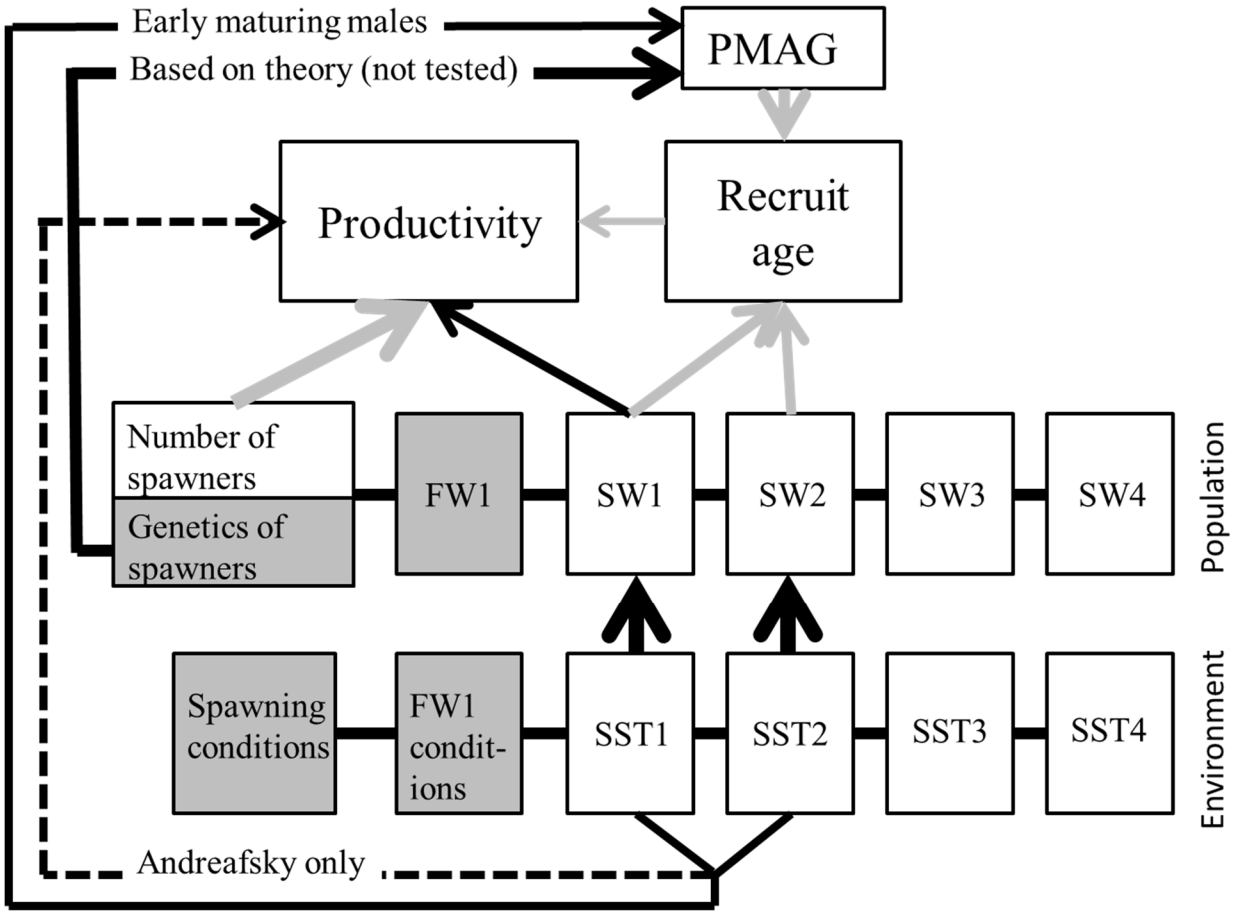

Figure 2.6. Theoretical model of the relationship between central Bering Sea surface temperatures (SSTs), growth, and life history metrics of western Alaskan Chinook salmon. Black arrows demonstrate positive and grey lines represent negative relationships. The thickness of the arrow demonstrates the strength of the relationship. SST1 represents marine temperatures during first year of rearing, SST2 during the second year of rearing, and so on. Dashed arrow connecting early marine SSTs to productivity represents relationship observed only in Andreafsky River.

Conclusion

This study demonstrates that the congruent analysis of population dynamics in multiple tributary populations can be utilized as a tool to investigate region-wide trends. Growth and productivity were shown to be highly correlated between the Andreafsky River and the Kogrukluk River Chinook salmon populations, despite the populations being located in separate river drainages. Additionally, the two populations demonstrated similar patterns of sexual-dimorphism in SW2 growth, and had comparable relationships between growth and age at maturation as established by the analysis of stage-specific probabilistic maturation reaction norms. These results suggest that the two populations are regulated by many of the same regional environmental processes. This approach also provides increased confidence that results are not spurious by confirming the same patterns in multiple datasets. Adding more populations to analyses would strengthen conclusions and help distinguish sub-regional patterns amongst populations.

Results from Chapter 1 indicate sex-specific responses between growth and age at maturation in the western Alaskan Chinook salmon. This is consistent with the view of age at maturity in Chinook salmon as a sexually antagonistic trait, where selection for a trait in one sex can be maladaptive in the other sex. Results suggest that the average age of males will increase to a greater extent than the average age of females during periods of low growth due to plasticity in the expression of age at maturation. Additionally, sex-specific genetic control is expected when sexually antagonistic traits are present (Rice 1984), thus the sexes may also adapt distinctly to changes in selection pressures. Accordingly, when possible the sexes should be considered independently when analyzing the characteristics and causes of declines of western Alaskan Chinook salmon.

There is concern that the terminal Chinook salmon fisheries in western Alaska, which are believed to have disproportionately harvested larger/older fish, may be responsible for declining age as a consequence of fisheries-induced evolution. This study expanded on the probabilistic maturation reaction norms (PMRN) approach in Chapter 1 to determine if declines in age may be a consequence of an adaptive response to a change in selection pressures, as opposed to a plastic response to a change in the environment. Results suggest that declines in the average age of maturation in western Alaskan Chinook salmon have in part been a consequence of adaptive (genetic) change, as demonstrated by an increase in PMAG over time in all maturity decisions analyzed. While estimates showing that the terminal fisheries have harvested older fish disproportionately in these populations are presented, this investigation does attempt to relate selection pressures to declines in age and it is recognized that environmental change could also produce selection pressures on the population. Further research is necessary to determine if selection pressures from the fisheries are consistent with observed trends.

While results suggest that declines in age have been adaptive, observational methods to distinguish between genetic and adaptive change, as with any model, represent a simplification of more complicated relationships. Accordingly, there are unaccounted for environmental effects of the PMRN method that could cause a trend in PMRNs as a consequence of a plastic response. Caveats that have been discussed in the literatures include; growth history, temperature, and fish condition. Due to this study being retrospective, and thus only representative of survivors, it is recognized that a directional change in late marine mortality (increased mortality of fish that delay maturation) could also have caused a trend in the presented measure of maturation reaction norms. This study attempts to address two out of four of these recognized caveats, growth history and temperature. The presented new measure of maturation reaction norms, the "probability of maturation with average growth" (PMAG) accounts for growth history on an annual life history basis by dividing the single considered effect in the traditional PMRN approach, size-at-age, into separate effects of annual growth increments. Additionally, analyses in Chapter 2 found that most maturity decisions, with the exception of the male 1.2 maturity decision (early male maturation), were largely independent of marine temperatures. This result, combined with a lack of a temporal trend during the period of analysis (1977-2013), suggests that SST alone cannot explain documented age declines of western Alaskan Chinook salmon.

The caveats of a directional change in fish condition or late marine mortality remain unaddressed in the study. One possible source of changes in fish condition and/or late marine mortality is the documented increase in Russian pink salmon *O. gorbuscha* abundance during the study period (Ruggerone and Irvine 2015). Russian pink salmon abundance in the Bering Sea has affected growth and maturation of other Pacific salmon species (Ruggerone et al. 2003, Ruggerone and Nielsen 2004, Kaga et al. 2013) and may also have had a detrimental effects on Chinook salmon growth and condition through interspecific competition as a consequence of substantial diet overlap (Davis et al. 2004). Accordingly, the effect of pink salmon and other potential influences on late marine growth and survival of western Alaskan Chinook salmon should be further investigated.

While marine temperatures do not appear to be the primary cause of past declines in age at maturity, analyses in Chapter 2 suggest that they play a major role in the life history of western Alaskan Chinook salmon. Warmer ocean temperatures during the first two years of marine residency were found to have led to higher productivity in the Andreafsky River population, though no effect was found for the Kogrukluk River population. Results suggest that ocean temperatures exert strong control over growth during the first two years of marine residency. Consequently, ocean temperatures indirectly affect the expression of age at maturity as consequence of faster growing individuals maturing earlier. Additionally, ocean temperatures appear to exert direct control of the age at maturation of males as a consequence of lower maturation thresholds for early male maturity at higher temperatures. This suggests

that western Alaskan Chinook salmon may become younger, with age structures similar to more southern populations, as a consequence of predicted warming of the Bering Sea during the 21st century.

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Appendix: Chinook salmon run reconstructions for the East Fork of the Andreafsky River (brood years 1990-2005) and the Kogrukluk River (brood years 1981-2006) in western Alaska

Introduction

Methods are provided for run reconstructions of the Chinook salmon populations in the East Fork Andreafsky River (brood years 1990-2005) and the Kogrukluk River (brood years 1981-2006), tributaries of the Yukon River and Kuskokwim River respectively. These time series include years with unreliable/missing weir data and age/sex sampling. These methods fill in these missing data gaps to create a continuous time series for each population. When analyzed in conjunction, correlation of life history characteristics between the two populations (and possibly others in the future) could demonstrate representation of western Alaskan Chinook salmon, as opposed to being unique to each population. Thus these run reconstructions will provide another tool to complement the combined population run reconstructions to investigate population dynamics of western Alaskan Chinook salmon.

Data sources

The majority of data used for these analyses came from the escapement weir monitoring projects on the East Fork of the Andreafsky River and the Kogrukluk River and were gathered from published reports summarizing results from these projects. The East Fork Andreafsky River weir is run by the US Fish and Wildlife Service (USFWS) and the Kogrukluk River weir is run by ADF&G. Weir operations are designed to produce unbiased escapement estimates, as well as age, sex and length distribution of the escapement estimates. Scales are collected and used to estimate age distributions. Sex is determined visually by weir crews on both rivers through secondary characteristics, including snout prominence in males and roundness of the belly, and the extension of the genital opening in females. For a more detailed description of weir sampling methods, refer to Mears (2015) for the East Fork of the Andreafsky River and Williams and Shelden (2011) for the Kogrukluk River.

Escapement estimates for the East Fork Andreafsky River and the Kogrukluk River, produced in both populations using a Bayesian approach to estimate missed migration, were acquired from ADF&G and USFWS respectively. These estimates are considered the best available for both systems (superior to published estimates) though substantial uncertainty remains during a few years when the weirs were largely not operational as a result of high water (Zach Liller, ADF&G, personal communication; Jeremey Mears, USFWS, personal communication).

Harvest data in the commercial, subsistence and sport fisheries on the Yukon and Kuskokwim rivers was collected and reported by ADF&G. Harvest data was apportioned by age classes in both the Yukon and Kuskokwim Rivers. These data were primarily gathered from published ADF&G documents. Some harvest data was acquired as unpublished data from ADF&G following communication with agency biologists.

Terminology

Brood year: The year that spawning took place to produce a cohort of fish of the same age.

Return year: The year that a mature fish returns to spawn.

Escapement: Fish that make it back to the spawning beds within a return year. In this case, it is defined as those that make it past the escapement monitoring weirs.

Returns: Mature fish in a return year that return to the river to spawn. The term includes those that survive to escapement plus those harvested in the terminal fisheries within a single return year.

Brood recruits: All returns from a single brood year that survive to return to their respective river system. The term includes the escapement plus those fish harvested in the terminal fishery. Brood recruits mature and return at different ages over multiple return years.

East Fork Andreafsky Run Reconstruction

Escapement

Escapement estimates are provided for return years 1994-2012 (Table A.1). For all return years, with the exception of 2001, total escapement estimates were produced from weir data using a stratified sampling method with a Bayesian approach to estimate missed sampling (Jeremey Mears, USFWS, unpublished data). During these years, age and sex sampling was considered sufficient to characterize the run. During 2001, the weir was not running long enough to produce representative data. Thus an escapement estimate from ADF&G aerial survey conversions was used instead (Volk et al. 2009).

Weir age-sex-length (ASL) sampling was used by USFWS to produce estimates of the distribution of the escapement by age at maturity and sex. For all years with the exception of 2001, ASL

sampling was considered sufficient to produce unbiased estimates of age and sex proportions. Accordingly, estimates from a stratified sampling approach published in the annual weir reports were used (USFWS 1995-1999 and 2003-2013). While weir reports for return years 1999 and 2000 were not obtained, the data for these years was acquired directly from the agency (Jeremy Mears, USFWS, unpublished data). The weir was largely non-operational during the run in 2001 and thus the average age and sex proportions from the years with quality weir data (1994-2000, 2002-2012) were used to estimate the age and sex distribution for this year. East Fork of the Andreafsky River escapement numbers by age and sex combinations (Table A.1) were calculated by multiplying estimated age and sex proportions by total escapement estimates.

Harvest and exploitation

To estimate harvest it was assumed that all populations in the lower stock group of the Yukon River were exploited proportionally in the fisheries below the confluence with the Andreafsky River. Harvest estimates by Yukon River stock groups for each fishing district were retrieved from the annual ADF&G "Origin of Chinook salmon in the Yukon fisheries" reports (ADF&G 1996-2015). The harvest data is published apportioned by age class (but not by sex within ages). Accordingly, we estimated annual harvest for each age class separately (Table A.2) using the following equation:

$$Ha_{y,a} = \frac{Ea_y}{(El_y + Hu_y)} * (H1_{y,a} + H2_{y,a} * P_y)$$

where *Ha* is the estimated harvest of the East Fork Andreafsky stock in year *y* for fish of age class *a*, *Ea* is the estimated East Fork Andreafsky escapement, *El* is the estimated escapement of the lower stock group in the Yukon River (Hamazaki in review), *Hu* is the estimated harvest of the lower stock group above the confluence with the Andreafsky River, *H1* is the estimated harvest of the lower stock group in district 1, *H2* is the estimated harvest of the lower stock group in district 2, and *P* is an annual estimate of the proportion of the district 2 harvest taken below the confluence with the Andreafsky River (Larry Dubois, ADF&G, unpublished data). Lower stock group harvest upstream of the confluence with the Andreafsky River (*Hu*) is estimated for each return year by subtracting the estimated lower stock group harvest below the confluence from the estimated total lower stock group harvest using the equation:

$$Hu_y = Hl_y - (H1_y + H2_y * P_y)$$

where *Hl* is the total estimated harvest for the total lower river stock group. Exploitation rate by age class (Table A.3) was calculated by dividing age-specific harvest estimates by the estimates of age-specific returns, the sum of age-specific harvest and escapement estimates.

Returns

Annual East Fork Andreafsky returns by age class and sex (Table A.4) were estimated as the sum of annual harvest estimates and annual escapement estimates. Each sex was assumed to be harvested at the same rate within an age class. Thus harvest estimates by each age class were apportioned to each sex proportional to the estimated escapement. Brood year was calculated by subtracting the age at maturity from the return year. The data were reorganized and presented by brood year returns (Table A.5).

Average age and productivity

Average age of the escapement by return year and average age of recruits by brood year (Table A.6) were estimated using the following equation:

$$\frac{\sum n_a * a}{N}$$

where *n* is the number of fish of age *a*, and N is the total number of fish of all ages. Productivity (Table A.6) was calculated as the number of returns from a brood year cohort divided by the escapement during the corresponding brood year. Productivity was found to be peak in year 2000 while being below replacement levels during brood years in the mid-1990s, 2002, and 2004 (Figure A.1).

Changes in the average age of brood recruits and of the escapement over time were analyzed using ordinary least squares linear regression for the total population, males, and females separately (Figure A.2). While none of the Andreafsky River brood recruit models were significant ($p < 0.05$), all demonstrated trends towards a younger age of maturity. Average age of all brood recruits was estimated to have declined from 5.17 to 5.06 from brood years 1990-2005 ($F = 0.7036$, $df_1 = 1$, $df_2 = 14$, $P = 0.42$). Average age of male brood recruits was estimated to have declined from 4.92 to 4.72 ($F = 1.257$, $df_1 = 1$, $df_2 = 14$, $P = 0.28$). Average age of female brood recruits was estimated to have declined from 5.61 to 5.51 ($F = 0.521$, $df_1 = 1$, $df_2 = 14$, $P = 0.48$).

Changes in the average age of the escapement were minimal and not significant. Smaller changes in the average age of the escapement in comparison to returns is a consequence of a decline in age-selective harvests during the time period of analysis allowing a higher portion of older fish to survive to escapement (Table A.3). Average age of the total escapement was estimated to have decreased from 5.08 to 5.00 from return year 1994-2012 ($F = 0.4503$, $df_1 = 1$, $df_2 = 17$, $P = 0.51$). Average age of the male escapement was estimated to have decreased from 4.84 to 4.71 ($F = 0.6357$, $df_1 = 1$, $df_2 = 17$, $P = 0.44$). Average age of the female escapement was estimated to have stayed relatively constant, moving from 5.53 to 5.54 during the time series ($F = 0.0003$, $df_1 = 1$, $df_2 = 17$, $P = 0.99$).

Kogrukluk River Run Reconstruction

Escapement

Escapement data for return years 1981-2013 were taken from ADF&G estimates from the Kogrukluk River weir data produced using a stratified Bayesian approach to fill in for missed sampling when the weir was not operational (Zach Liller, ADF&G, unpublished data). In the majority of the years, less than 20% of the escapement was estimated allowing for relatively precise estimates. In a few years (1982, 1987, 1989, 2007, and 2012) more than 50% of the escapement was estimated and thus escapement estimates for these years have a high degree of uncertainty.

For all years in the time series, with the exception of 2012, age and sex proportions of the escapement were estimated from weir ASL sampling (Molyneaux et al. 2009, Williams and Shelden 2010, 2011, Brodersen et al. 2013, Hansen and Blain 2013, Liller et al. 2015). For the majority of years, samples were considered sufficient to produce unbiased estimates for the entire escapement using a stratified sampling approach. For seven return years (1987, 1989, 1992, 1993, 1994, 1998, and 2013) age and sex sampling was limited and thus estimates may be inaccurate but were used due to a lack of a superior alternative. No stratified estimate was produced for 2013 and thus proportions utilized were straight sample proportions. Samples for 2012 were considered too inaccurate to use for age and sex proportions due to collection being limited to the very beginning and end of the run. Average age proportions estimated for the entire Kuskokwim River escapement were used for the 2012 Kogrukluk age distribution estimates (Zach Liller, ADF&G, unpublished data). These data did not have age classes separated out by sex. Thus for 2012, escapement for each age at maturity was distributed by sex using the average proportion of each sex by age at maturity in the escapement calculated from years with quality age/sex distribution data (1981-1986, 1988, 1990-1991, 1995-1997, and 1999-2011). For all other years,

Kogrukluk River escapement numbers by age and sex (Table A.7) were calculated by multiplying estimated age and sex proportions by the total escapement estimates.

Exploitation by age class

Harvest in the Kogrukluk was assumed to be proportional to harvest in the entire Kuskokwim River. Exploitation by age class in the Kuskokwim River returns (Table A.8) was estimated by dividing estimates of harvest for each age class in the Kuskokwim River terminal fisheries by estimates of the total return (Zach Liller, ADF&G, unpublished data). Harvest estimates by age class and sex (Table A.9) were calculated using the following equation:

$$H_{y,a} = X_{y,a} * \frac{E_{y,a}}{(1 - X_{y,a})}$$

where H is the harvest in year y for fish of age class a, E is the estimated escapement and X is the respective estimated exploitation rate. The harvest data are published apportioned by age classes (but not by sex within age classes) and thus the above equation was applied within each age class to produce individual age class harvest estimates.

Returns

Each sex within the same age class was assumed to be harvested at the same rate. Returns by return year (Table A.10) were estimated by adding harvest and escapement together. Brood year was calculated by subtracting the age at maturity of individual spawners from the return year. The data were reorganized by brood year returns (Table A.11).

Average age and productivity

Average age of the escapement for each return year and returns for each brood year (Table A.12) were estimated using the following equation:

$$\frac{\sum n_a * a}{N}$$

where n is the number of fish of age a, and N is the total number of fish in the return. Productivity (Table A.12) was calculated as the number of returns from a brood year cohort divided by the escapement during the corresponding brood year. Productivity was found to peak in brood years 1983 and 2000 while being below replacement levels during brood years in the early 1980's, early 1990s, and mid-2000s (Figure A.3).

Changes in the average age of brood recruits and of the escapement over time were analyzed using ordinary least squares linear regression for the total population, males, and females separately (Figure A.4). Average age of all brood recruits was estimated to have declined from 5.37 to 5.12 from brood year 1977-2006 ($F = 3.97$, $df_1 = 1$, $df_2 = 28$, $P = 0.057$). Average age of male brood recruits was estimated to have declined from 5.07 to 4.82 ($F = 3.54$, $df_1 = 1$, $df_2 = 28$, $P = 0.070$). Average age of female brood recruits was estimated to have declined from 6.00 to 5.74 ($F = 7.81$, $df_1 = 1$, $df_2 = 28$, $P = 0.012$).

Declines in the average age of the escapement were steeper than those of brood recruits. This is a result of age selectivity in Kuskokwim River harvest becoming stronger following the year 2000 in our estimates (Table A.8). Average age of the total escapement was estimated to have decreased from 5.46 to 4.94 between return years 1981-2013 ($F = 20.3$, $df_1 = 1$, $df_2 = 31$, $P < 0.001$). Average age of males in the escapement was estimated to have decreased from 5.18 to 4.64 between return years 1981-2013 ($F = 24.77$, $df_1 = 1$, $df_2 = 31$, $P < 0.001$). Average age of females in the escapement was estimated to have decreased from 6.02 to 5.69 between return years 1981-2013 ($F = 15.22$, $df_1 = 1$, $df_2 = 31$, $P < 0.001$).

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Table A.1. Escapement estimates by sex (M. is male and F. is female) and age class for the East Fork of the Andreafsky River Chinook salmon population. Age 1.2 Females may be misidentified males.

Year	M. 1.1	M. 1.2	M. 1.3	M. 2.2	M. 1.4	M. 2.3	M. 1.5	M. 2.4	Male	F. 1.1	F. 1.2	F. 1.3	F. 2.2	F. 1.4	F. 2.3	F. 1.5	F. 2.4	Female	Escapement
1994 a	0	627	4,293	11	717	0	0	0	5,649	0	0	518	0	1,562	0	226	0	2,306	7,956 e
1995 a	0	1,989	681	0	691	0	27	0	3,389	0	177	309	0	1,889	0	79	0	2,454	5,844 e
1996 a	22	107	1,522	0	123	0	7	31	1,812	8	94	770	0	242	0	56	0	1,170	2,982 e
1997 a	0	1,339	421	0	236	0	0	0	1,996	0	217	134	0	842	0	0	0	1,192	3,188 e
1998 a	0	723	2,196	0	203	6	0	0	3,128	0	49	673	0	258	0	36	0	1,015	4,143 e
1999 b	13	1,100	1,007	0	380	0	8	0	2,508	0	77	151	0	717	0	6	0	952	3,459 e
2000 b	0	128	647	0	231	0	2	0	1,008	0	107	291	0	418	0	0	0	816	1,824 e
2001 c	3	534	798	2	183	1	3	2	1,525	0	51	314	1	472	1	18	0	856	2,381 d
2002 a	0	1,240	1,531	0	386	0	6	0	3,163	0	18	277	0	619	0	47	0	961	4,124 e
2003 a	23	586	1,477	0	258	0	0	0	2,345	0	140	719	0	1,099	0	40	0	1,997	4,342 e
2004 a	0	2,668	2,559	0	218	0	0	0	5,445	0	610	727	0	1,542	0	53	0	2,932	8,377 e
2005 a	0	286	750	0	155	0	0	0	1,191	0	73	779	0	338	0	1	0	1,191	2,382 e
2006 a	0	1,138	2,756	0	481	0	0	0	4,375	0	241	1,547	0	1,650	0	0	0	3,438	7,813 e
2007 a	0	2,114	831	0	486	0	17	0	3,449	0	0	520	0	1,335	0	2	0	1,857	5306 e
2008 a	0	108	2,354	0	217	0	27	3	2,709	0	0	827	0	700	16	48	0	1,591	4,270 e
2009 a	2	995	529	2	663	2	2	0	2,196	0	0	90	0	1,689	0	18	0	1,797	3,992 e
2010 a	2	1,354	566	42	22	20	0	0	2,007	0	0	892	14	286	14	25	1	1,231	3,237 e
2011 a	0	2,209	1,830	0	177	0	0	0	4,216	0	42	390	0	611	0	11	0	1,054	5,271 e
2012 a	18	445	2,286	0	319	0	0	0	3,068	0	0	448	0	837	0	5	0	1,290	4,359 e

a: Age/sex distribution from weir data (Andreafsky weir reports).

b: Age/sex distribution from weir data (data provided by Jeremy Mears).

c: No reliable age/sex data. Estimated as average of weir monitored years.

d: Escapement from aerial conversions.

e: Escapement from weir data

Table A.2. Harvest estimates for the East Fork of the Andreafsky River Chinook salmon population by age class and return year.

Year	1.1	1.2	1.3	2.2	1.4	2.3	1.5	2.4	1.6	2.5	Total
1994	0	19	807	0	570	0	58	0	0	0	1,454
1995	0	73	253	0	1,008	2	37	0	1	0	1,375
1996	0	7	248	0	1,076	11	844	2	0	0	2,188
1997	0	110	109	0	795	0	3	0	0	0	1,017
1998	0	74	797	0	310	0	40	0	0	0	1,222
1999	0	44	205	0	1,230	1	17	3	0	0	1,500
2000	0	5	112	0	225	0	9	1	0	0	352
2001	0	9	28	0	161	0	14	0	0	0	212
2002	0	48	155	0	276	0	42	0	0	0	521
2003	0	9	139	0	151	0	6	0	0	0	306
2004	1	187	378	1	744	0	16	0	0	0	1,326
2005	0	24	259	0	120	0	5	0	0	0	407
2006	0	49	545	0	594	2	1	2	0	0	1,192
2007	0	96	133	0	317	1	5	13	0	0	565
2008	0	18	118	0	62	1	4	1	0	0	204
2009	0	13	12	0	41	0	1	0	0	0	67
2010	1	142	260	0	97	3	8	1	0	0	512
2011	0	63	151	0	92	1	2	2	0	0	312
2012	0	27	111	0	82	1	2	1	0	0	225

Table A.3. Estimated Chinook salmon exploitation rates (terminal harvest/return) by age class and for the entire population and each sex separately for the East Fork of the Andreafsky River. Only well represented age classes are shown due to limited samples of other age classes producing inaccurate estimates.

Year	1.2	1.3	1.4	1.5	Male	Female	Total
1994	0.030	0.144	0.200	0.205	0.140	0.188	0.155
1995	0.033	0.204	0.281	0.258	0.133	0.258	0.190
1996	0.032	0.097	0.746	0.930	0.262	0.570	0.425
1997	0.066	0.164	0.424	0.858	0.150	0.358	0.242
1998	0.088	0.217	0.402	0.529	0.207	0.285	0.228
1999	0.036	0.150	0.529	0.555	0.209	0.469	0.303
2000	0.022	0.107	0.257	0.814	0.144	0.182	0.161
2001	0.015	0.024	0.197	0.397	0.047	0.138	0.082
2002	0.037	0.079	0.216	0.439	0.084	0.194	0.112
2003	0.012	0.060	0.100	0.139	0.053	0.081	0.066
2004	0.054	0.103	0.297	0.233	0.090	0.211	0.137
2005	0.062	0.145	0.195	0.809	0.134	0.158	0.146
2006	0.034	0.112	0.218	1.000	0.107	0.162	0.132
2007	0.044	0.090	0.148	0.216	0.075	0.133	0.094
2008	0.139	0.036	0.063	0.055	0.043	0.048	0.045
2009	0.013	0.020	0.017	0.035	0.016	0.017	0.017
2010	0.095	0.151	0.240	0.237	0.112	0.174	0.136
2011	0.027	0.064	0.104	0.126	0.048	0.088	0.056
2012	0.058	0.039	0.067	0.234	0.045	0.058	0.049
Avg.	0.047	0.106	0.247	0.425	0.110	0.199	0.146

Table A.4. Chinook salmon return estimates (escapement + terminal harvest) by age class and sex for the East Fork of the Andreafsky River. Age 1.2 females may be misidentified males.

Year	M. 1.1	M. 1.2	M. 1.3	M. 2.2	M. 1.4	M. 2.3	M. 1.5	M. 2.4	Male	F. 1.1	F. 1.2	F. 1.3	F. 2.2	F. 1.4	F. 2.3	F. 1.5	F. 2.4	F. 1.6	Female	Total
1994	0	646	5,013	11	897	0	0	0	6,568	0	0	605	0	1,953	0	284	0	0	2,842	9,410
1995	0	2,056	855	0	961	1	37	0	3,911	0	183	388	0	2,627	1	106	0	1	3,306	7,217
1996	0	111	1,687	0	487	6	104	33	2,426	8	97	853	0	955	6	804	0	0	2,722	5,148
1997	0	1,434	504	0	409	0	1	0	2,348	0	232	160	0	1,463	0	3	0	0	1,858	4,206
1998	0	792	2,805	0	340	6	0	0	3,944	0	53	860	0	431	0	75	0	0	1,420	5,364
1999	0	1,141	1,185	0	806	0	18	3	3,154	0	80	178	0	1,521	0	13	0	0	1,793	4,947
2000	0	131	724	0	311	0	11	1	1,178	0	109	326	0	563	0	0	0	0	998	2,176
2001	0	542	818	0	228	0	5	0	1,592	0	51	321	0	588	0	30	0	0	991	2,584
2002	0	1,287	1,662	0	492	0	11	0	3,453	0	19	300	0	789	0	84	0	0	1,192	4,645
2003	0	593	1,571	0	287	0	0	0	2,451	0	142	765	0	1,221	0	46	0	1	2,174	4,624
2004	1	2,820	2,853	1	310	0	0	0	5,986	0	645	811	0	2,194	0	69	0	0	3,718	9,704
2005	0	305	877	0	192	0	0	0	1,374	0	77	911	0	420	0	6	0	0	1,415	2,789
2006	0	1,178	3,105	0	615	1	0	2	4,901	0	249	1,743	0	2,110	1	1	0	0	4,104	9,005
2007	0	2,211	913	0	571	0	22	12	3,729	0	0	571	0	1,567	0	2	1	0	2,143	5,872
2008	1	126	2,441	1	231	0	29	4	2,832	0	0	858	0	747	17	50	0	0	1,672	4,504
2009	0	1,008	540	2	675	2	2	0	2,229	0	0	92	0	1,718	0	19	0	0	1,828	4,057
2010	1	1,496	667	42	29	22	0	0	2,258	0	0	1,051	14	376	15	32	2	0	1,490	3,748
2011	0	2,272	1,955	0	198	1	0	1	4,426	0	43	417	0	683	1	12	0	0	1,155	5,581
2012	0	472	2,379	0	342	1	0	2	3,195	0	0	466	0	897	1	7	0	0	1,370	4,565

Table A.5. Chinook salmon brood recruit estimates by age class and sex for the East Fork of the Andreafsky River. Age 1.2 females may be misidentified males.

Brood Year	M. 1.1	M. 1.2	M. 1.3	M. 2.2	M. 1.4	M. 2.3	M. 1.5	M. 2.4	Male	F. 1.1	F. 1.2	F. 1.3	F. 2.2	F. 1.4	F. 2.3	F. 1.5	F. 2.4	F. 1.6	Female	Total
1987	-	-	-	-	-	-	0	0	-	-	-	-	-	-	-	284	0	1	-	-
1988	-	-	-	-	897	0	37	0	-	-	-	-	0	1,953	0	106	0	0	-	-
1989	-	-	5,013	11	961	1	104	33	-	-	-	605	0	2,627	1	804	0	0	-	-
1990	-	646	855	0	487	6	1	0	1,995	-	0	388	0	955	6	3	0	0	1,352	3,347
1991	0	2,056	1,687	0	409	0	0	0	4,153	0	183	853	0	1,463	0	75	0	0	2,574	6,726
1992	0	111	504	0	340	6	18	3	982	0	97	160	0	431	0	13	0	0	701	1,683
1993	0	1,434	2,805	0	806	0	11	1	5,059	8	232	860	0	1,521	0	0	0	0	2,622	7,680
1994	0	792	1,185	0	311	0	5	0	2,293	0	53	178	0	563	0	30	0	0	825	3,118
1995	0	1,141	724	0	228	0	11	0	2,104	0	80	326	0	588	0	84	0	1	1,078	3,182
1996	0	131	818	0	492	0	0	0	1,440	0	109	321	0	789	0	46	0	0	1,266	2,706
1997	0	542	1,662	0	287	0	0	0	2,491	0	51	300	0	1,221	0	69	0	0	1,641	4,132
1998	0	1,287	1,571	0	310	0	0	0	3,168	0	19	765	0	2,194	0	6	0	0	2,984	6,152
1999	0	593	2,853	1	192	0	0	2	3,642	0	142	811	0	420	0	1	0	0	1,373	5,016
2000	0	2,820	877	0	615	1	22	12	4,347	0	645	911	0	2,110	1	2	1	0	3,670	8,018
2001	1	305	3,105	0	571	0	29	4	4,014	0	77	1,743	0	1,567	0	50	0	0	3,439	7,453
2002	0	1,178	913	0	231	0	2	0	2,324	0	249	571	0	747	17	19	0	0	1,603	3,927
2003	0	2,211	2,441	1	675	2	0	0	5,329	0	0	858	0	1,718	0	32	2	0	2,610	7,940
2004	0	126	540	2	29	22	0	1	720	0	0	92	0	376	15	12	0	0	495	1,214
2005	1	1,008	667	42	198	1	0	2	1,919	0	0	1,051	14	683	1	7	0	0	1,754	3,673
2006	0	1,496	1,955	0	342	1	-	-	-	0	0	417	0	897	1	-	-	-	-	-
2007	1	2,272	2,379	-	-	-	-	-	-	0	43	466	-	-	-	-	-	-	-	-

Table A.6. Estimates of Chinook salmon recruits, escapement, and average age for the East Fork of the Andreafsky River by brood year.

Brood year	Recruits	Average brood age			Escapement	Average spawner age			Productivity
		Total	Males	Females		Total	Males	Females	
1990	3347	5.24	4.92	5.72	-	-	-	-	-
1991	6726	4.97	4.60	5.56	-	-	-	-	-
1992	1683	5.38	5.28	5.52	-	-	-	-	-
1993	7680	5.09	4.88	5.49	-	-	-	-	-
1994	3118	5.03	4.79	5.69	7957	5.26	5.02	5.87	0.39
1995	3182	4.93	4.58	5.63	5842	5.11	4.63	5.76	0.54
1996	2706	5.42	5.25	5.61	2984	5.10	5.03	5.21	0.91
1997	4132	5.25	4.90	5.80	3188	4.85	4.45	5.52	1.30
1998	6152	5.20	4.69	5.73	4143	4.94	4.84	5.28	1.48
1999	5016	4.98	4.89	5.20	3459	4.98	4.71	5.68	1.45
2000	8018	4.92	4.51	5.40	1824	5.23	5.11	5.38	4.40
2001	7453	5.26	5.08	5.46	2382	5.05	4.77	5.54	3.13
2002	3927	4.90	4.59	5.34	4124	4.96	4.73	5.72	0.95
2003	7940	5.03	4.71	5.68	4342	5.15	4.84	5.52	1.83
2004	1214	5.28	4.90	5.84	8377	4.83	4.55	5.35	0.14
2005	3673	4.97	4.58	5.40	2382	5.06	4.89	5.22	1.54
2006	-	-	-	-	7813	5.10	4.85	5.41	-
2007	-	-	-	-	5306	4.95	4.54	5.72	-
2008	-	-	-	-	4300	5.23	5.06	5.51	-
2009	-	-	-	-	3992	5.35	4.85	5.96	-
2010	-	-	-	-	3238	4.70	4.34	5.29	-
2011	-	-	-	-	5271	4.73	4.52	5.56	-
2012	-	-	-	-	4359	5.16	4.95	5.66	-
Avg.	4748	5.12	4.82	5.57	4489	5.04	4.77	5.54	1.51

Year	M. 0.2	M. 1.1	M. 1.2	M. 1.3	M. 2.2	M. 1.4	M. 2.3	M. 1.5	M. 2.4	Male	F. 1.2	F. 1.3	F. 2.2	F. 1.4	F. 2.3	F. 1.5	F. 2.4	F. 1.6	Female	Total
1981	0	48	1,158	4,489	0	3,105	0	209	0	9,010	32	386	0	6,259	0	418	0	0	7,095	16,089
1982	0	0	840	2,731	0	2,534	0	236	0	6,341	0	354	0	5,947	0	473	0	0	6,775	13,129
1983	0	4	358	337	0	532	0	13	0	1,243	0	14	0	469	0	63	0	0	546	1,791
1984	0	5	1,098	2,254	0	482	0	49	0	3,888	5	89	0	817	0	118	0	5	1,034	4,922
1985	0	0	720	1,488	0	786	0	49	0	3,043	0	98	0	1,208	0	93	0	4	1,404	4,443
1986	0	15	331	1,888	0	381	0	66	0	2,682	0	69	0	882	0	212	0	0	1,164	3,853
1987 [ab]	0	23	893	777	0	732	0	23	0	2,447	0	23	0	754	0	0	0	0	777	3,224
1988	0	0	642	3,572	0	899	0	80	0	5,194	0	658	0	1,622	0	562	0	0	2,842	8,028
1989 ab	0	0	2,095	3,349	0	3,729	0	128	0	9,301	0	256	0	4,540	0	128	0	0	4,924	14,231
1990 c	0	293	2,432	4,875	0	262	0	0	0	7,862	0	1,332	0	868	0	30	0	0	2,231	10,093
1991	0	0	437	1,593	21	1,422	0	0	0	3,472	0	451	0	2,843	0	75	0	0	3,370	6,835
1992 b	0	0	1,340	2,470	0	604	0	39	0	4,453	20	226	0	1,780	0	53	20	0	2,098	6,568
1993 b	0	0	4,250	2,751	0	1,636	0	88	0	8,725	37	298	0	2,777	0	497	37	0	3,646	12,376
1994 ab	0	0	1,611	7,688	64	1,755	0	0	0	11,118	0	1,994	0	2,728	0	105	0	0	4,826	15,951
1995	0	0	3,588	3,628	0	4,084	20	0	20	11,340	198	1,429	0	6,839	0	40	0	0	8,506	19,846
1996	0	0	1,735	6,859	0	1,667	55	152	0	10,467	0	702	0	1,818	0	785	0	0	3,306	13,773
1997	0	0	4,406	2,454	0	2,177	0	0	0	9,036	40	237	0	3,812	0	53	0	0	4,142	13,191
1998 b	0	0	281	2,223	0	765	0	72	0	3,341	0	1,048	0	1,533	0	66	0	0	2,646	5,987
1999	0	17	299	1,186	17	1,081	0	0	0	2,600	0	211	0	2,650	0	83	0	0	2,944	5,544
2000	0	0	321	1,359	0	227	0	0	0	1,907	0	237	0	1,041	0	58	0	0	1,336	3,243
2001	0	0	1,115	2,701	0	1,489	0	45	0	5,350	30	239	0	1,788	0	67	0	0	2,125	7,483
2002	0	0	1,745	4,583	0	1,083	0	50	0	7,461	0	431	0	2,046	0	90	0	0	2,567	10,028
2003	0	0	2,245	4,815	0	1,201	0	0	0	8,261	0	300	0	3,122	0	336	0	0	3,758	12,007
2004	0	0	8,748	6,645	0	1,191	0	0	0	16,585	119	519	0	2,483	0	119	0	0	3,240	19,819
2005	0	65	5,276	6,888	0	1,942	0	87	0	14,259	44	3,247	0	4,161	0	109	0	0	7,560	21,819
2006	0	101	7,051	4,647	0	1,475	0	182	0	13,455	0	1,596	0	4,465	0	687	0	0	6,748	20,203
2007	0	0	4,473	3,642	0	1,689	0	97	0	9,901	0	928	0	2,700	0	305	0	0	3,933	13,848
2008	0	49	3,481	3,471	0	449	0	49	0	7,498	20	761	0	1,414	20	49	0	0	2,262	9,750
2009	0	0	1,972	4,230	67	572	0	0	0	6,841	143	762	0	1,610	38	133	0	0	2,687	9,528
2010	0	0	2,558	1,343	0	366	0	23	0	4,291	0	331	0	1,128	0	64	0	0	1,523	5,814
2011	0	0	3,181	1,780	20	379	0	0	0	5,359	0	419	0	945	0	0	0	0	1,364	6,733
2012 ad	37	0	3,288	7,054	0	1,303	41	15	0	11,738	33	1,272	0	2,497	66	52	0	0	3,919	15,665
2013 e	0	0	448	388	0	89	0	0	0	925	29	270	0	597	0	0	0	0	896	1,821

a: Weir inoperable for a majority of the season

b: Age and sex composition represents stratefied estimate from limited samples. Considered best estimate available

c: Potential age errors.

d: Estimated age and sex composition from the entire Kuskokwim used

e: Age and sex composition represents samples collected only.

Table A.7. Escapement estimates by sex and age class for the Kogrukluk River Chinook salmon population. All total escapement numbers from ADF&G estimates implementing Bayesian methods to estimate missed sampling (Zach Liller, ADF&G, unpublished data). 2012 age and sex proportions assumed to be the same as entire Kuskokwim estimates due to limited sampling (Zach Liller, ADF&G, unpublished data).

Table A.8. Estimated Kuskokwim River Chinook salmon exploitation proportions in the terminal fisheries by age class (Zach Liller, ADF&G, unpublished data). Sample size for estimating harvest age proportions is shown. Only well represented age classes are shown due to limited samples of other age classes producing inaccurate estimates.

Year	Sample Size	Total Run	1.2	1.3	1.4	1.5	Males	Females	Total
1981	1,294	389,791	0.297	0.343	0.241	0.247	0.302	0.248	0.279
1982	1,137	187,354	0.746	0.637	0.518	0.441	0.616	0.521	0.572
1983	1,733	166,333	0.391	0.604	0.453	0.474	0.492	0.461	0.483
1984	2,070	188,238	0.279	0.431	0.592	0.560	0.428	0.576	0.467
1985	1,706	176,292	0.522	0.464	0.435	0.481	0.472	0.439	0.462
1986	850	129,168	0.570	0.516	0.597	0.378	0.535	0.565	0.545
1987	696	193,465	0.497	0.598	0.504	0.770	0.539	0.507	0.532
1988	1,542	207,818	0.778	0.557	0.632	0.468	0.617	0.591	0.608
1989	600	241,857	0.549	0.596	0.428	0.695	0.532	0.452	0.507
1990	805	264,802	0.566	0.508	0.840	0.959	0.550	0.748	0.617
1991	1,111	218,705	0.706	0.578	0.420	0.652	0.552	0.455	0.509
1992	2,393	284,846	0.367	0.496	0.504	0.590	0.466	0.506	0.479
1993	1,064	269,305	0.167	0.460	0.426	0.288	0.338	0.410	0.361
1994	935	365,246	0.277	0.264	0.444	0.647	0.302	0.390	0.331
1995	1,141	360,513	0.306	0.446	0.335	0.877	0.367	0.368	0.367
1996	1,293	302,603	0.324	0.331	0.434	0.116	0.346	0.358	0.349
1997	933	303,189	0.144	0.481	0.281	0.818	0.299	0.320	0.306
1998	643	213,873	0.779	0.417	0.546	0.673	0.522	0.508	0.516
1999	586	189,939	0.501	0.555	0.316	0.674	0.468	0.360	0.416
2000	586	136,618	0.340	0.552	0.537	0.526	0.525	0.539	0.531
2001	1,797	223,707	0.154	0.317	0.408	0.370	0.319	0.395	0.343
2002	4,365	246,296	0.123	0.305	0.449	0.506	0.299	0.432	0.339
2003	4,200	248,789	0.093	0.276	0.350	0.471	0.248	0.358	0.286
2004	5,483	388,136	0.108	0.299	0.400	0.527	0.220	0.385	0.253
2005	5,429	366,601	0.096	0.263	0.304	0.317	0.215	0.286	0.242
2006	4,910	307,662	0.095	0.354	0.402	0.266	0.245	0.379	0.296
2007	4,603	273,060	0.078	0.405	0.532	0.476	0.329	0.503	0.390
2008	4,910	237,074	0.249	0.493	0.511	0.518	0.404	0.504	0.430
2009	5,299	204,747	0.282	0.382	0.502	0.479	0.368	0.460	0.397
2010	3,021	118,507	0.247	0.678	0.664	0.616	0.508	0.665	0.562
2011	2,412	133,059	0.227	0.586	0.541	0.671	0.421	0.556	0.455
2012	871	99,807	0.173	0.225	0.271	0.627	0.217	0.262	0.229
2013	1,018	94,166	0.217	0.492	0.571	0.691	0.401	0.543	0.480
Avg	2,165	234,290	0.341	0.452	0.466	0.542	0.408	0.456	0.422

Table A.9. Estimated Chinook salmon harvest by sex and age class for the Kogrukluk River.

Year	M. 0.2	M. 1.1	M. 1.2	M. 1.3	M. 2.2	M. 1.4	M. 2.3	M. 1.5	M. 2.4	Male	F. 1.2	F. 1.3	F. 2.2	F. 1.4	F. 2.3	F. 1.5	F. 2.4	F. 1.6	Female	Total
1981	0	4	490	2,342	0	986	0	69	0	3,890	14	201	0	1,988	0	137	0	0	2,340	10,121
1982	0	0	2,464	4,794	0	2,720	0	187	0	10,164	0	622	0	6,384	0	373	0	0	7,380	27,707
1983	0	11	230	513	0	440	0	11	0	1,206	0	22	0	388	0	57	0	0	466	2,878
1984	0	14	426	1,705	0	701	0	63	0	2,908	2	67	0	1,187	0	150	0	0	1,407	7,222
1985	0	0	786	1,290	0	604	0	45	0	2,726	0	85	0	929	0	86	0	0	1,100	6,552
1986	0	32	439	2,015	0	566	0	40	0	3,091	0	74	0	1,309	0	129	0	0	1,512	7,695
1987	0	0	881	1,157	0	743	0	75	0	2,858	0	34	0	766	0	0	0	0	800	6,515
1988	0	0	2,250	4,491	0	1,546	0	71	0	8,357	0	828	0	2,789	0	494	0	0	4,110	20,825
1989	0	0	2,553	4,932	0	2,792	0	292	0	10,568	0	377	0	3,399	0	292	0	0	4,068	25,205
1990	0	13	3,172	5,042	0	1,370	0	0	0	9,597	0	1,378	0	4,543	0	715	0	0	6,636	25,830
1991	0	0	1,052	2,184	12	1,029	0	0	0	4,277	0	619	0	2,058	0	141	0	0	2,818	11,373
1992	0	0	778	2,431	0	614	0	57	0	3,880	11	223	0	1,808	0	76	33	0	2,150	9,911
1993	0	0	850	2,348	0	1,212	0	35	0	4,446	7	254	0	2,058	0	200	14	0	2,534	11,427
1994	0	0	616	2,764	20	1,400	0	0	0	4,800	0	717	0	2,176	0	192	0	0	3,085	12,684
1995	0	0	1,579	2,916	0	2,053	13	0	11	6,572	87	1,149	0	3,438	0	283	0	0	4,957	18,101
1996	0	0	832	3,393	0	1,276	16	20	0	5,537	0	347	0	1,392	0	103	0	0	1,842	12,915
1997	0	0	739	2,271	0	849	0	0	0	3,860	7	220	0	1,488	0	237	0	0	1,952	9,671
1998	0	0	989	1,592	0	922	0	148	0	3,651	0	750	0	1,847	0	136	0	0	2,733	10,035
1999	0	7	301	1,479	3	499	0	0	0	2,289	0	263	0	1,223	0	172	0	0	1,658	6,235
2000	0	0	165	1,675	0	264	0	0	0	2,104	0	292	0	1,209	0	65	0	0	1,565	5,773
2001	0	0	202	1,256	0	1,026	0	26	0	2,510	5	111	0	1,232	0	40	0	0	1,388	6,409
2002	0	0	244	2,009	0	884	0	51	0	3,188	0	189	0	1,670	0	93	0	0	1,952	8,328
2003	0	0	231	1,840	0	647	0	0	0	2,718	0	115	0	1,682	0	300	0	0	2,097	7,532
2004	0	0	1,054	2,830	0	795	0	0	0	4,679	14	221	0	1,658	0	132	0	0	2,026	11,384
2005	0	0	562	2,461	0	849	0	41	0	3,913	5	1,160	0	1,820	0	51	0	0	3,035	10,861
2006	0	26	744	2,541	0	991	0	66	0	4,368	0	873	0	2,999	0	249	0	0	4,121	12,857
2007	0	0	378	2,482	0	1,917	0	88	0	4,865	0	632	0	3,065	0	276	0	0	3,973	13,703
2008	0	30	1,155	3,373	0	468	0	52	0	5,078	6	739	0	1,475	21	52	0	0	2,295	12,451
2009	0	0	774	2,614	10	577	0	0	0	3,975	56	471	0	1,625	14	122	0	0	2,288	10,239
2010	0	0	837	2,831	0	723	0	37	0	4,428	0	699	0	2,226	0	103	0	0	3,027	11,883
2011	0	0	935	2,519	0	447	0	0	0	3,901	0	594	0	1,113	0	0	0	0	1,707	9,509
2012	0	0	687	2,052	0	485	0	26	0	3,250	7	370	0	929	0	87	0	0	1,393	7,892
2013	0	0	124	376	0	119	0	0	0	619	8	261	0	796	0	0	0	0	1,065	2,302

Table A.10. Estimated total Chinook salmon returns (terminal harvest + escapement) by sex and age class for the Kogrukluk River.

Year	M. 0.2	M. 1.1	M. 1.2	M. 1.3	M. 2.2	M. 1.4	M. 2.3	M. 1.5	M. 2.4	Male	F. 1.2	F. 1.3	F. 2.2	F. 1.4	F. 2.3	F. 1.5	F. 2.4	F. 1.6	Female	Total
1981	0	52	1,648	6,831	0	4,091	0	278	0	12,900	46	588	0	8,246	0	555	0	0	9,435	22,335
1982	0	0	3,304	7,525	0	5,254	0	423	0	16,505	0	977	0	12,331	0	846	0	0	14,154	30,659
1983	0	15	588	850	0	972	0	24	0	2,449	0	36	0	857	0	119	0	0	1,013	3,461
1984	0	19	1,523	3,959	0	1,183	0	112	0	6,796	7	156	0	2,004	0	268	0	5	2,440	9,236
1985	0	0	1,506	2,779	0	1,391	0	94	0	5,770	0	182	0	2,137	0	180	0	5	2,504	8,273
1986	0	47	770	3,903	0	947	0	105	0	5,773	0	143	0	2,191	0	341	0	0	2,676	8,449
1987	0	23	1,774	1,934	0	1,475	0	98	0	5,305	0	56	0	1,521	0	0	0	0	1,577	6,859
1988	0	0	2,892	8,063	0	2,445	0	151	0	13,552	0	1,486	0	4,410	0	1,056	0	0	6,952	20,503
1989	0	0	4,648	8,281	0	6,520	0	420	0	19,870	0	633	0	7,939	0	420	0	0	8,992	28,862
1990	0	306	5,604	9,917	0	1,632	0	0	0	17,459	0	2,710	0	5,411	0	745	0	0	8,866	26,325
1991	0	0	1,490	3,776	33	2,451	0	0	0	7,750	0	1,070	0	4,902	0	216	0	0	6,188	13,937
1992	0	0	2,118	4,901	0	1,218	0	96	0	8,333	31	449	0	3,587	0	128	53	0	4,248	12,582
1993	0	0	5,100	5,099	0	2,849	0	123	0	13,171	45	552	0	4,835	0	697	51	0	6,180	19,324
1994	0	0	2,227	10,453	83	3,155	0	0	0	15,918	0	2,711	0	4,904	0	297	0	0	7,911	23,829
1995	0	0	5,167	6,544	0	6,138	33	0	30	17,912	286	2,578	0	10,277	0	323	0	0	13,463	31,406
1996	0	0	2,567	10,252	0	2,943	71	171	0	16,004	0	1,050	0	3,210	0	888	0	0	5,148	21,152
1997	0	0	5,145	4,725	0	3,026	0	0	0	12,896	46	457	0	5,300	0	290	0	0	6,094	18,989
1998	0	0	1,270	3,815	0	1,687	0	220	0	6,992	0	1,798	0	3,379	0	202	0	0	5,379	12,371
1999	0	24	601	2,665	19	1,580	0	0	0	4,889	0	473	0	3,873	0	255	0	0	4,602	9,490
2000	0	0	486	3,034	0	491	0	0	0	4,011	0	529	0	2,250	0	123	0	0	2,901	6,912
2001	0	0	1,317	3,957	0	2,515	0	71	0	7,861	35	351	0	3,020	0	107	0	0	3,514	11,374
2002	0	0	1,989	6,592	0	1,967	0	102	0	10,649	0	620	0	3,716	0	183	0	0	4,519	15,168
2003	0	0	2,476	6,654	0	1,848	0	0	0	10,979	0	415	0	4,804	0	636	0	0	5,855	16,834
2004	0	0	9,802	9,475	0	1,987	0	0	0	21,264	133	740	0	4,142	0	251	0	0	5,267	26,494
2005	0	65	5,838	9,349	0	2,791	0	128	0	18,171	48	4,407	0	5,981	0	160	0	0	10,596	28,803
2006	0	127	7,795	7,188	0	2,465	0	248	0	17,823	0	2,469	0	7,464	0	936	0	0	10,869	28,692
2007	0	0	4,851	6,124	0	3,607	0	185	0	14,766	0	1,560	0	5,765	0	581	0	0	7,906	22,672
2008	0	79	4,636	6,844	0	917	0	101	0	12,576	26	1,499	0	2,889	41	101	0	0	4,557	17,133
2009	0	0	2,747	6,844	77	1,149	0	0	0	10,816	199	1,233	0	3,236	52	256	0	0	4,975	15,792
2010	0	0	3,396	4,174	0	1,089	0	61	0	8,719	0	1,030	0	3,354	0	167	0	0	4,550	13,269
2011	0	0	4,116	4,298	20	826	0	0	0	9,260	0	1,013	0	2,058	0	0	0	0	3,071	12,309
2012	37	0	3,975	9,106	0	1,788	41	42	0	14,988	40	1,642	0	3,426	66	139	0	0	5,312	20,300
2013	0	0	572	764	0	208	0	0	0	1,544	37	531	0	1,393	0	0	0	0	1,961	3,505

Table A.11. Estimated Chinook salmon brood year recruits by age class and sex for the Kogrukluk River.

Brood Year	M. 0.2	M. 1.1	M. 1.2	M. 1.3	M. 2.2	M. 1.4	M. 2.3	M. 1.5	M. 2.4	Male	F. 1.2	F. 1.3	F. 2.2	F. 1.4	F. 2.3	F. 1.5	F. 2.4	F. 1.6	Female	Total
1975	-	-	-	-	-	4,091	0	423	0	-	-	-	-	8,246	0	846	0	0	-	-
1976	-	-	-	6,831	0	5,254	0	24	0	-	-	588	0	12,331	0	119	0	5	-	-
1977	-	-	1,648	7,525	0	972	0	112	0	10,256	46	977	0	857	0	268	0	5	2,153	12,409
1978	0	52	3,304	850	0	1,183	0	94	0	5,484	0	36	0	2,004	0	180	0	0	2,220	7,704
1979	0	0	588	3,959	0	1,391	0	105	0	6,043	0	156	0	2,137	0	341	0	0	2,633	8,677
1980	0	15	1,523	2,779	0	947	0	98	0	5,362	7	182	0	2,191	0	0	0	0	2,381	7,742
1981	0	19	1,506	3,903	0	1,475	0	151	0	7,054	0	143	0	1,521	0	1,056	0	0	2,720	9,774
1982	0	0	770	1,934	0	2,445	0	420	0	5,569	0	56	0	4,410	0	420	0	0	4,887	10,456
1983	0	47	1,774	8,063	0	6,520	0	0	0	16,405	0	1,486	0	7,939	0	745	0	0	10,169	26,574
1984	0	23	2,892	8,281	0	1,632	0	0	0	12,828	0	633	0	5,411	0	216	0	0	6,261	19,089
1985	0	0	4,648	9,917	0	2,451	0	96	0	17,112	0	2,710	0	4,902	0	128	53	0	7,793	24,905
1986	0	0	5,604	3,776	33	1,218	0	123	0	10,754	0	1,070	0	3,587	0	697	51	0	5,405	16,160
1987	0	306	1,490	4,901	0	2,849	0	0	0	9,545	0	449	0	4,835	0	297	0	0	5,580	15,125
1988	0	0	2,118	5,099	0	3,155	0	0	30	10,403	31	552	0	4,904	0	323	0	0	5,810	16,213
1989	0	0	5,100	10,453	83	6,138	33	171	0	21,978	45	2,711	0	10,277	0	888	0	0	13,920	35,898
1990	0	0	2,227	6,544	0	2,943	71	0	0	11,785	0	2,578	0	3,210	0	290	0	0	6,078	17,862
1991	0	0	5,167	10,252	0	3,026	0	220	0	18,664	286	1,050	0	5,300	0	202	0	0	6,837	25,502
1992	0	0	2,567	4,725	0	1,687	0	0	0	8,979	0	457	0	3,379	0	255	0	0	4,092	13,071
1993	0	0	5,145	3,815	0	1,580	0	0	0	10,540	46	1,798	0	3,873	0	123	0	0	5,840	16,381
1994	0	0	1,270	2,665	19	491	0	71	0	4,516	0	473	0	2,250	0	107	0	0	2,830	7,346
1995	0	0	601	3,034	0	2,515	0	102	0	6,251	0	529	0	3,020	0	183	0	0	3,732	9,983
1996	0	24	486	3,957	0	1,967	0	0	0	6,434	0	351	0	3,716	0	636	0	0	4,703	11,137
1997	0	0	1,317	6,592	0	1,848	0	0	0	9,757	35	620	0	4,804	0	251	0	0	5,711	15,468
1998	0	0	1,989	6,654	0	1,987	0	128	0	10,757	0	415	0	4,142	0	160	0	0	4,716	15,474
1999	0	0	2,476	9,475	0	2,791	0	248	0	14,990	0	740	0	5,981	0	936	0	0	7,657	22,648
2000	0	0	9,802	9,349	0	2,465	0	185	0	21,802	133	4,407	0	7,464	0	581	0	0	12,585	34,387
2001	0	0	5,838	7,188	0	3,607	0	101	0	16,733	48	2,469	0	5,765	0	101	0	0	8,383	25,117
2002	0	65	7,795	6,124	0	917	0	0	0	14,901	0	1,560	0	2,889	41	256	0	0	4,746	19,647
2003	0	127	4,851	6,844	0	1,149	0	61	0	13,031	0	1,499	0	3,236	52	167	0	0	4,953	17,984
2004	0	0	4,636	6,844	77	1,089	0	0	0	12,646	26	1,233	0	3,354	0	0	0	0	4,613	17,259
2005	0	79	2,747	4,174	0	826	0	42	0	7,866	199	1,030	0	2,058	0	139	0	0	3,425	11,292
2006	0	0	3,396	4,298	20	1,788	41	0	0	9,543	0	1,013	0	3,426	66	0	0	0	4,505	14,048
2007	0	0	4,116	9,106	0	208	0	-	-	-	0	1,642	0	1,393	-	-	-	-	-	16,465
2008	0	0	3,975	764	0	-	-	-	-	-	40	531	0	-	-	-	-	-	-	5,309

Table A.12. Estimated Kogrukluk River Chinook salmon recruits, escapement, average age, and productivity.

Brood Year	Recruits	Average Brood Age Total	Males	Females	Escapement	Average Spawner Age Total	Males	Females	Productivity
1977	12,409	5.07	4.96	5.63	-	-	-	-	-
1978	7,704	5.04	4.63	6.06	-	-	-	-	-
1979	8,677	5.44	5.17	6.07	-	-	-	-	-
1980	7,742	5.23	4.92	5.92	-	-	-	-	-
1981	9,774	5.40	5.03	6.34	16,089	5.58	5.25	6.00	0.61
1982	10,456	5.74	5.45	6.07	13,129	5.69	5.34	6.02	0.80
1983	26,574	5.53	5.28	5.93	1,791	5.44	5.15	6.09	14.84
1984	19,089	5.24	4.90	5.93	4,922	5.11	4.86	6.03	3.88
1985	24,905	5.13	4.88	5.68	4,443	5.35	5.05	6.00	5.61
1986	16,160	5.06	4.62	5.94	3,853	5.38	5.06	6.12	4.19
1987	15,125	5.41	5.08	5.97	3,224	5.18	4.93	5.97	4.69
1988	16,213	5.41	5.11	5.95	8,028	5.39	5.08	5.97	2.02
1989	35,898	5.37	5.06	5.86	14,231	5.47	5.20	5.97	2.52
1990	17,862	5.26	5.07	5.62	10,093	4.82	4.65	5.42	1.77
1991	25,502	5.15	4.91	5.79	6,835	5.58	5.28	5.89	3.73
1992	13,071	5.23	4.90	5.95	6,568	5.19	4.85	5.91	1.99
1993	16,381	5.03	4.66	5.70	12,376	5.11	4.72	6.04	1.32
1994	7,346	5.25	4.86	5.87	15,951	5.19	5.01	5.61	0.46
1995	9,983	5.55	5.34	5.91	19,846	5.37	5.05	5.79	0.50
1996	11,137	5.58	5.22	6.06	13,773	5.27	5.03	6.03	0.81
1997	15,468	5.38	5.05	5.92	13,191	5.13	4.75	5.94	1.17
1998	15,474	5.30	5.02	5.95	5,987	5.38	5.19	5.63	2.58
1999	22,648	5.38	5.05	6.03	5,544	5.64	5.29	5.96	4.09
2000	34,387	5.04	4.68	5.67	3,243	5.33	4.95	5.87	10.60
2001	25,117	5.15	4.88	5.71	7,483	5.32	5.09	5.89	3.36
2002	19,647	4.82	4.53	5.73	10,028	5.17	4.92	5.87	1.96
2003	17,984	4.99	4.71	5.73	12,007	5.23	4.87	6.01	1.50
2004	17,259	4.99	4.72	5.72	19,819	4.75	4.54	5.80	0.87
2005	11,292	5.01	4.75	5.62	21,819	5.05	4.77	5.57	0.52
2006	14,048	5.14	4.84	5.78	20,203	5.02	4.60	5.87	0.70
2007	-	-	-	-	13,848	5.05	4.74	5.84	-
2008	-	-	-	-	9,750	4.84	4.60	5.67	-
2009	-	-	-	-	9,528	5.04	4.80	5.66	-
2010	-	-	-	-	5,814	4.85	4.50	5.82	-
2011	-	-	-	-	6,733	4.72	4.48	5.69	-
2012	-	-	-	-	15,665	5.04	4.83	5.67	-
2013	-	-		-	1,821	5.12	4.61	5.63	-
Avg.	16,844	5.24	4.94	5.87	10,231	5.21	4.91	5.86	2.96

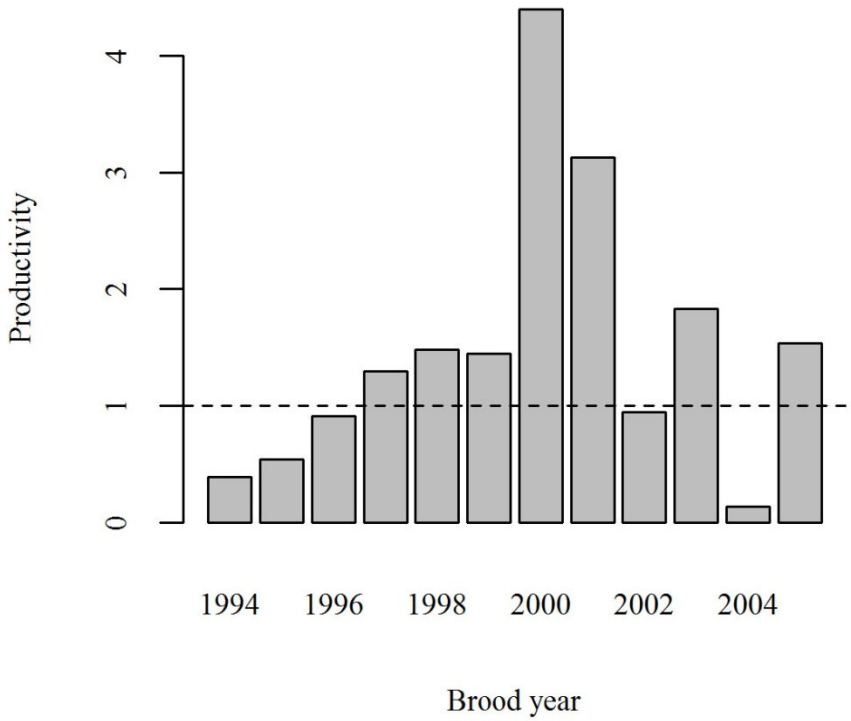

Figure A.1. Estimated productivity (recruits-per-spawner) by brood year from run reconstruction for the East Fork of the Andreafsky Chinook salmon population. Brood year is defined as the year of the escapement which produced recruits. Spawners are estimated as the escapement above monitoring weir in a return year. Recruits are estimated as all returns (escapement plus harvest) originating from a single brood year. Replacement level is shown by dashed line.

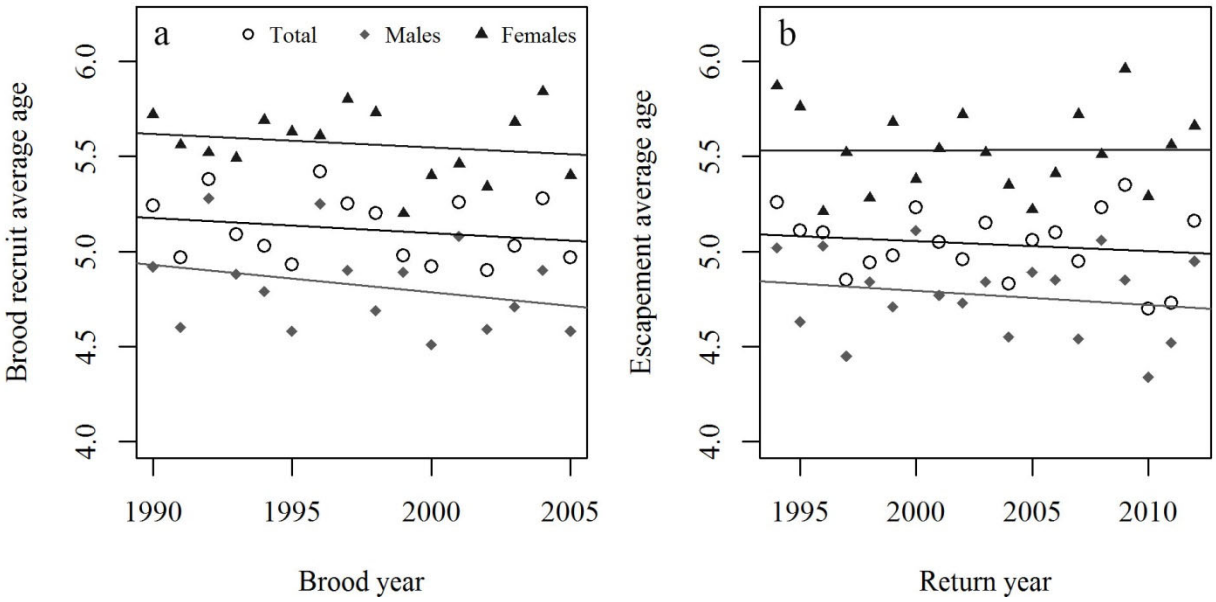

Figure A.2. Estimated average escapement age (a) and brood recruit age (b) by return year and brood year respectively for the Chinook salmon population of the East Fork of the Andreafsky River. Average age of the total population and both males and females are all shown separately. Age 1.1 fish were not available for the estimation of average age in brood year 1990 and their absence was ignored due to their rarity or absence in all other brood years (Table 5).

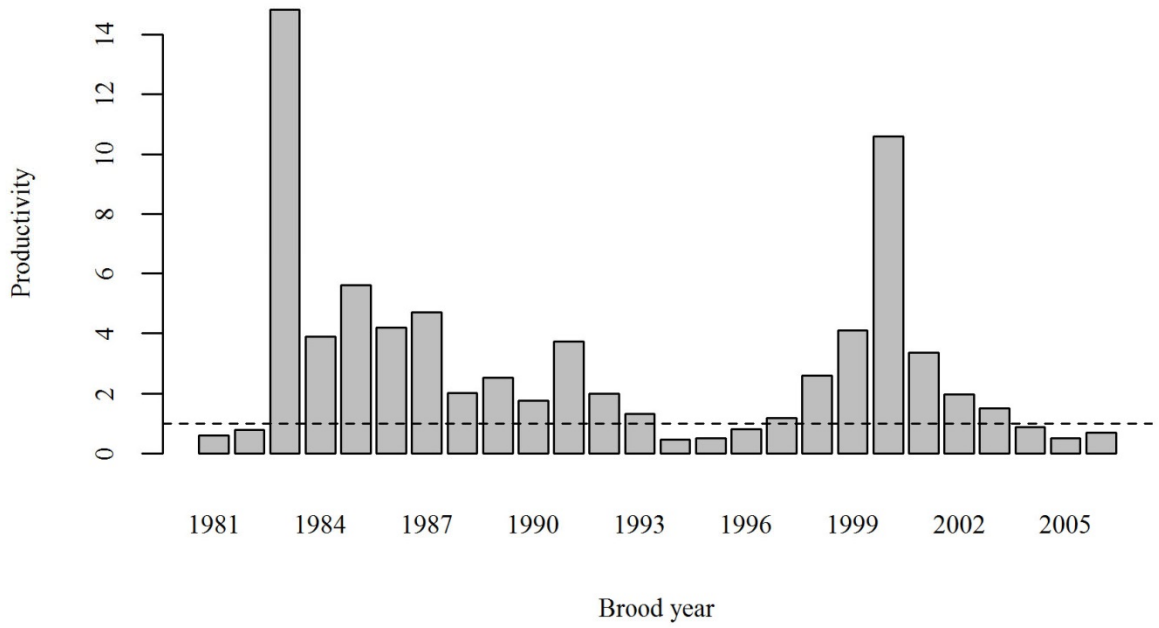

Figure A.3. Estimated productivity (recruits/spawner) by brood year from run reconstruction for the Kogrukluk River Chinook salmon population. Brood year is defined as the year of the escapement which produced recruits. Spawners are estimated as the escapement above monitoring weir in a single return year. Recruits are estimated as all returns (escapement plus harvest) originating from a single brood year. Replacement level is shown by dashed line.

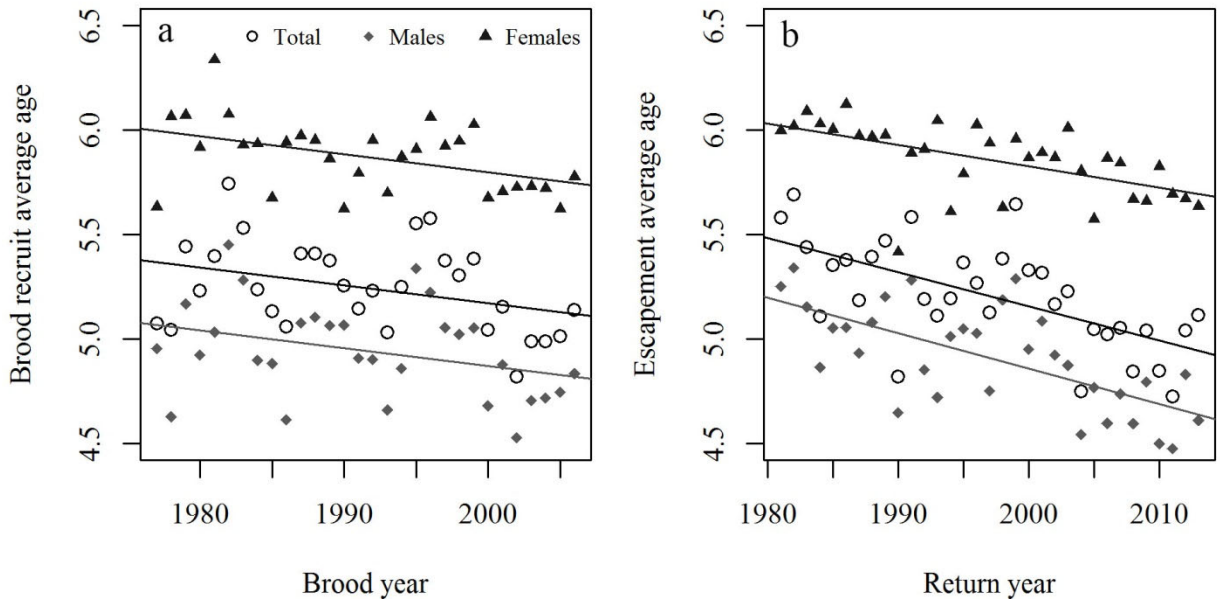

Figure A.4. Estimated average escapement age (a) and brood recruit age (b) by return year and brood year respectively from run reconstruction for the Chinook salmon population of the Kogrukluk River. Average age of the total population and both males and females are all shown separately. Age 1.1 fish were not available for the estimation of average age in brood year 1977 and their absence was ignored due to their rarity or nonexistence in all other brood years (Table 11).