Effects of Marine Growth on Yukon River Chinook Salmon Fecundity

R&M# 21-10

Project Proponents: Kathrine G. Howard, Alaska Department of Fish and Game, Division of Commercial Fisheries, Anchorage, Alaska and Jeffrey Bromaghin, U.S. Geological Survey, Alaska Science Center, Anchorage

1. Introduction:

Summary:

Strategies for investing energy in the development of reproductive tissue and optimizing the trade-off between egg size and egg number (fecundity) are important determinants of both individual fitness and population productivity in Pacific salmon (Smith and Fretwell 1974; Einum and Fleming 2000; Einum et al. 2004). Not surprisingly, the optimum strategy appears to vary among populations. Both fecundity and egg size vary latitudinally in Chinook *Oncorhynchus tshawytscha*, coho *O. kisutch*, sockeye *O. nerka*, and masu *O. masou* salmon, with northern populations tending to have less total ovarian mass, smaller eggs, and greater fecundity (Fleming and Gross 1990; Beacham and Murray 1993; Morita et al. 2009). Healey and Heard (1984) found that fecundity varied both temporally and spatially among populations of Chinook salmon *O. tshawytscha* throughout the northeastern Pacific and the Bering Sea. Egg size and the proportion of total somatic energy allocated to egg development in Chinook salmon appear to be inversely related to the difficulty of migration (Beacham and Murray 1993; Kinnison et al. 2001). The apparent tendency for populations with more arduous migrations to invest less energy in ovaries may reflect an adaptation to maximize fitness under the constraint of increased energetic demands for migration (Roff 1988; Healey 2001).

Bromaghin et al. (2011) summarize an extensive investigation of the fecundity of Yukon River Chinook salmon. They obtained fecundity information from 403 females sampled from lower-river test fishery catches in 2008. Matched tissue samples and a new generalized mixture model were used to estimate the mean and variance of fecundity as a function of length and stock origin within the drainage. They found that the relationship between mean fecundity and length differed among broad regions within the drainage. In Chinook salmon from the lower portions of the drainage, mean fecundity was comparatively high and appeared to be nearly independent of length. In the middle and upper portions of the drainage, Chinook salmon tended to have fewer eggs and fecundity was more strongly dependent on fish length (Figure 1). Bromaghin et al. (2011) also found a high degree of variability among available data sources, suggesting that fecundity might have a high degree of inter-annual variability.

Although the models of Bromaghin et al. (2011) capture broad trends in mean fecundity as a function of length and region of origin, the variation in fecundity among individual fish of a similar size and origin is extremely high. For example, the fecundity of females with length 850mm ranges from approximately 5,000 to 12,000 eggs (Figure 1). While this high variation may be caused by chance, we suspect that unmeasured variables other than fish length may be important determinants of below- or above-average fecundity for individual fish. For example, Campbell et al. (2006) found that growth during the 6 months prior to maturation had the greatest correlation with reproductive parameters at spawning among captively-reared Coho salmon.

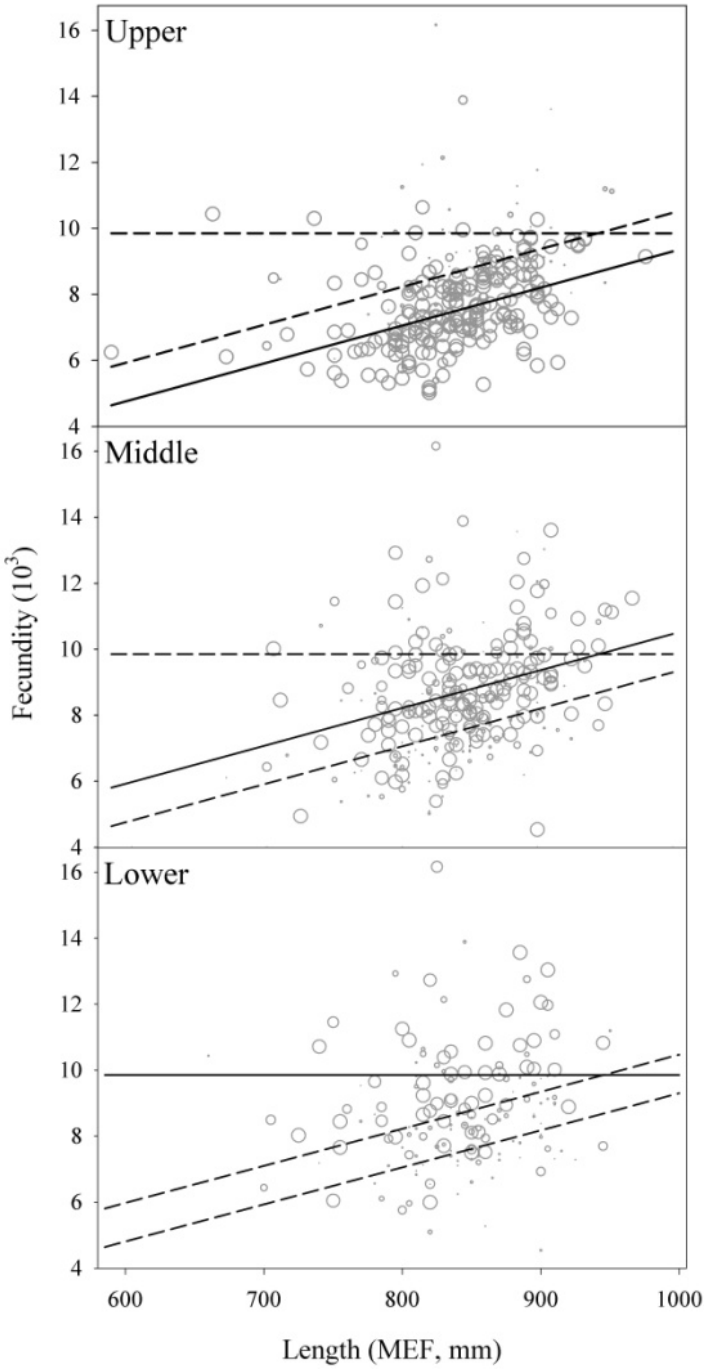

Figure 1. Mean fecundity as a function of length for each of three stock groups, taken from Bromaghin et al. (2011).

A number of recent investigations have reemphasized the importance of scale metrics as indirect indices of environmental conditions, availability of prey, and inter-specific competition on salmon growth and population dynamics (e.g., Ruggerone et al. 2003, 2004, 2009). Bromaghin et al. (2011) obtained scale samples from individual fish in their fecundity study. The present study examines those scales and uses scale growth increments to index seasonal somatic growth. Fecundity from the Bromaghin et al. (2011) analysis are modeled as a function of growth metrics obtained from the scales in an exploratory fashion to identify aspects of growth that are associated with the establishment of fecundity. Identification of critical growth and periods of growth will provide further insights into the importance of ecological conditions on

growth, link information on growth to both individual and population productivity, and assist managers in crafting biologically-relevant measures of the quality of escapement.

Objectives:

The primary objective is to test the hypothesis that the growth history of female Chinook salmon is an important predictor of their fecundity (number of eggs per female). The results of this investigation are expected to contribute to an improved understanding of the influence of the marine environment on Chinook salmon and their productivity. In addition, an improved understanding of the factors influencing Chinook salmon fecundity and productivity will facilitate ongoing early efforts to incorporate escapement quality into management systems and escapement goals**.**

2. Methods:

Bromaghin et al. (2011) describes methodology for the collection of fecundity, length (mid-eye to fork of tail), age, and genotype data from 403 female Chinook salmon caught in the Lower Yukon River Test Fishery in 2008. Scales collected in the Bromaghin et al. project were digitized by the Alaska Department of Fish and Game (ADF&G) Mark, Tag, and Age (MTA) Lab in Juneau, Alaska.

Individuals were excluded from this study if their scales were regenerated or there was a discrepancy in age determination between the original reading made by ADF&G Yukon Area research staff and MTA staff. Individuals used in this study spent one year in freshwater and three to five years in saltwater before returning to the river to spawn. Ages are recorded using European notation, where the number of freshwater annuli is separated by a decimal from the number of marine annuli succeeding it. A total of 386 individuals met these criteria: 71 Age-1.3, 273 Age-1.4, and 24 Age-1.5. Growth measurements from the scales were merged with existing data on fecundity, length, age, and genotype.

Scale digitization followed standard procedures (Hagen et al. 2001), where scales were scanned into microfiche readers, stored as digital files, and then distances between circuli were measured with imaging software. Zone distance, the distance within a growth zone, was measured in mm. Growth zones included FW1 (first year in freshwater), FW1PL (additional growth in the spring prior to ocean entry), SW1, 2, 3, 4, 5 (first through fifth years in saltwater, respectively) and SWPL (additional growth after the last annulus). Circuli within a growth zone were also counted.

Initial analyses were exploratory in nature, consisting of bivariate correlations and scatter plot graphics to investigate coarse-scale relationships between fecundity and measures of growth. Subsequently, linear regression models were developed for fecundity, length, stock and growth information. Data were modeled to include each of the twelve stock groups (Table 1), lengths for each stock group, and each growth zone apparent in each of the age classes (Age-1.3, 1.4 and 1.5). Fecundity data were log transformed to meet normality assumptions. In the first model, stock groups not significantly different from one another were combined, and then insignificant terms associated with scale measurements were subsequently dropped from the model. The second model was identical to the first but insignificant terms associated with scale measurements were dropped first, and stock groups were pooled afterwards. The third model was based upon residuals of the previous Bromaghin et al (2011) model fit of fecundity to length and stock of origin variables; i.e., the difference between observed and predicted fecundity

(Figure 1). Parameters used in this linear regression include residuals for each of the growth zone at age metrics.

Table 1 Stock groups reporting regions assigned to individual fish, as in Bromaghin et al. (2011).

	Stock Group
1	Andreafsky-Anvik
2	Gisasa
3	Tozitna
4	Upper Koyukuk
5	Tanana
6	Upper US
7	Lower Canada
8	Stewart-Mayo
9	Tincup
10	Pelly
11	Canada Mainstem
12	Upper Canada

3. Results:

For all age classes, growth tended to be lowest during their freshwater phase and tended to peak in the first year in saltwater (Figure 2). Afterwards, relative growth gradually declined in age 1.4 and 1.5 fish but remained high in age 1.3 fish. Higher growth measurements in SW1 appear to correspond to younger age at maturity (Figure 2).

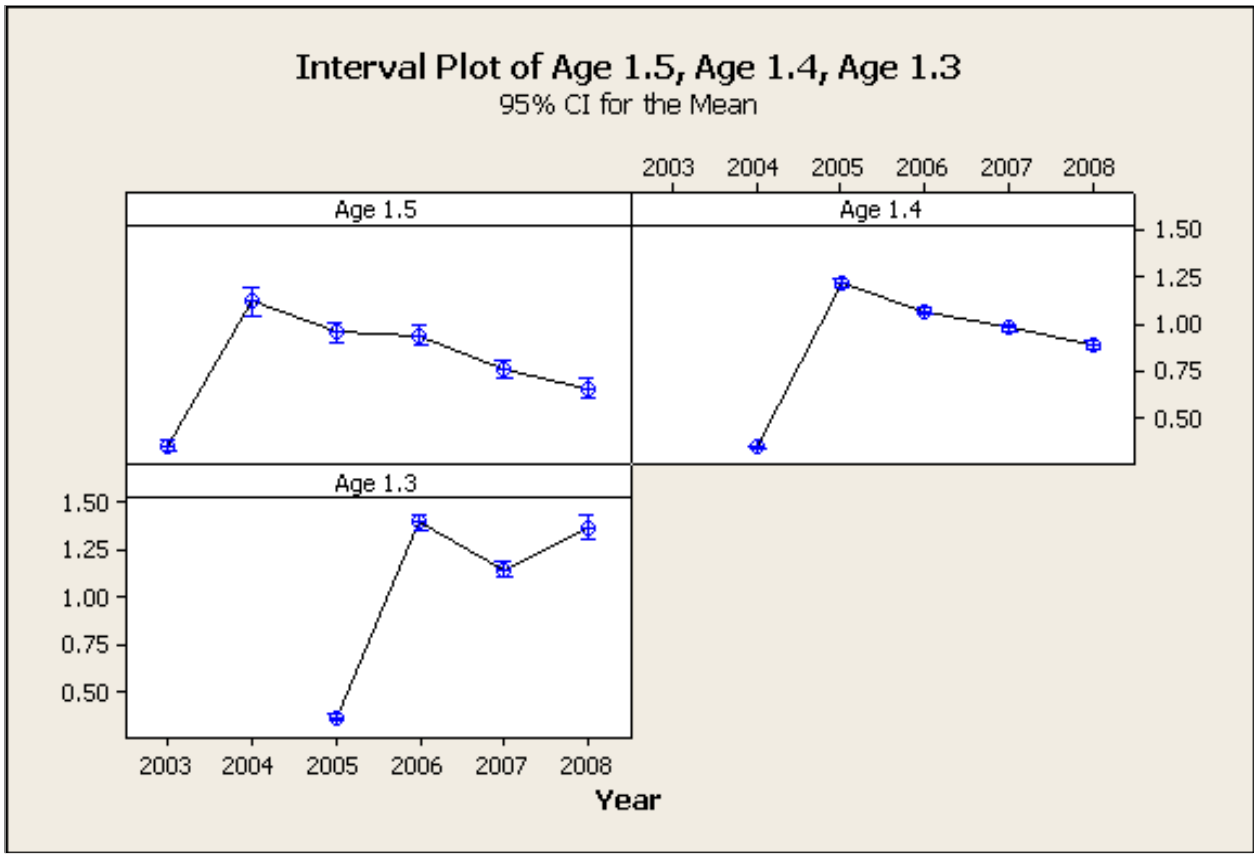

Figure 2 Scale growth in each year (FW1, SW1, SW2, etc.) for each of the three age classes. FW1 phase occurred in 2003 for age 1.5, 2004 for 1.4, and 2005 for 1.3.

Initial correlations suggested that growth for SW1 and in the year prior to maturation may weakly influence fecundity parameters (Figure 3 and 4). However, further modeling was not supportive of growth zone distance having significant influence on fecundity.

For the first model, prior to pooling stock groups, the only significant growth metric was SW1 for Age 3 fish (Table 2, p=0.017728). Pooling left four significantly different stock groups of 1-3, 4, 5-8 and 8-12. Under the pooled model, no growth zone by age parameters were significant at p=0.05 but Age-3 SW1 and SW3 were close to significance (Table 2, 0.0532 and 0.0768, respectively). Growth zone by age variables were eliminated consecutively, beginning with the least significant metrics. Throughout this process, Age-3 SW1 and SW3 remained only marginally close to significance.

In the second model, insignificant terms for scale growth were dropped first, leaving Age-3 SW1 as the only significant scale variable (Table 2, $p=2.2e^{-16}$). Stocks were subsequently pooled and model results were similar to Model 1.

The third model using residuals from the previous Bromaghin et al. (2011) model did not suggest significance for any of the growth zone at age parameters, although Age-3 SW1 was near significance (Table 2, p=0.0634). The overall model, however, was not significant. Insignificant terms were sequentially removed. After the removal of two parameters (Age-5 SW4 and Age-3

FW1), both the overall model and the Age-3 SW3 growth parameter were significant (Table 2, p=0.0496 and 0.0426, respectively). This model was further reduced to Age-3 SW3 only.

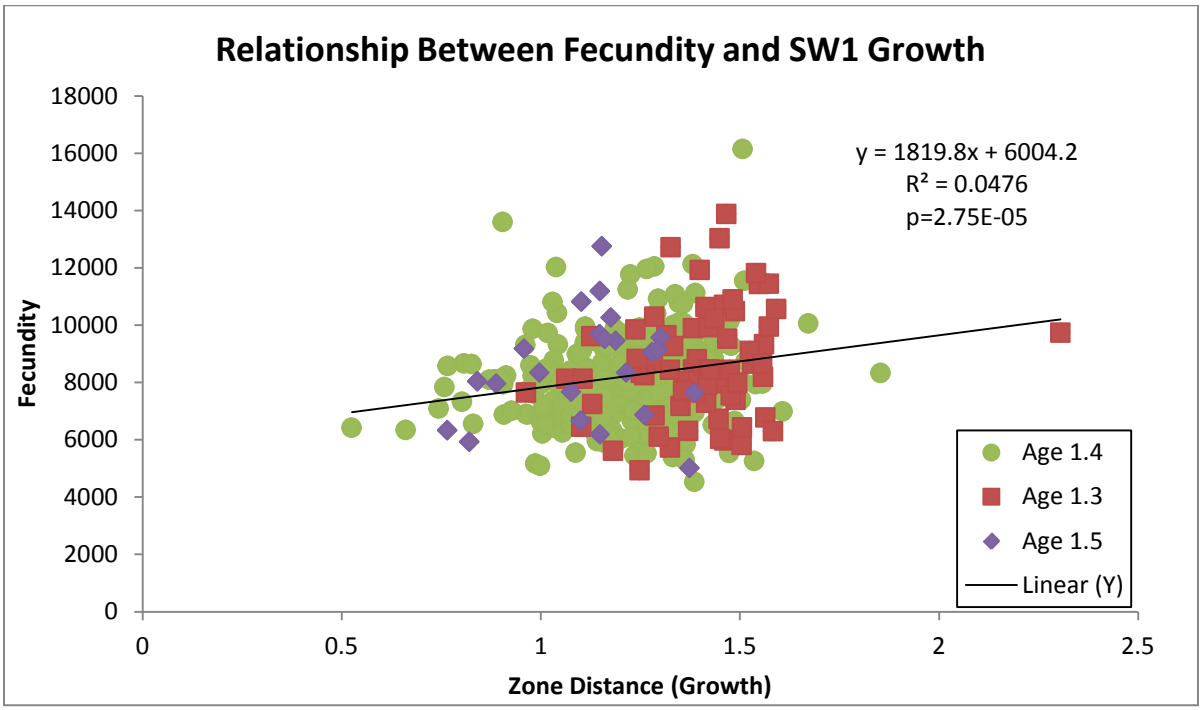

Figure 3 Weak relationship between fecundity and growth during the first year at sea. Zone distance is the scale distance of annual growth, used as a metric for somatic growth.

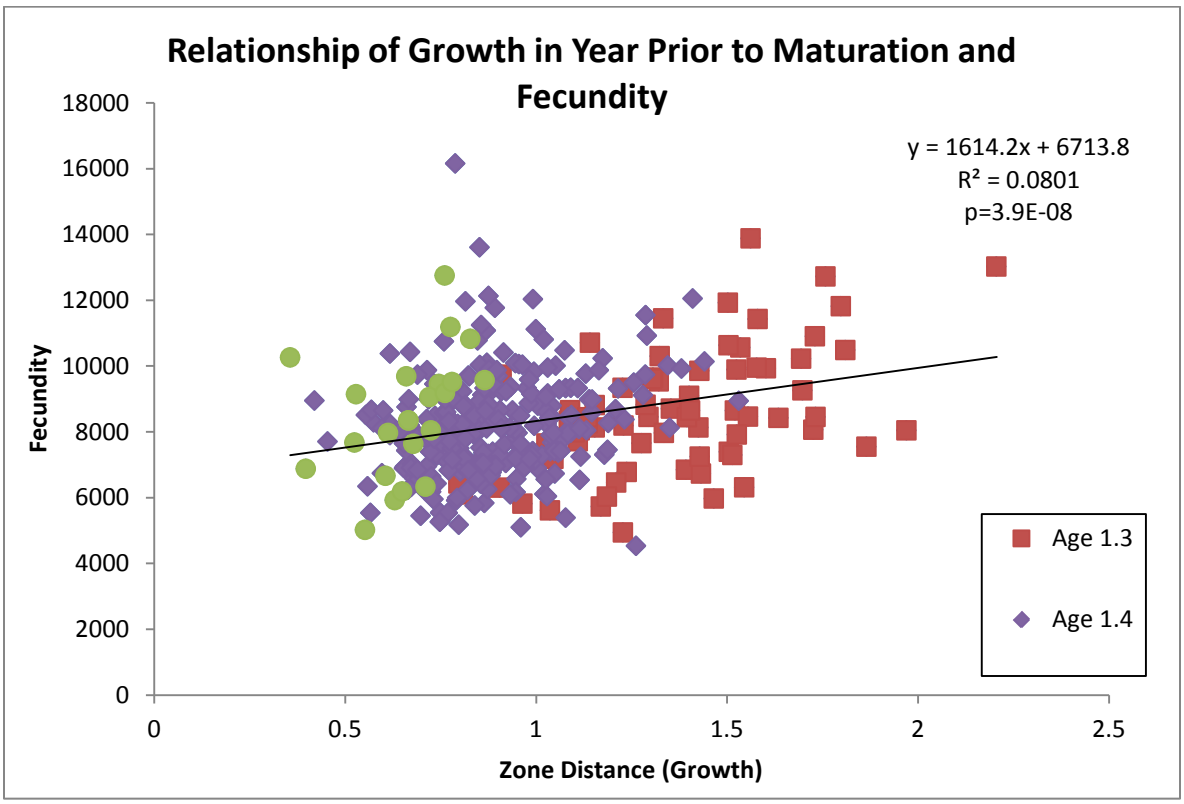

Figure 4 Weak relationship between fecundity and growth during the year prior to maturation. Zone distance is the scale distance of annual growth, used as a metric for somatic growth.

Table 2 Pertinent information from the three models explored in this study.

Model	**Residual Standard Error**	**Multiple R-squared**	**Adjusted R-squared**	**F-statistic**	**p-value**
1	0.1539 on 325 DF	0.4388	0.3732	6.687 on 38 and 325 DF	$2.2e^{-16}$
1 Pooled stock groups	0.1569 on 341 DF	0.3875	0.348	9.805 on 22 and 341 DF	$2.2e^{-16}$
2	0.1539 on 325 DF	0.4388	0.3732	6.687 on 38 and 325 DF	$2.2e^{-16}$
2 Age 3 SW1 only	0.1536 on 339 DF	0.4168	0.3755	10.09 on 24 and 339 DF	$2.2e^{-16}$
3	1370 on 348 DF	0.06109	0.0262	1.509 on 15 and 348 DF	0.09914
3	1366 on 350 DF	0.06104	0.02617	1.75 on 13 and	0.04962

Reduced by Age-5 SW4 and Age-3 FW1				350 DF	
3 Age-3 SW3 only	1360 on 362 DF	0.03721	0.03455	13.99 on 1 and 362 DF	0.0002134

4. Discussion:

Contrary to our hypothesis, it does not appear that growth metrics explain variation in fecundity for Chinook salmon in this study. While some weak correlations were initially observed, these could not be supported by more rigorous model assessment. As such, it appears that other factors may affect individual fecundity, while growth may be more important to an individuals' maturation schedule.

Factors such as egg size and condition of fish were not included in this study. A wealth of literature support the importance of both egg size and energetic condition in life history trade-offs related to fecundity (Beacham and Murray 1993; Smith and Fretwell 1974; Einum and Fleming 2000; Kinnison et al. 2001; Einum et al. 2004). For fish of the same size, some individuals may choose more eggs while others may choose to provide fewer, larger eggs with more lipids. Either life history strategy may confer better fitness, dependent upon local conditions and the likelihood of offspring from either life history strategy to survive to maturity in highly variable environments. Moreover, females with poorer energetic condition may choose different life history strategies than robust females, to maximize fitness given energy limitations. Because this study was located at the mouth of the Yukon River and egg development was variable (depending upon the spawning distance from the mouth of the river), it was not possible to measure egg size in these fish in a consistent manner. Many of the eggs examined were undeveloped and were observed prior to lipid sequestrations, while others already initiated lipid sequestration. Consequently, examination of the influence of either egg size or female energetic condition were not possible across fish at different stages in egg development. Had these measurements been taken, however, it may have been possible to examine the influence of these factors on fecundity for fish within a stock assignment. Future efforts should endeavor to either examine fecundity and these other factors at individual spawning locations, which has been a traditional methodology, or to study these factors within stock reporting regions for which individual assignment of fish is possible.

Outcomes and insight from this study could have been improved by expanding the study across multiple years. All fish examined in this study matured in 2008. If growth in the year prior to maturation is important to fecundity, as was suggested by Campbell et al. (2006), then interannual variation could be more important than intrannual variation in growth metrics. Additional sampling in other years could shed light on the relative variation within and between years immediately prior to maturation. Additionally, it may be that sampling in this study could have been biased. Salmon returns in 2008 were dominated by Age-5 fish (1.3), however sample size of the Age-6 fish (1.4) dwarfed the sample size of Age-5 fish in this study. All samples came from the Lower Yukon Test Fishery that employs large mesh gear, which is biased towards larger individuals. It is possible that smaller individuals with potentially differing growth metrics may be absent from the present study, thereby limiting the range of observations

available relative to what is naturally occurring. Future efforts should be made to ensure that sampling is fully representative of salmon returns.

While growth in this study may not have explained variation in fecundity, it may be an important predictor of maturity schedules. Growth rate thresholds have been demonstrated to determine maturity schedules in Atlantic salmon *Salmo salar* (Hutchings and Jones 1998), chum salmon *Oncorhynchus keta* (Morita and Fukuwaka 2006), Chinook salmon *O. tshawytscha* (Scheuerell 2005), and others. In the present study, Age-1.3 fish tended to have highest growth in the first year at sea and maintained high growth throughout ocean residency. Meanwhile, 1.4 and 1.5 fish growth was each successively lower in the first year at sea and tended to gradually decline thereafter. Bromaghin et al.'s 2011 study demonstrated that size of fish may influence fecundity in some but not all stocks, and even then other factors may play significant roles in determining fecundity. Given this, if mortality potential over an additional year at sea outweighs potential fecundity gains by increased growth, then an individual's fitness would increase by choosing to mature earlier and forego any modest gains in fecundity with larger size.

If growth determinants (such as above average marine temperatures or prey abundances) can be identified and growth-based maturity thresholds ascertained, then future run abundance forecasting may be enhanced by applying growth determinant knowledge for years during cohort duration at sea to growth-based maturity thresholds. This information could benefit both Sibling and spawner-recruit model run projections by better predicting the relative returns of different age classes from a given cohort. Additionally, this information could assist in long term projections of age class composition trends and future productivity of Yukon River stocks. Based on the preliminary information from this study, growth in the first year at sea may be critical for determining the ultimate maturity schedule for an individual. Future research should investigate marine ocean conditions that may influence growth rate of Yukon River Chinook salmon and the identification of growth-based maturity thresholds.

References:

Beacham, T. D., and C. B. Murray (1993) Fecundity and egg size variation in North American Pacific salmon (*Oncorhynchus*). Journal of Fish Biology 42:485-508.

Bromaghin J. F., D. F. Evenson, T. H. McLain and B. G. Flannery (2011) Using a genetic mixture model to study phenotypic traits: differential fecundity among Yukon River Chinook salmon. Transactions of the American Fisheries Society 140: 235-249

Campbell, B., B. R. Beckman, W. T. Fairgrieve, J. T. Dickey, and P. Swanson (2006) Reproductive investment and growth history in female coho salmon. Transactions of the American Fisheries Society 135:164-173.

Einum, S., and I. A. Fleming (2000) Highly fecund mothers sacrifice offspring survival to maximize fitness. Nature 405:565-567.

Einum, S., M. T. Kinnison, and A. P. Hendry (2004) Evolution of egg size and number. Pages 126-153 in A. P. Hendry, and S. C. Stearns, editors. Evolution illuminated: Salmon and their relatives. Oxford University Press, New York, New York.

Fleming, I. A. and M. R. Gross (1990) Latitudinal clines: A trade-off between egg number and size in Pacific salmon. Ecology 71:1-11.

Hagen, P. T., D. S. Oxman, and B. A. Agler (2001) Developing and deploying a high resolution imaging approach for scale analysis. Doc. 567. North Pacific Anadromous Fisheries Commission, 889 Pender Street, Vancouver, Canada. 11 p.

Healey, M. C. (2001) Patterns of gametic investment by female stream- and ocean-type chinook salmon. Journal of Fish Biology 58:1545-1556.

Healey, M. C., and W. R. Heard (1984) Inter- and intra-population variation in the fecundity of Chinook salmon (*Oncorhynchus tshawytscha*) and its relevance to life history theory. Canadian Journal of Fisheries and Aquatic Sciences 41:476-483.

Hutchings, J. A. and M. E. B. Jones (1998) Life history variation and growth rate thresholds for maturity in Atlantic salmon, *Salmo salar*. Canadian Journal of Fisheries and Aquatic Sciences. 55: 22-47.

Kinnison M. T., M. J. Unwin, A. P. Hendry, T. P. Quinn (2001) Migratory costs and the evolution of egg size and number in introduced and indigenous salmon populations. Evolution 55: 1656

Morita, K. and M. Fukuwaka (2006) Does size matter most? The effect of growth history on probabilistic reaction norm for salmon maturation. Evolution. 60 (7): 1516-1521.

Morita, K., T. Tamate, Y. Sugimoto, Y. Tago, T. Watanabe, H. Konaka, M. Sato, Y. Miyauchi, K. Ohkuma, and T. Nagasawa (2009) Latitudinal variation in egg size and number in anadromous masu salmon *Oncorhynchus masou*. Journal of Fish Biology 74:699-705.

Roff, D. (1988) The evolution of migration and some life history parameters in marine fishes. Environmental Biology of Fishes 22:133-146.

Ruggerone, G. T., and F. A. Goetz. 2004. Survival of Puget Sound Chinook salmon (Oncorhynchus tshawytscha) in response to climate-induced competition with pink salmon (Oncorhynchus gorbuscha). Canadian Journal of Fisheries and Aquatic Sciences 61:1756-1770.

Ruggerone G. T., J. L. Nielsen, B. A. Agler (2009) Climate, growth and population dynamics of Yukon River Chinook salmon. North Pacific Anadromous Fish Commission Bulletin 5: 279-285

Ruggerone, G. T., M. Zimmermann, K. W. Myers, J. L. Nielson, and D. E. Rogers (2003) Competition between asian pink salmon (oncorhynchus gorbuscha) and alaskan sockeye salmon (O. nerka) in the North Pacific ocean. Fisheries Oceanography 12:209-219.

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

Smith, C. C., and S. D. Fretwell (1974) The optimal balance between size and number of offspring. The American Naturalist 108:499-506.