Evaluation of Growth, Survival, and Recruitment of Chinook Salmon in Southeast Alaska Rivers

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Final report

First, I would like to express my appreciation for being awarded the PCCRC Fellowship. Without your support I would not have been able to complete my project.

Since receiving the PCCRC Fellowship extension I have completed the following activities: 1) orally presented the results of my thesis research at the national American Fisheries Society (AFS) meeting, 2) completed and defended my thesis, 3) and started preparing manuscripts for publication in peer-reviewed journals.

1) Presentations

1. Graham, C. J, and T. M. Sutton. 2016. Evaluation of growth, survival, and recruitment of Chinook salmon in southeast Alaska. 147th Annual Meeting of the American Fisheries Society, August 2016, Kansas City, Kansas.

2) Thesis completion

I successfully defended my thesis on October 6th, 2016 and the Graduate School accepted it on November 16th, 2016.

3) Manuscripts

I am currently preparing two manuscripts for publication in Transactions of the American Fisheries Society.

Introduction

Chinook salmon *Oncorhynchus tshawytscha* are culturally and economically important in southeastern Alaska (SEAK; Der Hovanisian et al. 2011). Recently, spawning run sizes of Chinook salmon have been dramatically reduced across Alaska, prompting researchers to identify the cause of these declines (ADF&G Chinook Salmon Research Team 2013). Previous research suggests that salmon abundance is mediated by size-dependent mortality, with the time period during freshwater and early marine residence being critical for influencing survival patterns and, ultimately, recruitment to the spawning stock (Beamish and Mahnken 2001). I used a time series of freshwater and marine scale growth patterns to determine the effects and relationships of freshwater and marine growth on survival to the age of reproduction for female Chinook salmon by brood year in the Taku and Unuk rivers in southeastern Alaska.

Study goals

1) Characterize the importance of freshwater (FW) and annual saltwater growth (e.g., SW1, SW2, etc.) in determining the recruitment success of Chinook salmon in SEAK.
2) Determine if growth dependency is present in Chinook salmon in SEAK.
3) Investigate the relationship between Chinook salmon smolt body size and survival to reproductive maturity.

Methods

Scale samples

A time series of freshwater- and marine-growth patterns for female Chinook Salmon from the Taku (1979 – 1986, 1990 – 2000, 2002 – 2008) and Unuk (1976, 1978 – 1989, 1993 – 2006) rivers was constructed by brood year (BY) using scales collected by the Alaska Department of Fish and Game (ADF&G). In both systems, scales were collected from the preferred area: two rows above the lateral line between the posterior end of the dorsal fin and the anterior end of the anal fin (Hagen et al. 2001).

Recruitment benchmarks

Estimates relating to the recruitment success (e.g., abundance, total return, marine survival) of Chinook Salmon stocks from the Taku and Unuk rivers were obtained from ADF&G. In both systems, biological data such as age, sex, and length (ASL) data were collected during their annual stock assessment programs, which allowed escapement, survival, and marine harvest to be estimated (Hendrich et al. 2008; McPherson et al. 2010). Total return was calculated as the sum of estimated in-river run and marine harvest for 1.2 to 1.5 age fish within a given BY. Marine survival was calculated as the ratio of BY total return and the estimated BY smolt abundance.

Relationship between annual growth zones and recruitment benchmarks

To determine the influence of annual growth on recruitment success, scale-growth patterns for the Taku and Unuk rivers were related to Chinook Salmon recruitment benchmarks (i.e., total return, productivity) using multiple regression analyses. Multiple regression models were constructed separately for each system due to their distinct freshwater and marine rearing locations. Prior to analyzing the data, weighted averages that accounted for differences in the BY abundances of age-1.3 and 1.4 fish were calculated for each annual growth zone and each BY class. The weighted averages for each system were then used to explain the variability in log-transformed BY recruitment benchmarks.

The influence of annual growth on marine survival of stocks from both systems was assessed using weighted simple linear regression. Models were fitted using weighted averages of annual growth zones as explanatory variables and log-transformed marine survival as the response variable. The current literature has demonstrated the importance of large body size in determining the survival and recruitment success of multiple species of Pacific salmon (Mortensen et al. 2000; Beamish et al. 2004; Moss et al. 2005; Farley et al. 2007; Murphy et al. 2013); therefore, statistical significance ($P < 0.05$) of explanatory variables was determined using a one-tailed t-test.

All parameters in the multiple regression and simple linear regression models were estimated using weighted-least-squares regression, with each BY in the model being weighted by the number of scale samples in that BY. Residuals obtained from fitting models were used to test the assumptions of multiple and simple regression analyses (i.e., normality, constant variance, and independence of errors; Quinn and Keough 2002).

Relationship between growth zones

The relationships between adjacent growth zones were examined using mixed-effects modeling. To determine if the growth of individual Chinook Salmon from each system was dependent on their previous growth, random intercept mixed-effects models were fitted by regressing each individual's annual growth zone on that individual's subsequent annual growth zone (e.g., FW1 versus SW1, SW1 versus SW2, etc.). The relationship between growth zones and BY represented the fixed effect and random effect, respectively.

Size-selective mortality at ocean entry

The relationship between smolt body size and survival to reproductive maturity was investigated by examining the skew of FW1 by BY. Previous research has shown that the length distribution of age-0 Chinook Salmon from the Taku River was normally distributed, and that size-selective mortality of small individuals results in positively skewed weight and length distributions of Chinook Salmon stocks (Murphy et al. 1989; Murphy et al. 2013; Woodson et al. 2013). Because the measured distance of the freshwater growth zone has been used as an index of size at marine entry for both Pacific and Atlantic salmon (Hogan and Friedland 2010; Leon 2013), the freshwater growth distribution (i.e., FW1) was used to represent the length-frequency distribution at ocean entry. Therefore, evidence for size-selective mortality at ocean entry was identified by examining the skew of FW1 distributions by BY. To determine the presence and nature of skew of the FW1 distribution, g_1 was calculated as:

$$g_1 = k_3/s^3,$$

where s^3 and k_3 represent the second and third moments around the mean, respectively (Zar 1999). Positive g_1 values indicated skewed right (positively skewed) distributions and, therefore,

g_1 values that were significantly greater than zero implied size-selective mortality during early marine residence. To determine if g_1 values were significantly greater than zero, one-tailed 95% confidence interval (CI) of BY g_1 values was constructed by bootstrapping the FW1 distributions of each BY class, using 100,000 replicates for each system. The high number of replicates was necessary to produce stable CIs due to BY with large sample sizes.

Results

Brood-year weighted annual growth was highest during the first year at sea, and declined each subsequent year for Chinook Salmon from the Taku and Unuk rivers (Table 1). There were no significant trends in the measured distance of any annual growth zone for either system (Table 1). Annual growth during freshwater residence displayed significantly lower variability than any other growth zone for Chinook Salmon from the Taku River (1.3-age [ANOVA: $F_{3,88} = 138.6$, $P < 0.001$] and 1.4-age [ANOVA: $F_{4,110} = 75.25$, $P < 0.001$]) and Unuk River (1.3-age [ANOVA: $F_{3,68} = 138.6$, $P < 0.001$] and 1.4-age [ANOVA: $F_{4,85} = 138.6$, $P < 0.001$]).

Relationship between brood year recruitment success and annual growth

For the Taku River, FW1 and SW2 were negatively related to total return, while SW1, SW3, and SW4 were positively related to total return (Figure 1). There were no significant relationships between any of the annual growth zones and BY total return or productivity when using sample sizes as weights in the regression model (Figure 1; Table 2). Overall, annual growth explained little variation in either total return ($R^2_{adj} = 0.07$) or productivity ($R^2_{adj} = 0.07$), when fitting models with weights. However, there appeared to be a positive-linear relationship between total return and first-year marine growth. When both models were fitted without using scale samples sizes as weights and SW1 as the only explanatory variable, first year marine growth explained significant amounts of variation in total return (R^2 = 0.21; P = 0.04) but not productivity (R^2 = 0.22; P = 0.09). The 1993 BY had the lowest weight and also had the lowest total return (16,840), productivity (0.21), and weighted first year marine growth (1.08 mm). This BY provided important contrast within the time series and lowering its weight affected the results of the analyses.

In contrast to the Taku River, all annual growth zones were positively related to total return in the Unuk River (Figure 1). There was a significant, positive relationship between SW1 and BY total return (Figure 1), and no other annual growth zone was significantly related to total return for this stock. Annual growth of Unuk River Chinook Salmon explained more variation in total return (R^2_{adj} = 0.33) than did annual growth for the Taku River model (R^2_{adj} = 0.07). Similar to the Taku River, no annual growth zones were significant predictors of log-transformed productivity when all of the growth zones were included in the model (Table 2). Although there was a strong positive relationship between SW1 and productivity (P = 0.1), annual growth explained little variation in productivity (R^2_{adj} = 0.06). Because of this relationship, another model was fitted using only SW1 to explain variance in BY productivity. When SW1 was the only explanatory variable in the model, there was a significant, positive relationship between growth during the first year at sea and stock productivity for Unuk River Chinook Salmon (Table 2; R^2 = *0.26*; P = 0.03).

Relationship between annual growth and marine survival

Weighted first-year marine growth was linearly related to marine survival of Taku and Unuk river Chinook Salmon stocks (Figure 2). In the Unuk River, there was a significant, positive relationship between marine survival and SW1 (Table 3; $R^2 = 0.37$; $P < 0.01$). No other growth zone was significantly related to marine survival for this stock. Similar to the Unuk River, there was a significant positive relationship between marine survival and SW1 of Taku River Chinook Salmon (Table 3; $R^2 = 0.32$; $P = 0.04$). There was also a significant positive relationship between SW3 and Taku River Chinook Salmon marine survival (Table 3; $R^2 = 0.30$; $P = 0.04$).

Relationship between growth zones

For Unuk River Chinook Salmon, there were no significant relationships between any of the adjacent growth zones (Table 4; Figure 3). In contrast, there were significant positive relationships between FW1 and SW1 and SW1 and SW2 for Taku River Chinook Salmon (Table 4; Figure 3). After the second year at sea, there were no significant relationships between any of the remaining adjacent growth zones for Taku River Chinook Salmon (Table 4).

Size-selective mortality at ocean entry

In both systems, there was evidence of size-selective mortality at ocean entry. For the Taku River, a total of 33 BY FW1 distributions were examined. Overall, 24 out of the 33 examined BY FW1 distributions had skew values that were greater than zero (Figure 4). Further, seven out of thirty-three one tailed 95% CIs were significantly greater than zero. In the Unuk River, 26 BYs FW1 distributions were investigated. Of those 26 BYs, 22 had measured skew values that were greater than zero and 12 of the 26 95% CIs were significantly greater than zero (Figure 4).

For Unuk River Chinook Salmon, there was a negative relationship between smolt abundance and the skew of FW1 distribution ($R^2 = 0.25$; $P = 0.07$). Further, there was also a negative relationship between smolt size and the skew of the BY FW1 distribution ($R^2 = 0.27$; $P = 0.06$). For Taku River Chinook Salmon, there was a negative relationship between smolt abundance and skew of the FW1 distribution; however, this relationship was weaker than for the Unuk River ($R^2 = 0.03$; $P = 0.44$).

Discussion

Influence of annual growth on survival

A retrospective scale analysis was conducted using two regionally important salmon-producing systems in an attempt to understand how annual growth influences the survival and recruitment success of Chinook Salmon stocks in SEAK. One important finding of this study was the significant, positive relationship between first-year marine growth and marine survival of Chinook Salmon from the Taku and Unuk rivers. This finding contributes to the considerable literature indicating the importance of growth and body size during the first marine year in determining marine survival and recruitment success of Pacific salmon (Beamish and Mahnken 2001; Mortensen et al. 2000; Beamish et al. 2004; Moss et al. 2005; Farley et al. 2007; Tomaro et al. 2012; Murphy et al. 2013; Miller et al. 2014). High growth rates during the first year at sea have been associated with greater survival rates of Coho *O. kisutch*, Pink *O. gorbuscha*, Chum *O. keta*, and Chinook Salmon stocks (Healey 1982; Beamish et al. 2004; Farley et al. 2007; Mortensen et al. 2000; Duffy and Beauchamp 2011; Murphy et al. 2013; Woodson et al. 2013; Miller et al. 2014). The positive relationship between growth during early marine residence and survival can be explained by size-selective mortality (Sogard 1997; Beamish and Mahnken 2001). Pacific salmon are thought to experience high rates of size-selective mortality during their first year at sea (Beamish et al. 2004; Farley et al. 2007). Based on the critical size, critical period hypothesis, rapid growth during early marine residence may increase Pacific salmon survival by allowing small individuals to outgrow size classes vulnerable to predation and/or store enough energy to survive the food-limited, first-year marine winter (Sogard 1997; Beamish and Mahnken 2001).

In the current study, the timing of mortality was unknown; therefore, it was not possible to attribute the observed relationship between SW1 and marine survival to reduced size-selective predation during the first few months at sea or to higher survival during the first marine winter. Chinook Salmon stocks within the region are thought to overwinter in the coastal waters of SEAK prior to migrating offshore; therefore, the timing of size-dependent mortality may be determined by sampling Chinook Salmon throughout their first marine year and comparing scale circuli spacing between sampling periods (Beamish et al. 2004; Orsi et al. 2013). Although the timing of mortality was unknown, the results of the current study highlight the importance of regional conditions that control growth and, ultimately, survival for Chinook Salmon stocks in SEAK. Further, these results suggest that the recent regional declines in Chinook Salmon abundance and productivity may be related to changes in growth conditions during the first year at sea.

Another important finding of the current study was the negligible effect of size at ocean entry (i.e., FW1) on marine survival of Chinook Salmon stocks from both systems. While large smolt body size has been shown to lead to higher survival in Atlantic Salmon and Pacific salmon (Jutila et al. 2006; Woodson et al. 2013), growth during early marine residence appears to have a greater influence on survival than does size at ocean entry in Pacific salmon (Duffy and Beauchamp 2011; Tomaro et al. 2012; Miller et al. 2014). For example, growth during the first 20 days at sea explained more variation in Snake River Chinook Salmon survival than did size at marine entry (Miller et al. 2014). However, large body size may still confer a survival advantage for Pacific salmon smolts, because the probability of experiencing size-selective mortality declines with increases in body size (Murphy et al. 2013). Large-bodied smolts appear to have a survival advantage; however, this advantage appears to be dependent on other factors such as cohort recruitment success and/or growth conditions during early marine residence (Holtby et al. 1990; Woodson et al. 2013; C. Graham, University of Alaska Fairbanks, unpublished data). For example, large smolt body size conferred a survival advantage Chinook and Coho Salmon smolts in years characterized by low, but not high, survival (Holtby et al. 1990; Woodson et al. 2013; Graham, unpublished). Holtby et al. (1990) found that the interannual variations in Coho Salmon survival were driven by early ocean growth rates, which in turn, were strongly correlated with oceanic conditions associated with high biological productivity. This led the authors to speculate that the relationship between smolt body size and survival may be dependent on early ocean growth conditions. Because the relationship between smolt body size and survival may depend on cohort survival and/or growth conditions during early marine residence, future research should focus on of how these factors interact to better understand the relative importance of growth in freshwater versus marine residence in determining the marine survival of Chinook Salmon within SEAK.

Size-selective mortality is the proposed mechanism that explains the positive relationship between growth and survival; therefore, the majority of current research examining the factors that influence Pacific salmon survival has focused on processes that occur when salmon inhabit size classes that are thought to be most susceptible to size-based predation (i.e., freshwater residence, early marine residence; Sogard 1997; Beamish and Mahnken 2001; Murphy et al. 2013; Woodson et al. 2013; Miller et al. 2014). However, because Chinook Salmon stocks may spend upwards of seven years in the marine environment, causes of mortality that occur after early ocean residence must be considered when examining the mortality dynamics of this species. Greene et al. (2005) examined the relationship between Skagit River Chinook Salmon return rates and environmental conditions during freshwater, estuarine, and marine residence and found a significant relationship between a factor negatively related to SSTs and positively related to sea level pressure and coastal upwelling during the third marine year and stock productivity. The authors postulated that conditions during the third year at sea could influence the energetic efficiency of spawning migrations with poor conditions (i.e., high SSTs) leading to increased energy expenditures and reduced survival. In the current study, enhanced growth during the third year at sea was associated with higher marine survival of Chinook Salmon from the Taku River. This stock of Chinook Salmon is thought to rear in the Gulf of Alaska and Bering Sea where they may be selectively targeted by predators such as Killer Whales *Orcinus orca* and/or Salmon Sharks *Lamna ditropis* (Ford et al. 1998; Nagasawa 1998; Ford and Ellis 2006). Because of the positive relationship between body size and swimming ability, high growth during the third year at sea may increase survival by allowing Chinook Salmon to escape potential predators. Current research using satellite pop-up-satellite tags suggests that Chinook Salmon with a mean fork length of 69 cm (range, 57 – 89 cm) in the Bering Sea and Gulf of Alaska may experience predation by both homeothermic and poikilothermic predators (M. Courtney, University of Alaska Fairbanks, personal communication). Therefore, size-selective mortality may explain the observed relationship between growth during the third year at sea and marine survival of Taku River Chinook Salmon.

Growth dependency

Results of the current study indicate that annual growth of individual Chinook Salmon from the Taku River is dependent on their previous annual growth through the second year at sea. Growth dependency between adjacent growth zones has also been found in individual Chinook Salmon from the Yukon and Kuskokwim rivers (Ruggerone et al. 2009; Leon 2013). As noted by Ruggerone et al. (2009), growth dependency may be the result of developmental changes in prey availability and the highly piscivorous diet of Chinook Salmon (Quinn 2005; Davis et al. 2009). In general, as Chinook Salmon increase in size, their diets contain higher proportions of fish (Schabetsberger et al. 2003). High growth rates during freshwater residence could allow an earlier transition to fish-based diets, which in turn, could increase growth rates during the first year at sea due to their higher energy content (Boldt and Haldorson 2002; Pazzia et al. 2002).

Size-selective mortality at ocean entry

The results of the current study indicate that Chinook Salmon from the Taku and Unuk rivers may experience size-selective mortality at ocean entry. Pacific salmon smolts are thought to face high rates of size-selective predation when entering predator-rich coastal environments (Quinn 2005; Murphy et al. 2013). Murphy et al. (2013) compared the weight distributions of juvenile and mature Chinook Salmon from the Yukon River and found that heavier smolts were more likely to survive their ocean residence than lighter individuals within the cohort. Due to the strong positive relationship between length and weight in Chinook Salmon smolts (Tattam et al. 2015), the results from Murphy et al. (2013) implied that longer fish also had higher survival. In addition, Woodson et al. (2013) found that large-bodied Chinook Salmon smolts from California's Central Valley were more likely to survive the first month at sea than smaller members of their cohort. In the current study, FW1 distributions of stocks from both systems were positively skewed more than would be expected by chance, with 21% of the Taku River Chinook Salmon and 46% of the Unuk River Chinook Salmon BY FW1 distributions exhibiting significant, positive skew. The higher percentage of significantly skewed FW1 distributions for Unuk River Chinook Salmon may be attributed to their relatively lower smolt abundance than Taku River Chinook Salmon. High abundances have been shown to reduce the per-capita predation rates of Sockeye Salmon *O. nerka* (Furey et al. 2016). However, few studies have investigated how prey abundance affects the size selectivity of predators. Cunningham et al. (2013) found that in years of high Sockeye Salmon abundances, Brown Bears *Ursus arctos* exhibited lower rates of size selectivity. In the current study, smolt abundance and skew of the freshwater growth distributions were negatively related for both systems, which implied lower levels of size-selective mortality when Chinook Salmon abundances were high. Therefore, if high smolt abundances reduce the rate of size-selective mortality, then freshwater growth may be more important for reducing size-selective mortality at ocean entry for smaller stocks within the region.

One limitation of the use of the skewness of FW1 distributions to identify size-selective mortality at ocean entry was the unknown length distribution of outmigrating smolts. If Pacific salmon face high rates of size-selective mortality during freshwater residence, their length distributions may become positively skewed prior to ocean entry. In addition, large fish may become dominant and, as a result, become better able to compete for resources (Abbott and Dill 1989); consequently, the observed skew in freshwater growth distributions may also be the result of larger fish growing at faster rates than smaller individuals within these stocks. Previous research indicates that freshwater length distribution of age-0 Chinook Salmon from the Taku River was is normally distributed (Murphy et al. 1989). The results of the current study (i.e., negative relationship between both smolt abundance and size and skew of the FW1 distribution) in conjunction with previous research, which found evidence of size-selective mortality at ocean entry, suggest that the observed skew of FW1 distributions from both systems is the result of size-selective mortality during early marine residence. In addition, the variability of the in BY FW1 distributions was significantly lower than any other annual growth zone for Chinook Salmon from both systems, suggesting selection for a minimum smolt body size to survive to reproductive maturity. Future research that compares the freshwater growth increment of smolts sampled during or shortly after their outmigration with mature fish sampled during their spawning migration could provide more convincing evidence of size-selective mortality at ocean entry (Murphy et al. 2013).

Conclusions

The results of the current study highlight the importance of growth during the first marine year in influencing the survival of Pacific salmon stocks in SEAK and suggest that the current declines in Chinook Salmon abundance within the region may be attributed to changes in growth or growth conditions during the first year at sea. While growth during freshwater residence was not related to the survival or recruitment success of either stock, it may still influence Chinook Salmon survival patterns by facilitating early ocean growth rates and reducing size-selective mortality at ocean entry. Finally, while the majority of the current research has focused on processes during freshwater and early marine residence when trying to describe variability in recruitment success and survival, results of this study indicate that survival may be influenced by processes happening later in the life of Chinook Salmon (i.e., third year of marine growth).

Literature cited

Abbott, J. C., and L. M. Dill. 1989. The relative growth of dominant and subordinate juvenile Steelhead Trout (*Salmo gairdneri*) fed equal rations. Behaviour 108:104–113.

ADF&G Chinook Salmon Research Team. 2013. Chinook Salmon assessment and research plan, 2013. Alaska Department of Fish and Game, Special Publication No. 13−01, Anchorage.

Beamish, R. J., and C. Mahnken. 2001. A critical size and period hypothesis to explain natural regulation of salmon abundance and the linkage to climate and climate change. Progress in Oceanography 49:423–437.

Beamish, R. J., C. Mahnken, and C. M. Neville. 2004. Evidence that reduced early marine growth is associated with lower marine survival of Coho Salmon. Transactions of the American Fisheries Society 133:26–33.

Boldt, J., and L. J. Haldorson. 2002. A bioenergetics approach to estimating consumption of zooplankton by juvenile Pink Salmon in Prince William Sound, Alaska. Alaska Fishery Research Bulletin 9:111–127.

Cunningham, C. J., G. T. Ruggerone, and T. P. Quinn. 2013. Size selectivity of predation by Brown Bears depends on the density of their Sockeye Salmon prey. The American Naturalist 181:663–673.

Davis, N. D., A. V. Volkov, A. Y. Efimkin, N. A. Kuznetsova, J. L. Armstrong, and O. Sakai. 2009. Review of BASIS salmon food habits studies. North Pacific Anadromous Fish Commission Bulletin 5:197–208.

Der Hovanisian, J., S. McPherson, E. Jones, P. Richards, R. Chapell, B. Elliott, T. Johnson, and S. Fleischman. 2011. Chinook Salmon status and escapement goals for stocks in

Southeast Alaska. Alaska Department of Fish and Game, Special Publication No. 11−19, Anchorage.

Duffy, E. J., and D. A. Beauchamp. 2011. Rapid growth in the early marine period improves the marine survival of Chinook Salmon (*Oncorhynchus tshawytscha*) in Puget Sound, Washington. Canadian Journal of Fisheries and Aquatic Sciences 68:232–240.

Farley, E. V., J. H. Moss, and R. J. Beamish. 2007. A review of the critical size, critical period hypothesis for juvenile Pacific salmon. North Pacific Anadromous Fish Commission Bulletin 4:311–317.

Ford, J. K. B., and G. E. Ellis. 2006. Selective foraging by fish-eating Killer Whales *Orcinus orca* in British Columbia. Marine Ecology Progress Series 316:185–199.

Ford, J. K. B., M. E. Graeme, L. G. Barrett-Lennard, A. B. Morton, R. S. Palm, and K. C. Balcomb III. 1998. Dietary specialization in two sympatric populations of Killer Whales (*Orcinus orca*) in coastal British Columbia and adjacent waters. Canadian Journal of Zoology 76:1456–1471.

Furey, N. B., S. G. Hinch, A. L. Bass, C. T. Middleton, V. Minke-Martin, and A. G. Lotto. 2016. Predator swamping reduces predation risk during nocturnal migration of juvenile salmon in a high-mortality landscape. Journal of Animal Ecology 85:948–959.

Greene, C. M., D. W. Jensen, G. R. Press, E. A. Steel, and E. Beamer. 2005. Effects of environmental conditions during stream, estuary, and ocean residency on Chinook Salmon return rates in the Skagit River, Washington. Transactions of the American Fisheries Society 134:1562–1581.

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

Anadromous Fish Commission Document 567, Juneau.

Healey, M. C. 1982. Timing and relative intensity of size-selective mortality of juvenile Chum Salmon (*Oncorhynchus keta*) during early sea life. Canadian Journal of Fisheries and Aquatic Sciences 39:952–957.

Hendrich, C. F., J. L. Weller, S. A. McPherson, D. R. Bernard. 2008. Optimal production of Chinook Salmon from the Unuk River. Alaska Department of Fish and Game, Fishery Manuscript No. 08–03, Anchorage.

Hogan, F., and K. D. Friedland. 2010. Retrospective growth analysis of Atlantic Salmon *Salmo salar* and implications for abundance trends. Journal of Fish Biology 76:2502–2520.

Holtby, L. B., B. C. Andersen, and R. K. Kadowaki. 1990. Importance of smolt size and early ocean growth to interannual variability in marine survival of Coho Salmon (*Oncorhynchus kisutch*). Canadian Journal of Fisheries and Aquatic Sciences 47:2181–2194.

Jutila, E., E. Jokikokko, and M. Julkunen. 2006. Long-term changes in the smolt size and age of Atlantic Salmon, *Salmo salar* L., in a northern Baltic river related to parr density, growth opportunity and postsmolt survival. Ecology of Freshwater Fish 15:321–330.

Leon, J. M. 2013. Freshwater growth and recruitment of Yukon and Kuskokwim river Chinook Salmon: a retrospective growth analysis. Master's thesis, University of Alaska, Fairbanks.

McPherson, S. A., E. L. Jones III, S. J. Fleischman, and I. M. Boyce. 2010. Optimal production of Chinook Salmon from the Taku River through the 2001 year class. Alaska Department of Fish and Game, Fishery Manuscript Series No. 10–03, Anchorage.

Miller, J. A., D. J. Teel, W. T. Peterson, and A. M. Baptista. 2014. Assessing the relative importance of local and regional processes on the survival of a threatened salmon population. PLoS One 9(6):e99814.

Mortensen, D., A. Wertheimer, S. Taylor, and J. Landingham. 2000. The relation between early marine growth of Pink Salmon, *Oncorhynchus gorbuscha*, and marine water temperature, secondary production, and survival to adulthood. Fishery Bulletin 98:319–335.

Moss, J. H., D. A. Beauchamp, A. D. Cross, K. W. Myers, E. V. Farley Jr. J. M. Murphy, and J. H. Helle. 2005. Evidence for size-selective mortality after the first summer of ocean growth by Pink Salmon. Transactions of the American Fisheries Society 134:1313–1322.

Murphy, J., K. Howard, L. Eisner, A. Andrews, W. Templin, C. Guthrie, K. Cox, and E. Farley. 2013. Linking abundance, distribution, and size of juvenile Yukon River Chinook Salmon to survival in the northern Bering Sea. North Pacific Anadromous Fish Commission Technical Report No. 9:25–30.

Murphy, M. L., J. Heifetz, J. F. Thedinga, S. W. Johnson, and K. V. Koski. 1989. Habitat utilization by juvenile Pacific salmon (*Oncorhynchus*) in the glacial Taku River, Southeast Alaska. Canadian Journal of Fisheries and Aquatic Sciences 46:1677–1685.

Nagasawa, K. 1998. Predation by Salmon Sharks (*Lamna ditropis*) on Pacific salmon (*Oncorhynchus* spp.) in the North Pacific Ocean. North Pacific Anadromous Fish Commission Bulletin 1:419–433.

Orsi, J. A., M. V. Sturdevant, E. A. Fergusson, W. R. Heard, and E. V. Farley Jr. 2013. Chinook Salmon marine migration and production mechanisms in Alaska. North Pacific Anadromous Fish Commission Technical Report 9:240–243.

Pazzia, I., M. Trudel, M. Ridgway, and J. B. Rasmussen. 2002. Influence of food web structure on the growth and bioenergetics of Lake Trout (*Salvelinus namaycush*). Canadian Journal of Fisheries and Aquatic Sciences 59:1593–1605.

Quinn, G. P., and M. J. Keough. 2002. Experimental design and data analysis for biologists. Cambridge University Press, United Kingdom.

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

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

Schabetsberger, R., C. A. Morgan, R. D. Brodeur, C. L. Potts, W. T. Peterson, and R. L. Emmett. 2003. Prey selectivity and diel feeding chronology of juvenile Chinook (*Oncorhynchus tshawytscha*) and Coho (*O. kisutch*) Salmon in the Columbia River plume. Fisheries Oceanography 16:523–540.

Sogard, S. M. 1997. Size-selective mortality in the juvenile stage of teleost fishes: a review. Bulletin of Marine Science 60:1129–1157.

Tattam, I. A., J. R. Ruzycki, J. L. McCormick, and R. W. Carmichael. 2015. Length and condition of wild Chinook Salmon smolts influence age at maturity. Transactions of the American Fisheries Society 144:1237–1248.

Tomaro, L. M., D. J. Teel, W. T. Peterson, and J. A. Miller. 2012. When is bigger better? early marine residence of middle and upper Columbia River spring Chinook Salmon. Marine Ecology Progress Series 452:237–252.

Woodson, L. E., B. K. Wells, P. K. Weber, R. B. MacFarlane, G. E. Whitman, and R. C. Johnson. 2013. Size, growth, and origin-dependent mortality of juvenile Chinook Salmon *Oncorhynchus tshawytscha* during early ocean residence. Marine Ecology Progress Series 487:163–175.

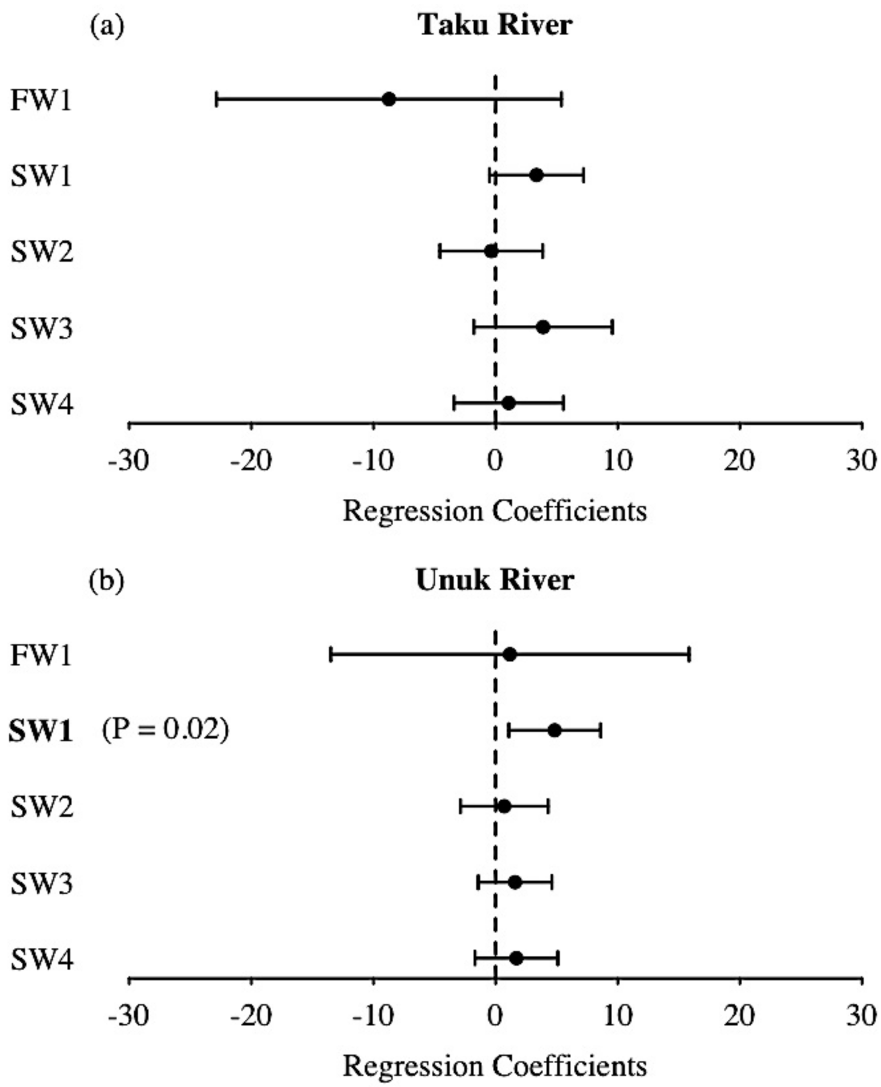


Figure 1. Visualization of the multiple regression models that were fitted using weighted annual growth zones (freshwater growth [FW1], first [SW1], second [SW2], third [SW3], and fourth [SW4] years of marine growth) on the y axis to explain variance in brood-year total return in the (a) Taku and (b) Unuk rivers. On the x axis are the estimated regression coefficients and their 95% CIs. The dashed vertical line is at zero; coefficients that fall to the right and left of the line indicate a positive and negative relationship between that annual growth zone and brood-year total return, respectively. Weighted annual growth zones in bold were found to explain statistically significant ($P < 0.05$) amounts of variance in brood-year total return.

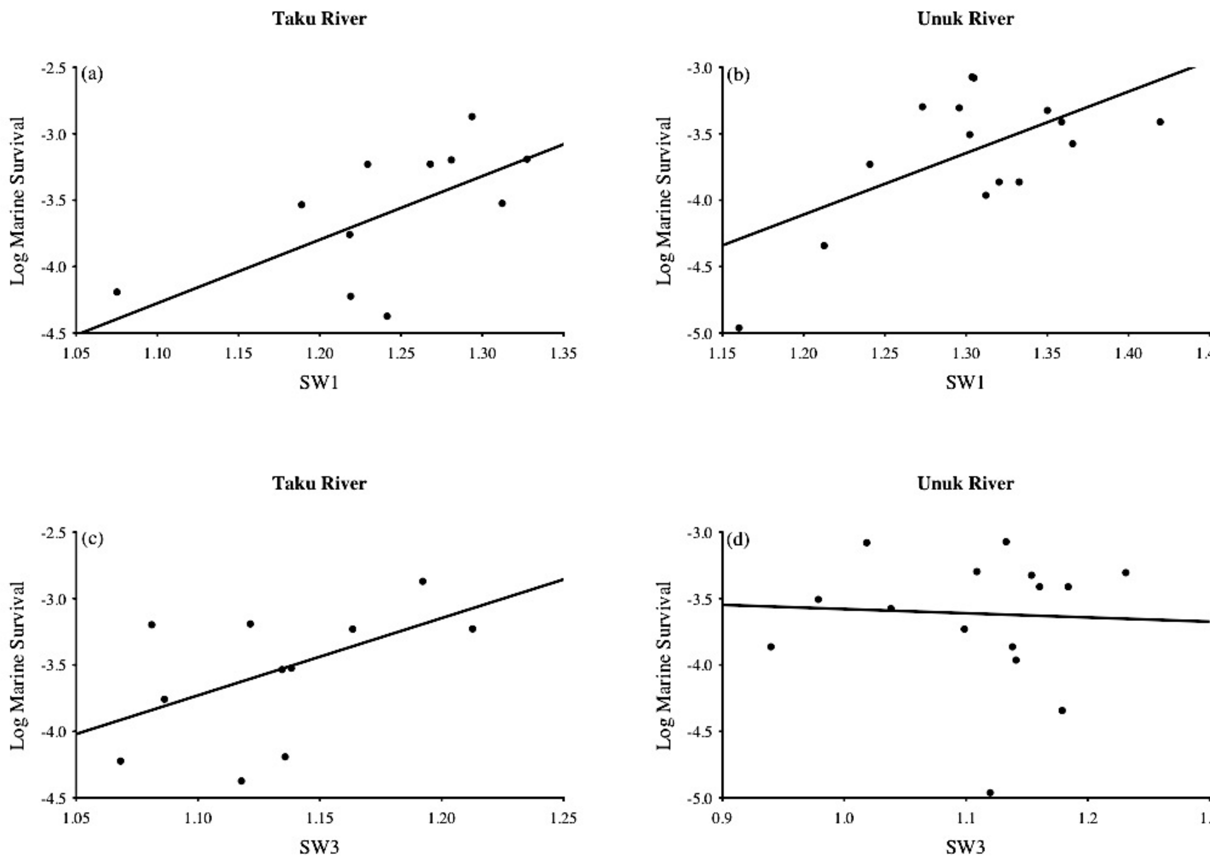


Figure 2. Scatter plots showing relationships between first- and third-year marine growth and marine survival for (a, c) Taku and (b, d) Unuk river Chinook Salmon. The solid black line was obtained from simple linear regression models that used annual growth to explain variance in marine survival.

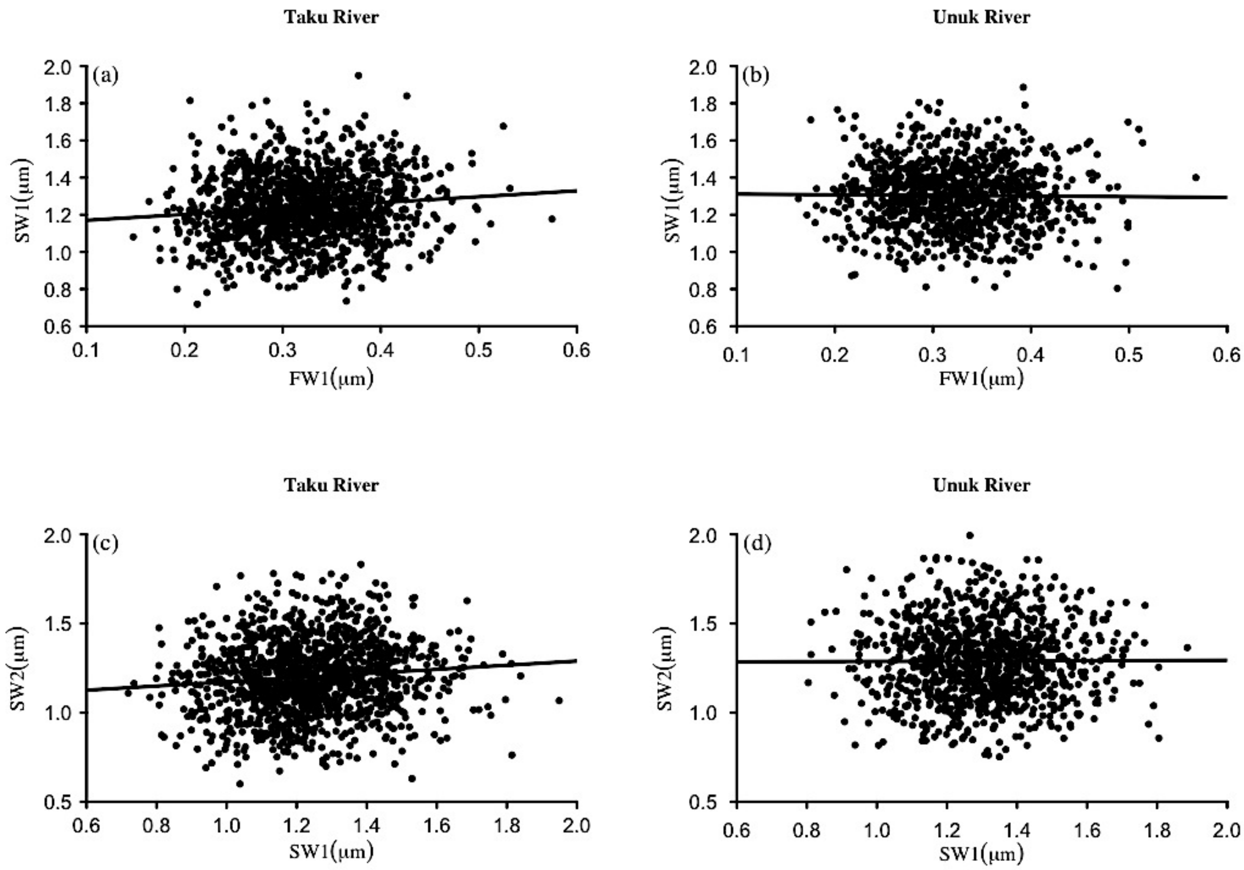
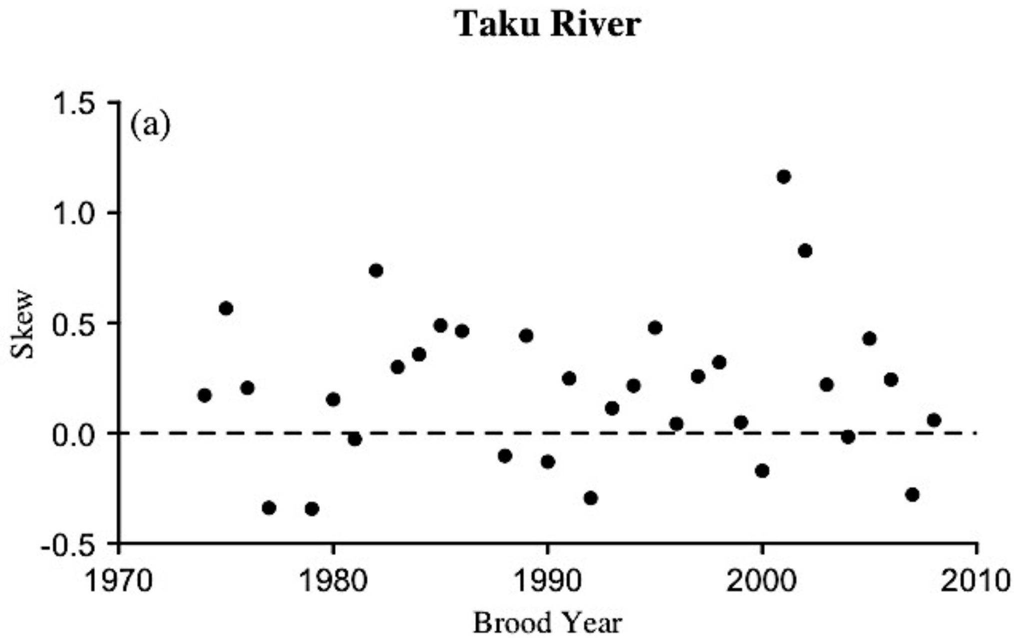


Figure 3. Relationships between adjacent growth zones in (a, c) Taku and (b, d) Unuk river Chinook Salmon stocks. The lines were obtained by fitting simple linear regression models using the previous growth zone to predict the subsequent growth zone.



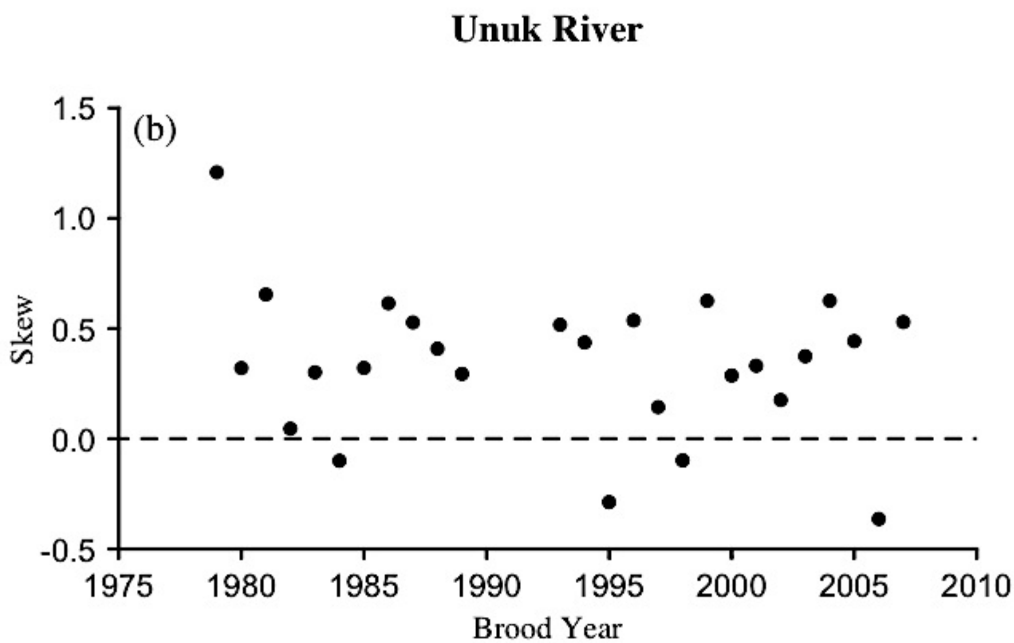


Figure 4. Scatter plot with skew of brood-year freshwater growth distributions on the y axis and brood year on the x axis for the (a) Taku and (b) Unuk rivers. The dashed line is at zero; points that fall above the line indicate positive skew of freshwater growth distribution.

Table 1. Mean distance, range, and standard deviation of weighted annual growth zones (freshwater growth [FW1], first [SW1], second [SW2], third [SW3], and fourth [SW4] years of marine growth), by brood year, for Taku and Unuk river Chinook Salmon stocks. Regression coefficients (β), standard errors, t-values, and *P*-values were obtained from simple linear regression models that regressed each annual growth zone on brood year to determine if there were trends in annual growth across the time series.

System	Growth zone	Mean growth	Range	SD	β	Standard error	t-value	*P*-value
Taku River	FW1	0.32	0.28 – 0.35	0.02	< -0.001	< 0.001	-0.47	0.64
	SW1	1.25	1.08 – 1.35	0.07	< -0.001	0.002	-0.36	0.72
	SW2	1.21	1.09 – 1.31	0.07	0.001	0.002	0.88	0.39
	SW3	1.11	0.99 – 1.21	0.05	< -0.001	0.001	-0.14	0.89
	SW4	0.79	0.69 – 0.96	0.06	-0.002	0.001	-1.46	0.16
Unuk River	FW1	0.32	0.29 – 0.36	0.02	< -0.001	0.001	-1.82	0.09
	SW1	1.30	1.16 – 1.41	0.07	-0.002	0.002	-0.98	0.34
	SW2	1.29	1.15 – 1.43	0.08	0.002	0.002	0.92	0.37
	SW3	1.11	0.94 – 1.23	0.08	-0.004	0.002	-1.48	0.16
	SW4	0.76	0.69 – 0.92	0.07	-0.003	0.002	-1.79	0.09

Table 2. Results of weighted multiple regression models (regression coefficient [β]) that examined the influence of weighted annual growth (freshwater growth [FW1], first [SW1], second [SW2], third [SW3], and fourth [SW4] years of marine growth) on log-transformed brood-year productivity for Taku and Unuk river Chinook Salmon.

		Model				
Dependent variable	Independent variable	β	Standard error	t-value	*P*-value	Adjusted R-squared
Taku River						
Productivity	FW1	2.97	9.96	0.30	0.77	0.07
	SW1	3.05	2.72	1.12	0.28	
	SW2	-5.09	2.97	-1.71	0.11	
	SW3	3.12	4.00	0.78	0.45	
	SW4	-0.26	3.16	-0.08	0.94	
Unuk River						
Productivity	FW1	5.51	11.63	0.47	0.64	0.06
	SW1	5.31	2.98	1.78	0.10	
	SW2	1.24	2.84	0.44	0.67	
	SW3	1.32	2.39	0.55	0.59	
	SW4	1.56	2.69	0.58	0.57	
Productivity	SW1	5.14	2.12	2.43	0.03	0.22

Table 3. Results of weighted simple linear regressions (regression coefficient [β]) that examined the influence of weighted annual growth during the first (SW1) and third (SW3) years at sea on the marine survival of Taku and Unuk river Chinook Salmon.

		Model				
Dependent variable	Independent variable	β	Standard error	t-value	*P*-value	R-squared
Taku River						
Marine survival	SW1	4.79	2.35	2.04	0.04	0.32
	SW3	5.82	2.99	1.94	0.04	0.30
Unuk River						
Marine survival	SW1	4.63	1.69	2.74	< 0.01	0.37

Table 4. Pearson's product-moment correlation coefficient (r) and results of mixed-effects models (regression coefficient [β], and degrees of freedom [DF]) that examined the relationships between adjacent growth zones (freshwater growth zone [FW1], and first [SW1], second [SW2], third [SW3], and fourth [SW4] year marine growth zones) of individual fish collected in the Taku and Unuk rivers.

			Model				
Dependent variable	Independent variable	r	β	Standard error	DF	t-value	*P*-value
Taku River							
SW1	FW1	0.11	0.32	0.078	1273	4.040	< 0.001
SW2	SW1	0.10	0.12	0.031	1273	3.916	< 0.001
SW3	SW2	-0.03	-0.02	0.027	1178	-0.677	0.50
SW4	SW3	-0.08	-0.04	0.036	481	-1.089	0.28
Unuk River							
SW1	FW1	-0.01	0.08	0.089	966	0.948	0.34
SW2	SW1	0.01	-0.04	0.040	965	-1.008	0.31
SW3	SW2	-0.07	-0.03	0.033	739	-0.873	0.38
SW4	SW3	0.05	0.04	0.057	211	0.781	0.44