Linking marine and freshwater growth in western Alaska Chinook salmon Oncorhynchus tshawytscha

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The hypothesis that growth in Pacific salmon Oncorhynchus spp. is dependent on previous growth was tested using annual scale growth measurements of wild Chinook salmon Oncorhynchus tshawytscha returning to the Yukon and Kuskokwim Rivers, Alaska, from 1964 to 2004. First-year marine growth in individual O. tshawytscha was significantly correlated with growth in fresh water. Furthermore, growth during each of 3 or 4 years at sea was related to growth during the previous year. The magnitude of the growth response to the previous year’s growth was greater when mean year-class growth during the previous year was relatively low. Length (eye to tail fork, LETF) of adult O. tshawytscha was correlated with cumulative scale growth after the first year at sea. Adult LETF was also weakly correlated with scale growth that occurred during freshwater residence 4 to 5 years earlier, indicating the importance of growth in fresh water. Positive growth response to previous growth in O. tshawytscha was probably related to piscivorous diet and foraging benefits of large body size. Faster growth among O. tshawytscha year classes that initially grew slowly may reflect high mortality in slow growing fish and subsequent compensatory growth in survivors. Oncorhynchus tshawytscha in this study exhibited complex growth patterns showing a positive relationship with previous growth and a possible compensatory response to environmental factors affecting growth of the age class.

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INTRODUCTION

Growth in Pacific salmon Oncorhynchus spp. has a strong influence on survival to maturity, life-history characteristics and reproductive success (Beamish et al., 2004; Vøllestad et al., 2004; Quinn, 2005). Greater growth of Oncorhynchus spp. in fresh water (Henderson & Cass, 1991; Koenings et al., 1993), early marine life (Ruggerone & Goetz, 2004; Moss et al., 2005; Farley et al., 2007) and during the second year at sea (Ruggerone et al., 2003) has been associated with greater survival. Mechanisms linking growth to survival involve higher rates of predation on smaller slow growing individuals and higher lipid content of faster growing individuals that may enable Oncorhynchus spp. to survive through the winter when prey are less available (Beamish & Mahnken, 2001). Outside of harvest, however, the cause of

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death at sea is rarely quantified. Growth also affects key salmonid life-history traits, such as age at maturation, fecundity and egg size (Healey, 1986; Jonsson et al., 1996; Quinn et al., 2004). Larger Oncorhynchus spp. have greater competitive ability during mating, although large body size is disadvantageous in shallow streams (Blair et al., 1993; Hamon & Foote, 2005). The evolution of anadromy in Oncorhynchus spp. is probably a response to increased growth and associated benefits gained by migrating to sea where numerous large prey can be found (Gross et al., 1988; Helle, 1989; Quinn & Myers, 2005).

Genetic and environmental factors influence the growth rates of Oncorhynchus spp. In nature, some fishes may encounter periods of low prey availability or low temperatures leading to reduced growth. Compensatory growth is a phase of accelerated growth when favourable conditions are restored after a period of depressed growth (Ali et al., 2003). Although reduced growth may lead to higher risks of predation and mortality, a variety of studies indicate individual fishes can undergo compensatory growth such that their growth rate exceeds that of fishes that were initially larger (Bilton & Robins, 1973; Damsgard & Dill, 1998; Ali et al., 2003).

Salmonids can exhibit enhanced growth at different life stages, such as during an ontogenetic shift in diet from zooplankton to forage fishes and squid (Kaeriyama et al., 2000; Kelley, 2001). At higher latitudes, fish growth at sea is typically faster than growth in fresh water (Gross, 1987; Vøllestad et al., 2004). Faster growing fishes may be more capable of capturing larger prey at an earlier age, leading to greater metabolic efficiency, increased growth and higher survival rates (Mortensen et al., 2000; Quinn, 2005). Timing of an ontogenetic shift in diet among pink Oncorhynchus gorbuscha (Walbaum) and sockeye salmon Oncorhynchus nerka (Walbaum) in the North Pacific Ocean may be important for subsequent growth (Aydin, 2000, Aydin et al., 2005). Salminen (1997, 2002) reported that large Atlantic salmon Salmo salar L. smolts experienced enhanced growth relative to small members of the cohort because large salmon had greater access to large and energy-rich herring Clupea harengus L.

The hypotheses of compensatory, enhanced or random growth responses of fishes to previous growth were tested among Chinook salmon Oncorhynchus tshawytscha (Walbaum). These tests examined whether O. tshawytscha growth at sea was dependent on preceding growth in fresh water and the extent to which growth dependency continued through each of 3 or 4 years of marine residence. The approach utilized a long-term collection of scales, which provide an index of growth during each life stage (Clutter & Whitesel, 1956; Bilton, 1975; Fukuwaka & Kaeriyama, 1997; Fisher & Pearcy, 2005). Growth of individual O. tshawytscha during each year or life stage, based on scale annuli, was compared with growth during the previous year. A positive correlation within each year class of O. tshawytscha would indicate growth enhancement, a negative correlation would suggest growth compensation and a lack of correlation would suggest random growth.

**MATERIALS AND METHODS**

**SCALE COLLECTION AND MEASUREMENTS**

The study utilized scales from adult wild O. tshawytscha returning to the Yukon (64° 00' N; 164° 14' W) and Kuskokwim Rivers (59° 58' N; 162° 26' W), Alaska, from 1964 to 2004.
These catchments, the largest in Alaska, have supported annual *O. tshawytscha* harvests (commercial and subsistence) averaging 147,000 and 99,000 fish, respectively, since 1961 (Bue & Hayes, 2006; Whitmore et al., 2008). Scales were obtained from the Alaska Department of Fish and Game (ADFG) archive in Anchorage, Alaska (http://www.adfg.state.ak.us/). For the Yukon River, scales were selected for measurement only when they were from *O. tshawytscha* captured with set gillnets (21·6 cm stretched mesh) located in the lower river (river km 20–30). Fewer scales were available from fish harvested in the Kuskokwim River; therefore, these scales were selected from multiple gear types. In most years, Kuskokwim *O. tshawytscha* scales were selected from fish captured by gillnets (15·2 or 21·6 cm mesh) in the mainstem river near Bethel, but some scales were sampled at tributary weirs. The scales were typically obtained from one gear type within a given year. In both catchments, scales were primarily collected from June to July in an attempt to consistently select fish from the same stocks.

Approximately 50 scales from each of the two dominant *O. tshawytscha* age groups from both the Yukon and Kuskokwim Rivers were measured, *i.e.* c. 200 scales per year. These fish spent one winter in fresh water (*i.e.* river-type fish) and three (age 1·3) or four winters (age 1·4) in the ocean. Scales were selected for measurement only when: (1) the age determination agreed with the one previously made by ADFG, (2) the scale shape indicated the scale was removed from the preferred area (Koo, 1962) and (3) the circuli and annuli were clearly defined and not affected by scale regeneration or significant resorption along the measurement axis.

Scale measurements followed procedures described by Hagen et al. (2001). After selecting a scale for measurement, the scale was scanned from a microfiche reader and stored as a high resolution digital file. The high resolution image (3352 × 4425 pixels) allowed the entire scale to be viewed and provided enough pixels between narrow circuli to ensure accurate measurements of circuli spacing. The digital image was loaded in Optimas 6·5 image processing software (www.mediacy.com) to collect measurement data using a customized programme. The scale image was displayed on an LCD monitor, and the scale measurement axis was defined as the longest axis extending from the scale focus. Distance (mm) between circuli was measured within each growth zone, *i.e.* growth through the first winter in fresh water from the scale focus to the outer circulus of the first freshwater annulus (FW1), spring plus growth zone (FWPL) extending from the last FW1 circulus to the first marine circulus (smolt transition period), each annual ocean growth zone (SW1, SW2, SW3 and SW4), and from the last ocean annulus to the edge of the scale (SWPL). Data associated with each scale, such as date of collection, location, sex, fish length (mid-eye to tail fork, *L* ETF) and capture method, were included in the dataset.

**DATA ANALYSIS**

Linear regressions were performed to determine whether scale growth during each life stage (FWPL, SW1, SW2, SW3, SW4 and SWPL) could be explained by scale growth during the previous stage. Regressions were performed annually for scale growth measurements of individual fish from each stock (Yukon and Kuskokwim) and each age group (ages 1·3 and 1·4). Sample groups having <20 scale measurements were excluded from regression analysis. Exploratory analyses indicated that the best explanatory variable was the distance across the five widest (adjacent) circuli during the previous stage (four circuli in FW1). Total annual scale growth could have also been used as the primary explanatory variable. It yielded comparable results, but peak circuli growth consistently provided the highest correlation. When comparing growth during the smolt transition period (FWPL) with growth in fresh water, the entire FW1 scale growth was used because juvenile size has been shown to affect timing of *Oncorhynchus* spp. smolt migration and therefore growth during this brief transition period (Burgnner, 1962).

It was hypothesized that growth of individual *O. tshawytscha* during the past four decades was dependent on the previous year’s growth. A *t*-test was used to examine whether regression slopes (mm per mm of scale growth) calculated for each year class, age group, stock and life stage were statistically different from zero (*α* = 0·05).

Growth of *O. tshawytscha* during each life stage was expected to vary from year to year. Therefore, additional regressions were calculated to determine whether the regression slopes (scale growth *v.* previous year’s growth) were related to mean scale size of the year class.
during the previous life stage. In other words, was the magnitude of the growth response dependent on prior mean scale growth of the fish year class? Scale growth values were based on the mean of ages 1-3 and 1-4 fish. Mean scale size was calculated from the mean of normalized values (s.d. > or < the long-term mean) for males and females, which may experience differential growth. This analysis only involved Yukon River fish because scales from Yukon River fish were collected consistently across all years (same location, gear and mesh size), thereby minimizing possible bias in annual mean values associated with different sampling methods. The Durbin–Watson statistic (Kutner et al., 2005) was used to test for autocorrelation among regression residuals. If the presence of autocorrelation was significant or inconclusive, then the slope of the previous year class was included in a multiple regression as a means to remove autocorrelation. Partial residual analysis (Larsen & McCleary, 1972) was used to show the relationship between the regression slope of a year class and the growth during the previous year after removing the autocorrelation effect.

The adult $L_{ETF}$ of individual *O. tshawytscha* (all stocks and ages combined) was compared with their scale measurements using regression analysis to examine whether scale growth was related to $L_{ETF}$. Exploratory analyses indicated a variety of scale measurements were correlated with adult $L_{ETF}$, but the analysis presented here was based on cumulative scale growth from the second year at sea (SW2) through to the third circulus of the homeward migration period (SWPL). The outer SWPL zone was excluded due to scale resorption beyond the third circuli in some scales.

Correlation between adult $L_{ETF}$ and scale growth in fresh water 4 to 5 years earlier was expected to be weak. Correlation coefficients were calculated for each stock, age group and year of adult return. Two methods were used to test for positive correlation across all years. First, a $\chi^2$ test using Yates correction for continuity was used to test the null hypothesis that the frequency of positive correlations across the past four decades was random (i.e. 0.5), as expected if growth in fresh water had no effect on adult $L_{ETF}$. Second, a $t$-test was used to evaluate whether the mean annual correlation coefficient during the past four decades was >0.

**RESULTS**

**GROWTH RELATIONSHIPS WITHIN INDIVIDUAL *ONCORHYNCHUS TSHAWYTSCHA***

A total of 690 regressions were performed to evaluate the relationship between annual scale growth of individual *O. tshawytscha* and previous year’s growth for each year of adult return from 1964 to 2004. Age 1-4 scales from *O. tshawytscha* returning to the Yukon River in 1991 provided an example of these regressions during each life stage (Fig. 1). Annual growth during each life stage at sea was correlated with the previous year’s growth ($P < 0.001$), with one exception. Annual growth during the smolt transition from fresh to marine waters (brief transition and minimal growth) was not correlated with freshwater growth ($P > 0.05$).

On average, 48% of the 131 regressions of early marine growth (SW1) on freshwater growth (FW1) were positively correlated and statistically significant ($P < 0.05$), indicating that growth during the first year at sea was related to growth during freshwater residence (Table I). This pattern held for each stock and age group. Negative correlations represented only 15% of the total, and none were statistically significant. The variability in early marine growth explained by peak growth in fresh water was 13%, on average, but it reached as much as 55% for age 1-3 fish returning to the Kuskokwim River in 1975 (Table I).

The relationship of scale growth to the previous year’s growth increased during later life stages in the ocean. On average, 71% of the 131 regressions of SW2 on SW1 growth had a positive slope and were statistically significant ($P < 0.05$), and 98% of
Table I. Percentage of annual life-stage growth regressions for each stock and age group of *Oncorhynchus tshawytscha* during the past three to four decades that were statistically significant (*P* < 0.05). Dependent variables were total scale growth during each life stage, and independent variables were either peak or total (FWPL on FW1 only) scale growth during the previous life stage. The mean percentage of annual regressions, including non-significant regressions, having a positive slope and the mean and maximum annual correlation coefficient (*r*²) for each life stage are shown.

<table>
<thead>
<tr>
<th>Stock &amp; Age</th>
<th>Number of years</th>
<th>Average scales per year</th>
<th>Regression</th>
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<tbody>
<tr>
<td></td>
<td></td>
<td>FWPL on FW1</td>
<td>SW1 on FW1</td>
</tr>
<tr>
<td>Age 1-3</td>
<td>34</td>
<td>42.7</td>
<td>0%</td>
</tr>
<tr>
<td>Age 1-4</td>
<td>39</td>
<td>50.0</td>
<td>13%</td>
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<tr>
<td>Kuskokwim (1964–2004)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Age 1-3</td>
<td>29</td>
<td>37.0</td>
<td>3%</td>
</tr>
<tr>
<td>Age 1-4</td>
<td>29</td>
<td>40.7</td>
<td>21%</td>
</tr>
<tr>
<td>Mean ± s.d. % significant regressions</td>
<td></td>
<td>9 ± 9%</td>
<td>48 ± 13%</td>
</tr>
<tr>
<td>Mean ± 1 s.d. % positive slopes</td>
<td></td>
<td>41 ± 14%</td>
<td>85 ± 12%</td>
</tr>
<tr>
<td>Maximum coefficient of determination (<em>r</em>²)</td>
<td></td>
<td>0.05 ± 0.01</td>
<td>0.13 ± 0.03</td>
</tr>
</tbody>
</table>

FWPL, scale growth during the smolt transition period in spring from fresh water to the ocean; FW1, scale growth during the first year in fresh water; SW1, scale growth during the first year at sea; SW2, scale growth during the second year at sea; SW3, scale growth during the third year at sea; SW4, scale growth during the fourth year at sea; SWPL, scale growth during the homeward migration.
all correlations were positive. Likewise, 64, 60 and 90% of the correlations involving the dependent variables SW3, SW4 and SWPL had a positive slope and were statistically significant with previous year’s growth (Table I). The percentage of positive correlations ranged from 84 to 99% of the total. On average, 15 to 40% of the variability in marine scale growth was explained by the previous year’s growth, depending on life stage. For some cohorts, previous growth explained up to 48 to 81% of the variability in marine growth, depending on life stage. The strength of the relationships tended to be greater for age 1·4 fish rather than age 1·3 fish during each life stage.
In contrast, *O. tshawytscha* scale growth during FWPL was typically not related to growth during the previous year in fresh water. Only 9% of the 131 regressions were statistically significant, including both positive and negative relationships (Table I). The few significant correlations could be due to chance.

**GROWTH RELATIONSHIPS ACROSS YEARS**

When comparing across all years, the mean slope of the annual regressions of growth on the previous year’s growth was statistically greater than zero for each stock, age group and life stage of *O. tshawytscha* (*P* < 0.001), except during FWPL (Fig. 2), indicating that growth was related to previous year’s growth throughout most life stages during the study period. Mean slope of the regressions of FWPL on freshwater growth during the previous year was significantly <0 for three of the four tests (Fig. 2), indicating a unique relationship involving FWPL and FW1 growth. Annual regression slopes of most life stages did not vary with time or with ocean climate shifts observed in 1977, 1989 and 1997 (Kruse, 1998; Hare & Mantua, 2000), except the magnitude of slopes for FWPL (*r* = 0.66) and SW1 (*r* = 0.42) were positively correlated with time (*P* < 0.05).

**GROWTH RELATIONSHIPS RELATIVE TO MEAN SCALE GROWTH OF THE YEAR CLASS**

The relationship of *O. tshawytscha* scale growth with previous year’s growth was stronger when previous year’s growth of the population was relatively low, especially during early marine life. Slope of the annual regressions of scale growth on the previous year’s growth was negatively correlated with mean scale growth of the year class during the previous year for all life stages except those during late marine life, *i.e.* SW4 and SWPL (Fig. 3). Autocorrelation was non-significant (*P* > 0.05) when comparing the SW1 and SW2 slopes with mean growth during the previous year. The potential effect of autocorrelation, based on inconclusive statistical tests, on the FWPL and SW3 relationships was removed by inclusion of the slope from the previous year class (*P* < 0.05). In these multiple regression models, the negative relationship between mean SW2 growth and SW3 slope was significant (partial *P* < 0.05), whereas the negative relationship between mean growth in fresh water (FW1) and FWPL slope was not significant (*P* > 0.05).

**ADULT *L*\textsubscript{ETF} AND SCALE GROWTH**

Regressions of individual adult *O. tshawytscha* *L*\textsubscript{ETF} and scale measurements (SW2 to SWPL) were statistically significant for 97% of the annual regressions since 1964 (*P* < 0.05). On average, 32% of the variability in adult *L*\textsubscript{ETF} was explained by cumulative scale growth during the second year at sea to the homeward migration period (SWPL first three circuli). In some years, adult *L*\textsubscript{ETF} was highly correlated with scale growth (Fig. 4).

Adult *L*\textsubscript{ETF} was significantly, albeit weakly, related to growth during the freshwater period. Adult *L*\textsubscript{ETF} of individual age 1·3 and 1·4 Yukon and Kuskokwim fish was positively correlated with total growth in FW1 for 63 and 64% of the annual tests, respectively. These percentages include statistically significant and non-significant

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Fig. 2. Mean rate of scale growth change in relation to previous year’s growth during each life stage and age class (1·3 and 1·4) of Yukon River (Y) and Kuskokwim River (K) *Oncorhynchus tsawytscha*. Rate of scale growth change is mean ± 95% CI slope calculated from annual regressions of scale growth on previous year’s growth (see Fig. 1). Slope values were statistically significant (*P* < 0·001) except as noted.


Fig. 3. Regressions of normalized annual scale growth slopes of Yukon River Oncorhynchus tshawytscha on normalized mean scale growth (Z) of the year class during the previous year (see Fig. 1). Scale slopes were calculated from regressions of scale growth of individual O. tshawytscha on the previous year’s growth. The FWPL and SW3 plots were based on partial residuals of multiple regressions that included the slope of the previous year class to remove autocorrelation. In these cases, \( r^2 \) is based on the partial correlation coefficient. All correlations were statistically significant (\( P < 0.05 \)) except the FWPL slope (partial \( P > 0.05 \)). Regressions involving SW4 and SWPL life stages were non-significant and are not shown (\( P > 0.05 \)).

correlations. \( \chi^2 \) analysis indicated that the frequency of positive v. negative correlations was not random among Yukon River (\( \chi^2, n = 73, P < 0.05 \)), Kuskokwim River (\( \chi^2, n = 58, P < 0.05 \)) and both stocks combined (\( \chi^2, n = 131, P < 0.05 \)). Likewise, annual correlation coefficients (\( r \)) were statistically >0 for both Yukon (\( t \)-test, mean \( r = 0.07 \), d.f. = 76, \( P = 0.001 \)) and Kuskokwim (mean \( r = 0.07 \), d.f. = 59, \( P < 0.01 \)) *O. tshawytscha*.

**DISCUSSION**

Analysis of Yukon and Kuskokwim *O. tshawytscha* scale growth within each year during the past four decades indicated that annual growth of individuals was related to growth during the previous year. This relationship was maintained between fresh water and early marine life stages and among each life stage in the ocean. The degree of growth relationship, as indicated by the magnitude of the regression slope, was greater when mean growth of the year class was relatively low during the previous year. Adult \( L_{ETF} \) of *O. tshawytscha* was most closely correlated with cumulative scale growth after the first year at sea. Adult \( L_{ETF} \), however, was also weakly related to growth that occurred during freshwater residence 4 to 5 years earlier.
The relationship of individual *O. tshawytscha* growth to the previous year’s growth may relate to their piscivorous feeding habits and their tendency to select relatively large prey including squid while foraging in the ocean (Major *et al*., 1978; Healey, 1991; Farley *et al*., 2009). Greater growth may beget greater growth because larger *Oncorhynchus* spp. can consume larger prey (Ruggerone, 1992; Juanes, 1994), thereby enhancing overall availability and energy content of prey for larger *Oncorhynchus* spp. (Salminen, 1997; Aydin *et al*., 2005). Somatic growth may be especially important for *O. tshawytscha* because they mature at a large size relative to other species of *Oncorhynchus* spp. Rapid growth and large body size may enhance survival (Healey, 1982) and lead to greater fecundity at a given age (Quinn, 2005).
Investigations to determine whether *Oncorhynchus* spp. smolt size has an effect on post-smolt growth have led to inconsistent findings. Studies on *S. salar* indicated growth was compensatory or negatively correlated with smolt size (Skilbrei, 1989; Nicieza & Brana, 1993; Einum *et al*., 2002), independent of smolt size (Friedland *et al*., 2006) or positively correlated with smolt size (Salminen, 1997). Friedland *et al*. (2006) also reported that growth at sea of *S. salar* during summer was positively correlated with their growth during spring. Post-smolt growth of steelhead *Oncorhynchus mykiss* (Walbaum) was positively correlated with smolt size, whereas post-smolt growth of coho salmon *Oncorhynchus kisutch* (Walbaum) was either negatively correlated or not correlated with smolt size (Johnsson *et al*., 1997; Snover *et al*., 2005). In Bristol Bay, Alaska, scale growth of individual *O. nerka* during the second year at sea was not correlated with growth during the first year (G. T. Ruggerone, unpubl. data). The relationship between growth and size may depend, in part, on whether the fish is consuming relatively large mobile prey versus smaller less mobile prey.

The degree of growth enhancement (magnitude of positive regression slope) among *O. tshawytscha* varied from year to year. It was greatest when the mean growth of the year class was relatively low indicating the tendency for fish growth to increase even more when previous growth was relatively low. This form of compensatory growth, or ‘catch-up’ growth, might be related to both physiological and ecological factors. The *O. tshawytscha* scales used in this study were from fish that survived 3 or 4 years at sea. Conceivably, mortality may have been relatively high for slower growing individuals, leading to the observed rapid growth increase when body size of the population was relatively small. This pattern was also observed among Bristol Bay *O. nerka* in which mean growth of the population during the second year at sea was inversely correlated with early marine growth (Ruggerone *et al*., 2005).

*Oncorhynchus tshawytscha* scale growth during the FWPL tended to be negatively correlated with growth in fresh water during the previous year, although the relationships were weak. This relationship probably reflects a behavioural response of *O. tshawytscha* rather than compensatory growth. Smaller, slow growing *Oncorhynchus* spp. tend to delay the date of smoltification, leading to greater time and growth during the spring transition period from fresh to marine waters (Burgner, 1962). This transition growth was reflected in the FWPL measurements.

Adult $L_{ETF}$ of *O. tshawytscha* was correlated with scale growth, but variability explained by scale measurements was only 32%, on average. The low $L_{ETF}$ and scale correlation at the adult stage compared with the juvenile and immature stages (Fukuwaka & Kaeriyama, 1997; Fisher & Pearcy, 2005) probably reflects a change in the length and scale relationship caused by rapid growth of maturing *Oncorhynchus* spp., as they migrate toward their natal river (Brett, 1995) followed by reduced feeding and resorption of the scale with the onset of maturation (Bilton, 1985; Price & Schreck, 2003). Still, the adult $L_{ETF}$ and scale relationship provides evidence that the observed scale growth relationships between adjacent life stages were related to body growth rather than an artifact of scale growth.

Evidence suggests that climate shifts and associated oceanic conditions can influence *Oncorhynchus* spp. abundance through their effects on growth during early marine life (Peyronnet *et al*., 2007; Ruggerone *et al*., 2007). Abundance of western Alaska *O. tshawytscha*, including those in the Yukon and Kuskokwim Rivers, increased after the 1977 regime shift, then declined after the 1997 to 1998 El Niño.
(Kruse, 1998). The present study did not identify distinct and immediate shifts in *O. tshawytscha* growth in relation to climate shifts, possibly because *O. tshawytscha* feed in the ocean at a relatively high trophic level that involves complex species interactions (Hunt *et al*., 2002) that may delay a response to climate shifts. Furthermore, the present study indicated that growth of *O. tshawytscha* was influenced, in part, by growth during earlier life stages, suggesting that effects of climate shifts on growth may be mediated by earlier growth.

The dependency of early marine growth and adult $L_{ETF}$ of *O. tshawytscha* on growth in fresh water has important implications for maintaining habitat quality in fresh water. *Oncorhynchus* spp. habitat from California to the Pacific Northwest is often degraded by human activities leading to depleted stocks and protection under the United States Endangered Species Act (Yoshiyama *et al*., 1998; Good *et al*., 2005). Atmospheric warming is predicted to lead to amplification of precipitation extremes affecting freshwater systems (Allen & Ingram, 2002). Predicted increases in extreme precipitation events correlate with changes in sea surface temperature (Allan & Soden, 2008) and by implication change in the ocean prey resource for salmonids. Although *O. tshawytscha* may compensate for small size in fresh water, the present study suggests that rapid growth during early life stages, including the freshwater period, is important to subsequent growth and presumably survival throughout life. Thus, growth in freshwater habitats may be especially important during periods of low ocean productivity because large size at ocean entry may enable fish to consume a wider spectrum of prey.

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