ARTICLE

Interactions between Marine Growth and Life History Diversity of Steelhead from the Situk River, Alaska

Matthew R. Catterson

Alaska Department of Fish and Game and College of Fisheries and Ocean Sciences, University of Alaska Fairbanks, Juneau, Alaska 99801, USA

David C. Love

Alaska Department of Fish and Game, Sport Fish Division, Douglas, Alaska 99824, USA

Trent M. Sutton and Megan V. McPhee*

College of Fisheries and Ocean Sciences, University of Alaska Fairbanks, Fairbanks, Alaska 99775, USA

Abstract

Steelhead (the anadromous form of Rainbow Trout *Oncorhynchus mykiss*) exhibit a complex life history that is described by variable freshwater and ocean residency and maturation schedules. This diversity confers resilience but complicates their monitoring and management. The Situk River in Southeast Alaska has the longest running set of biological data and scale samples for steelhead in the state, and it is of particular interest because it supports the largest known population of steelhead in Alaska and is free of hatchery influence. We used a retrospective analysis of scales that were collected from 525 individuals over 11 years (1999–2012) to examine the relationships among freshwater growth, early ocean growth, and life history in a mixed-effects modeling framework. Specifically, we examined the relationships among annual growth stanzas and adult length and we determined how age at maturity varied by sex and growth history while allowing these relationships to vary randomly among calendar years of growth. Within individuals, freshwater and first ocean-year growth were positively correlated, while second ocean-year growth was negatively correlated with earlier growth stanzas. Early-maturing steelhead (returning after two ocean years) grew more quickly during their first ocean year, and they then grew more slowly during their second ocean year and attained smaller adult length than did later-maturing steelhead (those that returned after three ocean years). Second ocean-year growth was more variable than first ocean-year growth and adult length were. Males tended to mature earlier than females did, and later-maturing males attained larger freshwater growth than their earlier-maturing male counterparts did and grew larger in overall length than did females. Our analyses identified divergent growth trajectories that were associated with age at maturity that began in freshwater periods but were most pronounced during early ocean residency. We found retrospective scale-growth analysis to be a useful tool for better understanding the connections between ocean growth and demography in this important sport fish.

Steelhead, the anadromous form of Rainbow Trout *Oncorhynchus mykiss,* are a highly valued species that contributes to recreational fisheries in the Pacific Northwest, British Columbia, and Alaska. In recent years, steelhead populations in Washington, Oregon, and California have suffered declines that are associated with the cumulative effects of habitat degradation, hydroelectric development, fishery harvest, and hatchery effects (Ruckelshaus et al. 2002; Augerot 2005; Good et al. 2005). However, more remote and northerly regions in British Columbia, Alaska,

*Corresponding author: mvmcphee@alaska.edu

and eastern Russia persist as strongholds for healthy populations of wild steelhead (Augerot 2005). Steelhead spend 2–5 years rearing in fresh water before migrating to the ocean (Harding 2008), which is the longest freshwater rearing period exhibited by anadromous members of the genus. The complex life history of steelhead is mediated by some combination of heritable variation and growth history, and it diversifies the suite of ecological forces that affect individual survival and regulate population productivity (Kendall et al. 2015). Life history diversity also buffers populations against variability by creating asynchronous population dynamics that disperse mortality over space and time (Moore et al. 2014). This "portfolio effect" of biodiversity, which has been characterized in other salmonid populations (Schindler et al. 2010), may also support the persistence of the small (<200 anadromous adults) steelhead populations that are characteristic of most of Southeast Alaska (Fowler 2017).

While steelhead management opportunities are primarily limited to freshwater environments, a better understanding of the relationships between juvenile growth and life history complexity in both freshwater and marine ecosystems may help inform ongoing management strategies to preserve biodiversity and maintain population productivity in this species (Shapovalov and Taft 1954; Ward and Slaney 1988). The small size and remote location of many Alaskan steelhead populations challenge intensive research on their ecology and population dynamics, but information from populations that are monitored across Southeast Alaska indicates stable abundance (Harding and Coyle 2011). These small populations are protected by conservative sport fishing regulations that are designed to allow angling opportunity while conserving populations. However, a lack of population-specific information, potential overexploitation in recreational and subsistence fisheries, unknown levels of interception in commercial fisheries, and changes to marine and freshwater habitat quality are tangible threats to steelhead populations in Southeast Alaska (Love and Harding 2009). Much remains to be studied regarding steelhead ecology and population dynamics in Southeast Alaska, and the ecological processes regulating growth, life history, and survival remain largely unknown.

Retrospective scale-pattern analysis is well suited for evaluating the relationships between growth and life history in the steelhead populations in Southeast Alaska because it is noninvasive, less costly, and less labor-intensive than are alternative methods of assessing fish growth (Beakes et al. 2014). This process also provides information on growth over the entire lifespan of the fish. The relationships between growth and life history have been investigated by using analyses of scale growth increments for multiple salmon species (e.g., Fisher and Pearcy 2005; Morita and Fukuwaka 2006) including

steelhead (Shapovalov and Taft 1954; Ward and Slaney 1988; Daugherty et al. 2003; Quinn et al. 2011; Friedland et al. 2014; Hodge et al. 2016). Ruggerone et al. (2009) used scale-pattern analysis to identify positive correlations between freshwater growth and first-year marine growth in Chinook Salmon *O. tshawytscha*, while subsequent marine growth was also related to previous years' growth. Conversely, Marco-Rius et al. (2012) identified a compensatory growth pattern in juvenile anadromous Brown Trout, which was described by a negative relationship between freshwater growth and growth occurring after migration to the marine environment. The large size of juvenile steelhead when they first enter the ocean (Love et al. 2013) and their rapid offshore migration (Burgner et al. 1992; Quinn and Myers 2005) suggest that they may immediately be capable of consuming abundant marine resources for growth and development. Therefore, we might expect to observe positive relationships among juvenile freshwater growth, marine growth, and adult fish length in steelhead. Second, anadromous salmonids typically exhibit a relationship between faster growth and earlier age at maturity (Vøllestad et al. 2004; Morita and Fukuwaka 2006; Siegel et al. 2018), leading to the expectation that steelhead from Southeast Alaska that mature earlier will show greater freshwater growth (i.e., a larger smolt size) and early marine growth.

For retrospective scale studies of steelhead life history to be informative, several methodological considerations must be addressed. First, age validation is necessary to demonstrate that a scale-aging technique is accurate (Beamish and MacFarlane 1983) and this requires that scales be taken from known-age fish or from recaptures of previously marked fish for the life history stage of interest (Campana 2001). In addition to age validation, measures of systematic differences (bias) and precision in the scale-reading methods that are used are required to evaluate the consistency of the age interpretations (Campana et al. 1995). Finally, steelhead have more complicated life histories than the Pacific salmon species do, including the potential for iteroparity (repeat spawning), which makes accurate reading of their scales more difficult (Shapovalov and Taft 1954; Copeland et al. 2018). Fortunately, several steelhead monitoring projects in Southeast Alaska have included collecting scales and PIT-tagging emigrating smolts or kelts (postspawn adults) along with scale collections from returning adults, including recaptured PIT-tagged individuals. These data have been used to validate the saltwater age of steelhead and to develop a standardized methodology for assigning freshwater and saltwater annuli and identifying "checks" (regions of closely spaced circuli) that are associated with spawning in such a way that minimizes bias and variability among readers (Love 2016). This previous work supports the application of

scale-pattern analysis to the study of the life history complexity of steelhead in Southeast Alaska.

Here, we report on a study that used scales to analyze variation in growth and life history in steelhead from the Situk River, near Yakutat in Southeast Alaska. There were two primary goals for this study. First, we validated saltwater age by using PIT-tagged individuals of known emigration year (as smolts). Second, we explored sex-specific relationships among freshwater and marine growth and adult size, age at maturation, and the frequency of repeat spawning. Using adult steelhead scale samples that were collected from the Situk River, Alaska, between 1999 and 2012, we applied a mixed-effects modeling approach to scale growth data in order to (1) assess the correlations among juvenile growth increments and adult length at capture and (2) determine how age at maturity differed by sex and growth patterns. Treating cohort (indexed by the year of emigration, or "smolt year") as a random effect accounted for the nonindependence of individuals that were growing during the same calendar year and allowed us to investigate coarse-scale (i.e., climatic) environmental influences on life history beyond those that were captured by individual growth. Retrospective growth investigations such as this study incorporate juvenile growth into the long-term tracking of stock demography and life history variation, underscoring the benefits of more in-depth population assessment and monitoring protocols for steelhead in Alaska.

Study Site

The Situk River is located approximately 16 km southwest of Yakutat, Alaska (Figure 1). A small river, its mean summer discharge ranges between 5.7 and 8.5 m³/s (Gubernick and Paustian 2007), with a total watershed area of 397 ha (Marston et al. 2012). Originating in two headwater lakes (Mountain and Situk lakes) and fed by two tributaries (the West Fork Situk and the Old Situk rivers), the main-stem Situk River flows 29 km into the Gulf of Alaska via Situk–Ahrnklin lagoon. The Situk River drops approximately 500 m from headwater lakes to mouth and is characterized by slow, meandering riffle–pool channels that pass through old growth Sitka spruce *Picea sitchensis* timber stands and muskeg meadows. The Situk River joins with the Ahrnklin River, Seal Creek, Lost River, and several smaller streams in a tidally influenced lagoon before exiting into the Gulf of Alaska.

For its size, the Situk River is among the most productive rivers in Alaska, supporting the largest known population of steelhead in Alaska and large populations of all five North American Pacific salmon *Oncorhynchus* spp., Dolly Varden *Salvelinus malma*, nonanadromous Rainbow Trout, and Eulachon *Thaleichthys pacificus*. Historically, about 450,000 Pacific salmon return to the Situk River annually and contribute to commercial, subsistence, and

sport fisheries (Thedinga et al. 1993). The Situk River's unusually high salmonid productivity has been attributed to its stable hydrologic regime and high base flow, which is mediated by two headwater lakes and substantial groundwater inflow (Thedinga et al. 1993). An abundance of complex, low-gradient riffle–pool habitat and bountiful forage create a diversity of high-quality spawning and juvenile rearing habitat for salmonids (Thedinga et al. 1993). The Situk River is an important economic driver for the nearby community of Yakutat, with over 200,000 salmon being harvested in the Situk River commercial fisheries in 2015 (Zeiser and Woods 2016). The Situk River also supports an important sport fishery, accounting for an average of 16% annually of all of the freshwater sport fishing effort in Southeast Alaska since 1996 (ADFG 2016). The steelhead sport fishery in the Situk River is the largest in the region, with an average of 67% of the steelhead catch in Southeast Alaska occurring in this system since 1996 (ADFG 2016). Over our study period (1999–2012), catches of steelhead averaged ~11,000 fish annually, while the average catch of other salmonids in the Situk River exceeded 45,000 fish (ADFG 2019). Although salmon fisheries in the Situk River are customary and traditional to the community of Yakutat, subsistence harvest of steelhead is minimal.

METHODS

Steelhead sampling.— Steelhead have been counted in the Situk River by the U.S. Fish and Wildlife Service (USFWS) or the Alaska Department of Fish and Game (ADFG) since the 1950s, with a standardized protocol in place since the early 1990s (Bain et al. 2003). The current aluminum bipod-and-picket weir structure, with a 10-m floating polyethylene resistance board section, stretches 40 m across the Situk River at a location that is approximately 1.9 km upstream from the lower landing (Marston et al. 2012). Steelhead kelts are counted as they move downstream by using an underwater video system, which allows personnel to remotely count fish in a nearby cabin. An aluminum picket trap and holding pen is constructed on the downstream side of the weir in the deepest section of water adjacent to the floating weir section to capture and sample a portion of the run each year.

Age, sex, and length sampling protocols at the Situk River steelhead weir have evolved over the duration of operation in response to changes in the project objectives (Bain et al. 2003; Marston and Power 2016). Over our study period (1999–2012), the weir was operated from early May to mid-June. Sampling occurred on two nights each week, with the sample-size goals calculated by multiplying the fish that were counted at the last sampling event by 5% (Marston and Power 2016). Early weir studies observed diel variation in emigration, with older fish
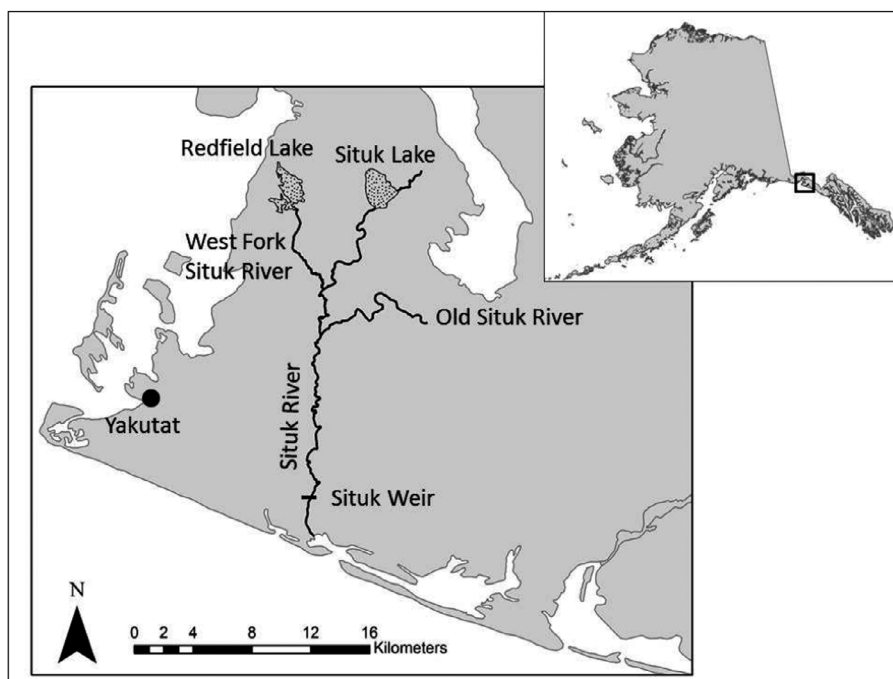
FIGURE 1. Map of the Situk River, showing the location of the weir and the neighboring village of Yakutat.

moving downstream earlier in the evening (Johnson and Jones 1998). To account for this variation, steelhead were sampled after midnight on the first weekly sampling event and prior to midnight on the second event (Marston et al. 2012). The captured steelhead were sampled for sex and standard length (SL). Four scales were taken from each side of the fish from the preferred area above the lateral line on a diagonal between the posterior end of the dorsal fin and the anterior end of the anal fin. All of the scales were immediately affixed to gum cards that were labeled with the date, species, river system, and sampler information (Marston 2014). Due to changes in the project objectives, the regular collection of scales from sampled steelhead was terminated in 2014.

Beginning in 2000, individuals from a subsample of steelhead kelts were implanted with 20-mm PIT tags. To validate the saltwater age determinations, saltwater age-2 steelhead that were returning to spawn for the first time were targeted for tagging and sampling as described by Marston et al. (2012). The criteria for PIT-tagging required the fish to be ≤ 750 mm total length, have a "bright" color classification, and lack any significant wounds or body fungus growth (Marston et al. 2012). Eight scales were collected from the preferred area (Hagen et al. 2001) at the time of tagging. A PIT tag antenna was attached to the upstream weir trap opening so that all of the emigrating steelhead kelts passed through the reception field during normal counting and sampling. A tagged steelhead that passed through the antenna field would

have its tag code recorded, and the PIT tag reader would emit an audible tone via a speaker system, allowing the weir personnel to remotely close the trap doors and capture the fish (Marston et al. 2012). The recaptured PIT-tagged steelhead were sampled again for sex, length, and scales.

Scale measurements.— We analyzed steelhead scales from 1999 through 2012, excluding 2002 through 2004 (when samples and/or accompanying sex, length, and sample date data were unavailable). The scales were read and measured from digitized photos that were made from acetate impressions of gum cards that were archived at the ADFG scale laboratory in Douglas, Alaska, following a standardized protocol that is outlined in detail in Hagen et al. (2001). We also followed the scale quality criteria for inclusion as is described in Hagen et al. (2001).

Scale-pattern analysis is complicated in steelhead by their diverse life histories and iteroparity (Seamons et al. 2009; Copeland et al. 2018). Irregular regions of scale reabsorption (or "checks") that are associated with smoltification, feeding cessation upon marine exit, and spawning can obscure the record of circuli and annuli formation. Scale reabsorption that is associated with illness or starvation during marine residency may lead to the false identification of spawning checks (Love 2016). Therefore, we followed the specific guidance for steelhead scale aging and identification of spawning checks that is outlined in Love (2016). This protocol was developed from known-age steelhead from Southeast Alaska, so it provided the

best available criteria for the scale analysis of steelhead in the Situk River.

We followed the age designation process of Koo (1962), where the figure to the left of the decimal denotes the years spent in fresh water and the figure to the right of the decimal denotes years spent in saltwater prior to spawning. Additionally, an "s1" was used to denote the occurrence of reabsorption of annuli in a spawning check and an additional year of marine growth (Love 2016). For example, a steelhead with an estimated age of X.2s1 spent an unknown number of years rearing in fresh water and 2 years in the ocean prior to returning to spawn. It then survived another year at sea and returned to spawn again. We defined the scale growth stanza as follows: FW referred to the distance along a predefined axis of the scale (Hagen et al. 2001) from focus to the end of the freshwater growth zone (i.e., smolt check); SW1 was distance from the edge of the freshwater growth zone to the outer edge of the first saltwater annulus, SW2 was the distance from the outer edge of the first saltwater annulus to the outer edge of the second saltwater annulus, and so on (Figure 2). We did not attempt to quantify or measure annuli within the freshwater growth zone because the freshwater growth zone was small and compressed and annuli could not be discerned.

Age validation, precision, and bias.— Although known-age freshwater and first-ocean marine samples were not available for the scales of steelhead from the Situk River, the scales from PIT tag recaptures of adult steelhead that had been tagged at Sitkoh Creek (~340 km from the Situk River) as juveniles provided a useful proxy for the ocean-growth characteristics of scales from steelhead in the Situk River. We used an age-estimation technique that was established in the reference collection of scales from steelhead from the Sitkoh River with known ocean age (Love 2016). Furthermore, a small sample ($n = 10$) of recaptured PIT-tagged steelhead from the Situk River was also available to assess aging accuracy and to allow for partial (marine) age validation of repeat spawners, as the number of years between adult kelt tagging and recapture were known. The scales from the recaptured PIT-tagged steelhead in the Situk River and scale-aging methods based on the validated scale morphological characteristics from the fish from Sitkoh Creek provided the most accurate validation method possible in the absence of known-age samples from the Situk River.

In order to address bias and precision in aging, three blind and nonconsecutive age readings were completed by the same reader for each sampled scale as is described by Love et al. (2013). If none of the age estimates agreed, the sample was considered unreadable and omitted from further analysis unless an additional scale from the same fish was independently aged to verify a modal age estimate (Love et al. 2013). The modal age of the three or four successful scale-age readings was considered to be the most precise age and was recorded as such. Pairwise age-bias plots (Campana et al. 1995) compared each of the three aging reads to the modal age to identify the occurrence and direction of bias occurring during age estimation (Supplementary Figure S1 available in the online version of this article). For all of the age estimates, the precision
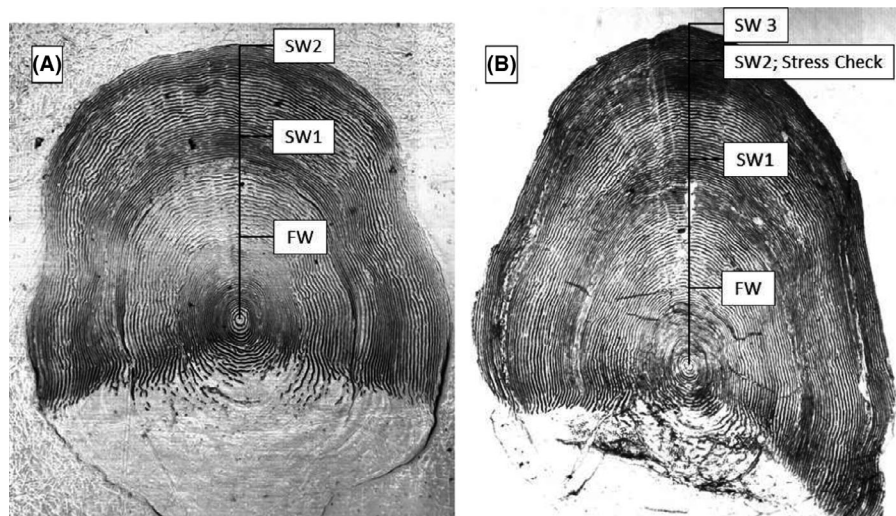

FIGURE 2. Annotated steelhead scales from the Situk River displaying freshwater (FW) and the first (SW1), second (SW2), and third (SW3) ocean-years of growth. **(A)** Age X.2 scale, where X refers to indeterminate number of years in freshwater and 2 refers to 2 years in saltwater. **(B)** Age X.2s1 scale, with X (indeterminate) years in freshwater and 2 years in saltwater followed by a spawning event ("s" denotes a stress check) and an additional 1 year in saltwater.

or reproducibility of the repeated measurements were assessed by using the coefficient of variation (CV):

$$CV_j = 100 \times \frac{\sqrt{\frac{\sum_{i=1}^{R}(X_{ij}-X_j)^2}{R-1}}}{X_j},$$

where CV_j was the age precision estimate of the jth steelhead, X_{ij} was the ith age estimate of the jth steelhead, X_j was the mean age estimate of the jth steelhead, and R was the number of times age was estimated for each steelhead (after Campana 2001). The CV_j was averaged across all of the steelhead to assess the general consistency of the aging method and stratified by steelhead saltwater age to assess the variability in age estimates that was related to the ocean age of the steelhead that were sampled (Table 1).

Relationships between growth zones.—Linear mixed-effects models were used to assess the pairwise relationships between FW growth, SW1 growth, SW2 growth, and adult length at capture. Separate models were fitted for each measure of annual growth as a function of a preceding annual growth measurement (e.g., SW1 vs. FW1). Adult length was modeled separately as a function of FW, SW1, or SW2. Scale and adult length measurements were each standardized to a mean of 0 and standard deviation of 1 prior to modeling, although the original scale of measurement (mm) was retained for plotting purposes.

Calendar year of growth rather than brood year was included as a random term to account for correlations among individuals that were growing at the same time (e.g., McPhee et al. 2016). Smolt year (first spring/summer at sea) was used to index this cohort effect due to the uncertainty in assigning freshwater age. We only included data from smolt years with a minimum sample size of 10 fish, which led to the exclusion of 11 individuals that had originated from five smolt years: 1994–1996, 2001, and

TABLE 1. Summary of assessed steelhead scales by saltwater age, repeat-spawning status (where "s" indicates a spawning event; e.g., *X*.2s1 indicates 2 years at sea, followed by a spawning check, followed by an additional year of marine growth), percentage of females, sample size (n), and the average of the coefficient of variation in an individual's age estimates (CV) by estimated saltwater age.

Years at sea	Age	% Female	n	Average CV
2	*X*.2	54	192	4.69
3	*X*.2s1	84	99	4.42
3	*X*.3	73	164	4.04
4	*X*.2s1s1	100	22	5.26
5	*X*.2s1s1s1	100	4	4.33
4	*X*.3s1	79	33	18.02
5	*X*.3s1s1	82	9	12.37
6	*X*.2s1s1s1s1	100	2	0.00
Total			525	5.41

2002. To evaluate the appropriate random-effects model structure, we compared linear models with no random effect, models with a random effect that affected only the intercept, and models with a random effect that affected both the intercept and slope by using Akaike's information criterion corrected for small sample sizes (AIC_c), as is demonstrated in Zuur et al. (2009). This preliminary analysis (results not shown) suggested that a random-intercept model structure was preferable to a model with no random effect and models with random intercepts and slopes, so our models took the following form:

$$y_{ij} = \beta_0 + \beta_1 x_{ij} + u_j + \varepsilon_{ij},$$

where y_{ij} was the size of an annual scale zone or adult length of individual i in cohort j, x_{ij} was the size of a preceding annual scale zone of the same individual, u_j was the random intercept for cohort j, and ε_{ij} was residual variance.

The statistical significance of the correlations between adjacent growth zones and between adult length and growth zones was assessed by using likelihood ratio tests against the corresponding null (random-effect only) model ($\alpha < 0.05$). Conditional and marginal coefficients of determination were calculated for the mixed-effects models per Nakagawa et al. (2017). All of the statistical analyses were completed by using the open source statistical program R (version 3.1.2; R Core Team 2014), with mixed-effects models being fit by using the R package lme4 v. 1.1.14 (Bates et al. 2015) and coefficients of determination being calculated in the R package MuMIn v. 1.40.0 (Bartón 2017). We evaluated the model assumptions of normality, constant variance, and independence graphically, and found no violations after the removal (from the adult length models) of one individual with an erroneous adult length value of 45 mm.

Relationships among sex, growth, and life history.—A multivariate binomial mixed model was used to examine the relationships among sex, freshwater growth, early marine growth, and age at maturity. An exploratory analysis (not shown) suggested that a sex-by-freshwater growth interaction was likely influencing age at maturity, so we included that interaction in our full candidate model. We modeled the probability of maturing "early" (after the second rather than third ocean year) as a function of sex and normalized growth increments FW, SW1, and SW2, while treating cohort (measured as smolt year) as a random effect:

$$\ln \frac{p}{(1-p)} = \beta_0 + \beta_1 Sex_{ij} + \beta_2 FW_{ij} + \beta_3 SW1_{ij} + \beta_4 SW2_{ij} + \beta_5 (Sex_{ij} \times FW_{ij}) + u_{ij} + \varepsilon_{ij},$$

where p is the event of maturing early and FW_{ij}, $SW1_{ij}$, and $SW2_{ij}$ are the standardized widths of the freshwater,

first ocean-year, and second ocean-year annual scale zones, respectively, for individual i in cohort j. Previously described sample-size criteria and outlier removal were applied. We compared the AIC_c values of all possible combinations of fixed effects (including the null model with only the cohort random effect) to determine which growth increments were related to age at maturity with statistical support. The fit of the preferred model was evaluated by examining the scaled residuals (calculated in the R package DHARMa; Hartig 2019) in quartile–quartile and residual vs. fixed-effect plots. Conditional and marginal coefficients of determination were calculated according to the procedures that are described in Nakagawa et al. (2017).

To investigate potential climatic correlates of age at maturity beyond those that are manifested as growth variability, we extracted random effects (i.e., cohort-specific deviations from the overall model intercept) and related those to the North Pacific Gyre Oscillation (NPGO). The NPGO is the second empirical orthogonal function of sea-surface temperature and height anomalies in the Northeast Pacific (Di Lorenzo et al. 2008). Catterson (2017) found correlations between the annual average value of the NPGO index and the abundance of steelhead in the Situk River, suggesting that this index might characterize large-scale climate dynamics that are affecting this steelhead population. We examined the correlations between the annual NPGO (the average of monthly values, January–December) and the cohort effect, lagged according to growth increment (i.e., no lag for SW1 because individuals would experience their first summer of marine growth during their year of emigration, −1 year for FW, and +1 year for SW2). The values for the NPGO were extracted on November 20, 2019 from http://www.o3d.org/npgo/npgo.php.

To visualize the relationships between individual growth increments, sex, and age at maturity while accounting for within- and among-year variability, we plotted univariate binomial mixed models that modeled the fixed effect of one growth increment at a time for a single sex along with the cohort random effect. We also calculated the CVs of the FW, SW1, and SW2 growth increments, total scale radius, and adult length to compare the variability in growth among different periods of life history.

Females dominated the repeat-spawning individuals (Table 1), so we only included females in the comparisons of freshwater and early marine growth between first-time and repeat spawners. To account for among-year growth variation, we examined residual growth from a random (cohort) effect-only model, based on the full data as described previously, and compared the residuals between first-time and repeat spawners. Inferences were limited because we did not know whether the individuals that were classified as first-time spawners would become repeat spawners in the future, so the residuals in FW, SW1, and SW2 were examined graphically and not tested statistically.

RESULTS

Age Estimation and Validation

A total of 525 steelhead that were sampled over a period of 11 years (1999–2012, excluding 2002–2004 for which samples were not available) had scales that were suitable for analysis (Table 1). We characterized 356 individuals as first-time spawners (i.e., their scales lacked a spawning check). In contrast, 169 individuals had scales with a spawning check, indicating that they were repeat spawners. Repeat-spawning fish were found to have ocean ages from 3 to 6 years (Table 1). All of the sampled steelhead, including the repeat spawners, returned to spawn for the first time after their second or third ocean year.

The age estimates of all 10 scale pairs from the PIT-tagged and recovered fish matched the interval between the sampling events, corroborating the saltwater age estimation technique (Supplementary Table S1 available in the online version of this article). The age-bias plots (Supplementary Figure S1) illustrated that minimal aging bias was evident for ocean age-2 and age-3 steelhead, ocean age-4 estimates were biased low, and ocean age-5 fish were underestimated most frequently.

The average CV of the individual age estimates was 5.4% over all of the samples, and the age-specific CVs ranged from 0.0–18.02% (Table 1). The CVs of the dominant age-classes were lower than the average over the entire sample. Repeat-spawning steelhead that spent 3 years at sea before spawning had the largest CVs, reflecting the complexity of their scale patterns. Two fish, both female, were estimated to have successfully spawned four times prior to returning and spawning again in the year that they were sampled, and both had matured after 2 years at sea (scale designation $X.2s1s1s1s1$). These individuals had CVs of zero, indicating they were aged consistently in each of the three scale reads.

Relationships between Growth Zones

Adjacent scale growth zones tended to be statistically correlated, but the associations were weak. The FW and SW1 growth zones were positively correlated, whereas SW2 tended to be smaller when SW1 was greater (Figure 3), but these relationships explained < 2% of the overall variation in scale growth (Table 2). Adult length was statistically uncorrelated with FW growth, increased slightly with increasing SW1 growth, and increased significantly with increasing SW2 growth (Figure 3; Table 2). Scale growth explained a negligible amount of variation in adult length with the exception of SW2 (Table 2).

Relationships among Sex, Growth, and Life History

Age at maturity was related to sex and growth (Figure 4, Table 3). Males were more likely to mature early, and earlier maturation was associated with faster first ocean-year growth and slower second ocean-year growth in both sexes. The relationship between freshwater growth and age at maturity differed by sex. Earlier maturation was associated with faster freshwater growth in females but slower freshwater growth in males. The top model (lowest AIC_c) contained sex and the two saltwater growth increments, but the full model (containing all three growth increments, sex, and the sex-by-freshwater growth interaction) was within 0.38 AIC_c units of the top model. Given this minimal AIC_c difference, we based the model validation and analysis of random effects on the full model. A quartile–quartile plot of the scaled residuals from the full model revealed no major deviations from uniformity (Supplementary Figure S2). We detected no temporal trend in the random effects (i.e., the cohort-specific deviations from the overall model intercept; Figure 5A), supporting modeling cohort as a random rather than fixed effect.

The cohort random effect explained a greater proportion of variation in the probability of earlier maturation than did the fixed effects of sex and growth. When including both fixed and random effects, the model explained nearly 50% of the variation, while the fixed effects alone explained <10% (Table 3). The cohort effect tended to increase with the NPGO index for all three of the growth increments (FW, SW1, and SW2), although the relationship was most pronounced for SW1 (Figures 5B–D).

For all of the growth zones and adult length, there was considerable variation among calendar years of growth (Supplementary Figures S3–S6). Variation among individuals (CV, summed across all years) was greatest for SW2 growth (22.8%), followed by FW growth (19.2%), SW1 growth (17.5%), and total scale radius (10.4%). Adult length was the least variable (9.5%). A visual comparison of FW, SW1, and SW2 scale growth after accounting for among-year variation indicated no difference in average growth between first-time and repeat-spawning females (Supplementary Figure S7).

DISCUSSION

Growth and Life History of Steelhead in the Situk River

The archived steelhead scales that were studied here provided fundamental information on the patterns of juvenile freshwater and marine growth for steelhead in Southeast Alaska. We found positive associations between smolt size and first ocean-year growth, negative associations between first and second ocean-year growth, and sex-specific relationships between growth and age at maturity. The availability of 10 recaptured PIT-tagged individuals allowed us to validate saltwater age in steelhead in the Situk River, and the use of mixed-effects models allowed us to maximize the information that we obtained from the individual fish while accounting for the correlations among individuals from the same growth year (see also McPhee et al. 2016; Debertin et al. 2017).

The positive correlation between smolt size and first ocean-year growth may be a general aspect of steelhead biology. A review by Marco-Rius et al. (2012) determined that the majority of studies of salmonid growth found no significant relationship between smolt size and ocean growth and negative correlations occurred more frequently
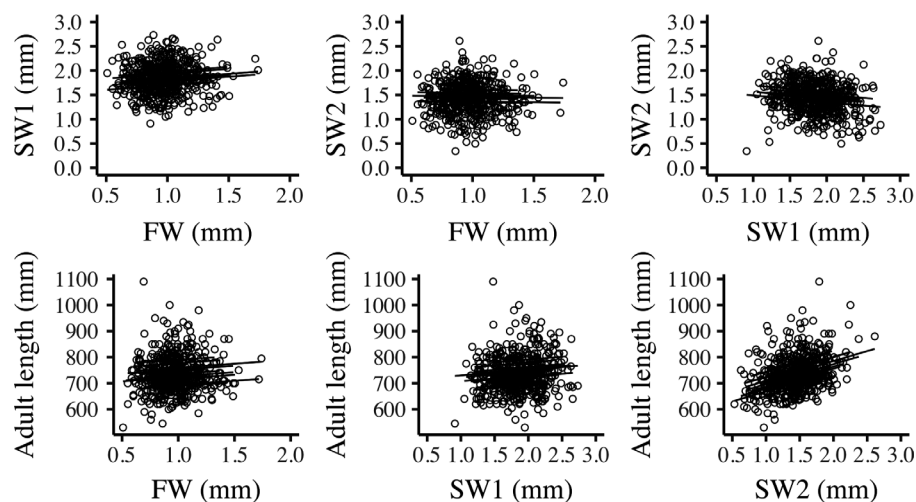

FIGURE 3. Relationships among scale growth stanzas (top row) and between scale growth stanzas and adult body length (bottom row). The abbreviations are FW = freshwater growth, SW1 = first ocean-year growth, and SW2 = second ocean-year growth. The lines show the fitted cohort-specific linear regressions from a mixed-effect model with cohort as a random effect (intercept only).

TABLE 2. Mixed-effects model results describing the relationships between annual scale growth and previous growth of individual steelhead as well as between adult length and annual scale-growth stanzas (FW = freshwater growth, SW1 = first ocean-year growth, and SW2 = second ocean-year growth). The χ^2 value is for the likelihood ratio test of the fitted model against the null (random-effects only) model. The marginal coefficient of determination (R^2m) quantifies the proportion of variance that is explained by fixed effects, while the conditional coefficient of determination (R^2c) describes that explained by both fixed and random effects.

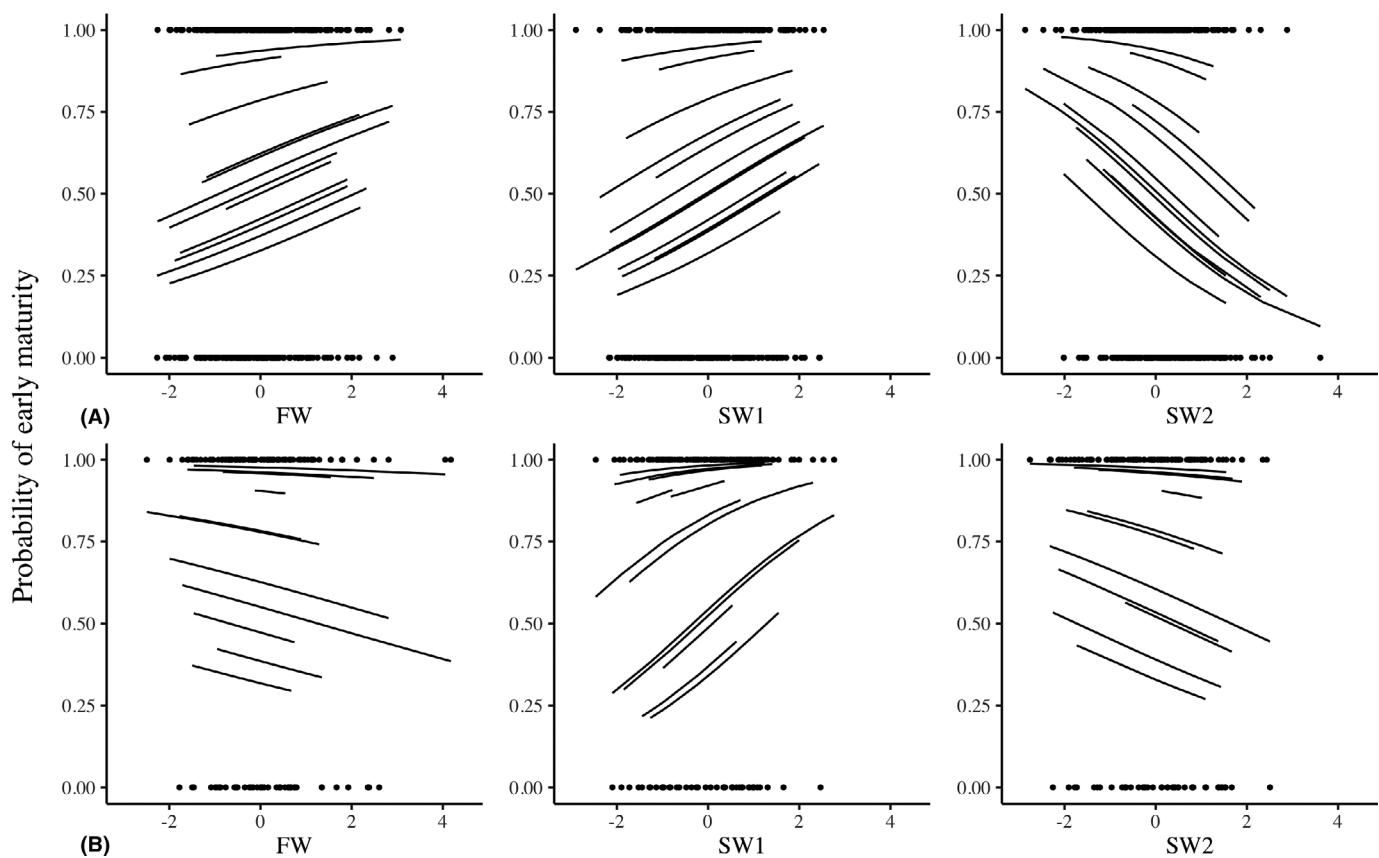| Y	X	Intercept (SE)	β (SE)	χ^2 (1)	P	R^2m	R^2c
SW1	FW	−0.10 (0.10)	0.11 (0.04)	6.78	0.009	0.01	0.10
SW2	SW1	0.06 (0.09)	−0.13 (0.04)	9.36	0.002	0.02	0.08
SW2	FW	0.07 (0.09)	−0.02 (0.04)	0.17	0.68	0.00	0.08
Adult length	FW	0.04 (0.14)	0.08 (0.04)	3.60	0.06	0.01	0.21
Adult length	SW1	0.05 (0.14)	0.10 (0.04)	5.39	0.02	0.01	0.20
Adult length	SW2	0.01 (0.14)	0.35 (0.04)	74.6	<0.0001	0.12	0.31

FIGURE 4. Probability of maturing early (after the second ocean year) as a function of normalized growth increment (FW = freshwater growth, SW1 = first ocean-year growth, and SW2 = second ocean-year growth). The points represent individual steelhead, and the lines represent cohort-specific predictions from univariate (one sex, one growth increment) binomial mixed models. The panels indicate (A) females and (B) males.

than positive ones did. However, Johnsson et al. (1997) found a weakly positive correlation between freshwater presmolt growth and marine postsmolt growth in steelhead, consistent with our results. Steelhead exhibit early marine migratory and bioenergetics patterns that differ from those of other Pacific salmon species by moving rapidly offshore during their first year at sea and foraging on a more dispersed but higher energy prey base of juvenile fishes and squid (Burgner et al. 1992; Atcheson et al. 2012a). Atcheson et al. (2012b) identified ontogenetic shifts in steelhead diet, with individuals consuming more larval and juvenile fish species during their first ocean year and older steelhead consuming more squid. Steelhead in Alaska typically spend 3 years rearing in fresh water

TABLE 3. Summary of the top (ΔAIC = 0), comparable (ΔAIC < 2), and null (random-effect only) binomial mixed models for the probability of maturing after 2 rather than 3 years of ocean growth as a function of sex, freshwater growth (FW), first ocean-year growth (SW1), second ocean-year growth (SW2), and an interaction between sex and freshwater growth. The random effect of smolt year is given as the standard deviation (σ_{SY}). The marginal (fixed effect only) and conditional (fixed and random effects) R^2 values are also given.

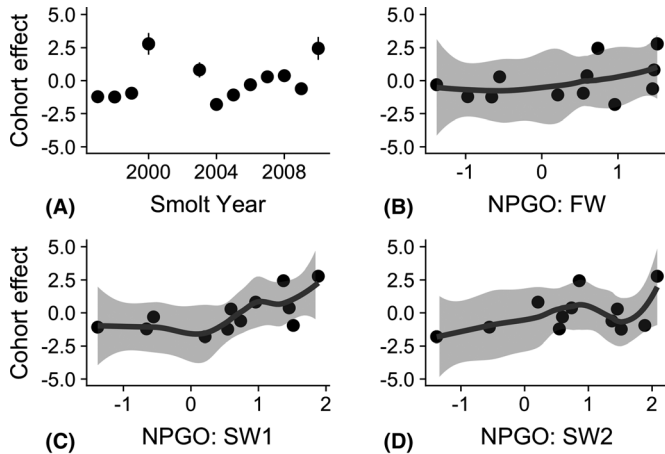| Intercept	Sex (female)	FW	SW1	SW2	Sex (female) $\times$ FW	ΔAIC	σ_{SY}	R^2m	R^2c
1.35 (0.52)	−0.64 (0.24)		0.32 (0.11)	−0.41 (0.11)		0	1.56	0.07	0.47
1.37 (0.52)	−0.66 (0.25)	−0.24 (0.20)	0.32 (0.11)	−0.41 (0.11)	0.44 (0.24)	0.38	1.56	0.08	0.47
1.35 (0.51)	−0.64 (0.24)	0.07 (0.11)	0.31 (0.11)	−0.41 (0.11)		1.64	1.55	0.07	0.46
0.78 (0.47)						27.9	1.53		0.41

FIGURE 5. The effect of cohort (i.e., smolt-year-specific intercepts from the full model) **(A)** on the probability of early maturation over time versus **(B)** the North Pacific Gyre Oscillation (NGPO) index during the final year of freshwater growth, **(C)** first ocean-year growth, and **(D)** second ocean-year growth.

before emigrating to the ocean (Harding 2008), which allows them to attain a relatively large body size upon ocean entry. Their large smolt size, early marine strategy of rapid offshore migration, and consumption of high-energy prey allow steelhead to achieve first ocean-year growth that is not observed for Pacific salmon species until their second year at sea (Atcheson et al. 2012a). These migratory and foraging patterns may help explain the positive relationship between freshwater and first ocean-year growth because larger individuals can consume larger pelagic fish and squid (see Ruggerone et al. 2009 for a similar interpretation in piscivorous Chinook Salmon).

The sex-specific relationships between growth and age at maturity are also likely a general aspect of steelhead biology. Faster growth is typically associated with early maturation in Pacific salmon (e.g., Morita and Fukuwaka 2006; Siegel et al. 2018) and Atlantic Salmon *Salmo salar* (Hutchings and Jones 1998; Jonsson and Jonsson 2007). This was certainly the case with first ocean-year growth, which was associated with early maturation in both male and female steelhead in our study. On the other hand, we observed greater total freshwater growth in early-maturing females but the opposite pattern in early-maturing males. This apparent contradiction might be resolved by considering partial anadromy, a common feature of steelhead life history. In partially anadromous systems, the fastest growing males mature without ever leaving fresh water (reviewed in Kendall et al. 2015) and because we only sampled anadromous individuals, we likely missed a substantial portion of the male population. The female-skewed sex ratio of first-time spawners in the Situk River (63%; Table 1) coupled with evidence for partial anadromy in other steelhead populations in Southeast Alaska (Lohr and Bryant 1999; Ohms et al. 2014) supports this inference. Furthermore, because we were unable to validate freshwater age, we only examined total freshwater growth, which better reflected smolt size than growth rate because it was confounded by (unknown) smolt age. It is possible that the slowest growing males delayed smoltification, thereby obtaining the most total freshwater growth while also being the later-maturing males in the population. Interestingly, Ward and Slaney (1988) detected a positive relationship between smolt age and early maturity in both male and female steelhead in the Keogh River, British Columbia, but they also found relatively even sex ratios in returning anadromous adults, suggesting that partial anadromy was not a prominent feature of that population.

The relationship between growth and maturation could also explain the negative correlation between first and second ocean-year growth that we observed in the steelhead population in the Situk River, although compensatory growth (Ali et al. 2003)—specifically faster second ocean-year growth as a response to slower first ocean-year growth—could not be ruled out. Early-maturing steelhead grew faster during their first ocean year, but they then grew more slowly during their second ocean year, perhaps as a consequence of allocating energy away from somatic growth to gamete development. Support for this interpretation is provided by the univariate maturity models (Figure 4), which showed a steeper relationship between age at maturity and second ocean-year growth for females than for males, as female steelhead are expected to divert greater energy towards fecundity than are males (Ward

and Slaney 1988). Divergent patterns of energy allocation between early- and later-maturing fish during second ocean-year growth could also explain why we saw the greatest among-individual variation in this growth stanza.

While the relationship between growth and age at maturity was supported in this study, growth explained very little of the variation in the probability of maturing early relative to the cohort effect (i.e., among-year variation). That environmental variation can lead to changes in maturation in salmonids is well understood from captive rearing studies, where individuals that are fed a higher ration grow faster and mature earlier (e.g., Shearer et al. 2006). We were only able to infer growth rates from scales, reflecting annual growth in length. It is possible that this measure either did not capture the aspects of growth that are most closely related to maturation, such as lipid content (Shearer and Swanson 2000) or energy stores (Silverstein et al. 1997), or was of insufficient temporal resolution to adequately capture the relevant growth variation. We found that the cohort effect tended to increase with higher NPGO values during early growth, suggesting that conditions that are favorable for upwelling in the Alaskan Gyre and downwelling in the Alaska Coastal Current (i.e., positive NPGO phase; Di Lorenzo et al. 2008) are conducive to earlier maturation in the steelhead population in the Situk River beyond the effects of growth as is reflected in scales. However, similar to studies of growth and age at maturity in Chinook Salmon (Siegel et al. 2017, 2018), we were not able to distinguish this "bottom-up" environmental hypothesis from an alternative hypothesis that variation in mortality rates of older fish could drive temporal patterns in age at maturity of salmonids (e.g., Ohlberger et al. 2018). Allelic variation (e.g., Martyniuk et al. 2003; Barson et al. 2015) could also contribute to among-year variation in age at maturity in steelhead in the Situk River, particularly if smolt-year cohorts originate from only a few consecutive brood years. Ultimately, the cohort effect most likely integrates both environmental and genetic variation, reflecting the current understanding of maturation in salmonids as a probabilistic reaction norm (Hutchings and Jones 1998; Sloat et al. 2014).

The measurement of annual growth increments depends on the accurate and precise identification of scale annuli, including correctly assigning them to a particular year or period of life history. While absolute age-validation methods were somewhat limited in this study, established steelhead aging protocols (Love 2016) and precision assessment tools provided quantitative measures of confidence. While no formal a priori standard of precision has been agreed upon, Campana (2001) suggested that CVs below 7.6% are sufficient to support further analysis and that an informal target CV of 5% is sought by many researchers. The average age-specific CV values in this study ranged from 0.0–18.02%, but for the dominant saltwater ages at maturity (2 and 3 years), the average CVs were 4.69% and 4.04%, respectively, for first-time spawners. Age-bias plots corroborated these findings, indicating minimal aging bias for the dominant age-classes but some underestimation of older age fish. Difficulties in aging the scales from older individuals were expected, as these scales contain complex annuli and circuli patterns that may be obscured or disrupted by scale reabsorption at the spawning check. Scale samples from tagged and recaptured fish provided an additional level of validation, confirming our age estimates for the period of time between capture events. Our estimates of age and repeat-spawning rates also matched those that have been found in previous scale analysis studies of steelhead in Southeast Alaska (Harding and Coyle 2011; Love et al. 2012, 2013).

Our inability to validate freshwater age prevented our marine growth and life history models from accounting for differences in growth that were related to freshwater age. Lakes at the headwaters of the Situk River may have provided overwintering habitat where juvenile steelhead could continue to feed and grow, thus obscuring freshwater annuli. Given the complexity of the freshwater rearing period for juvenile steelhead (ranging from 2 to 5 years in our study region; Harding 2008), it is likely that freshwater growth and residency duration affected the subsequent marine growth patterns and life history variation. The overall study design and age-validation protocols could be improved by tagging and collecting scales from juvenile steelhead rearing in fresh water, as has been done in other Southeast Alaska systems (e.g., Love et al. 2012, 2013). Additionally, future studies could synthesize the freshwater growth-measurement methodologies from this study with scales from juvenile steelhead from Southeast Alaska to define quantitative relationships among freshwater age, freshwater growth, and age at maturity. Such research would provide a validated methodology for estimating total steelhead age from adult steelhead scales and increased insight into the environmental and population characteristics that support life history diversity and subsequent recruitment and survival.

Management Implications

Across the geographic range of steelhead, there is great diversity in the characteristics of populations, habitats, and the approaches that are used to address specific management concerns. Furthermore, steelhead encapsulate the continuum of Pacific salmonid anadromous life history strategies, e.g., the sympatric occurrence of anadromous and nonanadromous forms, gene flow between forms, and the production of offspring that express either form (McPhee et al. 2007; Sloat and Reeves 2014; Kendall et al. 2015). Hodge et al. (2016) identified 38 unique life history categories that are displayed by *O. mykiss*, varying in

freshwater and ocean-rearing periods, maturation, and reproductive characteristics.

Over three hundred watersheds in Southeast Alaska are known to support populations of steelhead, though many are comprised of fewer than 200 anadromous adults (Fowler 2017). The small size and remote location of these populations challenge management, and regional population-monitoring studies are currently limited to survey counts of index streams (Harding and Coyle 2011; Fowler 2017). The stock assessment objectives for steelhead in the Situk River focus on abundance monitoring and the tracking of fish sex and length characteristics (Marston and Power 2016) to inform management responses to changes in stock characteristics and fishery effects. However, current management is limited in its consideration of how changing marine and freshwater aquatic habitats may affect steelhead across Southeast Alaska.

Scale-growth analysis offers an underused source of information on the patterns of steelhead growth and demography in Alaska and beyond, and it is well suited to steelhead research because it is relatively noninvasive and affordable compared with alternative sampling methods (Love 2016). Standardized, representative scale sampling methodology coupled with standardized analyses of steelhead scales may better inform our understanding of the early marine ecology, life history diversity, and growth dynamics that contribute to the stability and resilience of steelhead populations (Moore et al. 2014). This may be particularly relevant in Southeast Alaska where numerous populations exhibit relatively stable abundance trends (Fowler 2017) despite their small size and potential effects from targeted recreational fisheries, interception in commercial fisheries, and variable freshwater and marine environmental conditions. The management applications of scale growth analysis in larger, more thoroughly studied populations in the Pacific Northwest and British Columbia are likely specific to the research and conservation priorities of those fisheries, but the collection and incorporation of scale-derived metrics of juvenile steelhead growth into population-monitoring protocols would provide baseline information that may inform management in the face of increasingly unpredictable environmental change.

ORCID

Megan V. McPhee https://orcid.org/0000-0001-9614-4137

REFERENCES

ADFG (Alaska Department of Fish and Game). 2016. Alaska sport fishing survey database, 1996–2015 [online database]. ADFG, Sport Fish Division, Anchorage. Available: https://intra.sf.adfg.state.ak.us/swhs_est/. (January 2020).

ADFG (Alaska Department of Fish and Game). 2019. Alaska sport fishing survey database 1996–current [online database]. ADFG, Sport Fish Division, Anchorage. Available: https://intra.sf.adfg.state.ak.us/swhs_est/. (January 2020).

Ali, M., A. Nicieza, and R. J. Wootton. 2003. Compensatory growth in fishes: a response to growth depression. Fish and Fisheries 4:147–190.

Atcheson, M. E., K. W. Myers, D. A. Beauchamp, and N. J. Mantua. 2012a. Bioenergetic response by steelhead to variation in diet, thermal habitat, and climate in the North Pacific Ocean. Transactions of the American Fisheries Society 141:1081–1096.

Atcheson, M. E., K. W. Myers, N. E. Davis, and N. J. Mantua. 2012b. Potential trophodynamic and environmental drivers of steelhead (*Onchorhynchus mykiss*) productivity in the North Pacific Ocean. Fisheries Oceanography 21:321–335.

Augerot, X. 2005. Atlas of Pacific salmon: the first map-based assessment of salmon in the north Pacific. University of California Press, Berkeley.

Bain, C. S., S. T. Elliot, R. Johnson, and G. Woods. 2003. Situk River steelhead: a review of historical data through 1996. Alaska Department of Fish and Game, Fishery Manuscript 03-01, Anchorage.

Barson, N. J., T. Aykanat, K. Hindar, M. Baranski, G. H. Bolstad, P. Fiske, C. Jacq, A. J. Jensen, S. E. Johnston, S. Karlsson, M. Kent, T. Moen, E. Niemelä, T. Nome, T. F. Næsje, P. Orell, A. Romakkaniemi, H. Sægrov, K. Urdal, J. Erkinaro, S. Lien, and C. R. Primmer. 2015. Sex-dependent dominance at a single locus maintains variation in age at maturity in salmon. Nature 528:405–408.

Bartón, K. 2017. MuMIn: multi-model inference. R package version 1.40.0. R Foundation for Statistical Computing, Vienna.

Bates, D., M. Machler, B. Bolker, and S. Walker. 2015. Fitting linear mixed-effects models using lme4. Journal of Statistical Software [online serial] 67(1).

Beakes, M. P., R. Sharron, R. Charish, J. W. Moore, W. H. Satterthwaite, E. Sturm, B. K. Wells, S. M. Sogard, and M. Mangel. 2014. Using scale characteristics and water temperature to reconstruct growth rates of juvenile steelhead *Oncorhynchus mykiss*. Journal of Fish Biology 84:58–72.

Beamish, R. J., and G. A. MacFarlane. 1983. The forgotten requirement for age validation in fisheries biology. Transactions of the American Fisheries Society 112:735–743.

Burgner, R. L., J. T. Light, L. Margolis, T. Okazaki, A. Tautz, and S. Ito. 1992. Distribution and origins of steelhead trout (*Oncorhynchus*

mykiss) in offshore waters of the North Pacific Ocean. International North Pacific Fisheries Commission Bulletin 51.

Campana, S. E. 2001. Accuracy, precision and quality control in age determination, including a review of the use and abuse of age validation methods. Journal of Fish Biology 59:197–242.

Campana, S. E., C. M. Annand, and J. I. McMillan. 1995. Graphical and statistical methods for determining the consistency of age determinations. Transactions of the American Fisheries Society 124:131–138.

Catterson, M. R. 2017. Early marine growth patterns of Situk River steelhead, *Oncorhynchus mykiss*. Master's thesis. University of Alaska, Fairbanks, Fairbanks.

Copeland, T., K. Hernandez, M. T. Davison, and K. Wright. 2018. Validation of spawn checks and saltwater age assignments based on scales from known repeat-spawning steelhead. North American Journal of Fisheries Management 38:1050–1058.

Daugherty, D. J., T. M. Sutton, and R. W. Greil. 2003. Life-history characteristics, population structure, and contribution of hatchery and wild steelhead in a Lake Huron tributary. Journal of Great Lakes Research 29:511–520.

Debertin, A. J., J. R. Irvine, C. A. Holt, G. Oka, and M. Trudel. 2017. Marine growth patterns of southern British Columbia Chum Salmon explained by interactions between density-dependent competition and changing climate. Canadian Journal of Fisheries and Aquatic Sciences 74:1077–1087.

Di Lorenzo, E., N. Schneider, K. M. Cobb, P. J. S. Franks, K. Chhak, A. J. Miller, J. C. McWilliams, S. J. Bograd, H. Arango, E. Curchitser, T. M. Powell, and P. Rivière. 2008. North Pacific Gyre Oscillation links ocean climate and ecosystem change. Geophysical Research Letters 35:L08607.

Fisher, J. P., and W. G. Pearcy. 2005. Seasonal changes in growth of Coho Salmon (*Oncorhynchus kisutch*) off Oregon and Washington and concurrent changes in the spacing of scale circuli. U.S. National Marine Fisheries Service Fishery Bulletin 103:34–50.

Fowler, P. 2017. Southeast Alaska steelhead snorkel surveys of regional index streams, 2014 and 2015. Alaska Department of Fish and Game, Fishery Data Series 17-13, Anchorage.

Friedland, K. D., B. R. Ward, D. W. Welch, and S. A. Hayes. 2014. Postsmolt growth and thermal regime define the marine survival of steelhead from the Keogh River, British Columbia. Marine and Coastal Fisheries: Dynamics, Management, and Ecosystem Science [online serial] 6:1–11.

Good, T. P., R. S. Waples, and P. Adams. 2005. Updated status of federally listed ESUs of west coast salmon and steelhead. NOAA Technical Memorandum NMFS-NWFSC-66.

Gubernick, R., and S. Paustian. 2007. Hubbard Glacier, Russell Fiord and Situk River—a landscape in motion. U.S. Forest Service PNW-GTR 689:401–418.

Hagen, P. T., D. S. Oxman, and B. A. Agler. 2001. Developing and deploying a high resolution imaging approach for scale analysis. North Pacific Anadromous Fish Commission, Document 567, Vancouver.

Harding, R. 2008. Southeast Alaska steelhead and Dolly Varden management. Alaska Department of Fish and Game, Special Publication 08-21, Anchorage.

Harding, R. D., and C. L. Coyle. 2011. Southeast Alaska steelhead, trout, and Dolly Varden management. Alaska Department of Fish and Game, Special Publication 11-17, Anchorage.

Hartig, F. 2019. DHARMa: residual diagnostics for hierarchical (multilevel/mixed) regression models. R package version 0.2.4. R Foundation for Statistical Computing, Vienna.

Hodge, B. W., M. A. Wilzbach, W. G. Duffy, R. M. Quiñones, and J. A. Hobbs. 2016. Life-history diversity in Klamath River steelhead. Transactions of the American Fisheries Society 145:227–238.

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:S22–S47.

Johnson, R. E., and J. D. Jones. 1998. Southeast Alaska steelhead studies, 1997: Situk River weir and surveys of index streams. Alaska Department of Fish and Game, Fishery Data Series 98-45, Anchorage.

Johnsson, J. I., J. Blackburn, W. C. Clarke, and R. E. Withler. 1997. Does presmolt growth rate in steelhead trout (*Oncorhynchus mykiss*) and Coho Salmon (*Oncorhynchus kisutch*) predict growth rate in seawater? Canadian Journal of Fisheries and Aquatic Sciences 54:430–433.

Jonsson, N., and B. Jonsson. 2007. Sea growth, smolt age and age at sexual maturation in Atlantic Salmon. Journal of Fish Biology 71:245–252.

Kendall, N. W., J. R. McMillan, M. R. Sloat, T. W. Buehrens, T. P. Quinn, G. R. Pess, K. V. Kuzishcin, M. M. McClure, and R. W. Zabel. 2015. Anadromy and residency in steelhead and Rainbow Trout (*Oncorhynchus mykiss*): a review of the processes and patterns. Canadian Journal of Fisheries and Aquatic Sciences 72:319–342.

Koo, T. S. Y. 1962. Age designation in salmon. Pages 37–48 *in* T. S. Y. Koo, editor. Studies of Alaska red salmon. University of Washington Press, Seattle.

Lohr, S. C., and M. D. Bryant. 1999. Biological characteristics and population status of steelhead (*Oncorhynchus mykiss*) in Southeast Alaska. U.S. Forest Service General Technical Report PNW-GTR-407.

Love, D. C. 2016. Manual for aging steelhead trout scales based on scale sampling from Sitkoh Creek, Big Ratz Creek, and other Southeast Alaska streams, 2003–2011. Alaska Department of Fish and Game, Special Publication 16-13, Anchorage.

Love, D. C., and R. D. Harding. 2009. Steelhead trout production studies at Sitkoh Creek, Alaska, 2005–2006. Alaska Department of Fish and Game, Fishery Data Series 09-68, Anchorage.

Love, D. C., R. D. Harding, and D. J. Reed. 2013. Steelhead trout production studies at Big Ratz Creek, Alaska, 2010–2011. Alaska Department of Fish and Game, Fishery Data Series 13-02, Anchorage.

Love, D. C., D. J. Reed, and R. D. Harding. 2012. Steelhead trout production studies at Sitkoh Creek, Alaska, 2003–2009, and 2009, Final Report. Alaska Department of Fish and Game, Fishery Data Series 12-82, Anchorage.

Marco-Rius, F., P. Caballero, P. Moran, and C. Garcia de Leaniz. 2012. And the last shall be first: heterochrony and compensatory marine growth in Sea Trout (*Salmo trutta*). PLoS (Public Library of Science) ONE [online serial] 7:e45528.

Marston, B. H. 2014. Situk River steelhead stock assessment, 2014–2015. Alaska Department of Fish and Game, Division of Sport Fish, Regional Operational Plan SF.IJ.2014.09, Anchorage.

Marston, B. H., R. E. Johnson, and S. J. H. Power. 2012. Steelhead studies from the Situk River in Southeast Alaska, 2002–2008. Alaska Department of Fish and Game, Fishery Data Series 12-40, Anchorage.

Marston, B. H., and S. J. H. Power. 2016. Situk River steelhead stock assessment, 2016–2017. Alaska Department of Fish and Game, Division of Sport Fish, Regional Operational Plan SF.1J.2016.03, Anchorage.

Martyniuk, C. J., G. M. L. Perry, H. K. Mogahadam, M. M. Ferguson, and R. G. Danzmann. 2003. The genetic architecture of correlations among growth-related traits and male age at maturation in Rainbow Trout. Journal of Fish Biology 63:746–764.

McPhee, M. V., J. M. Leon, L. I. Wilson, J. E. Siegel, and B. A. Agler. 2016. Changing growth and maturity in western Alaskan Chinook Salmon *Oncorhynchus tshawytscha*, brood years 1975–2005. North Pacific Anadromous Fish Commission Bulletin 6:307–327.

McPhee, M. V., F. Utter, J. A. Stanford, K. V. Kuzishchin, K. A. Savvaitova, D. S. Pavlov, and F. W. Allendorf. 2007. Population

structure and partial anadromy in *Oncorhynchus mykiss* from Kamchatka: relevance for conservation strategies around the Pacific Rim. Ecology of Freshwater Fish 16:539–547.

Moore, J. W., J. D. Yeakel, D. Peard, J. Lough, and M. Beere. 2014. Life-history diversity and its importance to population stability and persistence of migratory fish: steelhead in two large North American watersheds. Journal of Animal Ecology 83:1035–1046.

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

Nakagawa, S., P. C. D. Johnson, and H. Schielzeth. 2017. Coefficient of determination R^2 and intra-class correlation coefficient from generalized linear mixed-effects models revisited and expanded. Journal of Royal Society Interface 14:20170213.

Ohlberger, J., E. J. Ward, D. E. Schindler, and B. Lewis. 2018. Demographic changes in Chinook Salmon across the Northeast Pacific Ocean. Fish and Fisheries 19:533–546.

Ohms, H. A., M. R. Sloat, G. H. Reeves, C. E. Jordan, and J. B. Dunham. 2014. Influence of sex, migration distance, and latitude on life history expression in steelhead and Rainbow Trout (*Oncorhynchus mykiss*). Canadian Journal of Fisheries and Aquatic Sciences. 71:70–80.

Quinn, T. P., and K. W. Myers. 2005. Anadromy and the marine migrations of Pacific salmon and trout: Rounsefell revisited. Reviews in Fish Biology and Fisheries 14:421–442.

Quinn, T. P., T. R. Seamons, L. A. Vøllestad, and E. Duffy. 2011. Effects of growth and reproductive history on the egg size-fecundity trade-off in steelhead. Transactions of the American Fisheries Society 140:45–51.

R Core Team. 2014. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna.

Ruckelshaus, M. H., P. Levin, J. B. Johnson, and P. M. Kareiva. 2002. The Pacific salmon wars: what science brings to the challenge of recovering species. Annual Review of Ecology and Systems 33:665–706.

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.

Schindler, D. E., R. Hilborn, B. Chasco, C. P. Boatright, T. P. Quinn, L. A. Rogers, and M. S. Webster. 2010. Population diversity and the portfolio effect in an exploited species. Nature 465:609–613.

Seamons, T. R., M. B. Dauer, J. Sneva, and T. P. Quinn. 2009. Use of parentage assignment and DNA genotyping to validate scale analysis for estimating steelhead age and spawning history. North American Journal of Fisheries Management 29:396–403.

Shapovalov, L., and A. C. Taft. 1954. Life histories of the steelhead Rainbow Trout (*Salmo gairdneri gairdneri*) and Silver Salmon (*Oncorhynchus kisutch*). California Department of Fish and Game Bulletin 98:1–303.

Shearer, K., P. Parkins, B. Gadberry, B. Beckman, and P. Swanson. 2006. Effects of growth rate/body size and a low lipid diet on the incidence of early sexual maturation in juvenile male spring Chinook Salmon (*Oncorhynchus tshawytscha*). Aquaculture 252:545–556.

Shearer, K. D., and P. Swanson. 2000. The effect of whole body lipid on early sexual maturation of 1 + age male Chinook Salmon (*Oncorhynchus tshawytscha*). Aquaculture 190(3–4):343–367.

Siegel, J. E., M. D. Adkison, and M. V. McPhee. 2018. Changing maturation reaction norms and the effects of growth history in Alaskan Chinook Salmon. Marine Ecology Progress Series 595:187–202.

Siegel, J. E., M. V. McPhee, and M. D. Adkison. 2017. Evidence that marine temperatures influence growth and maturation of western Alaskan Chinook Salmon *Oncorhynchus tshawytscha*. Marine and Coastal Fisheries: Dynamics, Management, and Ecosystem Science [online serial] 9:441–456.

Silverstein, J. T., H. Shimma, and H. Ogata. 1997. Early maturity in Amago Salmon (*Oncorhynchus masu ishikawai*): an association with energy storage. Canadian Journal of Fisheries and Aquatic Sciences 54:444–451.

Sloat, M. R., D. J. Fraser, J. B. Dunham, J. A. Falke, C. E. Jordan, J. R. McMillan, and H. A. Ohms. 2014. Ecological and evolutionary patterns of freshwater maturation in Pacific and Atlantic salmonines. Reviews in Fish Biology and Fisheries 24:689–707.

Sloat, M. R., and G. H. Reeves. 2014. Individual condition, standard metabolic rate, and rearing temperature influence steelhead and Rainbow Trout (*Oncorhynchus mykiss*) life histories. Canadian Journal of Fisheries and Aquatic Sciences 71:491–501.

Thedinga, J. F., S. W. Johnson, K. V. Koski, J. M. Lorenz, and M. L. Murphy. 1993. Potential effects of flooding from Russell Fiord on salmonids and habitat in the Situk River, Alaska. Alaska Fisheries Science Center, Processed Report 93-01, Juneau.

Vøllestad, L. A., J. Peterson, and T. P. Quinn. 2004. Effects of freshwater and marine growth rates on early maturity in male Coho and Chinook salmon. Transactions of the American Fisheries Society 133:495–503.

Ward, B. R., and P. A. Slaney. 1988. Life history and smolt-to-adult survival of Keogh River steelhead (*Salmo gairdneri*) and the relationship to smolt size. Canadian Journal of Fisheries and Aquatic Sciences 45:1110–1122.

Zeiser, N. L., and G. F. Woods. 2016. Annual Management Report of the 2015 Yakutat Area commercial salmon fisheries. Alaska Department of Fish and Game, Fishery Management Report 16-22, Anchorage.

Zuur, A. F., E. N. Ieno, N. J. Walker, A. A. Saveliev, and G. M. Smith. 2009. Mixed effects models and extensions in ecology with R. Springer, New York.

SUPPORTING INFORMATION

Additional supplemental material may be found online in the Supporting Information section at the end of the article.