

Density dependence and its impact on individual growth rates in an age-structured stream salmonid population

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Abstract. In organisms with flexible and indeterminate growth, demographic density dependence can affect both individual fitness and population dynamics. Recent work in stream salmonids suggests that individual growth rates can be depressed even at low population densities, which warrants examination of populations previously assumed to be below carrying capacity. We investigated the effects of population density on individual growth rates in a threatened population of steelhead (*Oncorhynchus mykiss*) in a tributary to the Clearwater River in Idaho, USA. We followed a mark-recapture design where we visited 16 study sites on average five times per year from 2010 to 2012. The 95% confidence interval for average growth rates (% change in body mass per day) for subyearlings were [0.82, 1.0] and [0.16, 0.30] for yearling steelhead. Variance decomposition showed that the variation in growth rates could be attributed equally to individual- and visit-level factors in subyearlings, whereas almost two-thirds of the variance in yearling growth rates could be attributed to individual-level factors. Growth rates in the subyearling age class were negatively related to the densities of yearling steelhead, but not vice versa. Yearling growth rates showed no evidence of density dependence. Finally, density in interaction with water temperature did not affect growth rates of either age class. Our results demonstrate that density dependence can pose constraints on individual growth rates at low population densities (<1 fish m⁻²) in stream salmonids, and underscore the importance of considering age classes separately when studying density dependence in age-structured populations.

Key words: inter-cohort competition; intraspecific competition; *Oncorhynchus mykiss*; population dynamics; regulation; steelhead.

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INTRODUCTION

Wild populations are regulated if they persist for many generations, are bounded at some level above zero and below infinity, and show a return tendency towards some long-term mean (Turchin 1995, Hixon et al. 2002). The mechanism responsible for population regulation is demographic density dependence, because abiotic factors alone cannot produce a return tendency (Haldane 1953, Hixon et al. 2002).

Density dependence occurs when present or past population size affects the population's per capita growth rate (Sinclair and Pech 1996, Turchin 1999). In closed populations (i.e., no migration), the change in abundance is determined by the difference in birth- and death rates. Thus, the change in the population's growth rate can be affected by changes in both demographic rates (Morris and Doak 2002). Whereas mortality directly affects the numbers of individuals in an age class, birth rates can be

affected via subsequent changes to the individuals' fitness, which in turn can affect reproductive success and future population size (Rose et al. 2001).

In organisms with flexible and indeterminate growth, such as fishes, individual fitness and life-history expression can be largely determined by growth performance during juvenile stages (Sogard 1997, Rose et al. 2001, Lorenzen and Enberg 2002, Achord et al. 2003). Depressed growth can result in decreased survival via prolonged stage duration, which can increase predation risk and size-dependent mortality (Werner and Gilliam 1984, Ward and Slaney 1988, Quinn and Peterson 1996), and lower reproductive success through altered fecundity, egg quality, and spawning location (Morita and Takashima 1998, Einum and Fleming 1999, Rose et al. 2001, Lorenzen and Enberg 2002). A useful diagnosis of density dependence is hence to measure the effects of population density on individual performance metrics, such as body mass and growth rate (Walters and Post 1993).

Recent work in populations of stream salmonids suggests that the effects of population density are manifested in mortality rates at high densities, and in individual growth rates at lower densities (Elliott 1994, Grant and Imre 2005, Einum et al. 2006, Lobón-Cerviá 2007, Kaspersson et al. 2013, Walters et al. 2013). High densities typically occur during the early post-emergent stage, when individuals have limited energy reserves to withstand even short periods of starvation, and consequently die if they cannot find food and shelter (Elliott 1994, Rose et al. 2001, Einum et al. 2006). Later in their development, individuals are on average larger and can better tolerate periods of starvation. Their fat reserves hence create a buffer against mortality, but the effects of competition can be manifested in depressed growth rates (Einum et al. 2006). For example, Jenkins et al. (1999) found stronger negative effects of density on brown trout (*Salmo trutta*) mass at densities $<1 \text{ fish m}^{-2}$, with greater effects on subyearling growth than that of yearling fish. Further, in a meta-analysis of 19 stream salmonid populations, Grant and Imre (2005) found significant decreases in growth rates with increasing densities in 15 populations, with most of the decrease occurring at densities

$<1 \text{ fish m}^{-2}$.

Density dependence is often neglected in studies of small populations because it is often assumed to be of lesser importance than stochastic, density-independent factors (Achord et al. 2003, Lobón-Cerviá 2007, Walters et al. 2013). However, with the potentially strong influence of density on individual growth rates, and the consequences for life history expression and fitness, it is important to understand the extent to which density dependence is manifested at the individual level (Sogard 1997, DeAngelis and Mooij 2005, Kaspersson et al. 2013). These effects can be particularly important in age-structured populations, in which the presence of one cohort can alter the behavior of another (Rosenfeld and Boss 2001, Kaspersson and Höjesjö 2009), and in populations experiencing abiotic conditions which can exacerbate the effects of competition (Crozier et al. 2010, Parra et al. 2012). Here we study the effects of population density on individual growth rates in juvenile age classes of steelhead (*Oncorhynchus mykiss*) in a population listed as threatened under the Endangered Species Act (NMFS 2010). We hypothesize that individual growth rates in both subyearling and yearling steelhead are negatively related to the density of their age class (Imre et al. 2005, Lobón-Cerviá 2007), and that subyearling growth rates are more negatively affected by yearling densities than vice versa (Jenkins et al. 1999, Kaspersson and Höjesjö 2009).

MATERIALS AND METHODS

Study area and population

The study was conducted in the 694 km² Lapwai Creek watershed of north-central Idaho, United States (Fig. 1). Details on the study area and the population were given in Myrvold and Kennedy (2015). The watershed is located on the boundary between the Columbia River Plateau and Northern Rockies ecoregions (level IV regions 10f and 15f; McGrath et al. 2002), and is dominated by canyon topography through a mix of coniferous forest at higher elevations and grasslands at lower elevations. Mean annual precipitation is 490 mm, primarily falling as rain and snow from October through May. The hydrograph follows a typical snowmelt-driven

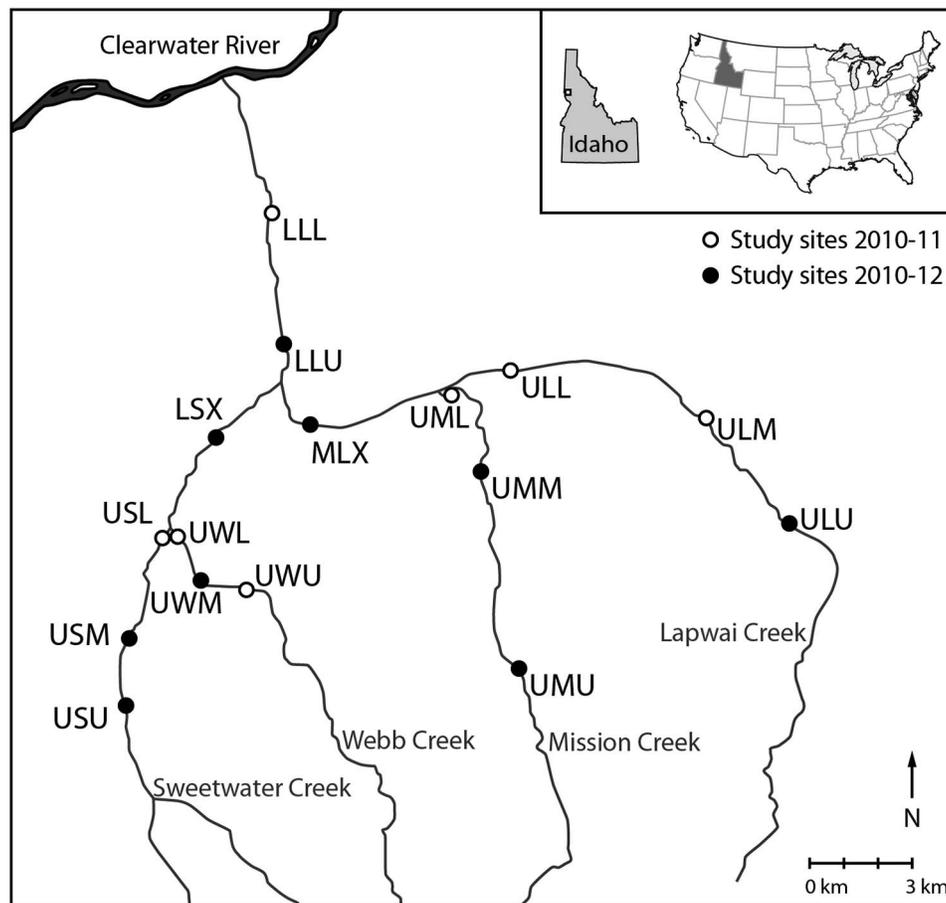


Fig. 1. The map shows the four major streams of the Lapwai Creek watershed and its location in north-central Idaho, United States (inset). All 16 study sites were sampled in 2010 and 2011, and nine were sampled in 2012 (a subset of the 16). The watershed is located within the Columbia River Basin.

pattern with a few rain-on-snow events occurring during winter, and baseflow conditions with very few rain-driven spates from July through October (K. M. Myrvold, *personal observation*). The watershed is designated as critical habitat for wild Snake River steelhead (NMFS 2010) and there is no hatchery supplementation of the population. Study sites were defined using a stratified random approach (Frissell et al. 1986) to capture a gradient of the physiographic conditions and land uses within the basin. Other fish species include, in order of abundance, longnose dace (*Rhinichthys cataractae*), sculpin (*Cottus* spp.), bridgelip sucker (*Catostomus columbianus*), redbelt shiner (*Richardsonius balteatus*), northern pikeminnow (*Ptychocheilus oregonensis*), and chiselmouth (*Acrocheilus alutaceus*). In recent

years juvenile coho salmon (*Oncorhynchus kisutch*) have been stocked as part of a reintroduction program in lower reaches of the system, but are generally not sympatric in space or time with steelhead.

Sampling methods and data

Sampling methods have been described elsewhere (Myrvold and Kennedy 2015), but we review key details in the following. Field data were collected monthly at each study site over five months from mid-June to late October each year from 2010 to 2012. We set block nets to ensure a closed population, and conducted three-pass depletion electrofishing using a Smith-Root LR-24 backpack electroshocker (Smith-Root, Vancouver, Washington, USA). We conducted the

sampling during early morning hours when the water temperatures did not exceed 18°C, and kept the voltage, frequency, and duty cycle within 20% of their mean values of 350 V, 30 Hz, and 15%, respectively. Fish were held in aerated water at ambient stream temperatures and anesthetized with tricaine methanesulfonate (MS-222) prior to handling. We measured fork length in millimeters and weight to the nearest 0.1 gram. Steelhead were scanned for PIT tags using a FS-2001F-ISO reader (Destron Fearing, St. Paul, Minnesota, USA) and data on the individuals were recorded in program P3 (PIT-Tag Information System for the Columbia Basin). For untagged individuals 65 mm and larger we inserted 134.2 kHz PIT tags (Biomark, Boise, Idaho, USA) into the ventral body cavity. Prior to release, fish were first allowed to recover in buckets with aerated water, and were then moved to a live-well placed in the stream channel outside the sampling reach. Upon completion of sampling, we removed the block nets and released fish back to the study reach. We sampled 16 sites in 2010 and 2011, and nine sites in 2012 (a subset of the 16; Fig. 1).

Each individual steelhead was classified as subyearling (hatched in the late spring in the same calendar year) or yearling (hatched in the previous year) based on an examination of the length frequency histogram of each sampling visit (called *visit* in the following). We calculated densities using Carle and Strub's (1978) maximum weighted likelihood estimator of multiple-pass removal data. Due to the small size and low discharge of these streams we obtained high capture probabilities (season averages and their associated standard deviations were 0.63 [0.14] in 2010, 0.62 [0.13] in 2011, and 0.64 [0.13] in 2012) and consequently narrow confidence intervals around our population estimates. The density distribution is shown in Fig. 2. Densities were expressed as numbers per 100 m² and natural log-transformed in the analyses to ensure that statistical assumptions were met. Growth rates from recaptured individuals were calculated as percent change in body mass per day between capture events, and are displayed in Fig. 3. The majority of the individuals from which we could calculate growth rates were encountered in one set of consecutive visits (i.e., from month *i* to month *i* + 1). We only included

visits with more than four growth measurements to ensure reliable representation (Maas and Hox 2005). All sampling procedures were permitted as part of the Section 7 consultation for the Lewiston Orchards Biological Opinion (NMFS 2010), and reviewed and approved by Idaho Department of Fish and Game and the University of Idaho Institutional Animal Care and Use Committee. Finally, water temperature (°C) data were collected every 30 minutes at each study site using HOBO TidbiT v.2 temperature loggers (Onset Computer, Pocasset, Massachusetts, USA). We used the average temperature in the week prior to sampling as the basis in the modeling to level out the daily fluctuations.

Analytical approach

In our analyses we had to account for the clustered design (i.e., visits to discrete study sites) and the hierarchical structure of the data (i.e., individual-level response and population-level predictors). We therefore used a hierarchical linear model, which is also known as mixed-effects models in biometric applications and covariance-components models in statistics (Raudenbush and Bryk 2002, McMahan and Diez 2007). Hierarchical linear models use nested regression equations to investigate relationships between variables at different levels, such as an individual-level response (growth rate) and a population-level predictor variable (density).

Variance decomposition for growth rates.—To quantify how much variation in growth rates that could be attributed to the different levels (individual, visit, and site), and subsequently how many levels we would explicitly model, we performed a one-way analysis of variance (Raudenbush and Bryk 2002). The model for the variance components for the site-, visit-, and individual level (the unconditional model) can be written as

$$\text{Growth}_{ijk} = \gamma_{000} + v_{00k} + u_{0jk} + r_{ijk} \quad (1)$$

where γ_{000} is the grand mean growth rate of all steelhead in an age class; v_{00k} is the random "site effect," that is the deviation of site *k*'s mean from the grand mean; u_{0jk} is the random "visit effect," that is the deviation of visit *jk*'s mean from the site mean; and r_{ijk} is the random individual effect,

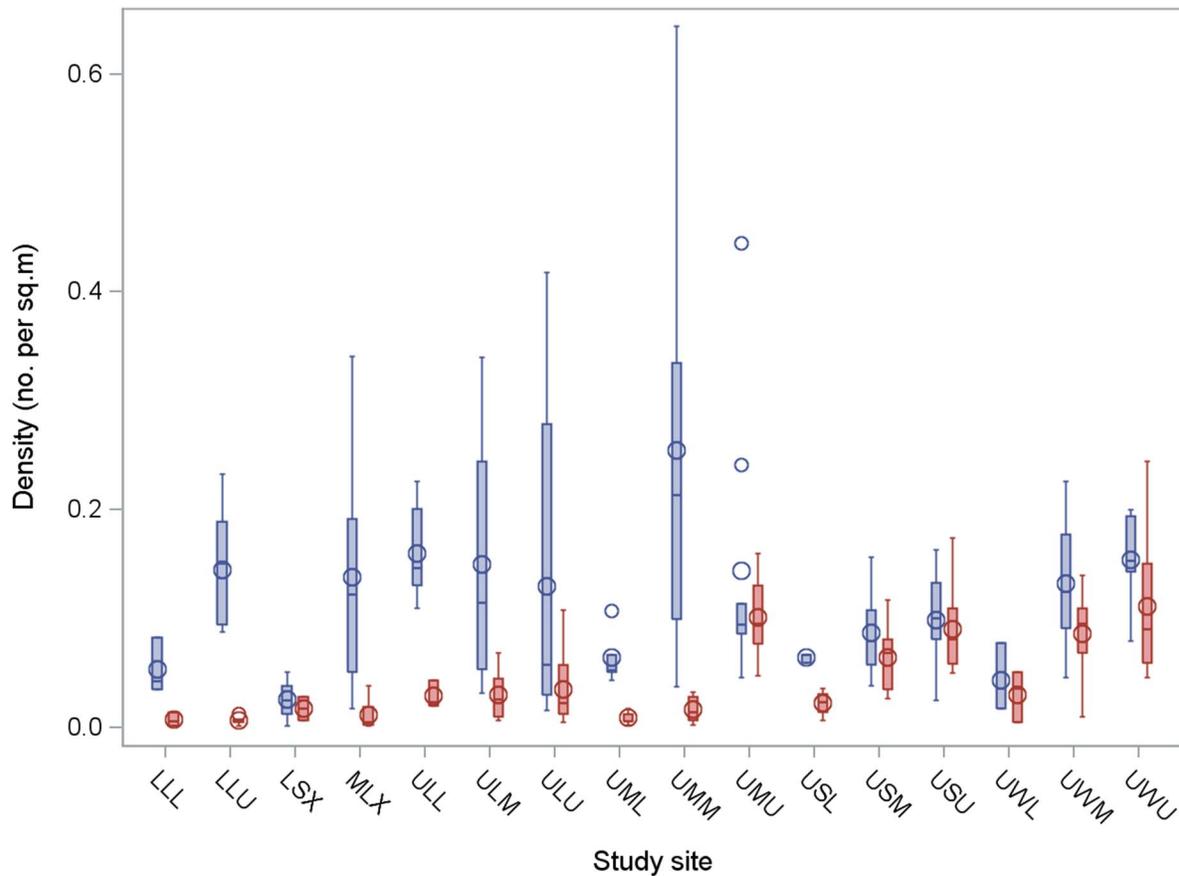


Fig. 2. Densities (m^{-2}) of subyearling (blue bars) and yearling (red bars) steelhead estimated for the study sites in the Lapwai Creek watershed between 2010 and 2012. The data are based on an average of five visits to each site each year. The boxes contain density values within the 25th and 75th percentiles, and the whiskers delimit the minimum and maximum values within 1.5 times this interquartile range. The bar inside each box represents the median density, and the circle marker represents the mean. Outliers greater than 1.5 times the inter-quartile range are marked as circles above or below the whiskers.

i.e., the deviation of fish ijk 's growth rate from the visit mean. Because study sites and visits were randomly sampled from a larger statistical population of potential sites and visits, and because individuals could move freely between sampling events and thus were sampled at random, we can assume that $v_{00k} \sim N(0, \tau_v)$; $u_{0jk} \sim N(0, \tau_u)$; and $r_{ijk} \sim N(0, \sigma^2)$. Because the means of these random effects are zero, the unconditional model effectively consists of their variance terms τ_v , τ_u , and σ^2 . We also considered a model with two levels, *individual* and *visit*. It has the same properties as the three-level model, and can be written as

$$\text{Growth}_{ij} = \gamma_{00} + u_{0j} + r_{ij} \quad (2)$$

where individual i at visit j is related to a grand mean (γ_{00}), a visit-level variance (u_{0j}) around this mean, and an individual-level error (r_{ij}), with $u_{0j} \sim N(0, \tau_{00})$ and $r_{ij} \sim N(0, \sigma^2)$. The proportion of the variance in growth rates that is attributable to each level is called the intraclass correlation (ρ), and is calculated as the proportion of the variance at each level divided by the total variance (Raudenbush and Bryk 2002):

$$\rho = \text{variance at one level} / \text{sum of variances all levels.}$$

The variance decomposition showed significant clustering of the data (Table 1), which warranted a hierarchical modeling approach. However, steelhead growth rates did not vary appreciably

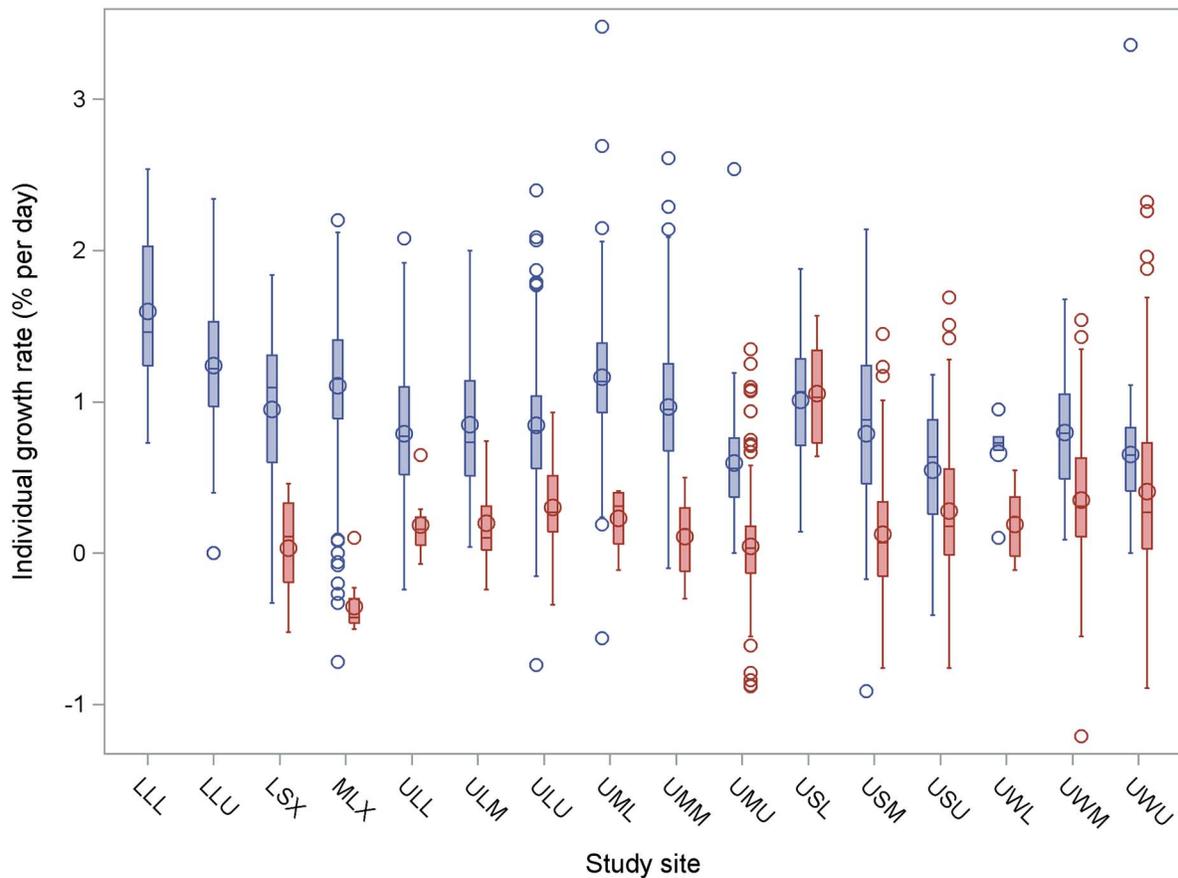


Fig. 3. Growth rates (% change in body mass day⁻¹) of individually tagged subyearling (blue bars, $n = 1228$) and yearling (red bars, $n = 983$) steelhead in the Lapwai Creek watershed between 2010 and 2012. The growth histories are grouped by study site, and the variation within each site reflects individual variation.

between sites (the 95% confidence interval for the site-level variance τ_v included zero for both age classes), which meant that a two-level model was sufficient for our analysis. The variance decomposition in the two-level models showed that 37% of the variance in subyearling growth rates and 52% of the variance in yearling growth rates were attributable to visit-level factors and the rest to individual-level factors (Table 1).

Models of density dependence.—The primary factor we were interested in was the effect of age class density on individual growth rates, and how water temperature could affect these relationships. However, because growth rates (as measured by a change in body mass over a given time increment) tend to decrease as a fish ages, we had to account for fish mass. Further, there is evidence in the salmonid literature of inter-

cohort competition in age-structured populations (Nordwall et al. 2001, Kaspersson and Höjesjö 2009). To examine these potentially differential effects of age class density on individual growth rates, we explicitly modeled the effects of each age class and the total density. An individual-level model of growth as a function of body mass for fish i at visit j can be written as

$$\text{Growth}_{ij} = \beta_{0j} + \beta_{1j}\text{mass}_{ij} + r_{ij}. \quad (3)$$

To introduce the visit-level covariate density, and allowing the intercept to vary as a random effect according to each visit, we can write

$$\beta_{0j} = \gamma_{00} + \gamma_{01}\text{density}_j + u_{0j}$$

$$\beta_{1j} = \gamma_{10} + \gamma_{11}\text{density}_j.$$

Table 1. Variance decomposition by model structure and age class. Shown for each model are the grand mean growth rate estimate and the estimates of the variance components, both with standard errors in parentheses, and the P -value of the test (H_0 : estimate = 0). Shown for the variance components are the intraclass correlation coefficients (ρ).

Level, by structure and age class	Variance term	Estimate (SE)	ρ	P
Three levels: $\text{Growth}_{ijk} = \gamma_{000} + \gamma_{00k} + u_{0jk} + r_{ijk}$				
Subyearling				
Mean	γ_{000}	0.900 (0.0629)		<0.0001
Individual	σ^2	0.143 (0.00598)	47.8	<0.0001
Visit	τ_u	0.125 (0.0253)	41.9	<0.0001
Site	τ_v	0.0307 (0.0243)	10.3	0.10
Yearling				
Mean	γ_{000}	0.224 (0.0483)		0.0017
Individual	σ^2	0.108 (0.00506)	59.0	<0.0001
Visit	τ_u	0.0640 (0.0138)	34.9	<0.0001
Site	τ_v	0.0113 (0.0126)	6.1	0.19
Two levels: $\text{Growth}_{ij} = \gamma_{00} + u_{0j} + r_{ij}$				
Subyearling				
Mean	γ_{00}	0.908 (0.0455)		<0.0001
Individual	σ^2	0.143 (0.00598)	48.3	<0.0001
Visit	τ_{00}	0.153 (0.00598)	51.7	<0.0001
Yearling				
Mean	γ_{00}	0.230 (0.0346)		<0.0001
Individual	σ^2	0.108 (0.00506)	62.9	<0.0001
Visit	τ_{00}	0.0742 (0.0506)	37.1	<0.0001

Combining into Eq. 3, this model structure becomes a random intercept model:

$$\text{Growth}_{ij} = \gamma_{00} + \gamma_{01}\text{density}_j + \gamma_{10}\text{mass}_{ij} + \gamma_{11}\text{mass}_{ij} \times \text{density}_j + u_{0j} + r_{ij}. \quad (4)$$

To allow the slope to vary randomly within each visit, we considered the following visit-level model for the slope parameter in Eq. 3:

$$\beta_{1j} = \gamma_{10} + \gamma_{11}\text{density}_j + u_{1j}$$

which, combined with the level-1 model (Eq. 3), is a random-intercept-and-slope model:

$$\text{Growth}_{ij} = \gamma_{00} + \gamma_{01}\text{density}_j + \gamma_{10}\text{mass}_{ij} + \gamma_{11}\text{mass}_{ij} \times \text{density}_j + u_{1j}\text{mass}_{ij} + u_{0j} + r_{ij}. \quad (5)$$

In both models, the gammas are fixed effects (equivalent to betas in normal regression), and u and r are random effects. As in the unconditional model, r_{ij} is assumed $N(0, \sigma^2)$ for fish i in site j , and σ^2 is referred to as the individual-level variance; u_{0j} is the residual of visit j from the grand mean growth rate, and its variance τ_{00} is a conditional variance at the visit level, i.e., the visit-level variance after controlling for density. A full explanation of the parameters is given in Table 2.

Next, we considered the densities of the two age classes as separate covariates in a random

intercept model. To introduce the age classes separately into Eq. 3 we can write

$$\beta_{0j} = \gamma_{00} + \gamma_{01}\text{yearling}_j + \gamma_{02}\text{subyearling}_j + u_{0j}$$

$$\beta_{1j} = \gamma_{10} + \gamma_{11}\text{yearling}_j + \gamma_{12}\text{subyearling}_j$$

which becomes

$$\begin{aligned} \text{Growth}_{ij} = & \gamma_{00} + \gamma_{01}\text{yearling}_j + \gamma_{02}\text{subyearling}_j \\ & + \gamma_{10}\text{mass}_{ij} + \gamma_{11}\text{mass}_{ij} \times \text{yearling}_j \\ & + \gamma_{12}\text{mass}_{ij} \times \text{subyearling}_j + u_{0j} + r_{ij}. \end{aligned} \quad (6)$$

Here, *yearling* and *subyearling* refer to the densities of these two age classes. In addition to these density models, we examined the effects of water temperature on individual growth rates. We included water temperature as a level-2 covariate. We considered temperature alone, and as an interaction with density (Crozier et al. 2010, Bærum et al. 2013), both as random intercept models. The structure of the first model, with only temperature as a predictor, is the same as Eq. 4:

$$\beta_{0j} = \gamma_{00} + \gamma_{01}\text{temp}_j + u_{0j}$$

$$\beta_{1j} = \gamma_{10} + \gamma_{11}\text{temp}_j.$$

In combined notation we get:

Table 2. Parameter interpretation for the two-level model with random intercept (Eq. 4).

Parameter	Description
growth_{ij}	the estimated growth rate (% body mass per day) of individual steelhead i at visit j (in site k)
mass_{ij}	the initial mass of individual steelhead i at visit j
density_j	density of steelhead at visit j (note: density varies by age class in the modeling)
γ_{00}	the intercept of the visit-level density-growth relationship
γ_{01}	the mean effect of visit-level density on growth
γ_{10}	the average slope of the relationship between fish mass and growth rate
γ_{11}	the average effect of density on the relationship between mass and growth
u_{0j}	the random effect of visit j on growth, holding density constant
r_{ij}	the random (individual-level residual) effect on growth

$$\text{Growth}_{ij} = \gamma_{00} + \gamma_{01}\text{temp}_j + \gamma_{10}\text{mass}_{ij} + \gamma_{11}\text{mass}_{ij} \times \text{temp}_j + u_{0j} + r_{ij}. \quad (7)$$

The structure of the model relating temperature, density, and their interaction to individual growth was

$$\beta_{0j} = \gamma_{00} + \gamma_{01}\text{density}_j + \gamma_{02}\text{temp}_j + \gamma_{03}\text{density}_j \times \text{temp}_j + u_{0j}$$

$$\beta_{1j} = \gamma_{10} + \gamma_{11}\text{density}_j + \gamma_{12}\text{temp}_j + \gamma_{03}\text{density}_j \times \text{temp}_j$$

which in combined notation becomes

$$\begin{aligned} \text{Growth}_{ij} = & \gamma_{00} + \gamma_{01}\text{density}_j + \gamma_{02}\text{temp}_j \\ & + \gamma_{03}\text{density}_j \times \text{temp}_j + \gamma_{10}\text{mass}_{ij} \\ & + \gamma_{11}\text{mass}_{ij} \times \text{density}_j + \gamma_{12}\text{mass}_{ij} \\ & \times \text{temp}_j + \gamma_{13}\text{mass}_{ij} \times \text{density}_j \\ & \times \text{temp}_j + u_{0j} + r_{ij}. \end{aligned} \quad (8)$$

The properties of these models are the same as explained above for the density models.

Finally, for the best supported models we calculated the information contribution of the covariates by comparing the reduction in the variance for each level. For the visit-level, this is calculated as

$$\begin{aligned} \text{proportion variance explained} = \\ (\tau_{00}\text{unconditional} - \tau_{00}\text{density}) / \tau_{00}\text{unconditional}. \end{aligned}$$

Equivalently, the variance reduction can be calculated for the individual level. This gives an estimate of how much of the explainable variation was explained by the inclusion of the covariate at that level.

Model selection

We used an information-theoretic criterion to assess the relative plausibility of these candidate models (Akaike 1973, Burnham and Anderson 2002). Akaike's information criterion (AIC) is given as

$$\text{AIC} = -2\ln(L(\hat{\theta} | \text{data})) + 2K$$

where $\ln(L(\theta | \text{data}))$ is the value given the estimated parameters, and K is the number of estimable parameters in that model. The model with the lowest AIC value is the best approximating model of the data (Burnham and Anderson 2002). Because information criteria can only be used on models examining the same set of response variables, we performed two selections within each age class, denoted *comparison* in Table 3.

We also examined the estimated variance components to inform the model structure. The variance component for slope (τ_{11}) was very small in all cases (Table 3). The null hypothesis of no difference in slopes across visits could therefore not be rejected at the critical value of $\alpha = 0.05$. Although some of the random slope models had lower AIC values (Table 3), this suggested that a simpler model structure would describe the data just as well. We therefore present parameter estimates for the best supported random intercept models (Eq. 4) for each comparison (Table 4). For the additive density (Eq. 6), temperature (Eq. 7), and density \times temperature interaction (Eq. 8) models we present parameter estimates for those models which received substantial relative support in each comparison, i.e., AIC-values better than or within two points of the AIC_{min} model presented in Table 4 (Table 5; Burnham and Anderson 2002). We used SAS v.9.2 Proc MIXED (SAS Institute, Cary, North Carolina, USA) specified with the Kenward and Roger (1997) approximation of denominator degrees of freedom, and maximum likelihood as the estimator in all the analyses. We verified that model assumptions

Table 3. Model selection results for the two age classes of juvenile steelhead. For each age class, the table shows the density terms, the structure of the random effects, the sample size (n), the number of parameters in the model (K), the AIC value, and whether the variance components for the random effects were significantly different from zero at the $\alpha = 0.05$ level (Z -test). Asterisks denote significant values ($P < 0.0001$ in all cases) and ellipses denote insignificant values ($P > 0.05$) of variance components.

Predictor variable(s) by comparison	ID	Random term	N	K	AIC	Intercept (τ_{00})	Slope (τ_{11})	Covariance (τ_{01})	Residual (σ^2)
Subyearling 1									
Subyearling density	1	intercept, mass	1228	8	1300.5	*	*
Subyearling density	2	intercept	1228	6	1300.2	*	n/a	n/a	*
Total density	3	intercept, mass	1228	8	1295.9	*	*
Total density	4	intercept	1228	6	1295.5	*	n/a	n/a	*
Temperature	5	intercept	1128	6	1300.3	*	n/a	n/a	*
Temperature + subyearling density + interaction	6	intercept	1228	9	1300.7	*	n/a	n/a	*
Temperature + total density + interaction	7	intercept	1228	9	1296.4	*	n/a	n/a	*
Subyearling 2									
Yearling density	8	intercept, mass	1133	8	1157.0	*	*
Yearling density	9	intercept	1133	6	1158.0	*	n/a	n/a	*
Yearling density + subyearling density	10	intercept	1133	8	1160.4	*	n/a	n/a	*
Temperature + yearling density + interaction	11	intercept	1133	9	1160.5	*	n/a	n/a	*
Yearling 1									
Yearling density	12	intercept, mass	983	8	710.6	*	*	...	*
Yearling density	13	intercept	983	6	712.3	*	n/a	n/a	*
Total density	14	intercept, mass	983	8	713.9	*	*	...	*
Total density	15	intercept	983	6	715.6	*	n/a	n/a	*
Temperature	16	intercept	983	6	714.9	*	n/a	n/a	*
Temperature + yearling density + interaction	17	intercept	983	9	715.5	*	n/a	n/a	*
Temperature + total density + interaction	18	intercept	983	9	718.4	*	n/a	n/a	*
Yearling 2									
Subyearling density	19	intercept, mass	661	8	429.5	*	*
Subyearling density	20	intercept	661	6	429.6	*	n/a	n/a	*
Subyearling density + yearling density	21	intercept	661	8	430.8	*	n/a	n/a	*
Temperature + subyearling density + interaction	22	intercept	661	9	429.0	*	n/a	n/a	*

Table 4. Parameter estimates for the random intercept models (Eq. 4) on the form $Growth_{ij} = \gamma_{00} + \gamma_{01}density_j + \gamma_{10}mass_{ij} + \gamma_{11}mass_{ij} \times density_j + u_{0j} + r_{ij}$. The variance term τ_{00} refers to the random intercept (u_{0j}), and σ^2 refers to individual-level residuals (r_{ij}); ρ_{ind} refers to the variance explained at the individual level by the inclusion of mass, and ρ_{visit} refers to the variance explained by the inclusion of the density covariate of interest. Standard errors are given in parentheses.

Age class and model (density variable)	Fixed effects				Random effects		ρ_{ind}	ρ_{visit}
	γ_{00}	γ_{01}	γ_{10}	γ_{11}	τ_{00}	σ^2		
Subyearling #4 (total density)	1.31 (0.238)	-0.111 (0.0833)	0.00963 (0.0242)	-0.0106 (0.00846)	0.145 (0.0256)	0.140 (0.00587)	2.0	5.1
Subyearling #9 (yearling density)	1.16 (0.0592)	-0.154 (0.0460)	-0.0253 (0.00527)	-0.00503 (0.00497)	0.124 (0.0234)	0.137 (0.00597)	4.1	18.8
Yearling #13 (yearling density)	0.256 (0.132)	0.0423 (0.0637)	0.000197 (0.00216)	-0.00196 (0.000973)	0.0762 (0.0144)	0.102 (0.00475)	5.7	0
Yearling #20 (subyearling density)	0.174 (0.123)	-0.0668 (0.0530)	-0.00098 (0.00212)	-0.00106 (0.000895)	0.0755 (0.0159)	0.0915 (0.00525)	15.4	0

Table 5. Parameter estimates for the additive age class and temperature-density interaction models which were better or within two AIC points of the best approximating density models in Table 3.

Variable, by age class and model	Parameter estimate (SE)	ρ_{ind}	ρ_{visit}
Subyearling #7			
Intercept γ_{00}	0.649 (0.423)
Temperature γ_{02}	0.0399 (0.0217)
Total density γ_{03}	-0.112 (0.0825)
Mass γ_{10}	-0.0993 (0.128)
Mass total density γ_{11}	0.0362 (0.0482)
Mass \times temperature γ_{12}	0.00653 (0.00756)
Mass \times total density \times temperature γ_{13}	-0.00278 (0.0028)
Random intercept τ_{00}	0.137 (0.0247)	...	11.5
Residual σ^2	0.140 (0.00587)	2.0	...
Yearling #22			
Intercept γ_{00}	0.200 (0.328)
Temperature γ_{02}	-0.00174 (0.0195)
Subyearling density γ_{03}	0.0663 (0.0530)
Mass γ_{10}	0.00515 (0.0170)
Mass \times subyearling density γ_{11}	0.000719 (0.00722)
Mass \times temperature γ_{12}	-0.00039 (0.0010)
Mass \times subyearling density \times temperature γ_{13}	-0.00011 (0.00043)
Random intercept τ_{00}	0.0725 (0.0153)	...	0
Residual σ^2	0.0908 (0.0052)	19.2	...
Yearling #21			
Intercept γ_{00}	0.0629 (0.164)
Yearling density γ_{02}	0.0733 (0.0760)
Subyearling density γ_{03}	0.0465 (0.0564)
Mass γ_{10}	0.00180 (0.00268)
Mass \times yearling density γ_{11}	-0.00202 (0.00119)
Mass \times subyearling density γ_{12}	-0.00042 (0.00097)
Random intercept τ_{00}	0.0775 (0.0164)	...	0
Residual σ^2	0.09085 (0.00521)	39.6	...

were met (i.e., that each variance component and the residual error had means of zero and constant variance) by examining the residual plots of each model using the SAS *ods graphics* option (SAS Institute 2008).

RESULTS

Densities of both subyearling and yearling age classes varied considerably between and within study sites (Fig. 2). The density of subyearlings was always higher than that of yearling fish, but their combined numbers were always less than one individual per m^2 . Within each site there was substantial variation in density among the visits. Individual growth rates were on average higher for subyearling steelhead (Fig. 3), with considerable variation among individuals within sites. Because of the large variation in growth rates within sites, the differences in growth rates between study sites were not significant (Table 1). This implies that individual- and visit-level variation in growth rates were greater than any consistent spatial differences in growth across the

study sites.

We found evidence of density-dependent growth in the subyearling age class (Table 4). Subyearling growth rates were negatively related to the density of yearling steelhead as estimated in the γ_{01} parameter. By examining the intraclass correlation coefficients, it was clear that *density*, a visit-level covariate, provided more information than did the individual-level covariate *mass* for the subyearling age class. Yearling density explained approximately 19% of the explainable variation at the visit level for subyearling growth rates.

There were no effects of total density or intra-age class densities on the growth rates in either age class (Fig. 4). Here, the γ_{01} parameters were small relative to their standard errors, indicating estimates statistically indistinguishable from zero (Table 4). Yearlings thus showed no evidence of density-dependent growth. The inclusion of any density metrics into the model of yearling growth did not provide any reduction in the visit-level variance, strongly suggesting that growth in yearling steelhead in the Lapwai Creek water-

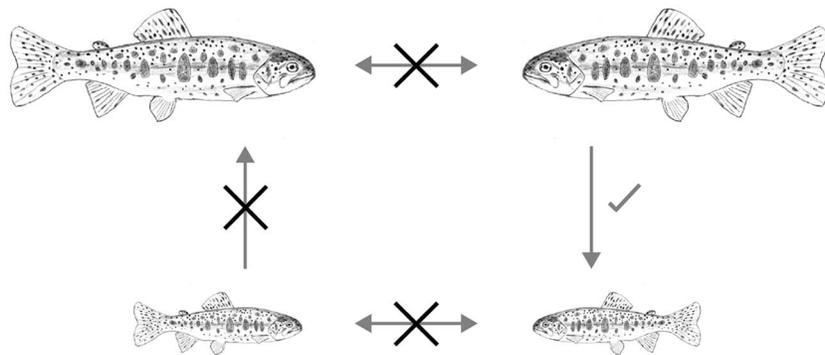


Fig. 4. Depressed growth rates in subyearling steelhead were caused by the density of yearling conspecifics in the age-structured population examined in this study.

shed was not constrained by density.

In the Yr-2 comparison we found that the temperature-density interaction model was the best approximating model for yearling growth. However, the parameter estimates were small relative to their standard errors, and thus statistically indistinguishable from zero (Table 5). Similarly, for subyearling steelhead, the parameter estimates for model 7 were insignificant (Table 5). We were therefore unable to conclude whether the interacting effects of temperature and density affected juvenile steelhead growth rates in the system.

Collectively, our results suggest that density-dependent impacts on individual growth may be subtle and masked by age structure, especially when considering a range of population densities, seasons, and physiographic conditions. Examination of density dependence in age-structured populations should therefore consider the potentially disproportionate effects of particular age or size classes on population demographic rates.

DISCUSSION

In this study we documented density-dependent growth in individually marked juvenile steelhead in a relatively sparse, age-structured population. Growth rates in the subyearling age class were overall negatively related to the densities of older fish, but not vice versa. These results support recent research on the sequence of regulation of salmonid populations, notably that density dependence can be manifested in

growth rates at relatively low population densities (Achord et al. 2003, Einum et al. 2006, Lobón-Cervía 2007) and that inter-cohort competition can occur in age-structured populations (Nordwall et al. 2001, Kaspersson and Höjesjö 2009). Our results showed no conclusive effects of temperature on growth rates, either as a stand-alone factor or in interaction with age class density.

Density-dependent growth occurs when individual feeding rates are depressed due to the presence of conspecifics (Rose et al. 2001, Lorenzen and Enberg 2002). The primary mechanism for density-dependent growth is competition, and in territorial stream salmonids the primary resources are access to space (interference competition, Grant and Kramer 1990) and food (exploitative competition, Bohlin et al. 1994). Via both mechanisms, competition imposes a net negative effect on individual performance such as growth and survival, but in observational studies it is difficult to identify the exact mechanism (i.e., whether food or space is more limiting) because predictions from these hypotheses overlap (Ward et al. 2007). Due to individual differences, however, the outcome of intraspecific competition is usually asymmetric, i.e., it affects some individuals more than others (Jenkins 1969, Keeley 2001, Reid et al. 2011). When ascribing an effect of a group-level factor such as density on an individual-level response such as growth rate, it is therefore imperative to partition the effect between the individual and the average response (DeAngelis and Mooij 2005).

Notable were the relatively low densities at which density dependence was operating. For organisms competing for access to food and space, greater per capita impacts of one unit increase in density occur at low densities. Einum et al. (2006) proposed a sequence of regulation in stream salmonid populations which suggests that density dependence is manifested in increased mortality rates with relatively little effect on growth rates early in ontogeny (at the early free-swimming stage), and larger effects on growth and dispersal, but lesser effects on mortality, as individuals grow in size (i.e., the parr stage, as the present study examined). The densities of Atlantic salmon (*S. salar*) parr in their field experiment were lower than 1 fish per m², and the primary density-dependent effect was depressed growth rates. The effect of relatively low densities on individual growth rates has also been shown by other studies. Grant and Imre (2005) conducted a meta-analysis of 19 populations of stream-dwelling salmonids to explore whether growth rates were depressed at such lower population densities. In the majority of these populations, density dependence manifested itself in depressed growth rates, with the strongest growth rate reduction occurring at densities <1 fish m⁻². Jenkins et al. (1999) combined a multiscale field study with experimental manipulations, and found that density affected individual brown trout growth rates more strongly at densities <1 fish m⁻², and that subyearlings were more affected than yearling fish.

Studies that have investigated competition between age classes in population-level studies have reported conflicting results. Elliott (1985) found no evidence of competition between age classes of brown trout in England, whereas Nordwall et al. (2001) reported on depressed growth in younger age classes with increased densities of older age classes in brown trout in Sweden. In two recent studies on brown trout in Sweden, Kaspersson and Höjesjö (2009) found that the presence of yearling fish was associated with an overall reduction in subyearling growth rates, and Kaspersson et al. (2013) reported on reduced growth rates, rather than increased mortality rates and movement, in small individuals when experimentally adding large brown trout to stream sections. Oppositely, Kvingedal

and Einum (2011) found that subyearling brown trout densities in Norway were associated with depressed size-at-age for both subyearling and yearling fish, and that yearling density did not cause depressed sizes in either age class. Parra et al. (2012) reported on density-dependent effects both within and among cohorts of brown trout in northern Spain, and notably that the size of overyearling fish was negatively associated with densities of younger cohorts. This finding could owe to marginally better rearing conditions for younger fish in habitats suitable for several age classes, and that the energetic cost of fending off subyearling competitors could depress growth rates in older fish in these habitats (Parra et al. 2012).

Our findings likely owe to a combination of competition through exclusion and to life-history choices. First, in stream salmonids, age-structured populations often show differential habitat use among the age classes (Bjornn and Reiser 1991, Quinn 2005). In most species, subyearlings tend to utilize stream margins or slow-flowing pockets in riffle habitats, whereas older individuals tend to use pool habitats and deeper sections of the channel (Bjornn and Reiser 1991). Whether this segregation owes to competition or preference likely depends on a number of factors, such as availability of critical habitat features, densities of conspecifics and other species, food availability, and the dynamics of energetically profitable positions (Vehanen et al. 1999, Nislow et al. 2000, Rosenfeld and Boss 2001, Kaspersson et al. 2013). For example, Rosenfeld and Boss (2001) reported that habitat selection by cutthroat trout (*O. clarkii*) in the wild does not accurately reflect habitat choice in absence of competition. When removing larger individuals, subyearling cutthroat trout utilized pool habitats which maximized their growth rates. In our study, if both subyearlings and yearlings were selecting for the same features, but yearling steelhead consistently occupied better feeding stations, there would likely be an effect of yearling density on subyearling growth because subyearlings would be displaced to energetically less favorable territories (Rosenfeld and Boss 2001) or show stress responses (Ejike and Schreck 1980). The most likely mechanisms causing the negative relationship between subyearling growth rate and yearling density thus appears to be compe-

tion over space, or increased levels of stress in subyearlings with the presence of yearlings.

Secondly, we did not find any evidence of density-dependent growth in yearling steelhead, although there was substantial variation among visits. In some sites there were sufficient densities to produce depressed growth rates among yearlings, but for the Lapwai Creek watershed as a whole, this was not the case. The reason for this could owe to life-history choices. Previous research in the system has shown higher outmigration rates with increasing local densities, and that individual outmigration probability increases with relative body size (Hartson and Kennedy 2015). The resultant densities as observed in the summer and fall might therefore not reach levels that affect individual growth rates. In an evolutionary perspective, this behavior is a driving factor in the development of anadromy (Gross 1987, Kendall et al. 2015).

The interacting effects of density and temperature have been studied in several recent works (Crozier et al. 2010, Parra et al. 2012, Bærum et al. 2013), and reveal complex constraints on individual growth and size-at-age. Whereas we did not find any conclusive effects of temperature and density interactions on juvenile steelhead growth rates, Crozier et al. (2010) found that the negative effects of density on individual Chinook salmon (*O. tshawytscha*) size were exacerbated at high temperatures, and that growth correlated positively to temperature at relatively low densities. Parra et al. (2012) reported on a positive relationship between temperature and size early in ontogeny, and that density-dependent effects posed more important constraints on the size of larger brown trout. In a cold stream in Norway, Bærum et al. (2013) found a positive effect of water temperature on brown trout growth. Food supply and activity is linked with water temperature in the system, and the results suggest that the improved feeding opportunities associated with relatively higher temperatures could offset the negative density-dependent effects. The contrast of these results to the findings by Crozier et al. (2010) is compelling, and speaks to the fact that the relative importance of density-dependent and -independent factors varies according to the biological and abiotic context of the study system (Begon et al. 1996, Karels and Boonstra 2000).

The role of individual performance on population dynamics is receiving increased attention as a driver of ecological and evolutionary processes (De Roos et al. 2003, DeAngelis and Mooij 2005). Because growth is largely indeterminate in fishes, density-dependent changes in individual growth rates can affect other fitness components such as survival and fecundity at subsequent life stages (Werner and Gilliam 1984, Morita and Takashima 1998, Eium and Fleming 1999). Although anadromous salmonids depend on more than juvenile rearing habitat to complete a generation, rapid growth and large body size has been shown to confer fitness advantages through increased survival (Ward and Slaney 1988, Ward et al. 1989, Kahler et al. 2001). Growth during juvenile stages can therefore have important ramifications for population dynamics (Sogard 1997, Rose et al. 2001), particularly in small populations inhabiting or navigating highly altered habitats to complete their life cycle. The flow regime of the Columbia River has undergone vast changes during the last century (NRC 1996), which not only affects returning adults but also the energy expenditure and predation risk for outmigrating smolts (Petersen and Kitchell 2001, Kuehne et al. 2012). Under such conditions, individual body size is a key trait that could increase the likelihood of successful migration.

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