

# Spatial and temporal patterns of growth and consumption by juvenile spring/summer Chinook salmon *Oncorhynchus tshawytscha*

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Received: 10 July 2013 / Accepted: 2 January 2014 / Published online: 21 January 2014  
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**Abstract** Somatic growth is often used as a metric of habitat quality, but such an approach has limitations because growth results from complex interactions between abiotic and biotic factors. In this study, we derived estimates of weekly growth (based on otolith growth increments) across several months for four populations of threatened Chinook salmon, *Oncorhynchus tshawytscha*, from the Salmon River Basin, Idaho, USA. Although mean stream temperature varied by 2–5 °C across populations, growth across the season did not vary significantly by population. To investigate this further, we applied a bioenergetics model that produced estimates of consumption rates. We then examined how growth and consumption rates varied according to rearing stream and day in the season. Using generalized least squares models, somatic growth ( $\text{g}\cdot\text{day}^{-1}$ ) was best explained by stream and date,

yet a model with only date had moderate support, and thus indicated limited support for stream effects. Specific consumption rate ( $\text{g}\cdot\text{g}^{-1}\cdot\text{day}^{-1}$  and  $\text{J}\cdot\text{g}^{-1}\cdot\text{day}^{-1}$ ) was best explained using a model that included main effects of stream and date. These findings are consistent with the hypothesis that higher temperatures confer higher metabolic costs that require greater consumption to produce similar growth rates in cooler streams. This highlights that similarity in growth rate among streams may mask changes in individual behavior and/or energetic acquisition associated with differences in temperatures among streams. Results of this study represent the first steps towards identifying factors that underlie important population level and habitat quality differences.

**Electronic supplementary material** The online version of this article (doi:10.1007/s10641-014-0230-2) contains supplementary material, which is available to authorized users.

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**Keywords** Generalized least squares models · Somatic growth and consumption rate · Proportion of maximum consumption

## Introduction

A populations' replenishment, augmentation, or colonization is a consequence of the survival of individuals to reproductive age and their production of viable progeny. The likelihood of an individual contributing offspring to a population(s) is positively related to the individuals' performance and success during early life history stages (see Lundqvist et al. 1988; Elliot 1989; Letcher et al. 2002; Sponaugle and Grorud-Colvert 2006; Hamilton et al. 2008). Body size has been shown to be positively related to fitness (Kingsolver and Huey 2008) and

survival (Sogard 1997), and therefore somatic growth is often used as an indicator of individual performance and habitat quality (e.g., Meng et al. 2000; Le Pape et al. 2003; Necaïse et al. 2005).

For fish, growth has been shown to be related to factors and processes such as food quality (Beauchamp et al. 2007), food availability (Graeb et al. 2004; Limm and Marchetti 2009), temperature (Elliott 1994), competition (DeVries and Frie 1996; Crozier et al. 2010), and predation (Baumann et al. 2003). But because ecosystems are inherently complex, growth is often the product of interactions among these or other ecosystem components (Searcy et al. 2007), and such interactions potentially limit the usefulness of growth as a metric of habitat quality. For example, the relationship between growth and temperature can be mediated by the abundance of conspecifics (Crozier et al. 2010). Therefore, a more mechanistic understanding of how these components interact to influence growth can provide a deeper understanding of how growth responds to ecosystem variability. Understanding these relationships is particularly important in assessing the potential impacts of major anthropogenic disturbance, including climate change, on ecosystems.

Spring/summer populations of Chinook salmon (*Oncorhynchus tshawytscha*, Walbaum 1792) within the Salmon River Basin, USA, are listed as threatened under US Endangered Species Act (Fig. 1). These populations face difficult challenges on the road to delisting and sustainability because of anthropogenic influences such as pollution, habitat degradation and loss, and hydropower and flood control projects that limit access to rearing areas and hinder migration. For efficient and successful management of these degraded populations it is critical to understand what factors influence an individual's performance and by what mechanism this influence occurs. In this study, to provide insight into the processes that determine somatic growth patterns, variability in growth of juvenile Chinook salmon was examined both spatially (among populations) and temporally (within a summer). Using otoliths, stomach contents, environmental monitoring, and bioenergetics modeling we explored relationships between growth rates and consumption rates of fish subjected to different temperatures.

## Materials and methods

Chinook salmon (*Oncorhynchus tshawytsch*) is an anadromous species that is distributed from Alaska to

California, U.S.A. Spring/summer runs of Chinook salmon (i.e., spawning in spring/summer) spawn in freshwater streams and rivers where they deposit fertilized eggs into gravel substrate. Approximately 3 months later eggs hatch and the majority of fish (90th percentile) pass Lower Granite Dam on the Snake River by June (Achor et al. 2006). Individuals eventually migrate to the ocean where they spend up to 3 years before returning to spawn (Quinn 2005).

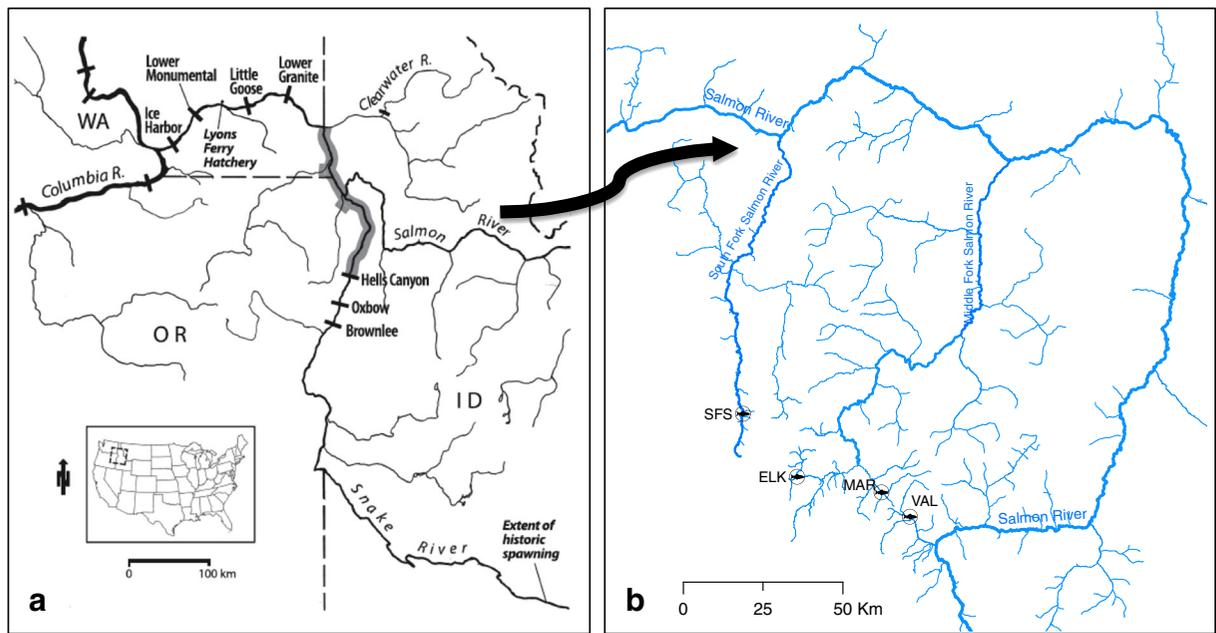
To assess how somatic growth and consumption rates vary spatially and temporally, and how interactions between ecosystem components might influence consumption and subsequent growth, we collected water temperature data, prey items from sampled stomachs, and growth from sampled otoliths. The aforementioned data was then used in a bioenergetics model to estimate consumption rates and the proportion of maximum consumption (Fig. 2).

Four streams of the Salmon River Basin, Idaho, were visited July and September 2004 so as to obtain information on water temperature and to collect juvenile Chinook salmon. Daily stream temperature (°C) was determined by averaging temperatures recorded every 5 min with a Hobo<sup>1</sup> temperature logger (Proccasset, MA, U.S.A.), which was placed in each stream at the start of the first sampling period and retrieved at the final sampling period (Table 1; Fig. 2). Chinook salmon were captured by backpack electrofishing, euthanized with tricaine methanesulfonate (MS-222), wet-weighed (g), measured (fork length, mm), and then frozen.

To determine the items in Chinook salmon diets we extracted stomachs from individuals (prior to freezing) collected in July and September (Table 1). Stomachs were preserved in 90 % ethanol and later prey were identified to family and enumerated. Proportions of each prey item were then calculated and values of nutritional value (i.e., energy density) obtained from peer-reviewed literature (Fig. 2, Online Resource Table 1 and Fig. 1).

To estimate fish mass and somatic growth rate we relied upon the microstructural analysis of otoliths that were extracted from Chinook salmon collected in September (Table 1). Otoliths are calcified-balance structures that grow throughout a fish's life. As otoliths grow, visible daily increments are formed in proportion to somatic growth, and these increments and the distance between them, are commonly used to estimate age and somatic

<sup>1</sup> Use of trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.



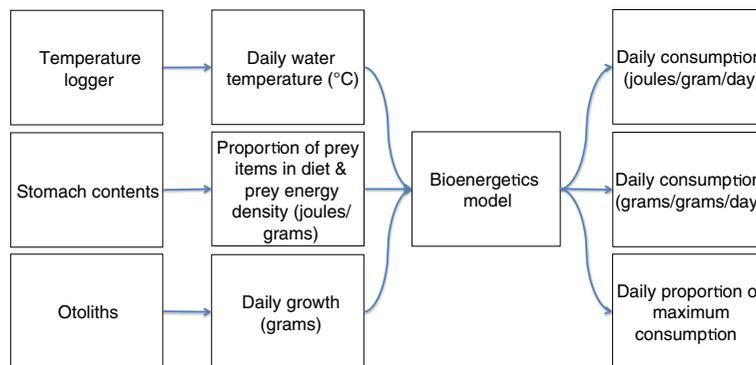
**Fig. 1** Map showing the Columbia, Clearwater, and Salmon Rivers (a) and a close-up of the Salmon River Basin, Idaho (b) within which the location of sampled rearing streams (fish

symbol); South Fork of the Salmon River (SFS), Elk Creek (ELK), Marsh Creek (MAR), and Valley Creek (VAL)

growth, respectively (Campana and Neilson 1985; Gauldie 1991; Zabel et al. 2010).

Sagittal otoliths were polished in a sagittal plane (using grit sizes of 1 and 5 alumina micropolish and a grinding wheel with Buehler 1500 and micro-polishing pads; Lake Bluff, IL, U.S.A.) so that each otolith core was exposed (Table 1; note that sample sizes are small due to ESA restrictions, which limit handling and

removal). Polished otoliths were digitally photographed at 20× magnification using a Cybernetics camera mounted on a Zeiss light microscope (Thornwood, NY, U.S.A.). Using an image analysis system (Image Pro MediaCybernetics, Bethesda, MD, U.S.A.), radius (i.e., distance from the otolith core to its margin) was measured along the same axis of each otolith (i.e., all measurements were made at 90° angle to the



**Fig. 2** Schematic representation of bioenergetics modeling framework. For each rearing stream we obtained estimates of daily water temperature, and from sampled Chinook salmon otoliths and stomachs, we obtained estimates of daily somatic growth and proportion of each prey item, respectively. Prey energy density

was obtained from the literature (see Online Resource Table 1). These three pieces of data were input into the bioenergetics model to produce daily estimates of consumption (in terms of joules and grams) and proportion of maximum consumption

**Table 1** Rearing streams and dates juvenile *O. tshawytscha* were collected along with mean daily water temperature (standard deviation) for a 42 day interval from July 28 to September 7, 2004. Sample sizes are of juvenile Chinook used for diet and growth

Rearing stream (code)	Sampling dates (# of days of temperature data)	Mean daily water temperature (°C)(st. dev.)	Sample sizes for diet analysis (July & September)	Sample sizes for growth analysis (September only)	Mean FL (mm) (st.dev.)
South Fork of the Salmon River (SFS)	07/27/04 & 09/12/04 (48 days)	9.8 (2.0)	5 & 5	7	63 (12)
Elk Creek (ELK)	07/15/04 & 09/15/04 (63 days)	13.2 (2.1)	5 & 5	3	67 (3)
Marsh Creek (MAR)	07/16/04 & 09/13/04 (60 days)	10.8 (1.4)	5 & 5	4	68 (12)
Valley Creek (VAL)	07/17/04 & 09/13/04 (59 days)	13.8 (1.9)	11 & 2	7	66 (11)

analysis. Individuals used in the diet analysis were from both sampling dates and are indicated separately, while individuals used in the growth analysis were limited to those collected in September

longitudinal axis on the ventral side of the left otolith). Along this radius, daily increments (Neilson and Geen 1982) were marked from the otolith margin towards the core. Next, widths between daily increments were determined for days for which we had daily temperature data common to all streams. Specifically, width was measured between 42 daily increments that corresponded to calendar dates of July 28 to September 7 (Table 1). Matching otolith growth increments to temperature data was necessary for our use of a bioenergetics model (see below).

Estimates of daily fish length (mm) were back-calculated through part of the summer growing season by using previously published relationships between fish length and otolith size, which were developed using fish from the same basin (quadratic predictive function; Zabel et al. 2010). Next, fish mass (g) was calculated using the estimated fish length in the following equation (generated by pooling all rearing streams;  $R^2=0.94$ ) between fish mass and fish length:

$$M = 6.0 \cdot 10^{-6} \cdot L^{3.15} \quad (1)$$

where  $M$  is mass (g) and  $L$  is fork length (mm). Estimates of daily mass were then calculated for each fish and these estimates were used in the bioenergetics model (Fig. 2). The use of back-calculated weights in the bioenergetics model allowed us to track the average growth trajectories of specific individuals instead of calculating the mean mass of fish sampled from each stream (Beauchamp et al. 2007).

To estimate consumption rates we used a bioenergetics model, which is an energy-balance equation (see Kitchell et al. 1977) that determines how much prey is needed to achieve a specified growth under a set of environmental conditions (Koehler et al. 2006). The bioenergetics model requires inputs of water temperature, somatic growth, proportion of prey items in diet, and prey nutritional value (Fig. 2). Most studies taking a bioenergetics approach to estimate consumption rely on a measurement of growth derived from the difference in body size between two points in time (e.g., Madenjian et al. 2004; Duffy and Beauchamp 2008). Our study, however, has the advantage of using otoliths to back-calculate size, and thus growth, at any previous age, thereby allowing us to investigate temporal changes in consumption (see below).

A bioenergetics model was developed in the R statistical software using formulas and *O. tshawytscha* parameters from Wisconsin Fish Bioenergetics 3.0 (Hanson et al. 1997; see the Online Resource 1 for model equations and Online Resource Table 2 for parameter values), and the aforementioned inputs of fish mass ( $M$ , g), daily growth ( $g \cdot \text{day}^{-1}$ ), mean daily temperature ( $^{\circ}\text{C}$ ), proportion of prey items (Online Resource Fig. 1), and prey energy density ( $\text{J} \cdot \text{g}^{-1}$ ) (Fig. 2). Madenjian et al. (2004) indicated that a *O. tshawytscha* bioenergetics model performed relatively well (i.e., unbiased estimates) in predicting consumption rates, and other researchers have applied this general approach to estimate the effects of habitat quality on fish growth for a variety of fish species (e.g., radiated shanny, *Ulvaria subbifurcata*, Baumann

et al. 2003; European anchovy, *Engraulis encrasicolus*, Basilone et al. 2004). When compared, the R based bioenergetics model yielded the same consumption results as the Wisconsin software. Because most parameter values for juvenile *O. tshawytscha* are not available, parameter values from adult Chinook were used (see Online Resource Table 2, parameter values taken from Stewart and Ibarra 1991, see Wisconsin bioenergetics 3.0). Although using parameters from a different life stage is not ideal we feel it is acceptable given our goal to report trends among and within the four study populations (see Ney 1993).

The bioenergetics model was run on a daily time step for each individual for a 42-day period common to all populations (July 28–September 7, 2004). From the bioenergetics model, the following daily outputs were obtained for each individual: consumption (g of prey·day<sup>-1</sup> and J of prey·day<sup>-1</sup>), and proportion of maximum consumption (*P*, unitless) (Fig. 2). *P* accounts for ecological constraints on an individual to feed at its maximum rate and thus it may be used as an index of whether feeding was limited by access to food (Post 1990); *P* of 0 indicates limited access to food and *P* of 1 indicates high food availability. *P* was adjusted iteratively in order to optimize the fit of model predictions to individual growth estimates. Growth and consumption were standardized by fish mass to produce the following variables for further analysis: growth (*G*, g·g<sup>-1</sup>·day<sup>-1</sup>, i.e., grams per grams of body mass per day), and consumption (*C<sub>g</sub>*, g·g<sup>-1</sup>·day<sup>-1</sup> and *C<sub>j</sub>*, J·g<sup>-1</sup>·day<sup>-1</sup>). Next, means of the above values (*M*, *G*, *C<sub>g</sub>*, and *C<sub>j</sub>*) were calculated for six 7-day periods so as to smooth out day-to-day variability and to potentially account for any lag effects to define the following variables:  $\bar{M}_{i,s,t}$ ,  $\bar{G}_{i,s,t}$ ,  $\bar{C}_{g,i,s,t}$ , and  $\bar{C}_{j,i,s,t}$ , where *i* represents the individual, *s* represents the stream, *t* represents the 7 day time period. We also calculated  $\bar{T}_{s,t}$  and  $\bar{D}_{s,t}$ , which represent the mean temperature and mean day number, respectively, by stream and time period.

Although the quantities  $\bar{G}_{i,s,t}$ ,  $\bar{C}_{g,i,s,t}$ , and  $\bar{C}_{j,i,s,t}$  were divided by fish mass, they still scale by allometric relationships and cannot be compared directly among fish of different mass. Therefore, to allow for direct comparison among fish and across time steps, these quantities were further standardized by the following allometric relationship:

$$\bar{Y}_{i,s,t} = a \cdot \exp(-b \cdot \bar{M}_{i,s,t}) \tag{2}$$

where *Y* is a generic term representing *G*, *C<sub>g</sub>*, or *C<sub>j</sub>*. Nonlinear regression was used to estimate the *a* and *b* coefficients. We then removed the expected relationship (see below), and rescaled the equation to represent a 2.5-g fish, which was approximately average size:

$$\bar{Y}_{i,s,t}^* = \bar{Y}_{i,s,t} - \hat{a} \cdot \exp(-\hat{b} \cdot \bar{M}_{i,s,t}) + \hat{a} \cdot \exp(-\hat{b} \cdot 2.5) \tag{3}$$

and in this manner defined new standardized response variables  $\bar{G} \rightarrow_{i,s,t}$ ,  $\bar{C}_{g \rightarrow_{i,s,t}}$ , and  $\bar{C}_{j \rightarrow_{i,s,t}}$  that are directly comparable among streams and through time.

### Generalized least squares models

Generalized least squares models (Pinheiro and Bates 2000) were used to assess how related response variables (somatic growth rate and consumption rate) varied according to rearing stream and date. Individual fish were replicates for the stream from which they were collected, and we also included first order autocorrelation in the error term so as to reflect that the response variables are repeated measures of the same individual. An example of a general model is:

$$Y_{ist} = \beta_0 + \beta_s + \beta_t \cdot D_t + \varepsilon_t + \rho \cdot \varepsilon_{t-1} \tag{4}$$

where *Y* is the response variable, the  $\beta$  are model coefficients, with  $\beta_s$  a dummy variable for stream, *D<sub>t</sub>* is mean Julian date for the *t*th time period,  $\varepsilon$  is a normally distributed error term, and  $\rho$  is a first-order autocorrelation coefficient. Note that the error term contains two sources of error: process error, due to lack of model fit, and sampling error, due to the fact that somatic growth rates were reconstructed with inherent errors. Although methods exist to attempt to separate these types of error, they are beyond the scope of this study. Generalized least squares models were also considered that contained interactions between stream and date. We did not include temperature as a factor in the statistical models because temperature was included in the bioenergetics model. In addition, models were considered where date was either treated as a continuous or categorical variable, and thus with regards to the latter the effect of date was unconstrained throughout the season.

For each response variable, eight models (including a null model with no effects) were run to determine the importance of added factors. In addition, for comparison purposes, each model was run as a standard linear model (no autocorrelation).

All model parameters were estimated by maximizing the likelihood function. To compare models, Akaike's Information Criterion corrected for sample size (AICc, Akaike 1973; Burnham and Anderson 2002) was calculated for each model, such that smaller AICc values indicated "better" models. When comparing two models, the difference in AICc values ( $\Delta\text{AICc}$ ) was computed, and according to Burnham and Anderson (2002), a  $\Delta\text{AICc}$  of less than 2 indicates little difference between competing models; a  $\Delta\text{AICc}$  of 2–10 indicates moderate support for a difference between the models, and a  $\Delta\text{AICc}$  of greater than 10 indicates strong support.

#### Generalized least squares model prediction and confidence intervals

The best-fitting model for each response variable was used to predict how mean model response varied by population (i.e. stream) across the season (i.e., date). Confidence intervals (95 %) were calculated, which represent uncertainty in parameters. Standard errors about the predicted means were calculated as

$$\mathbf{se}_{\bar{y}} = \mathbf{X}\Sigma\mathbf{X}' \quad (5)$$

where  $\mathbf{se}$  is a vector of standard errors for each predicted mean,  $\mathbf{X}$  is the model-specific design matrix, and  $\Sigma$  is the variance-covariance matrix of the model parameters excluding the autocorrelation term.

#### Sensitivity analysis and prediction of bioenergetics model

The sensitivity of consumption rates to temperature was tested by investigating how standardized consumption rates (in terms of both  $\text{g}\cdot\text{g}^{-1}\cdot\text{day}^{-1}$  and  $\text{J}\cdot\text{g}^{-1}\cdot\text{day}^{-1}$ ) varied across a range of temperatures experienced by the fish. Further, the bioenergetics model included spatially and temporally explicit measurements of fish growth and water temperature, but this study did not have direct measurements of *O. tshawytscha* activity or diet energy content. Thus, the sensitivity of these parameters to our bioenergetic estimates was explored. The model parameter for activity multiplier uses literature values for salmon (ACT=9.7 taken from Stewart and Ibarra 1991; see Online Resource Table 2) and the sensitivity analysis was conducted to understand how model behavior responded to changes in activity multiplier.

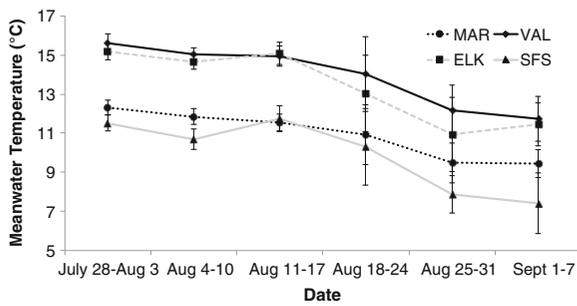
The approach was to run the bioenergetics model several times, each time varying the activity multiplier. Activity multiplier values were 2, 4, 6, 8, 10, and 12, which covered the range of values used in bioenergetics modeling of freshwater and marine species (see Hanson et al. 1997 and references therein), and in our opinion represent a natural starting point to assess the influence of activity multiplier in an anadromous species (see Boisclair and Sirois 1993 for a discussion on activity rates in brook trout, *Salvelinus fontinalis*). Only the activity multiplier was allowed to vary (i.e., all other parameters were fixed) since combinations of other parameter values could produce the same result, and the purpose of this analysis was to understand the influence of the activity multiplier. Consumption rates were then predicted across the season to determine how changes in activity multiplier altered the model predictions.

A sensitivity analysis was also performed to assess the influence of variation in prey energy density parameters on model predictions. Despite having field estimates for prey energy density, diet sampling was conducted only near the beginning and end of the studied growth period (for each stream). A sensitivity analysis served to underscore the potential variation in bioenergetics predictions from interpolated energy density values. For this sensitivity analysis we varied energy density across eight values (ranging from 3,900 to 4,600  $\text{J}\cdot\text{g}^{-1}$ ), representing the observed range of values in this study, and repeated the analyses of those described for the activity multiplier.

## Results

Water temperature recorded during this study ranged from 5 to 18 °C, 6 to 22 °C, 8 to 19 °C, and 4 to 17 °C, for MAR, VAL, ELK, and SFS, respectively. Temperature decreased during our study period and there were consistent differences among streams, with Elk and Valley Creek experiencing temperatures 2–5 °C warmer than those in Marsh Creek and South Fork Salmon River (Fig. 3). This contrast in temperature across populations was important for the ability to distinguish between the effects of temperature and date.

Generalized least squares models of somatic growth rate and specific consumption rate that contained a term to account for autocorrelation of individual fish, performed substantially better than models without this

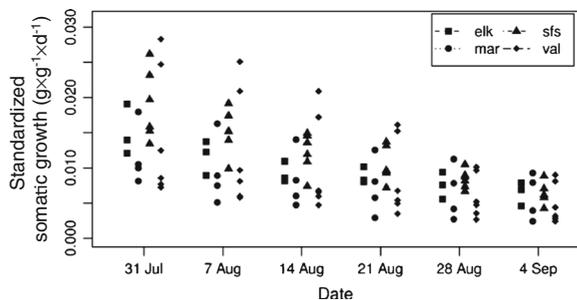


**Fig. 3** Mean water temperature (°C) for six 7-day intervals (from July 28 to September 7, 2004) for each of four rearing streams; South Fork of the Salmon River (SFS), Elk Creek (ELK), Marsh Creek (MAR), and Valley Creek (VAL). Whiskers represent standard deviations

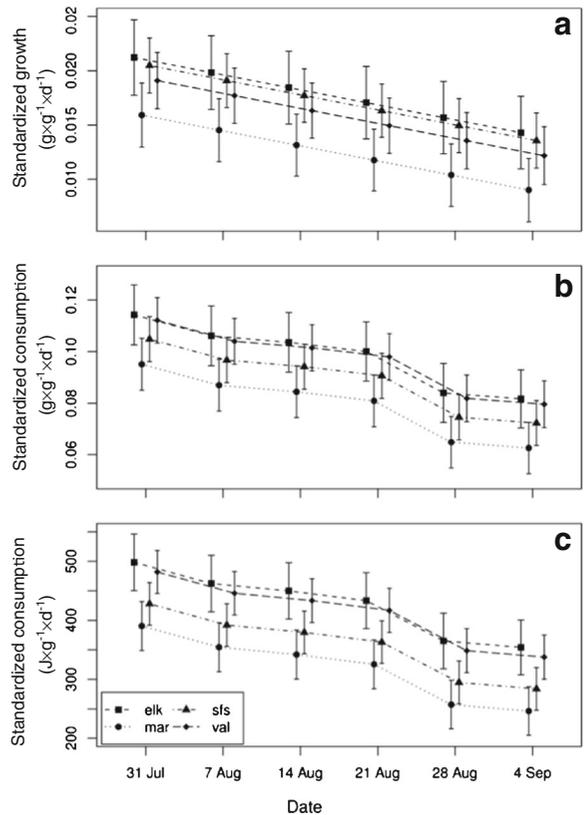
autocorrelation term. Therefore, in the presentation of results that follows, we only refer to models with this autocorrelation term.

Somatic growth

Mean standardized somatic growth rates ranged from 0.003 to 0.029  $g \cdot g^{-1} \cdot day^{-1}$  across streams and dates (Figs. 4 and 5a). Growth rates did not differ among streams given the overlap in 95 % CI (Fig. 5a). The most prominent factor related to growth was date in the season, with lower AICc values produced for generalized least square models with date as a term (i.e., comparing model c and f to model a in Table 2). In addition, a model where growth decreased through the season that had date as a continuous variable (models c–e) better represented the data than when date was a categorical variable (models f–h). The best-fitting model for growth contained stream and date in the season (Table 2, models d), but a model with only date performed nearly as well



**Fig. 4** Otolith derived back-calculated estimates of individual somatic growth rates ( $g \cdot g^{-1} \cdot day^{-1}$ ) over the study period (July 28 to September 7) for fish collected from each rearing stream; South Fork of the Salmon River (SFS), Elk Creek (ELK), Marsh Creek (MAR), and Valley Creek (VAL). Within each date, rearing stream symbols (i.e., individuals) were jittered to improve figure clarity



**Fig. 5** a Somatic growth rate ( $g \cdot g^{-1} \cdot day^{-1}$ ), b consumption rate ( $g \cdot g^{-1} \cdot day^{-1}$ ), and c consumption rate ( $J \cdot g^{-1} \cdot day^{-1}$ ) for six 7-day intervals from July to September for each of four rearing streams; South Fork of the Salmon River (SFS), Elk Creek (ELK), Marsh Creek (MAR), and Valley Creek (VAL). Whiskers represent 95 % confidence intervals. Note that the growth and consumptions rates were standardized to a 2.5 g individual

(Table 2, model c). The lack of a strong stream effect was demonstrated by overlap in confidence intervals among most streams (Fig. 5a) and the lack of difference in AICc between the null model and one with a stream term (Table 2). Thus, the overriding factor determining growth rate in our models were date in the season.

Consumption

Mean consumption rates varied from 0.07 to 0.11  $g \cdot g^{-1} \cdot day^{-1}$  and from 250 to 500  $J \cdot g^{-1} \cdot day^{-1}$  across streams and dates (Fig. 5b and c, respectively). Consumption rates (in grams) did not differ significantly among streams (overlap in the 95 % CI, see Fig. 5b). However, consumption rates (in joules) were significantly different, such that individuals from MAR had significantly lower consumption rates than VAL & ELK

**Table 2** Generalized least squares results obtained from eight models that assess how somatic growth rate ( $G$ ,  $\text{g}\cdot\text{day}^{-1}$ ) and specific consumption rate ( $C_g$ ,  $\text{g}\cdot\text{g}^{-1}\cdot\text{day}^{-1}$ ;  $C_j$ ,  $\text{J}\cdot\text{g}^{-1}\cdot\text{day}^{-1}$ ) vary with respect to date in the season and rearing stream

Model	G (g/day)			C <sub>g</sub> (g/g/day)			C <sub>j</sub> (J/g/day)		
	AICc	ΔAIC	Weight	AICc	ΔAIC	Weight	AICc	ΔAIC	Weight
a) NULL	-941.3	71.0	0.00	-617.1	108.1	0.00	1,296.0	121.5	0.00
b) Stream	-942.1	70.2	0.00	-618.0	107.2	0.00	1,290.2	115.7	0.00
Date as a continuous variable									
c) Date	-1,010.1	2.2	0.21	-711.2	14.0	0.00	1,195.3	20.8	0.00
d) Stream + Date	-1,012.3	0.0	0.79	-715.0	10.2	0.01	1,184.7	10.2	0.01
e) Stream*Date	-1,009.5	2.8	0.19	-713.5	11.7	0.00	1,185.0	10.5	0.01
Date as a categorical variable									
f) Date	-1,003.1	9.2	0.01	-721.8	3.4	0.14	1,184.9	10.4	0.01
g) Stream + Date	-1,004.8	7.5	0.02	-725.2	0.0	0.99	1,175.0	0.0	0.99
h) Stream*Date	-971.3	41.0	0.00	-695.3	29.9	0.00	1,205.0	28.1	0.00

ΔAIC is the difference between each model and the model with the lowest AIC, and weight is the AIC weight for each model with respect to each of the response variables

(Fig. 5c). The patterns of generalized least square model performance were similar between models with consumption expressed as grams or joules of prey as the response variable (Table 2). As with growth, the dominant factor for determining consumption rate was date in the season, with large decreases in AICc associated with the inclusion of date (models c–h, Table 2). In contrast to growth, model fit the consumption data better when date was a categorical variable (models f–h, Table 2). The best-fitting model contained both stream and date (model g, Table 2). The effects of date on consumption rates (Fig. 5b, c, Table 2) appears driven by changes in temperature (Fig. 3) such that the greatest decrease in temperature (between August 21st and 28th) is associated with the greatest decrease in consumption rates. In addition, fish from the warmer streams, Elk and Valley creeks, consumed more prey than those from the cooler streams, Marsh Creek and South Fork of the Salmon River.

#### Model diagnostics

We tested for violations of model assumptions for the full model for growth and the two consumption models. In particular, we tested whether individual fish were positively correlated by conducting pair-wise comparisons of all individuals within each population. Only one comparison yielded a significant correlation (Pearson's correlation,  $\alpha=0.05$ ) for each of the two consumption

models, and none were significant for the growth model. In addition, qq-plots yielded no obvious deviations from the assumption of normality for all three models.

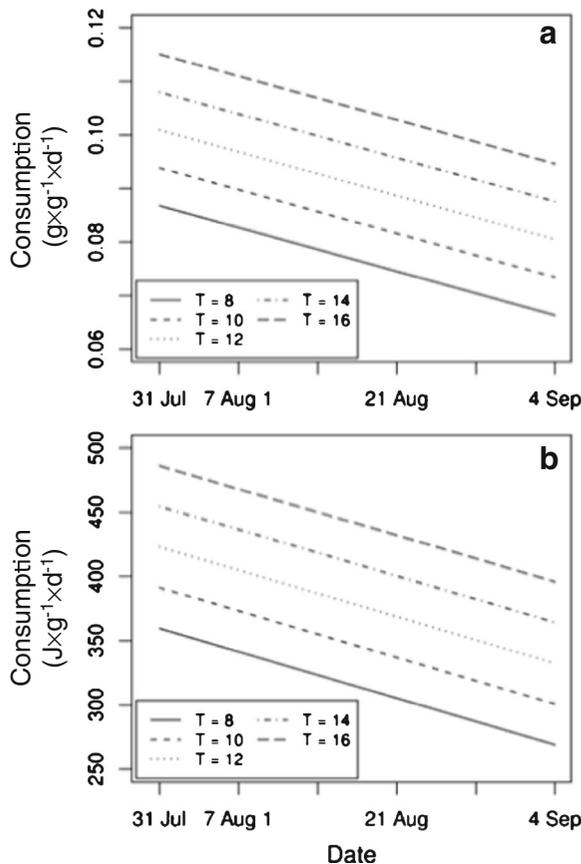
#### Proportion of maximum consumption

Estimates of the proportion of maximum consumption ( $P$ ) ranged from approximately 0.25 to 0.5 with high overlap among streams; average (and standard deviation)  $P$  were 0.34 (0.07), 0.43 (0.07), 0.41 (0.09), and 0.38 (0.10), for Marsh, Elk, South Fork of the Salmon River, and Valley creeks, respectively.

#### Sensitivity analysis and prediction of bioenergetics model

To investigate model response, consumption rates (in terms of both grams and joules of prey) were predicted across a range of temperatures experienced by the fish (Fig. 6). Consumption responded strongly to both temperature and date, with a comparable response (i.e., parallel lines) of each consumption rate across the range of both variables.

Results of the sensitivity analysis indicated a negative relationship between the parameter of prey energy density and predicted consumption rates, such that an increase in energy density resulted in a roughly comparable decrease in consumption rate in terms of mass ( $\text{g}\cdot\text{g}^{-1}\cdot\text{day}^{-1}$ ) or a negligible change in terms of energy



**Fig. 6** Sensitivity analysis testing the response of consumption rates (**a**  $\text{g}\cdot\text{g}^{-1}\cdot\text{day}^{-1}$  and **b**  $\text{J}\cdot\text{g}^{-1}\cdot\text{day}^{-1}$ ) across a range of temperatures (denoted T in the legend and expressed in °C) and dates

( $\text{J}\cdot\text{g}^{-1}\cdot\text{day}^{-1}$ ) (Fig. 7a, b). These analyses demonstrate that the estimate of energy density of prey has a strong influence in the mass of prey consumed but little influence on the total energy of prey consumed. A positive relationship was observed between the parameter of activity multiplier and predicted consumption rate (Fig. 7c, d), such that a six-fold increase in activity multiplier resulted in approximately an 18 % increase in consumption.

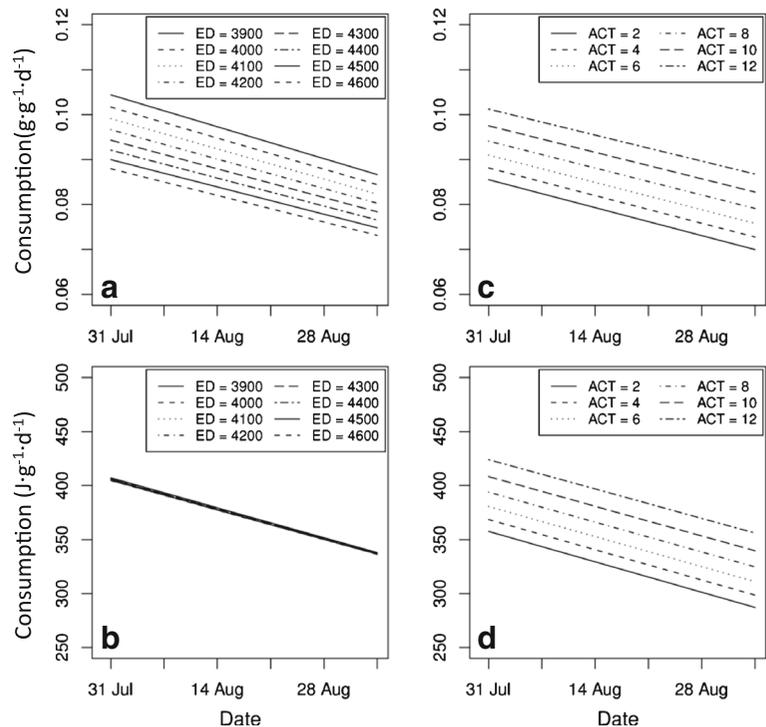
### Discussion

This study examined spatial and temporal patterns of somatic growth in spring/summer Chinook juveniles from the Salmon River basin. Although growth rate did not vary substantially among four populations (Figs. 4 and 5a, and Table 2 model d), stream-specific differences in temperature were present resulting in

estimates of consumption rates to be quite dissimilar among populations (Fig. 5c). In particular, mean stream temperatures were approximately 2–5 °C warmer in two of the four streams (ELK and VAL; Fig. 3), yet temperatures in all streams were below the 19 °C optimum for Chinook salmon reported by Brett et al. (1982). Assuming that the bioenergetics model accurately reflects an increase in metabolic demands when temperatures are warmer (yet below a physiological upper threshold, 25 °C; Brett et al. 1982), corresponding elevated differences in consumption rates were modeled for ELK and VAL (Fig. 5b, c). In fact the bioenergetics model reflects this optimum by having a parameter value, CTM (see Online Resource Table 1), of 18 °C represent the temperature at which an individual is at 98 % of its maximum consumption. The greater consumption we modeled for fish residing in warmer streams could not be explained by stream productivity reported in Sanderson et al. (2009), in which the same streams were studied (B. Sanderson pers. com.). Further, the modeled dynamics were partially driven by the relatively low feeding rates observed in these populations (*P* consistently less than 0.5), which in effect, made metabolic costs relatively expensive (Crozier et al. 2010).

These results demonstrated that using juvenile growth exclusively as a measure of ecosystem or habitat components misses fundamental differences among ecosystems. Several disparate ecosystem components can lead to the same growth rate, and thus growth is not always a satisfactory measure of juvenile salmon habitat. Thus, we advocate for modeling and monitoring, similar to that described in this study, to further understand spatial and temporal variability in growth rates. In terms of modeling, feeding models (see Hughes et al. 2003) and individual-based population models (see Van Winkle et al. 1993; Elliott 1994) could further clarify relationships among populations. Similarly, the monitoring of several important factors that interact to influence growth at scales relevant to the individual, such as density of intra and interspecific competitors and predators, food availability, and habitat structure, could greatly improve our understanding of growth variability. Furthermore, expanding this study to monitor these factors over multiple years and sites will help to resolve their relative contributions. This type of understanding will be crucial for providing insight into how threatened populations will respond to future conditions under climate change or how mitigation actions can improve growth rates.

**Fig. 7** Sensitivity analysis testing the response of consumption rates (**a** and **c**,  $\text{g}\cdot\text{g}^{-1}\cdot\text{day}^{-1}$  and **b** and **d**  $\text{J}\cdot\text{g}^{-1}\cdot\text{day}^{-1}$ ) across a range of energy density (ED) values (**a** and **b**) and activity multiplier (ACT) values (**c** and **d**). The line in plot **b** contains all (8) of the energy density values used to compute consumption



In relationships that had growth or consumption rates as response variables, strong relationships were observed between the response variables and date. Most previous field studies of growth rate have not had the temporal resolution to uncover intra-seasonal effects. The use of otoliths to estimate growth trajectories (in this study) provided this capability, which conferred clear advantages: bioenergetic model results indicated an intra-seasonal trend in consumption, with consumption rates decreasing through time. In fact, the effects of temperature and date were approximately equivalent over the ranges examined (Fig. 6). That is, the range of consumption rates modeled across temperature values on a given date was similar to consumption rates modeled within a temperature across dates. In addition to the observed decreases in temperature throughout the season, this within-season trend could have been due to decreasing daylight, as Cromwell (2009) observed more foraging during daytime than nighttime for closely related populations of Chinook (see also McCormick et al. 1995; Björnsson et al. 2000). We do not believe the decrease in growth rate through time is mediated by a negative relationship between fish growth rate (expressed in units of length) and fish size (e.g., von Bertalanffy growth relationship) because our previous

modeling of these fish did not detect such an effect (unpublished data).

It is important to acknowledge that this analysis relied on a bioenergetics model using literature values and on assumptions such as a constant activity coefficient across populations. Because of such limitations, Ney (1993) suggested that bioenergetic models be used to investigate trends and for relative comparisons, as is the case in the present study. Furthermore, uncertainty is lower when models calculate consumption from growth (like reported here) instead of growth from consumption (Boisclair and Leggett 1989; Ney 1993). In addition, our sensitivity analysis demonstrated that estimates of consumption rate (expressed in grams of prey) were sensitive to energy density of prey, and we acknowledge that our data on energy density was limited. However, our sensitivity analysis also demonstrated that estimates of consumption rate (expressed in Joules) were not sensitive to energy density of prey. Therefore, we believe that expressing consumption rates in terms of energy consumed is preferable to expressing in terms of grams of prey. That being said, and given the relatively small sample sizes (owing to ESA restrictions), the conclusions of this study should be regarded as a working hypothesis on the mechanisms underlying the observed

variability in growth rates. The sensitivity analysis, for example, demonstrated that large differences in activity across populations could have led to patterns in growth rate across populations that were similar to those we observed. These types of issues will need to be resolved with observational field studies such as those by Cromwell (2009) and Macneale et al. (2010).

In this study a relatively low food consumption was observed in these populations, with  $P$  ranging from approximately 0.25 to 0.5 (see also Sauter and Connolly 2010). This was in contrast to other studies, which estimated greater rates of food consumption for *O. tshawytscha* in Lake Washington ( $P$  range 0.58–0.95, Koehler et al. 2006), Puget Sound ( $P$  range of 0.55–0.90; Duffy 2009), and Lake Ontario ( $P$  range 0.43–0.83, Murry et al. 2009). Given the nutrient-limited condition of this study's streams (Sanderson et al. 2009), our results were not necessarily surprising, and suggest that food limitation is one factor influencing consumption rates and potentially regulating growth across all sites. We note, though, that other factors can contribute to variability in feeding rates. For example, Cromwell (2009) observed that foraging rate was related to a variety of factors, including density of conspecifics and other fish species and distance to cover (also see Achord et al. 2003).

Several studies have demonstrated the importance of juvenile size to various processes in these populations. For instance, Zabel and Achord (2004) related juvenile survival to fish length, and Zabel and Williams (2002) and Duffy and Beauchamp (2011) related survival to adulthood to fish size while a juvenile. In addition, larger juveniles have been observed to migrate earlier (Zabel 2002), and juvenile migrants arriving in the estuary at an earlier date typically return at a greater rate (Scheuerell et al. 2009). These studies help highlight that understanding the mechanisms that underlie juvenile growth processes can help in the recovery of these federally listed populations.

Results of this study represent the first steps towards identifying factors that underlie important population level and habitat quality differences. Further, this study highlights that ecosystem components, such as temperature, influence somatic growth in complex ways, thus potentially limiting the use of growth as a metric of habitat quality. Additional research is needed to better understand how these and other ecosystem components contribute to variation in the growth and size of individuals.

**Acknowledgments** We thank C. Vizza, A. Goodwin, C. Tran, H. Coe, and S. Achord, for collecting fish samples. We thank L.

Crozier for providing the map of Salmon River basin populations, C. Harvey for assistance with bioenergetic components. M. Carey and B. Burke provided valuable comments that greatly improved an earlier draft. Collection permits were obtained from ESA (Sect 10 permit # 1406) and USFS (biological opinion #1-4-04-F-289).

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