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Using scale characteristics and water temperature to reconstruct growth rates of juvenile steelhead *Oncorhynchus mykiss*

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Juvenile steelhead *Oncorhynchus mykiss* from a northern California Central Valley population were reared in a controlled laboratory experiment. Significantly different rates of growth were observed among fish reared under two ration treatments and three temperature treatments (8, 14 and 20° C). Wider circulus spacing and faster deposition was associated with faster growth. For the same growth rate, however, circulus spacing was two-fold wider and deposited 36% less frequently in the cold compared to the hot temperature treatment. In a multiple linear regression, median circulus spacing and water temperature accounted for 68% of the variation in observed *O. mykiss* growth. These results corroborate previous research on scale characteristics and growth, while providing novel evidence that highlights the importance of water temperature in these relationships. Thus, this study establishes the utility of using scale analysis as a relatively non-invasive method for inferring growth in salmonids.

Key words: circuli; life history; rainbow trout; salmonids; scale analysis.

INTRODUCTION

Individual growth of salmonids, and other fishes, is intrinsically linked with vital aspects of their basic biology and life history (Wedemeyer *et al.*, 1980; Schlosser, 1991; Nislow, 2001). For example, elevated growth rates in numerous salmonid species have been shown to facilitate the transition between freshwater and saltwater ecosystems, partly due to increased hypo-osmoregulatory capacity and salinity tolerance (Wedemeyer *et al.*, 1980). In addition, several studies have shown that juvenile salmonid growth rates drive variation in fish size at ocean entry, which affects predation mortality and early marine survival (Healey, 1982; Holtby *et al.*, 1990; Bond *et al.*, 2008; Woodson *et al.*, in press). Variation in growth rates during the early life

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of salmonids such as steelhead *Oncorhynchus mykiss* (Walbaum 1792) and Atlantic salmon *Salmo salar* L. 1758 is also associated with the expression of disparate life histories (Thomaz *et al.*, 1997; Hutchings & Jones, 1998; Thorpe *et al.*, 1998; Mangel & Satterthwaite, 2008; Satterthwaite *et al.*, 2009, 2010). For example, Metcalfe *et al.* (1988, 1989) concluded that the anadromous phenotype of *S. salar* was more probable in fish achieving accelerated growth rates during the first summer after emergence. Similarly, Beakes *et al.* (2010) found that laboratory-reared *O. mykiss* with rapid initial growth were more likely to adopt an anadromous life history. Overall, variation in growth has been shown to affect pivotal transitions during the life cycle of many salmonids. Thus, quantifying individual growth, especially during the early life stages, can be an important component of understanding the dynamics of salmonid life histories and populations.

Scale analysis has been used extensively in fisheries science for reconstructing growth in salmonids (Bhatia, 1932; Barber & Walker, 1988; Fukuwaka & Kaeriyama, 1997; Heidarsson *et al.*, 2006; Wells *et al.*, 2008). Generally, the removal and analysis of scales for estimating growth is an attractive tool because it is relatively non-invasive and requires relatively little effort compared to alternative methods for estimating fish growth (Fisher & Pearcy, 1990; Stolarski & Hartman, 2008). Research has shown that growth is significantly and positively correlated with scale growth (Ricker, 1992; Heidarsson *et al.*, 2006; Bond *et al.*, 2008). In addition, a series of concentric rings (circuli) is deposited as scales grow. Previous work has found that spacing between circuli increases with increased growth rate (Healey, 1982; Fisher & Pearcy, 1990, 2005; Fukuwaka & Kaeriyama, 1997). Thus, the characteristics of scales (*i.e.* length and circulus spacing) can provide a chronological record of an individual's growth over discrete time periods.

Environmental conditions such as water temperature may also contribute to variation in scale characteristics (Bhatia, 1932; Bilton, 1975; Barber & Walker, 1988; Fisher & Pearcy, 1990; Fukuwaka, 1998). The primary impact of water temperature on scale development is believed to occur through mediating growth rates, a widely accepted, but rarely tested assumption (Bilton, 1975; Barber & Walker, 1988; Fisher & Pearcy, 1990; Fukuwaka, 1998). There have been few controlled experiments that have explicitly tested the interactive effects of water temperature and growth on scale development and those that have been published report mixed results. For example, Bhatia (1932) reported that water temperature had no effect on the production of scale annuli in rainbow trout *O. mykiss*, or periodic zones (*i.e.* a concentric series of narrowly spaced circuli followed by a series of widely spaced circuli), when fish were fed a uniform ration. Fukuwaka (1998) similarly found no evidence for a direct effect of temperature on the scale development of chum salmon *Oncorhynchus keta* (Walbaum 1792). Skurdal & Andersen (1985), however, found that in brown trout *Salmo trutta* L. 1758 circulus deposition occurred at a significantly greater rate for an equal size fish when reared at 7° C compared to 2° C, presumably leading to differences in circulus spacing. In addition, Boyce (1985) argued that temperature is one of the predominant environmental factors driving variation in scale characteristics of *O. mykiss*, such as the formation of scale annuli. This uncertainty in the literature confounds the understanding of the mechanisms underpinning the development of scales (Fukuwaka, 1998). To optimize the analysis of scale patterns for reconstructing growth in salmonids, and other fishes, the relationship between scale characteristics, growth and the environment must be better understood (Fisher & Pearcy, 1990, 2005; Fukuwaka, 1998).

The use of scales to reconstruct growth necessitates studies that quantify the relationship between growth, temperature and scale characteristics. To address this challenge, juvenile *O. mykiss* were reared in a full factorial experiment, with replicated aquaria under high and low rations, and three temperatures to test for the interactive effects of temperature and food availability on scale characteristics and growth. Two central questions were addressed: (1) Are scale characteristics (*i.e.* circulus spacing and deposition rate) correlated with growth? (2) What effect does water temperature have on scale development and what is the underlying relationship between scale characteristics and growth?

Evidence from prior studies indicates that colder water temperatures should be associated with narrower circulus spacing with a slower deposition rate due to inhibited fish growth, but have no independent effect on scale development. The direct and indirect effects of water temperature and growth on scale development are clarified in this study using data that could be reasonably attained in field studies. This study thus adds to the utility of scale analysis as a non-invasive tool for inferring growth rates in juvenile salmonids.

MATERIALS AND METHODS

STUDY SYSTEM

The relationship between scale development and growth rates was examined in *O. mykiss* from Coleman National Fish Hatchery (CNFH) on Battle Creek, CA, U.S.A., a tributary of the Sacramento River. This population is part of the Central Valley *O. mykiss* Distinct Population Segment (DPS; USFWS & NMFS, 1996), which is listed as threatened under the Endangered Species Act (ESA). *Oncorhynchus mykiss* returning to Battle Creek from the ocean and spawned in the CNFH are predominantly of hatchery origin although both wild and hatchery fish contribute to the fertilization process. It is considered that *O. mykiss* from CNFH are a reasonable proxy for northern California Central Valley *O. mykiss* with regard to growth rates and scale characteristics.

REARING ENVIRONMENT, INDIVIDUAL GROWTH AND SCALES

On 2 May 2007, *O. mykiss* fry (*i.e.* recently emerged and feeding) were transported from CNFH to the aquarium facility of the National Marine Fisheries Service (NMFS) South West Fisheries Science Center (SWFSC) in Santa Cruz, CA. The experiment lasted 103 days, from 2 May to 13 August 2007. *Oncorhynchus mykiss* were randomly segregated into 18 tanks (110 l) with six fish per tank, and tanks assigned to one of three temperatures and one of two rations, thus providing three replicate tanks and 18 fish of each temperature and ration treatment. Fish were acclimated to ambient water temperatures of $14 \cdot 0 \pm 0 \cdot 8^\circ$ C, mean $\pm$ S.D.) until 8 May. After the acclimation period, the temperature in each tank was adjusted by *c*. 2° C per day until the target treatment temperatures of cold (8° C), warm (14° C) and hot (20° C) were reached. Each tank was supplied with a continuous flow of oxygenated water (*c*. 15 ml s^{-1}) that was pumped in from a temperature-regulated reservoir (245 l). Digitally controlled heaters (Process Technology; www.processtechnology.com) and chillers (Aquanetics 1/5 Hp; www.aquaneticsparts.com) were used to regulate the water temperature in each treatment reservoir in order to maintain temperatures within $0 \cdot 5^\circ$ C of the target within each tank.

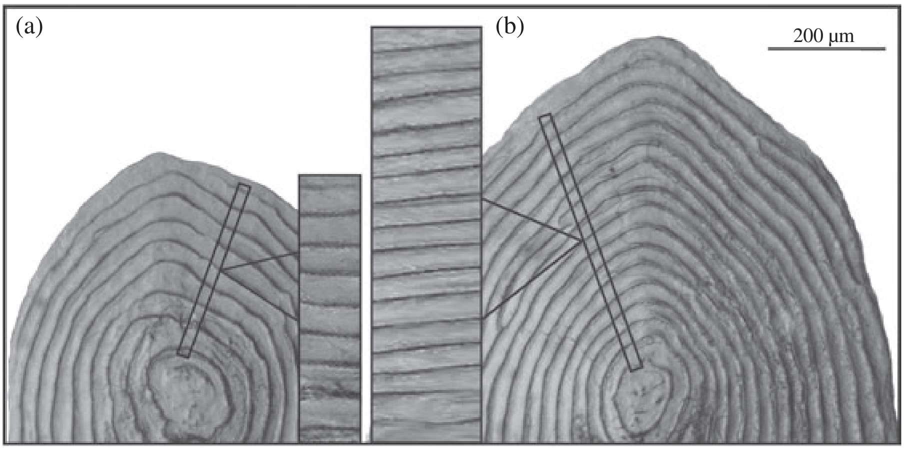

FIG. 1. Scale image depicting variation in circulus spacing from two *Oncorhynchus mykiss* that were reared for the same amount of time. Scales shown are from fish reared in the (a) low ration and cold and (b) high ration and hot treatments. Images and insets are scaled to the same magnification.

From 2 to 20 May, a daily food ration equal to 3% of the total wet fish biomass in each tank was distributed. On 21 May, a high (6% daily) and low (2%, 4 days week^{-1}) ration treatment was initiated, which lasted until the end of the experiment on 13 August. Individual fish were tracked throughout the experiment by marking each fish with an elastomer tag (Northwest Marine Tech.; www.nmt.us) in a unique combination of colour and body position. Every 2 weeks from 21 May to 13 August, all fish from each tank were removed except for a control fish, lightly anaesthetized (MS 222), and the fork length (L_F) of each fish in mm and wet mass in g were measured. Control fish were marked with a highly fluorescent yellow elastomer tag that could be illuminated from above the tank using a VI light (Northwest Marine Tech.), thus allowing for their identification and preventing their capture during measuring events. The control fish were left unhandled until the final measurement on 13 August to provide information on the potential effects of handling stress. After each measuring event, the food ration levels were adjusted according to the observed change in biomass for each tank. The tank mean was used to estimate the mass of control fish.

The *O. mykiss* reared in this experiment should have been in the initial stages of scale development by 21 May based on their L_F at that time (37·0 ± 2·7 mm, mean ± S.D.; Kesner & Barnhart, 1972; Hopelain, 1998). Besides, minimal or no evidence of scale development could be found on 21 May from a sub-set of fish that were excluded from the experiment. Thus, it was assumed that all scale growth occurred after initiating the ration treatments. On 18 June, 16 July and 13 August, a small sample of scales was removed from above the lateral line on a diagonal between the posterior insertion of the dorsal fin to the anterior insertion of the anal fin. A scale sample from the control fish was only removed on the last sampling occasion on 13 August. Only samples and measurements taken on 13 August were included in data analysis. These fish were *c*. 130 days old. For analysis, individual scales representative of the sample were chosen, avoiding scales that were damaged or regenerated. Each scale was photographed using a Nikon SMZ 1500 microscope with an attached Nikon Coolpix 5400 camera (5·1 megapixels; www.nikon.com/). All images were taken at ×9 magnification using a micrometer as a scale reference (Fig. 1). The scale radius, number of circuli and spacing between circuli were measured along a 20° radial line (Clutter & Whitesel, 1956) using imageJ software version 1.45 s with objectJ plug-in (Rasband, 2012).

TREATMENT EFFECTS ON GROWTH AND SCALES

A series of contrasts were conducted to test for significant differences in growth rates and scale characteristics as a function of temperature and ration treatments. The average daily growth and circulus deposition rate of fish from the onset of ration treatments on 21 May to the end of the experiment on 13 August (84 days) and the median circulus spacing of the final scale sample taken on 13 August were used for statistical comparison. All possible combinations of each treatment and response variable (*i.e.* mean growth rate, circulus spacing and circulus deposition rate) were tested with a two-way ANOVA, and the P-values were adjusted for multiple comparisons *via* Tukey's HSD correction. In addition, a factor to identify control and experimental fish was included to test if there was a difference in the growth and scale characteristics of the two groups.

MODELLING GROWTH WITH SCALES

The primary focus in this experiment was to test whether scale characteristics are linked to individual growth. To improve the transferability of results from this experiment to studies in the field, the data used in analyses were restricted to the types of data that would be available in field research (*i.e.* fish scales and water temperature). A multiple linear regression (MLR) including factors for temperature and ration treatments was used to test for differences in the relationship between scale radius and fish L_F. In addition, an MLR incorporating median scale circulus spacing and temperature treatment tested these variables as predictors of individual growth rates. Circulus spacing and water temperature were focused on, as these factors do not depend on the age of the fish or the amount of food a fish has been consuming. The mean growth rates for the duration of the experiment and scale measurements from the final 13 August sample were used. A set of five candidate models including a model with all factors and interactions and all possible sub-models was built. Akaike information criterion, corrected for small sample sizes, (AICc; Akaike, 1974; Hurvich & Tsai, 1989; Burnham & Anderson, 2002) was used to rank model performance. A 'top' model was identified with the lowest AICc score, which is indicative of greater parsimony and balance between model fit and model complexity. A difference >4 AICc units between models can be interpreted as evidence for model superiority (Burnham & Anderson, 2002). All computations and analysis were conducted with programme R (R development core team; www.r-project.org/), and 95% C.I. were approximated as ± 1.96 S.E. for model coefficients and model fit. Control fish were not included in the dataset used to parameterize the AICc selected model. Model validation was conducted by comparing observed growth rates to the predicted growth rates of the control fish from each temperature and ration treatment using the AICc top model.

RESULTS

INDIVIDUAL GROWTH

At the end of the 103 day experiment, there was 100% survival in the cold ($n = 36$) and warm ($n = 36$) temperature treatments, and 100% survival of control fish. In the hot temperature treatment, there were four mortalities in the low-ration treatment ($n = 14$ remaining, two mortalities in two tanks), and three mortalities in the high-ration treatment ($n = 15$ remaining, one mortality in each tank). Over the course of the experiment, growth was *c.* linear [Fig. 2(a), (b)]. There was not a significant difference in the average growth rate of control fish compared to the experimental fish (ANOVA, $F_{1,91} = 0.05$, $P > 0.05$).

Growth was significantly affected by temperature (ANOVA, $F_{2,95} = 26.63$, $P < 0.001$) and ration (ANOVA, $F_{1,95} = 185.97$, $P < 0.001$). There was also a significant interaction between temperature and ration (ANOVA, $F_{2,95} = 31.38$, $P < 0.001$), indicating that the effect of ration on growth rate was different among temperature treatments [Figs 2(a), (b) and 3(a)]. For example, in the warm-temperature treatment the average growth rate was 33% faster in the high-ration

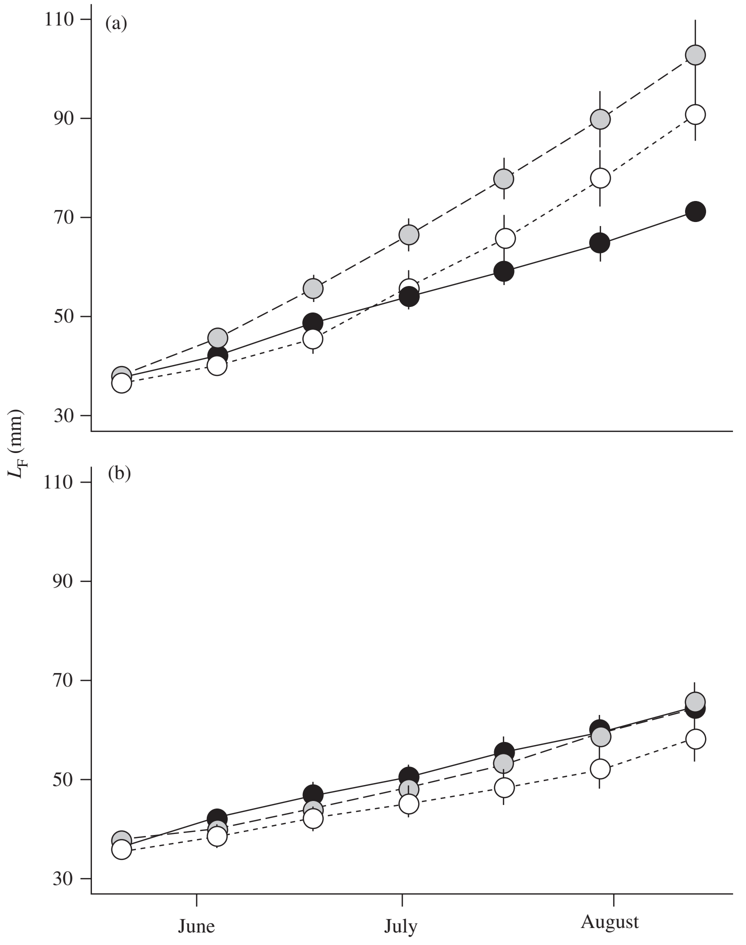

FIG. 2. *Oncorhynchus mykiss* fork lengths (L_F) over the duration of the experiment for temperature treatments of 8 (—●—), 14 (- ◎ -) and 20° C (···○···) provided (a) high and (b) low rations. Error bars are 95% C.I. around the mean (*i.e.* ±1·96 S.E.).

compared to the low-ration treatment. In contrast, there was no significant difference in growth between the high- and low-ration tanks in the cold treatment [Tukey's HSD, $P > 0{\cdot}05$; Fig. 3(a)]. The fastest observed growth was supported in the warm temperature and high-ration treatment, which had a mean ± S.E. $= 0{\cdot}77 \pm 0{\cdot}04$ mm day^{-1}, and was significantly faster than any other temperature and ration treatment combination [Tukey's HSD, $P < 0{\cdot}01$; Fig. 3(a)]. The slowest observed growth occurred in the hot temperature and low-ration treatment, which had a mean ± S.E. $= 0{\cdot}26 \pm 0{\cdot}06$ mm day^{-1}, but was not significantly slower than low-ration growth rates in the cold and warm treatments [Tukey's HSD, $P > 0 \cdot 05$; Fig. 3(a)].

FACTORS CONTROLLING SCALE DEVELOPMENT

Scale circulus spacing was different in fish reared in the cold compared to warm or hot treatments (Fig. 1 inset). Circulus spacing (μm) was significantly wider (ANOVA,

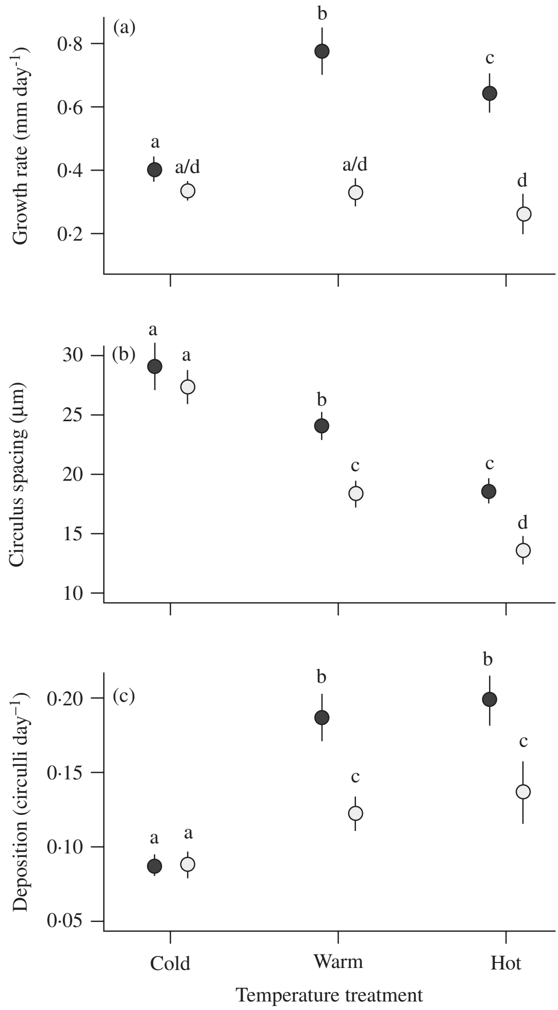

FIG. 3. (a) Estimated growth, (b) median circulus spacing and (c) circulus deposition rate as a function of temperature and high (●) *v*. low (○) ration treatments in *Oncorhynchus mykiss*. Temperature treatments (*x*-axis) were labelled cold (8° C), warm (14° C) and hot (20° C). Growth and circulus deposition rates were calculated as a daily average from 21 May to 13 August. Median circulus spacing was calculated from scales sampled on the last measuring event on 13 August 2007. Error bars represent an approximated 95% C.I. around the mean (*i.e*. ±1·96 S.E.), and significant differences between treatments are indicated with dissimilar lower case letters.

$F_{2,95} = 160{\cdot}50$, $P < 0{\cdot}001$) as temperatures declined from the hot to the cold treatment [Fig. 3(b)]. The mean circulus spacing in the cold and high-ration treatment was 57% wider than the average spacing in the hot and high-ration treatment [Fig. 3(b)]. Within a temperature treatment, high rations significantly increased mean circulus spacing [ANOVA, $F_{1,95} = 55{\cdot}05$, $P < 0{\cdot}001$; Fig. 3(b)]. The effect of ration was, however, dissimilar among temperature treatments [ANOVA, $F_{2,95} = 5{\cdot}31$, $P < 0{\cdot}01$; Fig. 3(b)] and was not significant in the cold treatment [Tukey's HSD, $P > 0 \cdot 05$; Fig. 3(b)].

Patterns in the rate of circulus deposition (circuli day^{-1}) among treatment groups were driven by temperature and ration treatments [Fig. 3(c)]. There was a significant increase in the rate of circulus deposition in the warm and hot temperature treatments relative to the cold treatment [ANOVA, $F_{2,95} = 82{\cdot}51$, $P < 0{\cdot}001$; Fig. 3(c)]. Compared to the low-ration treatment, a 52 and 45% increase in the mean circulus deposition rate was observed within the high-ration and warm and hot temperature treatments respectively [ANOVA, $F_{1,95} = 53{\cdot}34$, $P < 0{\cdot}001$; Fig. 3(c)]. Similar to circulus spacing, a significant interaction between temperature and ration treatments was found [ANOVA, $F_{2,95} = 15{\cdot}29$, $P < 0{\cdot}001$; Fig. 3(c)], due partly to the non-significant difference in circulus deposition rate within the cold temperature treatment [Tukey's HSD, $P > 0{\cdot}05$; Fig. 3(c)]. There was no significant difference in the mean circulus spacing (ANOVA, $F_{1,91} = 0{\cdot}32$, $P > 0{\cdot}05$), or the rate of circulus deposition (ANOVA, $F_{1,91} = 0{\cdot}27$, $P > 0{\cdot}05$) of control fish compared to experimental fish. Thus, the additional handling of experimental fish had limited effects on growth and development of scale characteristics relative to temperature and ration treatments.

PREDICTING GROWTH AND MODEL VALIDATION

Fish that were longer had scales with a larger radius (Fig. 4). Specifically, for every mm of increased L_F, scale radius was mean ± s.e. = 5·0 ± 0·2 μm longer, and over 87% of the variation in scale radius could be explained by L_F (MLR, adjusted $r^2 = 0{\cdot}87$, $P < 0{\cdot}001$; Fig. 4). No evidence for an effect of water temperature (MLR, $P > 0{\cdot}05$) or ration level (MLR, $P > 0{\cdot}05$) on the underlying relationship between L_F and scale radius was found. The median circulus spacing within scales from individual fish was, however, strongly associated with fish growth and, importantly, depended on water temperature (Fig. 5).

The amount of variation in fish growth that could be explained with scale circulus spacing and water temperature was examined with MLR. The most strongly supported model for estimating fish growth contained factors for circulus spacing, temperature and an interaction between circulus spacing and temperature (Table I). The 'top' AICc model was considerably more supported than other models in the candidate set (Δ AICc > 24). In total, 68% of the observed variation in individual growth was accounted for by the top model (MLR, adjusted $r^2 = 0{\cdot}68$, $P < 0{\cdot}01$; Fig. 5). Increased growth rates were significantly associated with wider circulus spacing; however, the slope and intercept of the regression differed significantly with temperature (Table II). There was strong agreement between the predicted and observed growth rates of the control fish indicating that an accurate estimate of control fish growth was generated with the AICc selected model (linear regression: adjusted $r^2 = 0{\cdot}72$, $P < 0{\cdot}01$; Fig. 6). The slope between predicted and observed growth was estimated with linear regression (LR) as 0·93 ± 0·14 (mean ± s.e.), and the intercept was not significantly different than 0 (LR: intercept = 0·03 ± 0·07 mean ± s.e., $P > 0{\cdot}05$). The residual error between predicted and observed growth appeared to be randomly distributed with the data combined. The uncertainty in predicted growth and variation in observed growth for the control fish reared in the warm and hot treatments was, however, greater than the cold treatment (Fig. 6). The disparate uncertainty in predicted and observed growth among treatments probably reflects the overall increased variance in growth rates in the warm and hot treatment temperatures

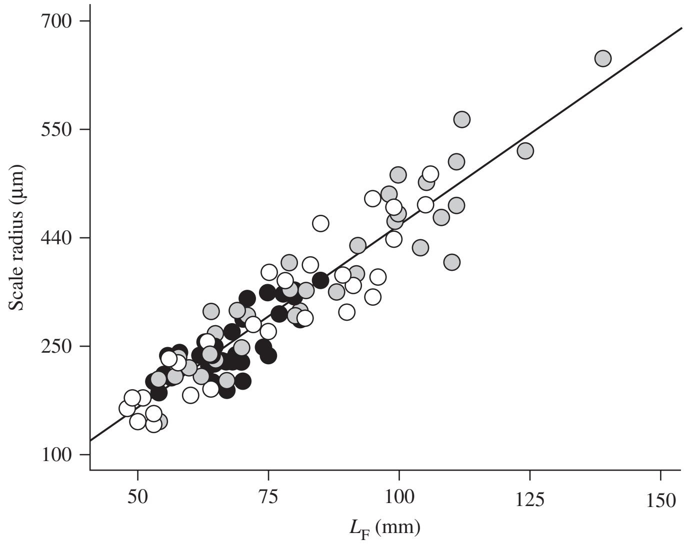

FIG. 4. Fitted linear regression (——) plotted to depict the *Oncorhynchus mykiss* fork length (L_F) and scale radius relationship. High and low rations are combined within 8° C (●), 14° C (◎) and 20° C (○) temperature treatments. The linear regression was fitted by $y = -86{\cdot}9310 + 5{\cdot}0408x$.

[Fig. 2(a), (b)] and the uncertainty in temperature treatment coefficients in the AICc selected MLR (Table II).

DISCUSSION

This study provides insight into the interpretation and application of scale analyses to reconstruct growth of *O. mykiss*. The laboratory experiment manipulated both water temperature and food availability to generate a gradient in growth of juvenile *O. mykiss*. Not surprisingly, warmer water temperature and higher ration size was associated with higher growth rates. Scale characteristics were strongly related to growth rate. These results are consistent with several other studies examining the effects of food availability on growth and scale development of *Oncorhynchus* spp. (Bhatia, 1932; Bilton & Robins, 1971*a*, *b*; Fisher & Pearcy, 1990). The relationship between scale radius and fish length was independent of ration and temperature treatments (Fig. 4). Temperature, however, modulated the relationship between scale characteristics (*e.g.* circulus spacing) and growth rates (Fig. 5). This study therefore highlights the importance of incorporating temperature into research that uses scale characteristics to reconstruct fish growth.

Scale length was predictably associated with fish length. Regardless of the thermal environment, scales continue to grow proportionally to fish length (Fig. 4). As such, scale radius can be used to reconstruct fish length at specific time periods such as size at ocean out-migration (Bond *et al.*, 2008; Wells *et al.*, 2008; Woodson *et al.*, in press). This study thus supports this application of using scale radius to reconstruct fish length across different environmental conditions as these relationships appear to be robust to temperature variation.

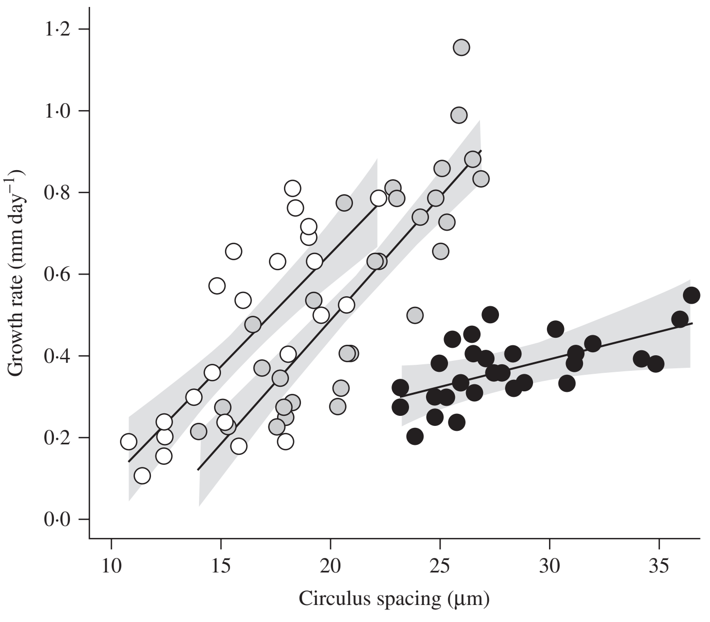

FIG. 5. Fitted Akaike information criterion, corrected for small sample sizes (AICc) selected multiple linear regression of growth rate & circulus spacing for the cold (●; $y = -0{\cdot}0129 + 0{\cdot}0135x$), warm (◎; $y = -0{\cdot}7196 + 0{\cdot}0604x$) and hot (○; $y = -0{\cdot}4521 + 0{\cdot}0554x$) temperature treatments for *Oncorhynchus mykiss*. The grey polygon encompasses the 95% C.I. of the model fit.

Scale characteristics such as circulus spacing were positively associated with growth, but these relationships were modified by temperature (Fig. 5). There was strong support for a direct effect of temperature on circulus spacing independent of fish growth. Contrary to the assumptions of previous studies, an increase in circulus spacing in the cold, compared to the warm and hot temperature treatments was observed. Within the low-ration treatment, circulus spacing was two-fold wider on average in the cold treatment compared to the hot treatment despite non-significant differences in growth. In addition, the deposition rate of circuli was 36% slower in the cold temperature treatment, suggesting that under cold-water conditions, the mechanisms controlling circulus deposition are being suppressed. Scales continue to grow proportionally to fish length, thus at cold temperatures a depressed rate of circulus deposition will naturally lead to wider spacing between deposits. This study thus indicates that temperature can strongly influence scale characteristics, particularly scale circuli, contrary to the conclusions of previous studies (Bhatia, 1932; Fukuwaka, 1998).

This study illuminates how scale characteristics and temperature can be used to predict growth. Specifically, the pattern of circuli generated as scales develop is a function of growth and water temperature. As fish grow faster the space between circuli also increases, but this relationship is mediated by water temperature. Thus, fish growth can be best predicted by water temperature and circulus spacing, as demonstrated by the reconstruction of control fish growth rates with an AICc supported MLR that included water temperature and circulus spacing. Studies that quantify temperature can thus use the relationships developed in this study to estimate growth

TABLE I. The competing models used for predicting growth rate of *Oncorhynchus mykiss* ranked in order of Akaike information criterion, corrected for small sample sizes (AICc). Parameters are defined as median circulus spacing (M.S) and temperature treatment (T). The separation of factors are labelled with a +, and interactions between factors are labelled with a colon. Ration was not included in the predictive model because ration size is not generally known at the individual level or in field applications

Rank	Model parameters	d.f.	Log-like	AICc	Δ AICc
1	M.S + T + T:M.S	7	58·62	−101·75	0
2	M.S + T	5	43·95	−77·11	24·64
3	T	4	14·38	−20·26	81·50
4	M.S	3	10·59	−14·88	86·88
5	Null	2	8·48	−12·80	88·95

based on scale characteristics. On the other hand, this study suggests that using circulus spacing to predict growth without considering temperature may produce erroneous results.

In natural water bodies, water temperatures fluctuate on diel and annual cycles. In this study, however, temperatures were held constant at the target treatment levels of 8, 14 and 20° C in order to isolate the effect of temperature from growth and food availability. As a consequence, further research is needed in order to discern how conclusions from this study may change if temperatures are allowed to oscillate on natural cycles.

Over recent years, many salmonid population numbers have declined across a large extent of their range (Gustafson *et al.*, 2007). Growth of juvenile salmonids can have profound impacts on vital population dynamics and life histories, thus obtaining data on growth of salmonids in small size classes is pertinent for conservation and management efforts (Metcalfe *et al.*, 1989; Schlosser, 1991; Nislow, 2001; Satterthwaite *et al.*, 2009; Beakes *et al.*, 2010). Individual growth of the smaller size classes of salmonids is challenging, or impossible, to measure with common tagging technologies owing to the invasive nature and physical size restrictions (Nislow, 2001; Gibbons & Andrews, 2004). Furthermore, tagging studies are often expensive and logistically demanding. The analysis of alternative calcified structures such as otoliths

TABLE II. Regression coefficients obtained from the most parsimonious multiple linear regression used to estimate growth as a function of scale circulus spacing and temperature treatment in *Oncorhynchus mykiss*. Parameters are defined as median circulus spacing (M.S), warm and hot temperature treatment

Parameter	*b*	S.E.	*t*-value	*P*
Intercept	−0·0129	0·1764	−0·073	>0·05
M.S	0·0135	0·0062	2·174	<0·05
Hot	−0·4391	0·2248	−1·953	>0·05
Warm	−0·7067	0·2194	−3·221	<0·01
M.S × hot	0·0419	0·0105	4·009	<0·001
M.S × warm	0·0469	0·0087	5·391	<0·001

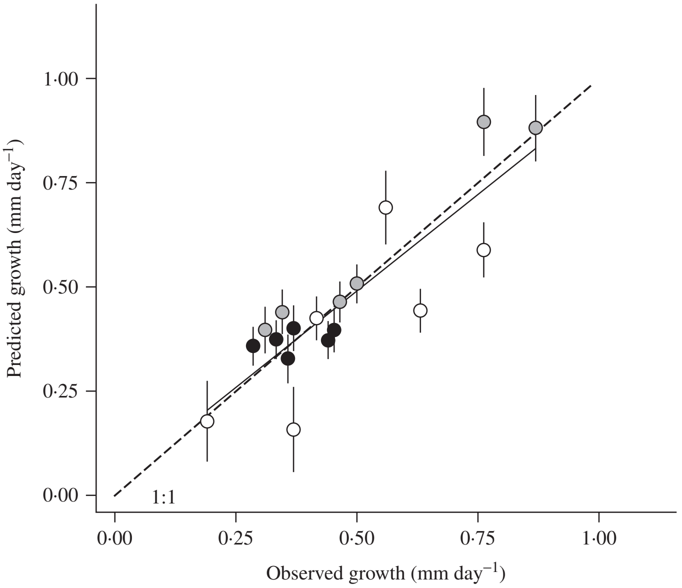

FIG. 6. Predicted *v*. observed growth for the control *Oncorhynchus mykiss* from the cold (●), warm (◎) and hot (○) temperature treatments. Error bars represent 95% C.I. from model predictions. Linear model fit (——; $y = 0{\cdot}0275 + 0{\cdot}9271x$) and 1:1 line (-----) is plotted to illustrate agreement between predicted and observed values.

require that captured individuals are killed, which may be unethical when working with threatened and endangered animals. In this study, the time spent during scale analysis averaged <15 min for each sample, including mounting scales on slides, photographing and data extraction. Thus, scale analysis is a relatively inexpensive, non-invasive and efficient method for reconstructing growth of a species with a broad global distribution (MacCrimmon, 1971) and results from this study are probably applicable to other fishes. This study highlights the potential for scale analysis as an effective tool for estimating growth of young salmonids, and thus aids the conservation and management of commercially, culturally and ecologically important species.

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REFERENCES

Akaike, H. (1974). A new look at the statistical model identification. *IEEE Transactions on Automatic Control* **19,** 716–723.

Barber, W. E. & Walker, R. J. (1988). Circuli spacing and annulus formation: is there more than meets the eye? The case for sockeye salmon, *Oncorhynchus nerka*. *Journal of Fish Biology* **32,** 237–245.

Beakes, M. P., Satterthwaite, W. H., Collins, E. M., Swank, D. R., Merz, J. E., Titus, R. G., Sogard, S. M. & Mangel, M. (2010). Smolt transformation in two California steelhead populations: effects of temporal variability in growth. *Transactions of the American Fisheries Society* **139,** 1263–1275.

Bhatia, D. (1932). Factors involved in the production of annual zones on the scales of rainbow trout (*Salmo irideus*) II. *The Journal of Experimental Biology* **9,** 6–11.

Bilton, H. T. (1975). Factors influencing the formation of scale characters. *International North Pacific Fisheries Commission Bulletin No* **32,** 102–108.

Bilton, H. T. & Robins, G. L. (1971a). Effects of feeding level on circulus formation on scales of young sockeye salmon (*Oncorhynchus nerka*). *Journal of the Fisheries Research Board of Canada* **28,** 861–868.

Bilton, H. T. & Robins, G. L. (1971b). Effects of starvation, feeding, and light period on circulus formation on scales of young sockeye salmon (*Oncorhynchus nerka*). *Journal of the Fisheries Research Board of Canada* **28,** 1749–1755.

Bond, M. H., Hayes, S. A., Hanson, C. V. & MacFarlane, R. B. (2008). Marine survival of steelhead (*Oncorhynchus mykiss*) enhanced by a seasonally closed estuary. *Canadian Journal of Fisheries and Aquatic Sciences* **65,** 2242–2252.

Boyce, R. B. (1985). Effects of feeding level, temperature, and photoperiod on growth and selected scale characteristics of juvenile steelhead trout. MSc. Thesis, Oregon State University, Oregon, USA. Available at http://scholarsarchive.library.oregonstate.edu/xmlui/handle/1957/21708/

Burnham, K. P. & Anderson, D. R. (2002). *Model Selection and Multimodel Inference: A Practical-Theoretic Approach*, 2 edn. New York, NY: Springer-Verlag.

Clutter, R. I. & Whitesel, L. E. (1956). Collection and interpretation of sockeye salmon scales. *International North Pacific Fisheries Commission Bulletin No.* **9,** 1–159.

Fisher, J. P. & Pearcy, W. G. (1990). Spacing of scale circuli versus growth rate in young coho salmon. *Fisheries Bulletin* **88,** 637–643.

Fisher, J. P. & Pearcy, W. G. (2005). Seasonal changes in growth of coho salmon (*Oncorhynchus kisutch*) off Oregon and Washington and concurrent changes in the spacing of scale circuli. *Fisheries Bulletin* **103,** 34–51.

Fukuwaka, M. (1998). Scale and otolith patterns prove growth history of Pacific salmon. *North Pacific Anadromous Fish Commission Bulletin* **1,** 190–198.

Fukuwaka, M. & Kaeriyama, M. (1997). Scale analyses to estimate somatic growth in sockeye salmon, *Oncorhynchus nerka*. *Canadian Journal of Fisheries and Aquatic Sciences* **54,** 631–636.

Gibbons, J. W. & Andrews, K. M. (2004). PIT tagging: simple technology at its best. *BioScience* **54,** 447–454.

Gustafson, R. G., Waples, R., Myers, J. M., Weitkamp, L. A. & Bryant, G. J. (2007). Pacific salmon extinctions: quantifying lost and remaining diversity. *Conservation Biology* **21,** 1009–1020.

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

Heidarsson, T., Antonsson, T. & Snorrason, S. S. (2006). The relationship between body and scale growth proportions and validation of two back-calculation methods using individually tagged and recaptured wild Atlantic salmon. *Transactions of the American Fisheries Society* **135,** 1156–1164.

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

Hurvich, C. M. & Tsai, C. L. (1989). Regression and time series model selection in small samples. *Biometrika* **79,** 297–307.

Hutchings, J. A. & Jones, M. E. B. (1998). Life-history variation and growth rate thresholds for maturity in Atlantic salmon, *Salmo salar*. *Canadian Journal of Fisheries and Aquatic Sciences* **55,** 22–47.

Kesner, W. D. & Barnhart, R. A. (1972). Characteristics of the fall-run steelhead trout (*Salmo gairdneri*) of the Klamath River system with emphasis on the half-pounder. *California Fish and Game* **58,** 204–220.

MacCrimmon, H. R. (1971). World distribution of rainbow trout (*Salmo gairdneri*). *Journal of the Fisheries Research Board of Canada* **28,** 663–704.

Mangel, M. & Satterthwaite, W. H. (2008). Combining proximate and ultimate approaches to understand life history variation in salmonids with application to fisheries, conservation, and aquaculture. *Bulletin of Marine Science* **83,** 107–130.

Metcalfe, N. B., Huntingford, F. A. & Thorpe, J. E. (1988). Feeding intensity, growth rates, and the establishment of life-history patterns in juvenile Atlantic salmon *Salmo salar*. *Journal of Animal Ecology* **57,** 463–474.

Metcalfe, N. B., Huntingford, F. A., Graham, W. D. & Thorpe, J. E. (1989). Early social status and the development of life-history strategies in Atlantic salmon. *Proceedings of the Royal Society of London B: Biological Sciences* **236,** 7–19.

Nislow, K. H. (2001). International symposium on the implications of salmonid growth variation. *Reviews in Fish Biology and Fisheries* **10,** 521–527.

Ricker, W. E. (1992). Back-calculation of fish lengths based on proportionality between scale and length increments. *Canadian Journal of Fisheries and Aquatic Sciences* **49,** 1018–1026.

Satterthwaite, W. H., Beakes, M. P., Collins, E. M., Swank, D. R., Merz, J. E., Titus, R. G., Sogard, S. M. & Mangel, M. (2009). Steelhead life history on California's central coast: insights from a state-dependent model. *Transactions of the American Fisheries Society* **138,** 532–548.

Satterthwaite, W. H., Beakes, M. P., Collins, E. M., Swank, D. R., Merz, J. E., Titus, R. G., Sogard, S. M. & Mangel, M. (2010). State-dependent life history models in a changing (and regulated) environment: steelhead in the California Central Valley. *Evolutionary Applications* **3,** 221–243.

Schlosser, I. J. (1991). Stream fish ecology: a landscape perspective. *BioScience* **41,** 704–712.

Skurdal, J. & Andersen, R. (1985). Influence of temperature on number of circuli of first year scales of brown trout, *Salmo trutta* L. *Journal of Fish Biology* **26,** 363–366.

Stolarski, J. T. & Hartman, K. J. (2008). An evaluation of the precision of fin ray, otolith, and scale age determinations for brook trout. *North American Journal of Fisheries Management* **28,** 1790–1795.

Thomaz, D., Beall, E. & Burke, T. (1997). Alternative reproductive tactics in Atlantic salmon: factors affecting mature parr success. *Proceedings of the Royal Society B* **264,** 219–226.

Thorpe, J. E., Mangel, M., Metcalfe, N. B. & Huntingford, F. A. (1998). Modeling the proximate basis of salmonid life-history variation, with application to Atlantic salmon, *Salmo salar* L. *Evolutionary Ecology* **12,** 581–599.

USFWS & NMFS (1996). Policy regarding the recognition of distinct vertebrate population segments under the Endangered Species Act. *Federal Register* (7 February 1996) **61,** 4722–4725.

Wedemeyer, G. A., Saunders, R. L. & Clarke, W. C. (1980). Environmental factors affecting smoltification and early marine survival of anadromous salmonids. *Marine Fisheries Review* **42,** 1–14.

Wells, B. K., Grimes, C. B., Sneva, J. G., McPherson, S. & Waldvogel, J. B. (2008). Relationships between oceanic conditions and growth of Chinook salmon (*Oncorhynchus tshawytscha*) from Alaska, Washington, and California, USA. *Fisheries Oceanography* **17,** 101–125.

Woodson, L. E., Wells, B. K., Weber, P. K., MacFarlane, R. B., Whitman, G. & Johnson, R. C. (in press). Growth, size, and origin-dependent mortality of juvenile Chinook salmon

Oncorhynchus tshawytscha during early ocean residence. *Marine Ecology Progress Series* doi:10.3354/meps10353.

Electronic References

Hopelain, J. S. (1998). Age, growth, and life history of Klamath River Basin steelhead (*Oncorhynchus mykiss irideus*) as determined from scale analysis. Inland Fisheries Division, California Fish and Game, Sacramento, California. *Administration Report No. 98–3*. Available at http://aquaticcommons.org/2898/1/IFD_AdminReport98-3.pdf/ (accessed 11 September, 2011).

Rasband, W. S. (1997–2012). *ImageJ*. Bethesda, MD: US National Institutes of Health. Available at http://imagej.nih.gov/ij/