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ARTICLE

A laboratory-calibrated model of coho salmon growth with utility for ecological analyses

Christopher V. Manhard, Nicholas A. Som, Russell W. Perry, and John M. Plumb

Abstract: We conducted a meta-analysis of laboratory- and hatchery-based growth data to estimate broadly applicable parameters of mass- and temperature-dependent growth of juvenile coho salmon (*Oncorhynchus kisutch*). Following studies of other salmonid species, we incorporated the Ratkowsky growth model into an allometric model and fit this model to growth observations from eight studies spanning ten different populations. To account for changes in growth patterns with food availability, we reparameterized the Ratkowsky model to scale several of its parameters relative to ration. The resulting model was robust across a wide range of ration allocations and experimental conditions, accounting for 99% of the variation in final body mass. We fit this model to growth data from coho salmon inhabiting tributaries and constructed ponds in the Klamath Basin by estimating habitat-specific indices of food availability. The model produced evidence that constructed ponds provided higher food availability than natural tributaries. Because of their simplicity (only mass and temperature are required as inputs) and robustness, ration-varying Ratkowsky models have utility as an ecological tool for capturing growth in freshwater fish populations.

Résumé : Nous avons réalisé une méta-analyse de données sur la croissance obtenues en laboratoire et en écloserie afin d'estimer des paramètres largement applicables de la croissance dépendant de la masse et de la température pour les saumons cohos (*Oncorhynchus kisutch*) juvéniles. À l'instar d'études sur d'autres espèces de salmonidés, nous avons incorporé le modèle de croissance de Ratkowsky dans un modèle allométrique et calé ce modèle sur des observations sur la croissance provenant de huit études portant sur dix populations différentes. Pour expliquer des variations des motifs de croissance en fonction de la disponibilité de nourriture, nous avons reparamétré le modèle de Ratkowsky pour ajuster à la ration l'échelle de plusieurs de ses paramètres. Le modèle en découlant est robuste pour une grande fourchette d'allocations de rations et de conditions expérimentales, expliquant 99 % de la variation de la masse corporelle finale. Nous avons calé ce modèle sur des données de croissance pour des saumons cohos habitant des affluents et des étangs aménagés dans le bassin du fleuve Klamath en estimant des indices de disponibilité de nourriture propres à l'habitat. Les résultats du modèle indiquent que les étangs aménagés présentent une plus grande disponibilité de nourriture que les affluents naturels. En raison de leur simplicité (les seules entrées requises sont la masse et la température) et leur robustesse, les modèles de Ratkowsky à rations variables constituent un outil écologique utile pour décrire la croissance dans les populations de poissons d'eau douce. [Traduit par la Rédaction]

Introduction

In Pacific salmon (*Oncorhynchus* spp.), growth rates of juvenile fish are an important factor underlying productivity (Koenings et al. 1993; Beamish and Mahnken 2001; Ebersole et al. 2006; Connor and Tiffan 2012). Consequently, the estimation of growth rates is often an objective of ecological studies of salmonid populations. Growth rate is a consequence of numerous factors, including body mass, temperature, food availability, seasonality, and behavior (Fry 1971; Ostrovsky 1995; Forseth et al. 2011). While it is logistically difficult to design ecological studies that jointly account for each of these factors, laboratory-based growth models provide a potential tool for evaluating growth in wild populations, as they can control for two primary governing factors: body mass and temperature (Forseth et al. 2001; Jonsson et al. 2001). Body mass and temperature measurements are generally attainable in ecological studies, and once controlled for, environmental factors underlying growth may be identified.

The Ratkowsky growth model (Ratkowsky et al. 1983) was developed to predict growth of bacterial cultures, but has been successfully extended to laboratory-based observations of growth of Atlantic salmon (*Salmo salar*; Elliott and Hurley 1997; Forseth et al. 2001), Arctic char (*Salvelinus alpinus*; Larsson et al. 2005), and Chinook salmon (*Oncorhynchus tshawytscha*; Perry et al. 2015). This model is well-suited for ecological studies because of its simplicity; it requires only temperature and initial body mass as inputs to predict growth over a given period. Growth is commonly measured by the specific growth rate (G_M; $g \cdot g^{-1} \cdot day^{-1}$), but this metric declines with mass (M) at a rate that is estimated by the allometric mass exponent (b). Scaling mass by b yields the mass-standardized growth rate (Ω), which controls for mass and thereby enables growth rates to be compared among fish of different sizes.

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Table 1. Data sources used in the meta-analysis of coho salmon growth.

Study code	Source	Water body	Feed	R	T (°C)	Initial mass, M_0 (g)	Period, t (days)	n
A	Bilton et al. 1974	Big Qualicum River, B.C.	Oregon Moist Pellet	0.39–1.66	2.4–16.1	1.0–16.8	14	19
B	Griffioen and Narver 1974	Big Qualicum River, B.C.	Oregon Moist Pellet	0.16–2.70	3.6–9.1	5.0–19.1	27–31	31
C	Larsen et al. 2001	Puget Sound, Wash.	BioDiet Grower Pellet	0.16–1.82	2.5–10.0	18.6–29.9	14–25	9
D	Stauffer 1973	White River, Wash.	Oregon Moist Pellet	0.30–1.10	5.0–12.3	0.5–11.7	30	7
E	Stauffer 1973	Columbia River, Wash.	Oregon Moist Pellet	0.25–1.49	9.7–10.5	2.7–9.7	30	10
F	Stauffer 1973	Big Creek, Oreg.	Oregon Moist Pellet	0.21–0.75	4.9–13.6	2.2–41.2	30	22
G	Stauffer 1973	Klaskanine River, Oreg.	Oregon Moist Pellet	0.42–0.52	9.1–16.1	7.6–14.5	30	3
H	Carline 1968	Unknown, Oreg.	Fly larvae	0.53–1.14	5.9–12.3	0.8–6.8	12–17	7
I	Everson 1973	Tobe Creek, Oreg.	Oregon Moist Pellet	0.34–1.10	11.0–22.3	1.5–2.9	30	18
J	Hutchins 1974	Fall Creek, Oreg.	Fly larvae	0.56–0.80	15.0	2.5–3.8	10–11	3
K	Culp 1972	Unknown, Oreg.	Oregon Moist Pellet	0.71–2.01	12.0–17.0	0.4–10.8	30–40	15

Note: Sample size (n) is the number of growth trials from each study that were used in the analysis ($n_{\text{total}} = 144$). Ration (R) denotes daily grams of food fed to fish per gram of body mass expressed as a fraction of the maximum daily consumption rate. Temperature (T) ranges correspond to those observed among growth trials. Temperature ranges within growth trials were small.

$$G_M = \Omega M^{-b} \tag{1}$$

Estimates of b of 0.31 in brown trout (*Salmo trutta*; Elliott 1975), 0.31 in Atlantic salmon (Elliott and Hurley 1997), and 0.34 in Chinook salmon (Perry et al. 2015) are sufficiently close to suggest that this exponent is similar among salmonids.

Despite having features that are well-suited to ecological analyses, application of the Ratkowsky model has been limited to predicting growth of fish that are putatively feeding near ad libitum levels. Given that food availability may limit growth in many salmonid populations (Amundsen and Gabler 2008; Armstrong and Schindler 2011; Kennedy et al. 2008), the assumption of ad libitum feeding rates is not necessarily reasonable for predicting growth in the wild, but may provide a baseline for drawing useful comparisons. The Ratkowsky model provides several biologically meaningful parameters, such as the maximum growth rate (c) and the temperature at which growth is maximized (T_M), which might be expected to increase with increasing food availability (Brett et al. 1969). Consequently, greater flexibility may be needed to account for variable food availability when applying the Ratkowsky model to ecological studies.

The life history of coho salmon (*O. kisutch*) makes them well-suited to evaluate the effects of temperature on salmonid growth. Coho salmon are considered the most temperature-sensitive species of Pacific salmon (Brett 1952). Because they exhibit thermal stress at temperatures as low as 16 °C, evidence of deleterious effects of temperatures on growth may be evident in ecological data. Moreover, the high fidelity of juvenile coho salmon to thermal and flow refugia during their freshwater phase (Nielsen 1992) indicates they occupy relatively small ranges for extended periods, an attribute conducive to estimating the thermal experience of individual fish based on data collected at local temperature gauges. Although an ample background on growth of captive coho salmon exists, studies to date have largely focused on observations of single populations across limited size and temperature ranges. Hence, a synthesis of this literature is needed to estimate growth parameters for ecological analyses of coho salmon that are robust across populations, sizes, and temperatures.

To develop a general growth model for coho salmon, we conducted a meta-analysis of data gathered from both experimental studies and hatchery trials that monitored growth of juveniles under controlled conditions. A version of the Ratkowsky model parameterized to incorporate allometric growth (Larsson et al. 2005) and variable ration allocations was fit to growth observations from a geographically diverse set of fish populations to estimate broadly applicable growth parameters. Our goal was to develop an analytical tool for predicting growth in the wild with accessible ecological data.

Methods

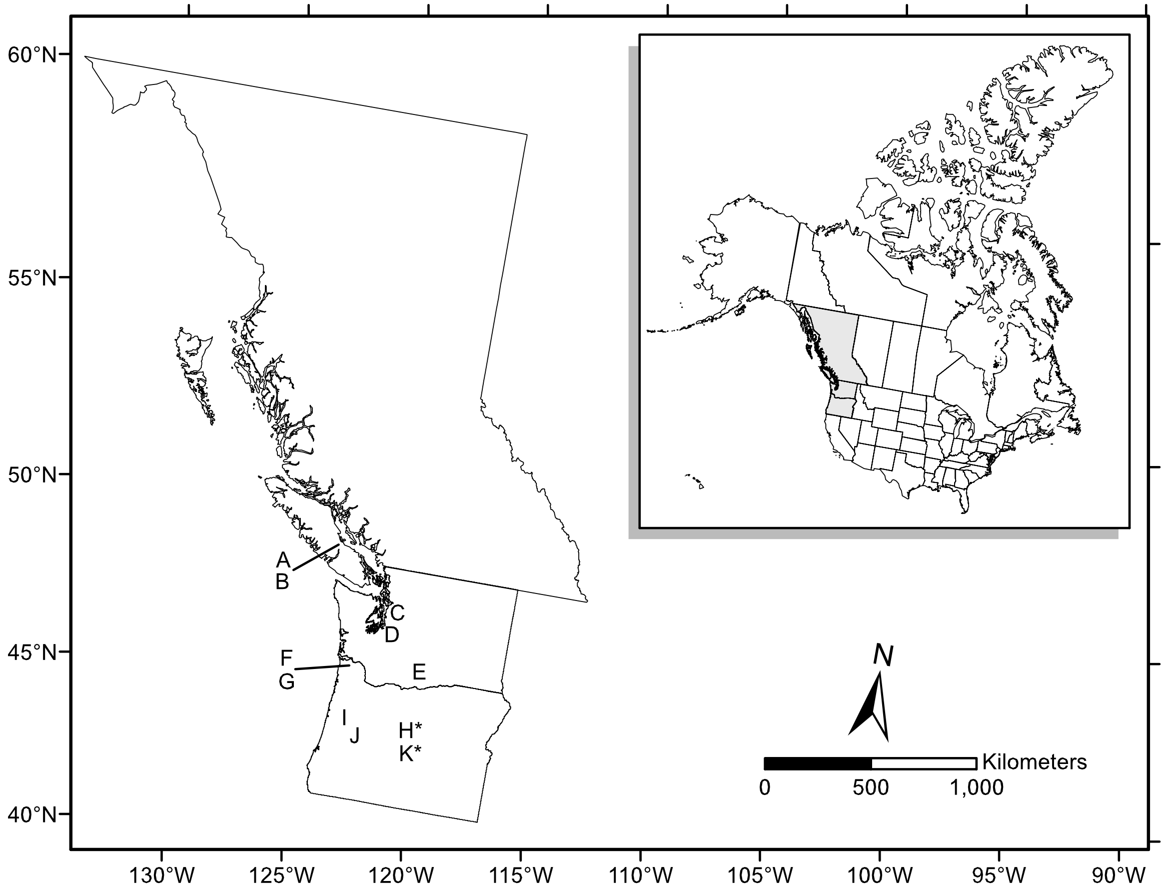
Data sources

A broad literature search was performed to identify studies that documented growth of juvenile coho salmon under controlled conditions. The objectives of the search were to assemble a dataset adequate to (*i*) estimate Ratkowsky model parameters that are broadly applicable to coho salmon, (*ii*) quantify the effect of ration on the growth parameters, and (*iii*) develop an ecologically tractable model for growth of juvenile coho salmon. To meet these objectives, growth data were expected to comprise a wide range of fish masses, rearing temperatures, and ration allocations, and to include fish from geographically diverse sources. We limited our input dataset to studies that documented initial mass (M_0), final mass (M_t) after t days of growth, mean temperature (T), and ration.

The literature search led to the inclusion of growth data (Table 1) from eight different studies conducted with broodstock sources that ranged from Oregon to British Columbia (Fig. 1). Growth data recorded were from tables in published reports (studies A, D–K in Table 1) and were digitized from figures with the package *digitize* (Poisot 2011) in R (R Core Team 2015) when tabular data were not available (studies B and C in Table 1). The data included observations of fish reared at a broad range of masses (0.46–41.20 g) and temperatures (2.4–22.3 °C). While there were large temperature ranges observed among growth trials, temperature ranges within growth trials typically only spanned 1–2 °C.

We evaluated the ecological utility of the growth model by analyzing growth data from wild coho salmon collected at seven different sites in the Klamath Basin, California (Fig. 2). Data were collected as part of a study in which a mark–recapture framework with passive integrated transponder (PIT) tagged fish was used to monitor growth of juveniles in natural tributaries and constructed ponds (Witmore 2014). Fish captured at study sites were tagged and weighed to the nearest 0.1 g before being returned to their habitat. Repeated sampling of sites from July through September in 2012 led to many instances in which an initial mass, M_0, and a mass after t days of growth, M_t, were recorded for an individual tagged fish, thereby providing a basis for computing growth. We limited input data to 335 observations where the growth period ranged between 10 and 50 days and where daily water temperature data were available over the growth period (Table 2). Daily measurements of water temperature in natural tributaries were obtained from surveys conducted by the US Forest Service. Measurements of daily water temperatures in constructed ponds were obtained by data loggers installed near sampling locations (S. Witmore, NOAA, personal communication).

Fig. 1. Sources of fish from hatchery- and laboratory-based studies of juvenile coho salmon growth. Study sources (A–K) correspond to those described in Table 1. Asterisk-marked sources (H and K) were collected from unspecified locations in Oregon. (ESRI 2016, ArcGIS Desktop Release 10.4.1, Environmental Systems Research Institute, Redlands, Calif., USA).



Food availability

There was considerable variability in ration fed to fish in the experimental growth dataset. To incorporate different ration levels into the model framework, we estimated an index of ration relative to the maximum ration. This index was based on Stauffer's (1973) equations for daily ration on a dry mass basis (R_{dry}) and maximum ration ($R_{\max}$). Daily ration was estimated as

$$R_{\mathrm{dry}} = [(1 - m_{\mathrm{d}})/(1 - m_{\mathrm{f}})]R_{\mathrm{wet}} \tag{2}$$

where m_{d} is the moisture content of the diet, m_{f} is the moisture content of fish flesh, and R_{wet} is daily ration on a wet mass basis. The value of m_{f} was assumed to be 75% in each growth trial, based on previous estimates in salmonids (Brett et al. 1969; Phillips 1969). Two brands of commercial foods were used in the selected studies: Oregon Moist Pellets, which were reported to have an m_{d} value of 33% (Crawford and Law 1972), and BioDiet Grower Pellets, which were reported to have an m_{d} value of 16%. Several studies (H–J) provided estimates of R_{dry}, which were used instead of estimates from eq. 2. The maximum ration was estimated as

$$R_{\max} = [-8.82 + 2.51\log_{\mathrm{e}}(1.8T + 32)]\left(0.17M_0^{-0.33}\right) \tag{3}$$

where T is the mean temperature during a feeding period expressed in degrees Celsius, and M_0 is the mass at the beginning of the feeding period. Finally, an index of ration relative to the maximum ration, R, was computed as

$$R = R_{\mathrm{dry}}/R_{\max} \tag{4}$$

Calculations of R (Table 1) indicated that the growth trials from the selected studies encompassed a broad range of rations (0.16–2.70).

Growth parameter estimation

We estimated mass- and temperature-dependent growth parameters by using initial fish mass, M_0, to predict mass after t days of growth, M_t, as follows:

$$M_t = \left(M_0^b + \frac{\Omega bt}{100}\right)^{1/b} \tag{5}$$

where b is the allometric growth exponent and Ω is the mass-standardized growth rate, corresponding to the specific growth rate of a 1 g fish (Ostrovsky 1995). Mass-standardized growth rate was expressed as a function of temperature with a reparameterized version of the Ratkowsky growth model (Forseth et al. 2001; Perry et al. 2015),

$$\Omega = d(T - T_{\mathrm{L}})[1 - \mathrm{e}^{g(T - T_{\mathrm{U}})}] \tag{6}$$

$$T_{\mathrm{U}} = T_{\mathrm{M}} + \frac{\log_{\mathrm{e}}[1 + g(T_{\mathrm{M}} - T_{\mathrm{L}})]}{g} \tag{7}$$

where d and g are shape parameters, T is the mean temperature during the growth period, T_{M} is the temperature at which growth

Fig. 2. Locations of passive integrated transponder tag monitoring sites in the Klamath Basin where growth data were collected from juvenile coho salmon. Monitoring was conducted in four natural tributaries and in three constructed ponds. (ESRI 2016, ArcGIS Desktop Release 10.4.1, Environmental Systems Research Institute, Redlands, Calif., USA). [Colour online.]

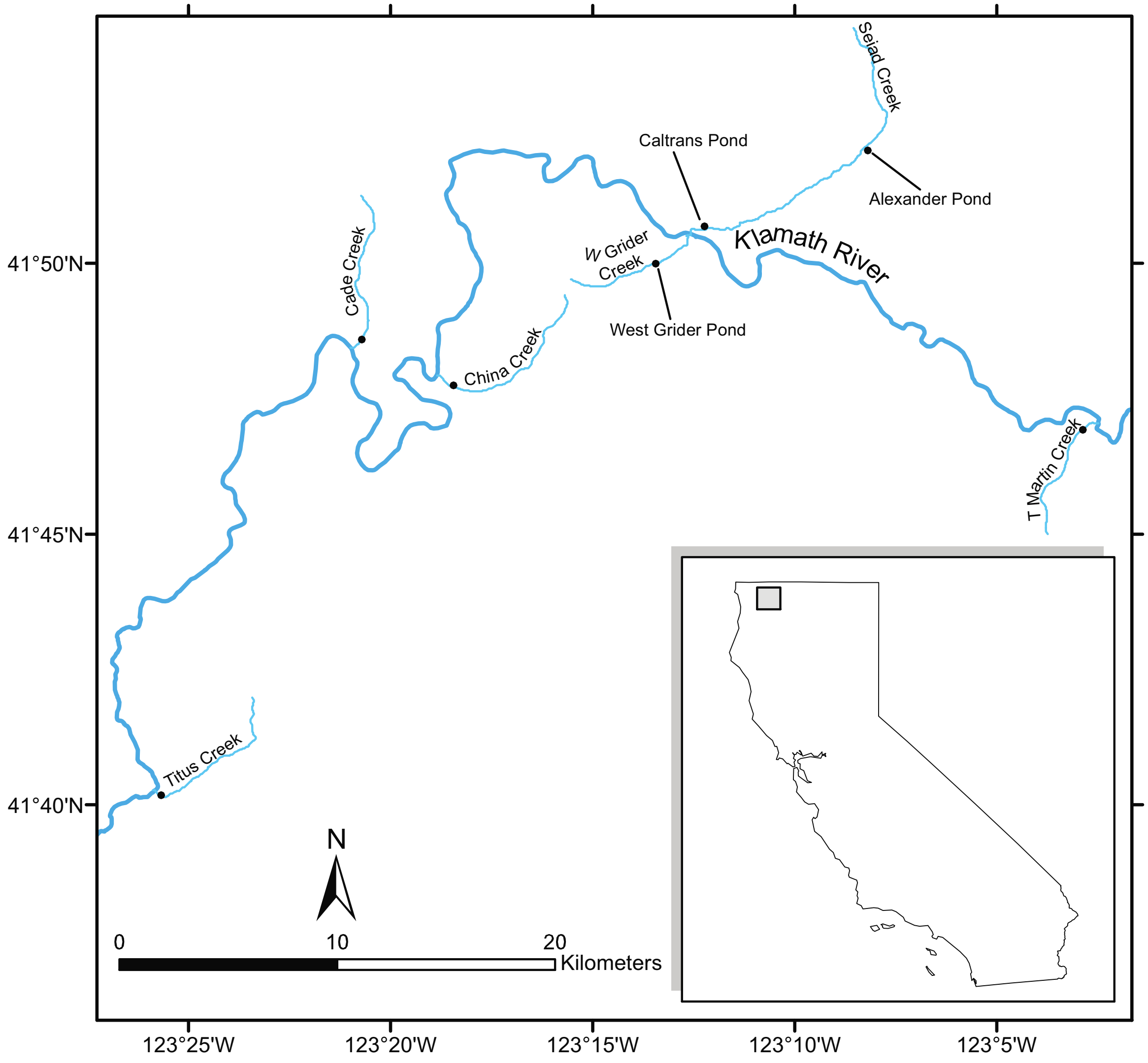


Table 2. Sources of coho salmon growth data used in applying the growth model.

Survey location	Latitude	Longitude	Habitat type	T (°C)	Initial mass M_0 (g)	Period t (days)	n
Alexander Pond	41.869	–123.138	Constructed pond	16.8–17.3	4.1–8.4	12–43	10
Caltrans Pond	41.846	–123.202	Constructed pond	14.1–16.0	2.8–5.7	12–47	70
West Grider Pond	41.834	–123.221	Constructed pond	14.4–14.9	3.5–7.3	13–29	17
Cade Creek	41.813	–123.343	Tributary	14.7–15.5	3.1–7.7	13–42	42
China Creek	41.796	–123.310	Tributary	15.1–16.1	2.1–7.9	13–43	45
Titus Creek	41.670	–123.429	Tributary	14.5–15.1	2.9–9.4	15–49	113
Tom Martin Creek	41.784	–123.045	Tributary	14.3–15.0	3.2–16.6	13–27	38

Note: Growth was monitored at various sites in the Klamath Basin by recapturing passive integrated transponder tagged juveniles. Survey locations included constructed ponds and natural tributaries. Sample size (n) is the number of observations from each study that were used in the analysis ($n_{\mathrm{total}} = 335$).

is maximized, and T_L and T_U are the lower and upper thermal limits, respectively, at which growth rate is zero. Experimental studies of salmonid growth have demonstrated that T_M and T_U change as a function of ration (Brett et al. 1969). Therefore, we reparameterized our growth model to enable these parameters to vary continuously with ration by expressing g and T_M as functions of R.

$$(8) \qquad \begin{aligned} T_{M_j} &= e^{\alpha + \beta_{T_M} \times R_j} \\ g_j &= \beta_g \times R_j \end{aligned}$$

where g_j and T_{M_j} are functions of the ration fed to the jth observation, which were substituted into eq. 7. Preliminary model runs produced minimal evidence of a nonzero intercept for g, and so it was excluded from the function.

Each parameter of the growth model was estimated under a Bayesian framework. Samples from the posterior distribution of each parameter were drawn via Markov chain Monte Carlo, which was implemented in R by using the package *rjags* (Plummer 2016) to call JAGS (Plummer 2003) from R. We assumed that M_t was log-normally distributed (Larsson et al. 2005; Perry et al. 2015).

$$\begin{aligned} & M_t \sim \text{lnN}[\log_e(\hat{M}_t), \tau] \\ & \sigma = \sqrt{1/\tau}; \quad \sigma \sim \text{U}(0, 10) \end{aligned} \tag{9}$$

where $\hat{M}_t$ is the predicted mass after t days of growth, and τ is the inverse of the variance, which was given a vague prior. The prior for the lower thermal limit, T_L, was constrained to biologically realistic boundaries for salmon (Brett 1952).

$$T_\text{L} \sim \text{U}(0, 30) \tag{10}$$

The prior for b was constrained based on similar estimates of this parameter in multiple salmonid species that ranged from 0.31 to 0.34 (Elliott 1975; Elliott and Hurley 1997; Perry et al. 2015), and the prior for d was constrained to a biologically realistic range to improve convergence.

$$b \sim \text{U}(0, 1); \quad d \sim \text{U}(0, 1) \tag{11}$$

Noninformative priors were used for the intercept (α) and slope (β_{T_M}) of T_M. The prior for the slope (β_g) of g was constrained over a biologically realistic range to improve convergence.

$$\begin{aligned} & \alpha \sim \text{N}(0, 1000); \quad \beta_{T_\text{M}} \sim \text{N}(0, 1000) \\ & \beta_g \sim \text{U}(0, 5) \end{aligned} \tag{12}$$

Three separate chains were simulated for the growth model; each chain consisted of 400 000 iterations with a burn-in period of 300 000 and a thinning interval of 20, which reduced autocorrelation among posterior samples. Convergence was confirmed by Gelman–Rubin convergence statistics of $\hat{R} < 1.1$ for all parameters (Gelman and Rubin 1992).

Model application

We evaluated the capacity of our growth model to predict masses of wild coho salmon by analyzing growth data from PIT-tagged juveniles in the Klamath Basin. Mass after t days of growth, M_t, was predicted from the initial mass, M_0, by setting the parameters of the growth model at their posterior means. Because we did not have estimates of food availability at these sites, we estimated R in eq. 8 in the Ratkowsky growth model.

$$R \sim \text{U}(0, 10) \tag{13}$$

where the prior for R was constrained to a biologically realistic range of values. Posterior distributions of R were estimated for each survey location and for each habitat type with Markov chain Monte Carlo as previously described.

Results

By using observations of growth from multiple studies spanning a wide range of experimental conditions, we simultaneously estimated mass-, temperature-, and ration-dependent growth parameters (Table 3). The posterior means of b (0.386, SE = 0.030), d (0.341, SE = 0.048), and T_L (1.287, SE = 0.696) were estimated independent of ration and are therefore broadly applicable to coho salmon. The posterior means of the slopes for the ration-varying parameters, β_g (0.142, SE = 0.025) and β_{T_M} (0.306, SE = 0.095), were positive with minimal posterior density near zero, providing evidence of a positive effect of ration on each of these parameters.

Table 3. Posterior means, standard errors, and 95% Bayesian credible intervals (BCI) of mass-, temperature-, and ration-dependent parameters from the Ratkowsky model of juvenile coho salmon growth.

Parameter	Mean	SE	95% BCI	Sample*
b	0.386	0.030	0.328–0.446	17 000
d	0.341	0.048	0.268–0.453	13 000
β_g	0.142	0.025	0.096–0.194	14 000
T_L	1.287	0.696	0.098–2.658	30 000
α	2.483	0.060	2.361–2.597	6 600
β_{T_M}	0.306	0.095	0.131–0.506	5 700
σ	0.099	0.006	0.088–0.112	19 000

Note: b, allometric growth exponent; d, shape parameter; β_g, slope of shape parameter g; T_L, the lower thermal limit at which growth is zero; α, intercept of T_M; β_{T_M}, slope of T_M; σ, variance of the body mass.

*The effective number of samples is listed for each parameter.

We divided the growth dataset into a high-ration group in which R was ≥0.6 and a low-ration group in which R was <0.6. We then used our model to estimate ration-dependent growth over the range of temperatures in the dataset by setting ration equal to the mean from each of these groups (R_low = 0.43 and R_high = 1.19). Additionally, we estimated growth at an intermediate ration level by setting ration equal to the mean over the entire dataset (R_medium = 0.87). The resulting growth curves indicated that our model produced a good approximation of the expected growth patterns across rations (Fig. 3). In particular, the model accounted for substantial increases in T_M and T_U with ration. The model fit the observed data very well, describing 99% of the total variation in M_t (r^2 = 0.99). Deviations of predicted mass from observed mass exhibited little evidence of a systematic pattern with respect to M_t (Fig. 4). This was supported by a regression of predicted versus observed mass, wherein the intercept did not differ significantly from 0 (b = −0.009, SE = 0.113; P = 0.934) and the slope was close to 1 (β = 1.005, SE = 0.008). We did not observed a latitudinal pattern in model residuals across source populations (Fig. 5).

We applied the growth model to observations of wild coho salmon by fixing the parameters at their posterior means and estimating R for each survey site. Our posterior estimates of R revealed considerable variation in food availability among survey sites (Fig. 6). In particular, there were large differences between habitat types; excluding China Creek, estimates of R in constructed ponds were significantly higher than in tributaries. China Creek was noteworthy in that its estimate of R was nearly four times larger than the next closest tributary.

Discussion

Our analyses estimated mass-, temperature-, and ration-dependent growth parameters that provide new insight into coho salmon growth. Our b estimate of 0.386 was close to the value of 0.333 that has been considered generally applicable to salmonids (Iwama and Tautz 1981), providing further support for the use of a universal allometric mass exponent across salmonids. Our literature search produced an abundance of growth observations at temperatures between 0 and 15 °C, which comprised a wide range of source populations. These data attributes were conducive to obtaining precise and broadly applicable estimates of the lower thermal limit, T_L, in coho salmon. Our T_L estimate of 1.3 °C in fish fed a broad range of rations was similar to an estimate of 1.8 °C in Chinook salmon fed ad libitum (Perry et al. 2015), suggesting that the lower thermal limit is robust across species and ration levels. By contrast, we produced evidence that the optimal temperature for growth, T_M, and the upper thermal limit, T_U, are sensitive to changes in ration. For instance, increasing R from 0.5 to 1.0 re-

Fig. 3. Observed mass-standardized growth rates (Ω) of juvenile coho salmon as a function of temperature and ration. Study codes are indicated by corresponding letters from Table 1. Observations were divided into a low-ration group (blue text) and a high-ration group (red text). Three separate growth curves were estimated with the Ratkowsky model at the mean ration allocation in the low-ration group (solid blue line), the high-ration group (solid red line), and across all data (dashed black line). The dotted grey line depicts ration-dependent changes in the maximum growth rate and the temperature that maximizes growth.

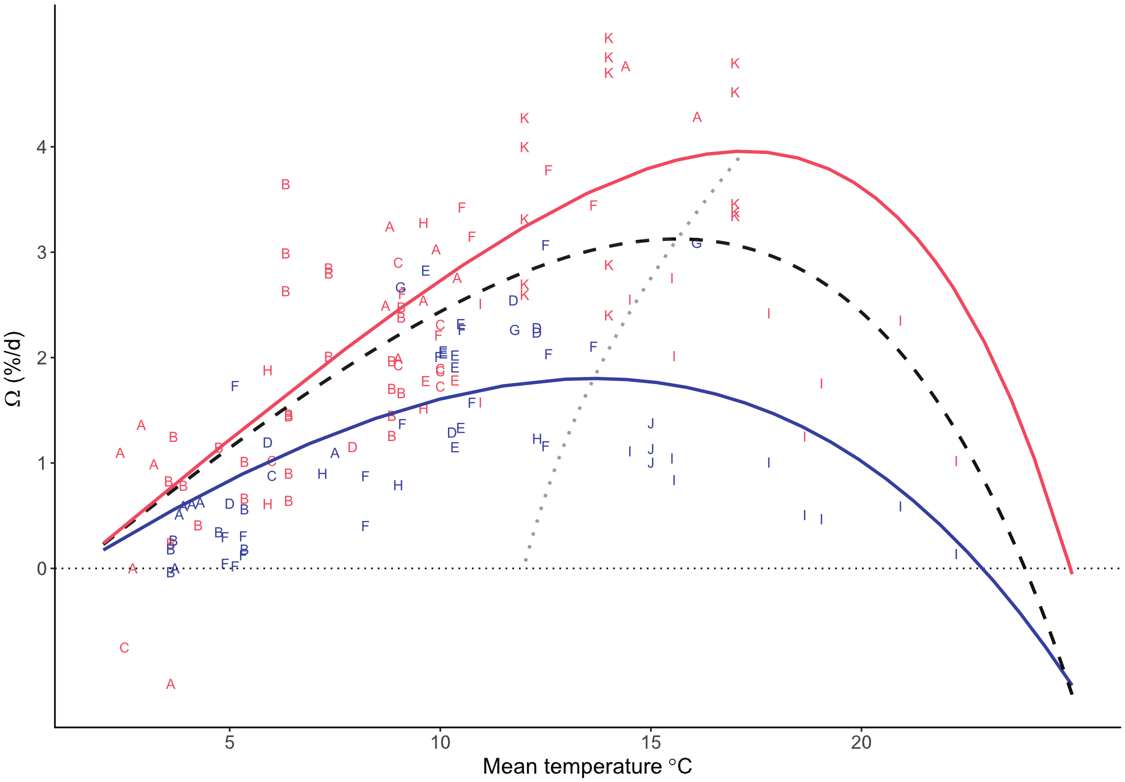
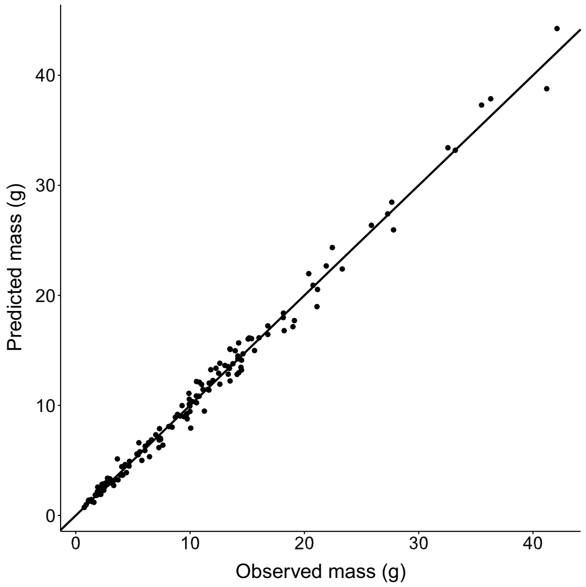


Fig. 4. Mass of juvenile coho salmon, M_t, predicted by the Ratkowsky model versus observed mass, depicted against a 1:1 reference line.



sulted in a 2.3 °C increase in T_M and a 1.3 °C increase in T_U. In comparison with studies that estimated growth parameters at ad libitum, our estimate of T_M at $R = 1.0$ was 16.3 °C, which was considerably lower than estimates of 19.0 °C in Chinook salmon (Perry et al. 2015) and 18.4 °C in Atlantic salmon (Forseth et al. 2001), potentially reflecting adaptation to cooler water in juvenile coho salmon (Brett 1952).

Because of limited data availability, our meta-analysis was confined to a narrower range of source populations than in Perry et al. (2015). In particular, there were no representative populations from the southern end of the geographic range of coho salmon. Growth of juvenile salmon may be locally optimized to temperatures that are characteristic of the average environment that they rear in, which could limit the ability of our model to make inferences outside of the geographic range of the source populations included in our analysis. If there are regional differences in growth, we would expect to observe latitudinal differences in growth rates among source populations. However, Perry et al. (2015) did not observe a latitudinal gradient in residuals across a relatively broad geographic range of source populations (British Columbia to Northern California). That observation, when considered alongside a similar lack of a pattern in residuals in our study (Fig. 5), suggests that latitudinal growth differences were small enough to enable robust model performance across locations. These observations support the utility of our model as a broadly relevant tool for capturing growth in coho salmon, including in populations that are located near the southern end of the species' range.

We demonstrated the ecological utility of our growth model by fitting it to observations of growth in wild coho salmon through the estimation of an index of food availability, R, which scales g and T_M. In the process, we obtained predictions of final mass and habitat-specific estimates of R. Importantly, our model cannot resolve food abundance and quality, and estimates of R therefore encompass both of these of components of nutrition. Nonetheless, R provides a meaningful index of the ability of a habitat to nourish juvenile fish. We observed substantial variation of R

Fig. 5. Distributions of growth model residuals from each study source (bold line within box = median; ends of box = 25th and 75th percentiles; ends of lines = 5th and 95th percentiles). Study source codes correspond to letters from Fig. 1 and are arranged from north to south.

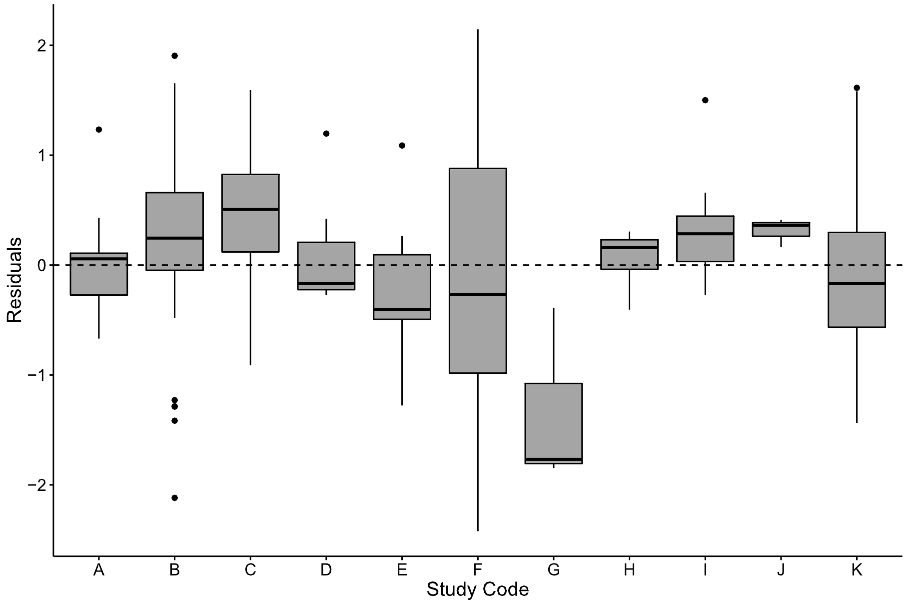
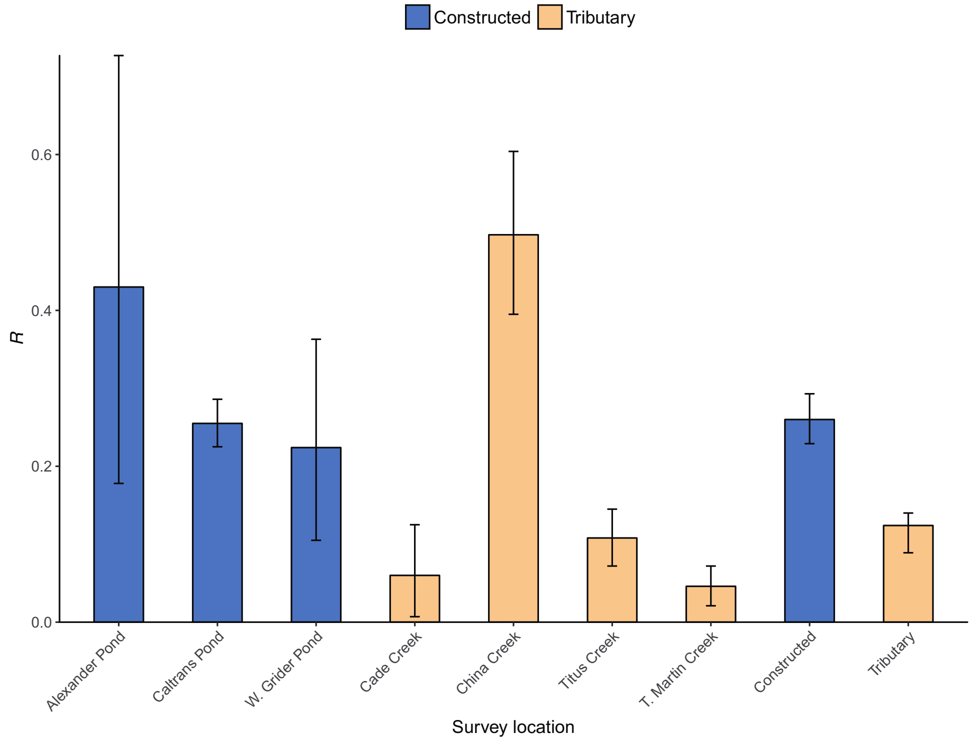


Fig. 6. Estimates of food availability, *R*, in constructed ponds and tributaries of the Klamath Basin where summer growth of passive integrated transponder tagged coho salmon was monitored. Whiskers depict 95% Bayesian credible intervals. [Colour online.]



among survey locations, including significantly higher estimates of *R* in constructed ponds compared with natural tributaries (Fig. 6). Previous analyses of this dataset demonstrated similar variation in growth among survey locations, but found no systematic association with physical habitat characteristics, leaving the possibility that the variation reflected differences in food abundance or quality among habitats (Witmore 2014). In particular, the standing waters in constructed ponds provide prey resources, including mosquito larvae and amphibian eggs, which are not typically present in tributaries and may underlie differences in estimates of *R*. While reduced growth in tributaries may also reflect increased energetic demands of orienting in constant flowing water, the tendency of juvenile coho salmon to locate and remain in low-velocity habitat suggests that this is a less likely explanation for the growth differences between habitat types.

The Wisconsin bioenergetics model has been commonly applied to predict growth in salmon populations (Stewart and Ibarra 1991; Koehler et al. 2006). The Wisconsin model uses consumptive inputs to estimate ration as a proportion of consumption (often referred to as a *P* value) relative to a theoretical maximum consumption ($C_{\max}$) and requires 30 parameters, which are informed from parameter estimates that have been borrowed from multiple species (Stewart et al. 1983; Stewart and Ibarra 1991; Hanson et al. 1997) that were fit by eye to a deterministic equation. In contrast, our formulation of the Ratkowsky model does not require consumptive inputs, requires just six parameters, and has been calibrated to growth data from a particular species. However, our estimates of *R* under the Ratkowsky model are analogous to estimates of the *P* value under the Wisconsin model and provide similar interpretations of the consumptive behavior of fish.

Classic laboratory experiments with sockeye salmon (*Oncorhynchus nerka*) have demonstrated that the range of temperatures that support growth and the optimum temperature for growth both decline with ration, a pattern that likely reflects an increase in the energy intake required for basal metabolism at higher temperatures and a corresponding decrease in the scope for growth (Brett et al. 1969). Our growth model captured this pattern, demonstrating declines with ration of the upper thermal limit, temperature of optimal growth, and maximum growth rate (Fig. 3). By demonstrating ration-dependent growth patterns consistent with Brett's work in growth data from diverse source populations and experimental conditions, we have provided some of the strongest empirical support to date for an interaction between temperature and food availability. Food availability is a critical factor governing the dynamics of fish populations because it is a primary mechanism by which density dependence manifests. Because food availability would be expected to decline with the density of juveniles occupying natural habitats (Rosenfeld et al. 2005), our demonstration of an interaction between temperature and food availability implies than an interaction can exist between temperature and population density. Support for this hypothesis was provided by a study of growth in 13 Chinook salmon populations, which observed a negative interaction between water temperature and population density, thereby demonstrating an intensification of density-dependent effects on growth at higher temperatures (Crozier et al. 2010). This interaction could be integral in shaping the response of fish populations to a warming climate, and it therefore has important implications for the conservation of imperiled populations.

In conclusion, our meta-analysis of a diverse collection of studies and populations produced a broadly applicable set of parameters for estimating mass- and temperature-dependent aspects of growth in juvenile coho salmon. The addition of ration-scaling parameters is unique among applications of growth models to fish and imparts the flexibility to tailor the model to fish populations in the wild. Moreover, our parameterization of the model, wherein temperature and mass are controlled for and ration is estimated, provides a means of estimating indices of food availability in wild populations. By estimating food availability, our model provides valuable information about habitat suitability that is difficult to acquire through sampling.

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