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NOTE

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Abstract

Researchers have cautioned against the borrowing of consumption and growth parameters from other species and life stages in bioenergetics growth models. In particular, the function that dictates temperature dependence in maximum consumption (C_{max}) within the Wisconsin bioenergetics model for Chinook Salmon *Oncorhynchus tshawytscha* produces estimates that are lower than those measured in published laboratory feeding trials. We used published and unpublished data from laboratory feeding trials with subyearling Chinook Salmon from three stocks (Snake, Nechako, and Big Qualicum rivers) to estimate and adjust the model parameters for temperature dependence in C_{max} . The data included growth measures in fish ranging from 1.5 to 7.2 g that were held at temperatures from 14°C to 26°C. Parameters for temperature dependence in C_{max} were estimated based on relative differences in food consumption, and bootstrapping techniques were then used to estimate the error about the parameters. We found that at temperatures between 17°C and 25°C, the current parameter values did not match the observed data, indicating that C_{max} should be shifted by about 4°C relative to the current implementation under the bioenergetics model. We conclude that the adjusted parameters for C_{max} should produce more accurate predictions from the bioenergetics model for subyearling Chinook Salmon.

In fisheries biology, bioenergetics models have become increasingly important as tools for examining the effects of climate change (Mruscia et al. 2009; Pörtner and Peck 2010; Gale et al. 2011; Hasler et al. 2012), predicting the consequences of habitat alterations and restorations (Boughton et al. 2007; Wehrly et al. 2007; Beer and Anderson 2011), better understanding nutritional physiology and toxicology,

evaluating aquaculture systems (Jobling 1994; Dumas et al. 2009), and comparing consumptive behaviors in the wild (Armstrong and Schindler 2011). These models have been parameterized by using empirical data from individual fish or groups of fish across a wide range of species, locations, and life stages (Kitchell et al. 1977; Beauchamp et al. 1989; Stewart and Ibarra 1991; Rand et al. 1993; Railsback and Rose 1999; Tyler and Bolduc 2008). In constructing bioenergetics models, parameters for the population of interest are often borrowed from other species, locations, or life stages due to a lack of data describing the target population. However, the borrowing of parameters may introduce bias into growth or consumption predictions from the models (Ney 1993; Chipps and Wahl 2008; Tyler and Bolduc 2008; Dumas et al. 2009; Van Poorten and Walters 2010). Researchers have also cautioned that parameters derived from older or larger fish may not accurately fit the juvenile stages (Hanson et al. 1997; Tyler and Bolduc 2008). Juvenile fish often have temperature-dependent consumption and growth relationships that differ from those of adults of the same species (Post 1990; King et al. 1999; Schoenbeck et al. 2008; Ohlberger et al. 2012); thus, the borrowing of parameter values from other species or life stages may lead to systematic departures in bioenergetics estimates (Bajer et al. 2004; Trudel et al. 2005).

In bioenergetics models, the purpose of the function for temperature dependence in maximum consumption (C_{max} ; Thornton and Lessem 1978; Hanson et al. 1997) is to scale the food consumed by the fish according to the temperature of the water (and fish). The resulting curve describes the relative change in consumption from the temperature that provides maximum consumption for the given species or life stage.

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Consumption parameters have not been measured for sub-yearling fall Chinook Salmon *Oncorhynchus tshawytscha*; therefore, Stewart and Ibarra (1991), who reported the first bioenergetics model for Chinook Salmon, borrowed consumption parameters from Coho Salmon *O. kisutch*. Furthermore, Stewart and Ibarra (1991) based their temperature-dependent curve for C_{max} on six data points. The C_{max} curve for Coho Salmon peaked at about 16.5°C. Brett et al. (1982) found that subyearlings of both coastal and inland Chinook Salmon stocks exhibited their highest consumption at 20–21°C, which is 3.0–4.5°C higher than the value used by Stewart and Ibarra (1991) for the Chinook Salmon bioenergetics model. Geist et al. (2010) reported optimal growth of Chinook Salmon at about 20°C and also suggested that the peak of the consumption curve might be higher than that currently used in the Wisconsin bioenergetics model for this species.

Given these observations, we were motivated to re-evaluate the temperature-dependent consumption parameters for sub-yearling Chinook Salmon. Our focus was to (1) compile data on temperature-dependent consumption by subyearlings; (2) estimate the parameters (and error) for subyearlings under the Wisconsin bioenergetics model (Thornton and Lessem 1978; Hanson et al. 1997); and (3) compare the adjusted parameters and resultant curve with those currently implemented for the species.

METHODS

Fish Stocks, Laboratory Procedures, and Data Sources

We compiled data from studies conducted in our own laboratory and from published sources that included information about food consumption by sub-yearling Chinook Salmon at different water temperatures (Brett et al. 1982; Yanke 2006).

Snake River stock.—Experiments on Snake River sub-yearling Chinook Salmon obtained as fertilized eggs from Lyons Ferry Hatchery (Washington Department of Fish and Wildlife, Starbuck) were conducted by Yanke (2006) over two consecutive years in our laboratory at the College of Natural Resources, University of Idaho. Sub-yearling fish tested in 2003 (mean initial weight = 7.1 g; $N = 180$ fish/tank) were placed into triplicate tanks for one of three thermal treatments over an 80-d period. The treatments consisted of 30 d of acclimation from an initial temperature of 12°C to a final target temperature ($\pm 1^\circ\text{C}$) of 16°C, 20°C, or 24°C (Table 1; Figure 1). Sub-yearlings tested in 2004 (mean initial weight = 4.2 g; $N = 240$ fish/tank) were subjected to thermal treatments over 42 d and were acclimated over a 21-d period from 14°C to a target temperatures ($\pm 1^\circ\text{C}$) of 16°C, 20°C, or 24°C (triplicate tanks for each treatment). For the 2003 and 2004 experiments, the average rate of increase in temperature was less than 0.4°C per day during the acclimation period and was less than 0.23°C per day over the full duration of the trial.

All fish were fed commercial pellets (BioDiet Grower, Bio-Oregon, Warrenton, Oregon) ad libitum twice daily. The

amount of food consumed each day by each tank of fish was estimated by subtracting the amount of food remaining on the bottom of the tank from the amount of food introduced to the tank during each daily feeding event over the course of the experiment. At the end of each feeding session, the number of uneaten pellets that were present on the bottom of each tank was estimated. To avoid administering small, crumbling feed, the feed was sifted before weighing the rations. Although crumbling feed and other factors can lead to error in consumption estimates, this was unlikely to have been a large source of error in our study because we measured the relative change in food consumption over a range of temperatures (see below). Fish were sampled, weighed, and removed from the tanks for physiological assay on a weekly basis. To account for the changing number of fish (and grams of fish) in each tank and to estimate the total amount of food consumed per gram of fish, we used (1) the daily feeding amount (after accounting for the uneaten portion), (2) the weekly starting and ending fish weights (from the sampled fish that were euthanized for physiological assay), and (3) the daily number of fish in the tank to interpolate over each week the daily amount of food consumed per gram of fish (i.e., g food/g fish).

British Columbia stocks.—Data from Brett et al. (1982) provided details on food consumption, growth, and conversion efficiency for groups of sub-yearling Chinook Salmon (~25–30 fish) that were held in tanks and reared for 28 d at temperatures from 14°C to 24°C. The fish (initial mean weight = 2.9 g) were from a coastal stock (Big Qualicum River) and an upriver stock (Nechako River, a Fraser River tributary) in British Columbia, Canada. Fish of the coastal stock were obtained as eggs from the Big Qualicum River Hatchery. Fish of the upriver stock were captured as sac fry in the wild and were then transported to the laboratory and held in tanks. The two stocks were comparable in size at the beginning of the trials, and all fish were fed Oregon Moist pellets ad libitum three times daily. In the Brett et al. (1982) study, total food consumption was measured by weighing the food provided to the tanks of fish and then subtracting the estimated portion of food that remained uneaten after each feeding.

Estimation of Temperature-Dependent Consumption

We used the consumption function in the Wisconsin bioenergetics model to estimate temperature-dependent consumption: $C = C_{max} \cdot p \cdot f(T)$, where C is the specific consumption rate (g food·g fish⁻¹·d⁻¹), C_{max} is the maximum specific consumption rate at the optimal temperature for consumption, p is the proportion of C_{max} that was consumed, and $f(T)$ is a function of temperature (T) that scales C relative to C_{max} . The form of $f(T)$ used in the Chinook Salmon bioenergetics model was given by Thornton and Lessem (1978) as $f(T) = K_A \cdot K_B$, where K_A and K_B are values resulting from two logistic equations (representing the increasing and decreasing portions of the curve).

TABLE 1. Mean tank temperature, initial weight, and total food consumed by subyearling Chinook Salmon in laboratory studies (river of origin, length of the feeding trial at constant temperature, and source for each data set are provided). Ranged consumption values were calculated from dry weights during the Brett et al. (1982) studies and from wet weights during the experiments at the University of Idaho (Yanke 2006).

Mean temperature (°C)	Mean initial weight (g)	Total consumption (g)	Total consumption (g food/g fish)	Ranged consumption
Big Qualicum River Stock, 28 d (Brett et al. 1982)				
24.8	3.2	32.1	0.336	0.292
23.9	3.2	70.0	0.727	0.630
24.0	3.4	69.4	0.674	0.584
23.0	3.2	85.3	0.900	0.780
22.0	3.3	101.4	1.012	0.877
21.8	3.3	100.8	1.006	0.872
20.9	3.4	116.0	1.154	1.000
19.9	3.2	108.3	1.114	0.965
19.9	3.1	107.5	1.141	0.989
19.0	3.3	100.5	1.015	0.880
18.1	3.3	111.5	1.130	0.979
16.0	3.3	88.5	0.902	0.782
13.9	3.4	90.5	0.900	0.780
Nechako River Stock, 28 d (Brett et al. 1982)				
23.9	2.1	58.1	0.927	0.682
23.7	2.5	65.2	0.876	0.645
23.0	2.5	83.2	1.114	0.820
21.9	2.6	90.2	1.174	0.865
21.8	2.5	91.7	1.233	0.908
21.0	2.3	93.7	1.358	1.000
20.0	2.5	94.9	1.286	0.947
19.9	2.6	85.1	1.074	0.791
19.0	2.3	90.6	1.325	0.975
15.9	2.3	90.3	1.303	0.960
Snake River Stock, 21 d (University of Idaho, Yanke 2006)				
23.7	8.7	511.3	0.300	0.581
19.4	8.4	993.9	0.517	1.000
19.4	8.5	816.1	0.429	0.830
23.7	7.6	624.6	0.370	0.715
19.4	8.3	714.4	0.364	0.705
15.4	7.8	747.3	0.411	0.796
15.4	8.2	809.7	0.426	0.824
23.7	8.7	716.8	0.387	0.750
15.4	7.8	753.6	0.422	0.818
Snake River Stock, 46 d (University of Idaho, Yanke 2006)				
23.9	14.6	1,240	0.494	0.448
19.9	16.2	3,790	0.951	0.863
19.9	16.1	4,006.8	1.084	0.984
23.9	14.7	1,177	0.560	0.508
19.9	16.7	4,170	1.049	0.952
16.0	14.6	3,730	1.102	1.000
16.0	16.6	3,956	0.963	0.874
23.9	14.8	1,175	0.462	0.420
16.0	16.7	3,858	1.015	0.921

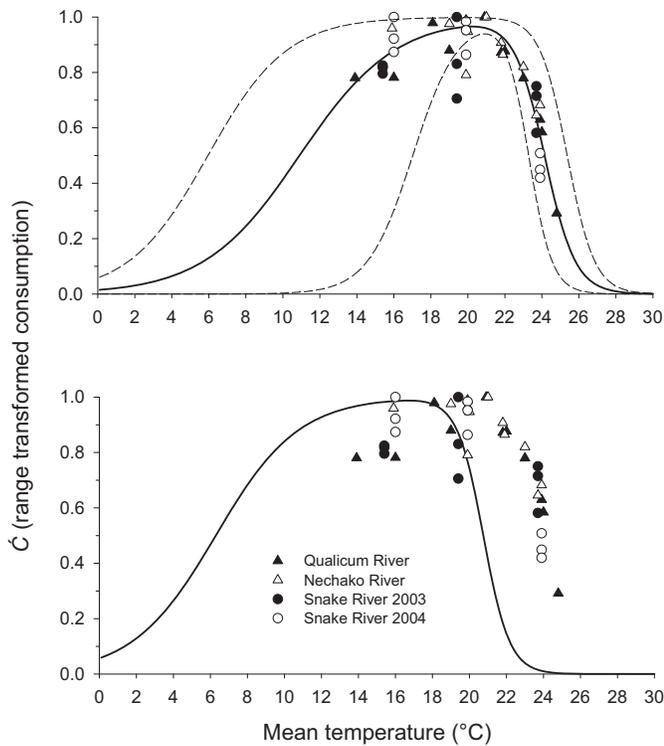


FIGURE 1. Adjusted (upper panel) and unadjusted (lower panel) temperature-dependent consumption curves for Chinook Salmon based on the Thornton and Lessem (1978) equation and the coefficients provided in Table 2. Individual plots of the proportion of maximum food consumption in relation to mean water temperature are provided for data from laboratory trials by Brett et al. (1982) for the Big Qualicum River and Nechako River stocks and from University of Idaho laboratory trials with Snake River stocks (Yanke 2006). Dashed lines in the upper panel represent the bootstrapped 95% confidence bounds for the adjusted consumption curve.

Following the notation of Hanson et al. (1997), K_A and K_B can be expressed as

$$K_A = \frac{CK1 \cdot L1}{1 + [CK1 \cdot (L1 - 1)]},$$

where $L1 = e^{[G1 \cdot (T - CQ)]}$, with

$$G1 = \frac{1}{CTO - CQ} \cdot \log_e \left[\frac{0.98 \cdot (1 - CK1)}{CK1 \cdot 0.02} \right];$$

and

$$K_B = \frac{CK4 \cdot L2}{1 + [CK4 \cdot (L2 - 1)]},$$

where $L2 = e^{[G2 \cdot (CTL - T)]}$, with

$$G2 = \frac{1}{CTL - CTM} \log_e \left[\frac{0.98(1 - CK4)}{CK4 \cdot 0.02} \right].$$

In these relationships, T is water temperature. For the increasing portion of the curve, CQ is the lower water temperature at which temperature dependence is a small fraction ($CK1$) of

the maximum rate, and CTO is the water temperature corresponding to 0.98 of C_{max} . Similarly, for the decreasing portion of the curve, CTM is defined as the water temperature at which dependence is still 0.98 of the maximum, and CTL is the temperature at which dependence is some reduced fraction ($CK4$) of the maximum.

We used the food consumption data from Brett et al. (1982) and the data collected during the laboratory studies by Yanke (2006) to estimate the six consumption-dependent parameters used by Thornton and Lessem (1978; Tables 1, 2). Consumption data for the j th tank or treatment group of tanks within an experiment were transformed to a scale ranging from 0 to 1 as

$$\hat{C} = \frac{C_{tot, ij}}{\max(C_{tot, ij})},$$

where $C_{tot, ij}$ is the total amount of food eaten during the i th study by the j th tank or treatment group over a growth period (Legendre and Legendre 1998). Thus, when $\hat{C} = 1$, then $C_{tot, ij}$ equals $\max(C_{tot, ij})$. Consumption data from Brett et al. (1982) were collected under fairly constant temperatures. To maintain comparability among studies and to fulfill the assumption of a fixed x -axis, we used only the consumption data from periods when temperatures were constant and within 1°C of the experimental target temperature (days 34–80 in 2003; days 21–42 in 2004). These \hat{C} -values and the associated mean tank temperatures were used to estimate the Thornton and Lessem (1978) parameters by minimizing the sum of the squared deviations. To provide a measure of uncertainty about the parameter values, we bootstrapped the residuals about the fitted line, and we then used the percentile method to obtain the 95% confidence limits (CLs) for the parameter values (Efron and Tibshirani 1993).

RESULTS

The amount of food consumed varied among tanks and among studies, largely due to differences in the growth period length, fish size variation, and number of experimental fish (Table 1). For example, the total amount of food eaten (g) over the 28-d studies by Brett et al. (1982) ranged from 32.1 to 116 g for the Big Qualicum River stock and from 58.1 to 94.9 g for the Nechako River stock. The amount of food consumed by the Snake River stocks ranged from 511 to 994 g over the 21-d feeding trial at our laboratory and from 1,175 to 4,007 g over the 46-d feeding trial. The mean daily temperature at which food consumption was maximum was about 20.9°C for the Big Qualicum River fish and 21.0°C for the Nechako River fish (Brett et al. 1982). During the Yanke (2006) experiments, consumption ($\text{g food} \cdot \text{g fish}^{-1} \cdot \text{d}^{-1}$) was maximized at mean temperatures of 16 – 20°C , although consumption was measured at only three temperatures.

Parameter estimates from fitting $f(T)$ to the consumption data supported a shift in consumption toward higher

TABLE 2. Parameter values (with bootstrapped 95% confidence limits in parentheses) estimated for the Thornton and Lessem (1978) multiplier used to determine thermal dependence in maximum consumption (C_{max}) within the Wisconsin bioenergetics model for Chinook Salmon.

Symbol	Parameter description	Unadjusted value	Adjusted value
CQ	Lower temperature ($^{\circ}\text{C}$) for C_{max}	5	4.97 (0.74, 14.12)
CTO	Optimum temperature ($^{\circ}\text{C}$) for C_{max}	15	20.93 (14.3, 21.8)
CTM	Maximum temperature ($^{\circ}\text{C}$) for C_{max}	18	20.93 (20.86, 22.48)
CTL	Upper temperature ($^{\circ}\text{C}$) for C_{max}	24	24.05 (23.9, 25.17)
CK1	Proportion of C_{max} at CQ	0.36	0.09 (0.08, 0.09)
CK4	Proportion of C_{max} at CTL	0.01	0.53 (0.28, 0.57)

temperatures than are currently specified in the bioenergetics model for Chinook Salmon (Table 2; Figure 1). The unadjusted model specified C_{max} at 16.5°C (i.e., $[\text{CTO} + \text{CTM}]/2$), whereas the adjusted parameter values resulted in an estimated C_{max} of 20.9°C (lower, upper 95% CLs = 18.2°C , 21.8°C). Thus, there was a 4.4°C difference between models; this difference was consistent over the temperature range, although we had little data with which to inform $f(T)$ at low temperatures. Although optimum consumption was measured at higher temperatures than previously estimated, the curve for optimum temperatures was relatively flat from about 12°C to 21°C . Consequently, the adjusted and unadjusted models produced similar estimates of \dot{C} over a wide swath of the thermal range, indicating the existence of a relatively wide range in temperatures that permit consumption rates similar to consumption at the optimum temperature. Nonetheless, the estimated curve for \dot{C} more closely followed the observed data than did $f(T)$ from the unadjusted model; in particular, the unadjusted model produced \dot{C} -estimates that were increasingly inaccurate as temperatures went beyond near-optimum temperatures. The unadjusted model resulted in an r^2 of 0.24 and residuals that were heterogeneous over the predicted range, whereas the adjusted model had an r^2 of 0.77 and homogeneous residuals over the predicted range. These findings clearly support that (1) the adjusted model provides a better fit to the data than does the unadjusted model; and (2) C_{max} for subyearlings occurs at higher temperatures than currently implemented under the Wisconsin bioenergetics model for Chinook Salmon.

DISCUSSION

Our re-evaluation of the parameters from Thornton and Lessem (1978) should improve consumption and growth estimates when the Wisconsin bioenergetics model is used in application to juvenile Chinook Salmon. The unadjusted parameters that were developed by Stewart and Ibarra (1991) for Chinook Salmon used lower optimal temperatures in the thermal multiplier equation for C_{max} (Thornton and Lessem 1978). We found that adjustments in the thermal multiplier parameters better accounted for the effect of temperature on C_{max} across the range of rearing temperatures for which we had data. We acknowledge that all of the fish in these

experiments were fed high-energy, easily digestible diets, which potentially influenced our results. However, if our findings on juvenile feeding behavior at specific temperatures in the laboratory are at all comparable to performance in the natural environment, the use of our adjusted model parameters should produce better estimates of consumption and growth for juvenile fall Chinook Salmon (Koehler et al. 2006; Armstrong and Schindler 2011). This may be especially important at the upper end of the thermal range, where the effects of temperature on consumption are acute (Brett et al. 1982; Stewart and Ibarra 1991).

Given the paucity of data collected with the specific intent to measure temperature dependence in C_{max} for subyearling Chinook Salmon and given the difficulty in evaluating and obtaining these key bioenergetics model parameters (Chippis and Wahl 2008), we believe that the model predictions can be improved for subyearling Chinook Salmon by applying the adjustments. The unadjusted parameters of the Wisconsin bioenergetics model were developed without using consumption data from Chinook Salmon, thus likely influencing the variable performance of this model (Madenjian et al. 2004; Chippis and Wahl 2008). The unadjusted parameter values for temperature dependence in C_{max} were calibrated by Beauchamp et al. (1989) for Sockeye Salmon *O. nerka*. Stewart and Ibarra (1991) later evaluated the Beauchamp et al. (1989) calibration by using food consumption data from Coho Salmon (Edsall et al. 1974, 1999; Stewart 1980; Stewart et al. 1983) but not from Chinook Salmon. Therefore, use of existing data to re-parameterize the Thornton and Lessem (1978) model for C_{max} provided a relatively inexpensive opportunity to evaluate and improve a submodel of the Wisconsin bioenergetics model over a wide range of conditions that are known to be important for fish consumption and, in turn, growth.

The early life stage and smaller fish sizes examined in this study likely influenced our results. Madenjian et al. (2004) found good agreement between observed values and predicted values from the unadjusted bioenergetics model for Chinook Salmon, suggesting an appropriate function for C_{max} . However, those authors conducted their laboratory evaluation using much larger Chinook Salmon (>400 g) that were fed natural food (i.e., Alewives *Alosa pseudoharengus*) rather than pelleted feed and that were reared at a cooler and narrower

temperature range (10.7–13.0°C) than we evaluated. Sauter et al. (2001) experimentally showed that the thermal preference of subyearling fall Chinook Salmon from the lower Columbia River decreased from about 18°C to 11°C as smoltification progressed, indicating that optimal temperatures for consumption and growth may also decline as the fish mature and prepare for ocean entry. In a study of fall Chinook Salmon subyearlings from the lower Columbia River, Banks et al. (1971) demonstrated a shift in the thermal growth curve toward cooler temperatures with greater fish size, which also supports the occurrence of C_{max} at lower temperatures as fish grow. It seems reasonable that the optimal temperatures for consumption and growth in fall Chinook Salmon would have evolved to decline and become more similar to those of other salmon stocks (e.g., stream-type Chinook Salmon) and species (e.g., Coho Salmon and Sockeye Salmon) as the fish mature and approach the time of ocean entry. Temperatures that are experienced by adults in the ocean would be more homogeneous and similar among species relative to the temperatures experienced by juveniles in freshwater habitats (e.g., inland headwater streams and lakes versus lower main-stem rivers and estuaries). Our estimates are very similar to those currently used in the Wisconsin bioenergetics model for steelhead *O. mykiss*, which tend to have longer periods of stream residence (1–7 years; Pevan et al. 1994) than Chinook Salmon (<2 years). Killen et al. (2010) reviewed resting metabolic rates for 89 teleost species and found that intraspecific scaling of metabolic rate varied with spatial habitat as well as temperature. The unadjusted model parameters for C_{max} may be more appropriate for adult Chinook Salmon, whereas our adjusted parameters may be more universally applicable to juvenile Chinook Salmon irrespective of whether the fish originated from inland versus coastal rivers (e.g., lower Snake River versus Big Qualicum River) or, perhaps, northern versus southern portions of the species' range (e.g., Nechako River versus the Sacramento and San Joaquin rivers, California; Brett et al. 1982; Kjelson et al. 1982; Myrick and Cech 2004).

The validity of parameter adjustments could be improved by conducting further a priori laboratory tests that are designed to calibrate and corroborate the model parameters, especially CQ, which is the parameter for consumption at the lower end of the thermal range (<10°C). Given the post hoc nature of our analysis, we believe our simple approach and adjustment of the parameter values were prudent and were sufficient to test the hypothesis that subyearling fall Chinook Salmon exhibit higher consumption at higher temperatures than previously believed. Trends in consumption and growth follow one another over the range in temperature, but the peak temperatures for consumption are typically about 1.0–1.5°C higher than the peak temperatures for growth (Brett et al. 1982; Forseth et al. 2001). Perry et al. (2015, this issue) measured peak growth at 19°C for subyearling Chinook Salmon across nine populations, two of which were used in this study. Therefore, we measured a peak temperature for C_{max} (20.9°C) that was

within expectations from other studies that have evaluated consumption and growth in other salmonids over a range of temperatures (Forseth et al. 2001).

Our analysis identifies and potentially provides correction for a systematic consumption-dependent error in the Wisconsin bioenergetics model for juvenile Chinook Salmon. Bajer et al. (2004) found that systematic consumption-dependent errors were widespread in bioenergetics models, and Trudel et al. (2005) indicated that improvements could be made to the energy density–mass equations in the Wisconsin bioenergetics model for juvenile Chinook Salmon. Improvements in bioenergetics model output (i.e., between the current and adjusted parameters) are unlikely to be apparent over much of the central portion of the temperature range, where the two functions overlap (Figure 1). However, improvements should be most apparent at the upper end of the thermal range, which may be important for researchers using bioenergetics models to assess the effects of climate change on fish consumption and growth. Our study results suggest that at a minimum, the Wisconsin bioenergetics model for Chinook Salmon should be revisited before predicting juvenile growth and consumption at the upper end of the thermal range, where changes in consumption and growth are most rapid.

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