



Re-estimating temperature-dependent consumption parameters in bioenergetics models for juvenile Chinook salmon

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2 juvenile Chinook salmon

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22 **ABSTRACT**

23 Researchers have cautioned against the borrowing of consumption and growth parameters from
24 other species and life stages in bioenergetics growth model projections. In particular,
25 temperature dependent consumption in the Wisconsin bioenergetics model for Chinook salmon
26 *Oncorhynchus tshawytscha* produced estimates of maximum consumption (C_{\max}) at lower
27 temperatures than measured in published laboratory feeding trails. In this paper we used
28 published and unpublished data from laboratory feeding trials for three stocks of subyearling
29 Chinook salmon: the Snake/Columbia River, the Nechako/Fraser River, and the Big Qualicum
30 River to estimate and adjust parameters for temperature dependence in C_{\max} used in the
31 Wisconsin bioenergetics model. Our data included growth measures from fish ranging from 1.5
32 to 7.2 g, and at temperatures that ranged from 14 to 26°C. We estimated parameters for
33 temperature dependence in C_{\max} based on relative differences in food consumption and then used
34 bootstrapping techniques to estimate the error about the parameters. We found that the current
35 parameter values miss-estimated the observed data at temperatures between 17 and 25 °C,
36 confirming that the C_{\max} should be shifted by about 4°C relative to the current implementation
37 under the bioenergetics model. We conclude the adjusted parameters for C_{\max} should produce
38 more accurate predictions from the bioenergetics model for subyearling Chinook salmon.

39

40 INTRODUCTION

41 Bioenergetics models have become increasingly important tools in fisheries biology to examine
42 the effects of climate change (Mruscia et al. 2009; Pörtner and Peck 2010; Gale et al. 2011;
43 Hasler et al. 2012), predict the consequences of habitat alterations and restorations (Boughton et
44 al. 2007; Wehrly et al. 2007; Beer and Anderson 2011), better understand nutritional physiology
45 and toxicology, evaluate aquaculture systems (Jobling 1994; Dumas et al. 2009), and compare
46 consumptive behaviors in the wild (Armstrong and Schindler 2011). These models have been
47 parameterized using empirical data from individuals or groups of fish across a wide range of
48 species, locations, and life stages (Kitchell et al. 1977; Beauchamp et al. 1989; Stewart and
49 Ibarra 1991; Rand et al. 1993; Railsback and Rose 1999; Tyler and Bolduc 2008). In
50 constructing bioenergetics models, parameters for the population of interest are often borrowed
51 from other species, locations, or life stages due to lack of data about the target population.
52 However, such borrowing of parameters may introduce bias into growth or consumption
53 predictions from bioenergetics models (Ney 1993; Chipps and Wahl 2008; Tyler and Bolduc
54 2008; Dumas et al. 2009; Van Poorten and Walters 2010). Researchers have also cautioned that
55 parameters derived from older or larger fish may not accurately fit juvenile stages (Hanson et al.
56 1997; Tyler and Bolduck 2008). Juvenile fish often have different temperature-dependent
57 consumption and growth relationships compared to adults of the same species (Post 1990; King
58 et al. 1999; Schoenbeck et al. 2008; Ohlberger et al. 2012), and thus borrowing parameter values
59 from other species or life stages may lead to systematic departures in bioenergetics estimates
60 (Bajer et al. 2004; Trudel et al. 2005).

61 In bioenergetics models, the purpose of the function for temperature dependence in
62 maximum consumption (C_{\max} ; Thornton and Lessem 1978; Hanson et al. 1997) is to scale the

63 food consumed by the fish according to the temperature of the fish. The function provides a
64 curve that describes the relative change in consumption from the temperature providing
65 maximum consumption for the given species or life stage. Consumption parameters have not
66 been measured for subyearling Fall Chinook Salmon; therefore, Stewart and Ibarra (1991), who
67 first published the bioenergetics model for Chinook Salmon, borrowed consumption parameters
68 from coho salmon, *O. kisutch*. Furthermore, the authors based their temperature-dependent
69 curve for C_{\max} on six data points. The maximum consumption curve for coho salmon peaked at
70 about 17°C. Brett et al. (1982) found that both coastal and inland stocks of subyearling Chinook
71 salmon exhibited their highest consumption at 20-21°C — 3-4°C higher than used in the Stewart
72 and Ibarra (1991) bioenergetics model for Chinook salmon. Geist et al. (2010) reported optimal
73 growth at about 20°C, and also suggested that the peak of the consumption curve for Chinook
74 salmon might be higher than currently used in bioenergetics model for Chinook salmon. These
75 findings suggest that C_{\max} peaks at higher temperatures than currently implemented in the
76 bioenergetics model for Chinook salmon.

77 Given these observations, we were motivated to re-evaluate the temperature dependent
78 consumption parameters for subyearling Chinook salmon. Our focus was to: 1) compile data on
79 temperature-dependent consumption for subyearling Chinook salmon, and 2) estimate the
80 parameters (and error) for subyearling Chinook salmon under the Wisconsin bioenergetics model
81 (Thornton and Lessem 1978; Hanson et al. 1997), and 3) compare these results to the
82 relationship currently implemented for the species.

83

84 **METHODS**

85

86 We compiled data laboratory studies conducted in our own laboratory, and from published

87 sources that included information about food consumption by subyearling Chinook salmon at
88 different water temperatures (Brett et al. 1982; Yanke 2006).

89
90 Fish Stocks, Laboratory Procedures, and Data Sources

91
92 *Snake River stock* — We conducted laboratory experiments on Snake River subyearling
93 Chinook salmon obtained as fertilized eggs from Lyons Ferry hatchery (Washington Department
94 of Fish and Wildlife, Starbuck, Washington). Experiments were conducted in the fisheries
95 laboratory of the College of Natural Resources over two consecutive years (Yanke 2006).
96 Subyearling fish tested in 2003 (mean initial weight = 7.1 g; $N = 180$ fish/tank) were placed into
97 triplicate tanks for one of three thermal treatments over an 80-d period. The treatments consisted
98 of a 30-d period of acclimation from an initial temperature of 12°C to final target temperatures
99 within 1°C of 16°C, 20°C, or 24°C (Table 1 and Figure 1). Subyearlings tested over 42 d in
100 2004 (mean initial weight = 4.2 g) and were acclimated over a 21 d period from 14°C to target
101 temperatures within 1°C of 16°C, 20°C, and 24°C ($N = 240$ fish per tank; triplicate tanks for
102 each treatment). The average rates of increase in temperature during the acclimation periods
103 over the 2003 and 2004 experiments was < 0.4 °C/d, and were < 0.23 °C/d over the full duration.

104 All fish were fed commercial pellets (Bio Diet Grower, Bio-Oregon, Warrenton, Oregon)
105 *ad libitum* twice daily. The daily food consumed by each tank of fish, was estimated by
106 subtracting the amount of food remaining on the bottom of each tank from the amount of food
107 introduced to each tank on each daily feeding event over the course of our experiments. Because
108 fish were sampled and removed from the tanks for physiological assay on a weekly basis, the
109 changing numbers of fish (and grams of fish) in the tanks had to be accounted for in our estimate
110 of the total food consumed. So, we used (1) the daily feeding amount (after accounting for the
111 uneaten portion), (2) the weekly starting and ending fish weights (from the sampled fish taken

112 for physiological assay), and (3) the daily numbers of fish in the tanks to interpolate over each
113 week the daily amount of food consumed (g) for each tank per gram of fish (i.e., g/g).

114 *British Columbia Stocks*) — Data from Brett et al. (1982) provided details on food
115 consumption, growth, and conversion efficiency for groups of (~25-30 fish) subyearling Chinook
116 salmon held in tanks and reared in temperatures from 14 to 24°C for 28 d. The salmon tested
117 (initial mean weight = 2.9 g) were from coastal and upriver stocks in British Columbia, Canada.
118 The coastal stock was obtained from the Big Qualicum River hatchery as eggs. Fish from the
119 Nechako River stock (tributary to the Fraser River) were captured as sac fry, transported to their
120 lab and held in tanks. Both stocks were comparable in size at the beginning of trials, and all fish
121 were fed Oregon Moist pellets *ad libitum* three times daily. In their study, the total food
122 consumption was measured by weighing the food provided to the tanks of fish and subtracting
123 the estimated uneaten portions after each feeding.

124

125 Estimating Temperature-Dependent Consumption

126 We used the consumption function in the Wisconsin model: $C = C_{\max} \cdot p(C_{\max}) \cdot f(T)$, where C is
127 the specific consumption rate in grams of food consumed per gram of fish per day, C_{\max} is the
128 maximum specific consumption rate at the optimal temperature for consumption, $p(C_{\max})$ is the
129 proportion of C_{\max} that was consumed, and $f(T)$ is a function of temperature (T) that scales C
130 relative to consumption at the temperature where consumption is at the maximum, C_{\max} . The
131 form of $f(T)$ used in the Chinook bioenergetics model is given by Thornton and Lessem (1978):
132 $f(T) = K_A \cdot K_B$ where K_A and K_B are values resulting from two logistic equations (one increasing
133 and one decreasing).

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

$$135 \quad K_A = (CK1 \cdot LI) / (1 + CK1 \cdot (LI - 1))$$

$$136 \quad LI = e^{(G1 \cdot (T - CQ))}$$

$$137 \quad G1 = (1 / (CTO - CQ)) \cdot \ln((0.98 \cdot (1 - CK1)) / (CK1 \cdot 0.02))$$

$$138 \quad K_B = (CK4 \cdot L2) / (1 + CK4 \cdot (L2 - 1))$$

$$139 \quad L2 = e^{(G2 \cdot (CTL - T))}$$

$$140 \quad G2 = (1 / (CTL - CTM)) \cdot \ln((0.98 \cdot (1 - CK4)) / (CK4 \cdot 0.02))$$

141

142 In these relationships T is the water temperature. For the increasing portion of the curve; CQ is
 143 the lower water temperature at which temperature dependence is a small fraction ($CK1$) of the
 144 maximum consumption rate; and CTO is the water temperature that is 0.98 of the maximum
 145 consumption rate. Similarly, for the decreasing portion of the curve, CTM is defined as the water
 146 temperature at which dependence is still 0.98 of the maximum, and CTL is the temperature at
 147 which dependence is some reduced fraction ($CK4$) of the maximum consumption rate. Please
 148 see Thornton and Lessem (1978) for greater detail on the general construct of this model for
 149 biological rates.

150 We used the food consumption data provided by Brett et al. (1982) and collected during
 151 our laboratory studies to estimate the six consumption-dependent parameters used by Thornton
 152 and Lessem (1978) (Tables 1 and 2). Consumption data for the j th tank or treatment group of
 153 tanks within an experiment were transformed to a scale ranging from 0 to 1 as $\hat{C} = C_{totij} /$
 154 $\max(C_{totij})$ where C_{totij} is the total amount food eaten during the i th study by the j th tank or
 155 treatment group over a growth period (Legendre and Legendre 1998). Thus when $\hat{C} = 1$ then
 156 $C_{totij} = \max(C_{totij})$. Consumption data collected by Brett et al. (1982) were collected under fairly
 157 constant temperatures. To maintain comparability among studies and fulfill the assumption of a

158 fixed x -axis, we used only the consumption data when temperatures were constant and within
159 1°C of the experimental target temperature (day 34 to 80 in 2003 and day 21 to 42 in 2004).
160 These \dot{C} values and the associated mean tank temperatures were used to estimate the Thornton
161 and Lessem (1978) parameters. To provide a measure of uncertainty about the parameter values
162 we bootstrapped the residuals about the fitted line, and used the percentile method to obtain the
163 95% confidence limits (CL) about the parameter values (Efron and Tibsharini 1993).

164

165 RESULTS

166 The amount of food consumed varied among tanks and studies, largely due to differences in the
167 length of the growth periods, fish sizes, and the numbers of fish (Table 1). For example, the total
168 amount of food eaten (g) over the 28-d Brett et al. (1982) study ranged from 32.1g to 116 g for
169 the Qualicum River fish, and 58.1g to 94.9 g for Nechako River fish. The amount of food
170 consumed by Snake River stocks ranged from 511 g to 994 g over our 21-d feeding trails, and
171 1175.0 g to 4007g over our 46-d feeding trails. The temperature at which the maximum amount
172 of food was eaten occurred at mean daily temperatures of about 20.9 °C for Qualicum River fish
173 and 21.0 °C for Nechako River fish in the Brett et al. (1982) studies. During our studies,
174 consumption (g/g/d) was maximized at mean temperatures of 16°C to 20 °C, though we only
175 measured consumption at three temperatures.

176 Parameter estimates from fitting $f(T)$ to the consumption data supported a shift in
177 consumption towards higher temperatures than currently specified in the bioenergetics model for
178 Chinook salmon (Table 2 and Figure 1). The unadjusted model specified C_{\max} at 16.7 °C,
179 whereas the adjusted parameter values estimated C_{\max} at 20.9 °C (lower 95% CL =18.2, Upper
180 95% CL 21.8 =), a 4.2 -°C difference between models. This difference between the unadjusted

181 and adjusted model was consistent over the temperature range, although we had little data on
182 which to inform $f(T)$ at low temperatures, and so there was large uncertainty about the parameter
183 values at low end of the temperature range. Nonetheless, the estimated curve for temperature
184 dependence in maximum consumption more closely followed the observed data than did $f(T)$
185 from the unadjusted model. For example, the unadjusted model resulted in an $r^2 = 0.24$ and
186 residuals that were heterogeneous over the predicted range, whereas the adjusted model had an r^2
187 $= 0.77$ and homogeneous residuals over the predicted range. These findings clearly support a
188 better fit to the data for the adjusted model and a shift towards C_{\max} at higher temperatures for
189 subyearlings than currently implemented under the Wisconsin bioenergetics model for Chinook
190 salmon.

191

192 **DISCUSSION**

193 Our re-evaluation of the Thornton and Lessem (1978) parameters should improve consumption
194 and growth estimates when using the Wisconsin based bioenergetics model in application to
195 juvenile Chinook salmon. The unadjusted parameters developed for Chinook salmon by Stewart
196 and Ibarra (1991) used lower optimal temperatures in the thermal multiplier equation for C_{\max}
197 from Thornton and Lessem (1978). We found that adjustments in the thermal multiplier
198 parameters better accounted for the effect of temperature on C_{\max} across the range of rearing
199 temperatures for which we had data. However, we acknowledge that all fish in these
200 experiments were fed high energy, easily digestible diets, which potentially influenced our
201 results. Nonetheless, if our findings about juvenile feeding behavior at specific temperatures in
202 the laboratory are at all comparable to performance in the natural environment, use of our
203 adjusted model parameters should produce better estimates of consumption and growth for

204 juvenile fall Chinook salmon (Koehler et al. 2006; Armstrong and Schindler 2011).

205 With the paucity of carefully collected data, and the difficulty in evaluating and obtaining
206 these key bioenergetics model parameters (Chips and Wahl 2008), we believe model predictions
207 can be improved for subyearling Chinook salmon with adjustments. The unadjusted model
208 parameters of the Wisconsin model were developed without consumption data from Chinook
209 salmon, likely influencing the variable performance of this model (Madenjian et al. 2004; Chips
210 and Wahl 2008). The unadjusted model parameter values for the temperature-dependence in
211 C_{\max} were calibrated by Beauchamp et al. (1989) for sockeye salmon, *O. nerka*. Stewart and
212 Ibarra (1991) later compared the Beauchamp et al. (1989) calibration using food consumption by
213 coho salmon, *O. kisutch* (Edsall et al. 1974, 1999; Stewart 1980; Stewart et al. 1983), but not
214 Chinook salmon. So using existing data to re-parameterize the Thornton and Lessem (1978)
215 model for C_{\max} , provided a relatively inexpensive opportunity to evaluate and improve a sub-
216 model to the Wisconsin bioenergetics model over a wide range of conditions known to be
217 important to fish consumption, and in turn growth estimates.

218 The early life stage and smaller fish sizes likely contributed to our results. Madenjian et
219 al. (2004) found good agreement between observed and predicted values for the unadjusted
220 bioenergetics model for Chinook salmon, suggesting an appropriate function for C_{\max} . However,
221 the authors conducted their laboratory evaluation using much larger Chinook salmon (> 400 g)
222 that were fed natural (i.e., alewife, *Alosa pseudoharengus*) rather than pelleted feed, and fish were
223 reared at a cooler and narrower temperature range (10.7–13 °C) than evaluated by this study.
224 Sauter et al. (2001) experimentally showed that the thermal preference of subyearling fall
225 Chinook salmon (from the lower Columbia River) decreased from about 18 to 11 °C with the
226 progression of smoltification, indicating that optimal temperatures for consumption (and growth)

227 may also presumably decline as the fish mature and prepare for ocean entry. Banks et al. (1971)
228 demonstrated a shift in the thermal-growth curve in Lower Columbia River subyearling fall
229 Chinook salmon towards cooler temperatures with greater fish maturity and size, which also
230 supports C_{\max} at lower temperatures with greater fish maturity and size. It seems reasonable that
231 optimal temperatures for consumption and growth for fall Chinook salmon would have evolved
232 to decline and become more similar to other salmon stocks (e.g., stream-type Chinook salmon)
233 and species (e.g. coho and sockeye salmon) as the fish mature and near ocean-entry.
234 Temperatures experienced by adult fish in the ocean would be more homogeneous and similarly
235 shared among species compared to those experienced by juvenile fish in freshwater habitats (e.g.,
236 inland headwater streams and lakes versus lower main stem rivers and estuaries). Our estimates
237 are very similar to those currently used in Wisconsin bioenergetics model for steelhead, *O.*
238 *mykiss*, which tend towards longer stream residences (1 – 7 y; Pevan et al. 1994) than Chinook
239 salmon (< 2 y). Killen et al. (2010) reviewed resting metabolic rates for 89 teleost species, and
240 found that intraspecific scaling of metabolic rate varied with spatial habitat, as well as
241 temperature. The unadjusted Wisconsin model parameters for C_{\max} may be more appropriate for
242 adult Chinook salmon, whereas our adjusted model may be more universally applied to juvenile
243 Chinook salmon irrespective of whether the fish originated from inland versus coastal rivers
244 (e.g., lower Snake versus Big Qualicum rivers), or northern versus southern portions of their
245 range (e.g., Nechako versus Sacramento-San Joaquin rivers; Brett et al. 1982; Kjelson et al.
246 1982; Myrick and Cech 2004).

247 The validity of parameter adjustments could be improved by further *a priori* laboratory
248 tests designed to calibrate and corroborate the model parameters, especially those for CQ – the
249 parameter for consumption at the lower end of thermal range (< 10 °C). Given the *post-hoc*

250 nature of our analysis, we believe our simple approach and adjustment to the parameter values
251 was prudent and was sufficient to test the hypothesis that subyearling fall Chinook salmon may
252 exhibit higher consumption at higher temperatures than previously believed. Trends in
253 consumption and growth follow one another over the range in temperature, but peaks
254 temperatures for consumption are typically about 1 – 1.5 °C higher than peak temperature for
255 growth (Brett et al. 1982; Foreseth et al. 2001). Perry et al. (2014 in review) measured peak
256 growth at 19 °C across 11 populations of subyearling Chinook salmon, two of which were used
257 in this study, and so we measure peak temperatures for C_{\max} (20.4 °C) that were within
258 expectations of other studies that have evaluated both consumption and growth by other
259 salmonids over a range in temperatures (Foreseth et al. 2001).

260 Our analysis identifies and potentially provides correction for a systematic consumption-
261 dependent error in the bioenergetics model for juvenile Chinook salmon. Bajer et al. (2004)
262 found widespread systematic consumption-dependent errors in bioenergetics models, and Trudel
263 et al. (2005) indicated that improvements could be made to the energy density-mass equations in
264 the Wisconsin bioenergetics model for juvenile Chinook salmon. Improvements to bioenergetics
265 model output is unlikely to be apparent between the current and adjusted parameters over much
266 of the central portion of the temperature range (where the two functions overlap; Figure 1), but
267 model improvements should be most apparent at the upper end of the thermal range, which may
268 be important for those using bioenergetics models to assess the effects of climate change on fish
269 consumption and growth. At a minimum, our study suggests that the bioenergetics model should
270 be revisited before predicting growth and consumption by juvenile Chinook salmon at the upper
271 end of the thermal range where changes in consumption and growth are most rapid.

272

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415 **Figure Captions**

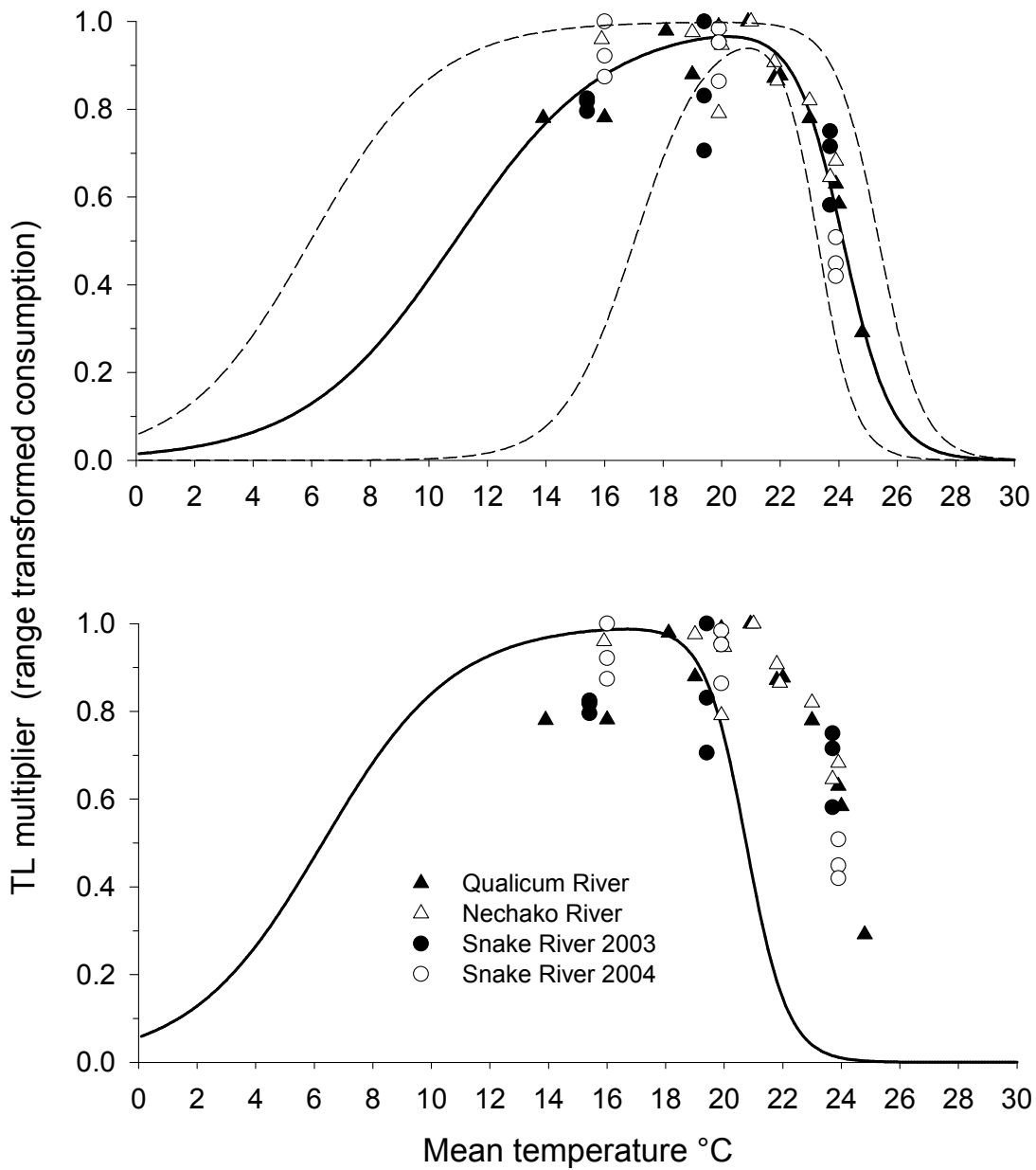
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417 Figure 1. Adjusted (upper panel) and unadjusted (lower panel) temperature dependent
418 consumption curves using the Thornton and Lessem (1978) equation and coefficients provided in
419 Table 1. Individual plots of the proportion of maximum food consumption by mean water
420 temperatures are provided for data from laboratory trials of Brett et al (1982) for Qualicum River
421 and Nechako River stocks, and Snake River stocks reared in our laboratory. Dashed lines in the
422 upper panel represent the bootstrapped 95% confidence bounds about the adjusted consumption
423 curve.

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426 Figure 1
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472 Table 1. — Mean tank temperatures, initial weights, and the total food consumed by subyearling
 473 Chinook salmon by river origin, length of feeding trial at constant temperature, and data source.
 474 Ranged food values were calculated from dry weights during the Brett et al. (1982) studies and
 475 calculated from wet weights during U of Idaho studies.

Mean temperature °C	Mean initial weight (g)	Total consumption (g)	Total consumption (g/g)	Ranged consumption
Qualicum River 28 d (Brett et al. 1982)				
24.8	3.2	32.1	0.336	0.292
23.9	3.2	70	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	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 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 21 d (U of Idaho)				
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

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481 Table 1.— continued.

Mean temperature °C	Mean initial weight (g)	Total consumption (g)	Total consumption (g/g)	Ranged consumption
Snake River 46 d (U of Idaho)				
23.9	14.6	1240	0.494	0.448
19.9	16.2	3790	0.951	0.863
19.9	16.1	4006.8	1.084	0.984
23.9	14.7	1177	0.560	0.508
19.9	16.7	4170	1.049	0.952
16.0	14.6	3730	1.102	1.000
16.0	16.6	3956	0.963	0.874
23.9	14.8	1175	0.462	0.420
16.0	16.7	3858	1.015	0.921

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 490 Table 2. — Parameter values and their bootstrapped 95% confidence limits estimated for the
 491 Thronton and Lessem (1978) multiplier to determine thermal-dependence in maximum
 492 consumption in the Wisconsin bioenergetics model for Chinook salmon.

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

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