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# What We Don't Know About the Effects of Temperature on Salmonid Growth

Steven F. Railsback  
Lang Railsback & Associates  
250 California Avenue  
Arcata CA 95521 USA

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Running head: Temperature and salmonid growth

## 20 **ABSTRACT**

21 Salmonid biologists use both mental models—simple assumptions—and bioenergetics-  
22 based mathematical models to understand and predict effects of temperature regime on growth.  
23 Bioenergetics model results, however, sometimes conflict with common assumptions. Previous  
24 studies plus “Wisconsin model” bioenergetics simulations lead to four conclusions that conflict  
25 with some management assumptions. (1) Food consumption is at least as important as  
26 temperature in explaining growth; we cannot understand temperature effects without  
27 understanding food consumption. (2) At natural food consumption rates, there is no “optimal  
28 temperature for growth”; growth peaks in model results are artifacts of food consumption  
29 assumptions, and in laboratory studies are (apparently) artifacts of ad libitum feeding. (3) Effects  
30 of temperature on growth can be stronger during cooler seasons than in summer; traditional  
31 temperature criteria are not useful for managing such effects. (4) Salmonid populations adapted  
32 to survive higher temperatures may be more, not less, vulnerable to temperature effects on  
33 growth, due to their higher metabolic rates. Temperature-growth relations observed under ad  
34 libitum feeding seem risky for managing wild populations. Model predictions of growth need to  
35 consider food consumption assumptions carefully. For predicting effects of increased  
36 temperature, the traditional assumption that consumption is a constant fraction of maximum  
37 consumption rate appears especially uncertain and incautious, with its hidden assumption that  
38 consumption increases with temperature; assuming a constant ration is simpler and more  
39 cautious. Growth can be predicted more reliably with feeding models and individual-based  
40 population models that consider how consumption and energetic costs depend on processes such  
41 as habitat selection, competition, and adaptive behaviors that trade off food intake and predation  
42 risk. Two research needs are clear: empirical observations for parameterizing and testing the  
43 Wisconsin model comprehensively under natural conditions (which we lack despite the extensive  
44 energetics literature), and methods for predicting salmonid food production responses to  
45 temperature and flow regimes.

## 46 **INTRODUCTION**

47 The effect of temperature regime on stream salmonids has long been an important  
48 management concern, and its importance is increasing rapidly. Management and research

49 biologists often address temperature effects at scales from local to regional, e.g., how  
50 temperature interacts with physical habitat and other variables to drive adaptive behaviors such  
51 as when and where to feed (Railsback et al. 2021a), how changes in flow and temperature regime  
52 resulting from (e.g.) hydropower licensing and forest harvest (Leach et al. 2012) affect trout  
53 abundance, and how climate change interacts with other stressors to affect population viability  
54 (Ayllón et al. 2021). These questions usually depend less on acute temperature stress and more  
55 on sublethal effects such as how temperature affects growth, because sublethal effects happen  
56 over wider and lower ranges of temperature.

57 Salmonid biologists use both mental models—assumptions—and mathematical models to  
58 understand and predict effects of temperature on growth. Unfortunately, some widely used  
59 assumptions sometimes conflict with the mathematical models, as I explore below. These  
60 conflicts indicate that, despite an extensive literature, important uncertainties about how  
61 temperature affects salmonid growth persist.

62 The specific mathematical model of temperature effects on growth I refer to is the  
63 “Wisconsin” bioenergetic model (Hanson et al. 1997; Deslauriers et al. 2017), which includes a  
64 conceptual model and specific equations and parameters for various species and life stages. The  
65 conceptual model is an energy balance, treating growth rate as the difference between the rates of  
66 energy intake from food and energy costs of basal metabolism, activity, and digestion. The  
67 conceptual and mathematical models are of course great simplifications of complex  
68 physiological mechanisms. For example, Wisconsin model applications typically ignore the  
69 energetics of reproduction and adaptive energy allocation (e.g., growth in size vs. storage as  
70 lipids).

71 However, bioenergetics modeling is popular as a way to relate fish growth to temperature  
72 and other variables *because* it is simple. Unlike another widely used energetics approach  
73 (Dynamic Energy Budget theory; Kooijman 2010; Nisbet et al. 2000), the Wisconsin model has  
74 two characteristics making it useful for management modeling. First, it uses only a minimal set  
75 of variables to link temperature and growth: growth rate, energy intake, temperature, fish size,  
76 activity. Second, the model’s energy compartments and mechanisms are clearly related to actual  
77 physiology and therefore measurable, at least in principle. We can put fish in the laboratory and  
78 measure, e.g., how metabolic energy demand varies with temperature and swimming speed.  
79 Therefore, the Wisconsin model provides a framework for combining observations from various

80 experiments into a predictive tool. It has become a very important tool not just by itself but as the  
81 growth component of numerous models (cited throughout this article) of phenomena from  
82 individual growth to population dynamics to regional productivity.

83         Unfortunately, despite extensive literature on relevant mechanisms, we still lack  
84 conclusive empirical evidence for evaluating both mental and mathematical models of  
85 temperature effects on salmonid growth. To my knowledge, there has not been a single study on  
86 real fish that carefully controlled and independently varied the four drivers of growth in the  
87 Wisconsin model (energy intake, temperature, fish size, and swimming speed) while observing  
88 growth. Salmonid biologists are blessed with probably hundreds of studies of how *some* of these  
89 variables affect growth, but none that we can use as a thorough and conclusive test of the  
90 Wisconsin model.

91         The fundamental problem with the empirical literature is that quantitative results depend  
92 on factors that always vary among experiments; examples include species and stock, exercise  
93 condition, life history stage, food type, and measurement methods (Hartman and Brandt 1993).  
94 Consequently, results from different experiments often conflict (even when experiments use very  
95 similar methods and equipment; e.g., Forseth and Jonsson 1994; Myrick and Cech 2000), and  
96 combining them into a useful set of equations and parameters requires judgement and  
97 assumptions that introduce uncertainty. Other problems with many laboratory studies include the  
98 use of ad libitum feeding and artificial food, which are convenient but produce unnaturally food-  
99 rich, high-energy conditions; not taking observations at the extreme temperatures that are often  
100 of management concern, or not observing enough temperatures to define the sharp changes that  
101 can occur at high temperatures; and unmeasurable variation in food intake and swimming speed  
102 due to competitive interactions among multiple fish kept in the same tank (e.g., Forseth and  
103 Jonsson 1994).

104         My objective here is to identify conflicts between management assumptions and models  
105 and examine them in light of the available evidence, thereby illuminating key research needs and  
106 ways we can improve both mental and mathematical models. I identify four assumptions about  
107 how temperature affects growth that I have noted in the literature and in interactions with  
108 salmonid biologists. I then examine how well these assumptions agree with the bioenergetic  
109 model and, sometimes, empirical evidence. The Discussion examines key conflicts between our

110 mental and mathematical models, suggests alternative assumptions, and identifies research  
111 objectives to reduce key uncertainties.

## 112 **MANAGEMENT ASSUMPTIONS AND MODEL PREDICTIONS**

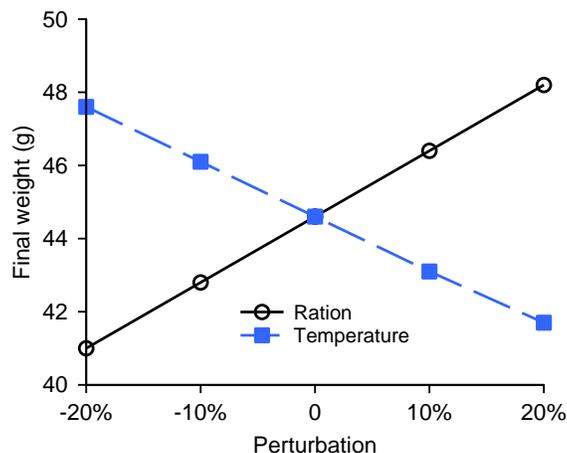
### 113 **Assumption 1: Growth is Driven by Temperature**

114 Perhaps the most fundamental assumption salmonid biologists make about temperature is  
115 that it has a strong, even predominant, effect on growth: if we see that trout in one stream are  
116 larger than those in another stream, we often assume that the difference results from the first  
117 stream being warmer. This assumption also appears in management models. For example, Mims  
118 et al. (2019) used temperature as the sole habitat variable driving growth in a large-scale  
119 metapopulation model, and Lopez Arriaza et al. (2017) modeled growth in juvenile Steelhead  
120 Trout as a function of fish activity, competition, and temperature as the only habitat variable.

121 The Wisconsin model offers the alternative assumption that differences in growth can  
122 also be explained by differences in energy intake, either via higher food consumption or higher  
123 prey energy density. In fact, a comprehensive parameter sensitivity analysis of three versions of  
124 the Wisconsin model (none for salmonids, however) found that parameters affecting food intake  
125 had the strongest effect on results (Bartell et al. 1986). Stewart et al. (1983) and Beauchamp et  
126 al. (1989) found high sensitivity to food intake parameters in salmonid applications of the model.

127 I examined the relative effects of temperature and food consumption with a simple  
128 sensitivity experiment: I executed the Wisconsin model for both temperature and ration ranging  
129 from -20% to +20% of baseline values. (Following Deslauriers et al. 2017, I use “ration” as an  
130 individual’s mass rate of food consumption, g/d; energy intake rate is equal to ration times a prey  
131 energy density.) I used Version 1.1.3 of the Fish Bioenergetics Model 4 software (Deslauriers et  
132 al. 2017), its standard formulation for adult Rainbow Trout, and its default prey and predator  
133 energy densities of 3000 and 4500 J/g. I simulated growth of a 40-g trout over 30 days with  
134 constant temperature and ration. The baseline value of ration, 2.06 g/d, was calculated as that  
135 producing zero growth at 20°, representing realistic intake in a natural, relatively oligotrophic  
136 environment. The baseline temperature was 15°. Therefore, I varied temperature 12–18° with  
137 ration of 2.06 g/d, then ration 1.65–2.47 g/d with temperature at 15°.

138 The results of this experiment (Figure 1) indicate that food—energy intake rate—affects  
139 growth as much or more than temperature does. Food intake seems even more important when  
140 we consider that it often varies far more widely than temperature among sites, seasons, and  
141 perhaps management scenarios such as alternative flow regimes; a decrease in flow, for example,  
142 may produce an increase of several degrees in summer temperature but a large decrease in drift  
143 food delivery (e.g., Harvey et al. 2006). Therefore, it appears risky to assume that differences in  
144 growth (among sites, over time, etc.) are due to temperature alone and not also to food  
145 availability. In fact, we should also consider other factors that affect the energy balance, e.g.,  
146 differences in activity (e.g., between low- and high-slope sites) or food quality (e.g., between  
147 times when food is dominated by immature aquatic vs. adult or terrestrial insects).  
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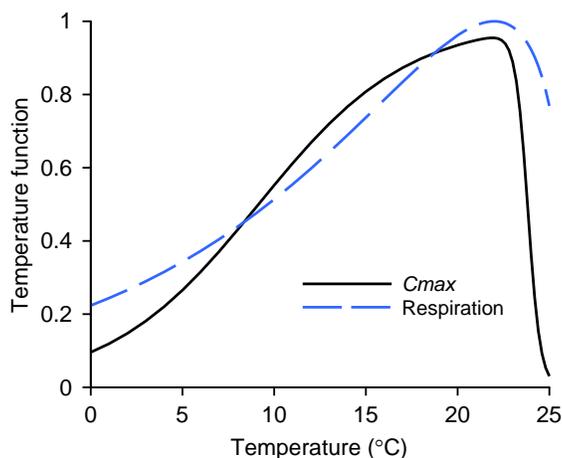


149 Figure 1. Results of the temperature and ration sensitivity experiment for adult rainbow trout. The X axis is ration or  
150 temperature, as the percentage change from its baseline value, and the Y axis is predicted fish weight after 30 days.  
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### 153 **Assumption 2: There is an Optimal Temperature for Growth**

154 The second assumption I examine is that growth typically increases with temperature up  
155 to an “optimal” temperature, above which it decreases. A number of studies have tried to  
156 quantify optimal growth temperatures (e.g., Forseth and Jonsson 1994; Myrick and Cech 2000),  
157 and the assumption has been used in management models (e.g., Fullerton et al. 2017; Lopez  
158 Arriaza et al. 2017) and recommendations (e.g., Zeigler et al. 2013), and in other analyses of  
159 temperature effects (e.g., Huntsman et al. 2021).

160 I evaluated this assumption simply by running the Wisconsin model for adult Rainbow  
 161 Trout over a range of temperatures, holding food consumption constant. However, I repeated the  
 162 experiment using three definitions of food consumption. One is absolute ration, g food per day.  
 163 Second is relative ration, g food per g fish per day, so absolute ration increases as the fish grows.  
 164 Third is  $p$ , a measure peculiar to the Wisconsin model. The value of  $p$  is ration as a fraction of  
 165 the fish's maximum consumption rate ( $C_{max}$ , g/d); the model represents  $C_{max}$  as a nonlinear  
 166 function of both fish weight and temperature (Figure 2). Assuming a constant  $p$  therefore means  
 167 that absolute ration increases with weight and varies with temperature; for the adult Rainbow  
 168 Trout formulation, ration at a constant  $p$  increases sharply with temperature up to  $>20^{\circ}\text{C}$ .  
 169



170  
 171 Figure 2. Temperature functions for  $C_{max}$  and, for comparison, respiration, in the adult Rainbow Trout formulation  
 172 provided with the Fish Bioenergetics 4.0 software of Deslauriers et al. (2017).

173  
 174 As in the first experiment, I selected consumption parameter values representing  
 175 moderate energy intake, producing zero growth at  $20^{\circ}\text{C}$ : absolute ration = 2.06 g/d, relative  
 176 ration =  $0.0515 \text{ g} \cdot \text{g}^{-1} \cdot \text{d}^{-1}$ , and  $p = 0.265$ . I also simulated high energy intake: absolute ration =  
 177 4.50 g/d, relative ration =  $0.0910 \text{ g} \cdot \text{g}^{-1} \cdot \text{d}^{-1}$ , and  $p = 0.500$ . These high intake rates produce 20 g  
 178 of growth over 30 d at  $20^{\circ}\text{C}$ , an average of 1.4% body weight per day; for comparison, Myrick  
 179 and Cech (2000) observed growth in the range of 3.0–3.7%/d at 19 and  $22^{\circ}\text{C}$  with ad libitum  
 180 feeding of high-energy pellets. I simulated 30 d of growth for a trout starting at 40 g, at eight  
 181 constant temperatures from 5 to  $22.5^{\circ}\text{C}$ .

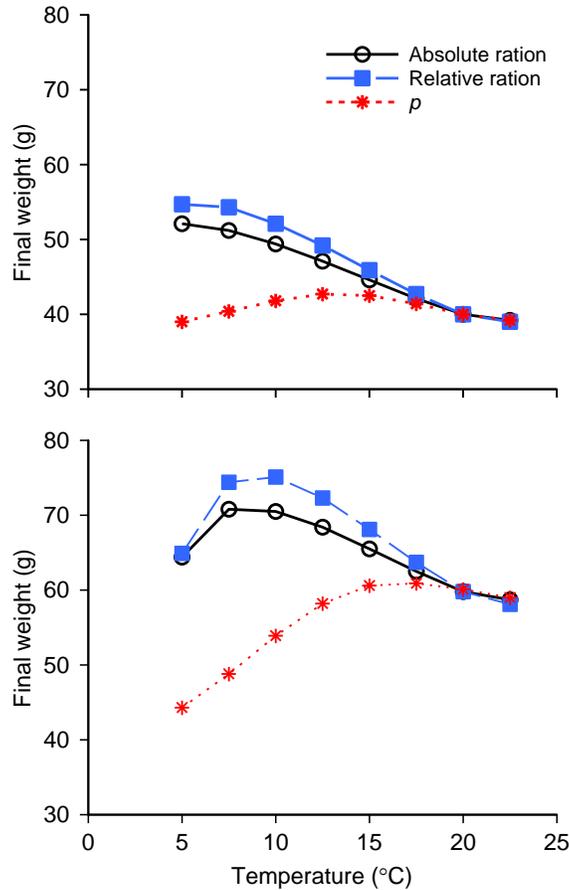
182           The results for moderate energy intake (Figure 3, top panel) show that an “optimal”  
183 growth temperature only occurs when we assume food consumption is a constant fraction of  
184  $C_{max}$ , not when we simulate a constant energy intake rate. When the model assumes fish have  
185 the same absolute energy intake, and metabolic energy demands increase with temperature (up to  
186 a peak at 22°C, in this case; Figure 2), then growth rate can only decline as temperature  
187 increases. However, when the model assumes that food consumption follows the complex  
188 function for  $C_{max}$ , which also increases with temperature, then a peak in growth as temperature  
189 increases is possible as an artifact of the  $C_{max}$  temperature function. (Using similar methods,  
190 Beachamp 2009 showed that the temperature producing highest predicted growth depends on  $p$ .)

191           With high energy intake (Figure 3, bottom panel), there are peaks in growth at relatively  
192 low temperatures when intake is modeled as a constant absolute or relative ration. These peaks  
193 occur because the Wisconsin model limits the food consumption rate to the value of  $C_{max}$ ,  
194 which at low temperatures is lower than the specified absolute and relative rations; the simulated  
195 fish actually gets less food than the assumed intake rates.

196           If this simulation experiment indicates that peaks in simulated growth with temperature  
197 are artifacts of assumptions about  $C_{max}$ , why have “optimal” temperatures been found in  
198 laboratory studies of real salmonids? One answer appears to be that such studies typically use ad  
199 libitum feeding (e.g., Zeigler et al. 2013; Myrick and Cech 2000; Forseth and Jonsson 1994) so  
200 growth is limited by digestion rate instead of the balance between a limited energy intake and  
201 metabolic costs that increase with temperature. (In fish such as grazers that use less-digestible  
202 food, temperature appears to have strong effect on growth because digestion rates are strongly  
203 temperature-dependent, and energy assimilation is typically limited by digestion instead of intake  
204 rates; e.g., Hofer et al. 1982.) Slower digestion at lower temperatures is likely what causes the  
205 appearance of an optimal growth temperature in experiments with ad libitum feeding (and the  
206 reason  $C_{max}$  is low at low temperatures). However, at more natural food consumption rates the  
207 energy assimilation of salmonids is unlikely to be limited by digestion rate, except perhaps at  
208 low temperatures. There is some evidence to support this potential explanation. Wurtsbaugh and  
209 Davis (1977) observed growth in juvenile Rainbow Trout under three temperature regimes and  
210 several ration levels. At low rations, growth always decreased with temperature, but temperature  
211 had positive effects on growth at higher rations. Cui and Wootton (1988) observed growth of  
212 minnows fed on small invertebrates at five ration levels and four temperatures; they too found

213 growth to only decrease with temperature at low rations, but peak or increase with temperature at  
 214 high rations. The concept of an optimal temperature for growth may be useful in situations where  
 215 food is essentially unlimited and energy-rich—hatcheries and prey pulses (Furey et al. 2016)—  
 216 but appears questionable for salmonids feeding on invertebrate prey, in which case growth is  
 217 much more likely to be limited by food capture rate than digestion rate.  
 218

219



220

221 Figure 3. Results of the optimal temperature for growth simulation experiment: response of simulated trout growth  
 222 (as in Figure 1) for three food consumption assumptions. Top panel: moderate food intake producing zero growth at  
 223 20°C. Bottom panel: high intake that produces 1.4% d<sup>-1</sup> growth at 20°C.

224

225 This experiment clearly shows that the response of growth to temperature depends, even  
 226 qualitatively, on what happens to food consumption. The differences among ration assumptions  
 227 in Figure 3 have important management implications. For example, when we assume absolute  
 228 ration is constant, then growth under moderate energy intake is most sensitive to temperature at

229 intermediate temperatures,  $\sim 7\text{--}17^\circ$ ; when we assume constant  $p$ , then growth is insensitive to  
230 temperature at  $\sim 10\text{--}17^\circ$  and most sensitive above and below that range. Management  
231 recommendations based on temperature-growth relations observed under ab libitum feeding  
232 (e.g., Zeigler et al. 2013) seem especially risky.

### 233 **Assumption 3: Temperatures Effects are Important Only in Summer**

234 We often naturally assume that the highest summer temperatures are our biggest  
235 management concern for salmonids. This assumption is reflected in the widespread use of  
236 temperature criteria for assessing temperature effects of management alternatives (e.g., by  
237 evaluating how frequently a criterion of  $20^\circ\text{C}$  is exceeded under each alternative). Peak  
238 temperatures are an obvious concern in streams where natural climate and human impacts drive  
239 them to levels making growth difficult and acute effects likely (e.g., Ayllón et al. 2013).

240 Studies applying bioenergetics models to year-round growth at sites with less-extreme  
241 thermal regimes, however, have found that temperature can have strong effects on growth during  
242 seasons other than summer. Railsback and Rose (1999) analyzed temperature effects on growth  
243 using the Wisconsin model and trout sizes observed in spring and fall at a number of sites in the  
244 Sierra Nevada, California. They concluded that temperature had stronger effects from fall to  
245 spring than from spring to fall. Similarly, Armstrong et al. (2021) applied the model of Fullerton  
246 et al. (2017), which also uses a Wisconsin model formulation to represent growth, to year-round  
247 temperatures throughout several watersheds in the Pacific Northwest. They concluded that  
248 lower-elevation sites offering low summer growth due to higher temperatures provided important  
249 high-growth habitat at other times of year.

250 These analyses illustrate that changes in temperature regime can have strong effects on  
251 salmonid growth during cooler seasons. Figure 3 illustrates why the Wisconsin model predicts  
252 this: for all the ration assumptions, the sensitivity of growth to temperature is high at low to  
253 intermediate temperatures.

### 254 **Assumption 4: Warm-adapted Populations Grow Better at Higher Temperatures**

255 Clear evidence shows that some salmonid populations are better adapted to high  
256 temperatures than others, even within a species (e.g., Eliason et al. 2011; Chen et al. 2015, 2018).  
257 This evidence is mostly derived from measurements of acute thermal effects such as critical  
258 thermal maximum (the temperature at which a fish loses swimming ability during rapidly

259 increasing temperatures) and aerobic scope (the difference between resting and maximum  
260 metabolic rates at elevated temperatures, which reflects how resting metabolic rate increases and  
261 maximum rate decreases with temperature; e.g., Eliason et al. 2011). Larger hearts and increased  
262 cardiac performance appear to be key mechanisms conveying acute temperature tolerance (Chen  
263 et al. 2018).

264 We might naturally assume that warm-adapted salmonid populations have lower  
265 sublethal effects: that populations evolved to tolerate higher temperature extremes are also likely  
266 to grow over a wider range of temperatures. However, the mechanism of adaptation—increased  
267 heart size and pumping rate—seems likely to come at a cost of higher metabolic rate. In fact,  
268 recent evidence indicates the validity of this concern. Data from two southern California  
269 Steelhead populations indicate that the population from a warmer stream has higher tolerance of  
270 extreme temperatures and approximately double the resting metabolic rate, measured over  
271 temperatures of 18–21°C (Eliason, pers. comm.). It seems reasonable to assume that this  
272 difference in resting metabolic rate would extend to lower temperatures as well.

273 If higher tolerance of extreme temperature has a cost of higher metabolic rates, then we  
274 should not think of “warm-adapted” populations (and, perhaps, species) as less subject to effects  
275 of temperature on growth. Just the opposite appears to be true: such fish may be able to grow and  
276 thrive only when able to consume considerably more food than others, to keep up with their  
277 higher metabolic costs. This evidence also implies that we should reconsider Wisconsin model  
278 respiration parameters to avoid overestimation of growth, or underestimation of food  
279 requirements, for warm-adapted populations.

## 280 **DISCUSSION**

### 281 **Conflicts Between Management Assumptions and Bioenergetics Modeling**

282 The Wisconsin bioenergetics model has proven extremely useful as a temperature  
283 management tool. It is useful not because it is “realistic”—it is not—but, in contrast, because it is  
284 as simple as possible while still linking the management variables we need to evaluate, via  
285 mechanisms we can measure. The model provides a way to assemble relations observed in  
286 diverse laboratory studies into a predictive tool. My comparison of Wisconsin model results to

287 management assumptions leads to the following conclusions, some of which challenge how we  
288 commonly think about temperature effects.

289 **Growth is driven by food as much or more than by temperature.** When trying to  
290 explain differences or changes in growth, we should consider food consumption, not  
291 temperature, as the primary driver. Further, there is no way to understand the effects of  
292 temperature without understanding food consumption; Figure 3 shows that even the shape of the  
293 growth response to temperature depends on what we assume about food consumption.

294 **There may be no optimal temperature for growth under typical natural conditions.** I  
295 found a peak in simulated growth rate with temperature only as an artifact of assuming ration  
296 varies with  $C_{max}$ , not under simpler and perhaps more realistic consumption assumptions.  
297 Optimal growth temperatures found in laboratory studies seem likely an artifact of ad libitum  
298 feeding, which makes growth limited by digestion rate instead of food intake rate. While there  
299 may be situations (including low temperatures) when wild salmonids can capture food more  
300 rapidly than they can digest it, under typical natural feeding conditions (e.g., drift-feeding on  
301 invertebrates), salmonid growth is much more likely limited by food intake than by digestion.  
302 Therefore, relations between growth and temperature observed under unnaturally food-rich  
303 laboratory conditions seem a risky basis for management of wild populations.

304 **Peak temperatures may not be the most important to manage.** Temperature can have  
305 strong effects on growth during cool seasons, which implies that traditional temperature criteria  
306 have limited value for assessing and avoiding growth effects.

307 **Warm-adapted salmonid populations may be more, not less, vulnerable to**  
308 **temperature effects on growth.** The higher metabolic rates that allow survival of higher  
309 extreme temperatures in some populations also require higher food intake to maintain growth.  
310 Consequently, populations that have evolved tolerance of higher temperatures must be assumed  
311 more vulnerable to elevated temperatures that are not accompanied by higher food availability.

## 312 **Representing Consumption in Bioenergetics Analyses**

313 The main lesson from my analyses is that we should not ignore food in modeling how  
314 temperature affects salmonid growth. Unfortunately, while temperature is easy to measure and  
315 model, food availability and consumption by fish are complex, expensive to observe, and  
316 impossible to predict with certainty. Therefore, we almost always rely on simple assumptions

317 about food; typically, we calibrate a consumption parameter by fitting the model to growth  
318 observed under one temperature regime and then use that parameter value to predict growth  
319 under other temperature regimes.

320         What is a good assumption about food consumption for predicting growth under  
321 alternative temperatures? If management conclusions drawn from analyses based on the  
322 Wisconsin model are likely to change if we assume different consumption rates, can those  
323 analyses have any credibility? These questions are especially important when examining  
324 management actions, e.g., changes in flow, that are likely to affect food production as well as  
325 temperature.

326         The Wisconsin model literature and software long promoted the practice of representing  
327 consumption as a constant value of  $p$ , an assumption that seems especially risky and difficult to  
328 justify. That assumption causes absolute ration and energy intake rate to vary with temperature  
329 according to the complex relation assumed between  $C_{max}$  and temperature (Figure 2). This  
330 variation makes it harder to interpret results and understand exactly what drove predicted growth  
331 (Railsback and Rose 1999). Because  $C_{max}$  typically increases with temperature except at high  
332 temperatures, assuming constant  $p$  includes a hidden assumption that ration increases with  
333 temperature; therefore, it could underestimate effects of increased temperature on growth (but  
334 see below concerning temperature effects on ration). Other problems with this assumption  
335 include the lack of an ecological reason why a fish would or could adjust its consumption to  
336 maintain constant  $p$  as temperature changes (I discuss behavioral aspects of consumption below),  
337 and that  $C_{max}$  is a particularly challenging variable to define precisely and measure (Hartman  
338 and Brandt 1993)—it can vary with factors that are rarely controlled and not included in the  
339 model, such as exercise condition of the fish, food type, activity, and measurement time scale.  
340 Figure 2 makes it clear that uncertainty in the Rainbow Trout  $C_{max}$  temperature function has  
341 especially strong effects on predicted growth at temperatures  $>20^{\circ}\text{C}$ . (This uncertainty is why I  
342 simulated growth at temperatures no higher than  $22.5^{\circ}$ .) Further, the physiological mechanism  
343 driving  $C_{max}$ —digestion rate—is unlikely to limit growth under consumption rates typical of  
344 natural conditions (except, possibly, when temperatures are low and food availability high).

345         The alternative assumption of constant ration (either absolute or relative) is simpler and  
346 more conservative, by not including the hidden assumption that ration increases with  
347 temperature. Calibrating the Wisconsin model to estimate a constant ration that is then used to

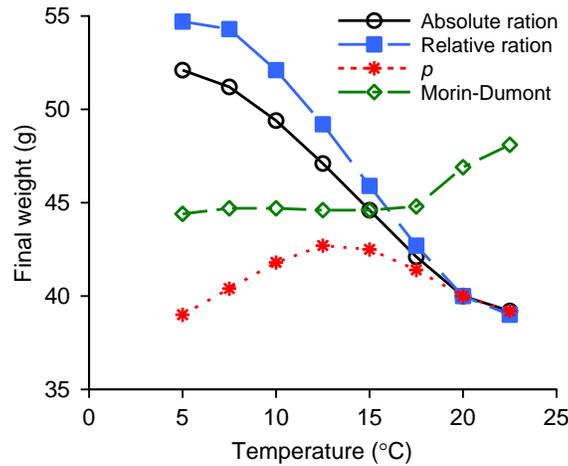
348 estimate effects of other temperature regimes seems simple and clear, and cautious for examining  
349 temperatures above those used for calibration. As an example, Hawkins et al. (2020) modified  
350 their previous model that assumed a constant  $p$  (Fullerton et al. 2017) to instead use a constant  
351 relative ration.

352 On the other hand, assuming a constant ration ignores how the productivity of aquatic  
353 ecosystems actually can vary with temperature; it is not unreasonable to expect a positive  
354 relationship between salmonid food intake and temperature. Filbert and Hawkins (1995)  
355 observed drift food concentrations roughly an order of magnitude higher in summer than winter,  
356 in a reservoir tailwater. From a meta-analysis of published benthic insect growth rates, Morin  
357 and Dumont (1994) produced a regression model of growth rate vs. temperature for a  
358 combination of Diptera, Ephemeroptera, Plecoptera, and Trichoptera, observed over  
359 temperatures from  $<5$  to  $>20^{\circ}\text{C}$ . This model predicts insect growth to increase as an exponential  
360 function of temperature (growth is proportional to  $e^{0.058T}$  where  $T$  is temperature,  $^{\circ}\text{C}$ ). Neglecting  
361 complexities such as how insect growth translates to drift rate and how drift depletion by fish  
362 varies with temperature, we can use this regression model as a speculative example of how food  
363 availability could vary with temperature.

364 To explore the speculation that trout food consumption increases with temperature  
365 according to the growth equation of Morin and Dumont (1994), I repeated the simulation  
366 experiment of Figure 3 while assuming that food consumption varies, above and below  $15^{\circ}\text{C}$ ,  
367 according to their exponential function. I used an absolute ration (g/d) equal to  $0.87e^{0.058T}$ , which  
368 at  $15^{\circ}\text{C}$  produces the same ration of 2.06 g/d assumed in the “Absolute ration” results of Figure 3  
369 (top panel). The results (Figure 4) are completely different from those of the other consumption  
370 assumptions: growth is insensitive to temperature up to  $17.5^{\circ}$ , then *increases* with temperature  
371 up to  $22.5^{\circ}$ .

372 This simulation provides only a very simplistic view of potential effects of food  
373 availability increasing with temperature and should not be used to inform management decisions;  
374 however, it further confirms the importance of food consumption assumptions when predicting  
375 temperature effects on growth, and to some extent even brings into question the generalization  
376 that increased temperature always has negative effects on salmonid growth and population  
377 biomass accumulation. It raises the possibility that increased benthic productivity could largely  
378 offset the increased metabolic demands of fish; as Railsback and Rose (1999) suggest, the

379 strongest effect of temperature on trout growth could be an indirect effect via food production.  
380 Such increased productivity could help explain the persistence of warm-adapted populations  
381 despite their higher metabolic rates.  
382



383  
384 Figure 4. Growth simulations as in the top panel of Figure 3, with the additional assumption that food consumption  
385 follows the temperature term of the insect growth equation of Morin and Dumont (1994).

386  
387 Unfortunately, even the range of assumptions illustrated in Figure 4 is a gross  
388 simplification of food consumption. The consumption rate of each individual fish in a population  
389 can also depend on competition for food, and on behavior. Feeding behavior—where an  
390 individual feeds, how often, and at what times of day—is now understood and modeled as an  
391 adaptive tradeoff between meeting energy demands and avoiding predation risk (Railsback et al.  
392 2020). This understanding suggests that the most reasonable simple assumption about food  
393 consumption is that each individual feeds enough to meet its metabolic demands and, during  
394 relevant life stages, to accumulate the size and energy needed for future survival and  
395 reproduction (e.g., Biro et al. 2005). Consequently, the effects of temperature could manifest as  
396 changes not in growth but in survival: if increased temperatures raise metabolic rates but not  
397 prey availability, salmonids are likely to respond by feeding more often, or in more productive  
398 but riskier places and times, and hence to maintain their growth but experience more predation.  
399 Lower temperature or higher food availability could result in less time spent feeding and higher  
400 survival, instead of (or in addition to) higher growth.

401           Given all these complexities in estimating consumption, is it possible to make useful and  
402 credible predictions of growth (and survival) responses to temperature? At a minimum, we can  
403 try several simple food assumptions and see whether and how the conclusions of management  
404 studies differ among them (e.g., the food availability experiment of Railsback et al. 2021a).

405           Incorporating the Wisconsin formulation within individual feeding models and  
406 individual-based population models (IBMs) is a second way to deal with food consumption  
407 complexities. Models that predict individual food intake from habitat conditions have a long  
408 history (e.g., Fausch 1984; Hughes and Dill 1990; Naman et al. 2020). Fullerton et al. (2017),  
409 Mims et al. (2019), and Railsback et al. (2021a, b) provide examples of IBMs, for different  
410 purposes, that combine the Wisconsin formulation with models of how habitat, competition, and  
411 behavior affect food consumption.

412           InSTREAM and inSALMO (Railsback and Harvey 2002; Railsback et al. in prep.,  
413 2021b) are unique as salmonid population models that represent individual growth (and  
414 population abundance and biomass) as outcomes of prey production, physical habitat,  
415 temperature, competition, and behaviors that determine when and where individuals feed as a  
416 tradeoff between growth and predation risk. These two models are especially valuable for  
417 assessing changes in temperature that accompany changes in flow: they predict the combined  
418 effects of flow (e.g., on food delivery and habitat space) and temperature on populations  
419 (Railsback et al. 2021a, b). These models also facilitate experiments to examine sensitivity of  
420 results to alternative assumptions about food; for example, Railsback et al. (2021a) showed that  
421 conclusions about a range of instream flow and temperature management alternatives changed  
422 little when drift food availability was assumed concentrated during crepuscular periods instead of  
423 constant throughout the day. (InSTREAM and inSALMO have the additional benefit of  
424 representing temperature effects other than on growth; the application of Railsback et al. 2021b  
425 found temperature effects on egg mortality and incubation rate to clearly affect abundance.)

426           These models that predict food consumption from foraging behavior depend on a part of  
427 the Wisconsin model otherwise neglected here: the energy cost of swimming. The models treat  
428 selection of drift-feeding sites as a tradeoff between the food delivery benefits of higher velocity  
429 and its costs in reduced capture ability and increased activity respiration. (In developing the  
430 newest version of inSTREAM, we discovered an important flaw in the Wisconsin model's  
431 activity respiration formulation, which it adopts from Stewart et al. 1983. It treats activity

432 respiration as a function only of swimming speed, neglecting the effect of fish size. See  
433 Railsback et al. in prep. for an alternative formulation, plus reviews of other components of the  
434 Wisconsin salmonid formulations in light of recent empirical data.)

### 435 **Research Needs**

436 As a simple representation of complex physiological and ecological processes, the  
437 Wisconsin model depends on empirical data for parameterization and validation; yet we lack  
438 even a single comprehensive data set for salmonids, as widely studied and important as trout and  
439 salmon are. While a few parameterizations have been based mostly on a single set of laboratory  
440 experiments designed specifically for that purpose (e.g., Mesa et al. 2013 for Bull Trout feeding  
441 on fish), or shown to predict growth well under limited conditions (Mesa et al. 2013; Madenjian  
442 et al. 2004, for Chinook Salmon feeding on fish), many (including the formulation for Rainbow  
443 Trout used here) have been cobbled together from multiple studies of questionable compatibility  
444 (Railsback and Rose 1999) and, in retrospect, limited value for formulating or testing the model.  
445 In fact, the Rainbow Trout formulation produces implausible results above 22.5°C, a critical  
446 range for temperature assessment, clear evidence that it needs improvement.

447 To make results reliable and credible, we need laboratory experiments designed  
448 specifically to parameterize and test the Wisconsin model as applied to natural conditions.  
449 Traditionally measured variables such as *C<sub>max</sub>* and temperature “tolerance” are not useful for  
450 this purpose. Instead, we need observed growth of individual fish of various sizes, exposed to  
451 many combinations of temperature, energy intake rate, and swimming speed over wide ranges of  
452 these variables (including extremes), in experiments that carefully control the many other factors  
453 that affect growth. Data on how metabolic rates of the same fish vary with temperature and  
454 swimming speed would help parameterize those components of the model and test the overall  
455 energy balance assumptions. Such experiments are likely to be challenging and expensive, yet  
456 well within the capabilities of existing laboratory technology.

457 The evidence that growth depends as much or more on food consumption as on  
458 temperature indicates that we also need useful observations and models of how production of  
459 salmonid food depends on the variables we predict growth responses to, especially flow and  
460 temperature regimes. IBMs that predict how population-level abundance and biomass depend on  
461 temperature regime, considering complexities such as competition and behavior, still depend on

462 assumptions about food production rates. Even though salmonid food production is notoriously  
463 variable and uncertain, additional studies to observe it and learn how it varies should improve  
464 our ability to predict temperature effects. To improve our ability to predict how temperature (and  
465 flow) regimes affect salmonids, we do not need a comprehensive understanding of food  
466 production dynamics; instead, we need to understand those dynamics just well enough to select  
467 simple yet valid assumptions of how food availability varies among those regimes.

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