

FEATURED PAPER

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

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Abstract

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

The effect of temperature regime on stream salmonids has long been an important management concern, and its importance is increasing rapidly. Management and research biologists often address temperature effects at scales from local to regional: for example, how temperature interacts with physical habitat and other variables to drive adaptive behaviors such as when and where to feed (Railsback et al. 2021b), how changes in flow and temperature regime resulting from (for instance) hydropower licensing and forest harvest (Leach et al. 2012) affect trout abundance, and how climate change interacts with other stressors to affect population viability (Ayllón et al. 2021).

These questions usually depend less on acute temperature stress and more on sublethal effects, such as how temperature affects growth, because sublethal effects happen over wider and lower ranges of temperature.

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

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

However, bioenergetics modeling is popular as a way to relate fish growth to temperature and other variables *because* it is simple. Unlike another widely used energetics approach (dynamic energy budget theory; Nisbet et al. 2000; Kooijman 2010), the Wisconsin model has two characteristics that make it useful for management modeling. First, it uses only a minimal set of variables to link temperature and growth: growth rate, energy intake, temperature, fish size, and activity. Second, the model’s energy compartments and mechanisms are clearly related to actual physiology and therefore are measurable, at least in principle. We can put fish in the laboratory and measure, for instance, how metabolic energy demand varies with temperature and swimming speed. Therefore, the Wisconsin model provides a framework for combining observations from various experiments into a predictive tool. It has become a very important tool not just by itself but as the growth component of numerous models (cited throughout this article) of phenomena from individual growth to population dynamics to regional productivity.

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

The fundamental problem with the empirical literature is that quantitative results depend on factors that always vary among experiments; examples include species and stock, exercise condition, life history stage, food type, and measurement methods (Hartman and Brandt 1993). Consequently, results from different experiments often conflict (even when experiments use very similar methods and

equipment; e.g., Forseth and Jonsson 1994; Myrick and Cech 2000), and combining them into a useful set of equations and parameters requires judgment and assumptions that introduce uncertainty. Other problems with many laboratory studies include (1) the use of ad libitum feeding and artificial food, which are convenient but produce unnaturally food-rich, high-energy conditions; (2) not taking observations at the extreme temperatures that are often of management concern or not observing enough temperatures to define the sharp changes that can occur at high temperatures; and (3) unmeasurable variation in food intake and swimming speed due to competitive interactions among multiple fish kept in the same tank (e.g., Forseth and Jonsson 1994).

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

MANAGEMENT ASSUMPTIONS AND MODEL PREDICTIONS

Assumption 1: Growth Is Driven by Temperature

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

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

Beauchamp et al. (1989) found high sensitivity to food intake parameters in salmonid applications of the model.

I examined the relative effects of temperature and food consumption with a simple sensitivity experiment: I executed the Wisconsin model for both temperature and ration ranging from -20% to $+20\%$ of baseline values. (Following Deslauriers et al. [2017], I use “ration” as an individual’s mass rate of food consumption [g/d]; energy intake rate is equal to ration times a prey energy density.) I used version 1.1.3 of Fish Bioenergetics 4.0 software (Deslauriers et al. 2017), its standard formulation for adult Rainbow Trout, and its default prey and predator energy densities of 3,000 and 4,500 J/g. I simulated growth of a 40-g Rainbow Trout over 30 d with constant temperature and ration. The baseline value of ration, 2.06 g/d, was calculated as that producing zero growth at 20°C , representing realistic intake in a natural, relatively oligotrophic environment. The baseline temperature was 15°C . Therefore, I varied temperature from 12°C to 18°C with a ration of 2.06 g/d and then varied the ration from 1.65 to 2.47 g/d with a temperature of 15°C .

The results of this experiment (Figure 1) indicate that food—energy intake rate—affects growth as much as or more than temperature does. Food intake seems even more important when we consider that it often varies far more widely than temperature among sites, seasons, and perhaps management scenarios, such as alternative flow regimes; a decrease in flow, for example, may produce an increase of several degrees in summer temperature but a large decrease in drift food delivery (e.g., Harvey et al. 2006). Therefore, it appears risky to assume that

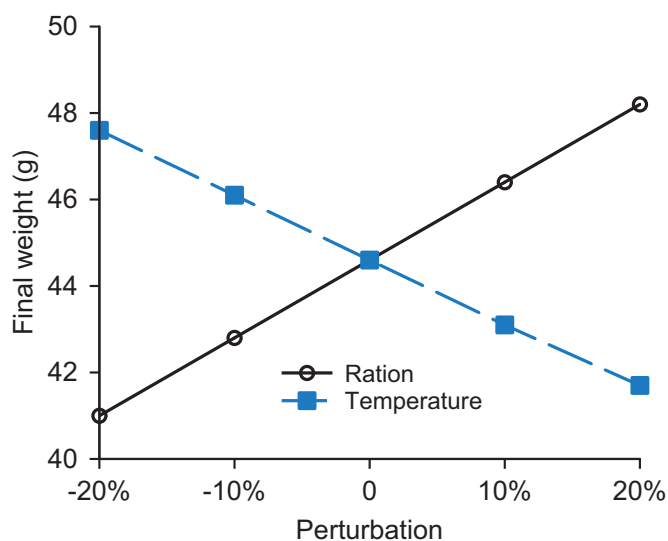


FIGURE 1. Results of the temperature and ration sensitivity experiment for adult Rainbow Trout. The X-axis is ration or temperature, expressed as the percentage change from its baseline value, and the Y-axis is predicted fish weight after 30 d.

differences in growth (among sites, over time, etc.) are due to temperature alone and not also to food availability. In fact, we should also consider other factors that affect the energy balance, such as differences in activity (e.g., between low- and high-slope sites) or food quality (e.g., between times when food is dominated by immature aquatic insects versus adult or terrestrial insects).

Assumption 2: There Is an Optimal Temperature for Growth

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

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

As in the first experiment, I selected consumption parameter values representing moderate energy intake, producing zero growth at 20°C : an absolute ration of 2.06 g/d, a relative ration of $0.0515 \text{ g}\cdot\text{g}^{-1}\cdot\text{d}^{-1}$, and p of 0.265. I also simulated high energy intake: an absolute ration of 4.50 g/d, a relative ration of $0.0910 \text{ g}\cdot\text{g}^{-1}\cdot\text{d}^{-1}$, and p of 0.500. These high intake rates produce 20 g of growth over 30 d at 20°C , an average of 1.4% of body weight per day. For comparison, Myrick and Cech (2000) observed growth in the range of 3.0–3.7% per day at 19°C and 22°C with ad libitum feeding of high-energy pellets. I simulated 30 d of growth for a Rainbow Trout starting at 40 g under eight constant temperatures from 5.0°C to 22.5°C .

The results for moderate energy intake (Figure 3, top panel) show that an “optimal” growth temperature only occurs when we assume that food consumption is a constant fraction of C_{max} , not when we simulate a constant

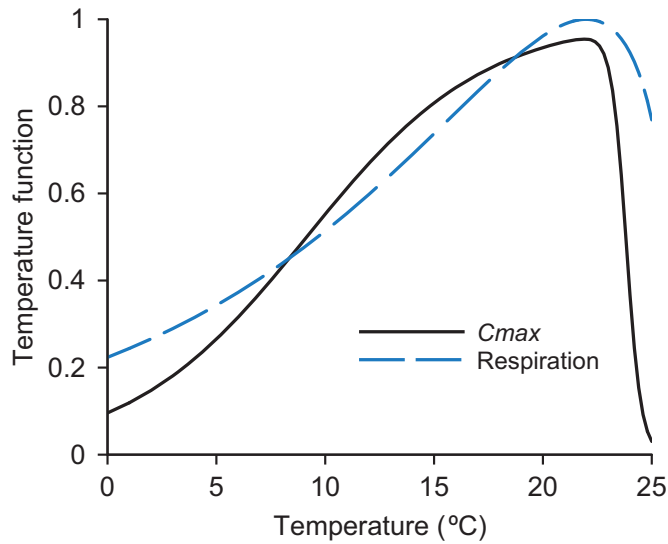


FIGURE 2. Temperature functions for maximum consumption rate (C_{max}) and (for comparison) respiration in the adult Rainbow Trout formulation provided with Fish Bioenergetics 4.0 software (Deslauriers et al. 2017).

energy intake rate. When the model assumes that fish have the same absolute energy intake, and metabolic energy demands increase with temperature (up to a peak at 22°C, in this case; Figure 2), then growth rate can only decline as temperature increases. However, when the model assumes that food consumption follows the complex function for C_{max} , which also increases with temperature, then a peak in growth as temperature increases is possible as an artifact of the C_{max} temperature function. (Using similar methods, Beauchamp [2009] showed that the temperature producing the highest predicted growth depends on p .)

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

If this simulation experiment indicates that peaks in simulated growth with temperature are artifacts of assumptions about C_{max} , then why have “optimal” temperatures been found in laboratory studies of real salmonids? One answer appears to be that such studies typically use ad libitum feeding (e.g., Forseth and Jonsson 1994; Myrick and Cech 2000; Zeigler et al. 2013), so growth is limited by the digestion rate instead of the balance between a limited energy intake and metabolic costs that increase with temperature. (In fish such as grazers that use less-digestible food, temperature appears to have a strong

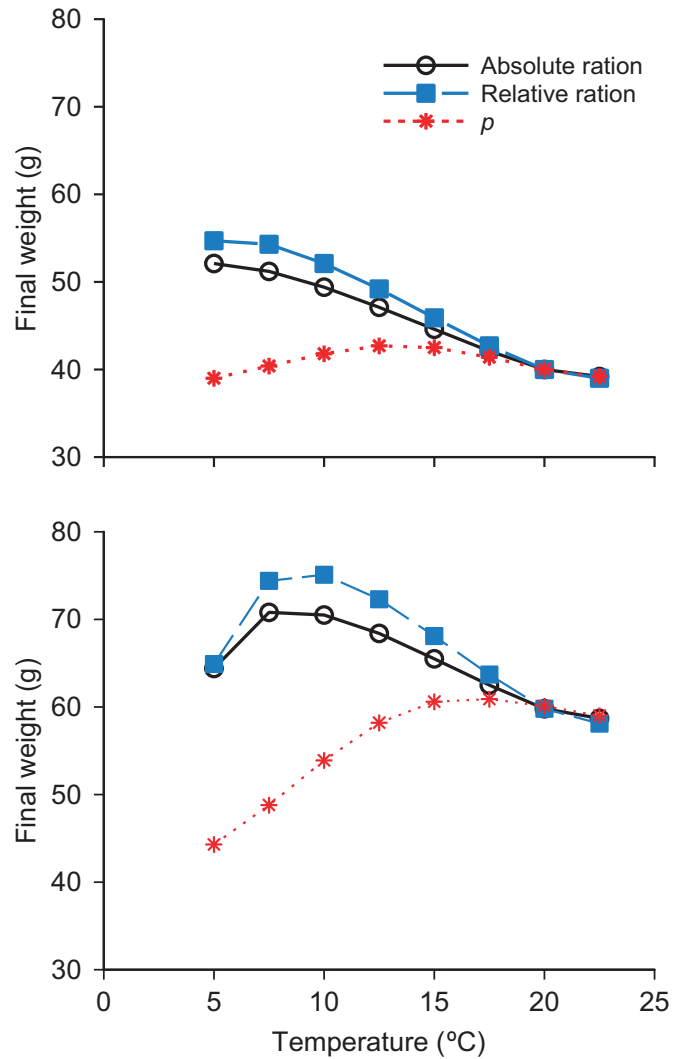


FIGURE 3. Results of the simulation experiment examining the optimal temperature for growth: response of simulated Rainbow Trout growth (as in Figure 1) for three assumptions about food consumption. The top panel depicts moderate food intake, producing zero growth at 20°C. The bottom panel depicts high intake that produces growth of 1.4% of body weight per day at 20°C.

effect on growth because digestion rates are strongly temperature dependent, and energy assimilation is typically limited by digestion instead of intake rates; e.g., Hofer et al. [1982].) Slower digestion at lower temperatures is likely what causes the appearance of an optimal growth temperature in experiments with ad libitum feeding (and the reason that C_{max} is low at low temperatures). However, at more natural food consumption rates the energy assimilation of salmonids is unlikely to be limited by digestion rate except perhaps at low temperatures. There is some evidence to support this potential explanation. Wurtsbaugh and Davis (1977) observed growth in juvenile Rainbow Trout under three temperature regimes and

several ration levels. At low rations, growth always decreased with temperature, but temperature had positive effects on growth at higher rations. Cui and Wootton (1988) observed growth of Eurasian Minnows *Phoxinus phoxinus* that received small invertebrates at five ration levels and that were held at four temperatures; they too found growth to only decrease with temperature at low rations, whereas growth peaked or increased with temperature at high rations. The concept of an optimal temperature for growth may be useful in situations where food is essentially unlimited and energy rich—for instance, hatcheries and prey pulses (Furey et al. 2016)—but it appears questionable for salmonids feeding on invertebrate prey, in which case growth is much more likely to be limited by food capture rate than by digestion rate.

This experiment clearly shows that the response of growth to temperature depends, even qualitatively, on what happens to food consumption. The differences among ration assumptions in Figure 3 have important management implications. For example, when we assume that absolute ration is constant, then growth under moderate energy intake is most sensitive to temperature at intermediate levels of about 7–17°C; when we assume constant p , then growth is insensitive to temperature at approximately 10–17°C and is most sensitive above and below that range. Management recommendations based on temperature–growth relations observed under *ad libitum* feeding (e.g., Zeigler et al. 2013) seem especially risky.

Assumption 3: Temperatures Effects Are Important Only in Summer

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

Studies applying bioenergetics models to year-round growth at sites with less-extreme thermal regimes, however, have found that temperature can have strong effects on growth during seasons other than summer. Railsback and Rose (1999) analyzed temperature effects on growth using the Wisconsin model and trout sizes observed in spring and fall at a number of sites in the Sierra Nevada, California. They concluded that temperature had stronger effects from fall to spring than from spring to fall. Similarly, Armstrong et al. (2021) applied the model of Fullerton et al. (2017), which also uses a Wisconsin model formulation to represent growth, to year-round temperatures throughout several watersheds in the Pacific

Northwest. They concluded that lower-elevation sites offering low summer growth due to higher temperatures provided important high-growth habitat at other times of year.

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

Assumption 4: Warm-Adapted Populations Grow Better at Higher Temperatures

Clear evidence shows that some salmonid populations are better adapted to high temperatures than others, even within a species (e.g., Eliason et al. 2011; Chen et al. 2015, 2018). This evidence is mostly derived from measurements of acute thermal effects, such as critical thermal maximum (the temperature at which a fish loses swimming ability during rapidly increasing temperatures) and aerobic scope (the difference between resting and maximum metabolic rates at elevated temperatures, which reflects how resting metabolic rate increases and maximum rate decreases with temperature; e.g., Eliason et al. 2011). Larger hearts and increased cardiac performance appear to be key mechanisms conveying acute temperature tolerance (Chen et al. 2018).

We might naturally assume that warm-adapted salmonid populations have lower sublethal effects: that populations that have evolved to tolerate higher temperature extremes are also likely to grow over a wider range of temperatures. However, the mechanism of adaptation—increased heart size and pumping rate—seems likely to come at a cost of higher metabolic rate. In fact, recent evidence indicates the validity of this concern. Data from two southern California steelhead populations indicate that the population from a warmer stream has a higher tolerance of extreme temperatures and approximately double the resting metabolic rate, measured over temperatures of 18–21°C (E. J. Eliason, Department of Ecology, Evolution, and Marine Biology, University of California–Santa Barbara, personal communication). It seems reasonable to assume that this difference in resting metabolic rate would extend to lower temperatures as well.

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

overestimation of growth or underestimation of food requirements for warm-adapted populations.

DISCUSSION

Conflicts between Management Assumptions and Bioenergetics Modeling

The Wisconsin bioenergetics model has proven extremely useful as a temperature management tool. It is useful not because it is “realistic”—it is not—but, in contrast, because it is as simple as possible while still linking the management variables we need to evaluate, via mechanisms we can measure. The model provides a way to assemble relations observed in diverse laboratory studies into a predictive tool. My comparison of Wisconsin model results to management assumptions leads to the following conclusions, some of which challenge how we commonly think about temperature effects.

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

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

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

Warm-adapted salmonid populations may be more, not less, vulnerable to temperature effects on growth. The higher metabolic rates that allow survival of higher extreme temperatures in some populations also require higher food intake to maintain growth. Consequently,

populations that have evolved tolerance of higher temperatures must be assumed more vulnerable to elevated temperatures that are not accompanied by higher food availability.

Representing Consumption in Bioenergetics Analyses

The main lesson from my analyses is that we should not ignore food in modeling how temperature affects salmonid growth. Unfortunately, while temperature is easy to measure and model, food availability to and consumption by fish are complex, expensive to observe, and impossible to predict with certainty. Therefore, we almost always rely on simple assumptions about food; typically, we calibrate a consumption parameter by fitting the model to growth observed under one temperature regime and then use that parameter value to predict growth under other temperature regimes.

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

The Wisconsin model literature and software have long promoted the practice of representing consumption as a constant value of p , an assumption that seems especially risky and difficult to justify. That assumption causes absolute ration and energy intake rate to vary with temperature according to the complex relation assumed between C_{max} and temperature (Figure 2). This variation makes it harder to interpret results and to understand exactly what drove predicted growth (Railsback and Rose 1999). Because C_{max} typically increases with temperature except at high temperatures, assuming constant p includes a hidden assumption that ration increases with temperature; therefore, it could underestimate the effects of increased temperature on growth (but see below concerning temperature effects on ration). Other problems with this assumption include the lack of an ecological reason why a fish would or could adjust its consumption to maintain constant p as temperature changes (I discuss behavioral aspects of consumption below) and that C_{max} is a particularly challenging variable to define precisely and measure (Hartman and Brandt 1993)—it can vary with factors that are rarely controlled and are not included in the model, such as exercise condition of the fish, food type, activity, and measurement time scale. Figure 2 makes it clear that uncertainty in the Rainbow Trout C_{max} temperature function has especially strong effects on predicted growth at temperatures greater than 20°C. (This uncertainty is why I simulated growth at temperatures no higher than

22.5°C.) Further, the physiological mechanism driving C_{max} —digestion rate—is unlikely to limit growth under consumption rates that are typical of natural conditions (except, possibly, when temperatures are low and food availability is high).

The alternative assumption of a constant ration (either absolute or relative) is simpler and more conservative by not including the hidden assumption that ration increases with temperature. Calibrating the Wisconsin model to estimate a constant ration that is then used to estimate effects of other temperature regimes seems simple and clear as well as cautious for examining temperatures above those used for calibration. As an example, Hawkins et al. (2020) modified their previous model that assumed a constant p (Fullerton et al. 2017) to instead use a constant relative ration.

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

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

This simulation provides only a very simplistic view of the potential effects of food availability increasing with temperature and should not be used to inform management decisions; however, it further confirms the importance of assumptions about food consumption when predicting temperature effects on growth and, to some

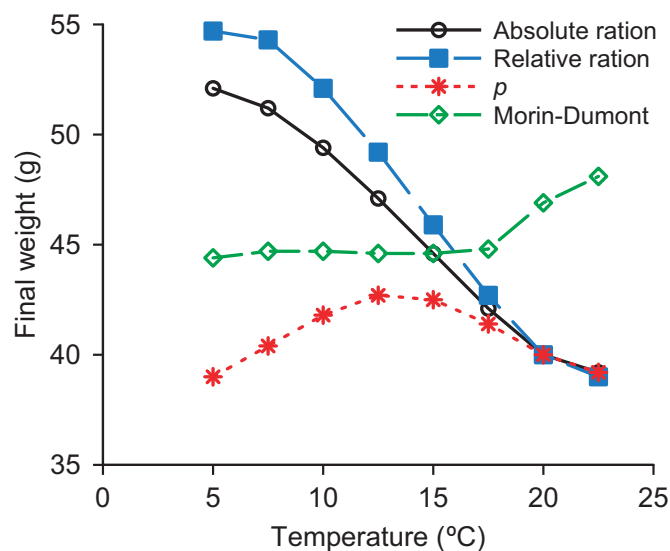


FIGURE 4. Growth simulations as in the top panel of Figure 3, with the additional assumption that food consumption follows the temperature term of the insect growth equation provided by Morin and Dumont (1994).

extent, even brings into question the generalization that increased temperature always has negative effects on salmonid growth and population biomass accumulation. It raises the possibility that increased benthic productivity could largely offset the increased metabolic demands of fish; as Railsback and Rose (1999) suggested, the strongest effect of temperature on trout growth could be an indirect effect via food production. Such increased productivity could help to explain the persistence of warm-adapted populations despite their higher metabolic rates.

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

time spent feeding and higher survival instead of (or in addition to) higher growth.

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

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

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

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

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

Research Needs

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

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

The evidence that growth depends on food consumption as much as or more than on temperature indicates that we also need useful observations and models of how the production of salmonid food depends on the variables to which we predict growth responses, especially flow and temperature regimes. Individual-based population models that predict how population-level abundance and biomass depend on temperature regime, while considering complexities such as competition and behavior, still rely on assumptions about food production rates. Even though salmonid food production is notoriously variable and uncertain, additional

studies to observe food production and learn how it varies should improve our ability to predict temperature effects. To improve our ability to predict how temperature (and flow) regimes affect salmonids, we do not need a comprehensive understanding of food production dynamics; instead, we need to understand those dynamics just well enough to select simple yet valid assumptions of how food availability varies among those regimes.

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