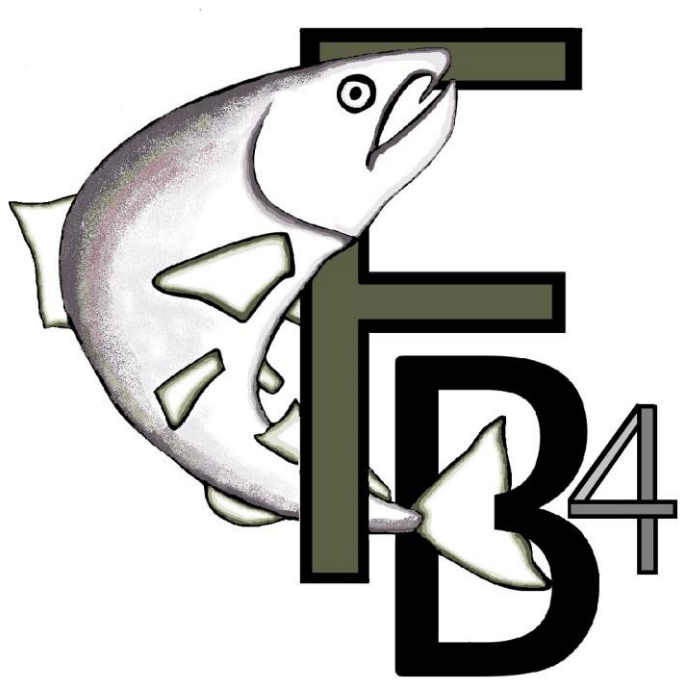
FISH BIOENERGETICS 4.0:
AN R-BASED MODELING APPLICATION

USERS MANUAL



FB4 v1.0

12.06.2017

Fish Bioenergetics 4.0

Fish Bioenergetics 4.0 (FB4) is the product of countless communications involving many colleagues and students -- unfortunately, too many to list here – and we thank them all.

Our goal in developing FB4 as an open source application was to expand the availability and science of bioenergetics modeling. Visit our website at fishbioenergetics.org to learn more about FB4 and obtain information for installing the application.

 is an open source programming language and software environment for statistical computing.

Shiny by RStudio, is an interactive web application that serves as a graphical user interface for FB4.

Shiny application developed by *David Deslauriers.*

R code written by *David Deslauriers* and *James Breck.*

This work was supported in part by the U.S. Army Corps of Engineers (D. Deslauriers, doctoral research), the U.S. Geological Survey (S. Chipps and C. Madenjian), North Carolina State University (J. Rice), and the South Dakota Department of Game, Fish and Parks (S. Chipps).

Suggested citation:

Deslauriers, D., S.R. Chipps, J.E. Breck, J.A. Rice and C.P. Madenjian. 2017. Fish Bioenergetics 4.0: An R-based modeling application. Fisheries 42(11):586-596.

ACKNOWLEDGMENTS

This manual represents the fourth version of what first appeared as the "Wisconsin model" by Hewett and Johnson (1987) and subsequent versions by Hewett and Johnson (1992) and Hanson *et al.* (1997). We thank Steven W. Hewett, Barry L. Johnson, Paul C. Hanson, Timothy B. Johnson, Daniel E. Schindler, James F. Kitchell, David A. Beauchamp, Kyle J. Hartman, Jason T. Breck, and Marc Trudel for technical assistance and support during development of Fish Bioenergetics 4.0. We are particularly indebted to Tim Johnson for providing initial data for new species models and the University of Wisconsin Sea Grant Institute for allowing us to reproduce text and instructional materials in previous editions of the manual.

We thank the many students and workshop participants who provided critical feedback for improving earlier versions of FB4. We especially thank North Carolina State University students from J. Rice's course (Fish Bioenergetics Modeling) for their inputs and suggestions that greatly improved FB4.

FOREWORD

Development and application of bioenergetics modeling has flourished in recent years, due in part, to the complexity of issues being faced by fisheries biologists. Bioenergetics models provide a sound, theoretical approach for estimating energy allocation in animals by partitioning consumed energy into three basic components: 1) metabolism, 2) wastes, and 3) growth (Winberg 1956). Because the models are based on mass balance equations, they are often used to estimate growth or consumption, given information on other variables. Bioenergetics models are particularly attractive for estimating food consumption by free-ranging fishes given the time and effort required of more traditional approaches (Kitchell *et al.* 1977). Today, these models are widely used in fisheries management and research to address issues related to climate change, invasive species, sportfish management, and endangered species – just to mention a few.

Like other mathematical models, bioenergetics models are simplifications of reality. How well they describe the real world depends on appropriate parameterization of the model and the accuracy of input data used to drive them (Bartell *et al.* 1986). Fortunately, as development and application of bioenergetics models have increased, so too have efforts for parameterizing model input (Hartman and Hayward 2007) and evaluating model output (Chipps and Wahl 2008) with the goal of reducing uncertainty in bioenergetics models. As our colleague Dr. James Kitchell once noted, "*The model cannot be wrong because it is based on a budget that must be right. It will improve in proportion to our ability to estimate the physiological parameters that regulate growth and the errors or bias of data employed as inputs*".

However, not all models are of the same quality, and a model developed for one particular application or set of conditions may not be appropriate for another. Before applying any of the models in FB4, the user should read the publication(s) documenting the model's development, and become familiar with its assumptions and limitations.

We also urge users to be cautious when applying fish bioenergetics models beyond the range of conditions for which they were developed. In statistics, we are taught to be wary about extrapolating a regression equation beyond the range of the predictor variables. A similar idea applies here. Because bioenergetics models incorporate descriptions of the component processes of growth, we expect that the models will perform robustly for a wide range of conditions and for combinations of conditions not explicitly measured in the laboratory. However, if fish are exposed to extreme conditions, the component physiological processes are likely to respond differently than they would to conditions within the normal range. For example, osmoregulation may begin to fail at very low temperatures; enzymes will become denatured and lose their function at very high temperatures; respiration rate will decline if the dissolved oxygen level is too low. Bioenergetics models should not be expected to give correct predictions under such extreme conditions unless the component processes are modified to incorporate the additional processes involved. In fact, this would be a useful area for future research.

It has been 20 years since the last version of Fish Bioenergetics (version 3.0) was released. In that time, we have seen dramatic increases in the number of bioenergetics models that have been developed and novel ways in which they are being applied. Moreover, advances in computing technology and statistical software applications have opened the doors to new analytical platforms. The development of Fish Bioenergetics 4.0 stems from these advances and includes several new features compared to earlier versions: (1) FB4 is free. FB4 is an open-source application that uses an R-based operating platform linked

to a graphical user interface (Shiny by RStudio). (2) FB4 is adaptable. Unlike compiled programs, the code that drives the models can be modified by users familiar with the R language. Thus, any 'bugs' in the code can be quickly corrected. And while we've done our best to minimize these, there are always "unknown unknowns". (3) FB4's user-friendly environment. The Shiny application provides an easy-to-use interface with R-studio, so users need not be familiar with the R computing language. In addition to buttons and drop-down menus, we enhanced the Initial Settings page so that model parameter values and the original citation are provided for any model the user selects, as well as any notes about the model that the user should be aware of. We also added graphing features that allow users to instantly visualize input data prior to performing a simulation. (4) Fixed previous bugs. We corrected several calculation errors from the previous version, and 5) Number of models. As mentioned earlier, a variety of new models have been developed since the last release, increasing the total number of bioenergetics models available from 33 to 105. New models can be added as they are developed.

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Core Processes in Bioenergetics

Bioenergetics models represent an energy budget equation in which energy consumed by a fish is balanced by energy expended for total metabolism, waste losses and growth. As with earlier versions of Fish Bioenergetics software (Hewett and Johnson 1987, 1992; Hanson *et al.* 1997), FB4 uses taxon-specific physiological estimates of food consumption (or growth), respiration, egestion and excretion that drive the energy balance equation.

Consumption = metabolism + wastes + growth
= (respiration + active metabolism + specific dynamic action) + (egestion + excretion) + (somatic growth + gonad growth)
C = (R + A + SDA) + (F + U) + (SG + GG)

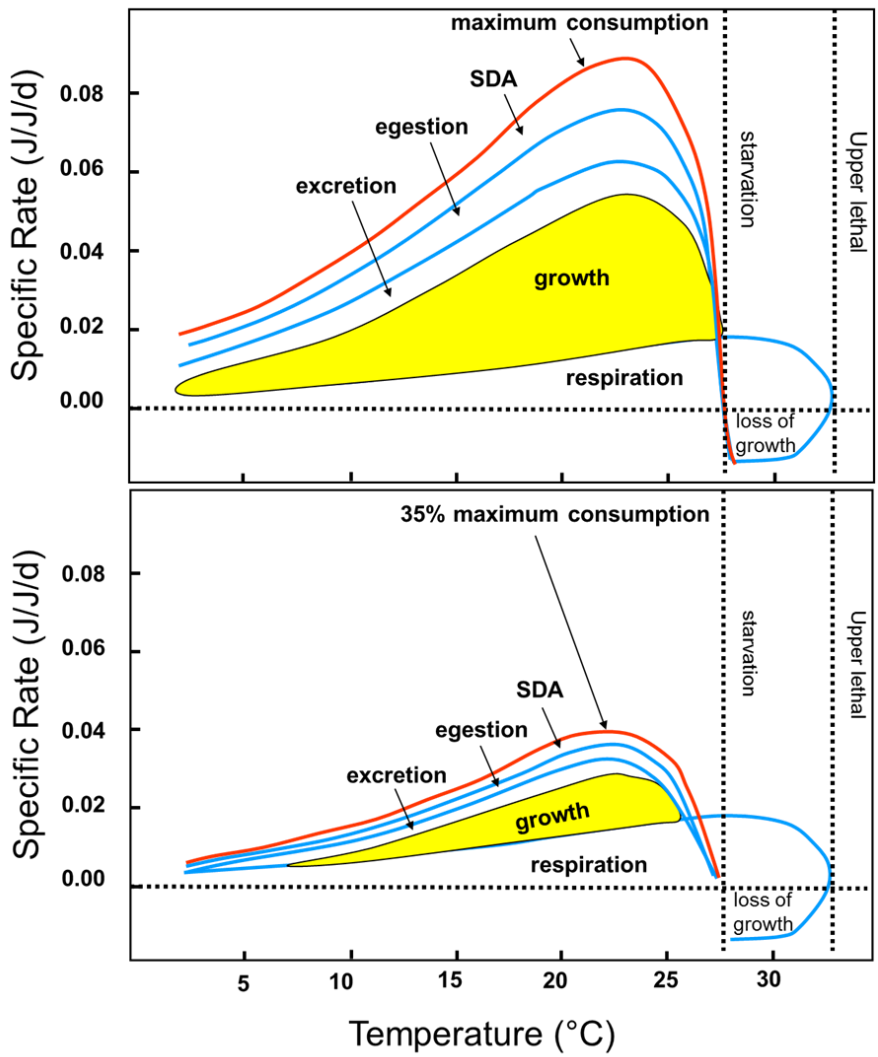


Figure 1. Generalized energy budget for a fish as a function of water temperature. The top panel depicts energy use and resultant growth for a fish feeding at its maximum feeding rate (maximum consumption, C_{max}=100%). The bottom panel depicts similar energy allocation, but for a fish feeding at 35% of its maximum consumption rate (adapted from J. Kitchell, pers. comm.).

Each of the physiological processes is described by a set of functions that are regulated primarily by water temperature and body size. The total number of physiological parameters ranges from 12 to over 30 depending on mathematical functions chosen by the user to describe the physiological process of each taxon or life-stage. The hierarchy of energy allocation is an important component of the bioenergetics modeling approach. Consumed energy is first allocated to metabolism (required for maintenance, activity, and specific dynamic action), some is lost as waste (feces and urine) and that left over can be allocated to growth (somatic and gonadal development). This hierarchy is similar to that of an economic 'balance sheet', where the first costs paid are for rent or mortgage (metabolism) that sustain the animal. The second set of costs (waste losses) are like taxes- they are proportional to income (food consumption) and must be paid. And finally, the remaining funds may then be allocated to savings (growth) or invested in the next generation (gonad development). Like an account balance, a record of growth shows how well the organism has resolved the complexities of its environment (Hanson *et al*. 1997).

The next section defines the individual parameters needed to describe the energy budget of a fish. For each of the major physiological processes (consumption, metabolism, egestion and excretion), several different forms of the underlying equations are given to provide flexibility in describing the unique physiologies of different species. Methods for directly measuring bioenergetics components can be found in Adams and Breck (1990) and Hartman and Hayward (2007). To date, parameter sets have been determined for 70 species of fish and 3 invertebrate species and, where possible, modified to recognize important ontogenetic shifts in physiology between larval, juvenile and adult fish. All calculations in the model are based on specific rates (e.g., Joules of prey per Joules of predator per day) and are calculated on a daily time step. Where necessary, predator and prey energy densities (Joules per gram of wet weight) are used to convert between mass and energy density.

Consumption

C_{max} and P-value

Food consumption is estimated as the proportion of maximum daily food consumed by a fish at a given mass (W, in g) and water temperature (°C). Maximum daily consumption (C_{max}) is expressed as a specific rate (g of prey consumed per g body mass per day) and is estimated as an allometric function of mass from *ad libitum* feeding experiments conducted at the optimum temperature for a particular fish species (Hartman and Hayward 2007) as,

$$C_{max} = CA \cdot W^{CB},$$

where **CA** and **CB** are the intercept and slope coefficients, respectively. Maximum daily consumption is then modified by a temperature dependence function (**F(T)**) and a proportionality constant (P-value, **p**) that accounts for ecological constraints on the maximum feeding rate (C_{max}). The P-value theoretically ranges from 0 to 1, with 0 representing no feeding, and 1 indicating the fish is feeding at its maximum rate based on its size and water temperature. The basic form of the consumption equation is,

$$C = C_{max} \cdot p \cdot F(T).$$

In Fish Bioenergetics 4.0, users can specify a P-value to be used in a simulation, or can set consumption as a constant daily ration in grams or percent body weight per day (in these cases the consumption function in the model is bypassed). Alternatively, the user can specify a final weight or final total consumption value,

and FB4 will iteratively solve for a constant P-value to reach that specified final value. To achieve this fit, the model uses an initial P-value (p=0.5) to balance the bioenergetics equation every day, then re-calculates the P-value iteratively using a binary search algorithm, until the simulation process generates a final output that equals the specified output (i.e., the model is fit to the user-defined final weight or consumption value; Figure 2).

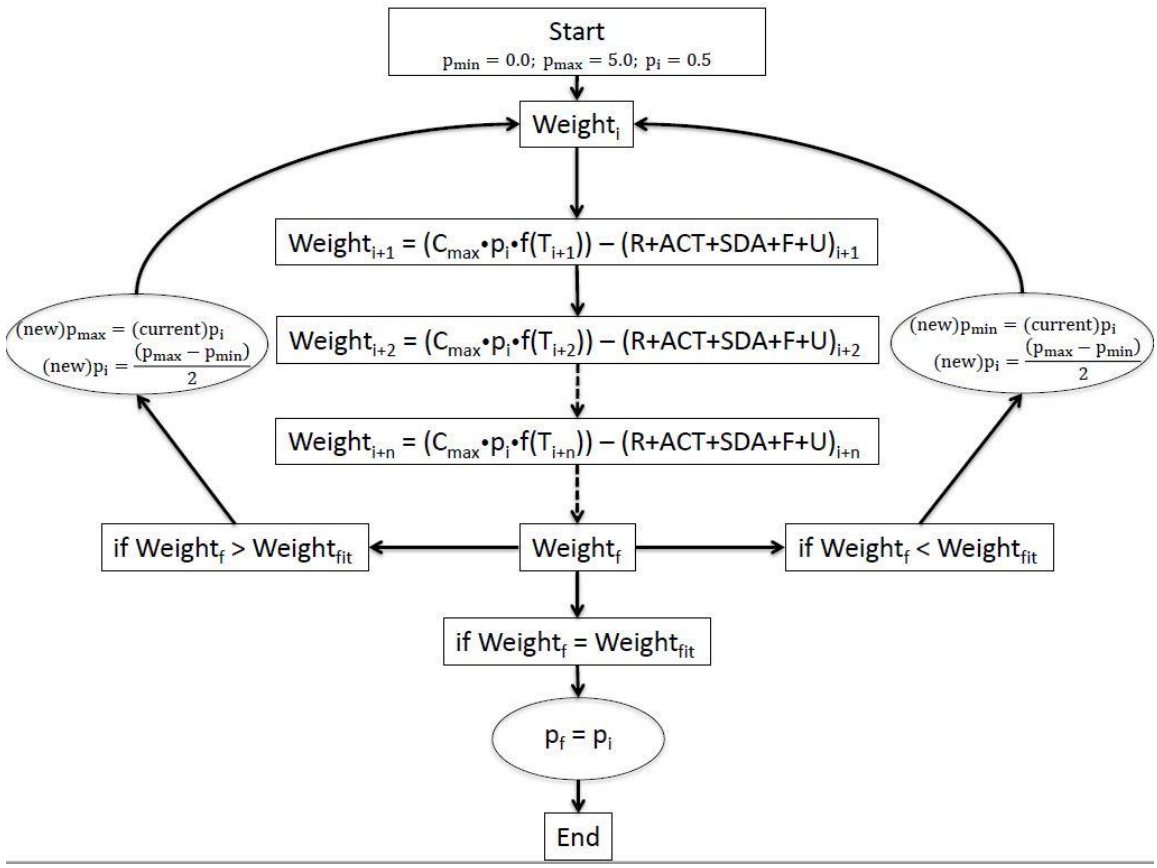


Figure 2. Binary search algorithm used to estimate the P-value in a Wisconsin-type bioenergetics model. Initial weight ($Weight_i$) and specified final weight ($Weight_{fit}$) are used as inputs to calculate a P-value (p_i) through an iterative process. The initial P-value (p_i) is set to 0.50, and the initial upper and initial lower limits of the P-value are set (e.g., P_{min} is set to 0.000 and P_{max} is set to 5.000). The model runs one iteration, generating $Weight_{i+n}$ values for every day of the simulation, including a final weight ($Weight_f$) value. If the final weight is less than the specified $Weight_{fit}$ then the needed P-value must be larger than the current P-value (p_i), so P_{min} is reset to the current value of p_i. If the final weight is greater than the specified $Weight_{fit}$ then the needed P-value must be smaller than the current P-value, so P_{max} is reset to the current value of p_i. Then a new trial value of p_i is calculated from P_{min} and P_{max} and the model runs the next iteration. The iterative process ends once $Weight_f$ and $Weight_{fit}$ are equivalent (within 0.001), and the final P-value (p_f) is returned. The initial P_{min} and P_{max} (e.g., 0.000 and 5.000, respectively) are boundaries that cannot be exceeded by the P-value estimated from the search algorithm. If these boundaries would need to be exceeded to match the specified final weight (for example, if the user specified a final weight that was less than the final weight of a starving fish with a P-value of zero), then the search algorithm will be terminated, and an error message will be issued.

The interpretation of P-values can be useful in exploring factors such as prey availability, spatiotemporal foraging patterns, and in making management decisions (Rice *et al.* 1983; Robel and Fisher 1999). High P-values (e.g., >0.5), for example, imply greater feeding rates and are often linked to favorable values of factors such as prey abundance, prey quality and(or) water temperature. A word of caution however; in

many bioenergetics models, laboratory-derived C_{max} estimates are generally calculated from the weight of the prey (g) consumed rather than the amount of energy consumed (i.e., Joule, J). Thus, if the energy density of prey used to derive a C_{max} estimate varies substantially from that of the diet, resulting P-values could be misleading in their ability to characterize the true proportion of maximum food consumed. P-values are best viewed in relative terms; for example, "How does a 20% increase or decrease in food consumption (i.e., P-value) influence fish growth?"

Temperature dependent functions F(T) for consumption

Four forms of the temperature dependence function (F(T)) are available in FB4:

Model 1: Exponential equation (Stewart *et al.* 1983)

$$F(T) = e^{(CQ \cdot T)}$$

This simple exponential function is useful when ambient temperatures are at or below the physiological optimum for the species. In this formulation, **CQ** is the water temperature-dependent coefficient of consumption. When determining C_{max}, **CA** is the intercept of the mass dependence function (equivalent to C_{max} for a 1-gram fish) at 0 °C and **CB** is the mass dependence coefficient. Consumption Model 1 has been used for coldwater salmonids such as Lake Trout (Stewart *et al.* 1983).

Model 2: Q_{10}, T_{opt} and T_{max} (Kitchell *et al.* 1977)

$$F(T) = V^X \cdot e^{(X \cdot (1-V))}$$

where:

$$V = (CTM - T)/(CTM - CTO)$$

$$X = (Z^2 \cdot \left(1 + \left(1 + \frac{40}{Y}\right)^{0.5}\right)^2)/400$$

$$Z = ln(CQ) \cdot (CTM - CTO)$$

$$Y = ln(CQ) \cdot (CTM - CTO + 2)$$

This water temperature dependence function is most appropriate for warmwater species. With this model, **CA** is the intercept of the mass dependence function (equivalent to C_{max} for a 1-gram fish) at the optimum water temperature (**CTO**, the optimal temperature for consumption, i.e., the temperature at which consumption peaks in laboratory feeding trials), **CB** is the coefficient of the mass dependence, **CTM** is the maximum water temperature above which consumption ceases (typically approximated by the upper incipient lethal temperature), and **CQ** approximates a Q_{10} (the rate at which the function increases over relatively low water temperatures).

Model 3: Sigmoid function (Thornton and Lessem 1978)

$$F(T) = K_A \cdot K_B$$

where:

$$K_A = (CK1 \cdot L1)/(1 + CK1 \cdot (L1 - 1)$$

$$L1 = e^{(G1 \cdot (T - CQ))}$$

$$G1 = (\frac{1}{CTO - CQ}) \cdot \ln(\frac{0.98 \cdot (1 - CK1)}{CK1 \cdot 0.02})$$

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

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

$$G2 = (\frac{1}{CTL - CTM}) \cdot \ln(\frac{0.98 \cdot (1 - CK4)}{CK4 \cdot 0.02})$$

The Thornton and Lessem algorithm provides a better fit for some cool- and coldwater species, especially at lower water temperatures. It is essentially the product of two sigmoid curves - one fit to the increasing portion of the temperature dependence function (**K_A**) and the other to the decreasing portion (**K_B**). **CA** is the intercept of the mass dependence function (equivalent to C_{max} for a 1-gram fish) at the optimum water temperature and **CB** is the coefficient of the mass dependence. For the increasing portion of the curve, **CQ** is the lower water temperature at which the temperature dependence is a small fraction (**CK1**) of the maximum rate and **CTO** is the water temperature corresponding to 0.98 of the maximum consumption rate. For the decreasing portion of the curve, **CTM** is the water temperature (≥ **CTO**) at which dependence is still 0.98 of the maximum and **CTL** is the temperature at which dependence is some reduced fraction (**CK4**) of the maximum rate. Consumption Model 3 has been used to model a variety of species including Chinook and Coho Salmon (Stewart and Ibarra 1991).

Model 4: Cubic polynomial (Bevelhimer *et al.* 1985)

$$F(T) = e^{(CQ \cdot T + CK1 \cdot T^2 + CK4 \cdot T^3)}$$

This temperature dependence model has been successfully applied in esocid consumption models where **CQ**, **CK1**, and **CK4** are species-specific temperature-dependent constants (Bevelhimer *et al.* 1985).

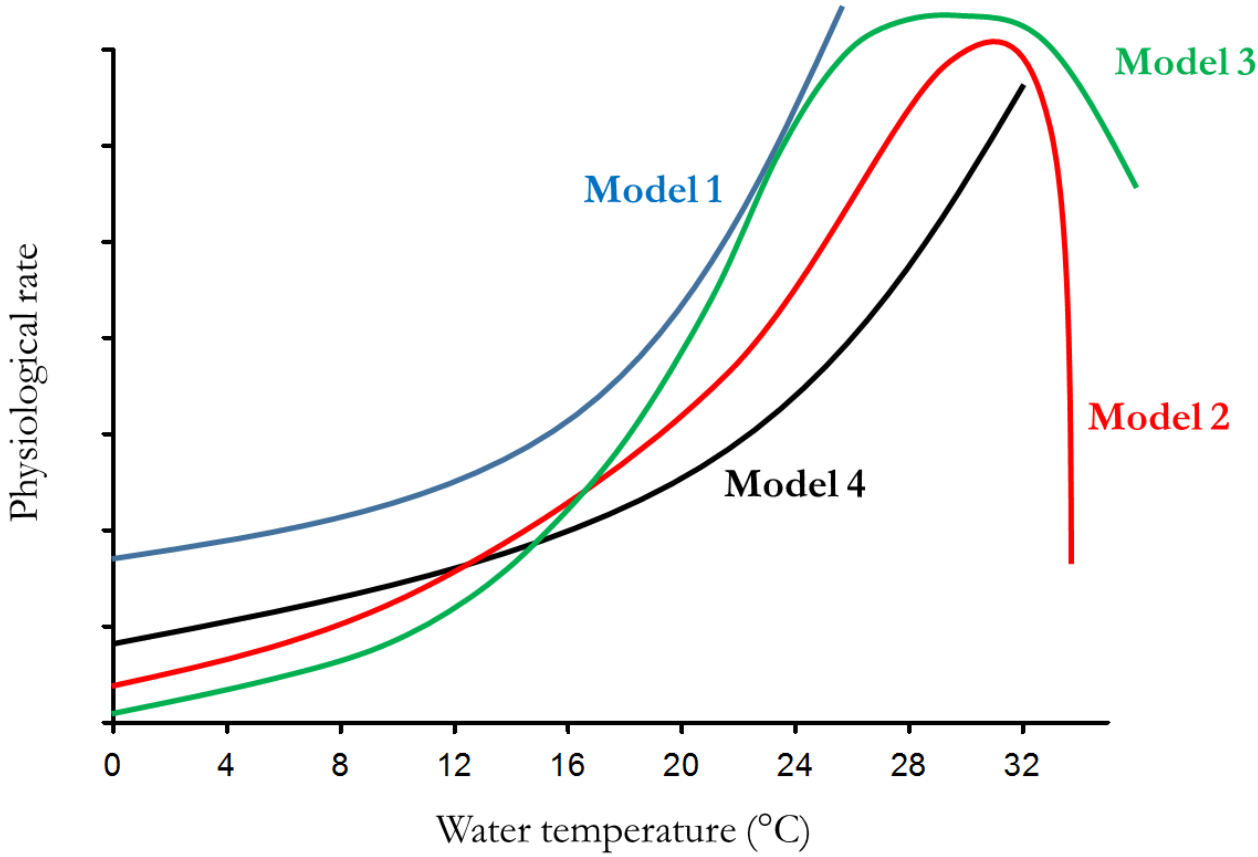


Figure 3. Generalized form of temperature dependence functions used to estimate consumption rate (Models 1, 2, 3 and 4) or respiration rate (Models 1 and 2) in bioenergetics models.

Respiration

Respiration (**R**; specific rate of respiration in g O_2/g fish/d) is dependent on fish size (W), water temperature (F(T)) and a function representing activity (*ACTIVITY*) as,

$$R = RA \cdot W^{RB} \cdot F(T) \cdot ACTIVITY$$

where **RA** and **RB** are the intercept and slope for the allometric mass function.

Because the output generated from the basic respiration equation returns a value that represents the specific amount of oxygen consumed over the course of a day (g O_2/g fish/d), it must be converted to an energy-equivalent value compatible with bioenergetics modeling. In this case, an oxy-calorific coefficient is used to convert O_2 consumption into Joules. The oxy-calorific coefficient used should be dependent on fish diet (Elliot and Davison 1975); as such FB4 provides users an option to input an oxy-caloric coefficient value. As a default value, FB4 uses 13,560 J/g O_2, which is the same value that was used for Lake Trout bioenergetics modeling (Stewart *et al.* 1983) and in Fish Bioenergetics 3.0 (Hanson *et al.* 1997).

The total metabolic cost for a fish is estimated by summing the costs of respiration (***R***) and the assimilated energy (**S**) lost to specific dynamic action. Specific dynamic action (**SDA**) is generally modeled as a constant proportion of assimilated energy (i.e., consumption minus egestion). Typical values of **SDA** lie between 0.15 and 0.2. Egestion (**F**) is calculated as a constant proportion of consumption or as a function of mass, temperature and ration size (see Waste Losses section) (Hanson *et al.* 1997).

$$S = SDA \cdot (C - F)$$

Temperature dependent F(T) and activity (*ACTIVITY*) functions for respiration

Model 1: Exponential with swimming speed (Stewart *et al.* 1983)

$$F(T) = e^{(RQ \cdot T)}$$

$$ACTIVITY = e^{(RTO \cdot VEL)}$$

where:

$$VEL = RK1 \cdot W^{RK4} \cdot e^{(RK5 \cdot T)}, when\ T > RTL$$

$$VEL = ACT \cdot W^{RK4} \cdot e^{(BACT \cdot T)}, when\ T \leq RTL$$

In this first model, a simple exponential relationship describes the temperature dependence of metabolism and activity as a function of swimming speed. Three different formulations of the activity function can be used: 1) swimming speed is a function of mass alone above a cutoff temperature (e.g., Bloater, Rudstam *et al.* 1994), 2) swimming speed is a function of mass and water temperature below a cutoff temperature (e.g., Lake Trout, Stewart *et al.* 1983), or 3) swimming speed is a constant (e.g., Largemouth Bass, Rice *et al.* 1983).

For mass dependence, **RA** is the specific mass of oxygen (g 0_2/g/d) consumed by a 1-gram fish at 0 °C and zero swimming speed, **RB** is the slope of the allometric mass function for standard metabolism, and **RQ** approximates the Q_{10} (the rate at which the function increases over relatively low water temperatures). When swimming speed is modeled as a function of mass or mass and temperature, **RTO** is the coefficient for swimming speed dependence of metabolism (s/cm), **RTL** is the cutoff temperature at which the activity relationship changes (°C), **RK1** is the intercept for swimming speed above the cutoff temperature (cm/s), **RK4** is the mass dependence coefficient for swimming speed at all water temperatures, **RK5** is the water temperature dependence coefficient of swimming speed at water temperatures above **RTL** (Klumb *et al.* 2003), **ACT** is the intercept (cm/sec for a 1-gram fish at 0 °C) of the relationship for swimming speed versus mass at water temperatures less than **RTL**, and **BACT** is the water temperature dependence coefficient of swimming speed at water temperatures below **RTL**. In either case, **RTM** is set to 0.

If swimming speed is a constant then **RTL**, **RK4, RK5** and **BACT** are set to 0, and **RK1** and **ACT** are set to the desired velocity (cm/s) (Hanson *et al.* 1997).

Model 2: Temperature-dependent with activity multiplier (Kitchell *et al.* 1977)

$$F(T) = V^X \cdot e^{(X \cdot (1-V))}$$

$$ACTIVITY = ACT$$

where,

$$V = (RTM - T)/(RTM - RTO)$$

$$X = (Z^2 \cdot \left(1 + \left(1 + \frac{40}{Y}\right)^{0.5}\right)^2)/400$$

$$Z = ln(RQ) \cdot (RTM - RTO)$$

$$Y = ln(RQ) \cdot (RTM - RTO + 2)$$

With this formulation, the temperature dependence of respiration is adjusted by an activity multiplier (**ACT**). **RTO** (°C) is the optimum temperature for respiration (where respiration is highest), **RTM** (°C) is the maximum (lethal) water temperature, and **RQ** approximates the Q_{10} (the rate at which the function increases over relatively low water temperatures). **RA** is the oxygen (g O_2/g/d) consumed by a 1-gram fish at **RTO** and **RB** is the slope of the allometric mass function for standard metabolism. Activity (**ACT**) is set to a constant multiplier of standard or resting metabolism, the "Winberg multiplier'' (Winberg 1956). Several recent studies have shown that activity may be a large and variable component of the total energy budget and is influenced by a number of environmental and physiological factors (Boisclair and Leggett 1989; Boisclair and Sirois 1993; Lucas *et al.* 1993; Madon and Culver 1993).

Waste Losses (Egestion and Excretion)

Egestion (fecal waste, **F**) and excretion (nitrogenous waste, **U**) can be computed as a constant proportion of consumed energy or as functions of water temperature and consumption. Waste losses are computed as grams of waste per gram of fish per day (Hanson *et al.* 1997).

Model 1: Proportional to consumption (Kitchell *et al.* 1977)

$$F = FA \cdot C$$

$$U = UA \cdot (C - F)$$

In this model, egestion (F) is computed as a constant proportion (**FA**) of consumption and thus represents waste loss of non-assimilated energy. Because excretion (U) represents waste loss from assimilated energy (consumption minus egestion), it is computed as a constant proportion (**UA**) of C-F. This formulation suffices for most species. For models in which UA was originally expressed as a proportion of C, the value of UA has been modified in FB4 to yield the equivalent result.

Model 2: Dependent on temperature and ration (Elliott 1976)

$$F = FA \cdot T^{FB} \cdot e^{(FG \cdot p)} \cdot C$$

$$U = UA \cdot T^{UB} \cdot e^{(UG \cdot p)} \cdot (C - F)$$

This model incorporates both water temperature and feeding rate. It is most appropriate when the diet is either all invertebrate or all fish. **FA** is the intercept of the proportion of consumed energy egested versus water temperature and ration and **FB** is the coefficient of water temperature dependence of egestion. **FG** is the coefficient for dependence of egestion on feeding level (P-value). **UA**, **UB**, and **UG** can be similarly defined for excretion (Hanson *et al.* 1997).

Note that at positive temperatures very close to 0 °C or at negative temperatures, the Model 2 equations yield inaccurate estimates of waste losses (Kao *et al.* 2015a, 2015b). To circumvent problems arising from this issue, the FB4 user may elect to assign a value of 0.1 °C to all temperatures in the temperature input file less than 0.1 °C (Kao *et al.* 2015a, 2015b). Eventually, researchers may need to develop new equations to accurately portray waste losses at very cold temperatures.

Model 3: Similar to Model 2 with correction for indigestible prey (Stewart *et al.* 1983)

$$F = PF \cdot C$$

$$U = UA \cdot T^{UB} \cdot e^{(UG \cdot p)} \cdot (C - F)$$

where,

$$PF = \left(\frac{PE - 0.1}{0.9}\right) \cdot (1 - PFF) + PFF$$

$$PE = FA \cdot T^{FB} \cdot e^{FG \cdot p}$$

$$PFF = \sum_{1}^{n} (PREY[n] \cdot DIET[n])$$

This model allows the user to incorporate corrections for the indigestible component of the prey.
It is most useful when the diet shifts between highly digestible prey (e.g., fish) to less digestible prey (e.g., large crustaceans). **FA**, **FB**, and **FG** and **UA**, **UB**, and **UG** are as defined for Model 2. PREY[n] (indigestible proportion of n^{th} prey) and DIET[n] (proportion of n^{th} prey in diet) are input by the user (Hanson *et al.* 1997). **Note** that for temperatures less than 0.1 °C, the same caution mentioned in the Model 2 section applies to the Model 3 equations.

Model 4: Similar to Model 2 without the effect of ration size (Luo and Brandt 1993).

$$F = FA \cdot T^{FB} \cdot C$$

$$U = UA \cdot T^{UB} \cdot (C - F)$$

FA is the intercept of the proportion of consumed energy egested versus water temperature and **FB** is the coefficient of water temperature dependence of egestion. **UA** and **UB** can be similarly defined for excretion. **Note** that for temperatures less than 0.1 °C, the same caution mentioned in the Model 2 section applies to the Model 4 equations.

Reproduction

Production of reproductive tissue occurs during normal growth and loss occurs during spawning. If a bioenergetics simulation includes a spawning date for mature fish, a user-defined proportion of fish mass is lost on that day. While separate runs can be conducted for male and female fish to account for sex differences in gonad mass, the usual practice is to estimate the average gonad proportion for both sexes combined (Hanson *et al.* 1997). In FB4, the model can accommodate fish that experience multiple spawning events throughout the year. One of the main assumptions from this approach is that the gonad energy density is equal to the whole body energy density of the spawning fish. This likely will underestimate the energetic loss in spawning females but overestimate in males.

Predator Energy Density

Predator energy density (**ED** in joules per gram wet mass) can be input from a .csv data file (Model 1) or modeled as a function of body mass by selecting Model 2 (Stewart *et al.* 1983) or Model 3 (Cerino *et al.* 2013). The Model 2 formulation estimates predator energy density as,

$$ED = \alpha + \beta \cdot W$$

where **α** and **β** are the intercept and slope coefficients for the allometric mass function. Predator energy density can be defined using two size ranges with respective intercepts and slopes (**α1**, **β1** and **α2**, **β2**). Model 2 switches from equation set 1 to equation set 2 at the **mass cutoff**. To run only one equation, set the mass cutoff to either a value higher than the largest fish to use only **α1** and **β1**, or to 0 to use only **α2** and **β2**.

Predator energy density (**ED** in joules per gram wet mass) can be also be estimated as a power function of body mass by selecting Model 3:

$$ED = \alpha \cdot W^{\beta}$$

where **α** and **β** are the intercept and slope coefficients for the allometric mass function.

For a balanced energy budget it must be the case that the total body energy at the start of the day ($W_t \cdot ED_t$) plus the net energy gained that day (E_t) must equal the total body energy at the start of the next day ($W_{t+1} \cdot ED_{t+1}$). To balance the daily energy budget under Model 1, FB4 uses an algorithm in which the weight

at the end of any daily time step (W_{t+1}) is dependent on the predator energy density on the following (ED_{t+1}) day as

$$W_{t+1} = \frac{E_t + (ED_t \cdot W_t)}{ED_{t+1}}$$

Here, E_t is equal to the net energy (J) gained from the food eaten by the fish during day t, also accounting for any energy lost in reproduction that day. This approach results in an accurate balancing of the daily energy budget of the fish and also has been shown to improve bioenergetics model performance in the laboratory (Madenjian *et al.* 2012; Canale and Breck 2013).

When predator energy Models 2 or 3 are selected, the value of ED_{t+1} depends on W_{t+1}, and the following equations are used to solve for W_{t+1} for Model 2 (Stewart *et al.* 1983):

$$W_{t+1} = \frac{-\alpha \pm \sqrt{\alpha^2 + (4 \cdot \beta \cdot (W_t \cdot (\alpha + \beta \cdot W_t) + (E_t))}}{2 \cdot \beta}$$

and for Model 3

$$W_{t+1} = \left(\frac{(E_t + (ED_t \cdot W_t))}{\alpha}\right)^{1/(\beta+1)}$$

Note that for Model 2, when $\beta > 0$ and when $\beta < 0$, the positive radical from the above-mentioned equation for Model 2 is used to solve for W_{t+1}. For the special case of $\beta = 0$, the above-mentioned equation for Model 2 is bypassed to avoid division by zero, and the daily energy budget is balanced using the algorithm for constant predator energy density over time. For Model 2, whenever weight crosses the cutoff value during a day's growth, that day's growth is computed in two parts: growth to the cutoff, then growth beyond the cutoff. The appropriate ED-weight relationship is used on each side of the cutoff. This keeps the energy budget in balance. For Model 3, α must be > 0.

Prey Energy Density

Energy density of prey types (J/g wet weight) contained in fish diets is a measured parameter that must be input as a .csv file by FB4 users. Nonetheless, we include a brief overview of prey energy density here because it is a sensitive input parameter in most modeling scenarios (Bartell *et al.* 1986). Three general approaches to estimating prey-specific energy density include:

Obtaining values from the literature

The diets of fish are usually characterized by diverse, partially digested remains of consumed food items. While food items can often be easily weighed (or counts extrapolated to weights) to characterize diet composition, quantifying energy density (J/g wet wt) for individual food types can be challenging. One approach relies on obtaining prey-specific energy density from published studies, and using these values as input in bioenergetics models. The large compendium by Cummins and Wuycheck (1971) summarizes the caloric equivalents of many plant and animal species and is a frequently cited paper in the

bioenergetics literature. Because energy density of food types can vary across taxa, body size, season, and geographic location, energy values obtained from the literature may not be representative of those found in the diet. Other methods include direct (bomb calorimetry) measurement of prey energy density derived from food items collected from the fish's diet and(or) from the environment where fish sampling occurred or estimation using established relationships between energy density and tissue dry-to-wet weight ratio.

Bomb calorimetry

Bomb calorimetry is a direct method for quantifying energy density of plant and animal tissue. Whole diet items are weighed for wet mass, then dried to a constant weight before being ground into a powder. Dried, pressed pellets of the ground material are then combusted in a bomb calorimeter to obtain energy density estimates (usually as calories/gram dry weight). These values can then be converted to calories/gram wet weight and multiplied by 4.184 to obtain Joules/gram wet weight (note that 1 Calorie = 1000 calories). As with most things, the time and cost of processing samples using bomb calorimetry is dependent on sample size, and large sample sizes can require considerable time to process. An alternative approach, that can be less time consuming than bomb calorimetry, is the application of empirical relationships to estimate energy density for fish and invertebrates.

Dry-to-wet weight ratio

A number of studies have documented the relationship between energy density and dry-to-wet weight ratio of fishes and invertebrates (Hartman and Brandt 1995; Ciancio *et al.* 2007; James *et al.* 2012). This approach relies on obtaining wet and dry weights of whole prey from the diet and(or) field, and estimating energy density (ED) as a function of dry mass (either as a percent or proportion).

<u>Fish</u>

Hartman and Brandt (1995) developed an equation to reliably estimate fish energy density (ED) as,

$$ED\ (J/g\ wet\ wt) = 45.29\ DW^{1.507},$$

where DW represents percent dry weight of the sample (n=587, r^2=0.95, p<0.002).

More recently, Johnson *et al.* (2017) developed a multi-species model to predict fish energy density based on water content and found close agreement between predictions of their model and those of Hartman and Brandt (1995) and Schreckenbach *et al.* (2001). Fish energy density in the Johnson *et al.* (2017) model can be predicted as,

$$ED\ (J/g\ wet\ wt) = 32.678\ DW^{1.604}$$

where DW represents percent dry weight of the sample (n=299, r^2=0.95, p<0.0001).

<u>Invertebrates</u>

As with fish, James *et al.* (2012) showed that ED of aquatic invertebrates can be predicted as,

$$ED\ (J/g\ wet\ wt) = (22{,}960\ PDW)-174.2,$$

where PDW represents the proportional dry weight of the sample (n=88, r^2=0.96, p<0.0001).

Scaling from Individuals to Populations

The previous sections describe the functions used to characterize the physiology of an individual fish. These models can be used to estimate the rates of predation of individual fish and how these rates vary with changes in diet, thermal regimes, growth rates, etc. However, we are often more interested in estimating the impact of fishes at the population level. In this section, we describe how to scale up from an individual to the population level (Hanson *et al.* 1997).

Cohort(s) as a Population

We define a cohort of fish as a group of similar sized (aged) fish of the same species experiencing identical environmental conditions (temperature, diet, growth and reproductive losses). For instance, a single cohort of perch may be 500 individuals growing from 60 to 85 g in a given lake during one year. All of these perch consume exclusively zooplankton, reside in water temperatures ranging from 4 °C during the winter to 20 °C in July and August and do not spawn. While there will be individual variability in diet, distribution, growth and consumption within this group of perch, the physiological parameters and environmental conditions used in the model will represent the average individual. Therefore, the estimated amount of food consumed for these 500 perch is simply 500 times that consumed by an individual, assuming no mortality occurs. A second cohort may represent a different age group of perch, or fish growing at a faster or slower rate (i.e., discrete stocks where diet or thermal history may be different). By combining multiple cohorts into a simulation FB4 permits the user to model entire populations of fish at one time (i.e., account for size/age structure, stock structure, etc.) so that patterns in consumption or growth can be compared between cohorts or combined to provide a single prediction for the entire population of fish (Hanson *et al.* 1997).

Population Mortality

Once the analysis is extended beyond a single fish to a cohort, mortality may become an important regulator of population level processes. Mortality can come from a variety of sources (starvation, predation, fishing, etc.) and each may act for a different period of time at varying intensity. For instance, a Yellow Perch cohort may experience a discrete natural rate of mortality of 0.2 per annum, with an additional 0.3 fishing mortality between June 1 and October 1. These two sources of mortality act together to reduce an initial population of 500 individuals on January 1 to 280 by December 31. For each cohort, mortality is modeled using a simple exponential decay model:

$$N_{t+1} = N_t \cdot e^{\left(\frac{\ln(1-n)}{t_n} + \frac{\ln(1-m)}{t_m} - \left(\frac{\ln(1-n)}{t_n} \cdot \frac{\ln(1-m)}{t_m}\right)\right)}$$

where $\mathbf{N_t}$ and $\mathbf{N_{t+1}}$ represent the number of fish at time t and time t+1, respectively, **n** and **m** are the discrete natural and fishing mortality rates acting at time t, respectively, and $\mathbf{t_n}$ and $\mathbf{t_m}$ are the time intervals (in days) for which the natural and fishing mortality rates are observed. It is important to note that the time interval for both mortality types might differ (e.g., t_n = 365 and t_m = 122), and that the amount of mortality input by the user (as a discrete rate) will occur during the period specified by the user. For example, if discrete mortality is set to 0.3 for the entire year, then 30% of the fish would die over the course of the year, whereas if discrete mortality was set to 0.3 for one month, 30% of the fish would die

in that month. When multiple sources of mortality act together on a cohort, each type of mortality is applied to the cohort each day, and the number surviving the combined mortality is projected forward to the following day. Remember that while the daily instantaneous rates of mortality are additive ($m_{natural}$ + $m_{fishing}$ + ...), the actual probabilities of mortality are not. For instance, if the natural rate of mortality (n) is 0.3 per year, and the rate of fishing mortality (m) is 0.2 per year, the combined total mortality is 0.45 per year (n+m-nm). This expression simply means that a fish can die from natural mortality or fishing mortality, but the same fish cannot die from both types of mortality (Hanson *et al.* 1997).

The order of daily events for a fish is: eat, grow, spawn and die. Spawning and mortality only occur if required by the user input. The importance of this chronology will be trivial for most bioenergetics runs, however, the user should realize that daily consumption values will be calculated before the fish dies.

It is important to realize that like previous versions, FB4 is not a population model because we do not consider recruitment. However, by accounting for mortality rates, the net predatory impact of a group of fish can be estimated (Hanson *et al.* 1997).

Nutrient Regeneration and Contaminant Accumulation

The utility of reconstructing energy budgets of fishes to estimate predation rates in aquatic systems has been extended to allow estimation of flow rates of other materials that are transferred through interactions of fishes and their prey. The impetus for this development derived from the recognition that fishes play pivotal roles in transfers of limiting nutrients between ecosystem compartments (Kitchell *et al.* 1977), and because contaminant accumulation in fish tissue that has potentially important toxicity implications for humans and wildlife that consume them (Cordle *et al.* 1982; Fein *et al.* 1984; Mac 1988). As with estimating the rates of energy transfer between food web components, estimating nitrogen and phosphorus regeneration rates and contaminant accumulation rates in fish tissues has proven difficult. Using measured growth rates as a constraint on energy budgets, we can calculate predation rates with relatively minimal errors. We capitalize on this strength of bioenergetics models to estimate flow of other materials through fishes.

By coupling mass balance models to bioenergetics models, we can estimate the rates at which materials are transferred into and through fishes. The mass balance models that are coupled with energetic models fall into two distinct types depending on the behavior of the material of interest in fish tissue. Some materials, for example nitrogen (N) and phosphorus (P), are maintained at relatively constant concentrations in fish tissue through homeostatic mechanisms. In these instances, the concentration of the material in fish tissue is usually known, and we are interested in the rates at which the material is transferred into fishes and the rate at which it is eliminated. The best example of this is evaluating the role that fish play in lake nutrient (N and P) cycles by regenerating these primary production-limiting nutrients through excretion (Kraft 1992; Carpenter *et al.* 1992; Schindler *et al.* 1993). By linking the elemental composition of fishes and their prey (e.g., Davis and Boyd 1975; Penczak 1985) to bioenergetics models, we can estimate nutrient regeneration rates by fishes.

The other general class of materials that we are often interested in are those that are bioaccumulated (i.e., not maintained at homeostatic concentrations). Whether a material is bioaccumulated is largely a function of its lipophilicity that determines the efficiency with which it is eliminated from tissue. Examples include the bioaccumulation of heavy metals (e.g., mercury) and organic contaminants such as polychlorinated

biphenyls (PCBs). In these instances, we are generally more concerned with predicting the concentration of the material in fish tissue and how different environmental conditions (e.g., varying temperatures, changes in diet or changes in growth rate) alter concentrations.

In this section we describe how functions that are linked to the core bioenergetics models are used to estimate nutrient regeneration and contaminant bioaccumulation by fishes.

Nutrient Regeneration

Kraft (1992) adapted the original Hewett and Johnson (1987) bioenergetics model to a mass balance model of nutrient allocation in fishes (Nakashima and Leggett 1980) to estimate nutrient regeneration rates by fishes. The strength of Kraft's (1992) approach is that it couples estimates of predation rates by fishes to the elemental composition (i.e., N and P) of fishes and their prey, to estimate nutrient regeneration rates.

Nakashima and Leggett (1980) described a mass balance model of phosphorus (P) allocation in fishes according to:

$$C_p = G_p + F_p + U_p$$

where:

$$C_p = mass\ of\ P\ consumed\ (g)$$
$$G_p = mass\ of\ P\ allocated\ to\ growth\ (g)$$
$$F_p = mass\ of\ P\ lost\ in\ feces\ (g)$$
$$U_p = mass\ of\ P\ lost\ in\ urine\ (g)$$

P in urine (U_p) is lost in soluble form that is readily available for uptake by aquatic primary producers (Brabrand 1990; Lall 1991). Therefore, excreted P is generally of interest to those estimating the role of fishes in P cycles of aquatic systems. In this regard, the previous equation is more useful when written as:

$$U_p = C_p - G_p - F_p$$

Excreted P can be estimated as the difference between the P gained through consumption, and that lost in feces and allocated to growth. Fecal losses can be accounted for as a direct proportion of consumption (Nakashima and Leggett 1980a) by determining a gross assimilation efficiency (AE_p) for a given prey type. Nakashima and Leggett (1980a) reported that P assimilation efficiency was about 0.72 for most types of animal prey. Lall (1991) reports greater variation in P assimilation efficiencies of fishes fed a variety of aquaculture feeds.

By accounting for fecal losses of P with an assimilation efficiency coefficient (AE_p), the previous equation simplifies to:

$$U_p = \left(AE_p \cdot C_p\right) - G_p$$

The mass of P consumed (C_p) is calculated as the product of the mass of prey consumed (C, in grams) and the concentration of P in prey tissue (g P/g).

$$C_p = C \cdot [P]_{prey}$$

In the previous section we discussed how bioenergetics can be used to calculate mass consumption (C). The nutrient regeneration model uses this value of C determined from the energetics component of the model. The P concentration of prey is expressed as g P/g of wet mass determined for individual prey types.

The amount of P allocated to growth (G_p) is the product of the increase in mass due to growth, and the P concentration in fish tissue. Phosphorus concentrations are about 0.005 g P/g of wet mass in adult fishes. Davis and Boyd (1975) and Penczak *et al.* (1985) give species-specific P (and N) concentrations for many fish species.

To estimate N regeneration by fishes, the nutrient mass balance can be coupled to the energetics model, as was done for estimating P regeneration. To do this the user needs data to describe N concentrations (g N/g wet weight) in the predator and prey, and the assimilation efficiency of N (AE_N). Brett and Groves (1979) estimated that the N assimilation efficiency was about 0.8 for carnivorous fishes. This value of AE_N will probably be lower for herbivorous fishes. However, the model is easily modified to incorporate other values of AE_N (Hanson *et al.* 1997)

FB4 couples both the P and the N mass balance to the energetics submodel in a way that the N:P ratio of excreted and egested nutrients can be estimated.

Contaminant Accumulation

There are several good reasons to use fish bioenergetics models to predict contaminant bioaccumulation in fish. Bioenergetics models are good at predicting several of the rates that are needed to quantify the dynamics of contaminant uptake and elimination.

- **Food consumption rate** is calculated as a function of body weight and water temperature. Knowing contaminant concentration in prey items and the contaminant uptake efficiency from food allows calculation of the contaminant **uptake rate from the food** pathway. This is typically the dominant uptake route for highly lipophilic contaminants, such as PCBs, and for contaminants such as methyl mercury that bind to certain amino acid groups.
- **Metabolic rate** can be quantified as **oxygen uptake rate** and varies with body weight and water temperature. Knowing oxygen concentration in the water allows calculation of the volume of water per day from which oxygen is extracted, and hence, the volume of water from which contaminants may also be taken up. The **gill uptake** route is typically the dominant uptake pathway for moderately lipophilic contaminants -- those with K_{ow} (octanol:water partition coefficient) smaller than about 10,000.
- **Metabolic rate** generally influences the **clearance rate** of contaminants from the fish's body, so that clearance varies with body weight and temperature.
- **Growth rate** is calculated for fish, and this can account for the influence of **growth dilution** on the contaminant concentration in fish.
- **Reproduction** can be included in bioenergetics simulations, and this could be used to quantify a pathway of contaminant loss.

- **Body fat concentration** influences the dynamics of contaminants in fish, both directly by influencing the body:water partitioning of lipophilic contaminants, and indirectly by influencing the amount of food required per gram of growth. The current version of FB4 considers fat concentration indirectly via its influence on energy density of the predator. Future versions of FB4 will likely include fat as a separate fish compartment (along with protein, ash and water); this model development is underway. Similarly, future versions of FB4 will likely include **protein** as another body compartment. The size of the protein compartment is of interest for contaminants such as methylmercury, which binds to the sulfur-containing amino acids (e.g., cysteine) in proteins.

Fishes accumulate compounds by bioconcentration across their gills and through bioaccumulation from ingested food. Uptake of contaminants across the gills can be substantial for moderately lipophilic contaminants -- those with K_{ow} (octanol:water partition coefficient) smaller than about 10,000 (Post *et al.* 1996; Barber 2003; Stadnicka *et al*. 2012). For highly lipophilic contaminants – those with K_{ow} greater than about 1,000,000, the bulk of accumulation usually occurs through extraction from ingested food (Rowan and Rasmussen 1992; Rasmussen *et al.* 1990; Thomann and Connolly 1984; Thomann 1989; Rodgers 1994; Barber 2008). The current modeling approach in FB4 follows FB3 and assumes that uptake from water through the gills is negligible compared to that taken up through dietary exposure. We are developing a new contaminant model following Arnot and Gobas (2004) that can account for both gill uptake and dietary uptake, but this version is not yet ready for release.

Estimating the accumulation of compounds that are not maintained at homeostatic concentrations in fishes can be modeled by mass balance models of uptake and elimination coupled to the bioenergetics models. Examples of bioaccumulated compounds include mercury (Hg), primarily as monomethylmercury (MMHg; Bloom 1992)), and organic contaminants such as polychlorinated biphenyls (PCBs).

We present two methods to model contaminant accumulation in fishes. Both methods assume that contaminant uptake from water is insignificant, and that fishes incorporate contaminants into tissue entirely due to uptake from ingested food. The first model assumes that elimination of contaminants from body tissue is negligible and that contaminant uptake can be modeled simply as a constant fraction of the amount of contaminants consumed by a fish. Model 1 is recommended for simulating accumulation of highly lipophilic organic contaminants such as PCBs, when the parameters for the more complex model are not known. The second contaminant model accounts for variation in contaminant elimination rate due to body size and environmental temperature (Trudel and Rasmussen 1997). Model 2 was derived specifically for methylmercury (MMHg) accumulation in fishes whose elimination kinetics are better established (Trudel and Rasmussen 1997; Van Walleghem *et al.* 2007; Van Walleghem *et al.* 2013).

Model 1. Simple net trophic transfer efficiency with no elimination (e.g., PCBs).

$$dX_{pred}/dt = (C \cdot W) \cdot Prey_X \cdot TE_X$$

X_{pred} = total quantity of contaminant X in predator (µg).
C = weight-specific consumption during the time step (g/g/d).
W = fish weight (g).
$Prey_X$ = mean concentration of contaminant X in prey (µg/g).
TE_X = net transfer efficiency of contaminant X from prey to predator (fraction).

Table 1. TE_X values reported for invertebrate and fish prey.

Taxa	Contaminant	Value (µg/g)	Citation
Invertebrates			
Diporeia	PCB	0.30-0.50	Kukkonen *et al.* 2005
Fish			
Chinook Salmon	PCB	0.53-0.60	Jackson and Schindler 1996; Madenjian *et al.* 2004
Coho Salmon	PCB	0.50	Jackson and Schindler 1996; Madenjian *et al.* 1998
Lake Trout	PCB; Hg	0.81; 0.77	Madenjian *et al.* 2000, 2012b
Whitefish	Hg	0.63	Madenjian *et al.* 2008

Model 2. Gross assimilation efficiency with Hg elimination dependent on body size and temperature.

$dHg_{pred}/dt = (C \cdot W) \cdot Prey_{Hg} \cdot AE_{Hg} - K_{Hg} \cdot Hg_{pred}$

Hg_{pred} = total quantity of Hg in predator (µg).
C = weight-specific consumption during the time step (g/g/d).
W = fish weight (g).
$Prey_{Hg}$ = mean concentration of Hg in prey (µg/g).
AE_{Hg} = gross assimilation efficiency of Hg from prey (fraction).
K_{Hg} = fraction of Hg_{pred} eliminated from predator per day (d^{-1}).

Elimination rate, K_{Hg}, is estimated as,

$K_{Hg} = e^{(0.066T - 0.20(Ln(W)) - 6.56)}$

where W is fish weight (g of wet weight) and T is water temperature (°C) (Trudel and Rasmussen 1997; Van Walleghem *et al.* 2013).

Gross assimilation efficiency, AE_{Hg}, is equal to $1 - F_{Hg}$, where F_{Hg} is the proportion of consumed MMHg lost in feces.

Table 2. AE_{Hg} values reported for invertebrates and fishes.

Taxa	Value	Citation
Invertebrates		
Amphipods	0.95	Lawson and Mason 1998
Blue Crabs	0.76	Evans *et al.* 2000
Copepods	0.78	Lawson and Mason 1998
Crayfish	0.95	Headon *et al.* 1996
Mussels	0.85	Wang *et al.* 2004
Oysters	0.90	Blackmore and Wang 2004
Shrimp	0.72	Evans *et al.* 2000
Fish		
Blackhead Sea Bream	0.90	Dang and Wang 2012
Grunt	0.90	Dang and Wang 2010
Killifish	0.68[a]; 0.89[b]	Goto and Wallace 2008
Largemouth Bass	0.79	Bowling et al 2011
Lake Trout	0.84	Boudou and Ribeyre 1997
Rainbow Trout	0.75	Rodgers and Beamish 1982
Sheepshead Minnow	0.76	Lawson and Mason 1998
Spotted Sweetlips	0.80	Wang and Wong 2003
Tilapia	0.90[c]; 0.85[d]	Wang *et al.* 2010
Yellow Perch	0.80	Norstrom *et al.* 1976; Rodgers 1994

[a] prey = amphipods; [b] prey = Chironomidae; [c] prey = invertebrates, [d] prey = algae

It is important to note that for both contaminant models (Model 1 and Model 2), predator contaminant concentration generated by FB4 represents whole body concentration, and not muscle concentration. Because fish muscle is a major storage site for MMHg and is consumed by humans, fish muscle concentration is often an important metric in contaminant monitoring programs (Van Walleghem *et al.* 2013). Although whole body and muscle MMHg concentrations are related, whole body concentrations predicted by FB4 may be different than muscle concentration. Some studies suggest that MMHg concentration in whole fish and muscle are similar (Becker and Bigham 1995; Trudel and Rasmussen 2001), whereas others show greater MMHg concentration in muscle tissue compared to whole fish (Peterson *et al.* 2005; Van Walleghem 2006; Van Walleghem *et al.* 2013). Thus, we encourage users to review these (and related studies) if interest lies in estimating MMHg concentration in fish muscle. An empirical, statistical model presented by Peterson *et al.* (2005) could be used to convert whole-body MMHg concentration to muscle MMHg concentration or vice versa.

Getting Started – Fish Bioenergetics 4.0 in R

The main purpose of FB4 is to estimate the energy required for an individual fish to grow from an initial weight to a final weight in a specified amount of time, given a certain diet and temperature regime, and accounting for energy density of the fish and the food. The model accounts for the influences of body mass and temperature on the physiological processes of consumption, respiration, specific dynamic action, egestion, excretion, and gamete production. The model can estimate energy required (prey consumption) by a cohort of identical fish if the initial number of fish and the mortality rate are specified. An alternative purpose of FB4 is to estimate final weight, given an initial weight and a specified level of consumption, energy density, and the temperature regime. Other capabilities of FB4 include estimating the accumulation of chemical contaminants by fish and estimating the release of nitrogen and phosphorus to the water, accounting for the physiological processes of a fish that is growing under specified conditions. Users can modify their copy of this open-source model in order to address other questions, taking advantage of this specification of the physiology of fish growth and accounting for the major effects of body weight and temperature.

FB4 Installation

Fish Bioenergetics 4.0 (FB4) uses **R** as a computing language and **Shiny** through **RStudio** as the supporting interface. You will need both of these programs in order to be able to run FB4 on your computer.

Note: Steps 1, 2, 3 and 6 only need to be performed once. All other steps need to be performed every time you want to use FB4, except as noted.

1. Go to: http://cran.r-project.org and download the latest version of R that is compatible with your computer (Windows or Mac).

2. Go to: http://www.rstudio.com/products/rstudio/download/, click on the button to download the free RStudio Desktop version, then download the latest version of RStudio under "**Installers for supported platforms**" that is compatible with your computer (Windows or Mac) operating system.

3. Once both programs have been installed, save the FB4 folder (can be found at fishbioenergetics.org or http://www.fishdata.org/software) onto your desktop or another suitable location.

4. In RStudio, select **File -> Open File…** and double click on the "server.R" file found in the FB4 folder you just saved. This step only needs to be repeated if the server.R file has been modified or a different one is used, or if a different FB4 folder is used.

5. In RStudio, go to **Session -> Set Working Directory -> Choose Directory …** and select the FB4 folder you just saved. Once the folder has been selected, press the select (in Windows) or open (in Mac) tab. This step only needs to be performed once if the same FB4 folder is continually used. However, this step will have to be repeated if a different FB4 folder is created.

6. You will now need to download the "Shiny" package, which will allow you to run the application. To do so, go to **Tools -> Install Packages …** and type **Shiny** under **Packages (separate multiple with space or comma):**. Then, click on **Install**. This might take 1-2 minutes.

7. You are now all set to run the application. To do so, press the down-arrow icon to the right of the **Run App** tab found in the upper right corner of the script window (upper left window) and select **Run External**. Once this is done, press the **Run App** tab and FB4 will start in a new window in your browser.

   Note: In some versions of RStudio, the **Run App** tab does not appear. In that case, type runApp() in the **Console** window (lower left window) and insert the FB4 folder path inside the parentheses. The folder path should be inside quotation marks and should look something like:
   runApp("/users/daviddeslauriers/Desktop/PhD/Fish Bioen 4.0")
   Once done, press **ENTER** and the application should run.

8. **Warning**: Any alteration to the R script will cause the application to either be modified or not function. If you inadvertently modify the code, just make sure you do not save the **server.R** or **ui.R** files before closing and re-opening them again (or save them under a different name).

Required components

Input Files

All user input files are in comma-separated-values (*.csv) format and can be found in the **Main Input** or **Sub-Models** folders found in the FB4 folder. Each data file consists of a two-dimensional array where the day of the year is in the first column and the data are in the remaining columns. The daily values are interpolated, if necessary, between the values specified in the input files (except for the mortality file; see below). For example, if the temperature file gives a value of 4.0 on day 1 and a value of 13.0 on day 10, the model will use 4.0 °C on day 1, 5.0 °C on day 2, 6.0 °C on day 3, …, 12.0 °C on day 9, and 13.0 °C on day 10. Any modifications to the default datasets must be saved as .csv using the same file names before FB4 will be able to recognize them.

The mortality file is the one case where daily values are not interpolated. The value specified for one day remains in effect until a different value is specified.

Note: All input files **must** start on day 1. Failure to do so will result in FB4 using the wrong set of days for the simulation.

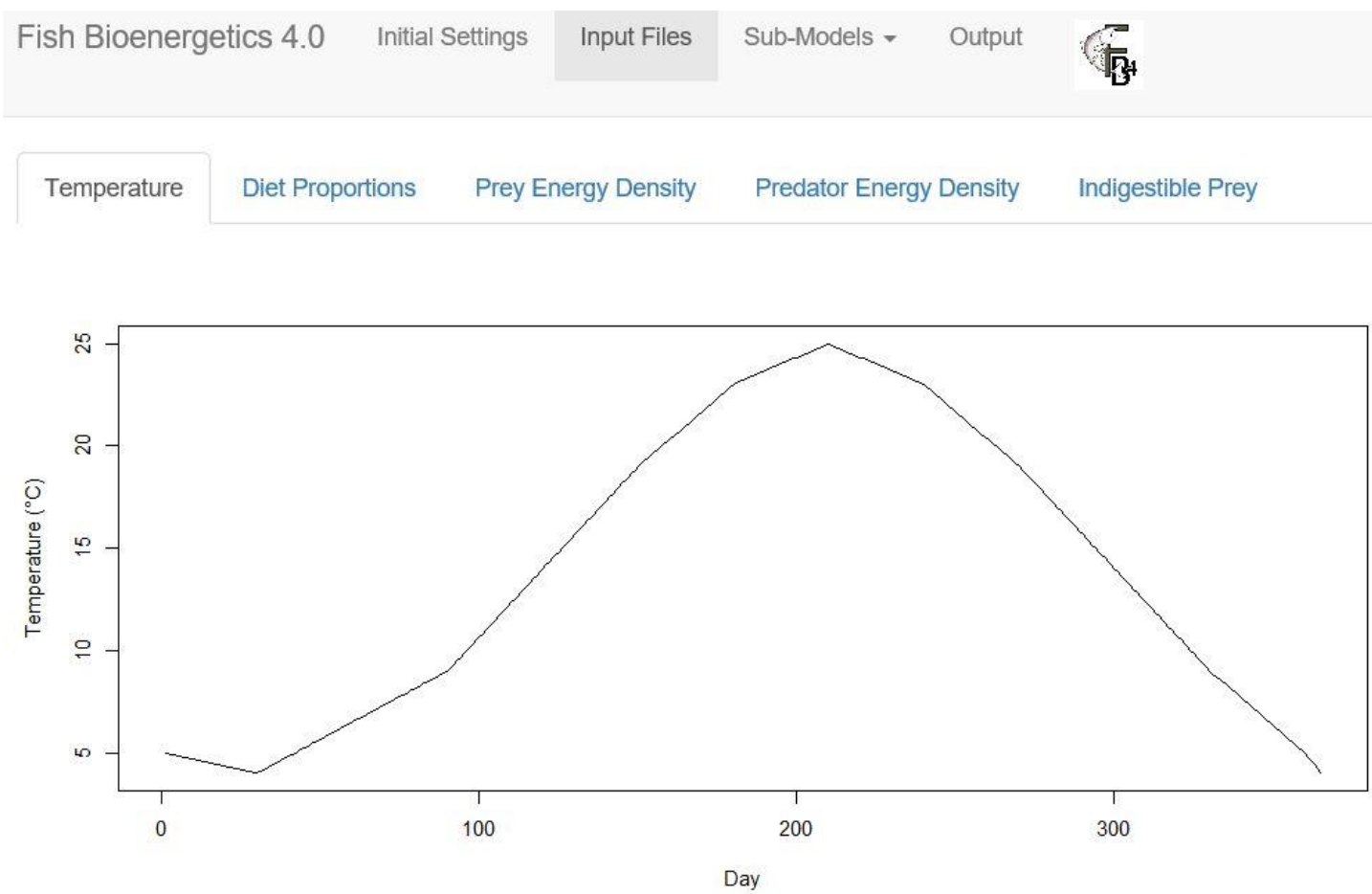
The next section describes the input data files that are necessary for any simulation to run. File names are in parentheses. Although users can assign specific names to folders that contain input files, the **input file names should not be changed,** because they are included in the R code.

Input Files

Temperature in °C (Temperature.csv)

This example temperature file shows monthly values. The model linearly interpolates to determine daily values to use in the simulation.

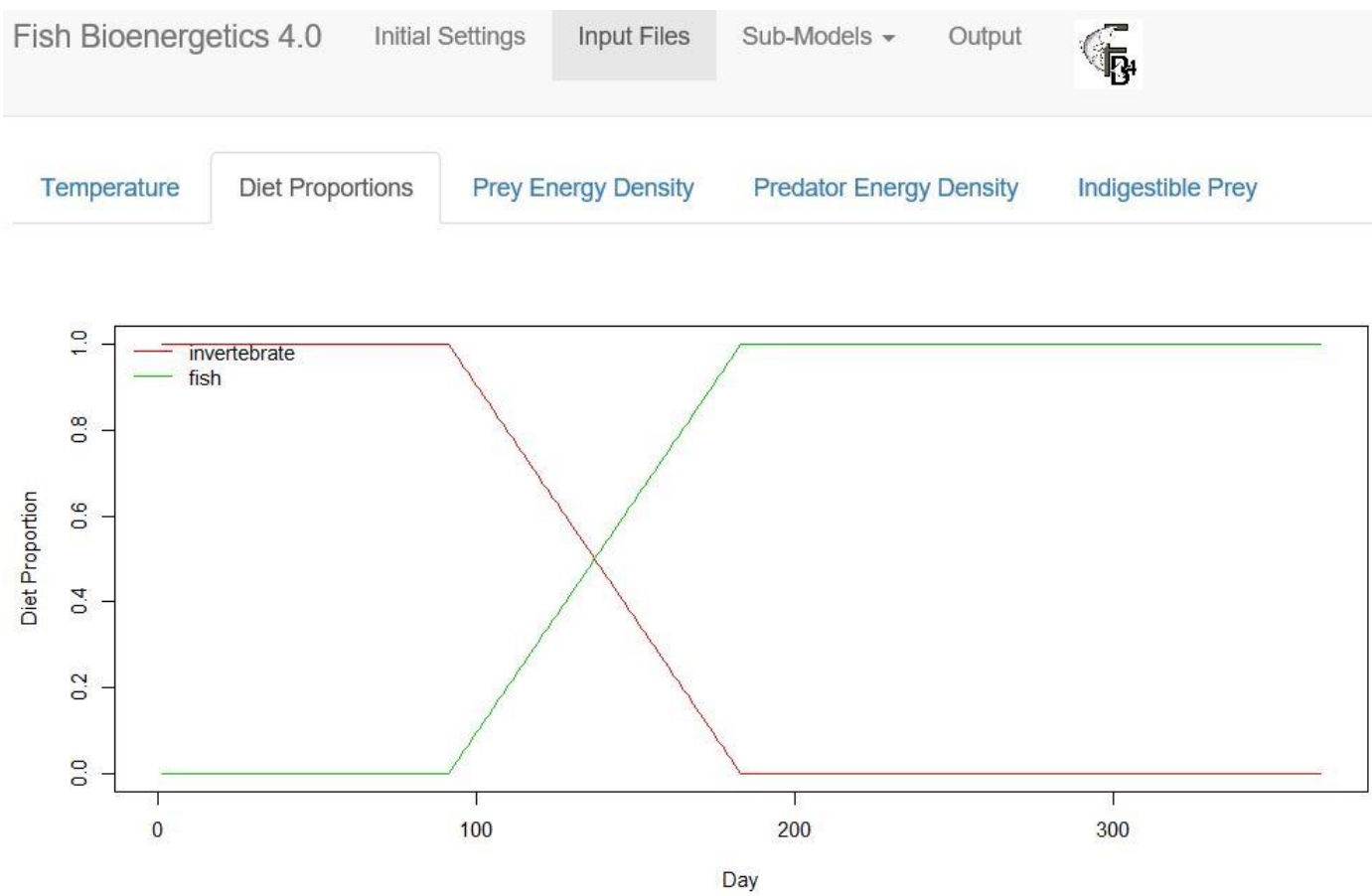
day	temperature
1	5
30	4
90	9
120	14
150	19
180	23
210	25
240	23
270	19
300	14
330	9
360	5
365	4



Diet Proportions (Diet_prop.csv)

This example diet file indicates the proportions of two prey types: invertebrate and fish. Notice a diet switch from invertebrate to fish occurring between days 92 and 183. Users can add columns to include additional prey types. However, the proportions in each row must sum to 1. **Note**: It is important that diet data be represented as the proportion by wet weight of each prey type – and NOT the proportion by number or dry weight. Additionally, it is important that the number of prey species (columns) and the labels for each column are identical for both the Diet Proportions file and Prey Energy Density file.

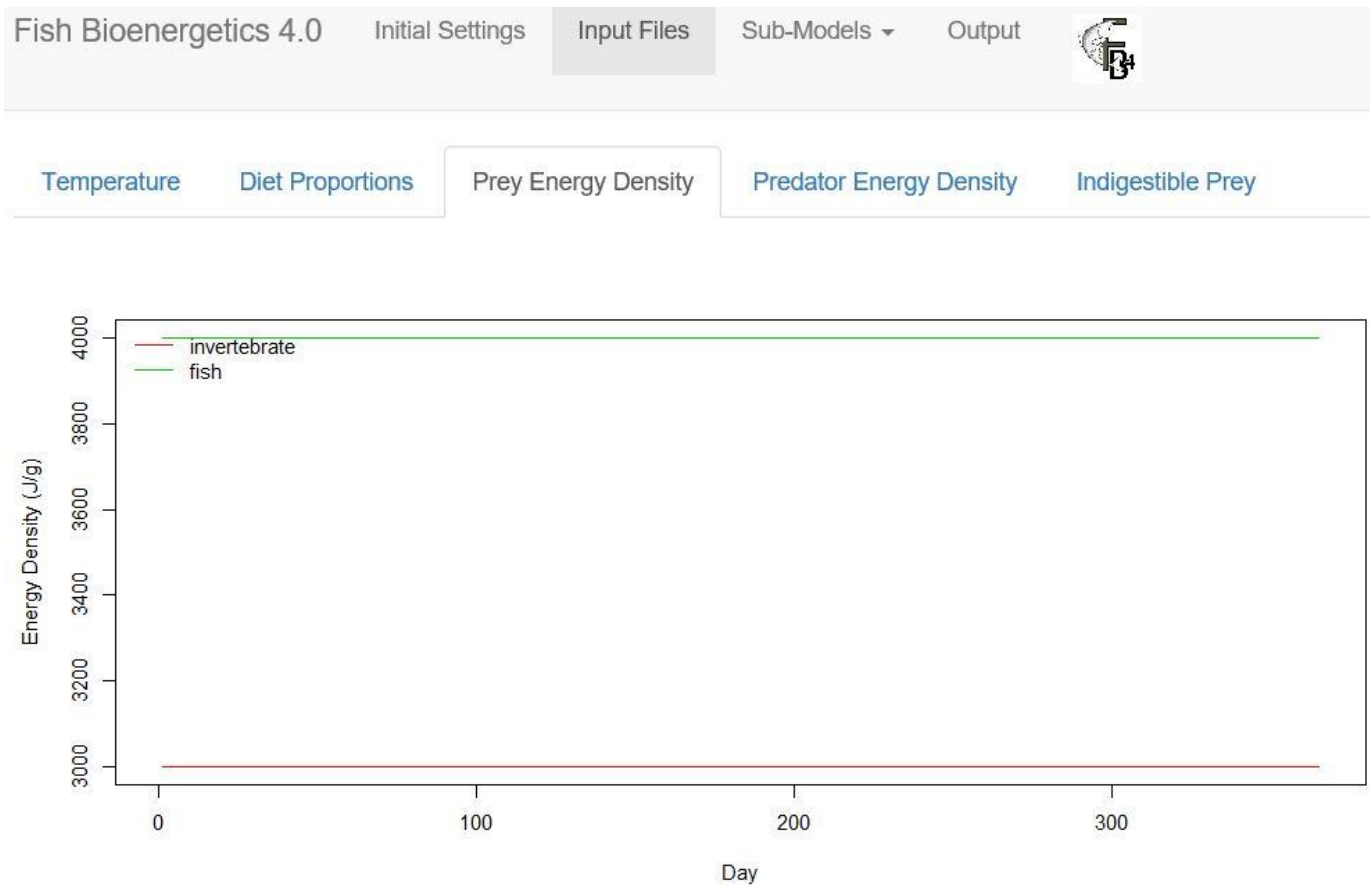
day	invertebrate	fish
1	1	0
91	1	0
183	0	1
365	0	1



Prey Energy Density in J/g (Prey_E.csv)

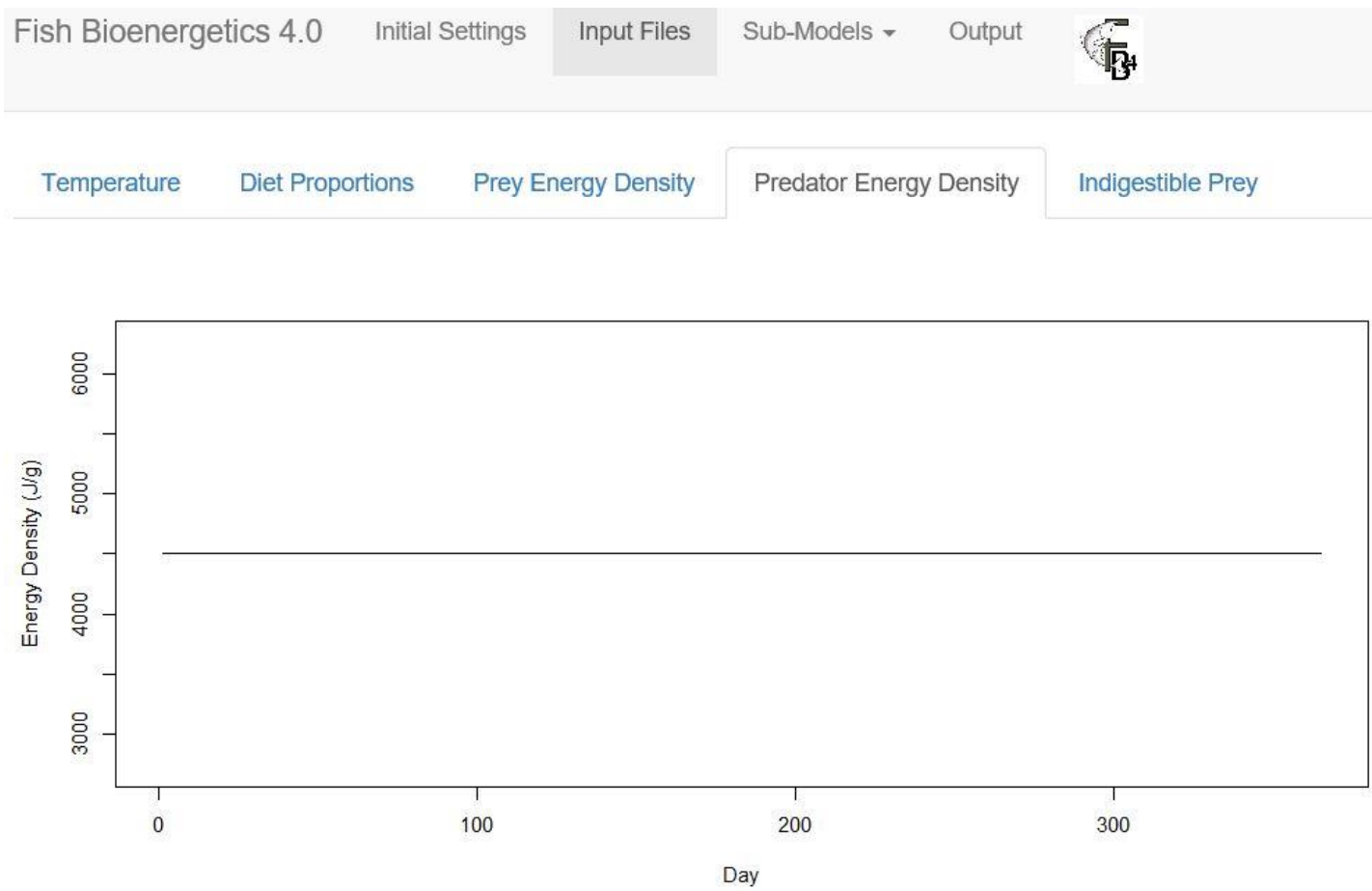
This example file indicates the energy density of the two prey types. No seasonal changes are occurring in this example. Notice how prey types in this file match those in the Diet Proportions file. This is necessary as FB4 will return an error if the prey types in both files do not match.

day	invertebrate	fish
1	3000	4000
365	3000	4000



Predator Energy Density in J/g (Pred_E.csv)
This example file indicates the energy density of the simulated fish (the predator). No seasonal changes are occurring in this example. These values will be used in cases where Predator Energy Density Model 1 is used (see *Predator Energy Density* section).

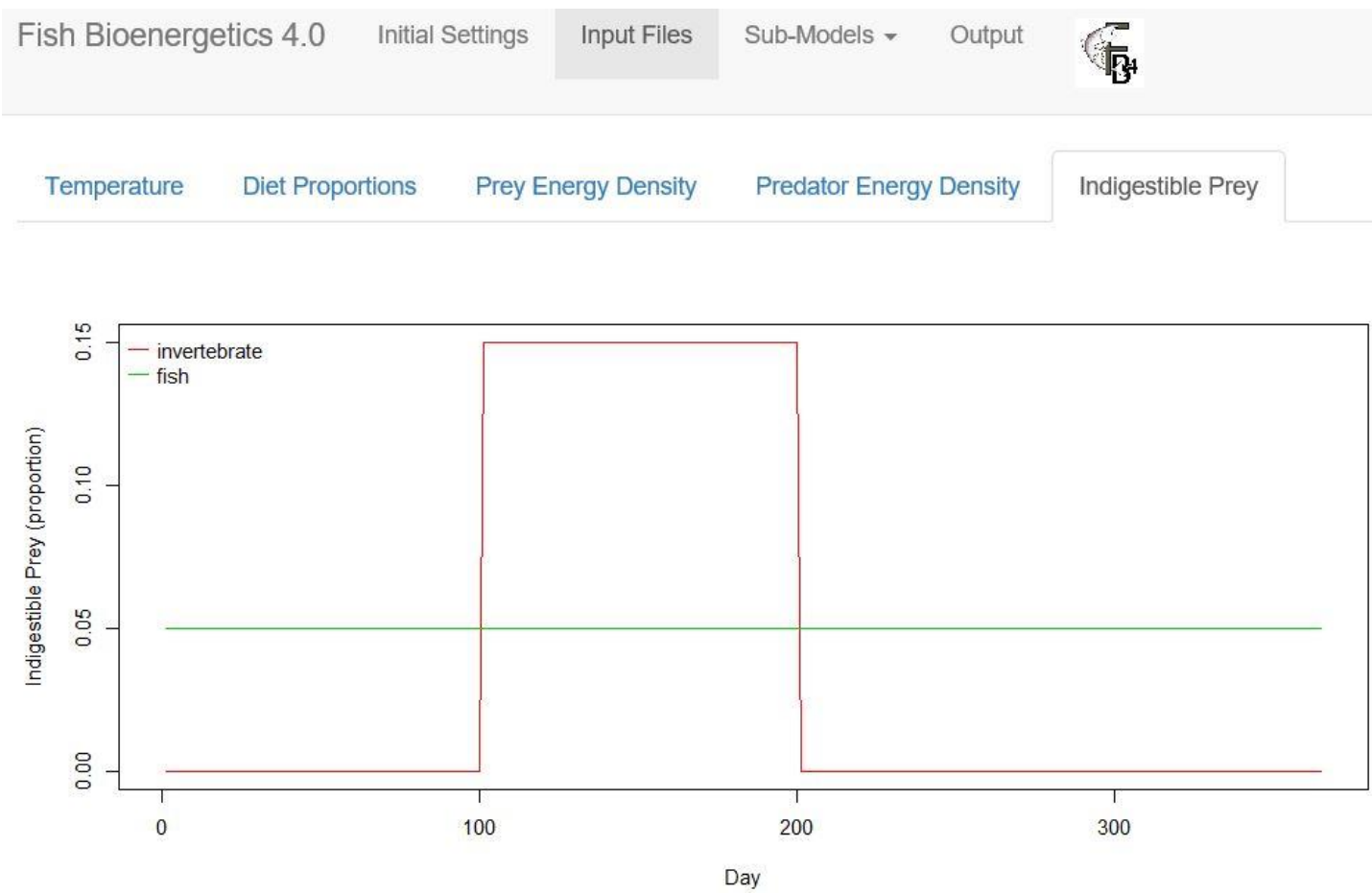
day	Yellow Perch
1	4500
365	4500



Indigestible Prey as a proportion (Indigestible_Prey.csv)

Waste loss Model 3 (Stewart *et al.* 1983) allows for the user to specify the proportion of each prey type that is indigestible. This example file indicates the percent indigestible content for two prey types: invertebrate and fish. **Important:** Notice how prey types in this file match those in the Diet Proportions and Prey Energy Density file. This is necessary as FB4 will return an error if the prey types in all files do not match.

day	invertebrate	fish
1	0	0.05
100	0	0.05
101	0.15	0.05
200	0.15	0.05
201	0	0.05
365	0	0.05



Predator Physiological Parameters (Parameters_official.csv)

When you select a species to model in FB4, you're really opening a set of physiological parameters that is unique to the species and life stage that you wish to work with. How the fish's growth, consumption, respiration, egestion and excretion result from your input data are dependent upon the fish's physiological parameters. For the most part, these parameters have been determined experimentally in the laboratory and do not change. FB4 contains a database of physiological parameters for many different species and life stages of fish and several aquatic invertebrates. The parameter set for each model constitutes one row in the Parameters.Official.csv file in the FB4 folder. Each parameter set in FB4 comes from one or more published studies (references are noted in the parameters file). In some cases parameters have been modified for use in FB4 to insure that they function as intended by the original authors. For example, FB4 calculates Excretion and SDA as a fraction of Consumption-Egestion (C-F), but some authors expressed these variables as a fraction of Consumption. In these instances the parameter value has been changed so that it yields a result equivalent to that from the author's initial formulation. These alterations are described in the Notes section for the model in the parameters file.

The full list of parameters for a given bioenergetics model can be seen on the **Initial Settings** page once the **Species** has been selected. Users can modify parameter estimates by changing them in the "Parameters_official.csv" file and saving the file. This is also where you can enter a new bioenergetics model. To do so, insert a blank row (models are ranked alphabetically according to their common name) and enter the appropriate information under the different column headings. Once the file is saved, the new model will be available for use in FB4. The complete set of parameters is explained in more detail in the *Core Processes in Bioenergetics* section. It is important to keep in mind that the use of some parameters is dependent on the type of model selected, and that the same parameter names may serve different purposes in different models.

The example below indicates all of the physiological parameters (along with their definitions) necessary to run the adult Yellow Perch model (Kitchell *et al.* 1977) in FB4. Rows have been transposed to columns for demonstration purposes.

Table 3. Parameter descriptions for the Yellow Perch (adult) bioenergetics model. Parameters and values for all models can be found in the **Parameters_official.csv** file.

Parameter	Value	Description
Species	Yellow perch (adult)	Common name with life stage in () if there is more than one model for the same species
Sci_Name	*Perca flavescens*	Scientific name
Family	Percidae	Fish family
Order	Perciformes	Fish order
LifeStage	adult	Life stage
Source	Kitchell *et al.* 1977	Original reference
CEQ	2	Consumption equation used
CA	0.25	Intercept for the consumption allometric mass function
CB	-0.27	Slope for the consumption allometric mass function
CQ	2.3	Water temperature-dependent coefficient of consumption (approximates a Q_{10})
CTO	23	Optimal temperature for consumption
CTM	28	Maximum water temperature above which consumption ceases
CTL	NA	Temperature at which consumption is some reduced fraction (CK4) of the max. rate
CK1	NA	Small fraction of the maximum rate
CK4	NA	Reduced fraction of the maximum rate
REQ	2	Respiration equation used
RA	0.0108	Intercept of the allometric mass function for standard metabolism
RB	-0.2	Slope of the allometric mass function for standard metabolism
RQ	2.1	Q_{10} rate at which the function increases over relatively low temperatures
RTO	28	Optimum temperature for respiration
RTM	33	Maximum (lethal) water temperature

Parameter	Value	Description
RTL	NA	Cutoff temperature at which the activity relationship changes
RK1	NA	Intercept for the swimming speed above the cutoff temperature
RK4	NA	Mass dependence coefficient for swimming speed at all water temperatures
RK5	NA	Temperature-dependent coefficient for swimming speed
ACT	1	Activity multiplier
BACT	NA	Water temperature dependence coefficient of swimming speed at water temperature below RTL
SDA	0.172	Specific dynamic action
EGEQ	2	Egestion equation used
FA	0.158	Egestion
FB	-0.222	Coefficient of water temperature dependence of egestion
FG	0.631	Coefficient for feeding level dependence (P-value) of egestion
EXEQ	2	Excretion equation used
UA	0.0253	Excretion
UB	0.58	Coefficient of water temperature dependence of excretion
UG	-0.299	Coefficient for feeding level dependence (P-value) of excretion
PREDEDEQ	1	Predator energy density equation used
ED	4186	Predator energy density
Alpha1	NA	Intercept of the allometric mass function for first size range
Beta1	NA	Slope of the allometric mass function for first size range
Cutoff	NA	End of first size range
Alpha2	NA	Intercept of the allometric mass function for second size range
Beta2	NA	Slope of the allometric mass function for second size range
Notes	NA	Important information to consider when using this model

Optional Input Files

1. **Mortality** (Mortality.csv)
   This example mortality file specifies the mortality due to natural causes and the mortality due to fishing, each expressed as discrete mortality from that source, occurring during the period specified. **Note:** FB4 does not use linear interpolation for the mortality file. Rather, each specified mortality is converted to a daily instantaneous rate and is applied each day until a different mortality value is specified. For this example file, the natural mortality rate is applied at an annual discrete rate of 0.2 during days 1 to 365. Fishing mortality is applied at a discrete rate of 0.1 during the interval from day 1 to 100, at a rate of 0 during days 101 to 249, and at a discrete rate of 0.15 during days 250 to 365. **Note**: a row with the final day of the simulation is needed to allow for the Mortality.csv to be read.

day	natural	fishing
1	0.2	0.1
101	0.2	0
250	0.2	0.15
365	0.2	0.15

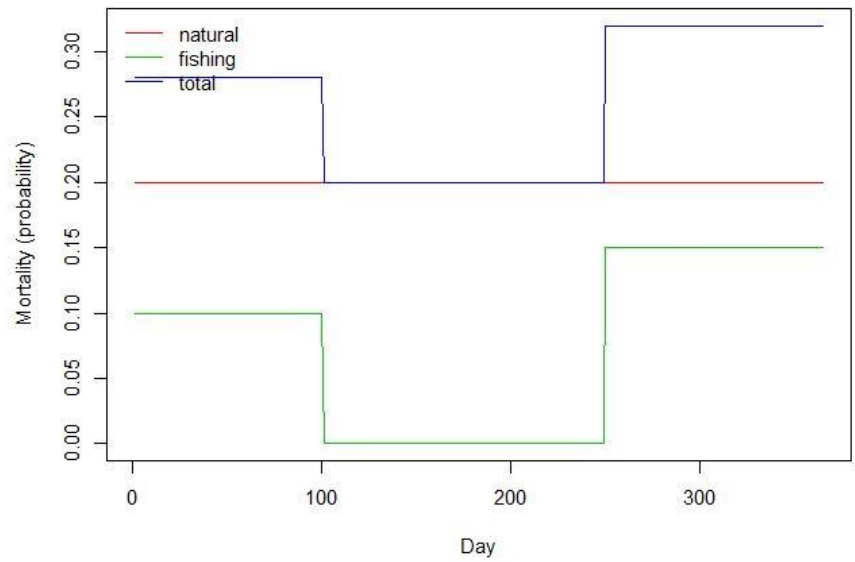
To account for mortality, choose the **Population** option under the **Sub-models** tab, select the **Mortality** box (this turns on the sub-model) and input your **Initial Population Size**. On the right hand side you will see two plots. The first plot indicates the mortality probability (based on the Mortality.csv input file) associated with the different mortality types, along with a total mortality probability. The second plot shows the decline in population numbers over time as a result of these mortality probabilities.

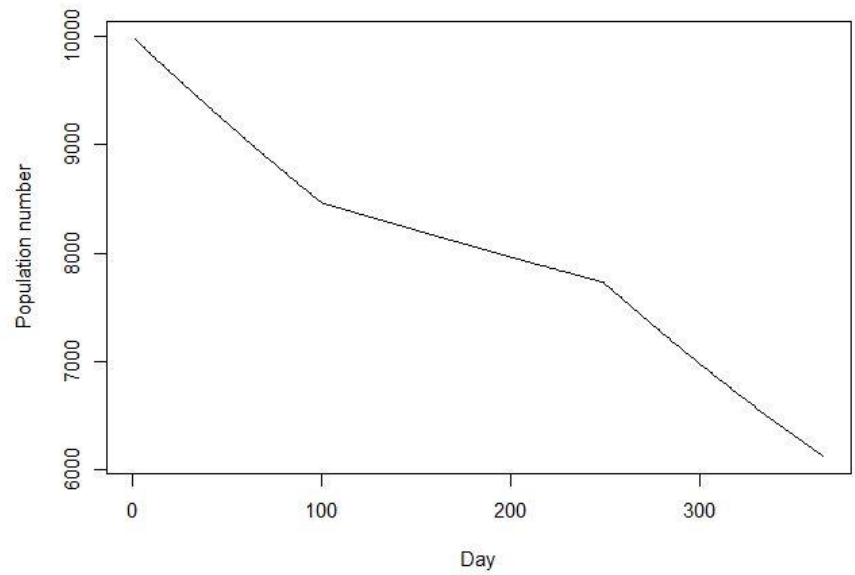
Fish Bioenergetics 4.0 Initial Settings Input Files Sub-Models Output

☑ Mortality

Initial Population Size

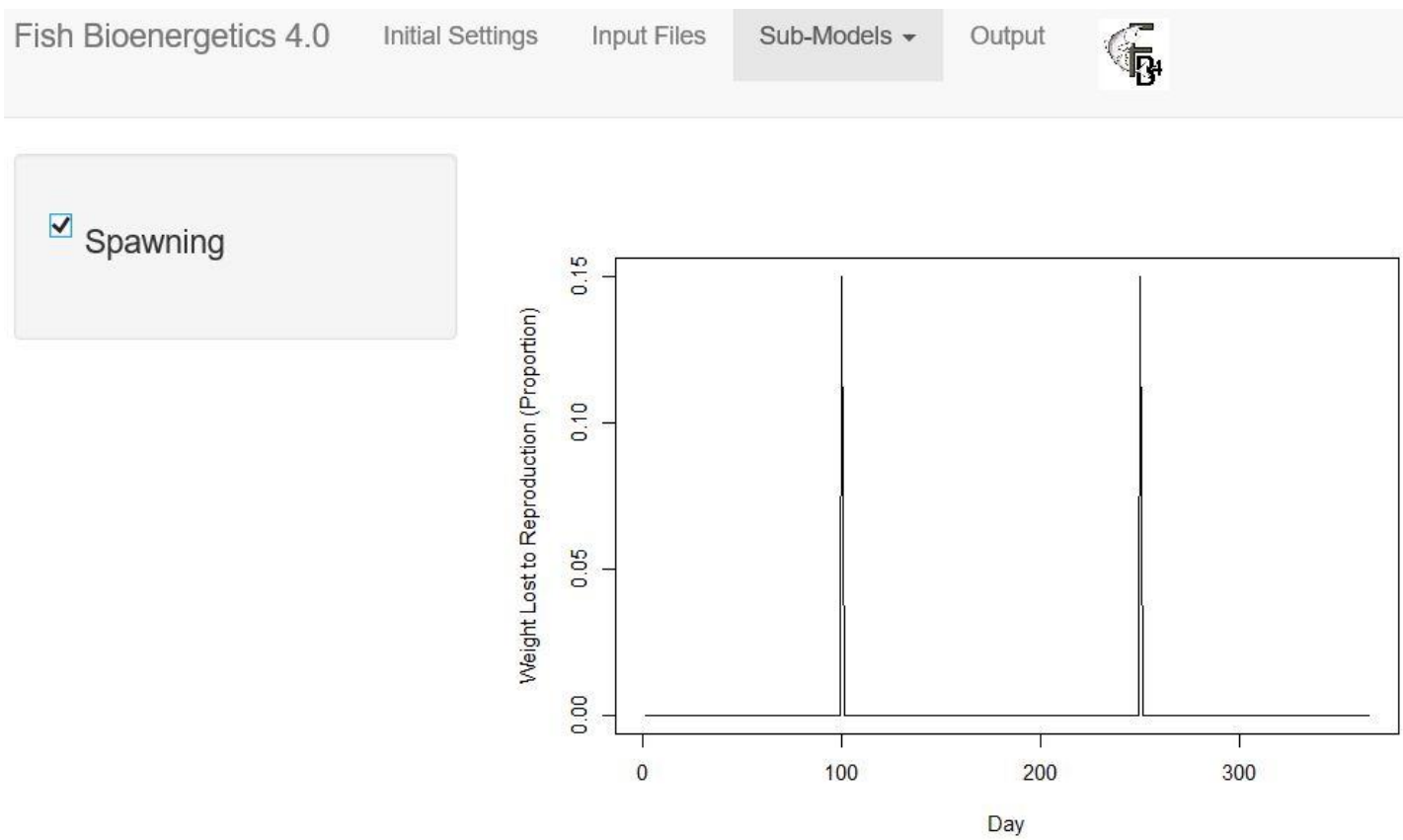
10000





2. **Reproduction** (Reproduction.csv)
   The Reproduction sub-model allows the user to account for energy and weight loss via spawning by specifying in the input file Reproduction.csv the day(s) the fish will spawn and the proportion of body weight lost as reproductive products each spawning day. To simulate spawning losses, choose the **Reproduction** option under the **Sub-models** tab and select the **Spawning** box to turn on the submodel. In this example the fish is shown to spawn on two different occasions.

day	proportion
1	0
100	0.15
101	0
250	0.15
251	0
365	0



3. **Nitrogen Assimilation Efficiency** (Nit_Ae.csv), **Nitrogen Concentration in Prey** (Nit_Conc_Prey.csv), and **Nitrogen Concentration in Predator** (Nit_Conc_Pred.csv)

The Nutrient Regeneration sub-model allows the model to estimate the amounts of nitrogen and phosphorus consumed, and the total mass of N and P excreted and egested. Under the **Nutrient Regeneration** sub-model tab, select the **Nutrient Regeneration** box. The sub-model uses the following input data files: Nit_Ae.csv, Nit_Conc_Pred.csv, Nit_Conc_Prey.csv, Phos_Ae.csv, Phos_Conc_Pred.csv, and Phos_Conc_Prey.csv. Plots will be instantly generated based on these input files and can be visualized by selecting the plot of interest on the right-hand side of the window. **Note:** The file structures and data types are the same for Phosphorus regeneration as they are for Nitrogen regeneration.

Nitrogen Assimilation Efficiency

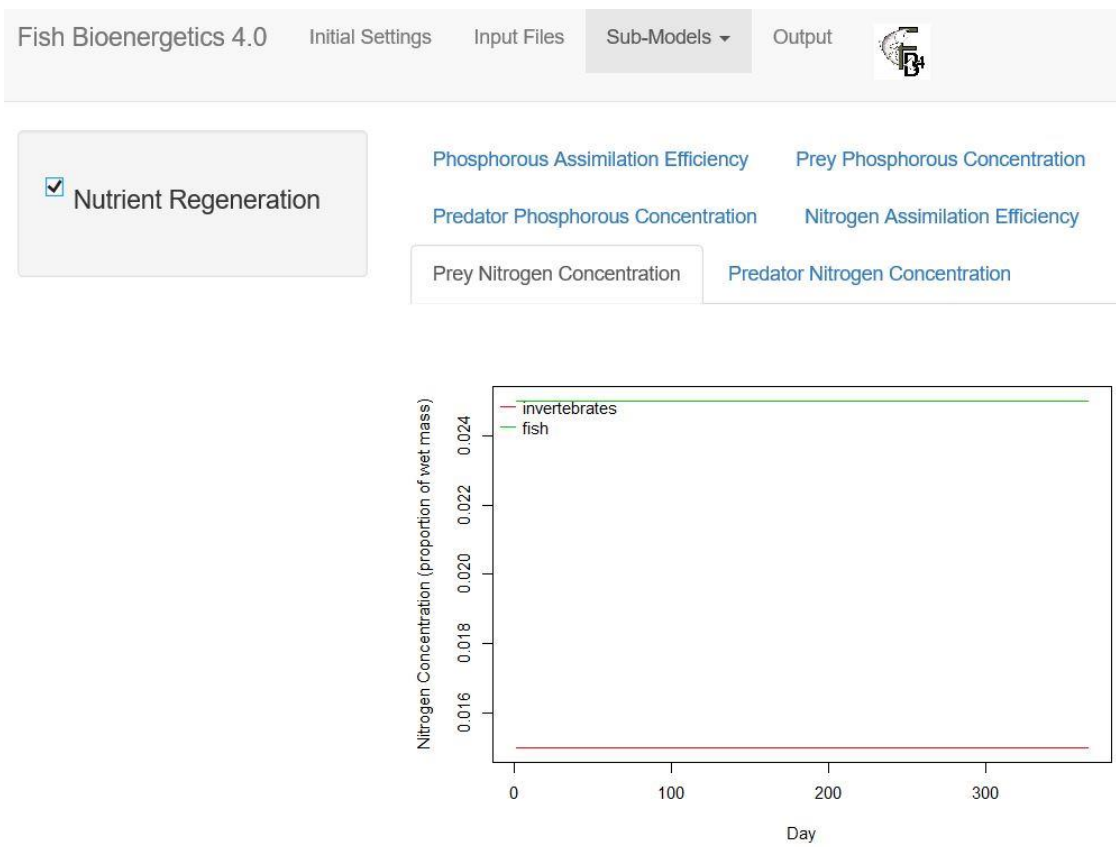
day	invertebrates	fish
1	0.8	0.8
365	0.8	0.8

Nitrogen Concentration in Prey (g/g wet weight)

day	invertebrates	fish
1	0.015	0.025
365	0.015	0.025

Nitrogen Concentration in Predator (g/g wet weight)

day	predn
1	0.025
365	0.025



4. **Contaminant Assimilation Efficiencies in Prey Items** (Contaminant Assimilation.csv), **Contaminant Concentrations in Prey Items** (Contaminant Concentration.csv), and **Transfer Efficiency of the contaminant from prey to predator** (Transfer Efficiency.csv)

   The contaminant accumulation sub-model allows the model to estimate contaminant accumulation in the predator, as well as clearance and uptake rates. Under the **Contaminant Accumulation** sub-model tab, select the **Contaminant Accumulation** box. You then need to decide on which model to use (Model 1 or 2; See Contaminant Accumulation section). You will also need to input an **Initial Predator Concentration (µg/g)** for both models. Based on your input files (Contaminant Assimilation.csv, Contaminant Concentration.csv, and Transfer Efficiency.csv), FB4 will generate three plots to the right side of the window.

   Contaminant Assimilation Efficiency from Prey

day	invertebrate	fish
1	0.9	0.8
365	0.9	0.8

   Contaminant Concentration in Prey

day	invertebrate	fish
1	0.03	0.05
365	0.03	0.05

   Transfer Efficiency of Contaminant from Prey to Predator

day	invertebrate	fish
1	0.50	0.55
365	0.50	0.55

Outputs

FB4 allows users to select over 50 output variables to summarize their simulations. Some variables are only available when specific sub-models are selected. Below is a summary of output parameters by category along with a brief description of each variable.

Individual Variables	Units	Description
Day	day	Day of year (the downloaded Excel output table will also include the day of the simulation in the first column).
Temperature	°C	Temperature on the current day.
Weight	g	Wet mass of the fish at the end of the day.
Net Production	g	Increase in mass of the cohort on the current day excluding losses to metabolism and mortality.
Net Production	J	Increase in energy of the cohort on the current day excluding losses to metabolism and mortality.
Cumulative Net Production	g	Cumulative increase in mass of the cohort excluding losses to metabolism and mortality.
Cumulative Net Production	J	Cumulative increase in energy of the cohort excluding losses to metabolism and mortality.
Gross Production	g	Total increase in mass of the cohort on the current day (includes mass used in metabolism and lost through mortality).
Gross Production	J	Total increase in energy of the cohort on the current day (includes energy used in metabolism and lost through mortality).
Cumulative Gross Production	g	Cumulative increase in mass of the cohort (includes mass used in metabolism and lost through mortality).
Cumulative Gross Production	J	Cumulative increase in energy of the cohort (includes energy used in metabolism and lost through mortality).
Specific Growth Rate	g/g/d	The mass of prey allocated to growth per gram of predator on the current day.
Specific Growth Rate	J/g/d	The energy of prey allocated to growth per gram of predator on the current day.
Specific Consumption Rate	g/g/d	The mass of prey consumed per gram of predator on the current day.
Specific Consumption Rate	J/g/d	The energy of prey consumed per gram of predator on the current day.
Consumption	g	The total mass of all prey consumed by an individual fish on the current day.
Consumption	J	The total energy of all prey consumed by an individual fish on the current day.
Cumulative Consumption	g	Cumulative mass of all prey types consumed by an individual fish.

Cumulative Consumption	J	Cumulative energy of all prey types consumed by an individual fish.
Consumption of prey type i on the current day	g	Mass of prey type i consumed by an individual fish on the current day.
Consumption of prey type i on the current day	J	Energy of prey type i consumed by an individual fish on the current day.
Specific Egestion Rate	J/g/d	The energy egested per gram of predator on the current day.
Specific Excretion Rate	J/g/d	The energy excreted per gram of predator on the current day.
Specific Respiration Rate	J/g/d	The energy required for metabolism per gram of predator on the current day.
Specific SDA Rate	J/g/d	The energy allocated to SDA per gram of predator on the current day.
Initial Predator Energy Density	J/g	Predator energy density at the beginning of the day.
Final Predator Energy Density	J/g	Predator energy density at the end of the day.
Mean Prey Energy Density	J/g	Mean weighted prey energy density on the current day.
Gametic Production	g	The total mass of gametes lost via spawning on the current day.
Gametic Production	J	The total energy of gametes lost via spawning on the current day.
Population Variables		
Population Number	Individuals	Total number of fish alive at the end of the current day
Population Biomass	g	Total mass of the cohort at the end of the current day
Consumption by Population	g	The total mass of all prey consumed by the entire cohort on the current day.
Consumption by Population	J	The total energy of all prey consumed by the entire cohort on the current day.
Cumulative Consumption by Population	g	Cumulative mass of all prey consumed by the population.
Cumulative Consumption by Population	J	Cumulative energy of all prey consumed by the population.
Consumption of prey type i by population	g	Mass of prey type i consumed by the population on the current day.
Consumption of prey type i by population	J	Energy of prey type i consumed by the population on the current day.
Mortality	Individuals	Number of fish removed from the population on the current day.
Mortality	g	The mass of fish removed from the population on the current day.

Nutrient Regeneration Variables		
Nitrogen Egestion	g	Total mass of N egested.
Phosphorous Egestion	g	Total mass of P egested.
N:P Egestion	mass ratio	N:P ratio of egested nitrogen and phosphorous.
Nitrogen Excretion	g	Total mass of N excreted.
Phosphorous Excretion	g	Total mass of P excreted.
N:P Excretion	mass ratio	N:P ratio of egested nitrogen and phosphorous.
Nitrogen Consumption	g	Total mass of N consumed.
Phosphorous Consumption	g	Total mass of P consumed.
N:P Consumption	mass ratio	N:P ratio of consumed nitrogen and phosphorous.
Nitrogen Growth	g	Mass of N allocated to growth.
Phosphorous Growth	g	Mass of P allocated to growth.
N:P Growth	mass ratio	N:P ratio of nitrogen and phosphorous allocated to growth.
Contaminant Analysis Variables		
Contaminant Clearance Rate	µg/d	Product of elimination rate (d^{-1}) times contaminant burden (µg)
Contaminant Uptake	µg	Mass of contaminant consumed.
Contaminant Burden	µg	Mass of contaminant in predator
Contaminant Predator Concentration	µg /g	Concentration of contaminant in predator tissue.

Putting it all together

The most fundamental unit of analysis is a cohort. In FB4, a cohort is a single species of fish in a specific life stage. A cohort can represent one or many fish. You create a cohort every time you run a simulation using user input parameters and data. Multiple cohorts are created by running multiple simulations using either different user input parameters, data, or both. User input data are imported through .csv files found in the **Main Inputs** and **Sub-Models** folders in the FB4 folder. New bioenergetics models and physiological parameters can be added to the "Parameters_official.csv" file found in the FB4 folder.

An Important Note about Editing and Saving Input Files

While Excel is very useful for viewing and editing input files, there are some idiosyncrasies that users should be aware of. After you open and edit an input file in Excel, when you choose "Save" or "Save As" a dialog box will open that says:

"Some features in your workbook might be lost if you save it as CSV (Comma delimited).
Do you want to keep using that format?"

If you choose Yes, Excel does not actually save the file. When you close Excel you will be asked if you want to save your changes to the file. If you choose Save, your file will be saved.

If you will be making a lot of changes to your input files and want to avoid this inconvenience, follow these steps to change your default format to .csv:

Select the Files tab, click on Options (bottom of the list), and then select Save. In the top dialog box select .csv as the format in which files will be saved.

After this is set, if you choose Save or Save As, you will still see the dialog box asking if you want to keep the .csv format, but if you choose Yes your file will actually be saved. This lets you leave the file open in case you want to go back to look at it, or will want to change it and save it again soon.

Recognize that once you do this, .csv format will be the default for any files you save in Excel until you repeat the process and change the format back to .xlsx.

The following exercises will introduce you to the Fish Bioenergetics 4.0 modeling platform. Exercises are designed around specific questions to familiarize users with different types of modeling scenarios and output. *Prior to beginning, copy and paste the* FB4 *folder onto your desktop or another preferred location*. You can make multiple copies of the FB4 folder and assign a different file name of your choosing to each (e.g., FB4_2, YellowPerch, etc…). But keep in mind that you will need to set your working directory so that FB4 is able to recognize which folder you are working with for a given simulation.

EXERCISES

Input Dataset 1:

These are the main input data saved as the default Excel .csv files in FB4. Main inputs (*file names*) include water temperature in °C (*Temperature.csv*), prey composition as proportion of wet mass (*Diet_prop.csv*), prey energy density as J/g wet mass (*Prey_E.csv*), and predator energy density as J/g wet mass (*Pred_E.csv*).

Water temperature

day	temperature
1	5
30	4
90	9
120	14
150	19
180	23
210	25
240	23
270	19
300	14
330	9
360	5
365	4

Prey composition

day	inverts	fish
1	1	0
91	1	0
183	0	1
274	0	1
365	0	1

Prey energy density

day	inverts	fish
1	3000	4000
365	3000	4000

Predator energy density

day	predator
1	4500
365	4500

Indigestible prey

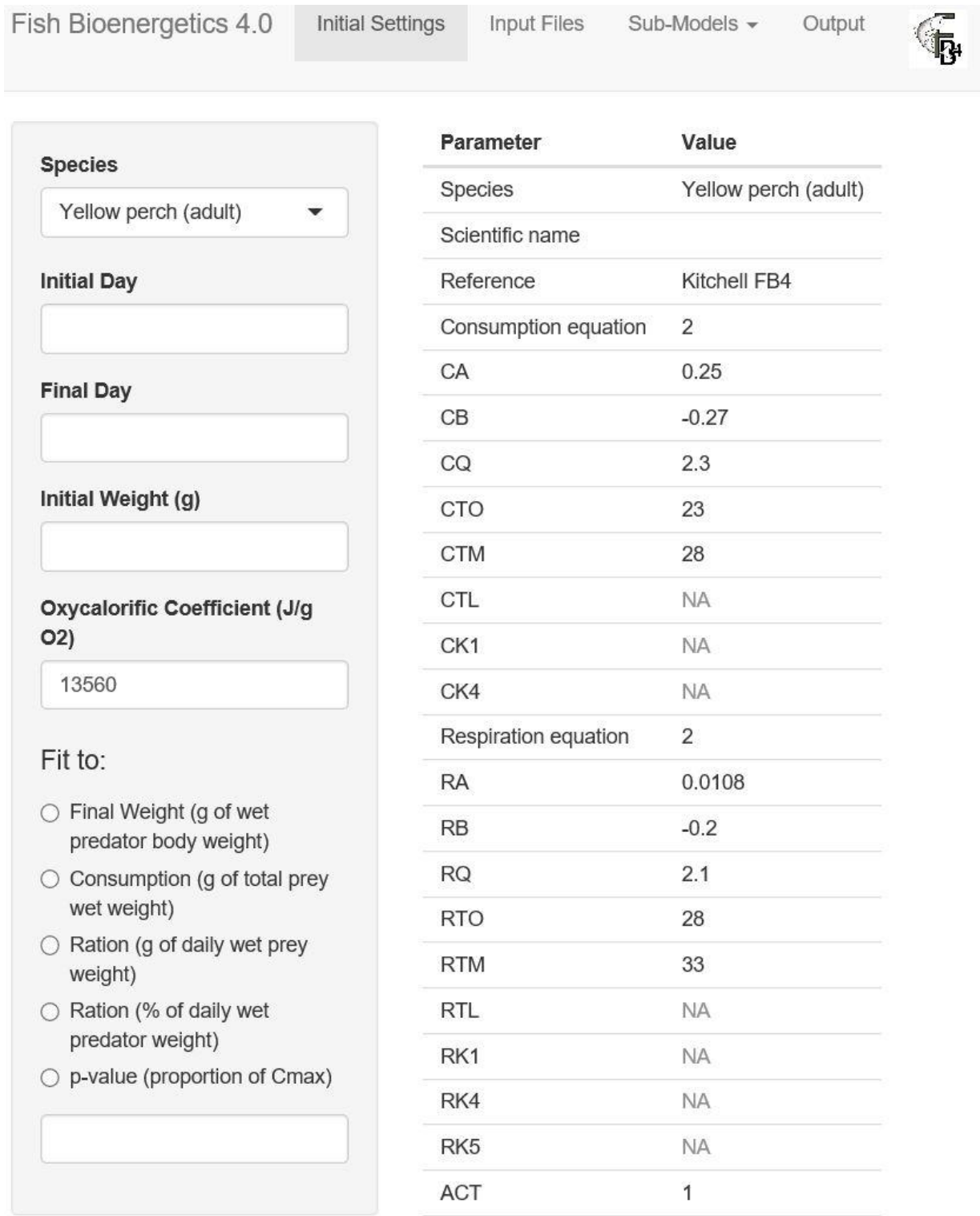
day	inverts	fish
1	0	0
365	0	0

Example 1: Creating a cohort using a simple growth simulation

In general, you need to complete five steps to create and analyze a new cohort. To demonstrate this, we will estimate the amount of food required for an average, age-2 Yellow Perch to grow from 65 to 122 g over 1 year. To successfully create a cohort FB4 requires that all input data files are correctly populated (see **Main Input Files** section). In addition to growth data, we also collected water temperature data every month, we determined diet composition for Yellow Perch at different times of the year, and we obtained energy density estimates for Yellow Perch and their prey categories. Values shown in **Input Dataset 1** above represent default values in the **Main Input Files**. Using the default data, follow the five steps below to guide you through a bioenergetics simulation of Yellow Perch growth and consumption.

Step 1. Species Selection

Once FB4 has been launched, select your species/model of interest under the **Species** dropdown menu, which is found under the **Initial Settings** tab. Information pertaining to that model (i.e., equations, parameters, references) can been seen in table format on the right hand side of the window once a species/model has been selected. FB4 will use these physiological parameters to run the bioenergetics simulations. In this example, we will select the Yellow Perch (adult) model.

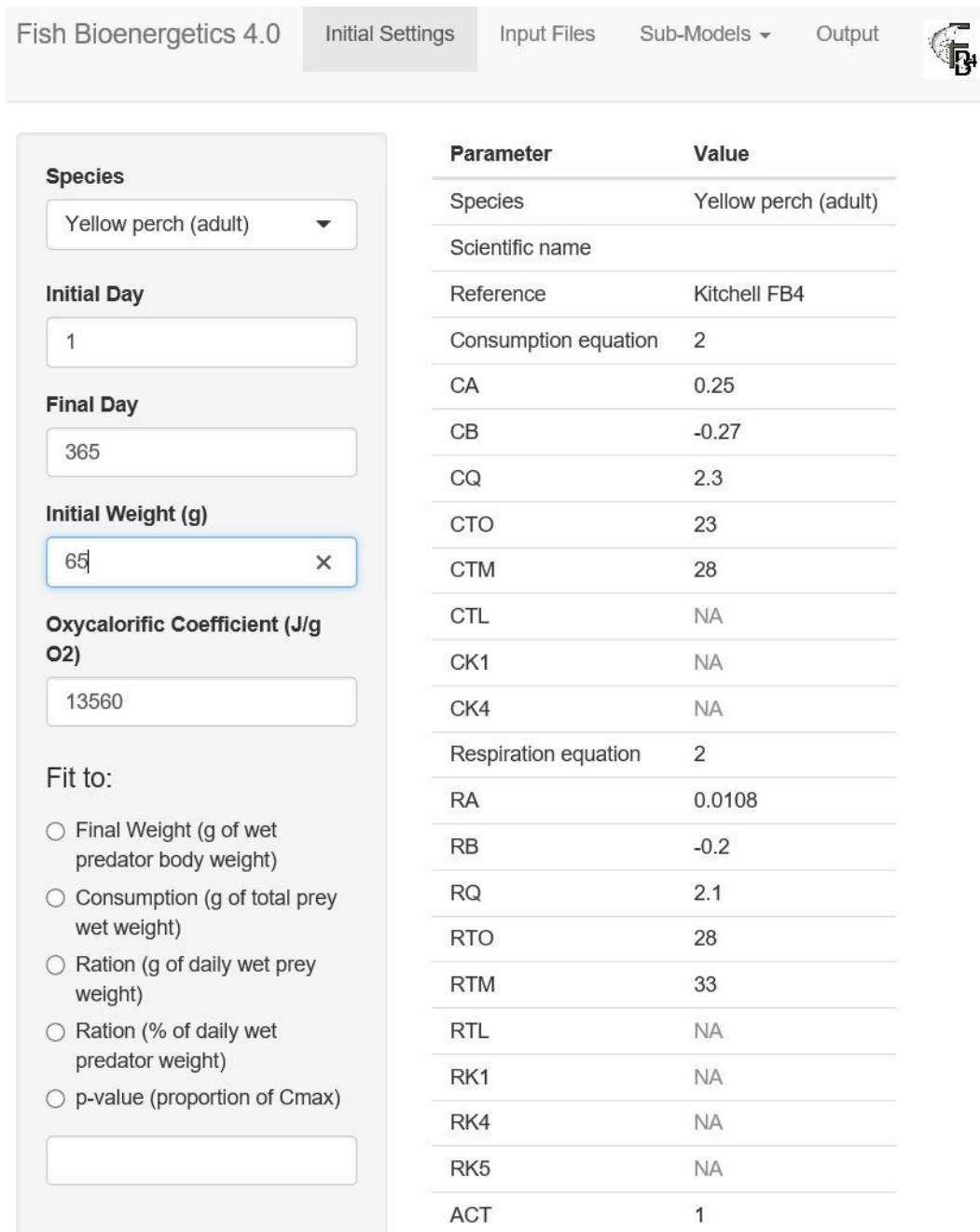


Parameter	Value
Species	Yellow perch (adult)
Scientific name	
Reference	Kitchell FB4
Consumption equation	2
CA	0.25
CB	-0.27
CQ	2.3
CTO	23
CTM	28
CTL	NA
CK1	NA
CK4	NA
Respiration equation	2
RA	0.0108
RB	-0.2
RQ	2.1
RTO	28
RTM	33
RTL	NA
RK1	NA
RK4	NA
RK5	NA
ACT	1

Step 2. Setup

In the **Initial Settings** tab, fill out the **Initial Day** (1) and **Final Day** (365) of the simulation. Care must be taken to ensure that this time interval is within the days range given in the input data files. Once the initial and final days are entered, you can visualize the input data that will be used for the simulation. To do so, select the **Input Files** tab to view the temperature, diet proportions, prey energy density, predator energy density, or indigestible prey (not applicable in this example) data that will be used. These plots will adjust automatically every time the **Initial** and(or) **Final Days** are modified under the **Initial Settings** tab.

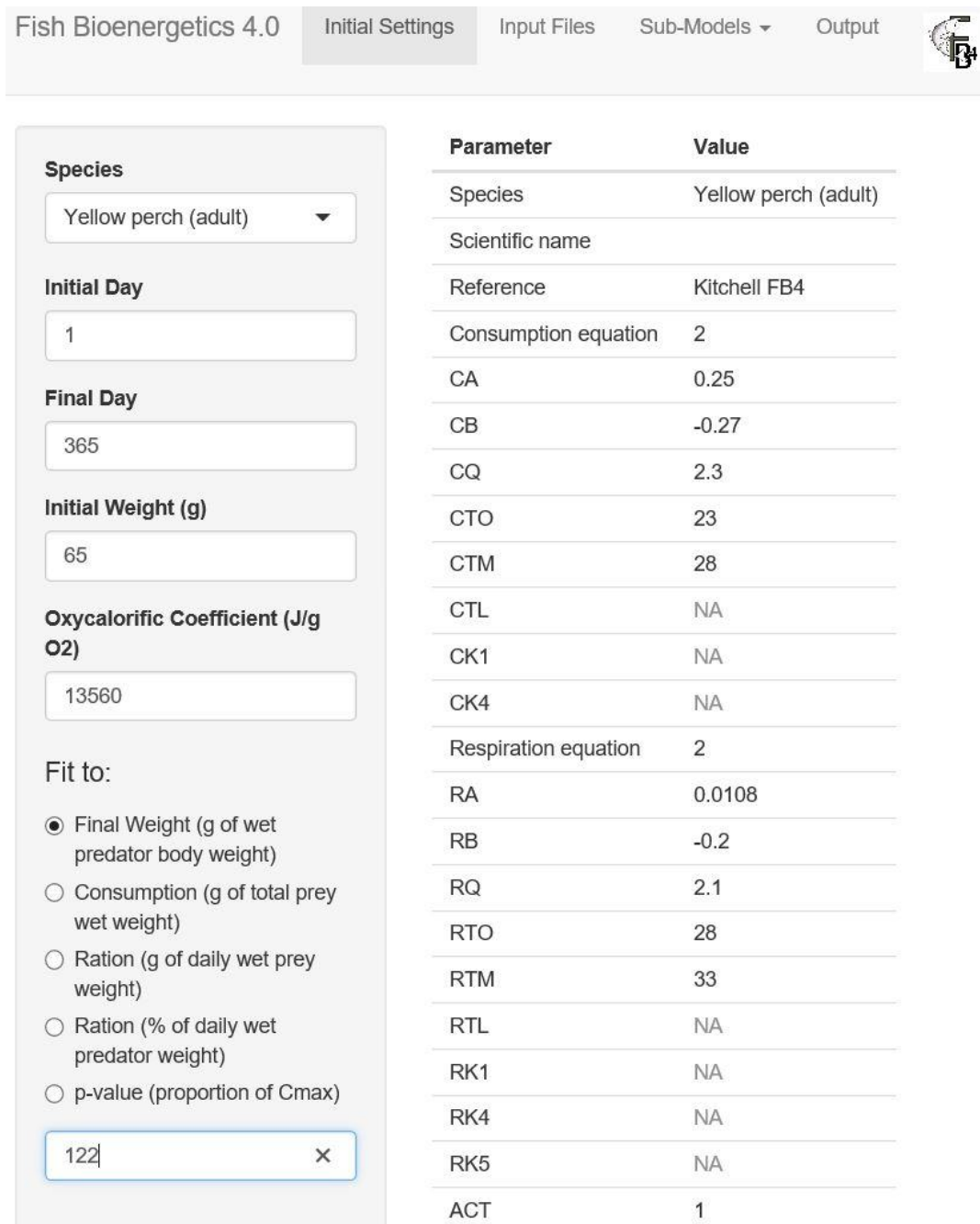
Next, you must enter the **Initial Weight** (65 g of wet weight) you wish your fish to be at the beginning of the simulation. Lastly, FB4 offers the option to modify the **Oxycalorific Coefficient**, which has been set to 13,560 J/g O_2 as a default value. We will not change it for this example.



Step 3. 'Fit to:' options

FB4 gives you five different fitting options, one of which must be selected before any simulation can begin. The fitting options are found at the bottom left section of the **Initial Settings** tab. One fitting option must be selected and an appropriate value must be entered in the box below. Please note that the fitting options have different units. For this example, we will select **Final Weight**, but take notice of the other four options:

(1) Final Weight: User specifies the mass in g of wet weight the fish will reach at the end of the simulation (122 g wet weight for this example). FB4 uses this information to iteratively calculate a P-value (proportion of C_{max}) that will allow for the simulated final weight to equal the input final weight (see ***Consumption*** section).



(2) Consumption: User specifies the total amount of food (in g of wet weight of prey) that will be consumed by an individual fish during the simulation. FB4 uses this information to iteratively calculate a P-value (proportion of C_{max}) that will allow for the simulated final cumulative consumption to equal the input final cumulative consumption.

(3) Ration (g per day of prey, wet weight): User specifies a constant mass of prey eaten by an individual fish on each day of the simulation. With this option the model uses user-specified consumption rather than the consumption estimation function in the model. **Note**: the user should confirm that the specified rate is reasonable (i.e., ≤ C_{max}) on each day of the simulation.

(4) Ration (% per day of predator weight): user specifies a constant percentage of predator body weight eaten by an individual fish on each day of the simulation. With this option the model also uses user-specified consumption rather than the consumption estimation function in the model. Again, the user should confirm that the specified rate is reasonable (i.e., ≤ C_{max}) throughout the simulation.

(4) P-value: The proportion of C_{max} (size- and temperature-dependent) applied to each day of your simulation.

Step 4. Run your simulation

Once steps 1-3 have been completed, you are now ready to run a simulation. To do so, simply select the **Output** tab and the simulation will begin. For simulations that take more than a second, an indicator at the bottom-right or top-right (depending on the Shiny version) will show "Calculating…" confirming that the program is running.

Important: It is important to note that input files cannot be modified and used while running FB4 without reloading the whole program. For example, if the temperature profile is modified in the Temperature.csv file while FB4 is running, the new information will not be accessible automatically. One approach is to simply click the refresh icon on your web browser (or F5 on the keyboard). While this will reload FB4 to incorporate changes you made to input files, it will clear all information from the **Initial Settings** page. A short cut that will not clear this information is to delete and then retype a value in one of the data entry boxes on the **Initial Settings** page. For example, deleting the value for Initial Day and then retyping the same (or different) value will reload the model to read the revised input data files while maintaining other values entered in the **Initial Settings** page.

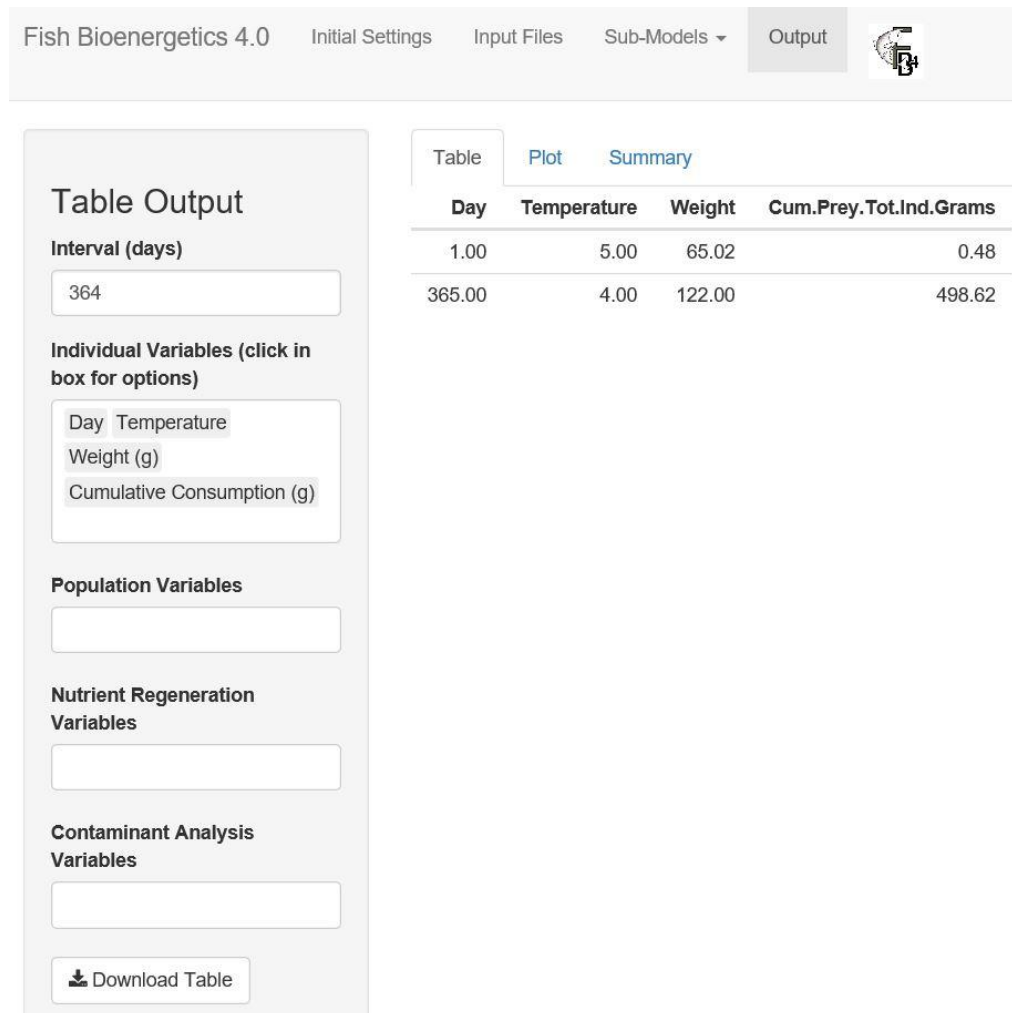
Step 5. Visualizing your output.

In FB4 you are able to visualize your outputs in three different ways: Table, Plot, or Summary. All three of these options are found under the **Output** tab in FB4 and are available once the simulation is completed.

(1) Tabulated Output

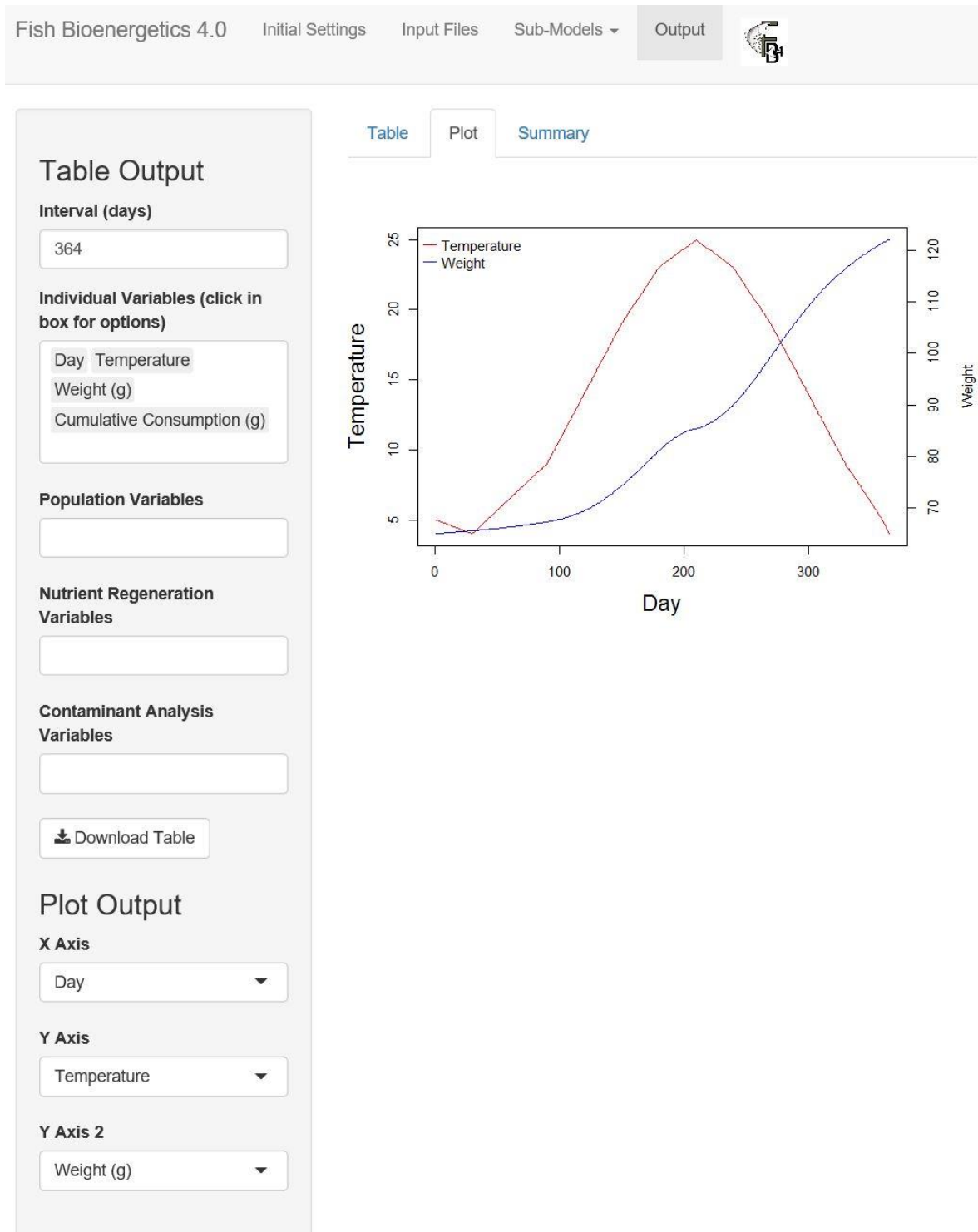
This is where you can access the simulated data for each one of the daily time steps. Once the Table appears after the simulation has finished running, three default variables will appear: **Day** of the simulation, water **Temperature**, and fish **Weight** at the end of the day. You can also decide on the **Intervals (days)** for which you wish your table to be displayed. You can select different output options under the **Individual Variables** and **Population Variables** boxes on the left. Click your cursor inside the box to view the different options. You can scroll down the list, or start typing the name of the variable you want. **Note:** Most **Individual** and **Population Variables** will be identical when the population number is equal to 1 (default). To delete a variable from the display, click on its name in the box and hit delete. Lastly, the **Download Table** button allows you to download your output table to a .csv file for further analyses and data visualization. On-screen values are rounded to two decimal places, but downloaded values are not.

In our Yellow Perch simulation, scroll down through the **Individual Variables** box and select the **Cumulative Consumption (g)** variable. You can see that a 65 g Yellow Perch will need to consume 498.62 g of food throughout the year to grow to 122 g.



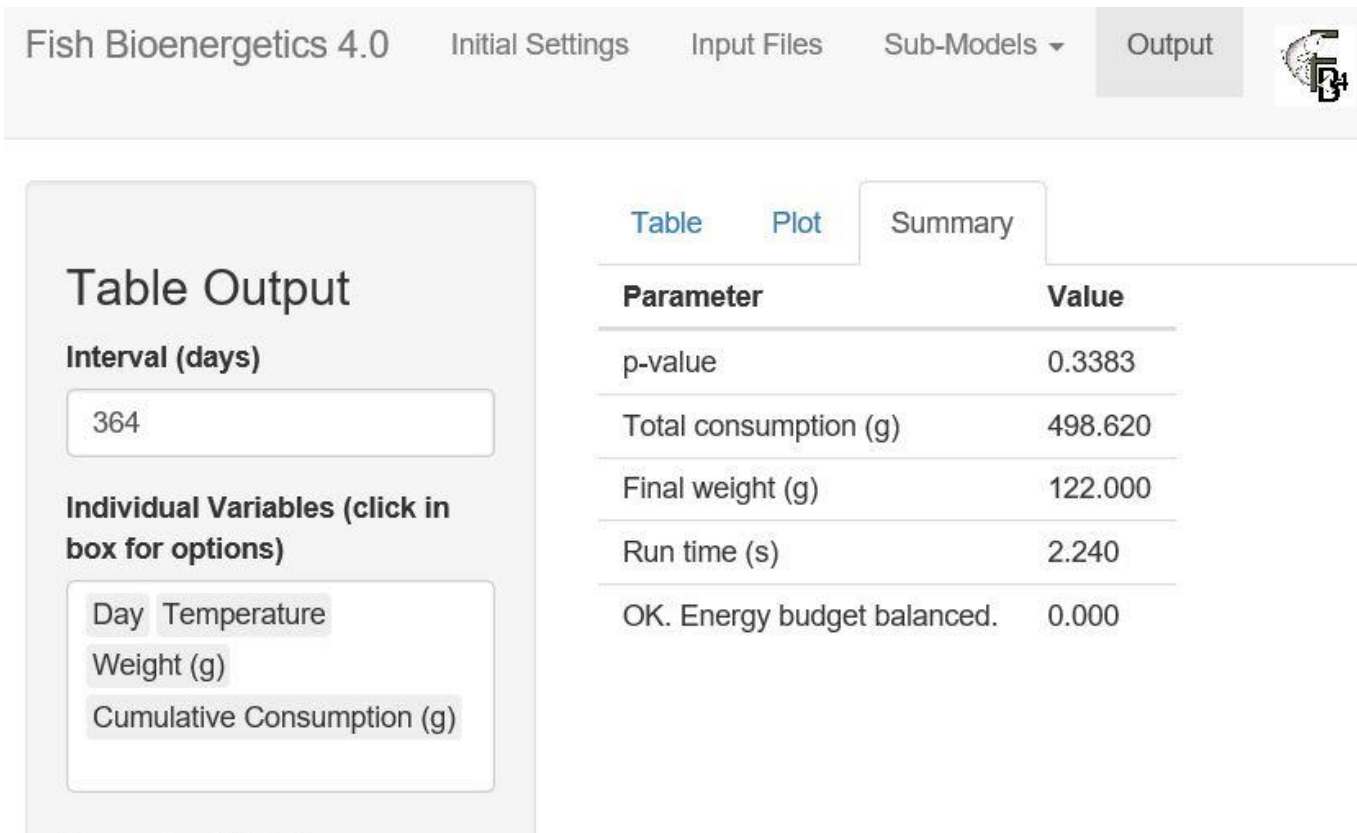
(2) Plot Output

Results can also be quickly visualized using a two y-axes plot under the **Plot** tab. You have the option to choose from the same variables found in the Table Output section. You will have to select a variable for the x-axis (usually simulation day) and two variables for the y-axes. The plot will be instantly generated based on the variables selected. The default plot is set to have simulation **Day** on the x-axis and **Weight** and **Temperature** on the y-axes.



(3) Summary

The last output option is the summary table, accessed through the **Summary** tab. This table consists of three values that are generated after each simulation run. The first value is the P-value, which is the proportion of C_{max} used to balance the energy budget for the duration of the simulation. In this example, adult Yellow Perch ate at an average of 33.83% of their maximum capacity throughout the simulation period. The second value is total consumption (g), which represents the total amount of food consumed by our fish during the entire simulation period. Notice how this value (498.620 g) is the same as the one generated in the *Tabulated Output*. Lastly, the Final weight (g) value indicates the weight of our Yellow Perch at the end of the simulation. You will notice that this value is equal to the **Final Weight** value entered under the **Initial Settings** tab. These three values are useful to get a quick glimpse at the fish's performance during the simulation. It is important to note that if the simulation is fitted to a constant ration (%) that no P-value will be returned.



Scenario A: Now we will determine how much food an age-2 perch requires for maintenance (e.g., no net growth). Re-run the model with an initial and ending weight equal to 65 g and fill in the results for scenario A in Table E1.

Note: to check your answers, the correct output for all exercises is listed in Appendix A.

Scenario B: Let's assume that no forage fish were available so that invertebrates represented 100% of the Yellow Perch diet. Hint: You will need to change values in the prey composition file (Diet_prop.csv) to represent this diet change and then reload FB4 using the browser refresh button or delete and reenter a value on the **Initial Settings** page. Re-run the model with an initial and ending weight equal to 65 g and fill in information for scenario B in Table E1.

Scenario C: Finally, what happens if the caloric density of invertebrates is changed from 3,000 to 4,500 Joules/g wet weight? Re-run the model using invertebrate prey only with an initial and ending perch weight equal to 65 g; fill in information for scenario C in Table E1.

Table E1.

Scenario	P-value (proportion of maximum consumption)	Total, annual prey consumption (g)
A (65 to 65 g)		
B (no fish prey)		
C (increase in Prey E)		

Example 2: Seasonal Energy Requirements

NOTE: Be sure to restore all **Main Input** data to the default values in **Input Dataset 1**.

Now let's assume that a 150 g Yellow Perch does not gain weight, so that its initial and final weight on day 1 and 360 are the same. Run simulations for three time periods: days 1-120, 121-240, and 241-360, keeping the initial and final weight of the Yellow Perch at 150 g, and complete Table E2 below.

Table E2.

Period (days)	Average Temperature (°C)	P-value	Total Consumption (g)
1-120	**7.3**		
121-240	**21.4**		
241-360	**13.9**		

During which period does the fish require the least amount of energy to maintain its weight? Why?

What is the highest P-value you obtained from the three simulations? How would you interpret this?

Example 3: Modeling Climate Change Effects

NOTE: Be sure to restore all **Main Input** data to original values in **Input Dataset 1**.

Now let's model the effects of global warming on food consumption and growth of age 5 Largemouth Bass in North Carolina. To do this, estimate the P-value and annual food consumption for an age-5 Largemouth Bass with an initial weight of 540 g on day 1 and a final weight of 660 g on day 365, and enter your results in Table E3 under "Baseline". Let's assume that average, daily water temperature in High Rock Lake increases by 2 °C. For the next simulation, adjust water temperature values in the .csv file by increasing each value +2. Then re-run your analysis assuming that feeding rate does not change. To do this, check the Fit to: P-value option, and enter the P-value from your Baseline run. Enter total consumption and final weight under "Global warming". Calculate net change from Baseline conditions as [(Global warming-Baseline)/Baseline x 100].

Table E3.

Baseline			Global warming		% Net change	
P-value	Total consumption (g)	Final weight (g)	Total consumption (g)	Final weight (g)	Total consumption (g)	Final weight (g)

How does 'global warming' affect food consumption for age 5 Largemouth Bass? Why?

What if 'extra' prey isn't available for Largemouth Bass under our climate change scenario, and prey abundance is similar to our Baseline conditions (i.e., total consumption value above)? Estimate what Largemouth Bass growth (i.e., final weight) will be based on the warmer temperatures you entered. To do this, you will be modeling growth, rather than consumption – and will need to select the "Fit to: Consumption" option in Initial Settings, and enter the grams of food consumed from your Baseline estimate above.

What is the final, predicted size of an age-5 Largemouth Bass?

What if food consumption is 10% less than Baseline **(1,541 g)**? Re-run your growth simulation and estimate the final size of a Largemouth Bass under this scenario.

What is the final, predicted size of an age-5 Largemouth Bass?

Example 4: Population Mortality

To increase predator abundance and enhance fishing opportunities, a total of 1,223 adult Lake Trout were recently stocked into Deerfield Reservoir, South Dakota. The average initial weight of each fish was about 4536 g. Although diet information is lacking, we hope they prey on introduced Rock Bass that are very abundant in the lake. So we would like to know how many Rock Bass (mean size = 80 g) would be needed to support an annual growth of 90 g (or 2%/y) for an individual Lake Trout, corresponding to a mean, final weight of 4626 g on day 365. You will note on the **Initial Settings** page that the adult Lake Trout model uses predator equation 2. This equation estimates Lake Trout energy density as a function of body mass each day, so users do not need to provide an energy density value. **Note**: Users can input their own estimates of energy density if desired, by opening the **Parameters_official.csv** file and changing the value in the predator energy density model column (PREDEDEQ) from "2" to "1". When using Model 1, the predator energy density file (Pred_E.csv) is used for simulations. The prey in this simulation (Rock Bass) have an energy density of 4000 J/g. In addition, total mortality of adult Lake Trout is assumed to be 8% per year. Files for population analysis can be found in the **Sub-models** folder in the main FB4 folder. To perform a population analysis in FB4, click on **Submodels** → then **Population** → then be sure to check the box labeled **Mortality** and enter the initial population size (i.e., 1,223). Run a simulation to estimate total, annual consumption of Rock Bass by the Lake Trout population in Deerfield Reservoir, using values shown below for **Input Dataset 2**. We assume fishing mortality to be low (2%) given the minimum size regulations, so we will assume natural mortality is 6% (for total mortality=8%) in the **Mortality**.csv file. Add your results to Table E4 below.

Input Dataset 2:

Water temperature

day	temperature
1	5
30	4
90	8
120	10
150	12
180	13
210	15
240	12
270	10
300	8
330	6
360	5
365	4

Prey composition

day	inverts	fish
1	0	1
91	0	1
183	0	1
274	0	1
365	0	1

Prey energy density

day	inverts	fish
1	3000	4000
365	3000	4000

Indigestible prey

day	inverts	fish
1	0	0
365	0	0

Mortality

day	natural	fishing
1	0.06	0.02
365	0.06	0.02

Table E4.

Estimate	Value on day 365
Cumulative prey consumption by population (g)	
Population biomass (g)	
Population number	

Assuming Lake Trout feed exclusively on young Rock Bass, how many bass (i.e., total number) would be needed for the Lake Trout population to be able to grow to their desired weight of 4,626 g/fish?

Example 5: Nutrient Regeneration

This exercise will introduce you to nutrient analysis using bioenergetics models. We will model phosphorus (P) regeneration by Gizzard Shad using the input data shown below in **Input Dataset 3**. The input data needs for nutrient analysis include prey P concentration (weight of P in fish/total weight of fish), predator P concentration, and assimilation efficiency, which is set to 0.72.

Based on our sampling of Lake Bigfish, we find that invertebrates (zooplankton) have a P concentration of 0.0025 g/g and detritus has a P concentration of 0.002 g/g. We will assume Gizzard Shad have a P concentration of 0.005 g/g. These data are used to populate the files for nutrient analysis found in the **Sub-models** folder in the main FB4 folder. To perform nutrient analysis, click on **Submodels** → then **Nutrient Regeneration** → then be sure to check the box labeled **Nutrient Regeneration**. Using the input data below, run a nutrient analysis from day 150 to day 250, with an initial and final weight of 80 g for a juvenile Gizzard Shad. Use the model output to calculate total Phosphorus excretion for a juvenile Gizzard Shad during the simulation period, and fill in table 5. Next, re-run the analysis using an initial and final weight of 300 g – indicative of an adult Gizzard Shad. Calculate total Phosphorus excretion for an adult fish and fill in table 5.

Input Dataset 3:

Water temperature

day	temperature
1	5
30	4
90	9
120	14
150	19
180	23
210	25
240	23
270	19
300	14
330	9
360	5
365	4

Prey composition

day	inverts	detritus
1	1	0
91	1	0
183	0.8	0.2
274	0.3	0.7
365	0	1

Prey energy density

day	inverts	detritus
1	3000	3300
365	3000	3300

Predator energy density

day	predator
1	4200
365	4200

Indigestible prey

day	predator	detritus
1	0	0
365	0	0

Table E5.

Life-stage	Weight (g)	Total P excretion (g)	Total g P/acre
Juvenile	80		
Adult	300		

How does body size affect nutrient excretion in Gizzard Shad?

Now let's standardize Gizzard Shad biomass – and see how this jives with your answer above. Setting equal biomass for Juvenile and Adult Gizzard Shad to 13,600 g/acre for each population, calculate total P excreted for each life stage and add to the last column in Table E5. Which life-stage excretes more P per acre? Why?

Appendix A. Answers to example exercises

Example 1: Creating a cohort using a simple growth simulation

Table E1.

Scenario	P-value (proportion of maximum consumption)	Total, annual prey consumption (g)
A (65 to 65 g)	0.262	303
B (no fish prey)	0.329	398
C (increase in Prey E)	0.219	265

Example 2: Seasonal Energy Requirements

Table E2.

Period (days)	Average Temperature (°C)	P-value	Total Consumption (g)
1-120	**7.3**	**0.311**	**126**
121-240	**21.4**	**0.293**	**316**
241-360	**13.9**	**0.247**	**179**

Which period does the fish require the least amount of energy to maintain its weight? Why?

What is the highest P-value you obtained from the three simulations? How would you interpret this?

Example 3: Modeling Climate Change Effects

Table E3.

Baseline			Global warming		% Net change	
P-value	Total consumption (g)	Final weight (g)	Total consumption (g)	Final weight (g)	Total consumption (g)	Final weight (g)
0.49	**1713**	**660**	**2175**	**808**	**33**	**30**

How does 'global warming' affect food consumption for age 5 Largemouth Bass? Why?

What is the final, predicted size of an age-5 Largemouth Bass (climate change scenario, with no extra prey)? ***619 g; P-value=0.42.***

What is the final, predicted size of an age-5 Largemouth Bass (climate change scenario, with 10% less prey)? ***551 g; P-value=0.39***

Example 4: Population Mortality

Table E4.

Estimate	Value on day 365
Cumulative prey consumption by population (g)	**10,271,108 g**
Population biomass (g)	**5,212,933 g**
Population number	**1,126**

Assuming Lake Trout feed exclusively on young Rock Bass, how many bass (i.e. total number) would be needed for the Lake Trout population to be able to grow to their desired weight of 4,626 g/fish?

128,388 Rock Bass per year to support the Lake Trout population.

Example 5: Nutrient Regeneration

Table E5.

Life-stage	Weight (g)	Total P excretion (g)	Total g P/acre
Juvenile	80	**0.5**	**85**
Adult	300	**1.42**	**64**

How does body size affect nutrient excretion in Gizzard Shad?

Which life-stage excretes more P per acre? Why?

Troubleshooting

Here is a list of common errors (and their explanations) that can occur in FB4.

1. Under **Input Files** and **Sub-Models** tabs

Error
Error: NA/NaN argument

Solution
- Make sure you enter an Initial Day and Final Day under the Initial Settings tab.

Error
Error: missing value where TRUE/FALSE needed

Solution
- Make sure you selected a species before running your simulation

2. Under **Output** tab

Error
Error: NA/NaN argument

Solution
- Make sure the Final Day you entered does not exceed the number of days found in the input files.

Error
Error: missing value where TRUE/FALSE needed

Solution
- Make sure you selected a species before running your simulation

Error
Error: argument is of length zero

Solution
- Make sure you selected a fitting option and entered a value in the box below.

Error
Error: undefined columns selected

Solution
- Make sure the number of prey types is the same in all input files. Also make sure all prey types are labeled the same across input files.

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