


FEATURE

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Fish Bioenergetics 4.0: An R-Based Modeling Application

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Bioenergetics modeling is a widely used tool in fisheries management and research. Although popular, currently available software (i.e., Fish Bioenergetics 3.0) has not been updated in over 20 years and is incompatible with newer operating systems (i.e., 64-bit). Moreover, since the release of Fish Bioenergetics 3.0 in 1997, the number of published bioenergetics models has increased appreciably from 56 to 105 models representing 73 species. In this article, we provide an overview of Fish Bioenergetics 4.0 (FB4), a newly developed modeling application that consists of a graphical user interface (Shiny by RStudio) combined with a modeling package used in the R computing environment. While including the same capabilities as previous versions, Fish Bioenergetics 4.0 allows for timely updates and bug fixes and can be continuously improved based on feedback from users. In addition, users can add new or modified parameter sets for additional species and formulate and incorporate modifications such as habitat-dependent functions (e.g., dissolved oxygen, salinity) that are not part of the default package. We hope that advances in the new modeling platform will attract a broad range of users while facilitating continued application of bioenergetics modeling to a wide spectrum of questions in fish biology, ecology, and management.

INTRODUCTION

The bioenergetics modeling approach provides a sound, theoretical tool for quantifying energy allocation in fishes by partitioning consumed energy into three basic components: (1) metabolism, (2) wastes, and (3) growth (Winberg 1956; Ney 1993). The models are often used to estimate growth or food consumption and are particularly attractive for estimating feeding rates of free-ranging fishes given the time and effort required by traditional techniques (Kitchell et al. 1977).

Based on the second law of thermodynamics, bioenergetics models are formulated as an energy balance equation:

$$C = R + A + SDA + F + U + G,$$

where energy input (i.e., consumed food, C) is balanced by metabolic demands (standard metabolism, R ; energy expenditure due to activity, A ; and specific dynamic action, SDA, or the energy required to digest food), waste losses due to egestion (F) and excretion (U), and somatic and/or gonadal growth (G); units for all terms are typically joules per day.

Traditionally, bioenergetics models have been used to evaluate factors affecting fish growth through diet or environmental constraints (Bevelhimer and Adams 1993) or to quantify the impact a predator may have on its prey (Stewart et al. 1981, 1983). Currently, bioenergetics models are widely used as an analytical tool to address a broad range of questions in physiology, ecology, aquaculture, and fisheries management (Hartman and Hayward 2007; Chipps and Wahl 2008; Bevelhimer and Breck 2009; Armstrong and Schindler 2011; Madenjian 2011; Canale et al. 2013). Bioenergetics modeling has also improved our understanding of feeding and growth of fish at different life stages (Post 1990; Madon and Culver 1993; Beauchamp 2009; Lawrence et al. 2015). As new challenges have arisen, researchers have found new bioenergetics model applications in fisheries management and research (Hartman and Kitchell 2008). Special symposia held at annual meetings of the American Fisheries Society (1989 in Anchorage, Alaska; 1992 in Rapid City, South Dakota; 2004 in Madison, Wisconsin) have advanced the science by broadening the application of bioenergetics modeling, identifying limitations to model inference, and recommending future directions for the field (Bartell et al. 1986; Beauchamp et al. 1989; Boisclair and Leggett 1989; Brandt and Hartman 1993; Hansen et al. 1993; Ney 1993; Megrey et al. 2007; Chipps and Wahl 2008; Hartman and Kitchell 2008; Madenjian et al. 2012). More recently, bioenergetics models have been used to explore whole-life growth patterns of fish (Rose et al. 1999; Hayes et al. 2000), to evaluate the impact of invasive species on aquatic ecosystems (Cooke and

Hill 2010; Cerino et al. 2013), to assess contaminant accumulation by fish (Stafford and Haines 2001; Trudel and Rasmussen 2006), and to quantify the effects of habitat alterations on fish survival (Niklitschek and Secor 2009; Rose et al. 2013). Increasingly, researchers are turning to bioenergetics modeling as a robust approach for evaluating effects of climate change on foraging, growth, and mortality of fishes (Petersen and Kitchell 2001; Megrey et al. 2007; Kishi et al. 2010; Breeggemann et al. 2015).

Often referred to as the “Wisconsin model,” the popular modeling approach used today was based on the pioneering work of James F. Kitchell and collaborators at the University of Wisconsin–Madison Center for Limnology (Kitchell et al. 1977), which in turn built upon earlier work on energy partitioning in fish (Ivlev 1939; Fry 1947; Winberg 1956; Brett 1971). This foundation, and the growing interest in bioenergetics modeling applications to research and management, sparked development of computer software applications that included Fish Bioenergetics 1.0 (Hewett and Johnson 1987), Fish Bioenergetics 2.0 (Hewett and Johnson 1992), and Fish Bioenergetics 3.0 (Figure 1; Hanson et al. 1997). The 1997 release of Fish Bioenergetics 3.0 by the Wisconsin Sea Grant Program has been tremendously popular among fisheries scientists worldwide, due to the sound biological foundation of bioenergetics models, the user-friendly environment of the application, and the relatively low cost of the software (Hanson et al. 1997). Since its release, Fish Bioenergetics 3.0 has been cited over 600 times in the scientific literature (Google Scholar Citations).

Although the modeling approach offered by Fish Bioenergetics 3.0 remains popular, the software is 20 years old and out of date with regards to new information and computer technologies. That version, for example, is a 32-bit program that is incompatible with newer 64-bit Microsoft Windows operating systems (and it was never compatible with non-Windows operating systems). In addition, a number of long-standing bugs in the program have been recognized (Madenjian et al. 2012; Canale and Breck 2013) and needed to be corrected in future versions. Most important, prior applications were not amenable to user modifications or additions, a commonly noted limitation (Hartman and Hayward 2007). The new version presented here assures that bioenergetics modeling will continue to be an accessible, user-friendly tool for addressing contemporary fisheries questions. The purpose of this article is to provide an overview of Fish Bioenergetics 4.0, a newly developed modeling application that (1) incorporates new species models; (2) corrects known bugs; (3) offers an adaptable, user-friendly working environment; and (4) updates the user’s guide.

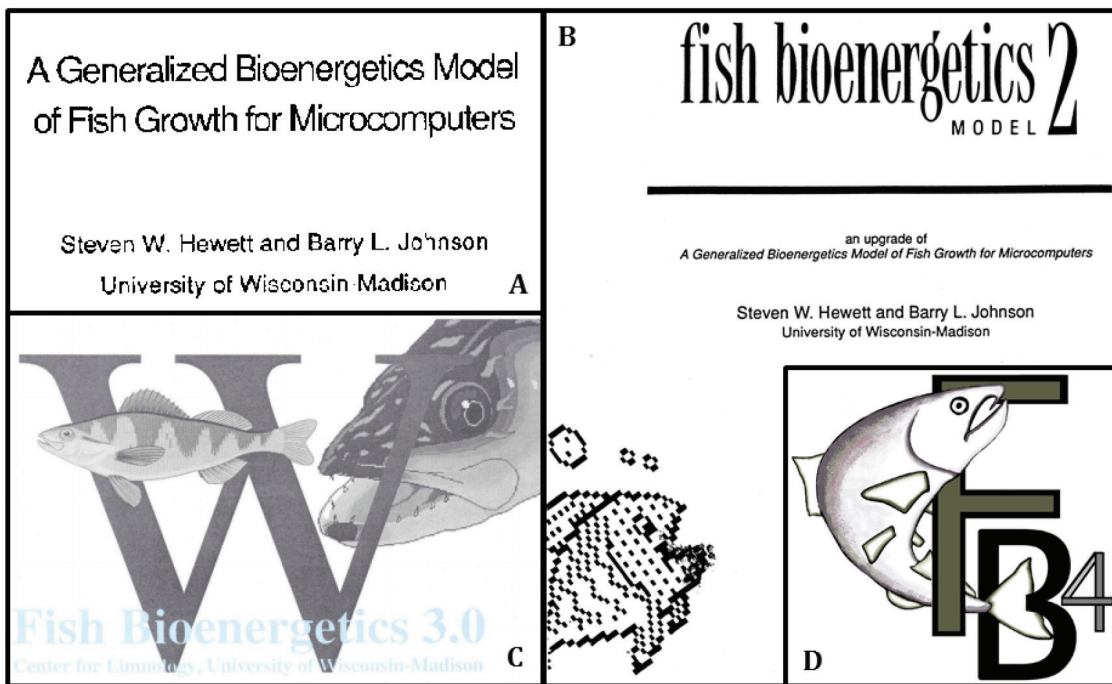


Figure 1. User's guide cover pages for previously developed Fish Bioenergetics software. (A) Fish Bioenergetics 1 (Hewett and Johnson 1987), (B) Fish Bioenergetics 2 (Hewett and Johnson 1992), (C) Fish Bioenergetics 3.0 (Hanson et al. 1997), and (D) Fish Bioenergetics 4.0.

FISH BIOENERGETICS 4.0 R-Based Application

The popularity and widespread use of bioenergetics modeling was linked, in no small part, to the availability and user-friendly attributes of previous software versions. The graphical user interface of Fish Bioenergetics 3.0 allowed users to easily navigate the modeling environment. However, because Fish Bioenergetics 3.0 was developed as a compiled program (i.e., C++), users were unable to access the code to fix bugs, customize analyses, or address other program issues. In contrast, Fish Bioenergetics 4.0 (hereafter referred to as FB4) uses an R-based analytical approach that consists of a graphical user interface application (Shiny by RStudio; Chang et al. 2015) and an independent modeling package to be used in the R computing environment (R Core Team 2015). The programming approach of FB4 enables timely updates and bug fixes and can rely on feedback from users to continuously improve the application. We also note that the error in the algorithm to balance the fish's daily energy budget found in Fish Bioenergetics 3.0 (see Madenjian et al. [2012] and Canale and Breck [2013] for more details) has been corrected in FB4. Users will also be able to formulate and incorporate modifications such as habitat-dependent functions (e.g., dissolved oxygen, salinity) and submodels that are not part of the default package and can easily add parameter sets for additional species without modifying the R code. Because the core model code is accessible to users, it can be incorporated as a module in larger models if desired.

Our goal in developing FB4 was to provide a user-friendly, menu-driven environment for bioenergetics modeling that appeals to users with little or no experience in R programming. During development of FB4, we conserved many aspects of the previous version (Fish Bioenergetics 3.0) while adding features that improved efficiency and ease of working from the user interface. It is our hope that advances in the new modeling platform

will attract a broad range of users while facilitating continued use of bioenergetics modeling to address ecological and management questions.

Open Access

FB4 is free, open-access software that is available for download at fishbioenergetics.org and on the Fisheries Information and Technology Section website of the American Fisheries Society (www.fishdata.org/software). Once downloaded, FB4 offers users the ability to run bioenergetics simulations on a personal computer without access to the Internet. In addition to program files, instructions for Getting Started, as well as an updated User's Guide are available for download on these websites.

Updated Species Models

Bioenergetics models are now available for a wide range of freshwater and marine fish species, as well as for several aquatic invertebrate species (Table 1). The number of published bioenergetics models has increased appreciably from five models covering three species in the late 1970s to 105 models covering 73 species in 2017 (Figure 2). In addition, a number of studies have been published that provide revisions of alternative formulations for previously existing models (Table 1).

Working Environment

The user interface allows users to manage initial settings for a model simulation, review input data, and view and download simulation output. Once a species is selected from the drop-down list on the Initial Settings page, the parameter set for that model is displayed (Figure 3). After the user specifies the initial and final day of the simulation and starting weight of the fish, he or she can choose among several options for the type of simulation to run the following:

Table 1. List of models included in Fish Bioenergetics 4.0 (FB4). Bioenergetics models that are new to FB4 are indicated by an asterisk (*). † denotes new or revised versions of existing models found in previous versions of Fish Bioenergetics software. A = adult, J = juvenile, L = larvae.

Family	Species	Number of models; life stages	References
Acipenseridae	Pallid Sturgeon <i>Scaphirhynchus albus</i> *	2; L, J	Chipps et al. (2009); Heironimus (2015)
Cambaridae	Rusty Crayfish <i>Orconectes rusticus</i> *	1; A	Roth et al. (2006)
Centrarchidae	Largemouth Bass <i>Micropterus salmoides</i>	1; A	Rice et al. (1983)
	Smallmouth Bass <i>Micropterus dolomieu</i>	3; J, A	Shuter and Post (1990); Whitley et al. (2003)†
	White Crappie <i>Pomoxis annularis</i> *	1; A	Zweifel (2000); Bajer et al. (2004)
	Bluegill <i>Lepomis macrochirus</i>	2; J, A	Kitchell et al. (1974)
	Sacramento Perch <i>Archoplites interruptus</i> *	1; A	Bliesner (2005)
Channidae	Snakehead <i>Channa striatus</i> *	1; J	Qin et al. (1997)
Cichlidae	Blue Tilapia <i>Oreochromis aureus</i>	1; A	Nitithamyong (1988)
Clupeidae	Alewife <i>Alosa pseudoharengus</i>	4; L, J, A	Stewart and Binkowski (1986); Klumb et al. (2003)†
	Atlantic Menhaden <i>Brevoortia tyrannus</i> *	1; L	Rippetoe (1993); Annis et al. (2011)†
	Baltic Herring <i>Clupea harengus</i> *	1; J	Arrhenius (1998); Rudstam (1988); Blaxter (1960)
	Gizzard Shad <i>Dorosoma cepedianum</i> *	1; J, A	Sebring (2002)
	Herring <i>Clupea harengus</i>	2; J, A	Rudstam (1988)
Cottidae	Prickly Sculpin <i>Cottus asper</i> *	1; J, A	Moss (2001)
Cyprinidae	Bighead Carp <i>Hypophthalmichthys nobilis</i> *	1; J, A	Cooke and Hill (2010)
	Dace <i>Phoxinus</i> spp.	1; J, A	He (1986); Trudel and Boisclair (1994)
	Fathead Minnow <i>Pimephales promelas</i> *	1; J, A	Duffy (1998)
	Humpback Chub <i>Gila cypha</i> *	1; J, A	Petersen and Paukert (2005)
	Northern Pikeminnow <i>Ptychocheilus oregonensis</i> *	1; J, A	Petersen and Ward (1999)
	Red River Shiner <i>Notropis bairdi</i> *	1; A	Offill (2003)
	Roach <i>Rutilus rutilus</i> *	1; A	Karjalainen et al. (1997)
	Silver Carp <i>Hypophthalmichthys molitrix</i> *	1; J, A	Cooke and Hill (2010)
	Zebra Mussel <i>Dreissena polymorpha</i> *	1; A	Schneider (1992)
Engraulidae	Bay Anchovy <i>Anchoa mitchilli</i> *	1; J, A	Luo and Brandt (1993)
	European Anchovy <i>Engraulis encrasicolus</i> *	3; L, J, A	Politikos et al. (2011)
Esocidae	Muskellunge <i>Esox masquinongy</i>	1; A	Bevelhimer et al. (1985)
	Northern Pike <i>Esox lucius</i>	1; A	Bevelhimer et al. (1985)
	Tiger Muskellunge <i>Esox lucius</i> x <i>E. masquinongy</i>	2; J, A	Bevelhimer et al. (1985); Schoenebeck et al. (2008)†
Fundulidae	California Killifish <i>Fundulus parvipinnis</i> *	1; J, A	Madon et al. (2001)
	Plains Killifish <i>Fundulus zebrinus</i> *	1; J, A	Offill (2003)
Gadidae	Atlantic Cod <i>Gadus morhua</i> *	2; J, A	Hansson et al. (1996); Mateo (2007)
	Walleye Pollock <i>Theragra chalcogramma</i>	5; J, A	Buckley and Livingston (1994)
Gasterosteidae	Threespine Stickleback <i>Gasterosteus aculeatus</i> *	1; J, A	Hovel et al. (2015)
Gobiidae	Round Goby <i>Neogobius melanostomus</i> *	1; J, A	Lee and Johnson (2005)
Hexagrammidae	Lingcod <i>Ophiodon elongatus</i> *	1; A	Beaudreau and Essington (2009)
Latidae	Nile Perch <i>Lates niloticus</i>	1; J	Kitchell et al. (1997)
Lotidae	Burbot <i>Lota lota</i> *	1; J, A	Pääkkönen et al. (2003)
Moronidae	Striped Bass <i>Morone saxatilis</i>	5; L, J, A	Hartman and Brandt (1995); Johnson (1995)
	White Bass <i>Morone chrysops</i> *	1; L	Johnson (1995)
Mysidae	Mysis <i>Mysis diluviana</i>	1; A	Rudstam (1989); Rudstam et al. (1999)†
Osmeridae	European Smelt <i>Osmerus eperlanus</i> *	1; L, J	Karjalainen et al. (1997)
	Rainbow Smelt <i>Osmerus mordax</i>	3; L, J, A	Lantry and Stewart (1993)
Paralichthyidae	Southern Flounder <i>Paralichthys lethostigma</i> *	1; J, A	Burke and Rice (2002)
Percidae	Eurasian Perch <i>Perca fluviatilis</i> *	3; L, J, A	Karas and Thoreson (1992); Karjalainen et al. (1997)
	Ruffe <i>Gymnocephalus cernuus</i> *	1; J, A	Tarvainen et al. (2008)
	Saugeye <i>Sander vitreus</i> x <i>S. Canadensis</i> *	1; A	Zweifel et al. (2010)

Table 1. (Continued).

Family	Species	Number of models; life stages	References
	Walleye <i>Sander vitreus</i>	2; L, J, A	Kitchell et al. (1977); Madon and Culver (1993)
	Yellow Perch <i>Perca flavescens</i>	3; L, J, A	Kitchell et al. (1977); Post (1990)
	Zander <i>Zander zander</i> *	1; A	Keskinen et al. (2008)
Petromyzontidae	Sea Lamprey <i>Petromyzon marinus</i>	1; A	Kitchell and Breck (1980)
Poeciliidae	Western Mosquitofish <i>Gambusia affinis</i> *	1; J, A	Chippis and Wahl (2004)
Pomatomidae	Bluefish <i>Pomatomus saltatrix</i>	1; L, J, A	Hartman and Brandt (1995)
Salmonidae	Baikal Grayling <i>Thymallus arcticus baicalensis</i> *	1; J, A	Hartman and Jensen (2017)
	Bloater Chub <i>Coregonus hoyi</i>	1; A	Rudstam et al. (1994)
	Brook Trout <i>Salvelinus fontinalis</i> *	1; J, A	Hartman and Sweka (2003); Hartman and Cox (2008)
	Brown Trout <i>Salmo trutta</i> *	1; J, A	Dieterman et al. (2004)
	Bull Trout <i>Salvelinus confluentus</i> *	1; J, A	Mesa et al. (2013)
	Chinook Salmon <i>Oncorhynchus tshawytscha</i>	1; J, A	Stewart and Ibarra (1991); Plumb and Moffitt (2015)
	Coho Salmon <i>Oncorhynchus kisutch</i>	1; J, A	Stewart and Ibarra (1991)
	Cutthroat Trout <i>Oncorhynchus claki</i>	1; J, A	Beauchamp et al. (1995)
	Generalized coregonid <i>Coregonus</i> spp.	1; A	Rudstam et al. (1994)
	European Whitefish <i>Coregonus lavaretus</i> *	1; L, J	Huuskonen et al. (1998)
	Lake Trout <i>Salvelinus namaycush</i>	1; A	Stewart et al. (1983)
	Lake Whitefish <i>Coregonus clupeaformis</i> *	1; A	Madenjian et al. (2006, 2013)
	Lenok <i>Brachymystax lenok</i> *	1; A	Hartman and Jensen (2017)
	Pink Salmon <i>Oncorhynchus gorbuscha</i>	1; J, A	Beauchamp et al. (1989)
	Rainbow Trout <i>Oncorhynchus mykiss</i> *	2; J, A	Railsback and Rose (1999); Tyler and Bolduc (2008)
	Sockeye Salmon <i>Oncorhynchus nerka</i>	1; J, A	Beauchamp et al. (1989)
	Steelhead <i>Oncorhynchus mykiss</i>	1; J, A	Rand et al. (1993)
	Vendace <i>Coregonus albula</i> *	1; L, J	Karjalainen et al. (1997)
Sciaenidae	Weakfish <i>Cynoscion regalis</i>	2; L, J, A	Hartman and Brandt (1995)
Scomberesocidae	Pacific Saury <i>Cololabis saira</i> *	2; J, A	Ito et al. (2004); Mukai et al. (2007)
Scorpaenidae	Indo-Pacific lionfish <i>Sander lucioperca</i>	1; J, A	Cerino et al. (2013)

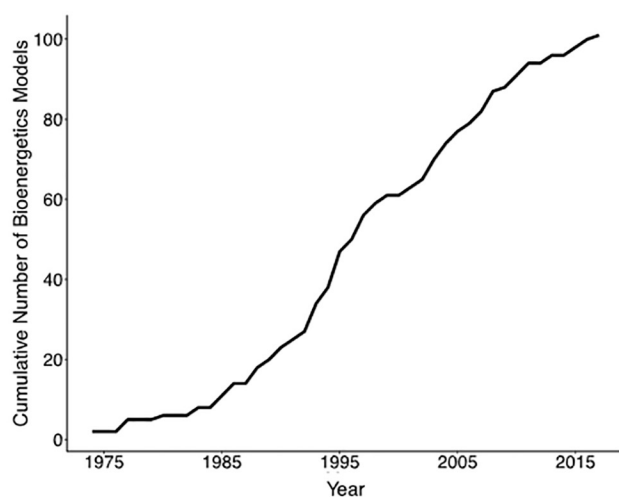


Figure 2. Cumulative number of published bioenergetics models, 1974–2017, representing 70 fish species (some at multiple life stages) and three invertebrate species.

1. *fit to final weight*, where the user specifies the mass in grams of wet weight the fish will reach at the end of the simulation; FB4 uses this information to iteratively calculate a *P* value (proportion of maximum consumption, i.e., *C*_{max}) that will allow for the simulated final weight to equal the input final weight;
2. *fit to cumulative food consumption*, where the user specifies the total amount of food (in grams 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. *fit to a fixed ration*, where the user specifies a constant mass of prey eaten by an individual fish on each day of the simulation;
4. *fit to ration*, where the user specifies a constant percentage of predator body weight eaten by an individual fish on each day of the simulation; or
5. *fit to a proportion of C_{max} (P value)*, to calculate consumption that will be applied to each day of the simulation.



Parameter	Value
Species	Yellow Perch (adult)
Scientific name	<i>Perca Flavescens</i>
Reference	Kitchell et al (1974)
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
BACT	NA
SDA	0.15
Egestion equation	2
FA	0.158
FB	-0.22
FG	0.631
Excretion equation	2
UA	0.0292
UB	0.58
UG	-0.299
Predator equation	1
Energy density	4186
Alpha 1	NA
Beta 1	NA
Cutoff	NA
Alpha 2	NA
Beta 2	NA
Notes	

Species
Yellow Perch (adult) ▾
Initial Day
1
Final Day
365
Initial Weight (g)
60
Oxycaloric Coefficient (J/g O₂)
13560
Fit to:
<ul style="list-style-type: none"> ● Final Weight (g of wet predator body weight) ○ Consumption (g of total prey wet weight) ○ Ration (g of daily wet prey weight) ○ Ration (% of daily wet predator weight) ○ p-value (proportion of C_{max})
120

Figure 3. User interface for FB4 showing Initial Settings page. Parameter values are shown at right for the species selected by the user, providing original reference(s) and values used in the bioenergetics model.

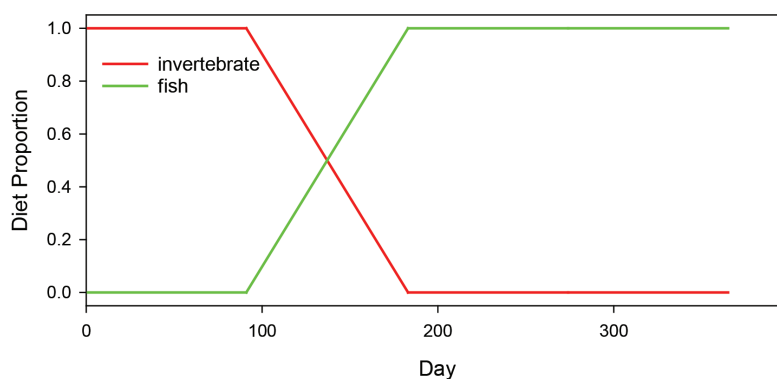
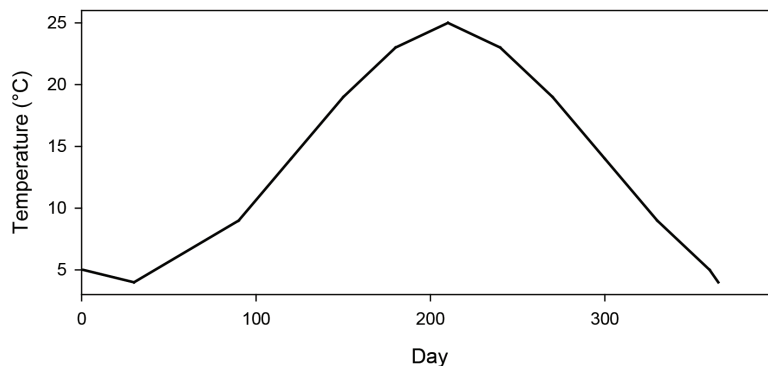


Figure 4. Example of temperature (top panel) and diet proportion (bottom panel) input data in FB4. The Input Files page allows users to quickly visualize their input data to ensure accuracy prior to performing a simulation. Note: Data are linearly interpolated for missing data points.

The file structure of FB4 is organized into three primary folders: a “Fish Bioenergetics” (or user defined) main folder and two subfolders, “Main Inputs” and “Sub-models.” All user input (and output) data are saved as comma-delimited (.csv) files that can be easily modified in Microsoft Excel or other spreadsheet programs. Species-specific bioenergetics parameter estimates derived from published models are contained in a file listed in the main folder. The Main Inputs folder contains files of input data for diet proportions, proportion of indigestible prey, predator energy density, prey energy density, and water temperatures. The content of these files can be visualized instantly in a plot format,

which allows the user to quickly verify whether data were entered correctly (Figure 4).

The Sub-models page has options to simulate a population, incorporate spawning losses, or track contaminant uptake or nutrient regeneration by fishes. As for the main inputs, contents of data files for these submodels (e.g., mortality rates, prey contaminant concentrations) can be visualized instantly for verification.

Once a simulation is run, users can select from a large number of output variables to be visualized in plot format or tabulated in spreadsheet format before being downloaded as a .csv file for further analyses (Figure 5).



Table Output

Interval (days)
33

Individual Variables (click box for options)
Day Temperature Weight (g)

Population Variables

Nutrient Regeneration Variables

Contaminant Analysis Variables

Download Table

Plot Output

X Axis
Day ▾

Y Axis
Temperature ▾

Y Axis 2
Weight ▾

Day	Temperature	Weight
1.00	5.00	60.03
34.00	4.33	60.87
67.00	7.08	61.95
100.00	10.67	63.71
133.00	16.17	67.84
166.00	21.13	75.31
199.00	24.27	82.70
232.00	23.53	87.37
265.00	19.67	97.17
298.00	14.33	107.88
331.00	8.87	115.43
364.00	4.20	119.91

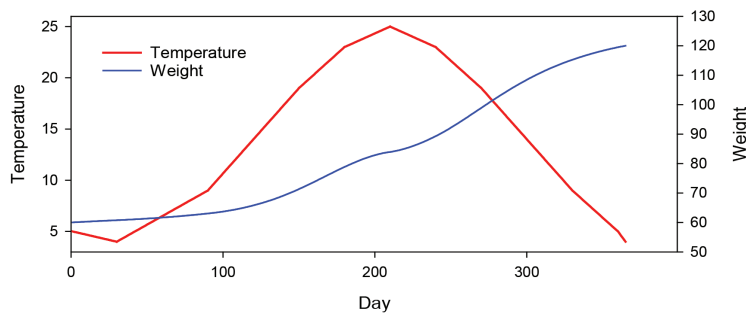


Figure 5. Tabulated (top panel) and plotted (bottom panel) output options available in FB4. The tabulated output can be downloaded as a .csv file using the “Download Table” button. Note that the output variables shown here are only a small subset of those available.

USER'S GUIDE

The user's guide for FB4 is organized around core concepts with an emphasis on topics such as the “Science of Bioenergetics” and “Learning the Software.” In addition, we added sections describing “Model Limitations” and “Case Study Examples” — along with other topics applicable to a variety of modeling scenarios.

Bioenergetics Community

Last, a listserv has been created to facilitate the exchange of ideas, announce updates, and report any issues associated with FB4. If you wish to participate in this growing community, please send an e-mail to fish-bioen4@googlegroups.com to be added to the list.

Model Verification

We have used several approaches to ensure that the application functions as intended and accurately reflects specific models as presented in the literature. Equations and parameters for each model were thoroughly reviewed by the authors to assure that they were consistent with the information provided in the original source publication(s). Model outputs from FB4 were compared with those generated using the same models coded in Excel spreadsheets. Functionality of the program was also tested extensively by participants in a graduate-level bioenergetics modeling course (taught at North Carolina State University by J. A. Rice) and by participants in two FB4 training workshops held at the 76th Midwest Fish and Wildlife Conference and the 146th Annual Meeting of the American Fisheries Society.

User Responsibilities

Although FB4 is intended to facilitate bioenergetics modeling applications without extensive coding by the user, we emphasize that it is the user's responsibility to understand the assumptions and limitations of the model being used and to assure that it is being applied appropriately for the question being asked. We have made every effort to ensure that the models in FB4 accurately reflect their original sources, but the fact remains that there is substantial variation among models in the rigor with which they were derived. The onus is on the user to understand how the model works and to examine the original model publication(s) to learn how it was developed and what assumptions it relies upon (e.g., parameters borrowed from other species models; Chipps and Wahl 2008). Are the assumptions inherent in the original model application suitable for the intended use? Was the original model developed for the size and age range of fish and the range of environmental conditions (e.g., temperature) to be modeled? Are the most appropriate energy densities being used for predators and prey? How will errors or uncertainties in the model or input data affect interpretation of results for the questions being asked? Have questions or concerns been raised in the literature regarding this model and, if so, what are the implications for the intended application? With adequate attention to these kinds of questions, FB4 will be a powerful and informative tool for fisheries researchers and managers.

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