A Generalized Bioenergetics Model of Fish Growth for Microcomputers

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INTRODUCTION

Why use bioenergetics models? Bioenergetics models enable fish growth or food consumption to be estimated over a range of environmental conditions. Much effort has gone into developing methods for estimating prey consumption by fish, including measures of the gastric evacuation rate, stomach content analysis, etc. (Elliott and Perrson 1978; Mann 1978; Eggers 1979; Adams et al. 1982). In many cases, comparable estimates of consumption can be obtained, with much less effort, by measuring growth and using an energetics model to estimate how much food was consumed (Rice and Cochran 1984).

Bioenergetics modeling enables us to ask questions about fish growth and food consumption under known conditions and to predict how fish might grow (or how much they would consume) under a different set of conditions. Growth is an integrator of food consumption over time. Energetics models can be used to calculate food consumption based on growth that has occurred over any given interval.

This document will describe how to use a bioenergetics model of fish growth and food consumption developed at the Center for Limnology, University of Wisconsin-Madison, with support from the UW Sea Grant College Program. The model is comprised of a set of menu-driven computer programs which use data on fish physiology, diet composition, temperature and energy density to estimate fish growth and food consumption. Separate programs allow the user to create and edit data files, run the bioenergetics model with those data files and create an output file on disk, then view the output in numeric or graphic form. The model represents a synthesis of many previous modeling efforts. It can be adapted to many different species by using different parameter values and model options. These options add enhancements to the basic model and allow for modeling seasonal or ontogenetic changes in energy density of predator and prey, seasonal changes in diet proportions among prey types, energy loss due to spawning , and a "no-growth" period at low temperatures.

Our purpose in developing this model and documentation was to provide users who may be unfamiliar with bioenergetics or computer modeling with a basic understanding of the bioenergetics modeling approach and to allow them to begin using this tool without having to create their own model. The model comes with a set of species-specific data files containing the physiological data needed for modeling 12 species of fish: sea lamprey (*Petromyzon marinus*), alewife (*Alosa psuedoharengus*), lake trout (*Salvelinus namaycush*), coho salmon (*Onchorhynchus kisutch*), chinook salmon (*O. tshawytscha*),northern pike (*Esox lucius*), muskellunge (*E. masquinongy*), dace (*Phoxinus* spp.), bluegill (*Lepomis macrochirus*), largemouth bass (*Micropterus salmoides*), yellow perch (*Perca flavescens*) and walleye (*Stizostedion vitreum vitreum*). New data files can be created to simulate other species. In this document, we discuss options available for different components of the model and recommend the options most appropriate for particular species or groups of fishes. Chapter 1 provides a brief introduction to bioenergetics modeling and how bioenergetics models have been used as an approach to different research questions. Chapter 2 is a tutorial guide to using our microcomputer model. In Chapter 3, the bioenergetics equations and various options of the model are discussed in more detail. Chapter 4 provides some guidance on modeling new species, strategies for modeling and making modifications to the programs.

Acknowledgments

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CHAPTER 1

Uses of Bioenergetics Modeling

Consumption Estimation

Bioenergetics models of fish growth have been a useful tool for answering 0a variety of ecological questions about fish growth and consumption. The direct measurement of the feeding rate of fish is difficult. Field estimates of food consumption rates, derived from stomach contents and gastric evacuation rates, are highly variable and require extensive effort to produce point estimates of consumption (Cochran and Adelman 1982; Adams et al. 1982). However, the growth shown by an animal in the field is an integrator of the consumption that has occurred over time.

Energetics models offer an alternative method for estimating consumption from growth data. Given information on the physiological energetics of a species (from laboratory experiments), and growth and temperature data from the field, we can estimate the amount of food consumed over time by that fish. Alternately, we can estimate the growth (and final weight) of a fish, given a specific ration and the fish's thermal history, over a set time. Both approaches have been used in previous applications of these models. The first approach (that of predicting consumption, given growth) has been shown to be more reliable than using the model to predict growth, given ration, as will be discussed in the succeeding chapters (Bartell et al. 1986). General discussions of bioenergetics modeling are available in Kitchell (1983) and Tytler and Calow (1985).

Previous Applications

Previous applications of bioenergetics modeling have addressed questions regarding growth, consumption and predator-prey interactions for a wide range of species. One approach has been to use modeling to sort out the influence of different environmental parameters on growth. Kitchell et al. (1977) modeled the growth of yellow perch in the western and eastern basins of Lake Erie. Observed differences in growth rate between perch from the western and eastern basins could be explained solely on the basis of the slight delay in the warming of the eastern basin as opposed to the western basin. Rice et al. (1983) used bioenergetics modeling to explore possible explanations for the decline in condition factor of largemouth bass in Parr Pond, a heated reservoir in South Carolina. They determined that a seasonal decline in prey abundance was the most likely cause of the decline rather than increased activity by bass or the effect of a heated effluent.

Bioenergetics models have been used to determine patterns and magnitude of consumption between known end points of growth, both seasonally and over the lifetime of fish. Kitchell and Breck (1980) used energetics to determine the time of year when sea lamprey would have the highest rate of consumption and thus the greatest effect on prey populations. They predicted that the highest mortality for fish preyed upon by sea lamprey would occur in fall. Stewart et al. (1981) determined different consumption patterns over the life span of salmon and trout stocked in Lake Michigan. They used the estimates of consumption rates and stocking rates for the various salmonid species to estimate total predation pressure on the primary forage species, the alewife. Stewart et al. (1981) predicted that stocking trends at that time would result in a decline of the alewife population of Lake Michigan, which in fact has occurred.

Another application derived from estimating consumption is modeling the uptake of contaminants by fish. Weininger (1978) modeled PCB uptake by lake trout both through active uptake from the water and from bioaccumulation through the food chain.

With data on diet composition for a predator, modeling can be used to partition predation impact among prey types. Cochran and Rice (1982) used an energetics model to predict the numbers and biomass of bluegill and young largemouth bass eaten by older bass in Lake Rebecca, Minnesota. Model estimates of both numbers and biomass agreed well with independent field estimates of predator impact. Lyons (1984) extended this approach to determine what proportion of total mortality for perch, minnows and darters was due to predation by walleye during years of high and low perch recruitment.

The bioenergetics approach has many management applications and is particularly useful for exploring scenarios and evaluating potential management actions before going into the field. Carline et al. (1984) used data on the diet of largemouth bass, bioenergetics estimates of predation rates by bass and data on forage fish production to determine that bass were unlikely to control bluegill populations when gizzard shad (*Dorosoma cepedianum*) were available as alternative prey. Bevelhimer et al. (1985) used bioenergetics models to determine which esocid might be best suited for stocking in Ohio reservoirs with different thermal regimes and which size of fish and time of year were best for stocking.

Tests of model predictions are rare because the necessary data are difficult to obtain, which is why models are often used in the first place. However, a test does exist for the bioenergetics modeling of largemouth bass. Rice and Cochran (1984) modeled the growth of largemouth bass in Lake Rebecca, Minnesota, over a summer for which there was an independent study of bass feeding and growth. The bioenergetics model predicted a seasonal cumulative consumption within 8.5% of the estimate extrapolated from field data. Rice and Cochran also found that the bioenergetics model best fit the seasonal pattern of growth if they broke the summer into three periods of different prey availabilities: the first with no young-of-the-year (YOY) fish available, the second with YOY largemouth bass, and the third with YOY largemouth bass and YOY bluegill.

The use of the bioenergetics model to predict consumption, given the observed growth over an interval of time, is less open to error than using the model to predict growth with a given ration. When you estimate consumption from growth, the end points of growth constrain the model and limit the effects of errors in determining temperature cycles, energetics parameters, etc. The primary difficulty in predicting growth is the accurate assessment of feeding rates. The model appears fairly sensitive to variations in the availability of food (Bartell et al. 1986). Most applications of the model have involved some aspect of predicting consumption from observed growth.

Among the physiological parameters used in the model, results are typically most sensitive to the parameters in the allometric functions for routine metabolism and, in the case of modeling percids, the allometric functions for consumption (Rice et al. 1983; Stewart et al. 1983). Bartell et al. (1986) have recently introduced a more comprehensive method for determining model sensitivities to errors in parameter estimation.

Summary

Bioenergetics modeling represents a powerful approach to some research and management questions that are not easily addressed by conventional methods. Direct measurements of the consumption rates of fish in the field are difficult and, in many instances, impossible. However, bioenergetics models can couple measurements of the allometric functions for consumption and metabolism from laboratory studies with observed growth under field conditions to estimate consumption. Along with the estimates of energetics parameters, field data needed to run the model include the beginning and final weights for the fish over an interval of time, thermal conditions over that interval and some diet information. This modeling approach can be used to estimate growth under different thermal, environmental or prey conditions, or to estimate the amount and dynamics of prey consumption over time. A wide variety of questions can be addressed with these two approaches to bioenergetics modeling.

CHAPTER 2

Bioenergetics Model Tutorial

Hardware, Disks and Data Required

The bioenergetics model is available in versions for two different computer systems. An Apple version, written in Apple PASCAL, requires an Apple IIe or IIc microcomputer with 64K of memory, an 80-column card, two disk drives and a printer. An IBM version, written in TURBO PASCAL, requires an IBM (or compatible) microcomputer with 512K of memory, two disk drives and a printer. Although both versions are written in PASCAL, the PASCAL language system is not needed unless you wish to modify the programs (see Chapter 4). For both versions, the model is provided on two 5 1/4-inch floppy disks, both sides of which contain files:

(1) **BIOENERGETICS MODEL.**
The working versions of the programs.

(2) **SAMPLE DATA.**
The sample data files and the PASCAL text files.

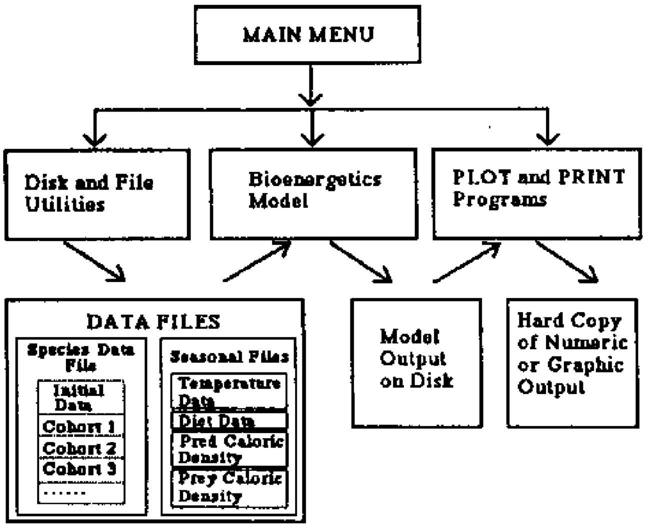
A listing and description of the volume directories of each disk is included in Appendix 1A (Apple version) and Appendix 1B (IBM version).

The first thing to do is make backup copies of the disks! For the Apple disks, it is best to copy each side of the two disks to a new disk. You can make backup disks using any copy program or utility. For convenience, a utility program that will copy PASCAL disks is provided on the Apple version of the model.

To run the bioenergetics model, you need a data disk (like the SAMPLE DATA disk provided) that contains a complete set of data files for the species to be modeled. There are three required files, and two additional files may be necessary for some species (Figure 1). The three required files are (1) **species data file,** which contains species-specific bioenergetics parameters, initial and final weights, length of time interval modeled and population data; (2) **temperature file,** which contains temperature data over time; and (3) **diet file,** which contains diet proportion data across prey types and time. The two additional files are (4) **predator energy density file,** which contains data on energy value (calories) per gram wet weight of predator over time (this file is not needed if predator energy density can be modeled as a function of weight); and (5) **prey energy density file,** which contains the same type of caloric data for prey items (this file is not needed if the prey energy densities can be considered constant across time).

FIGURE 1

Flow Chart for the Energetics Model



These data files fall into two types based on file structure. The **species data file** contains a variety of information types and is created and edited with its own utility program (see menu options below). The remaining files (**temperature, diet, energy density**), called seasonal files, all have the same basic structure and are created and edited with their own utility program. Seasonal files all consist of a series of day numbers followed by the value (temperature, diet proportion, or energy density) for that day. Values for dates between file days are calculated by linear interpolation.

Species data files for 12 species are included on the SAMPLE DATA disk (see Appendix 1). In addition, there are temperature, diet and predator energy density files for yellow perch, and temperature, diet and prey energy density files for lake trout on the SAMPLE DATA disk. Files for other species can be stored on the same disk; however, we recommend storing the files for each species on separate disks to minimize your losses if a disk is lost or destroyed.

Starting the Model: The Main Menu

Apple Version: Insert the **back side** of the BIOENERGETICS MODEL disk into drive 1 and insert the SAMPLE DATA disk (or your own data disk) into drive 2. In general, the model programs follow the Apple PASCAL conventions for naming disk drives as volumes, with drive 1 referred to as PASCAL volume #4 and drive 2 as volume #5. Turn the computer on. You will see the following prompt:

REPLACE DISK WITH BIOMODEL DISKETTE.

Remove the BIOENERGETICS MODEL disk, turn it over, put back into drive 1 (volume #4) and press **RETURN**. The menu program will then start.

IBM Version: We are not able to give out IBM system software with the model disks, thus the IBM version will not boot in the form received. To make the IBM version bootable, follow the instructions in your DOS manual for copying the DOS system files onto your backup BIOENERGETICS MODEL disk. Once you have done this, insert the model disk into drive **A** and turn on the computer. When the computer has booted, or if you have already booted from the machine from another disk, execute the file **MENU**.

Menu Options: The bioenergetics model runs from a central menu program (Figure 1). This program directs you to the programs for data entry, modeling, or model output. All other programs return you to this central menu program. The model menu offers the following choices:

```
    MODEL MENU

A) pfit / bioenergetics model
B) species file utilities
C) cal, temp, & diet file utilities
D) print model output
E) plot model output
        NOT AVAILABLE FOR IBM
F) file / disk utilities
        NOT AVAILABLE FOR IBM
G) program information
H) change default data drive
        NOT AVAILABLE FOR APPLE

CHOICE: Q)uit -> []
```

Options **E** and **F** are not available on the IBM version. To plot output from the IBM version, you must transfer the model output files to another graphics software package (e.g., Lotus 1-2-3, STATISTIX, etc.) that is compatible with your system. Programs for disk and file utilities on an IBM (e.g., copying, formatting, renaming, etc.) are available within MS DOS. Option **H** is not available on the Apple version. When using an Apple, the data disk must be in drive 2 (volume #5).

In the remainder of this chapter, we will describe these menu options in the order they would be used if you were starting from scratch, rather than the order of the items on the menu. Descriptions of running the model and viewing the output will follow the descriptions of data entry. If you wish to run the model using the data files already on the SAMPLE DATA disk, go to the section describing menu option **A) p-fit / bioenergetics model.**

File/Disk Utilities (Option F)

This option is available only in the Apple version of the bioenergetics model. For the IBM version, all of these utility functions are available through MS DOS commands. The utility program allows you to do various general functions, such as formatting and copying disks, copying or deleting files, listing directories, etc. Under this option, you will see a second menu:

```
FILE/DISK UTILITIES
1) Format diskettes
2) Delete files
3) Copy diskettes
4) Copy file
5) List/edit directory

Choice Q)uit --> []
```

When you choose any of these options, the computer will prompt you for the necessary information. The procedures are fairly self-explanatory. As in other programs, disk drives are referred to under the Apple PASCAL volume numbering system, where the boot drive (drive 1) is volume #4 and the second drive is volume #5. You must use these volume numbers in specifying which diskette to use for a particular function.

To use either copy option (**3** or **4**), you must remove the model disk from volume #4 and use that volume to hold one of the disks for copying. When copying an entire disk, the new disk does not have to be formatted first. However, when copying individual files, you must first format the new disk using menu option 1.

Option **5**, **List/edit directory**, allows you to list a disk directory to the screen or printer, to change disk or file names, or to print out a text file. The only text files on your disks will be the program text files contained on the SAMPLE DATA disk. These are the text versions of the programs in the bioenergetics model, and this option can be used to get a printed copy of the programs.

Change Default Data Drive (Option H)

This option, available only on the IBM version, allows the user to designate which disk drive will contain the data files. In the Apple version, the data disk must reside in drive 2 (volume #5). In the IBM version, you may designate either of the floppy disk drives, or the hard disk, as the data drive. This will also be the drive to which the output files will be sent. The bioenergetics model must reside in the logged drive.

Species Data File Utilities (Option B)

The **species data file** contains general species information, bioenergetics parameters, growth and population data, and some diet information for the fish to be modeled. We have included lists of the required bioenergetics parameters for a number of species previously modeled so that you do not have to gather this data yourself. The SAMPLE DATA disk comes with **species data files** for 12 species (see Appendix 1). Appendix 2 contains a listing of the **species data file** for lake trout entitled "LAKTROUT.BIO". Appendices 3, 4 and 5 contain lists of energetics parameters for all of the12 species.

In **species data files**, data are stored in two types of subfiles: "initial data" and "cohort data" (Figure 1). "Initial data" consists of information that applies to all fish of the species being modeled. For the purposes of the model, a cohort is defined as a group of fish with the same growth end points over some interval of time. Thus each cohort has a specific beginning and ending weight for that time interval. A **species data file** can contain separate data for up to 30 cohorts. Cohort data consists of physiological parameters, weight and time interval data, and information on prey digestibility and energy density. In general, cohorts are modeled on a yearly basis, using the mean weights at the beginning and end of the year. When used in this manner, a model cohort represents a single year class or age class of fish growing over one year. If more information is available on seasonal patterns of growth, each cohort may represent growth over a shorter interval of time such that data for an entire year of growth may be spread across several cohorts within the **species data file.**

This utility program produces a new menu, which allows you to edit, print or create a species file:

```
SPECIES FILE UTILITIES

A) Create New Data File
B) Edit Data File
C) List Data File

CHOICE: Q)uit -> []
```

Under any of these menu options, the program will first ask for the title of the file. Titles for all **species data files** may have up to eight identifying characters (any combination of letters or numbers, but **no** spaces), followed by the suffix ".BIO".

Creating a New File: To create a new **species data file**, choose option **A**. Creating a species file requires you to enter the initial data section of the file and to reserve space for the number of cohorts you will need. First, all the files on your data disk will be listed on the right side of the screen (Apple version only). The program will ask you for the prefix (i.e., the letters preceding ".BIO") for the title of your new file. If you use the same name as an existing file, the existing file will be overwritten. You will then move to the following screen, which shows default values for the "Initial Data" section of the file (Figure 2; see Appendix 2).

The initial data section contains explicit information about how to model energetics for this species. The information is stored only once for the species and applies to all cohorts. This section defines the options for the specific versions of the consumption, respiration and egestion equations (see Chapter 3), whether to include spawning weight losses, whether fish energy density is to be read from a data file or calculated as a function of weight, whether the prey energy densities should be considered constants or read from a data file and whether a temperature exists below which the fish feeds only at a maintenance level (i.e. , does not grow). When first created, this section contains default values which produce the simplest form of the energetics model. All equations for model terms and energy densities take their most common form, and spawning losses and maintenance ration temperatures are not included.

To edit this screen (and any similar screen in these programs), follow the prompts at the bottom of the screen. Use the arrow keys to move the cursor to the parameter you wish to change, type **E** for edit, type in the new value and then press **RETURN** . When finished editing, type **A** to advance. The program will save the newly entered values in the new datafile on the disk.

The first specific entry for this screen is "Species Name," which can be up to 25 characters long. The next three entries, "Consumption Model," "Respiration Model" and "Egest/Excret Model," refer to numbers from the right side of the screen corresponding to the appropriate form of equation for each of these model terms. (See Chapter 3 for a discussion of the equation forms.)

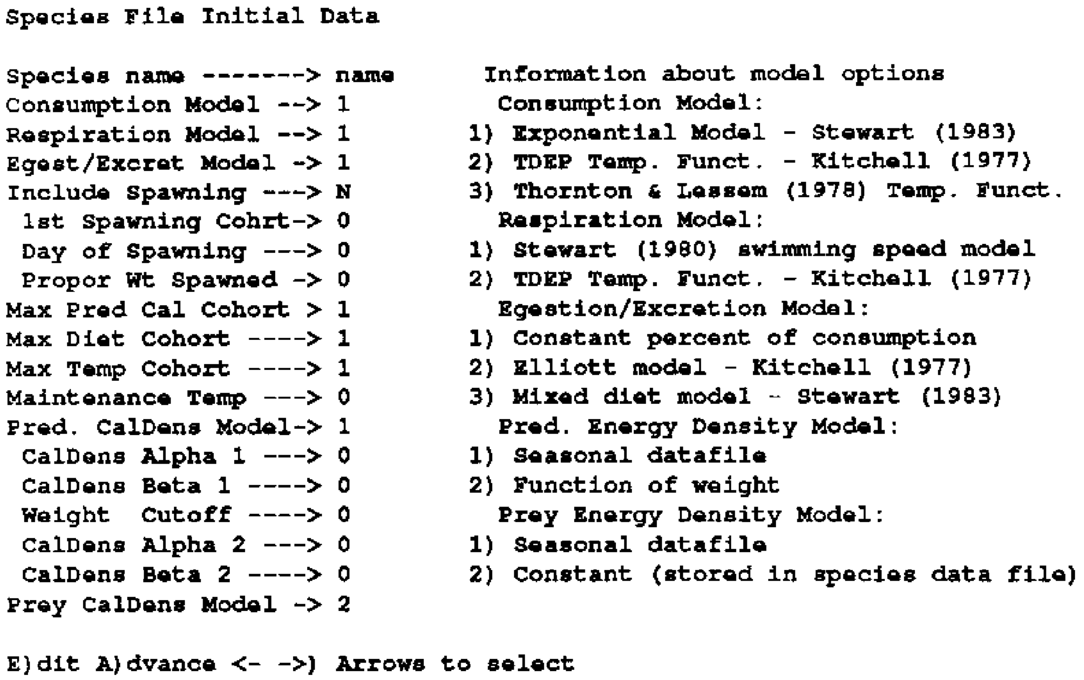
The next four entries refer to modeling spawning losses (see Chapter 4). Set "Include Spawning " to "Y" if you want to include spawning losses in the model. "1st Spawning Cohrt" is set to the first cohort that participates in spawning, "Day of Spawning" is the numerical day of the year when spawning occurs and "Propor Wt Spawned" is the proportion (0-1) of body weight lost during spawning.

The entries "Max Pred Cal Cohort," "Max Diet Cohort" and "Max Temp Cohort" are initially set to "1". These entries tell the model how many cohorts of information to read from each of the data files containing predator energy density, diet and temperature data, respectively (see section below, "Cal, Temp & Diet File Utilities"). "Maintenance Temp" is entered if the fish feeds at maintenance levels (i.e., doesn't grow) below a specific temperature (see Chapter 4). If not, this entry is set to zero or some temperature below the lowest observed temperature.

The rest of the entries on this screen refer to modeling energy density of the fish and its prey. "Pred. CalDens Model" refers to the number from the right side of the screen that determines the method of modeling energy density of the predator. If model 1 is chosen, then caloric density data are read from the **predator caloric density file**, which you must create, and the "Alpha," "Beta" and

FIGURE 2

Initial Data Screen



```
Species File Initial Data

Species name -------> name      Information about model options
Consumption Model --> 1          Consumption Model:
Respiration Model --> 1        1) Exponential Model - Stewart (1983)
Egest/Excret Model -> 1        2) TDEP Temp. Funct. - Kitchell (1977)
Include Spawning ---> N        3) Thornton & Lessem (1978) Temp. Funct.
 1st Spawning Cohrt-> 0          Respiration Model:
 Day of Spawning ---> 0        1) Stewart (1980) swimming speed model
 Propor Wt Spawned -> 0        2) TDEP Temp. Funct. - Kitchell (1977)
Max Pred Cal Cohort > 1          Egestion/Excretion Model:
Max Diet Cohort ----> 1        1) Constant percent of consumption
Max Temp Cohort ----> 1        2) Elliott model - Kitchell (1977)
Maintenance Temp ---> 0        3) Mixed diet model - Stewart (1983)
Pred. CalDens Model-> 1          Pred. Energy Density Model:
 CalDens Alpha 1 ---> 0        1) Seasonal datafile
 CalDens Beta 1 ----> 0        2) Function of weight
 Weight  Cutoff ----> 0          Prey Energy Density Model:
 CalDens Alpha 2 ---> 0        1) Seasonal datafile
 CalDens Beta 2 ----> 0        2) Constant (stored in species data file)
Prey CalDens Model -> 2

E)dit A)dvance <- ->) Arrows to select
```

"Cutoff" values are ignored. If model 2 is chosen, caloric density is modeled as a function of weight (e. g., in modeling lake trout). The "Alpha" and "Beta" values are parameters in the weight-dependence function (see the *Growth* section of Chapter 3). You may input two sets of parameters (Alpha1, Beta1, and Alpha2, Beta2) so that separate weight-dependent functions can be used for young and adult fish. "Weight Cutoff" is the weight at which the model switches from equation 1 to equation 2. Values for these parameters for some species are given in Appendix 5.

"Prey CalDens Model" refers to the number at the right for the method of modeling prey energy density. Under model 1, prey energy density is read in from the **prey caloric density file**. Under model 2, prey energy density is considered constant. These constant values are stored in the cohort data section of the **species data file.**

When you advance from this screen, the computer will ask for the maximum number of cohorts to be contained in this file. We suggest you set the file up for more cohorts than you think you will need (maximum of 30). You do not have to enter values for later cohorts if they are not used, but, unless you reserve room now, you may not be able to add cohorts later (especially on an Apple).

Editing a File: At this point, you have created a new species file on the disk and will have returned to the "SPECIES FILE UTILITY" menu. You must now use option `B) Edit Datafile` to enter specific data for each of the cohorts in the new file. A list of all the files on your data disk will appear on the right side of the screen (again, only for the Apple version). The program will ask you for the prefix for the datafile you wish to edit and then ask for the first and final cohort numbers that you wish to edit (1 to 1 will edit only the information for cohort 1; 2 to 4 will edit cohorts 2, 3 and 4, etc.). The **species data files** are split into seven separate groups of parameters to make editing simpler. After entering the name of the file and number of cohorts to edit, another menu will list these seven groupings:

```
Species Data File Changes Menu

Initial Data Parameters--------> N
Wts / Dates / P-val Parameters-> N
Consumption Parameters---------> N
Respiration Parameters---------> N
Egestion / Excretion Parameters> N
Mortality Parameters-----------> N
Prey Information Parameters----> N

E)dit A)dvance <- ->)Arrows to select
```

The first of these groups, "Initial Data Parameters," is the section of the file entered when the file was created. See the paragraphs above for editing this group. The other six groupings contain data that are entered for each cohort individually. The above menu allows you to choose which of the parameter groups (one or more) you would like to examine or edit. Move the cursor to each group using the arrow keys, type **E** for edit and **Y** to include that parameter group for editing. Press **A** to advance. After you have chosen a data group to examine, the information for each cohort will appear in sequence.

The "Wts/Dates/P-val Parameters" group contains data on the first and last date of the simulation interval. These dates can be any day of the calendar year, and the interval length can any portion of a year (up to one year maximum). The only restriction is that day 1 must be the same across all files (species and seasonal) used in any one model run. Beginning and ending weights are weights (grams wet weight) on the first and last simulation date. Weight on the last simulation date is used only for calculating the P-value in the P-fit portion of the model program. P-value is the proportion of maximum consumption realized (Chapter 3) and is calculated by the model under main menu option **A** (see section below on "P-fit / Bioenergetics Model"). Other values entered in this data group include the initial population size (the number of fish in the cohort on the first simulation day) and the number of prey items contained in the diet (maximum of10).

The "Consumption Parameters," "Respiration Parameters" and "Egestion / Excretion Parameters" groups are set up similarly. Each allows you to enter parameter values for each version of the equations for these model terms (three versions for consumption and egestion, two versions for respiration). See Chapter 3 for descriptions of the various equations and the parameters contained in each.

The "Mortality Parameters" group is needed only for population level modeling. This group allows you to break a year into as many as 12 intervals, with different daily mortality rates for each. Values are constant within each of these intervals. You must designate the starting day for each interval. In the model, daily mortality rates are expressed as the proportion of the cohort dying each day. Editing mortality parameters begins with an option to calculate daily proportional mortality rates from total proportion of the cohort dying in an interval. You must write these values down as they are determined and enter them into the file using the subsequent data entry screen. Mortality can also be broken into natural mortality ("Mort") and harvest mortality ("Harv"). Total mortality for the cohort is the sum of these two values. If harvest mortality is zero, then natural mortality equals total mortality.

The "Prey Information Parameters" group contains data on the energy density (calories per gram, wet weight) of each prey item (necessary if you are using prey energy density model 2) and the proportion (0-1) of each item that is indigestible (needed only for egestion/excretion model 3).

When you finish editing, *if you were editing a single cohort* (1 to 1, or 5 to 5, for example), a prompt will ask "Save this file for other cohorts also? Y/N". Responding **Y** will allow you to save the data just entered for any of the cohorts in this file. Answer the next prompt, "Save as cohort #," with the number of the cohort for which you want to save this data. This feature is designed to speed up initial data entry by minimizing the number of times you must enter the same data. Because much of the data for each cohort will be the same, it is simpler to enter the bioenergetics data just once (usually for cohort 1), save it in several cohorts, then go back and edit only the specific information (such as initial and final weights and P-values) that differs for each cohort. This multiple-save feature is not invoked if you edit more than one cohort at once (e.g., 1 to 2, or 4 to 7, etc.).

Listing a File: The final option in this submenu, `C) List Datafile`, allows you to list a species file to the console or printer. You may list a single cohort or any number of cohorts in sequence.

Files Contained on Sample Disk: There are **species data files** for 12 species on the SAMPLE-DATA disk (Appendix 1). All these files were set up for 10 cohorts of data, and each cohort contains the appropriate energetics parameters for a fish of that species and age. The yellow perch file (YELPERCH.BIO) and lake trout file (LAKTROUT.BIO) also contain initial and final weights and P-values. The perch file has weights for cohorts 1 through 3, and the lake trout file, for cohorts 1 through 9. For both of these files, the simulation period is one year, thus each cohort represents one age class. A simulation year begins on January 1 for yellow perch and on July 1 for lake trout. You can use these two files, along with their associated seasonal files (see next section) to make practice runs of the bioenergetics model.

Cal, Temp & Diet File Utilities (Option C)

The seasonal files, **predator caloric density** (Table 1), **temperature** (Table 2), **prey caloric density** (Table 3) and **diet** (Table 4), are all set up similarly. Each file contains data for up to 36 different days within a year. Day 1 and day 365 must be entered, and any dates within the year for which you have specific data can be entered. The simulation interval (defined by the "Start" and "Final" day entries in the cohort data) can be less than 365 days, but the seasonal files must contain data covering the entire year. Day 1 may represent any day of the year which is convenient for the simulations (day one of the sample lake trout files is July 1) but must be consistent between files. Values for days between the dates in the file are estimated by linear interpolation (Figure 3).

TABLE 1

Predator Caloric Density Data File. (calories per gram, wet weight)

Day	Energy Density
1	1000.0
121	1200.0
289	1030.0
324	1140.0
350	1140.0
365	1260.0

TABLE 2

Temperature (^{o}C) Data File.

Day	Temperature
1	10
105	10
118	9
159	6
248	2.75
271	2.75
306	4
330	8
335	10
365	10

TABLE 3

Prey Caloric Density Data File. (calories/g wet weight, by diet item)

Day	Diet1	Diet2	Diet3	Diet4
1	1000	1200	1000	1150
150	1000	1275	1200	1150
250	1000	1350	1200	1150
365	1000	1350	1000	1150

The **temperature** and **predator energy density** files have one value associated with each date in the file. The **diet** and **prey energy density** files have a value for each diet item on each date. In the **diet** file, the sum of proportions for all diet items must be 1.0 for each date. All energy density data are in calories per gram, wet weight. Temperatures are in degrees centigrade.

Prey caloric density files contain one set (annual cycle) of caloric data for each diet item which applies to all

TABLE 4

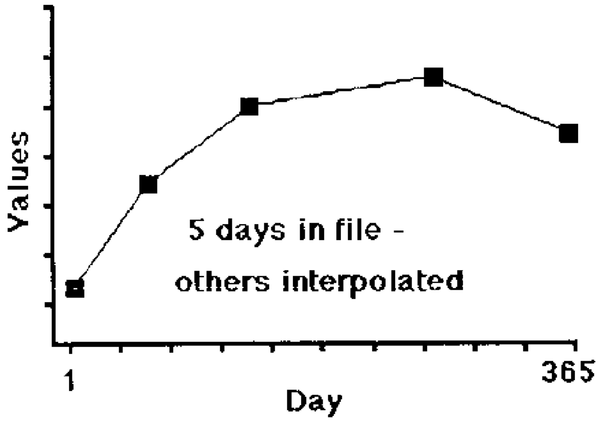
Diet Data File.
(proportion of each item in the diet)

Day	Diet1	Diet2	Diet3	Diet4
1	0.21	0.00	0.04	0.75
121	0.66	0.00	0.04	0.30
151	0.54	0.00	0.16	0.30
331	0.53	0.00	0.10	0.37
365	0.53	0.00	0.00	0.47

cohorts. However, **temperature**, **diet** and **predator caloric density** files can have separate data for each cohort being modeled. In these files, if data for succeeding cohorts are the same, data for those remaining cohorts need not be entered. For example, the sample **diet file** for lake trout (LAKTROUT.DIE) contains separate data for seven cohorts, while the **species data file** contains data for nine cohorts. The model assumes that the diets of cohorts 7, 8 and 9 are all identical, and any model runs for cohorts 8 and 9 will use the diet data for cohort 7. The sample **temperature file** (LAKTROUT.TEM) contains data for only one cohort, thus the model assumes that all cohorts are subject to the same seasonal temperature regime. The "Initial data" section of the **species data file** (Appendix 2) contains specifications (the "MAX COHORT" entries) for the number of the last cohort entered in each seasonal file.

FIGURE 3

Sample Graph of Data File



Creating and Editing Files: The mechanics of creating and editing seasonal files are similar among file types and also similar to species data files. You first choose the type of file you want to create, edit or print:

```
CAL/TEMP/DIET FILE UTILITIES

A) Temperature File
B) Diet file
C) Predator Energy Density File
D) Prey Energy Density File

CHOICE: Q)uit -> []
```

To create a new temperature file for one cohort, choose **A** and enter 1 for the initial cohort and 1 for the final cohort. The next screen will list all the current files on your data disk (Apple version only) and ask what name you would like to save the file under. Names of seasonal files all have a three-letter suffix, designating the type of file, which follows up to eight identifying characters (any combination of letters or numbers, but no spaces). The suffixes are ".TEM" for **temperature** files, ".DIE" for **diet** files, ".PDC" for **predator caloric density** files and ".PYC" for **prey caloric density** files.

Once you have named the file, you can start entering data following the prompts on the screen. The first day entered must be day 1, the last must be 365, and days must be entered in increasing order (to a maximum of 36 different days).

When all the points are entered, press **A** to advance from data entry to the next screen and answer **Y** to the prompt asking if you want to save the file to disk. If you are modeling prey energy density using a seasonal file, you must be careful that the number and sequence of diet items are consistent between the **diet** file and **prey caloric density** file. Because the **prey caloric density** file contains only one annual cycle, all items in the fish's diet, over the entire period of time you will simulate, must be represented in this file. Some cohorts may not feed on all the items listed in this file. However, the **diet** file, which can contain diet proportions for more than one cohort, must have an entry for each diet item listed in the **prey caloric density** file. Thus, items not eaten by a particular cohort must have "0" entered across all days. For example, Table 3 (the prey calorie file) shows seasonal caloric density cycles for four diet items, but the cohort represented in Table 4 (the diet file) does not feed on diet item 2, so that column is all zeros.

Files Contained on Sample Disk: The SAMPLE DATA disk contains seasonal data files to accompany the lake trout and yellow perch species data files (Appendix 1, identified by the species name and appropriate suffix). For yellow perch, predator energy density is constant over time, thus a predator caloric density file (YELPERCH.PDC) is required. For lake trout, predator energy density is modeled as a function of weight, thus a predator caloric density file is not needed. However, the energy density of lake trout prey fluctuates over time, so a prey caloric density file (LAKTROUT.PYC) is required. All the sample seasonal files contain data for one cohort, except the diet files. The lake trout diet file (LAKTROUT.DIE) contains data for four diet items and seven cohorts. The yellow perch diet file (YELPERCH.DIE) contains data for two diet items and three cohorts. Day 1 for lake trout files is July 1 and for yellow perch files is January 1. These seasonal files may be used with the species data files as input to a bioenergetics model run.

P-fit / Bioenergetics Model (Option A)

Running the bioenergetics model is usually a two-step process. Before running the model to generate output, you must enter a P-value for each cohort in the **species data file.** P-value is a proportionality constant representing the proportion of maximum ration actually consumed by the fish (Chapter 3; Kitchell et al. 1977) over the time interval simulated. You can think of P-value as representing prey availability. Thus, the P-value acts as a scaler for consumption rate. If P-value is 1, then the fish is feeding at its maximum rate (based on current temperature and fish size). If P-value is 0.5, then the fish is feeding at one-half its maximum rate. During any one simulation interval, P-value is constant. It is this P-value that allows the model to fit predicted growth to observed growth and thus determine the consumption rate and total amount of food required to attain that observed growth. The sample species files for lake trout and yellow perch already contain P-values fitted to the starting and final weights of each cohort.

It is possible to run the bioenergetics model using any assumed P-value and thus predict growth. However, most model applications involve fitting P-value to the observed growth, then comparing the resulting growth and consumption patterns to patterns obtained by changing one or more factors (e.g., temperatures, diet proportions, equation parameters, P-value, etc.).

Under this model option you will see a second menu:

```
BIOENERGETICS MODEL OPTIONS

A) P-fit
B) Bioenergetics Run

Choice Q)uit --> []
```

A word of caution: If either of these options refuses to run, or runs but gives strange results (e.g., starvation), the first thing to do is check the data files. Small errors in the data files can result in strange model behavior. Make sure all necessary parameter values are included and are correct (it's easy to misplace a decimal point). Other likely sources of error to check are: (1) make sure day 1 in all files refers to the same day of the year, (2) check that the number of cohorts in each of the seasonal files is correct, and (3) make sure the number of diet items, and the order in which they are listed, is the same in the species data file, diet file and prey caloric density file (if required).

P-Fit Option: The P-fit program solves for the P-value that will give observed growth by running simulations iteratively and adjusting P-value until predicted weight at the end of the interval equals observed weight (i.e., final weight from the **species data file** ± 0.05 %). The program operates on one cohort at a time, begins with initial weight, and uses all appropriate data from the species, temperature, diet and energy density files. The program requires an initial estimate of P-value, which is read from the **species data file** (0.3 is often a good initial estimate). After each cohort simulation, if the predicted weight does not agree with final weight (± 0.05 %), the program estimates a new P-value and runs the simulation again. The P-fit output is sent to the printer as each cohort is calculated (Table 5). P-fits can be run for a single cohort or any number of successive cohorts. Once the P-values have been calculated for any cohorts, *you must manually enter those new values* (which have been printed out) into the **species data file** using the cohort data file utility program. You cannot go directly to the bioenergetics run without first editing the data files and saving the new P-values. If you do, your old estimates for P-values will be used instead of the new, correct values.

TABLE 5

Output from P-Fit Run of Model.

```
Cohort:1 Iteration:1
Old PValue:0.700 Next PValue:0.8283
Final Weight:165.73 Target Weight:260

Cohort:1 Iteration:2
Old PValue:0.8283 Next PValue:0.8291
Final Weight:259.29 Target Weight:260

Cohort:1 Iteration:3
Final PValue:0.8291
Final Weight:260.03 Target Weight:260
```

Bioenergetics Option: After all data files are complete and P-values have been determined and saved, the bioenergetics model can be run. To run the bioenergetics program, select item **B** from the submenu. You will then have a series of options for structuring the model run. All output from the model is stored on the data disk (see the subsection below on model output). The first option is for the interval (number of simulation days) at which output will be saved to the disk. All simulations are run in a daily time step, but you have two options for saving output: once per mortality period (as defined in the cohort data), or at any set interval that you specify.

The second option specifies how many cohorts to simulate in this run. You can run a single cohort or any number of sequential cohorts. For instance, beginning with cohort 1 and ending with cohort 1 simulates the first cohort only. Beginning with cohort 3 and ending with cohort 6 simulates cohorts 3 through 6. The time interval that these simulations represent depends on how you are defining a cohort (see Chapter 4).

The third option determines how to sum the output data. There are three possibilities: (1) summing over each output interval, (2) over each cohort or (3) over all cohorts. Your choice may depend on whether you are modeling a single cohort over time, or several different cohorts all living during the same simulation interval. When summing over each interval, the summed variables in the output file are zeroed at the beginning of each interval. Thus, if you are saving data every 30 days, variables will be summed over each 30-day interval. When summing over each cohort, the summed variables in the output file are zeroed at the beginning of each new cohort. This is useful when determining consumption in each simulation interval for a single cohort, or for each cohort in a population within a single simulation interval. When summing over all cohorts, the summed variables are zeroed only at the start of a simulation, and data for all cohorts simulated accumulate over the entire run. This is useful when determining consumption of a single cohort over its lifespan, or all cohorts in a population in a single simulation interval. If you simulate only one cohort, summing over each cohort and all cohorts will give identical results.

Once you have selected the run options, the program will ask for the specific data files to be used for this simulation. It will read the **species data file** first, then ask for the other files needed, depending on the choice of equation options designated in the **species data file**. Before beginning the model run, the computer allows you to type in a comment to be stored with the output, then asks for the prefix to identify the output files from this run.

Model Output: Output from each model run is sent to the data disk and resides in three files with identifying suffixes of ".LAB", ".KEY" and ".WRK" in the titles. Each of these file names will have the prefix you designated to identify this particular model run. The .LAB and .KEY files contain titles and "bookkeeping" information. The .WRK file contains the numeric output from the model at each of the predetermined intervals. Data for each output day (one row of the output data matrix) are stored in this file as 36 variables (36 columns of the output data matrix), which include cohort number, day of year, specific daily rates for each term in the energy equation, daily individual and population consumption by prey type (up to four prey currently) and cumulative consumption values by prey type. Appendix 6 lists the variables saved at each output day. The specific variables saved can be changed by editing the bioenergetics model text files and recompiling the programs. One area where your may want more output is in consumption by prey type. The model currently saves data for only the first four items in the diet file. Model calculations are carried out using all the items in the diet file, but only the data for the first four items is written to the output file. If you need output for more than four diet items, you can change the variables saved. Conversely, you can get by without changing the variables by running the model a second time using a modified diet file. For information on using such modeling tricks and on changing the program text files, see Chapter 4, "Modifying the Bioenergetics Programs."

You can keep results from different model runs on the same data disk by using different prefixes to identify each run. The number of runs that can be stored on one data disk depends on the size and number of other data files already on the disk, the number of cohorts in a run and the output interval. In general, if data files are kept to a minimum, about 750 output days can be stored on a single data disk. As a data disk begins to fill up, you can get more room by transferring the three output files for any one run (.LAB, .KEY and .WRK, all with the same prefix) to another disk (see section on File / Disk Utilities). If you try to run a simulation without enough room on the data disk to store all output, you will get an error message, such as "no room on volume," and the program will stop. You must then transfer some files off the data disk and start the run over. If you intend to run several simulations for one species, we recommend that you transfer the output to another disk after each run, thus keeping the maximum amount of storage available on your data disk.

Differences in Apple and IBM Results: If the Apple and IBM versions of the model are run using identical data files, the output from each version will be similar but not exactly the same. This discrepancy is due to differences in the precision with which numbers are represented in Apple (8-bit) versus IBM (16-bit) computers. However, the discrepancy usually occurs in the fifth or sixth significant digit, resulting in a difference of < 0.01% between the two versions. Thus, for all practical purposes, differences in results can be ignored.

Printing Model Output (Option D)

The print program allows you to list any combination of the variables contained in a .WRK file. The SAMPLE DATA disk contains output files (LAKTROUT.LAB, LAKTROUT .KEY and LAKTROUT.WRK) for a simulation run using the lake trout sample data files. Appendix 7 shows some of the printed output from this sample output file. This simulation was run with output intervals of once every 50 days. The run began with cohort 1 and ended with cohort 3 (i.e., covered three cohorts). Data were summed over all cohorts, thus the cumulative variables (SI Cons, SP Cons, Cum Prod and CmCalCons, Appendix 6) represent total consumption, or production, summed over the entire simulation, up to each output day.

To print an output file, choose option **D** from the model menu. The computer will list all the files on your data disk (Apple version only) and ask for the prefix of the workfile to be listed. The next screen will list all the fields (variables) in the output file and ask for the number of fields you want to list, where the list is to be sent and which specific fields to include. The listing can be sent to the console, a printer (up to four specific printer options are available, depending on which version of the model you have), or a text file on another disk. The text file option produces an ASCII file that can be read by the PASCAL or TURBO editor or can be transferred to other data analysis or plotting software (e.g., Lotus 1-2-3, STATISITX, etc.). In the Apple version, the text file can be sent to either disk drive. In the IBM version, the text file is sent to the default data drive.

The next screen lists the record range (number of rows of data) contained in the designated output file. You can list all the records (each record being the output from a particular day)or any sequential group of records and at any interval (e.g., every second or third row). The computer will ask for the designations for low record, high record and the interval.

Plotting Model Output (Option E)

This option is available only on the Apple version. For the IBM version, model output can be plotted through graphics routines on other software packages (e.g., Lotus 1-2-3, STATISTIX, etc.). To use these packages, the model output file must be converted into an ACSII file using menu option D (see previous section). These graphics programs can read the ASCII output files into their own data structures and produce a variety of graphs.

For the Apple version, simulation results can be plotted, and those plots printed, through menu option **E**. This program has a number of sub-options, each of which uses instruction screens to help you step through the procedure. Under this option you will see a second menu:

```
PLOT PROGRAM

1) Scatter plot
2) Read photofile
3) Save photofile
4) View/edit graph
5) Send graph to printer
6) Open .WRK file

Choice Q)uit ->[]
```

Option `1) Scatter plot` allows you to plot any pair of variables (Figure 4) and will plot up to three pairs on a single screen at once. You may use different symbols for each pair and may plot data as single points or connected. You may also overlay plots on the current screen thus ending up with more than three plots on a single screen. The plot program can automatically scale the axes to the range of the variables plotted, or you may set the axes limits yourself. You may also perform arithmetic transformation on any variable before plotting. Transformation is required if values of the variable are greater than the integer limit of the computer (-32,676 to 32,676) because integers are used in the graphics calculations.

FIGURE 4

Growth Curve of a Salmonid over Time from a Bioenergetics Simulation Run

The program will allow you to search any field and plot only those records corresponding to a value or set of values you select. For example, if your model run covered cohorts 1 to 3 and you wish to plot weight versus time for cohort 2 only, you would plot field 5 (WEIGHT, Appendix 6) versus field 2 (DAY YEAR) and search in field 1 (COHORT) for values of 2. The program also allows you to set the low and high record number and interval between records to be plotted (every second record, every third record, etc.). Thus you can plot any subset of records in the output data and at any interval. Option `6) Open .WRK file` must be used to open an output file before any graphs can be plotted. When the plot is completed, pressing **RETURN** gets you back to the menu.

After a plot is produced, option `4) View/edit graph` allows you to insert text to label the graph. When the graph appears on the screen, type **?** to see a help screen listing the various methods of moving the cursor and entering text. When finished editing, press **Esc** to return to the menu.

The photofile programs, options `3) Save photofile` and `2) Read photofile`, allow you to store or retrieve a graphics screen on a disk file. Graphs of model output can be stored in a photofile, then read back into the program later and edited. Disks must be formatted before graphs can be saved. Option `5) Send graph to printer` can be used to get a hard copy of your graphs if you have an Epson, Anadex or Imagewriter printer, or a Grappler card in any brand printer.

Program Information (Option G)

This option shows a screen of information about the authors and acknowledgments of funding support for the development of these programs.

Summary

This chapter introduced the various programs making up the bioenergetics modeling package. We have tried to be brief and have not listed all the screens of information or questions that will arise while running the model. The programs are relatively user friendly, but it will require some amount of time for you to become familiar with them. We suggest that you "play" with the model using your backup copies and try entering some of your own files, making new energetics runs and printing and plotting the output.

CHAPTER 3

Energetics Equations and Options

This chapter gives an overview of the basic bioenergetics equations and describe the various options for the functions used in the energetics calculations. Several functions have been modeled in different ways by different researchers. Because these different functions seem to work best for different species, they have been included as options within this model. For example, different researchers have used different temperature-dependence functions for modeling consumption and respiration. The source references for the different functions we have used for modeling energetics often have different notations for the equations used, so we cannot be consistent with all the references in the parameter names that we use. We will list both the equations and the variable names (used in the computer model text files) corresponding to each of the parameters in the bioenergetics equations separately. This will introduce you to the equation form and allow you to compare the equations to the variable names in the text of the programs and to the equations in the various references.

The Balanced Energy Equation

The bioenergetics model is essentially an accounting of the energy intake and use by a fish. The balanced energy equation is:

Growth = Consumption - (Respiration + Waste Losses)

Different options, which you specify within the model, allow the terms of this equation to be calculated in different ways. Energy loss through reproduction can also be included in the terms on the loss side of the equation. Within the model, the calculations are based on specific rates (i.e., grams consumed per gram of weight, all terms in units of wet weight). Specific rates are then converted to rates per fish and per population. In addition, at each step all weights are corrected for caloric density of both the fish and the various prey items consumed. All calculations are made on a daily basis.

Consumption

Consumption is the amount of food consumed by the fish. In its general form, consumption is determined by calculating the maximum specific consumption rate (grams consumed per gram of body weight per day) as an allometric function of weight. The maximum specific rate is then modified by a temperature-dependence function and by a proportionality constant representing prey availability. The basic equations for consumption rate are:

$$C_{max} = a * W^{b}$$

$$C = C_{max} * \text{P-value} * F(T)$$

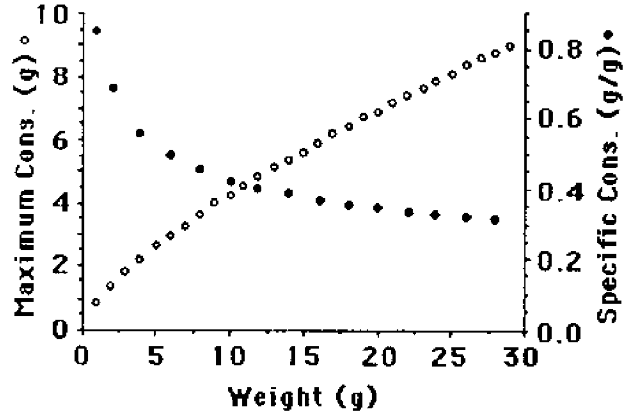
where:

C_{max} = the maximum specific consumption rate ($g*g^{-1}*d^{-1}$),
W = fish weight (g),
a = the intercept of the allometric function,
b = the slope of the allometric function,
C = specific rate of consumption ($g*g^{-1}*d^{-1}$),
P-value = a proportionality constant,
T = temperature (°C),
F(T) = the temperature-dependence function.

Figure 5 shows C_{max} and the equivalent specific rate of consumption as a function of weight for yellow perch (at optimum temperature). Three separate functions for the temperature dependence of consumption are included in this program. The equations for each function will be discussed separately.

FIGURE 5

Maximum Consumption (o) and Specific Consumption (+) vs Weight for Yellow Perch at Optimum Temperature



Consumption Model 1:

$$F(T) = e^{(\theta * T)}$$

Parameters used: a, b, θ
Function variables: CA, CB, CQ

Model 1 is an exponential function for temperature dependence. This is the consumption function presented by Stewart et al. (1983) for lake trout. This form is most appropriate for fishes in thermally stratified systems where they can select preferred temperatures (i.e., they never approach stressfully warm temperatures). The main advantage of this function -- simplicity -- is offset partly by its being invalid above some temperature (about 12° C for lake trout). **a** is the intercept for a one-gram fish at 0° C, **b** is the weight-dependence coefficient and θ is the temperature-dependence coefficient.

Consumption Model 2:

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

Where:

$$V = (T_M - T) / (T_M - T_O)$$

$$X = (W^2 * (1 + (1 + 40 / Y)^{0.5})^2) / 400$$

$$W = \mathrm{Ln}(\theta) * (T_M - T_O)$$

$$Y = \mathrm{Ln}(\theta) * (T_M - T_O + 2)$$

Parameters used: a, b, θ, T_O, T_M
Function variables: CA, CB, CQ, CTO, CTM

This temperature-dependence function was used by Kitchell et al. (1977) for perch and walleye (TDEP in Figure 6). It has also been used for bluegill and bass (Kitchell et al. 1974; Rice1981; Rice et al. 1983). This function is most appropriate for warm-water species. In this function, **a** is the intercept for the weight dependence of consumption at the *optimum* temperature (T_O), **b** is the weight-dependence coefficient, **T_M** is the maximum temperature, T_O is the optimum temperature and θ approximates a Q_{10} for the rate the function increases over relatively low temperatures. This function increases from 0 (at low temperatures) to 1 at the optimum temperature and back to 0 at the maximum temperature.

Consumption Model 3:

$$F(T) = K_A * K_B$$

Where:

$$K_A = (K1 * L1) / (1 + K1 * (L1 - 1))$$

$$L1 = e^{(G1 * (T - \theta))}$$

$$G1 = (1 / (T_O - \theta)) * \mathrm{LN}((0.98 * (1 - K1)) / (K1 * 0.02))$$

$$K_B = (K4 * L2) / (1 + K4 * (L2 - 1))$$

$$L2 = \mathrm{EXP}(G2 * (T_L - T))$$

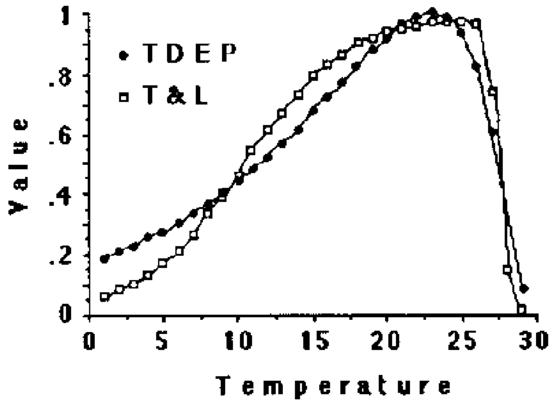
$$G2 = (1 / (T_L - T_M)) * \mathrm{Ln}((0.98 * (1 - K4)) / (K4 * 0.02))$$

Parameters used: a, b, θ, T_O, T_M, T_L, K1, K4
Function variables: CA, CB, CQ, CTO, CTM, CTL, CK1, CK4

Model 3 is the Thornton and Lessem (1978) algorithm (T & L in Figure 6), which has been used for alewife, coho salmon and chinook salmon (Stewart et al. 1981; Stewart and Binkowski 1986). This function is essentially the product of two sigmoid curves, one fitting the increasing portion of the temperature dependence (K_A) and the other fitting the decreasing portion of the temperature-dependence (K_B) curve. This function seems to provide a better fit for the temperature dependence of maximum consumption in some cool- and cold-water species, especially at lower temperatures. **a** is the intercept for the weight dependence of consumption at the optimum temperature, and **b** is the weight-dependence coefficient. For the increasing portion of the function, θ is the low temperature at which the temperature dependence is **K1** (a low value, such as 0.15) times the maximum rate, and T_O is the higher temperature at which the temperature dependence is 0.98 of maximum. For the decreasing portion of the function, $\mathbf{T_M}$ is the temperature (above or equal to T_O) at which the temperature dependence is still 0.98 of maximum, and $\mathbf{T_L}$ is the upper temperature at which the temperature dependence is **K4** (usually around 0.01) of the maximum rate. For more detail on this function, see Thornton and Lessem (1978).

FIGURE 6

Temperature-Dependence Functions



Respiration

Respiration is the amount of energy (converted to weight equivalents) used by the fish in carrying out body processes and includes standard metabolism and active metabolism. The respiration term is determined by calculating resting metabolism as an allometric function of weight and modifying that by a temperature function and a factor representing active metabolism. Specific dynamic action is calculated separately and added to the other metabolic rates. The basic equations for respiration are:

$$R = \alpha * W^{\beta} * F(T) * ACTIVITY$$

$$S = SDA * (C - F)$$

where:

R = the specific rate of respiration ($g*g^{-1}*d^{-1}$),
W = fish weight (g),
α = the intercept of the allometric function,
β = the slope of the allometric function,
T = temperature (° C),
$F(T)$ = the temperature-dependence function,
ACTIVITY = the increment for active metabolism,
S = the energy accounted for by specific dynamic action,
SDA = the proportion of assimilated energy lost to specific dynamic action,
C = specific rate of consumption,
F = specific rate of egestion.

Two separate sets of functions for respiration are included in this program, each with a slightly different method of modeling the temperature dependence of respiration and activity metabolism. Each function will be described separately.

Respiration Model 1:

$$F(T) = e^{(\theta * T)}$$

$$ACTIVITY = e^{((T_O - (T_M * T)) * VEL)}$$

where:

$$VEL = K1 * W^{(K4)} \qquad \{\text{if } T > T_L\}$$

or

$$VEL = (ACT * e^{(BACT * T)}) * W^{(K4)} \qquad \{\text{if } T \leq T_L\}$$

Parameters used: α, β, θ, T_O, T_M, T_L, K1, K4, ACT, BACT, SDA

Function variables: RA, RB, RQ, RTO, RTM, RTL, RK1, RK4, ACT, BACT, SDA

α is measured as g $O_2 * d^{-1}$ and is the intercept for specific standard metabolism vs. weight, temperature and swimming speed (value for a one-gram fish at 0° C and 0 swimming speed). α is corrected for the relative energy density of the fish and its prey items on each day within the model. This is an improvement over the method of estimating α in terms of grams body weight used in some of the publications using earlier versions of this model (Kitchell et al. 1977; Kitchell and Breck 1980). β is the weight-dependence coefficient for standard metabolism.

Model 1 includes an exponential function for temperature dependence of standard respiration and the swimming speed function developed for lake trout (Stewart et al. 1983). This function provides a lot of latitude in modeling swimming speed. Swimming speed is modeled as a function of weight alone (above a cutoff temperature of T_L) or as a function of weight and temperature (below the cutoff temperature of T_L). Swimming speed for any species can be modeled in either (or both) of these methods by choosing an appropriate **T_L**. Swimming speed can also be modeled as a constant velocity. Constant velocity can be modeled by setting **T_O** to an appropriate value, setting **K1** and **ACT** to 1.0, and setting **K4**, **BACT**, and **T_M** to 0.0.

θ is the temperature-dependence coefficient for standard metabolism. **T_O** is the coefficient for swimming speed dependence of metabolism. **T_M** and **T_O** together allow for a possible linear relationship between the coefficient for swimming speed dependence of metabolism and temperature. This relationship has not yet been fully examined; at the present time, we always leave **T_M** set to a value of 0.0 (i.e., no relationship). The units for swimming speed (**VEL**) are centimeters per second. **T_L** is the cutoff temperature above which swimming speed is dependent on weight only and below which swimming speed is dependent upon weight and temperature. **K1** is the intercept for weight dependence of swimming speed above the cutoff temperature (**T_L**). **K4** is the slope for weight dependence of swimming speed at all temperatures. **ACT** is the intercept of the relationship for swimming speed vs. temperature and weight below **T_L** (swimming speed in centimeters per second of a one-gram fish at 0° C). **BACT** is the coefficient for the temperature dependence of swimming speed below **T_L**. See Stewart et al. (1983) and Stewart and Binkowski (1986) for a more complete description of these parameters.

Respiration Model 2:

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

ACTIVITY = ACT

Where:

$$V = (T_M - T) / (T_M - T_O)$$

$$X = (W^2) * (1 + (1 + 40 / Y)^{0.5})^2) / 400$$

$$W = LN(\theta) * (T_M - T_O)$$

$$Y = LN(\theta) * (T_M - T_O + 2)$$

Parameters used: α, β, θ, T_M, T_O, ACT, SDA
Function variables: RA, RB, RQ, RTM, RTO, ACT, SDA

Model 2 uses the same function for modeling the temperature dependence of respiration (Kitchell et al. 1977) as model 2 for the temperature dependence of consumption. α is measured as g O_2*d^{-1} and is the intercept for specific standard metabolism vs. weight at optimum temperature (value for a one-gram fish at the optimum temperature; i.e., **T_O**). (Note the difference between the temperature at which α is measured for this option vs. option 1). β is the weight dependence coefficient, and θ is the temperature coefficient for the temperature-dependence function. **T_O** is the optimum temperature for respiration and **T_M** is the maximum temperature for the temperature-dependence function.

Activity is modeled as a constant (**ACT**) times the resting metabolism (sometimes called the "Winberg multiplier" [Winberg 1956]). Typical values used for this parameter have ranged from 1 to 2.5 (Kitchell et al. 1977).

Waste Losses (Egestion/Excretion)

Egestion is waste products lost as fecal matter, and excretion is metabolic waste lost mainly as nitrogenous wastes. Units for both terms in the model are grams of waste per gram of fish per day. There are three separate options for modeling egestion and excretion either as constant proportions of consumption (C in option 1) or as functions of temperature and consumption (T and C in options 2 and 3).

Egestion/Excretion Model 1:

$F \text{ (egestion)} = FA * C$

$U \text{ (excretion)} = UA * (C - F)$

Parameters used: FA, UA
Function variables: FA, UA

Model 1 assumes that egestion is a constant proportion of consumption (Kitchell et al. 1974). Excretion is a constant proportion of consumption minus egestion (since egested calories cannot be excreted). The more complicated relationships described below do not vary much from a straight proportion model. In most cases, option 1 is probably sufficient for modeling egestion and excretion if you are interested in growth or consumption (Bartell et al. 1986). If you are using the model to ask questions about egestion or excretion processes, then the more complicated functions (models 2 and 3) are probably more appropriate.

Egestion/Excretion Model 2:

$F \text{ (egestion)} = \alpha_F * T^{(\beta_F)} * e^{(\gamma_F * \text{P-value})} * C$

$U \text{ (excretion)} = \alpha_U * T^{(\beta_U)} * e^{(\gamma_U * \text{P-value})} * (C\text{-}F)$

Parameters used: α_F, β_F, γ_F, α_U, β_U, γ_U
Function variables: FA, FB, FG, UA, UB, UG

Model 2 is from Elliott (1976) and is described in Kitchell et al. (1977). α_F is the intercept for the proportion of consumption egested vs. temperature and ration, β_F is the coefficient for temperature dependence of egestion and γ_F is the coefficient for feeding level (P-value) dependence of egestion. Similarly, α_U is the intercept for the proportion of assimilated consumption excreted vs. temperature and ration, β_U is the coefficient for the temperature dependence of excretion and γ_U is the coefficient for the feeding level (P-value) dependence of excretion. Elliott's formulation (1976) was based on a study of brown trout (*Salmo trutta*) feeding on all invertebrate prey. This option is most appropriate when diet items are either all invertebrates or all fish. If the diet is a mixture of invertebrate and vertebrate prey, then option 3 is more accurate.

Egestion/Excretion Model 3:

$F \text{ (egestion)} = PF * C$

$U \text{ (excretion)} = \alpha_U * T^{\beta_U} * e^{(\gamma_U * \text{P-value})} * (C - F)$

Where:

$PF = ((PE - 0.1) / (1 - 0.1)) * (1 - PFF) + PFF$

$PE = \alpha_F * T^{\beta_F} * e^{(\gamma_F * \text{P-value})}$

$PFF = \Sigma\, (PREYK[n] * DIET[n])$
for n = 1 to number of prey

PREYK[n] = indigestible proportion of nth prey

DIET[n] = proportion of *n* th prey in diet

Parameters used: α_F, β_F, γ_F, α_U, β_U, γ_U
Function variables: FA, FB, FG, UA, UB, UG

Model 3 is developed from Elliott (1976) and is described in Stewart et al. (1983). The calculations of **PFF** and **PF** are correction factors for diets that include both vertebrate and invertebrate prey. **PREYK** and **DIET** values are read from datafiles (**species data file** and **diet file**, respectively). Excretion is calculated as in model 2, and all parameters used are as described in model 2.

Growth

Growth is the increase or decrease in body weight of a fish and is calculated directly from the terms of the balanced energy equation:

Growth = Consumption - (Respiration + Waste Losses)

Growth is calculated as a specific rate (grams of food per gram of fish per day). The total grams available for growth is this specific rate times the weight of the fish. The total must then be corrected for the relative energy density (calories per gram, wet weight) of both the prey and the predator. The actual correction factor depends on whether the caloric density of the predator is based on a seasonal energy density file or is a function of body weight.

If the caloric density is input from a seasonal file (predator energy density model 1), the correction is straightforward. The weight of the fish on the next day is equal to the total number of calories in the fish on the current day plus the total number of calories in the prey on that day, all divided by what the caloric density will be on the next day. If the energy density of the fish is a function of body weight (predator energy density model 2), then the "Alpha" and "Beta" parameters from the "Initial Data" section of the species data file are used and the calculations are more complicated (see Stewart et al. 1983). The equation for predator caloric density model 2 is:

$$CD = \alpha + \beta * W$$

where:

CD = caloric density (cal/g, wet weight),
α = intercept,
β = slope,
W = weight.

The model allows you to have two sets of "Alpha" and "Beta" values, which define equations for young and adult fish. "Weight Cutoff" is the weight at which the model switches from equation 1 to equation 2. Caloric density can be modeled as a constant if "β" is set to zero and "α " is set to the desired caloric density.

These corrections allow for predator and prey energy densities to vary independently and allow for all calculations for weights and consumption amounts to be in terms of grams (wet weight) corrected for energy density. The importance of the energy density information depends on the question being asked of the model and on the relative differences between the energy density of the fish and its prey, and whether either show strong seasonal or ontogenetic changes in energy density. For an example of where the prey show strong seasonal dynamics in energy density and where energy density of the fish varies ontogenetically, see Stewart et al. (1983).

The model also allows for loss of weight by the fish due to spawning. Growth of reproductive tissue is considered part of the growth term. However, if the simulation interval includes the date that spawning occurs, weight of reproductive products lost can be subtracted from fish weight (see Chapter 4).

For further information on the bioenergetics options, please refer to the references mentioned here and in the bibliography.

CHAPTER 4

Extended Topics

Simulation Intervals

Typical simulation intervals are to use each cohort within the model to represent growth over one year. However, cohorts within the model can represent growth over any period of time. Thus, the first five cohorts in a **species data file** can represent growth over the first year of life, and the next three model cohorts in the same file can represent the second year of life. When using multiple model cohorts to represent growth periods within years, care must be taken to make sure that the proper seasonal data files are used with each cohort. In the above example (five cohorts for year 1 and three for year 2), if temperature cycles are different for fish of age 1 and 2, then six cohorts must be present in the **temperature data file**. The first five cohorts in the **temperature data file** are all identical and represent the temperatures for fish in their first year, and the sixth cohort in the **temperature data file** represents the temperature cycle for fish in their second year. In the **species data file**, the maximum temperature cohort would be listed as 6. If all ages showed the same seasonal diet proportions, then only one cohort needs to be entered in the **diet data file**. Each of the seasonal data files must contain a full year's data within each cohort, whether or not that cohort is modeled over the entire year.

Usually, it is best to divide a year's growth into several simulation intervals if you want to estimate the seasonal patterns of consumption and if prey abundances vary seasonally. Under these conditions, the assumptions of constant P-value are usually not met. However, the only way to get more detailed consumption information is to have good weight estimates for periods corresponding to the changing prey abundances. For a good example of seasonally changing prey availability to largemouth bass, see Rice and Cochran (1984). If the only weight data available are annual, then you cannot model shorter intervals.

Model Enhancements

Energy Density: The energy density of both predator and prey are important values for the modeling of growth and consumption. The accuracy of energy density information needed for the model depends on the question that you seek to answer through the model and on the characteristics of the particular species in question. For example, in modeling salmonid consumption of alewife in Lake Michigan, good caloric data is important because the prey undergo drastic energy density changes during an annual cycle, and the predators continue to increase in energy density as they grow larger. When you are estimating the annual growth cycle for a fish that does not show large changes in caloric density (e.g., yellow perch), it is not as important to "fine tune" the energy density information. For species without drastic changes in caloric density and without large amounts of fat, a constant value of 1,000 calories per gram (wet weight) has been used in several of the studies previously cited (Kitchell et al. 1977; Kitchell and Breck 1980).

Maintenance Consumption: For some species, available data suggest little or no weight change during part of the winter months (Stewart and Binkowski 1986; Kitchell et al. 1977). To produce a better fit to the annual growth cycle in those instances, we have included an option that will calculate daily P-values for maintenance ration when the temperature is below some specific value (set in the **species data file**). While this option was originally introduced to better fit the pattern of growth shown by perch and alewife in cold water, it can also be used to examine how maintenance ration changes as a function of weight or temperature. This approach may have valuable applications in aquaculture. For example, it could be used to determine the maintenance ration level for a particular size of fish across a range of temperatures. That information could then be used to estimate the food costs of different temperature and ration levels.

Spawning Losses: The model includes spawning losses as a fixed proportion loss of weight on a particular day of the year for all cohorts older than a cut-off cohort number. The proportional weight loss is the same for all cohorts that are mature (i.e., different cohorts cannot have different spawning weight losses). In modeling a population, the model assumes that all individuals of mature cohorts spawn. Remember that the model is set up to model the average individual in a population and that all individual calculations are then multiplied by the estimated population size on a given day to produce the population estimates.

Modeling New Species

To model different species, only the data files need to be changed. As described in the previous chapter, programs within the model allow you to create and edit new data files. Therefore, you don't need to modify the programs themselves. Modeling new species is obviously easier if all the necessary bioenergetics parameters have been estimated for that species. Usually that is not the case. However, for many fish, some of the required bioenergetics parameters have been estimated, or parameters are available for related species. Some parameters, such as those for egestion and excretion, do not show a lot of variation across species (except when comparing piscivores to herbivores). The model estimates of growth and consumption are relatively insensitive to changes in the egestion and excretion parameters (Bartell et al. 1986). When starting to model a new species, it is best to start out with the simplest model you can. You can later increase its complexity and determine if various enhancements lead to a significant change in the results.

For respiration and consumption parameters, the temperature dependences are of much greater importance. Several papers list information on temperature preferences (Jobling 1981), and this information can often be combined with bioenergetics parameters from similar species to make a good initial estimate of the parameters for the species of interest. It is a good idea to do some error or perturbation analysis (Kitchell et al. 1977; Stewart et al. 1983; Bartell et al. 1986) of the model if you must make informed guesses about some of the bioenergetics parameters. This will give you some estimates of the precision of the results of your modeling efforts.

Model Limitations

One of the main assumptions of this model is that the prey availability remains constant across each growth interval. As discussed previously, if this is not the case, the best solution is to split the time period into smaller growth periods with a separate P-value calculated for each growth period (see Rice and Cochran 1984). While day-to-day variation in prey availability obviously occurs to some extent, this model is designed to model the average individual in a population. The better the growth data and temperature data, the better the predictions of the model.

Temperature preferences show some variation across the geographic range of a species. Therefore, temperature parameters reported here and in the literature may not be appropriate for all populations of a given species. When possible, check the literature sources of these parameters for the geographic area of the fish used in the study.

Most of the parameters for various species have come from laboratory studies using fish of a size easy to handle and appropriate to the size of laboratory apparatus. Also, such studies tend to be done at temperatures which do not stress the fish. Therefore, one should be cautious about modeling growth at extreme temperatures or extreme sizes. For some of the species examined, growth at cold temperatures has proved difficult to model accurately. This problem is most apparent when modeling cool- or warm-water species at cold temperatures. Because of the allometric relationships between size and the components of bioenergetics, extending the parameters measured on larger fish to very small fish (larvae and early young-of-the-year) may result in significant biases. Small errors at larger sizes will become magnified at smaller sizes. In addition, very small fish may "behave" energetically more like invertebrates than vertebrates. The energetics of small fish is an area requiring further research, and we hope that energetics models can be extended to cover fish larvae and help answer some of the basic questions of larval fish ecology.

Modifying the Bioenergetics Programs

Modifying the programs comprising the bioenergetics model is not difficult if you have a working knowledge of PASCAL. You must have the Apple PASCAL language system or, for IBM, TURBO PASCAL 3.0 to make any changes in the text files. If you have not programmed in either of these languages, you may find it easier to work around any changes you might want to make. The main reason you might want to change the programs is to modify the variables that are saved to the output file. For example, the model only saves output variables from the first four (of a maximum of 10) prey items. One way to get around this particular limitation without rewriting part of the model program is to set up several diet files with different prey items ordered as the first four in the file. If you want to model eight prey types and want output on all eight, create two diet files with different prey items in the first four categories. Be sure to change the appropriate prey caloric density information also. By running the model twice, using different prey files each time, you can obtain all the prey consumption information without rewriting the model program.

If you need to change the output variables from the current list, two sections of code must be changed. The first saves a file of titles for each of the variables, and the second saves the value of each variable during the output steps of the model. Be sure to make your changes in both places when modifying the output variables. Because PASCAL is a compiled language, the programs must be recompiled using the appropriate PASCAL compiler whenever any program text files are changed. We are not able to give out the text files for the disk utilities or plotting routines on the Apple.

When making any changes to the models (or to the data files), be sure to do so only on backup copies of the diskettes. It is always a good idea to make copies of the original disks and always work off of the copies only. Please feel free to write to the authors (c/o Center for Limnology, University of Wisconsin, Madison, WI 53706) with any suggestions or comments you may have regarding these models. We hope that they provide a tool that helps to improve our understanding and management of our fishery resources.

APPENDICES

APPENDIX 1A

Directories of Model Disks: Apple Version

```
BIOENERGETICS MODEL DISK
  MODEL:   Energetics Programs  (Front Side)
     SYSTEM.PASCAL       | System
     SYSTEM.CHARSET      | System
     SYSTEM.MISCINFO     | System
     SYSTEM.LIBRARY      | System
     SYSTEM.STARTUP      | Startup program (from MENU.TEXT)
     BOOTCODE.DATA       | System
     UTILITY.CODE        | Utility program, format disks, etc.
     PLOT.CODE           | Plotting program
     MODEL.CODE          | Model program
     CHANGECOH.CODE      | Edit species data files
     TEMPDIET.CODE       | Edit temp, diet, calorie files
  MODEL.B:   Energetics Programs  (Back Side)
     SYSTEM.APPLE        | System


SAMPLE DATA DISK
  DATA:      Sample Data Files  (Front Side)
     YELPERCH.BIO        | Species data file for perch
     YELPERCH.TEM        | Temperature file for perch
     YELPERCH.DIE        | Diet file for perch
     YELPERCH.PDC        | Predator caloric file for perch
     LAKTROUT.BIO        | Species data file for lake trout
     LAKTROUT.DIE        | Diet file for lake trout
     LAKTROUT.PYC        | Diet calorie file for lake trout
     LAKTROUT.TEM        | Temperature file for lake trout
     COHO.BIO            | Species data file for coho salmon
     CHINOOK.BIO         |   "      "    "    "  chinook salmon
     LMBASS.BIO          |   "      "    "    "  largemouth bass
     WALLEYE.BIO         |   "      "    "    "  walleye
     BLUEGILL.BIO        |   "      "    "    "  bluegill
     SEALAMP.BIO         |   "      "    "    "  sea lamprey
     DACE.BIO            |   "      "    "    "  dace
     ALEWIFE.BIO         |   "      "    "    "  alewife
     NORTHERN.BIO        |   "      "    "    "  northern pike
     MUSKY.BIO           |   "      "    "    "  muskellunge
     LAKTROUT.KEY        | Output file for lake trout
     LAKTROUT.LAB        | Output file for lake trout
     LAKTROUT.WRK        | Output file for lake trout
```

APPENDIX 1A (con't.)

SAMPLE DATA DISK

```
 TEXT:    Text Files   (Back Side)
   MENU.TEXT           | Menu program
   MODEL.TEXT          | 1 of 6  Model program, main file
    MDGETFILE.TEXT     | 2 of 6  Include file for Model program
    MDFILESET.TEXT     | 3 of 6     "       "   "  Model program
    MDINCLUDE.TEXT     | 4 of 6     "       "   "  Model program
    MDENERGY.TEXT      | 5 of 6     "       "   "  Model program
    MDINITIAL.TEXT     | 6 of 6     "       "   "  Model program
   CHANGECOH.TEXT      | 1 of 6  Species file utilities, main file
    CGPRINTIT.TEXT     | 2 of 6  Include file for species file program
    CGFIRST.TEXT       | 3 of 6     "       "   "  species file program
    CGABCCALC.TEXT     | 4 of 6     "       "   "  species file program
    CGREADKEYS.TEXT    | 5 of 6     "       "   "  species file program
    CGGETVALS.TEXT     | 6 of 6     "       "   "  species file program
   TEMPDIET.TEXT       | 1 of 2 Seasonal file utilities, main file
    TEMPSEGS.TEXT      | 2 of 2  Include file for seasonal file program
```

APPENDIX 1B

Directories of Model Disks: IBM Version

BIOENERGETICS MODEL DISK

MODEL: Energetics Programs

MENU.COM	Model program
MENU.000	Overlay program for MENU.COM
MENU.001	" " " MENU.COM
MENU.002	" " " MENU.COM
MENU.003	" " " MENU.COM
MENU.004	" " " MENU.COM

SAMPLE DATA DISK

DATA: Sample Data Files and PASCAL Text Files

YELPERCH.BIO	Species data file for perch
YELPERCH.TEM	Temperature file for perch
YELPERCH.DIE	Diet file for perch
YELPERCH.PDC	Predator caloric file for perch
LAKTROUT.BIO	Species data file for lake trout
LAKTROUT.DIE	Diet file for lake trout
LAKTROUT.PYC	Diet calorie file for lake trout
LAKTROUT.TEM	Temperature file for lake trout
COHO.BIO	Species data file for coho salmon
CHINOOK.BIO	" " " " chinook salmon
LMBASS.BIO	" " " " largemouth bass
WALLEYE.BIO	" " " " walleye
BLUEGILL.BIO	" " " " bluegill
SEALAMP.BIO	" " " " sea lamprey
DACE.BIO	" " " " dace
ALEWIFE.BIO	" " " " alewife
NORTHERN.BIO	" " " " northern pike
MUSKY.BIO	" " " " muskellunge
LAKTROUT.KEY	Output file for lake trout
LAKTROUT.LAB	Output file for lake trout
LAKTROUT.WRK	Output file for lake trout
MENU.PAS	Text file for main menu
MODEL.PAS	" " " energetics code
CHANGECO.PAS	" " " species file utilities
TEMPDIET.PAS	" " " seasonal file utilities

APPENDIX 2

Contents of Species Data File for Lake Trout (LAKTROUT.BIO) on Sample Data Disk

```
INITIAL DATA:
Species Name ----------> LAKE TROUT
Consumption Model -----> 1
Respiration Model -----> 1
Egest/Excret Model ----> 3
Pred CalDens Model ----> 2
Prey CalDens Model ----> 1
Include Spawning ------> Y
 First cohort to spawn > 5
 Day of spawning ------> 120
 Prop. spawning wt loss> 0.068
Maximum cohort for Pred Cal File > 1
Maximum cohort for Diet File ----> 7
Maximum cohort for Temp. File ---> 1
Temp. for maintenance growth ---->  0.00000
Values for weight relationship
of caloric density for predator.
   CalDens Alpha1>  1.36200E3
   CalDens Beta1->  7.36000E-1
   Weight Cutoff->  1.44200E3
   CalDens Alpha2>  2.17200E3
   CalDens Beta2->  1.86000E-1

Values for COHORT  1
Start Day =     1 Final Day =  365 Initial Pop Size =    1.00000E6
Start Wgt =  20.000 Final Wgt =  260.000 P-val =  0.89705   4 Prey
Season Firstday   Mortality     Harvest
    1       1       0.001265    0.00000
    2      32       0.001265    0.00000
    3      63       0.001265    0.00000
    4      93       0.001265    0.00000
    5     124       0.001265    0.00000
    6     154       0.001265    0.00000
    7     185       0.001265    0.00000
    8     213       0.001265    0.00000
    9     244       0.001265    0.00000
   10     274       0.001265    0.00000
   11     305       0.001265    0.00000
   12     335       0.001265    0.00000
Consumption: CA  = 0.05890  CB = -0.307     CQ = 0.1225
             CTO = 0        CTM = 0         CTL = 1.0
             CK1 = 0        CK4 = 0
Respiration: RA  = 0.004630 RB = -0.29500   RQ = 0.05900
             RTO = 0.023    RTM = 0.00      RTL = 11.0
             RK1 = 1.0      RK4 = 0.0500    ACT = 11.700
             BACT= 0.04050 SDA = 0.1720
Egestion:     FA = 0.2120   FB = -0.2220    FG = 0.6310
Excretion:    UA = 0.0314   UB = 0.5800     UG = -0.2990
Propor. Prey Indigest. 0.100 0.033 0.033 0.033
```

APPENDIX 2 (con't)

```
Values for COHORT  2
Start Day =    1 Final Day =  365 Initial Pop Size =    6.30000E5
Start Wgt =  260.000 Final Wgt =  659.000 P-val =  0.58156   4 Prey
Season Firstday   Mortality    Harvest
    1      1       0.001265    0.00000
    2     32       0.001265    0.00000
    3     63       0.001265    0.00000
    4     93       0.001265    0.00000
    5    124       0.001265    0.00000
    6    154       0.001265    0.00000
    7    185       0.001265    0.00000
    8    213       0.001265    0.00000
    9    244       0.001265    0.00000
   10    274       0.001265    0.00000
   11    305       0.001265    0.00000
   12    335       0.001265    0.00000
Consumption:  CA = 0.05890  CB = -0.307   CQ = 0.1225
             CTO = 0        CTM = 0       CTL = 0
             CK1 = 0        CK4 = 0
Respiration:  RA = 0.004630 RB = -0.29500 RQ = 0.05900
             RTO = 0.023    RTM = 0.00    RTL = 11.0
             RK1 = 1.0      RK4 = 0.0500  ACT = 11.700
             BACT= 0.04050 SDA = 0.1720
Egestion:     FA = 0.2120   FB = -0.2220  FG = 0.6310
Excretion:    UA = 0.0314   UB = 0.5800   UG = -0.2990
Propor. Prey Indigest. 0.100 0.033 0.033 0.033

Values for COHORT  3
Start Day =    1 Final Day =  365 Initial Pop Size =    3.96900E5
Start Wgt =  659.000 Final Wgt =  1216.00  P-val =  0.56872   4 Prey
Season Firstday   Mortality    Harvest
    1      1       0.001265    0.00000
    2     32       0.001265    0.00000
    3     63       0.001265    0.00000
    4     93       0.001265    0.00000
    5    124       0.001265    0.00000
    6    154       0.001265    0.00000
    7    185       0.001265    0.00000
    8    213       0.001265    0.00000
    9    244       0.001265    0.00000
   10    274       0.001265    0.00000
   11    305       0.001265    0.00000
   12    335       0.001265    0.00000
Consumption:  CA = 0.05890  CB = -0.307 CQ = 0.1225
             CTO = 0        CTM = 0     CTL = 0
             CK1 = 0        CK4 = 0
Respiration:  RA = 0.004630 RB = -0.29500 RQ = 0.05900
             RTO = 0.023    RTM = 0.00    RTL = 11.0
             RK1 = 1.0      RK4 = 0.0500  ACT = 11.700
             BACT= 0.04050 SDA = 0.1720
Egestion:     FA = 0.2120   FB = -0.2220  FG = 0.6310
Excretion:    UA = 0.0314   UB = 0.5800   UG = -0.2990
Propor. Prey Indigest. 0.100 0.033 0.033 0.033
```

APPENDIX 3

Suggested Consumption Models and Associated Parameter Values for Various Species

Consumption Models:
Model 1: Exponential Temperature Function (Stewart 1980).
Uses parameters CA,CB,CQ.
Model 2: TDEP Temperature Function (Kitchell et al. 1977).
Uses parameters CA,CB,CQ,CTO,CTM.
Model 3: Thornton-Lessem Temperature Function (Stewart 1980).
Uses all parameters.
Multiple values of CQ, CTO, CTM and CTL are for fish of different ages, beginning with age 0.

Parameter	Largemouth Bass	Yellow Perch	Walleye	Bluegill	Sea Lamprey	Dace
Consumption Model....	2	2	2	2	2	2
CA........	0.33	0.25	0.25	0.182	0.30	0.36
CB........	-0.325	-0.27	-0.27	-0.274	-0.35	-0.31
CQ........	2.65	2.3	2.3	2.3	2.3	2.3
CTO.......	27.5	29.,23	22.	31.,27	18.	26.
CTM.......	37.	32.,28	28.	37.,36	25.	29.
CTL.......	.	.	.	.	.	.
CK1.......	.	.	.	.	.	.
CK4.......	.	.	.	.	.	.

Parameter	Lake Trout	Alewife	Coho/Chinook Salmon	Northern Pike[a]	Muskellunge[a]
Consumption Model....	1.	3.	3	2	2
CA........	0.0589	0.8464	0.3033	0.2045	0.2215
CB........	-0.307	-0.3	-0.2754	-0.18	-0.18
CQ........	0.1225	5.,4.,3.	5.	2.59	2.53
CTO.......	.	24.,20.,16	15.	24.	26.
CTM.......	.	26.,22.,18	18.	34.	34.
CTL.......	.	29.,27.,25	24.	.	.
CK1.......	.	0.17	0.36	.	.
CK4.......	.	0.01	0.01	.	.

---

[a] Parameter values for northern pike and muskellunge are preliminary and have not been thoroughly tested. Most were estimated from data in Bevelhimer et al. (1985).

APPENDIX 4

Suggested Respiration Models and Associated Parameter Values for Various Species

Respiration Models:

Model 1: Exponential with swimming speed (Stewart 1980; Stewart et al. 1983). Uses all parameters.

Model 2: TDEP with activity multiplier (Kitchell et al. 1977). Uses parameters RA,RB,RQ,RTO,RTM,ACT,SDA.

Parameter	Largemouth Bass	Yellow Perch	Walleye	Bluegill	Sea Lamprey	Dace
Respiration Model...	1.	2.	2.	2.	2.	2.
RA[a].......	0.008352	0.0108	0.0108	0.0154	0.0324	0.04
RB........	-0.355	-0.2	-0.2	-0.2	-0.05	-0.20
RQ........	0.0313	2.1	2.1	2.1	2.1	2.1
RTO[b]......	0.0196	32.,28.	27.	37.,36.	25.	29.
RTM[b]......	0.	35.,33.	32.	41.,40.	30.	32.
RTL.......	0.	.	.	.	.	.
RK1.......	1.0	.	.	.	.	.
RK4.......	0.	.	.	.	.	.
ACT.......	1.0	1.0	1.0	1.0	1.5	2.
BACT......	0.	.	.	.	.	.
SDA.......	0.163	0.172	0.172	0.172	0.172	0.15

---

[a] RA for these species has been converted from units in the original reference to g $O_2*g^{-1}*d^{-1}$.

[b] Multiple values for RTO and RTM are for fish of different ages, beginning with age 0.

Parameter	Lake Trout	Alewife	Coho/Chinook Salmon	Northern Pike/ Muskellunge[c]
Respiration Model...	1.	1.	1.	1.
RA.......	0.00463	0.00367	0.00264	0.00246
RB.......	-0.295	-0.2152	-0.217	-0.18
RQ.......	0.059	0.0548	0.06818	0.055
RTO......	0.0232	0.03	0.0234	0.1222
RTM......	0.	0.	0.	0.
RTL......	11.	9.	25.	0.
RK1......	1.	22.08	1.	1.0
RK4......	0.05	-0.045	0.128	0.
ACT......	11.7	5.78	9.7	1.0
BACT.....	0.0405	0.149	0.0405	0.
SDA......	0.172	0.175	0.172	0.14

---

[c] Parameter values for northern pike and muskellunge are preliminary and have not been thoroughly tested. Most were estimated from data in Bevelhimer et al. (1985).

APPENDIX 5

Suggested Egestion/Excretion and Predator Energy Density Models and Associated Parameter Values for Various Species

Egestion/Excretion Models:

- Model 1: Constant proportions of consumption.
  Uses parameters FA,UA.
- Model 2: Function of weight, temperature and ration (Elliott 1976).
  Uses all parameters.
- Model 3: Model 2 with correction for invertebrates in diet (Stewart 1980).
  Uses all parameters.

Parameter	Largemouth Bass	Yellow Perch	Walleye	Bluegill	Sea Lamprey	Dace
Egest/Excret						
Model....	1.	2.	2.	2.	1.	1.
FA........	0.104	0.158	0.158	0.158	0.03	0.40
FB........	.	-0.222	-0.222	-0.222	.	.
FG........	.	0.631	0.631	0.631	.	.
UA........	0.068	0.0253	0.0253	0.0253	0.15	0.10
UB........	.	0.58	0.58	0.58	.	.
UG........	.	-0.299	-0.299	-0.299	.	.
Pred. Energy						
Dens. Model	1	1	1	1	1	1
Cal Density	1000	1000	1000	1000	1000	1196

Parameter	Lake Trout	Alewife	Coho Salmon	Chinook Salmon	Northern Pike/ Muskellunge[a]
Egest/Excret.					
Model...	3.	1.	3.	3.	1.
FA.......	0.212	0.16	0.212	0.212	0.20
FB.......	-0.222	.	-0.222	-0.222	.
FG.......	0.631	.	0.631	0.631	.
UA.......	0.0314	0.10	0.0314	0.0314	0.07
UB.......	0.58	.	0.58	0.58	.
UG.......	-0.299	.	-0.299	-0.299	.
Pred. Energy					
Dens. Model	2	1	2	2	1
Cal Density	.	seasonal[b]	.	.	860
Alpha1...	1362.	.	1377.	1377.	.
Beta1....	0.736	.	0.2356	0.2356	.
Cutoff...	1442.	.	4000.	4000.	.
Alpha2...	2172.	.	1377.	1816.	.
Beta2....	0.186	.	0.2356	0.1258	.

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[a] Parameter values for northern pike and muskellunge are preliminary and have not been thoroughly tested. Most were estimated from data in Bevelhimer et al. (1985).

[b] See Stewart and Binkowski (1986).

APPENDIX 6

List of Variables Saved to the Output File for Each Energetics Run

Note: Variables 1 through 22 and 27 through 30 are daily values that apply only to the specific day for which the data were saved. Variables 23 through 26 and 31 through 36 are cumulative values which are summed in the manner designated by the user. Variable 35, "CUM PROD", includes spawning losses as part of production.

Field Number	Variable Name	Description of Variable
1	COHORT	Cohort number
2	DAY YEAR	Day of year
3	DAY LIFE	Age (days) since first day of this run
4	TEMP	Temperature (C)
5	WEIGHT	Weight (grams)
6	POPSIZE	Population size (number)
7	POPMASS	Population mass (grams)
8	SP GROWTH	Specific growth rate ($g*g^{-1}*d^{-1}$)
9	SP CONS	Specific consumption rate ($g*g^{-1}*d^{-1}$)
10	SP EGEST	Specific egestion rate ($g*g^{-1}*d^{-1}$)
11	SP EXCRET	Specific excretion rate ($g*g^{-1}*d^{-1}$)
12	SP RESP	Specific respiration rate ($g*g^{-1}*d^{-1}$)
13	SP SDA	Specific SDA rate ($g*g^{-1}*d^{-1}$)
14	CAL DENS	Predator Caloric Density (calories * g^{-1})
15	% PREY 1	Proportion of prey 1 in diet (0-1)
16	% PREY 2	Proportion of prey 2 in diet
17	% PREY 3	Proportion of prey 3 in diet
18	% PREY 4	Proportion of prey 4 in diet
19	ID CONS 1	Individual daily cons. prey 1 (grams)
20	ID CONS 2	Individual daily cons. prey 2
21	ID CONS 3	Individual daily cons. prey 3
22	ID CONS 4	Individual daily cons. prey 4
23	SI CONS 1	Cumulative individual cons. prey 1 (grams)
24	SI CONS 2	Cumulative individual cons. prey 2
25	SI CONS 3	Cumulative individual cons. prey 3
26	SI CONS 4	Cumulative individual cons. prey 4
27	PD CONS 1	Population daily cons. prey 1 (grams)
28	PD CONS 2	Population daily cons. prey 2
29	PD CONS 3	Population daily cons. prey 3
30	PD CONS 4	Population daily cons. prey 4
31	SP CONS 1	Cumulative population cons. prey 1 (grams)
32	SP CONS 2	Cumulative population cons. prey 2
33	SP CONS 3	Cumulative population cons. prey 3
34	SP CONS 4	Cumulative population cons. prey 4
35	CUM PROD	Cumulative population production (grams)
36	CMCALCONS	Cumulative calories consumed per individual

APPENDIX 7

Partial Listing of Output from a Bioenergetics Run (Apple Version) for Lake Trout Contained in LAKTROUT.WRK on the Sample Data Disk

Note: This simulation used data files with the LAKTROUT prefix (Appendix 1) and was run for cohorts 1 to 3. Output was summed over all cohorts, and saved at 50-day intervals and on "Start" and "Final" weight day for each cohort.

```
                        Variable Name and Field Number
                   Day    Day
Record   Cohort   Year   Life    Temp    Weight    Sp Growth      Sp Cons      Cal Dens
Number     1        2      3       4        5          8              9            14

   1:      1.       1.     1.    10.0      20.3    0.0217         0.0717       1376.72
   2:      1.      50.    50.    10.0      37.2    0.0177         0.0595       1389.07
   3:      1.     100.   100.    10.0      61.6    0.0149         0.0509       1406.94
   4:      1.     150.   150.     6.9      97.9    0.0103         0.0302       1433.46
   5:      1.     200.   200.     4.2     128.5    5.69041E-3     0.0198       1456.21
   6:      1.     250.   250.     2.8     152.2    3.93819E-3     0.0158       1473.72
   7:      1.     300.   300.     3.8     175.8    4.68925E-3     0.0172       1490.97
   8:      1.     350.   350.    10.0     232.9    0.0115         0.0338       1532.23
   9:      1.     365.   365.    10.0     260.0    0.0117         0.0327       1551.91
  10:      2.       1.   366.    10.0     261.2    6.28025E-3     0.0212       1553.36
  11:      2.      50.   415.    10.0     323.4    5.91088E-3     0.0198       1599.01
  12:      2.     100.   465.    10.0     408.6    6.54133E-3     0.0184       1661.22
  13:      2.     150.   515.     6.9     478.0    2.64633E-3     0.0120       1713.29
  14:      2.     200.   565.     4.2     522.3    2.02244E-3     8.35905E-3   1745.90
  15:      2.     250.   615.     2.8     551.4    1.37596E-3     6.91033E-3   1767.48
  16:      2.     300.   665.     3.8     577.1    1.66484E-3     7.72905E-3   1786.30
  17:      2.     350.   715.    10.0     635.3    4.50118E-3     0.0161       1828.45
  18:      2.     365.   730.    10.0     658.9    4.51740E-3     0.0159       1845.80
  19:      3.       1.   731.    10.0     660.7    4.59057E-3     0.0155       1847.02
  20:      3.      50.   780.    10.0     748.0    4.47338E-3     0.0150       1911.18
  21:      3.     100.   830.    10.0     865.5    5.25876E-3     0.0143       1996.86
  22:      3.     150.   880.     6.9     957.3    2.11142E-3     9.48517E-3   2065.91
  23:      3.     200.   930.     4.2    1029.1    1.91478E-3     6.63753E-3   2118.59
  24:      3.     250.   980.     2.8    1075.8    1.33180E-3     5.50387E-3   2153.24
  25:      3.     300.  1030.     3.8    1115.2    1.52938E-3     6.17386E-3   2182.18
  26:      3.     350.  1080.    10.0    1188.6    3.64242E-3     0.0130       2235.51
  27:      3.     365.  1095.    10.0    1216.0    3.68751E-3     0.0129       2255.62
```

APPENDIX 7 (con't.)

	Variable Name and Field Number						
Record Number	ID Cons1 19	ID Cons2 20	ID Cons3 21	SI Cons1 23	SI Cons2 24	SI Cons3 25	Cum Prod 35
1:	1.0755	0.3011	0.0574	1.0755	0.3011	0.0574	2.78683E5
2:	1.6403	0.4593	0.0875	67.4257	18.8792	3.5960	1.66299E7
3:	2.3310	0.6527	0.1243	166.594	46.6462	8.8850	3.88374E7
4:	0.8796	1.9351	0.1173	240.672	119.450	15.0051	6.97235E7
5:	0.7621	1.3718	0.4065	280.572	191.270	36.2850	9.43478E7
6:	0.7210	1.2979	0.3846	317.412	257.582	55.9330	1.12201E8
7:	0.9034	1.6261	0.4818	356.798	328.478	76.9391	1.28842E8
8:	2.3466	1.0168	4.4585	436.745	412.705	179.254	1.66516E8
9:	2.5313	1.0969	4.8095	473.393	428.586	248.885	1.83703E8
10:	0.5499	2.9146	0.0	473.943	431.500	248.885	1.84446E8
11:	0.6378	3.3804	0.0	503.072	585.886	248.885	2.22381E8
12:	0.7496	3.9729	0.0	537.633	769.061	248.885	2.71173E8
13:	0.5731	1.7765	3.3810	571.427	906.187	361.468	3.08785E8
14:	0.4360	3.1393	0.0	595.639	1080.51	361.468	3.31218E8
15:	0.3807	2.7411	0.0	615.831	1225.89	361.468	3.45044E8
16:	0.4456	3.2082	0.0	635.911	1370.47	361.468	3.56464E8
17:	1.0197	5.4042	0.0	672.773	1598.75	361.468	3.80646E8
18:	1.0458	5.5427	0.0	688.276	1680.91	361.468	3.90120E8
19:	0.0	5.4299	0.0	688.276	1686.34	361.468	3.90794E8
20:	0.0	5.9180	0.0	688.276	1964.59	361.468	4.24353E8
21:	0.0	6.5435	0.0	688.276	2275.35	361.468	4.66691E8
22:	0.0	3.1751	5.8965	688.276	2508.66	559.236	4.98080E8
23:	0.0	3.8892	0.0	688.276	2725.76	559.236	5.20997E8
24:	0.0	3.3727	0.0	688.276	2905.21	559.236	5.34984E8
25:	0.0	3.9216	0.0	688.276	3082.54	559.236	5.46030E8
26:	0.0	8.1631	0.0	688.276	3391.76	559.236	5.65256E8
27:	0.0	8.2928	0.0	688.276	3515.24	559.236	5.72175E8

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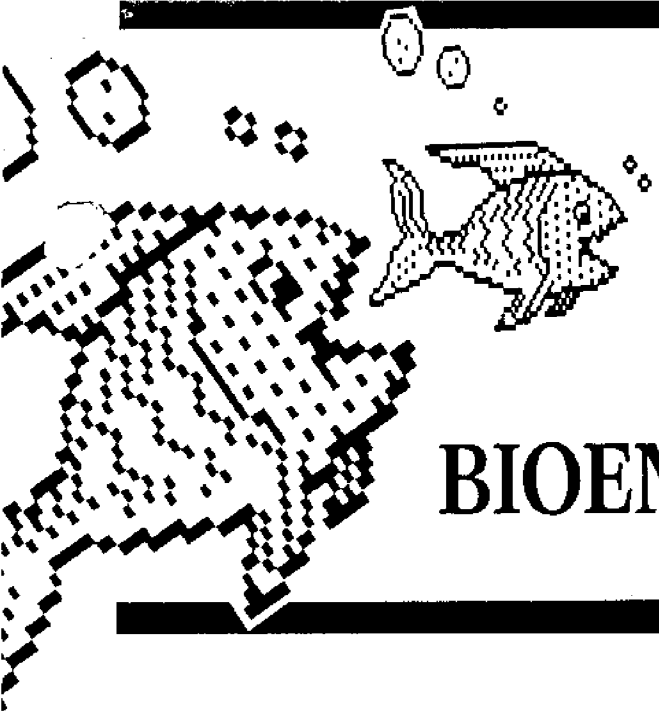

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Providing program information and tips for
A Generalized Bioenergetics Model
of Fish Growth for Microcomputers

BIOENERGETICS BOOTER

WELCOME to the first issue of Bioenergetics Booter, part of the support system provided by the University of Wisconsin Sea Grant Institute and the UW-Madison Center for Limnology for users of the generalized fish bioenergetics model (Hewett and Johnson 1987). The support system for model users has two main components: the newsletter and workshops. This first issue of Bioenergetics Booter contains an overview of user support services, a description of educational uses, suggestions for modeling young fish and setting caloric densities, and answers to technical questions we have received.

As of March 1988, 223 copies (29 Apple II and 194 IBM/compatible versions) of the bioenergetics model have been distributed. Both Apple and IBM versions of the model are still available for US$20 from the UW Sea Grant Institute, Madison, Wis. (see ordering information on the back page).

LOADING NEW OPTIONS

University of Wisconsin Sea Grant Institute and the UW-Madison Center for Limnology

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User Support for the Generalized Fish Bioenergetics Model

■ *Bioenergetics Booter*

The purpose of this newsletter is to provide a communication link among users of the generalized fish bioenergetics model and to provide a conduit for feedback from users to help in future model development. Formal user support for the model by the UW Sea Grant Institute will continue for two years (January 1988 through January 1990). The Bioenergetics Booter will be published semiannually during that period.

The Bioenergetics Booter will include answers to questions regarding model operation and strategies, descriptions of new or innovative applications of the model, corrections to the model or its documentation, new information or parameters for modeling new species or life stages, comments and letters from users, and announcements of workshops and other modeling activities. Each issue will be an addendum to the model documentation that can be inserted directly into the three-ring binder provided with the original documentation.

This newsletter is sent to all registered bioenergetics model owners (i.e., everyone who purchased the model from UW Sea Grant and returned the registration form contained in the package). If you know of a model owner or other users who have not returned the registration form, please urge them to do so, or send their names and addresses to UW Sea Grant.

To make this effort a success, we need feedback from you, the users of our model. We welcome all questions, from specific details of operating the model to general modeling strategies and applicability. For example, the most common problem reported by users so far is answered in this issue (see "Most Common IBM Error: Defining Default Data Drive").

We also urge you to write us with any comments, suggestions, ideas, new data or new applications of the model for research, management or education. Please address your correspondence to Bioenergetics Booter, Advisory Services, UW Sea Grant Institute, 1800 University Avenue, Madison, WI 53705, USA.

■ *Training In Model Use: Bioenergetics Workshops*

The generalized fish bioenergetics model is a powerful and cost-effective tool for addressing questions of fish growth, production and consumption, but it requires some experience to use efficiently. One of the most effective ways to become proficient at using the model is to be instructed in its operation by an experienced user.

UW-Madison Center for Limnology personnel are available to conduct on-site hands-on modeling workshops for interested users. The objectives and length of a workshop can be tailored to the needs of any particular group, from a general introduction to bioenergetics concepts and model operation, to a detailed analysis of data and output for a specific research or management question.

The hosting institution is expected to provide all computer facilities and local arrangements for a workshop. We provide the instructors, instructional materials and expertise. The number of participants, computers and instructors is flexible, but for a hands-on workshop we have found that two people per computer and one instructor for every four people is optimal. We recommend a maximum of 16 participants for a hands-on workshop. We offer workshops on a cost basis, where the hosting institution pays travel costs and per-diem expenses for the required number of instructors. No consulting fees or honorariums are required (though some great food would go a long way toward making us happy!). A site visit prior to the workshop is necessary to finalize local arrangements and set up the objectives and data sets that will fulfill the workshop's goals.

Given these guidelines, a hands-on workshop for 12 people, for example, would require six computers, three instructors and enough money to pay round-trip air fare and daily expenses for four (three instructors plus the pre-planning trip).

If you are interested in scheduling a workshop, contact Barry Johnson, Center for Limnology, 680 N. Park St., Madison, WI 53706 (phone 608/262-3087). Our 1988 schedule is already becoming quite full.

Besides workshops, we will be offering a two-day course on bioenergetics modeling Sept. 10-11, 1988, as part of the American Fisheries Society meetings at Toronto, Canada. The course will cover the basic concepts of bioenergetics, model operation and modeling strategies, and is limited to 20 participants. Through an agreement with the American College Testing Service, the American Fisheries Society will grant course participants 1.5 continuing education credits. Participants will be asked to bring their own data and create the files necessary to address a question of concern to them. A registration fee of US$200 is required. A formal course announcement will appear in the American Fisheries Society publication "Fisheries" later this spring, but registered model users will receive a course announcement from the UW Sea Grant Institute in the near future. -*Barry Johnson, Center for Limnology*

Using the Bioenergetics Model in the Classroom

Bioenergetics modeling has a long history of use in research and management. Now, with the development of the generalized fish model, the educational potential of bioenergetics modeling can be better developed. Through modeling, students can explore and evaluate the effect of a variety of physiological and ecological variables on the dynamics of fish growth and consumption. Incorporating population sizes and mortality rates into the model allows investigation of the effects of different management actions on the production, consumption, and harvest of predators. Estimates of consumption can be translated into effects on prey population dynamics.

Energetics modeling can act as a surrogate for laboratory experimentation (a particularly attractive application, given current concerns for laboratory animal care). Alternatively, modeling can be used as a guide for developing logical hypotheses, which can then lead to critical and incisive experimental work. Typically, student lab experiments involve responses of fishes to acute or chronic stressors (e.g., temperature, nutrition,osmoregulation, etc.), and virtually any stressor can be translated into effects on growth, reproduction or mortality rates, which are the primary dependent variables of the energetics model. Incorporating published data into parameters used in modeling gives students the ability to develop and evaluate the equivalent of extensive experimentation.

At the University of Wisconsin, we have used the bioenergetics model as the focus of a four-week series of laboratory exercises in the Ecology of Fishes course. Students were introduced to bioenergetics concepts and the model through a class lecture and a demonstration. In laboratory sections, students were given a disk containing data files (entered previously by the instructor) for a single cohort of either a piscivore (walleye) or planktivore (yellow perch). The students worked in pairs and made an initial run of the model using these data sets. Output from this initial run represented the baseline conditions. Next, students were given a handout of specific energetics questions (appended), and each pair of students was assigned one question to answer. Finding an answer required modifying the data files and making an additional model run or two to compare to the baseline run. Each student was required to submit a report that included a description of the initial conditions for the model, the modifications needed to answer the question and their likely physiological and ecological significance, assumptions made in answering the question, and an analysis of the results of the modified runs (including graphs).

This procedure worked well for explaining the concepts of bioenergetics modeling and for developing both the technical and analytical skills necessary to use the model. Some initial effort is required on the part of the instructor to develop appropriate data files as well as clear and insightful questions. Having the students use previously entered data files allows them to immediately (and successfully) run the model and get some output, which keeps student interest levels high. Answering structured questions that require simple changes in the data files helps students learn the editing functions of the programs and allows them to evaluate the importance of specific parameters and inputs on model outcomes.

The student response to this approach was enthusiastic. They recognized the merits of substituting simulation studies for dead fish; of developing the logic required to translate experimental results into the integrated context of survival, growth and reproduction; and of being able to conduct the equivalent of many months or years of experimental work through a few hours of computer time. They also appreciated the familiarity with computer systems derived from the time spent applying and modifying the model. This exercise could be expanded to allow students to define and answer their own bioenergetics question. If you are an educator, we encourage you to try the model in your courses and to write to the Bioenergetics Booter regarding the specifics of your approach and your success and/or criticisms of the outcome. -- *Barry Johnson and Jim Kitchell, Center for Limnology.*

■ *Sample Questions Given to Students as Part of a Laboratory Exercise Using the Generalized Fish Bioenergetics Model*

Before receiving these questions, the students made initial runs of the model using standard data files (in this case, representing walleye and yellow perch in Lake Mendota, Wis.) and used the output from those runs as the baseline state. Following each question is a description of the changes needed in the model to answer the question (students did not get this information). P-value remains constant between runs unless specifically stated. Generally, only one additional model run is needed to answer each question. In all simulations, day 1 was April 1.

❶ This was a very warm summer in Madison. Assume that as a result hypolimnetic oxygen depletion occurred in Lake Mendota, and walleyes were forced to reside in an epilimnion that was two degrees warmer during the months of July, August and September. How are growth, total consumption and specific rates affected?

Model Changes Needed: In the temperature file, increase temperatures from July 1 through September 30 by 2 °C.

❷ Suppose that a power plant was built on Lake Mendota. Its thermal plume attracts perch in the winter, keeping them at 8°C from November 15 through March 31. For the remainder of the year, the perch leave the effluent and go about their usual business. How are total growth and consumption and their annual patterns different from those recorded before the plant went on line?

Model Changes Needed: In the temperature file, set temperature from Nov. 15 through March 31 to 8°C.

❸ Assume that forage fishes had a very poor year and that walleye were forced to eat 25% less fish and 25% more invertebrates from April through October. How would walleye growth and annual production be affected? How much does predatory pressure on invertebrates change?

Model Changes Needed: In the diet file, decrease the proportion of fish in the diet during April-October by 0.25 and increase invertebrates by 0.25. (Note: The caloric density of the fish must be different from invertebrates, or there will be no changes in growth and production between runs.) An alternative approach to this question is to assume growth remains constant and fit a new P-value using the modified diet file.

❹ Assume this was a poor year for forage production. As a result, walleyes had to double their searching activity in order to catch the same amount of prey. What effect does this have on growth, consumption and efficiency of food conversion?

Model Changes Needed: In the species file, double the respiration activity parameter (ACT).

❺ Assume this was an excellent year for forage production. As a result, Lake Mendota perch increased their feeding rate by 10% during the April-August period. How would this affect the annual totals and seasonal patterns of consumption and growth?

Model Changes Needed: Answering this question requires two model runs. In the first run, the P-value (in the species file) is increased by 10% and the model is run from April 1 through August 31. Then the P-value is reset to its original value, and the final weight on August 31 from the first run is entered into the species file as the beginning weight on September 1. The second run then covers September 1 through March 31. The sum of the results from the two runs provides the annual totals.

❻ Assume that the length limit for walleyes in Lake Mendota is reduced from 12 to 10 inches. The cohort containing fish of this size experiences an increase in daily harvest mortality of 0.001 from May 16 through October 15. What effect does this management action have on walleye population size and on consumption of walleye prey?

Model Changes Needed: In the species file, increase daily harvest mortality rates from May 16 through October 15 by 0.001.

❼ Many fishes exhibit seasonal changes in fat content and, therefore, in caloric density. Suppose that yellow perch in Lake Mendota cycle from 1,200 cal/g wet weight on January 1 to 900 cal/g on April 1 to 1,500 cal/g on October 1. How are patterns of growth and consumption and their annual totals different from the previous assumption of constant caloric density?

Model Changes Needed: In the predator caloric density (.PDC) file, change the value on day 1 (April 1) and day 365 (March 31) to 900, and add values of 1,200 for January 1 and 1,500 for October 1.

⑧ Suppose someone developed a new, transplantable gene that reduced the standard metabolism of any ectotherm by 15%. DNR hatchery managers bought a case and injected the brood stock from which they will get the walleyes to stock into Lake Mendota. How will these new fish feed and grow relative to the previously stocked, "unengineered" fish (i.e., do they offer any advantages over the old stock)? Will their effect on the forage base be different from the old stock?

Model Changes Needed: In the species file, reduce the intercept for the respiration function (RA) by 15%.

⑨ Assume that the next year class of perch is twice as large as the current year class. As a result, perch growth (i.e., their annual weight increment) is reduced by 50%. What is the net effect of this combination of increased year class size and growth compensation on rate of consumption (i.e., P-value), total consumption and production by this cohort?

Model Changes Needed: Answering this question is a bit complicated. First, subtract the starting weight from the ending weight of the standard cohort to determine its annual weight increment. Add half of that increment to the beginning weight to get the new ending weight for the larger cohort. Next, in the species file, enter the number of fish in the new cohort (twice the standard number) and new ending weight. Then run "P-fit" to get a new P-value, and enter that new value into the species file. The file is now complete, and you can run the model to get new output.

Modeling Growth / Consumption Dynamics of Young Fish

There has been much interest recently in modeling growth, consumption and production dynamics of larval and juvenile fish. Recruitment studies have frequently identified positive correlations between high growth rates and year class success. For some species, the majority of a cohort's consumption and production throughout its lifespan is within the first year or two of life. Thus, a bioenergetics modeling approach to growth, consumption and production of larval and juvenile fish would be useful.

Most physiological work has been conducted on adult fish. The species parameters listed in appendices 3, 4 and 5 in the model documentation are generally derived from adults. Using these data to model larval and juvenile fish results in back-extrapolation of 1-3 orders of magnitude in weight from the adult relationships. Attempts at applying these models to early life history stages have met with limited success. When the yellow perch model was applied to data from a field study in which growth and consumption were determined for young-of-year (YOY) perch with wet weights of 0.01-2.00 g, the model underestimated consumption rates and overestimated conversion efficiencies (Post 1987). When the model was applied to YOY yellow perch (range 0.01-10.0 g) from Lake Mendota, fish consistently lost weight even when P-values were set to nearly 2. Hewett and Stewart (in prep.) found evidence that larval alewife might have different metabolic rates than older fish, which would require higher consumption rates as well. These results indicate that the energetics parameters for adult fish do not adequately describe the growth of larvae and juveniles. There are a variety of reasons why these results may have occurred. In the above situations, the researchers took two different approaches (1) changing parameters for metabolism and consumption and (2) reducing caloric densities to develop reasonable models for very young fish.

Post (1987) suggested that both metabolic and consumption rates for very small perch may be higher than predicted by extrapolating weight-dependent relationships for adults. Laboratory experiments by Mills and Forney (1981) on YOY yellow perch support this contention regarding metabolism. Post modified the model by replacing the intercept for maximum standard respiration (model variable RA, originally set to 0.0108: see documentation Appendix 4), with an intercept for maximum feeding respiration (new RA = 0.0293) determined from Mills and Forney's (1981) data. To address consumption by young fish, Post (1987) ran a series of field enclosure experiments with *ad libitum* natural prey to determine maximum feeding rates. He then modified the intercept for the maximum

TABLE 1

Caloric Densities and Dry Weight as a Percentage of Wet Weight for Various Organisms Reported in the Literature

The bioenergetics model uses wet weight caloric density (cal/g ww).
Multiplying the percentage dry weight by dry weight caloric density (cal/g dw)
will provide an estimate of caloric density

Organism	% Dry Weight	cal/g dw	cal/g ww	Seasonal or ontogenetic effects considered ?
Rotifers	10[a]			
Cladocerans	10–12[b,c]	5,451–5,463[d,e,f]		yes[g]
Copepods	11-14[a,b,h]	4,124–6,278[f,h]		yes[h]
Leptodora	4[e]	5,182–6,150[e]		yes[e]
Mysids	16[a]		1,030[e]	
Amphipods	24–28[e]	4,072[e]	1,058[e]	
Diptera larvae	5–12[c,e]	4,936[e]		yes[c]
Yellow Perch	24–28[i]	4,362–5,198[i]	1,075–1,410[i]	yes[i]
Juveniles	12[j]	4,946[k]		yes[k]
Alewife	20-35[l]		1,200–2,270[l]	yes[l,m]
larvae			800[n]	
Salmonids		3,598[p]	1,256–2,868[p]	yes[p]

a–Downing and Rigler (1984)
b–Dumont et al. (1975)
c–Lueke (in prep.)
d–Lei and Armitage (1980)
e–Cummins and Wuycheck (1971)
f–Vijverberg and Frank (1976)
g–Snow (1972)
h–Schindler et al. (1975)
i–Craig (1977)
j–derived from infomation in Lin (1975) and Mills and Forney (1981)
k–Mills and Forney (1981)
l–Stewart and Binkowski (1986)
m–Flath and Diana (1985)
n–Hewett and Stewart (in prep.)
p–cited in Stewart et al. (1983)

consumption function (new CA = 0.52) and slope for maximum consumption (new CB = -0.41) to fit the empirically determined growth patterns in the enclosures. The modified bioenergetics model, incorporating higher metabolic and maximum consumption rates, adequately represented the observed growth and consumption dynamics of larval and juvenile yellow perch in the field and resulted in consumption estimates 2-3 times greater than values estimated using adult parameters (Post 1987).

Hewett and Stewart (in prep.) modeled alewife from hatching through the first growing season. They used two different slopes for the respiration function (RB) during the larval period (hatching to day 40); one was the normal adult value as listed in documentation Appendix 4, and the other was a higher value based on data for Pacific herring (Eldridge et al. 1977). The higher respiration rate also required an increase in the slope of the consumption curve (CB) to a value slightly higher than RB. These two respiration models were chosen to represent bounds on a range of metabolic rates for larval clupeids based on literature sources. Over the 40-day larval period, the higher metabolic rate resulted in a 15%-20% increase in consumption required to attain any specific weight increment.

In addition to differences in physiology, the caloric density of juvenile fishes may be lower than for adults (e.g., Flath and Diana 1985). For yellow perch, wet-weight caloric density of juveniles is about 50% of values for adults (Table 1). Post (1987) assumed that caloric density of perch in his model was equivalent to their food source. Because most of their diet was zooplankton, this assumption resulted in a modeled caloric density of about 600 cal/g wet weight (Table 1). In the Lake Mendota perch study mentioned above where P-values could not be fitted, caloric density was initially set at 1,200 cal/g. When density was lowered to 800, the P-fit algorithm yielded a value of 0.73.

Hewett and Stewart (in prep.) used a seasonal data file to model two patterns of increasing caloric density of larval alewife. In the first, they set caloric density at hatching to 800 cal/g, then increased it to 1,000 cal/g by day 40. In the second, caloric density was constant at 600 cal/g for the entire 40 days. These simulations were chosen to represent a range of caloric densities suggested by the literature. Over the 40-day period, using the higher caloric values (and either of the previously described metabolic functions) resulted in an increase in consumption of about 12%.

There are obviously many unanswered questions about the bioenergetics of larval and juvenile fish. We need some good lab and field studies of the physiology and energetic dynamics of very young fish to determine the best methods and parameters for modeling the processes involved. Until such time, parameter modifications as described above can produce workable models and reasonably accurate output. Such models can be very useful for a wide variety of applications, especially those involving comparisons between model runs. --*John Post, Center for Limnology*

Modeling Caloric Density Change

As described in the previous section, caloric density of both predator and prey can have large effects on estimates of consumption, production, conversion efficiency and P-values. In addition to differences between juvenile and adult fish, seasonal and size-related variation in caloric density of older fish has been observed (e.g., Craig 1977; Stewart et al. 1983).

The importance of modeling changes in caloric density will depend on the species involved and the question asked. If you are primarily interested in annual totals, using a constant caloric density that approximates the average over the year will provide fairly accurate results. (In addition, estimates of production are likely more affected by errors in population size and mortality rates than in caloric density.) If you are interested in seasonal patterns, then including changes in caloric density may be important. For example, Stewart and Binkowski (1986) found that inclusion of the seasonal cycle of caloric content in alewives had a relatively small effect on annual estimates of production and consumption (less than 10%) but a large effect on seasonal estimates.

Given the importance of caloric densities and the fact that they are seldom collected in routine fish surveys, we have compiled a list of caloric densities reported in the literature for a variety of organisms (Table 1). This list is not exhaustive and is best used as a general guideline for estimating caloric density and as an introduction to the literature on the subject. Some of the variation in reported values results from the different methodologies used by researchers. You should consult the specific references for these details. Reviews of energy content and methodology are contained in Cummins and Wuycheck (1971), Schindler et al. (1971), Bottrell et al. (1976), Vijverberg and Frank (1976) and Downing and Rigler (1984).

Table 1 lists caloric density on both a dry and wet weight basis. The bioenergetics model uses caloric density per gram wet weight (i.e., as the organism exists in nature). Most studies report caloric density on a dry weight basis. Conversion from dry to wet weight basis requires an estimate of the percentage of water or wet weight to dry weight ratios. Unfortunately, these are seldom reported. Wet to dry weight ratios can be valuable for investigating seasonal or ontogenetic changes in energy density in fish because much of the variation in wet weight caloric density over time results from changes in the water content of the organism, which is inversely related to lipid content (Craig 1977).

Estimation of the wet weight caloric density for zooplankton and other small aquatic invertebrates is especially problematic because the methodology for estimating wet weight has not been clearly defined. In a practical sense, it is difficult to remove water from the surface of the carapace, legs and swimming apendages without also reducing water content of the organism. From the data available, we can suggest some guidelines for a variety of organisms. In general, dry weight ranges from 10%-15% of wet weight for zooplankton, 10%-25% for larger aquatic invertebrates, and 25%-30% for mature fish. Dry weight caloric density ranges from 4,000-6,000 cal/g for most organisms.

If you are unsure of how important caloric density is in your particular application, you can always make additional model runs with caloric density set to different values and examine the changes in output (sort of a small sensitivity analysis). The range of values reported in the literature (Table 1) can help provide bounds for your estimates. As in all cases of specific changes in model assumptions, the most important issue is whether this modification causes you to draw different conclusions with regard to the original question. Determining caloric density of fish requires the use of bomb calorimetry (Cummins and Wuycheck 1971). Estimating wet to dry weight ratios for fish and prey from a specific study area is not difficult and may explain much of the seasonal dynamics of caloric content of organisms. Dry weight is determined by drying whole fish at 60°C until the weight no longer changes (this requires a few days for small fish, weeks for large fish). We encourage researchers to measure and report dry weights as well as wet weights. --*Chris Luecke, Center for Limnology*

Technical Questions/Corrections

■ *Most Common IBM Error: Defining Default Data Drive*

So, you got a copy of the model and want to try a run using the files on the Sample Data Disk. You select the "Bioenergetics Model" option from the menu and correctly type in all the requested information, but the first time the program tries to access a data file, you get a cryptic message that says, "`ERROR 1 while opening [drive]:[filename]`".

You have just fallen prey to the most common problem encountered by users of the IBM version of the model: forgetting to define the default data drive. When you first execute the model, the default data drive is set to the currently selected drive, and the program will look there for data. If your data files are somewhere else, you will get the message above. (You will also get this message if you misspell the file name.)

The solution is to go to the main menu and use option `H) change default data drive` to tell the computer where the data files will be. On an IBM, the files can be in any drive, including a hard drive. If you exit the model and then re-enter it, you will need to define the data drive again.

None of the above applies to the Apple II version, because data files must always reside in Volume 5 (Drive 2) on Apple systems.

■ *Comparisons of Run Speeds and Use of Math Accelerators*

Repetitive runs of the bioenergetics model can be time consuming, but the time required is largely dependent on the hardware used. Computers come with different processors that run at different speeds, which are measured in megahertz (MHz). Quite simply, faster processors mean faster run times. Most computers can also be equipped with accelerators. These are add-on cards or chips (coprocessors) that speed up math calculations (i.e., the number crunching that is the guts of the bioenergetics model).

We tested the time required to run a 365-day simulation on different microcomputers with and without math coprocessors. The tests were run using the files for yellow perch, cohort 2, as contained on the Sample Data Disk provided with the model. Output was saved only once, at the end of day 365. The test results (Table 2) confirm that using a computer with a faster processor does improve run time. However, you are likely to get dramatic decreases in run time (3x to 6x) relatively cheaply by adding a coprocessor to your present system. In all cases, if output were saved to a disk periodically during the run, speeds would increase by some amount, depending on disk speed and access time (hard drives being fastest), and the difference between run times for regular and accelerated versions would be reduced. The ease with which you can make use of an accelerated machine for modeling will depend on which model version (Apple or IBM) you are using. The Apple version is written in Apple Pascal 1.2 and should run as-is with all accelerator cards (at least to our knowledge—ask before putting money down).

For an IBM system, it's not quite that simple. The IBM version is written in TURBO Pascal 3.0, and, as received, it will run on machines with a coprocessor but will not recognize the coprocessor. To make use of a coprocessor, you must recompile the program (file MENU.PAS) using the TURBO-87 compiler (called TURBO-87.COM or TURBO87.COM on the TURBO Pascal system disk). This compiler is an option when you buy TURBO Pascal, thus you may not have it on your disk. If not, find someone who does. See the instructions for using this compiler in the TURBO Pascal reference manual.

Be aware that a program compiled using TURBO-87 will *not* run on a machine that does not have a coprocessor installed. Once you have recompiled the program, you still have some work to do. Unfortunately, because of differences in file structure, data files created with the regular version of the model (e.g., those on the Sample Data Disk) cannot be read by the TURBO-87 version, and vice versa.

You must create new data files using the editor in the TURBO-87 version. We are working on methods for translating files but have not yet completed that work; for now, you will have to decide whether the trade-offs between decreased run times, the inability to use the model on unaccelerated machines, or creating new files make it worthwhile for you to use the TURBO-87 version.

TABLE 2

Time Required for a 365–Day Run of the Generalized Bioenergetics Model[a] with Different Computer Systems and Processors

The standard run was conducted using yellow perch cohort 2 from the data files on the Sample Data Disk included with the model. Output interval was 365 days and data were not saved for the first and last day of the run. (See text for tradeoffs involved in using a coprocessor with an IBM system.)

Computer System	Processor	Speed	Time for a 365–Day Run (minutes:seconds)		
			Normal	Accelerated	Coprocessor
Apple IIe	6802	1 MHz	7:21	2:07	TransWarp[b]
IBM XT (& 4.77 MHz clones)	8088	4.77 MHz	2:15	0:23	8087
IBM PS/2 Mod.30	8086	8 MHz	0:55		
NEC MultiSpeed (a laptop)	NEC V-30	9.54 MHz	0:55		
IBM AT (& 10 MHz clones)	80286	10 MHz	0:35	0:10–0:14	80287
IBM PS/2 Mod. 50	80286	10 MHz	0:31	0:07	80287
Zenith Z–386	80386	16 MHz	0:18		

a– Hewett and Johnson (1987)

b– Registered trademark of Applied Engineering

■ *Documentation Errata: Modeling Constant Caloric Density*

On page 22, paragraph 1, in the model documentation, we explain how to model caloric density as a function of fish weight (predator caloric density model 2). The function used is a linear regression and thus requires parameters for slope ("Beta") and intercept ("Alpha").

In the paragraph noted, we state that "Caloric density can be modeled as a constant if 'β' is set to zero, and 'α' is set to the desired caloric density." That statement is wrong: Setting Beta to zero results in a "divide by zero" error, and the program will not run.

To model constant caloric density, you must use a predator caloric density (.PDC) file with the required caloric density entered for day 1 and day 365 (see documentation section on "Cal, Temp & Diet File Utilities," page 10, for how to create this file).

■ *Clarification on Defining Mortality Periods*

When editing the mortality parameters contained in the species (.BIO) files, you see a screen which allows you to define up to 12 periods with different mortality rates (natural and/or harvest mortality). On this screen, the 12 periods are called "months," but mortality does not have to be defined on a monthly basis. Mortality periods can cover any period of time. You define these periods by entering the starting day for each period on this screen. Mortality rate remains constant during any period, thus if annual mortality is constant in the population you are modeling, you need only enter that rate for day 1. If no other mortality periods are defined, that rate will apply to the entire year.

■ *A Caution on Saving Data for Multiple Cohorts*

When editing a species (.BIO) file, if you edit only one cohort, you have the option of saving that data for other cohorts. Be aware that using this feature will save all the data for the cohort you just edited to the new cohort number you enter.

For example, if you edit the mortality parameters in cohort 1 and save to cohort 2, cohort 2 will be identical to cohort 1 including weights, dates, P-values, mortality parameters, etc. If you wish to change only the mortality parameters (or any other subset of the cohort data), you must edit each cohort individually. *--Cliff Kraft and Barry Johnson, Center for Limnology*

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The *Bioenergetics Booter* is provided free of charge to all registered users of the Generalized Fish Bioenergetics Model. The model, which includes manual, program and data diskettes and the Bioenergetics Booter newsletters, is available for $20.00 (postage and handling included). When ordering please be sure to specify whether you want the IBM/compatible or Apple II version of the model. Make checks or money orders payable to "UW Sea Grant Institute." Payment must be made in U.S. currency and drawn on a U.S. bank. Order from:

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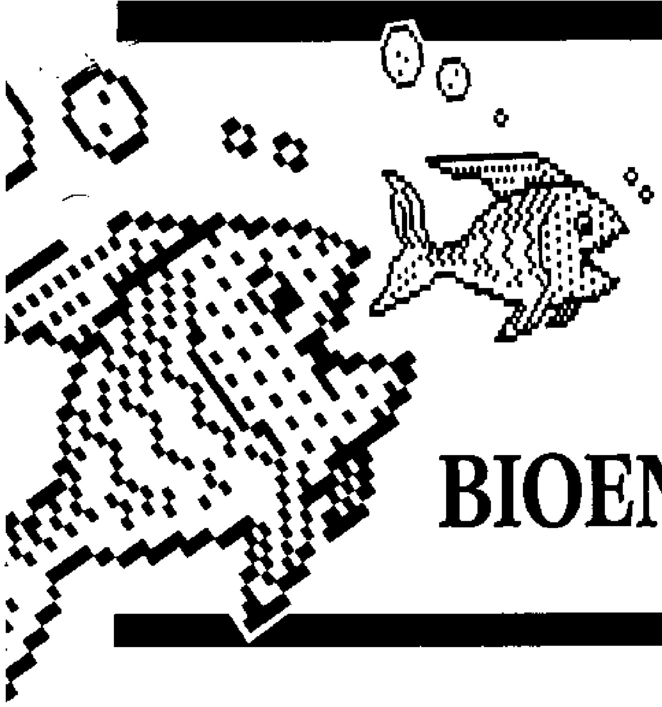

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Providing program information and tips for
A Generalized Bioenergetics Model
of Fish Growth for Microcomputers

BIOENERGETICS BOOTER

WELCOME to the second issue of Bioenergetics Booter, part of the support system provided by the University of Wisconsin Sea Grant Institute and the UW–Madison Center for Limnology for users of the generalized fish bioenergetics model. The support system for model users has two main components: the newsletter and workshops. This second issue of Bioenergetics Booter contains an update on recent modeling activities, a Julian date conversion table, information on how to run P–fits without a printer, some model corrections and a feedback page.

Your feedback will help improve our user support system. Please complete the feedback form and return it to us at your earliest convenience. If you have not received the first issue of the Booter (published in March 1988), contact the University of Wisconsin Sea Grant Institute at the address on the last page of the issue. Be sure to add this issue to the back of your model documentation.

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University of Wisconsin Sea Grant Institute and the UW–Madison Center for Limnology

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Modeling and Workshop Activities

■ *Summary of Workshop in Burlington, Vermont*

We conducted a two–day bioenergetics workshop in April 1988 to familiarize participants with fish bioenergetics and model operation and to devise strategies for studying the effects of lamprey control in Lake Champlain. The workshop was sponsored by the Vermont Department of Fish & Wildlife and the University of Vermont. Twenty-four biologists and researchers from the Vermont DFW, the University of Vermont, the New York Department of Environmental Conservation and the U.S. Fish & Wildlife Service participated.

Participants developed a food web diagram of Lake Champlain's fish community and used it to ask questions about the effects of a lamprey control program on the system. Then, they used data from Lake Champlain to develop data files and model runs to estimate consumption by sea lamprey, lake trout and Atlantic salmon populations before and after lamprey control, and increased predation pressure on smelt as a consequence of lamprey control. Participants also used the model to study walleye growth in Lake Champlain and the energetics of trout in Vermont's inland waters and New York's Finger Lakes.

The group was eager and energetic (pun intended), and response to the workshop was quite positive. Participants identified a number of topics—including predator–prey interactions in lakes Champlain and Ontario, production estimates, causes of slow walleye growth, hatchery applications, and directing field sampling—where they hoped to use energetics modeling in the future. The instructors learned a lot themselves and are eager for the next workshop (see below).—*Barry Johnson, Center for Limnology*

■ *Upcoming Workshop at American Fisheries Society Meetings in Toronto, Ontario*

We will conduct a bioenergetics workshop Sept. 10–11, 1988, at the Royal York Hotel in Toronto immediately prior to the American Fisheries Society meetings there. The workshop is offered through AFS as a Continuing Education Course carrying 1.5 credits. We will discuss the basics of fish bioenergetics, data requirements and strategies for model application, and then participants will create data files, run the model and analyze the output on IBM microcomputers. The registration fee is US$200. For more information, contact Cathy Catanzaro at UW Sea Grant Advisory Services, phone (608) 262-0645.

■ *A New Predator-Prey Bioenergetics Model*

A predator–prey version of the bioenergetics model is being developed by Dr. Jim Breck of the Institute for Fisheries Research, Michigan Department of Natural Resources, Ann Arbor. The new version of the model will run multiple species concurrently to allow prey and predators to interact dynamically. In the new version, the daily ration of piscivores (e.g., walleye or large-mouth bass) can vary with the sizes and abundance of available prey (e.g., bluegill or sunfish). The new version also will implement compensatory growth of bluegills or other forage fish, allowing their ration to increase as predation reduces bluegill density. This work—part of efforts to develop a fish community model in the Michigan DNR's inland lakes program—will help better manage stunted bluegill populations. A more complete description of the predator-prey model, some preliminary results and a revised set of energetics parameters for bluegill will appear in a future issue of the Bioenergetics Booter.—*Jim Breck, Institute for Fisheries Research*

Converting Calendar Dates to Model Days

One of the more confusing procedures in the bioenergetics model involves specifying the appropriate day number for use in seasonal files and for the beginning and ending days of the simulation. Field data are usually available on a calendar day basis, but they must be converted to a Julian day basis to be entered into the model. To help you make this conversion, we developed a table that lets you quickly convert calendar dates to Julian-type model days when your model year begins on the first day of a month (Table 3).

For example, your modeling year starts March 1, and you need the model day for October 15. Go across the top of the table to the column for March 1 and down to the row for October. Add the date in October (i.e., 15) to the number at the intersection of the column and row in the table below (i.e., 214). The model day for October 15 in a modeling year that started March 1 is 214 + 15 = 229. —*Barry Johnson, Center for Limnology*

TABLE 3

Converting Calendar Dates to Day Number for the Bioenergetics Model

To convert from a calendar day to a model day, add the date of the month to the number at the intersection of the row that corresponds to the month and the column that corresponds to the start of your modeling year.

For model year starting on . . .

For calander dates during month of . . .	*Jan 1*	*Feb 1*	*Mar 1*	*Apr 1*	*May 1*	*Jun 1*	*Jul 1*	*Aug 1*	*Sep 1*	*Oct 1*	*Nov 1*	*Dec 1*
Jan	0	334	306	275	245	214	184	153	122	92	61	31
Feb	31	0	337	306	276	245	215	184	153	123	92	62
Mar	59	28	0	334	304	273	243	212	182	151	121	96
Apr	90	59	31	0	334	304	274	243	212	182	151	121
May	120	89	61	30	0	334	304	273	242	212	181	151
Jun	151	120	92	61	31	0	335	304	273	243	212	182
Jul	181	150	122	91	61	30	0	334	303	273	242	212
Aug	212	181	153	122	92	61	31	0	334	304	273	243
Sep	243	212	184	153	123	92	62	31	0	335	304	274
Oct	273	242	214	183	153	122	92	61	30	0	334	304
Nov	304	273	245	214	184	153	123	92	61	31	0	335
Dec	334	303	275	244	214	183	153	122	91	61	30	0

Technical Changes and Corrections

■ *Changing the Model to Write P–Fit Data to a Disk File*

When running a P–fit with the bioenergetics model, output is automatically sent to the printer. However, with the proliferation of "lap–top" computers and networks where several computers are connected to one printer, it is not always convenient to print out the P–fit values immediately. By making a small change in the program, you can save P–fit information to a file on a disk without having a printer hooked up to your computer and print this file later to the screen or a printer to see the results of the P–fit run.

To make this program change, you must first add a line to the program code and then recompile the model, so you will need access to the appropriate Pascal language system for your version of the model. If you are not familiar with editing or compiling within Pascal, find someone who is. And remember, always work with backup copies!

IBM Version of the Model: To make this change you will need a copy of Turbo Pascal version 3.0. The change must be made in the file called MODEL.PAS. Go to line 336 of this file (you will be in "Procedure Menu"). Line 336 reads:

```
IF RUNCHOICE = 'A' THEN ANSWER := 'P'
```

You must replace this line with two lines that read:

```
IF RUNCHOICE = 'A' THEN

ANSWER := GETCHAR(['D','P'],'Print to D)isk
   P)rinter -> ',0,5)
```

Save the modified code back into the file called MODEL.PAS. Finally, recompile the entire bioenergetics model by compiling the file named MENU.PAS. It will take several minutes to compile the program, depending on the speed of your computer. After you incorporate this program change, every time you run a P–fit you will have the option of writing the results either to a disk file or to the printer. The P–fit procedure itself will still work as before. If you choose the option of writing to the disk, the data will be saved to a file labeled PFITDAT.DAT on the default data disk. You can then read or print out this file at your convenience.

Apple II Version: The same change in model code listed above is required on the Apple II version. You will need the Apple Pascal language system to modify and recompile the program. The program code is in "Procedure Menu" in a file called MDINITIAL.TEXT on your Sample Data Disk. Make the change as described above and save the modified code back into MDINITIAL.TEXT. Recompile the model segment of the programs by compiling the file named MODEL.TEXT. You will need to have MODEL.TEXT and the other 5 text files, which begin with "MD," on the same disk when compiling. This will produce a code file called MODEL.CODE, which must be transferred to your program disk.

The results of this modification will closely resemble the IBM version. When running a P–fit, you will be asked if you wish to send output to the printer or disk. If you choose disk, the data will be saved in a file labeled PFITDATA.TEXT on the data disk.

You can print this file by using main menu option "F) File/Disk Utilities" and then option "5) List/Edit Directory" on the submenu. However, this procedure will only print to a printer, not to the screen. As a result, you will still need a printer with your system. You also can list the file through the Apple Pascal language system to either the screen or a printer.
—*Cliff Kraft, University of Wisconsin Sea Grant Institute*

■ *Documentation Errata*

Page 18: The first equation under "Consumption Model 2" is missing a right parenthesis. Currently it reads:

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

It should read:

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

Page 19: Under "Respiration Model 1" the temperature inequalities in brackets are reversed. Currently they read:

$\{\text{If } T > T_L\}$ and $\{\text{If } T \leq T_L\}$.

The inequalities in these two expressions should be switched.

Page 20: The first equation under "Respiration Model 2" is missing an exponent. Currently it reads:

$$F(T) = V * e^{(X * (1-V))}.$$

It should read:

$$F(T) = V^{X} * e^{(X * (1-V))}.$$

Page 35: In Appendix 4, the RA parameter for sea lamprey is incorrect. The RA for Sea Lamprey was listed as 0.0324; the correct value is 0.00397.

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Providing program information and tips for
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BIOENERGETICS BOOTER

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This work was funded by the University of Wisconsin Sea Grant Institute under grants from the National Sea Grant College Program, National Oceanic & Atmospheric Administration, U.S. Department of Commerce, and from the State of Wisconsin. Federal Grant No. NA84AA-D-00065, Projects R/LR-29, R/GB-24, A/AS-1 and A/AS-2.

Modeling and Workshop Activities

■ *Symposium on Fish Bioenergetics at AFS Meetings*

A half-day symposium on fish bioenergetics models entitled "A Critical Examination of Bioenergetics Models and Their Uses" will be held at the American Fisheries Society meeting September 4-8, 1989, in Anchorage, Alaska.

Organized by Mark Bevelhimer, Oak Ridge National Laboratories, and David Wahl, Illinois Natural History Survey, the purpose of the symposium is to look critically and constructively at the parameters and uses of fish bioenergetics models.

The symposium will have three sections, covering model parameterization, predictive capabilities (predicted vs. observed), and considerations in applying these models.

This should be a great opportunity to learn about the state of the art in fish energetics modeling and to meet and talk with a group of current practitioners. Check future issues of the AFS publication, *Fisheries,* for more information on the meeting and the symposium.
— *Barry Johnson, Center for Limnology*

Bibliography Update

Research papers on bioenergetics modeling produced since the model documentation was published include:

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Cuenco, M.L.; R.R. Stickney and W.E. Grant. 1985. Fish bioenergetics and growth in aquaculture ponds: I. Individual fish model development. *Ecol. Model.* 27(1985):169-190.

Cuenco, M.L.; R.R. Stickney and W.E. Grant. 1985. Fish bioenergetics and growth in aquaculture ponds: II. Effects of interactions among size, temperature, dissolved oxygen, unionized ammonia and food on growth of individual fish. *Ecol. Model.* 27(1985): 191-206.

Cuenco, M.L.; R.R. Stickney and W.E. Grant. 1985. Fish bioenergetics and growth in aquaculture ponds: III. Effects of intraspecific competition, stocking rate, stocking size and feeding rate on fish productivity. *Ecol. Model.* 28(1985):73-95.

Hewett, S.W., and D.J. Stewart. (submitted). Zooplanktivory by alewife in Lake Michigan: ontogenetic, seasonal and historical patterns. *Trans. Amer. Fish. Soc.*

Hurley, D.A. 1986. Growth, diet, and food consumption of walleye (*Stizostedion vitreum vitreum*): an application of bioenergetics modeling to the Bay of Quinte, Lake Ontario, population. In: *Project Quinte: point-source phosphorous control and ecosystem response in the Bay of Quinte, Lake Ontario,* C.K. Minns, D.A. Hurley and K.H. Nicholls, eds., pp. 224-236. Can. Spec. Publ. Fish. Aquat. Sci. 86. 270 pp.

Kitchell, J.F., and L.B. Crowder. 1986. Predator-prey interactions in Lake Michigan: model predictions and recent dynamics. *Environ. Biol. Fish.* 16(1-3):205-211.

Kitchell, J.F., and S.W. Hewett. 1987. Forecasting forage demand and yield of sterile chinook salmon (*Onchorynchus tshawytscha*) in Lake Michigan. *Can. J. Fish. Aquat. Sci.* 44(Suppl. 2):384-389.

Lyons, J., and J.J. Magnuson. 1987. Effects of walleye predation on the population dynamics of small littoral-zone fishes in a northern Wisconsin lake. *Trans. Amer. Fish. Soc.* 116:29-39.

Post, J.R. (submitted). Metabolic allometry of larval and juvenile yellow perch: *in situ* estimates and bioenergetic models. *Can. J. Fish. Aquat. Sci.*

Ridgeway, M.; D.A. Hurley and K.A. Scott. (in press). The impacts of winter temperatures and predation on the abundance of alewife (*Alosa pseudoharengus*) in the Bay of Quinte, Lake Ontario. *J. Grt. Lakes Res.*

Rudstam, L.G. 1988. "Patterns of zooplanktivory in a coastal area of the northern Baltic proper." Ph.D. thesis, Dept. of Zool. and Asko Laboratory, University of Stockholm, Sweden. (This thesis contains the next 3 papers on energetics modeling.)

Rudstam, L.G. (in press). *Exploring the seasonal dynamics of herring predation in the Baltic Sea: applications of a bioenergetics model of fish growth.* Kieler Meeresforsch., Sonderh. (Also in Rudstam 1988.)

Rudstam, L.G. (submitted). A bioenergetic model for *Mysis* growth and consumption applied to a Baltic population of *Mysis mixta. J. Plankton Res.* (Also in Rudstam 1988.)

Rudstam, L.G.; S. Hansson, S. Johansson and U. Larsson. (manuscript). "Seasonal dynamics of zooplanktivory along a nutrient gradient in the northern Baltic proper." (Also in Rudstam 1988.)

Shuter, B.J., and J.R. Post. (submitted). Implications of climate change for fish whose northern distributional limit is shaped by winter starvation. *Trans. Am. Fish. Soc.*

Technical Changes and Corrections

■ *DOS Incompatibility on IBM Model Versions*

If you received an IBM version of the energetics model recently but couldn't read the disk onto your system, the problem may be DOS incompatibility.

Demand for the IBM version of the model outstripped our initial supply, and we made additional copies of the model with MS-DOS 3.3. We later discovered that these copies are not compatible with and cannot be read by machines using 3.2 or earlier versions of DOS. We have recopied these disks in DOS 3.2, but some of the DOS 3.3 copies were sent out in the interim. If you received such a disk, please return it to us for a replacement disk in the earlier version of IBM DOS.

In the meantime, you can correct this problem by finding an IBM or clone with the DOS 3.3, copying the model files onto the hard disk of that machine and then copying from the hard disk back onto floppies. In most cases, these copies will be readable by other machines using earlier DOS versions.—*Barry Johnson, Center for Limnology*

■ *Errata*

Page 36: In Appendix 5, the cutoff weight for switching between energy density equations in the lake trout model (parameter "Cutoff") is currently listed as 1,442 g; the correct value is 1,472 g.

Page 53: Table 1 in issue 1 of the Bioenergetics Booter lists the caloric density for salmonids as 3,978 cal/g dry weight. This value should be replaced with a range of 6,123 to 7,092 cal/g dry weight. Also, values of 28 to 38 for percentage dry weight of salmonids can be added to the table. These new numbers come from D.V. Rottiers and R.M. Tucker, 1982, Proximate composition and caloric content of eight Lake Michigan fishes, *U.S. Fish Wildl. Serv. Tech. Paper 108* (8 pp.).

Page 63: Under "Documentation Errata" in issue 2 of the Bioenergetics Booter, we listed a correction to the first equation in "Consumption Model 2" on page 18 in the model documentation. The correction contained a typographical error. The equation should read:

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

Page 63: Under "Documentation Errata" in issue 2 of the Bioenergetics Booter, we listed a correction for the temperature inequalities in "Respiration Model 1" on page 19 in the model documentation. Ignore that correction: Those inequalities were correct as originally published. Swimming speed is modeled as a function of both fish weight and temperature below a critical temperature (T_L), and as a function of weight only above the critical temperature.

The Bioenergetics Booter is provided free of charge to all registered users of *A Generalized Bioenergetics Model of Fish Growth for Microcomputers*. The model package—which includes manual, program and data diskettes, and all issues of the Bioenergetics Booter to date—is available for $20.00, including postage and handling.

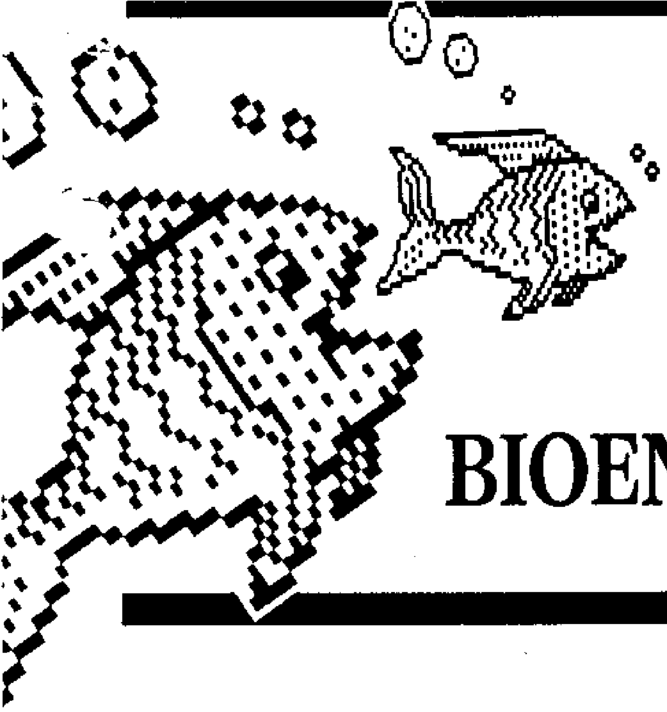
When ordering, please be sure to specify whether you want the IBM/compatible or Apple II version of the model. Make checks or money orders payable to "UW Sea Grant Institute." Payment must be made in U.S. currency drawn on a U.S. bank. Order from:

Communications Office
UW Sea Grant Institute
1800 University Avenue
Madison, WI 53705 USA

Phone (608) 263-3259

We welcome your questions, comments, suggestions, ideas, new data or new applications of the model for research, management or education. Please address your correspondence to:

Bioenergetics Booter
UW Sea Grant Institute
1800 University Avenue
Madison, WI 53705 USA



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Providing program information and tips for
A Generalized Bioenergetics Model
of Fish Growth for Microcomputers

BIOENERGETICS BOOTER

WELCOME to the fourth and final issue of the Bioenergetics Booter, part of the user support provided by the University of Wisconsin Sea Grant Institute and UW-Madison Center for Limnology for owners of *A Generalized Bioenergetics Model of Fish Growth for Microcomputers*. This issue announces the development of a new, revised version of the model, which will be available in 1990. Though this completes the Bioenergetics Booter series, UW Sea Grant will continue to support model users through on-site workshops and informal consultation. See the "User Workshops" section for more information.

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University of Wisconsin Sea Grant Institute and the UW-Madison Center for Limnology

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This work was funded by the University of Wisconsin Sea Grant Institute under grants from the National Sea Grant College Program, National Oceanic & Atmospheric Administration, U.S. Department of Commerce, and from the State of Wisconsin. Federal Grant No. NA84AA-D-00065, Projects R/LR-29, R/GB-24, A/AS-1 and A/AS-2.

New Version of Bioenergetics Model

Since the generalized bioenergetics model was first introduced in June 1987, we have received considerable feedback on how to improve the model from users, primarily at our training workshops and from individual consultations. Based on this feedback and our own experiences, we are currently revising the IBM version of the model. We expect to have this revised and, we hope, much improved version available in early 1990.

The revisions being made to the IBM version will make it much easier to enter data, run the model and evaluate output. These revisions will include:

- A friendlier user interface, with highlighted menu options, windows for file choices, simplified data entry and a greater selection of default values.
- Simpler ways of structuring model runs.
- A graphics package offering plotting, printing and the ability to store graphs in files.
- Seven additional variables in the output file, including total consumption over all prey items and number & weight of fish harvested.
- The ability to model a constant ration as percentage of body weight.
- The ability to use a math coprocessor with the model.

The basic energy budgeting process—which is the primary function of the model—will remain essentially unchanged.

The model documentation will be revised accordingly and will include a new tutorial chapter with a keystroke appendix to guide users through a sample model run. The new documentation will also feature updated references and species parameters, including some new species. As with the original model, you will also receive the program code files for changing and customizing the programs to your applications.

The Apple II version of the model is not being revised due to low demand. To date, UW Sea Grant has sold only 51 copies of the Apple II version vs. nearly 350 copies of the IBM version. Though we have been asked and would like to produce a version of the model for Apple Macintosh computers and a "windows"-compatible IBM version as well, we do not plan to do so at this time. If we do, registered users will receive an announcement.

The new IBM version will be distributed free of charge to all registered users of the original version of the model, including all users of the Apple II version (i.e., everyone who sent in the registration form enclosed with the model documentation). The model package will include a complete copy of the revised manual and new program and data disks.

Unregistered users, new users and registered users who need additional copies of the model will be able to order the new IBM version for $11.00 from UW Sea Grant Communications (see back page for details).

User Workshops

■ *How to Arrange for a Workshop*

The *Generalized Bioenergetics Model of Fish Growth* is a powerful and cost-effective tool for addressing questions of fish growth, production and consumption, but it requires some experience to use efficiently. One of the most effective ways to become proficient at using the model is to be instructed in its operation by an experienced user.

We will continue to offer on-site workshops through UW Sea Grant Advisory Services. One- and two-day, hands-on workshops have proven to be an effective and efficient method of teaching users how to operate and apply the model. The workshops also provide an excellent opportunity for biologists and researchers to discuss different approaches to using fish bioenergetics for addressing common management problems. The workshops have been a valuable source of feedback to us for improving the model as well.

These workshops are provided on a "at-cost," user-funded basis, where the host institution pays travel costs and per-diem expenses for the required number of instructors. In some cases, this may include a site visit prior to the workshop to finalize local arrangements and establish the objectives and data sets for fulfilling the goals of the workshop.

The hosting institution or agency is expected to provide all computer facilities and make all local arrangements for the workshop. We provide the instructors, instructional materials (including the latest version of the model) and expertise. No consulting fees or honorariums are requested.

The objectives and length of each workshop can be tailored to the particular needs of the participants, from a general introduction to bioenergetics concepts and model operation, to detailed analyses of data and model output for specific research or management questions. Whenever possible, we try to use data provided by the participants to create files and model runs that address questions of interest to them.

The number of participants, computers and instructors is flexible, but we recommend a maximum of about 16 participants, with at least one computer for every two participants and one instructor for every four to five participants.

If you are interested in scheduling a workshop, contact Clifford Kraft, University of Wisconsin Sea Grant Advisory Services, 105 Environmental Sciences Bldg., UW-Green Bay, Green Bay, WI 54301, phone (414) 465-2795.

■ *Workshops Held to Date*

To date, we have conducted ten instructional workshops:

- Lake Superior Lake Trout Technical Committee, Great Lakes Fish Commission, Ashland, Wis., April 1987.
- University of Wisconsin Sea Grant scientists and Advisory Services personnel, UW-Madison, Madison, Wis., May 1987.
- Bureau of Fish Management, Wisconsin Department of Natural Resources, Madison, Wis., November 1987.
- Vermont Fish & Game Department, New York Department of Environmental Conservation, U.S. Fish & Wildlife Service, University of Vermont (host), Burlington, Vt., April 1988.
- U.S. and Canadian public- and private-sector biologists, American Fisheries Society Continuing Education (host), Toronto, Ont., Canada, September 1988.
- Northwest District personnel, Wisconsin Department of Natural Resources, Brule, Wis., January 1989.
- North Carolina Wildlife Resources Commission, South Carolina Wildlife & Marine Resources Department, Carolina Power & Light, North Carolina State University, National Marine Fishery Service, Duke Power Co. (host), Huntersville, N.C., February 1989.
- Bureau of Research, Wisconsin Department of Natural Resources, Woodruff, Wis., March 1989.
- Oak Ridge National Laboratories, University of Wisconsin-Madison (host), Madison, Wis., July 1989.
- Minnesota Department of Natural Resources, Missouri Department of Conservation, U.S. Environmental Protection Agency, University of North Dakota, Minnesota Chapter of the American Fisheries Society (host), Hackensack, Minn., October 1989.

The Bioenergetics Booter was provided free of charge to registered users of the original version of *A Generalized Bioenergetics Model of Fish Growth for Microcomputers.*

A new IBM version of the model will be distributed free of charge to all registered users in early 1990. Additional copies of the new version of the model will be available for $11.00 each from:

Communications Office
UW Sea Grant Institute
1800 University Avenue
Madison, WI 53705
USA

Telephone (608) 263-3259

The model package includes user manual and program and data disks. Price includes postage and handling. Orders must be prepaid. Make checks and money orders payable to "UW Sea Grant Institute." Payment must be in U.S. currency drawn on a U.S. bank.

Our ultimate goal in this process of transferring bioenergetics technology is to produce a network of model users able to help each other and train new model users.

We welcome your questions, comments, suggestions, ideas, new data and reports of new applications of the model for research, management or education. Please address your correspondence to:

Bioenergetics Model
UW Sea Grant Advisory Services
1800 University Avenue
Madison, WI 53705
USA