fish bioenergetics MODEL 2

an upgrade of
A Generalized Bioenergetics Model of Fish Growth for Microcomputers

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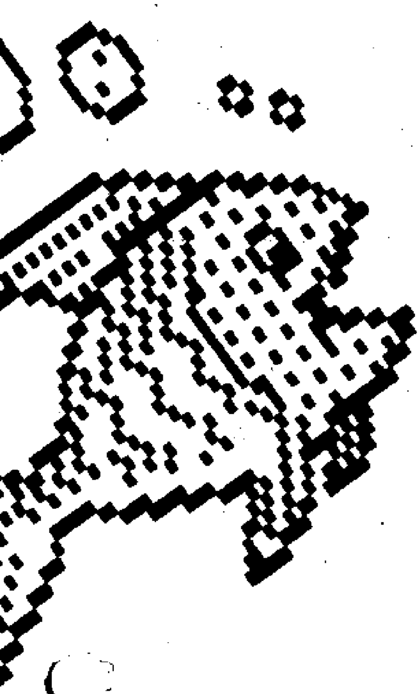

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Preface

Since the publication of *A Generalized Bioenergetics Model of Fish Growth for Microcomputers*:

- bioenergetics modeling has become an accepted tool for assessing predator-prey interactions,
- bioenergetics as the basis of growth relations has been incorporated in a variety of models, and
- new physiological parameter sets have been developed and published for more fish species and mysid invertebrates.

We as software developers have learned a tremendous amount about the transfer of modeling technology to users — through consultations, training workshops, and model applications in the literature. We have revised and refined the bioenergetics model to incorporate a variety of advances based on user feedback. *Model 2* has a more user-friendly interface and is easier to learn and run (Append. 1)

We encourage all users with older versions, including intermediate versions from the workshops, to upgrade. A free upgrade package is available to anyone who purchased our first model. For more information, contact: Communications Office, University of Wisconsin Sea Grant, 1800 University Ave., Madison, WI 53705-4094. (*Model 2* has been produced only for IBM/compatibles; low demand for the Apple II version precluded its production.)

Steve Hewett

Barry Johnson

Acknowledgments

Fish Bioenergetics Model 2 would never have seen the light of day without continued support from James Kitchell, University of Wisconsin-Madison Center for Limnology. Also, Jim Breck, Michigan Department of Natural Resources, provided all manner of advice and pieces of program code.

Many others contributed advice and constructive comments on the program and documentation, including Clifford Kraft, University of Wisconsin Sea Grant; Donald Stewart, State University of New York-Syracuse; John Lyons, Wisconsin Department of Natural Resources; and Jim Rice, North Carolina State University. Neil MacKay, UW-Madison Center for Limnology, contributed greatly to revising the documentation and wrote the keystroke guide (Append 5).

Further, we thank Brett Johnson, UW-Madison Center for Limnology; Chris Luecke, Utah State University; and John Post, University of British Columbia, who instructed bioenergetics-modeling workshops — and all workshop participants and UW-Madison students who suggested improvements, especially Paul Eiler, Minnesota Department of Natural Resources, and John Knight, Duke Power.

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Introduction

Why use fish bioenergetics models? Considerable effort has gone into developing other methods to derive consumption estimates, such as gastric evacuation rate and stomach content analyses (Elliott and Perrson 1978; Mann 1978; Eggers 1979; Adams et al. 1982). Comparable estimates of comsumption can be obtained, with much less effort, by measurig growth and using an energetics model to estimate consumption (Rice and Cochran 1984). Because growth is an integrator of consumption over time, bioenergetics models can be used to derive consumption estimates based on observed growth over some time period. Bioenergetics models can also be used to estimate growth rates given some estimate of consumption.

Fish Bioenergetics Model 2 — developed at the Center for Limnology, University of Wisconsin-Madison, with support from the University of Wisconsin Sea Grant Institute — synthesizes many previous modeling efforts. The model processes data on fish physiology, diet composition, energy density, and water temperature to generate consumption and/or growth estimates. Options within the bioenergetics model include seasonal or ontogenetic changes in predator or prey energy density, seasonal variation in diet proportions, constant ration, and weight loss due to spawning.

This model comes with 20 taxa-specific physiological parameter sets, including: sea lamprey (*Petromyzon marinus*); the clupeids, alewife (*Alosa pseudoharengus*) and Atlantic herring (*Clupea harengus*); *Coregonus* spp.; the salmonids, lake trout (*Salvelinus n. namaycush*), coho salmon (*Oncorhynchus kisutch*), chinook salmon (*O. tshawytscha*), and pink (*O. gorbuscha*) or sockeye (*O. nerka*) salmon; the esocids, northern pike (*Esox lucius*) and muskellunge (*E. masquinongy*); dace (*Phoxinus* spp.); the centrarchids, bluegill (*Lepomis macrochirus*), largemouth bass (*Micropterus salmoides*), and smallmouth bass (*M. dolomieui*); striped bass (*Morone saxatilis*); the percids, yellow perch (*Perca flavescens*) and walleye (*Stizostedion v. vitreum*); *Tilapia* spp.; and *Mysis* spp. Other species can be modeled by specifying additional parameter values.

The *Model 2* menu-driven program allows users to create and edit data files, process the data files, generate output files, and view the output files in numeric or graphic form. This documentation describes how to use the model, presenting available system options and recommending those most appropriate for particular taxa. The chapters (1) overview bioenergetics modeling, (2) describe model operations, (3) detail bioenergetics equations and *Model 2* options, and (4) provide guidance on specific applications. Nine appendices supplement the text; reference and bibliography lists specify sources of further information.

CHAPTER 1

Uses of Fish Bioenergetics Models

PRELIMINARIES

Direct measurement of the feeding rates of fish is problematic. Field estimates, derived from gastric evacuation rate models and stomach content analyses, are highly variable — and associated point estimates require extensive effort (Mann 1978; Cochran and Adelman 1982; Adams et al. 1982; Soofiani and Hawkins 1985). Bioenergetics modeling, however, uses growth rate data that are more readily obtainable and less variable to derive consumption estimates.

Bioenergetics models can generate consumption or growth estimates over given time intervals by processing data on metabolism, consumption, water temperature, diet composition, and energy density, according to taxa-specific physiological parameters.

While both consumption and growth estimates have been derived with bioenergetics models, estimating consumption from growth data has proven more reliable than estimating growth from consumption estimates (Bartell et al. 1986). For general discussions of bioenergetics modeling, see Kitchell (1983), Tytler and Calow (1985), Hewett (1989), and Ney (1990).

PREVIOUS APPLICATIONS

Consumption and Effects on Prey

Estimating patterns and amounts of consumption, over seasons and lifespans, has been the most common application of bioenergetics models (Kitchell and Breck 1980; Stewart et al. 1981; Stewart and Binkowski 1986; Carline 1987; Rudstam 1988, 1989; Hewett and Stewart 1989; Beauchamp et al. 1989; Kitchell 1990; Raat 1990).

Kitchell and Breck (1980) developed a model for sea lamprey (*Petromyzon marinus*) and estimated that feeding rate, and thus potential host mortality, was greatest in autumn. Kitchell (1990) further considered how the size of sea lamprey and host size affects host mortality.

Stewart et al. (1981) modeled lifespan consumption by salmonids stocked in Lake Michigan and assessed predation pressure on the primary forage species, alewife (*Alosa pseudoharengus*). They predicted that unabated salmonid stocking would mean a decline in the alewife population — which has occurred (Kitchell and Crowder 1986).

Stewart and Binkowski (1986) modeled patterns of consumption by individual alewife in Lake Michigan and estimated that almost 50% of annual consumption by adult alewife occurred in September-October, whereas summer appeared to be a period of food limitation. Hewett and Stewart (1989) extended this analysis to the population level. They estimated that young-of-year alewife accounted for 50% of consumption by the total population and that during the mid-1960s, when alewife populations peaked, potential consumption by the population would have approached 20% of zooplankton biomass per day, implicating food limitation as a cause of the mid-1960s population crash of alewive.

Carline (1987) used consumption estimates from bioenergetics to develop simplified regressions, based on fish size, weight gain, and degree days, for estimating total consumption by largemouth bass (*Micropterus salmoides*) and northern pike (*Esox lucius*) under typical field conditions.

Diet Composition

Some bioenergetics-modeling applications have extended estimates of total consumption to assess the impact on prey types. Cochran and Rice (1982) modeled the number and biomass of bluegill (*Lepomis macrochirus*) and young largemouth bass eaten by older largemouth bass in Lake Rebecca, Minnesota. Similarly, Lyons and Magnuson (1987) estimated what proportion of total mortality for perch, minnows, and darters was due to predation by walleye (*Stizostedion v. vitreum*) during years of high and low perch recruitment in Sparkling Lake, Wisconsin. Hurley (1986) estimated that forage production in the Bay of Quinte, Lake Ontario, exceeded consumption by walleye for all forage species except alewife — whose population was replenished each year by a spawning migration into the bay.

Another application derived from estimating consumption is modeling the uptake of contaminants. Weininger (1978) modeled PCB uptake by lake trout (*Salvelinus n. namaycush*) both from the water directly and from bioaccumulation through the food web.

Environmental Parameters

Kitchell et al. (1977b) modeled the growth of yellow perch (*Perca flavescens*) in Lake Erie and found that differences in growth rate between yellow perch from the eastern versus the western basin could be explained by a slight delay in the warming of the eastern versus the western basin.

When Rice et al. (1983) modeled the decline in condition of largemouth bass in Parr Pond, a heated reservoir in South Carolina, they postulated that a seasonal decline in prey availability was the probable cause, rather than increased largemouth bass activity or the effects of a heated effluent.

Hill and Magnuson (1990) used modeling to examine how climate warming could affect the growth of and consumption by lake trout, largemouth bass, and yellow perch over their lifespans in the Great Lakes.

Fisheries Management

Bioenergetics modeling has many fisheries management applications. It offers an alternative method for estimating fish production that can be useful in evaluating alternate management actions.

Stewart et al. (1981) provided a basis for developing a salmonid-stocking strategy for Lake Michigan that considers how the lifespans and the species mix of predators affect total forage demand over time (Kruger and Dehring 1986).

Carline et al. (1984) used data on largemouth bass diet composition, modeling estimates of largemouth bass predation rates, and data on forage fish production to conclude that largemouth bass are unlikely to control bluegill populations when gizzard shad (*Dorosoma cepedianum*) are available. Using a similar approach, Johnson et al. (1988) estimated total consumption by all predators in an Ohio reservoir at only 20% of young-of-year gizzard shad production.

Bevelhimer et al. (1985) used models to recommend which esocid to stock in Ohio reservoirs with different thermal regimes and which size of fish and time of year were best for the stocking.

Kitchell and Hewett (1987) investigated the possible effects of stocking sterile chinook salmon (*Oncorhynchus tshawytscha*) in Lake Michigan. They used the model developed by Stewart et al. (1981) but with different assumptions about growth and mortality to simulate the extended lifespan of sterile chinook. They estimated that a cohort of sterile chinook salmon, over its lifespan, would consume about 1.5 times as much as a normal cohort but would produce less total return to the fishery — although trophy-size (>22 kg) sterile chinook salmon would begin to appear about five years after stocking.

Aquaculture

Bioenergetics modeling has many potential applications in aquaculture. Nitithamyong (1988) used a model to estimate the costs of increased activity and egestion among cultured blue tilapia (*Oreochromis aureus*), that resulted from different doses of a synthetic steroid.

Field Verification

Tests of bioenergetics-modeling estimates are rare because the necessary field data are difficult to obtain, which also is often why models are used.

When Cochran and Rice (1982) modeled number and biomass of bluegill and young largemouth bass eaten by older largemouth bass in Lake Rebecca, Minnesota, the model estimates agreed well with independent field estimates. When Rice and Cochran (1984) modeled the growth of largemouth bass in the same waterbody, they estimated seasonal cumulative consumption within 8.5% of independent field estimates. The model best fit observed growth when simulated over three periods of different prey availability: the first with no young-of-year prey available, the second with young-of-year largemouth bass available, and the third with young-of-year largemouth bass and bluegill available.

Beauchamp et al. (1989) found close agreement between model and field estimates of consumption and energy budget for sockeye salmon (*Oncorhynchus nerka*) in three lakes in the United States, Canada, and the Soviet Union.

Comparisons of model and field estimates for consumption by yellow perch have been the subject of much debate (Hayward and Margraf 1988; Hayward 1990; Boisclair and Leggett 1989, 1990, 1991; Post 1990; Hewett et al. 1991).

Comparisons of model and field estimates for esocids (Wahl and Stein 1991) and yound-of-the-year walleye (Fox 1991) have resulted in suggested changes in parameter estimates for those models.

Model Sensitivity

Bioenergetics-modeling estimates of consumption per observed growth have been more precise than estimates of growth per given ration (Kitchell et al. 1977b; Bartell et al. 1986; Beauchamp et al. 1989). For estimating consumption, known growth parameters limit the effects of errors in temperature cycles, bioenergetics functions, and so on. Conversely, for estimating growth, a primary difficulty has been to accurately assess feeding rate, even given a known availability of food (Bartell et al. 1986). Most applications have estimated consumption per observed growth.

Modeling results have been most sensitive to parameters in the allometric functions for routine metabolism — and, when modeling percids, the allometric functions for consumption (Rice et al. 1983; Stewart et al. 1983). Bartell et al. (1986) developed a comprehensive method for determining model sensitivity to the parameters.

SUMMARY

Bioenergetics modeling provides an alternative approach to some research and management questions that have not been easily addressed by conventional methods.

Direct measurements of consumption are difficult or, in some instances, impossible to obtain in the field. Through modeling, however, estimates of consumption can be obtained by combining laboratory and field data. Models incorporate laboratory-derived allometric functions for consumption and metabolism with field-derived data on diet composition, energy density, fish growth and water temperature over time. Similarly, modeling can be used to estimate growth under various conditions.

Fish Bioenergetics Model 2 Overview

SET-UP AND GO

Model 2 is coded in Borland International TURBO PASCAL 5.5. For a descriptive listing of the program files, and the sample data files, that come with *Model 2*, see Appendix 2.

Model 2 diskette packages vary (by diskette size and density, compressed or not, and so on), depending on user/distributor options.

The first thing to do is copy your *Model 2* diskette package! Whatever your original diskette package type, your copy should have the sample data files on a separate diskette from the program files. Then, store the original in a safe place and use the copy thereafter — just in case...

Data Files

To compute output, *Model 2* uses species files and seasonal files (Fig.1).

Species files specify physiological parameters. Consumption, respiration, egestion/excretion, and predator energy density data for 20 species are in the sample data files that come with *Model 2* (Append. 3).

Seasonal files delineate field data as a series of day numbers and corresponding water temperature, diet composition, or energy density values. The sample data files also include a set of seasonal files (Append. 4) for walleye (filename prefix WALLEYE).

File Names

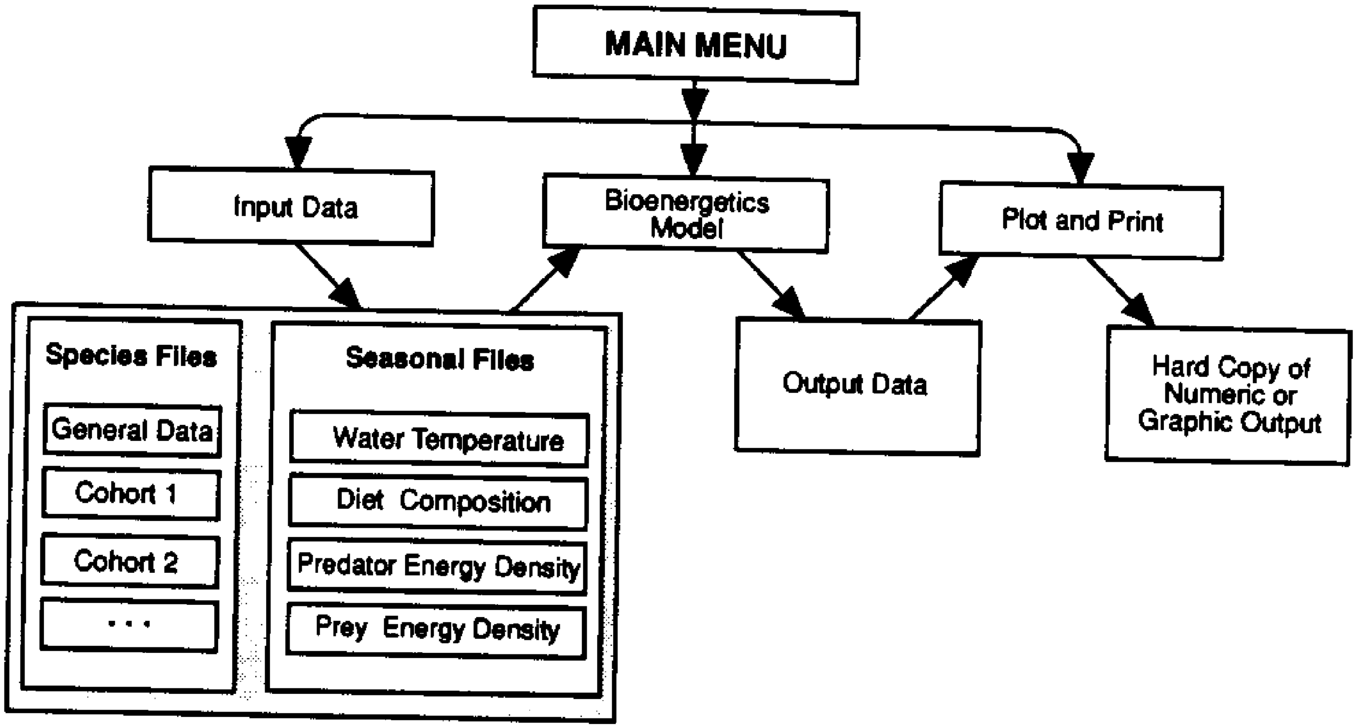
Model 2 data file names have a prefix of up to eight identifying characters (any combination of letters or numbers, but no spaces between them) followed by a period (.) and a three-character suffix. You can identify datafile type by filename suffix:

File Type	Suffix
input data	
species	.BIO
seasonal	
water temperature	.TEM
diet composition	.DIE
prey energy density	.PYC
predator energy density	.PDC
output data	
results	.WRK
bookkeeping	.LAB
	.KEY

Appendix 5 guides you through a WALLEYE run — after which you can compare your results with the WALLEYE.WRK sample data file (Append. 6).

Figure 1

Flowchart of *Fish Bioenergetics Model 2*



Loading

You can run *Model 2* on IBM/compatible PCs with at least 512K of memory and dual diskette drives (Append. 7) or a combination of diskette drive(s) with hard drive. A math coprocessor is recommended.

(Note: Files with suffixes .OBJ, .PAS, and .TPU are not required to run *Model 2*, although you do need them to change and recompile the program.)

Loading *Model 2* (on a combination of diskette drive(s) with hard drive)

READY
1. Turn on the computer and boot the system.
2. Bring up the hard drive prompt, C:\> .

SET
3. Type **md bioen** and then press **<Enter>**.
4. Type **cd bioen** and then press **<Enter>**.
5. Type **md data** and then press **<Enter>**.

GO
6. Insert program diskette(s) in drive A.
7. Type **copy a:*.* c:\bioen** and then press **<Enter>**.
8. Replace program diskette(s) with data diskette(s) in drive A.
9. Type **copy a:*.* c:\bioen\data** and then press **<Enter>**.
10. Remove your data diskette from drive A.

MODEL 2 MAIN MENU OPTIONS

After loading *Model 2*, you can run it. To begin, bring up your *Model 2* program files directory prompt, `BIOEN>`, and type **menu <Enter>**. *Model 2*, then, displays a welcome screen, specifying the current data directory and cuing you for verification.

To choose the response indicated by the cursor, press **<Enter>**. Otherwise, type your alternate choice. If you choose to change the current data directory, *Model 2* cues you to type in the new directory name and **<Enter>**, then cues you to verify the new name, and so on.

When you resolve the name of the current data directory, *Model 2* displays:

```
BIOENERGETICS MODEL
MAIN MENU

1) pfit/bioenergetics model
2) species file utilities
3) cal, temp, & diet file
   utilities
4) print model output
5) plot model output
6) edit defaults for run
   options & colors/graphics
7) program information
8) change default data drive
9) QUIT to DOS

Choice? -> 1
```

The current date is also displayed on the **MAIN MENU** screen, in the upper right corner. The default choice is highlighted and indicated by the cursor. To choose the default, press **<Enter>**. Otherwise, type your alternate choice. You can also use the arrow keys to move the cursor and highlight your choice, then press **<Enter>**.

Note: This chapter describes *Model 2* **MAIN MENU** options as if you are starting from scratch — rather than in numerical order as on the **MAIN MENU**.

8) change default data drive

This option enables you to change the current data directory without having to restart *Model 2*. The current data directory contains input files and receives output files. You can assign the current data directory to any drive or directory. However, both data and program files run much faster from a hard drive — preferably in separate subdirectories.

2) species file utilities

`.BIO` files contain ***general data***, which describe how this species is modeled, and ***cohort data***, which describe individuals with the same begin and end points of growth over a time interval.

To access `.BIO` files, choose **MAIN MENU** option **2**. *Model 2* displays:

```
SPECIES FILE UTILITY MENU

1) Create New Datafile
2) Edit Datafile
3) Print Datafile
4) Replicate Cohort in Datafile
5) ESCAPE

Choice? -> 2
```

Species File Utility Menu Options
When you choose a species file utility menu option, *Model 2* cues you to select a `.BIO` file and displays `.BIO` file names from your current data directory on the right side of the screen.

1) Create New Datafile. This option enables you to create a .BIO file, usually for a species not described in the sample data files. New .BIO files are completely blank, and you must input all data, including general physiological parameters. Therefore, to copy and edit an existing .BIO file is almost always easier than to create a new one.

When you choose this option, *Model 2* displays a warning and asks, **Do you want to continue?** If so, *Model 2* cues you to name the new .BIO file — you type in the prefix (up to eight characters); *Model 2* attaches the .BIO suffix. If you use an existing .BIO file name, the earlier version will be overwritten. Again, *Model 2* displays a warning and this time asks, **Do you want to write over that file? ...**

After you have named the new .BIO file, *Model 2* cues you to specify how many cohorts it will contain initially (default = 10, maximum = 40). Do that, and *Model 2* displays:

```
SPECIES FILE GENERAL DATA                  File name: ________.BIO
                                   Number of cohorts in this file = ___
                                   Model options (details in User's Guide)

Species Name ----------->
Cons Model ------------->  1      1=Exponential, 2=TDEP, 3=Thornton & Lessem
Resp Model ------------->  1      1=Stewart, 2=TDEP
Egest/Excret Model ----->  1      1=Constant %, 2=Elliot, 3=Mixed diet
Include Spawning ------->  N
 1st Spawning Cohrt ---->  0
 Day of Spawning ------->  0
 Propor Wt Spawned ----->  0.000
Maintenance Temp. ------>  0.0
Pred CalDens Model ----->  1      1=Seasonal datafile, 2=Function of weight
 CalDens Alpha1 -------->  0.0000 \
 CalDens Beta 1 -------->  0.0000  \
 Weight Cutoff --------->  0.0000   > parameters for Pred CalDens Model 2
 CalDens Alpha2 -------->  0.0000  /
 CalDens Beta 2 -------->  0.0000 /

<SPACE>)Edit A)dvance <-_->)Arrows to select
```

Species File General Data Options:

`Species Name` — up to 25 characters.

`Cons Model, Resp Model`, and `Egest/Excret Model` — per number choices (on-screen, to the right of each term) that correspond to alternative equations for modeling consumption, respiration, and egestion/excretion.

Include Spawning — Y to include spawning loss in computations; then, `Edit` spawning values accordingly.

- `1st Spawning Cohort` — number of the first cohort that spawns.
- `Day of Spawning` — day of model year when spawning occurs.
- `Propor Wt Spawned` — proportion (0-1) of body weight lost during spawning.

`Maintenance Temp.` — zero or water temperature (degrees centigrade) below which growth does not occur.

`Pred CalDens Model` — number (choices on-screen, to the right) that corresponds to the method of determining predator energy density. If 1, proceed no further here, but rather, input predator energy density data in a .PDC file. If 2, predator energy density is run as a function of weight, and you continue here.

- `Alpha` and `Beta` — function parameters. You can input two sets (`Alpha 1, Beta 1`, and `Alpha 2, Beta 2`) to separate young versus adult fish.
- `Weight Cutoff` — weight (grams wet weight) at which the run switches from young to adult fish parameters.

The blanks for `File name` and `Number of cohorts` display your earlier specifications. Now, you input the general physiological parameters for this new `.BIO` file. The default values produce the simplest bioenergetics configuration for *Model 2*, such that equations are in the most common form while `Spawning` and `Maintenance Temp` are set to zero.

Using the arrow keys to move the cursor around the screen, you can input the species name and change bioenergetics options.

To **Edit** an option — press the space bar or **<Enter>**, type your input, then press the space bar or **<Enter>** again.

The equations you choose for consumption, respiration, and egestion/excretion as well as your choices about spawning loss, maintenance temperature, and predator energy density are stored only once for the species and apply to all cohorts.

When you complete **General Data** inputs, type **A** to advance to the next screen. *Model 2* saves the new .BIO file to the current data directory. However, the cohort sections of the new .BIO file are still blank. You must input cohort data before running the new .BIO file.

2) Edit Datafile. This option enables you to edit data in a .BIO file, which you choose from the list of current data directory .BIO files on the right side of the screen. Use the arrow keys to highlight your choice, then press **<Enter>**.

Model 2 cues you to specify the first and last cohorts to be edited (1 to 1 for cohort 1 only; 2 to 4 for cohorts 2, 3, and 4; and so on).

Do that, and *Model 2* displays:

```
SPECIES DATAFILE EDITING MENU          File Name:________.BIO

Select portion(s) of species file you wish to edit.

Species General Data Parameters ------------------------------>N
Wt/Date/P-val/Popn Parameters -------------------------------->N
Consumption Parameters --------------------------------------->N
Respiration Parameters --------------------------------------->N
Egestion/Excretion Parameters -------------------------------->N
Mortality Parameters ----------------------------------------->N
% Prey Indigestible Parameters ------------------------------->N
(used only in Egest/Excrete Model 3)

<SPACE>)Toggle value A)dvance <-_->)Arrows to select <ESC>)Escape
```

The blank for **Filename** displays the name of the .BIO file you chose to edit. The **Species General Data Parameters** is the section of a .BIO file entered when the .BIO file is created, and is edited through the same **Species File General Data** screen. The other parameters are cohort-specific.

Select the parameter/s to edit, by using the arrow keys to move the cursor and toggling with the space bar between **N** and **Y**.

Selections made, type **A** to advance — the parameter options for each cohort to be edited will then appear in sequence.

Species Data File Cohort-Specific Parameters:

Wt/Date/P-val/Popn Parameters

Start Day and **Final Day** of the run interval, which can be up to a year. You designate dates as sequential days from 1 through 365. Day 1 can be any calendar date and represents that same calendar date across all data files when running the cohort.

Start Weight and **Final Weight** (grams wet weight) at the beginning and end of the run.

P-value — the proportion of maximum consumption realized, which *Model 2* computes.

Init.Pop.Size — the number of fish in the cohort on the first run day.

Consumption Parameters, Respiration Parameters, and **Egestion/Excretion Parameters** are all set up similarly.

Mortality Parameters enable population level modeling. You can specify up to 12 time intervals, with different daily instantaneous mortality rates for each interval. On a **MORTALITY HELP** screen, *Model 2* cues you to specify the total proportion of the cohort dying and the number of days in the interval. Do that, and *Model 2* displays the daily instantaneous mortality rate for each interval. Write these values down to input on the **Mortality Table** screen, which comes up next. You can apportion total mortality as natural mortality and fishing mortality (Ricker 1975).

% Prey Indigestible Parameters — data on the proportion (0-1) of each prey item that is indigestible. (These data are needed only when using Egestion/Excretion Equation Set III.)

3) Print Datafile.
This option enables you to list a .BIO file to the **P)rinter**, the **S)creen**, or a **F)ile**. You can list a single cohort or multiple cohorts in sequence.

4) Replicate Cohort in Datafile.
This option provides an easy way to create multiple cohorts. You can copy any selected cohort into any other cohort, then edit the copy as necessary, which is very useful for inputing cohort-specific data on newly created .BIO files.

Species Sample Data Files. All sample .BIO files contain appropriate **Species File General Data** and are set up with 10 cohorts, each containing appropriate physiological parameters. The WALLEYE.BIO file also contains a full set of cohort-specific parameters for cohort 1.

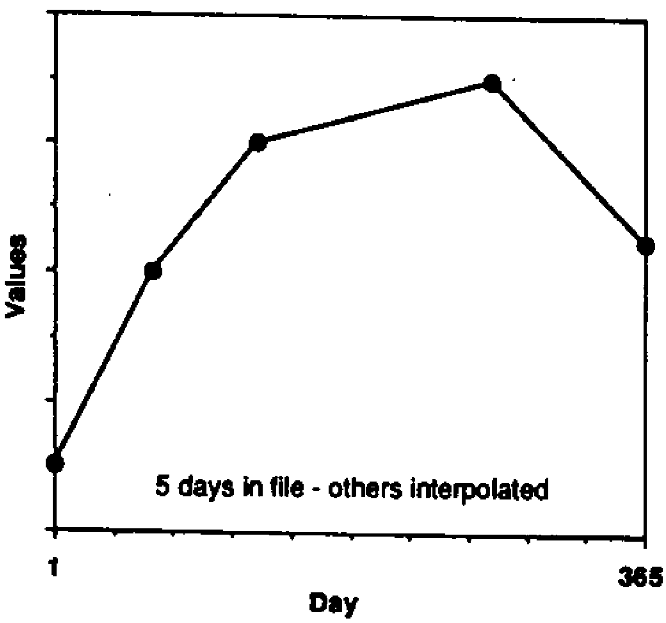
3) cal, temp & diet file utilities

The seasonal files — water temperature (.TEM), diet composition (.DIE), prey energy density (.PYC), and predator energy density (.PDC) — are all set up similarly. Each seasonal file accommodates data for up to 36 ***Input days*** over the timeframe of a year.

Day 1 can represent any date, but it ***must*** be consistent across all data files. The run interval can be less than 365 days, but you ***must*** input data for day 1 and day 365. You can also input data available for any other days, for up to 36 input days altogether. *Model 2* computes values for days between the input days through linear interpolation (Fig.2).

FIGURE 2

Sample Graph of Seasonal Data File



`.TEM` and `.PDC` files can contain one value per day. `.DIE` and `.PYC` files can contain values for up to 10 diet items per day. In `.DIE` files, the sum of proportions for all diet items ***must*** be 1.0 for each day.

Model 2 requires ***temperature in degrees centigrade*** and ***energy density data in calories per gram wet weight***, using calories to balance the predator-prey energy budget. The energy density of predator and prey, therefore, can be very important in determining consumption and growth.

Multiple Cohorts in Seasonal Files

All seasonal files can accommodate data for multiple cohorts, which correspond to cohorts in the `.BIO` file. However, you need not repeat identical cohort data at the end of a seasonal file. For example, if you have a `.DIE` file containing data for 3 cohorts, while the `.BIO` file contains data for 6 cohorts, *Model 2* assumes that the diets of cohorts 3, 4, 5, and 6 are identical.

Creating and Editing Seasonal Files

To access seasonal files, choose **`MAIN MENU`** option `3)`. *Model 2* displays:

```
CAL/TEMP/DIET FILE UTILITIES

Edit, Create or Print
the following data files:

1) Temperature File
2) Diet File
3) Predator Energy Density File
4) Prey Energy Density File
5) ESCAPE

Choice? -> 1
```

First, choose the type of seasonal file you want to create or edit.

When you **`Create`**, *Model 2* cues you to name the new seasonal file — you type in the prefix (up to eight characters); *Model 2* attaches the suffix. (If you use an existing seasonal file name, the earlier version will be overwritten.) Next, specify the number of cohorts. Then, input data chronologically, following the on-screen cues.

When you **`Edit`**, *Model 2* cues you for **`File Information`**. You confirm or change the **`Last cohort to be used in model run`**, which can be less than or equal to the **`total number of cohorts in file`**. (In a run, *Model 2* uses all directly corresponding seasonal and `.BIO` cohort files, then reuses **`Last cohort`** seasonal files with any additional `.BIO` cohort files.) **`File Information`** specified, you can proceed to edit data.

When you finish inputing or editing data, type **A** to return to **`CAL/TEMP/DIET FILE UTILITIES`**.

Converting Calendar Dates to *Model 2* Days
Field data, usually available by calendar date, must be input to *Model 2* by numerical day-of-year.

Using Table 1, you can quickly convert calendar dates to day-of-year numbers, if your run year begins on the first day of a month.

Table 1
Converting Calendar Dates to *Model 2* Days.

To convert calendar dates to day-of-year numbers, if your run year begins on the first day of a month:

1. Start at the column that corresponds to the start of your run year.
2. Move down the column to its intersection with the row that corresponds to the month of your calendar date.
3. Add the number at the intersection to the number of your calendar date for the *Model 2* day-of-year number.

For example, if your run year begins March 1, and your input data are for October 15:

1. Start at the "Mar 1" column.
2. Move down the "Mar 1" column to its intersection with the "Oct" row.
3. Add the number at the intersection (214) to the number of your calendar date (15) for the *Model 2* day-of-year number (229).

Run Year Start Date

Calendar Month	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

Seasonal Sample Data Files

The sample WALLEYE seasonal files contain data for one cohort. The WALLEYE.DIE and WALLEYE.PYC files contain data for two diet items. Item 1 is benthos; item 2 is fish. For walleye, predator energy density is not a function of weight, thus the WALLEYE.PDC file is required. Run day 1 is April 1.

1) pfit/bioenergetics model

Running *Model 2* usually involves two steps — a P-fit run and a bioenergetics run.

P-value

You specify a P-value, a proportionality constant, for each cohort in a .BIO file.

The P-value represents the proportion of maximum ration consumed by the fish over the run interval (Kitchell et al. 1977). If P-value is 1, then the fish is feeding at its maximum rate (based on its size and the water temperature); if P-value is 0.5, then the fish is feeding at half its physiological maximum; and so on.

At P-value of Ø, no feeding occurs. Thus, P-value is a scalar representing an ecological constraint on the physiological maximum feeding rate. This constraint could represent prey availability, competition, predator avoidance, disease, etc.

Using P-value, *Model 2* fits computed growth to observed growth, determining the consumption rate and total consumption required to compute observed growth. Alternately, *Model 2* can fit the P-value to observed consumption. You must include a non-zero starting estimate of P-value to run *Model 2*.

Troubleshooting

If any **pfit/bioenergetics model** options do not run — or do run, but with strange output — check the data files. For example, if *Model 2* displays an error message that you have no .BIO files, use **MAIN MENU** option 8) to verify the current data directory. To remedy other likely sources of error, use the following checklist:

- Are all necessary parameter values specified?
- Are all data input accurately?
- Does run day 1 correspond to the same calendar date in all seasonal files?
- Is the number of cohorts in each seasonal file correct?
- Is the number of diet items, and the order in which they are listed, the same in the .DIE and the .PYC files?

RUN OPTIONS

When you choose **MAIN MENU** option **1) pfit/bioenergetics model**, *Model 2* displays:

```
BIOENERGETICS GROWTH MODEL
RUN OPTIONS

1) P-FIT run - fit to end weight
2) P-FIT run - fit to consumption
3) BIOENERGETICS run - constant
   P-value
4) BIOENERGETICS run - constant
   ration
5) ESCAPE

Choice? -> 1
```

1) P-FIT run - fit to end weight

This option determines the P-value that fits observed growth. To do this, *Model 2* runs iteratively, adjusting P-value until computed final weight is ±0.05 percent of the final weight input on the .BIO file.

P-fit can be run for a single cohort or multiple successive cohorts. Beginning with an initial P-value estimate in the .BIO file (0.3 often works well), *Model 2* runs one cohort at a time — from start weight using all the applicable data in the .BIO, .TEM, .DIE, .PYC, and .PDC files. After each cohort run, if computed final weight does not agree with final weight data (±0.05%), *Model 2* estimates a different P-value and runs the cohort again, and so on.

As they are determined, cohort P-fits appear on-screen. You then choose whether or not to replace initial estimates with P-fit determinations.

2) P-FIT run - fit to consumption

This option determines the P-value that fits total consumption by an individual — not total consumption by the population. If you are running multiple cohorts, input a consumption value for each cohort.

This option is often useful for fish culture runs or for re-running consumption values to compute growth under different conditions, assuming consumption will remain constant.

3) BIOENERGETICS run
- constant P-value

This **BIOENERGETICS run** option simulates growth from the start weight, given consumption as a **constant P-value** for each cohort.

Model 2 first cues you for which .BIO file to run. Next, you select seasonal files and specify how many cohorts to simulate. Do that, and *Model 2* displays:

```
BIOENERGETICS RUN OPTIONS

Save Bioenergetics
   output to file at:->

"Set interval" for                    {used only when a "set interval"
   saving output is:->                option is chosen above}

Zero all cumulative
   output variables at:->

Save Bioenergetics output
   at start day of cohort->

Save Bioenergetics output
   on final day of cohort->

<- ->)Arrows to Select,  <SPACE> to Change/Edit Option

A)dvance,  <ESC>)Escape -> _
```

The initial **Bioenergetics Run Options** specify when to save output. To see the choices available, use the arrow keys to move the cursor to the top option and press the space bar repeatedly.

The *output day* choices should be self-explanatory. If you choose **A set interval relative to the day of the year**, select the **"Set interval"** next.

Options for Zeroing Cumulative Output:

- `After each cohort` — produces totals for each cohort.
- `After each output day` — produces totals over each output interval.
- `After every day 365` — produces totals over a run year (or part of a year if the run did not begin on day 1).
- `After every day` — produces daily totals.
- `Start of run only` — produces overall totals per cohort.

The last `Bioenergetics Run Options` determine whether data will be saved for the `start day` and `final day` of each cohort. Choose, using the arrow keys to position the cursor and the space bar to toggle, between `Y` and `N`. Selections made, type **A** to advance.

Before starting the run, *Model 2* cues you for an optional comment, which can be saved with output, and for a prefix to identify run output files. If you use an existing output filename prefix, the earlier version will be overwritten.

4) BIOENERGETICS run - constant ration

This `BIOENERGETICS run` option simulates growth from the start weight, given consumption as a `constant ration` daily, at a fixed proportion of weight. (The proportional constant is specified in the `.BIO` file with consumption parameters.)

Under this option, daily consumption rate equals ration, unless ration exceeds the physiological maximum consumption, which is then used instead.

`Bioenergetics Run Options` are the same as for a `constant P-value` run.

***Model 2* Output**

Output from every run goes to the current data directory in three output files, each with the identifying common prefix that you assigned and a differentiating suffix that *Model 2* attaches — `.LAB`, `.KEY`, or `.WRK`.

`.LAB` and `.KEY` files contain "bookkeeping" information; the `.WRK` file contains "results" data for each output day across 44 variables (Append. 8). All three output files are needed to print or plot output.

4) print model output

This option enables you to view any combination of up to 24 of the 44 variables in a `.WRK` file.

First, you select a `.WRK` file from the list displayed on-screen, in the upper right corner. Do that, and *Model 2* displays the `Model Output Listing` screen.

Then, you select how to view output — via the screen, a printer, or an ASCII text file (space delimited, tab delimited, or Lotus PRN). Text files are saved to the current data directory per file names you designate.

Next, you select which output variables to view, from numbered fields displayed on the right side of the screen. Type **0** at the end your variables list.

Selections made, you can type **C** to correct any errors. To advance, type **A**. On the next screen, you specify which output days to view.

Model 2 displays the number of output days for which you have saved data. You can view all, or any sequential group, and at any interval — type in the `low output day`, the `high output day`, and the `output day interval`.

5) plot model output

This option enables you to plot output variables against each other, using x : y or x : double-y axes.

First, you select a `.WRK` file from the list displayed on-screen, in the upper right corner. Do that, and *Model 2* displays:

```
PLOTTING MENU

1) Plot model output
2) Change to new *.WRK file
3) Load graph from disk file
4) Program information
5) Escape

Choice? -> 1
```

Making the Graph

Through **1) Plot Model Output**, you select the output variables to plot, choose graphic features, then view and, optionally, save the graph (Fig. 3).

You select which output variables to plot from the 44 numbered fields displayed on the right side of the **Plot Model Output** screen. *Model 2* first cues you for the x-axis field number, which is usually a time variable — therefore, 2 or 3 . Then, you select the y-axis field number/s.

Next, choose whether the data points should be connected or left unconnected as a scatter plot. You can plot all, or any sequential group of output days on record, and at any interval. *Model 2* displays the total number of output days on record, then cues you to choose a **Low**, a **High**, and an **Interval**.

Having input the data configurations, you can choose whether to **Save graph** to the current data directory. If so, then *Model 2* cues you for a filename prefix and attaches the suffix .PGF.

Before viewing the graph, however, you designate **GRAPHICS AXIS OPTIONS**. The defaults that appear on-screen are minimum and maximum values for the output variables you have chosen. To edit the options, cursor to the appropriate spot, then type **E**. To advance, and see the graph, type **A**.

FIGURE 3

Growth Curve of a Salmonid over Time, from a *Model 2* Bioenergetics Run

The Plot Thickens

Use **2) Change to new *.WRK file** to change .WRK files without leaving (and thus having to repeat) a plotting protocol.

Use **3) Load graph from disk file** to review a graph that was saved to a .PGF file.

Use **4) Program information** to access on-screen information about *Model 2* plotting routines and compatibility with different graphics cards and printers.

6) edit defaults for run options & colors/graphics

This option enables you to customize default values and screen colors and to designate a system graphics card and printer. *Model 2* default values operate from the BIOFILE.DEF file.

The **Bioenergetics Run Options** appear first for editing. Default values changed here are saved to the BIOFILE.DEF file — unlike **Bioenergetics Run Options** changed at the time of a run, which apply to the run only.

Next, you can edit various options for screen color, graphics card, printer, and so on. Use the arrow keys to position the curser, then press the space bar or <Enter> to see the choices available.

`S)et to original defaults` will set the options to the original *Model 2* default values `R)eset to user-defined defaults` will set the options to whatever values were last saved to the `BIOFILE.DEF` file.

A caution on screen colors: If you should inadvertently set `Text Color` and `Background Color` the same, your program will become invisible! The easiest way to recover is to reboot the computer, delete the BIOFILE.DEF file, then run the program again.

`7) program information`

This option provides information about the authors, acknowledges funding support, and overviews *Model 2* developments since the original, *A Generalized Bioenergetics Model of Fish Growth for Microcomputers*, was released in 1987.

CUSTOMIZING *MODEL 2*

Run Interval

Each *Model 2* cohort accommodates input data for a run interval of one year. Nonetheless, you can structure cohorts to represent growth over any shorter time period, up to one year.

For example, the first five cohorts in a `.BIO` file can represent growth over the first year of life, the next three cohorts in the same `.BIO` file can represent the second year of life, and so on. Then, for each `.BIO`-file cohort, you have a corresponding seasonal file. However, each seasonal file contains data for an entire year, whether or not the corresponding `.BIO`-file cohort represents an entire year.

So, if water temperature cycles differ for Age 1 versus Age 2 fish, the first five `.TEM` cohorts are identical and correspond to year 1, the next three `.TEM` cohorts are identical and correspond to year 2, and so on. Similarly, if all ages have the same diet, one `.DIE` cohort suffices for all the corresponding `.BIO`-file cohorts.

You can divide annual growth into several run intervals either to compute seasonal consumption patterns or if prey abundance varies seasonally (Rice and Cochran 1984) such that consumption rates show strong seasonal changes.

Spawning Loss

Model 2 computes spawning loss as a fixed proportion of weight, on a specific day of the year, for all cohorts older than the designated `1st Spawning Cohort`. The same proportional weight loss applies to all mature fish, per the typical mature individual in a population. Therefore, different cohorts cannot have different spawning loss, and mean proportional weight loss is an average of male and female data.

Maintenance Consumption

To better run annual growth cycles, *Model 2* can compute, on a daily basis, the consumption required to maintain current weight when water temperature is below a `.BIO`-specified value. You can also use this approach to determine maintenance ration as a function of fish weight or water temperature.

Energy Density

Energy densities of predator and prey can significantly affect *Model 2* computations of consumption, production, conversion efficiency, and P-value. Both seasonal and size-related energy density variations have been observed for many fish (Craig 1977; Stewart et al.1983).

Energy density variations can be significant when modeling seasonal patterns, whereas, average energy densities output fairly accurate annual values. Also, production outputs are less likely affected by energy density than by population size and mortality rate.

Stewart and Binkowski (1986) found that including the seasonal cycle of caloric content in alewives had a relatively small effect on annual production and consumption outputs (<10%) — but a large effect on seasonal outputs (70-100%).

Model 2 requires energy density in calories per gram wet weight. Many studies, however, report energy density in calories per gram dry weight. Generally, dry weight is: 10 to 15 percent of wet weight for zooplankton; 10 to 25 percent, for larger aquatic invertebrates; and 25 to 30 percent, for mature fish.

Table 2 provides dry/wet weight energy density values as reported for several organisms.

For more information on energy densities and the related research methods, see Cummins and Wuycheck (1971), Schindler et al. (1971), Bottrell et al. (1976), Vijverberg and Frank (1976), Craig (1977), Kitchell et al. (1977a), Driver (1981), and Downing and Rigler (1984).

(*Model 2* uses wet weight energy density, calories per gram wet weight — which can be estimated by multiplying dry-wet weight percentage by dry weight energy density, calories per gram dry weight.)

Table 2

Energy density and dry-wet weight percentage for several organisms.

Organism	Dry:Wet Weight Percentage	Calories per Gram Dry Weight	Calories per Gram Wet Weight	Seasonal or Ontogenetic Effects Considered?
Rotifers	10[a]			
Cladocerans	10-12[b,c]	5451-5463[d, e, f]	545-656	yes[g]
Copepods	11-14[a, b, h]	4121-6278[f, h]	454-880	yes[h]
Leptodora	4[e]	5182-6150[e]	207-246	yes[e]
Mysids	16[a]		710-1030[e, i]	
Amphipods	24-28[e]	4072[e]	1058[e]	
Diptera larvae	5-12[c, e]	4936[e]	250-592	yes[c]
Yellow perch	24-28[j]	4362-5198[j]	1075-1410[j]	yes[j]
juveniles	12[k]	4946[l]	600[m]	yes[l]
Alewife	20-35[n]		1200-2270[n]	yes[n, p]
larvae			800[q]	
Salmonids	28-41[r]	5421-7140[r]	1247-2739[r]	yes[r]

[a] Downing and Rigler (1984)
[b] Dumont et al. (1975)
[c] C. Luecke, Utah State Univ., Logan (per. comm.)
[d] Lei and Armitage (1980)
[e] Cummins and Wuychuck (1971)
[f] Vijverberg and Frank (1976)
[g] Snow (1972)
[h] Schindler et al. (1971)
[i] Rudstam (1989)
[j] Craig (1977)
[k] derived from information in Lin (1975) and Mills and Forney (1981)
[l] Mills and Forney (1981)
[m] Post (1990)
[n] Stewart and Binkowski (1986)
[p] Flath and Diana (1985)
[q] Hewett and Stewart (1989)
[r] Rottiers and Tucker (1982)

Bioenergetics Equations and Model 2 Options

This chapter describes *Model 2* bioenergetics calculations — beginning with the ***basic balanced energy equation***, then describing its ***component functions***.

Previous researchers developed diverse functions for modeling consumption, respiration, egestion/excretion, and predator energy density. Because different functions seem to work best for different species, several options are included.

However, the source notations are transcribed for *Model 2* program code. So, the following description of bioenergetics parameters uses both variable names from *Model 2* program code and the most common parameter names from source references.

THE BALANCED ENERGY EQUATION

Model 2 is essentially an accounting of energy intake and use by fish:

Consumption = (Metabolic Loss) + (Waste Loss)+(Growth)

or, using the balanced energy equation variables (defined in the remainder of this chapter):

$$C = (R + S) + (F + U) + (\Delta B)$$

Water temperature, fish size, energy density, and prey availability are the primary factors affecting the energy budget. The model balances the energy budget daily.

All computations are based on specific rates — grams of prey per gram of predator per day, wet weights — then converted to rates per fish and per population. Weights are adjusted for energy densities of both predator and prey.

CONSUMPTION

Consumption is the amount of food consumed by fish – generally determined by calculating maximum specific feeding rate (grams of prey consumed per gram of body weight per day) as an allometric function of weight. The maximum specific feeding rate is then modified by a water temperature dependence function and by a proportionality constant representing prey availability.

The basic equations for determining feeding rate are:

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

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

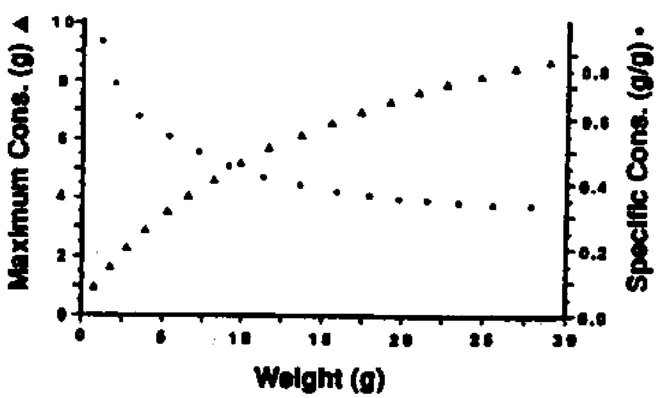
where:

C_{max} = maximum specific feeding rate ($g * g^{-1} * d^{-1}$)
W = fish weight (g)
a = intercept of the allometric function
b = slope of the allometric function
C = specific feeding rate ($g * g^{-1} * d^{-1}$)
P-value = a proportionality constant
T = water temperature (degrees centigrade)
f(T) = water temperature dependence function

Figure 4 shows C_{max} as a function of weight for yellow perch (*Perca flavescens*) at optimum water temperature. **P-value** is the y-axis scaling factor, denoting a proportion (from 0 to 1) of the maximum feeding rate actually exhibited by the fish. For example, a **P-value** of 0.5 indicates that the fish was feeding at half its maximum possible rate, over all water temperatures and fish weights, during the time modeled.

FIGURE 4

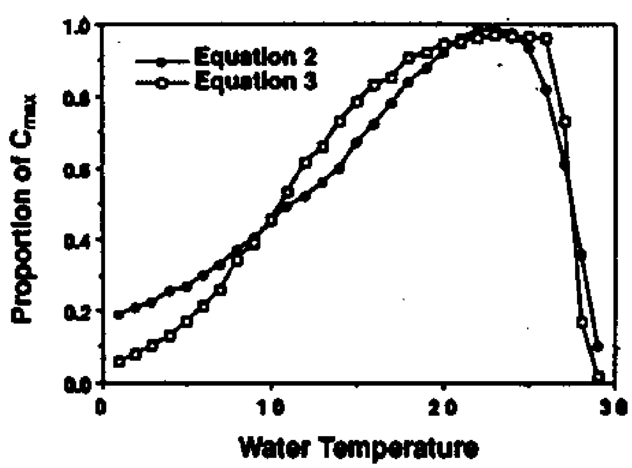
Maximum Consumption (▲) and Specific Consumption (●) versus Weight for Yellow Perch at Optimum Water Temperature



Model 2 includes three water temperature dependence functions, f(T), for consumption. Figure 5 shows sample functional curves.

FIGURE 5

Temperature Dependence Functions



f(T):Consumption Equation 1

$$f(T) = e^{(\theta \cdot T)}$$

with parameters and equivalent model variables:

a (= CA), b (= CB), θ (= CQ)

This is a simple exponential function, where θ is the water temperature dependence coefficient. It has no means of decreasing consumption as water temperature increases to stressful levels and thus is useful only when temperatures are at or below optimum.

For computing C_{max}, **a** is the intercept of the weight dependence function for 1-gram fish at 0 centigrade, and **b** is the weight dependence coefficient.

Stewart et al. (1983) used this function for lake trout.

f(T):Consumption Equation 2

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

where:

$$V = (T_M - T) / (T_M - T_O)$$
$$X = (Z^2 \cdot (1 + (1 + 40 / Y)^{0.5})^2) / 400$$
$$Z = \ln\theta \cdot (T_M - T_O)$$
$$Y = \ln\theta \cdot (T_M - T_O + 2)$$

with parameters:

a (= CA), b (= CB), θ (= CQ),
T_O (= CTO), T_M (= CTM)

This water temperature dependence function is most appropriate for warm-water species, ranging from near 0 at low water temperatures to 1 at optimum water temperatures and back to 0 at maximum water temperatures (Figure 5).

Herein, **a** is the intercept (at 1 g) for the weight dependence of consumption at optimum water temperature (T_O), **b** is the weight dependence coefficient, T_M is the maximum water temperature (above which consumption ceases), T_O is the optimum water temperature, and θ approximates a Q_{10} for the rate at which the function increases over relatively low water temperatures.

Kitchell et al. (1977b) used this function for yellow perch and walleye (*Stizostedion v. vitreum*). It has also been used for bluegill (*Lepomis macrochirus*) and largemouth bass (*Micropterus salmoides*) (Kitchell et al. 1974; Rice 1981; Rice et al. 1983).

f(T):Consumption Equation 3

$f(T) = K_A * K_B$

where:

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

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

$G1 = (1 / (T_O - \theta)) * Ln((0.98 * (1 - K1)) / (K1 * 0.02))$

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

$L2 = e^{(G2 * (T_L - T))}$

$G2 = (1 / (T_L - T_M)) * Ln((0.98 * (1 - K4)) / (K4 * 0.02))$

with parameters:

a (= CA), b (= CB), θ (= CQ), T_O (= CTO),
T_M (= CTM), T_L (= CTL), K1 (=CK1), K4 (=CK4)

This is the Thornton and Lessem (1978) algorithm, which provides a better fit for some cool- and cold-water species, especially at lower water temperatures. It is essentially the product of two sigmoid curves — one of which fits the increasing portion of the water temperature dependence curve (K_A); the other, the decreasing portion (K_B).

Overall, **a** is the intercept for the weight dependence of consumption at the optimum water temperature, and **b** is the weight dependence coefficient. For the increasing portion, θ is the lower water temperature at which dependence is K1 (a low value, such as 0.15) of the maximum rate, and T_O is the higher water temperature at which dependence is 0.98 of maximum. For the decreasing portion, T_M is the water temperature ($\geq T_O$) at which dependence is still 0.98 of maximum, and T_L is the water temperature at which dependence is K4 (a low value, usually around 0.01) of the maximum rate.

Stewart et al. (1981) used this function for coho salmon (*Oncorhynchus kisutch*) and chinook salmon (*O. tshawytscha*), and Stewart and Binkowski (1986) used it for alewife (*Alosa pseudoharengus*).

RESPIRATION AND SPECIFIC DYNAMIC ACTION

Respiration is the amount of energy (or weight equivalent) used by fish for metabolism — determined by calculating resting metabolism as an allometric function of weight, then increasing that value through a water temperature dependence function and a factor representing activity. Specific dynamic action (also called apparent heat increment) is calculated separately, then added to respiration to obtain ***total metabolic rate***.

The basic equations for determining respiration and specific dynamic action are:

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

$S = SDA * (C - F)$

where:

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

Energy lost to specific dynamic action is modeled as a proportion of the amount of energy assimilated (**SDA**, range 0 to 1), in other words, consumption minus egestion.

Model 2 includes two water temperature dependence functions, f(T), for respiration — which also compute activity metabolism differently.

f(T):Respiration Equation Set 1

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

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

where:

$VEL = K1 * W^{(K4)}$, if $T > T_L$
or
$VEL = ACT * e^{(BACT * T)} * W^{(K4)}$, if $T \leq T_L$

with parameters:

α (= RA), β (= RB), θ (= RQ), T_O (= RTO),
T_M (= RTM), T_L (= RTL), K1 (= RK1), K4 (= RK4),
ACT (= ACT), BACT (= BACT), SDA (= SDA)

In this simple exponential function, θ is the water temperature dependence coefficient.

For weight dependence,

- α is measured as grams of oxygen ($g\ O_2 * g^{-1} * d^{-1}$), which is an improvement over α measurements as grams of body weight (Kitchell et al. 1977b; Kitchell and Breck 1980). α is the intercept for specific standard metabolism versus weight, water temperature, and swimming speed (for 1-gram fish at 0 centigrade and 0 swimming speed), and is corrected daily for the relative energy density of the fish and its prey.

- β is the weight dependence coefficient for standard metabolism.

Activity is computed per the swimming speed function developed for lake trout by Stewart et al. (1983), which provides much latitude. Swimming speed can be a function of weight alone (above a cutoff water temperature of T_L), a function of weight and water temperature (below the cutoff water temperature of T_L), a constant velocity (by setting T_L, T_M, K4, and BACT to 0; setting K4 and ACT to 1; and setting T_s to desired velocity). The units for swimming speed are centimeters per second.

K1 is the intercept for weight dependence of swimming speed above the cutoff water temperature (T_L). K4 is the slope for weight dependence of swimming speed at all water temperatures.

- ACT is the intercept (in centimeters per second for a 1-gram fish at 0 centigrade) of the relationship for swimming speed versus water temperature and weight at water temperatures below T_L.

- BACT is the coefficient for water temperature dependence of swimming speed at water temperatures below T_L.

T_O and T_M are not water temperatures. T_O is the coefficient for swimming speed dependence of metabolism. T_O and T_M together allow for a linear relationship between the coefficient for swimming speed dependence of metabolism and water temperature, but this relationship has not yet been fully examined. (You can set T_M at 0 for no relationship.)

See Stewart et al. (1983) and Stewart and Binkowski (1986) for a more complete description of the parameters.

f(T):Respiration Equation Set 2

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

ACTIVITY = ACT

where:

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

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

$$Z = Ln\theta * (T_M - T_O)$$

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

with parameters:

α (= RA), β (= RB), θ (= RQ), T_O (= RTO),

T_M (= RTM), ACT (= ACT), SDA (= SDA)

Herein, T_O is the optimum water temperature for respiration (temperature at which respiration is highest), T_M is the maximum water temperature (lethal), and θ is the water temperature dependence coefficient.

For calculating C_{max}, α is measured as grams of oxygen ($g\ O_2 * g^{-1} * d^{-1}$) and is the value for specific standard metabolism (for 1-gram fish at optimum water temperature, T_O, not Ø centigrade as in Set I). β is the weight-dependence coefficient.

Activity is a constant (ACT) times resting metabolism, sometimes called the "Winberg multiplier" (Winberg 1956). Typical values range from 1 to 2 (Kitchell et al. 1977b), depending not only on how active the fish is in general but also on the actual metabolic level represented by the weight dependence function — in other words, basal versus resting versus active metabolism.

WASTE LOSSES (EGESTION AND EXCRETION)

Model 2 includes three equations for computing egestion (fecal waste) and excretion (nitrogenous waste) — either as constant proportions of consumption (1) or as functions of water temperature and consumption (2 and 3). Waste losses are computed in grams of waste per gram of fish per day.

Egestion/Excretion Equation Set 1

Egestion: $F = FA * C$

Excretion: $U = UA * (C - F)$

with parameters: FA (=FA), UA (=UA)

Simply stated, egestion is a constant proportion of consumption, C (Kitchell et al. 1974), and excretion is a constant proportion of consumption minus egestion (egested calories cannot be excreted). This formulation suffices for many growth/consumption computations (Bartell et al. 1986).

Egestion/Excretion Equation Set 2

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

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

with parameters:

α_F (= FA), β_F (= FB), γ_F (= FG), α_U (= UA),

β_U (= UB), γ_U (= UG)

This option includes both a water temperature term and a feeding rate term and is most appropriate when diet is either all invertebrate or all fish.

α_F is the intercept for the proportion of consumption egested versus water temperature and ration, β_F is the coefficient for water 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 versus water temperature and ration, β_U is the coefficient for the water temperature dependence of excretion, and γ_U is the coefficient for the feeding level (P-value) dependence of excretion.

This formulation is from Elliott (1976), based on a study of brown trout (*Salmo trutta*) feeding on all invertebrate prey, and is described in Kitchell et al. (1977b).

Egestion/Excretion Equation Set 3:

Egestion: $F = PF * C$

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

where:

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

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

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

PREYK[n] = indigestible proportion of nth prey

DIET[n] = proportion of nth prey in diet

with parameters:

α_F (= FA), β_F (= FB), γ_F (= FG), α_U (= UA),

β_U (= UB), γ_U (= UG)

This option includes correction factors (**PF** and **PFF**) for digestibility and is useful as diet changes over time–for example, from mostly crayfish (indigestible exoskeleton) in spring to mostly fish (entirely digestible).

`PREYK` and `DIET` values are read from data files (`.BIO` and `.DIE`, respectively). Excretion computations and parameters used are as described in Set II. This formulation is also from Elliott (1976) and is described in Stewart et al. (1983).

GROWTH AND SPAWNING LOSSES

Growth refers to either an increase or a decrease in fish body weight and can be stated in terms directly from the balanced energy equation as:

$\Delta B = C - (R + S) - (F + U)$

Growth is computed as a rate, in grams of prey per gram of predator per day, and growth rate times predator weight indicates the total grams of prey consumed that are available for growth. This total is then converted to grams of predator weight based on the relative energy density (calories per gram, wet weight) of both prey and predator. Thus, predator and prey energy densities vary independently.

Energy Density Conversion

Model 2 includes two energy density options for computing grams of growth — either based on a `.PYC` file or as a function of predator body weight. If predator energy density is based on a `.PYC` file, then calories in the fish plus calories available for growth (which can be negative) on the current day, divided by energy density on the next day, equals fish weight on that next day. If predator energy density is computed as a function of body weight, then **Alpha** and **Beta** parameters from the **Species General Data** section of the `.BIO` file are used (Stewart et al. 1983).

A simple linear regression denotes predator energy density as a function of body weight:

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

where:

CD = predator energy density (calories per gram, wet weight)

α = intercept

β = slope

W = predator weight (grams)

You can have two sets of **Alpha** and **Beta** values ($\alpha 1$, $\beta 1$ and $\alpha 2$, $\beta 2$) to define equations for two size ranges. You can also specify **Weight Cutoff**, when *Model 2* switches from equation 1 to equation 2. Thus, to run only one equation, set **Weight Cutoff** either (1) higher than the largest fish, for only $\alpha 1$ and $\beta 1$, or (2) to 0, for only $\alpha 2$ and $\beta 2$.

Note: Do not set β to 0 to run constant predator energy density; this results in a "divide by zero" error. Rather input the constant predator energy density for days 1 and 365 in the `.PYC` file.

The importance of energy density data depends on your question, the relative differences between predator and prey energy densities, and whether predator or prey show strong seasonal or ontogenetic energy density changes. For example, detailed energy density data were important in modeling salmonid consumption of alewife in Lake Michigan (Stewart et al. 1983) because alewife undergo drastic seasonal energy density changes and salmonids increase in energy density as they grow.

Spawning Loss

Model 2 computes reproductive tissue growth as part of growth and allows for weight loss due to spawning. If a run interval includes a spawning date for mature fish, spawning loss is computed as a proportion of weight, which is subtracted on that day.

Mean predator energy density at spawning applies to both somatic and gonadal tissue. This assumption is generally false, but the error is typically small. You can account for the higher energy density of gonadal tissue by increasing energy density before, or on the day of, spawning in the `.PDC` file.

CHAPTER 4

Modeling Tips and Strategies

EDUCATING MODEL USERS

Model 2 is a powerful and cost-effective tool for addressing questions of fish growth, production, consumption, and predator-prey interactions, but it requires some experience to use efficiently. To help educate model users, we have employed both training workshops and a college-level laboratory exercise.

Workshops

Wisconsin Sea Grant can organize workshops to instruct *Model 2* users. As of autumn 1991, we had conducted more than a dozen workshops attended by biologists from universities, governmental agencies, and the private sector. Workshop objectives can range from a general introduction to detailed analysis of a specific research or management question. Two-day workshops with up to 20 participants seem to work best. Wisconsin Sea Grant will arrange for instructors, instructional materials, and continuing education credit. The hosting institution provides computer facilities, local arrangements, and travel costs for instructors (usually one instructor per 4-5 participants). Participants should bring their own data to address questions of concern. For more information on workshops, contact Clifford Kraft, Sea Grant Advisory Services, ES-105, University of Wisconsin-Green Bay, Green Bay, WI 54311-7001; phone (414) 465-2795 and fax (414) 465-2376.

A College-Level Laboratory Exercise

Through *Model 2*, students can explore the effects of physiological and ecological variables on the dynamics of fish growth and consumption, right in the classroom. Bioenergetics modeling can also act as a surrogate for laboratory experimentation and be used as a guide for developing logical and incisive experimental work.

To introduce upper-level undergraduate and graduate students to bioenergetics modeling, we developed a laboratory exercise built around a series of structured questions (Append. 9). These questions relate to walleye in Lake Mendota and use the WALLEYE sample data files (Append. 4). The first question in the exercise requires students to conduct the baseline run as described in the "Keystroke Guide" (Append. 5).

STRUCTURING EFFICIENT RUNS

Model 2 can be applied through various strategies to address different research and management questions and complement field data. Learning to structure model runs efficiently can save considerable time and extend model usefulness.

Absolute versus Relative Estimates

Model 2 can be used to derive absolute estimates of consumption, growth, or production. This is particularly useful when field estimates would be difficult or time consuming to obtain. The accuracy of these estimates will depend on the quality of the input data and how well you meet model assumptions. Your questions will determine how accurate your answers must be.

An alternative to absolute estimates is determining the relative difference between a run under standard conditions and a second run depicting changes in environment, management, or predator-prey interactions. With this approach, any biases in the model or data are likely to have similar effects between runs and should cancel out when you subtract model estimates to derive the differences. For example, if your question is how much consumption could change under a size limit, frame your answer as a percentage change relative to the standard condition with no size limit.

Generating Patterns

Model 2 can also estimate what happened in the interval between data points and, by saving output at frequent intervals, generate patterns for outputs over time. This process can help define key indicators such as maximums and minimums, periods of rapid change, and time to reach threshold levels, which can also be difficult to discern in the field.

Bounding the Question

One of the most powerful applications of modeling is to set bounds on outcomes by evaluating the effects of variations in inputs. You can model a broad spectrum of possible effects, then evaluate outputs and focus further modeling or field efforts on those areas likely to be most important for addressing your question. When the effects of a variable, parameter, or policy are unknown, conduct model runs using values that span the likely range for that input. The results set bounds on model outputs as affected by that input. If output range is narrow, then that input is probably not important in answering this question. Otherwise, you can conduct additional runs at intermediate levels to define a response curve or a critical range of values for the input. This process can easily be expanded to multiple inputs.

This strategy is essentially a sensitivity analysis particular to your question. This approach can be used to analyze potential causes of an observed response (Rice et al. 1983) or to develop efficient data collection procedures for the field. Remember that the ultimate question is not, "How much will the output change?" but rather, "Will my conclusions change?"

Compensatory Responses

Model 2 estimates population level consumption and production, but contains no functional responses for predator-prey interactions, density dependence of growth, and so on. Users must define model scenarios that represent compensatory population responses. For example, to estimate increased consumption caused by a new minimum size limit, you can calculate the decrease in fishing mortality due to the size limit, then run *Model 2* for a new consumption estimate. However, increased predator numbers could reduce forage levels and growth rates. You must simulate that response by either reducing P-value or fish weight at the end of the run. The bounding approach described above can be used to investigate the range of possible compensatory responses.

The Constant P-value Assumption

Model 2 assumes that prey availability (P-value) is constant for each growth interval (cohort). Short-term variation in prey availability certainly occurs, but the model is designed to average that variability over time. The alternative is to split the growth interval into smaller periods with separate P-values. Estimates of total consumption are typically similar between simulations using constant P-values and those using shorter time intervals (Rice and Cochran 1984; Stewart and Binkowski 1986). However, seasonal patterns of consumption are usually best estimated by using shorter intervals with separate P-values (Hewett and Stewart 1989).

Typically, growth intervals for modeling are based on field sampling dates. If you have monthly weight data, you could model a year in 12 intervals. However, modeling the same year in a single interval allows you to assess the constant P-value assumption. If the modeled growth trajectory fits the intermediate points well, then the assumption of constant P-value is supported. Otherwise, you can break the year into smaller segments and run P-fits for each segment. Trends or shifts in P-value over successive intervals suggest changes in prey availability.

If you suspect seasonal changes in prey availability but have only annual weight data, you can still model suspected differences by changing P-values yourself. First, divide the year into shorter intervals (cohorts) of presumed differing prey availability. Run cohort 1 with the known beginning weight and an assumed P-value to estimate final weight. That final weight becomes the start weight for cohort 2. Input that weight for cohort 2, modify the P-value to match assumed prey availability in the second interval, then run the model to determine final weight for cohort 2. Follow this procedure until the last time interval. For the last interval, run a standard P-fit using computed final weight for the previous cohort as the start weight and the observed year-end weight as final weight. An extreme P-value, or the inability to fit ***any*** P-value, for this last cohort means your assumptions regarding prey availability were not plausible. You can then repeat the procedure, modifying your assumptions about prey availability. Exploration of various prey availability scenarios can tell you a lot about how the fishery could function and help design field efforts to evaluate prey resources.

Calculating Maintenance Ration

For exploring prey availability questions, it is often useful to calculate a maintenance P-value by assuming that the fish did not gain or lose weight over an interval. Two methods exist within this model for calculating a maintenance ration. Both produce similar numbers but differ in their methods and assumptions.

The easiest method is to input the same initial and final weights in the species data file. This method will calculate an average P-value that results in the final and initial weights being identical. Weight between the two dates, however, is free to vary as a function of temperature, prey energy density, and diet proportions.

The second method is to set the maintenance temperature in the `Species File General Data` screen. For any day that experiences a temperature at or below the maintenance temperature, the model calculates a P-fit for ***that day*** that results in no growth. This second method takes longer to run since each day has to be iteratively fit, but it has the advantage that weight stays constant for the entire interval of time that is being modeled.

Typically, maintenance P-values are between 0.10 and 0.25, indicating that the fish requires relatively little food to maintain itself and has considerable scope for growth at higher feeding rates. That growth potential may not be realized in the field due to food limitations, competitive interactions, predator avoidance, and so on.

High maintenance P-value (above 0.5) indicates that the fish requires considerable food to meet physiological demands and thus has little scope for growth at higher feeding rates. Possible reasons include extremes of temperature, low prey energy density, physiological stress, parasites, or disease. Extreme P-values could also result from errors in field data, such as biased weight estimates.

MULTIPLE COHORT RUNS

Efficient use of *Model 2* often involves simulating multiple cohorts in a single run. Time intervals for a cohort can be up to one year long. You cannot model different species in a single run because each species requires its own `.BIO` file.

Modeling One or Many Groups of Fish

Multiple cohort runs can represent a single group of fish over many time intervals (e.g., one year-class over successive years of life), many groups over a single time interval (e.g., all age-classes in a population over one year), or a combination of both. It is not necessary for the time intervals covered by successive cohorts to be of equal length or even to be contiguous.

When modeling a single group of fish over contiguous time intervals, the final weight and population size for one cohort will be the start weight and population size for the next cohort. However, if you model this group in successive years but only during spring through autumn of each year (the growing season), final weights and population sizes for one cohort will not be the starting values for the next cohort if any growth or mortality occurs during winter.

When you are modeling an entire population over one year, each cohort represents successive age classes within the population. The final weights and population sizes for one cohort will generally not be the starting values for the next because each age-class differs in year-class strength, growth, and mortality.

Many bioenergetics analyses will require a combination of run types listed above. For example, if you are modeling three year-classes, all growing over one year, but in six-month intervals (total of 6 cohorts), you could run cohorts 1 and 2, 3 and 4, and 5 and 6 representing successive six-month intervals for year classes 1, 2, and 3, respectively. Or, cohorts 1, 2, and 3 could represent the first six months for each year class and cohorts 4, 5, and 6, the second six months. Your choice of cohort structure depends on the type of output desired.

The choices for saving and zeroing output variables, under **`BIOENERGETICS RUN OPTIONS`**, give you many options for structuring multiple cohort runs. For totals for each cohort, save output with the `start day of cohort` and `final day of cohort` options and zero all cumulative variables `after each cohort`. For totals over the entire run, zero cumulative variables with the `start of run only` option. In addition, you can save data at more frequent intervals to generate totals during the run or patterns of outputs over time. Other options produce totals over each year, each mortality interval, or each output interval.

Correspondence of Cohorts between Data Files

For multiple cohort runs, *Model 2* matches each cohort in the **.BIO** files with the appropriate cohort in the seasonal files. You must structure the cohorts in the seasonal files to provide the correct match. The simplest method is to create one-to-one correspondence between seasonal and **.BIO** file cohorts.

For example, assume you are modeling eight **.BIO** cohorts. Cohorts 1 and 2 have the same diet, A, and all older cohorts have a different diet, B. Using one-to-one correspondence, the **.DIE** file would have 8 cohorts with cohorts 1 and 2 containing identical data for diet A, and cohorts 3 through 8 containing identical data for diet B.

However, it is not necessary to repeat the last cohort in a seasonal file when it applies to all later **.BIO** cohorts. In the example above, you could eliminate cohorts 4 through 8 in the **.DIE** file. When *Model 2* runs **.BIO** cohort 4, it cannot find **.DIE** cohort 4 so it substitutes **.DIE** cohort 3, the last cohort in the file. Similarly, if all ages had the same diet, one **.DIE** cohort would be sufficient. However, if age 8 fish had a different diet, C, eight **.DIE** cohorts would be necessary (two A cohorts, five B cohorts, and one C cohort).

Remember that each cohort in seasonal files must contain a full year of data, even if the growth interval for the corresponding **.BIO** cohort is less than a year.

MORE THAN SIX DIET ITEMS

Model 2 will use up to 10 diet items for calculating the energy budget, but saves output for only the first six items. Typically, this is not a problem. Total grams consumed over all diet items is contained in output fields **36 SITotCons** and **44 SPTotCons**. You can often condense more than six diet items to six or less by combining diet proportions and averaging energy densities.

For consumption data on more than six diet items, rearrange the **.DIE** file so that items 7 through 10 are now items 1 through 4, then rerun the model. Remember that you must also rearrange the energy densities in the **.PYC** file. Total consumption should be identical between runs because you are still using the same diet and energy density data, just in a different order.

MODEL LIMITATIONS

Model 2 can be a very useful and accurate tool for addressing a wide variety of fisheries questions, but, like any mathematical tool, it has limitations due to model structure and data quality.

Population Level Modeling

Model 2 is basically a single-fish model, and that single fish often represents the average individual in a group. Population level estimates are computed by multiplying single-fish values by population size, which is derived from your estimates of initial population size and mortality rates. Any error in field measurement of weight produces errors in consumption estimates for an individual fish. However, field estimates of population size or mortality rate often have confidence intervals of 50 percent or larger. Errors in these inputs are more likely to limit accuracy in estimates of population level consumption.

Modeling Extremes of Temperature or Size

Most physiological parameters used in *Model 2* are based on laboratory studies, which use fish of moderate size that are easy to handle and temperatures that are not extremely stressful. While these parameters can work well over the temperature and size range from which they were derived (which approximate the normal range found in the field), one should be cautious about modeling growth at extreme temperatures or sizes that extrapolate beyond these data.

Temperature Extremes

For some cool- or warm-water species, growth at cold temperatures has proved difficult to model accurately. Original parameters for largemouth bass (Rice et al. 1983) did not work well at temperatures below about 10 degrees Centigrade, but have been modified based on new data.

Modeling fish at stressfully high temperatures has also proved difficult. Few data exist to develop parameters describing high temperature physiology, which can change rapidly over small temperature increments. Also remember that Consumption Equation 1 (the lake trout equation) is exponential and **is not appropriate** at temperatures above optimum (about 10 to 11 degrees Centigrade for lake trout).

Fish Size

Attempts at applying model parameters derived from adult fish to early life history stages have met with limited success. Because of the allometric weight relationships contained in *Model 2*, using adult fish parameters to model larvae and young-of-year fish results in extrapolation of 1 to 3 orders of magnitude and can cause significant biases.

Generally, for fish larger than 10 grams, adult parameters work well. For fish smaller than 1 gram, parameter modifications are usually necessary. For fish from 1 to 10 grams, results have been mixed.

Researchers have taken two approaches to develop reasonable equations for young fish: (1) changing parameters for metabolism and consumption and (2) reducing energy densities. Post (1990) suggested that metabolic and consumption rates for small fish could be higher than predicted from adult parameters (but see Fox 1991). When he applied the yellow perch equation to field data for young-of-year perch of 0.01 to 2.00 grams, the model underestimated consumption rates and overestimated conversion efficiencies (Post 1990). He modified the physiological parameters, based on both laboratory and field experiments, to increase consumption and respiration (Append. 3) and produce good fits to observed growth and consumption.

Hewett and Stewart (1989) modeled larval alewives using both adult parameters and parameters modified to produce higher metabolic and consumption rates. The two parameter sets represented bounds on metabolic rates for larval clupeids, based on literature sources. Over the 40-day larval period, the higher metabolic rate resulted in a 15 to 20 percent increase in consumption.

Besides differences in physiology, the energy density of juvenile fish could be lower than for adults (Flath and Diana 1985). Hewett and Stewart (1990) used energy densities from 600 to 1,000 calories per gram, the range of suggested by literature sources. Over the 40-day larval period, higher energy density values resulted in a 12 percent increase in consumption. For yellow perch, energy density of juveniles is about half that of adults. Post (1990) assumed an energy density of about 600 calories per gram wet weight for larval perch.

The Constant Physiology Assumption

Generally, bioenergetics modeling assumes that the physiology of a species is constant over time and among populations. Thus, the model can be applied to different geographic locations without reestimating physiological parameters. Literature reports of model applications for a single species in different waterbodies support this assumption (see Bibliography listing for walleye and salmon). However, few data exist on physiology of a single species from different waterbodies.

The bioenergetics model is often used to explain field observations based on environmental factors (Kitchell et al. 1977b; Rice et al. 1983) without resorting to changes in physiology. In some cases, physiological differences can be manifest in ways accounted for by the model. For example, Schott et al. (1978) found hormonal differences between male and female yellow perch that resulted in increased consumption and growth rates for females. This could be accounted for within the model as differences in P-values between sexes.

When necessary, physiological parameters can be modified to fit the application at hand. The most common situation could be modeling fish of a different strain, or from a different geographic range, that have different temperature preferences. See "Modeling New Species" below for a list of references on temperature preference data.

Activity

Activity is a poorly understood component of fish bioenergetics (Boisclair and Leggett 1989, 1990, 1991; Fox 1991; Hewett et al. 1991). In *Model 2*, both temperature and weight affect the amount of energy expended for activity. These effects are constant within a model cohort, and we generally assume they are constant among cohorts and populations. However, few data are available with which to evaluate these assumptions. Parameters determining activity level can easily be changed to investigate the effects of variation in activity over time or between populations.

In Chapter 3, we indicated that the weight and temperature dependence terms for respiration define resting metabolism, but these terms will include any activity metabolism evident in the data from which they were derived. For yellow perch, respiration parameters derived from Solomon and Brafield (1972) include normal activity levels in laboratory aquariums. Thus, an activity multiplier of 1 (parameter ACT) could be appropriate for perch.

MODEL VERSUS FIELD ESTIMATES

The bioenergetics model can accurately estimate growth and consumption when applied to unbiased data under conditions meeting model assumptions. Model estimates can actually be more accurate than field estimates when unknown biases exist in field data.

Both model results and field data are estimates, derived from different sets of assumptions. If model and field estimates don't agree, it is not always obvious which are in error. The process of bounding outputs (described earlier in this chapter) can be used to assess the effects of errors in data or in model specifications, or of violating assumptions regarding sampling design or model application. Results can be used to design effective field studies or explicit tests of model predictions.

MODELING NEW SPECIES

To model new species, you must develop a set of physiological parameters for that species, then input those values into a new `.BIO` file (or modify an existing file). You do not need to modify program code.
For new species, start with the simplest model, then increase complexity, if necessary. Consult the references cited in Chapter 3 for procedures to estimate model parameters. Typically, all the necessary data are not available for any one species, so you must use parameters derived from related species. Across species, *Model 2* growth and consumption estimates are relatively insensitive to changes in egestion and excretion parameters (Bartell et al. 1986). Optimal temperatures often differ among species and several references list temperature preferences (Coutant 1977; Jobling 1981; Houston 1982; Wismer and Christie 1987).

When developing new species parameters ***for adults***, we suggest some rules of thumb:

- For Consumption Equation 2, the weight-dependence coefficient (parameter CB) is about -0.3 and CQ is about 2.3. CA typically ranges from 0.15 to 0.35 but should be derived from species specific data. Optimum (CTO) and maximum (CTM) temperatures can be approximated by preferred and upper lethal temperatures, respectively.
- For Respiration Equation Set 2, the weight-dependence coefficient (RB) is about -0.2 and RQ is typically 2.1. RTO can be approximated by the upper lethal temperature with RTM set about 3 degrees Centigrade higher. SDA is about 0.16.
- For Egestion/Excretion Equation Set 1, egestion (FA) is typically 0.15 and excretion (UA), about 0.1.

For any new model, it is a good idea to conduct error or perturbation analysis (Kitchell et al. 1977b; Stewart et al. 1983; Bartell et al. 1986).

MODIFYING PROGRAM CODE

Your *Model 2* diskette package contains program code files, which can be modified to suit your needs. However, to use *Model 2* code in another program, you must obtain copyright permission. *Model 2* is programmed in Borland International TURBO PASCAL 5.5, a compiled language, so the programs must be recompiled when modified. For compiling *Model 2*, the primary file is `MENU.PAS`, and all `.PAS` and the `.TPU` files listed in Appendix 1 must be accessible to the PASCAL compiler.

Appendices

Differences between *A Generalized Bioenergetics Model of Fish Growth for Microcomputers* and *Fish Bioenergetics Model 2* and Instructions for Updating Files Created in Version 1

Model 2 operates in the same basic manner as our first model, but incorporates a number of changes that make it easier to use. The bioenergetics equations are the same; so, the energy-budgeting process is unchanged. Specific changes include:

- a friendlier user interface with highlighted menu options, windows for file choices, simplified data entry, and extensive use of default values
- a simple graphics package, which allows plotting, printing and file storage of graphs
- a file containing user-defined default values, for run options and graphics, which can be edited from the main menu
- seasonal files (instead of species files) now store the number of cohorts for seasonal data and the number of prey items
- prey energy densities can no longer be stored in the species file, so all runs require that prey energy densities be listed in a seasonal file (identified by the `.PYC` suffix)
- the ability to replicate cohorts in both species and seasonal files
- results from P-fit runs can be written to the screen, printer, or a disk(ette) file, and you have the option of automatically updating P-values in the species files
- use of instantaneous mortality rates and the assumption of competition between natural and harvest mortality
- eight new variables (44 total) stored in the output file, including total consumption over all prey items and number and weight of fish harvested
- automatic recognition and use of a math coprocessor chip if your computer is so equipped
- an updated list of physiological parameters, including newly developed sets for a number of fish and revisions to many previously published parameter sets
- an expanded discussion of application strategies and a new appendix, providing a keystroke guide to a sample model run

Intermediate versions of our first model, which were used in workshops, will contain some, but not all, of the changes.

Updating Files

Some *Model 2* changes make files created with previous model versions incompatible. You will have to update those files. This can be done with the *Model 2* `FIXFILE.EXE` utility file. After choosing the data directory, you will see the following screen:

```
UPDATE BIOENERGETICS DATA FILES TO
VERSION 2

1) Update diet (.DIE) files
2) Update temperature (.TEM) files
3) Update prey calorie (.PYC) files
4) Update predator calorie
   (.PDC) files
5) Update species (.BIO) files
6) Change file directory
7) QUIT to DOS

Choice? -> 1
```

Use options `1)` through `5)` to convert your data files. When you choose a file type, *Model 2* updates all files of that type in the active data directory. Just advance through each screen — one per data file. (The more files you have, the more screens you will have to advance through.)

The species file editing program contains a help screen that can calculate daily instantaneous mortality rates from proportional rates. Also, check the parameters list (Append. 3) for any changes — besides new species, note modifications to the original parameters for lake trout (*Salvelinus n. namaycush*), largemouth bass (*Micropterus salmoides*), larval yellow perch (*Perca flavescens*), sea lamprey (*Petromyzon marinus*), and dace (*Phoxinus* spp.). Prey caloric density can no longer be stored in species files, but must be transferred to `.PYC` files.

You update output files created with version 1 by rerunning the simulations using *Model 2*.

Fish Bioenergetics Model 2 Program Files, and Sample Data Files, in the Diskette Package

Model 2 is programmed in Borland International
TURBO PASCAL 5.5.

MODEL 2 CODE FILES

MENU.EXE	*Model 2* program
FIXFILE.EXE	Program to update data files
BIOFILE.DEF	File for storing user-defined default values

MODEL 2 TEXT FILES

MENU.PAS	Text file for *Model 2*
GETSETUP.PAS	" " "
DRIVERS.PAS	" " "
TDCREAD.PAS	" " "
TDCUNIT.PAS	" " "
FILEDEC.PAS	" " "
WORKUNIT.PAS	" " "
STUFF.PAS	" " "
NWCHANGE.PAS	" " "
CHGVAL.PAS	" " "
MODEL.PAS	" " "
MODGRAF.PAS	" " "
CGA.OBJ	TURBO PASCAL object required for compiling program
EGAVGA.OBJ	" " " " " " "
HERC.OBJ	" " " " " " "
PC3270.OBJ	" " " " " " "
ATT.OBJ	" " " " " " "
GRAPH.TPU	TURBO PASCAL unit required for compiling program

The walleye files on the sample data disk contain data for age 3 walleye in Lake Mendota, Wisconsin. They are designed for use in a sample run of *Model 2*.

MODEL 2 SAMPLE DATA FILES

SEALAMP.BIO	Species data file for sea lamprey
ALEWIFE.BIO	" " " alewife
COREGONI.BIO	" " " generalized coregonid
HERRING.BIO	" " " herring
LAKTROUT.BIO	" " " lake trout
CHINOOK.BIO	" " " chinook salmon
COHO.BIO	" " " coho salmon
PINKSOCK.BIO	" " " pink or sockeye salmon
NORTHERN.BIO	" " " northern pike
MUSKY.BIO	" " " muskellunge
DACE.BIO	" " " dace
STRPBASS.BIO	" " " striped bass
LMBASS.BIO	" " " largemouth bass
SMBASS.BIO	" " " smallmouth bass
BLUEGILL.BIO	" " " bluegill
WALLEYE.BIO	" " " walleye
YELPERCH.BIO	" " " yellow perch
LARVALYP.BIO	" " " larval yellow perch
TILAPIA.BIO	" " " tilapia
MYSIS.BIO	" " " mysid zooplankter
WALLEYE.DIE	Diet file for 3-year-old walleye in L. Mendota
WALLEYE.PDC	Predator caloric density file for walleye in L. Mendota
WALLEYE.PYC	Prey caloric density file for walleye in L. Mendota
WALLEYE.TEM	Temperature file for walleye in L. Mendota
WALLEYE.LAB	Output file for walleye sample run
WALLEYE.KEY	Output file " " "
WALLEYE.WRK	Output file " " "

Physiological Parameter Values for the Sample Species (`.BIO`) Data Files — with Explanatory Notes and Citations

Parameter	Sea Lamprey[f]	Alewife	Generalized Coregonid[h]	Herring[i]	Lake trout
CONSUMPTION					
Equation[a].......	2	3	2	3	1
CA..................	0.30	0.8464	1.57	0.642	0.0589
CB..................	-0.35	-0.3	-0.523	-0.256	-0.307
CQ..................	2.3	5,4,3[q]	4.04	1	0.1225
CTO................	18	24,20,16[q]	15.8	15,13[i]	*
CTM................	25	26,22,18[q]	26	17,15[i]	*
CTL.................	*	29,27,25[q]	*	25,23[i]	*
CK1.................	*	0.17	*	0.10	*
CK4.................	*	0.01	*	0.01	*
RESPIRATION					
Equation Set[b]	2	1	1	1	1
RA[e].................	0.00397	0.00367	0.0018	0.0033	0.00463
RB..................	-0.05	-0.2152	-0.12	-0.227	-0.295
RQ..................	2.1	0.0548	0.047	0.0548	0.059
RTO................	25	0.03	0.025	0.03	0.0232
RTM................	30	0	0	0	0
RTL.................	*	9	0	0	11
RK1................	*	22.08	7.09	15	1
RK4................	*	-0.045	0.25	0.13	0.05
ACT.................	1.5	5.78	0	3.9	11.7
BACT..............	*	0.149	0	0.149	0.0405
SDA................	0.172	0.175	0.17	0.175	0.0172
EGESTION/EXCRETION					
Equation Set[c]	1	1	1	1	3
FA...................	0.03	0.16	0.25	0.16	0.212
FB...................	*	*	*	*	-0.222
FG..................	*	*	*	*	0.631
UA..................	0.15	0.10	0.10	0.10	0.0314
UB..................	*	*	*	*	0.58
UG..................	*	*	*	*	-0.299
PREDATOR CALORIC DENSITY					
Equation[d].......	1	1	2	1	2
Caloric density.........	1224	seasonal[g]	*	1322	*
Alpha1............	*	*	945	*	1362
Beta1..............	*	*	14	*	0.736
Cutoff..............	*	*	155	*	1472
Alpha2............	*	*	3119	*	2172
Beta2..............	*	*	0.001	*	0.186

Parameter	Chinook Salmon	Coho Salmon	Pink/Sockeye Salmon[j]	Northern Pike	Muskellunge
CONSUMPTION					
Equation[a]	3	3	3	2	2
CA..................	0.303	0.303	0.303	0.2045	0.2215
CB..................	-0.275	-0.275	-0.275	-0.18	-0.18
CQ..................	5	5	3	2.59	2.53
CTO...............	15	15	20	24	26
CTM...............	18	18	20	34	34
CTL................	24	24	24	*	*
CK1................	0.36	0.36	0.58	*	*
CK4................	0.01	0.01	0.50	*	*
RESPIRATION					
Equation Set[b]	1	1	1	1	1
RA[e].................	0.00264	0.00264	0.00143	0.00246	0.00246
RB..................	-0.217	-0.217	-0.209	-0.18	-0.18
RQ..................	0.06818	0.06818	0.086	0.055	0.055
RTO...............	0.0234	0.0234	0.0234, 0.033[j]	0.1222	0.1222
RTM...............	0	0	0	0	0
RTL................	25	25	25	0	0
RK1................	1	1	1	1	1
RK4................	0.13	0.13	0.13	0	0
ACT................	9.7	9.7	9.9	1	1
BACT.............	0.0405	0.0405	0.0405	0	0
SDA................	0.172	0.172	0.172	0.14	0.14
EGESTION/EXCRETION					
Equation Set[c]	3	3	3	1	1
FA..................	0.212	0.212	0.212	0.20	0.20
FB..................	-0.222	-0.222	-0.222	*	*
FG..................	0.631	0.631	0.631	*	*
UA..................	0.0314	0.0314	0.0314	0.07	0.07
UB..................	0.58	0.58	0.58	*	*
UG..................	-0.299	-0.299	-0.299	*	*
PREDATOR CALORIC DENSITY					
Equation[d]	2	2	2	1	1
Caloric density........	*	*	*	860	860
Alpha1...........	1377	1377	1250	*	*
Beta1.............	0.2356	0.2356	1.851	*	*
Cutoff.............	4000	4000	196	*	*
Alpha2...........	1816	1377	1588	*	*
Beta2.............	0.1258	0.2356	0.1254	*	*

Parameter	Dace[k]	Striped Bass	Largemouth Bass[m]	Smallmouth Bass	Bluegill
CONSUMPTION					
Equation[a]	2	2	2	2	2
CA..................	0.36	0.33	0.33	0.25	0.182
CB..................	-0.31	-0.30	-0.325	-0.31	-0.274
CQ..................	2.3	2.26	2.65	3.8	2.3
CTO................	26	25,22,20[q]	27.5	29	31,27[q]
CTM...............	29	30,27,25[q]	37	36	37,36[q]
CTL................	*	*	*	*	*
CK1................	*	*	*	*	*
CK4................	*	*	*	*	*
RESPIRATION					
Equation Set[b]	2	2	1	2	2
RA[e].................	0.0148	0.02192	0.00279[m]	0.009	0.0154
RB...................	-0.20	-0.234	-0.355[m]	-0.21	-0.2
RQ..................	2.1	2.5	0.0811	3.3	2.1
RTO...............	29	30,27,25[q]	0.0196	30	37,36[q]
RTM...............	32	35,32,30[q]	0	37	41,40[q]
RTL...............	*	*	0	*	*
RK1................	*	*	1	*	*
RK4................	*	*	0	*	*
ACT................	1	2	1	2	1
BACT..............	*	*	0	*	*
SDA................	0.15	0.172	0.163	0.16	0.172
EGESTION/EXCRETION					
Equation Set[c]	1	1	1	1	2
FA...................	0.40	0.104	0.104	0.104	0.158
FB...................	*	*	*	*	-0.222
FG...................	*	*	*	*	0.631
UA...................	0.10	0.068	0.068	0.068	0.0253
UB...................	*	*	*	*	0.58
UG...................	*	*	*	*	-0.299
PREDATOR CALORIC DENSITY					
Equation[d]	1	1	1	1	1
Caloric density.........	1196	1550	1000	1000	1000

Parameter	Walleye	Yellow Perch	Larval Yellow Perch[n]	Tilapia	Mysis spp.[p]
CONSUMPTION					
Equation[a]	2	2	2	2	3
CA..................	0.25	0.25	0.51	0.15	0.036
CB..................	-0.27	-0.27	-0.42	-0.36	-0.372
CQ.................	2.3	2.3	2.3	2.5	0
CTO..............	22	29,23[q]	29	30	9
CTM..............	28	32,28[q]	32	37	11
CTL...............	*	*	*	*	16
CK1...............	*	*	*	*	0.50
CK4...............	*	*	*	*	0.01
RESPIRATION					
Equation Set[b]	2	2	2	2	1
RA[e]...............	0.0108	0.0108	0.0065[n]	0.0274	0.00182
RB..................	-0.2	-0.2	-0.2	-0.348	-0.161
RQ.................	2.1	2.1	2.1	2.3	0.0752
RTO..............	27	32,28[q]	32	37	0
RTM..............	32	35,33[q]	35	41	0
RTL...............	*	*	*	*	0
RK1...............	*	*	*	*	0
RK4...............	*	*	*	*	0
ACT...............	1	1	4.4	1	0
BACT............	*	*	*	*	0
SDA..............	0.172	0.172	0.15	0.1	0.18
EGESTION/EXCRETION					
Equation Set[c]	2	2	1	1	1
FA..................	0.158	0.158	0.15	0.194	0.15
FB..................	-0.222	-0.222	*	*	*
FG..................	0.631	0.631	*	*	*
UA..................	0.0253	0.0253	0.15	0.028	0.18
UB..................	0.58	0.58	*	*	*
UG.................	-0.299	-0.299	*	*	*
PREDATOR CALORIC DENSITY					
Equation[d]	1	1	1	1	1
Caloric density........	1000	1000	600	1300	830

[a] Consumption:

Equation 1: Exponential Temperature Function (Stewart 1980).
Uses parameters CA, CB, CQ.

Equation 2: TDEP Temperature Function (Kitchell et al. 1977).
Uses parameters CA, CB, CQ, CTO, CTM.

Equation 3: Thornton-Lessem Temperature Function (Stewart 1980).
Uses all parameters.

[b] Respiration:

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

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

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

[c] Egestion/Excretion:

Equation Set 1: Constant proportions of consumption.
Uses parameters FA, UA.

Equation Set 2: Function of weight, temperature and ration (Elliott 1976).
Uses all parameters.

Equation Set 3: Model 2 with correction for invertebrates in diet (Stewart 1980).
Uses all parameters.

[d] Predator Caloric Density:

Equation 1: Values stored in Predator Caloric Density (.PDC) file.

Equation 2: A function of predator weight.

[e] When necessary, RA has been converted from units in the original references to $g\ O_2 \cdot g^{-1} \cdot d^{-1}$.

[f] Sea lamprey - RA and caloric density have been corrected from our first model.

[g] Alewife - See Stewart and Binkowski (1986) for the annual cycle of caloric density.

[h] Generalized coregonid (*Coregonus* spp.)-L. Rudstam and M.A. Miller (Center for Limnology, University of Wisconsin-Madison) and F. Binkowski (Center for Great Lakes Studies, University of Wisconsin-Milwaukee), unpublished manuscript, "A bioenergetics model for analysis of food consumption by bloater in Lake Michigan." For an alternative model, see Helminen et al. (1990).

[i] Herring (*Clupea harengus*) - (Rudstam 1988). Duplicate values for CTO, CTM, and CTL are for age 0 and 1 fish (first number) and for age 2 and older fish (second number).

[j] Pink/Sockeye salmon - Sockeye from Beauchamp et al. (1989), Pink from D. Stewart, (pers. comm.). For RTO, the larger value (0.033) was used for adult salmon migrating back to river mouths for spawning.

[k] Dace - RA and ACT have been modified from the values listed in our first model.

[m] Largemouth bass - RA and RQ have been modified from the original parameter for better performance at low temperatures (A. Trebitz, UW-Madison Center for Limnology, pers. comm.).

[n] Larval yellow perch - (Shuter and Post 1990; Post 1990). The lower RA value for larval yellow perch is due to lower caloric density of larval perch compared to adult perch.

[p] *Mysis mixta* - (Rudstam 1989). In this model, respiration parameters represent routine activity; no correction for swimming speed is added. Therefore, many of the parameters are set to zero.

[q] Multiple values of CQ, CTO, CTM, CTL, RTO and RTM are for fish of different ages,beginning with age 0.

Contents of WALLEYE Sample Data Files

In the walleye species data file (WALLEYE.BIO), the 0.5 P-value is an arbitrary initial value. The P-value that produces growth from 505 grams to 920 grams over April 1 to March 31, given conditions described in the seasonal files below, is approximately 0.418.

Species File

```
Bioenergetics Species Data File *WALLEYE.BIO
Date ->
Number of cohorts in this file = 10

Species Name ---------------------    > walleye
Consumption Model ----------------->  2
Respiration Model ----------------->  2
Egest/Excret Model ---------------->  2
Pred CalDens Model ---------------->  1
Include Spawning ------------------>  N
 First cohort to spawn ------------>  0
 Day of spawning ------------------>  0
 Prop. spawning wt loss ----------->  0.0000
Temp. for maintenance growth ------>  0.00
```

```
Values for COHORT  1

Start Day =   1          Final Day = 365   Initial Pop Size = 1.00000E+04
Start Wgt = 505.00000   Final Wgt = 920.00000    P-val = 0.500000

Firstday    Natural       Fishing
    1     0.001000000   .000000000
   31     0.001000000   .000500000
  198     0.001000000   .000000000
    0     0.000000000   .000000000
    0     0.000000000   .000000000
    0     0.000000000   .000000000
    0     0.000000000   .000000000
    0     0.000000000   .000000000
    0     0.000000000   .000000000
    0     0.000000000   .000000000
    0     0.000000000   .000000000
    0     0.000000000   .000000000
```

```
Consumption:  CA     =   0.2500000   CB  =  -0.2700000   CQ  =   2.3000000
              CTO    =  22.0000000   CTM =  28.0000000
              Ration =   0.0000000
Respiration:  RA     =   0.0108000   RB  =  -0.2000000   RQ  =   2.1000000
              RTO    =  27.0000000   RTM =  32.0000000
              ACT    =   1.0000000   SDA =   0.1720000
Egestion:     FA     =   0.1580000   FB  =  -0.2220000   FG  =   0.6310000
Excretion:    UA     =   0.0253000   UB  =   0.5800000   UG  =  -0.2990000
Propor. Prey Indigest: 0.000, 0.000, 0.000, 0.000, 0.000, 0.000, 0.000,
 0.000, 0.000, 0.000
```

Temperature File

File title -> WALLEYE.TEM
Date ->
Cohort # 1
Values in degrees centigrade

Day	Temperature
1	6.0
31	10.0
62	17.0
92	22.0
123	22.0
154	22.0
184	20.0
215	12.0
245	6.0
276	4.0
335	4.0
365	6.0

Diet File

File title -> WALLEYE.DIE
Date ->
Cohort # 1
Values in proportions (0-1)

Day	Diet 1	Diet 2
1	0.20	0.80
365	0.20	0.80

Predator Caloric Density File

File title -> WALLEYE.PDC
Date ->
Cohort # 1
Values in calories per gram wet weight

Day	Caloric Density
1	1200.0
365	1200.0

Prey Caloric Density File

File title -> WALLEYE.PYC
Date ->
Cohort # 1
Values in calories per gram wet weight

Day	Diet 1	Diet 2
1	750.0	1100.0
365	750.0	1100.0

Keystroke Guide to WALLEYE Sample Run
By Neil MacKay

This keystroke guide describes the process for loading *Model 2* programs onto a hard drive, starting the model, viewing and editing data files — and conducting a run using WALLEYE sample data files. These files describe the growth of age 3 walleye in Lake Mendota, Wisconsin.

A. Create directories for the data and the program on your hard drive.

We recommend running *Model 2* from a hard drive to improve speed, but it can be run from diskettes. To load *Model 2* onto the hard drive:

1. From drive `C:\`, type **md bloen <Enter>**.
2. Type **cd bloen <Enter>**.
3. Type **md data <Enter>**.

B. Load the contents of the *Model 2* diskette package onto your hard drive.

Note: If space is limited, it is not necessary to load files with suffixes `.PAS`, `.TPU`, and `.OBJ`. These files are not required to run the model. They are only needed to change and recompile the program.

1. Put your program files diskette in drive `A:` and type **copy a:*.* c:\bloen <Enter>**.
2. Replace the program files diskette in drive `A:` with the data files diskette and type **copy a:*.* c:\bloen\data <Enter>**.

C. Enter the program.

1. Return to subdirectory **`c:\bloen`** by typing **c: <Enter>**, then typing **cd \bloen <Enter>**.
2. Type **menu** <Enter>. *Model 2* displays a welcome screen, asking you if you would like to change the default data directory.
3. Type **y**. (Do not press **<Enter>**).
4. *Model 2* prompts you for the new data directory name. Type **c:\bloen\data <Enter>**. The model responds with the new data directory and gives you the option to correct any mistakes. If you type **y**, the new data directory is active, and you are sent to the main menu. If you type **n**, then you can correct any mistakes you have made.

D. You are now at the main menu.

Option 1 is highlighted as a default, indicating that this option is selected if you press **<Enter>**. Use the arrow keys to highlight different options, then press **<Enter>** to select that option. Alternately, you can select an option by typing its number.

E. Edit `.BIO` files.

1. First, select option `2)`**`species file utilities`**.
2. On the next screen, **`SPECIES FILE UTILITY MENU`**, select option `2)`**`Edit Datafile`**.
3. You should then see, on the right side of the screen, a list of all the `.BIO` files in the data subdirectory. (NOTE: If *Model 2* indicates that there are no `.BIO` files, then you either installed them incorrectly or set the default data drive incorrectly. Press **<Enter>**, then **<Esc>** to return to the main menu. Then, select option 8 and re-enter the default data drive. Go to C4 above.) From the list of `.BIO` files, use the arrow keys to highlight `WALLEYE.BIO`, then press **<Enter>**. If you inadvertently select the wrong file, *Model 2* allows you to backtrack by typing **n** then reselecting the file, or by pressing **<Esc>** to be bounced back to the **`SPECIES FILE UTILITY MENU`**. You can try both of these options now to become familiar with how *Model 2* allows you to correct mistakes.
4. Once you've selected `WALLEYE.BIO`, the next screen, **`Cohort Selection`**, asks you which cohort/s to edit. We wish to edit cohort 1 only, so at the prompt for **`First Cohort to use`**, type **1**, and at the next prompt for **`Last Cohort to edit`**, type **1** also. Press **<Enter>** at the next prompt to select **`Y`** (unless you've made a mistake, in which case you type **n**).

5. Next you see the **Species Datafile Editing Menu**. This screen lists seven sections of a .BIO file that can be edited separately. To select one of these sections for editing, use the arrow keys to move to that option, then press the space bar or <Enter> once. This toggles the N to Y or vice versa. For this tutorial, we look at the first six sections of the data file to see what they contain. So, highlight each option in turn and toggle the N to Y. Leave the **% Prey Indigestible Parameters** option at N, since we are not using this option for running walleye. Once you have turned the top six options to Y, then type a to continue.
6. You now see the **Species File General Data** screen. This screen designates the specific equations and options currently used to run walleye. You seldom need to edit this screen unless you wish to include spawning in *Model 2*. We have no changes to make here, so type a to advance to the next screen.
7. The second screen contains the **Individual and Population Parameters** and is a screen you edit quite often. To edit this screen, or any screen within the .BIO file, use the arrow keys to move the cursor to the value you want to edit, then press the space bar or <Enter>. This erases the old value and activates the editor, allowing you to type in a new value. At this point, if you decide you want the old value back, just press <Enter> again. Once you have changed a value, press the space bar or <Enter> again to turn off the editor. You won't be allowed to leave the line until you turn off the editor.

   On this screen, you should see that the **Start day** of our simulation is 1 and the **Final Day** is 365. In this simulation, day 1 corresponds to April 1. The **Start Weight** is set to 505 grams, the average size of age 3 walleye in Lake Mendota on April 1. This fish grows to 920 grams by March 31 of the next year. The P-value, or proportion of maximum consumption realized, is arbitrarily set to 0.5. This value is modified later when we fit it to the growth data. The initial population size is set at 10,000. Because we are dealing with only one cohort, you only see this screen once. If we were running multiple cohorts, you would need to edit this screen for each cohort.
   For this tutorial, we do not edit any values on this screen, so type a to advance to the next screen.
8. The next screen displays the consumption parameters specific to walleye. Many of the values are 0.0 because, for walleye, we use Consumption Equation II, which does not require values for all parameters. You do not need to edit here, so type a to advance.
9. The next screen contains the respiration parameters. No editing is necessary. Type a to advance.
10. This screen contains the egestion/excretion parameters. No changes are necessary. Type a to advance.
11. Next you see the **Mortality Help Screen**. This screen helps you convert mortality rates expressed as percentages to daily instantaneous rates. In the sample data file, natural mortality is 30 percent annually, and fishing mortality is 8 percent over the period from May 1 to October 15. We now calculate the daily instantaneous mortality rates corresponding to these percentages. First type y, then input 30, the natural mortality rate expressed as a percentage. This is an annual rate so for **Number of days in the interval**, input 365. *Model 2* responds with 0.000977, or approximately 0.001. Write this value down, then press <Enter>. Now type y again, input 8 for the fishing mortality rate, and 167 as the number of days in the interval from May 1 (run day 31) to October 15 (run day 198). *Model 2* responds with 0.000499, or approximately 0.0005. Again, write this value down and press <Enter>. Now type n to advance to the next screen.

    The next screen is **Mortality Table Parameters**. This data describes the natural and fishing mortality schedules that are applied to the population over time. For this walleye simulation, from day 1 through day 30, natural mortality operates at a daily instantaneous rate of 0.001 with no fishing mortality. Beginning on day 31 and continuing through day 197, both natural mortality at 0.001 and fishing mortality at 0.0005 operate. On day 198, fishing mortality ceases, but natural mortality continues through the rest of the year. Values on this screen are edited in the same manner as on previous screens. You do not need to edit these values now so type **a** to advance.

12. You have now cycled through each of the screens selected in step 5 and are back at the `SPECIES FILE UTILITY MENU`. We have finished editing the `.BIO` file, so select option 5 to return to the main menu.

F. Edit seasonal files (cal, temp, & diet file utilities).

The four types of seasonal files (temperature, diet, predator caloric density, and prey caloric density) have a similar format. Each describes an annual cycle for the associated data type. The WALLEYE files used for this simulation do not need to be edited, but we do view a temperature file to see the data format.

1. Highlight main menu option `3) cal, temp, & diet file utilities` and press <Enter>.
2. You now see the `CAL/TEMP/DIET FILE UTILITIES` menu. Select menu option `1) Temperature File`, which brings you to the `Temperature File Utilities` menu. From here, choose option `1) Edit file`. Now, select the walleye temperature file (`WALLEYE.TEM`), which should be the only file on the list. Again *Model 2* gives you a chance to correct any errors or to escape. To proceed, type **y**.
3. The `File Information` screen appears. It should say that there are 10 cohorts in this file and the last cohort to be used in the run is cohort 1. To edit this screen, type **c**, then you are cued for the number of the line to be edited. Only numbered lines can be edited. No editing is necessary, so type **a** to advance to the `Cohort Selection` screen.
4. Since this file has only one cohort, input **1**, then input **1** again, then type **y**. Now, you see the contents of cohort 1 in file `WALLEYE.TEM`. Note that the temperature remains at 22 degrees centigrade from day 92 to day 154. The assumption here is that walleye thermo-regulate at 22 degrees centigrade during the summer. As explained in F4, this file can be edited by typing **c** followed by the number of the line you wish to edit. Here, the available numbers range from 1 to 36. No editing is needed, so type **a** to advance to the next screen.
5. You are now back to the **CAL/TEMP/DIET FILE UTILITIES** menu. The three other types of seasonal files are edited similarly to the temperature file except that diet and prey caloric density files have entries for each prey item (to a maximum of 10) on each day. Type **5** to return to the main menu.

G. Doing a P-fit and bioenergetics run.

1. From the main menu, select option `1) pfit/bioenergetics model`. You see the `BIOENERGETICS GROWTH MODEL - RUN OPTIONS` screen. Select option `1) P-FIT run - fit to end weight` by typing **1**.
2. On the `P-fit Run Options` screen, type **s**, so the results of the P-fit are sent to the screen only. Now, you must select the files to use in the P-fit run. Highlight `WALLEYE.BIO` and press <Enter>. Type **y**, unless you made a mistake. Now, you must select the seasonal files. Select `WALLEYE.DIE`, `WALLEYE.TEM`, `WALLEYE.PDC`, and `WALLEYE.PYC` as they come up on the screen. *Model 2* then lists the files you selected and asks if they are correct. If you have erred, press **n** to re-select the seasonal files (or press <Esc> to go back and re-select everything.) If everything is correct, type **y**. You run a P-fit for cohort 1 only, so select the `First Cohort to use` by inputing 1 and the `Last Cohort to use` by inputing 1 again. Then, type **y** to advance. *Model 2* now calculates the P-value (proportion of maximum consumption). The process should require five iterations and reach a final value of 0.41796, indicating that in order for a walleye to grow from 505 grams to 920 grams under the conditions described in the seasonal files, the fish must consume at 42% of its physiological maximum consumption rate.

   When the P-fit is finished, type **y**, and *Model 2* records the new P-value for this cohort in the `WALLEYE.BIO` file.

3. You have now returned to the **BIOENERGETICS GROWTH MODEL - RUN OPTIONS** menu. This time select option **3) BIOENERGETICS run - constant P-value**. Now, select the WALLEYE data files again as you did for the P-fit run (step G2 above). Input **1** for first cohort and **1** for the last cohort, then type **y**.
4. The next screen is entitled **Bioenergetics Run Options**. This screen allows you to set a variety of options for how data are saved. The default settings you see are contained in a file called BIOFILE.DEF. The settings chosen are: **A set interval relative to day of year, 15 days, Start of run only, Y**, and **Y**. These defaults can be changed here, but the changes only apply to this session. If you exit *Model 2*, the original defaults appear the next time you start the program. To change the original defaults, use main menu option 6.
   To edit any options on the **Bioenergetics Run Options** screen, move the cursor to the that option and press **<Enter>**. For the second option (**"Set interval"**), you must input a number from 1 to 365. For all other options, press either the space bar or **<Enter>** to cycle through the different choices. It is not necessary to edit any of these values now, so type **a** to advance to the next screen.
5. The next screen allows you to type in a descriptive comment that appears on your printout of the bioenergetics output. For example, you could type **Age 3 walleye in Lake Mendota, thermoregulating**. The comment can be up to 60 characters long, which is the length of the dotted line on the screen. Press **<Enter>** when you have finished the comment.
6. Now *Model 2* cues you for a prefix for the output file. Although this could be your first run, there is already a sample output file, included in the *Model 2* diskette package, that was generated from the same run you are now conducting. This sample output file uses the prefix WALLEYE and should appear in the list of files on the upper right of your screen. If you type WALLEYE as your prefix, you erase the sample output. We suggest you keep the sample output file for comparison with output from this run, so type any other prefix of eight letters or less. Try to make it descriptive of this run, for example, **wallcool**, since the walleye are thermoregulating. Press **<Enter>** and, unless you've made a mistake, type **y** to continue. *Model 2* proceeds with the bioenergetics run, saving data every 15 days. When finished, *Model 2* prompts you to press **<Enter>**. You are now back at the BIOENERGETICS GROWTH MODEL - RUN OPTIONS menu. Type 5 to return to the main menu.

H. Printing output.

1. From the main menu, select option 4. On the next screen, highlight the work file you just created, WALLCOOL.WRK, and press **<Enter>**. Type **y** to continue, unless you have made a mistake.
2. You are now at the **Model Output Listing** screen. Your first choice here is to decide where the output should be sent. We suggest that you send the output to a printer. If you have an Epson printer or a printer that operates in an Epson emulation mode, type **e**. The Epson designation produces condensed print that allows you to get more fields of output per page. If you have another brand of printer, then type **o**. If you do not have a printer, type **s** to send output to the screen. The other choices for this option create files on the disk in different formats.
3. Next you must decide what output variables, or fields, you wish to see. The 44 different variables saved from a run are listed on the right side of the screen. For the variables to view now, input these numbers in order: **2** (day of year), **4** (temperature), **5** (weight), **14** (specific growth), **15** (specific consumption), and **23** (net production). Once these numbers are in, type a **0** to signify the end of the output list. If you typed in everything correctly, type **a** to advance. If you wish to correct anything, type **c**, then choose **A** or **B** to correct.
4. The next screen shows you the number of days of output saved in this file (should be 27) and asks if you wish to list all days. You can print a subset of the data by typing **n**, then following the instructions on the screen. For this example, we list all days, so type **y**, then **y** again

to proceed. *Model 2* then prints your results to the printer or the screen. Check some of the values against those from the sample data output file (Append. 6); they should be identical. Press **<Enter>** to return to the main menu.

I. Plotting output.

1. You are now at the main menu. Select option 5 to plot output from your run. On the next screen, select the `WALLCOOL.WRK` work file, just as you did for printing the output above. Type **y** to continue.
2. The next screen is the **`PLOTTING MENU`** screen. Choose option 1 from this menu.
3. You are now at the **`Plot Model Output`** screen and should see the list of output variables on the right side. For this example, we plot weight on the Y axis versus day of the year on the X axis. Thus, for the first entry, **`Enter X Field Number`**, input **2**. Next, select weight for the Y axis by inputing **5**. We don't want a second Y variable, so input **0**. We want the data points connected, so type **y**. We want to use all of the records, so type **y** again. We don't want to save the graph to a disk file, so type **n**. You are now at the end of this screen, so type **y** to continue or **n** to reenter the plotting options.
4. The next screen allows you to set the range and number of tick marks for the axes of the graph. The default values for the maximum and minimum on the X and Y axes are the extremes for these values as contained in the output file. We accept the defaults, so type **a** to advance. *Model 2* now plots your graph.

   Notice that even though the proportion of maximum consumption was constant over the year, growth was not. The seasonal changes in growth rate were due primarily to the seasonal thermal regime. Press **<Enter>** to advance out of the plot screen.
5. You should be on the screen entitled **`PLOTTING MENU`**. For a more direct illustration of the effect of temperature on growth, we plot specific growth rate and temperature versus day of the year. Select **1** from the **`PLOTTING MENU`**. On the next screen, again input **2**, day of the year, as the X axis. The first Y axis is temperature, so input **4**. The second Y axis is specific growth, so input **8**. Type **y** to connect the data points, **y** to use all records, and **n** to not save the graph to a disk file. Then, type **y** to continue or to correct any mistakes. Accept the default axis options by typing **a**. *Model 2* now plots the output. Note how sensitive growth rate is to temperature and that growth seems to maximized around 19 centigrade. Press **<Enter>** to return to the **`PLOTTING MENU`**, then type **5** to return to the main menu. This marks the end of the keystroke guide.

Model 2 is a powerful tool with many applications in fishery management and research. While the model includes many options that can add realism to a simulation, most questions can be addressed very effectively with simple but well planned runs. We have tried to make *Model 2* easy to use, but you will need some time to become familiar with it, as with any software. We encourage you to "play" with the model, to try different options and features, and to modify the data files to develop and simulate your own scenarios. In any event, HAVE FUN!

Partial Listing of `WALLEYE` Sample Run Output

This simulation used the sample data files with the `WALLEYE` prefix and was run for cohort 1. Output was saved at 15-day intervals and on the `start` and `final` days of the cohort. Cumulative variables were summed over the entire cohort — they were zeroed with the `Start of run only` option. All data were saved at the end of the output day, except for day 0, which represents data from the beginning of the first day of the simulation.

Variable Name and Field Number

Cohort 1	Day_Year 2	Temperat 4	Weight_g 5	Sp_Grwt_c 8	Sp_Cons_c 9	NetProd_g 23
1.0000	0.0000	6.0000	505.0000	0.0000	0.0000	0.0000
1.0000	1.0000	6.0000	505.5702	1.3550	5.9420	5696.7555
1.0000	15.0000	7.8667	514.6140	1.6695	7.1135	9.535E+04
1.0000	30.0000	9.8667	526.7414	2.0407	8.5476	2.138E+05
1.0000	45.0000	13.1613	542.6758	2.7087	11.3263	3.665E+05
1.0000	60.0000	16.5484	563.6890	3.2968	14.4477	5.635E+05
1.0000	75.0000	19.1667	588.1265	3.4086	16.5412	7.874E+05
1.0000	90.0000	21.6667	611.9822	2.8473	17.5436	1.001E+06
1.0000	105.0000	22.0000	632.8066	2.6546	17.4066	1.184E+06
1.0000	120.0000	22.0000	653.9490	2.6125	17.2526	1.365E+06
1.0000	135.0000	22.0000	675.4478	2.5715	17.1024	1.545E+06
1.0000	150.0000	22.0000	697.3018	2.5316	16.9559	1.724E+06
1.0000	165.0000	21.2667	720.6009	2.7793	16.7109	1.911E+06
1.0000	180.0000	20.2667	747.1299	2.9729	16.1664	2.118E+06
1.0000	195.0000	17.1613	775.8673	2.9684	13.7816	2.338E+06
1.0000	210.0000	13.2903	802.0871	2.3462	10.3001	2.535E+06
1.0000	225.0000	10.0000	822.3566	1.7331	7.6723	2.685E+06
1.0000	240.0000	7.0000	837.5364	1.2427	5.7286	2.796E+06
1.0000	255.0000	5.3548	848.9719	1.0102	4.8392	2.878E+06
1.0000	270.0000	4.3871	859.0252	0.8841	4.3684	2.949E+06
1.0000	285.0000	4.0000	868.1247	0.8338	4.1849	3.013E+06
1.0000	300.0000	4.0000	877.1950	0.8301	4.1731	3.075E+06
1.0000	315.0000	4.0000	886.3189	0.8264	4.1615	3.137E+06
1.0000	330.0000	4.0000	895.4964	0.8227	4.1499	3.198E+06
1.0000	345.0000	4.6667	905.0533	0.8980	4.4331	3.260E+06
1.0000	360.0000	5.6667	915.9915	1.0179	4.8933	3.331E+06
1.0000	365.0000	6.0000	919.9783	1.0594	5.0548	3.357E+06

How To Load *Model 2* on Dual Diskette Drives

To run *Model 2* on dual diskette drives, we recommend storing the program files on drive 1 and the data files that you want to use on drive 2. Your two drives can be any combination of 5.25-inch and 3.5-inch diskette drives.

We recommend creating a "bootable" diskette, using the DOS format command with the system option (`FORMAT A:/S`). See your DOS manual for directions on creating a "bootable" diskette for your system. Usually, you will have to copy the following files to a diskette formatted with the `/S` option:

```
COMMAND.COM
CONFIG.SYS
AUTOEXEC.BAT
```

After creating and testing a "bootable" diskette, you need to use the DOS copy command to copy over two *Model 2* program files: (1) `MENU.EXE` and (2) `BIOFILE.DEF`. This will be sufficient to run *Model 2* from your program diskette. You can copy other DOS utility programs to your program diskette as well, depending on the capacity of the drive you are using.

We recommend copying only the data files that you need for a specific run on to your data diskette. By creating separate data diskettes for different species or simulations, you reserve a maximum amount of diskette space for the creation of output data files.

To create a data diskette for walleye, for example, the following files should be copied:

```
WALLEYE.BIO
WALLEYE.TEM
WALLEYE.PDC
WALLEYE.PYC
WALLEYE.DIE
```

To create data diskettes for any other species, follow the same conventions and include at least one data file of each type (`*.BIO`, `*.TEM`, `*.PDC`, `*.PYC`, and `*.DIE`).

Variables Saved to Results (.WRK) Output Data Files for Each Bioenergetics Run

Field Number	Variable Name	Description of Variable
1	Cohort	Cohort number
2	Day_Year	Day of year in a simulation
3	Day_Life	Age of fish in simulation days
4	Temperat	Temperature on the current day (°C)
5	Weight_g	Weight on the current day (grams)
6	Pop_Size	Population number on the current day
7	Pop_Mass	Population biomass (g) on the current day
8	Sp_Grwt_c	Specific growth rate (calories/g of predator/day)
9	Sp_Cons_c	Specific consumption rate (" " " " ")
10	Sp_Eges_c	Specific egestion rate (" " " " ")
11	Sp_Excr_c	Specific excretion rate (" " " " ")
12	Sp_Resp_c	Specific respiration rate (" " " " ")
13	Sp_SDA_c	Specific SDA rate (" " " " ")
14	Sp_ConPry	Specific consumption rate (g of prey/g of predator/day)
15	Sp_GrwPrd	Specific growth rate (g of pred./g of predator/day)
16	PrdCalDen	Predator caloric density on current day (calories/g)
17	PryCalDen	Mean weighted prey caloric density on current day (calories/g)
18	Wt_Incrmt	Daily weight increment (today's wt. - yesterday's wt.)
19	GrosPrd_g	Cumulative gross production (g)
20	GrosPrd_c	Cumulative gross production (calories)
21	GamProd_g	Cumulative gametic production (g)
22	GamProd_c	Cumulative gametic production (calories)
23	NetProd_g	Cumulative net production (g)
24	NetProd_c	Cumulative net production (calories)
25	NumHarvst	Cumulative number of fish harvested
26	Wt_Harvst	Cumulative weight of fish harvested (g)
27	NumNatMrt	Cumulative number of fish dying naturally
28	WtNatMort	Cumulative weight of fish dying naturally (g)
29	SI_CalCon	Cumulative consumption by individual of all prey (calories)
30	SI_Cons_1	Cumulative consumption by individual of prey item 1 (g)
31	SI_Cons_2	Cumulative consumption by individual of prey item 2 (g)
32	SI_Cons_3	Cumulative consumption by individual of prey item 3 (g)
33	SI_Cons_4	Cumulative consumption by individual of prey item 4 (g)
34	SI_Cons_5	Cumulative consumption by individual of prey item 5 (g)
35	SI_Cons_6	Cumulative consumption by individual of prey item 6 (g)
36	SITotCons	Cumulative consumption by individual of all prey (g)
37	SP_CalCon	Cumulative consumption by population of all prey (calories)
38	SP_Cons_1	Cumulative consumption by population of prey item 1 (g)
39	SP_Cons_2	Cumulative consumption by population of prey item 2 (g)
40	SP_Cons_3	Cumulative consumption by population of prey item 3 (g)
41	SP_Cons_4	Cumulative consumption by population of prey item 4 (g)
42	SP_Cons_5	Cumulative consumption by population of prey item 5 (g)
43	SP_Cons_6	Cumulative consumption by population of prey item 6 (g)
44	SPTotCons	Cumulative consumption by population of all prey (g)

Notes regarding output fields:

Fields 8-15:
Specific rates in fields 8-13 are given in (calories/g of predator/day). Caloric values can easily be converted to grams of predator or prey by dividing by the appropriate caloric density (field 16 or 17). Two common conversions have already been calculated in Fields 14 (specific consumption in g of prey/g of predator/day) and 15 (specific growth in g of predator/g of predator/day).

Field 18:
Weight increment does not include losses due to spawning. Thus, the increment listed for the day that the fish spawned is the change in weight that would have occurred without spawning.

Fields 23,24:

Net production is calculated as gross biomass produced (Field 19) minus biomass lost through spawning (Field 21) and lost through mortality (both natural and fishing).

Fields 29-44:
For consumption variables, you can save daily values, instead of cumulative values, by selecting the option to zero cumulative output variables `After every day` from the `Bioenergetics Run Options` screen when setting up the run. Then, the variable names will all begin with "D" instead of "S" (for example, field 29 would become "DI_CalCon").

A Laboratory Exercise for College-Level Courses

The following handout for a classroom laboratory exercise is designed to introduce students to *Model 2*, to give them some structured experience running *Model 2*, and to help them discover some basic principles of bioenergetics on their own. This exercise should be preceded by classroom lectures describing the physiology of consumption and respiration as affected by temperature, body size, and food quality — and by a demonstration of *Model 2* in operation.

While students can work independently on this exercise, we found that having them work in pairs, with one computer for each pair, was the most efficient arrangement. Students were given the handout and a diskette containing the bioenergetics program and the walleye sample data files. The handout first instructs them to conduct the baseline run, using the files as they exist on the diskette, then poses a series of questions requiring them to change the data files and conduct a new run.

The following questions describe a number of situations where bioenergetics modeling can be used to estimate the effects of environmental influences or management actions on fish consumption and growth. Each question requires you to run the bioenergetics model to simulate a particular situation, print out the results, then fill in the required information in the blanks.

The computer diskette you received contains a copy of *Fish Bioenergetics Model 2* and all the data files needed to model walleye: the species file (WALLEYE.BIO) and the seasonal files (WALLEYE.TEM, WALLEYE.DIE, WALLEYE.PDC, WALLEYE.PYC). Each file contains a single cohort of data for age 3 walleye in Lake Mendota, Wisconsin, growing from 505 g on April 1 to 920 g on March 31. Initial population size for age 3 fish is 10,000 with natural mortality of 30% annually and harvest mortality of 8% during the fishing season (May 1 to October 15). The diet (.DIE) file contains two diet items: 1 = benthic invertebrates, 2 = fish. The temperature (.TEM) file assumes that walleye thermoregulate at 22°C during summer. Day 1 in all files is April 1.

For each of the following questions, print out results of the simulation run for the variables below:

- #3 - day of life
- #5 - weight
- #6 - population size
- #30 - cumulative individual consumption of diet item 1
- #31 - " " " " " " " " " " " " " " " " " " 2
- #36 - " " " " " " " " " " " " " " " all diet items
- #44 - cumulative population consumption of all diet items
- #19 - cumulative gross production
- #25 - number harvested
- #26 - weight harvested

Results from question 1 (the baseline run) will be compared with results from questions 2-7.

---

1) Boot your computer, set the directory to the drive containing the program diskette, then start *Model 2* by typing **menu**. First, print out the species (.BIO) file and each of the seasonal files so you have a record of the original (baseline) conditions. Next, do a "P-fit run - fit to end weight" using the 5 standard files and update the P-value in the .BIO file. Then, do a bioenergetics run saving the output at 15-day intervals and summing variables over the interval covered by the cohort (zero cumulative variables with the **After each cohort** option). Name this output file BASELINE.

Fill in the blanks below:

P-value __________

Weight gain __________

Individual conversion efficiency __________
(weight gain / total individual consumption)

Population conversion efficiency __________
(gross production / total population consumption)

2) Assume it was a very warm summer. As a result, hypolimnetic oxygen depletion occurred in Lake Mendota, and walleye were forced to reside in an epilimnion that was two degrees warmer during the months of July, August, and September. Edit the temperature (WALLEYE.TEM) file to increase the temperatures for these 3 months (days 92, 123, and 154) by 2°C. How are growth, total consumption, and conversion affected?

Weight gain __________

% change __________

Total individual consumption __________

% change __________

Individual conversion efficiency __________

% change __________

3) Assume that forage fish had poor recruitment this year resulting in a change in walleye diet. ***Create a new diet file*** in which you increase the proportion of invertebrates in the walleye diet by 0.25 and reduce the proportion of fish by 0.25 from May 1 to November 1. ***Also remember to change the temperature file back to 22°C.***

Run another simulation, using the new diet file and assuming that feeding rate (P-value) remains the same. How would walleye growth and annual production be affected?

New ending weight __________

Weight gain __________

% change from baseline __________

Total production __________

% change from baseline __________

How much does predation pressure on each diet item change from baseline conditions?

Total individual consumption of:

invertebrates __________

% change __________

fish __________

% change __________

Individual conversion efficiency __________

Total population consumption __________

% change __________

4) Assume that the length limit for walleye in Lake Mendota is reduced from 15 to 12 inches, which increases fishing mortality for age 3 walleye to 20% over the fishing season. Change the fishing mortality rate in the species data file, then run another simulation with this new mortality schedule, ***using diets from the baseline run.*** What effect does this management action have on walleye population size and prey consumption?

Population size on March 31 __________

% change __________

Total production __________

% change __________

Total number harvested __________

% change __________

Total population consump. __________

% change __________

5) Suppose someone developed a new transplantable gene that reduced the standard metabolism of any ectotherm by 10% (respiration parameter RA). DNR hatchery managers bought a case and injected it into the walleye they stock into Lake Mendota. Run another simulation with the lower RA value, but all other conditions as in the baseline. ***Remember to change fishing mortality back to baseline conditions!*** How will these new fish feed and grow relative to previously stocked "unengineered" fish, and will their effect on the forage base change?

New end weight __________

Weight gain __________

% change __________

Total individual consumption __________

% change __________

Individual conversion efficiency __________

Total population consumption __________

% change __________

Population conversion efficiency __________

6) Assume that the next year-class of walleye is twice as large as the current year-class. As a result, growth (the 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 (P-value), total consumption, production, and harvest for this cohort? (You will need to change ending weight and population size, run a new P-fit, then run another simulation with the new P-value) ***Remember to change RA back to its baseline value!***

New P-value __________

% change __________

Total population consumption __________

% change __________

Total production __________

% change __________

Number harvested __________

% change __________

Weight harvested __________

% change __________

7) Assume this was an excellent year for forage production. As a result, Lake Mendota walleye increased their feeding rate (P-value) by 10% during the period from April 1 through August 31. How would this affect growth and the annual totals for consumption? ***Remember to change population size back to its baseline value.***

(HINT: This will require 2 cohorts in the species file; one covering April 1 - August 31, and another covering September 1 - March 31. To create cohort 2, select "Species File Utility" from the main menu, then duplicate cohort 1 as cohort 2. Think about how you will determine starting weight and initial population size for cohort 2.)

New ending weight (on March 31) __________

Weight gain __________

% change ________

Population size (on March 31) __________

% change ________

Total population consump. (annual) __________

% change ________

Total production (annual) __________

% change ________

1) Approach: Make a standard run using default files to set baseline conditions.

P-value = 0.4180
Weight gain = 920 - 505 = 415 g

Individual conversion efficiency = 415 / 2752 = 15%

Population conversion efficiency = 3.361E6 / 2.229E7 = 15%

2) Approach: Change/edit temperature file for days 92, 123 and 154. Run second simulation using same P-value, etc.

Weight gain = 844 - 505 = 339g
% change = 339 vs 415 = - 18%

Total individual consumption = 2601 g
% change = 2601 vs 2752 = - 5.5%

Individual conversion efficiency = 339 / 2601 = 13%
% change = 13% vs 15% = - 13%

3) Approach: Create a new diet file with diet proportions of 0.45 for invertebrates (diet item 1) and 0.55 for fish (diet item 2) between May 1 (day 31) and November 1 (day 215). This could be done as a step function change (enter previous values in diet file for days 1, 30, 216 and 365; enter new values for days 31 and 215) or as a gradual change (interpolated) by entering data for days 1, 31, 215 and 365. I used the step function change in the following calculations.

New ending weight = 845 g

Weight gain = 845 - 505 = 340 g
% change = 340 vs 415 = - 18%

Total production = 2.745E6 g
% change = 2.745E6 vs 3.361E6 = - 18%

Invertebrates = 1002.6 g
% change = 1002.6 vs 550.4 = + 82%

Fish = 1640.5 g
% change = 1640.5 vs 2201.58 = - 25.5%

Individual conversion efficiency = 340 / 2643.05 = 12.9%

Total population consumption = 2.146E7 g
% change = 2.146E7 vs 2.229E7 = - 3.7%

4) Approach: Use baseline values plus a change in mortality rates for walleye during the fishing season (20%). Note that the 20% figure applies to part of the year only. New mortality to enter should be 0.001328. (Write down old value so that you can reset it after running this simulation). Be sure to use the baseline diet file.

Population size = 5561 fish
% change = 5561 vs 6386 = - 12.9%

Total production = 3.089E6 g
% change = 3.089E6 vs 3.361E6 = - 8%

Total number harvested = 1783 fish
% change = 1783 vs 716.8 = + 148%

Total population consumption = 2.047E7 g
% change = 2.047E7 vs 2.229E7 = - 8.2%

5) Approach: Use all baseline values with the following change: reduce RA by 10% (0.9 * 0.0108 = 0.00972).

New end weight = 1039.3 g

Weight gain = 534 g
% change = 534 vs 415 = + 28.7%

Total individual consumption = 2895 g
% change = 2895 vs 2752 = + 5.2%

Individual conversion efficiency = 534 / 2895=18.4%

Total population consumption = 2.338E7 g
% change = 2.338E7 vs 2.229E7 = + 5%

Population conversion efficiency = 4.315E6 / 2.338E7 = 18.5%

6) Approach: Use baseline values with these specific changes: annual growth increment is halved: (415 / 2 = 207.5; 207.5 + 505 = 712.5 end weight) and new population size is doubled (to 20,000). Run a new P-fit and then run new simulation.

New P-value = 0.35857

% change = 0.35857 vs 0.41805 = - 14%

Total population consumption = 3.47E7 g

% change = 3.47E7 vs 2.229E7 = + 55.7%

Total production = 3.378E6 g

% change = 3.378E6 vs 3.361E6 = + 0.5%

Number harvested = 1434 fish

% change = 1434 vs 717 = + 100%

Weight harvested = 8.258E5 g

% change = 8.258E5 vs 4.585E5 = + 80%

7) Approach: Create second cohort in file by duplicating the first cohort. Change P-value in first cohort (1.1 * 0.4180). Set end date of first cohort to August 31 (153). Run bioenergetics model for cohort 1 by itself and print out last day's values. Take the last day's weight and population size and add as input data for cohort 2 (initial weight and initial population size). Change beginning day for cohort 2 to September 1 (154). Keep the old P-value for cohort 2. Now make a final run of the bioenergetics model using both cohorts.

New ending weight = 1007.88 g
Weight gain = 502.88 g
% change = 502.88 vs 415 = + 21%

Population size = 6386 fish
% change = 6386 vs 6386 = 0%

Total population consumption = 2.479E7 g
% change = 2.479E7 vs 2.229E7 = + 11.2%

Total production = 4.121E6 g
% change = 4.121E6 vs 3.361E6 = + 22.6%

References

Adams, S.M., R.B. McLean, and M.M. Huffman. 1982. Structuring of a predator population through temperature-mediated effects on prey availability. *Can. J. Fish. Aquat. Sci.* 39:1175-1184.

Bartell, S.M., J.E. Breck, R.H. Gardner, and A.L. Brenkert. 1986. Individual parameter perturbation and error analysis of fish bioenergetics models. *Can. J. Fish. Aquat. Sci.* 43:160-168.

Beauchamp, D.A., D.J. Stewart, and G.L. Thomas. 1989. Corroboration of a bioenergetics model for sockeye salmon. *Trans. Amer. Fish. Soc.* 118:597-607.

Bevelhimer, M.S., R.A. Stein, and R.F. Carline. 1985. Assessing significance of physiological differences among three esocids with a bioenergetics model. *Can. J. Fish. Aquat. Sci.* 42:57-69.

Boisclair, D., and W.C. Leggett. 1989. The importance of activity in bioenergetics models applied to actively foraging fishes. *Can. J. Fish. Aq. Sci.* 46:1859-1867.

Boisclair, D., and W.C. Leggett. 1990. On the relationship between growth and consumption rates: response to comments by R.S. Hayward (1989). *Can. J. Fish. Aq. Sci.* 47:230-233.

Boisclair, D., and W.C. Leggett. 1991. If computers could swim or fish could be programmed: a response to comments by Hewett et al. (1991). *Can. J. Fish. Aq. Sci.* 48:1337-1344.

Bottrell, H.H., A. Duncan, Z.M. Gliwicz, E. Grygierek, A. Herzig, A. Hillbright-Ilkowska, H. Kurasawa, P. Larsson, and T. Weglenska. 1976. A review of some problems in zooplankton production studies. *Norwegian J. Zool.* 24:419-456.

Carline, R.F. 1987. Simplified method based on bioenergetics modeling to estimate food consumption by largemouth bass and northern pike. *Trans. Amer. Fish. Soc.* 116:224-231.

Carline, R.F., B.L. Johnson, and T.J. Hall. 1984. Estimation and interpretation of proportional stock density for fish populations in Ohio impoundments. *N. Amer. J. Fish. Manag.* 4:139-154.

Cochran, P.A., and I.R. Adelman. 1982. Seasonal aspects of daily ration and diet of largemouth bass (*Micropterus salmoides*), with an evaluation of gastric evacuation rates. *Env. Biol. Fish.* 7:265-275.

Cochran, P.A., and J.A. Rice. 1982. A comparison of bioenergetics and direct field estimates of cumulative seasonal food consumption by largemouth bass (*Micropterus salmoides*). In: *Gutshop '81: Fish Food Habits Studies*, G. Caillliet and C. Simenstad, pp. 88-96. Seattle: Washington Sea Grant.

Coutant, C.C. 1977. Compilation of temperature preference data. *J. Fish. Res. Bd. Can.* 34:739-745.

Craig, J.F. 1977. The body composition of adult perch *Perca fluviatilis* in Windemere, with reference to seasonal changes and reproduction. *J. Anim. Ecol.* 46:617-632.

Cummins, K.W., and J.C. Wuycheck. 1971. Caloric equivalents for investigations in ecological energetics. *Mitt. Int. Ver. Theor. Angew. Limnol.* 18:1-151.

Downing, J.A., and F.H. Rigler. 1984. *A manual on methods for the assessment of secondary productivity in fresh water.* Blackwell Scientific, Oxford.

Driver, E.A. 1981. Calorific values of pond invertebrates eaten by ducks. *Freshwater Biology* 11:579-581.

Dumont, H.J., I. Van de Velde, and S. Dumont. 1975. The dry weight estimate of biomass in a selection of cladocera, copepoda and rotifera from the plankton periphyton and benthos of continental waters. *Oecologia* 19:75-97.

Eggers, D.M. 1979. Comment on some recent methods for estimating food consumption by fish. *J. Fish. Res. Board Can.* 36:1018-1019.

Elliott, J.M. 1976. Energy losses in the waste products of brown trout (*Salmo trutta* L.). *J. Anim. Ecol.* 45:561-580.

Elliott, J.M., and L. Perrson. 1978. The estimation of daily rates of food consumption for fish. *J. Anim. Ecol.* 47:977-991.

Flath, L.E., and J.S. Diana. 1985. Seasonal energy dynamics of the alewife in southeastern Lake Michigan. *Trans. Amer. Fish. Soc.* 114:328-337.

Fox, M.G. 1991. Food consumption and bioenergetics of young-of-the-year walleye (*Stizostedion vitreum vitreum*): model predictions and population density effects. *Can. J. Fish. Aq. Sci.* 48:434-441.

Hayward, R.S. 1990. Comment on Boisclair and Leggett: can eating really stunt your growth? *Can. J. Fish. Aq. Sci.* 47:228-230.

Hayward, R.S., and F.J. Margraf. 1988. Ecology of yellow perch in Lake Erie. Commercial Fisheries Research and Development Project 3-379-R #1, Completion Report, 138 pp.

Helminen, H., J. Sarvala, and A. Hirvonen. 1990. Growth and food consumption of vendace (*Coregonus albula* (L.)) in Lake Pyhajarvi, SW Finland: a bioenergetics modeling analysis. *Hydrobiologia* 200/201:511-522.

Hewett, S.W. 1989. Ecological applications of bioenergetics models. *Amer. Fish. Soc. Symp.* 6:113-120.

Hewett, S.W., C.E. Kraft, and B.L. Johnson. 1991. Consumption, growth, and allometry: A comment on Boisclair and Leggett (1989a,b,c,d). *Can. J. Fish. Aq. Sci.* 48:1334-1337.

Hewett, S.W., and D.J. Stewart. 1989. Zooplanktivory by alewives in Lake Michigan: Ontogenetic, seasonal, and historical patterns. *Trans. Amer. Fish. Soc.* 118:581-596.

Hill, D.K., and J.J. Magnuson. 1990. Potential effects of global climate warming on the growth and prey consumption of Great Lakes fishes. *Trans. Amer. Fish. Soc.* 119:265-275.

Houston, A.H. 1982. Thermal effects upon fishes. Nat. Resch. Council Can., Assoc. Comm. Sci. Criteria Environ. Qual., Rep. 18566. 200 pp.

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.

Jobling, M. 1981. Temperature tolerance and the final preferendum - rapid methods for the assessment of optimum growth temperatures. *J. Fish Biol.* 19:439-455.

Johnson, B.M., R.A. Stein, and R.F. Carline. 1988. Use of a quadrat rotenone technique and bioenergetics modeling to evaluate prey availability to stocked piscivores. *Trans. Amer. Fish. Soc.* 117:127-141.

Kitchell, J.F. 1983. Energetics. pp. 312-338 In: *Fish Biomechanics*, P.W. Webb, and D. Weihs, New York: Praeger Publishing.

Kitchell, J.F. 1990. The scope for mortality caused by sea lamprey. *Trans. Amer. Fish. Soc.* 119:642-648.

Kitchell, J.F., and J.E. Breck. 1980. Bioenergetics model and foraging hypothesis for sea lamprey (*Petromyzon marinus*). *Can. J. Fish. Aq. Sci.* 37:2159-2168.

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.*

Kitchell, J.F., J.F. Koonce, R.V. O'Neill, H.H. Shugart, Jr., J.J. Magnuson, and R.S. Booth. 1974. Model of fish biomass dynamics. *Trans. Amer. Fish. Soc. 103:786-798.*

Kitchell, J.F., J.J. Magnuson, and W.H. Neill. 1977a. Estimation of caloric content for fish biomass. *Environ. Biol. Fish.* 2:185-188.

Kitchell, J.F., D.J. Stewart, and D. Weininger. 1977b. Applications of a bioenergetics model to yellow perch (*Perca flavescens*) and walleye (*Stizostedion vitreum vitreum*). *J. Fish. Res. Board Can.* 34:1922-1935.

Kruger, C.C., and T.D. Dehring. 1986. A procedure to allocate the annual stocking of salmonids in the Wisconsin waters of Lake Michigan. Wisc. Dept. Nat. Res., Bureau Fish Mgmt., Madison. Fish Mgmt. Rep. 127.

Lei, C., and K.B. Armitage. 1980. Population dynamics and production of *Daphnia ambigua* in a fish pond, Kansas. *Univ. Kansas Sci. Bull.* 51:687-715.

Lin, Y. 1975. Food and growth of young yellow perch during pelagic and demersal stages in Oneida Lake. Ph.D. thesis, Cornell University, 96 pp.

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.

Mann, K.H. 1978. Chapter 10: Estimating the food consumption of fish in nature. In: *Ecology of freshwater fish production*, S.D. Gerking, pp. 250-273. New York: John Wiley and Sons.

Mills, E.L., and J.L. Forney. 1981. Energetics, food consumption and growth of young yellow perch in Oneida Lake, New York. *Trans. Am. Fish. Soc.* 110:479-488.

Ney, J.J. 1990. Trophic economics in fisheries: assessment of demand-supply relationships between predators and prey. *Reviews in Aquatic Sciences* 2:55-81.

Nitithamyong, C. 1988. Bioenergetics approach to the study of anabolic effects of 17α-methytestosterone in blue tilapia, *Oreochromis aureus*. Ph.D. thesis, University of Wisconsin-Madison. 124 pp.

Post, J.R. 1990. Metabolic allometry of larval and juvenile yellow perch (*Perca flavescens*): *in situ* estimates and bioenergetic models. *Can. J. Fish. Aquat. Sci.* 47:554-560.

Raat, A.J.P. 1990. Production, consumption, and prey availability of northern pike (*Esox lucius*), pike-perch (*Stizostedion lucioperca*) and European catfish (*Silurus glanis*): a bioenergetic approach. *Hydrobiologia* 200/201:497-509.

Rice, J.A. 1981. Derivation and application of a bioenergetics model for largemouth bass (*Micropterus salmoides*). M.S. thesis, University of Wisconsin-Madison. 109 pp.

Rice, J.A., J.E. Breck, S.M. Bartell, and J.F. Kitchell. 1983. Evaluating the constraints of temperature, activity and consumption on growth of largemouth bass. *Environ. Biol. Fish.* 9:263-275.

Rice, J.A., and P.A. Cochran. 1984. Independent evaluation of a bioenergetics model for largemouth bass. *Ecology* 65:732-739.

Ricker, W.E. 1975. Computation and interpretation of biological statistics of fish populations. Fish. Res. Bd. Can. Bull. 191.

Rottiers, D.V., and R.M. Tucker. 1982. Proximate composition and caloric content of eight Lake Michigan fishes. U.S. Fish Wild. Serv. Tech. Paper 108: 8 pp.

Rudstam, L.G. 1988. Exploring the dynamics of herring consumption in the Baltic: applications of an energetics model of fish growth. Kieler Meeresforsch., *Sonderh.* 6:312-322.

Rudstam, L.G. 1989. A bioenergetic model for *Mysis* growth and consumption applied to a Baltic population of *Mysis mixta. J. Plankton Res.* 11:971-983.

Schindler, D.W., A.S. Clark, and J.R. Gray. 1971. Seasonal caloric values of freshwater zooplankton, as determined with a Phillipson bomb calorimeter modified for small samples. *J. Fish. Res. Bd. Canada* 28:559-564.

Schott, E.F., T.B. Kayes, and H.E. Calbert. 1978. Comparative growth of male versus female yellow perch fingerlings under controlled environmental conditions. *Amer. Fish. Soc. Spec. Publ.* 11:181-186.

Shuter, B.J., and J.R. Post. 1990. Climate, population viability, and the zoogeography of temperate fishes. *Trans. Am. Fish. Soc.* 119:314-336.

Snow, N.B. 1972. The effect of season and animal size on the caloric content of *Daphnia pulicaria. Limnol. Oceanogr.* 17:909-913.

Solomon, D.J., and A.E. Brafield. 1972. The energetics of feeding, metabolism and growth of perch (*Perca fluviatilis* L.). *J. Anim. Ecol.* 41:699-718.

Soofiani, N.M., and A.D. Hawkins. 1985. Field studies of energy budgets. In: *Fish energetics: new perspectives*, P. Tytler and P. Calow, eds., pp. 283-307. Baltimore: Johns Hopkins University Press.

Stewart, D.J. 1980. Salmonid predators and their forage base in Lake Michigan: a bioenergetics-modeling synthesis. Ph.D. thesis, University of Wisconsin-Madison. 225 pp.

Stewart, D.J., and F.P. Binkowski. 1986. Dynamics of consumption and food conversion by Lake Michigan alewives: an energetics modeling synthesis. *Trans. Am. Fish. Soc.* 115:643-661.

Stewart, D.J., J.F. Kitchell, and L.B. Crowder. 1981. Forage fishes and their salmonid predators in Lake Michigan. *Trans. Amer. Fish. Soc.* 110:751-763.

Stewart, D.J., D. Weininger, D.V. Rottiers, and T.A. Edsall. 1983. An energetics model for lake trout, *Salvelinus namaycush*: Application to the Lake Michigan population. *Can. J. Fish. Aq. Sci.* 40:681-698.

Thornton, K.W., and A.S. Lessem. 1978. A temperature algorithm for modifying biological rates. *Trans. Amer. Fish. Soc.* 107:284-287.

Tytler, P., and P. Calow, eds. 1985. *Fish energetics: new perspectives.* 349 pp. Baltimore: John Hopkins University Press.

Vijverberg, J., and T.H. Frank. 1976. The chemical composition and energy contents of copepods and cladocerans in relation to their size. *Freshwat. Biol.* 6:333-345.

Wahl, D. H., and R. A. Stein. 1991. Food consumption and growth of three esocids: Field tests of a bioenergetics model. *Trans. Amer. Fish. Soc.* 120:230-246.

Weininger, D. 1978. Accumulation of PCBs by lake trout in Lake Michigan. Ph.D. thesis, University of Wisconsin-Madison. 232 pp.

Winberg, G.G. 1956. *Rate of metabolism and food requirements of fishes.* Belorussian Univ., Minsk. 253 pp. (Transl. by Fish. Res. Board Can. Transl. Ser. No. 164, 1960).

Wismer, D.A., and A.E. Christie. 1987. Temperature relationships of Great Lakes fishes: A data compilation. Great Lakes Fish. Comm., Ann Arbor, Mich. Spec. Publ. 87-3.

Bibliography

This bibliography is not exhaustive but, when combined with the references section, will give readers an introduction to much of the literature relevent to *Model 2*. It begins with a section on general bioenergetics references and continues with sections listing references pertinent to each taxa we can currently model. In the sections on individual taxa, one or more references are listed as a **Primary Paper**. These are papers that first introduced the model for a particular fish or those that list modifications to that model. Other papers listed are those that make use of the model or that contain data upon which parameter estimates for that model were based.

General Bioenergetics

Bartell, S.M., J.E. Breck, R.H. Gardner, and A.L. Brenkert. 1986. Individual parameter perturbation and error analysis of fish bioenergetics models. *Can. J. Fish. Aquat. Sci.* 43:160-168.

Braaten, B.R. 1979. Bioenergetics — A review on methodology. Proc. World Symp. on Finfish *Nutrition and Fishfeed Technology* II:461-504.

Brett, J.R., and T.D.D. Groves. 1979. Physiological energetics. In: *Fish Physiology*, Vol. VIII, W.S. Hoar, D.J. Randall and J.R. Brett, pp. 279-352. New York: Academic Press.

Cochran, P.A., and K.J. Knutsen. 1988. Error in estimation of feeding rates from changes in mean body mass. *Can. J. Fish. Aquat. Sci.* 45:1494-1498.

Cummins, K.W., and J.C. Wuycheck. 1971. Caloric equivalents for investigations in ecological energetics. *Mitt. Int. Theor. Angew. Limnol.* 18:158 pp.

DeWitt, C.B., and R.M. Friedman. 1979. Significance of skewness in ectotherm thermoregulation. *Amer. Zool.* 19:195-209.

Eggers, D.M. 1979. Comment on some recent methods for estimating food consumption by fish. *J. Fish. Res. Board Can.* 36:1018-1019.

Elliott, J.M. 1979. Energetics of freshwater teleosts. In: *Fish Phenology: Anabolic Adaptiveness in Teleosts*, P.J. Miller, pp. 29-61. London: Zoological Society of London.

Elliott, J.M., and W. Davison. 1975. Energy equivalents of oxygen consumption in animal energetics. *Oecologia (Berlin)* 19:195-201.

Elliott, J.M., and L. Perrson. 1978. The estimation of daily rates of food consumption for fish. *J. Anim. Ecol.* 47:977-991.

Fischer, Z. 1979. Selected problems of fish bioenergetics. *Proc. World Symp. on Finfish Nutrition and Fishfeed Technology* I:17-44.

Hewett, S.W., and B.L. Johnson. 1989. A general bioenergetics model for fishes. *Amer. Fish. Soc. Symp.* 6:206-208.

Kitchell, J.F. 1983. Energetics. In: *Fish Biomechanics*, P.W. Webb and D. Weihs, pp. 312-338. New York: Praeger Publishing.

Jobling, M. 1981. Temperature tolerance and the final preferendum — rapid methods for the assessment of optimum growth temperatures. *J. Fish Biol.* 19:439-455.

Majkowski, J., and K.G. Waiwood. 1981. A procedure for evaluating the food biomass consumed by a fish population. *Can. J. Fish. Aq. Sci.* 38:1199-1208.

Mann, K.H. 1978. Chapter 10: Estimating the food consumption of fish in nature. In: *Ecology of Freshwater Fish Production*, S.D. Gerking, pp. 250-273. New York: John Wiley and Sons.

Thornton, K.W., and A.S. Lessem. 1978. A temperature algorithm for modifying biological rates. *Trans. Amer. Fish. Soc.* 107:284-287.

Tytler, P., and P. Calow, eds. 1985. *Fish energetics: new perspectives.* 349 pp. Baltimore: John Hopkins University Press.

Ursin, E. 1979. Principles of growth in fish. *Symp. Zool. Soc. Lond.* 44:63-87.

Ware, D.M. 1978. Growth, metabolism, and optimum swimming speed of a pelagic fish. *J. Fish. Res. Bd. Can.* 32:33-41.

Ware, D.M. 1978. Bioenergetics of pelagic fish: theoretical change in swimming speed and ration with body size. *J. Fish. Res. Bd. Can.* 35:220-228.

Webb, P.W. 1978. Partitioning of energy into metabolism and growth. In: *Ecology of Freshwater Fish Production*, S.D. Gerking, pp. 184-214. New York: John Wiley and Sons.

Winberg, G.G. 1956. Rate of metabolism and food requirements of fishes. Belorussian Univ., Minsk. 253 pp. (Transl. by Fish. Res. Board Can. Transl. Ser. No. 164, 1960).

Sea Lamprey

Beamish, F.W.H. 1973. Oxygen consumption of adult *Petromyzon marinus* in Michigan. *U.S. Fish. Wildl. Serv. Spec. Sci. Rep. Fish. Ser.* 55:237.

Cochran, P.A., and J.F. Kitchell. 1986. Use of modeling to investigate potential feeding strategies of parasitic lampreys. *Environ. Biol. Fish.* 16(1-3):219-223.

Farmer, G.J., F.W.H. Beamish, and G.A. Robinson. 1975. Food consumption of the adult landlocked sea lamprey, *Petromyzon marinus* L. Comp. *Biochem. Physiol.* 50A:753-757.

Farmer, G.J., F.W.H. Beamish, and P.F. Lett. 1977. Influence of water temperature on the growth rate of landlocked sea lamprey (*Petromyzon marinus*) and the associated rate of host mortality. *J. Fish. Res. Board Can.* 34:1373-1378.

Kitchell, J.F. 1990. The scope for mortality caused by sea lamprey. *Trans. Amer. Fish. Soc.* 119:642-648.

Kitchell, J.F., and J.E. Breck. 1980. Bioenergetics model and foraging hypothesis for sea lamprey (*Petromyzon marinus*). *Can. J. Fish. Aq. Sci.* 37:2159-2168. **(Primary Paper)**

Alewife

Brown, E.H., Jr. 1972. Population biology of alewives, *Alosa pseudoharengus*, in Lake Michigan, 1949-1970. *J. Fish. Res. Board Can.* 29:477-500.

Flath, L.E., and J.S. Diana. 1985. Seasonal energy dynamics of the alewife in southeastern Lake Michigan. *Trans. Am. Fish. Soc.* 114:328-337.

Hatch, R.W., P.M. Haack, and E.H. Brown, Jr. 1981. Estimation of alewife biomass in Lake Michigan, 1967-1978. *Trans. Am. Fish. Soc.* 110:575-584.

Henderson, B.A., and E.H. Brown, Jr. 1985. Effects of abundance and water temperature on recruitment and growth of alewife (*Alosa pseudoharengus*) near South Bay, Lake Huron, 1954-1982. *Can. J. Fish. Aq. Sci.* 42:1608-1613.

Hewett, S.W., and D.J. Stewart. 1989. Zooplanktivory by alewives in Lake Michigan: Ontogenetic, seasonal, and historical patterns. *Trans. Amer. Fish. Soc.* 118:581-596.

Stewart, D.J., and F.P. Binkowski. 1986. Dynamics of consumption and food conversion by Lake Michigan alewives: an energetics modeling synthesis. *Trans. Am. Fish. Soc.* 115:643-661. **(Primary Paper)**

Coregonids

Helminen, H., J. Sarvala, and A. Hirvonen. 1990. Growth and food consumption of vendace (*Coregonus albula* (L.)) in Lake Pyhajarvi, SW Finland: a bioenergetics modeling analysis. *Hydrobiologia* 200/201:511-522. (This paper offers alternative model parameters to those in Rudstam and Binkowski 1990.)

Rudstam, L.G., F.P. Binkowski, and M. A. Miller. (in prep.) A bioenergetics model for analysis of food consumption patterns by bloater in Lake Michigan. (Compared to Helminen et al. 1990, this model is based on more new data specific to coregonids.) **(Primary Paper)**

Herring

Rudstam, L.G. 1989. Exploring the dynamics of herring consumption in the Baltic: applications of an energetics model of fish growth. *Kieler Meeresforsch., Sonderh.* 6:312-322. **(Primary Paper)**

Rudstam, L.G., S. Hansson, S. Johansson, and U. Larsson. 1992. Dynamics of planktivory in a coastal area of the northern Baltic Sea. *Mar. Ecol. Prog. Ser.* (in press).

Lake Trout

Eck, G.W., and E.H. Brown, Jr. 1985. Lake Michigan's capacity to support lake trout (*Salvelinus namaycush*) and other salmonines: an estimate based on the status of prey populations in the 1970's. *Can. J. Fish. Aq. Sci.* 42:449-454.

Stewart, D.J., D. Weininger, D.V. Rottiers, and T.A. Edsall. 1983. An energetics model for lake trout, *Salvelinus namaycush*. Application to the Lake Michigan population. *Can. J. Fish. Aq. Sci. 40:681-698.* **(Primary Paper)**

Weininger, D. 1978. Accumulation of PCBs by lake trout in Lake Michigan. Ph.D. Thesis, University of Wisconsin-Madison. 232 pp.

Salmons

Beauchamp, D.A., D.J. Stewart, and G.L. Thomas. 1989. Corroboration of a bioenergetics model for sockeye salmon. *Trans. Amer. Fish. Soc.* 118:597-607. **(Primary Paper)**

Brett, J.R. 1983. Life energetics of sockeye salmon, *Oncorhynchus nerka*. In: *Behavioral energetics: the cost of survival in vertebrates*, W.P. Aspey and S.I. Lustick, eds., pp. 29-63. Columbus: Ohio State University Press.

Brett, J.R. 1986. Production energetics of a population of sockeye salmon, *Oncorhynchus nerka*. *Can. J. Zool.* 64:555-564.

Elliott, J.M. 1975. Weight of food and time required to satiate brown trout, *Salmo trutta* L. *Freshw. Biol.* 5:51-64.

Elliott, J.M. 1975. Number of meals in a day, maximum weight of food consumed in a day and maximum rate of feeding of brown trout, *Salmo trutta* L. *Freshw. Biol.* 5:287-303.

Elliott, J.M. 1976. Energy losses in the waste products of brown trout (*Salmo trutta* L.). *J. Anim. Ecol.* 45:561-580.

Elliott, J.M. 1976. The energetics of feeding, metabolism and growth of brown trout (*Salmo trutta* L.) in relation to body weight, water temperature and ration size. *J. Anim. Ecol.* 45:923-948.

Stewart, D.J. 1980. Salmonid predators and their forage base in Lake Michigan: a bioenergetics-modeling synthesis. Ph.D. Thesis, Univ. of Wisconsin-Madison. 225 pp. **(Primary Paper)**

Stewart, D.J., and M. Iberra. 1991. Predation and production by salmonine fishes in Lake Michgan, 1978-88. *Can. J. Fish. Aq. Sci.* 48:909-922. **(Primary Paper)**

Stewart, D.J., J.F. Kitchell, and L.B. Crowder. 1981. Forage fishes and their salmonid predators in Lake Michigan. *Trans. Amer. Fish. Soc.* 110:751-763.

Esocids

Bevelhimer, M.S., R.A. Stein, and R.F. Carline. 1985. Assessing significance of physiological differences among three esocids with a bioenergetics model. *Can. J. Fish. Aquat. Sci.* 42:57-69. **(Primary Paper)**

Diana, J.S. 1980. Diel activity patterns and swimming speeds of northern pike (*Esox lucius*) in Lac Ste. Anne, Alberta. *Can. J. Fish. Aquat. Sci.* 37:1454-1458.

Diana, J.S. 1982. An experimental analysis of the metabolic rate and food utilization of northern pike. *Comp. Biochem. Physiol.* 71A:395-399.

Diana, J.S. 1983. An energy budget for northern pike (*Esox lucius*). *Can. J. Zool.* 61:1968-1975.

Wahl, D. H., and R. A. Stein. 1991. Food consumption and growth of three esocids: field tests of a bioenergetics model. *Trans. Amer. Fish. Soc.* 120:230-246.

Cyprinids

Bowen, S.H. 1982. Feeding, digestion and growth — quantitative considerations. In: *The Biology of Tilapias*, R.S.V. Pullin and R.H. McConnell, pp. 141-156. Manila: International Center for Living Aquatic Resources Management.

Brett, J.R. 1944. Some lethal temperature relations of Algonquin Park fishes. *Publ. Ont. Fish. Res. Lab* 63:1-49.

Bryan, J.D., L.G. Hill, and W.H. Neill. 1984. Interdependence of acute temperature preference and respiration in the plains minnow. *Trans. Am. Fish. Soc.* 113:557-562.

Campbell, J.S., and H.R. MacCrimmon. 1970. Biology of the emerald shiner *Notropis atherinoides* Rafinesque in Lake Simcoe, Canada. *J. Fish Biol.* 2:259-273.

Cui, Y., and R.J. Wootton. 1989. Bioenergetics of growth of a cyprinid, *Phoxinus phoxinus* (L.): development and testing of a model. *J. Fish Biol.* 34:47-64.

He, X. 1986. Population dynamics of northern redbelly dace (*Phoxinus eos*), finescale dace (*Phoxinus neogaeus*), and central mudminnow (*Umbra limi*), in two manipulated lakes. M.S. Thesis, University of Wisconsin-Madison. **(Primary Paper)**

Kevern, N.R. 1966. Feeding rate of carp estimated by a radioisotope method. *Trans. Am. Fish. Soc.* 95:363-371.

McCormick, J.H. 1976. Growth and survival of young-of-the-year emerald shiners (*Notropis atherinoides*) at different temperatures. *J. Fish. Res. Board Can.* 33:839-842.

Tyler, A.V. 1966. Some lethal temperature relations of two minnows of the genus *Chrosomus*. *Can. J. Zool.* 44:349-364.

Wooten, R.J., J.R.M. Allen, and S.J. Cole. 1980. Effect of body weight and temperature on the maximum daily food consumption of *Gasterosteus aculeatus* L. and *Phoxinus phoxinus* L.: selecting an appropriate model. *J. Fish Biol.* 17:695-705.

Striped bass

Moore, C.M. 1988. Food habits, population dynamics, and bioenergetics of four predatory fish species in Smith Mountian Lake, Virginia. Ph.D. Thesis, Virginia Polytechnic Institute and State University, Blacksburg. **(Primary Paper)**

Largemouth Bass

Beamish, F.W.H. 1974. Apparent specific dynamic action of largemouth bass, *Micropterus salmoides*. *J. Fish. Res. Bd. Can.* 31:1763-1769.

Cochran, P.A., and I.R. Adelman. 1982. Seasonal aspects of daily ration and diet of largemouth bass (*Micropterus salmoides*), with an evaluation of gastric evacuation rates. *Env. Biol. Fish.* 7:265-275.

Cochran, P.A., and J.A. Rice. 1982. A comparison of bioenergetics and direct field estimates of cumulative seasonal food consumption by largemouth bass (*Micropterus salmoides*). In: *Gutshop '81: Fish Food Habits Studies*, G. Cailliet and C. Simenstad, pp. 88-96. Seattle: Washington Sea Grant.

Niimi, A.J., and F.W.H. Beamish. 1973. Bioenergetics and growth of largemouth bass (*Micropterus salmoides*) in relation to body size and temperature. *Can. J. Zool.* 52:447-456.

Rice, J.A. 1981. Derivation and application of a bioenergetics model for largemouth bass (*Micropterus salmoides*). M.S. Thesis, University of Wisconsin-Madison. 109 pp.

Rice, J.A., J.E. Breck, S.M. Bartell, and J.F. Kitchell. 1983. Evaluating the constraints of temperature, activity and consumption on growth of largemouth bass. *Environ. Biol. Fish.* 9:263-275. **(Primary Paper)**

Rice, J.A., and P.A. Cochran. 1984. Independent evaluation of a bioenergetics model for largemouth bass. *Ecology* 65:732-739.

Smallmouth Bass

Shuter, B.J., and J.R. Post. 1990. Climate, population viability, and the zoogeography of temperate fishes. *Trans. Am. Fish. Soc.* 119:314-336. **(Primary Paper)**

Bluegill

Breck, J.E., and J.F. Kitchell. 1979. Effects of macrophyte harvesting on simulated predator-prey interactions. In: *Aquatic Plants, Lake Management and Ecosystem Consequences of Lake Harvesting*, J.E. Breck, R.T. Prentki and O.L. Loucks, pp. 211-228. Madison: Center for Biotic Studies, Institute for Environmental Studies, University of Wisconsin-Madison.

Kitchell, J.F., J.F. Koonce, R.V. O'Neill, H.H. Shugart, Jr., J.J. Magnuson, and R.S. Booth. 1974. Model of fish biomass dynamics. *Trans. Amer. Fish. Soc.* 103:786-798. **(Primary Paper)**

Perch / Walleye

Fox, M. G. 1991. Food consumption and bioenergetics of young-of-the-year walleye (*Stizostedion vitreum vitreum*): model predictions and population density effects. *Can. J. Fish. Aq. Sci.* 48:434-441.

Hokanson, K.E.F. 1977. Temperature requirements of some percids and adaptations to the seasonal temperature cycle. *J. Fish. Res. Board Can.* 34:1524-1550.

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.

Kelso, J.R.M. 1972. Conversion, maintenance and assimilation for walleye, *Stizostedion vitreum vitreum*, as affected by size, diet and temperature. *J. Fish. Res. Board Can.* 29:1181-1192.

Kitchell, J.F., D.J. Stewart, and D. Weininger. 1977. Applications of a bioenergetics model to yellow perch (*Perca flavescens*) and walleye (*Stizostedion vitreum vitreum*). *J. Fish. Res. Board Can.* 34:1922-1935. **(Primary Paper)**

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.

Minton, J.W., and R.B. McLean. 1982. Measurements of growth and consumption of sauger (*Stizostedion canadense*): implications for fish energetics studies. *Can. J. Fish. Aq. Sci.* 39:1396-1403.

Post, J.R. 1990. Metabolic allometry of larval and juvenile yellow perch (*Perca flavescens*): *in situ* estimates and bioenergetic models. *Can. J. Fish. Aquat. Sci.* 47:554-560. **(Primary Paper)**

Solomon, D.J., and A.E. Brafield. 1972. The energetics of feeding, metabolism and growth of perch (*Perca fluviatilis* L.). *J. Anim. Ecol.* 41:699-718.

Thorpe, J.E. 1977. Morphology, physiology, behavior and ecology of *Perca fluviatilis* L. and *P. flavescens* Mitchell. *J. Fish. Res. Board Can.* 34:1504-1514.

Tilapia

Nitithamyong, C. 1988. Bioenergetics approach to the study of anabolic effects of 17α-methytestosterone in blue tilapia, *Oreochromis aureus*. Ph.D. Thesis, University of Wisconsin-Madison. 124 pp. **(Primary Paper)**

Mysis

Rudstam, L.G. 1989. A bioenergetic model for *Mysis* growth and consumption applied to a Baltic population of *Mysis mixta*. *J. Plankton Res.* 11:971-983. **(Primary Paper)**