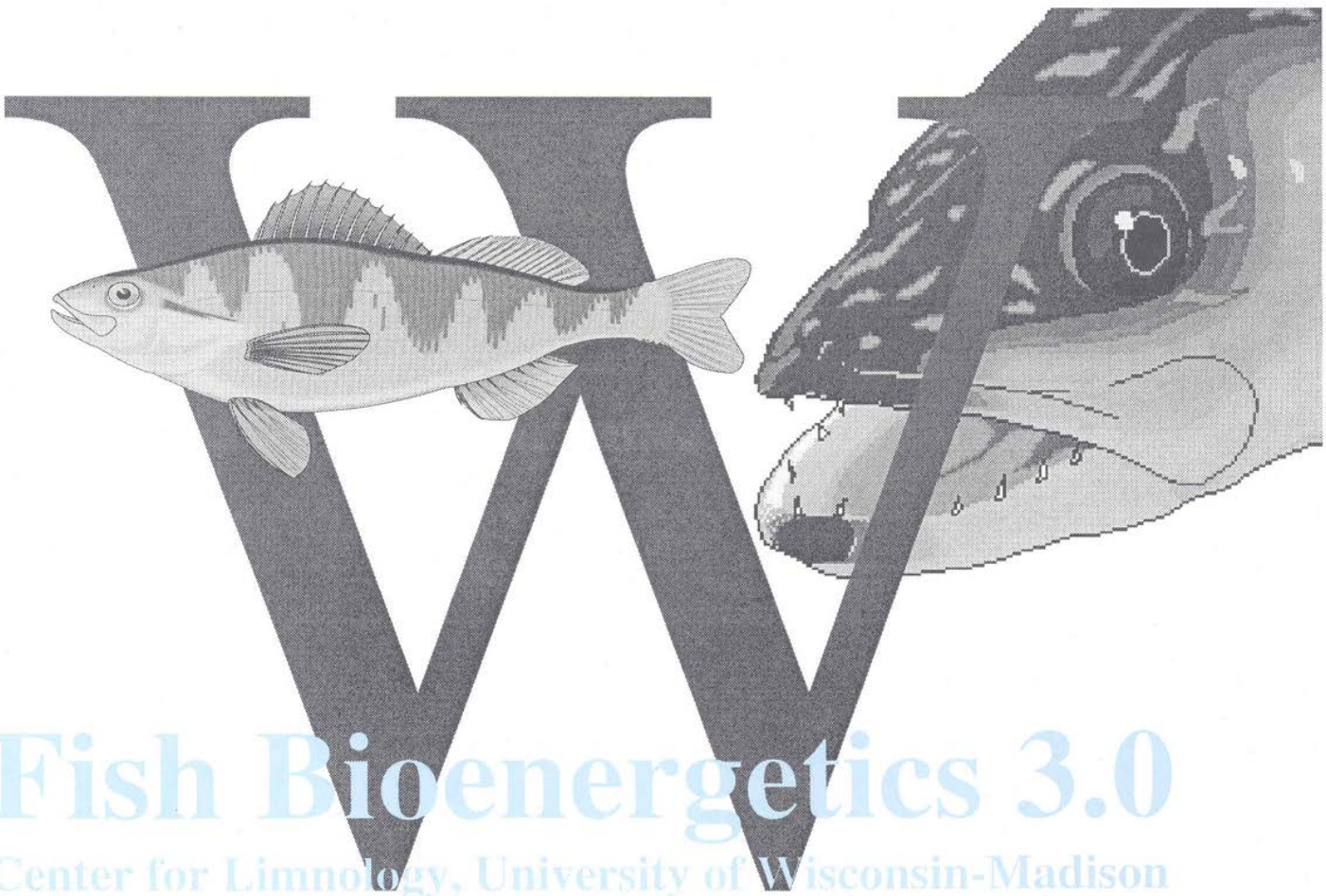

Fish Bioenergetics 3.0

Center for Limnology, University of Wisconsin-Madison

For Windows® 3.1, Windows® '95 and Windows® NT

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Fish Bioenergetics 3.0 for Windows

Contents

Bioenergetics Overview

The field of fish bioenergetics includes temporal scales that range from those of evolutionary time to cellular metabolism (Tytler and Calow 1985). It also includes spatial scales ranging from nutrition and growth in controlled aquaculture systems (Jobling 1994) to predator-prey systems in the largest ecological context (Adams and Breck 1990). Among the several reviews of the field, those by J. R. Brett offer the most insightful combination of basic laboratory studies and their application in the context most pertinent to fisheries science (Brett and Groves 1979). We recommend Brett's lead chapter (Brett 1995) in the new volume edited by Groot et al. (1995) for a thorough review of the extensive work conducted on energetics of Pacific salmonids and for an insightful assessment of areas where knowledge of energetics should be improved.

The underpinnings of energetics have a firm theoretical base in the laws of thermodynamics (Kleiber 1975). Working from an energy budget requires that you satisfy the terms of a simple equation; outputs must equal inputs and the budget must balance. As detailed in Chapter 2, the terms of the energy budget for fishes are well known and each can be measured independently. The model allows the user to specify the important external regulators: temperature and diet. For fishes, the most easily measured component of the energy budgeting process is expressed as growth. Growth integrates the array of environmental variables affecting an individual fish. Thus the evidence provided in the observed growth rate is the rich and varied foundation of scientific inquiry and the basis for better understanding.

The modeling approach presented in this manual derived from the extension of energetics principles used in ecosystem-scale models of trophic interactions developed during the International Biological Programme (Kitchell et al. 1974). These models focused on biomass dynamics. They often included formulations requiring an estimate of carrying capacity which was used to characterize density-dependent constraints for growth rates of a given trophic level. While those kinds of models have utility in an ecosystem context, they had three important shortcomings when applied to fishes. First, units of biomass per area or volume did not allow for resolution of cause and effect at the species or individual scale. After all, it is individual fish that feed, grow, reproduce and die. Further, as a fish grows from first-feeding larvae to reproductive adult, it may ascend through three or four trophic levels. Second, biomass models did not allow an effective interface with either the long history of population-based models in fisheries science or the models of predator-prey interactions developed in the ecological sciences. Third, biomass models required an estimate of environmental carrying capacity. The latter is difficult to do and, more importantly, likely to change as a consequence of the ecological effects due to fishery exploitation and/or anthropogenic effects on fish habitats.

An alternative to biomass models is an energetics-based approach focused on the processes that regulate growth by individual fish (Kitchell et al. 1977). This model assembled individuals in age- or size-based populations, separated the agents of mortality (natural vs. fishing) and specified the trophic ontogeny of predator-prey interactions. It focused on using the kinds of data most frequently collected by biologists – the habitat that is occupied (thermal history), size at age (growth curves), stomach contents, size or age at sexual maturity, and size- or age-related mortality rates. The development of size- or age-based cohorts is elaborated in Chapter 3.

1.1 The Modeling Strategy

Starting the process with observed growth rate is different from that of many kinds of modeling practices. In this case, the strategy of model building is based on specifying rules that define the limit conditions, i.e., the maximum and minimum possible rates of growth for members of a population. The physiological parameters used to represent the rules derive from readily and oft-measured processes such as temperature dependence, thermal tolerance, thermal preference, size dependence, assimilation efficiency, etc., that can be accurately measured in the laboratory. Those physiological parameters are assembled as empirical rules that define the effect of temperature, body size and food quality on maximum feeding rates. The minimum is similarly defined by rules describing the effect of temperature and body size on metabolic rates when food consumption is set to zero. These limits define the boundaries of the scope for growth. Observed growth is somewhere between those limits and allows the user to estimate how that growth rate is being regulated.

The hierarchy of energy allocation is an important component of this modeling approach. Consumed energy is first allocated to catabolic processes (maintenance and activity metabolism), then to waste losses (feces, urine and specific dynamic action) and that left over is allocated to somatic storage (body growth and gonad development). This hierarchy is analogous to practical economics. The first costs paid are those for rent or mortgage (metabolism) that sustain the organism. The second set of costs (waste losses) are like taxes – they are proportional to income (food consumption) and must be paid. The energy resource remaining may then be allocated to savings (growth) or invested in the next generation (gonad development). In an ecological or evolutionary context, it is easy to imagine selection for behaviors that maximize benefits (growth rate or gonad development) and minimize costs. Like an account balance, a record of growth reveals how well the organism has resolved the complexities of its environment.

In a thorough review of previous energetics work, Brett and Groves (1979) presented a generalization about energy budgets for two classes of fishes. If the energy budget is stated in the following terms:

Energy Consumed = Respiration + Waste + Growth,

and normalized to percentages when energy consumption = 100, then fishes growing at "typical" rates would have energy budgets approximated as below.

	Consumption	=	Respiration	+	Waste	+	Growth
For carnivores:	100	=	44	+	27	+	29
For herbivores:	100	=	37	+	43	+	20

These budgets reveal two important features. First, as expected, herbivores exhibit lower growth rates and higher waste-loss rates per unit of energy consumed. That is the logical consequence of eating foods of lower energy density and higher indigestible content. Second, both types of fishes demonstrate high rates of growth efficiency compared to those known for mammals and birds. Although these budgets can serve as a first approximation, the 95% confidence intervals for each component are substantial (e.g., plus or minus 20% of the mean). Of course, the energy budget for an average fish in a typical habitat may be very different from that of fishes in some unique ecological context. Fishes are known to exhibit among the highest growth efficiencies recorded (approaching 50%) and are known to exhibit strikingly negative energy budgets, as in the case of migrating salmon (Brett 1995). Note, too, that the hierarchy of energy allocation operates in all cases. Growth efficiency **is not** a constant, and growth rates in fishes are highly variable. Observed growth is the integrated answer to a complex question about prey resources and

environmental conditions. Deducing the quantitative components of cause and effect is the significant challenge.

In most of its applications, model users will seek an answer to questions about factors that constrain growth (e.g., diet quality or environmental stressors) or use the measured growth to estimate how much effect a predator has had on its prey populations. Assembled as a population, the model allows answers to those questions at the larger scales of ecological and management interest. This approach **does not** provide for feedback to future generations. Predator or prey population dynamics are not represented. Those must be characterized as simulations using specified assumptions about prey availability, mortality rates and environmental conditions.

We view the modeling process as having two general components. First is the "nuts-and-bolts" process of assembling the parameter tables and the input data. Much of the former is available in the manual or formatted in ways that welcome site-specific input. Second is the "arts-and-crafts" process of structuring analyses in ways that pose key questions and provide instructive answers. In these cases, it is often valuable to use the model as a way to create boundary conditions such as those for maximum possible growth or for maintenance requirements. Using the model in this way allows it to serve as a "deductive engine" in the more creative and challenging process of science (Walters 1986).

1.2 Previous Applications

This manual represents the third version of what appeared first as Hewett and Johnson (1989, 1992), which was sold (at cost) to more than 1,000 users and served as the basis for several score of shortcourses and workshops taught since 1988. That version was labeled the "Wisconsin model" (Ney 1993). As evidenced by the diversity of parameter tables presented in Appendix A, previous uses of this modeling approach are many and varied. They range from autecological studies of highly active subtropical tunas (Boggs and Kitchell 1991) to those of the sedentary, slowly growing burbot (Rudstam et al. 1995). They include omnivorous minnows (Schindler et al. 1993) and hyper-predaceous sea lampreys (Kitchell 1990). They provide estimates of zooplanktivory rates by small fishes in small lakes (Luecke et al. 1990, Post 1990) and rates of piscivory by a guild of salmonids predators preying on an assemblage of forage species in Lake Michigan (Stewart and Ibarra 1991). They include estimates of cannibalism (Rice and Cochran 1984) and quantitative estimates linking three trophic levels (LaBar 1993). In addition, the framework has been modified to develop models for some invertebrates (Rudstam 1989, Schneider 1992).

As summarized in Chapter 2, this model has been evaluated through a rigorous sensitivity analysis. Model results have also been compared to independently derived field data in several cases; those by Rice and Cochran (1984), Beauchamp et al. (1989) and Hansson et al. (1996) are particularly instructive. The approach has been praised for its promise and criticized for its inadequacies; both are represented in the proceedings of a recent symposium (Brandt and Hartman 1993, Hansen et al. 1993). We encourage the process of rigorous evaluation because that represents the path to improvements. The model cannot be wrong because it is based on a budget that must be right. It will improve in proportion to our ability to estimate the physiological parameters that regulate growth and the errors or bias of data employed as inputs.

This version of the model includes several new and important features. First, it is developed in the Windows environment and provides for inputs through a spreadsheet interface. Second, it employs the principles of mass balance to allow calculations in alternative currencies. Accordingly, it can be used to estimate the ecological significance of nutrient flux rates owing to fishes. In addition, it can be implemented to evaluate bioaccumulation of contaminants such as PCBs or heavy metals. The basic frameworks described in Chapter 4 invite additional applications.

References

Adams, M. S., and J. E. Breck. 1990. Bioenergetics. Pages 389-415 *In* C. B. Schreck and P. B. Moyle (eds.). Methods of Fish Biology. American Fisheries Society, Bethesda, Maryland.

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

Boggs, C.H., and J.F. Kitchell. l991. Tuna metabolic rate estimated from energy losses during starvation. Physiol. Zool. 64:502-524.

Brandt, S.B. and K.J. Hartman. 1993. Innovative approaches with bioenergetics models: future applications to fish ecology and management. Trans. Amer. Fish. Soc. 122:731-735.

Brett, J. R. 1995. Energetics. Pages 3-68 *In* C. Groot, L. Margois, and W. C. Clarke (eds.). Physiological Ecology of Pacific Salmon. Univ. British Columbia Press, Vancouver.

Brett, J. R., and T. D. D. Groves. 1979. Physiological energetics. Pages 279-352 *In* W. S. Hoar, D. J. Randall, and J. R. Brett. (eds.). Fish Physiology. Volume 8. Bioenergetics and Growth. Academic Press, New York.

Groot C., L. Margois, and W. C. Clarke (eds.). 1995. Physiological Ecology of Pacific Salmon. Univ. British Columbia Press, Vancouver.

Hansen, M. J., D. Boisclair, S. B. Brandt, S. W. Hewett, J. F. Kitchell, M. C. Lucas, and J. J. Ney. 1993. Applications of bioenergetics models to fish ecology and management: Where do we go from here? Trans. Amer. Fish. Soc. 122: 1019-1030.

Hansson, S., L. G. Rudstam, J. F. Kitchell, M. Hilden, B. L. Johnson and P. E. Peppard. 1996. Predation rates by North Sea cod (*Gadus morhua*) - predictions from models on gastric evacuation and bioenergetics. ICES J. Marine Sci. 51:107-114.

Hewett, S.W. and B.L. Johnson. 1987. A generalized bioenergetics model of fish growth for microcomputers. University of Wisconsin Sea Grant Institute, Madison, Wisconsin. 47 pp.

Hewett, S. W. and B.L. Johnson. 1992. A generalized bioenergetics model of fish growth for microcomputers. University of Wisconsin Sea Grant Institute, Madison, Wisconsin. UW Sea Grant Tech. Rep.WIS-SG-92-250. 79 pp.

Jobling, M. 1995. Fish Bioenergetics. Chapman and Hall, London.

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. Am. Fish. Soc. 103:786-798.

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

Kitchell, J.F. l990. The scope for mortality caused by sea lamprey. Trans. Amer. Fish. Soc. 119:642-648.

Kleiber, M. 1975. The Fire of Life: An Introduction to Animal Energetics. R. E. Krieger Publ, Huntington, New York.

LaBar, G. W. 1993. Use of bioenergetics models to predict the effect of increased lake trout predation on rainbow smelt following sea lamprey control. Trans. Amer. Fish. Soc. 122:942-950.

Luecke, C., M.J. Vanni, J.J. Magnuson, J.F. Kitchell, and P.T. Jacobson. 1990. Seasonal regulation of *Daphnia* populations by planktivorous fish: implications for the spring clear water phase. Limnol. Oceanogr. 35(8):1718-1733.

Ney, J. J. 1993. Bioenergetics modeling today: growing pains on the cutting edge. Trans. Amer. Fish. Soc. 122:736-748.

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.

Rice, J. A., and P. A. Cochran. 1984. Independent evaluation of a bioenergetics model for largemouth bass. Ecology 63:732-739.

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.

Rudstam, L.G., P.E. Peppard, T.W. Fratt, R.E.Bruesewitz, D.W.Coble, F.A. Copes and J. F. Kitchell. 1995. Prey consumption by the burbot (*Lota lota*) population in Green Bay, Lake Michigan, based on a bioenergetics model. Can. J. Fish. Aquat. Sci. 52: 1074-1082.

Schindler, D. E., J. F. Kitchell, X. He, S. R. Carpenter, J. R. Hodgson and K. L. Cottingham. 1993. Food web structure and phosphorus cycling in lakes. Trans. Amer. Fish. Soc. 122:756-772.

Schneider, D.W. l992. A bioenergetics model of zebra mussel feeding and growth in the Great Lakes. Can. J. Fish. Aquat. Sci. 49(7):1406-1416.

Stewart, D.J. and M. Ibarra. 1991. Predation and production by salmonine fishes in Lake Michigan, 1978-88. Can. J. Fish. Aquat. Sci. 48:909-922.

Tytler, P., and P. Calow (eds.). 1985. Fish Energetics: New Perspectives. Croom Helm, London.

Walters, C.J. 1986. Adaptive Management of Renewable Resources. Macmillan, New York.

Core Processes in Bioenergetics

A bioenergetics model is simply an energy balance equation in which energy consumed by a fish is balanced by total metabolism, waste losses and growth. As with earlier computer versions of the bioenergetics model (Hewett and Johnson 1987, 1992), *Fish Bioenergetics 3.0* uses species-specific physiological estimates of consumption or growth, respiration, egestion and excretion for the energy mass balance equation.

consumption = metabolism + wastes + growth
= (respiration +active metabolism + specific dynamic action) +
(egestion + excretion) + (somatic growth + gonad production)

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

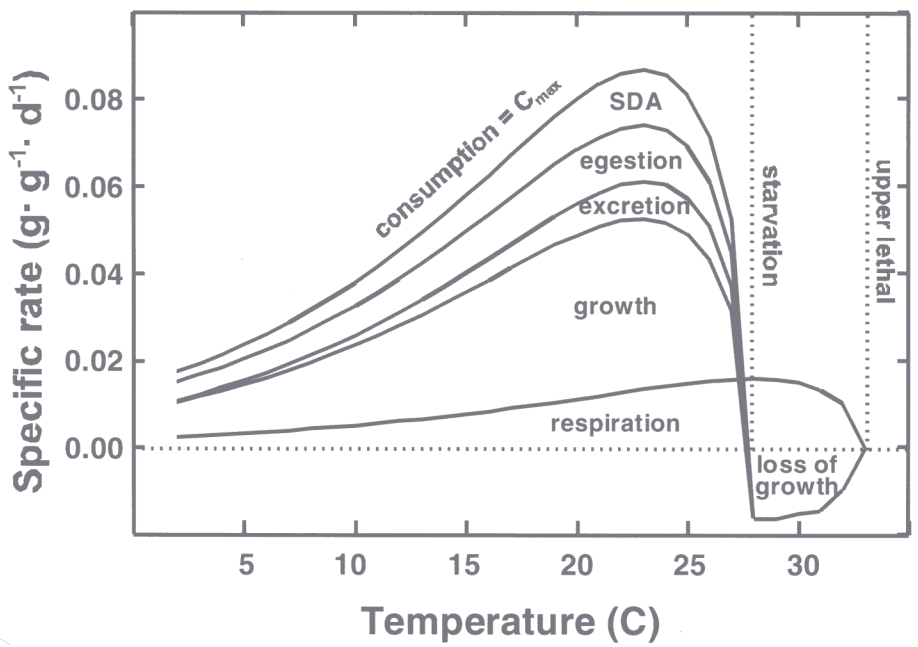


Figure 1: Energy budget for a 50g yellow perch (*Perca flavescens*) as a function of water temperature.

Each of the physiological processes is described by a species-specific set of physiological parameters. The total number of physiological parameters ranges from 12 to over 30 depending on the form of the function chosen by the user to describe the physiological process of each species. While some critics feel the models are overly complex (Ney 1990, 1993) and prone to errors in parameter estimation (Boisclair and Leggett 1989), the mass balance approach forces the energy budget to be balanced which acts to limit error propagation (Bartell et al. 1986).

This chapter defines the individual parameters necessary to describe the energy budget of a fish. For each of the major physiological processes (consumption, metabolism, egestion and excretion)

several different forms of the underlying equations are given to provide maximum latitude in describing the unique physiologies of different species. To date, parameter sets have been determined for 26 species of fish and, where possible, modified to recognize important ontogenetic shifts in physiology between larval, juvenile and adult fish. All calculations in the model are based on specific rates, e.g., grams of prey per gram of predator per day, and are calculated on a daily time step. Mass of predator and prey are corrected for energy density (joules per gram).

The final section of this chapter provides a more detailed explanation of the derivation of the individual parameters, including key citations describing how new species parameter lists were derived from laboratory studies and the published literature.

2.1 Consumption

Consumption is estimated as the proportion of maximum daily ration for a fish at a particular mass and temperature. Specifically, maximum daily consumption rate (g of prey per g body mass per day) is estimated as an allometric function of mass from *ad libitum* feeding experiments conducted at the optimum temperature for the particular fish species (Figure 2).

The basic form of the consumption function:

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

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

where:	C	specific consumption rate ($g \cdot g^{-1} \cdot d^{-1}$)
	C_{max}	maximum specific feeding rate ($g \cdot g^{-1} \cdot d^{-1}$)
	p	proportion of maximum consumption
	f(T)	temperature dependence function
	T	water temperature (°C)
	W	fish mass (g)
	CA	intercept of the allometric mass function
	CB	slope of the allometric mass function

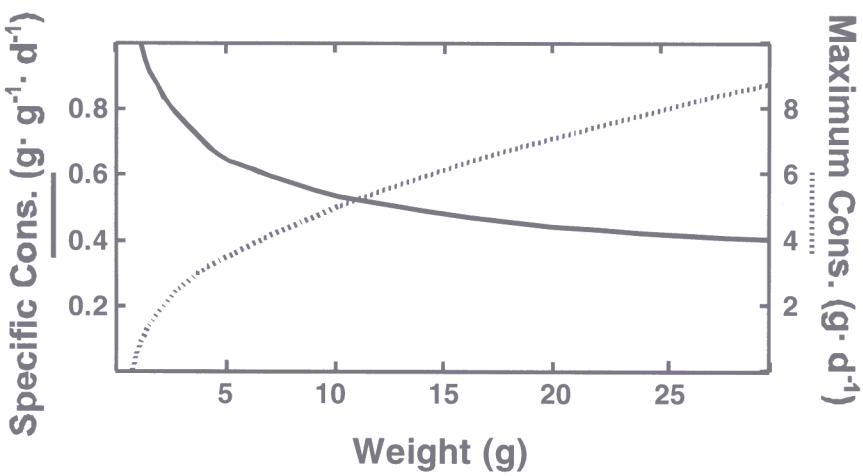


Figure 2: Maximum and specific consumption as a function of mass for a yellow perch (*Perca flavescens*) at optimum water temperature.

This maximum specific feeding rate is then modified by a water temperature dependence function and an additional proportionality constant (P-value) that accounts for ecological constraints on the maximum feeding rate (C_{max}). The P-value can range from 0 to 1, with 0 representing no feeding, and 1 indicating the fish is feeding at its maximum rate (based on its size and water temperature).

Three forms of the temperature dependence function (f(T)) are available with *Fish Bioenergetics 3.0* (Figure 3).

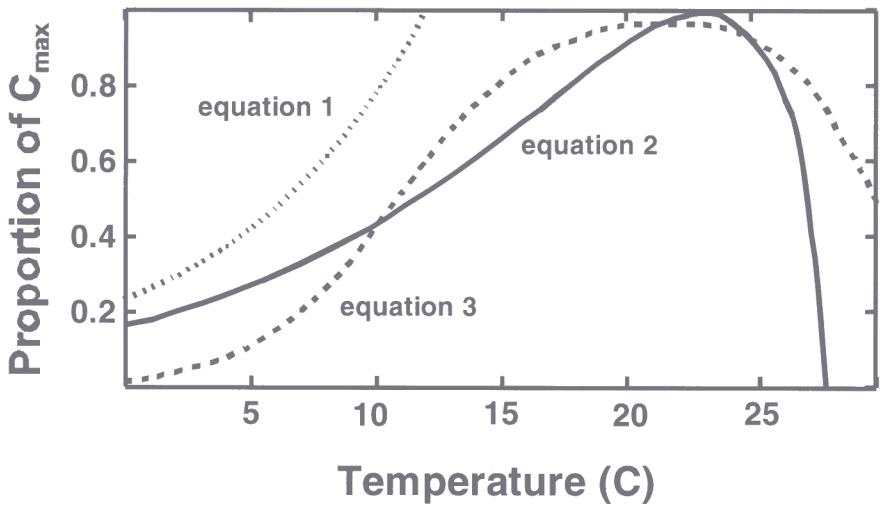


Figure 3: Temperature dependence of consumption as defined by the three equations available with *Fish Bioenergetics 3.0*.

Equation 1: Exponential (Stewart et al. 1983)

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

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

Equation 2: Temperature dependence for warm-water species (Kitchell et al. 1977)

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

where:

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

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

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

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

This water temperature dependence function is most appropriate for warm water species. With this equation, **CA** is the intercept of the mass dependence function for a 1 gram fish at the optimum water temperature (**CTO**, the laboratory temperature preferendum), **CB** is the coefficient of the mass dependence, **CTM** is the maximum water temperature above which consumption

ceases (approximated by the upper incipient lethal temperature), and **CQ** approximates a Q_{10} (the rate at which the function increases over relatively low water temperatures). Consumption equation 2 has been used to model a variety of warm water species including yellow perch and walleye (Kitchell et al. 1977).

Equation 3: Temperature dependence for cool- and cold-water species (Thornton and Lessem 1978)

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

where:

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

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

$$G1 = (1 / (CTO - CQ)) \cdot \ln((0.98 \cdot (1 - CK1)) / (CK1 \cdot 0.02))$$

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

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

$$G2 = (1 / (CTL - CTM)) \cdot \ln((0.98 \cdot (1 - CK4)) / (CK4 \cdot 0.02))$$

The Thornton and Lessem algorithm 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 fit to the increasing portion of the temperature dependence function (KA) and the other to the decreasing portion (KB). **CA** is the intercept of the mass dependence function for a 1 gram fish at the optimum water temperature and **CB** is the coefficient of the mass dependence. For the increasing portion of the curve, **CQ** is the lower water temperature at which the temperature dependence is a small fraction (**CK1**) of the maximum rate and **CTO** is the water temperature corresponding to 0.98 of the maximum consumption rate. For the decreasing portion of the curve, **CTM** is the water temperature (≥ CTO) at which dependence is still 0.98 of the maximum and **CTL** is the temperature at which dependence is some reduced fraction (**CK4)** of the maximum rate. Consumption equation 3 has been used to model a variety of species including chinook and coho salmon (Stewart and Ibarra 1991).

2.2 Respiration

Respiration (the amount of energy used by the fish for routine metabolism) is dependent on fish size, water temperature and activity. These losses are estimated by first calculating resting metabolism as a function of mass, and then increasing this value with a temperature dependent function (Figure 4) and a factor representing activity.

The total metabolic rate of the fish is estimated by adding the costs of respiration to the costs of digestion (specific dynamic action) of the fish. Specific dynamic action (SDA) is calculated as a constant proportion of assimilated energy (consumption minus egestion). Typical values of SDA lie between 0.15 and 0.2.

The basic form of the respiration and specific dynamic action functions:

$$R = RA \cdot W^{RB} \cdot f(T) \cdot ACTIVITY$$
$$S = SDA \cdot (C - F)$$

where:

R	specific rate of respiration ($g \cdot g^{-1} \cdot d^{-1}$)
W	fish mass (g)
RA	intercept of the allometric mass function ($g \cdot g^{-1} \cdot d^{-1}$)
RB	slope of the allometric mass function
f(T)	temperature dependence function
T	water temperature ($^{\circ}C$)
ACT	activity multiplier
S	proportion of assimilated energy lost to specific dynamic action
SDA	specific dynamic action
C	specific consumption rate ($g \cdot g^{-1} \cdot d^{-1}$)
F	specific egestion rate ($g \cdot g^{-1} \cdot d^{-1}$)

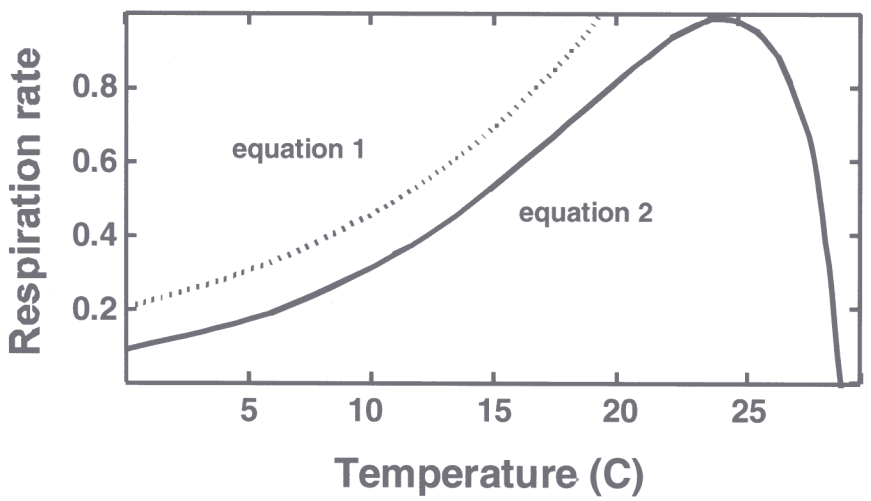


Figure 4: Temperature dependence of metabolism as defined by the two equations available with *Fish Bioenergetics 3.0*.

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

$$f(T) = e^{(RQ \cdot T)}$$
$$\text{ACTIVITY} = e^{(RTO \cdot VEL)}$$

where:

$$VEL = RK1 \cdot W^{RK4}, \text{ when T} > \text{RTL, or}$$
$$VEL = ACT \cdot W^{RK4} \cdot e^{(BACT \cdot T)}, \text{ when T} \leq \text{RTL.}$$

In this first equation, a simple exponential relationship describes the temperature dependence of metabolism and activity is a function of swimming speed. Three different formulations of the activity function can be used: 1) swimming speed is a constant (e.g. largemouth bass, Rice et al. 1983), 2) swimming speed is a function of mass alone above a cutoff temperature (e.g. bloater, Rudstam et al. 1994) and, 3) swimming speed is a function of mass and water temperature below a cutoff temperature (e.g. lake trout, Stewart et al. 1983).

For the mass dependence, **RA** is the specific weight of oxygen (g $O_2 \cdot g^{-1}$ d^{-1}) consumed by a 1 gram fish at 0 ° C and zero swimming speed, **RB** is the slope of the allometric mass function for standard metabolism, and **RQ** approximates the Q_{10} (the rate at which the function increases over relatively low water temperatures, $^{\circ}C^{-1}$).

Within the activity function **SDA** is the proportion of assimilated energy lost to specific dynamic action (the cost of assimilating foodstuffs, especially protein).

In *Fish Bioenergetics 3.0*, if swimming speed is a constant then **RTM**, **RTL**, **RK4** and **BACT** are set to 0, **RK1** and **ACT** are set to 1, and **RTO** is set to the desired velocity ($cm \cdot s^{-1}$).

If swimming speed is a function of mass or mass and temperature, **RTO** is the coefficient for swimming speed dependence on metabolism ($s \cdot cm^{-1}$), **RTL** is the cutoff temperature at which the activity relationship changes (° C), **RK1** is the intercept for swimming speed above the cutoff temperature ($cm \cdot s^{-1}$), **RK4** is the mass dependence coefficient for swimming speed at all water temperatures, **ACT** is the intercept ($cm \cdot sec^{-1}$ for a 1 gram fish at 0 ° C) of the relationship for swimming speed versus mass at water temperatures less than RTL, and **BACT** is the water temperature dependence coefficient of swimming speed at water temperatures below RTL ($^{\circ}C^{-1}$). In either case, **RTM** is always set to 0.

Equation 2: Temperature dependent with activity multiplier (Kitchell et al. 1977)

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

where:

$$V = (RTM - T) / (RTM - RTO)$$
$$X = (Z^2 \cdot (1 + (1 + 40 / Y)^{0.5})^2) / 400$$
$$Z = LN(RQ) \cdot (RTM - RTO)$$
$$Y = LN(RQ) \cdot (RTM - RTO + 2)$$

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

2.3 Waste Losses (Egestion and Excretion)

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

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

Egestion: $$F = FA \cdot C$$

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

Egestion is a constant proportion (**FA**) of consumption. Excretion is a constant proportion (**UA**) of assimilated energy (consumption minus egestion). This formulation suffices for most species.

Equation Set 2: Dependent on mass, temperature and ration (Elliott 1976)

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

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

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

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

Egestion: $$F = PF \cdot C$$

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

where:

$$PF = ((PE - 0.1) / 0.9) \cdot (1 - PFF) + PFF$$

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

$$PFF = \sum (PREY[n] \cdot DIET[n]) \text{ for n = 1 to number of prey}$$

This equation allows the user to incorporate corrections for the indigestible component of the prey. It is most useful when the diet shifts between highly digestible prey (e.g. fish) to less digestible prey (e.g. large crustaceans). **FA**, **FB**, and **FG** and **UA**, **UB**, and **UG** are as defined for equation 2. **PREY[n]** (indigestible proportion of n^{th} prey) and **DIET[n]** (proportion of n^{th} prey in diet) are input by the user.

2.4 Reproduction

Production of reproductive tissue occurs during normal growth and loss occurs during spawning. If a bioenergetic run includes a spawning date for mature fish, a user-defined proportion of fish mass is lost on that day. While separate runs can be conducted for male and female fish to account for gender differences in gonad mass, the usual practice is to estimate the average gonad proportion for both sexes combined.

2.5 Predator Energy Density

Predator energy density (joules per gram wet mass) can be either input from a .PYC data file or as a function of body mass:

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

where:

ED	predator energy density (joules·g^{-1} wet mass)
α	intercept of the allometric mass function (J·g^{-1})
β	slope of the allometric mass function
W	fish mass (g)

Predator energy density can be defined using two size ranges (**a1, b1** and **a2, b2**). The model switches from equation set 1 to equation set 2 at the **mass cutoff**. To run only one equation, set the mass cutoff to either a value higher than the largest fish to use only a1 and b1, or to 0 to use only a2 and b2.

2.6 Adapting existing models to new species

To model a new species, you will need to develop a set of physiological parameters for that species. Several different approaches can be taken to derive the necessary parameters: deriving them from published reports, estimating them from specifically designed field or laboratory studies, or borrowing parameters from closely related species. Most species parameters sets have been derived from a number of previously published reports, because few studies provide estimates of all the physiological parameters. Field and laboratory studies are very cost and labor intensive and require carefully regulated experimental conditions (Hartman and Brandt 1993; Lantry and Stewart 1993; Madon and Culver 1993). Species borrowing has met with some criticism (Ney 1990, 1993) however using parameters from closely related species or those with similar morphologies and life history attributes should provide a reasonable approximation until unique parameters can be derived. Irrespective of which approach is used, it is important to evaluate each of the physiological processes across as wide a range of temperatures and body sizes as possible. As such, caution must be applied when modeling extremes in temperature or body size, as the specific functions describing the physiology may not be adequately described in that region. For instance, using adult fish parameters to model larvae and young-of-the-year fish can produce significant biases because of the allometric mass relationships used. Generally for fish larger than 10 grams, adult parameters work well. For fish smaller than 1 gram, parameter modifications are necessary (Post 1990; Madon and Culver 1993; Johnson 1995). For fish between 1 and 10 grams, results are mixed.

When developing parameter sets for **adults** of new species, some general rules of thumb include:

1. Assume temperature dependent consumption (equation 2), setting CB around -0.3, CQ near 2.3 and CA typically between 0.15 and 0.35. CTO and CTM can be approximated by preferred and upper lethal temperatures, respectively.
2. Assume temperature dependent respiration (equation 2), setting RB near -0.2, and RQ around 2.1. RTO can be approximated by the upper lethal temperature, with RTM set about 3 ° C higher. SDA is typically near 0.175.
3. Assume egestion and excretion are proportional to consumption (equation 1), with FA near 0.15 and UA near 0.1

For any new model, it is a good idea to conduct error analyses. The parameters which have the greatest influence on model predictions include allometric parameters for the dependence of consumption and respiration on body mass (Kitchell et al 1977; Stewart et al 1983; Bartell et al 1986) and are therefore the prominent candidates for future research.

References

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

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

Boisclair, D. and Sirois, P. 1993. Testing assumptions of fish bioenergetics models by direct estimation of growth, consumption, and activity rates. Trans. Amer. Fish. Soc. 122:784-796.

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

Hartman, K.J. and Brandt, S.B. 1993. Systematic sources of bias in a bioenergetic model:examples for age-0 striped bass. Trans. Amer. Fish. Soc. 122:912-926.

Hewett, S.W. and Johnson, B.L. 1987. A generalized bioenergetic model of fish growth for microcomputers. Technical Report No. WIS-SG-87-245. University of Wisconsin Sea Grant Institute,
Madison, WI.

Hewett, S.W. and Johnson, B.L. 1992. Fish Bioenergetics Model 2. Technical Report No. WIS-SG-92-250. University of Wisconsin Sea Grant Institute, Madison, WI. 79 p.

Johnson, T.B. 1995. Long-term dynamics of the zooplanktivorous fish community in Lake Mendota, Wisconsin. Ph.D. thesis, University of Wisconsin - Madison. 203 p.

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

Lantry, B.F. and Stewart, D.J. 1993. Ecological energetics of rainbow smelt in the Laurentian Great Lakes: an interlake comparison. Trans. Amer. Fish. Soc. 122:951-976.

Lucas, M.C., Johnstone, A.D.F., and Priede, I.G. 1993. Use of physiological telemetry as a method of estimating metabolism of fish in the natural environment. Trans. Amer. Fish. Soc. 122:822-833.

Madon, S.P. and Culver, D.A. 1993. Bioenergetics model for larval and juvenile walleyes: an *in situ* approach with experimental ponds. Trans. Amer. Fish. Soc. 122:797-813.

Ney, J.J. 1990. Trophic economics in fisheries: assessment of demand-supply relationships between predators and prey. Rev. Aquat. Sci. 2:55-81.

Ney, J.J. 1993. Bioenergetic modeling today: growing pains on the cutting edge. Trans. Amer. Fish. Soc. 122:736-748.

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.

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. Env. Biol. Fishes 9: 263-275.

Rudstam, L.G., F.P. Binkowski, and M.A. Miller. 1994. A bioenergetics model for analysis of food consumption patterns of bloater in Lake Michigan. Trans. Amer. Fish. Soc. 123:344-357.

Stewart, D.J. and M. Ibarra. 1991. Predation and production by salmonine fishes in Lake Michigan, 1978-88. Can. J. Fish. Aquat. Sci. 48:909-922.

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

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

Winberg, G.G. 1956. Rate of metabolism and food requirements of fishes. Byelorussian University, Minsk. 253 p.

Scaling from Individuals to Populations

Chapter 2 described the functions used to characterize the physiology of an individual fish. These energetic models can be used to estimate the rates of predation of individual fish and how these rates vary with changes in diet, thermal regimes, growth rates, etc. However, we are often more interested in estimating the impact of fishes at the population level. Here we briefly describe how to scale up from an individuals predation rate to that of the population.

3.1 Cohort as a Population

Throughout this text, we define a **cohort** as a group of similar sized (aged) fish of the same species experiencing identical environmental conditions (temperature, diet, growth and reproductive losses). For instance, a single cohort of perch may be 500 individuals growing from 60 to 85 g in Lake Perca during one year. All of these perch consume exclusively zooplankton, reside in water temperatures ranging from 4 °C during the winter to 20 °C in July and August and do not spawn. While there certainly will be individual variability in diet, distribution, growth and thus consumption within this group of perch, the physiological parameters and environmental conditions used in the model will represent the average individual. Therefore the estimated amount of food consumed for these 500 perch is simply 500 times that consumed by an individual, assuming no mortality occurs. A second cohort may represent a different age group of perch, or fish growing at a faster or slower rate (i.e. discrete stocks where diet or thermal history may be different). By combining multiple cohorts into a **simulation** *Fish Bioenergetics 3.0* permits the user to model entire populations of fish at one time (i.e. account for size/age structure, stock structure, etc.) so that patterns in consumption or growth can be compared between cohorts or combined to provide a single prediction for the entire population of fish.

3.2 Population Mortality

Once the analysis is extended beyond a single fish to a cohort, mortality may become an important regulator of population level processes. Mortality can come from a variety of sources (starvation, predator-induced, fishing, etc.) and each may act for a different period of time at varying intensity. For instance, our yellow perch cohort may experience a natural rate of mortality of 20% per annum, with an additional 30% fishing mortality between June 1 and October 1. These two sources of mortality act together to reduce our initial population from 500 individuals on January 1 to 280 by December 31 (Figure 1).

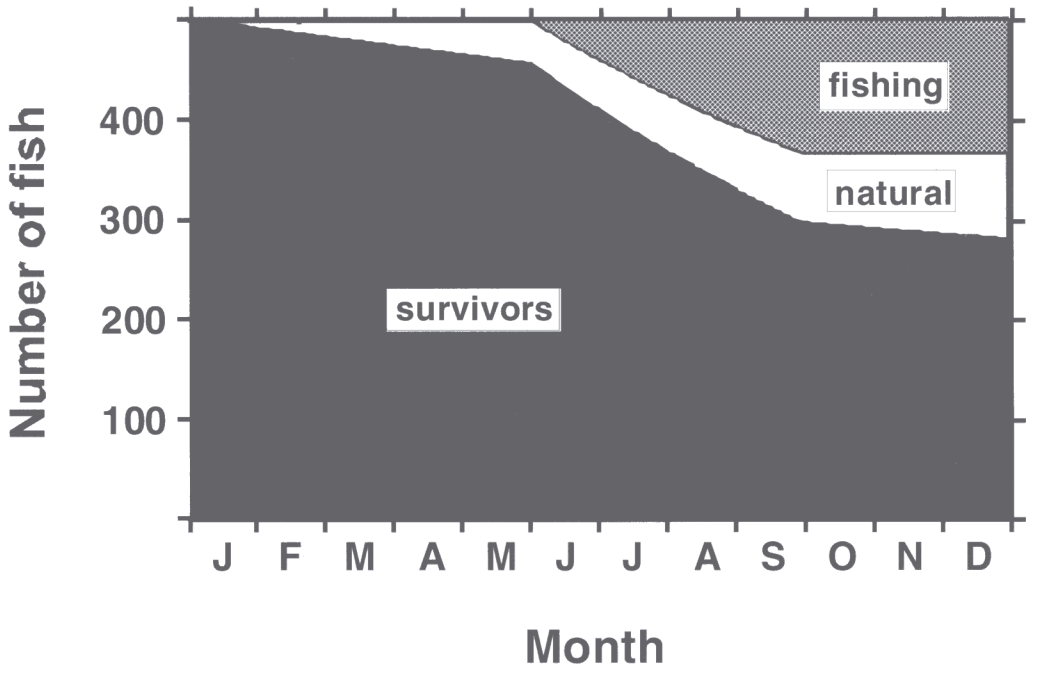


Figure 1. Population mortality by mortality type in one year.

Within *Fish Bioenergetics 3.0*, mortality is modeled for each cohort using a simple exponential decay model

$$N_t = N_0 e^{-m*t}$$

where N_0 and N_t represent the number of fish at time zero and time t, respectively, and m is the total daily instantaneous rate of mortality that occurred within the population. When multiple sources of mortality act together on a cohort, each type of mortality is applied to the cohort each day, and the number surviving the combined mortality is projected forward to the following day. Remember that while the daily instantaneous rates of mortality are additive ($m_{natural} + m_{fishing} + ...$), the actual probabilities of mortality are not. For instance, if the natural rate of mortality (n) is 30% per year, and the rate of fishing mortality (m) is 20% per year, the combined total mortality is 45% per year (n+m-nm). This expression simply states that a fish can die from natural mortality or fishing mortality, but the same fish can not die from both types of mortality.

Within *Fish Bioenergetics 3.0*, the order of daily events for a fish is: eat, grow, spawn and die. Spawning and mortality only occur if required by the user input. The importance of this chronology will be trivial for most bioenergetic runs, however, the user should realize that daily consumption values will be calculated before the fish dies. The reduction in consumption associated with the inclusion of mortality in the Lake Perca yellow perch cohort is shown in Figure 2.

It is important to realize that *Fish Bioenergetics 3.0* is not a population model because we do not explicitly consider recruitment. However, by accounting for mortality rates, the net predatory impact effect of a group of fish can be estimated.

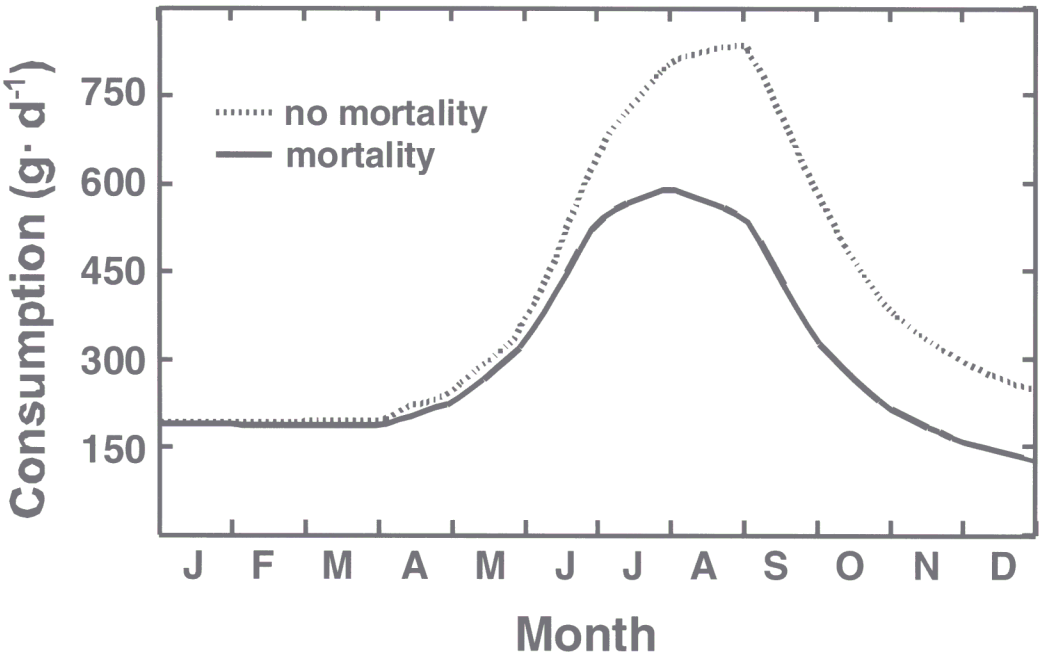


Figure 2. Population mortality effects on consumption.

Extended Topics: Analyses of Nutrient Regeneration and Contaminant Accumulation

The utility of reconstructing energy budgets of fishes to estimate predation rates in aquatic systems has been extended to allow estimation of flow rates of other materials that are transferred through interactions of fishes and their prey. The impetus for this development derived from the recognition that fishes play pivotal roles in transfers of limiting nutrients between ecosystem compartments (Kitchell et al. 1979), and because contaminant accumulation in fish tissue that has potentially important toxicity implications for humans and wildlife that consume them (Cordle et al. 1982; Fein et al. 1984; Mac 1988). As with estimating the rates of energy transfer between food web components, estimating nitrogen and phosphorus regeneration rates and contaminant accumulation rates in fish tissues has proven difficult. As discussed in Chapters 1 and 2, using measured growth rates as a constraint on energy budgets, we can calculate predation rates with relatively minimal errors. We capitalize on this strength of bioenergetic models to estimate flow of other materials through fishes.

By coupling mass balance models to bioenergetic models, we can estimate the rates at which materials are transferred into and through fishes. The mass balance models that are coupled with energetic models fall into two distinct types depending on the behavior of the material of interest in fish tissue. Some materials, for example nitrogen (N) and phosphorus (P), are maintained at relatively constant concentrations in fish tissue through homeostatic mechanisms. In these instances, the concentration of the material in fish tissue is usually known, and we are interested in the rates at which the material is transferred into fishes and the rate at which it is eliminated. The best example of this is evaluating the role that fish play in lake nutrient (N and P) cycles by regenerating these primary production-limiting nutrients through excretion (Kraft 1992; Carpenter et al. 1992; Schindler et al. 1993). By linking the elemental composition of fishes and their prey (e.g. Davis and Boyd 1975; Penczak 1980) to bioenergetics models, we can estimate nutrient regeneration rates by fishes.

The other general class of materials which we are often interested are those that are bioaccumulated (i.e. not maintained at homeostatic concentrations). Whether a material is bioaccumulated is largely a function of its lipophilicity that determines the efficiency with which it is eliminated from tissue. Examples include the bioaccumulation of heavy metals (e.g. mercury) and organic contaminants such as polychlorinated biphenyls (PCBs). In these instances, we are generally more concerned with predicting the concentration of the material in fish tissue and how different environmental conditions (e.g. varying temperatures, changes in diet or changes in growth rate) alter concentrations.

In this chapter we briefly describe the functions that are linked to the bioenergetics models described in Chapter 2, to estimate nutrient regeneration and contaminant bioaccumulation by fishes.

4.1 Nutrient Regeneration

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

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

$$C_p = G_p + F_p + U_p \qquad \text{equation 4.1}$$

where

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

P in urine ($\boldsymbol{U_p}$) is lost in soluble form that is readily available for uptake by aquatic primary producers (Brabrand 1990; Lall 1991). Therefore, excreted P is generally of interest to those estimating the role of fishes in P cycles of aquatic systems. In this regard, equation 4.1 is more useful when written as:

$$U_p = C_p - G_p - F_p \qquad \text{equation 4.2}$$

Excreted P can be estimated as the difference between the P gained through consumption, and that lost in feces and allocated to growth. Fecal losses can be accounted for as a direct proportion of consumption (Nakashima and Leggett 1980a) by determining a gross assimilation efficiency ($\boldsymbol{AE_p}$) for a given prey type. Nakashima and Leggett (1980a) reported that P assimilation efficiency was about 0.72, for most types of animal prey. Lall (1992) reports greater variation in P assimilation efficiencies of fishes fed a variety of aquaculture feeds.

By accounting for fecal losses of P with an assimilation efficiency coefficient ($\boldsymbol{AE_p}$), Equation 4.2 simplifies to:

$$U_p = (AE_p * C_p) - G_p \qquad \text{equation 4.3.}$$

The mass of P consumed ($\boldsymbol{C_p}$) is calculated as the product of the mass of prey consumed and the concentration of P in prey tissue.

$$C_p = C * [P]_{prey} \qquad \text{equation 4.4}$$

In Chapter 2 we discussed how bioenergetics can be used to calculate mass consumption ($\boldsymbol{C}$). The nutrient regeneration model uses this value of $\boldsymbol{C}$ determined from the energetics component of the model, in equation 4.4. The P concentration of prey is expressed as a percent of wet mass determined for individual prey types. Appendix D lists P concentrations ($\boldsymbol{[P]_{prey}}$) for several typical prey of fishes.

The amount of P allocated to growth ($\boldsymbol{G_p}$) is the product of the increase in mass due to growth, and the P concentration in fish tissue. Phosphorus concentrations are about 0.5% of wet mass in adult fishes. Davis and Boyd (1975) and Penczak et al. (1985) give species-specific P (and N)

concentrations for many fish species. Appendix D summarizes the N and P concentrations in several fish species.

To estimate N regeneration by fishes, the nutrient mass balance can be coupled to the energetics model, as was done for estimating P regeneration. To do this the user needs data to describe N concentrations in the predator and prey, and the assimilation efficiency of N (***AE_N***). N concentrations are relatively well known for a large number of prey taxa (Appendix C). Brett and Groves (1979) estimated that the N assimilation efficiency was about 0.8 for carnivorous fishes. This value of ***AE_N*** will probably be lower for herbivorous fishes. However, the model is easily modified to incorporate other values of ***AE_N*** .

Fish Bioenergetics 3.0 couples both the P and the N mass balance to the energetics submodel in a way that the N:P ratio of excreted and egested nutrients can be estimated. Chapter 6 of Section 2 describes in detail how to estimate nutrient regeneration from fishes.

Example of how nutrient regeneration is estimated using *Fish Bioenergetics 3.0.* The figure shows a 100 g yellow perch growing to 150 g in 365 days. The perch consumed 100% invertebrate prey with a tissue N:P ratio of 10 and an energy density of 3200 J/g until day 200. At day 201 the perch began to consume increasing proportions of fish prey with an N:P ratio of 5 and an energy density of 4800 J/g. As a result, after day 200 the growth rate increases, and the N:P ratio of nutrients excreted decrease. The proportion of fish in the perch diet is represented by the shaded region of the graph.

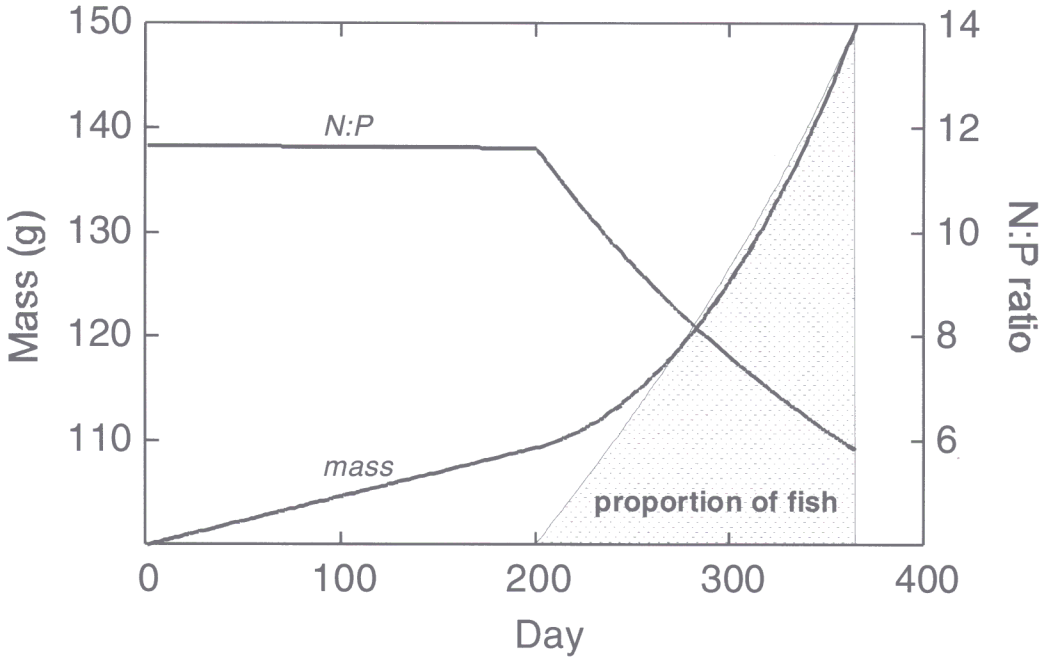


Figure 1. The effects of a diet shift to fish on predator growth and N:P ratio in excretion.

4.2 Contaminant Accumulation

Fishes accumulate compounds by bioconcentration across their gills and through bioaccumulation from ingested food. Although some studies suggest that uptake of contaminants across the gills can be substantial (Post et al. 1996), the bulk of accumulation usually occurs through extraction from ingested food (Rowan and Rasmussen 1992; Rasmussen et al. 1990; Thomann and Connolly 1984; Thomann 1989; Rodgers 1994). Our modeling approach assumes that uptake from water through the gills is negligible compared to that taken up through dietary exposure.

Estimating the accumulation of compounds that are not maintained at homeostatic concentrations in fishes can be modeled by mass balance models of uptake and elimination, to the bioenergetics models. Examples of bioaccumulated compounds include methyl-mercury (MeHg), and organic contaminants such as polychlorinated biphenyls (PCBs).

We present three alternative methods to model contaminant accumulation in fishes. All three are relatively simple compared to other models that have been developed to account for loss and uptake processes in a more mechanistic fashion (e.g. Barber et al. 1991). The methods we present assume that contaminant uptake from water is insignificant, and that fishes incorporate contaminants into tissue entirely due to uptake from ingested food. The first model we present assumes that elimination of contaminants from body tissue is constant and that contaminant uptake can be modeled simply as a constant fraction of the amount of contaminants consumed by a fish. This first model is the most parsimonious approach to estimating contaminant accumulation as it employs only one parameter to integrate across all possible uptake and loss processes of contaminants. We recommend using model 1 for simulating accumulation of highly lipophilic organic contaminants such as PCBs, when the parameters for the more complex models are not known. The second accumulation model accounts for contaminant elimination explicitly and assumes that elimination rates are dependent on body size of fish (i.e. mass-specific elimination rates are inversely proportional to body size). The third contaminant model accounts for changes in elimination rates due to both body size and environmental temperature. Models 2 and 3 scale elimination rate with mass-specific metabolic rates. We suggest using models 2 and 3 to model accumulation of contaminants that are relatively labile (e.g. mercury) and whose elimination kinetics are better established.

Model 1 - simple net trophic transfer efficiency with no elimination

Change in a predator's contaminant concentration ($[X]_{pred}$)can be calculated as:

$$dX_{pred}/dt = C * [X]_{prey} * TE_X \qquad \text{equation 4.5}$$

where ***C*** is the mass of prey consumed per unit time, $[X]_{prey}$ is the mean concentration of contaminant-X in the prey, and $\boldsymbol{TE_X}$ is the transfer efficiency of the contaminant from prey to predator. This transfer efficiency represents the net assimilation efficiency after accounting for all sources of elimination and transformation (Jackson and Schindler 1996).

Jackson and Schindler (1996) estimated that $\boldsymbol{TE_X}$ for total PCB transfer from prey fishes to Lake Michigan lake trout, chinook salmon and coho salmon were 0.55, 0.60 and 0.50 respectively. This means that, for example, 55% of the PCBs ingested by a lake trout are assimilated from prey tissue and incorporated into the predator tissue.

Example of using *Fish Bioenergetics 3.0* to estimate the effect of growth rates on contaminant accumulation by fishes. In this example, we show the PCB concentration for a coho salmon simulated under 3 growth-rate scenarios. A 500 g coho was grown to either 700 g (l), 1000 g (m), or 1500 g (h), by consuming prey with a PCB concentration of 1 ppm. The lines represent the PCB concentration of the coho for these three growth conditions. We see that higher growth rates lead to decreased PCB concentrations.

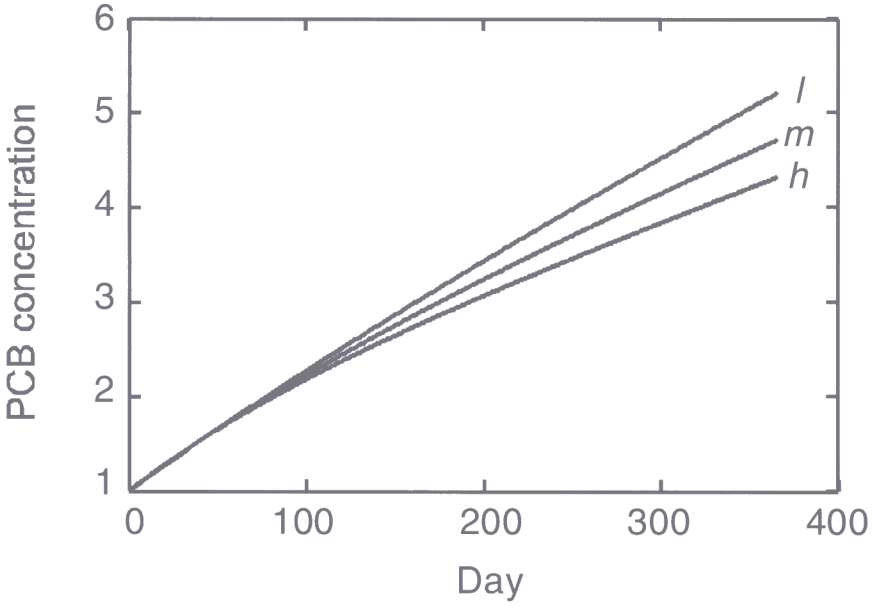


Figure 2. PCB concentrations in coho salmon as a function of growth rate.

Model 2 - gross assimilation efficiency with allometric scaling of clearance rate

The second contaminant accumulation model accounts for loss of contaminants in feces and metabolic clearance from tissue. In this model, loss of contaminants in feces is modeled as a constant proportion of that consumed, and clearance rate is scaled allometrically. The change in contaminant concentration per unit time is calculated as:

$$dX_{pred}/dt = C * [X]_{prey} * X_{ae} - \text{Clearance} \qquad \text{equation 4.6}$$

where: $\boldsymbol{X_{ae}}$ is the gross assimilation efficiency of contaminant-X from prey[1]

and

$$\text{Clearance} = \text{Mass}^{\zeta} * X_{pred} * K_{cl} \qquad \text{equation 4.7}$$

where ζ accounts for the effect of allometry on contaminant elimination.

[1] (i.e. 1- X_{ae} is the proportion of consumed X lost in feces); $\boldsymbol{X_{ae}}$ is likely to vary with prey type and with contaminant type. Rodgers (1994) successfully modeled MeHg accumulation in yellow perch and lake trout with $\boldsymbol{X_{ae}} = 0.8$.

The two parameters to describe clearance are not well described in the literature. Rodgers (1994) used $\zeta = -0.58$, and $K_{cl} = 0.029\ g^{-\zeta}/d$ to describe methyl mercury elimination in yellow perch and lake trout. These parameter values can be used as starting points for general exploratory studies.

Model 3 - gross assimilation efficiency with elimination rate dependent on body size and temperature

Model 2 can be elaborated to account for the increase in elimination rate with increases in environmental temperature. This is accomplished by using the same function as described in Model 2 (equations 4.6, 4.7), but by making the value of K_{cl} temperature dependent (Norstrom et al. 1975; Rodgers 1994) according to:

$$K_{cl}(T) = K_{cl} * 2^{((T - T_b)/10)} \qquad \text{equation 4.8}$$

where T is the environmental temperature

T_b is the base temperature of the temperature-dependence function

The T_b is going to vary with the thermal preference of the fish to be simulated. Extensive data do not exist regarding these parameters but Rodgers (1994) suggested a T_b value of 10 ° C for lake trout and 15 ° C for yellow perch.

Fish Bioenergetics 3.0 can be used to model contaminant bioaccumulation in fishes with data that describe the standard inputs to the bioenergetics models (Chapter 2) and estimates of contaminant concentrations in prey. Chapter 7 describes how to use *Fish Bioenergetics 3.0* to model contaminant accumulation in fishes. The largest unknowns involved in modeling contaminant accumulation rates are in estimating the elimination rates. The models we have presented here will be improved upon as better empirical data on elimination rates are described in the literature. Many of the parameters listed in this chapter should be viewed as preliminary and not as well known as the energetic parameters. Future research could be focused on better describing the functions to describe the temperature and allometric scaling of contaminant elimination, and of gross assimilation efficiencies of N, P and contaminants.

References

Barber, M.C., L.A. Suarez, and R.R. Lassiter. 1991. Modelling bioaccumulation of organic pollutants in fish with an application to PCBs in Lake Ontario salmonids. Can. J. Fish. Aquat. Sci. 48:318-337.

Brett, J.R., and T.D.D. Groves. 1979. Physiological energetics. *In* W.S. Hoar, D.J. Randall, and J.R. Brett (editors). Fish Physiology, Vol. VII: Bioenergetics and growth. Academic Press, New York.

Carpenter, S.R., C.E. Kraft, R. Wright, X. He, P.A. Soranno and J.R. Hodgson. 1992. Resilience and resistance of a lake phosphorus cycle before and after food web manipulation. Am. Nat. 140: 781-798.

Cordle, F., R. Locke, and J. Springer. 1982. Risk assessment in a federal regulatory agency: an assessment of risk associated with the human consumption of some species of fish contaminanted with polychlorinated biphenyls (PCBs). Environ. Health Perspect. 45:171-182.

Davis, J.A., and C.E. Boyd. 1975. Concentrations of selected elements and ash in bluegill (*Lepomis macrochirus*) and certain other freshwater fish. Trans. Am. Fish. Soc. 107:862-867.

Fein, G.G., J.C. Jacobson, S.W. Jacobson, P.M. Schwartz, and J.K. Dowler. 1984. Prenatal exposure to polychlorinated biphenyls: effects on birth size and gestation age. J. Pedriatr. 105:315-320.

Jackson, L.J., and D.E. Schindler. 1996. Field estimates of net trophic transfer of PCBs from prey fishes to Lake Michigan salmonids. Environmental Science & Technology 30:1861-1865.

Kraft, C.E. 1992. Estimates of phosphorus and nitrogen cycling by fish using a bioenergetics approach. Can. J. Fish. Aquat. Sci. 49:2596-2604.

Lall, S.P. 1991. Digestibility, metabolism and excretion of dietary phosphorus in fish. *In* C.B. Cowey and C.Y. Cho (editors). Nutritional strategies and aquaculture waste. Proceedings of the first international symposium on nutritional strategies in management of aquaculture waste. University of Guelph, Guelph, Ontario, Canada. 275 p.

Mac, M.J. 1988. Toxic substances and survival of Lake Michigan salmonids: field and laboratory approaches. Pages 389-401 in: M.S. Evans (editor) Toxic contaminants and ecosystem health: a Great Lakes focus. John Wiley and Sons, New York, NY.

Nakashima, B.S., and W.C. Leggett. 1980a. Natural sources and requirements of phosphorus for fishes. Can. J. Fish. Aquat. Sci. 37:679-686.

Nakashima, B.S., and W.C. Leggett. 1980b. The role of fishes in the regulation of phosphorus availability in lakes. Can. J. Fish. Aquat. Sci. 37:1540-1549.

Norstrom, R.J., A.E. McKinnon, and A.S.W. deFreitas. 1976. A bionenergetics-based model for pollutant accumulation by fish. Simulation of PCB and methylmercury residue levels in Ottawa River yellow perch (*Perca flavescens*). J. Fish. Res. Bd. Canada 33:248-267.

Penczak, T. 1985. Phosphorus, nitrogen, and carbon cycling by fish populations in two small lowland rivers in Poland. Hydrobiologia 120:159-165.

Post, J.R., R. Vandenbos, and D.J. McQueen. 1996. Uptake rates of food-chain and waterborne mercury by fish: field measurements, a mechanistic model, and an assessment of uncertainties. Can. J. Fish. Aquat. Sci. 53:395-407.

Rasmussen, J.B., R.J. Rowan, D.R.S. Lean, and J.H. Carey. 1990. Food chain structure in Ontario lakes determines PCB levels in lake trout (*Salvelinus namaycush*) and other pelagic fish. Can. J. Fish. Aquat. Sci. 47:2030-2038.

Rodgers, D.W. 1994. You are what you eat and a little bit more: bioenergetics-based models of methylmercury accumulation in fish revisited. Pages 427-439 *In* C.J. Watras and J.W. Huckabee (editors). Mercury pollution: integration and synthesis. Lewis Publishers, CRC Press, Boca Raton, FL.

Rowan, D.J., and J.B. Rasmussen. 1992. Why don't Great Lakes fish reflect environmental concentrations of organic contaminants? - An analysis of between-lake variability in the ecological partitioning of PCBs and DDT. J. Great Lakes Res. 18:724-741.

Schindler, D.E., J.F. Kitchell, X. He, S.R. Carpenter, J.R. Hodgson, and K.L. Cottingham. 1993. Food web structure and phosphorus cycling in lakes. Trans. Am. Fish. Soc. 122:756-772.

Thomann, R.V. 1989. Bioaccumulation model of organic chemical distribution in aquatic food chains. Environmental Science & Technology 23:699-707.

Thomann, R.V., and J.P. Connolly. 1984. Model of PCB in the Lake Michigan lake trout food chain. Environmental Science & Technology 18:65-71.

Index - Section 1

Before You Begin

1.1 General Conventions

Object or Formatting	Description
➡	Perform the action described by the following text.
Menu/Item	**Menu** describes a main menu option, such as **File** or **Edit**, found at the top of the Fish Bioenergetics main window, and **Item** describes an option, such as **New** or **Open**, listed in the pop-down menu.
Predator	The fish for which you are simulating bioenergetics. When you create a new cohort/document you select a predator species.
Cohort file/document	Document is a synonym for file, which represents a simulated cohort. The three terms are often interchanged. In Fish Bioenergetics 3.0 you can create two different file types, cohort and summary.

1.2 New Features in Version 3.0

- Unlimited number of cohorts
- Unlimited combinations of cohorts
- Unlimited number of prey
- Additional predator species
- Nutrient regeneration analysis
- Contaminant accumulation analysis
- First Impression built-in graphing program
- Formula One built-in spreadsheet
- Online help
- Runs in Windows 3.1, Windows '95 and Windows NT

Getting Started

2.1 System Requirements

Fish Bioenergetics 3.0 will run under Windows 3.1, Windows '95 and Windows NT.

Hardware Requirements

- Intel compatible PC running Windows 3.1, Windows '95, or Windows NT
- Minimum of 3 megabytes of hard disk space
- *Fish Bioenergetics 3.0* software media - note that the installation software is operating system specific. For example, if you're running Windows 3.1, be sure to run the installation program for Windows 3.1. On the installation CD you'll find subdirectories for the different versions of Windows.

2.2 Installing Software

- **Windows 3.1:** For *Fish Bioenergetics 3.0* to run in Windows 3.1, you must first install the 32-bit emulator called "Win32s". Because *Fish Bioenergetics 3.0* was written to run under a 32-bit operating system, such as Windows '95 or Windows NT, it requires interpretation to run under a 16-bit operating system, such as Windows 3.1. Some users who've installed other 32-bit programs in their Windows 3.1 environment may already have Win32s installed. If you're not sure whether or not to install Win32s, install it anyway.

  Win32s

  ➡ Insert the CD into the CD drive (or disk 1 into drive **A** if installing from floppies) and type **d:\win32s\setup** within the Program Manager **File/Run** menu option. Alternatively, you can double click the **setup.exe** file on disk 1 from the Windows File Manager if you are installing from floppies.

  Follow the prompts that Win32s provides, and Win32s will add 32-bit interpretation to Windows 3.1. If Win32s prompts you to replace files that are already on your computer with older Win32s files, be sure to indicate NO. Once you've completed Win32s installation and rebooted Windows, you can proceed with *Fish Bioenergetics 3.0* installation.

  Fish Bioenergetics 3.0 for Windows 3.1

  ➡ Insert the CD into the CD drive (or disk 1 into drive **A** if installing from floppies) and enter **a:\win31\setup** within the Program Manager **File/Run** menu option. Alternatively, you can double click the **setup.exe** file on disk 1 from the Windows File Manager if you are installing from floppies.

  Follow the prompts that the setup program provides, and *Fish Bioenergetics 3.0* will install the program files on your hard disk, sample files in a subdirectory named Samples, and some system files in the Windows/System subdirectory. Finally, the setup program will create a Bioenergetics program group in the Windows Program Manager.

- **Windows '95 or NT:** ➡ Insert the CD into the CD drive (or disk 1 into drive **A** if installing from floppies). Select **Add/Remove Programs** from the Windows control panels and press the **Install** button. Be sure to select the setup.exe file located in the d:\win95 subdirectory. Alternatively, you can double click the **setup.exe** file on disk 1 from within the Windows Explorer if you are installing from floppies.

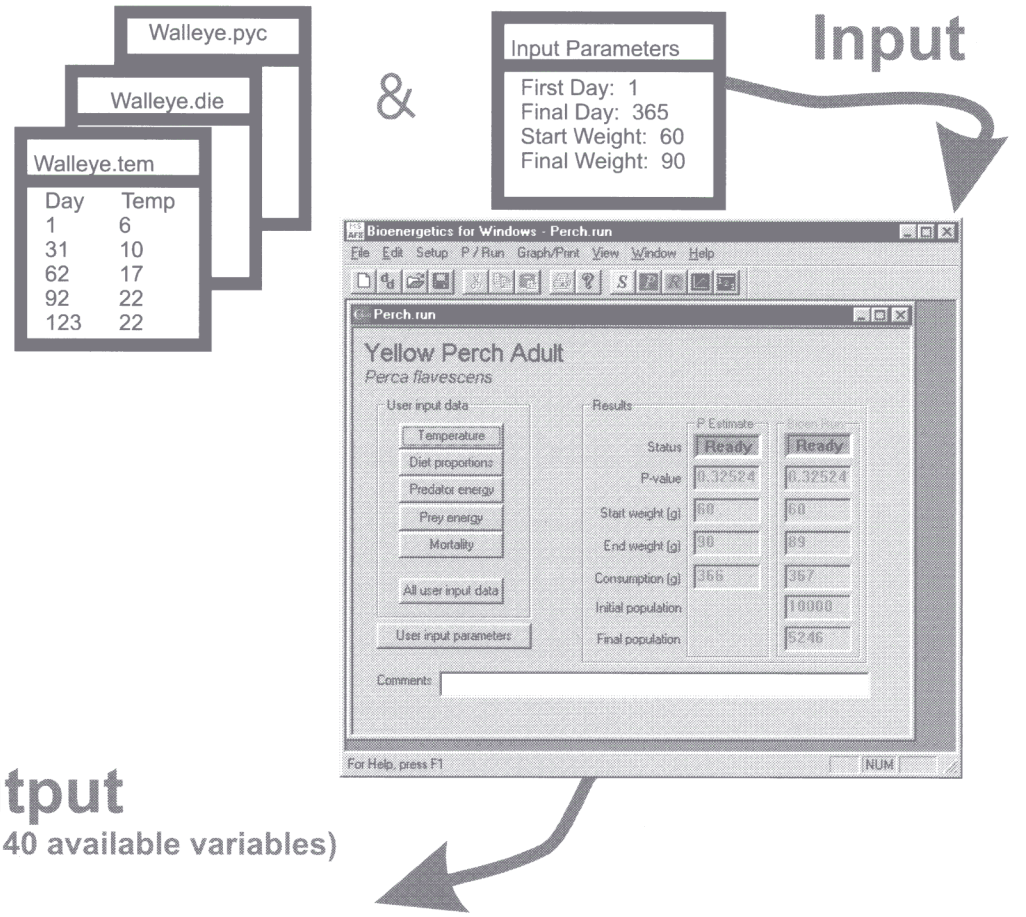
  Follow the prompts that the setup program provides, and *Fish Bioenergetics 3.0* will install the program files on your hard disk, sample files in a subdirectory named Samples, and some system files in the Windows/System subdirectory. Finally, the setup program will create a Bioenergetics entry in the Programs menu under your Start button.

Fish Bioenergetics 3.0 Installed Files

File Name	Description	Installed Location
regsvr32.exe	software that registers Fish Bioenergetics with the Windows operating system	temporarily in the program directory
data.bem	species physiological parameters	program directory
bioen.exe	program executable	program directory
perch.*	a number of perch sample files	samples subdirectory
vcf132.ocx	Formula One built-in spreadsheet	Windows\system directory
vcfl32.ocx	First Impression built-in graphing	Windows\system directory
msvcrt40.dll	Windows system file	Windows\system directory
mfc40.dll	Windows system file	Windows\system directory
olepro32.dll	Windows system file	Windows\system directory

2.3 Software Overview

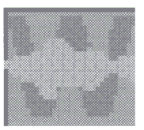
Fish Bioenergetics 3.0 allows you to combine your field data with known physiological fish parameters to create simulations depicting the consumption and growth characteristics of your fish. To run a simulation, you need user input data that you've estimated (temperature, diet, prey energy density, etc.); user input parameters, such as the date range of your simulation and the start and final mass of your predator; and *Fish Bioenergetics 3.0* to calculate daily consumption and growth.



Model components including input data, input parameters, software, and output.

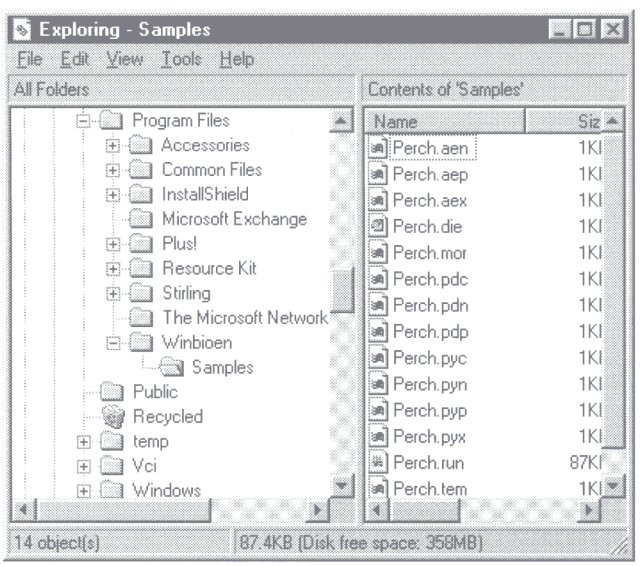
2.4 Starting Bioenergetics

To start *Fish Bioenergetics 3.0*, simply double click the *Fish Bioenergetics 3.0* icon located in the Bioenergetics group (Windows 3.1) or the Program menu under the Start button (Windows '95 or NT).



2.5 Sample Data and Bioenergetics Run

All of the examples used in the following chapters pertain to the simulation (PERCH.RUN) of a hypothetical yellow perch population living in Lake Perca. The data represent a cohort of age-3 perch which grow from 60 g on June 1 (simulation day 1) to 90 g on May 31 of the following year. The initial perch population size is 10,000 with a natural mortality rate of 30% per year, and a harvest mortality rate of 25% during the fishing season (June 1 to October 15) (PERCH.MOR). The diet (PERCH.DIE) gradually changes from all invertebrates on June 1 to all fish on December 1 with the perch remaining exclusively piscivorous to the end of the year. The energy density of both predator (PERCH.PDC) and prey (PERCH.PYC) remain constant throughout the year. The perch reside in a temperate lake where seasonal water temperatures range from 4 °C in the winter to 23 °C in the summer (PERCH.TEM). Industrial development has polluted the waters of Lake Perca such that the perch population accumulates PCBs from their diet (PERCH.PYX) at a constant assimilation efficiency of (PERCH.AEX). In addition, these perch act as a vector for nitrogen and phosphorus transport between the littoral zone (where they consume their prey) and the open lake. Files describing the nitrogen and phosphorus content of the perch (PERCH.PDN and PERCH.PDP) and their prey (PERCH.PYN and PERCH.PYP), and the gross assimilation efficiency (PERCH.AEN and PERCH.AEP) are provided.



Learning Bioenergetics

3.1 Required Components

Following are the minimum components required to get started with *Fish Bioenergetics 3.0*. You may find it helpful to examine the complete list of user input data in section 3.2, table: User Input Data Files and the complete list of user input parameters found in section 3.4, table: User Input Parameters. These two tables indicate all of the possible input information that you could supply if you were to run all facets of the model.

- **User Input Data:** Text files that include data for at least temperature, prey consumed as proportions of the total diet, and prey energy densities (see section 3.2, table: User Input Data Files). These data may be collected from the field, retrieved from your historical archives or pulled from scientific journals. You can use any text editor to create the files outside of the *Fish Bioenergetics 3.0* software, or you can enter the data manually using the built-in spreadsheet. Each data file consists of a two-dimensional array where simulation day is the first column and the data, such as temperature or prey energy densities, are in the remaining columns.

> Note that you have two options for providing user input data:
>
> 1) Creating tab delimited text files
> 2) Entering data into the built-in spreadsheet
>
> In general, the documentation will describe the data as if you were providing it via text file; however, most of the rules regarding the input data apply to both input methods.

- **User Input Parameters:**
  First Analysis Day: The first day of your simulation. All data files must include a day that is less than or equal to your first analysis day. The simulation days are arbitrary and do not fall under any kind of calendar constraints.
  Final Analysis Day: The last day of your simulation. Once again, data files must include a day that is greater than or equal to your final analysis day. Because simulation days are arbitrary, you can have a simulation day that's greater than 365.
  Start Weight: The mass in grams of your fish before you run your analysis. If your analysis runs from day 1 through day 200, start weight would be the mass of your fish at the beginning of day one. Incidentally, start weight and final weight apply to a single fish and are simply multiplied by the number of fish in a cohort to equal the mass of the starting population.
  Final Weight (alternatively Total consumption): The mass in grams of your fish when your analysis finishes. Although final weight is required entry, it is used only for estimating proportion of total possible consumption (P-value estimate), and not for actual predictive analyses. An alternative analysis would be to estimate the P-value and the final weight based on a known total consumption. In this case, you would first indicate **Fit to consumption** in **Simulation Setup** and then enter the total consumption of your fish in this field.
- **Software:** *Fish Bioenergetics 3.0* installed on your computer allows you to use your input data, first and final analysis days, and your start and final weights to model changes in fish and fish population energetics.

Example:

In June you sampled three-year-old perch and determined their average mass to be 60 g. In May of the following year you sampled the same population of perch which now weigh an average of 90 g. In addition, you've sampled the water temperature on and off throughout the season. You've been able to determine which prey the perch was likely to consume and in what proportions. Here's what your basic bioenergetics input data might look like:

First analysis day: 1 Final analysis day: 365
Start weight: 60 g Final weight: 90 g

Temperature input file

Perch.tem

	A	B
1	day	temperature
2	1	16
3	30	23
4	61	23
5	92	22
6	122	17
7	153	11
8	183	6
9	214	4
10	304	4
11	334	9
12	365	16

Perch

Diet input file

Perch.die

	A	B	C
1	day	invertebrates	fish
2	1	1	0
3	183	0	1
4	365	0	1
5			

Perch

Diet data represent proportions of total diet. On day 183, the perch switched from eating all invertebrates to all fish.

Prey energy density input file

Perch.pyc

	A	B	C
1	day	invertebrates	fish
2	1	3000	4000
3	365	3000	4000

Perch

In this example, the prey items and the predator maintained a constant energy density (joules/g) through the entire simulation

Note: Data is linearly interpolated for days not listed in user input data files.

Predator energy density input file

Perch.pdc

	A	B	C
1	day	Predator energy density	
2	1	4000	
3	365	4000	
4			

Perch

3.2 User Input Data Files

User input data files contain information that you may have collected in the field, retrieved from your historical archives, or pulled from scientific journals. These data files are created outside of *Fish Bioenergetics 3.0* and are loaded by the software during setup of the bioenergetics simulation. The data files that you need to run a simulation depend on the complexity of the simulation. For example, if you're interested only in the predator's consumption of a specific prey item, then you'll need only **Temperature**, **Diet**, **Prey energy density** (and possibly **Predator energy density**); however, if you're also interested in the quantity of PCBs that the predator consumed because of its diet, you'll need to add **Prey concentration** and **Assimilation efficiency** files for your contaminants.

Note that you have two options for providing user input data:

1) Creating tab delimited text files
2) Entering data into the built-in spreadsheet

In general, the documentation will describe the data as if you were providing it via text file; however, most of the rules regarding the input data apply to both input methods.

Below is a table of all possible user input data files. No matter how many files you need, keep in mind that all input data files must meet the following criteria:

- tab delimited
- first line must be column headers
- first column must be day

In addition, all data files have the following criteria in common:

- any non-number indicates no data
- days do not need to be contiguous
- days can encompass any valid integer range

User Input Data Files

Data	# of Cols	Units	File Extension[1]	Description
Temperature	2	degrees C	tem	water temperature in which the fish lives during the simulation; temperature can vary over time
Diet	Unlimited[2]	decimal proportion	die	on any given day the proportion of each prey species consumed by the predator; sum of all proportions on each day must equal 1; number of entries per day must equal the number of species in the prey energy density file; proportions can vary over time
Predator energy density	2	Joules per gram of predator body mass	pdc	Joules per gram wet body mass of the predator; energy density can vary over time
Prey energy density	Unlimited	Joules per gram of prey body mass	pyc	Joules per gram wet body mass of each prey item; number of entries per day must equal the number of species in the diet file; energy density can vary over time
Mortality	Unlimited	percentage	mor	probability of death over a time period; probabilities can vary over time; duration of any given mortality type (column) is independent of other mortality types
Phosphorus Analysis				
Prey concentration	Unlimited[2]	proportion of wet mass	pyp	phosphorus per gram body mass of each prey item; phosphorus concentration can vary over time
Assimilation efficiency	Unlimited[2]	proportion	aep	gross efficiency with which each prey item's phosphorus is taken up by the predator; assimilation efficiency can vary over time
Predator concentration	2	proportion of wet mass	pdp	phosphorus per gram body mass of the predator; phosphorus concentration can vary over time
Nitrogen Analysis				
Prey concentration	Unlimited[2]	proportion of wet mass	pyn	nitrogen per gram body mass of each prey item; nitrogen concentration can vary over time
Assimilation efficiency	Unlimited[2]	proportion	aen	gross efficiency with which each prey item's nitrogen is taken up by the predator; assimilation efficiency can vary over time
Predator concentration	2	proportion of wet mass	pdn	nitrogen per gram body mass of the predator; nitrogen concentration can vary over time
Contaminants Analysis				
Prey concentration	Unlimited[2]	mg/kg	pyx	contaminants per gram body mass of each prey item; contaminants concentration can vary over time
Assimilation efficiency	Unlimited[2]	proportion	aex	net efficiency with which each prey item's contaminants is taken up by the predator; assimilation efficiency can vary over time

Italicized files are optional and dependent upon the type of analysis you are running.

[1] Technically, you can give your files any extension, but *Fish Bioenergetics 3.0* will look first for the default extension.

[2] Files indicated as 'unlimited' columns must have the same number of columns found in the Prey Energy Density file and must have the same column names as those found in the Prey Energy Density file; however, beyond the day column the order of columns is not important.

3.3 User Input Data Files - Samples

Sample input files created from Excel® spreadsheets and saved as tab delimited text files.

Temperature input file

Perch.tem

	A	B	C
1	day	temperature	
2	1	16.3	
3	30	22.5	
4	61	23	
5	92	22.1	
6	122	17.3	
7	153	11.3	
8	183	6	
9	214	4	
10	304	4	
11	334	8.5	
12	365	16.3	

Perch

Note that you have two options for providing user input data:

1) Creating tab delimited text files
2) Entering data into the built-in spreadsheet

In general, the documentation will describe the data as if you were providing it via text file; however, most of the rules regarding the input data apply to both input methods.

Diet input file

Perch.die

	A	B	C
1	day	invertebrates	fish
2	1	1	0
3	183	0	1
4	365	0	1
5			

Perch

Prey energy density input file

Perch.pyc

	A	B	C
1	day	invertebrates	fish
2	1	3000	4000
3	365	3000	4000
4			

Perch

Predator energy density input file

Perch.pdc

	A	B	C
1	day	Predator energy density	
2	1	4000	
3	365	4000	
4			

Perch

Mortality

Perch.mor

	A	B	C
1	day	natural	fishing
2	1	0	0
3	137	no data	25
4	365	30	0
5			

Perch

Phosphorus concentration in prey items

Perch.pyp

	A	B	C	D
1	day	invertebrates	fish	
2	1	0.0025	0.005	
3	365	0.0025	0.005	
4				
5				

Perch

Phosphorus assimilation efficiencies of prey items

Perch.aep

	A	B	C	D
1	day	invertebrat	fish	
2	1	0.72	0.72	
3	365	0.72	0.72	
4				

Perch

Phosphorus concentration in predator

Perch.pdp

	A	B	C
1	day	predp	
2	1	0.005	
3	365	0.005	
4			

Perch

Nitrogen concentrations in prey items

Perch.pyn

	A	B	C
1	day	invertebrat	fish
2	1	0.025	0.025
3	365	0.025	0.025
4			

Perch

Nitrogen assimilation efficiencies of prey items

Perch.aen

	A	B	C
1	day	invertebrates	fish
2	1	0.8	0.8
3	365	0.8	0.8
4			
5			

PERCH

Nitrogen concentration of predator

Perch.pdn

	A	B
1	day	predn
2	1	0.025
3	365	0.025
4		

Perch

Contaminant concentrations in prey items

Perch.pyx

	A	B	C
1	day	invertebrates	fish
2	1	0.2	1
3	365	0.2	1
4			

PERCH

Contaminant assimilation efficiencies in prey items

Perch.aex

	A	B	C
1	day	invertebrates	fish
2	1	0.5	0.5
3	365	0.5	0.5
4			

PERCH

3.4 User Input Parameters

User input parameters provide the general framework in which your simulation will run. Unlike user input data files, which are two-dimensional sets of data that span some time period, each input parameter represents a single point of data, such as your fish's start weight. You can easily play with these parameters to see how their changes effect the results of your simulation. For example, your start weight and final weight can help you determine the proportion of maximal consumption (P-value) that your fish experienced to attain its growth. You can easily vary either the start weight or final weight and watch how the P-value changes. The table below describes each of the user input parameters in more detail.

User Input Parameters

Parameter	Units	Description
Maintenance temperature	degrees C	Temperature below which this fish cannot survive
First day	day as integer	The first day of your simulation. The value must be greater than or equal to all beginning dates in your user input data files.
Final day	day as integer	The final day of your simulation. The value must be less than or equal to all the final dates in your user input data files.
Start weight	grams	The mass of the individual fish before you run your analysis. If your analysis runs from day 1 through day 200, start weight would be the mass of your fish at the beginning of day 1.
Final weight (alternatively Total consumption)	grams	The mass in grams of your fish when your analysis finishes. Although final weight is required entry, it is used only for estimating proportion of total possible consumption (P-value estimate), and not for actual predictive analyses. An alternative analysis would be to estimate the P-value and the final weight based on a known total consumption. In this case, you would first indicate **Fit to consumption** in **Simulation Setup** and then enter the total consumption of your fish in this field.
Initial population size	Number of fish	The number of fish in your cohort at the beginning of the simulation.
Day of spawning	day as integer	The day of the simulation during which all fish in the cohort spawn.
Percentage of weight spawned	percentage	The percentage of the fishes mass that is immediately lost to spawn. Note that each cohort can spawn only once, and all spawn is applied to one day in the simulation.
Contaminant Analysis		
Initial predator concentration	mg/kg	The concentration of contaminants in your predator at the beginning of the simulation.
Allometric constant	none	Mass dependence of contaminant elimination.
Elimination constant	g^{-c}/d	Base line elimination rate.
Base temperature for elimination	degrees C	Scales the temperature dependence of elimination.

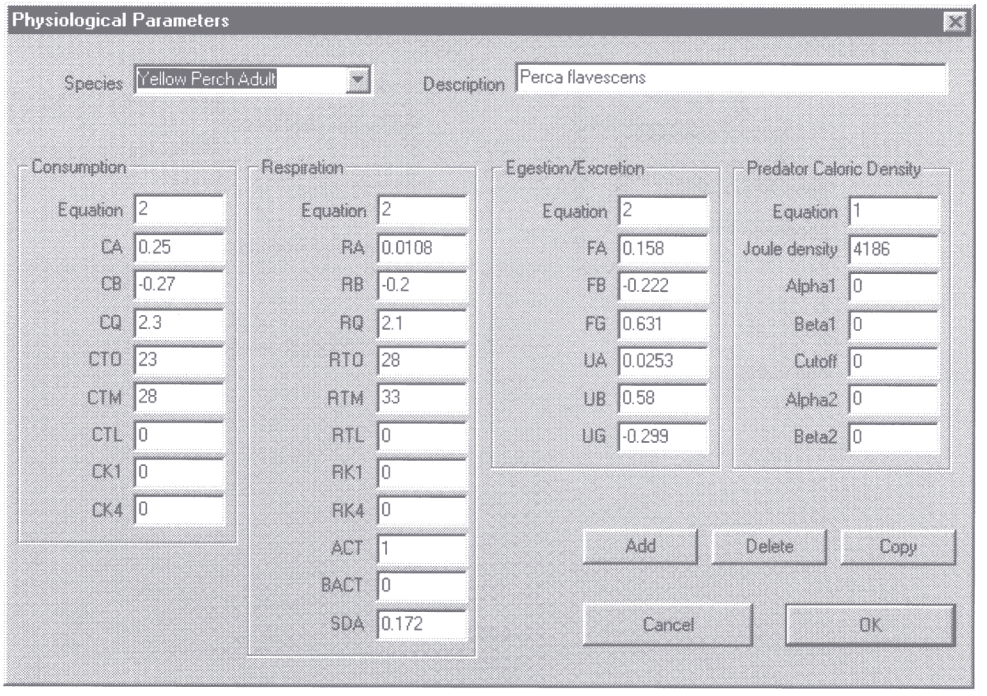
Italicized parameters are optional and dependent upon the type of analysis you are running.

3.5 Physiological Parameters in the Software

Fish Bioenergetics 3.0 contains a database of physiological parameters for many different species and life stages of fish. In essence, these parameters define how one species and life stage of fish differs from another. When you first create a cohort within the software, you are prompted to pick a species. When you pick your species, you're really opening a set of physiological parameters that is unique to the species and life stage you've chosen. How the fish's growth, consumption, respiration, egestion and excretion result from your input data are dependent upon the fish's physiological parameters.

For the most part, these parameters have been determined experimentally in the laboratory and do not change. You do not need to edit or even view any of the physiological parameters while running your simulation; however, you can change their values. For a more in-depth discussion of the parameter definitions, derivations and applications, read section 1, chapter 2 of the documentation, *Core Processes in Bioenergetics*. For a listing of the parameter values of different species, see *Appendix A, Fish Physiological Parameters*.

➡ Select **Edit/Physiological parameter defaults** to view the physiological parameter database. Note that the database will be permanently altered by any changes you make to these data; however, making changes in the database will have no effect on physiological parameters in cohort files that already exist.



Interface for editing the physiological parameter database.

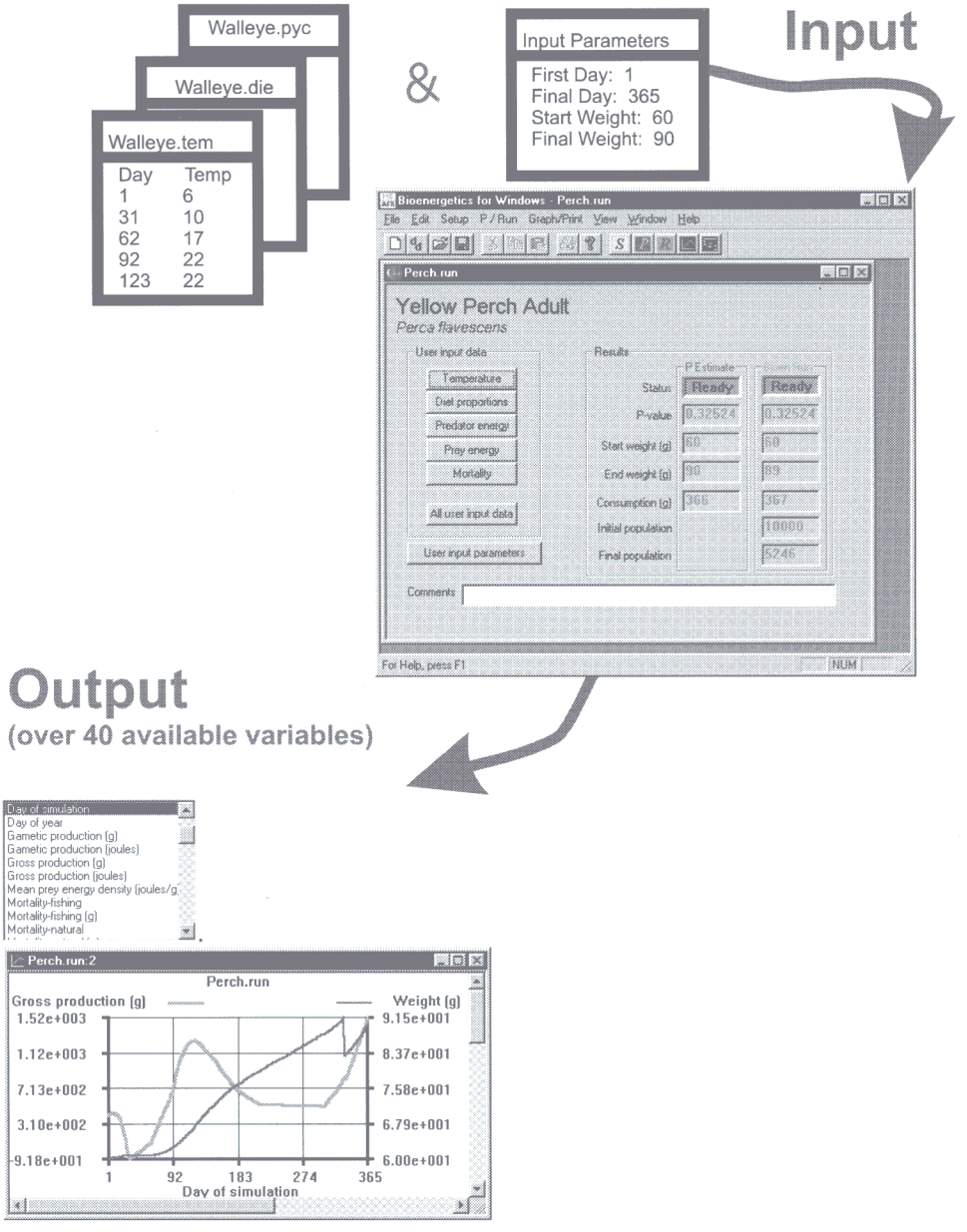
A conservative approach to editing a species' physiological parameters is to copy the species of interest and give it a new name, thus allowing you to test your changes before committing to permanently updating the database. You can always refer to Appendix A to view the original parameters.

3.6 Putting it All Together

A file is a cohort: The most fundamental unit of analysis is a cohort. In *Fish Bioenergetics 3.0*, a cohort is a single species of fish in a specific life stage, such as an adult perch. A cohort can represent one fish or many fish. In *Fish Bioenergetics 3.0*, each file is a cohort. You create a cohort when you open a new file, load your user input data, and use the software's physiological parameters appropriate for your species to analyze your data and make predictions. Multiple cohorts are created by creating multiple files, and you analyze the results of multiple cohorts by creating a second file type called a **summary** file.

Multiple document concept: *Fish Bioenergetics 3.0* is like many other Windows software packages because it allows you to open several documents concurrently, and to relate the information among documents. To help illustrate this concept, imagine a spreadsheet program that allows you to have several spreadsheets open at the same time. Imagine that this program allows you to create a special spreadsheet, called a summary sheet, that allows you to perform calculations involving data from all of the other open spreadsheets. This spreadsheet program would be analogous to *Fish Bioenergetics 3.0* in that a spreadsheet represents a cohort file and a summary sheet represents a bioenergetics summary file.

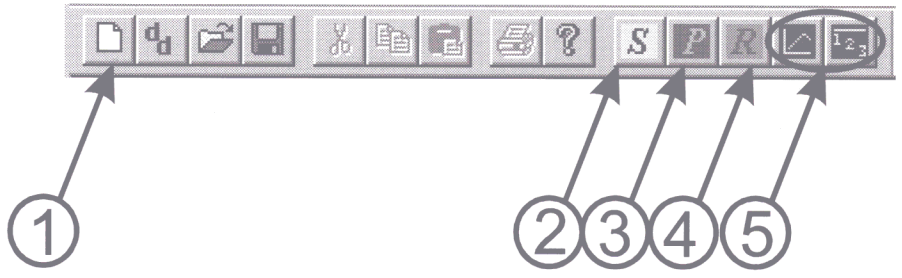
The Results: Although you can view over 40 variables as part of your results, you typically will concentrate on a few key ones, such as consumption, gross production, mass, mortality or population number. You can view your results as a graph or you can save them to a tab-delimited text file.



Creating a Cohort

4.1 The Five Major Steps

In general, you need to complete five steps to create and analyze a new cohort. Although each one of these steps can require some detailed information, you usually can successfully create a new cohort by hitting toolbar icons in the order shown below and accepting the default values. Being able to create a new cohort assumes that you've created your input data files and have given some thought to your user input parameters.

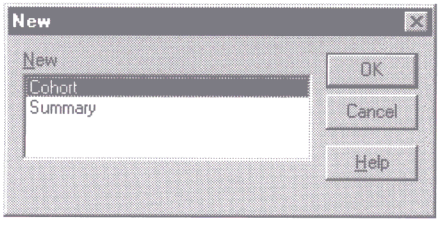


Icons will appear on the toolbar only after the previous icon has been selected and the ensuing steps have been completed. In other words, you'll be able to select only icon 1 when you first start, but after you've completed that step, you'll be able to select icon 2.

1. **New file** icon allows you to select a species and create a new cohort or summary
2. **Setup** icon selects options and loads data
3. **P-value** icon estimates the proportion of maximum consumption required to produce the input growth
4. **Run** icon executes a Bioenergetics run
5. **Graph or Spreadsheet** icon generates output

4.2 Step 1: New Cohort and Select a Species

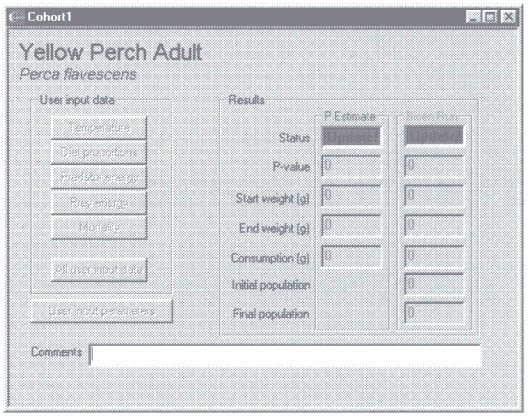
➡ From the main *Fish Bioenergetics 3.0* window, select **File/New** or press the new-file icon. The following window will appear.



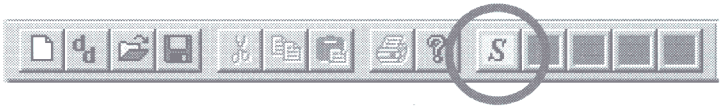
Fish Bioenergetics 3.0 presents two options for new files, **Cohort** and **Summary**. A cohort file represents a single species of fish at a single life stage, such as an age three perch. The cohort can represent one fish or many fish. A summary file allows you to summarize information from several open cohort files. For example, you might have two cohort files open – juvenile perch and adult perch. Within each cohort file you can determine the consumption by that cohort and its population, but you might be interested in determining the overall consumption by both juvenile and adult perch over the same time period. The summary file facilitates this type of calculation. Chapter 5, *Creating a Summary - Analyzing Multiple Cohorts* describe in detail the summary file.

➡ For now, highlight **Cohort** and press **OK**. The **Species List** window will appear.

➡ Select the species of your choice by highlighting it and pressing **OK**. If you select perch, your screen will look like this.



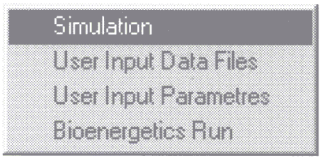
Notice how the Setup icon has now become available.



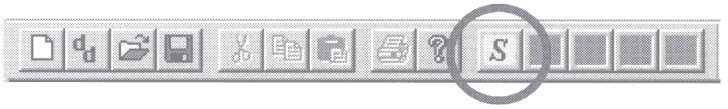
4.3 Step 2: Setup

There are three major steps to setting up your cohort: **Simulation Setup**, **Data File Setup**, and **Species Setup**.

➡ Select **Setup** from the main menu, and the following drop-down menu appears.

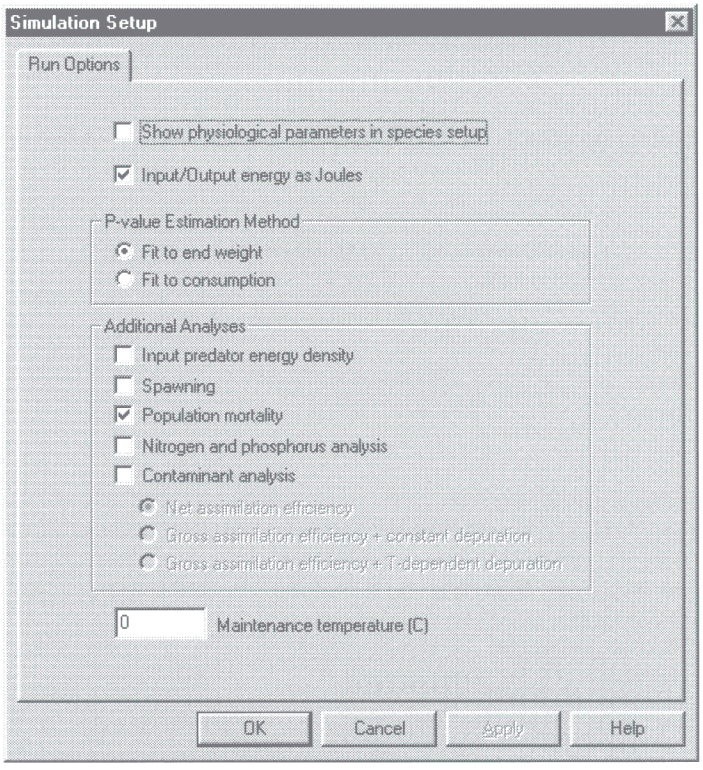


You'll see the three major setup steps (Bioenergetics Run setup will be covered later in this chapter). Depending on how far you've progressed through the setup process, some of these setup options might be grayed. As you complete each setup step, starting with **Simulation**, additional setup steps will become available. Pressing the setup icon from the toolbar has the same effect as selecting **Setup/Simulation** from the main window.



Simulation

➡ Select either **Setup/Simulation** or the setup icon from the toolbar. The **Simulation Setup** window appears.



➡ Press **OK** to accept the default values, or you can modify the Simulation Setup options to fit your specific needs.

Run Options

Show physiological parameters in species setup: Check this box if you would like to see and be able to edit the fish physiological parameters that have been copied from the software database into your new cohort. Although you will be able to edit these parameters, you should do so with the understanding that you're changing the basic physiology of the fish. Do not worry about corrupting the software database, because the parameters presented to you in a cohort file are a copy of the originals from the database. To view the original database values, select **Edit/Physiological parameter defaults**.

Input/Output energy as joules: This box is checked by default. Keep in mind that data from the two input data files, prey energy density and predator energy density, must be consistent with your selection in this check box. If you decide to use the default predator energy density that's provided with *Fish Bioenergetics 3.0* instead of inputting your own data, the software will automatically convert the energy density to the appropriate units. If you deactivate this box, you must use calories as the currency of energy (one cal = 4.186 joules).

P-value Estimation Method: Estimating the P-value really means determining the average proportion of maximal consumption that your cohort maintained to change from its start weight to its final weight during the duration of your simulation. For example, your cohort might grow from 60 to 90 grams in a year. Based on your input data files and the basic physiology of your cohort, it might have a maximum consumption of 5,600 grams of prey per year. Let's say that your fish ate at its maximum consumption rate (which is equivalent to a P-value of 1). Using a P-value of 1, the software would calculate your cohort's growth from 60 to 2,155 grams in a year. Well, your fish did

not grow to 2,155 grams, it grew to 90 grams, and so the software would try a P-value equal to 0.5 (or 50% of maximal consumption). The software iteratively recalculates the growth of your fish based on different P-values until it finds a P-value (or proportion of maximal consumption) that allows your fish to grow from 60 to 90 grams. Once the software has determined the P-value, it can use that P-value in subsequent **Run** calculations.

Calculating a P-value based on a change in mass is the most common method; however, you have the option of calculating your P-value based on total consumption during your simulation. For example, your cohort might grow to some unknown mass based on a known yearly consumption of 1,400 grams of food and a start mass of 200 grams. Based on your input data files and the basic physiology of your fish, it might have a maximum consumption (which is equivalent to a P-value of 1) of 6,800 grams of prey per year. Since your cohort didn't consume 6,800 grams of prey, the software will use a lower P-value and recalculate total consumption and repeat the process until calculated consumption equals the consumption of 1,400 grams that you entered. The resulting P-value might be around 0.48.

- **Fit to end weight:** Check this option if you would like the software to calculate your cohort's P-value (proportion of maximal consumption) based on its change in mass during the simulation.
- **Fit to consumption:** Check this option if you would like the software to calculate your cohort's P-value (proportion of maximal consumption) based on its total consumption of prey during the simulation.

Additional Analyses: With the possible exception of **Input predator energy density**, the additional analyses are optional.

- **Input predator energy density:** Predator energy density is the joules per gram wet body mass of your fish. In the real world your cohort's energy density will fluctuate over time. If you have prepared a predator energy density input file that represents these changes, then select the **Input predator energy density** option and you'll be prompted for that file in the **User Input Data Files** setup. Otherwise, you can accept the default value copied from the software's database for this species. If the software's database contains no default energy density, then you will be required to select this option.
- **Spawning:** Does your cohort spawn during your simulation? If so, select this option and you'll be prompted for the spawn day and percent body mass spawned in the **User Input Parameters** setup.
- **Population mortality:** Your cohort can represent a population of fishes if you select this option. This option assumes that you will provide mortality data (in the form of percent of population dying over time) during the **User Input Data Files** setup.
- **Nitrogen and phosphorus analysis:** Select this option if you would like to determine the conversion of nitrogen and phosphorus from that which is contained in the prey's flesh to that which is regenerated by the predator. If you select this analysis you will be prompted for prey concentration input data files and assimilation efficiency input data files during the **User Input Data Files** setup.
- **Contaminant analysis:** Select this option if you would like to model the changes in contaminant concentration in the predator based on the contaminant concentrations in its prey. If you select this analysis you will be prompted for a prey concentration input data file and an assimilation efficiency input data file during the **User Input Data Files** setup. In addition, you must decide upon the mechanism by which the predator will eliminate some of the contaminants it has consumed.

    - **Net assimilation efficiency:** Select this option if your predator will assimilate contaminants based solely upon data provided in the contaminant

assimilation input data file. The remaining contaminants are eliminated. You will need to know the initial predator concentration for the **User Input Parameters** setup.

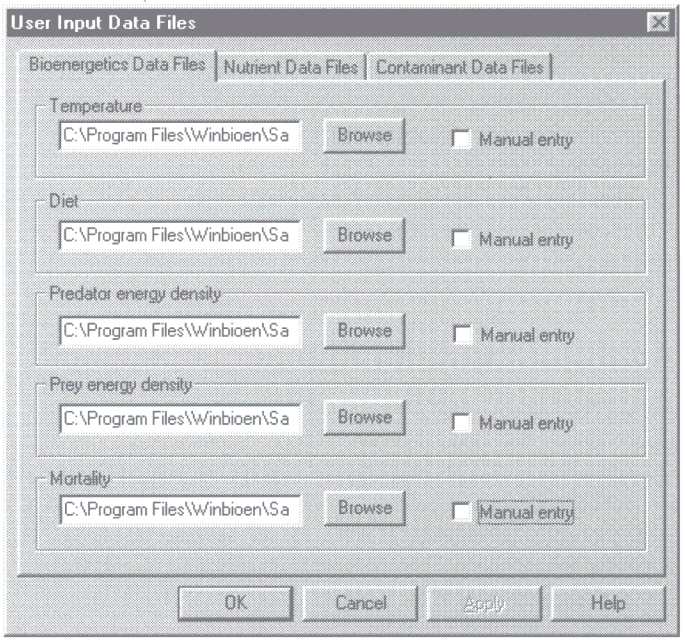
- **Gross assimilation efficiency + constant elimination:** If your predator assimilates at a rate indicated in your contaminant assimilation input data file, and yet loses some of those assimilated contaminants at a constant rate, select this option. You will need to know the initial predator concentration, and the elimination and allometric constants for the **User Input Parameters** setup.
- **Gross assimilation efficiency + T-dependent elimination:** If your predator assimilates at a rate indicated in your contaminant assimilation input data file, and yet loses some of those assimilated contaminants at a rate that's dependent upon temperature, select this option. You will need to know the initial predator concentration, the elimination and allometric constants, and the base temperature for elimination for the **User Input Parameters** setup.

Maintenance temperature: You can input a temperature (in degrees Celsius) below which your cohort will not survive. The software will then substitute this temperature whenever your user input data temperatures drop below this temperature.

User Input Data Files

➡ Select **Setup/User Input Data Files** from the main menu.

If you originally started the setup process from **Setup/Simulation** or the setup icon, you automatically will be forwarded into **User Input Data Files** setup when you select **OK** from **Simulation** setup. Otherwise, you can select **Setup/User input data files** from the program's main menu.



Load Data via Manual Entry:

➡ Check the **Manual entry** box and press the **Edit** button that appears.

This option allows you to type your data into a spreadsheet that pops-up. The data must conform to the same rules that apply to user input data files.

- OR -

Load Data via Data Files:

➡ Press the **Browse** button or type the full path and file name in the text box.

You can type in the full paths of your user input data files, or you can press the Browse button and search for your data files. If you did not select nitrogen and phosphorus analysis or contaminant analysis within the **Run Options** setup, you will not see the nitrogen and phosphorus Data Files and Contaminant Data Files tabs. You will always need to provide temperature, diet and prey energy density files. Depending upon the additional analyses you've selected in the **Run Options** setup, you might have to provide other files as well. For a complete discussion of User Input Data Files, see section 3.2, *User input data files.* Note that data files are loaded as soon as you exit the text field that applies to your file name or as soon as you've completed the **Browse** function for that file. Once you've loaded your data, you can check the Manual entry box and press the **Edit** button that appears to view or edit your data.

User Input Data Files (or manual entry)

General
Temperature
Diet
Predator energy density
Prey energy density
Mortality

Phosphorus Analysis
Prey concentration
Assimilation efficiency
Predator concentration

Nitrogen Analysis
Prey concentration
Assimilation efficiency
Predator concentration

Contaminants Analysis
Prey concentration
Assimilation efficiency

Italicized files are optional and dependent upon the type of analysis you are running.

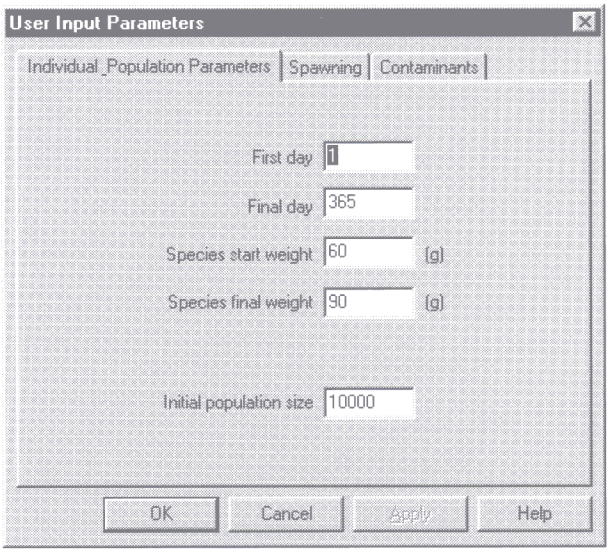
➡ Select **OK** to move onto **User Input Parameters** setup (don't forget nitrogen and phosphorus and contaminant files when applicable).

User Input Parameters

➡ Select **Setup/User Input Parameters** from the main menu.

If you were previously editing the **User Input Data Files** setup, you would automatically have been forwarded into **User Input Parameters** when you selected **OK** from **User Input Data Files** setup. The sheet that pops-up can contain as many as three tabbed dialogs depending upon the options you selected in **Run Options** setup.

Individual and Population Parameters

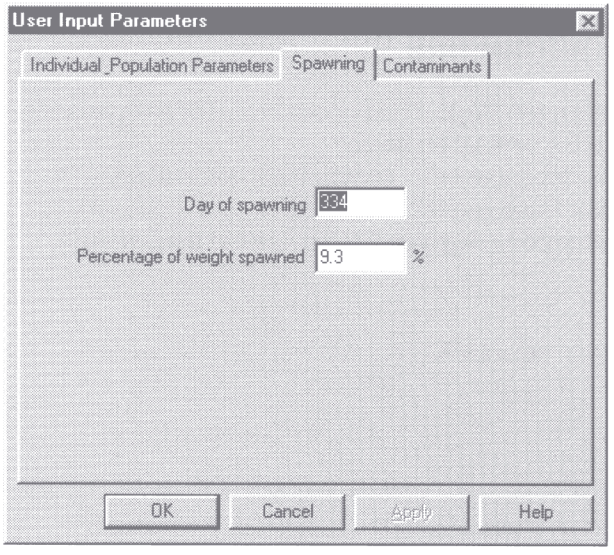


You must provide data for at least four of the six fields (P-value is for your information only, and **Initial population size** is available if you selected **Mortality** in your **Run** setup).

- **First day (integer):** The first day of your simulation. The value must be greater than or equal to all beginning dates in your user input data files.
- **Final day (integer):** The final day of your simulation. The value must be less than or equal to all the final dates in your user input data files.
- **Start weight (grams):** The mass of your fish before you run your analysis. If your analysis runs from day 1 through day 200, start weight would be the weight of your fish at the beginning of day 1. Incidentally, start weight and final weight apply to a single fish and are simply multiplied by the number of fish in a cohort to equal the mass of the starting population.
- **Final weight (grams) (alternatively Total consumption):** The mass in grams of your fish when your analysis finishes. Although final weight is required entry, it is used only for estimating proportion of total possible consumption (P-value estimate), and not for actual predictive analyses. An alternative analysis would be to estimate the P-value and the final weight based on a known total consumption. In this case, you would first indicate **Fit to consumption** in **Simulation Setup** and then enter the total consumption of your fish in this field.
- **Initial population size:** The number of fish in your cohort immediately before the beginning of your simulation.

➡ Once you've entered your parameters, select another parameter sheet if available, such as **Spawning** or **Contaminants**, or select **OK**.

Spawning

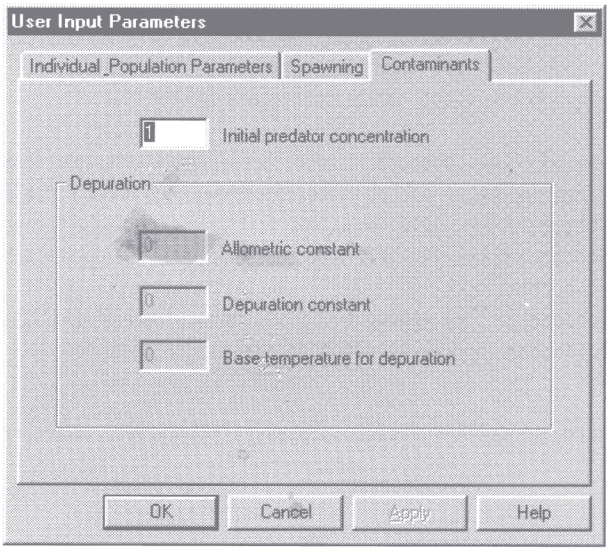


The **Spawning** parameter page is available only when you've selected **Spawning** as an option in your **Run** setup. You must provide data for both fields.

- **Day of spawning (integer):** This is the day during your simulation when all fish in the cohort spawn. Spawning day must be greater than or equal to **Start day** and less than or equal to **Final day**.
- **Percentage of weight spawned (%):** Enter the percent of your cohorts mass that is lost due to spawning.

➡ Once you've entered your parameters, select another parameter sheet if available, such as **Contaminants**, or select **OK**.

Contaminants



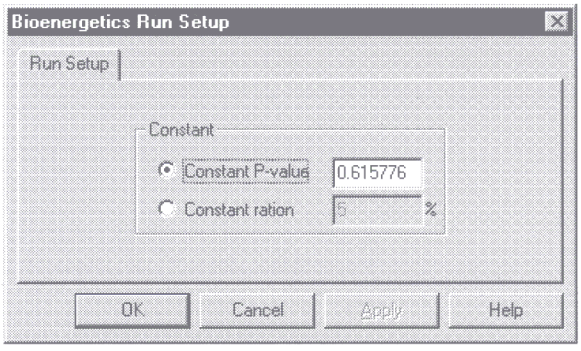
The **Contaminants** parameter page is available when you've selected **Contaminant analysis** as an option in your **Run** setup. Some or all of the fields will be available for editing depending on the type of contaminant analysis selected in your **Run** setup.

- **Initial predator concentration (mg/kg):** The concentration of contaminants in your predator immediately before the simulation begins.
- **Allometric constant :** Mass dependence of contaminant elimination.
- **Elimination constant ($g^{-\zeta}$/d):** Base line elimination rate.
- **Base temperature for elimination (degrees C):** Scales the temperature dependence of elimination.

➡ Once you've entered your parameters, select **OK**.

Bioenergetics Run

When you select **P/Run/Bioenergetics Run** from the main menu or the run icon you will automatically be forwarded to Bioenergetics Run setup first. Otherwise, you can select **Setup/Bioenergetics Run** at anytime from the main menu.



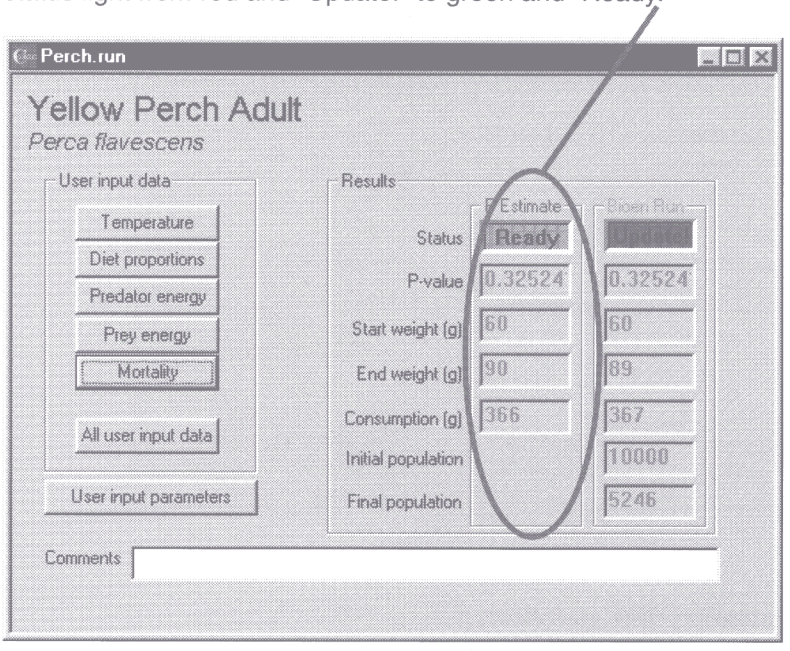
Before you can execute your Bioenergetics Run, you must decide which of two possible parameters, P-value or ration, to hold constant while varying the other. For most applications outside of the laboratory you'll assume a constant P-value while the amount of prey the cohort consumes (ration) will vary. But for some applications, such as raising fish in captivity, you might feed your fish a given amount of food daily. In this case, select constant ration.

- **Constant P-value (proportion):** The proportion of maximal consumption that will be applied to each day of your simulation. If you've recently executed a **Fit P-value**, the resulting P-value will be displayed here; otherwise, the P-value you used for your most recent **Bioenergetics Run** will be displayed. In either case, you can change this value.
- **Constant ration (% of mass/day):** The amount of prey consumed (in the form of % of an individual fish's mass) by your cohort on each day of the simulation

➡ Once you've entered your parameters, select **OK** and the **Bioenergetics Run** will execute.

4.4 Step 3: Estimating a P-value (optional)

➡ Select either **P/Run/Fit P-value** or the P icon from the toolbar. *Fish Bioenergetics 3.0* will estimate the P-value and display it in the P Estimate portion of the cohort window and change the status light from red and "Update!" to green and "Ready."



Why Estimate a P-value?

If estimating a P-value is optional, why do it? First, you must understand that estimating a P-value tells you the consumption behavior of your cohort based on your user input data and parameters. Recall that the P-value represents a proportion of maximum consumption at which the cohort is feeding. Let's say that you've setup your simulation, you execute a P-value estimate, and *Fish Bioenergetics 3.0* returns a P-value much higher than you anticipated. At this point you would review your input data and parameters to determine whether or not inaccuracies exist.

You also can see how estimating a P-value provides a mechanism for exploring input data and parameters and determining their effects on consumption. Why can't you do this in the actual Bioenergetics Run? Because the P-value estimate and Bioenergetics Run perform slightly different calculations:

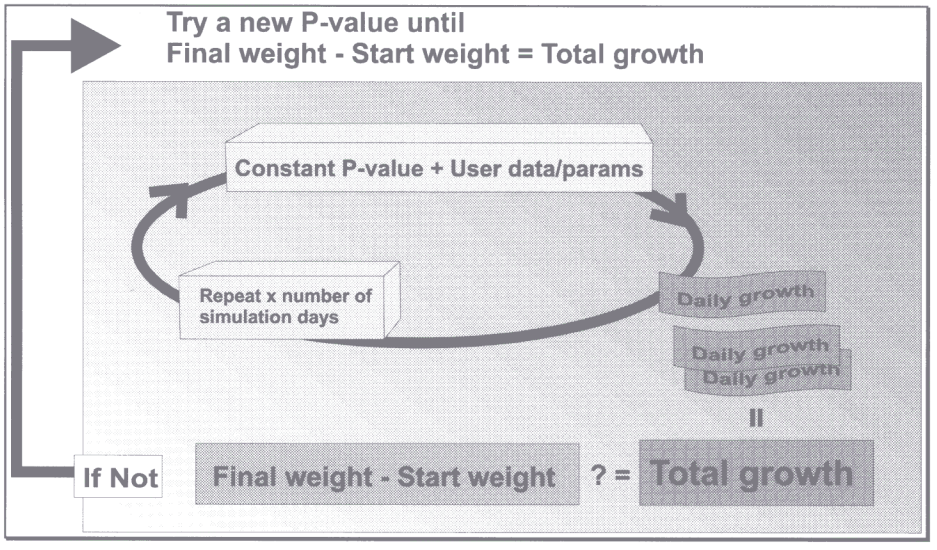
Why estimate a P-value?

1) Test the validity of your user input data and parameters.
2) See how changing user input data effects consumption.
3) Provide a starting point for executing Bioenergetics Runs.

P-value Estimate: Estimates the proportion of maximum consumption based on a start weight, final weight, and other user input data and parameters.

Bioenergetics Run: Calculates the cohort's final weight (and many other variables) based on a start weight, P-value, and other user input data and parameters.

How the P-value estimate calculation works



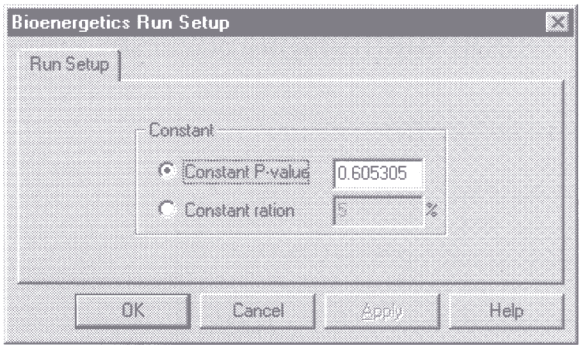
In pseudocode, the calculation runs as follows:

Until calculated growth = observed growth (final weight - start weight) do:
{
    Guess at a P-value
    For the total number of simulation days do:
    {
        Use the P-value *to calculate growth*
        Increment to the next day
        Total growth = previous growth plus today's growth
    }
    If total growth does not equal observed growth, repeat with a new P-value
}

Note that the P-value is considered acceptable when the percent difference between estimated total growth and observed growth is less than or equal to 0.001%

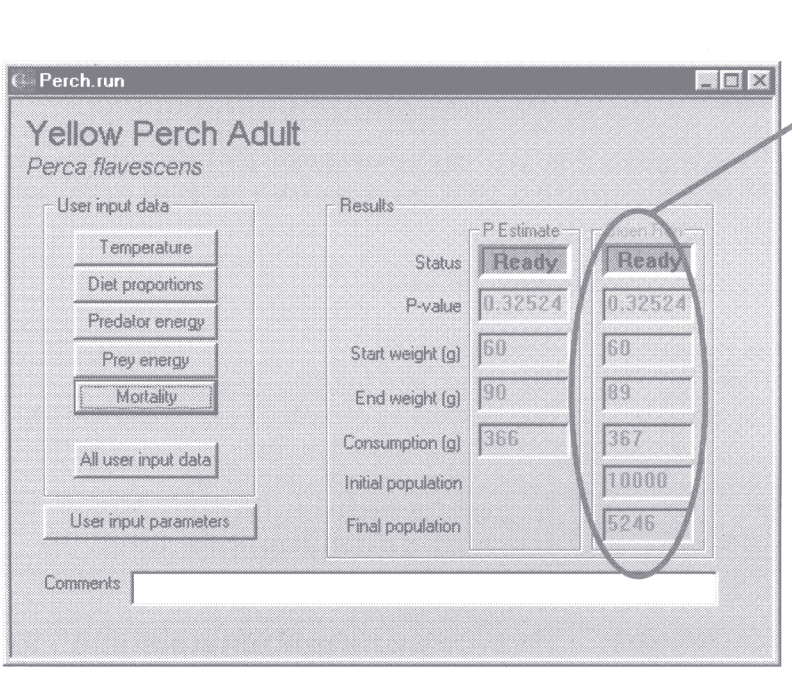
4.5 Step 4: Executing a Bioenergetics Run

➡ Select either **P/Run/Run Bioenergetics** or the R icon from the toolbar. The Bioenergetics Run Setup window appears.



➡ Select either **Constant P-value** or **Constant ration** in the Run Setup and press OK.

Fish Bioenergetics 3.0 will calculate a Bioenergetics Run and display it in the Bioen Run portion of the cohort window and change the status light from red and "Update!" to green and "Ready."



The P-Estimate values and the Bioen Run values may or may not be the same depending on whether or not you used the P-value from the P-value Estimate in your Bioenergetics Run. Even if you do use the same P-value, your results may be slightly different (percent difference < 0.5 %) because of rounding that occurs in the daily calculations. The values present on the screen represent just a few of the most commonly viewed variables and are intended to give you a quick look at your results.

How the Bioenergetics Run Works

On a daily basis, *Fish Bioenergetics 3.0* calculates growth based on the following equation:

Growth = Consumption - Respiration - SDA - Egestion - Excretion

Fish Bioenergetics 3.0 calculates parameters on a daily time step. Consequently, your finest resolution in output data is daily values. Calculations begin on day one of your simulation and continue through the final day.

Daily *Fish Bioenergetics 3.0* Run Calculations

- Retrieve user input data for the current day. Interpolate if necessary.
- For an individual fish, calculate consumption, egestion, excretion, respiration, SDA, and the resultant growth.
- Apply the calculations for an individual to the entire cohort population.
- If applicable, calculate nitrogen and phosphorus and contaminant analysis parameters.
- Calculate gross production for the population and gametic production when applicable.
- Determine the number of deaths in the population.
- Calculate net production.

Calculated Results

Once you've executed a Bioenergetics Run, you may view or graph the calculated results of nearly 70 parameters. The type and number of parameters available depends on the options chosen in your simulation setup.

Output Variables

Output Parameter	Units (type)	Description
Day of simulation	day (integer)	Age of fish in simulation days
Day of year	day (integer)	Day of year in a simulation (i.e. simulation can start on day 30 and run to any day)
Temperature	degrees C	Temperature on the current day
Weight	grams	Wet mass of the fish on the current day
Population number	number	Total number of fish alive on the current day
Population biomass	grams	Total biomass (population number x mass) of the cohort on the current day
Specific growth rate	joules/grams/day	The number of joules of energy allocated to growth per gram of predator mass on the current day
Specific consumption rate	joules/grams/day	The number of joules of energy consumed per gram of predator mass on the current day
Specific egestion rate	joules/grams/day	The number of joules of energy egested per gram of predator mass on the current day
Specific excretion rate	joules/grams/day	The number of joules of energy excreted per gram of predator mass on the current day

Output Variables (continued)

Specific respiration rate	joules/grams/day	The number of joules of energy required for metabolism per gram of predator mass on the current day
Specific SDA rate	joules/grams/day	The number of joules of energy allocated to SDA per gram of predator mass on the current day
Specific consumption rate	grams/gram/day	The number of grams of prey consumed per gram of predator mass on the current day
Specific growth rate	joules/gram/day	The number of grams of prey allocated to growth per gram of predator mass on the current day
Predator energy density	joules/day	Predator energy density on the current day
Mean prey energy density	joules/day	Mean weighted prey energy density on the current day
Daily weight increment	grams	Today's mass minus yesterday's mass
Gross production	grams	Total increase in biomass of the cohort on the current day (includes biomass used in metabolism and lost through mortality)
Gross production	joules	Total increase in energy of the cohort on the current day (includes biomass used in metabolism and lost through mortality)
Gametic production	grams	The total mass of gametes lost on the current day
Gametic production	joules	The net loss of energy associated with spawning on the current day
Net production	grams	Increase in biomass of the cohort on the current day excluding losses to metabolism and mortality
Net production	joules	Increase in energy content of the cohort on the current day excluding losses to metabolism and mortality
Prey-Total by indiv	grams	The total daily biomass of all prey consumed by an individual fish on the current day. Analogous parameters are generated for each specific prey type
Prey-Total by indiv	joules	The total daily energy content of all prey consumed by an individual fish on the current day. Analogous parameters are generated for each specific prey type
Prey-Total by pop'n	grams	The total daily biomass of all prey consumed by the entire cohort on the current day. Analogous parameters are generated for each specific prey type
Prey-Total by pop'n	joules	The total daily energy content of all prey consumed by the entire cohort on the current day. Analogous parameters are generated for each specific prey type
Mortality number		The number of fish removed from the population on the current day. A separate estimate is generated for each type of mortality
Mortality	grams	The biomass of fish removed from the population on the current day. A separate estimate is generated for each type of mortality
Nitrogen by prey item	% wet mass	Nitrogen concentration by individual prey items
Phosphorus by prey item	% wet mass	Phosphorus concentration by individual prey items
N/P ratio by prey item	mass ratio	N:P ratio in each of the prey items

Output Variables (continued)

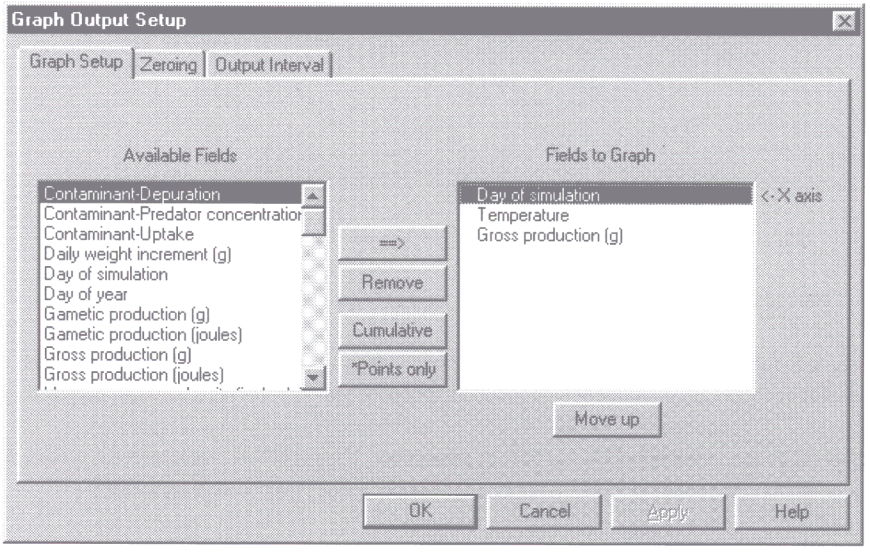
Nitrogen -Total egestion	grams	Total mass of N egested
Phosphorus -Total egestion	grams	Total mass of P egested
N/P-Total egestion	mass ratio	N:P ratio of egested nitrogen and phosphorus
Nitrogen -Total excretion	grams	Total mass of N excreted
Phosphorus -Total excretion	grams	Total mass of P excreted
N/P-Total excretion	mass ratio	N:P ratio of excreted nitrogen and phosphorus
Nitrogen -Total consumption	grams	Total mass of N consumed
Phosphorus -Total consumption	grams	Total mass of P consumed
N/P-Total consumption	mass ratio	N:P ratio of consumed nitrogen and phosphorus
Nitrogen -Total growth	grams	Mass of N allocated to growth
Phosphorus -Total growth	grams	Mass of P allocated to growth
N/P-Total growth	mass ratio	N:P ratio of nitrogen and phosphorus allocated to growth
Contaminant-Uptake	mg	Mass of contaminants consumed
Contaminant-Elimination	mg	Mass of contaminants eliminated
Contaminant-Predator concentration	mg/kg	Concentration of contaminants in predator tissue

4.6 Step 5: Graphing the Output and Generating an Output Spreadsheet

Creating a graph or generating spreadsheet output requires two major steps: 1) Setup, which includes selecting the output fields, how they will be zeroed, and the output interval; 2) Graph/Spreadsheet, which is the graphic or spreadsheet that you generate. *Fish Bioenergetics 3.0* includes two add-in programs, Formula One and First Impression, that help you view your results as a spreadsheet and graph your results as a chart. Both programs provide standard file functions, such as saving, opening, importing, etc. and are invoked automatically when you select the Graph or Spreadsheet output options.

Graph Output Setup (Spreadsheet Output Setup)

➡ Select either **Graph/Spreadsheet Graph Results** or the Graph icon from the toolbar. The Graph Output Setup window appears.



Graph Setup (Spreadsheet)

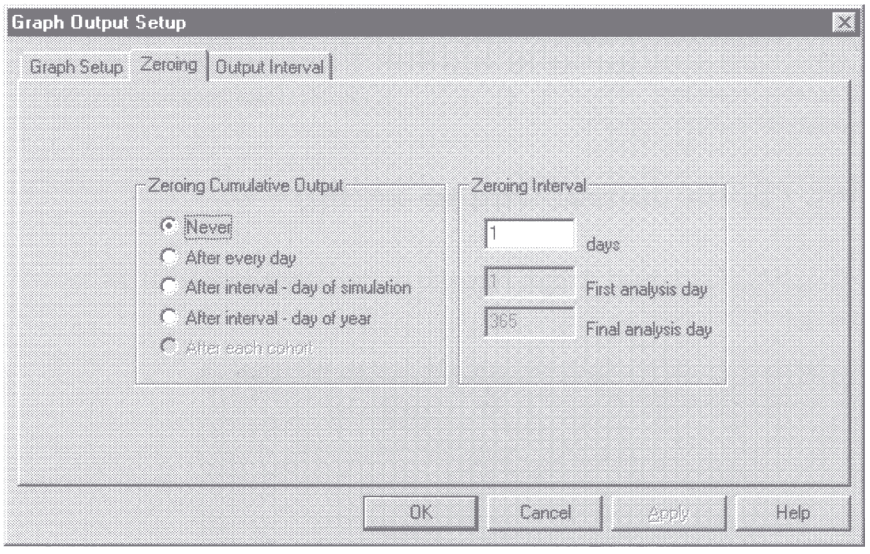
Available Fields: The list of fields, in alphabetical order, that are available to be graphed.

Fields to Graph (Fields to Display): The fields that are actually going to be graphed. The data from the first field in the list will represents the x-axis. The data from the second field represents the left y-axis, and the third field the right y-axis. Any fields in the list after the first three will be graphed on the second y-axis and will use the scaling of the third field. It follows that any fields after the third in the list should have data with values similar in scale to the data of the third field.

Display file header (spreadsheet output only): When this box is checked, *Fish Bioenergetics 3.0* will include information about the current file, such as the file name, date, and time in the spreadsheet output.

Display cohort parameters (spreadsheet output only): When this box is checked, *Fish Bioenergetics 3.0* will include all user input and physiological parameters in the spreadsheet output.

Zeroing



Never: The data simply accumulate throughout the entire analysis.

After every day: The cumulative data are returned to zero every day.

After interval - day of simulation: When this option is selected, cumulative data will be reset to zero after every n^{th} simulation day, where n equals a value that you enter into the **days** field.

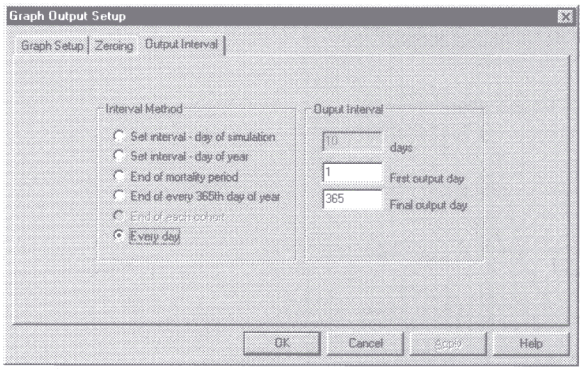
After interval - day of year: When this option is selected, cumulative data will be reset to zero after every n^{th} day of year, where n equals a value that you enter into the **days** field.

Days: The number of days in an interval when either **After interval - day of year** or **After interval - day of simulation** is selected.

First analysis day: For information only - the first analysis day in the summary.

Final analysis day: For information only - the final analysis day in the summary.

Output Interval



Set interval - day of simulation: Output will be generated only for those days that equal the simulation start day + x, where x equals the value typed in the Days field.

Set interval - day of year: Output will be generated only for those days that equal the day of year + x, where x equals the value typed in the Days field.

End of mortality period: This option provides output only on those days when a mortality period has ended. For example, if fishing mortality ended on day 200 of your simulation and natural mortality ended on day 365 of your simulation, the software would generate three data points, day 1, day 200, and day 365.

End of every 365th day of year: Assuming your assimilation spans at least 365 days, you can select this option to see data only on the 365th day of year.

End of each cohort: This option applies only to Summary files.

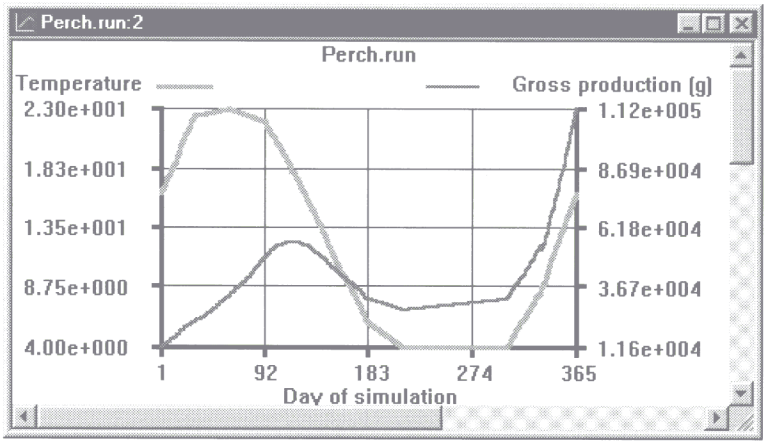
Every day (default): Select this option if you would like output generated for each day of the simulation.

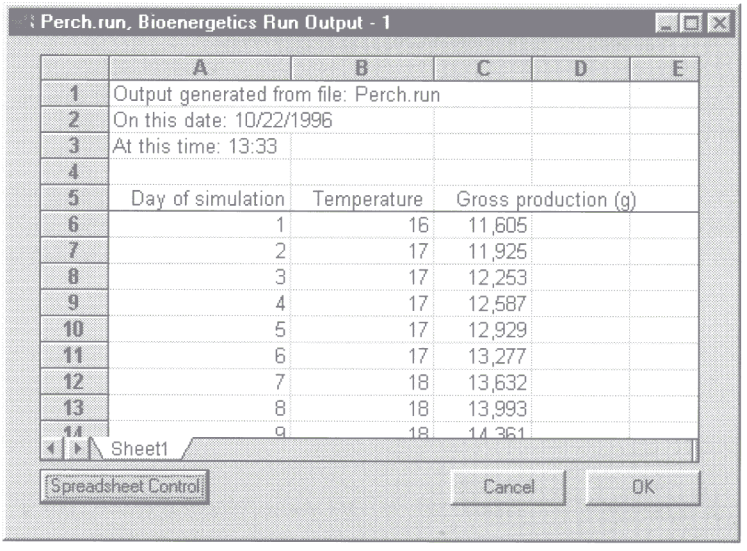
Days: Enter the number of days in your interval when you've selected either **Set interval - day of year** or **Set interval - day of simulation**.

First output day: If you would like to limit the range of days in your output, enter the first day of that range in this field.

Final output day: If you would like to limit the range of days in your output, enter the final day of that range in this field.

The Graph and Spreadsheet File





4.7 Saving

You can save all of the information within your cohort file by selecting **File/Save**. *Fish Bioenergetics 3.0* will save your user input data, user input parameters, setup, P-value estimate, and the results of latest Bioenergetics Run in a file with a *.run* extension. *Fish Bioenergetics 3.0* will not save graphs; however, you can save the spreadsheet output of a Bioenergetics Run using the method described in chapter 4, section 6, *Graphing the Output and Generating Output Spreadsheet*.

➡ To save, select either **File/Save** or the diskette icon from the toolbar.

4.8 Opening a Previously Saved Cohort File

You can open previously saved *Fish Bioenergetics 3.0* cohort files and resume working where you left off. For more information about the information that is saved in a cohort file, see chapter 4, section 7, *Saving*.

➡ To open a previously saved cohort file, select either **File/Open** or the open folder icon from the toolbar.

Creating a Summary - Analyzing Multiple Cohorts

You might be interested in the overall characteristics of a fish that passes through more than one life stage, or maybe you would like to determine the predation of a particular prey item by more than one cohort. Creating a summary allows you to combine the calculations of more than one cohort into one file.

What is a summary?

A summary is a file/document that combines the Bioenergetics Runs from one or more cohort files.

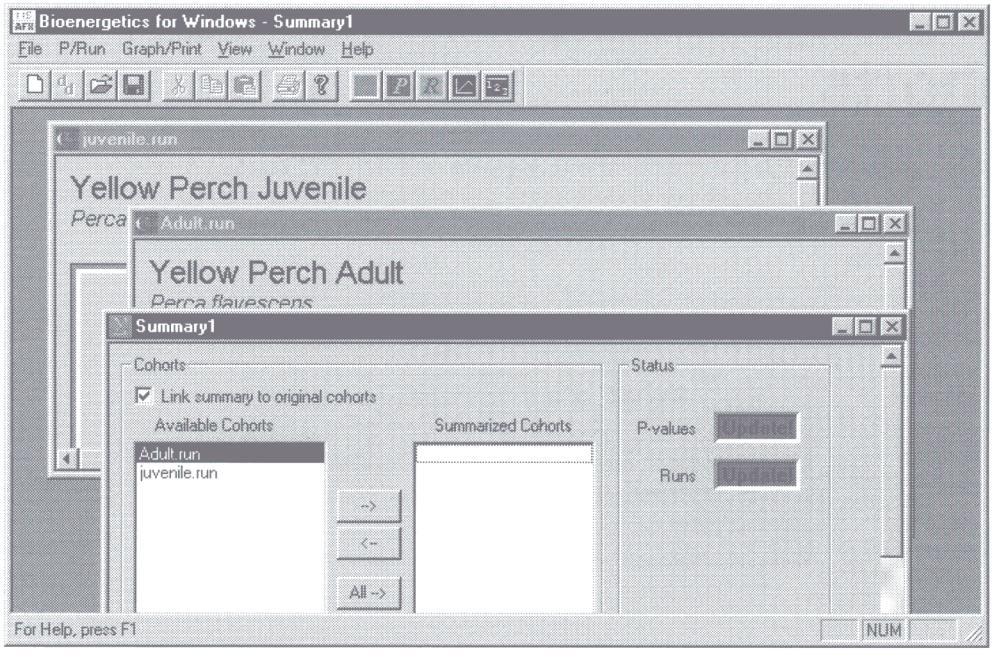
Why create a summary? To understand why a summary provides useful information about your analysis, you must first recall the definition of a cohort. A cohort file represents a single species of fish at a single life stage, such as an adult perch. The cohort can represent one fish or many fish. But let's say that your analysis includes the same species of fish at two different life stages, and you're interested in the total prey consumption by both life stages. You could create two separate cohort files, generate consumption output for each cohort, and add the outputs manually. A summary file makes this process easier.

Why create a summary?

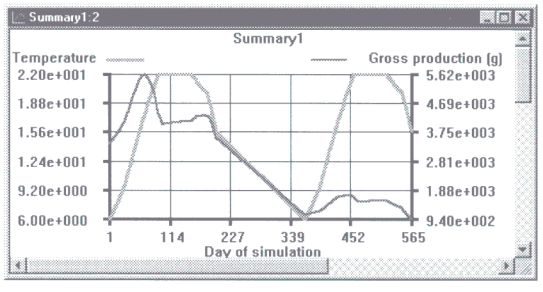
- Add the results of individual cohorts
- Follow ontogenetic changes over time
- Analyze diverse populations of cohorts
- Contrast differences among cohorts
- Combine different species to model complex species assemblages

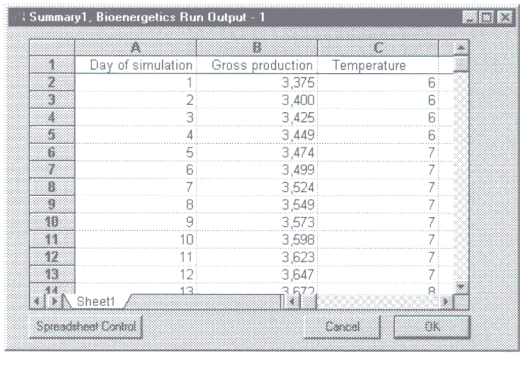
5.1 The Two Major Steps

Step 1: New Summary Setup



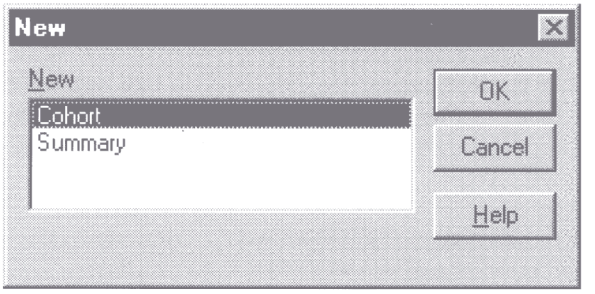
Step 2: Graphing the Output and Generating an Output Spreadsheet





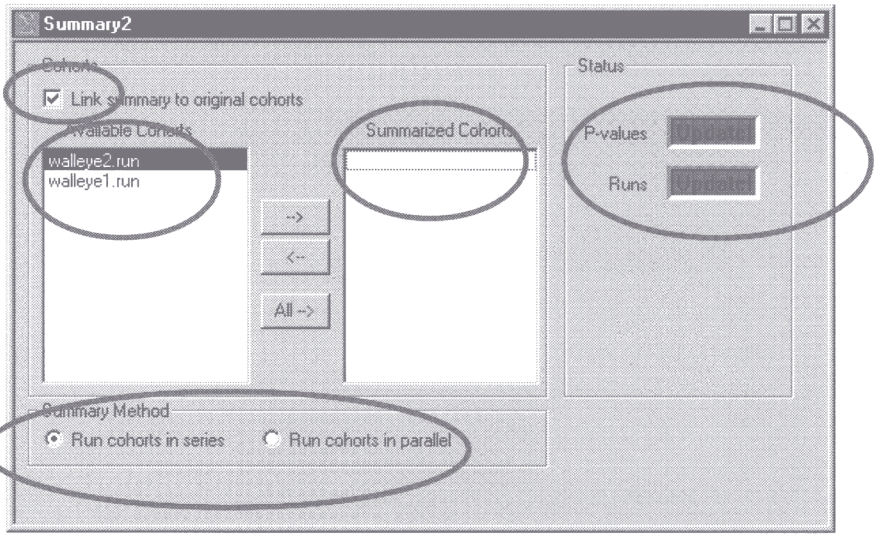
5.2 Step 1: New Summary Setup

➡ From the main *Fish Bioenergetics 3.0* window, select **File/New** or press the new-file icon. The following window will appear.



Fish Bioenergetics 3.0 presents two options for new files, **Cohort** and **Summary**. A cohort file represents a single species of fish at a single life stage, such as an adult perch. The cohort can represent one fish or many fish. A summary file allows you to summarize information from several open cohort files. For example, you might have two cohort files open – juvenile perch and adult perch. Within each cohort file you can determine the consumption by that cohort and its population, but you might be interested in determining the overall consumption by both juvenile and adult perch over the same time period. The summary file facilitates this type of calculation.

➡ Highlight **Summary** and press **OK**. *Fish Bioenergetics 3.0* will open a window similar to the following.



Minor Setup

Link summary to original cohorts: When this box is checked (default) then the following are true:

- Any changes made to the individual cohorts are automatically updated in the summary
- When a new cohort file is created, it is automatically displayed in the **Available cohorts** window of the summary file
- When a cohort file is closed, it is automatically removed from the summary file

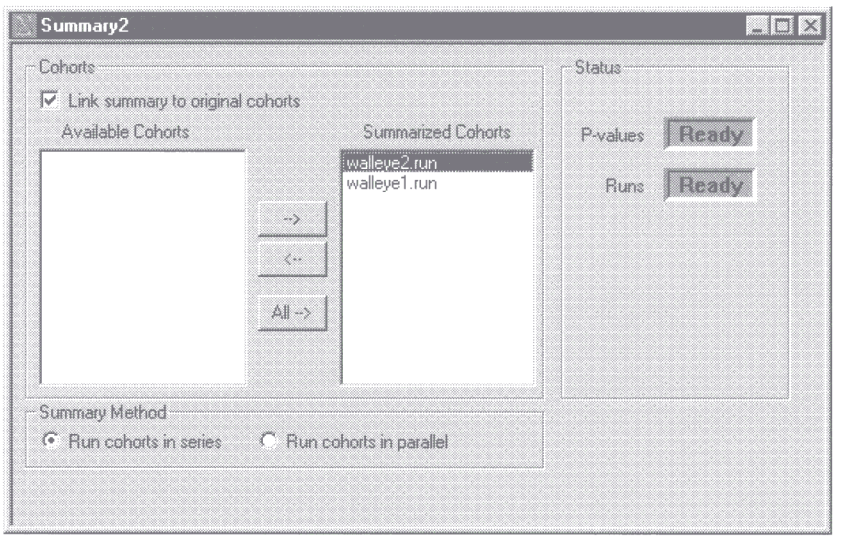
Available Cohorts: Any cohort files that are currently open are displayed in this window on the left side of the summary window. If a file is listed in this window, it is not included in summary calculations. These files need to be moved to the **Summarized Cohorts** window to be included in the summary analysis.

Summarized Cohorts: Any cohorts that are listed in the Summarized Cohorts window are included in the summary calculations. When cohorts are run in series, the cohorts are linked sequentially from top to bottom.

Status: The **Status** lights indicate whether or not the summarized cohorts have current P-value calculations and current Bioenergetics Runs. Only the **Runs** light has to be green for summary calculations to be executed.

Summary Method: Cohorts can be run in either series or parallel:

- **Series**: In series, the total number of days in the summary equals the sum of all the days in the analyzed cohorts, and each data point from each cohort becomes a data point in the summary.
- **Parallel**: In parallel, analysis days are matched among all the cohorts, and the data from the same days are added together. The start analysis day will equal the earliest start day from the cohorts, and the final analysis day will equal the latest final day from the cohorts.



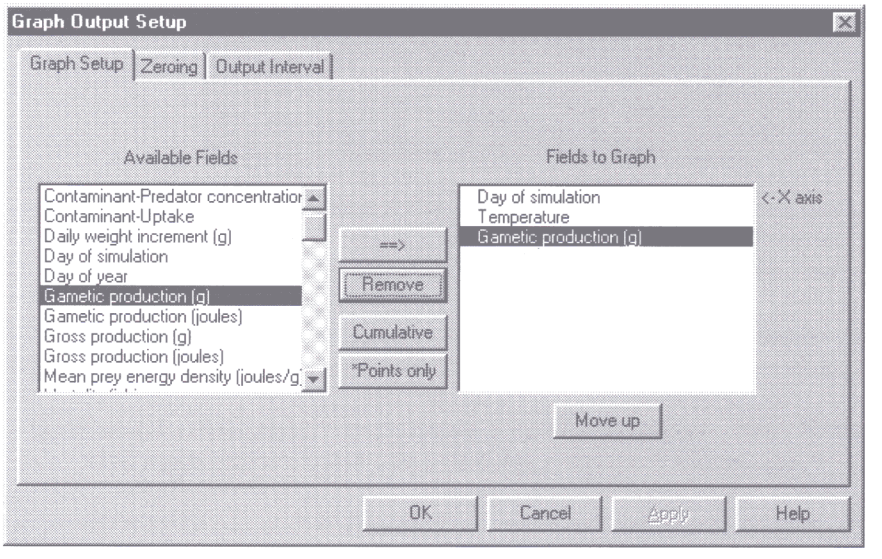
5.3 Step 2: Graphing the Output and Generating an Output Spreadsheet

Summary calculation notes

- Only files listed under **Summarized Cohorts** are part of the summary calculations
- As you make changes to the cohort files, those changes are automatically updated in the summary file (unless the **Link summary to original cohorts** box is NOT checked)
- You can analyze your cohorts in either series or in parallel. If you analyze in series, then the total number of days in the summary equals the sum of all the days in the analyzed cohorts, and each data point from each cohort becomes a data point in the summary. If you analyze in parallel, then analysis days are matched among all the cohorts, and the data from the same days are added together.

Graph Output Setup (Spreadsheet Output Setup)

➡ Select either **Graph/Spreadsheet Graph Results** or the Graph icon from the toolbar. The Graph Output Setup window appears.



Graph Setup (Spreadsheet)

Available Fields: An alphabetical listing of the available output fields that can be graphed.

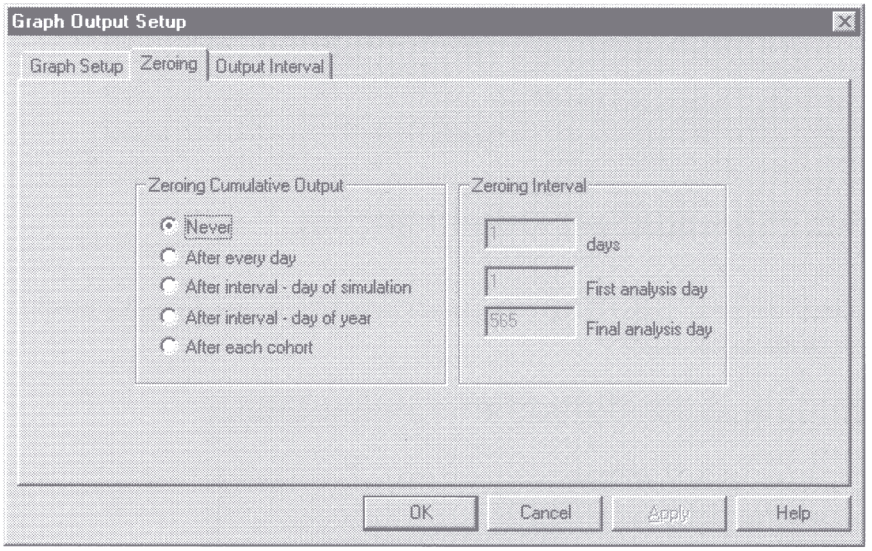
Fields to Graph (Fields to Display): The fields that are actually going to be graphed. The data from the first field in the list will represent the x-axis. The data from the second field represents

the left y-axis, and the third field the right y-axis. Any fields in the list after the first three will be graphed on the second y-axis and will use the scaling of the third field. It follows that any fields after the third in the list should have data with values similar in scale to the data of the third field.

Display file header (spreadsheet output only): When this box is checked, *Fish Bioenergetics 3.0* will include information about the current file, such as the file name, date, and time in the spreadsheet output.

Display cohort parameters (spreadsheet output only): When this box is checked, *Fish Bioenergetics 3.0* will include all user input and physiological parameters in the spreadsheet output.

Zeroing



Never: The data simply accumulate throughout the entire analysis.

After every day: The cumulative data are returned to zero every day.

After interval - day of simulation: When this option is selected, cumulative data will be reset to zero after every nth simulation day, where n equals a value that you enter into the **days** field.

After interval - day of year: When this option is selected, cumulative data will be reset to zero after every nth day of year, where n equals a value that you enter into the **days** field.

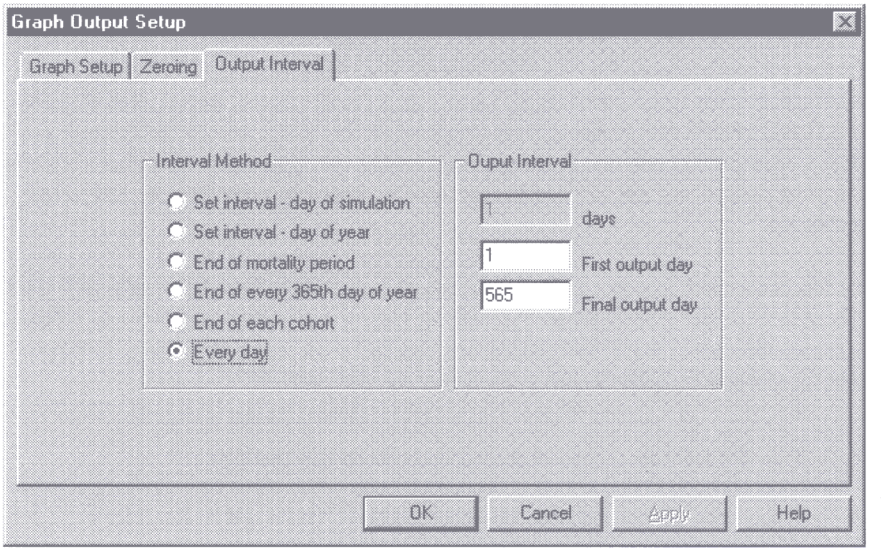
After each cohort: When cohorts are run in series, cumulative data are reset to zero after the final analysis day of each cohort.

Days: The number of days in an interval when either **After interval - day of year** or **After interval - day of simulation** is selected.

First analysis day: For information only - the first analysis day in the summary.

Final analysis day: For information only - the final analysis day in the summary.

Output Interval



Set interval - day of simulation: Output will be generated only for those days that equal the simulation start day + x, where x equals the value typed in the Days field.

Set interval - day of year: Output will be generated only for those days that equal the day of year + x, where x equals the value typed in the Days field.

End of mortality period: This option provides output only on those days when a mortality period has ended. For example, if fishing mortality ended on day 200 of your simulation and natural mortality ended on day 365 of your simulation, the software would generate three data points, day 1, day 200, and day 365.

End of every 365th day of year: Assuming your assimilation spans at least 365 days, you can select this option to see data only on the 365th day of year.

End of each cohort: Your summary file will probably contain multiple cohorts. If you're running your analysis in series, and you would like to see data only on the last day of each individual cohort's simulation, select this option.

Every day (default): Select this option if you would like output generated for each day of the simulation.

Days: Enter the number of days in your interval when you've selected either **Set interval - day of year** or **Set interval - day of simulation**.

First output day: If you would like to limit the range of days in your output, enter the first day of that range in this field.

Final output day: If you would like to limit the range of days in your output, enter the final day of that range in this field.

5.4 Saving

You can save all of the information within your summary file by selecting **File/Save**. *Fish Bioenergetics 3.0* will save your user input data, user input parameters, setup and the results of latest Bioenergetics Runs of all your cohorts that are part of the summary in a file with a *.sum* extension. *Fish Bioenergetics 3.0* will not save graphs; however, you can save the spreadsheet output using the method described in chapter 5, section 3, *Graphing the Output and Generating an Output Spreadsheet.*

Once the summary file is closed, it is no longer related to the cohort files from which it gathered its data. In other words, if you make changes to the cohort files these changes are not reflected in the summary. You can relink your summary to its original cohorts by using the techniques described in chapter 5, section 5, *Opening a previously saved summary.*

➡ To save, select either **File/Save** or the diskette icon from the toolbar.

5.5 Opening a Previously Saved Summary File

You can open previously saved *Fish Bioenergetics 3.0* summary files and resume working where you left off. For more information about the information that is saved in a summary file, see chapter 4, section 7, *Saving*. Keep in mind that once you open your summary file, it no longer will be linked to its original cohort files – as indicated by the absence of a check in the **Link summary to original cohorts** check box. In other words, you cannot make changes to the original cohort data and have these changes reflected in the summary document unless you check the **Link summary to original cohorts** check box. If you decide to relink to original cohorts, make sure these cohort files are open and that the file names mach those names listed in the **Summarized Cohorts** list in your summary file.

➡ To open a previously saved cohort file, select either **File/Open** or the open folder icon from the toolbar.

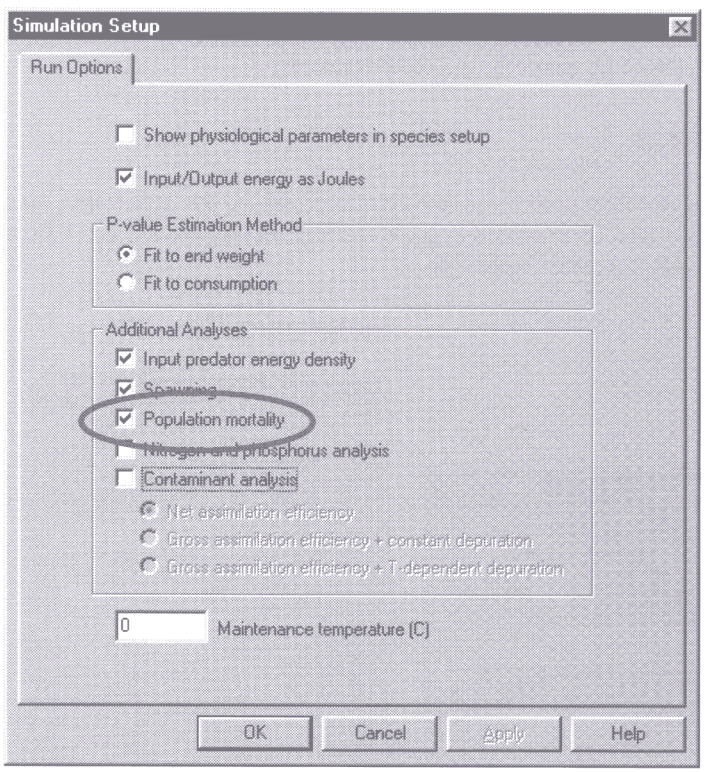
> If you decide to relink to original cohorts, make sure these cohort files are open and that the file names mach those names listed in the **Summarized Cohorts** list in your summary file.

Populations and Mortality

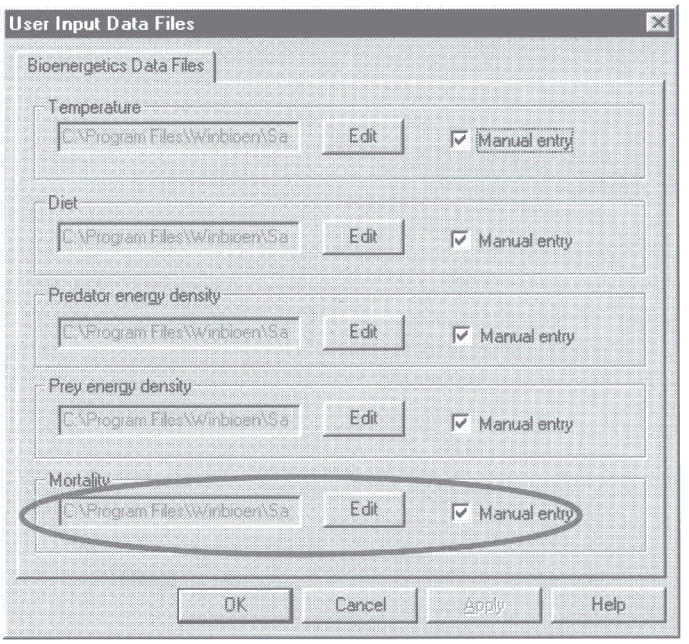
Fish Bioenergetics 3.0 allows you to extrapolate the simulation results of a single fish to an entire population of fishes, while at the same time accounting for mortality in the population. Recall that a cohort can be a single fish or a group of fish of the same species in the same life stage. To analyze a cohort that has more than one fish, you simply need to perform two setup steps: 1) Indicate that you would like to include mortality calculations in your simulation; and 2) Enter mortality user input data.

6.1 Mortality Setup and User Input Data

➡ From the main *Fish Bioenergetics 3.0* window, select **Setup/Simulation** or press the setup icon. The following window will appear.



➡ Check the **Population mortality** checkbox within **Additional Analyses**. Press the **OK** button, and the User Input Data Files window appears.

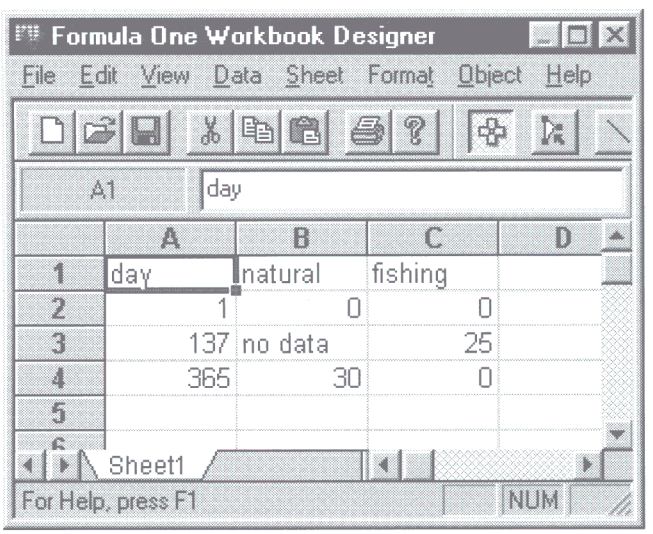


You'll see that the **Mortality** box becomes available. Load user input mortality data by either browsing for a tab delimited text file or by entering the data manually.

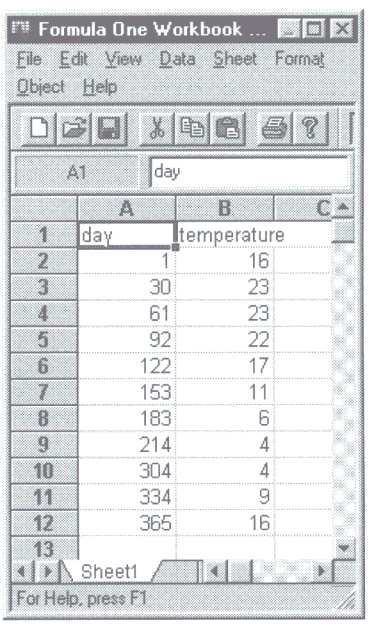
Mortality user input data

Although the format for entering mortality user input data is the same as for other data files, the software interprets the data differently. To illustrate this difference, let's compare the following mortality user input file and temperature user input file.

Mortality file



Temperature file



Notice that in the temperature file data must exist for every row of dates that have been entered; however, in the mortality file, day 137 of natural mortality reads "no data." The software interprets this to mean that over a range of 365 days every fish in the population has a 30% chance of dying from natural causes. Compare fishing mortality with natural and you'll see that day 137 of fishing mortality reads "25." The software interprets this to mean that from day zero through day 137 every fish has a 25% chance of dying from fishing. But from day 138 through day 365 no fish will die from fishing.

For the mortality user input data, the software interprets any non-number as being equivalent to "no data."

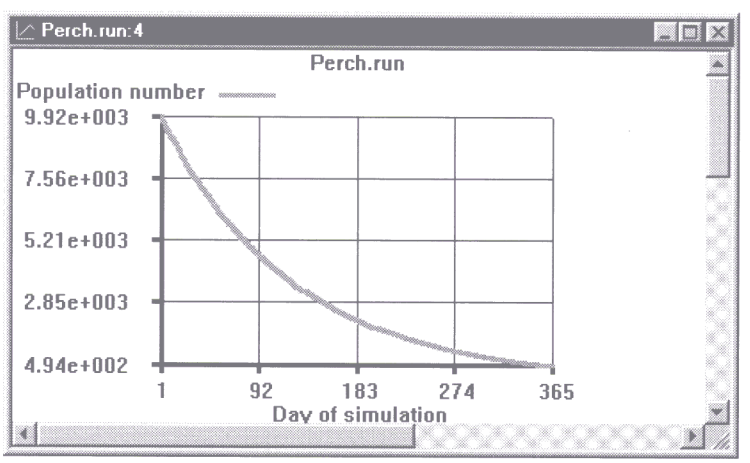
At a casual glance, you might expect your entire population of fishes to have a 55% (30% due to natural + 25% due to fishing) chance of dying during one year. In other words, given a starting population of 10,000 fish, only 4,500 would remain at the end of one year. But keep in mind that a fish cannot die from both fishing and natural causes, and so in our example above we actually end up with 5,250 fish at the end of the year. Instead of 55% percent of the fish dying, we have the sum of the two probabilities minus their product (0.30 + 0.25 - 0.30 * 0.25), or 47.5% of the fish dying.

Total probability (P_T) of mortality

$$P_T = P_1 + P_2 - (P_1 \times P_2)$$

6.2 Mortality Calculations

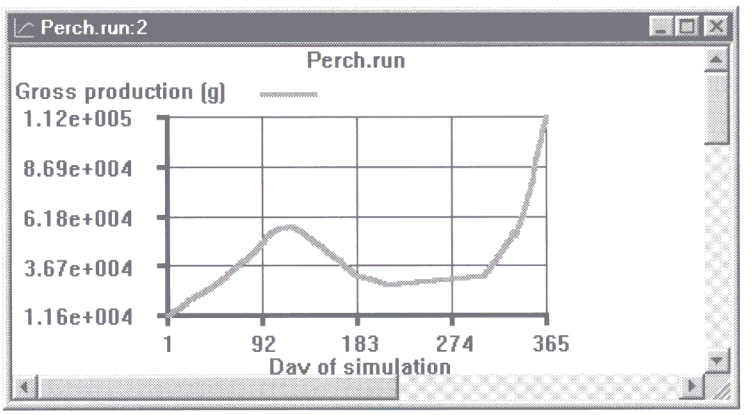
Fish Bioenergetics 3.0 looks at the entire mortality user input data before daily calculations begin. Because mortality is not a linear process, the software calculates a daily mortality rate that produces an exponential decrease in population. As a simple example, let's suppose that our fish population started at 10,000 and experienced a mortality rate of 95%. The resulting graph would look like this:

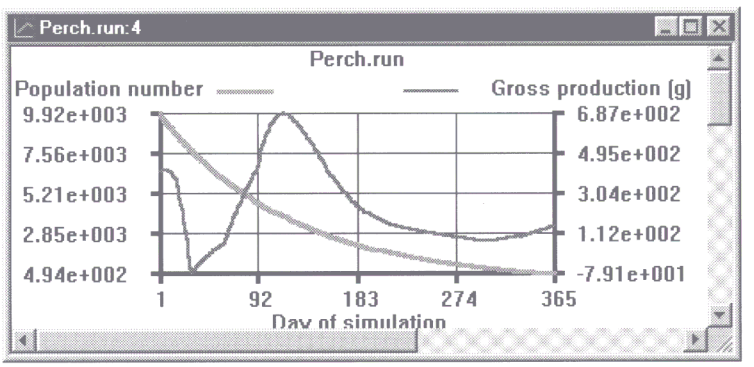


Bioenergetics calculations extrapolated to the population

The basic bioenergetics calculations and the mortality calculations are mutually exclusive; however, for every simulation day, the bioenergetics calculations (consumption, respiration, excretion, etc.) are multiplied by the fish population to provide an overall picture of the cohort's bioenergetics. As you might expect, some bioenergetics run results can be drastically different when you include population mortality as part of the simulation. For example, compare the two graphs below – the first represents gross production for a single fish, while the second represents

gross production when the fish population decreases from 10,000 to roughly 500 fish. Note that not only are the magnitudes different, but the shapes of the curves are different as well.





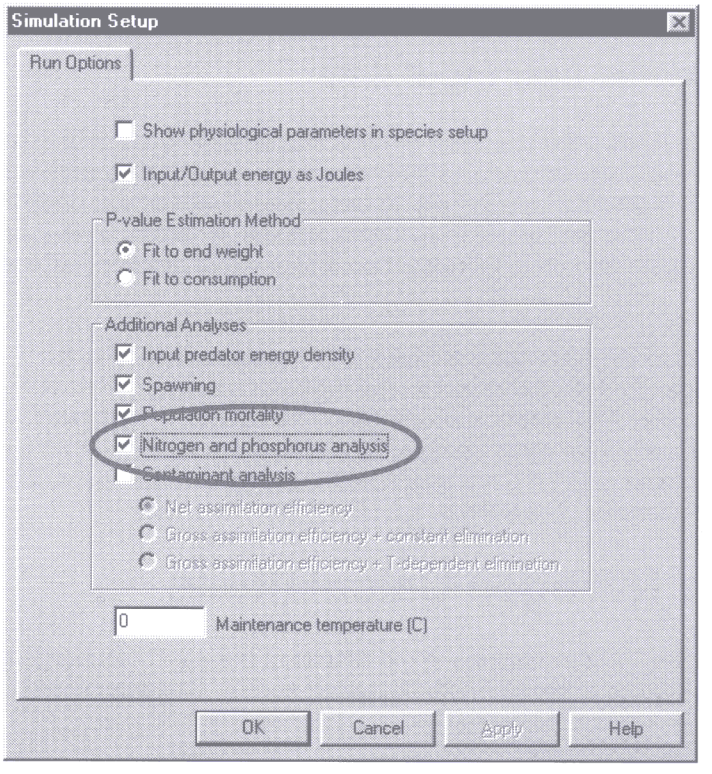
Nitrogen and Phosphorus Analysis

Fish Bioenergetics 3.0 allows you to extend the basic bioenergetics calculations to include nitrogen and phosphorus (N-P) analyses. Section 1, chapter 4, *Extended Topics: Nutrient and Contaminant Analyses* describes in detail the science underlying these analyses. To perform the N-P analysis, you simply need to perform two setup steps: 1) Indicate that you would like to include this calculations in your simulation; and 2) Provide the appropriate user input data.

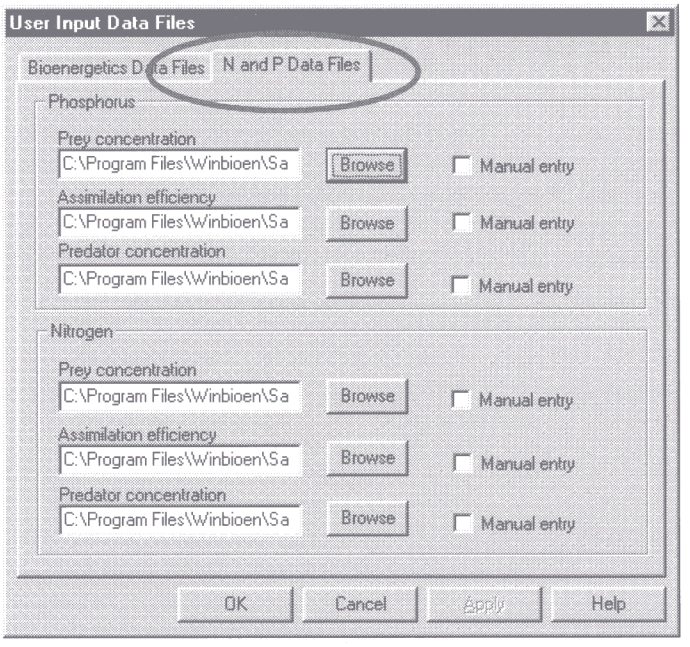
> Note that you must provide both nitrogen and phosphorus data, because Fish Bioenergetics 3.0 will automatically perform calculations on nitrogen, phosphorus, and nitrogen to phosphorus ratios.

7.1 Setup and User Input Data

➡ From the main *Fish Bioenergetics 3.0* window, select **Setup/Simulation** or press the setup icon. The following window will appear.



➡ Check the **Nitrogen and phosphorus analysis** checkbox within **Additional Analyses**. Press the **OK** button, and the **User Input Data Files** window appears.



You'll see that the **N and P Data Files** tab becomes available. Load user input data by either browsing for a tab delimited text file or by entering the data manually.

Nitrogen and Phosphorus user input data

User input data for N-P analysis follows the same set of rules that applies to other user input data as explained in chapter three. You'll also find analogies between the type of data entered for basic bioenergetics and for N-P analysis. For example, in basic bioenergetics you need data for the prey energy concentration and the predator energy concentration; whereas, in N-P analysis you also need data for prey nitrogen and phosphorus concentrations and predator nitrogen and phosphorus concentrations.

The difference between basic bioenergetics calculations and N-P calculations is in the assimilation of consumed nitrogen and phosphorus into the predator's tissue. This assimilation is quantified in the user input data file, **Assimilation efficiency**. The values for assimilation efficiency range from 0 to 1, with a typical value being around 0.7. This means that 30% of consumed nutrients are lost as feces and 70% are available for growth and excretion. For an example of N-P assimilation efficiencies, see section 3.2 *User Input Data Files*.

7.2 Phosphorus and Nitrogen Calculations

Fish Bioenergetics 3.0 applies the N-P calculations to the results of the basic bioenergetics calculations. Recall that bioenergetics is based on the following energy allocation equation:

Consumption = Growth + Respiration +SDA +Egestion + Excretion
or
C = G + R + SDA + F + U (where F = egestion and U = excretion)

Consumed phosphorus and nitrogen follows a similar but slightly simplified path. It has three fates: 1) assimilation into the predator's tissue (G); 2) loss in feces (F); 3) excretion in urine (U) - nutrients are not lost as a result of respiration or specific dynamic action (R and SDA respectively). These fates can be quantified in the equation (we'll use phosphorus as an example):

$$C_p = G_p + F_p + U_p$$

where

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

Because excreted nutrients are available for uptake by aquatic primary producers, we're usually interested in rearranging the equation to solve for U:

$$U_p = C_p - G_p - F_p$$

We can account for fecal losses through assimilation efficiency, and thus simplify the equation as follows:

$$U_p = (AE_p * C_p) - G_p$$

where

AE_p = assimilation efficiency read from the user input data file
C_p = mass consumption of prey from basic bioenergetics calculations multiplied by the user input prey concentrations of P
G_p = predator growth mass from basic bioenergetics calculations multiplied by the user input predator concentration of P

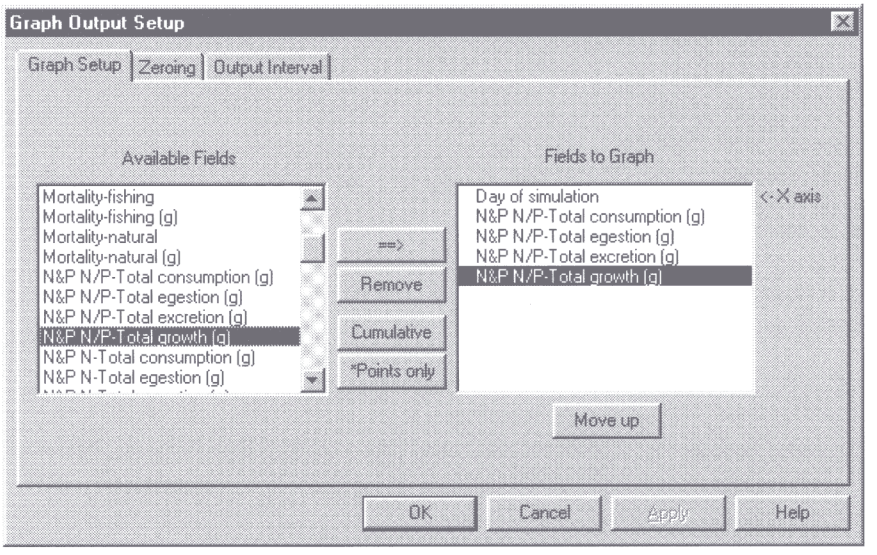
Results

As with basic bioenergetics calculations, *Fish Bioenergetics 3.0* calculates several N-P variables on a daily time step; consequently, your finest resolution in output data is daily values. Calculations begin on day one of your simulation and continue through the final day.

Daily *Fish Bioenergetics 3.0* Run Calculations

- Retrieve user input data for the current day. Interpolate if necessary.
- For an individual fish, calculate consumption, egestion, excretion, respiration, SDA and the resultant growth.
- Apply the calculations for an individual to the entire cohort population.
- **Calculate nitrogen and phosphorus and contaminant analysis parameters.**
- Calculate gross production for the population and gametic production when applicable.
- Determine the number of deaths in the population.
- Calculate net production.

Once you've executed a bioenergetics run, you can view the N-P output variables by selecting either the graph or text output options and highlighting the variables of choice.

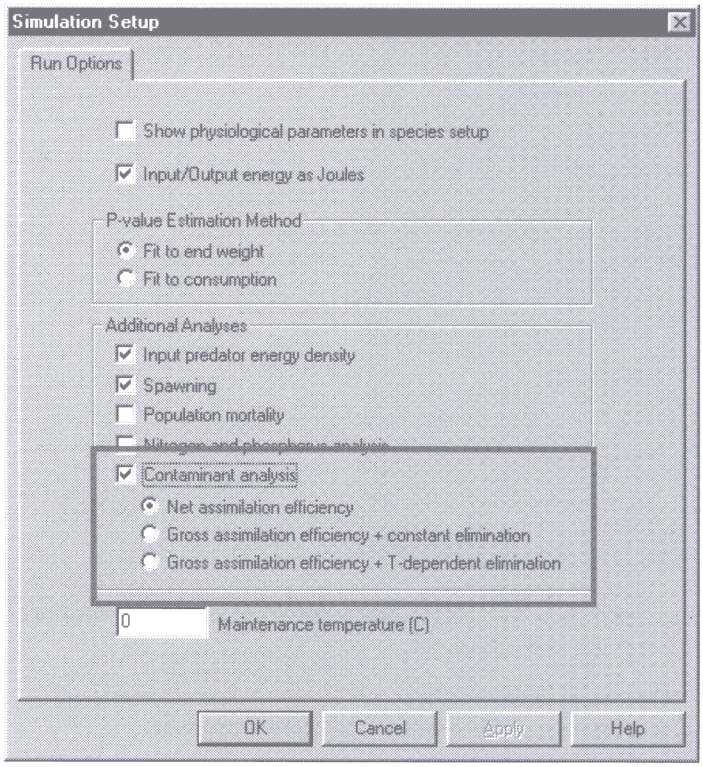


Contaminant Analysis

Fish Bioenergetics 3.0 allows you to extend the basic bioenergetics calculations to include contaminant analysis. Section 1, chapter 4, *Extended Topics: Nutrient and Contaminant Analyses* describes in detail the science underlying this analysis. To perform the contaminant analysis, you simply need to perform three setup steps: 1) Indicate that you would like to include this calculations in your simulation; 2) Provide the appropriate user input data; and 3) Enter user input parameters.

8.1 Setup, User Input Data, and User Input Parameters

➡ From the main *Fish Bioenergetics 3.0* window, select **Setup/Simulation** or press the setup icon. The following window will appear.



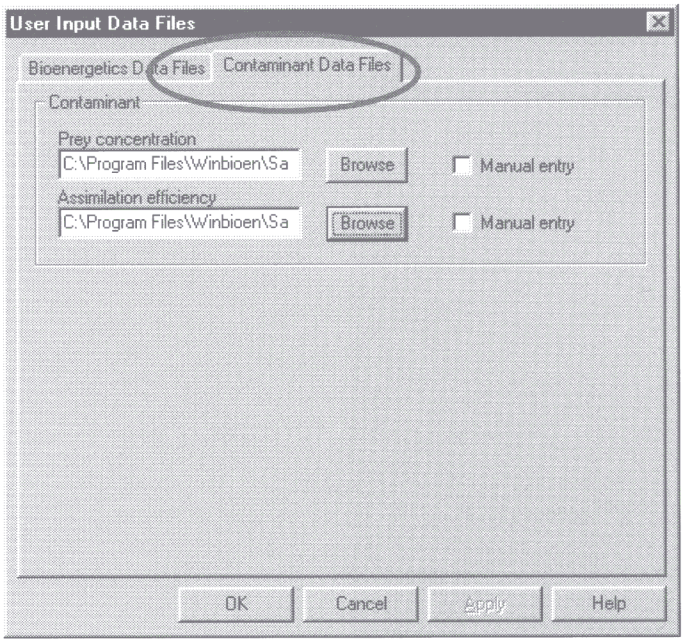
➡ Check the **Contaminant analysis** checkbox within **Additional Analyses**. The radio buttons immediately below the checkbox become available and require that you select one of the following three options.

- **Net assimilation efficiency:** Select this option if your predator will assimilate contaminants based solely upon data provided in the contaminant assimilation input data file. The remaining contaminants are eliminated. You

will need to know the initial predator concentration for the **User Input Parameters** setup.

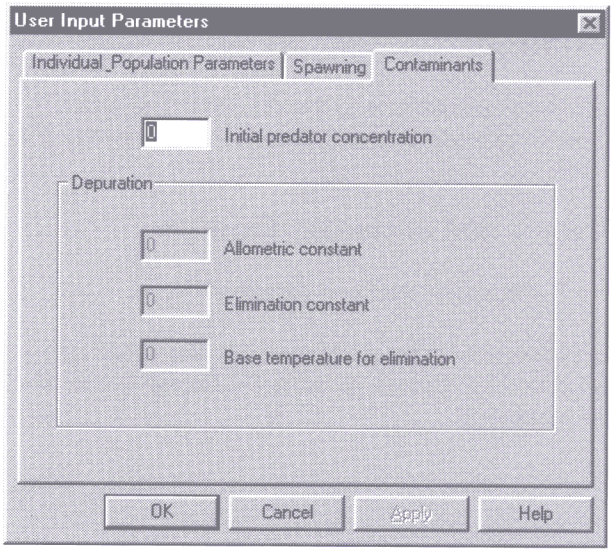
- **Gross assimilation efficiency + constant elimination:** If your predator assimilates at a rate indicated in your contaminant assimilation input data file, and yet loses some of those assimilated contaminants at a constant allometrically scaled rate, select this option. You will need to know the initial predator concentration, and the elimination and allometric constants for the **User Input Parameters** setup.
- **Gross assimilation efficiency + T-dependent elimination:** If your predator assimilates at a rate indicated in your contaminant assimilation input data file, and yet loses some of those assimilated contaminants at a rate that's dependent upon allometry and temperature, select this option. You will need to know the initial predator concentration, the elimination and allometric constants, and the base temperature for elimination for the **User Input Parameters** setup.

➡ Press the **OK** button, and the User Input Data Files window appears.



The **Contaminant Data Files** tab becomes available. Load user input data by either browsing for a tab delimited text file or by entering the data manually.

➡ Press the **OK** button, and the **User Input Parameters** window appears.



➡ Enter an initial predator concentration (or accept the default of 0), and enter the appropriate data in the additional edit boxes that have been activated for input. Note that activation of an edit box is dependent upon the type of elimination selected in your initial setup. Following are descriptions of the possible user input parameters:

- **Initial predator concentration (mg/kg):** The concentration of contaminants in your predator immediately before the simulation begins.
- **Allometric constant :** Mass dependence of contaminant elimination.
- **Elimination constant ($g^{-\zeta}$/d):** Base line elimination rate.
- **Base temperature for elimination (degrees C):** Scales the temperature dependence of elimination.

➡ Once you've entered your parameters, select **OK**.

Contaminant user input data

User input data for contaminant analysis follows the same set of rules that applies to other user input data as explained in chapter three. You'll also find analogies between the type of data entered for basic bioenergetics and for contaminant analysis. For example, in basic bioenergetics you need data for the prey energy concentration and the predator energy concentration; whereas, in contaminant analysis you need data for prey contaminant concentrations.

The differences between basic bioenergetics calculations and contaminant calculations is in the assimilation and bioaccumulation of consumed contaminants. The assimilation is quantified in the user input data file, **Assimilation efficiency**, and the bioaccumulation is quantified by the type of contaminant elimination selected its accompanying user input parameters. The values for assimilation efficiency range from 0 to 1, with a typical value being around 0.7. For an example of contaminant assimilation efficiencies, see section 3.2 *User Input Data Files*.

8.2 Contaminant Calculations

Fish Bioenergetics 3.0 applies the contaminant calculations to the results of the basic bioenergetics calculations. Recall that bioenergetics is based on the following energy allocation equation:

Consumption = Growth + Respiration + SDA + Egestion + Excretion
or
C = G + R + SDA + F + U (where F = egestion and U = excretion)

Consumed contaminants follow a similar but slightly more complex path, with the following three fates: 1) assimilation into the predator's tissue (X_c); 2) loss in feces (F); 3) metabolic elimination (E_c). These fates can be quantified in the equation:

$$C_c = X_c + F_c + E_c$$

where

C_c = mass of contaminants consumed (g)
X_c = mass of contaminants incorporated into predator (as a result of assimilation) (g)
F_c = mass of contaminants lost in feces (g)
E_c = mass of contaminants eliminated through metabolism (g)

Because most researchers are interested in contaminants present in the predator's tissue, we can rearranging the equation to solve for X_c:

$$X_c = C_c - E_c - F_c$$

We can account for fecal losses through assimilation efficiency, and thus simplify the equation as follows:

$$X_c = (AE_c * C_c) - E_c$$

where

AE_c = assimilation efficiency read from the user input data file
C_c = mass consumption of prey from basic bioenergetics calculations multiplied by the user input prey concentrations of contaminants
E_c = contaminant mass eliminated from the predator - dependent upon the elimination model selected in the simulation setup
X_c = predator growth mass from basic bioenergetics calculations multiplied by the user input predator concentration of P

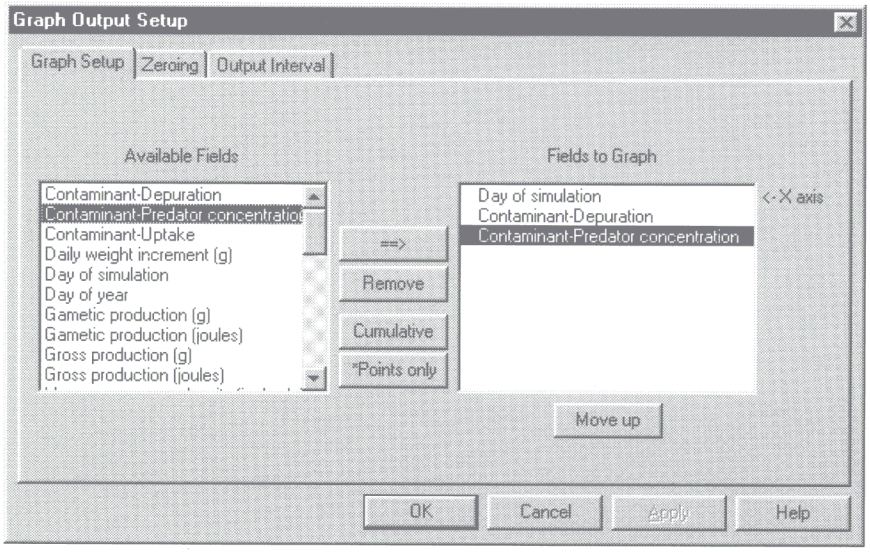
Results

As with basic bioenergetics calculations, *Fish Bioenergetics 3.0* calculates contaminant parameters on a daily time step; consequently, your finest resolution in output data is daily values. Calculations begin on day one of your simulation and continue through the final day.

Daily *Fish Bioenergetics 3.0* Run Calculations

- Retrieve user input data for the current day. Interpolate if necessary.
- For an individual fish, calculate consumption, egestion, excretion, respiration, SDA and the resultant growth.
- Apply the calculations for an individual to the entire cohort population.
- **Calculate nitrogen and phosphorus and contaminant analysis parameters.**
- Calculate gross production for the population and gametic production when applicable.
- Determine the number of deaths in the population.
- Calculate net production.

Once you've executed a bioenergetics run, you can view the contaminant output variables by selecting either the graph or text output options and highlighting the variables of choice.



Appendix A - Fish Physiological Parameters

Species	alewife	bloater chub	bluegill	coho salmon	chinook salmon
Latin name	*Alosa pseudoharengus*	*Coregonus hoyi*	*Lepomis macrochirus*	*Oncorhynchus kisutch*	*Oncorhynchus tshawytscha*
Age	YOY, juvenile, adult	adult	juvenile, adult	adult	adult
Source	Stewart and Binkowski 1986	Rudstam et al. 1994	Kitchell et al. 1974	Stewart and Iberra 1991	Stewart and Iberra 1991
CONSUMPTION					
Equation	3	2	2	3	2
CA	0.8464	1.61	0.182	0.303	0.303
CB	-0.3	-0.538	-0.274	-0.275	-0.275
CQ	5, 4, 3	3.53	2.3	5	5
CTO	24, 20, 16	16.8	31, 27	15	15
CTM	26, 22, 18	26	37, 36	18	18
CTL	29, 27, 25	*	*	24	24
CK1	0.17	*	*	0.36	0.36
CK4	0.01	*	*	0.01	0.01
RESPIRATION					
Equation	1	1	2	1	1
RA	0.00367	0.0018	0.0154	0.00264	0.00264
RB	-0.2152	-0.12	-0.2	-0.217	-0.217
RQ	0.0548	0.047	2.1	0.06818	0.06818
RTO	0.03	0.025	37, 36	0.0234	0.0234
RTM	0	0	41, 40	0	0
RTL	9	0	*	25	25
RK1	22.08	7.23	*	1	1
RK4	-0.045	0.025	*	0.13	0.13
ACT	5.78	0	1	9.7	9.7
BACT	0.149	0	*	0.0405	0.0405
SDA	0.175	0.17	0.172	0.172	0.172
EGESTION/ EXCRETION					
Equation	1	1	1	3	3
FA	0.16	0.25	0.158	0.212	0.212
FB	*	*	-0.222	-0.222	-0.222
FG	*	*	0.631	0.631	0.631
UA	0.1	0.1	0.0253	0.0314	0.0314
UB	*	*	0.58	0.58	0.58
UG	*	*	-0.299	-0.299	-0.299
PREDATOR ENERGY DENSITY					
Equation	1	2	1	2	2
Energy density	5233	*	4186	*	*
Alpha 1	*	3952	*	5764	5764
Beta 1	*	58.7	*	0.9862	0.9862
Cutoff	*	155	*	4000	4000
Alpha 2	*	13050	*	7602	5674
Beta 2	*	0.001	*	0.5266	0.9862

Fish Physiological Parameters

Species	dace	generalized coregonid	herring	lake trout	largemouth bass
Latin name	*Chrosomus spp.*	*Coregonus spp.*	*Clupea harengus*	*Salvelinus namaycush*	*Micropterus salmoides*
Age	adult	YOY, juvenile, adult	juvenile, adult	adult	adult
Source	He 1986	Rudstam et al. 1994	Rudstam 1989	Stewart et al. 1983	Rice et al. 1983
CONSUMPTION					
Equation	2	2	3	1	2
CA	0.36	1.61	0.642	0.0589	0.33
CB	-0.31	-0.32	-0.256	-0.307	-0.325
CQ	2.3	3.53	1	0.1225	2.65
CTO	26	16.8	15, 13	*	27.5
CTM	29	26	17, 15	*	37
CTL	*	*	25, 23	*	*
CK1	*	*	0.1	*	*
CK4	*	*	0.01	*	*
RESPIRATION					
Equation	2	1	1	1	1
RA	0.0148	0.0018	0.0033	0.00463	0.00279
RB	-0.2	-0.12	-0.227	-0.295	-0.355
RQ	2.1	0.047	0.0548	0.059	0.0811
RTO	29	0.025	0.03	0.0232	0.0196
RTM	32	0	0	0	0
RTL	*	0	0	11	0
RK1	*	7.23	15	1	1
RK4	*	0.025	0.13	0.05	0
ACT	1	0	3.9	11.7	1
BACT	*	0	0.149	0.0405	0
SDA	0.15	0.17	0.175	0.172	0.163
EGESTION/ EXCRETION					
Equation	1	1	1	3	1
FA	0.4	0.25	0.16	0.212	0.104
FB	*	*	*	-0.222	*
FG	*	*	*	0.631	*
UA	0.1	0.1	0.1	0.0314	0.068
UB	*	*	*	0.58	*
UG	*	*	*	-0.299	*
PREDATOR ENERGY DENSITY					
Equation	1	2	1	2	1
Energy density	5006	*	5534	*	4186
Alpha 1	*	3952	*	5701	*
Beta 1	*	58.7	*	3.0809	*
Cutoff	*	155	*	1472	*
Alpha 2	*	13050	*	9092	*
Beta 2	*	0.001	*	0.7786	*

Species	larval yellow perch	muskellunge	Mysis	Nile perch	northern pike
Latin name	*Perca flavescens*	*Esox masquinongy*	*Mysis mixta*	*Lates niloticus*	*Esox lucius*
age	larvae	adult			adult
Source	Post 1990	Bevelheimer et al. 1985	Rudstam 1989	Kitchell et al. unpubl.	Bevelheimer et al. 1985
CONSUMPTION					
Equation	2	2	3	2	2
CA	0.51	0.2215	0.036	0.3	0.2045
CB	-0.42	-0.18	-0.372	-0.27	-0.18
CQ	2.3	2.53	0	2.65	0.59
CTO	29	26	9	27.5	24
CTM	32	34	11	38	34
CTL	*	*	16	*	*
CK1	*	*	0.5	*	*
CK4	*	*	0.01	*	*
RESPIRATION					
Equation	2	1	1	2	1
RA	0.0065	0.00246	0.00182	0.011	0.00246
RB	-0.2	-0.18	-0.161	-0.2	-0.18
RQ	2.1	0.055	0.0752	2.5	0.055
RTO	32	0.1222	0	38	0.1222
RTM	35	0	0	43	0
RTL	*	0	0	*	0
RK1	*	1	0	*	1
RK4	*	0	0	*	0
ACT	4.4	1	0	2	1
BACT	*	0	0	*	0
SDA	0.15	0.14	0.18	0.163	0.14
EGESTION / EXCRETION					
Equation	1	1	1	1	1
FA	0.15	0.2	0.15	0.104	0.2
FB	*	*	*	*	*
FG	*	*	*	*	*
UA	0.15	0.07	0.18	0.068	0.07
UB	*	*	*	*	*
UG	*	*	*	*	*
PREDATOR ENERGY DENSITY					
Equation	1	1	1	1	1
Energy density	2512	3600	3474	5860	3600
Alpha 1	*	*	*	*	*
Beta 1	*	*	*	*	*
Cutoff	*	*	*	*	*
Alpha 2	*	*	*	*	*
Beta 2	*	*	*	*	*

Fish Physiological Parameters

Species	pink	sea lamprey	smallmouth bass	smelt	sockeye
Latin name	*Oncorhynchus gorbuscha*	*Petromyzon marinus*	*Micropterus dolomieui*	*Osmerus mordax*	*Oncorhynchus nerka*
age	adult		adult	YOY, juvenile, adult	adult
Source	Beauchamp et al. 1989	Kitchell and Breck 1980	Shuter and Post 1990	Lantry and Stewart 1993	Beauchamp et al. 1989
CONSUMPTION					
Equation	3	2	2	3	3
CA	0.303	0.3	0.25	0.18	0.303
CB	-0.275	-0.35	-0.31	-0.275	-0.275
CQ	3	2.3	3.8	3	3
CTO	20	18	29	16, 14, 10	20
CTM	20	25	36	21, 16, 12	20
CTL	24	*	*	26, 18, 18	24
CK1	0.58	*	*	0.4	0.58
CK4	0.5	*	*	0.01	0.5
RESPIRATION					
Equation	1	2	2	1	1
RA	0.00143	0.00397	0.009	0.0027	0.00143
RB	-0.209	-0.05	-0.21	-0.216	-0.209
RQ	0.086	2.1	3.3	0.036	0.086
RTO	0.0234	25	30	0	0.0234, 0.033
RTM	0	30	37	0	0
RTL	25	*	*	0	25
RK1	1	*	*	0	1
RK4	0.13	*	*	0	0.13
ACT	9.9	1.5	2	0	9.9
BACT	0.0405	*	*	0	0.0405
SDA	0.172	0.172	0.16	0.175	0.172
EGESTION / EXCRETION					
Equation	3	1	1	1	3
FA	0.212	0.03	0.104	0.16	0.212
FB	-0.222	*	*	*	-0.222
FG	0.631	*	*	*	0.631
UA	0.0314	0.15	1.068	0.1	0.0314
UB	0.58	*	*	*	0.58
UG	-0.299	*	*	*	-0.299
PREDATOR ENERGY DENSITY					
Equation	2	1	1	1	2
Energy density	*	5124	4186	4814	*
Alpha 1	5233	*	*	*	5233
Beta 1	7.7483	*	*	*	7.7483
Cutoff	196	*	*	*	196
Alpha 2	6647	*	*	*	6647
Beta 2	0.5249	*	*	*	0.5249

Species	steelhead	striped bass	striped bass	striped bass	tilapia
Latin name	*Oncorhynchus mykiss*	*Morone saxatilis*	*Morone saxatilis*	*Morone spp.*	*Sarotheradon spp.*
age	adult	age-1, age-2, adult	age-0	larvae	adult
Source	Rand et al 1993	Hartman and Brandt 1995	Hartman and Brandt 1995	Johnson 1995	Nitithamyong 1988
CONSUMPTION					
Equation	3	3	3	2	2
CA	0.628	0.3021	0.3021	0.48	0.15
CB	-0.3	-0.2523	-0.2523	-0.252	-0.36
CQ	5	6.6, 6.6, 7.4	2.6	2.8615	2.5
CTO	20	19, 18, 15	21.6	28.3	30
CTM	20	28, 29, 28	22.7	31.3	37
CTL	24	30, 32, 30	28.3	*	*
CK1	0.33	0.262, 0.255, 0.323	0.047	*	*
CK4	0.2	0.85, 0.9, 0.85	0.713	*	*
RESPIRATION					
Equation	1	1	1	2	2
RA	0.00264	0.00280	0.001456	0.0132	0.0274
RB	-0.217	-0.218	-0.2702	-0.265	-0.348
RQ	0.06818	0.0760	0.08339	2.1059	2.3
RTO	0.0234	0.5002	0.9014	31.3	37
RTM	0	0	0	34.3	41
RTL	25	0	0	*	*
RK1	1	1	1	*	*
RK4	0.13	0	0	*	*
ACT	9.7	1	1	1.5	1
BACT	0.0405	0	0	*	*
SDA	0.172	0.172	0.172	0.172	0.1
EGESTION / EXCRETION					
Equation	3	1	1	1	1
FA	0.212	0.104	0.104	0.15	0.194
FB	-0.222	*	*	*	*
FG	0.631	*	*	*	*
UA	0.0314	0.068	0.068	0.1	0.028
UB	0.58	*	*	*	*
UG	-0.299	*	*	*	*
PREDATOR ENERGY DENSITY					
Equation	2	1	1	1	1
Energy density	*	6488	5023	3349	5442
Alpha 1	5764	*	*		*
Beta 1	0.9862	*	*		*
Cutoff	4000	*	*		*
Alpha 2	7602	*	*		*
Beta 2	0.5266	*	*		*

Fish Physiological Parameters

Species	walleye	walleye	walleye pollock	walleye pollock	yellow perch
Latin name	*Stizostedion vitreum*	*Stizostedion vitreum*	*Theragra chalcogramma*	*Theragra chalcogramma*	*Perca flavescens*
age	adult	juvenile	juvenile	adult	juvenile, adult
Source	Kitchell et al. 1977	Madon and Culver 1993	Mason et al., unpubl.	Mason et al., unpubl.	Kitchell et al. 1977
CONSUMPTION					
Equation	2	2	2	2	2
CA	0.25	0.45	0.34	0.3	0.25
CB	-0.27	-0.27	-0.5875	-0.5875	-0.27
CQ	2.3	2.3	6	3.5	2.3
CTO	22	25	8	8	29, 23
CTM	28	28	15	15	32, 28
CTL	*	*	*	*	*
CK1	*	*	*	*	*
CK4	*	*	*	*	*
RESPIRATION					
Equation	2	2	2	2	2
RA	0.0108	0.0138	0.0195	0.0137	0.0108
RB	-0.2	-0.22	-0.26	-0.26	-0.2
RQ	2.1	2.1	4.6	3.3	2.1
RTO	27	27	15	15	32, 28
RTM	32	32	18	18	35, 33
RTL	*	*	*	*	*
RK1	*	*	*	*	*
RK4	*	*	*	*	*
ACT	1	3	1.4	1.4	1
BACT	*	*	*	*	*
SDA	0.172	0.1	0.125	0.125	0.172
EGESTION / EXCRETION					
Equation	2	1	1	1	2
FA	0.158	0.25	0.2	0.2	0.158
FB	-0.222	*	*	*	-0.222
FG	0.631	*	*	*	0.631
UA	0.0253	0.05	0.11	0.11	0.0253
UB	0.58	*	*	*	0.58
UG	-0.299	*	*	*	-0.299
PREDATOR ENERGY DENSITY					
Equation	1	1	1	1	1
Energy density	4186	3349	6070	6070	4186
Alpha 1	*	*	*	*	*
Beta 1	*	*	*	*	*
Cutoff	*	*	*	*	*
Alpha 2	*	*	*	*	*
Beta 2	*	*	*	*	*

Species	bluefish	weakfish	weakfish
Latin name	*Pomatomus saltatrix*	*Cynoscion regalis*	*Cynoscion regalis*
age	YOY, juvenile, adult	age-0	age-1 and older
Source	Hartman and Brandt 1995	Hartman and Brandt 1995	Hartman and Brandt 1995.
CONSUMPTION			
Equation	3	3	3
CA	0.5197	0.492	0.492
CB	-0.288	-0.2680	-0.2680
CQ	10.2	14.87	14.8
CTO	23	24.3	25
CTM	28	24.3	25
CTL	32	27.7	29
CK1	0.156	0.0334	0.195
CK4	0.85	0.561	0.970
RESPIRATION			
Equation	1	1	1
RA	0.00558	0.0009	0.003
RB	-0.264	-0.1254	-0.155
RQ	0.06925	0.0912	0.0508
RTO	0.6315	1.2326	0.9022
RTM	0	0	0
RTL	0	0	0
RK1	1	1	1
RK4	0	0	0
ACT	1	1	1
BACT	0	0	0
SDA	0.172	0.172	0.172
EGESTION / EXCRETION			
Equation	1	1	1
FA	0.104	0.104	0.104
FB	*	*	*
FG	*	*	*
UA	0.068	0.068	0.068
UB	*	*	*
UG	*	*	*
PREDATOR ENERGY DENSITY			
Equation	1	1	1
Energy density	6279	3558	5860
Alpha 1	*	*	*
Beta 1	*	*	*
Cutoff	*	*	*
Alpha 2	*	*	*
Beta 2	*	*	*

Appendix B - Prey Energy Densities

Organism	dry:wet mass (%)	joules/g dry mass	joules/g wet mass	seasonal / ontogenetic effects
rotifer	10[a]			
copepoda	11 to 14[a, b, c]	17251 to 26280[c, d]	1900 to 3684	yes[c]
cladocera	10 to 12[b, e]	22818 to 22868[d,f,g]	2281 to 2746	yes[h]
Leptodora	4[g]	21692 to 25744[g]	867 to 1030	yes[g]
Mysids	16[a]		2972 to 4312[g, i]	
amphipoda	24 to 28[g]	17045[g]	4429[g]	yes[j, k]
diptera larvae	5 to 12[e, g]	20662[g]	1047 to 2478	yes[e]
ephemeroptera	22 to 24[g, l]	22165 to 25493[g, l]	3675 to 5735[g]	
hirudinea	12 to 28[l]	22370 to 25083[l]		
gastropoda	29[l]	15944 to 20423[l]		
larval fish	10 to 25[m]	20930 to 27628[m]	2800 to 4596	yes[m]
alewife	20 to 35[n]		5023 to 9502[n]	yes[n, o]
yellow perch	24 to 28[p]	18259 to 21759[p]	4500 to 5902[p]	yes[p]
juvenile (perch)	12[e]	20704[q]	2512[r]	yes[q]
lake trout	28 to 41[s]	22692 to 29888[s]	5220 to 11465[s]	yes[s]

[a] Downing and Rigler (1984)
[b] Dumont et al. (1975)
[c] Schindler et al. (1971)
[d] Vijerberg and Frank (1976)
[e] Hewett and Johnson (1992)
[f] Lei and Armitage (1980)
[g] Cummins and Wuychuck (1971)
[h] Snow (1972)
[i] Rudstam (1989)
[j] Wissing and Hasler (1968)
[k] Wissing and Hasler (1971)
[l] Driver et al. (1974)
[m] Henderson and Ward (1978)
[n] Stewart and Binkowski (1986)
[o] Flath and Diana (1985)
[p] Craig (1977)
[q] Mills and Forney (1981)
[r] Post (1990)
[s] Rottiers and Tucker (1982)

Appendix C - Nitrogen and Phosphorus Concentrations for Selected Prey Species

Prey	P concentration (% of wet mass)	N concentration (% of wet mass)	Source
copepods	0.072	1.38	Andersen and Hessen (1991)
Bosmina	0.096	1.14	Andersen and Hessen (1991)
periphyton	0.05-0.1	0.7	Penczak (1985)
dipterans	0.11	1.22	Nakashima and Leggett (1980), Penczak (1985)
crayfish	0.16	1.6	Nakashima and Leggett (1980), Penczak (1985)
Daphnia	0.17	1.14	Andersen and Hessen (1991)
Mysis	0.18	1.72	Nakashima and Leggett (1980), Penczak (1985)
amphipods	0.18	1.72	Nakashima and Leggett (1980), Penczak (1985)
odonate larvae	0.18	3.03	Penczak (1985)
YOY fish	0.3-0.5	1.5-2.5	Kraft (1992)
fish	0.5	2.54	Penczak (1985), Davis and Boyd (1975)

Appendix D - Nitrogen and Phosphorus Concentrations In Selected Fish Species

Fish species	N concentration	P concentration	Units	Source
Gizzard shad	8.68	2.89	% dry mass	Davis and Boyd (1978)
Channel catfish	9.52	2.71	% dry mass	Davis and Boyd (1978)
Bluegill	10.51	4.02	% dry mass	Davis and Boyd (1978)
Largemouth bass	9.77	3.2	% dry mass	Davis and Boyd (1978)
Golden shiner	8.26	2.39	% dry mass	Davis and Boyd (1978)
Yellow perch	11.35	4.1	% dry mass	Davis and Boyd (1978)
Fathead minnow	10.4	2.64	% dry mass	Davis and Boyd (1978)
Rainbow trout	2.56	0.5	% wet mass	Penczak et al. (1985)
Whitefish (*Coregonus albula*)	2.62	0.53	% wet mass	Penczak et al. (1985)
Pike (*Esox lucius*)	2.56	0.6	% wet mass	Penczak et al. (1985)
Pike perch (*Stizostedion lucioperca*)	2.63	0.61	% wet mass	Penczak et al. (1985)
Roach (*Rutilis rutilis*)	2.67	0.59	% wet mass	Penczak et al. (1985)

References:

Davis, J.A., and C.E. Boyd. 1978. Concentrations of selected elements and ash in Bluegill (*Lepomis macrochirus*) and certain other freshwater fish. Trans. Am. Fish. Soc. 107:862-867.

Penczak, T., M. Molinski, W. Galicka and A. Prejs. 1985. Factors affecting nutrient budget in lakes of the R. Jorka watershed (Masurian Lakeland, Poland) VII. Input and removal of nutrients with fish. Ekologia Polska 33:301-309.

Appendix E - Publications That Reference Bioenergetics

Arnason, A.N., M.H. Papst, and G.E. Hopky. 1992. Modeling the Increase in Variance of Fish Weight. Can. J. Fish. Aquat. Sci. 49:2-16.

Arrhenius, F., and S. Hansson. 1993. Food-Consumption of Larval, Young and Adult Herring and Sprat in the Baltic Sea. Mar. Ecol. Prog. Ser. 96:125-137.

Arrhenius, F., and S. Hansson. 1994. *In-Situ* Food-Consumption by Young-of-the-Year Baltic Sea Herring *Clupea-Harengus* - A Test of Predictions from a Bioenergetics Model. Mar. Ecol. Prog. Ser. 110:2-3.

Beauchamp, D.A., D.J. Stewart, and G.L. Thomas. 1989. Corroboration of a Bioenergetics Model for Sockeye-Salmon. Trans. Am. Fish. Soc. 118:597-607.

Bevelhimer, M.S., and S.M. Adams. 1993. A Bioenergetics Analysis of Diel Vertical Migration by Kokanee Salmon, *Oncorhynchus-Nerka*. Can. J. Fish. Aquat. Sci. 50:2236-2349.

Binkowski, F.P., and L.G. Rudstam. 1994. Maximum Daily Ration of Great-Lakes Bloater. Trans. Am. Fish. Soc. 123:335-343.

Boisclair, D. 1992. Relationship Between Feeding and Activity Rates for Actively Foraging Juvenile Brook Trout (*Salvelinus- Fontinalis*). Can. J. Fish. Aquat. Sci. 49:2566-2573.

Boisclair, D., and W.C. Leggett. 1991. If Computers Could Swim or Fish Could Be Programmed - Reply. Can. J. Fish. Aquat. Sci. 48:1337-1344.

Boisclair, D., and W.C. Leggett. 1989. The Importance of Activity in Bioenergetics Models Applied to Actively Foraging Fishes. Can. J. Fish. Aquat. Sci. 46:1859-1867.

Boisclair, D., and P. Sirois. 1993. Testing Assumptions of Fish Bioenergetics Models by Direct Estimation of Growth, Consumption, and Activity Rates. Trans. Am. Fish. Soc. 122:784-796.

Boisclair, D., and M. Tang. 1993. Empirical-Analysis of the Influence of Swimming Pattern on the Net Energetic Cost of Swimming in Fishes. Journal Of Fish Biology 42:169-183.

Brandt, S.B. 1993. The Effect of Thermal Fronts on Fish Growth - A Bioenergetics Evaluation of Food and Temperature. Estuaries 16:142-159.

Brandt, S.B., and K.J. Hartman. 1993. Innovative Approaches with Bioenergetics Models - Future Applications to Fish Ecology and Management. Trans. Am. Fish. Soc. 122:731-735.

Brandt, S.B., and J. Kirsch. 1993. Spatially Explicit Models of Striped Bass Growth- Potential in Chesapeake Bay. Trans. Am. Fish. Soc. 122:845-869.

Brandt, S.B., D.M. Mason, E.V. Patrick, R.L. Argyle, and L. Wells. 1991. Acoustic Measures of the Abundance and Size of Pelagic Planktivores in Lake-Michigan. Can. J. Fish. Aquat. Sci. 48:894-908.

Breck, J.E. 1993. Hurry Up and Wait - Growth of Young Bluegills in Ponds and in Simulations with an Individual-Based Model. Trans. Am. Fish. Soc. 122:467-480.

Brodeur, R.D., R.C. Francis, and W.G. Pearcy. 1992. Food-Consumption of Juvenile Coho (*Oncorhynchus-Kisutch*) and Chinook Salmon (*O-Tshawytscha*) on the Continental- Shelf Off Washington and Oregon. Can. J. Fish. Aquat. Sci. 49:1670-1685.

Bryan, S.D., C.A. Soupir, W.G. Duffy, and C.E. Freiburger. 1996. Caloric Densities of 3 Predatory Fishes and Their Prey in Lake Oahe, South-Dakota. Journal Of Freshwater Ecology 11:153-161.

Buckel, J.A., N.D. Steinberg, and D.O. Conover. 1995. Effects of Temperature, Salinity, and Fish Size on Growth and Consumption of Juvenile Bluefish. Journal Of Fish Biology 47:696-706.

Cech, J.J., D.T. Castleberry, T.E. Hopkins, and J.H. Petersen. 1994. Northern Squawfish, *Ptychocheilus-Oregonensis,* O-2 Consumption Rate and Respiration Model - Effects of Temperature and Body-Size. Can. J. Fish. Aquat. Sci. 51:8-12.

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.

Cochran, P.A., and J.E. Marks. 1995. Biology of the Silver Lamprey, *Ichthyomyzon-Unicuspis*, in Green Bay and the Lower Fox River, with a Comparison to the Sea Lamprey, *Petromyzon-Marinus*. Copeia :409-421.

Coutant, C.C., and D.L. Benson. 1990. Summer Habitat Suitability for Striped Bass in Chesapeake Bay - Reflections on a Population Decline. Trans. Am. Fish. Soc. 119:757-778.

Craig, J.F., and J.A. Babaluk. 1989. Relationship of Condition of Walleye (*Stizostedion- Vitreum*) and Northern Pike (*Esox-Lucius*) to Water Clarity, with Special Reference to Dauphin Lake, Manitoba. Can. J. Fish. Aquat. Sci. 46:1581-1586.

Deangelis, D.L., L. Godbout, and B.J. Shuter. 1991. An Individual-Based Approach to Predicting Density-Dependent Dynamics in Smallmouth Bass Populations. Ecol. Modell. 57:1-2.

Eby, L.A., L.G. Rudstam, and J.F. Kitchell. 1995. Predator Responses to Prey Population-Dynamics - An Empirical-Analysis Based on Lake Trout Growth-Rates. Can. J. Fish. Aquat. Sci. 52:1564-1571.

Elser, J.J., C. Luecke, M.T. Brett, and C.R. Goldman. 1995. Effects of Food-Web Compensation After Manipulation of Rainbow-Trout in an Oligotrophic Lake. Ecology 76:52-69.

Filbert, R.B., and C.P. Hawkins. 1995. Variation in Condition of Rainbow-Trout in Relation to Food, Temperature, and Individual Length in the Green- River, Utah. Trans. Am. Fish. Soc. 124:824-835.

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. Aquat. Sci. 48:434-441.

Goyke, A.P., and S.B. Brandt. 1993. Spatial Models of Salmonine Growth-Rates in Lake-Ontario. Trans. Am. Fish. Soc. 122:870-883.

Halfon, E., N. Schito, and R.E. Ulanowicz. 1996. Energy-Flow Through the Lake-Ontario Food-Web - Conceptual-Model and an Attempt at Mass-Balance. Ecol. Modell. 86:1-36.

Hanratty, M.P., and F.S. Stay. 1994. Field-Evaluation of the Littoral Ecosystem Risk Assessment Models Predictions of the Effects of Chlorpyrifos. Journal Of Applied Ecology 31:439-453.

Hansen, M.J., D. Boisclair, S.B. Brandt, and S.W. Hewett. 1993. Applications of Bioenergetics Models to Fish Ecology and Management - Where Do We Go from Here. Trans. Am. Fish. Soc. 122:1019-1030.

Hansson, S., L.G. Rudstam, J.F. Kitchell, and M. Hilden. 1996. Predation Rates by North-Sea Cod (*Gadus-Morhua*) - Predictions from Models on Gastric Evacuation and Bioenergetics. Ices Journal Of Marine Science 53:107-114.

Hartman, K.J., and S.B. Brandt. 1995. Comparative Energetics and the Development of Bioenergetics Models for Sympatric Estuarine Piscivores. Can. J. Fish. Aquat. Sci. 52:1647-1666.

Hartman, K.J., and S.B. Brandt. 1995. Estimating Energy Density of Fish. Trans. Am. Fish. Soc. 124:347-355.

Hartman, K.J., and S.B. Brandt. 1995. Predatory Demand and Impact of Striped Bass, Bluefish, and Weakfish in the Chesapeake-Bay - Applications of Bioenergetics Models. Can. J. Fish. Aquat. Sci. 52:1667-1687.

Hartman, K.J., and S.B. Brandt. 1993. Systematic Sources of Bias in a Bioenergetics Model - Examples for Age-0 Striped Bass. Trans. Am. Fish. Soc. 122:912-926.

Hartman, K.J., and F.J. Margraf. 1993. Evidence of Predatory Control of Yellow Perch (*Perca-Flavescens*) Recruitment in Lake Erie, USA. Journal Of Fish Biology 43:109-119.

Hayward, R.S. 1991. Bias Associated with Using the Eggers Model for Estimating Fish Daily Ration. Can. J. Fish. Aquat. Sci. 48:1100-1103.

Hayward, R.S., and E. Arnold. 1996. Temperature-Dependence of Maximum Daily Consumption in White Crappie - Implications for Fisheries Management. Trans. Am. Fish. Soc. 125:132-138.

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 200:511-522.

Henry, E.A., L.J. Dodgemurphy, G.N. Bigham, and S.M. Klein. 1995. Modeling the Transport and Fate of Mercury in an Urban Lake (Onondaga Lake, NY). Water Air And Soil Pollution 80:1-4.

Hewett, S.W., and C.E. Kraft. 1993. The Relationship Between Growth and Consumption - Comparisons Across Fish Populations. Trans. Am. Fish. Soc. 122:814-821.

Hewett, S.W., C.E. Kraft, and B.L. Johnson. 1991. Consumption, Growth, and Allometry - A Comment. Can. J. Fish. Aquat. Sci. 48:1334-1337.

Hewett, S.W., and D.J. Stewart. 1989. Zooplanktivory by Alewives in Lake-Michigan - Ontogenic, Seasonal, and Historical Patterns. Trans. Am. 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 Fish. Trans. Am. Fish. Soc. 119:265-275.

Hodgson, J.R., S.R. Carpenter, and A.P. Gripentrog. 1989. Effect of Sampling Frequency on Intersample Variance and Food-Consumption Estimates of Nonpiscivorous Largemouth Bass. Trans. Am. Fish. Soc. 118:11-19.

Jackson, L.J. 1996. How Will Decreased Alewife Growth-Rates and Salmonid Stocking Affect Sport Fish PCB Concentrations in Lake- Ontario. Environ. Sci. & Technol. 30:701-705.

Johannsson, O.E., L.G. Rudstam, and D.C. Lasenby. 1994. Mysis-Relicta - Assessment of Metalimnetic Feeding and Implications for Competition with Fish in Lakes Ontario and Michigan. Can. J. Fish. Aquat. Sci. 51:2591-2602.

Karas, P., and G. Thoresson. 1992. An Application of a Bioenergetics Model to Eurasian Perch (*Perca-Fluviatilis L*). Journal Of Fish Biology 41:217-230.

Korhonen, P., M. Virtanen, and T. Schultz. 1995. Bioenergetic Calculation of Mercury Accumulation in Fish. Water Air And Soil Pollution 80:1-4.

Kraft, C.E. 1992. Estimates of Phosphorus and Nitrogen Cycling by Fish Using a Bioenergetics Approach. Can. J. Fish. Aquat. Sci. 49:2596-2604.

Labar, G.W. 1993. Use of Bioenergetics Models to Predict the Effect of Increased Lake Trout Predation on Rainbow Smelt Following Sea Lamprey Control. Trans. Am. Fish. Soc. 122:942-950.

Lantry, B.F., and D.J. Stewart. 1993. Ecological Energetics of Rainbow Smelt in the Laurentian Great-Lakes - An Interlake Comparison. Trans. Am. Fish. Soc. 122:951-976.

Leavitt, P.R., D.E. Schindler, A.J. Paul, and A.K. Hardie. 1994. Fossil Pigment Records of Phytoplankton in Trout-Stocked Alpine Lakes. Can. J. Fish. Aquat. Sci. 51:2411-2423.

Luecke, C., and D. Brandt. 1993. Estimating the Energy Density of Daphnid Prey for Use with Rainbow-Trout Bioenergetics Models. Trans. Am. Fish. Soc. 122:386-389.

Luecke, C., M.J. Vanni, J.J. Magnuson, and J.F. Kitchell. 1990. Seasonal Regulation of *Daphnia* Populations by Planktivorous Fish - Implications for the Spring Clear- Water Phase. Limnol. Oceanogr. 35:1718-1733.

Lunte, C.C., and C. Luecke. 1990. Trophic Interactions of *Leptodora* in Lake Mendota. Limnol. Oceanogr. 35:1091-1100.

Luo, J.G., and S.B. Brandt. 1993. Bay Anchovy *Anchoa-Mitchilli* Production and Consumption in Mid-Chesapeake Bay Based on a Bioenergetics Model and Acoustic Measures of Fish Abundance. Mar. Ecol. Prog. Ser. 98:223-236.

Madenjian, C.P. 1995. Removal of Algae by the Zebra Mussel (*Dreissena- Polymorpha*) Population in Western Lake Erie - A Bioenergetics Approach. Can. J. Fish. Aquat. Sci. 52:381-390.

Madenjian, C.P., and S.W. Gabrey. 1995. Waterbird Predation on Fish in Western Lake Erie - A Bioenergetics Model Application. Condor 97:141-153.

Madon, S.P., and D.A. Culver. 1993. Bioenergetics Model for Larval and Juvenile Walleyes - An *in-Situ* Approach with Experimental Ponds. Trans. Am. Fish. Soc. 122:797-813.

Magnuson, J.J. 1991. Fish and Fisheries Ecology. Ecol. Appl. 1:13-26.

Magnuson, J.J., J.D. Meisner, and D.K. Hill. 1990. Potential Changes in the Thermal Habitat of Great-Lakes Fish After Global Climate Warming. Trans. Am. Fish. Soc. 119:254-264.

Mason, D.M., A. Goyke, and S.B. Brandt. 1995. A Spatially Explicit Bioenergetics Measure of Habitat Quality for Adult Salmonines - Comparison Between Lakes Michigan and Ontario. Can. J. Fish. Aquat. Sci. 52:1572-1583.

Mason, D.M., and E.V. Patrick. 1993. A Model for the Space-Time Dependence of Feeding for Pelagic Fish Populations. Trans. Am. Fish. Soc. 122:884-901.

McDonald, M.E., C.A. Tikkanen, R.P. Axler, C.P. Larsen, and G. Host. 1996. Fish Simulation Culture Model (Fis-C) - A Bioenergetics Based Model for Aquacultural Wasteload Application. Aquacultural Engineering 15:243-259.

Ney, J.J. 1993. Bioenergetics Modeling Today - Growing Pains on the Cutting Edge. Trans. Am. Fish. Soc. 122:736-748.

Penczak, T. 1995. Food-Consumption by Fish Populations in the Warta River, Poland, Before and After Impoundment. Hydrobiologia 302:47-61.

Perezfuentetaja, A., D.J. McQueen, and C.W. Ramcharan. 1996. Predator-Induced Bottom-Up Effects in Oligotrophic Systems. Hydrobiologia 317:163-176.

Post, J.R. 1990. Metabolic Allometry of Larval and Juvenile Yellow Perch (*Perca-Flavescens*) - *Insitu* Estimates and Bioenergetic Models. Can. J. Fish. Aquat. Sci. 47:554-560.

Post, J.R., R. Vandenbos, and D.J. McQueen. 1996. Uptake Rates of Food-Chain and Waterborne Mercury by Fish - Field-Measurements, a Mechanistic Model, and an Assessment of Uncertainties. Can. J. Fish. Aquat. Sci. 53:395-407.

Rand, P.S., B.F. Lantry, R. Ogorman, R.W. Owens, and D.J. Stewart. 1994. Energy Density and Size of Pelagic Prey Fishes in Lake- Ontario, 1978-1990 - Implications for Salmonine Energetics. Trans. Am. Fish. Soc. 123:519-534.

Rand, P.S., D.J. Stewart, B.F. Lantry, and L.G. Rudstam. 1995. Effect of Lake-Wide Planktivory by the Pelagic Prey Fish Community in Lakes Michigan and Ontario. Can. J. Fish. Aquat. Sci. 52:1546-1563.

Rand, P.S., D.J. Stewart, P.W. Seelbach, M.L. Jones, and L.R. Wedge. 1993. Modeling Steelhead Population Energetics in Lakes Michigan and Ontario. Trans. Am. Fish. Soc. 122:977-1001.

Rice, J.A., L.B. Crowder, and K.A. Rose. 1993. Interactions Between Size-Structured Predator and Prey Populations - Experimental Test and Model Comparison. Trans. Am. Fish. Soc. 122:481-491.

Roell, M.J., and D.J. Orth. 1993. Trophic Basis of Production of Stream-Dwelling Smallmouth Bass, Rock Bass, and Flathead Catfish in Relation to Invertebrate Bait Harvest. Trans. Am. Fish. Soc. 122:46-62.

Rose, K.A., and J.H. Cowan. 1993. Individual-Based Model of Young-of-the-Year Striped Bass Population-Dynamics .1. Model Description and Base-Line Simulations. Trans. Am. Fish. Soc. 122:415-438.

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.

Rudstam, L.G., F.P. Binkowski, and M.A. Miller. 1994. A Bioenergetics Model for Analysis of Food-Consumption Patterns of Bloater in Lake-Michigan. Trans. Am. Fish. Soc. 123:344-357.

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. 80:2-3.

Rudstam, L.G., R.C. Lathrop, and S.R. Carpenter. 1993. The Rise and Fall of a Dominant Planktivore - Direct and Indirect Effects on Zooplankton. Ecology 74:303-319.

Rudstam, L.G., P.E. Peppard, T.W. Fratt, and R.E. Bruesewitz. 1995. Prey Consumption by the Burbot (*Lota-Lota*) Population in Green Bay, Lake-Michigan, Based on a Bioenergetics Model. Can. J. Fish. Aquat. Sci. 52:1074-1082.

Schindler, D.E. 1992. Nutrient Regeneration by Sockeye-Salmon (*Oncorhynchus- Nerka*) Fry and Subsequent Effects on Zooplankton and Phytoplankton. Can. J. Fish. Aquat. Sci. 49:2498-2506.

Schindler, D.E., J.F. Kitchell, X. He, and S.R. Carpenter. 1993. Food-Web Structure and Phosphorus Cycling in Lakes. Trans. Am. Fish. Soc. 122:756-772.

Schneider, D.W. 1992. A Bioenergetics Model of Zebra Mussel, *Dreissena- Polymorpha,* Growth in the Great-Lakes. Can. J. Fish. Aquat. Sci. 49:1406-1416.

Schultz, T., P. Korhonen, and M. Virtanen. 1995. Mercury Model Used for Assessment of Dredging Impacts. Water Air And Soil Pollution 80:1-4.

Shuter, B.J., and J.R. Post. 1990. Climate, Population Viability, and the Zoogeography of Temperate Fishes. Trans. Am. Fish. Soc. 119:314-336.

Stewart, D.J., and M. Ibarra. 1991. Predation and Production by Salmonine Fishes in Lake- Michigan, 1978-88. Can. J. Fish. Aquat. Sci. 48:909-922.

Stow, C.A., and S.R. Carpenter. 1994. PCB Accumulation in Lake-Michigan Coho and Chinook Salmon - Individual-Based Models Using Allometric Relationships. Environ. Sci. & Technol. 28:1543-1549.

Trudel, M., and D. Boisclair. 1996. Estimation of Fish Activity Costs Using Underwater Video Cameras. Journal Of Fish Biology 48:40-53.

Trudel, M., and D. Boisclair. 1993. An in-Situ Evaluation of the Day-to-Day Variation in the Quantity of Food Consumed by Fish. Can. J. Fish. Aquat. Sci. 50:2157-2165.

Trudel, M., and D. Boisclair. 1994. Seasonal Consumption by Dace (*Phoxinus-EOS X P-Neogaeus*) - A Comparison Between Field and Bioenergetic Model Estimates. Can. J. Fish. Aquat. Sci. 51:2558-2567.

Turner, A.M., and G.G. Mittelbach. 1990. Predator Avoidance and Community Structure - Interactions Among Piscivores, Planktivores, and Plankton. Ecology 71:2241-2254.

Walters, C.J., and J.R. Post. 1993. Density-Dependent Growth and Competitive Asymmetries in Size-Structured Fish Populations - A Theoretical-Model and Recommendations for Field Experiments. Trans. Am. Fish. Soc. 122:34-45.

Wu, L., and D.A. Culver. 1994. Daphnia Population-Dynamics in Western Lake Erie - Regulation by Food Limitation and Yellow Perch Predation. J. Gt Lakes Res. 20:537-545.

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