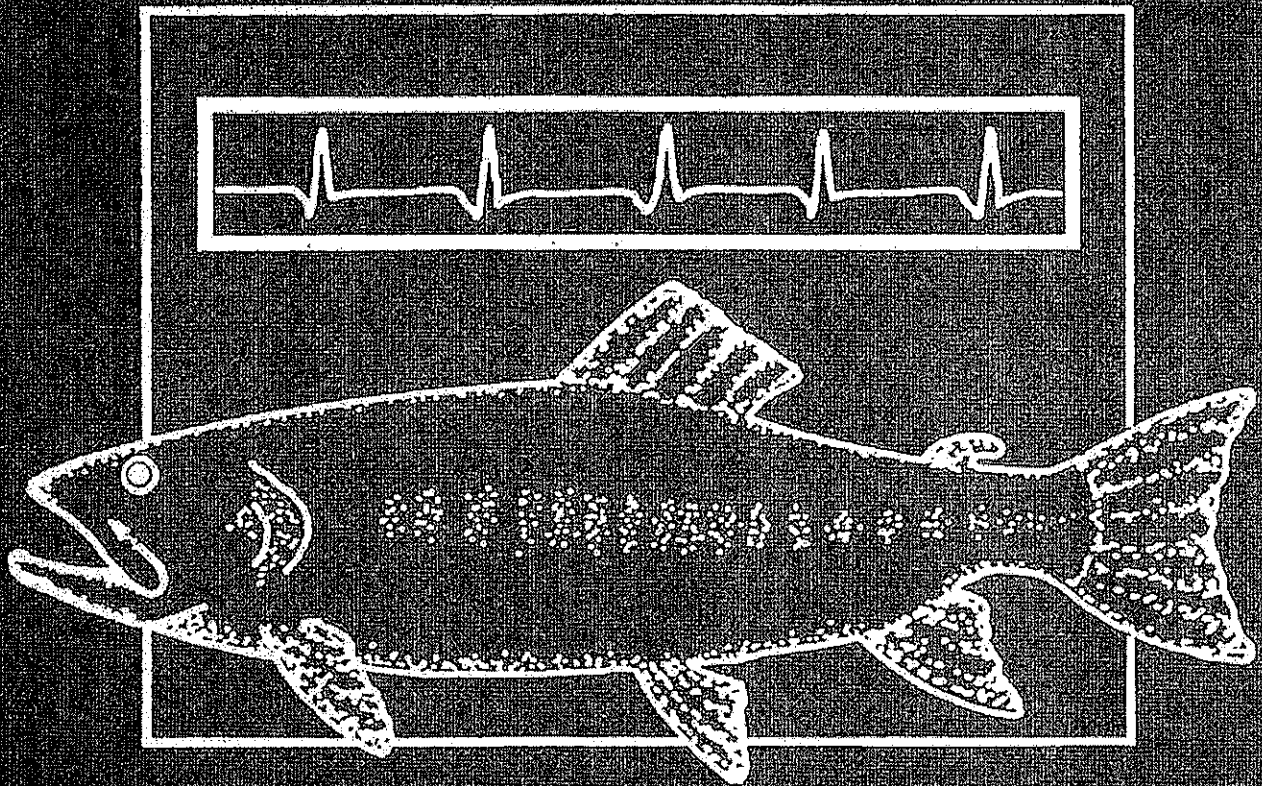


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# METHODS FOR FISH BIOLOGY



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# Chapter 12

## Bioenergetics

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### 12.1 INTRODUCTION

All energy acquired by an organism through ingestion must ultimately be used in metabolic processes, lost as wastes through excretion and egestion, or synthesized into new tissue (energy gain). Physiological energetics, or bioenergetics, is concerned with the rates of energy intake, transformations, losses, and uses as functions of the whole organism (Brett and Groves 1979). Bioenergetics provides a theoretical framework for relating growth rates and feeding rates of an organism to environmental conditions and provides some insight into causal relationships among these variables (Allen and Wootton 1982). The application of bioenergetics in fisheries involves partitioning ingested energy into the major physiological components of the basic energy budget equation of Winberg (1956):

$$p \cdot C = M + G; \quad (12.1)$$

$p$  = proportion of consumed food that is assimilated,  
 $C$  = food consumed,  
 $M$  = metabolism (catabolism), and  
 $G$  = growth (anabolism).

Equation (12.1) is usually expanded to yield the generalized form proposed by Warren and Davis (1967):

$$C = \underbrace{(M_r + M_a + \text{SDA})}_{\text{(metabolism)}} + \underbrace{(F + U)}_{\text{(waste)}} + \underbrace{(G_s + G_r)}_{\text{(growth)}}; \quad (12.2)$$

$C$  = rate of energy consumption,  
 $M_r$  = standard metabolic rate,  
 $M_a$  = metabolic rate increase (above the standard rate) due to activity,  
 $\text{SDA}$  = metabolic rate increase due to specific dynamic action,  
 $F+U$  = waste losses due to egestion (feces) and excretion (urine) rates,  
 $G_s$  = somatic growth rate due to protein synthesis and lipid deposition, and  
 $G_r$  = growth rate due to gonad (reproductive) synthesis.

All components of the energy budget must be expressed in the same units. The units can be biomass (wet or dry weight), energy (joules or calories), carbon, or nitrogen, and can be expressed as rates (e.g., cal/d) or as amounts gained or lost in some reference time period. Biomass estimates can be used directly only when the energy value of consumed food and the energy density of the fish are similar; otherwise, large errors can result in the balancing of the energy budget equation.

For example, the caloric density of alewife, the primary prey of lake trout in Lake Michigan, varies from 1.03 to 2.3 kcal/g of body weight over the year (Flath and Diana 1985), whereas the caloric density of lake trout varies with fish size between 1.26 and 3.35 kcal/g (Stewart et al. 1983). These energy content differences between predator and prey could cause estimates of alewife consumption by lake trout to err by a factor of 2 or more if they are not taken into account. Both the food (prey) and growth (predator) must be converted from biomass to common energy units to balance the budget; then the results can be converted back to biomass units if desired.

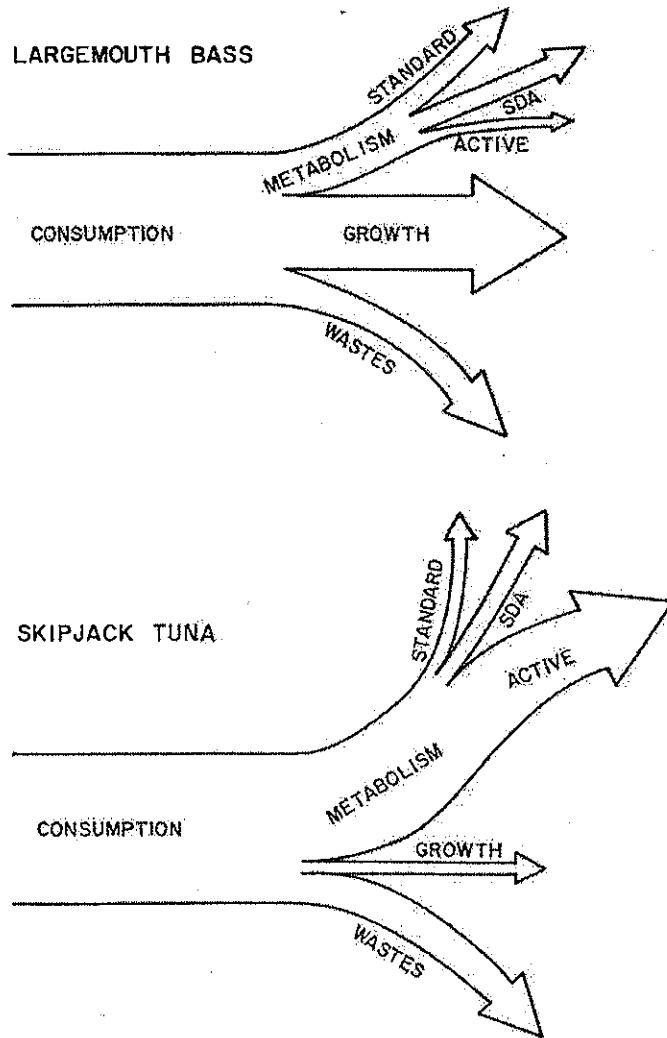
The life history of a fish dictates, to a large degree, how consumed energy is partitioned into its major functional processes of growth, metabolism, and production. For example, the generally sedentary largemouth bass, which employs an "ambush" type of feeding behavior, partitions ingested energy differently from the actively swimming skipjack tuna, which forages continuously. Both species allocate similar proportions of consumed energy to standard metabolism, specific dynamic action (food assimilation), and waste losses, but tunas devote a much larger fraction of their energy intake to activity than do basses (Figure 12.1). As a consequence, a much smaller proportion of the total energy intake of tunas is available for growth. However, tunas still achieve higher growth rates than basses by maintaining higher feeding rates.

### 12.1.1 Uses of Bioenergetics in Fishery Biology

Bioenergetic budgets have been applied in fishery biology for a variety of purposes. Common applications of the balanced energy budget have been estimation of growth or production (Paloheimo and Dickie 1966; Kerr 1971; Healey 1972; Ware 1975) and prediction of food consumption rates to evaluate the impacts of predators on their prey (Kitchell and Breck 1980; Stewart et al. 1981, 1983; Rice and Cochran 1984). Energy budgets can also be an efficient means of evaluating the relative importance of environmental factors that control growth, such as temperature or prey availability (Kitchell et al. 1977; Rice et al. 1983). The effects of multiple stresses on growth can also be examined with the bioenergetic budget (Vaughan et al. 1984; Rice 1990).

An understanding of how fish partition consumed energy into metabolic pathways, reproductive demands, and growth is important for studying life history strategies of fish (Williams 1961); these strategies include diel migration (Caulton 1978), seasonal feeding patterns (Kitchell and Breck 1980), and reproduction (MacKinnon 1972). Bioenergetic models have been used to estimate the rate at which pollutants such as PCBs are taken up by salmonids in the Great Lakes (Weininger 1978; Thomann and Connolly 1984), to determine the uptake of PCBs and methylmercury by yellow perch (Norstrom et al. 1976), and to evaluate the consequences of stress in fish (Rice 1990). Bioenergetics also has been applied to studies of early life history stages of fish (Cooney 1973; Laurence 1977; Eldridge et al. 1982).

Bioenergetic budgets can be used to address a variety of fishery-related needs and objectives (Table 12.1). The purpose of this chapter, therefore, is to provide practical guidelines for applying bioenergetics in fish biology. For more detailed discussions of the theoretical aspects of fish bioenergetics, see reviews by Beamish et al. (1975), Webb (1978), Brett and Groves (1979), Elliott (1979), Kitchell (1983), From and Rasmussen (1984), and Tyler and Calow (1985).



**Figure 12.1** Allocation of consumed energy into the major components of the bioenergetics budget at maximum rations in the relatively sedentary largemouth bass and the actively foraging skipjack tuna. Widths of arrows are scaled to represent actual proportions of consumed energy allocated to each process. SDA is specific dynamic action. (Data from Kitchell 1983.)

## 12.2 DIRECT MEASUREMENTS OF MAJOR BIOENERGETIC COMPONENTS

In very few studies have all components of the bioenergetic budget for fish been measured independently. More typically, one or more of the major components is estimated from other studies or calculated by difference to balance the budget (Kitchell 1983). Because they form a balanced equation, determinations (or well-founded estimates) of any three of the main components—growth, metabolism, waste, consumption—allow the fourth to be calculated by difference. All errors associated with the three determinations, however, become a pooled error in the fourth component (Brett and Groves 1979; Solomon and Brafield 1972). Methods of estimating the four basic components of the balanced energy budget, as well as their limitations, are discussed in the following sections.

**Table 12.1** Representative applications of bioenergetics to the study of fish biology.

Research use or objective	Species	Reference
<b>Basic bioenergetic components</b>		
Growth, consumption, metabolism	Northern pike	Diana (1983)
	Sauger	Minton and McLean (1982); Wahl and Nielsen (1985)
	Walleye	Swenson and Smith (1973)
	Largemouth bass	Adams et al. (1982b)
	Sockeye salmon	Brett (1976)
	Brown trout	Elliott (1976)
	Threespine stickleback	Allen and Wootton (1984)
	Eurasian perch	Thorpe (1977)
	Gizzard shad	Megrey (1978); Pierce (1977)
	Sand goby <sup>a</sup>	Healey (1972)
	Sargassumfish	Smith (1973)
	Rainbow trout	From and Rasmussen (1984)
	Six European species	Backiel (1971)
	Alewife	Stewart and Binkowski (1986)
<b>Accumulation of contaminants</b>		
Uptake of PCBs	Lake trout	Weininger (1978); Thomann and Connolly (1984)
Accumulation of PCBs and methylmercury	Yellow perch	Norstrom et al. (1976)
<b>Effects of environmental variables</b>		
Temperature effects on growth	Walleye, yellow perch	Kitchell et al. (1977)
Temperature effects on condition	Largemouth bass	Rice et al. (1983)
Prey availability on energy partitioning	Largemouth bass	Adams et al. (1982b)
Macrophyte harvesting on predator-prey relations	Bluegill	Breck and Kitchell (1979)
Prey availability and temperature on consumption	Walleye, sauger	Swenson (1977)
Food density	Atlantic menhaden	Durbin and Durbin (1983)
Food level, temperature	Largemouth bass	Rice (1990)
<b>Life history strategies</b>		
Diel migration	Tilapia <sup>b</sup>	Caulton (1978)
Feeding	Sea lamprey	Kitchell and Breck (1980)
Reproduction	American plaice	MacKinnon (1972)
	Threespine stickleback	Wootton et al. (1980)
	Northern anchovy	Hunter and Leong (1981)
Foraging	Skipjack tuna	Kitchell (1983)
<b>Effects of predators on their prey</b>		
	Lake trout	Stewart et al. (1981, 1983)
	Largemouth bass	Cochran and Adelman (1982)
	Sea lamprey	Kitchell and Breck (1980)
	Pacific sardine	Lasker (1970)
	Walleye	Lyons (1984)
<b>Fish culture and management</b>		
Manipulation of ponds	Channel catfish	Cuenca et al. (1985)
Optimal growth in hatcheries	Salmonids	Stauffer (1973)
Fishery management in Great Lakes	Salmonids and their prey	Stewart et al. (1981)
Stocking strategies	Esocids	Bevelhimer et al. (1985)
Population limitation processes	Yellowfin tuna	Sharp and Francis (1976)
Control of bluegill populations	Largemouth bass	Carline et al. (1984)
Closed-loop fish farming	Rainbow trout	Jorgensen (1976)

Table 12.1 Continued.

Research use or objective	Species	Reference
Energy balance of plant and animal food	Grass carp	Fisher (1972)
Energy balance of various foods	Salmonids	Cho et al. (1982)
<b>Energy budgets for larval and young-of-year fish</b>		
Growth, respiration	Blueback herring	Burbidge (1974)
Daily ration, growth, respiration	White bass	Wissing (1974)
Consumption, growth	Yellow perch	Mills and Forney (1981)
Growth, development	Striped bass	Eldridge et al. (1982)
Consumption, growth	Atlantic menhaden, spot, pinfish	Peters and Kjelson (1975)

<sup>a</sup> *Gobius minutus*.<sup>b</sup> *Tilapia rendalli*.

### 12.2.1 Growth

Growth or production of fish populations is the total elaboration or synthesis of fish tissue during a specified time interval, including tissue produced by individuals that do not survive to the end of an interval (Ivlev 1966). Growth can be calculated as changes in biomass (weight), energy (calories), carbon, or nitrogen during an interval of measurement and includes somatic (protein and lipid) growth and the development of gonads. For the purpose of a basic bioenergetic budget, protein synthesis and lipid storage are usually considered together as somatic growth; gonadal development is not usually measured separately except for mature female fish. Detailed techniques and approaches for measuring growth, including their uses and limitations in both the laboratory and field, are addressed in Chapter 11; see also Bagenal and Tesch (1978), Weatherley (1978), and Jearld (1983).

Even though changes observed in growth over a time interval may include energy deposition in protein, lipid, and reproductive components, fishery biologists are usually interested in the sum of energy changes occurring in the interval of measurement. Protein elaboration may be the major concern of fish culturists or fishermen for economic reasons, whereas deposition of energy into lipid and gonad compartments may be critical for the species' survival and reproductive success. Protein growth is usually a positive energy change throughout the year (except possibly for starving fish), but quantities of lipids and gonad sizes can undergo relatively large temporal fluctuations, including net losses during certain periods of the year. Fish usually accumulate lipids during the summer and fall, then use them during the winter when food consumption is low and also during the spring for spawning. During spawning, female fish can lose up to 85% of their somatic energy (Glebe and Leggett 1981). Temporal changes in lipid storage levels usually can be accounted for by caloric analysis, whereas the energy value of spawned eggs can be calculated from sudden reductions in the gonadosomatic index, the ratio of gonad weight to total body weight (Scott 1979; Ursin 1979). Energy values of gonadal material should be accounted for calorimetrically because the energy content of eggs can be different from that of most somatic tissue.

Growth can be estimated from field data or in the laboratory by methods detailed in Chapter 11. It also can be derived indirectly from the balanced energy

budget if metabolism, consumption, and assimilation are known. Direct measurement of growth has three principal advantages. (1) Growth data integrate feeding rate over time, and the effects of frequent variations in temperature and daily ration are minimized. (2) Growth rate is relatively easy to measure, and, of all the bioenergetic components, it is the one for which field data are most readily available. (3) The uncertainties of growth estimates in the energy budget are generally less than those of other components (Kitchell et al. 1977; Bartell et al. 1986). Growth estimates, obtained either directly or via the balanced budget, can be sensitive to proximate analysis of body constituents and, in particular, to caloric density; these measurements can have large effects on the energy budget's balance. Proximate analysis of the body constituents and calorimetry are addressed in Chapter 11.

### 12.2.2 Metabolism

Energy losses to metabolic demands are usually a large component of the bioenergetic budget of a fish (Figure 12.1). These energy costs can be partitioned into standard metabolism, metabolic costs of activity, and specific dynamic action (SDA).

#### 12.2.2.1 Standard Metabolism

Standard metabolism ( $M_r$  in equation 12.2) is the rate of energy use by a fasting fish at rest. It is primarily a function of water temperature and body size. Because standard metabolism defines the baseline or lower bound for the scope for growth, it is an important variable in the bioenergetic budget. Energy use for metabolism is typically measured as the rate of oxygen consumption. Oxygen units can be converted to energy units with the oxycaloric average of 3.20–3.24 cal/mg  $O_2$  (Brafield and Solomon 1972; Elliott and Davison 1975). Oxycaloric values can vary, however, according to the proportions of fat, carbohydrate, and protein catabolized (Elliott and Davison 1975). Detailed methods for measuring metabolic rates are discussed in Chapter 10. For many of the more common fish species, standard metabolic rates at various water temperatures and fish sizes can be obtained from the literature (some references are given in Table 12.1).

#### 12.2.2.2 Activity-Dependent Metabolism

The activity metabolism component in the bioenergetic budget accounts for metabolism above that of the standard metabolic rate, such as occurs during foraging or spawning migrations. Fry (1957) defined "active metabolism" as the maximum metabolic rate at which an animal can sustain a high level of activity. Because fish typically operate at activity levels requiring more than standard metabolism but less than active metabolism, Rice et al. (1983) suggested the term "activity-dependent metabolism" to refer to energy costs associated with standard metabolism plus activity (i.e.,  $M_r + M_a$ ).

Activity-dependent metabolism may vary with species, sex, and time of year. If activity costs are high and are not properly accounted for, large errors can result when the metabolism term is used in the bioenergetic equation to calculate another major component such as energy consumption or growth. For some species with sedentary life styles such as largemouth bass, activity-dependent metabolism can be approximated by standard metabolism (Adams et al. 1982b;

Rice et al. 1983). In other species such as skipjack tuna, activity-dependent metabolism ( $M_a$ ) can be a major fraction of total respiratory metabolism (Figure 12.1). Ware (1975) indicated that activity-dependent metabolism should be about 3 times standard metabolism for juvenile pelagic fish. Brett and Groves (1979) determined that the metabolic rate of migrating sockeye salmon was 8.5 times the standard. Minton and McLean (1982) reported that metabolic rates of sauger appear to be almost 4 times the standard during spring. Brett (1964) calculated that a 20-s burst of activity by a sockeye salmon cost as much energy as 179 min of standard metabolism.

Estimates of activity-dependent metabolism have been obtained by several methods. (1) Fish have been forced to swim against currents in laboratory respirometers (Brett 1964; Beamish 1970). (2) The Winberg multiplier (Winberg 1956) has been used, whereby the standard metabolic rate is doubled (Winberg II: Mann 1965; Gerking 1972) or tripled (Winberg III: Ware 1975) to estimate activity of fish in the wild. (3) Bioenergetic equations and models have been used to simulate activity-dependent metabolism as a function of fish size, swimming speed, and water temperature (Rice et al. 1983; Stewart et al. 1983). (4) The energy budget has been balanced by difference when there was little or no information about activity costs (Elliott 1976; Adams et al. 1982b).

#### 12.2.2.3 Specific Dynamic Action (SDA)

Specific dynamic action comprises the energetic costs of processing and assimilating food, such as deamination of proteins and transport and deposition of lipids. It is usually calculated as a constant fraction of the energy consumed, and averages about 15% for carnivorous and omnivorous fish (Muir and Niimi 1972; Beamish 1974; Schalles and Wissing 1976).

#### 12.2.3 Wastes: Egestion and Excretion

The energy lost with wastes can vary greatly among species, and depends on the nature of the diet. Winberg (1956) proposed that the assimilation efficiency of fish consuming a mixed diet was approximately 80%. Detritivores and herbivores, whose diets are high in fiber and ash, typically have efficiencies less than 80%; piscivores, whose diets are high in protein, commonly have efficiencies higher than 90% (Brett and Groves 1979). Even though Elliott (1976) found that egestion and excretion are functions of temperature and ration size, nonassimilated energy (egestion) and excretion can be estimated as a constant proportion of energy consumed (Beamish 1972, 1974; Niimi and Beamish 1974; Kitchell et al. 1977). Estimates of assimilation efficiency for many species are available in the literature. Direct measurements of assimilation efficiency can be made with the Conover (1966) method, the chromic oxide method (Windell and Bowen 1978), or fecal collection methods (Smith 1973).

#### 12.2.4 Food Consumption

Ingestion represents the only route of energy input into a consumer; the remainder of the bioenergetic components depend on this input. We emphasize consumption over the other components in this chapter because it is not addressed elsewhere in the book, because the uses and limitations of several widely applied consumption methodologies developed since 1977 have not been

summarized previously for practical use by fishery scientists, and because field estimates of consumption typically are infrequent and highly variable (Cochran and Adelman 1982; Diana 1983; Rice and Cochran 1984) and lack confidence limits (Diana 1979). The advantages and limitations of methods to estimate consumption rate must be recognized before the estimates are used in energy budget calculations.

Estimates of food consumed by fish in the field are influenced by many factors, including size of fish, amount of food eaten in a meal, number of meals in a day, rate of gastric clearing, water temperature, activity of the fish, type of food eaten, and prior feeding history (Windell 1978). Several of these variables are difficult to quantify outside the laboratory, so some investigators have used growth data coupled with metabolic estimates in the bioenergetic budget to predict consumption rates for fish in the wild (Kitchell and Breck 1980; Stewart et al. 1981; Kerr 1982; Rice and Cochran 1984).

The daily rations of fish have been estimated from field measurements (despite the problems mentioned), predicted from laboratory studies, and calculated from the balanced energy equation. Field estimates of daily ration are based primarily on measurements of gut contents and the rate at which the contents are evacuated from the stomach. Laboratory studies develop empirical relationships between food consumption and growth rates, which are applied to field measurements of growth to estimate consumption by wild fish (Warren and Davis 1967; Carline and Hall 1973; Wootton et al. 1980). The principal limitation of the laboratory approach is the expense in time and facilities necessary to study even a few of the many variables—temperature, day length, food density, fish activity, competition, etc.—that can affect growth and consumption in the field (Mann 1978). In this section, we discuss the methods used to directly estimate feeding rates in the field. For further discussions of methods for estimating consumption, see Mann (1978) and Windell (1978).

Field consumption rates have been estimated by three basic approaches. One is to assume that stomach contents decline exponentially with time for a given portion of food (as the remainder becomes increasingly refractory) and that feeding is continuous between sampling intervals. Another is to follow the chronology of feeding. The third is to assume that digestion is linear (i.e., a constant amount is digested per unit time) and that digestion times are long relative to periods of feeding.

#### 12.2.4.1 Continuous Feeding Models

In the method originally proposed by Bajkov (1935) and modified by Thorpe (1977) and Eggers (1979), feeding is assumed to be continuous and constant over a feeding cycle:

$$C = 24 \cdot s \cdot k; \quad (12.3)$$

$C$  = daily ration (percentage of body weight/d, or sometimes mg/[g · d]),

$s$  = average amount of food in the stomach or gut over 24 h (percentage or mg/g), and

$k$  = the instantaneous rate of gastric evacuation ( $\text{h}^{-1}$ ).

This formula gives valid consumption estimates only if the sampled fish have the same average amount of food in their stomachs at the beginning and end of 24 h,

and if the gastric evacuation rate is exponential (i.e., evacuation declines with the amount of material in the stomach).

Typically,  $s$  is estimated by sampling several fish at 2–6-h intervals during a 24-h period. The stomach contents of each interval are weighed, expressed as a proportion (percentage) of the fish's body weight to account for variations in body weight among individual fish, and averaged. Methods for calculating the amount of food present in the digestive tract of fish were described by Windell and Bowen (1978) and Bowen (1983). If nondestructive sampling is desired, the method of Seaburg and Moyle (1964) can be used to pump the stomach contents without killing the fish.

The stomach contents of many species vary substantially over the course of 24 h, violating a key assumption underlying equation (12.3). If this happens, the daily ration can be estimated from the stomach contents of fish sampled at various times of day. The amount of food ingested in the time between two sampling periods ( $C_t$ ) is

$$C_t = S_t - S_0 + A; \quad (12.4)$$

$S_0$  and  $S_t$  are the respective amounts of food in the stomach at the beginning and end of a sampling interval, and  $A$  is the amount of food evacuated from the stomach during the interval. Daily ration is calculated by summing the interval values for  $C_t$ .

The consumption model of Elliott and Persson (1978) is

$$C_t = \frac{(S_t - S_0 e^{-kt})kt}{1 - e^{-kt}}. \quad (12.5)$$

As before,  $S_0$  and  $S_t$  are amounts of food in the gut at the beginning and end of a sampling interval  $t$  hours long and  $k$  is the instantaneous rate of gastric evacuation. This model appears to be the most applicable one for estimating daily ration of fish collected in the field when (1) feeding is more or less continuous during daylight hours, (2) the amount of food in the gut at the start and at the end of a sampling interval is not necessarily the same, and (3) the digestion rate is exponential.

Equations (12.3) and (12.5) can be generally applied to species with a "fine-grained" diet (i.e., large numbers of small food particles) such as planktivores, detritivores, herbivores, and omnivores. It is less reliable with fish such as piscivores that typically consume and process a few large prey (Tyler 1970; Persson 1979; Cochran and Adelman 1982). The accuracy of consumption estimates obtained with these models increases with the frequency of sampling, because the assumption of constant feeding over a time interval is easier to meet when the interval is shorter (Elliott and Persson 1978).

*Determination of Stomach Evacuation Rate.* Stomach evacuation rate must be estimated accurately if calculations of daily rations are to be reliable (Darnell and Meierotto 1962; Jobling 1981; Allen and Wootton 1984). The form of the evacuation rate process (exponential or linear) is also important; compared to a linear digestion process, exponential digestion often gives lower estimates of consumption when digestion times are long. The coefficient ( $k$ ) of the exponential evacuation rate can be calculated as

$$k = (1/t) \log_e (S_0/S_t); \quad (12.6)$$

the terms are as defined for equation (12.5). As with most other physiological processes in fish, gastric evacuation rate increases with temperature; therefore, water temperature must be taken into account when  $k$  is estimated (Elliott 1972). Body size also influences stomach evacuation rate. Many workers have observed faster stomach evacuation rates in smaller fish (Flowerdew and Grove 1979; Mills et al. 1984). Failure to consider the effect of body size on evacuation rates can lead to underestimates of consumption for smaller fish and overestimates for larger fish.

To obtain  $k$  from field measurements, a time of day is selected during which fish are assumed not to feed. For fish that do not feed during darkness, for example, the decline in weight of stomach contents (relative to fish weight) during the night reflects evacuation of the stomach. Thus, the value of  $k$  over this nonfeeding period can be estimated from the slope of the regression of  $\log_e$  (stomach contents) against time. The serial-slaughter method of Windell (1967) can also be used to estimate  $k$  from the decline in mean weight of gut contents. In this procedure, some fish in the sample are examined immediately after capture, and others are examined after they have been held in food-free environments such as cages for different time intervals. Another method is to feed groups of starved fish known amounts of food (or, less accurately, feed them to satiation) in the laboratory, examine subsamples of these fish at regular intervals to determine the percentage of food remaining in the guts, and regress these percentages against time (Elliott 1972; Peters and Hoss 1974). Other less-often applied but potentially accurate methods for measuring gastric evacuation rate, such as the X-ray and radioisotopic procedures, were discussed by Windell (1978). Exponential digestion rate models were discussed in detail by Jobling (1981). A sample calculation for determining exponential gastric evacuation rate and daily ration for continuous feeders is presented in Box 12.1.

#### 12.2.4.2 Chronology-of-Feeding Methods

The chronology-of-feeding methods proposed by Keast and Welsh (1968) and Nakashima and Leggett (1978) to estimate consumption are based primarily on stomach content analyses for a large number of fish sampled over a 24-h period, and do not require information about stomach evacuation rate. Keast and Welsh (1968) summed the differences between successive maximum and minimum mean weights of stomach contents over a diel cycle to calculate consumption. Nakashima and Leggett (1978) summed mean food weights at feeding peaks over 24 h. Both methods assume noncontinuous or synchronous feeding of fish and no evacuation of food from the digestive tract during sampling. Fish with empty stomachs are included in the calculations.

A promising new method to estimate daily ration from a single collection of fish within a 24-h period was developed by Hayward and Margraf (1987). This procedure, which combines elements of both the Elliott-Persson model (equation 12.5) and the chronology-of-feeding method, was used to predict the daily ration of yellow perch in Lake Erie. First, 24-h feeding studies were done, trawl samples being taken every 3 h. These allowed daily consumption rates to be calculated, and established the times of peak feeding by yellow perch. Then, weight-specific food quantities were computed (dry weight of food divided by whole-body dry weight) for the time of maximum feeding. The median food quantity was

### Box 12.1 Calculation of Exponential Stomach Evacuation Rate and Consumption Rate for an Omnivorous Fish that Feeds Continuously

Assume that samples of fish are collected in close proximity to each other in the same stream at 1000 hours ( $t_0$ ), 1600 hours ( $t_1$ ), 2200 hours ( $t_2$ ), and 0400 hours ( $t_3$ ). Average food contents in the stomachs of fish sampled on each occasion are  $S_0 = 14$ ,  $S_1 = 23$ ,  $S_2 = 12$ , and  $S_3 = 4$  mg/g of fish.

For fish with "fine-grained" diets that feed more or less continuously during daylight hours but not at night, the exponential digestion rate coefficient ( $k$ ) is calculated for a nighttime interval when there is no new food intake:

$$k = (1/t) \log_e (S_2/S_3).$$

In this example,  $S_2 = 12$  and  $S_3 = 4$  mg/g; the time interval between these measurements is  $t = 6$  h:

$$k = (1/6) \log_e (12/4) = 0.18 \cdot \text{h}^{-1}.$$

The ration or consumption of this species for the first 6-h period can then be calculated from equation (12.5):

$$C_t = \frac{(S_1 - S_0 e^{-kt})kt}{1 - e^{-kt}};$$

$$C_{6h} = \frac{(23 - 14e^{-0.18(6)}) (0.18 \cdot 6)}{1 - e^{-0.18(6)}} = \frac{(23 - 4.75) (1.08)}{0.66};$$

$$C_{6h} = 30 \text{ mg/g in 6 h, or 3.0\% of body weight.}$$

multiplied by a temperature-dependent evacuation rate ( $k$  in equation 12.6) and regressed against calculated daily consumption. Thereafter, this calibration curve allowed daily consumption rate to be determined graphically from analysis of a single trawl sample taken during the peak feeding hours.

Most methods involving chronologies of feeding have two principal difficulties. First, they are likely to underestimate daily rations (Elliott and Persson 1978; Jobling 1981; Allen and Wootton 1984). Second, they generally require that large numbers of fish be collected at several intervals over a 24-h period, which may not be feasible for many species.

#### 12.2.4.3 Carnivore Feeding Models

Fish with "fine-grained" diets composed of a large number of small food items are generally herbivores, detritivores, planktivores, and omnivores that feed at lower trophic levels of the biological community. These fish usually feed more or less continuously during daylight hours, and their digestion process can be described by an exponential digestion function. In contrast, the top carnivores are generally piscivores that consume a few relatively large prey over a feeding cycle. In these fish, digestion rate is typically a linear process (Swenson and Smith 1973; Forney 1977; Diana 1979; Adams et al. 1982a), digestion time is long relative to the

length of the feeding period, and diurnal feeding patterns can be either synchronous (i.e., most or all of the fish feed at the same time) or asynchronous.

The methods for calculating daily ration of piscivores are of two types. The choice of method depends primarily on the length of digestion time relative to the length of time between meals, and on whether diurnal feeding patterns are synchronous or asynchronous. For coldwater fish such as northern pike, digestion time is considerably longer than the time between meals. For warmwater piscivores such as largemouth bass, digestion time can be less than the time between meals.

*Coldwater Fish.* For fish with digestion times considerably longer than 24 h, the model proposed by Diana (1979) can be used to calculate daily ration:

$$C = \frac{M \cdot n}{B' \cdot N}; \quad (12.7)$$

$C$  = daily ration (% body weight/d),

$M$  = average size of ingested meal (percentage of body weight),

$n$  = number of fish that contain food in the stomach,

$B'$  = number of days for gastric evacuation, and

$N$  = total number of fish, including those with empty stomachs.

This feeding model has the same form as equation (12.3) because the average meal size of the population is  $Mn/N$ , and the stomach evacuation rate per day ( $24 \cdot k$ ) has the same unit ( $d^{-1}$ ) as  $(1/B')$ . In equation (12.7), daily ration is calculated by (meal size)/(meal frequency), frequency ( $f$ ) being the ratio  $f = B'N/n$ . An important assumption inherent in consumption models based on meal size and frequency is that feeding by the population is asynchronous, and that a sample of predators taken at any time during the day would include prey representative of all levels of feeding.

The consumption model developed by Popova and Sytina (1977) is also applicable to coldwater piscivores whose digestion lasts several days:

$$C = \frac{n}{N} \sum_{i=1}^V \frac{(S_i/n_i)}{V}; \quad (12.8)$$

$C$  = daily ration (% body weight/d),

$N$  = total number of fish in the sample,

$n$  = number of fish in a sample that contained food,

$V$  = number of days for digestion at a given temperature,

$n_i$  = number of fish in the sample that contained food eaten on day  $i$ , and

$S_i$  = original undigested weight of all prey items eaten by  $n_i$  predators on day  $i$ , expressed as a percentage of body weight.

This type of consumption model has also been applied to the energy budget of sauger (Minton and McLean 1982). The feeding model developed by Swenson and Smith (1973) for walleye, and also applied to sauger by Wahl and Nielsen (1985), is similar to the Diana (1979) model for northern pike but takes into account ingestion of a range of prey size-classes by a predator and calculates the daily ration for several periods during a feeding cycle.

Examples of food consumption calculations by both methods for coldwater species are presented in Box 12.2.

*Warmwater Fish.* Predators that have short digestion times relative to periods between meals generally have digestion times of less than 24 h. For these fish, rates are calculated in units of hours, compared to units of days for coldwater piscivores, and calculation of daily ration is very sensitive to estimated digestion rate. The feeding model of Adams et al. (1982a) can be used to calculate the daily consumption ( $C$ ) of warmwater piscivores:

$$C = 100 \sum_{i=1}^N \frac{(Pw_i/Bw_i)}{N}; \quad (12.9)$$

$C$  = daily ration (% body weight/d),

$Pw_i$  = estimated total weight at capture of prey when ingested by predator  $i$  over a defined 24-h period,

$Bw_i$  = weight of predator  $i$  that consumed those prey, and

$N$  = total number of predators in a sample, including those with empty stomachs.

In addition to the large variations in digestion rate times, the principal differences between this consumption model and the one for coldwater predators are that this method (equation 12.9) does not require calculation of meal frequency or consumption estimates at separate intervals over a feeding cycle—provided that the time to 90 or 95% digestion is less than 24 h. The feeding model for warmwater piscivores is particularly applicable to fish that display synchronous feeding, such as the largemouth bass (DeAngelis et al. 1984). Calculation of daily ration based on meal frequency (equation 12.7) seems to be justified for asynchronous feeders, such as some of the coldwater piscivores (northern pike, sauger), but does not appear to be the most straightforward methodology for nonrandom or synchronous feeders.

An example calculation of food consumption for a warmwater fish is presented in Box 12.3.

#### 12.2.4.4 Determination of Feeding Model Components.

Calculation of daily ration for both cold- and warmwater piscivores requires estimates of the original weight of the ingested prey and the digestion rate of prey at various temperatures, and knowledge of whether the diurnal feeding pattern is synchronous or asynchronous.

*Weight of Ingested Prey.* Predators sampled from a population typically have stomach contents that range from freshly ingested prey to the hard remains (e.g., bones and chitin) of completely digested organisms. The original weights of consumed prey can be estimated in three ways. (1) Ingested prey can be compared to preserved specimens of prey that have been weighed, fed to predators, and digested for various periods before they were recovered (Darnell and Meierotto 1962; Popova 1978). (2) Prey lengths can be compared with preestablished length-weight regressions for the prey species; the regressions can be based on total length, standard length, backbone length, or some other appropriate measure

**Box 12.2 Calculation of Food Consumption for Coldwater Predators**

Example 1. Daily ration ( $C$ ) calculation for northern pike (equation 12.7)

$$C = \frac{M \cdot n}{B' \cdot N};$$

$M = 50$  g/kg (average meal size),

$n = 50$  (fish containing food),

$B' = 3$  d (gastric evacuation time),

$N = 100$  (total fish in sample).

$$C = \frac{(50 \text{ g/kg}) (50 \text{ fish})}{(3 \text{ d}) (100 \text{ total fish})} = 8.3 \text{ g/(kg} \cdot \text{d)}.$$

Example 2. Daily ration calculation for zander (equation 12.8).

$$C = \frac{n}{N} \sum_{i=1}^v \frac{(S_i/n_i)}{V};$$

$N = 50$  (total number of fish),

$n = 32$  (fish containing food),

$V = 3$  d (gastric evacuation time),

$n_1, n_2, n_3 = 10, 15, \text{ and } 7$ , respectively (number of fish in a sample that contained food on days 1, 2, and 3).

$S_1, S_2, S_3 = 15, 23.5, \text{ and } 18$ , respectively (sum of percent body weights consumed by all predators on days 1, 2, and 3; for example,  $S_3 = 1.6\% + 2.3\% + 4.7\% + 1.7\% + 1.1\% + 3.2\% + 3.4\% = 18\%$ ).

$$C = \left( \frac{32}{50} \right) \left( \frac{(15/10) + (23.5/15) + (18/7)}{3} \right) = 1.2 \text{ g/(kg} \cdot \text{d)}.$$

(Minton and McLean 1982). (3) The size or weight of relatively indigestible parts of prey (otoliths, bone fragments, gizzards, etc.) can be compared with standard regressions against whole body weight for the prey species to estimate the original weight of the ingested animal (Popova 1967; Minckley and Paulson 1976).

**Digestion Rates.** Methods used to determine digestion rates of carnivorous fish differ from those used with fish that have fine-grained diets, continuous feeding patterns, and exponential digestion rates. For piscivores, fish prey of known weights that were eaten voluntarily or force-fed are recovered at various intervals either by killing the predator or by pumping its stomach (Hunt 1960; Beamish 1972; Swenson and Smith 1973; Steigenberger and Larkin 1974; Diana 1979; McGee et al. 1979; Adams et al. 1982a; Minton and McLean 1982). For a particular experimental temperature, the fraction of original prey weight digested is graphed against hours since feeding, and the resulting regression is used to calculate digestion. In carnivorous fish, time to either 90 or 95% digestion is typically used as the endpoint of digestion time; digestion of the remaining 5–10% is slowed significantly because of hard parts such as skeletal remains and chitin.

**Box 12.3 Calculation of Daily Food Consumption for a Warmwater Predator**

For a warmwater piscivore such as largemouth bass, the daily ration of the population can be calculated, as percent of body weight, from equation (12.9):

$$C = 100 \sum_{i=1}^N \frac{(Pw_i/Bw_i)}{N}$$

Example. The stomachs of six largemouth bass contained fish prey in various stages of digestion. Reconstruction of the original weights of these prey is explained in Adams et al. (1982a).

Fish	Estimated weight of ingested prey (g)	Fish weight (g)
1	50, 34, 30	1,160
2	40	650
3	30, 29	710
4	70, 57	1,000
5	0	700
6	45	615

$$C = 100 \left( \frac{(114/1,160) + (40/650) + (59/710) + (127/1,000) + (0/700) + (45/615)}{6} \right)$$

= 7.4% of body weight or 74 mg/(g · d).

Water temperature, body sizes of predator and prey, meal size, and meal frequency all may affect digestion rate, as discussed by Windell (1978), Flowerdew and Grove (1979), and Mills et al. (1984). In addition, force-feeding of fish may prolong digestion because of handling stress, leading to underestimates of consumption (Swenson and Smith 1973).

*Diurnal Feeding Pattern.* Fish may feed synchronously (at particular periods of the day) or asynchronously (randomly), and this affects the choice of a consumption model. Calculation of daily ration based on meal frequencies requires that feeding be asynchronous throughout the day. To determine the diel feeding pattern of a fish, the average amount of food in the digestive tract (expressed as a percentage of body weight or as mg/g) or the number of prey in the gut should be measured at each of several intervals over a feeding cycle. To determine if gut contents are uniform over all sampling intervals (i.e., if the feeding pattern is asynchronous), average digestive tract contents (as percent weight or numbers) can be analyzed statistically by chi-square procedures (Minton and McLean 1982), nonparametric tests such as Kruskal-Wallis or Mann-Whitney (Godin 1981), one-way analysis of covariance combined with inferential analysis (Jenkins and Green 1977), or negative binomial distribution statistics (Sibert and Obrebski 1976).

### 12.3 ESTIMATION OF BIOENERGETIC COMPONENTS WITH EQUATIONS

In the previous section, guidelines were given for obtaining direct estimates of the major bioenergetic budget components from field or laboratory studies. These components can also be estimated indirectly with size- and temperature-dependent bioenergetic equations.

Fish size and water temperature are two of the most important variables that influence estimation of consumption and metabolism in bioenergetic equations. In the simple versions of the balanced energy budget (equations 12.1 and 12.2), none of the main components except respiration include adjustments for weight and temperature. Kitchell et al. (1974, 1977) and Elliott (1976) expanded the basic version of the energy budget to account for the influences of fish weight and water temperature on consumption, egestion, and excretion. The metabolism term, called "respiration" in their models (because metabolism is measured by respirometry) and denoted  $R$ , was also modified to explicitly include the costs of activity. The main components can be expressed as

$$C = R + F + U + \frac{dB}{B \cdot dt} \quad (12.10)$$

As before,  $C$ ,  $F$ , and  $U$  are consumption, egestion, and excretion rates, but total metabolism now is  $R$  and growth is  $dB/Bdt$ ,  $B$  being biomass and  $t$  being time.

As always,  $C$  can be estimated by addition if the other terms are known. It also can be estimated independently as a fraction of maximum consumption:

$$C = C_{\max} \cdot P \cdot r_c;$$

$C_{\max} = a_1 B^{b_1}$ , the weight-specific maximum consumption rate by fish fed ad libitum at their optimum temperature (g food/g fish);  $B$  is biomass in grams; and  $a_1$  and  $b_1$  are constants;

$r_c$  = a temperature-dependent proportional adjustment (0.0–1.0) of  $C_{\max}$  used when temperature is suboptimal ( $r_c = 1.0$  at optimum temperature), not to be confused with the  $r$  that denotes standard metabolism in equation (12.2); see Parker (1974), Kitchell et al. (1977), Thornton and Lessem (1978), and Weininger (1978) for alternative expressions of this term; and

$P$  = a scaling factor (0.0–1.0) that indicates the proportion of temperature-adjusted  $C_{\max}$  (i.e., of  $C_{\max} \cdot r_c$ ) that is actually consumed. The bioenergetic model of Hewett and Johnson (1987) uses an iterative technique to find the required  $P$  value.

The coefficient ( $a_1$ ), exponent ( $b_1$ ), and adjustment factors ( $r_c$ ) in this expression are determined from prior laboratory experiments.

The total metabolic or respiration rate has two terms:

$$R = R_{r+a} + s \cdot C; \quad (12.11)$$

$R_{r+a}$  is activity-dependent metabolism (standard plus activity metabolism, Section 12.2.2.2), and  $s$  is the coefficient for specific dynamic action ( $SDA = s \cdot C$ ,

Section 12.2.2.3). The coefficient  $s$ , usually around 0.15, is determined in laboratory studies.

Activity-dependent metabolism is affected by temperature ( $T$ , °C) and swimming speed ( $S$ , cm/s):

$$R_{r+a} = a_2 B^{b_2} e^{mT} e^{gS}; \quad (12.12)$$

again, the coefficients and exponents  $a_2$ ,  $b_2$ ,  $m$ , and  $g$  are determined empirically in the laboratory.

The function for  $R_{r+a}$  was first derived by Stewart et al. (1983) for lake trout, and Rice et al. (1983) applied it to largemouth bass. In the bioenergetic models developed for percids, the respiration equation is also a function of temperature and fish weight (Kitchell et al. 1977), but a different function is used for temperature dependence (a function similar to  $r_c$ ), and a single constant is used to adjust for the effects of activity rather than the activity metabolism term based on swimming speed as in equation (12.12).

For the waste loss components ( $F + U$ ) of equation (12.10), Elliott (1976) developed equations for the temperature dependence of egestion and excretion. However, such parameter resolution may not be necessary in all cases. Kitchell et al. (1977) showed that the sum of these two waste losses is essentially independent of temperature (the temperature effects nearly cancel out). For practical purposes, the waste term can be treated as an empirically determined, constant proportion of consumption (Section 12.2.3). Bartell et al. (1986) demonstrated that uncertainty in the waste loss parameters contributes only a relatively small amount to the uncertainty in predicted growth or consumption.

Use of the bioenergetics equation to calculate daily ration is demonstrated in Box 12.4.

Because temperature has a dominating influence on the metabolism, growth, digestion, and consumption rate of fish, the value of the temperature parameter used in bioenergetics models such as equation (12.11) is critical for accurate model predictions. When actual temperatures of the water occupied by fish living in a heterothermal environment (e.g., lakes or reservoirs that stratify in summer) are unknown, preferred temperature or optimal temperature for growth will provide a more realistic estimate for use in the bioenergetics equations than temperatures representing only one part of the environment. For example, bioenergetic simulations by Kitchell et al. (1977) showed that the predicted and observed growth of age-3 walleyes was similar only when the optimal temperature for growth (22°C) was used in the model instead of the observed surface water temperature of 27°C.

One of the most useful applications of the bioenergetics model is to estimate consumption from laboratory data on the physiological energetics of a species, field data on growth, and thermal history information (Hewett and Johnson 1987). Because growth is an integrator of food consumption over time, bioenergetics models generally have less error when they calculate consumption from growth data than when they predict growth from ration data (Bartell et al. 1986; Hewett and Johnson 1987).

Physiological data are unavailable for many fish species, but it still may be possible (and useful) to treat them in generalized bioenergetic models. Physiological parameters can be estimated from data on closely related species or

**Box 12.4 Calculation of Daily Consumption Rate with the Bioenergetic Equation**

**Problem:** calculate the daily ration of a 100-g largemouth bass that is growing at the average rate of 1 g/d at a temperature of 20°C as it swims at an average speed of 2 cm/s over a 24-h period. Use the empirically derived constants of Rice et al. (1983) with equations (12.10)–(12.12) of this chapter.

The governing bioenergetic equation is

$$C = R + F + U + (dB/Bdt);$$

$C$  = daily consumption (to be calculated),

$R$  = total metabolism (measured as respiration),

$F$  = egestion,

$U$  = excretion,

$B$  = biomass = 100 g (given),

$t$  = time = 1 d (given), and

$dB/Bdt$  = growth =  $1\text{g}/(100\text{g} \cdot \text{d}) = 0.010 \cdot \text{d}^{-1}$  (given).

Note that all of the components of the equation are weight-specific rates, that is,  $\text{g}/(\text{g} \cdot \text{d})$ .

Waste ( $F + U$ ) is assumed to be a constant proportion of consumption:

$$F + U = (f + u) \cdot C;$$

$f$  = egestion coefficient = 0.104 (from Rice et al.), and

$u$  = excretion coefficient = 0.079 (from Rice et al.).

Thus,

$$F + U = (0.104 + 0.079) \cdot C = 0.183C,$$

and the bioenergetic equation so far is

$$C = R + 0.183C + 0.010.$$

Total metabolism is

$$R = R_{r+a} + \text{SDA} = R_{r+a} + s \cdot c,$$

and activity-dependent metabolism ( $R_{r+a}$ ) is

$$R_{r+a} = a_2 B^{b_2} e^{mT} e^{gs};$$

SDA = specific dynamic action, assumed to be a constant proportion of consumption,

$s$  = SDA coefficient = 0.142 (from Rice et al.),

$a_2$  = 0.027 (expanded from hourly respiration in Rice et al. to account for caloric density:  $[0.348 \text{ mg O}_2/(\text{g} \cdot \text{h})] \times [24 \text{ h/d}] \times [3.24 \text{ cal/mg O}_2] \times [0.001 \text{ g/cal}]$ ),

$b_2$  = -0.355 (from Rice et al.),

$m$  =  $0.0313^\circ\text{C}^{-1}$  (from Rice et al.),

**Box 12.4 Continued.**

$T$  = temperature = 20°C (given),  
 $g$  = 0.0196 s/cm (from Rice et al.), and  
 $S$  = swimming speed = 2 cm/s (given).

Thus,

$$R_{r+a} = 0.027(100)^{-0.355} e^{0.0313(20)} e^{0.0196(2)} = 0.010 \text{ g/(g} \cdot \text{d)},$$

and

$$R = 0.010 + 0.142C.$$

The bioenergetic equation now is

$$C = 0.010 + 0.142C + 0.183C + 0.010;$$

$$C = 0.02/0.675 = 0.030 \text{ g/(g} \cdot \text{d)}.$$

Solution: the fish is consuming an average 3% of its body weight daily.

approximated from regressions based on data from many species (Robinson et al. 1983). Sensitivity analyses performed by Bartell et al. (1986) and Stewart and Binkowski (1986) on bioenergetics models indicate that, for some parameters, species-specific values impart little more precision to predicted growth or consumption than generalized values.

Bioenergetic models are now available for use on microcomputers (Hewett and Johnson 1987, 1989; Hewett 1989). To predict consumption, for example, the model of Hewett and Johnson (1987) requires input of the main physiological parameters, initial and final fish weights, and the thermal history of the fish. Documentation supplied with the models includes all the necessary physiological input parameters for lake trout, coho and chinook salmon, largemouth bass and bluegill, walleye and perch, lamprey, dace, and alewife.

Used with both species-specific parameters and parameters pooled from several species, bioenergetic models have been applied to more than 30 fish species to address a variety of research objectives and needs (Table 12.1). Most of these fish are important game and forage species representing primarily salmonids (Elliott 1976; Stewart et al. 1981, 1983), centrarchids (Breck and Kitchell 1979; Rice et al. 1983; Rice and Cochran 1984), percids (Kitchell et al. 1977), and esocids (Bevelhimer et al. 1985).

## 12.4 CRITERIA FOR APPLYING THE BIOENERGETICS APPROACH

A variety of factors should be considered when the bioenergetics (balanced energy budget) approach is applied in fishery biology. The importance of the research needs and objectives should be a large influence on the level of effort,

cost, and time allocated for development and application of a bioenergetics budget. For example, if the principal objective of a research project were to develop a management strategy for salmonids and their prey in the Great Lakes, this could require a much larger allocation of research resources than would the estimation of sunfish growth in a small farm pond.

In addition to the importance of the research objectives, the information available on the principal components of the energy budget should be an important consideration in the development and application of an energy budget for a particular research need. For several species of percids, salmonids, and centrarchids, the important bioenergetic parameters are available from previous studies (Table 12.1). For species in these groups, a relatively smaller effort would be required to estimate the major components of the energy budget with the equations (12.10 and 12.11) in section 12.3 than to do so by direct measurements (Section 12.2).

The accuracy and reliability of results will be affected both by the methods by which the bioenergetic components will be estimated and by the precision of the input terms. If the penalty for incorrectly predicting production (growth) is high, such as economic failure in a fish culture system, then increased effort and resources should be channeled into obtaining more precise estimates of such critical input parameters as temperature and feed consumption.

Sensitivity analysis is a useful way to evaluate how uncertainty or variation in the input parameters affects the uncertainty in predicted consumption or growth. Sensitivity analyses have been applied to bioenergetics models by Kitchell et al. (1977), Weininger (1978), Majkowski and Bramall (1980), Stewart et al. (1981), and Rice et al. (1983) and have been further evaluated by Bartell et al. (1986). These analyses can be used to assess the relative importance of the various input parameters for growth predictions, and thus can be employed to identify those model parameters and components that require further research efforts (e.g., allocation of research money), refinement, or simplification. For example, sensitivity analyses of growth models have indicated that uncertainty in parameter estimates for egestion and excretion contributes only a small amount to uncertainty in predicted growth or consumption (Bartell et al. 1986). Typically, the highest sensitivities for model parameters tend to be in the allometric functions for routine metabolism and consumption (Rice et al. 1983; Stewart et al. 1983).

Tests of bioenergetic model predictions are rare because the necessary data are difficult to obtain (Hewett and Johnson 1987). Model predictions can be tested by comparing independently measured bioenergetic components with those estimated by balancing the energy budget. Validation procedures for bioenergetics models have been discussed and applied by Rice and Cochran (1984). In the few studies in which the predictions of energy budgets have been compared with observed field values (Healey 1972; Adams 1976; Mills and Forney 1981; Diana 1983; Rice and Cochran 1984), the values have agreed reasonably well.

In summary, the use of bioenergetic budgets is a powerful approach for addressing a variety of research and management questions that may not be easily answered otherwise. Bioenergetics can be used to estimate patterns and magnitudes of growth and consumption, to evaluate the effects of environmental variables on fish dynamics and the effects of predators on their prey, to assess the effectiveness of various fish culture and management techniques, to predict the

uptake and accumulation of contaminants in fish, and to help interpretation of various life history strategies. This chapter has provided some practical methods and guidelines for obtaining estimates of the major energy budget components and has suggested ways to apply bioenergetics in fishery biology.

## 12.5 REFERENCES

- Adams, S. M. 1976. The ecology of eelgrass, *Zostera marina* (L.), fish communities. II. Functional analysis. *Journal of Experimental Marine Biology and Ecology* 22:293-311.
- Adams, S. M., R. B. McLean, and M. M. Huffman. 1982a. Structuring of a predator population through temperature-mediated effects on prey availability. *Canadian Journal of Fisheries and Aquatic Sciences* 39:1175-1184.
- Adams, S. M., R. B. McLean, and J. A. Parrotta. 1982b. Energy partitioning in largemouth bass under conditions of seasonally fluctuating prey availability. *Transactions of the American Fisheries Society* 111:549-558.
- Allen, J. R. M., and R. J. Wootton. 1982. The effect of ration and temperature on the growth of the three-spined stickleback, *Gasterosteus aculeatus* L. *Journal of Fish Biology* 20:409-422.
- Allen, J. R. M., and R. J. Wootton. 1984. Temporal patterns in diet and rate of food consumption of the three-spined stickleback (*Gasterosteus aculeatus* L.) in Llyn Frongock, an upland Welsh Lake. *Freshwater Biology* 14:335-346.
- Backiel, T. 1971. Production and food consumption of predatory fish in the Vistula River. *Journal of Fish Biology* 3:369-405.
- Bagenal, T. B., and F. W. Tesch. 1978. Age and growth. Pages 101-136 in T. Bagenal, editor. *Methods for assessment of fish production in fresh waters*. Blackwell Scientific Publications, Oxford, England.
- Bajkov, A. D. 1935. How to estimate the daily food consumption of fish under natural conditions. *Transactions of the American Fisheries Society* 65:288-289.
- Bartell, S. M., J. E. Breck, R. H. Gardner, and A. L. Brenkert. 1986. Individual parameter perturbation and error analysis of bioenergetics models of fish growth. *Canadian Journal of Fisheries and Aquatic Sciences* 43:160-168.
- Beamish, F. W. H. 1970. Oxygen consumption of largemouth bass, *Micropterus salmoides*, in relation to swimming speed and temperature. *Canadian Journal of Zoology* 48:1221-1228.
- Beamish, F. W. H. 1972. Ration size and digestion in largemouth bass, *Micropterus salmoides* Lacépède. *Canadian Journal of Zoology* 50:153-164.
- Beamish, F. W. H. 1974. Apparent specific dynamic action of largemouth bass, *Micropterus salmoides*. *Journal of the Fisheries Research Board of Canada* 31:1763-1769.
- Beamish, F. W. H., A. J. Niimi, and P. F. K. P. Lett. 1975. Bioenergetics of teleost fishes: environmental influences. Pages 187-209 in L. Bolis, H. P. Maddrell, and K. Schmidt-Nielsen, editors. *Comparative physiology—functional aspects of structural materials*. North-Holland Publishing, Amsterdam.
- Bevelhimer, M. S., R. A. Stein, and R. F. Carline. 1985. Assessing significance of physiological differences among three esocids with a bioenergetics model. *Canadian Journal of Fisheries and Aquatic Sciences* 42:57-69.
- Bowen, S. H. 1983. Quantitative description of the diet. Pages 325-336 in L. A. Nielsen and D. L. Johnson, editors. *Fisheries techniques*. American Fisheries Society, Bethesda, Maryland.
- Brafield, A. E., and D. J. Solomon. 1972. Oxy-caloric coefficients for animals respiring nitrogenous substrates. *Comparative Biochemistry and Physiology A, Comparative Physiology* 43:837-841.
- Breck, J. E., and J. F. Kitchell. 1979. Effects of macrophyte harvesting on simulated predator-prey interactions. Pages 221-228 in J. E. Breck, R. T. Prentki, and O. L. Loucks, editors. *Conference on aquatic plants, lake management and ecosystem consequences of lake harvesting*. Institute of Environmental Studies, University of Wisconsin, Madison.

- Brett, J. R. 1964. The respiratory metabolism and swimming performance of young sockeye salmon. *Journal of the Fisheries Research Board of Canada* 21:1183-1226.
- Brett, J. R. 1976. Scope for metabolism and growth of sockeye salmon, *Oncorhynchus nerka*, and some related energetics. *Journal of the Fisheries Research Board of Canada* 33:307-313.
- 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, editors. *Fish physiology*, volume 8. Academic Press, New York.
- Burbidge, R. G. 1974. Distribution, growth, selective feeding, and energy transformation of young-of-the-year blueback herring, *Alosa aestivalis* (Mitchill), in the James River, Virginia. *Transactions of the American Fisheries Society* 103:297-311.
- Carline, R. F., and J. D. Hall. 1973. Evaluation of a method for estimating food consumption rates of fish. *Journal of the Fisheries Research Board of Canada* 30:623-629.
- Carline, R. F., B. L. Johnson, and T. J. Hall. 1984. Estimation and interpretation of proportional stock density for fish populations in Ohio impoundments. *North American Journal of Fisheries Management* 4:139-154.
- Caulton, M. S. 1978. The importance of habitat temperatures for growth in the tropical cichlid *Tilapia rendalli* Boulenger. *Journal of Fish Biology* 13:99-112.
- Cho, C. Y., S. J. Slinger, and H. S. Bayley. 1982. Bioenergetics of salmonid fishes: energy intake, expenditure and productivity. *Comparative Biochemistry and Physiology B, Comparative Biochemistry* 73:25-41.
- Cochran, P. A., and I. R. Adelman. 1982. Seasonal aspects of daily ration and diet of largemouth bass *Micropterus salmoides* with an evaluation of gastric evacuation rates. *Environmental Biology of Fishes* 7:265-275.
- Conover, R. J. 1966. Assimilation of organic matter by zooplankton. *Limnology and Oceanography* 11:338-345.
- Cooney, T. D. 1973. Yolk sac stage energetics of the larvae of three Hawaiian fishes. Master's thesis. University of Hawaii, Honolulu.
- Cuenca, M. L., R. R. Stickney, and W. E. Grant. 1985. Fish bioenergetics and growth in aquaculture ponds: I. Individual fish model development. *Ecological Modelling* 27:169-190.
- Darnell, R. M., and R. R. Meierotto. 1962. Determination of feeding chronology in fishes. *Transactions of the American Fisheries Society* 91:313-320.
- DeAngelis, D. L., S. M. Adams, and J. E. Breck. 1984. A stochastic predation model: application to largemouth bass feeding. *Ecological Modelling* 24:25-41.
- Diana, J. S. 1979. The feeding pattern and daily ration of a top carnivore, the northern pike (*Esox lucius*). *Canadian Journal of Zoology* 57:2121-2127.
- Diana, J. S. 1983. An energy budget for northern pike. *Canadian Journal of Zoology* 61:1968-1975.
- Durbin, E. G., and A. G. Durbin. 1983. Energy and nitrogen budgets for the Atlantic menhaden, *Brevoortia tyrannus* (Pisces:Clupeidae), a filter-feeding planktivore. U.S. National Marine Fisheries Service Fishery Bulletin 81:177-199.
- Eggers, D. M. 1979. Comments on some recent methods of estimating food consumption by fish. *Journal of the Fisheries Research Board of Canada* 36:1018-1019.
- Eldridge, M. B., J. A. Whipple, and M. J. Bowers. 1982. Bioenergetics and growth of striped bass, *Morone saxatilis*, embryos and larvae. U.S. National Marine Fisheries Service Fishery Bulletin 80:461-474.
- Elliott, J. M. 1972. Rates of gastric evacuation in brown trout *Salmo trutta*. *Freshwater Biology* 2:1-18.
- Elliott, J. M. 1976. The energetics of feeding, metabolism and growth of brown trout (*Salmo trutta* L.) in relation to body weight, water temperature and ration size. *Journal of Animal Ecology* 45:923-948.
- Elliott, J. M. 1979. Energetics of freshwater teleosts. *Symposia of the Zoological Society of London* 44:29-61.
- Elliott, J. M., and W. Davison. 1975. Energy equivalents of oxygen consumption in animal energetics. *Oecologia (Berlin)* 19:195-201.
- Elliott, J. M., and L. Persson. 1978. The estimation of daily rates of food consumption by fish. *Journal of Animal Ecology* 47:977-991.

- Fisher, Z. 1972. The elements of energy balance in grass carp (*Ctenopharyngodon idella* Val.). Part III. Assimilability of proteins, carbohydrates, and lipids by fish fed with plant and animal food. Polish Archives of Hydrobiology 19:83-95.
- Flath, L. E., and J. S. Diana. 1985. Seasonal energy dynamics of the alewife in southeastern Lake Michigan. Transactions of the American Fisheries Society 114:328-337.
- Flowerdew, M. W., and D. J. Grove. 1979. Some observations of the effects of body weight, temperature, meal size and quality on gastric time in turbot, *Scophthalmus maximus* (L.), using radiography. Journal of Fish Biology 14:229-238.
- Forney, J. L. 1977. Reconstruction of yellow perch (*Perca flavescens*) cohorts from examination of walleye (*Stizostedion vitreum vitreum*) stomachs. Journal of the Fisheries Research Board of Canada 34:925-932.
- From, J., and G. Rasmussen. 1984. A growth model, gastric evacuation, and body composition in rainbow trout, *Salmo gairdneri* Richardson, 1836. Dana 3:61-139.
- Fry, F. E. J. 1957. The aquatic respiration of fish. Pages 1-63 in M. S. Brown, editor. The physiology of fish, volume 1. Academic Press, New York.
- Gerking, S. D. 1972. Revised food consumption estimate of a bluegill sunfish population in Wyland Lake, Indiana, USA. Journal of Fish Biology 4:301-308.
- Glebe, B. D., and W. C. Leggett. 1981. Latitudinal variations in energy allocation and use during the freshwater migrations of American shad (*Alosa sapidissima*) and their life history consequences. Canadian Journal of Fisheries and Aquatic Sciences 38:806-820.
- Godin, J.-G. J. 1981. Daily patterns of feeding behavior, daily rations, and diets of juvenile pink salmon (*Oncorhynchus gorbuscha*) in two marine bays of British Columbia. Canadian Journal of Fisheries and Aquatic Sciences 38:10-15.
- Hayward, R. S., and F. J. Margraf. 1987. Eutrophication effects on prey size and food availability to yellow perch in Lake Erie. Transactions of the American Fisheries Society 116:210-223.
- Healey, M. C. 1972. Bioenergetics of the sand goby (*Gobius minutus*) population. Journal of the Fisheries Research Board of Canada 29:187-194.
- Hewett, S. W. 1989. Ecological applications of bioenergetics models. American Fisheries Society Symposium 6:113-120.
- Hewett, S. W., and B. L. Johnson. 1987. A generalized bioenergetics model of fish growth for micro-computers. University of Wisconsin, Sea Grant Technical Report WIS-SG-87-245, Madison.
- Hewett, S. W., and B. L. Johnson. 1989. A general bioenergetics model for fishes. American Fisheries Society Symposium 6:206-208.
- Hunt, B. P. 1960. Digestion rate and food consumption of Florida gar, warmouth, and largemouth bass. Transactions of the American Fisheries Society 89:206-210.
- Hunter, J. R., and R. Leong. 1981. The spawning energetics of female northern anchovy, *Engraulis mordax*. U.S. National Marine Fisheries Society Fishery Bulletin 79:215-230.
- Ivlev, V. S. 1966. The biological productivity of waters. Journal of the Fisheries Research Board of Canada 23:1727-1759.
- Jearld, A. 1983. Age determination. Pages 301-324 in L. A. Nielsen and D. L. Johnson, editors. Fisheries techniques. American Fisheries Society, Bethesda, Maryland.
- Jenkins, B. W., and J. M. Green. 1977. A critique of field methodology for determining fish feeding periodicity. Environmental Biology of Fishes 1:209-214.
- Jobling, M. 1981. Mathematical models of gastric emptying and the estimation of daily rates of food consumption for fish. Journal of Fish Biology 19:245-257.
- Jorgensen, S. E. 1976. A model of fish growth. Ecological Modelling 2:303-313.
- Keast, A., and L. Welsh. 1968. Daily feeding periodicities, food uptake rates, and dietary changes with hour of day in some lake fishes. Journal of the Fisheries Research Board of Canada 25:1133-1144.
- Kerr, S. R. 1971. Prediction of fish growth efficiency in nature. Journal of the Fisheries Research Board of Canada 28:809-814.
- Kerr, S. R. 1982. Estimating the energy budgets of actively predatory fishes. Canadian Journal of Fisheries and Aquatic Sciences 39:371-379.

- Kitchell, J. F. 1983. Energetics. Pages 312–338 in P. Webb and D. Weihs, editors. Fish biomechanics. Praeger, New York.
- Kitchell, J. F., and J. E. Breck. 1980. Bioenergetics model and foraging hypothesis for sea lamprey (*Petromyzon marinus*). Canadian Journal of Fisheries and Aquatic Sciences 37:2159–2168.
- Kitchell, J. F., J. F. Koonce, R. V. O'Neill, H. H. Shugart, J. J. Magnuson, and R. S. Booth. 1974. Model of fish biomass dynamics. Transactions of the American Fisheries Society 103:786–798.
- Kitchell, J. F., D. J. Stewart, and D. Weininger. 1977. Application of a bioenergetics model to yellow perch (*Perca flavescens*) and walleye (*Stizostedion vitreum vitreum*). Journal of the Fisheries Research Board of Canada 34:1922–1935.
- Lasker, R. 1970. Utilization of zooplankton energy by a Pacific sardine population in the California current. Pages 265–284 in J. H. Steele, editor. Marine food chains. University of California Press, Los Angeles.
- Laurence, G. C. 1977. A bioenergetic model for the analysis of feeding and survival potential of winter flounder, *Pseudopleuronectes americanus*, larvae during the period from hatching to metamorphosis. U.S. National Marine Fisheries Service Fishery Bulletin 75:529–546.
- Lyons, J. 1984. Walleye predation, yellow perch abundance, and the population dynamics of an assemblage of littoral-zone fishes in Sparkling Lake, Wisconsin. Doctoral dissertation. University of Wisconsin, Madison.
- MacKinnon, J. C. 1972. Summer storage of energy and its use for winter metabolism and gonadal maturation in American plaice (*Hippoglossoides platessoides*). Journal of the Fisheries Research Board of Canada 29:1749–1759.
- Majkowski, J., and L. Bramall. 1980. Sensitivity of bioenergetic growth models of animals to changes in the energy balance parameters. Journal of Theoretical Biology 85:645–655.
- Mann, K. H. 1965. Energy transformation by a population of fish in the River Thames. Journal of Animal Ecology 34:253–275.
- Mann, K. M. 1978. Estimating the food consumption of fish in nature. Pages 250–273 in S. D. Gerking, editor. Ecology of freshwater fish production. Wiley, New York.
- McGee, M. V., J. S. Griffith, and R. B. McLean. 1979. Prey selection by sauger in Watts Bar Reservoir, Tennessee, as affected by cold-induced mortality of threadfin shad. Proceedings of the Annual Conference Southeastern Association of Fish and Wildlife Agencies 31:404–411.
- Megrey, B. A. 1978. Applications of a bioenergetics model to gizzard shad (*Dorosoma cepedianum*): a simulation of seasonal biomass dynamics in an Ohio reservoir. Master's thesis. Miami University, Oxford, Ohio.
- Mills, E. L., and J. L. Forney. 1981. Energetics, food consumption, and growth of young yellow perch in Oneida Lake, New York. Transactions of the American Fisheries Society 110:479–488.
- Mills, E. L., R. C. Ready, M. Jahneke, C. R. Hanger, and C. Trowbridge. 1984. A gastric evacuation model for young yellow perch, *Perca flavescens*. Canadian Journal of Fisheries and Aquatic Sciences 41:513–518.
- Minckley, C. O., and L. J. Paulson. 1976. Use of gizzard weights to determine total length and weight of threadfin shad eaten by predators. Transactions of the American Fisheries Society 105:409–410.
- Minton, J. W., and R. B. McLean. 1982. Measurements of growth and consumption of sauger (*Stizostedion canadense*): implication of fish energetic studies. Canadian Journal of Fisheries and Aquatic Sciences 39:1396–1403.
- Muir, B. S., and A. J. Niimi. 1972. Oxygen consumption of the euryhaline fish aholehole (*Kuhlia sandvicensis*) with reference to salinity, swimming, and food consumption. Journal of the Fisheries Research Board of Canada 29:67–77.
- Nakashima, B. S., and W. C. Leggett. 1978. Daily ration of yellow perch (*Perca flavescens*) from Lake Memphremagog, Quebec–Vermont, with a comparison of methods for in situ determinations. Journal of the Fisheries Research Board of Canada 35:1597–1603.

- Niimi, A. J., and F. W. H. Beamish. 1974. Bioenergetics and growth of largemouth bass (*Micropterus salmoides*) in relation to body weight and temperature. *Canadian Journal of Zoology* 52:447-456.
- Norstrom, R. J., A. E. McKinnon, and A. S. W. DeFreitas. 1976. A bioenergetics-based model for pollutant accumulation by fish. Simulation of PCB and methylmercury residue levels in Ottawa River yellow perch (*Perca flavescens*). *Journal of the Fisheries Research Board of Canada* 33:248-267.
- Paloheimo, J. E., and L. M. Dickie. 1966. Food and growth of fishes. III. Relations among food, body size, and growth efficiency. *Journal of the Fisheries Research Board of Canada* 23:1209-1248.
- Parker, R. A. 1974. Empirical functions relating metabolic processes in aquatic systems to environmental variables. *Journal of the Fisheries Research Board of Canada* 31:1550-1552.
- Persson, L. 1979. The effects of temperature and different food organisms on the rate of gastric evacuation in perch (*Perca fluviatilis*). *Freshwater Biology* 9:99-104.
- Peters, D. S., and D. E. Hoss. 1974. A radioisotopic method of measuring food evacuation time in fish. *Transactions of the American Fisheries Society* 103:626-629.
- Peters, D. S., and M. A. Kjelson. 1975. Consumption and utilization of food by various postlarval and juvenile fishes of North Carolina estuaries. *Estuarine Research* 1:447-472.
- Pierce, R. J. 1977. Life history and ecological energetics of the gizzard shad (*Dorosoma cepedianum*) in Acton Lake, Ohio. Doctoral dissertation. Miami University, Oxford, Ohio.
- Popova, O. A. 1967. The 'predator-prey' relationship among fish. Pages 359-376 in S. D. Gerking, editor. *The biological basis of freshwater fish production*. Blackwell Scientific Publications, Oxford, England.
- Popova, O. A. 1978. The role of predaceous fish in ecosystems. Pages 215-249 in S. D. Gerking, editor. *Ecology of freshwater fish production*. Wiley, New York.
- Popova, O. A., and L. A. Sytina. 1977. Food and feeding relations of Eurasian perch (*Perca fluviatilis*) and pikeperch (*Stizostedion lucioperca*) in various waters of the USSR. *Journal of the Fisheries Research Board of Canada* 34:1559-1570.
- Rice, J. A. 1990. Bioenergetics modeling approaches to evaluation of stress in fishes. *American Fisheries Society Symposium* 8:80-92.
- 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. *Environmental Biology of Fishes* 9:263-275.
- Rice, J. A., and P. A. Cochran. 1984. Independent evaluation of a bioenergetics model for largemouth bass. *Ecology* 65:732-739.
- Robinson, W. R., R. H. Peters, and J. Zimmerman. 1983. The effects of body size and temperature on metabolic rate of organisms. *Canadian Journal of Zoology* 61:281-288.
- Schalles, J. F., and T. E. Wissing. 1976. Effects of dry pellet diets on the metabolic rates of bluegill (*Lepomis macrochirus*). *Journal of the Fisheries Research Board of Canada* 33:2443-2449.
- Scott, D. B. C. 1979. Environmental timing and the control of reproduction in teleost fish. *Symposia of the Zoological Society of London* 44:105-132.
- Seaburg, K. G., and J. B. Moyle. 1964. Feeding habits, digestion rates, and growth of some Minnesota warmwater fishes. *Transactions of the American Fisheries Society* 93:269-285.
- Sharp, G. D., and R. C. Francis. 1976. An energetics model for the exploited yellowfin tuna, *Thunnus albacares*, population in the eastern Pacific Ocean. *U.S. National Marine Fisheries Service Fishery Bulletin* 74:36-51.
- Sibert, J., and S. Obrebski. 1976. Frequency distributions of food item counts in individual fish stomachs. Pages 107-114 in C. A. Simenstad and S. J. Lipovsky, editors. *Fish food habits. First Pacific Northwest technical workshop proceedings*. University of Washington, Washington Sea Grant Program, Seattle.
- Smith, K. L., Jr. 1973. Energy transformations by the sargassum fish *Histrio histrio* (L.). *Journal of Experimental Marine Biology and Ecology* 12:219-227.

- Solomon, D. J., and A. E. Brafield. 1972. The energetics of feeding, metabolism and growth of perch (*Perca fluviatilis* L.). *Journal of Animal Ecology* 41:699-718.
- Stauffer, G. D. 1973. A growth model for salmonids reared in hatchery environments. Doctoral dissertation. University of Washington, Seattle.
- Steigenberger, L. W., and P. A. Larkin. 1974. Feeding activity and rates of digestion of northern squawfish (*Ptychocheilus oregonensis*). *Journal of the Fisheries Research Board of Canada* 31:411-420.
- Stewart, D. J., and F. P. Binkowski. 1986. Dynamics of consumption and food conversion by Lake Michigan alewives: an energetics-modeling synthesis. *Transactions of the American Fisheries Society* 115:643-661.
- Stewart, D. J., J. F. Kitchell, and L. B. Crowder. 1981. Forage fishes and their salmonid predators in Lake Michigan. *Transactions of the American Fisheries Society* 110:751-763.
- Stewart, D. J., D. Weininger, D. V. Rottiers, and T. A. Edsall. 1983. An energetics model for lake trout, *Salvelinus namaycush*: application to the Lake Michigan population. *Canadian Journal of Fisheries and Aquatic Sciences* 40:681-698.
- Swenson, W. A. 1977. Food consumption of walleye (*Stizostedion vitreum*) and sauger (*S. canadense*) in relation to food availability and physical conditions in Lake of the Woods, Minnesota, Shagawa Lake, and western Lake Superior. *Journal of the Fisheries Research Board of Canada* 34:1643-1654.
- Swenson, W. A., and L. L. Smith. 1973. Gastric digestion, food conversion, feeding periodicity, and food conversion efficiency in walleye (*Stizostedion vitreum vitreum*). *Journal of the Fisheries Research Board of Canada* 30:1327-1336.
- Thomann, R. V., and J. P. Connolly. 1984. Model of PCB in the Lake Michigan lake trout food chain. *Environmental Science and Technology* 18:65-71.
- Thornton, K. W., and A. S. Lessem. 1978. A temperature algorithm for modifying biological rates. *Transactions of the American Fisheries Society* 107:284-287.
- Thorpe, J. E. 1977. Daily ration of adult perch *Perca fluviatilis* L. during summer in Lock Leven, Scotland. *Journal of Fish Biology* 11:55-68.
- Tyler, A. V. 1970. Rate of gastric emptying in young cod. *Journal of the Fisheries Research Board of Canada* 27:1177-1189.
- Tyler, P., and P. Calow. 1985. *Fish energetics: new perspectives*. Johns Hopkins University Press, Baltimore, Maryland.
- Ursin, E. 1979. Principles of growth in fishes. *Symposia of the Zoological Society of London* 44:63-87.
- Vaughan, D. S., R. M. Yoshiyama, J. E. Breck, and D. L. DeAngelis. 1984. Modeling approaches for assessing the effects of stress on fish populations. Pages 259-278 in V. W. Cairns, P. V. Hodson, and J. O. Nriagu, editors. *Contaminant effects on fisheries*. Wiley, New York.
- Wahl, D. H., and L. A. Nielsen. 1985. Feeding ecology of the sauger (*Stizostedion canadense*) in a large river. *Canadian Journal of Fisheries and Aquatic Sciences* 42:120-128.
- Ware, D. M. 1975. Growth, metabolism, and optimal swimming speed of a pelagic fish. *Journal of the Fisheries Research Board of Canada* 32:33-41.
- Warren, C. E., and G. E. Davis. 1967. Laboratory studies on the feeding, bioenergetics, and growth of fish. Pages 175-214 in S. D. Gerking, editor. *The biological basis of freshwater fish production*. Blackwell Scientific Publications, Oxford, England.
- Weatherley, A. H. 1978. Some aspects of age and growth. Pages 52-74 in S. D. Gerking, editor. *Ecology of freshwater fish production*. Wiley, New York.
- Webb, P. W. 1978. Partitioning of energy into metabolism and growth. Pages 184-214 in S. D. Gerking, editor. *Ecology of freshwater fish production*. Wiley, New York.
- Weininger, D. 1978. Accumulation of PCBs by lake trout in Lake Michigan. Doctoral dissertation. University of Wisconsin, Madison.
- Williams, G. C. 1961. *Adaptation and natural selection: a critique of some current evolutionary thought*. Princeton University Press, Princeton, New Jersey.
- Winberg, G. G. 1956. Rate of metabolism and food requirements of fishes. Byelorussian State University, Minsk. Translated from Russian: Fisheries Research Board of Canada Translation Series 194, 1960, Ottawa.

- Windell, J. T. 1967. Rates of digestion in fishes. Pages 151–153 in S. D. Gerking, editor. The biological basis of freshwater fish production. Blackwell Scientific Publications, Oxford, England.
- Windell, J. T. 1978. Digestion and daily ration of fishes. Pages 159–183 in S. D. Gerking, editor. Ecology of freshwater fish production. Wiley, New York.
- Windell, J. T., and S. H. Bowen. 1978. Methods for study of fish diets based on analysis of stomach contents. Pages 219–226 in T. Bagenal, editor. Methods for the assessment of fish production in fresh waters. Blackwell Scientific Publications, Oxford, England.
- Wissing, T. E. 1974. Energy transformations by young-of-the-year white bass *Morone chrysops* (Rafinesque) in Lake Mendota, Wisconsin. Transactions of the American Fisheries Society 103:32–37.
- Wootton, R. J., J. R. M. Allen, and S. J. Cole. 1980. Energetics of the annual reproductive cycle in female sticklebacks, *Gasterosteus aculeatus* L. Journal of Fish Biology 17:387–394.