ENERGETICS

Energy Utilization in Growth

Contents

Energetics of Growth

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Glossary

Anabolism Synthesis of materials via metabolic processes; a series of chemical reactions that builds larger molecules from smaller components, usually requiring energy in the process.

Bioenergetics Quantitative analysis of the energetic processes of living organisms.

Catabolism Metabolic processes that result in the release of energy from organic molecules.

Darwinian fitness Contribution of an individual to the gene pool of the next generation, often estimated as lifetime reproductive success (LRS).

Joule (J) Energy exerted by a force of 1 N acting to move an object through a distance of 1 m. It is the SI unit of energy.

Ontogeny Changes in the phenotype of an individual during its life span. Ontogeny is the outcome of a developmental program, encoded in an organism's genes, as well as interactions between the genotype of the individual and the environments it encounters, together with any maternal effects mediated through the egg itself.

**Parameter** A numerical constant in a quantitative relationship.

Somatic Body of an individual excluding the gonads.

Watt Rate of doing work, a measure of power as $J\ s^{-1}$.

Introduction

Growth, like all other physiological processes, is constrained by the laws of physics and chemistry. The laws of thermodynamics are of particular importance in the study of the bioenergetics of growth, forming the basis for the quantitative study of growth. The laws impose the constraints that during growth, energy can be neither created nor destroyed and that as useful work is done during the synthesis of materials required for growth, energy will be dissipated as heat. In studies of natural populations of fish or in aquaculture, growth is usually measured as changes in mass or length. However, growth can also be estimated as the change in energy content of fish, where energy content is measured by the heat generated when fish mass is burnt in an atmosphere of oxygen (bomb calorimetry), measured as joules (J), with the energy concentration $[E]$ expressed as $J\ g^{-1}$. The rate at which a fish uses energy can be expressed as power, measured in watts ($J\ s^{-1}$). Once growth is measured in energy units, energy conservation requires that growth = energy input − energy output, where energy input is the energy content of the food consumed and energy output is the energy lost in the form of fecal waste, excretory products (especially ammonia), maintenance metabolism, and as useful work is done. Growth is the energy retained in the body of the fish in the form of the energy of the chemical bonds in the organic molecules that have accumulated in the body. The relationship, growth = energy input − energy output, is a truism and can be applied, in principle, to any organism. The challenge is how to develop this principle in
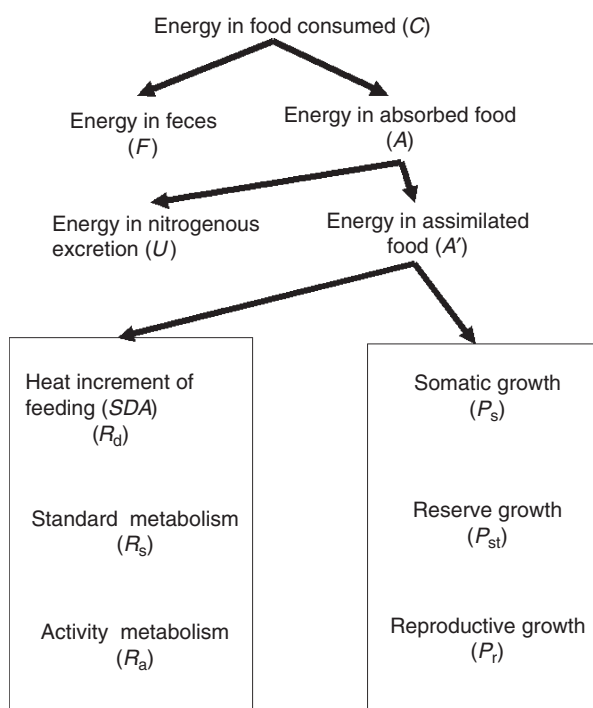
Figure 1 Pattern of energy allocation in individual fish described by Davis and Warren model.

a way that allows quantitative predictions to be made about the pattern of growth in specific circumstances for the identified species or groups of species of fish.

Growth has three components (**Figure 1**). The first is structural growth that builds the body of the fish, with its skeleton, muscles, nerve cells, and other tissues and organs, which allow the fish to function in its environment. In fish, the energy costs of this growth are predominantly the energy costs of the synthesis of proteins and structural lipids together with any costs of organizing the synthesized material into functioning components. The second component is reserve, or storage growth. This component provides a reservoir of energy that can be mobilized when the energy input in the form of food is insufficient to meet the individual's needs, but replenished when food availability is high. In fish, lipids generally form the main storage material, but some fish (e.g., the lungfish *Protopterus*) specialize in protein storage. Carbohydrates usually play only a minor role. The third component of growth is reproduction, represented by the germ cells, sperm, and eggs, which are eventually released during reproduction. For eggs, the main component is the yolk, made up of lipoprotein, while sperm are essentially packets of DNA wrapped in a lipid membrane.

Energy Budget

The three components of growth can be related to other aspects of the bioenergetics of the individual fish in the framework of an energy budget that itemizes the intake and output, the latter including growth over a defined time period. The budget must balance, because energy can neither be created nor destroyed (**see also Energetics**: General Energy Metabolism and **Energetic Models**: Bioenergetics in Aquaculture Settings). The basic equation is

$$C = F + U + R + P$$

where C is the food consumed, F the fecal waste, U the excretory losses produced by the metabolism of nitrogenous compounds, particularly proteins, R the heat lost during metabolism, and P is the total growth. All the items are measured in energy units. The heat-loss component, R, can be broken down into subcomponents:

$$R = R_S + R_D + R_A$$

where R_S is the standard metabolism, which is approximated as the heat expenditure of a resting, unfed individual; R_D the heat expenditure associated with the processing of the food consumed (sometimes called specific dynamic action, SDA); and R_A the additional heat expenditure of an active fish (**see also Energetics**: General Energy Metabolism). The growth component, P, can be subdivided as

$$P = P_S + P_{ST} + P_R$$

where P_S is the energy content of the structural growth, P_{ST} the energy content of the storage growth, and P_R the energy content of reproductive growth.

Conceptually, it is also useful to define absorbed energy (A) as $A = C - F$; and assimilated energy (A') as $A' = A - U$ or $A' = C - (F + U)$. A' is essentially the energy available to do useful work and to accumulate as growth.

Growth Efficiencies

The efficiency of a system is defined as output divided by input, where output and input are explicitly defined. Thus, in the context of the energy budget of an individual fish, the efficiency of growth can be defined. Three growth efficiencies are defined, depending on the input. For total growth, P, the efficiencies (expressed as percentages) are: $K_1 = 100 PC^{-1}$ in which growth is related to the food consumed; $K_2 = 100 PA'^{-1}$, where growth is related to assimilated energy; $K_3 = 100 P(C - C_{MAIN})^{-1}$, where growth is related to the energy of food consumed that is in excess of the maintenance ration (C_{MAIN}). C_{MAIN} is the level of food consumption when the individual fish is neither increasing nor decreasing in energy content, so growth and growth efficiency are zero.

Typically, for machines, including living organisms, it is not possible to maximize both the efficiency of a process and the maximum rate of that process. This suggests that a

growing fish cannot maximize its growth rate and its growth efficiency simultaneously.

Energy Allocation and Its Fitness Consequences

An individual is faced with the problem of how the energy obtained by its feeding activities should be allocated among the components of the energy budget (**Figure 2**). From moment to moment, the fish must solve the problem of what pattern of energy allocation will maximize its Darwinian fitness, which here can be defined as lifetime reproductive success (LRS). The allocation must be made in the context of limitations of the time available for energy acquisition, the need to shelter from predators or adverse physical conditions, the intensity of competition for food, and eventually the need to devote time to achieve reproductive success (**see also Food Acquisition and Digestion**: Energetics of Prey Capture: From Foraging Theory to Functional Morphology and Energetics of Foraging Decisions and Prey Handling). These limitations will mean that there are trade-offs. Energy allocated to maintenance, including expenditure on repair and defense against pathogens and parasites, will tend to increase the fitness component of survival. However, that energy is not available to be allocated to growth or reproduction. Energy allocated to somatic growth is not available for allocation to storage or reproductive growth. However, somatic growth means that the size of the fish increases, which also tends to increase the fitness component of survival. In addition, because fecundity in fish generally increases with fish size, allocation to somatic growth tends to increase future fecundity at the cost of allocation to present reproduction. Rapid somatic growth can also reduce the age at which the fish becomes sexually mature, thus decreasing the risk that it will die before reproducing. However, rapid growth can also diminish swimming performance. Allocation to storage growth has two possible advantages. It may allow the fish to survive adverse periods when feeding is poor, when the fish can mobilize its stored energy. Second, it may allow the fish to reproduce at times or in places that are advantageous to the progeny, but disadvantageous to the parents. Given these trade-offs, the optimal allocation of energy will change during the ontogeny of the individual fish and is dependent upon the abiotic and biotic environments. The pattern of energy allocation over the ontogeny of the fish defines the life-history pattern of that fish.

Growth Models of Fish Based on Bioenergetics

von Bertalanffy model

In studies of fish biology and fisheries, the von Bertalanffy model has been probably the most influential growth model based on bioenergetic principles (**Figure 3**). Its development is associated with the names of Pütter and von Bertalanffy, and it was proposed as a general model of animal growth. It argues that growth rate is the difference between the rate of synthesis (anabolism) and the rate of breakdown (catabolism) of proteins, lipids, and
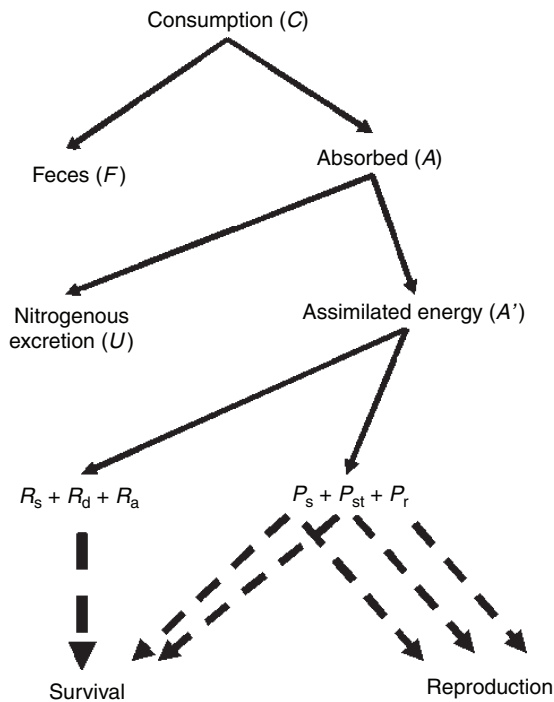
Figure 2 Effect of components of energy budget on components of fitness, that is, survival and reproduction, of an individual fish, indicated by broken lines.
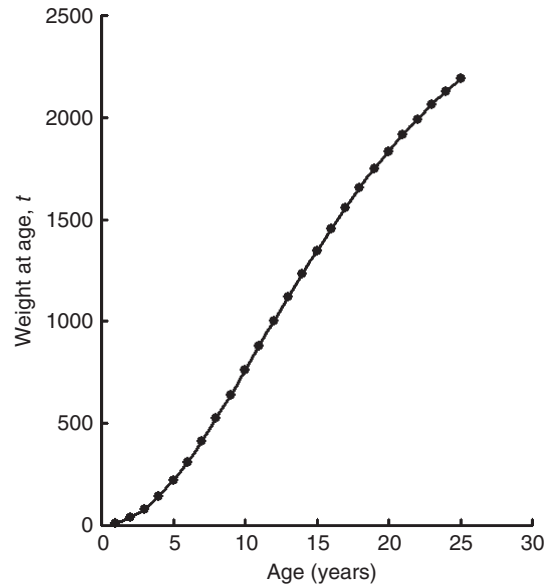
Figure 3 Example of von Bertalanffy growth model based on parameters describing growth of North Sea plaice (*Pleuronectes platessa*).

carbohydrates, with the anabolic and catabolic rates being related to body size. It then assumes that the rate of anabolism is determined by the surface area of the individual, but the rate of catabolism is directly proportional to body mass. Thus, growth rate $(\mathrm{d}W/\mathrm{d}t)$ is expressed as $\mathrm{d}W/\mathrm{d}t = hW^{2/3} - kW$, where W is the body mass, and h and k the coefficients of anabolism and catabolism, respectively. A further assumption is that as the individual grows, it does not change in shape, that is, growth is isometric. That is, mass, W, and body length, l, have the relationship: $W = al^3$, where a and b are parameters. From these assumptions, von Bertalanffy growth equations are derived. For length, the model is $l_t = l_\infty [1 - \mathrm{e}^{-k(t - t_0)}]$, and for mass, the model is $W_t = W_\infty [1 - \mathrm{e}^{-k(t - t_0)}]^3$, where l_t is the length at age t, l_∞ the asymptotic length, W_∞ the asymptotic mass, e the base of natural logarithms, k a constant that defines the rate at which the growth curve approaches the asymptote, and t_0 a constant that determines the hypothetical age at which the size of the fish is zero. The three constants, l_∞ (or W_∞), k, and t_0, determine the shape of the relationship between size and age, that is, the shape of the growth curve. Although based on physiological principles, the von Bertalanffy model has been used to fit curves to plots of size against age. In this role, it played a part in the derivation of the important Beverton and Holt model used in fisheries management.

A surprising feature of the von Bertalanffy model is that it does not include a term describing the rate of food intake. Growth cannot take place without an input of food that provides the required materials and energy; so, for a growth model to be predictive as well as descriptive, it has to include a term describing the rate of food consumption. This has led to a re-definition of the von Bertalanffy model in which the anabolic term is replaced by a term describing the rate of energy assimilation: $(j W_t^d)$, where j and d are parameters. The rate of food consumption, C, is given by $C = (j W_t^d)a^{-1}$, where a is the assimilation efficiency $(A'C^{-1})$.

If $d = 2/3$, then the von Bertafanffy model is now expressed in terms of food assimilation and catabolism. Simulation studies indicate that the estimates of food consumption using this model are highly sensitive to the value of the parameter d.

Winberg model
Well before the modifications to the von Bertalanffy model that replaced the anabolic term by an assimilation term, Winberg introduced a balanced energy budget to describe the relationship among food consumption, growth, and metabolism. He identified input as the energy content of food consumed (C) and the outputs as growth (P) and metabolic expenditure (R). From a survey of the data then available, he suggested that assimilated energy represented 70% of the consumed energy, that is, $0.7C$. The energy

budget was then expressed as $P = 0.7C - R$. Winberg argued that for fish in natural populations, R could be approximated as twice the standard metabolism measured under laboratory conditions; thus, $P = 0.7C - 2R_S$. In early studies of the bioenergetics of fish, this simple formulation provided a useful approximation of the magnitudes of growth and food consumption in natural populations. An early experimental study of the bioenergetics of the European perch, *Perca fluviatilis*, suggested that the Winberg equation could give a reasonable estimate of the maintenance metabolic rate, that is, when growth is zero, and of the metabolic rate of a fish on an unrestricted ration.

Davis and Warren model
A further step in the development of a bioenergetics model of growth was provided by the Davis and Warren model. This model is a flow diagram of the partitioning of the energy income among the energy outputs, the latter including any growth (**Figure 1**). The model thus provided a framework in which the pattern of energy allocation, in principle, could be described quantitatively. Each term in the energy budget equation for growth $P = C - (F + U) - R$ (see earlier) can be measured experimentally under defined conditions of individual body mass, water temperature, food availability, and other relevant environmental conditions. If four of the five terms in the energy budget equation are estimated empirically under defined conditions, the fifth can be obtained by calculation. For example, if C, F, U, and R are measured, P can be calculated, providing a prediction of growth under those conditions. That prediction can then be tested experimentally, by estimating the growth (in energy units) of individuals raised under the defined conditions.

The energy budget under defined conditions can be described in terms of the percentage allocation. The allocation by the grass carp, *Ctenopharyngodon idella*, when the fish were fed duckweed was summarized as $100C = 35F + 51R + 9P$, but, when fed tubificid worms, $100C = 9F + 8U + 61R + 22P$. This illustrates the effect of the better-quality animal diet on growth. A comparison of carnivorous with herbivorous species in terms of an energy budget suggested values of $100C = 27(F + U) + 44R + 27P$ for carnivores and $100C = 43(F + U) + 37R + 20P$ for herbivores.

Wisconsin growth model
The Davis and Warren model lies at the heart of the Wisconsin bioenergetics model that has found the most use as a predictive tool in fisheries biology (**see also Energetic Models**: Bioenergetics in Ecosystems). The model was made available as a computer package with a comprehensive manual, including data for a range of species on the parameters required to estimate the components of the energy budget. The model uses the energy

budget equation to predict the growth of a fish of a given initial mass over a selected time period, typically 24 h. The mass of the fish at the end of the 24 h is then used as the starting point for the prediction of growth over the next 24 h and so on for as many days as required. Relevant factors such as temperature can also be changed on a day-by-day basis. The computer package allows the growth in body size of fish in different age classes (cohorts) to be simulated and so the bioenergetics of the individual fish can be extended to the bioenergetics of the population of fish.

In the Wisconsin model, growth energy, P, is converted to the increase in mass, ΔW, by dividing P by the energy density of the fish $[E]$, so $\Delta W = P [E]^{-1}$. A flavor of the model can be given by describing some of the relationships used to quantify components of the Davis and Warren energy budget. Food consumption, C, is estimated as $C = p C_{MAX} f(T)$, where p is the proportion of C_{MAX} consumed, $f(T)$ is a function that describes the effect of temperature on food consumption, and the maximum rate of consumption $C_{MAX} = a W_t^b$, where a and b are parameters. C is converted into energy units for use in the mass-balance equation by multiplying by the energy density of the food $[E_{FOOD}]$. Metabolic expenditure, R, is estimated as $R = (ACT) R_S g(T) + R_D$, where ACT is a multiplier to define the level of activity and $g(T)$ is a function describing the effect of temperature on metabolism. If $ACT = 2$, then active metabolic rate is twice the resting rate. Each of the relationships used has to be defined for the species of interest.

The Wisconsin model has been used to guide management strategies, especially for the Great Lakes in North America. A list of its uses includes the following: (1) the evaluation of the factors that constrain fish growth; (2) the evaluation of the impact of fish predators on prey populations; (3) quantification of the dynamics of bioaccumulation of contaminants such as polychlorinated biphenyls (PCBs); (4) prediction of the waste loads produced by an aquaculture system; and (5) enhancement of an understanding of the role that fish play in ecological processes in aquatic systems. The Wisconsin model is also incorporated as a subcomponent of individual-based models of fish life history and population dynamics.

The Wisconsin model also illustrates some of the problems in using bioenergetics models to predict growth in natural populations. The first problem is obtaining a realistic estimate of the level of activity of fish in a natural population so that the metabolic costs of activity can be estimated. A second problem is estimating the rate of food consumption in natural populations in the context of the availability of suitable food items (**see also Food Acquisition and Digestion**: Energetics of Prey Capture: From Foraging Theory to Functional Morphology). This means that the Wisconsin model is often used to estimate food consumption on the basis of observed growth, rather
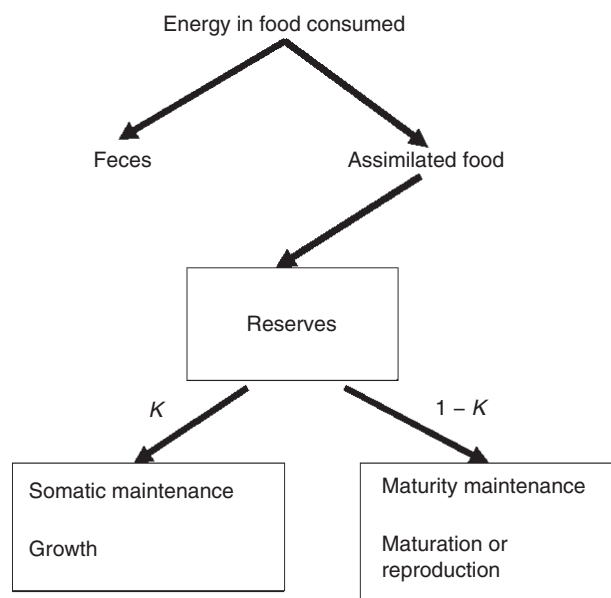
than growth from observed consumption. A third problem is that the Warren and Davis and its successor, the Wisconsin model, do not include an explicit model of how energy should be allocated between the different outputs to maximize fitness. Although the structure of the Wisconsin model is general for any fish species, to apply it to a specific population of a species requires knowledge of a high number of parameters to define the relationships among the components of the energy budget and body mass, temperature, and other relevant factors. This means that care must be taken to examine the sensitivity of the predicted growth to the values of the parameters used in the model.

Dynamic energy budget model

A comprehensive bioenergetics model has been developed by the Dutch biologist, SALM Kooijman. Although this model is, in principle, applicable to all living organisms, it has been adapted to simulate the growth of fish. The crucial feature of this model is that it does explicitly include a rule for the allocation of energy among outputs. It assumes that assimilation rate is proportional to body surface area, that is, to $V^{2/3}$, where V is the structural volume of the individual, while maintenance rate is proportional to body volume, V (these proportionalities recall those used in the von Bertalanffy model). The assimilated products then enter a reserve pool, from where they are allocated to maintenance, somatic growth, and reproduction. A fixed fraction of the reserve, K, is allocated to maintenance and growth, while the remaining fraction, $1 - K$, is allocated to development and reproduction. If the rate of assimilation is low, priority is given to maintenance, and if the rate of energy utilization from the reserves cannot meet the costs of somatic maintenance, the individual eventually dies.

The dynamic energy budget (DEB) model (**Figure 4**) uses two state variables to describe an individual fish: the volume of the somatic body, V, and energy density of the reserves $[E]$, which describes the quantity of reserves, E, per unit of structural body volume. The DEB model clearly distinguishes between structural body and reserves. With these assumptions, the DEB generates a growth equation, which is mathematically, if not conceptually, equivalent to the von Bertalanffy model. Extensions of the basic model apply to embryos, which do not feed or reproduce, and juveniles, which feed, but do not reproduce. In some extensions of the model, a further allocation rule is proposed, which governs the allocation between somatic growth and stored reserves. A disadvantage of the DEB model is that the parameters used to develop the model are difficult to estimate.

In a simplified form, the DEB model has provided some insight into the nature of compensatory growth in salmonid fishes, and the simulation of the growth of Atlantic salmon, *Salmo salar*, in a Scottish stream. Although the model is

Energy in food consumed

Feces   Assimilated food

Reserves

K $1 - K$

Somatic maintenance

Growth

Maturity maintenance

Maturation or
reproduction

Figure 4 Dynamic energy budget (DEB) model of energy allocation in individual fish, showing K-rule.

conceptually more realistic than the Wisconsin model, because it does incorporate an allocation rule, it has not matched the use of the Wisconsin model in practical studies of fish growth.

Conclusion

As bioenergetic models of growth are based firmly on the laws of thermodynamics, they offer the prospect of providing realistic simulations of growth under defined environmental conditions. Even under conditions of relatively stable long-term environmental conditions, the ability to predict the growth trajectories of fish in natural populations or in aquaculture is valuable for conservation and resource management. With the predicted long-term changes in global temperatures and the consequences for the climate, the ability to predict the effects of the changes on the growth rate and related traits of fish will be essential to devise strategies that will reduce, as far as is possible, the impact of these changes. The models also provide a framework within which physiological studies on the neuroendrocrine control of energy allocation in the individual fish can be conducted. There continues to be the need to verify and validate the bioenergetic model used, by carefully designed laboratory and field studies that result in improvements to the structures of the models and the estimates of the parameters used in the models.

See also: **Energetic Models**: Bioenergetics in Aquaculture Settings; Bioenergetics in Ecosystems. **Energetics**: General Energy Metabolism. **Food Acquisition and Digestion**: Energetics of Foraging Decisions and Prey Handling; Energetics of Prey Capture: From Foraging Theory to Functional Morphology.

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