



Comments on proper (and improper) solutions of bioenergetic equations for modeling fish growth



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ABSTRACT

This paper demonstrates that conventional bioenergetic models, that are commonly used to simulate fish growth or consumption, violate basic requirements of energy conservation when improperly applied for cases where the energy density of the fish is either a function of fish wet weight or an independent function of time. It appears that many previously published modeling results suffer from this deficiency unless the authors have made perspicuous provisions to avoid implicit imbalances that occur in the equations under these conditions. The incorrect solutions tend to overestimate fish growth and net energy consumption. The magnitude of these errors is a function of how rapidly the fish energy density changes as the fish increases in size. The errors can be as much as 30% for small fish in the range of 1 to 5 g per individual where the energy density changes rapidly. Although this mathematical error does not occur if fish energy density is modeled as a constant, this assumption is probably inadequate for most applications and results in a substantial “biological error.” It is recommended that published results for these various cases be critically reviewed and corrected where warranted. The errors can be readily eliminated when the bioenergetic model equations are handled properly as demonstrated in this paper.

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1. Introduction

Fish growth models have been used in aquaculture for many years. Some of the early models summarized empirical findings on the relationships among growth, ration, and temperature (Brett, 1974; Brett and Shelbourn, 1975; Brett et al., 1969; Elliott, 1975a, 1975b; Elliott et al., 1995; Iwama and Tautz, 1981). Fish growth models based on energy balance and bioenergetics are potentially more flexible and can make predictions for a wider range of conditions compared to empirical models (Brigolin et al., 2010; Csargo et al., 2012; Jobling, 2011; Madenjian, 2011). The models predict the growth or consumption of individual fish as a function of control variables such as temperature, food supply, and food composition. If such models can be calibrated and reliably validated, they can then be combined with mass balance equations for nitrogen and phosphorus and subsequently used as practical tools to optimize fish production and minimize environmental impacts. For example, Stigebrandt et al. (2004) describe this approach for fish farms for Atlantic salmon (*Salmo salar*) and Brigolin et al. (2010) have developed models for biomass

yields and environmental impacts of gilthead seabream (*Sparus aurata* L.) mariculture activities in the Adriatic seas.

2. Energy balance

Models for fish growth are based on equations that require conservation of energy. The energy available to fish to increase their body weight or energy density (\dot{E}_{Net}) is calculated from the energy provided by food consumption after accounting for various losses and non-growth metabolism. Eq. (1) describes a continuity equation for these processes, in which the rate of change of energy available (kJ/day) is the difference between the rate of energy intake and the rates of various energy losses (Brett and Groves, 1979). The dot above the E is a standard notation for rate of change, and the subscripts indicate the particular processes.

$$\dot{E}_{Net} = \dot{E}_C - \dot{E}_F - \dot{E}_E - \dot{E}_S - \dot{E}_R \quad (1)$$

\dot{E}_C is the rate of energy intake due to food consumed by an individual fish; \dot{E}_F is the rate of energy lost by egestion in feces; \dot{E}_E is the rate of energy lost by excretion of nitrogenous wastes in urine or by ammonia lost across the gills; \dot{E}_S is specific dynamic action or the rate of energy utilized for ingestion, digestion, and assimilation of food; and \dot{E}_R is the rate of energy used during standard and active

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respiration. Eq. (1) omits the energetic cost of reproduction, and therefore is only valid prior to sexual maturity.

The total body energy (kJ) associated with an individual fish is the product of the wet weight and the energy density of the fish. The rate of change of total body energy can be described by Eq. (2).

$$\frac{d[\varepsilon_{Fish} \cdot W]}{dt} = \dot{E}_{Net} \quad (2)$$

In Eq. (2), ε_{Fish} = the fish energy density (kJ/g), W = wet weight (g), and t = time (usually days). Note that the net energy available from the consumed food can be used to increase W with ε_{Fish} constant, or increase ε_{Fish} with W constant. However, extensive data in the literature indicate that ε_{Fish} is a function of W , and therefore solutions of Eq. (2) must account for changes in both components simultaneously. The general expression for the fish energy density (ε_{Fish}) can be formulated as a constant ($\bar{\varepsilon}_{Fish}$) or as various functions of fish weight or time $\varepsilon_{Fish}(W, t)$. Subsequent sections discuss the mathematical and biological implications of alternative formulations.

Implicit in Eq. (2) is the requirement that the energy associated with the fish at the end of any time interval (*End*) minus the energy associated with the fish at the beginning of the time interval (*Start*) must be equal to the sum or total net energy provided to the fish over the interval. Mathematically, this requirement is expressed by Eq. (3).

$$\varepsilon_{Fish}(End) \cdot W(End) - \varepsilon_{Fish}(Start) \cdot W(Start) = \int_{Start}^{End} \dot{E}_{Net} \cdot dt \quad (3)$$

All valid solutions of Eq. (2) must also satisfy Eq. (3).

In order to develop equations for the change in fish weight (dW/dt), the left side of Eq. (2) must first be expanded using the Chain Rule (also called the Product Rule) for the general case where the energy density can vary with either fish weight or time.

$$\frac{d[\varepsilon_{Fish}(W, t) \cdot W]}{dt} = \varepsilon_{Fish}(W, t) \cdot \frac{dW}{dt} + W \cdot \frac{d\varepsilon_{Fish}(W, t)}{dt} \quad (4)$$

Then Eqs. (2) and (4) can be used to solve for the rate of change of weight.

$$\frac{dW}{dt} = \frac{\dot{E}_{Net}}{\varepsilon_{Fish}(W, t)} - \left[\frac{W}{\varepsilon_{Fish}(W, t)} \frac{d\varepsilon_{Fish}(W, t)}{dt} \right] \quad (5)$$

Note that when the energy density of fish changes for any reason, the term in brackets on the right-hand side of Eq. (5) is a necessary adjustment to the rate of change in weight that is needed in order to balance the energy budget. Solutions that simply neglect the bracketed term overestimate fish growth when energy density typically increases with fish weight or time.

3. Fish energy density

Shearer (1994) published a comprehensive review of the factors that affect the proximate composition and energy density of cultured salmonids from eggs to sexual maturity. The review included endogenous factors such as size and life cycle, as well as exogenous factors such as temperature, diet composition, and ration level. The next section develops equations for fish growth that properly accommodate various formulations that have been used by researchers to describe the relationship between the energy density of a fish and its weight.

3.1. Case 1: fish energy density is constant

Munch and Conover (2002) developed bioenergetic models to simulate the growth of Atlantic silverside (*Menidia menidia*) populations.

Their model employs a constant value for silverside energy density. A similar approach was used by Libralato and Solidoro (2008) in their model to study the allometric and temperature functionality of feeding and respiration of gilthead seabream. Many other bioenergetic model applications have used a constant value for fish energy density (Breck, 1993; Pääkkönen et al., 2003; Rice et al., 1983). In these cases, $\varepsilon_{Fish}(W, t)$ reduces to a constant value ($\bar{\varepsilon}_{Fish}$) and the term in brackets on the right-hand side of Eq. (5) is zero (because the rate of change of a constant is zero). This results in Eq. (6).

$$\frac{dW}{dt} = \frac{\dot{E}_{Net}}{\bar{\varepsilon}_{Fish}} \quad (6)$$

It is important to note that Eq. (6) is valid only for the limited case where $\varepsilon_{Fish}(W, t)$ is constant and not a function of W or time.

Note that it is possible (in fact easy) to generate numerical solutions of Eq. (6) while incorrectly varying the fish energy density with either time or W . Although such solutions might upon casual glance seem reasonable, they violate the fundamental continuity condition described by Eq. (3), that is, the gain in energy associated with the fish biomass will not equal the sum of the net energy retained over the growth interval. For all other cases, as discussed below, $\varepsilon_{Fish}(W, t)$ cannot be factored out of the differential operator in Eq. (2).

3.2. Case 2: fish energy density is a linear function of W

Many investigators such as Stewart et al. (1983), Stewart and Ibarra (1991), Rudstam et al. (1994), Hanson et al. (1997), and Roy et al. (2004) have used linear or piece-wise linear functions to express the relationship between fish energy density and wet weight (see Eq. (7)).

$$\varepsilon_{Fish}(W) = \alpha + \beta \cdot W \quad (7)$$

The coefficients α and β are empirical constants. In this linear case, the rate of change of the energy density with respect to time is equal to $\beta \cdot dW/dt$. In order to develop an equation for the growth of the fish, Eq. (7) is inserted into Eq. (4), resulting in Eq. (8).

$$\frac{d[\varepsilon_{Fish}(W) \cdot W]}{dt} = \varepsilon_{Fish}(W) \cdot \frac{dW}{dt} + W \cdot \frac{d\varepsilon_{Fish}(W)}{dt} = (\alpha + 2 \cdot \beta \cdot W) \cdot \frac{dW}{dt} \quad (8)$$

Eq. (9) describes the growth of an individual fish for the case where fish energy density is a linear function of wet weight.

$$\frac{dW}{dt} = \frac{\dot{E}_{Net}}{(\alpha + 2 \cdot \beta \cdot W)} \neq \frac{\dot{E}_{Net}}{\varepsilon_{Fish}(W)} \quad (9)$$

The magnitude of the errors associated with incorrect application of Eq. (9) will be discussed in a following section.

3.3. Case 3: fish energy density is a power function of W

Craig (1977) as well as many others (e.g., Craig et al., 1978; Paine, 1971) have used measurements of proximate body composition to calculate the energy density of fish as in Eq. (10).

$$\varepsilon_{Fish} = \varepsilon_{Lipid} \cdot L + \varepsilon_{Protein} \cdot P \quad (10)$$

L and P are the lipid and protein fractions of whole fish wet weight, and ε_{Lipid} and $\varepsilon_{Protein}$ are the energy densities of lipid and protein (kJ/g). Eq. (10) follows the usual assumption that the contribution of carbohydrates is typically negligible (Craig, 1977). Thus if the fish proximate composition and wet weight are measured, the energy density is easily calculated. Shearer et al. (1997) and Gunther et al. (2005) as well as many others have found highly significant correlations between the log of lipid content and the log of wet weight and the log of protein

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