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Modeling Juvenile Salmonid Hatchery Growth Using a Local Equilibrium Assumption and Measured Water Fraction to Parameterize Fish Energy Density

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ABSTRACT

Previous reports have described bioenergetic models for juvenile salmonid growth that were validated using data from laboratory and production-scale feeding studies. Time variable functions and power correlations with body weight based on measurement of proximate composition were used to delineate the fish energy density in these models. Although model simulations for growth corresponded closely with measured data using either characterization of energy density, there is significant laboratory burden associated with the measurement of proximate composition throughout the simulation period, and this approach may therefore be impractical for many hatchery applications. Here measurements of fish water fraction are used to estimate the mass of protein and ash using correlations developed in a companion paper. Lipid is subsequently determined by difference, and energy content is calculated using the proximate composition. Model simulations of juvenile coho (*Oncorhynchus kisutch*) growth and proximate composition using this approach closely matched measured data when provided steady satiation and maintenance rations. The model was less successful predicting detailed protein and lipid dynamics following large abrupt decreases in the food supply rate. However, model simulation errors associated with fish growth were small because of the off-setting nature of the proximate composition model errors. It is concluded that coho water fraction measurements and correlations for protein and ash offer a practical and convenient alternative to direct measurement of fish energy density for many bioenergetic model hatchery applications.

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1. Background

Our long-term goal has been to develop reliable and practical models that can be used to predict food consumption, growth, and waste by-product generation associated with juvenile salmonid hatchery production. A bioenergetic model was initially validated for juvenile coho and Chinook salmon (*O. tshawytscha*) by comparing model simulations with growth data from two independent controlled laboratory feeding studies (Canale et al., 2013). Neely et al. (2008) compared the growth of an unselected wild strain (Skykomish) of coho salmon with a domestic strain (Dømsea) selected for its rapid growth characteristics. Model simulations were consistent with the observed growth for each strain when the consumption rate model coefficients were adjusted to characterize differences in the stomach size. Shearer et al. (1997) measured the growth and proximate composition of juvenile Chinook salmon in response to high and low lipid diets supplied at two different feeding rates. Model simulations were closely comparable to measured data when the model coefficients for the apparent respiration rate and

the fish energy density were adjusted to account for differences in ration and body lipid content. The efficacy of this model was extended using data from a production-scale growth and feeding study (Canale and Whelan, in press). In this study, the bioenergetic model calculations closely matched measured growth data when the apparent respiration rate and fish energy density were adjusted to account for different rations. Model calculations that employed time variable functions or used approximations for energy density based on correlations with coho body weight were equally successful in simulating growth.

In both of these efforts, the fish energy density must be a known function of time or be algebraically related to fish body weight in order to implement the model. This characterization must be done on a case-by-case basis because the energy density of fish with the same weight may be a function of diet, ration, and ration history. This poses a burdensome task and may be impractical for typical hatchery applications. In a companion paper, Breck (2014) extended earlier work by Groves (1970) and developed statistical correlations for body protein and body ash using only measurements of body weight and water fraction for several fish species including coho salmon. The correlations for coho salmon are used here to estimate proximate composition and energy density to support the requirements of a conventional bioenergetics model for coho growth. This approach will be called the

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GB method here after Groves (1970) and Breck (2014). The following sections examine the applicability of the GB approach for models that have been previously validated using growth measurements obtained during controlled production-scale feeding studies (see below).

2. Energy Balance

Bioenergetic models are based on a well-known equation that requires conservation of energy. The equation simply specifies that the rate of net energy available to the fish ($\dot{E}_{Net}$) is equal to the rate of net energy available from food sources after discounting for losses and non-growth metabolic requirements. Eq. (1) describes the rate equation for these processes. The dot above the E terms is standard notation for rate of change, and the subscripts indicate the particular processes. All the terms in Eq. (1) have units of calories per day (cal/day).

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

$\dot{E}_C$ is the energy from consumed food; $\dot{E}_F$ is the energy lost by egestion of feces; $\dot{E}_E$ is the 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 energy utilized for ingestion, digestion, and assimilation of food (SDA); and $\dot{E}_R$ is the energy used by respiration (standard plus active). Eq. (1) neglects the energetic cost of reproduction, and therefore is only valid prior to sexual maturity.

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

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

where ε_{Fish} is the energy density of the fish in cal/g of whole wet weight of fish, W is the whole wet weight of an individual fish in grams, and t is time (usually days). Note that if $\dot{E}_{Net}$ is greater than zero the energy content of the fish increases. This can result in an increase in the weight of the fish with the energy density constant, an increase in the energy density with the weight constant, or more likely some combination of an increase in both weight and energy density. If $\dot{E}_{Net}$ is less than zero then the energy content of the fish decreases and can be manifested as a decrease in either fish weight or energy density.

Note that Eq. (2) describes changes in the total energy content of the fish. Although this may be useful on occasion, we are generally more interested in predicting changes in the weight of the fish and its composition. Eq. (2) cannot be used to directly calculate the growth of the fish without further assumptions. Researchers have taken three basic approaches to separate W from the left-hand side of Eq. (2). The fish energy can be (1) input to the model as an independent forcing function of time; (2) modeled dynamically as a system of kinetic differential equations; or (3) assumed to be in local equilibrium with body weight and related algebraically to body weight. These alternatives will be discussed below.

2.1. Fish Energy Density is a Forcing Function of Time

The first approach used to isolate W in Eq. (2) is to simply measure the energy density of the fish as a function of time $\varepsilon(t)_{Fish}$, substitute this known function into the left hand side of Eq. (2), and solve for $W(t)$. This is a type of forcing function because the calculated growth must comply with the measured time variable function for the energy density and simultaneously be consistent with energy conservation. Although this approach necessitates the fewest assumptions, it demands no recognition of the biochemical mechanisms associated with the energy density dynamics. Furthermore, the requirement to

have *a priori* knowledge of the energy density dynamics may not be convenient or practical for many applications.

Note that when $\varepsilon(t)_{Fish}$ varies with time it cannot be simply factored out of the left hand side of Eq. (2) without violating continuity. Instead the Chain Rule must be employed (Canale and Breck, 2013) resulting in the following differential equation that can be solved for $W(t)$:

$$\frac{dW}{dt} = \frac{\dot{E}_{Net} - W \cdot \dfrac{d\varepsilon_{Fish}}{dt}}{\varepsilon(t)_{Fish}} \tag{3}$$

Megrey et al. (2007) used piece-wise linear functions of time to specify the energy density in a bioenergetics model for Pacific herring (*Clupea harengus pallasi*). Madenjian et al. (2012) employed a linear time-variable function to describe the energy density of walleye (*Sander vitreus*) in a model to describe growth in laboratory studies. Canale and Whelan (in press) used linear and polynomial functions of time to model production-scale growth of coho salmon for four different rations.

2.2. Kinetic Model for Fish Energy Density

Rather than treating the energy density as a forcing function of time, Bar et al. (2007) and Bar and Radde (2009) developed dynamic models for fish growth and composition. These models incorporate detailed kinetic equations that describe the main metabolic pathways (protein, lipid, and central metabolism) that play major roles in growth and body composition. The models consist of a system of non-linear differential equations where fish weight and composition are the model dependent variables. The models simulate growth and body composition on a time scale of several months and the flow of metabolites and nutrients through various pathways on the scale of a few hours. This is referred to as a dynamic or kinetic approach for modeling of proximate composition. This type of model has numerous coefficients and has substantial data requirements for development and validation and is perhaps best oriented toward research applications. It has not been applied for typical hatchery operations.

2.3. Fish Energy Density Employing the Local Equilibrium Assumption

The next approach uses algebraic equations to describe the relationship between body weight and energy density. The algebraic equations do not depend on time, and implicit in this approach is the assumption that composition responds quickly to changes in body weight compared to longer-term seasonal or life cycle changes in body weight. Applications where a local equilibrium assumption is employed (sometimes called the quasi-steady state assumption) occur in a variety of settings in chemistry and biology (Chapra, 1997; Fogler, 2005; Valocchi, 1985). The major emphasis of this paper will be an analysis of various local equilibrium assumptions that have been used in association with bioenergetic models for fish growth.

2.3.1. Fish Energy Density is Constant

The simplest local equilibrium assumption is that the fish energy density is a constant equal to $\overline{\varepsilon}_{Fish}$. In this case the energy density can be easily separated from Eq (2), resulting in Eq. (4) that can be used to solve directly for $W(t)$.

$$\frac{dW}{dt} = \frac{\dot{E}_{Net}}{\overline{\varepsilon}_{Fish}} \tag{4}$$

It is important to note that Eq. (4) is valid only for limited cases where energy density is constant and not a function of W or time. However, it is well known that the energy density is typically not constant and large errors in predicted values for W can result from inappropriate application of Eq. (4) (Canale and Breck, 2013).