STUDY PERFORMANCE REPORT

State: Michigan

Project No.: F-80-R-14

Study No.: 230756

Title: Development of management scenarios for lake and stream habitat and fisheries under current and future land-use and climate conditions

Period Covered: October 1, 2012 to September 30, 2013

Study Objectives: The overall objective of this project is to develop a tool that incorporates land-use and climate change scenarios and societal values of lakes and streams to identify management priorities based on assessed sensitivity and risk. The specific objectives of this study are to:

1. Assess habitat conditions for all lakes and streams statewide under current land-use and climate conditions.
2. Determine how current habitat conditions influence sport fish populations and fish community structure in lakes and streams.
3. Determine the potential changes in habitat suitability, sport fish populations, and fish community structure in response to changes in land-use and climate conditions.
4. Identify and map the lakes and streams that are most at risk to change.
5. Develop statistical models to predict how anglers use lake and stream resources at a statewide scale.
6. Generate information for evaluating non-fisheries uses of lake and stream resources at a statewide scale using GIS techniques.
7. Prioritize lakes and streams for management based on their habitat and fisheries risks and social uses and values.

Summary: Boosted regression tree models were developed that predict abundance and growth of fish species in 6,500 lakes. Nutrient loading models and a new temperature model were developed for use in predicting habitat changes in lakes. Recently developed predictions from 14 downscaled climate data were obtained and summarized for all lakes and stream reach catchments in Michigan. Changes in thermal regime and fish species suitability were estimated for all lakes greater than or equal to 10 acres. Maps identifying lakes vulnerable to species changes were developed for 14 different climate scenarios for mid-century and late century time steps. Manuscripts were written describing errors in bioenergetics models and methods for estimating fish proximate composition.

Findings: Jobs 2-4 and 7-10 were active this year. The progress of each active job is reported below.

Job 2. Title: Develop lake profile models. —No progress was made on this job because of personnel changes.

Job 3. Title: Develop community/habitat models. —Boosted regression tree models were developed that predict abundance and growth of fish species as a function of lake temperature, morphology, position, and hydrology. A new lake temperature model was developed that better accounts for
maximum temperatures expected under future climate warming. Loading models were developed to predict nutrient inputs to lakes based on land use characteristics.

**Job 4. Title: Develop bioenergetics models.**—In the process of developing bioenergetics models for several species of Michigan fishes, two types of errors were discovered in some common implementations of bioenergetics models. One type of error is mathematical, and the other is biological. The mathematical error involves the manner of implementation of the basic equation for change in body energy. If a fish’s energy density is changing through time (the most common situation), then the equation for fish growth in weight must properly account for that changing energy density. Failure to properly account for changing energy density will result in simulations that do not obey the law of conservation of energy: (initial fish energy) + (energy consumed) will not equal (new fish energy) + (energy lost as waste). A type of biological error can arise if it is assumed that fish energy density is constant when in reality it is changing. Many applications of bioenergetics models involve fish that are either increasing or decreasing in weight, and energy density is very likely to be changing under these situations. Although the type of mathematical error described above does not occur when fish density is constant, the assumption of constant energy density may introduce a type of biological error into the results of bioenergetic modeling, producing model results that differ from reality (Canale and Breck 2013). When both types of potential error are handled appropriately, bioenergetic simulations of fish growth can produce very good matches to laboratory data on fish growth (Canale et al. 2013). In the course of carefully examining previously published data on fish energy density and proximate composition, a very strong pattern was found in the relationship between mass of water and mass of protein. Data sets for several species show that the mass ratio of water and protein is constant for a given water mass, and the ratio changes slightly but statistically significantly with water mass. Smaller fish have more water per unit protein than larger fish. A similar pattern was found for mass of water and mass of ash. Used together, these very strong relationships can be used to predict mass of protein, ash, and lipid from mass of water (= wet weight * fraction water). Energy density can then be calculated from protein, lipid, and wet weight.

**Job 7. Title: Assess future habitat and fish changes.**—New downscaled climate data from 14 models were summarized for all lake and stream catchments for use in predicting habitat and fish species’ responses to climate change. Changes in thermal regime and fish species suitability were estimated for 6,500 lakes using these 14 climate scenarios for mid-century and late-century.

**Job 8. Title: Identify and map vulnerable waters.**—Maps were created that show the total number of species changes (additions and subtractions) in 6,500 lakes under different climate warming scenarios.

**Job 9. Title: Write annual performance reports.**—This performance report was prepared as scheduled.

**Job 10. Title: Write manuscripts.**—A manuscript describing the mathematical errors in bioenergetics models was written and published (citation below). A manuscript describing how to estimate proximate composition was written and has been submitted for publication.

Literature Cited


Prepared by: Kevin Wehrly
Date: September 30, 2013
Comments on proper (and improper) solutions of bioenergetic equations for modeling fish growth

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A B S T R A C T

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; Cargue 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 (ENet) 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 $\dot{E}$ is a standard notation for rate of change, and the subscripts indicate the particular processes.

$$ ENet = \dot{E}_c - \dot{E}_p - \dot{E}_e - \dot{E}_s - \dot{E}_r. $$ (1)

$\dot{E}_c$ is the rate of energy intake due to food consumed by an individual fish; $\dot{E}_p$ 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
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).

\[
\frac{d\epsilon_{\text{Fish}}}{dt} \cdot W = \dot{E}_{\text{Net}}.
\]  

(2)

In Eq. (2), \( \epsilon_{\text{Fish}} \) = 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 \( \epsilon_{\text{Fish}} \) constant, or increase \( \epsilon_{\text{Fish}} \) with \( W \) constant. However, extensive data in the literature indicate that \( \epsilon_{\text{Fish}} \) 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 \( (\epsilon_{\text{Fish}}) \) can be formulated as a constant \( \epsilon_{\text{Fish}}(t) \) or as various functions of fish weight or time \( \epsilon_{\text{Fish}}(W, t) \). 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).

\[
\epsilon_{\text{Fish}}(\text{End}) \cdot W(\text{End}) - \epsilon_{\text{Fish}}(\text{Start}) \cdot W(\text{Start}) = \int_{\text{Start}}^{\text{End}} \dot{E}_{\text{Net}} \ dt.
\]  

(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.

\[
\frac{d\epsilon_{\text{Fish}}(W, t)}{dt} \cdot W = \epsilon_{\text{Fish}}(W, t) \cdot \frac{dW}{dt} + W \cdot \frac{d\epsilon_{\text{Fish}}(W, t)}{dt}.
\]  

(4)

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

\[
\frac{dW}{dt} = \frac{\dot{E}_{\text{Net}}}{\epsilon_{\text{Fish}}(W, t)} - \left[ \frac{W}{\epsilon_{\text{Fish}}(W, t)} \cdot \frac{d\epsilon_{\text{Fish}}(W, t)}{dt} \right].
\]  

(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 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 silversides (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, \( \epsilon_{\text{Fish}}(W, t) \) reduces to a constant value \( \epsilon_{\text{Fish}} \) 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).

\[
\frac{dW}{dt} = \frac{\dot{E}_{\text{Net}}}{\epsilon_{\text{Fish}}}
\]  

(6)

It is important to note that Eq. (6) is valid only for the limited case where \( \epsilon_{\text{Fish}}(W, t) \) 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, \( \epsilon_{\text{Fish}}(W, t) \) 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)).

\[
\epsilon_{\text{Fish}}(W) = \alpha + \beta \cdot W.
\]  

(7)

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

\[
\frac{d\epsilon_{\text{Fish}}(W)}{dt} \cdot W = \epsilon_{\text{Fish}}(W) \cdot \frac{dW}{dt} + W \cdot \frac{d\epsilon_{\text{Fish}}(W)}{dt} = (\alpha + 2 \cdot \beta \cdot W) \cdot \frac{dW}{dt}
\]  

(8)

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

\[
\frac{dW}{dt} = \frac{\dot{E}_{\text{Net}}}{(\alpha + 2 \cdot \beta \cdot W)} \neq \frac{\dot{E}_{\text{Net}}}{\epsilon_{\text{Fish}}(W)}
\]  

(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).

\[
\epsilon_{\text{Fish}} = \epsilon_{\text{lipid}} \cdot \text{L} + \epsilon_{\text{protein}} \cdot \text{P}
\]  

(10)

\( L \) and \( P \) are the lipid and protein fractions of whole fish wet weight, and \( \epsilon_{\text{lipid}} \) and \( \epsilon_{\text{protein}} \) 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 content and the log of wet weight respectively.
content and the log of wet weight. Such correlations can be used along
with Eq. (10) to calculate energy density. Alternatively, these correla-
tions can be approximated by a power relationship for energy density
as a function of wet weight as in Eq. (11).
\[ \varepsilon_{\text{fish}}(W) = \alpha W^\beta. \] (11)

The coefficients \( \alpha \) and \( \beta \) are empirical constants. Brigolin et al.
(2010) as well as many others have used power equations to express
the relationship between fish energy density and fish weight in fish
bioenergetic models. In this power case, the rate of change of the en-
ergy density with respect to time is equal to \( \beta \cdot \alpha \cdot W^{\beta - 1} \cdot \frac{dW}{dt} \). Again, the left hand side of Eq. (2) must incorporate Eq. (11) and be
expanded using the Chain Rule, resulting in Eq. (12).
\[ \frac{d[\varepsilon_{\text{fish}}(W) \cdot W]}{dt} = \frac{d\varepsilon_{\text{fish}}(W)}{dt} \cdot W + \varepsilon_{\text{fish}}(W) \cdot \frac{dW}{dt} = (1 + \beta) \cdot \alpha \cdot W^\beta \cdot \frac{dW}{dt}. \] (12)

Eq. (13) describes the growth of an individual fish.
\[ \frac{dW}{dt} = \frac{\dot{E}_{\text{Net}}}{(1 + \beta) \cdot \varepsilon_{\text{fish}}(W)} \neq \frac{\dot{E}_{\text{Net}}}{\varepsilon_{\text{fish}}(W)}. \] (13)

Thus, it is observed once again that Eq. (6) is no longer valid when
the fish energy density is a function of \( W \). The magnitude of the
errors associated with incorrect application of Eq. (13) will be
discussed in a following section.

3.4. Case 4: fish energy density is function of time

Sometimes model developers employ time-variable functions to
account for variations in the fish energy density caused by increases
in body weight or changes in composition, and this may be appropri-
ate and expedient for some cases. However, this approach is less
satisfactory because it does not require the analyst to specify the
underlying mechanisms associated with the changes in energy den-
sity. Nevertheless, Megrey et al. (2007) found it convenient to use this
approach in a bioenergetic model for Pacific herring (Clupea
harengus pallasi). This model treated the energy density of the herring
as a piece-wise linear function of time. Madenjian et al. (2010) also
employed a linear time-variable function to describe the increase in
walleye (Sander vitreus) energy density during laboratory experi-
ments. Eq. (14) describes the fish energy density as a linear function
of time.
\[ \varepsilon_{\text{fish}}(t) = \alpha + \beta \cdot t. \] (14)

The rate of change of the energy density with respect to time is
equal to \( \beta \), and Eqs. (4) and (14) must be used to obtain Eq. (15)
that correctly describes the growth of an individual fish.
\[ \frac{dW}{dt} = \frac{\dot{E}_{\text{Net}}}{\varepsilon_{\text{fish}}(t)} \cdot \frac{W^{\beta - 1} \cdot \frac{dW}{dt}}{\varepsilon_{\text{fish}}(t)} = \frac{\dot{E}_{\text{Net}}}{\varepsilon_{\text{fish}}(t)}. \] (15)

Thus, as expected, Eq. (6) is no longer valid. The magnitude of the
errors associated with this incorrect application will be examined in a
following section.

3.5. Case 5: fish energy density is an arbitrary function of \( W \)

If the fish energy density is a multifunction of wet weight or time
and represented as a polynomial, power, exponential, or other com-
licated function (for example, Bajer et al., 2003; Csargo et al.,
2012; Hayes et al., 2000; Zhou et al., 2005), it may not be pos-
sible to develop convenient equations for the growth of the fish as
in Eqs. (9), (13), and (15). In these cases it is necessary to solve com-
plex algebraic equations for \( W \) at each time step using some iterative
search technique such as the Bisection or False Position method (see
Chapter 5 in Chapra and Canale, 2009). These cases will be briefly
discussed in the next section.

4. Numerical solutions

Numerical methods are normally used to calculate approximate
solutions of Eqs. (9), (13), and (15) because the right-hand sides of
these equations are typically complex functions of the wet weight of
the fish, temperature, ration, and food composition. Chapra and
Canale (2009) describe techniques such as the fourth-order Runge-
Kutta and predictor–corrector methods that can be used to generate
numerical solutions. Complex high-order methods are used when
the right-hand side of the equations changes rapidly over the integra-
tion time-step. However, for practically all fish growth applications,
the magnitude of the right-hand side of the equations changes slowly
over a one-day time-step. Therefore a simple Euler method can be
used to advantage because of its simplicity and ease of application.
For example, the Euler Method for the case where the energy density
is a power function of the fish weight (Eq. (13)) is given by the fol-
lowing difference equation:
\[ W_{i + \Delta t} = W_i + \frac{\dot{E}_{\text{Net}}(W_i)}{(1 + \beta) \cdot \varepsilon_{\text{fish}}(W_i)} \cdot \Delta t. \] (16)

Note that the weight at the end of each time step \( (t + \Delta t) \) can be
calculated from known values at the start of each time step \( t \). This
can be applied in a step-wise manner (as in a spreadsheet) to gener-
solve the equation over the entire interval from Start to End.

Note that \( W \) is the dependent variable in Eqs. (9), (13), and (15).
This was done for ease of visual comparison with Eq. (6), a form
that is often seen in scientific literature. However, sometimes it is ad-
vantageous to define the product of the fish weight and the energy
density as the dependent variable. This avoids the use of the Chain
Rule and the Euler Method can be applied directly to Eq. (2):
\[ \varepsilon_{\text{fish}}(W_{i + \Delta t}) \cdot W_{i + \Delta t} = \varepsilon_{\text{fish}}(W_i) \cdot W_i + \dot{E}_{\text{Net}}(W_i) \cdot \Delta t. \] (17)

This approach generates numerical values for the product of the
weight and energy density at the end of each new time step. This nu-
merical value can be used to calculate the weight at the end of the
new time step using Eq. (18) for the case where the energy density
is a power function of weight.
\[ W_{i + \Delta t} = \left[ \frac{\varepsilon_{\text{fish}}(W_{i + \Delta t}) \cdot W_{i + \Delta t}}{\varepsilon_{\text{fish}}(W_i)} \right]^{1/(1 + \beta)}. \] (18)

If the algebraic function relating energy density and weight is too
complex to obtain a simple result similar to Eq. (18), an iterative
search technique is needed to calculate the weight at the end of
each time step as discussed above.

Observe that for the special case where the energy density is spec-
dified as a function of only time rather than weight, Eq. (17) can be
written as
\[ W_{i + \Delta t} = \frac{\varepsilon_{\text{fish}}(t) \cdot W_i + \dot{E}_{\text{Net}}(W_i) \cdot \Delta t}{\varepsilon_{\text{fish}}(t + \Delta t)}. \] (19)

This equation is equivalent to the preferred model described by
Madenjian et al. (2012). This approach is limited and practical only
when a priori knowledge of the energy density is available at the end
of each integration time step.
5. Example application

The previous sections have described how the basic equations of energy balance can be violated by inappropriate application of Eq. (6) for cases where fish energy density is either a function of fish weight or time. The next step is to evaluate the magnitude of these errors for a practical application. Brigolin et al. (2010) have described a bioenergetic model for estimating seabream production and assessing the environmental impact of mariculture activities in the Adriatic seas. This publication has sufficient information to examine the ramifications of the above error analysis for a realistic case. The Brigolin et al. (2010) model can be summarized by Eq. (20).

\[
\frac{d[\text{E}_{\text{net}}]}{dt} = \alpha W^b - \beta W^d > 0.
\]

(20)

The \( \alpha \) coefficient in Eq. (20) is a function of the maximum consumption rate, temperature, food availability, the food energy density, and the assimilation efficiency of the lipid, protein, and carbohydrate components of the food. The \( \beta \) coefficient characterizes the respiration rate and is a function of temperature. Values of \( \alpha = 0.89 \) and \( \beta = 0.0325 \) were calculated for a constant temperature of 20 °C assuming that the seabream at the Bisceglie site were provided satiation rations. These conditions simplify the calculations and facilitate interpretation of the simulation results. The \( b \) and \( d \) coefficients characterize the allometric functionality of consumption and respiration. Numerical values for this example are \( b = 0.6 \) and \( d = 1.0 \). The energy density of the seabream as specified by Brigolin et al. (2010) is given by Eq. (11) with \( \alpha = 4.66 \) and \( \beta = 0.14 \). Fig. 1 shows a plot of this power function of fish wet weight, as well as linear and constant-value approximations.

Fig. 2a shows the model-calculated growth of the seabream using Eq. (13) and the power function to describe changes in energy density. The solutions were determined using the Euler method with a one-day time step. Virtually identical results were obtained using Eqs. (17) and (18). Solutions using a fourth-order Runge–Kutta method (not shown) differed from the Euler results by only about 0.1%. The growth shown in Fig. 2b also assumes that the energy density is a power function of W, but these results were obtained by the incorrect use of Eq. (6). The deviation between the calculated growth curves results in a mathematical error of about 18% at the end of 400 days (Table 1). Furthermore, energy continuity, as required by Eq. (3), is not preserved and results in an imbalance of about 14% (Table 1). As expected, similar mathematical errors occur if the energy density is assumed to be a linear function of fish weight or a function of time (see Table 1).

Fig. 2c shows the calculated growth response using Eq. (6) when the energy density is constant (see Fig. 1). Although this result contains no mathematical error, a “biological error” of about 18% is introduced when the energy density is approximated as a constant rather than the more appropriate power function used by Brigolin et al. (2010). The magnitude of this “biological error” depends on how rapidly the fish energy density changes during the integration period (see discussion below).

6. Discussion

It is interesting to note that various researchers have reported errors in bioenergetic models similar to Table 1. Sometimes the errors are attributed to biological inadequacies in the model such as “species borrowing”, “metabolic compensation or plasticity”, or differences in life stage (Bajer et al., 2004a, 2004b; Chipps and Wahl, 2008; Huuskonen et al., 1998; Whitledge et al., 2010). Although empirical data are often available to independently corroborate such phenomena, it is also essential that model simulations designed to analyze these mechanisms use the correct form of the energy balance equation and appropriate functions to describe fish energy density. Model analyses that do not conform to these requirements cannot be used to distinguish between real biological phenomena and poor estimates of model coefficients or inaccurate model forcing functions.

It is easy to compensate for the incorrect use of the energy balance equation (that tends to overestimate growth and production) by

![Fig. 1. Alternative energy density functions used for simulations of gilthead seabream growth. (a) Solid line: power function (Eq. (11); with \( \alpha = 4.66 \) and \( \beta = 0.14 \), from Brigolin et al., 2010). (b) Dotted line: linear approximation (Eq. (7); with \( \alpha = 7.94 \) and \( \beta = 0.0073 \)). (c) Dashed line: constant value with \( \text{EN}_{\text{net}} = 9.65 \) kJ/g.]

![Fig. 2. Model simulations for the growth of gilthead seabream. (a) Solid line: mathematically correct solution based on Eq. (13) or Eqs. (17) and (18) when the energy density is a power function of wet weight. (b) Dotted line: mathematically incorrect solution based on improper use of Eq. (6) when the energy density is a power function of wet weight. (c) Dashed line: mathematically correct, but biologically inadequate solution that results from constant energy density assumption.]

| Table 1 Mathemathical errors that result from the incorrect application of the energy balance equations for the Brigolin et al.’s (2010) model coefficients for seabream. The percent error is shown for different formulations for the energy density. |
|---------------------------------|-----------------|-----------------|
| Energy density formulation | Percent mathematical error in the weight (W) after 400 days. | Percent mathematical error in energy balance (Eq. (3)) after 400 days. |
| Power function of W | 18 | 14 |
| Linear function of W | 20 | 22 |
| Time-variable | 24 | 18 |
lowering the model coefficient value for the consumption rate or increasing the respiration rate. For example, visually appealing (but mathematically incorrect) simulations of the seabream growth can be obtained if the model coefficient for consumption ($a$) in Eq. (20) is lowered to about 0.81 or if the respiration coefficient ($c$) is increased to about 0.04. The errors generated by using the incorrect form of the energy balance equation and the distorted coefficient values compensate for one another. The incorrect model coefficient values could result in misleading conclusions about a number of biological factors such as food availability, the energy density of the food, maximum consumption and respiration rates, and incorrect temperature and allometric functions. These errors can be detected and corrected if Eq. (3) is used to verify that the calculated change in the energy content of the fish is consistent with the total net energy provided. It is recommended that all pre-programmed software applications of bioenergetic growth models implement this imperative audit.

Note that the magnitude of the mathematical errors associated with the incorrect application of Eq. (6) depends on how rapidly the energy density changes as a function of fish weight or how fast the fish energy density changes with time. As seen in many studies, the most rapid changes occur for the smallest size of fish (e.g., Brett, 1983; Gunther et al., 2005). Fishes in the family Salmonidae tend to have relatively large eggs and sizes at first feeding compared to many other fishes (Miller et al., 1988; Winemiller and Rose, 1992), and the early changes in energy density are rapid (Brett, 1983; Gunther et al., 2005; Reinitz, 1983). It is likely that the early changes are even faster for fishes that hatch at smaller sizes. Failure to account for such rapid changes in energy density with weight could lead to substantial differences in estimates of the bioenergetics of growth of age-0 fish, with implications for recruitment and dynamics of prey (Breck, 1993; Hewett and Stewart, 1989; Stewart and Binkowski, 1986). Therefore, the smaller the initial sizes of fish, the more important it is to consider non-linear, size-dependent changes in energy density.

As an example, Neely et al. (2008) compared the growth, feed intake, and nutrient efficiency of a domestic strain of coho salmon (Oncorhynchus kisutch) selected for its rapid growth characteristics (Damarco) with its source stock (Skykomish). Fig. 3 shows the calculated energy density of the Skykomish strain based on measurements of proximate composition. Incorrect use of Eq. (6) will result in large errors (about 30%) for simulations of weight between 1 and 4 g. Smaller but still significant errors are expected for the entire range between weights of 1 and 14 g.

7. Conclusion

From the analyses presented here, it is concluded that two major pitfalls must be avoided when using bioenergetic models to simulate fish growth or energy consumption. First, large mathematical errors can result from the incorrect application of conventional bioenergetic models for cases where the energy density of the fish is anything other than constant. Second, it has been shown that constant fish energy density assumptions are biologically inadequate for many bioenergetic modeling applications. This is particularly true for small fish where the energy density may change rapidly as the fish increase in size. Apparent “successful” model calibrations using equations that do not conserve energy are incorrect and may result in misleading characterizations of fundamental biological processes and ultimately the magnitude and impact of waste products from cultured fish. It is recommended that previously published results for these cases be critically reviewed and corrected where relevant. The errors can be eliminated when the bioenergetic model equations are handled properly as demonstrated in this paper.

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References


Fig. 3. Calculated energy density for smaller and larger weight categories in relation to wet weight of Skykomish strain of coho salmon based on measurements of proximate composition (Neely et al., 2008). (a) Long-dash line: Eq. (11) fitted to data for fish from 1.2 to 4.2 g gives $\alpha = 4.651$ and $\beta = 0.249$. (b) Solid line: Eq. (11) fitted to data for fish from 1.2 to 13.8 g gives $\alpha = 5.010$ and $\beta = 0.142$. 