

Integrating dynamic energy budget (DEB) theory with traditional bioenergetic models

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10.1242/jeb.071845

There was an error published in the online (Full Text and PDF) version of *J. Exp. Biol.* **215**, 892-902.

In Table 3 (p. 896), a typographical error was introduced into Eqns A3 and A4 during the production process. The correct version is given below.

Table 3. Equations of the standard DEB model

A1	$\frac{d}{dt}E = \dot{\rho}_A - \dot{\rho}_C$
A2	$\frac{d}{dt}V = \frac{1}{[E_G]} \dot{\rho}_G = \frac{1}{[E_G]} (\kappa \dot{\rho}_C - \dot{\rho}_S)$
A3	$\frac{d}{dt}E_H = (1 - \kappa) \dot{\rho}_C - \dot{\rho}_J \quad \text{if } E_H < E_H^p, \quad \text{else } \frac{d}{dt}E_H = 0$
A4	$\frac{d}{dt}E_R = 0 \quad \text{if } E_H < E_H^p, \quad \text{else } \frac{d}{dt}E_R = (1 - \kappa) \dot{\rho}_C - \dot{\rho}_J$
A5	with $\dot{\rho}_A = c(T) f(X) \{\dot{\rho}_{Am}\} L^2 \quad \text{if } E_H \geq E_H^p, \quad \text{else } \dot{\rho}_A = 0$
A6	$\dot{\rho}_C = c(T) \{\dot{\rho}_{Am}\} L^2 \frac{ge}{g + e} \left(1 + \frac{L}{gL_m} \right);$
	with $e = \frac{[E]}{[E_m]} = \frac{E}{V \{\dot{\rho}_{Am}\}}$ and $L = V^{1/3}$
A7	$\dot{\rho}_S = c(T) (\{\dot{\rho}_M\} L^3 + \{\dot{\rho}_T\} L^2)$
A8	$\dot{\rho}_J = c(T) \dot{\kappa}_J E_H$
A9	$f(X) = \frac{X}{X + K}$
A10	$c(T) = \exp\left(\frac{T_A}{T_1} - \frac{T_A}{T}\right)$

Notation is described in Table 2.

We apologise to all authors and readers for any inconvenience caused.

This error does not occur in the print version of this article.

REVIEW

Integrating dynamic energy budget (DEB) theory with traditional bioenergetic models

Roger M. Nisbet^{1,*}, Marko Jusup^{2,3}, Tin Klanjscek^{1,2} and Laure Pecquerie¹

¹Department of Ecology, Evolution and Marine Biology, University of California, Santa Barbara, CA 93106-9610, USA,

²Rudjer Boskovic Institute, Department for Marine and Environmental Research, Bijenicka cesta 54, POB 180, HR-10002 Zagreb, Croatia and ³Faculty of Environment and Information Sciences, Yokohama National University, 79-7, Tokiwadai, Hodogaya-ku, Yokohama, Kanagawa 240-8501, Japan

*Author for correspondence (nisbet@lifesci.ucsb.edu)

Accepted 5 October 2011

Summary

Dynamic energy budget (DEB) theory offers a systematic, though abstract, way to describe how an organism acquires and uses energy and essential elements for physiological processes, in addition to how physiological performance is influenced by environmental variables such as food density and temperature. A ‘standard’ DEB model describes the performance (growth, development, reproduction, respiration, etc.) of all life stages of an animal (embryo to adult), and predicts both intraspecific and interspecific variation in physiological rates. This approach contrasts with a long tradition of more phenomenological and parameter-rich bioenergetic models that are used to make predictions from species-specific rate measurements. These less abstract models are widely used in fisheries studies; they are more readily interpretable than DEB models, but lack the generality of DEB models. We review the interconnections between the two approaches and present formulae relating the state variables and fluxes in the standard DEB model to measured bioenergetic rate processes. We illustrate this synthesis for two large fishes: Pacific bluefin tuna (*Thunnus orientalis*) and Pacific salmon (*Oncorhynchus* spp.). For each, we have a parameter-sparse, full-life-cycle DEB model that requires adding only a few species-specific features to the standard model. Both models allow powerful integration of knowledge derived from data restricted to certain life stages, processes and environments.

Key words: bioenergetic models, dynamic energy budget, salmon, tuna.

Introduction

Empiricism alone does not offer a practical way to understand how environmental change impacts the physiology and viability of organisms. This is for three distinct reasons. First, there is an overwhelming number of different organism–environment combinations to consider, including many for which experimentation is impractical, prohibitively expensive, or unethical. Second, experimental studies yield information that is restricted to specific aspects of some system, with extrapolation to new contexts, and possibly entirely novel conditions, requiring verbal, statistical or mechanistic theory. Third, we know that climate change is likely to alter the frequency of extremes, and thus the time history of events; as a consequence, measurements that characterize average conditions and/or currently observed levels of variability have limited predictive value. This paper focuses on dynamic, mechanistic theory based on general biological principles that can help integrate bioenergetic information from experiments and field studies involving different combinations of organism and environment, and thereby help contribute to predictions for new situations.

There is a long tradition of simple bioenergetic models in ecology. Ecologists use bioenergetic models to address questions at single levels of biological organization – physiological and behavioral properties of individual organisms, population and community dynamics, or ecosystem processes – but models with bioenergetic components can also relate processes at different levels of organization (Brown et al., 2004; Nisbet et al., 2000). For instance, recent work has shown that energetic constraints may in part determine how a species’ niche responds to environmental

change (Buckley et al., 2008; Buckley et al., 2010; Kearney et al., 2010; Kearney et al., 2012).

‘Traditional’ bioenergetic models of individual animals describe energy acquisition from feeding, and its partitioning among processes such as growth, reproduction, respiration, excretion and activity. These processes are commonly defined operationally; for example, growth and reproduction may be measured directly and converted to energy units, activity may be defined through changes in respiration rate, and other terms may relate to data on heat balance or mechanical work done. Consequently, the traditional bioenergetics models are powerful data synthesis tools with a strong empirical foundation. Yet they are typically parameter-rich (Ney, 1993), with further assumptions required to relate parameters for different species (Chipps and Wahl, 2008; Ney, 1993).

By contrast, a much more theoretical approach known as dynamic energy budget (DEB) theory considers many of the same processes as the empirical models, but from a different perspective. The most sophisticated approach to DEB theory (Kooijman, 1993; Kooijman, 2010; Nisbet et al., 2000) starts from a set of well-defined assumptions and provides a characterization of the complete life cycle (embryo, juvenile and adult) of an animal through a ‘standard’ model with 12 parameters. It predicts both interspecific and intraspecific variation in the many energy and mass fluxes in any biologically relevant environment. The price paid for this enhanced generality is greater abstraction: the state variables of the model itself are not directly measurable, and observable fluxes such as respiration rate or heat loss are commonly linear combinations of individually unobservable fluxes.

The two contrasting approaches, outlined in the following two sections of this paper, can be characterized as data driven (Overview of traditional bioenergetic models) and theory driven (Kooijman's DEB theory). They have sufficient conceptual overlap that they should inform each other, but it is currently a challenge to figure out how to relate the powerful formalism of DEB theory to the bioenergetic data that are available in many applications. Making the connection requires precise recipes that relate individual measurements to DEB concepts. In the fourth section (Relating Kooijman's DEB theory to other bioenergetic approaches) we provide the explicit formulae for quantities where the connection is straightforward and we outline a systematic method for handling subtler situations. The connections are further illustrated in the fifth and sixth sections, where we review and synthesize data on two fish species with large adults, Pacific bluefin tuna (*Thunnus orientalis*) and Pacific salmon (*Oncorhynchus* spp.). For each, there is a full-life-cycle DEB model, constructed to connect knowledge deriving from data restricted to certain life stages, processes and environments. The paper ends with a discussion of some challenges in further integrating traditional approaches with DEB theory and simplifying DEB theory to make the connections more transparent.

Kooijman's DEB theory

DEB theory is a powerful theoretical framework for relating suborganismal (biochemical, genetic and physiological) processes to organismal performance and, thereby, to populations, ecosystems and their temporal evolution at many time scales. DEB theory focuses on the individual organism, with differential equations describing the rates at which the organism assimilates and utilizes energy and elemental matter from food for its maintenance, growth, reproduction and development (Kooijman, 1986; Kooijman, 2000; Kooijman, 2001; Kooijman, 2010; Nisbet et al., 2004; Nisbet et al., 2010; Nisbet et al., 2000).

There are a number of different approaches to DEB model formulation, but the 'standard' DEB model (Kooijman, 2010; Sousa et al., 2010) is the only model known to the authors that describes the interconnections among the processes of assimilation, maintenance, development, growth and reproduction of an organism throughout all stages of its life cycle, and in a dynamic environment. In this section, we describe the standard model for a heterotrophic ectotherm, and refer the reader to Kooijman's (Kooijman, 2010) book for discussion of other types of organism.

The state variables and energy flows are illustrated in Fig. 1. The animal's biomass is the sum of contributions from three compartments: structure, reserve and (for adults) reproductive reserve. Structure is defined as biomass that requires energy expenditure for maintenance; reserve is defined as biomass that does not require maintenance. (Note that some terms, notably structure and reserve, are very precisely defined in Kooijman's DEB theory. This is done in order to achieve maximum generality, but has the consequence that their interpretation in particular contexts may differ from common usage in biology. We retain Kooijman's terminology here for consistency with cited literature.) An immediate implication of these definitions is that individual compartments cannot be directly identified with specific organs or with chemical compounds such as proteins or lipids. However, in most applications it is safe to associate the term structure with some measure of an organism's physical length. The composition of the biomass in each compartment is constant but the composition of reserve and structure differ. Although each compartment contains a mixture of many compounds, it is represented as a 'generalized

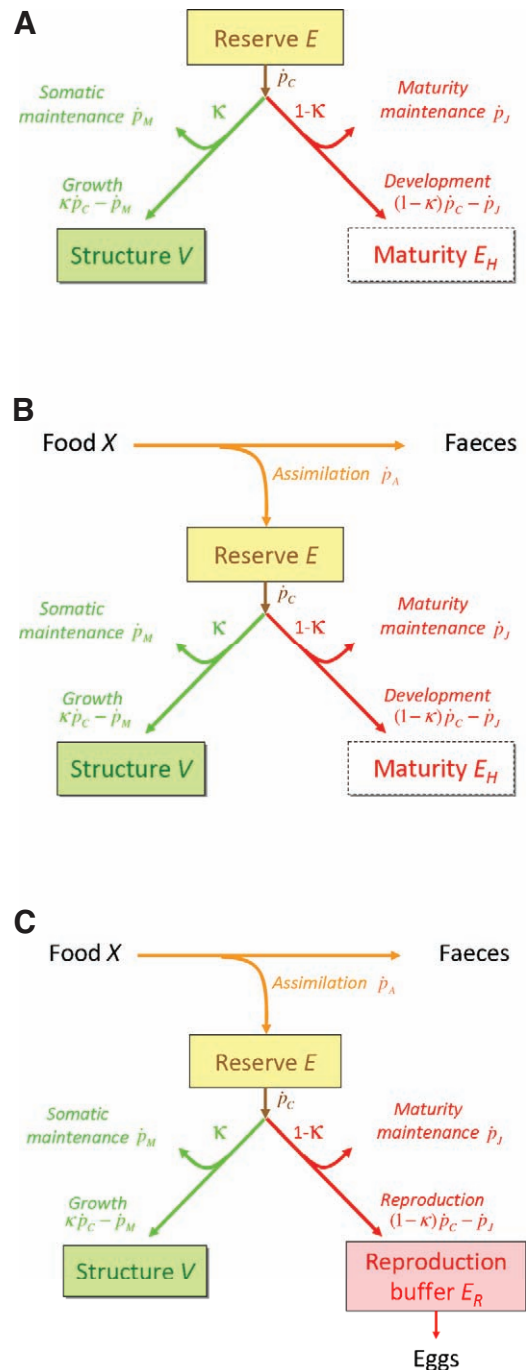
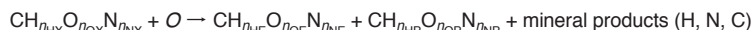


Fig. 1. Schematic representation of the three life stages of the 'standard' DEB model (Kooijman, 2010). (A) An embryo uses reserve to grow and develop. (B) At 'birth', a juvenile starts feeding, and (C) at 'puberty', an adult starts allocating energy to reproduction.

compound' with fixed stoichiometry, e.g. a molecule of structure V has a formula $\text{CH}_{n_{\text{HV}}}\text{O}_{n_{\text{OV}}}\text{N}_{n_{\text{NV}}}$. It is conventional to specify the composition of the generalized compounds with a single carbon atom. Thus, for example, n_{NV} represents the molar N:C ratio. With this convention, the natural unit for measuring mass is Cmol (Kooijman, 2010), and chemical potentials have dimension energy per Cmol. Each generalized compound has a specified chemical potential (Gibbs energy per Cmol). The relative masses of each component may vary over time; for example, during a period of

Table 1. Dynamic energy budget (DEB) theory defines three types of transformations: assimilation, growth and dissipation

Assimilation is the transformation of two substrates, food (X) and dioxygen (O), into five products, reserve (E), carbon dioxide (C), water (H), N-waste (N) and feces (P):

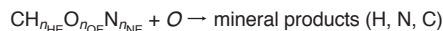


Growth involves the transformation of two substrates, reserve (E) and dioxygen (O), into four products, structure (V), carbon dioxide (C), water (H) and N-waste (N):



with an analogous equation for reproduction

Dissipation encompasses the transformations of two substrates, reserve (E) and dioxygen (O), into three products, carbon dioxide (C), water (H) and N-waste (N):



Unbalanced equations for each transformation in an aerobic heterotroph are shown.

starvation, the ratio of reserve to structure will decrease, possibly leading to a change in the overall composition of biomass.

The life cycle in the standard DEB model is described by three life stages: embryo, juvenile and adult. An embryo mobilizes maternal reserve for development, growth and maintenance processes. Once the individual has achieved a particular threshold of energy into invested in development, the individual is complex enough to start feeding, which marks 'birth', the transition between the embryo and the juvenile stage. Further investment in development leads to a second transition, awkwardly termed 'puberty' in the DEB literature, but not restricted to sexually reproducing organisms. After puberty, the organism starts to commit energy to reproduction.

Four state variables characterize the organism: the stored Gibbs energy in the three compartments and a variable called 'maturity' that characterizes increase in complexity through embryonic and juvenile development. The principal metabolic processes shown in Fig. 1 are of four types: (1) assimilation (food \rightarrow reserve); (2) 'dissipation', defined as metabolic work that does not lead to the production of new biological material, i.e. somatic and maturity maintenance along with the overheads of growth and reproduction (reserve \rightarrow mineral products); (3) growth (reserve \rightarrow structure); and (4) reproduction (reserve \rightarrow reproductive reserve). [Dissipation is another term with a precise definition for the standard DEB model that does not always match its use in other subdisciplines. We present a formula in the fourth section (Relating Kooijman's DEB theory to other bioenergetic approaches).] The chemical equations characterizing these transformations are presented in Table 1, and the model dynamics are summarized in Tables 2 and 3. The stoichiometry of the chemical equations leads to a formula for calculating respiration rate, defined as rate of oxygen consumption or CO₂ production. Respiration thus defined can be expressed as a weighted sum of contributions from assimilation, growth, dissipation and (for adults) reproduction.

The 'standard' version of the DEB model has 12 parameters (listed in Table 2). Estimating these parameters *ab initio* requires extensive data (Kooijman et al., 2008), but it is possible to make a first cut at estimation by taking advantage of theoretical predictions of interspecific body-size scaling relationships or co-variation of parameters [chapter 8 of Kooijman (Kooijman, 2010); see also Nisbet et al. (Nisbet et al., 2000) for an ecologically oriented overview of the underlying concepts]. In brief, the parameters in DEB theory may be classified as 'intensive' or 'extensive', with the values of the former roughly invariant among related species and the latter varying in a predictable way with size. Extensive parameters scale directly with a 'zoom factor' z , which is defined

as the ratio of the maximum length of the species of interest to the maximum length of the reference species $z=L_m/L_{m,ref}$. Where applicable, the size dependence is indicated in Table 2. Parameters for the model of Pacific salmon were, for instance, estimated with the help of these relationships (Pecquerie et al., 2011).

Relating Kooijman's DEB model to bioenergetic data is greatly facilitated by the work of Sousa et al. (Sousa et al., 2006). These authors placed Kooijman's DEB model in a rigorous thermodynamic framework. They assume that energy expenditure on mechanical work is commonly small and that the associated expenditure of chemical energy can be regarded as part of maintenance. They propose that entropy changes within an aerobic organism are likewise small, implying that the chemical transformations of an aerobe in the DEB model simply involve conversion of Gibbs energy to heat. They also highlight subtleties [see table 2 of Sousa et al. (Sousa et al., 2006)], not included in the current brief summary, that arise when considering anaerobic processes. Each of these considerations may be relevant when integrating information from bioenergetic data into DEB models.

Overview of traditional bioenergetic models

Traditional bioenergetic models similarly start from an equation describing energy or mass balance requirements, and describe the fate of chemical energy stored in food. We follow conventions from bioenergetic models of fish growth, for which the equations are frequently expressed in terms of energy per day per units of (wet or dry) weight.

The traditional models are in fact a particularly simple special case of a DEB model with a single state variable. The 'input' is the feeding rate (C); the 'outputs' include egestion (F) and excretion rates (U), growth rate (G) and total metabolic rate. Each term may in turn be decomposed into component terms. Thus, depending on the focus of the study, it may be useful to distinguish the contributions to growth rate from somatic growth, gonad production and storage of fats and lipids. Total metabolic rate can be decomposed into specific dynamic action (SDA; represented in equations by S) and maintenance, with the latter commonly described as the product of standard (or basal) maintenance (M) and a dimensionless factor called 'activity' (A). Note that maintenance here has a different meaning from its use in DEB theory. Ignoring the different components of growth, the energy balance equation then takes the form:

$$C = G + MA + S + F + U. \quad (1)$$

Notwithstanding the similarity of the underlying principles, the definition of rate processes in traditional bioenergetic models rests

Table 2. State variables, forcing variables and parameters of the standard DEB model with maximum length $L_m = zL_{m,ref}$ for a dimensionless zoom factor z defined as the ratio of the maximum length for a particular species to a reference length, $L_{m,ref}$, of 1 cm

Symbol	Value	Units	Definition
State and forcing variables			
E		J	Reserve energy
V		cm ³	Structural volume
E_H		J	Cumulated energy invested into development
E_R		J	Reproduction buffer energy
X		J cm ⁻³	Food density (per unit of environmental volume)
T		K	Temperature
$f(X)$			Scaled functional response
$\alpha(T)$			Temperature correction factor
Primary parameters			
$\{F_m\}$	6.51	cm ³ cm ⁻² d ⁻¹	Specific searching rate
κ_X	0.8		Assimilation efficiency
$\{\dot{\rho}_{Am}\}$	22.5z	J cm ⁻² d ⁻¹	Maximum surface-area-specific assimilation rate
$[\dot{\rho}_M]$	18	J cm ⁻³ d ⁻¹	Volume-specific somatic maintenance rate
$\{\dot{\rho}_T\}$	0	J cm ⁻² d ⁻¹	Surface-area-specific somatic maintenance rate
$[E_G]$	2800	J cm ⁻³	Volume-specific cost for structure
\dot{v}	0.02	cm d ⁻¹	Energy conductance
κ	0.8		Fraction of utilized reserve to growth + maintenance
k_j	0.002	d ⁻¹	Maturity maintenance rate coefficient
E_H^0	275z ³	mJ	Maturity threshold at birth
E_H^1	166z ³	J	Maturity threshold at puberty
κ_R	0.95		Fraction of the reproduction buffer fixed into eggs
Auxiliary and compound parameters			
T_A		K	Arrhenius temperature
δ			Shape coefficient
d_V		g cm ⁻³	Structure density
μ_V		J mol ⁻¹	Chemical potential of structure
μ_E		J mol ⁻¹	Chemical potential of reserve
w_V		g mol ⁻¹	Molar (wet) weight of structure
w_E		g mol ⁻¹	Molar (wet) weight of reserve
L_m		cm	Maximum volumetric length
g	$\kappa\{\dot{\rho}_{Am}\}/[\dot{\rho}_M]$		Energy investment ratio
K	$\dot{v}[E_G]/(\kappa\{\dot{\rho}_{Am}\})$	J cm ⁻³	Half-saturation coefficient
$[E_m]$	$\{\dot{\rho}_{Am}\}/\dot{v}$	J cm ⁻³	Maximum reserve density
κ_G	$\mu_V d_V / (w_V [E_G])$		Growth efficiency

All primary parameters that covary with z are called extensive parameters. Compound parameters including $\{\dot{\rho}_{Am}\}$ are thus extensive parameters (Kooijman 2010; Sousa et al., 2010). Rates are given at the reference temperature of $T_1=293$ K (=20°C).

on strikingly different principles from those invoked in Kooijman’s DEB theory. The state variables in Kooijman’s models are defined in an abstract way, with relationships among measurable quantities defined implicitly *via* these variables. In contrast, some terms in Eqn 1 are typically defined operationally through measured (or measurable) changes in metabolic rates, most commonly through changes in measured respiration rate under different experimental conditions.

The price paid for this practical approach to defining fluxes is a subtle difference in meaning for each term in different applications. For example, although SDA is widely defined as the increase in respiration due to the costs of processing and utilizing food, individual investigators operationalize this definition in different ways. A recent extensive review (Secor, 2009) defines SDA in terms of the integrated energy expenditure (relative to basal metabolic rate) over the complete transient response of respiration rate in an animal, following a meal. In contrast, a few studies focus on the steady state respiration rate of animals feeding at different rates, e.g. a study by Bohrer and Lampert (Bohrer and Lampert, 1988) of respiration in *Daphnia*.

Activity is defined as the proportional increase in respiration rate in ‘active’ *versus* ‘resting’ animals, and is widely used to characterize the metabolic energy costs of mechanical work. For fish, activity thus defined may be estimated by nonlinear

regressions of oxygen consumption against sustained swimming speed (Padapopoulos, 2008), but the resulting fits must be used with care, as other physiological processes, notably feeding rate, may covary with swimming speed.

For fish, activity can alternatively be estimated from the mechanical power requirements (e.g. Brett, 1963; Petrell and Jones, 2000; Schultz and Webb, 2002). Estimating activity in this manner requires answering two questions: (1) what is the mechanical power needed to generate the thrust that propels the fish to a given speed; and (2) how does the produced mechanical power relate to the rate of metabolic (chemical) energy consumption by the muscle?

In 1971, Paul Webb was among the first to attempt to answer these questions for rainbow trout in an integrative study, combining mechanical and physiological data (Webb, 1971a; Webb, 1971b; Ellerby, 2010). Following Webb’s pioneering work, the research on mechanics and physiology of fish swimming was, for the most part, conducted separately (for reviews, see Blake, 2004; Schultz and Webb, 2002).

Significant advances in understanding the mechanical aspects of swimming were achieved through visualization of flow close to living and robotic fish (Peng and Dabiri, 2008; Brucker and Bleckmann, 2007; Anderson et al., 2001), as well as development of complex hydrodynamic models (Borazjani and Sotiropoulos, 2010; Zhu et al., 2002; Wolfgang et al., 1999). One particular line

Table 3. Equations of the standard DEB model

A1	$\frac{d}{dt}E = \dot{p}_A - \dot{p}_C$
A2	$\frac{d}{dt}V = \frac{1}{[E_G]}\dot{p}_G = \frac{1}{[E_G]}(\kappa\dot{p}_C - \dot{p}_S)$
A3	$\frac{d}{dt}E_H = (1 - \kappa)\dot{p}_C \kappa \dot{p}_J \quad \text{if } E_H < E_H^p, \quad \text{else } \frac{d}{dt}E_H = 0$
A4	$\frac{d}{dt}E_R = 0 \quad \text{if } E_H < E_H^p, \quad \text{else } \frac{d}{dt}E_R = (1 - \kappa)\dot{p}_C \kappa \dot{p}_J$
A5	with $\dot{p}_A = c(T)f(X)\{\dot{p}_{Am}\}L^2 \quad \text{if } E_H \geq E_H^p, \quad \text{else } \dot{p}_A = 0$
A6	$\dot{p}_C = c(T)\{\dot{p}_{Am}\}L^2 \frac{ge}{g+e} \left(1 + \frac{L}{gL_m}\right);$ with $e = \frac{[E]}{[E_m]} = \frac{E}{V} \frac{\dot{v}}{\{\dot{p}_{Am}\}}$ and $L = V^{1/3}$
A7	$\dot{p}_S = c(T)(\{\dot{p}_M\}L^3 + \{\dot{p}_T\}L^2)$
A8	$\dot{p}_J = c(T)\dot{\kappa}_J E_H$
A9	$f(X) = \frac{X}{X+K}$
A10	$c(T) = \exp\left(\frac{T_A}{T_1} - \frac{T_A}{T}\right)$

Notation is described in Table 2.

of research helped link the kinematic parameters of swimming to optimal thrust generation, reduced boundary layer separation, and energy extraction from oncoming vortical flows using a bionic model (a 1.2 m long RoboTuna), digital particle image velocimetry and computational fluid dynamics (Triantafyllou et al., 2002; Zhu et al., 2002; Wolfgang et al., 1999; Barrett et al., 1999). Nonetheless, a number of questions concerning the total power consumption and propulsive efficiency were not resolved. New approaches, stressing conceptual and practical difficulties in separating drag and thrust (Schultz and Webb, 2002; Anderson et al., 2001), called for quantifying the power dissipated as vorticity in the wake to put limits on relative performances of various fishes (Tytell, 2007). It has even been hypothesized that, in the aquatic environment, mechanisms minimizing wake losses may be a more plausible evolutionary end-result than drag relief adaptations (Webb and Cotel, 2010).

Even with substantial knowledge about the mechanical power requirements of swimming, formidable difficulties must be resolved to determine how this power relates to the rate of metabolic (chemical) energy consumption, estimated by measuring respiration at endurable levels of exercise. In a typical experimental setup for a fasting, preferably non-growing fish, the sum of metabolic rates can be obtained by measuring respiration rates at various swimming speeds in a water tunnel. Statistical models are then applied to estimate and subtract the standard metabolic rate. After subtraction, the remainder is assumed to represent the metabolic cost of swimming. The method is not completely reliable, however, because respiration may be affected by numerous factors, including: (1) stress (Sloman et al., 2000), (2) shift from active to ram ventilation (Farrell and Steffensen, 1987), (3) use of various gaits (Korsmeyer et al., 2002), (4) contribution of anaerobic metabolism at higher speeds (Jayne and Lauder, 1994) and (5) changes in proportion of increased oxygen consumption actually received by locomotory muscles (Kiceniuk and Jones, 1977). In addition, studies involving respirometry provide little insight into the mechanical power produced by the muscle tissue. Patterns of muscle function in this context are studied rather independently, using a combination of electromyography measurements *in vivo* and myomere power output *in vitro* (Altringham and Ellerby, 1999).

Relating Kooijman's DEB theory to other bioenergetic approaches

The previous two sections offered brief overviews of complementary approaches to modeling energy acquisition and utilization by animals. 'Traditional' bioenergetic models emphasize operationally defined quantities such as SDA, activity, swimming, or standard metabolism. Relating these quantities to the more abstract concepts in Kooijman's DEB theory involves looking carefully at the operational definitions and their magnitude, and interpreting them in terms of DEB processes. We first establish those links that are unambiguous between the terms in the balance equation (Eqn 1) and DEB processes presented in Fig. 1, and then discuss possible interpretations of some of the terms in the balance equation. Our treatment has some overlap with chapter 11 of Kooijman (Kooijman, 2010), but differs in a number of details, for example our treatment of SDA.

As the different components of an energy budget are often expressed in energy per day per unit of (wet) weight, we first define the (wet) weight of an individual W_w :

$$W_w = W_V + W_E + W_R = d_V V + \frac{w_E}{\mu_E} (E + E_R). \quad (2)$$

where W_V is the structural weight (g), W_E is the reserve weight, W_R is the weight of the reproduction buffer, d_V is the density of the structural volume, and w_E and μ_E are the molar weight and the chemical potential of reserve, respectively.

Food consumption

The standard DEB model considers one type of food with density denoted by X , and assumes constant assimilation efficiency κ_X ($0 < \kappa_X < 1$). We express the food consumption rate, C , as follows:

$$C = \frac{1}{W_w} \dot{p}_X = \frac{1}{W_w \kappa_X} \dot{p}_A, \quad (3)$$

where \dot{p}_X is the ingestion rate and $\dot{p}_A = \kappa_X \dot{p}_X$ is the assimilation rate.

Growth

In a DEB model, the term 'growth' refers only to increase in structure (Fig. 1). In traditional bioenergetic models, growth (G) is defined as the amount of energy fixed in new tissues per day and per unit of weight. In DEB terms, it thus includes the energy fixed in reserve, in structure, and (for adults) in the reproduction buffer:

$$G = \frac{1}{W_w} \left(\frac{d_V \mu_V}{w_V} \frac{dV}{dt} + \frac{dE}{dt} + \frac{dE_R}{dt} \right), \quad (4)$$

where w_V and μ_V are the molar weight and the chemical potential of structure, and dE/dt , dV/dt and dE_R/dt are given in Eqns A1, A2 and A4 in Table 3. The growth term can thus be expressed as follows:

$$G = \frac{1}{W_w} (\dot{p}_A - (1 - \kappa_G) \dot{p}_G - \dot{p}_D). \quad (5)$$

In this equation, $(1 - \kappa_G) \dot{p}_G$ represents the overheads of growth (of structure) and $\dot{p}_D = \dot{p}_S + \dot{p}_J + (1 - \kappa_R) \dot{p}_R$ represents the 'dissipation' terms, which encompass all processes not associated with the production of new reserve and new structure. The parameter $\kappa_G = \mu_V d_V / (w_V [E_G])$ ($0 < \kappa_G < 1$) is the fraction of energy for growth that is fixed into structure. As mentioned earlier, this definition of dissipation is distinctive to the DEB literature; other processes linked to assimilation and growth may lead to products such as CO_2 that are sometimes used to characterize dissipative processes. Formulae for the different energy fluxes are given in Table 3.

Metabolic losses

The sum of all metabolic losses in a traditional bioenergetic approach has an unambiguous link with DEB processes:

$$F + U + S + MA = \frac{1}{W_w} \left[(1 - \kappa_X) \dot{p}_X + (1 - \kappa_G) \dot{p}_G + \dot{p}_D \right]. \quad (6)$$

In this equation, $(1 - \kappa_X) \dot{p}_X$ represents the overheads of assimilation. The fluxes \dot{p}_G , \dot{p}_S and \dot{p}_J are given in Eqns A2, A7 and A8 in Table 3. The final term, $(1 - \kappa_R) \dot{p}_R$, has different interpretation for each life stage. For adults, it represents the overheads of reproduction (conversion of the reproduction reserve into eggs). For embryos and juveniles, the flux \dot{p}_R represents energy committed to development. This is entirely metabolic loss, so we set $\kappa_R = 0$ for embryos and juveniles.

We now discuss the individual components of this metabolic loss equation: egestion (F), excretion (U), specific dynamic action (S) and the product of standard metabolism and activity (MA).

Egestion

This term also has a unique link with DEB processes:

$$F = \frac{1}{W_w} \kappa_P \dot{p}_X = \frac{1}{W_w} \frac{\kappa_P}{\kappa_X} \dot{p}_A, \quad (7)$$

with κ_P the fraction of the ingestion rate transformed into feces ($\kappa_P < 1 - \kappa_X$).

Excretion

In a traditional bioenergetic approach, excretion (U) is subtracted from the digestible energy to obtain the metabolizable energy that fuels growth and maintenance (e.g. Brett and Groves, 1979). Excretion is thus primarily associated with assimilation. However, excretion of previously assimilated nitrogen (e.g. during protein turnover) is regarded as one of the components underpinning trophic isotopic enrichment in $\delta^{15}\text{N}$ in animals (Ponsard and Averbuch, 1999). This highlights the importance of considering that all metabolic processes can potentially contribute to the formation of nitrogen waste products (e.g. ammonia or urea). As with respiration, the excretion term in the standard DEB model is not a single process but can be expressed as a sum of the contributions from the three basic transformations (see Table 1): assimilation, growth and dissipation:

$$U = \frac{1}{W_w} \mu_N (\dot{J}_{\text{NA}} + \dot{J}_{\text{NG}} + \dot{J}_{\text{ND}}), \quad (8)$$

with μ_N (J Cmol^{-1}) denoting the chemical potential of the nitrogen waste produced and \dot{J}_{NA} , \dot{J}_{NG} and \dot{J}_{ND} (Cmol day^{-1}) denoting the mass fluxes of nitrogen waste produced during assimilation, growth and dissipation, respectively. Each component of the nitrogen waste flux is fully determined by the mass balance equations, and so does not require extra parameters, provided the elemental composition of food, reserve, structure and feces is specified. It should be noted that determining the elemental composition of reserve and structure experimentally can be very demanding because of the very precise definition of these quantities in standard DEB theory (see Kooijman's DEB theory). However, with certain information-rich data, it is possible to establish the full mass balance of C, H, O and N for each transformation [see section 4.3.4 in Kooijman (Kooijman, 2010)]. This becomes an issue of considerable practical importance in applications where fluxes are derived from respiration measurements involving CO_2 production or O_2 consumption.

Specific dynamic action

As previously noted, there are a number of subtly different uses of the term specific dynamic action (SDA; S). Kooijman identifies SDA with the 'heat increment of feeding' [see fig. 11.2 in Kooijman (Kooijman, 2010)], and includes it in the overheads of assimilation [see section 4.4.2 and eqn 4.56 in Kooijman (Kooijman, 2010)]. In this case, if there is no fermentation, SDA is equal to the overheads of assimilation minus egestion minus excretion due to assimilation:

$$S = \frac{1}{W_w} \left[(1 - \kappa_X) \dot{p}_X - \kappa_P \dot{p}_X - \mu_N \dot{J}_{\text{NA}} \right]. \quad (9)$$

This definition assumes that the transient response of respiration rate of an animal following a meal (Secor, 2009) is a fast process when compared with the mobilization of reserve, i.e. that the increase in the mobilization flux following the increase in reserve during the assimilation process is negligible. However, if the mobilization flux \dot{p}_C is increasing over the duration of the transient, then S certainly includes contributions from the overheads on growth, and from development or reproduction. This is likely the case when measuring the change in steady state respiration rate of animals feeding at different rates (Bohrer and Lampert, 1988). Thus there is no simple formula for translating SDA measurements into DEB language; each experiment has to be modeled explicitly. Computing the DEB equivalent of Secor's (Secor, 2009) characterization of the SDA, for instance, involves numerically solving the differential equations in Table 3 with initial conditions representing a food impulse and calculating all the dissipated fluxes (dissipation + overheads of growth and assimilation; Table 1) before and after the food impulse.

Standard metabolism and activity

The standard metabolic rate of an animal is defined as the metabolism (M) of an inactive fish that is not digesting food. If we define activity (A) as the amount of energy spent on movement necessary to survive (e.g. to respire, to eat), then we can link the product MA to the following combination of DEB processes: overheads of growth + somatic maintenance + maturity maintenance + development or the overheads of reproduction – excretion during growth and dissipation processes:

$$M \times A = \frac{1}{W_w} \left[(1 - \kappa_G) \dot{p}_G + \dot{p}_D - \mu_N \dot{J}_{\text{NG}} - \mu_N \dot{J}_{\text{ND}} \right]. \quad (10)$$

Many current models that use Kooijman's model structure assume that mechanical work (which is a component of activity) by animals is either small and hence can be neglected, or that it is a component of maintenance. Thus, we cannot directly link activity to a specific component of the standard DEB model. The assumption that mechanical work is a component of somatic maintenance was made in the most detailed DEB-based discussion known to us – a model of Pacific bluefin tuna (Jusup et al., 2011). The validity and limitations of this assumption are discussed in the next section.

Example: Pacific bluefin tuna

Efforts in research and management of Pacific bluefin tuna (PBT) may benefit from an integrative approach based on a DEB model (Jusup et al., 2011). The model offers new insights, notwithstanding the existence of a substantial body of process-specific and environment-specific physiological and bioenergetic data. These include: (1) numerous measurements of metabolic rates by respirometry (Dewar and Graham, 1994; Sepulveda and Dickson,

2000; Blank et al., 2007) and energy losses of starved fish (Boggs and Kitchell, 1991); (2) comprehensive measurements related to embryonic development, including temperature dependence of time required from spawning to hatching (Miyashita et al., 2000); (3) extensive morphological and physiological descriptions of the larval stage, including measurements of body size as a function of time (Miyashita et al., 2001; Sawada et al., 2005); (4) various measurements of growth and feeding rates, feed conversion ratios, and reproductive output of fish in captivity (Aguado-Gimenez and Garcia-Garcia, 2005; Masuma, 2009); (5) detailed studies of cardiovascular function and SDA in response to feeding bouts (Fitzgibbon et al., 2007; Clark et al., 2008); and (6) thorough investigations of PBT heat budget by means of lumped system thermal analysis (Kitagawa et al., 2006; Kitagawa et al., 2007; Kubo et al., 2008).

The DEB modeling framework reveals connections between these data sets, taking into account differences in attributes of the fish (e.g. length, weight) as well as the environmental conditions (e.g. temperature, food density) in which data were gathered. Recognizing this, Jusup et al. (Jusup et al., 2011) formulated a complete life cycle DEB model for PBT – from an egg to an adult female and its eggs. The ‘standard’ DEB model (Sousa et al., 2010) was supplemented with a limited number of assumptions on PBT morphology and thermogenesis. The model was calibrated to emulate physiological characteristics of PBT and used to investigate knowledge gaps such as: (1) reasons for different growth rates between cultivated and wild PBT; (2) origins of similarities in the weight–length relationship of cultivated and wild PBT; (3) estimates of average number of batches produced per spawning season; (4) estimates of food abundance experienced by wild PBT; (5) reasons behind acceleration of growth rate in the larval stage; and (6) causes of deceleration of growth rate in the early juvenile phase.

The DEB model of Jusup et al. (Jusup et al., 2011) predicts energy fluxes (Fig. 1) that can be compared with previous bioenergetic measurements. For an individual growing from 30 to 40 kg, in conditions representative of the wild fish (mean scaled functional response $f=0.905$, mean body temperature 19°C) the model predicts an average assimilation flux of 35.5 W. The utilization flux (totaling 35.1 W) is split between somatic maintenance (64.2%), growth (13.8%), maturity maintenance (21.4%), and maturation (0.6%).

The high expenditure on maintenance relates to a well-recognized problem in tuna aquaculture, the exceptionally high ratio of dry feed weight to wet fish weight gain, traditionally called the feed conversion ratio (FCR). FCR for large bluefin tuna in Mediterranean aquaculture (average initial and final weights of 219 and 255 kg, respectively) is as high as 7.4. Even though a somewhat lower FCR of 4.6 has been reported (Aguado-Gimenez and Garcia-Garcia, 2005) for smaller fish (average initial and final weights of 32 and 63 kg, respectively), it is still high in comparison to an FCR of 1 to 2 characteristic of other fishes. From the bioenergetic point of view, high FCR is an indication that a large fraction of input energy from feed is lost in the form of heat and metabolic products that most likely originate from continuous swimming. The DEB model, which includes cost of swimming in the somatic maintenance flux, captures this dynamics very well.

Further connecting the DEB model predictions to traditional measurements requires data on respiration rates (see Overview of traditional bioenergetic models). The most complete relevant body of data known to us based on the standard interpretation of respirometry measurement is for (smaller) yellowfin tuna, *Thunnus*

albacares (Dewar and Graham, 1994; Korsmeyer et al., 1996; Korsmeyer and Dewar, 2001). These indicate: standard metabolic rate (11%), average contribution from aerobic swimming (27%), oxygen debt recovery (38%), SDA (18%) and growth (6%). When comparing with the DEB model, oxygen debt recovery (aerobic energy expenditure to cover costs of processing metabolites from anaerobic activity, replenishing fuel stores, etc.) should be interpreted as a part of locomotory costs, and included in somatic maintenance. The recovery period can last from a minute to several days, but is typically short except for the largest fish. Thus as the standard DEB model ‘averages’ fast processes, the most appropriate comparison regards the total expenditure associated with anaerobic processes (direct + recovery) as part of somatic maintenance. In yellowfin tuna, this combined cost of movement and oxygen debt recovery accounts for 65% of total respiration, and total dissipation (standard metabolism added) represents 76% of total respiration.

As noted earlier, in DEB theory, respiration is a weighted sum of assimilation, dissipation and growth fluxes; but without explicit assumptions on the stoichiometry of reserves and structure, the weights cannot be calculated *a priori*. However, data on SDA suggest that assimilation should be assigned a lower weight than the other fluxes. The DEB model suggests that assimilation accounts for 9–34% of respiration in PBT, and growth accounts for 12–9% of respiration (depending on the contribution from assimilation). Dissipation, defined previously, is the major component, accounting for 57–79% of respiration depending on the assumed weight of the assimilation. These results are qualitatively consistent with the interpretation of aerobic metabolism for yellowfin tuna in the preceding paragraph, where SDA accounts for 18%, growth for 6%, and dissipative processes for the remaining 76% of total respiration.

These analyses, suggesting that movement costs represent a high proportion of somatic maintenance, can be compared with information on the mechanical requirements for swimming. Theoretical studies involving fluid dynamics and experiments on a robotic fish indicate that the power required to overcome drag at normal swimming speeds is low: a RoboTuna (see Overview of traditional bioenergetic models) of approximately 120 cm fork length achieved a speed of 0.7 ms^{-1} ($0.58 \text{ s}^{-1} \times \text{fork length}$) with a power input of only 0.5283 W. Accompanying numerical modeling, showing a good agreement with experiments in terms of mean power, estimated the propulsive efficiency at over 90% and mean mechanical power, depending on the value of kinematic parameters, between 1.15 and 3.05 W at constant speed ($0.66 \text{ s}^{-1} \times \text{fork length}$). At higher sustained speeds, respiration studies suggest that the costs rise by a factor of approximately 10 at three times the typical cruising speed. Assuming a 20–30% conversion efficiency of chemical energy to mechanical work (Syme and Shadwick, 2002; Smith et al., 2005; Ellerby, 2010), these data suggest that energetic requirements for swimming are much lower than actual expenditure related to swimming as described above.

Further insight is obtained by comparing the mechanical energy requirements for swimming with *in vitro* measurements of power delivery by red muscle. A living tuna similar in size to RoboTuna (120 cm fork length; 35 kg body weight) would have between 4 and 13% red muscle mass as percentage of body weight (Bernal et al., 2001), indicating that the mechanical power required to overcome drag relative to red muscle mass is of the order of 1.0 W kg^{-1} red muscle at typical cruising speeds, with the highest plausible estimates yielding 2.2 W kg^{-1} red muscle. However, *in vitro* peak mechanical power production in red muscle of yellowfin tuna has been shown to exceed 60 W kg^{-1} red muscle, with power

production exceeding 20 W kg⁻¹ red muscle over a wide range of tail beat frequencies (Shadwick and Syme, 2008). Even higher values (44–75 W kg⁻¹ red muscle) were observed for skipjack tuna, *Katsuwonus pelamis* (Syme and Shadwick, 2002). Comparison of these values with the mechanical requirements for sustained swimming (preceding paragraph) demonstrates that a tuna's power capacity much exceeds the requirements for sustained swimming.

In summary, the characterization of the energy fluxes in tuna obtained from a parameter-sparse DEB model describing a tuna's full life cycle is consistent with short-term measurements of changes in respiration rates associated with different processes (e.g. feeding and swimming). A high proportion of the somatic maintenance rate is associated directly or indirectly with swimming costs, with this expenditure of chemical energy being much greater than is required for the mechanical work being performed. Direct measurement of the power output of red muscle indicates that the animal is capable of delivering much greater mechanical power than is required for sustained swimming. Better understanding of these mismatches requires a deeper exploration of the short-term changes in physiological rates than is possible here.

Example: Pacific salmon

Numerous bioenergetic approaches previously developed to study salmonid growth (e.g. Aydin et al., 2005; Ballantyne et al., 2003; Beauchamp et al., 2004; Brodeur et al., 1992; Cech and Myrick, 1999; Madenjian et al., 2004; Petrell and Jones, 2000; Stewart and Ibarra, 1991) are often limited to a particular size range of individuals and to a particular species. However, to fully understand the cumulative impact of stressors at different life stages, and how management and restoration actions could impact salmon populations, we need tools that connect the different life stages and their environments. For example, the effects of sublethal stress in early life (in rivers) may be manifest much later in the life cycle.

To overcome these limitations, Pecquerie et al. (Pecquerie et al., 2011) and Nisbet et al. (Nisbet et al., 2011) proposed a full-life-cycle DEB model applicable to all species of Pacific salmon. This work drew on both of the distinctive strengths of Kooijman's DEB theory highlighted in the Introduction: the full-life-cycle treatment and the theory for interspecific comparisons. The model supplements the standard model (Tables 2 and 3) with a limited number of assumptions on anadromy and semelparity. The body-size scaling relationships implied by DEB theory, i.e. the application to certain parameters of a zoom factor z (defined in Table 2) to express species-specific differences in physiology, capture most variations in life-history traits such as egg size, fry size and fecundity among five species of Pacific salmon: pink (*Oncorhynchus gorbusha*), sockeye (*O. nerka*), coho (*O. kisutch*), chum (*O. keta*) and chinook (*O. tshawytscha*). Initial discrepancies between data and model predictions for one particular species – sockeye – are resolved by adjusting one parameter value, assuming that sockeye lay eggs in finer substrate beds and that smaller eggs are more adapted to these substrates. This result is particularly encouraging for the development of a 'generalized' Pacific salmon model, with a potential method to fill the species-specific data gap and study-species- and population-specific adaptations.

Nisbet et al. (Nisbet et al., 2011) have also worked on modeling one particular species, chinook salmon (*O. tshawytscha*), with an initial aim of studying how variations in environmental conditions affect age and size of spawning adults. Qualitative examination of the intraspecific variations in life-history traits shows that the observed patterns are also well reproduced. The observation that

fast-growing individuals migrate back to the river to spawn at an earlier age and smaller size than slow-growing individuals (Parker and Larkin, 1959) is well reproduced. Quantitatively, preliminary simulation results for chinook broadly agreed with experimental studies on chinook growth and development rates, but further work is required on fecundity patterns. Energy loss during upstream migration is a potential cause of a mismatch of predictions with data on fecundity.

Overall, the findings support the validity of modeling all the different life stages of a Pacific salmon in a common framework. However, further refinement of chinook model for quantitative modeling of specific populations requires making a connection with existing studies on chinook bioenergetics (e.g. Beer and Anderson, 1997; Madenjian et al., 2004; Petrell and Jones, 2000). As a first step, we compare the overall energy budget established for a 3 kg chinook by Petrell and Jones (Petrell and Jones, 2000) with the chinook-specific DEB model presented in Nisbet et al. (Nisbet et al., 2011) following the equations detailed in the fourth section of this paper (Relating Kooijman's DEB theory to other bioenergetic approaches).

For a mean scaled functional response $f=0.9$ (high food level), the model predicts that the mobilization flux is split between somatic maintenance (50%), growth (10%), maturity maintenance (11.5%) and allocation to reproductive reserve (28.5%). When we compare these processes with the bioenergetic model presented by Petrell and Jones (Petrell and Jones, 2000), we find that growth (of structure, reserve and reproduction reserve) accounts for 34% of the amount of energy ingested. This value is in agreement with the 29±6% estimated by Brett and Groves (Brett and Groves, 1979), cited by Petrell and Jones (Petrell and Jones, 2000), for 15 fish species.

As in a standard DEB model, the costs of swimming in the salmon DEB model were considered as part of the maintenance costs. But to look at specific local river management scenarios, swimming costs need to be detailed. River flow regimes, determined in part by management decisions, impact the earliest and latest life stages because they determine temperature and oxygen supply for embryos, and body temperature and swimming requirements (and hence swimming costs) for juveniles that feed and aim to sustain their location in the river. More obviously, flow regimes impact swimming costs of adults that migrate upstream to reach the spawning grounds.

We are considering two approaches for introducing swimming costs in a DEB model for Pacific salmon. First, we note that adults do not feed during their upstream migration to the spawning grounds (Armstrong, 2010), which may last several months. We could therefore compare the energy expenditure due to total maintenance costs and egg production predicted by the salmon DEB at a given temperature for the duration of the migration for non-feeding individuals with the energy expenditure reported for sockeye salmon during their migration (Cooke et al., 2006a; Cooke et al., 2006b; Cooke et al., 2008; Crossin et al., 2009; Hanson et al., 2008; Rand et al., 2006). Associated costs may depend on elevation gain, flow regime, water temperature and many other factors. We need to evaluate whether introducing these factors (and thus adding more complexity to the model) is necessary to understand the variations in energy allocated to reproduction after migration.

Second, as in the tuna case, we could incorporate theoretical estimates of swimming costs in the DEB model. Petrell and Jones (Petrell and Jones, 2000), for example, evaluated the drag and power requirement of swimming for chinook and Atlantic salmon

(*Salmo salar*) by calculating the drag coefficient and planform area using body measurements and swimming speed. These authors suggested that the difference in energy expenditure due to drag could explain 20% of the observed difference in FCR between the two species. To obtain this estimation, they used a classical bioenergetic approach to evaluate how the growth – in weight, not in structure – is reduced in chinook because of a higher cost of swimming, largely due to a larger girth compared with an Atlantic salmon of the same weight, and thus a higher drag. For DEB applications, it is necessary to interpret the differences in power requirement for swimming in terms of structure-specific costs (and not weight-specific costs). This would allow comparison of budgets of individuals of the same weight of two different species in the DEB context. Deviations from DEB predictions could then be hypothesized as arising from differences in power requirement due to species-specific body form. Such interpretation would inform more precisely how we transfer parameter values among related species.

Finally, introducing specific swimming costs in our salmon DEB model would allow us to complement environmental flow assessment studies for juvenile salmon. We could potentially perform studies similar to that of Hayes et al. (Hayes et al., 2007), who evaluated energy uptake and expenditure in different river flow regimes for brown trout (*Salmo trutta*), which required modeling the trade-off between the costs in mechanical energy of life in high flows and the benefits of enhanced delivery rates of food (drifting invertebrates).

Discussion

Kooijman's DEB theory is emerging as a powerful tool for relating metabolic organization within organisms to those aspects of physiological performance that impact higher levels of biological organization, especially population dynamics and ecosystem processes. But the theory is highly abstract with neither the state variables nor the internal energy or material fluxes being directly measurable. The high level of abstraction acts as a deterrent to its wider use, but is the key to its generality. In this review we have provided formulae for common bioenergetic measurements in terms of the state variables and fluxes in a 'standard' DEB model. Although our examples involve fish, the equations presented here (Relating Kooijman's DEB theory to other bioenergetic approaches) are general and can be used to interconnect bioenergetic measurements with DEB variables and fluxes for any animal.

Nisbet et al. (Nisbet et al., 2010) recently reviewed the extent to which the individual–population connection could be achieved with simpler, empirically based models where the state of an animal was characterized by one variable (size). They concluded that remarkably simple mass-balance models, well supported by empirical data and resembling those described here as traditional bioenergetic models, are often adequate for connecting the performance of a well-studied organism to the history of its environment. But they also highlighted the serious downsides of such pragmatism: (1) the loss of connection to theory describing interspecific variation in physiological rates, and (2) the parameter richness of empirically based models for a complete life cycle.

The motivation for the two applications in this paper of Kooijman's more abstract approach to DEB theory came from recognition of these limitations. Each fish model was a variant of Kooijman's 'standard' DEB model (Sousa et al., 2010), and relied for parameter estimation on the capacity of DEB theory to offer a unified description of the full life cycle. The salmon study also exploits the body-size scaling relationships. The decision to use the

full DEB model in each application was therefore justified, even on pragmatic grounds. Yet there is a large body of empirical literature on the bioenergetics and biomechanics of both species that is constructed around the simpler paradigm. We faced (and still face) challenges figuring out how to relate these data to the DEB models, thereby giving added precision to the models in applications. In this paper, we made connections that relied on the formulae presented, and identified further issues that must be part of future research.

A more ambitious ecological motivation for better understanding the interconnections between the different modeling approaches is that there are some systems where the simplifying assumptions of 'standard' DEB theory may be invalid. We have already noted the potential importance of changes in the theory that are required to cover anaerobic processes (Childress and Somero, 1990), and we have discussed situations where mechanical work represents a significant contribution to the energy budget. Both situations require extensions of the thermodynamic underpinnings of DEB theory (Sousa et al., 2006).

Notwithstanding the remaining challenges, our take-home message for ecologists is that the rigorous conceptual framework offered by Kooijman's theory has the potential to allow better experimental design, open the door for creative utilization of hard-earned data, and help predict individual growth and reproduction in hitherto unobserved environments. We have tried to demystify the theory by clarifying the connections to measurements commonly obtained in physiological ecology. Further case studies are needed to further sharpen our understanding of the connections; over time, these should in turn lead to improved theory.

Acknowledgements

We thank Mark Denny for the organization of the symposium on Biophysics, Bioenergetics and Mechanistic Approaches to Ecology in March 2011. We thank Bill Gurney, Michael Kearney, Bas Kooijman, Ed McCauley, Erik Muller, Tania Sousa and others for discussions of DEB theory, and for sharing unpublished work.

Funding

This work was supported by the US National Science Foundation (grant EF-0742521); NOAA (subaward from NA100AR4320156); the Croatian Ministry for Science, Education and Sport (grant 098-0982934-2719); the US National Science Foundation and the US Environmental Protection Agency under Cooperative Agreement Number EF 0830117; the Society for Conservation of Fisheries Resources and Marine Environment (CoFRaME), project "Modeling approach for efficient bluefin tuna aquaculture"; and The Japanese Ministry of Education, Culture, Sports, Science & Technology (MEXT), scholarship no. 080755.

References

- Aguado-Gimenez, F. and Garcia-Garcia, B. (2005). Growth, food intake and feed conversion rates in captive Atlantic bluefin tuna (*Thunnus thynnus* Linnaeus, 1758) under fattening conditions. *Aquacult. Res.* **36**, 610-614.
- Altringham, J. F. and Ellerby, D. J. (1999). Fish swimming: patterns in muscle function. *J. Exp. Biol.* **202**, 3397-3403.
- Anderson, E. J., McGillis, W. R. and Grosenbaugh, M. A. (2001). The boundary layer of swimming fish. *J. Exp. Biol.* **204**, 81-102.
- Armstrong, J. B. (2010). Comment on "Egg consumption in mature Pacific salmon (*Oncorhynchus* spp.)". *Can. J. Fish. Aquat. Sci.* **67**, 2052-2054.
- Aydin, K. Y., McFarlane, G. A., King, J. R., Megrey, B. A. and Myers, K. W. (2005). Linking oceanic food webs to coastal production and growth rates of Pacific salmon (*Oncorhynchus* spp.), using models on three scales. *Deep-Sea Res. Part II* **52**, 757-780.
- Ballantyne, A. P., Brett, M. T. and Schindler, D. E. (2003). The importance of dietary phosphorus and highly unsaturated fatty acids for sockeye (*Oncorhynchus nerka*) growth in Lake Washington—a bioenergetics approach. *Can. J. Fish. Aquat. Sci.* **60**, 12-22.
- Barrett, D. S., Triantafyllou, M. S., Yue, D. K. P., Grosenbaugh, M. A. and Wolfgang, M. J. (1999). Drag reduction in fish-like locomotion. *J. Fluid Mech.* **392**, 183-212.
- Beauchamp, D. A., Sergeant, C. J., Mazur, M. M., Scheuerell, J. M., Schindler, D. E., Scheuerell, M. D., Fresh, K. L., Seiler, D. E. and Quinn, T. P. (2004). Spatial-temporal dynamics of early feeding demand and food supply for sockeye salmon fry in Lake Washington. *Trans. Am. Fish. Soc.* **133**, 1014-1032.

- Beer, W. N. and Anderson, J. J. (1997). Modelling the growth of salmonid embryos. *J. Theor. Biol.* **189**, 297-306.
- Bernal, D., Dickson, K. A., Shadwick, R. E. and Graham, J. B. (2001). Analysis of the evolutionary convergence for high performance swimming in lamnid sharks and tunas. *Comp. Biochem. Physiol.* **129A**, 695-726.
- Blake, R. W. (2004). Fish functional design and swimming performance. *J. Fish Biol.* **65**, 1193-1222.
- Blank, J. M., Farwell, C. J., Morrisette, J. M., Schallert, R. J. and Block, B. A. (2007). Influence of swimming speed on metabolic rates of juvenile Pacific bluefin tuna and yellowfin tuna. *Physiol. Biochem. Zool.* **80**, 167-177.
- Boggs, C. H. and J. F., Kitchell (1991). Tuna metabolic rates estimated from energy-losses during starvation. *Physiol. Zool.* **64**, 502-524.
- Bohrer, R. N. and Lampert, W. (1988). Simultaneous measurement of the effect of food concentration on assimilation and respiration in *Daphnia magna* Straus. *Funct. Ecol.* **2**, 463-471.
- Borazjani, I. and Sotiropoulos, F. (2010). On the role of form and kinematics on the hydrodynamics of self-propelled body/caudal fin swimming. *J. Exp. Biol.* **213**, 89-107.
- Brett, J. R. (1963). Energy required for swimming by young sockeye salmon with a comparison of drag force on a dead fish. *Trans. R. Soc. Can.* **1**, 441-457.
- Brett, J. R. and Groves, T. D. D. (1979). Physiological energetics. In *Bioenergetics and Growth*, Vol. 8 (ed. W. S. Hoar, D. J. Randall and J. R. Brett), pp. 279-352. New York: Academic Press.
- Brodeur, R. D., Francis, R. C. and Pearcey, W. G. (1992). Food consumption of juvenile coho (*Oncorhynchus kisutch*) and chinook salmon (*O. tshawytscha*) on the continental shelf off Washington and Oregon. *Can. J. Fish. Aquat. Sci.* **49**, 1670-1685.
- Brown, J. H., Gillooly, J. F., Allen, A. P., Savage, V. M. and West, G. B. (2004). Toward a metabolic theory of ecology. *Ecology* **85**, 1771-1789.
- Brucker, C. and Bleckmann, H. (2007). Vortex dynamics in the wake of a mechanical fish. *Exp. Fluids* **43**, 799-810.
- Buckley, L. B., Rodda, G. H. and Jetz, W. (2008). Thermal and energetic constraints on ectotherm abundance: a global test using lizards. *Ecology* **89**, 48-55.
- Buckley, L. B., Urban, M. C., Angilletta, M. J., Crozier, L. G., Rissler, L. J. and Sears, M. W. (2010). Can mechanism inform species' distribution models? *Ecol. Lett.* **13**, 1041-1054.
- Cech, J. J. and Myrick, C. A. (1999). *Steelhead and Chinook Salmon Bioenergetics: Temperature, Ration, and Genetic Effects. Technical Completion Report*, vol. 885, pp. 74. Davis, CA: University of California Water Resources Center.
- Childress, J. J. and Somero, G. N. (1990). Metabolic scaling: a new perspective based on scaling of glycolytic enzyme activities. *Am. Zool.* **30**, 161-173.
- Chipps, S. R. and Wahl, D. H. (2008). Bioenergetics modeling in the 21st century: reviewing new insights and revisiting old constraints. *Trans. Am. Fish. Soc.* **137**, 298-313.
- Clark, T. D., Taylor, B. D., Seymour, R. S., Ellis, D., Buchanan, J., Fitzgibbon, Q. P. and Frappell, P. B. (2008). Moving with the beat: heart rate and visceral temperature of free-swimming and feeding bluefin tuna. *Proc. R. Soc. Lond. B* **275**, 2841-2850.
- Cooke, S. J., Hinch, S. G., Crossin, G. T., Patterson, D. A., English, K. K., Healey, M. C., Shrimpton, J. M., Van Der Kraak, G. and Farrell, A. P. (2006a). Mechanistic basis of individual mortality in pacific salmon during spawning migrations. *Ecology* **87**, 1575-1586.
- Cooke, S. J., Hinch, S. G., Crossin, G. T., Patterson, D. A., English, K. K., Shrimpton, J. M., Van der Kraak, G. and Farrell, A. P. (2006b). Physiology of individual late-run Fraser River sockeye salmon (*Oncorhynchus nerka*) sampled in the ocean correlates with fate during spawning migration. *Can. J. Fish. Aquat. Sci.* **63**, 1469-1480.
- Cooke, S. J., Hinch, S. G., Farrell, A. P., Patterson, D. A., Miller-Saunders, K., Welch, D. W., Donaldson, M. R., Hanson, K. C., Crossin, G. T., Mathes, M. T. et al. (2008). Developing a mechanistic understanding of fish migrations by linking telemetry with physiology, behavior, genomics and experimental biology: an interdisciplinary case study on adult Fraser River sockeye salmon. *Fisheries* **33**, 321-338.
- Crossin, G. T., Hinch, S. G., Cooke, S. J., Cooperman, M. S., Patterson, D. A., Welch, D. W., Hanson, K. C., Olsson, L., English, K. K. and Farrell, A. P. (2009). Mechanisms influencing the timing and success of reproductive migration in a capital breeding semelparous fish species, the sockeye salmon. *Physiol. Biochem. Zool.* **82**, 635-652.
- Dewar, H., and Graham, J. B. (1994). Studies of tropical tuna swimming performance in a large water tunnel. *J. Exp. Biol.* **192**, 13-31.
- Ellerby, D. J. (2010). How efficient is a fish? *J. Exp. Biol.* **213**, 3765-3767.
- Farrell, A. P. and Steffensen, J. F. (1987). An analysis of the energetic cost of the branchial and cardiac pumps during sustained swimming in trout. *Fish Physiol. Biochem.* **4**, 73-79.
- Fitzgibbon, Q. P., Seymour, R. S., Ellis, D. and Buchanan, J. (2007). The energetic consequence of specific dynamic action in southern bluefin tuna *Thunnus maccoyii*. *J. Exp. Biol.* **210**, 290-298.
- Hanson, K. C., Cooke, S. J., Hinch, S. G., Crossin, G. T., Patterson, D. A., English, K. K., Donaldson, M. R., Shrimpton, J. M., Van der Kraak, G. and Farrell, A. P. (2008). Individual variation in migration speed of upriver-migrating sockeye salmon in the Fraser River in relation to their physiological and energetic status at marine approach. *Physiol. Biochem. Zool.* **81**, 255-268.
- Hayes, J. W., Hughes, N. F. and Kelly, L. H. (2007). Process-based modelling of invertebrate drift transport, net energy intake and reach carrying capacity for drift-feeding salmonids. *Ecol. Model.* **207**, 171-188.
- Jayne, B. C. and Lauder, G. V. (1994). How swimming fish use slow and fast muscle fibers: implications for models of vertebrate muscle recruitment. *J. Comp. Physiol. A* **175**, 123-131.
- Jusup, M., Klanjscek, T., Matsuda, H. and Kooijman, S. A. L. M. (2011). A full life cycle bioenergetic model for bluefin tuna. *PLoS ONE* **6**, e21903.
- Kearney, M. R., Simpson, S. J., Raubenheimer, D. and Helmuth, B. (2010). Modelling the ecological niche from functional traits. *Philos. Trans. R. Soc. Lond. B* **365**, 3469-3483.
- Kearney, M. R., Matzelle, A. and Helmuth, B. (2012). Biomechanics meets the ecological niche: the importance of temporal data resolution. *J. Exp. Biol.* **215**, 922-933.
- Kiceniuk, J. W. and Jones, D. R. (1977). The oxygen transport system in trout (*Salmo gairdneri*) during sustained exercise. *J. Exp. Biol.* **69**, 247-260.
- Kitagawa, T., Kimura, S., Nakata, S. and Yamada, H. (2006). Thermal adaptation of Pacific bluefin tuna *Thunnus orientalis* to temperate waters. *Fish. Sci.* **72**, 149-156.
- Kitagawa, T., Kimura, S., Nakata, S. and Yamada, H. (2007). Why do young Pacific bluefin tuna repeatedly dive to depths through the thermocline? *Fish. Sci.* **73**, 98-106.
- Kooijman, S. A. L. M. (1986). Population dynamics on the basis of energy budgets. In *The Dynamics of Physiologically Structured Populations*, vol. 68 (ed. J. A. J. Metz and O. Diekmann), pp. 266-297. Berlin: Springer-Verlag.
- Kooijman, S. A. L. M. (1993). *Dynamic Energy Budgets in Biological Systems: Theory and Applications in Ecotoxicology*. New York: Cambridge University Press.
- Kooijman, S. A. L. M. (2000). *Dynamic Energy and Mass Budgets in Biological Systems*. New York: Cambridge University Press.
- Kooijman, S. A. L. M. (2001). Quantitative aspects of metabolic organization: a discussion of concepts. *Philos. Trans. R. Soc. Lond. B* **356**, 331-349.
- Kooijman, S. A. L. M. (2010). *Dynamic Energy Budget Theory for Metabolic Organization*, 3rd edn. Cambridge, UK: Cambridge University Press.
- Kooijman, S. A. L. M., Sousa, T., Pecquerie, L., van der Meer, J. and Jager, T. (2008). From food-dependent statistics to metabolic parameters, a practical guide to the use of dynamic energy budget theory. *Biol. Rev.* **83**, 533-552.
- Korsmeyer, K. E. and Dewar, H. (2001). Tuna metabolism and energetics. *Fish Physiol.* **19**, 35-78.
- Korsmeyer, K. E., Dewar, H., Lai, N. C. and Graham, J. B. (1996). The aerobic capacity of tunas: adaptation for multiple metabolic demands. *Comp. Biochem. Physiol.* **113A**, 17-24.
- Korsmeyer, K. E., Steffensen, J. F. and Herskin, J. (2002). Energetics of median and paired fin swimming, body and caudal fin swimming, and gait transition in parrotfish (*Scarus schlegelii*) and triggerfish (*Rhinocanthus aculeatus*). *J. Exp. Biol.* **205**, 1253-1263.
- Kubo, T., Sakamoto, W., Murata, O. and Kumai, H. (2008). Whole-body heat transfer coefficient and body temperature change of juvenile Pacific bluefin tuna *Thunnus orientalis* according to growth. *Fish. Sci.* **74**, 995-1004.
- Madenjian, C. P., O'Connor, D. V., Chernyak, S. M., Rediske, R. R. and O'Keefe, J. P. (2004). Evaluation of a chinook salmon (*Oncorhynchus tshawytscha*) bioenergetics model. *Can. J. Fish. Aquat. Sci.* **61**, 627-635.
- Masuma, S. (2009). Biology of Pacific bluefin tuna inferred from approaches in captivity. *Collect. Vol. Sci. Pap. ICCAT* **63**, 207-229.
- Miyashita, S., Tanaka, Y., Sawada, Y., Murata, O., Hattori, N., Takii, K., Mukai, Y. and Kumai, H. (2000). Embryonic development and effects of water temperature on hatching of the bluefin tuna, *Thunnus thynnus*. *Suisanzoushoku* **48**, 199-207 (in Japanese).
- Miyashita, S., Sawada, Y., Okada, T., Murata, O. and Kumai, H. (2001). Morphological development and growth of laboratory-reared larval and juvenile *Thunnus thynnus* (Pisces: Scombridae). *Fish. Bull.* **99**, 601-616.
- Ney, J. J. (1993). Bioenergetics modeling today-growing pains on the cutting edge. *Trans. Am. Fish. Soc.* **122**, 736-748.
- Nisbet, R. M., Muller, E. B., Lika, K. and Kooijman, S. A. L. M. (2000). From molecules to ecosystems through dynamic energy budget models. *J. Anim. Ecol.* **69**, 913-926.
- Nisbet, R. M., McCauley, E., Gurney, W. S. C., Murdoch, W. W. and Wood, S. N. (2004). Formulating and testing a partially specified dynamic energy budget model. *Ecology* **85**, 3132-3139.
- Nisbet, R. M., McCauley, E. and Johnson, L. R. (2010). Dynamic energy budget theory and population ecology: lessons from *Daphnia*. *Philos. Trans. R. Soc. Lond. B* **365**, 3541-3552.
- Nisbet, R. M., Anderson, K. E., Pecquerie, L. and Harrison, L. (2011). Integrating bioenergetics, spatial scales, and population dynamics for environmental flow assessment. *California Energy Commission, PIER* **500-02-004**.
- Papadopoulos, A. (2008). On the hydrodynamics-based power-law function and its application in fish swimming energetics. *Trans. Am. Fish. Soc.* **137**, 997-1006.
- Parker, R. R. and Larkin, P. A. (1959). A concept of growth in fishes. *J. Fish. Res. Board Can.* **16**, 721-745.
- Pecquerie, L., Johnson, L. R., Kooijman, S. A. L. M. and Nisbet, R. M. (2011). Analyzing variations in life-history traits of Pacific salmon in the context of dynamic energy budget (DEB) theory. *J. Sea Res.* **66**, 424-433.
- Peng, J. and Dabiri, J. O. (2008). An overview of a Lagrangian method for analysis of animal wake dynamics. *J. Exp. Biol.* **211**, 280-287.
- Petrel, R. J. and Jones, R. E. (2000). Power requirement of swimming in chinook salmon and Atlantic salmon and implications for food conversion and growth performance. *Aquacult. Eng.* **22**, 225-239.
- Ponsard, S. and Averbuch, P. (1999). Should growing and adult animals fed on the same diet show different delta N-15 values? *Rapid Commun. Mass Spectrom.* **13**, 1305-1310.
- Rand, P. S., Hinch, S. G., Morrison, J., Foreman, M. G. G., MacNutt, M. J., Macdonald, J. S., Healey, M. C., Farrell, A. P. and Higgs, D. A. (2006). Effects of river discharge, temperature, and future climates on energetics and mortality of adult migrating Fraser River sockeye salmon. *Trans. Am. Fish. Soc.* **135**, 655-667.
- Sawada, Y., Okada, T., Miyashita, S., Murata, O. and Kumai, H. (2005). Completion of the Pacific bluefin tuna *Thunnus orientalis* (Temminck et Schlegel) life cycle. *Aquacult. Res.* **36**, 413-421.
- Schultz, W. W. and Webb, P. W. (2002). Power requirements of swimming: do new methods resolve the old questions? *Integr. Comp. Biol.* **42**, 1018-1025.

- Secor, S. M.** (2009). Specific dynamic action: a review of the postprandial metabolic response. *J. Comp. Physiol. B* **179**, 1-56.
- Sepulveda, C. and Dickson, K. A.** (2000). Maximum sustainable speeds and cost of swimming in juvenile kawakawa tuna (*Euthynnus affinis*) and chub mackerel (*Scomber japonicus*). *J. Exp. Biol.* **203**, 3089-3101.
- Shadwick, R. E. and Syme, D. A.** (2008). Thunniform swimming: muscle dynamics and mechanical power production of aerobic fibres in yellowfin tuna (*Thunnus albacares*). *J. Exp. Biol.* **211**, 1603-1611.
- Sloman, K. A., Motherwell, G., O'Connor, K. I. and Taylor, A. C.** (2000). The effect of social stress on the standard metabolic rate (SMR) of brown trout, *Salmo trutta*. *Fish Physiol. Biochem.* **23**, 49-53.
- Smith, N. P., Barclay, C. J. and Loisel, D. S.** (2005). The efficiency of muscle contraction. *Prog. Biophys. Mol. Biol.* **88**, 1-58.
- Sousa, T., Mota, R., Domingos, T. and Kooijman, S. A. L. M.** (2006). Thermodynamics of organisms in the context of dynamic energy budget theory. *Phys. Rev. E Stat. Nonlin. Soft Matter Phys.* **74**, 051951.
- Sousa, T., Domingos, T., Poggiale, J. C. and Kooijman, S. A. L. M.** (2010). Dynamic energy budget theory restores coherence in biology Introduction. *Philos. Trans. R. Soc. Lond. B* **365**, 3413-3428.
- Stewart, D. J. and Ibarra, M.** (1991). Predation and production by salmonine fishes in Lake Michigan, 1978-88. *Can. J. Fish. Aquat. Sci.* **48**, 909-922.
- Syme, D. A. and Shadwick, R. E.** (2002). Effects of longitudinal body position and swimming speed on mechanical power of deep red muscle from skipjack tuna (*Katsuwonus pelamis*). *J. Exp. Biol.* **205**, 189-200.
- Triantafyllou, M. S., Techet, A. H., Zhu, Q., Beal, D. N., Hover, F. S. and Yue, D. K. P.** (2002). Vorticity control in fish-like propulsion and maneuvering. *Integr. Comp. Biol.* **42**, 1026-1032.
- Tytell, E. D.** (2007). Do trout swim better than eels? Challenges for estimating performance based on the wake of self-propelled bodies. *Exp. Fluids* **43**, 701-712.
- Webb, P. W.** (1971a). The swimming energetics of trout: I. Thrust and power output at cruising speeds. *J. Exp. Biol.* **55**, 489-520.
- Webb, P. W.** (1971b). The swimming energetics of trout: II. Oxygen consumption and swimming efficiency. *J. Exp. Biol.* **55**, 521-540.
- Webb, P. W. and Cotel, A. J.** (2010). Turbulence: does vorticity affect the structure and shape of body and fin propulsors? *Integr. Comp. Biol.* **50**, 1155-1166.
- Wolfgang, M. J., Anderson, J. M., Grosenbaugh, M. A., Yue, D. K. P. and Triantafyllou, M. S.** (1999). Near-body flow dynamics in swimming fish. *J. Exp. Biol.* **202**, 2303-2327.
- Zhu, Q., Wolfgang, M. J., Yue, D. K. P. and Triantafyllou, M. S.** (2002). Three-dimensional flow structures and vorticity control in fish-like swimming. *J. Fluid Mech.* **468**, 1-28.