

Integrating Dynamic Energy Budget (DEB) theory with traditional bioenergetic models

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Abstract

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; also how physiological performance is influenced by environmental variables such as food density and temperature. A “standard” DEB model due to S.A.L.M. Kooijman describes the performance (growth, development, reproduction, respiration, etc) of *all* life stages of an animal (e.g. egg, embryo, juvenile, adult), and predicts both intra- and inter-specific 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.

1. Introduction

Empiricism alone does not offer a practical way to understand how environmental change impacts the physiology and viability of organisms. This is for two 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, and just as important, experimental studies yield information that is restricted to specific aspects of some system, with extrapolation to new contexts requiring verbal, statistical or mechanistic theory. This paper focuses on 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 relate processes at different levels of organization (Brown et al., 2004; Nisbet et al., 2000). 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., submitted).

“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 bioenergetic 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 (Chippis 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, 2010b; Nisbet et al., 2000) starts from a set of well-defined assumptions and provides a characterization of the complete life cycle (egg, embryo, juvenile, adult) of an animal through a “standard” model with 12 parameters. It predicts both inter- and intra-specific 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 (for example) respiration rate or heat loss are commonly linear combinations of individually unobservable fluxes.

The two contrasting approaches, outlined in sections 2 and 3 of this paper, can be characterized as data driven (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 section 4 we provide the recipe for two quantities where the connection is straightforward and we outline a systematic method for handling subtler situations. The connections are further illustrated in sections 5 and 6, where we review and synthesize data on two fish 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 (section 7) of some challenges in further integrating traditional approaches with DEB theory and in simplifying DEB theory to make the connections more transparent.

2. Kooijman’s Dynamic Energy Budget (DEB) theory

DEB theory is a powerful theoretical framework for relating suborganismal (biochemical, genetic, 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, 2010b; 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 (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*¹ as biomass that requires energy expenditure for maintenance; reserve is *defined* as biomass that does not require maintenance. An immediate implication of these definitions is the 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 different and involves a mixture of many compounds, but is represented as a “generalized compound” with fixed stoichiometry, e.g. a molecule of structure (V) has formula² $\text{CH}_{n_{HV}} \text{O}_{n_{OV}} \text{N}_{n_{NV}}$. Each generalized compound has a specified chemical potential (Gibbs energy per C-mol). The relative masses of each component may vary over time, as, for example, during a period of starvation when the ratio of reserves 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

¹ 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.

² 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 units for measuring mass is C-mol (Kooijman 2010), and chemical potentials have dimension energy per C-mol.

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 three types: (i) assimilation (food \rightarrow reserve), (ii) “dissipation” defined³ as metabolic work that do not lead the production of new biological material, i.e. somatic and maturity maintenance along with the overheads of growth (reserve \rightarrow mineral products), and (iii) growth (reserve \rightarrow structure). Allocation of reserve to reproduction is not considered a transformation, since “reserve” and “reproductive reserve” are assumed to have the same chemical composition. Conversion of reproductive reserve into eggs has some inefficiency, but is not considered as part a ‘basic’ transformation. . The chemical equations characterizing the three basic 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 recipe 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 – see section 4.

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 inter-specific *body-size scaling relations* or *co-variation of parameters* (chapter 8 of Kooijman 2010; see also 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 species and the latter varying in a predictable way with size. In practice, extensive parameters scale directly with a “zoom factor” z which is defined as the ratio of the maximum length of the species of interest divided by the maximum length of the

³ Dissipation is another term with a precise definition for the standard DEB model that does not match its use in other areas of biology. Section 2.5 of Kooijman (2010) discusses this in detail. Note in particular that the overhead on reproduction is not included in Kooijman’s definition.

reference species $L = L_m / L_{m,ref}$. Where applicable, the size dependence is indicated in Table 2. Parameters for the model of Pacific salmon in this paper were, for instance, estimated with the help of these relations (Pecquerie et al. submitted).

Relating Kooijman's DEB model to bioenergetic data is greatly facilitated by the work of 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 subtleties⁴, 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.

3. 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 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" (abbreviated as SDA and 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 components of growth, the balance equation (BE) then takes the form

$$C = G + MA + S + F + U \tag{BE}$$

⁴ See Table II of Sousa et al.(2006).

Notwithstanding the similarity of the principles underlying the balance equations, the definition of the fluxes in the bioenergetic models rests 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 eq. (BE) 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 subtle differences 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, different 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 (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, e.g. feeding rate, may covary with swimming speed.

Activity can alternatively be estimated from the mechanical power requirements of fish (e.g. Brett, 1963, Petrell and Jones, 2000, Schultz and Webb, 2001). 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?
- 2) How does the produced mechanical power relate to the metabolic (chemical) energy used by the muscle?

A long standing approach to the first question uses measurements of drag on dead, or model, fish pulled at differing speeds through water (Brett, 1963; Smit, 1965). However, fish are well known to achieve higher efficiencies than are inferred from such calculations. Recently,

particular success in defining the mechanical requirements of swimming has been achieved by techniques commonly referred to as the Vortex Interaction (Manipulation) Models (Schultz and Webb, 2001). These techniques involve experimentation on robotic models and live fish combined with the Particle Image Velocimetry (PIV), computational methods and hydrodynamic modeling. Research in the area of Vortex Interaction Models was motivated by the observation that the fish achieve remarkably higher efficiencies than the traditional human-made underwater vehicles, while older fish-inspired designs performed poorly (Triantafyllou and Triantafyllou, 1995). Examinations, involving a robotic model of a 1.2 m long bluefin tuna (called *RoboTuna*), PIV around live fish, and hydrodynamic modeling, concluded that the self-propelled fish-like locomotion reduces drag by as much as 50% (Barrett et al., 1999).

The second question, relating the produced mechanical power to the metabolic (chemical) energy used by the muscle, is equally challenging (Ellerby, 2010). Uncertainties to be resolved include quantifying: (i) the contribution of anaerobic energy expenditure and (ii) oxygen utilized to satisfy needs other than the locomotion?

4. 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 (BE – above) and DEB processes presented in Fig. 1 and then discuss possible interpretations of some of the terms in the balance equation (BE). Our treatment has some overlap with chapter 11 of Kooijman (2010), but differs in some details, for example our treatment of SDA. Equation numbers in this section refer to equations in Table 3.

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 :

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

Food consumption C. The standard DEB model assumes constant assimilation efficiency κ_X for one type of food X . We thus express food consumption C as follows:

$$C = \frac{1}{W_w} \dot{p}_X = \frac{1}{W_w \kappa_X} \dot{p}_A$$

with the ingestion rate $\dot{p}_X = \frac{\dot{p}_A}{\kappa_X}$.

Growth G. In a DEB model, the growth process only refers to the 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 in the reproduction buffer in adults:

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

with $\frac{dE}{dt}$, $\frac{dV}{dt}$, and $\frac{dE_R}{dt}$ given in Eqs (1), (2) and (4) (Table 3).

Metabolic losses: F + U + S + MA. The sum of all metabolic losses in a traditional bioenergetic approach has an unambiguous link with DEB processes:

$$\begin{aligned} F + U + S + MA &= \frac{1}{W_w} \left((1 - \kappa_X) \dot{p}_X + (1 - \kappa_G) \dot{p}_G + \dot{p}_D \right) \\ &= \frac{1}{W_w} \left((1 - \kappa_X) \dot{p}_X + (1 - \kappa_G) \dot{p}_G + \dot{p}_S + \dot{p}_J + (1 - \kappa_R) \dot{p}_R \right) \end{aligned}$$

In this equation, $(1 - \kappa_X) \dot{p}_X$ represents the overhead of assimilation, $(1 - \kappa_G) \dot{p}_G$ represents the overheads of growth, and \dot{p}_D is the dissipation term. The parameter $\kappa_G = \frac{\mu_V d_V}{w_V [E_G]}$ is the fraction of energy for growth that is fixed into structure. The fluxes \dot{p}_G , \dot{p}_S and \dot{p}_J are given in eqs. (2), (7)

and (8) 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. This term also has a unique link with DEB processes:

$$F = \frac{1}{W_w} \kappa_P \dot{p}_X = \frac{1}{W_w} \frac{\kappa_P}{\kappa_X} \dot{p}_A$$

with the constraint $\kappa_P < 1 - \kappa_X$

Excretion U. Excretion U is subtracted from the digestible energy to obtain the metabolizable energy that fuels the growth and maintenance processes in a traditional bioenergetic approach (e.g. Brett and Groves, 1979). Excretion is thus primarily associated with the ingestion process. However, excretion of nitrogen previously assimilated, during protein turn-over for instance, is regarded as one of the components underpinning trophic isotopic enrichment in $\delta^{15}N$ in animals (Ponsard and Averbuch, 1999). This highlights the importance of considering excretion in *all* metabolic processes, and in particular assimilation and somatic maintenance,. 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: assimilation, growth and dissipation, i.e. there is potentially production of N-waste (e.g. ammonia, urea, ...) during all metabolic processes:

$$U = \frac{1}{W_w} \mu_N (J_{NA} + J_{NG} + J_{ND})$$

with μ_N (J.Cmol⁻¹) denoting the chemical potential of the N-waste produced and J_{NA} , J_{NG} and J_{ND} (Cmol.d⁻¹) denoting the mass fluxes of N-waste produced during assimilation, growth, and dissipation, respectively. For example, the product $\mu_N J_{NA}$ (J.d⁻¹) is thus the energy flux associated with the excretion of ammonia. Each component of the flux of N-waste is fully determined by

the mass balance equations, and so does not require extra parameters, provided the elemental composition of food, reserve, structure and faeces is specified. It should be noted that determining the elemental composition of reserve and structure experimentally can be very demanding due to the very precise definition of these quantities in standard DEB theory (section 2). 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 2010).

Specific Dynamic Action S. As previously noted, there are a number of subtly different uses of the term Specific Dynamic Action (SDA). Kooijman (2010, Fig. 11.2) identifies SDA with the “heat increment of feeding”, and includes it in the overhead of assimilation (see section 4.4.2 and eq. 4.56 in Kooijman 2010). In this case, if there is no fermentation, $SDA = \text{overheads of assimilation} - \text{egestion} - \text{excretion due to assimilation}$:

$$S = \frac{1}{W_w} \left((1 - \kappa_x) \dot{p}_x - \kappa_p \dot{p}_x - \mu_N \dot{J}_{NA} \right)$$

This definition here assumes that the transient response of respiration rate of an animal following a meal (Secor, 2009) is a fast process when compared to 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 over the duration of the transient, the mobilization flux \dot{p}_c is increasing, then S certainly includes contributions from the overheads on growth, and from development or reproduction. This is likely in 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 recipe for translating SDA measurements into DEB language; each experiment has to be modeled explicitly. Computing the DEB equivalent of Secor’s (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 M and Activity A. The standard metabolic rate of a fish is defined as the metabolism of an inactive fish that is not digesting food. If we define activity, 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.

$$M \times A = \frac{1}{W_w} \left((1 - \kappa_G) \dot{p}_G + \dot{p}_S + \dot{p}_J + (1 - \kappa_R) \dot{p}_R \right),$$

with $\kappa_R = 0$ in embryos and juveniles.

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 BFT (Jusup et al., submitted). The validity and limitations of this assumption are discussed in the next section.

5. Example: Pacific Bluefin Tuna (PBT)

Efforts in research and management of Pacific Bluefin Tuna (PBT) may benefit from an integrative approach. There are large gaps in knowledge of PBT ecology, mostly due to uniqueness of tuna's physiology and its large range in the wild. Tuna (Scombridae; mainly *Thunnus* spp.) are distinctive because of regional endothermy (Graham and Dickson, 2004), excess red muscle tissue not observed in other fishes (Katz, 2002), elevated standard metabolic rate, high food requirements for increase in biomass, and high aerobic capacity (Korsmeyer et al., 2001).

These distinctive characteristics, coupled with economic significance of PBT and the resulting desire to appropriately manage wild populations and successfully culture PBT, have led to significant research efforts. As it is expensive and impractical to track and observe tuna in the wild, research has been focusing on observations of captured and cultured tuna (but see Butler et al., 2010; Walli et al., 2005), resulting in a substantial body of process-specific and environment-specific physiological and bioenergetic data including:

- 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)

- comprehensive measurements related to the embryonic development, including temperature dependence of time required from spawning to hatching (Miyashita et al., 2000)
- 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)
- 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)
- detailed studies of cardiovascular function and specific dynamic action in response to feeding bouts (Fitzgibbon et al., 2007; Clark et al., 2008)
- 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 can reveal connections between these data sets, taking account of both differences in attributes of the fish (e.g. length, weight) and the environmental conditions (e.g. temperature, food density) in which data were gathered.

Jusup et al. (submitted) formulated a complete life cycle DEB model for PBT – from an egg to an adult female and its eggs. The standard DEB model 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 like (i) reasons for different growth rates between cultivated and wild PBT, (ii) origins of similarities in the weight-length relationship of cultivated and wild PBT, (iii) estimates of average number of batches produced per spawning season, (iv) estimates of food abundance experienced by wild PBT, (v) reasons behind acceleration of growth rate in the larval stage, and (vi) causes of deceleration of growth rate in the early juvenile phase.

The DEB model of Jusup et al. 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 35.5W. The utilization flux (totaling 35.1W) 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 weight 219 and 255 kg) is as high as 7.4. Even though somewhat lower FCR of 4.6 is reported (Aguado-Gimenez and Garcia-Garcia, 2005) for smaller fish (average initial and final weight 32 and 63 kg), it is still high in comparison to FCR of 1-2 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 (section 3). 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%, and total dissipation (standard metabolism added) represents 76% of total respiration.

The total respiration flux can then be interpreted with an estimate based on DEB concepts. 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 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 for 12% to 9% (depending on the contribution from assimilation). Dissipation (define again) 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 the 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: *RoboTuna* (see section 3) of around 120cm fork length achieved speed of 0.7 m/s ($0.58\text{s}^{-1} \times \text{fork length}$) with a power input of only 0.5283W. Accompanying numerical modeling, showing a good agreement with experiments in terms of mean power, estimated the propulsive efficiency at over 90%, estimating mean mechanical power, depending on the value of kinematic parameters, between 1.15-3.05 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 around 10 at 3 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 4-13% 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 order $1.0\text{ W (kg red muscle)}^{-1}$ at typical cruising speeds, with the highest plausible estimates yielding $2.2\text{ W (kg red muscle)}^{-1}$. However, *in vitro* peak mechanical power production in red muscle of yellowfin tuna has been shown to exceed $60\text{ W (kg red muscle)}^{-1}$ with power production exceeding $20\text{ W (kg red muscle)}^{-1}$ over a wide range of tail beat frequencies (Shadwick and Syme, 2008). Even higher values (44-75 W

(kg red muscle)⁻¹) 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 (feeding, 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.

6. Example: Pacific salmon

Efforts in research and management of Pacific salmon also benefit from an integrative approach. Throughout their life cycle, these fish experience the entire range of aquatic habitats, from tributary, river and estuary to coastal and open ocean, migrating as juveniles from their natal river to the ocean and migrating back to spawn to their natal river as adults. This anadromous life cycle implies serious physiological stress and morphological changes at the transitions to and from the ocean but also implies that individuals experience a large variety of stressors throughout their life cycle. To fully understand the cumulative impact of these stressors 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 stresses experienced in rivers as juveniles, may be manifest later in the life cycle.

Numerous bioenergetic approaches have been previously developed to study salmonids 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). But these approaches are often specific to a particular size range of individuals and to a particular species.

To overcome these limitations, Pecquerie et al. (submitted) and 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 inter-specific 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 of a zoom factor z on certain parameters (see 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 (*O. gorbuscha*), 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 species-specific data-gap and study species and population-specific adaptations.

Pecquerie et al. also have work in progress modeling one particular species, Chinook salmon (*O. tshawytscha*) (Nisbet et al., 2011), with an initial aim of studying how variations in environmental conditions affect age and size of spawning adults. Qualitative examination of the *intra*-specific 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. But further refinement of the chinook DEB model 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 here compare the overall energy budget established for a 3kg Chinook by Petrell and Jones (2000) with the Chinook DEB model presented in Nisbet et al. (2011) following the recipes detailed in section 4.

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 to the bioenergetic model presented by Petrell and Jones (2000), we obtain that growth (of structure, reserve and reproduction reserve) accounts for 34% of the amount of energy ingested. This value is in agreement with the $29 \pm 6\%$ estimated by Brett and Groves (1979, cited by 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. They determine temperature and oxygen supply for embryos, body temperature and swimming requirements (and hence swimming costs) for juveniles that feed and aim to sustain their location. More obviously, they 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 that the salmon DEB model predicts 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, we could use the estimation of swimming costs by Petrell and Jones (2000). These authors evaluated drag and power requirement of swimming for Chinook and Atlantic salmon (*Salmo salar*) by calculating 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 due to higher cost of swimming, largely due to a larger girth compared to 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 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 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).

7. Discussion

Kooijman's dynamic energy budget 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 and 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 recipes for common bioenergetic measurements in terms of the state variables and fluxes in a “standard” DEB model. 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 down-side of

such pragmatism, which is (i) the loss of connection to theory describing interspecific variation in physiological rates; and (ii) 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 relations. The decision to use the full DEB model in each application was therefore justified, even on pragmatic grounds. Yet there is a large empirical literature on the bioenergetics and biomechanics of both species that is constructed round 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 recipes in section 4, 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 and to open the door for creative utilization of hard-earned data. 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, and over time should in turn lead to improved theory.

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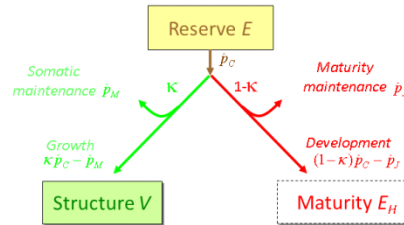
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Syme, D. A. and Shadwick, R. E. (2002). Effects of longitudinal body position and swimming speed on mechanical power of deep red muscle from skipjack tuna (*Katsuwonus pelamis*). *Journal of Experimental Biology* 205, 189-200.

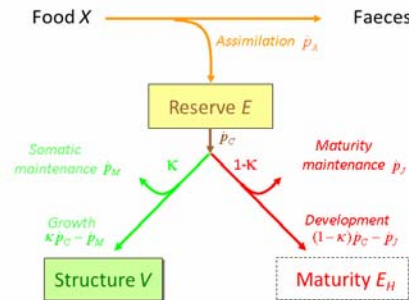
Triantafyllou, M. S. and Triantafyllou, G. S. (1995). An Efficient Swimming Machine. *Scientific American* 272, 64-70.

Figure 1: Schematic representation of the three life stages of the “standard” DEB model described by Kooijman and by Sousa et al. . An embryo uses reserve to grow and develop. At “birth” a juvenile starts feeding and at “puberty” an adult starts allocating energy to reproduction

(a) Embryo



(b) Juvenile



(c) Adult

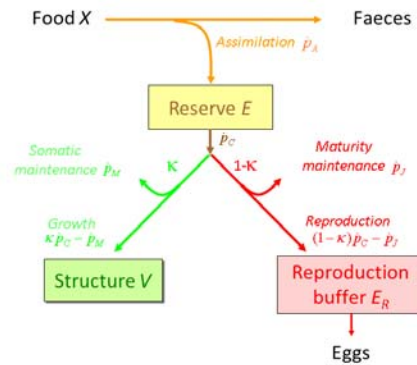
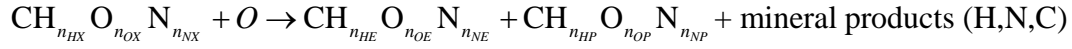


Table 1: DEB theory defines three types of transformations: assimilation, growth and dissipation. Unbalanced equations for each transformation in an aerobic heterotroph are shown.

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 :



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

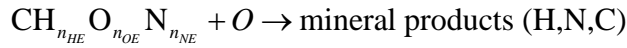


Table 2: State variables, forcing variables and parameters of the standard DEB model with maximum length $L_m = zL_m^{ref}$ for a dimensionless zoom factor z and $L_m^{ref} = 1$ cm. All primary parameters that covary with z are called extensive parameters. Compound parameters including $\{\dot{p}_{Am}\}$ are thus extensive parameters. (Kooijman 2010, Sousa *et al.* 2010). Rates are given at the reference temperature $T_1 = 293$ K (=20°C).

Symbol		Units	Description
<i>State and forcing variables</i>			
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
T		K	Temperature
$f(X)$			Scaled functional response
$c(T)$			Temperature correction factor
<i>Primary parameters</i>			
$\{\dot{F}_m\}$	6.51	cm ⁻² .d ⁻¹	Specific searching rate
\mathcal{K}_X	0.8		Assimilation efficiency
$\{\dot{p}_{Am}\}$	22.5 z	J.cm ⁻² .d ⁻¹	Maximum surface-area-specific assimilation rate
$[\dot{p}_M]$	18	J.cm ⁻³ .d ⁻¹	Volume-specific somatic maintenance rate
$\{\dot{p}_T\}$	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
\mathcal{K}	0.8		Fraction of utilized reserve to growth + maintenance
\dot{k}_J	0.002	d ⁻¹	Maturity maintenance rate coefficient
E_H^b	275 z^3	mJ	Maturity threshold at birth
E_H^p	166 z^3	J	Maturity threshold at puberty
\mathcal{K}_R	0.95		Fraction of the reproduction buffer fixed into eggs
<i>Auxiliary and compound parameters</i>			
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	Molecular (wet) weight of structure
w_E		g.mol ⁻¹	Molecular (wet) weight of reserve
L_m	$\frac{\kappa\{\dot{p}_{Am}\}}{[\dot{p}_M]}$	cm	Maximum volumetric length
g	$\frac{\dot{v}[E_G]}{\kappa\{\dot{p}_{Am}\}}$		Energy investment ratio

K	$\frac{\{\dot{p}_{Am}\}}{\kappa_X \{\dot{F}_m\}}$	J cm^{-3}	Half-saturation coefficient
$[E_m]$	$\frac{\{\dot{p}_{Am}\}}{\dot{v}}$	J cm^{-3}	Maximum reserve density
κ_G	$\frac{\mu_V d_V}{w_V [E_G]}$		Growth efficiency

Table 3: Equations of the standard DEB model. Notation is described in Table 2.

$$\frac{d}{dt}E = \dot{p}_A - \dot{p}_C \quad (1)$$

$$\frac{d}{dt}V = \frac{1}{[E_G]} \dot{p}_G = \frac{1}{[E_G]} (\kappa \dot{p}_C - \dot{p}_S) \quad (2)$$

$$\frac{d}{dt}E_H = (1 - \kappa) \dot{p}_C - \dot{p}_J \quad \text{if } E_H < E_H^p, \text{ else } \frac{d}{dt}E_H = 0 \quad (3)$$

$$\frac{d}{dt}E_R = 0 \quad \text{if } E_H < E_H^p, \text{ else } \frac{d}{dt}E_R = (1 - \kappa) \dot{p}_C - \dot{p}_J \quad (4)$$

$$\text{with } \dot{p}_A = c(T) f(X) \{\dot{p}_{Am}\} L^2 \quad \text{if } E_H \geq E_H^b \text{ else } \dot{p}_A = 0 \quad (5)$$

$$\dot{p}_C = c(T) \{\dot{p}_{Am}\} L^2 \frac{ge}{g+e} \left(1 + \frac{L}{gL_m} \right); \text{ with } e = \frac{[E]}{[E_m]} = \frac{E}{V} \frac{\dot{v}}{\{\dot{p}_{Am}\}} \text{ and } L = v^{1/3} \quad (6)$$

$$\dot{p}_S = c(T) ([\dot{p}_M] L^3 + \{\dot{p}_T\} L^2) \quad (7)$$

$$\dot{p}_J = c(T) \dot{k}_J E_H \quad (8)$$

$$f(X) = \frac{X}{X+K} \quad (9)$$

$$c(T) = \exp\left(\frac{T_A}{T_1} - \frac{T_A}{T}\right) \quad (10)$$
