



# Can we reach consensus between marine ecological models and DEB theory? A look at primary producers



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## ABSTRACT

In the last decades we have witnessed an explosion in marine modeling efforts, both at the development and application levels. A general agreement is expected between ecological models and metabolic theories, and one should be able to use ideas and principles from both views. Nevertheless, there are marked differences that can vary from differences in formulation of processes to baseline assumptions. So far, efforts to reconcile these models of natural systems have been limited. Here, we critically compare ERSEM (European Regional Seas Ecosystem Model), a state of the art ecological model in marine biogeochemical modeling, with a DEB (Dynamic Energy Budget) model (based on the metabolic theory DEB), highlighting similarities and showing where the approaches differ. This study focuses on primary producers and is driven by two main questions: (1) Is it possible to harmonize the philosophy and structure of models like ERSEM with the general scope of unifying metabolic theories such as DEB? (2) Can we bring the current paradigms in ecological modeling for marine communities to consensus with metabolic theories?

We analyze the links between the underlying processes in the DEB and ERSEM models. We found that the processes of assimilation and mobilization are the most difficult to reconcile between the two models. However, we also find a number of clear analogies between the parameters, state variables and fluxes of the two models, which allow for the transference of knowledge between them.

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## 1. Introduction

The last decades have witnessed an explosion in marine ecological modeling efforts, both at the development and the application levels. Several models with different degrees of complexity have been created, mostly to address the increasing problems of nutrient enrichment in marine systems. Model applications now range from simple hydrodynamic settings with coupled physical–ecological processes, to more complex applications with biogeochemical models for the regional scale. In the past decade the ERSEM (the European Regional Seas Ecosystem Model) (Baretta et al., 1995; Baretta-Bekker et al., 1994, 1995, 1997, 1998) is one of the most complex ecological model for the continental shelf and oceanic areas. Thus it has been considered the state of the art in marine biogeochemical modeling (James, 2002; Moll and Radach, 2003; Vichi et al., 2007a,b).

The ERSEM model was originally conceived in the ERSEM project that aimed at developing an ecosystem model (named after the project) to simulate the pelagic food web, using the North Sea as a test case. It

was a joint collaboration of several research teams, resulting in a model that deals with the organic matter dynamics, major element cycles and biological groups in plankton. The continuous effort in development led to ERSEM II, with improved features regarding the carbon and nutrient dynamics in organisms, and in the photosynthesis processes (Baretta-Bekker et al., 1997, 1998; Ebenhoh et al., 1997). ERSEM has been widely accepted among marine ecologists and modelers that have adopted and developed its basic original setup (Blackford et al., 2004; Mateus, 2012; Vichi et al., 2007a,b).

Metabolic theories in ecology aspire at achieving a general theory of energy budgets in organisms and communities. These theories, based on energy conservation, rely on simple mechanistic descriptions of how individual organisms take up and use energy and material. One of these theories, that has had some developments, is the Metabolic Theory of Ecology (MTE) advanced by Brown et al. (2004). This theory is based on earlier findings on how the metabolic rate of individual organisms varies with body temperature and size (Gillooly et al., 2001; West et al., 1997). Another such theory, the Dynamic Energy Budget (DEB), has at its starting point the energetics of the individual and was advanced almost three decades ago (Kooijman, 1986a,b,c). Since it was proposed, it has been used as a paradigm in different research fields (Sousa et al., 2008; Sousa et al., 2010). Both theories have growth models containing fundamental energy budget parameters

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and describe energy supply rate and maintenance rate as functions of body size.

Recently, van der Meer (2006) has compared MTE and DEB to see whether theories agree, and to perform a consistency check on some of their claims. He concluded that, at the organism level, the few insights provided by MTE have already been advanced by DEB, and that MTE appears to be inconsistent under close scrutiny (see also Kearney and White, 2013; Maino et al., 2013). Based on these observations, we found it redundant to address both theories in our study. As such, from here on we will use DEB theory as the baseline metabolic theory in ecology.

Metabolic theories focus on the basic physiological processes known to be identical in all living organisms, providing a model that accounts for processes at all levels of organization. As such, they address detailed physiological cellular processes and trace their influence up to the ecosystem scale, through matter and energy fluxes. Apparently, marine ecological models follow the same rationale and try to achieve a similar purpose. However, these models are used to study specific features of a system at an ecosystem scale and, most recently, are being applied as tools for management support and human activity impact assessment. To avoid detailed parameterization of processes, minimize computational requirements and simplify the interpretation of results, they rely on a number of assumptions and simplifications.

The use of DEB theory in the description of population dynamics is not straightforward and its structured population approach is to some extent incompatible with the approach of models such as ERSEM. To deal with this apparent gap between both modeling approaches we must eliminate the distinction between individuals and populations. This is achieved by treating primary producers as V1-morphs<sup>1</sup> in DEB theory (Kooijman, 2010; Lorena et al., 2010), which makes them an ideal paradigm for the connection between structured and non-structured populations. For V1-morphs the distinction between an individual and a population is mathematically non-existent in DEB models; because V1-morph individuals have their area proportional to their volume, it is unnecessary to distinguish between the individual and the population level. In other words, this makes it irrelevant to distinguish if we are addressing one single large V1-morph or a population of many small ones. The structured population of V1-morphs collapses to a non-structured one, with the mass of the population equal to the sum of the individual masses.

Agreement should in general be expected between ecological models and metabolic theories, and one should be able to use ideas and principles from both views. Nevertheless, there are marked differences that can vary from differences in formulation of processes to baseline assumptions (Table 1). So far, efforts to bridge both models of the natural systems have been limited and knowledge transfer from one to the other is difficult. Here we critically compare both ERSEM and DEB models, highlighting similarities and show where the approaches differ. This study focuses on primary producers and is driven by two main questions: (1) Is it possible to harmonize the philosophy and structure of models like ERSEM with the general scope of unifying metabolic theories such as DEB? (2) Can we bring the current paradigms in ecological modeling for marine communities to consensus with metabolic theories? As we will show, the ERSEM model cannot be seen as a special case of DEB theory but many links between models can be drawn.

## 2. Theory

Ecological models can be represented as systems of differential equations. There are no specific universal equations generally used to

determine the flux of material between the compartments of an ecological model. Wiegert (1979) formulated a general equation of population growth for a closed system, accommodating most of the limiting processes (but just considering multiplicative limitation):

$$\frac{dX_j}{dt} = \sum_{i=1}^m (e_{ij}\tau_j p_{ij} f_{ij} X_i) - (\mu_j + \varphi_j + \rho_j) X_j - \sum_{k=1}^m (\tau_k p_{jk} f_{jk} X_k) \quad (1)$$

where  $X_j$  represents the biomass. The equation is composed of three terms: the first addresses the assimilated ingestion (uptake) by species  $j$  of all other species (prey) or food sources (organic matter), losses by physiological or external causes are represented in the middle term, and the last term addresses the predation on species  $j$  by other species. Subscripts  $i$ ,  $j$  and  $k$  stand for species/resource  $i$ , and species  $j$  and  $k$ , respectively. The coefficients are as follows:  $e_{ij}$  is the assimilation efficiency of species  $j$  using resource  $i$ ,  $\tau_j$  the maximum specific uptake rate of  $j$ ,  $p_{ij}$  is the preference of  $j$  for resource  $i$ ,  $f_{ij}$  the limitation of ingestion of resource  $i$  by  $j$ ,  $\mu_j$  is the specific loss rate due to mortality,  $\varphi_j$  is the specific loss due to excretion, and  $\rho_j$  the specific loss due to respiration. These coefficients usually depend on various physiological and behavioral interactions which make them non-linear functions of the species or resource.

A quick look at available ecological models shows that the equations used are not as clear as physical equations for transport and diffusion. A reason for this is that biological equations in models are usually not based on known quantitative laws, such as physical laws. So it is common to simplify most of these coefficients to either constant values, or functions of other variables or forcing. However, in one way or another, organisms are usually modeled according to the concept of the Standard Organism (Baretta et al., 1995), considering universal biological processes such as resource uptake, growth, excretion, respiration/maintenance, and mortality (Fig. 1). According to this concept, the fundamental equation describing the net growth of a standard organism can be expressed as:

$$\frac{dX}{dt} = (up - rsp - exc - mrt)X, \quad (2)$$

in which the biomass ( $X$ ) depends on the specific uptake rate ( $up$ ), total respiration rate ( $rsp$ ), total excretion rate ( $exc$ ), and mortality rate ( $mrt$ ). In Fig. 1 we present this fundamental equation in schematic form.

For many decades, nitrogen was used as the currency in models, causing the biomass to be expressed in nitrogen concentration (or converted to carbon using the Redfield ratio), the basic philosophy of NPZ models (Fasham et al., 1990). Recent modeling approaches, however, explicitly address the crucial element cycles in marine systems (i.e. carbon and nitrogen). So, variable stoichiometry presupposes that nutrient content variation is in part determined by processes controlling the carbon dynamics (Anderson, 1992; Baretta-Bekker et al., 1997, 1998; Grover, 2003). A similar rationale is applied to light through the modeling of chlorophyll synthesis as a function of N-uptake and ambient light conditions (Geider et al., 1996, 1998; Mateus et al., 2012), allowing a stoichiometric fluctuation of C:Chl ratios.

The generic arrangement of DEB theory around the fundamental biological processes of living organisms includes these processes. Because it aims to capture the quantitative aspects of the organization of metabolism at the organism level, DEB theory is more sophisticated in its assumptions and detailed in the modeling approach. The theory assumes that energetic processes depend on either surface area or body volume. Essentially DEB theory describes empirical patterns related to (1) the metabolic processes common to all organisms (feeding, growth, reproduction, maturation and maintenance), (2) the life stages (embryo, juvenile and adult), and (3) the stoichiometry of organisms (Sousa et al., 2008). From this introduction to the basic modeling approaches one can expect not only some convergence in parameterization and modeling philosophy, but also some fundamental differences.

<sup>1</sup> In DEB theory a V1-morph is an organism in which surface area involved in uptake grows proportional to its volume.

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