



Dynamic energy budgets in syntrophic symbiotic relationships between heterotrophic hosts and photoautotrophic symbionts

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ABSTRACT

In this paper we develop and investigate a dynamic energy budget (DEB) model describing the syntrophic symbiotic relationship between a heterotrophic host and an internal photoautotrophic symbiont. The model specifies the flows of matter and energy among host, symbiont and environment with minimal complexity and uses the concept of synthesizing units to describe smoothly the assimilation of multiple limiting factors, in particular inorganic carbon and nitrogen, and irradiance. The model has two passive regulation mechanisms: the symbiont shares only photosynthate that it cannot use itself, and the host delivers only excess nutrients to the symbiont. With parameter values plausible for scleractinian corals, we show that these two regulation mechanisms suffice to obtain a stable symbiotic relationship under constant ambient conditions, provided those conditions support sustenance of host and symbiont. Furthermore, the symbiont density in the host varies relatively little as a function of ambient food density, inorganic nitrogen and irradiance. This symbiont density tends to increase with light deprivation or nitrogen enrichment, either directly or via food. We also investigate the relative benefit each partner derives from the relationship and conclude that this relationship may shift from mutualism to parasitism as environmental conditions change.

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1. Introduction

Symbiotic relationships have been found in virtually every ecosystem where they have been sought, and in many cases, they fulfill ecologically important roles. Surprisingly, however, they have received relatively little emphasis from theoretical ecologists, as evidenced by the well known paradigmatic models for competition and predator–prey interactions that are found in introductory ecology texts, but the near-absence of exposition of the substantial literature involving similar models for symbioses or mutualisms.

Many theoretical models suggest that mutualisms and symbioses can accelerate exponential population growth, with ultimate stabilization attributed to the interaction of the symbioses with other factors. For example, simple modifications of the Lotka–Volterra competition equations suggest that obligate mutualistic interactions may induce instability and promote explosive growth of both populations (Vandermeer and Boucher, 1978). These effects can be counteracted by stabilizing

mechanisms (e.g. Holland et al., 2002, 2004), as has been shown for demographically open populations (Amarasekare, 2004; Thompson et al., 2006).

Even during exponential population growth in a two species system with symbiotic interactions, it is of obvious interest to ask if the *ratio* of the sizes of the two populations is regulated, and if it is, to identify the regulatory mechanisms. Situations where such stabilization would be anticipated include nutritional symbioses such as the association of digestive bacteria with the gastrointestinal system of metazoans (Karasov and Martinez del Rio, 2007). More subtle interactions are found in syntrophic symbioses, where each partner is involved in the acquisition of resources required by the other. The objective of this paper is to elucidate regulatory mechanisms for syntrophic symbiosis under a range of environmental conditions. As a model system to focus our investigations, we have selected tropical scleractinian corals harboring intracellular dinoflagellates in the genus *Symbiodinium*, but our theory has fundamental application to other syntrophic symbioses such as those based on chemoautotrophic symbionts, or where the symbionts are in direct physical contact with the environment.

Our approach is to develop a dynamic energy budget (DEB) model for syntrophic symbiosis (Kooijman et al., 2003, 2004;

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Kooijman, 1993, 2001; Nisbet et al., 2000). A DEB model describes the rates at which an organism acquires nutrition and subsequently utilizes the energy and nutrients therein for production and maintenance. There are multiple approaches to DEB modeling, but the theoretical framework developed by Kooijman (2000) is especially suitable for our purpose because of four desirable features. First, it has previously been successfully applied to a wide variety of prokaryotic and eukaryotic taxa. Second, it is rigorous in specifying mass and energy balances, which are, for obvious reasons, critical for describing syntrophic symbiotic relationships. Third, its structure is modular, and, finally, it aims at evolutionary consistency. The benefits of the latter two qualities are subtle and thus merit further elaboration.

The grand aim of the DEB modeling approach is to bring together the acquisition and expenditure of resources of all organisms in a single framework (Kooijman et al., 2003; Kooijman, 2001). The rationale behind unification is that since organisms share ancestry, organisms must have a common energetic basis. This consideration is particularly important for theory describing syntrophic symbiotic relationships, since in the course of evolution syntrophic symbiotic partners may merge and yield a single organism in which symbionts have degraded to organelles, such as in the case of merging prokaryotes giving rise to the eukaryotic cell. It would be hard, if not impossible, to describe this gradual merging without describing the common energetic basis in a consistent way (Kooijman and Troost, 2007).

However, this common energetic basis is necessarily simplistic, and the question that immediately arises is whether this basis is not too simplistic in view of the diversity and complexity in nature. DEB theory addresses this question by using a modular approach: at the core lies the unifying framework and, appended to that, are taxon- or problem-specific modules. For instance, we can start by conceiving a heterotrophic organism that reproduces by fission and retains geometric similarity during its life time. A minimal characterization of this organism recognizes two types of biomass: structural and reserves. Structural biomass is defined to be the minimum amount of biomass that an organism of a given size needs to perform vital functions, and as such requires a constant expenditure of energy to remain viable (i.e. maintenance). All other biomass is called “reserves”. Note that this definition of reserves DEB reserves are not entirely identical with traditional storage compounds, since part of the DEB reserves is actively engaged in performing metabolic functions. The model of this simple heterotroph can be amended with modules in order to account for complexity or problem specific questions. In this way, reproduction, autotrophy, toxic effects, multiple resource limitation, and tumor development, among others, have been added to the model structure. Key to this process of adding modules is that internal and evolutionary consistency is maintained.

Evolutionary consistency is not only important in the context of the “grand aim” described above. It is essential for our immediate aim of modeling symbiotic assemblages over time scales of societal importance. This is because many symbiotic relationships commonly involve some components with short generation times that may experience rapid evolution in response to environmental change (Parmesan, 2006). Once again corals provide an example, with recent modeling work (Baskett et al., 2009; Day et al., 2008) illustrating that rapid evolution of autotrophic symbionts may impact the timing of bleaching events.

In this paper, we develop a DEB model that describes the syntrophic symbiotic relationship between a heterotrophic host and an internal photoautotrophic symbiont. We aim for minimal complexity, but without compromising rigor in our characterization of key processes for acquisition and processing of energy and nutrients. We analyze the biological stability of this symbiotic

assemblage by investigating the ratio of symbiont to host structure in a constant environment as function of ambient levels of nutrients, food and irradiance. We also study the mutual benefits of symbiosis for both partners. As a system of reference, we choose the symbiotic assemblage of dinoflagellates and anthozoa in scleractinian corals. We parameterize the model with values we deem relevant for scleractinian corals, but we re-emphasize that our focus is on *theory for syntrophic symbiosis*, and not on a “coral model” that could require additional taxon specific assumptions as described above. We revisit this distinction in the discussion.

2. Model description

We now introduce a DEB model of the syntrophic symbiotic interaction between a heterotrophic host and photoautotrophic symbiont. We confine ourselves to symbiotic assemblages in which the symbiont does not have immediate access to the environment, i.e. the host supplies all nutrients to the symbiont. We only model explicitly the flows of two elements, carbon and nitrogen; other nutrients can be included at the expense of adding mathematical (but not conceptual) complexity. The flows of energy and elemental matter are shown in Fig. 1.

Our model is an extension of an existing DEB model (Kooijman et al., 2003; Muller and Nisbet, 2000); Table 1 summarizes the assumptions of that model that are most relevant to this paper. The exposition in this section emphasizes the new features, and we refer the reader to the earlier publications for the rationale behind the basic DEB theory. Table 2 defines common terms like “reserves” and “structure” that have a specific interpretation in DEB modeling. Table 3 summarizes our notation, which is very close to that proposed by Kooijman (2000).

We make a number of simplifying assumptions. First, we assume that the surface area to volume ratio of both symbiont and host remains constant during growth. Second, we do not distinguish among species of inorganic carbon, i.e. we assume that the ratio of carbon dioxide, bicarbonate and carbonate in the environment, host and symbiont is constant. Third, we assume ammonia is the sole nitrogen-containing nutrient. This choice implies that the host is able to assimilate ammonia; indeed, several symbiotic invertebrates are known to assimilate ammonia (Yellowlees et al., 2008 and references therein). This choice also implies that ammonia is the sole nitrogen containing compound being exchanged between host and symbiont, an implication that disregards, for modeling purposes, the variety of nitrogen containing compounds being exchanged. This assumption is obviously a gross simplification of much complex biochemistry; the reader who is uncomfortable with it should regard the word “ammonia” in this paper as representing *all* compounds with reduced nitrogen involved in the exchange among host, symbiont and environment.

3. Host

The host has two energy sources: prey and reduced carbon sources from the symbiont. In a homogenous food environment with prey density X_1 , Assumption 4 in Table 1 implies a type II functional response, i.e. the host feeds at a rate (for definitions and values of symbols, see Table 3)

$$J_{X1} = \frac{J_{Xm} M_{VH} X_1}{X_1 + X_{K1}}. \quad (1)$$

Assuming a constant assimilation efficiency, the rate at which the host assimilates energy from prey, $J_{EHA,H}$, is proportional to

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