A simplified dynamic bioenergetic model for coral-*Symbiodinium* symbioses

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Abstract

This is the abstract.

Introduction

The nutritional exchange between corals and *Symbiodinium* directly underlies the capacity of corals to build coral reef ecosystems, worth trillions of US Dollars annually (Costanza, Groot, and Sutton 2014). However, the complex symbiotic metabolism of corals is vulnerable to disruption by numerous anthropogenic environmental perturbations (Baker and Cunning 2015), jeopardizing their future persistence. In order to understand and predict coral responses to complex changes in the environment, a mechanistic understanding of how multiple interacting factors drive the individual and emergent physiology of both symbiotic partners is necessary. Such a task is well suited for theoretical modeling frameworks such as Dynamic Energy Budget (DEB) theory (Kooijman 2010), although the complexity of such theory makes these efforts inaccessible to many biologists (Jager, Martin, and Zimmer 2013). In order to bridge this gap, we present here a simplified dynamic bioenergetic model for coral-*Symbiodinium* symbioses that aims to mechanistically integrate the impacts of complex environmental change on the physiological ecology of reef corals.

In reef coral symbioses, intracellular *Symbiodinium* translocate photosynthetically-fixed carbon to support coral metabolism, and utilize the animal's metabolic waste products, including nitrogenous compounds and carbon dioxide, in return (Muscatine and Porter 1977). Previous application of DEB theory to this syntrophic system (Muller et al. 2009) demonstrated a stable symbiotic relationship and qualitatively realistic growth and biomass ratios across gradients of ambient irradiance, nutrients, and food. This model assumed that 1) *Symbiodinium* has priority access to carbon through photosynthesis, 2) the coral animal has priority access to dissolved nitrogen through contact with seawater, and 3) each partner shares with the other only what it cannot use itself. In its simplest form, this principle of sharing the surplus sufficiently describes diverse syntrophic interactions among organs and organisms (e.g., trees, duckweeds, corals), suggesting the mechanism is mathematically and evolutionarily robust (Nisbet et al., submitted).

While the work of Muller et al. (2009) applying DEB formalism to this system represents the most significant theoretical contribution in coral symbiosis research to date, we aim to strengthen the role of theory and broaden its potential application in three primary ways:

1. *Develop a detailed module of environmental stress.* Of primary interest to coral biologists and ecologists is symbiosis dysfunction under environmental stress, resulting in coral "bleaching"–the loss of algal symbionts from the association (Jokiel and Coles 1977). Photooxidative stress in *Symbiodinium* is considered a primary trigger of bleaching in response to high temperature and/or light (Weis 2008), and prolonged or severe bleaching can result in mortality, though corals sometimes recover their symbionts. Bleaching susceptibility, severity, and recovery may by influenced by interacting factors such as heterotrophy and

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nutrient availability (Wooldridge 2014b), and the genetic identity of *Symbiodinium* (Glynn et al. 2001). To simulate these bleaching-related phenomena, we develop a generalized framework linking overreduction of the photosynthetic light reactions to downstream impacts of photoinhibition and photodamage.

2. *Reduce theoretical and mathematical complexity.* Following the logic of Jager, Martin, and Zimmer (2013), we exclude certain features of formal DEB models in order to capture behaviors of interest with the simplest possible formulation. Here, we present a model without reserves, maturity, or reproduction (see Kooijman 2010). This formulation restricts the model's scope to the bioenergetics of growth and symbiosis dynamics in adult corals, but greatly reduces theoretical complexity and parameter numbers, which is advantageous given the relative paucity of data for corals. However, our primary motivation for reducing complexity was to increase accessibility and applicability for biologists and ecologists without requiring significant expertise in DEB theory.
3. *Provide well-documented, open-access code.* In order to facilitate the continued development and application of theoretical modeling tools for coral symbioses, we provide open access to the model in the form of detailed, commented code written in the R language (R Core Team 2014). With an accessible and modular framework, we envision this as a resource for futher development by the scientific community to include additional complexity and problem-specific components. The R language was chosen because it is freely available and in common use by biologists and ecologists, to widen the audience for this work.

With these as our primary motivations, we describe a simplified approach to dynamic bioenergetic modeling of coral-algal symbioses that tracks carbon and nitrogen acquisition and sharing between partners. This theoretical framework dynamically integrates the influence of external irradiance, nutrients, and prey availability on coral growth and symbiosis dynamics (i.e., symbiont:host biomass ratios), allowing for the possibility of coral bleaching in the event of photooxidative stress. In the following sections, we describe the formulation of this model and justify its structure and parameter values based on relevant literature. We then demonstrate the model's behavior and discuss some of its major implications and outcomes, and the wide range of potential applications for this model in the study of cnidarian-algal symbioses.

Model description

In this model of coral-algal symbiosis, carbon and nitrogen are acquired by each partner and used to construct biomass. A graphical representation of the model is presented in Fig. 1. We use C-moles as the unit of biomass for consistency with the rigorous mass balance of DEB theory: 1 C-mole is equivalent to the amount of biomass containing 1 mole of Carbon atoms. Coral biomass, symbiont biomass, and prey biomass have fixed, but different, molar N:C ratios (Table 1). Carbon and nitrogen are combined to produce biomass by synthesizing units (SU), which are mathematical specifications of the formation of a product from two substrates; we use the "parallel complementary" formulation of Kooijman (2010) to specify these fluxes. The two state variables in this dynamical system are symbiont biomass and coral biomass; because resources are acquired proportionally to surface area (and surface area is assumed proportional to volume for corals (i.e., they are "V1-morphs" in DEB terminology (Kooijman 2010))), biomass increases exponentially during growth. The rate of increase in coral biomass (i.e. growth) and the ratio of symbiont to host biomass are the (i.e. symbiosis dynamics) are the responses of interest of the system. Below we describe the formulation of each flux involved in producing these responses.

Coral animal fluxes

The coral animal acquires both carbon and nitrogen from feeding on prey from the environment. Prey acquisition is specified by Michaelis-Menten kinetics using a maximum area-specific feeding rate and half-saturation constant:

$$U_X = \frac{UX_m \cdot X}{X + X_{KX}} \tag{1}$$

Additionally, the coral animal can acquire nitrogen from the surrounding seawater. This nitrogen source is assumed to represent ammonium, the primary form utilized by corals (Wang and Douglas 1998; Yellowlees, Rees,

and Leggat 2008). The uptake of nitrogen from the environment is specified by Michaelis-Menten kinetics using a maximum area-specific uptake rate and half-saturation constant:

$$U_N = \frac{UN_m \cdot N}{N + X_{KN}} \tag{2}$$

Coral biomass formation is specified by a parallel complementary SU that combines carbon and nitrogen to form biomass. In addition to the carbon and nitrogen acquired by direct uptake (Eqs. 1 and 2), the coral recycles a portion of the nitrogen liberated by biomass turnover (r_{NR}), and receives surplus fixed carbon shared by the symbiont (ρ_C), such that the total biomass formation is specified as:

$$Q_R = \left(\frac{1}{Q_{Rm}} + \frac{1}{\rho_C + U_X} + \frac{1}{(U_N + n_{NX}U_X + r_{NR})n_{NR}^{-1}} - \frac{1}{\rho_C + U_X + (U_N + n_{NX}U_X + r_{NR})n_{NR}^{-1}} \right)^{-1} \tag{3}$$

where Q_{Rm} is the maximum specific growth rate. Finally, a fixed portion of coral biomass is turned over to pay maintenance costs:

$$T_R = \gamma_R \tag{4}$$

$$\frac{dR}{dt} = Q_R - \gamma_R \tag{5}$$

where γ_R is the parameter specifying the turnover rate.

The amount of nitrogen input to the coral biomass SU in excess of what is actually consumed in biomass formation (i.e., surplus nitrogen, or the "rejection flux" in SU terminology) is then made available to the symbiont, and is specified as:

$$\rho_N = U_N + n_{NX}U_X + r_{NR} - n_{NR}Q_R \tag{6}$$

Due to the inherent "leakiness" of the parallel complementary SU formulation, there will always be some nitrogen shared with the symbiont even when coral biomass formation is strongly nitrogen-limited. Likewise, there is always a non-zero rejection flux of carbon from the coral biomass SU, which is assumed to be lost to the environment.

Symbiodinium *fluxes*

The symbiont produces fixed carbon through photosynthesis, a process represented here by a single SU with two substrates: light (photons) and inorganic carbon (CO_2). The amount of light absorbed by the symbiont depends on the scalar irradiance at the site of light absorption, which is modified substantially relative to external downwelling irradiance owing to multiple scattering by the coral skeleton and self-shading by surrounding symbionts [Enríquez, Méndez, and Iglesias-Prieto (2005); Wangpraseurt et al., in prep.]. The ratio of internal scalar irradiance to external downwelling irradiance can take a theoretical maximum value of 3 for a "flat coral model" (Marcelino et al. 2013), and may be reduced below 1 at high symbiont densities due to self-shading. We used data from Wangpraseurt et al. (in prep) to empirically derive this ratio as a function of symbiont density (expressed as symbiont to host biomass ratio), and subsequently multiply this quantity by the external downwelling irradiance L and the effective light-absorbing surface area of symbiont biomass ds to specify the amount of light absorbed:

$$U_L = 3 \cdot \exp(-4.905 \cdot S/R) \cdot L \cdot ds \tag{7}$$

We then specify two pathways for input of inorganic carbon to the photosynthesis SU: 1) passive diffusion of CO_2 from the external environment, and 2) active delivery of CO_2 to the symbiont by the host. The passive flux

ensures that some CO_2 is always available to photosynthesis, and the active flux encompasses the potentially diverse mechanisms by which the host may enhance CO_2 availability for the symbiont, including active transport of bicarbonate, carbonic anhydrase-catalyzed conversion of bicarbonate to CO_2 to promote diffusion toward the symbiont, and acidification of the symbiosome to increase localized CO_2 concentrations. Since the host physically separates the symbiont from the external environment, both the passive and active flux rates are proportional to host surface area. A more rigorous, mechanistic model of inorganic carbon processing would require spatially explicit internal pools accounting for pH and carbon speciation, which is beyond the current scope of this work. Instead, the specification of CO_2 delivery rates offers the user the opportunity to compare different rates of CO_2 delivery that may characterize different coral species (Wooldridge 2014a). The input of CO_2 to the photosynthesis SU is therefore specified as:

$$UCP = UCP_p + UCP_a \tag{8}$$

In addition to the inputs CO_2 specified in Eqs. 7, additional CO_2 representing the metabolic production of CO_2 in the host liberated from host biomass turnover (note: recylced C from symbiont was removed so that photodamage turnover does not make tons of C available), is made available to the photosynthesis SU. fixed carbon is produced by the photosynthesis SU according to:

$$UCS = \left(\frac{1}{UCS_m} + \frac{1}{U_L \cdot n_{LC}} + \frac{1}{UCP + r_{CR}} - \frac{1}{U_L \cdot n_{LC} + UCP + r_{CR}} \right)^{-1} \div ROS \tag{9}$$

where UCS_m is the maximum specific rate of photosynthesis, and ROS is the photooxidative stress multiplier (see below). Dividing by ROS causes the rate of photosynthesis to decline in response to photo-oxidative stress, a phenomenon known as photoinhibition.

Light energy absorbed in excess of what is used to fix carbon is specified by the SU "rejection flux", according to:

$$e_L = U_L - UCS \cdot n_{LC} \tag{10}$$

This excess light energy must be quenched by alternative pathways in order to prevent photo-oxidative damage. *Symbiodinium* may utilize a variety of pathways for non-photochemical quenching (NPQ; Roth 2014), which we collect in a total capacity for NPQ as a parameter of the symbiont (NPQ). If light energy exceeds the total capacity of both carbon fixation and NPQ, then damaging reactive oxygen species (ROS) may be produced, which may have negative downstream consequences. We specify a generalized photo-oxidative stress flux ROS which takes a value of 1 in the absence of stress, and increases as the amount of excess excitation energy increases.

$$ROS = 1 + \left[\left(\frac{e_L/S - NPQ}{L50} \right)^k \right]_+ \tag{11}$$

where NPQ, $L50$, and k are parameters of the symbiont that determine the overall susceptibility to photo-oxidative stress. Importantly, ROS as specified here is not a function of absolute light absorption, but rather the amount of excess light energy e_L after accounting for carbon fixation and NPQ. A direct consequence of this formulation is that carbon-limitation of photosynthesis can lead to photo-oxidative stress, a mechanism of biological importance (Wooldridge 2009) that was not captured by previous representations of photo-oxidative stress (Eynaud, Nisbet, and Muller 2011). Moreover, this formulation allows functional diversity among symbiont types to be explored by changing the parameters NPQ, $L50$, and k.

Carbon fixed by photosynthesis (UCS) is then used in conjunction with nitrogen shared by the host (ρ_N) to build symbiont biomass, following the SU equation:

$$Q_S = \left(\frac{1}{Q_{Sm}} + \frac{1}{UCS} + \frac{1}{(\rho_N + r_{NS}) n_{NR}^{-1}} - \frac{1}{UCS + (\rho_N + r_{NS}) n_{NR}^{-1}} \right)^{-1} \tag{12}$$

The rejection flux of carbon from this SU represents the amount of fixed carbon produced by photosynthesis in excess of what can be used to produce symbiont biomass; this surplus ρ_C is translocated to the coral host:

$$rho_C = UCS - Q_S \tag{13}$$

The rejection flux of nitrogen from the symbiont biomass SU is lost to the environment.

Finally, symbiont biomass is lost at a rate of

$$T_S = \gamma_S \cdot 5 \cdot ROS \tag{14}$$

Model behavior evaluation

Discussion - Potential applications/utility

References

Baker, Andrew C, and Ross Cunning. 2015. "Coral 'Bleaching' as a Generalized Stress Response to Environmental Disturbance." In *Diseases of Coral*, 396–409. Hoboken, NJ: John Wiley & Sons, Inc. doi:10.1002/9781118828502.ch30.

Costanza, R, R de Groot, and P Sutton. 2014. "Changes in the global value of ecosystem services." *Global Environmental ...* 26: 152–58. doi:10.1016/j.gloenvcha.2014.04.002.

Enríquez, Susana, Eugenio R Méndez, and Roberto Iglesias-Prieto. 2005. "Multiple scattering on coral skeletons enhances light absorption by symbiotic algae." *Limnology and Oceanography* 50 (4): 1025–32.

Eynaud, Yoan, Roger M Nisbet, and Erik B Muller. 2011. "Impact of excess and harmful radiation on energy budgets in scleractinian corals." *Ecological Modelling* 222 (7). Elsevier: 1315–22. http://www.sciencedirect.com/science/article/pii/S0304380011000263.

Glynn, Peter W, Juan L Maté, Andrew C Baker, and MO Calderón. 2001. "Coral bleaching and mortality in Panama and Ecuador during the 1997-1998 El Niño-Southern Oscillation event: Spatial/temporal patterns and comparisons with the 1982-1983 event." *Bulletin of Marine Science* 69 (1): 79–109. http://www.scopus.com/record/display.url?fedsrfIntegrator=MEKPAPERS-SCOCIT&origin=fedsrf&view=basic&eid=2-s2.0-0034761826.

Jager, Tjalling, Benjamin T Martin, and Elke I Zimmer. 2013. "DEBkiss or the quest for the simplest generic model of animal life history." *Journal of Theoretical Biology* 328: 9–18. doi:10.1016/j.jtbi.2013.03.011.

Jokiel, Paul L, and SL Coles. 1977. "Effects of temperature on the mortality and growth of Hawaiian reef corals." *Marine Biology* 43 (3): 201–8. http://www.scopus.com/record/display.url?fedsrfIntegrator=MEKPAPERS-SCOCIT&origin=fedsrf&view=basic&eid=2-s2.0-0000237488.

Kooijman, SALM. 2010. *Dynamic Energy Budget Theory for Metabolic Organization*. 3rd ed. Cambridge University Press.

Marcelino, Luisa A, Mark W Westneat, Valentina Stoyneva, Jillian Henss, Jeremy D Rogers, Andrew Radosevich, Vladimir Turzhitsky, et al. 2013. "Modulation of Light-Enhancement to Symbiotic Algae by Light-Scattering in Corals and Evolutionary Trends in Bleaching." *PLoS ONE* 8 (4): e61492. doi:10.1371/journal.pone.0061492.s008.

Muller, Erik B, Sebastiaan A L M Kooijman, Peter J Edmunds, Francis J Doyle, and Roger M Nisbet. 2009. "Dynamic energy budgets in syntrophic symbiotic relationships between heterotrophic hosts and photoautotrophic

symbionts." *Journal of Theoretical Biology* 259 (1): 44–57. doi:10.1016/j.jtbi.2009.03.004.

Muscatine, Leonard, and James W Porter. 1977. "Reef corals: mutualistic symbioses adapted to nutrient-poor environments." *Bioscience* 27 (7): 454–60.

R Core Team. 2014. "R: A Language and Environment for Statistical Computing." Vienna, Austria: R Foundation for Statistical Computing. http://www.R-project.org/.

Roth, M S. 2014. "The engine of the reef: Photobiology of the coral-algal symbiosis." *Frontiers in Microbiology*. http://journal.frontiersin.org/Journal/10.3389/fmicb.2014.00422/pdf.

Wang, J, and Angela E Douglas. 1998. "Nitrogen recycling or nitrogen conservation in an alga-invertebrate symbiosis?" *The Journal of Experimental Biology* 201: 2445–53.

Weis, Virginia M. 2008. "Cellular mechanisms of Cnidarian bleaching: stress causes the collapse of symbiosis." *The Journal of Experimental Biology* 211 (Pt 19): 3059–66. doi:10.1242/jeb.009597.

Wooldridge, Scott A. 2009. "A new conceptual model for the warm-water breakdown of the coral-algae endosymbiosis." *Marine and Freshwater Research* 60 (June): 483–96.

———. 2014a. "Differential thermal bleaching susceptibilities amongst coral taxa: re-posing the role of the host." *Coral Reefs* 33 (1). Springer Berlin Heidelberg: 15–27. doi:10.1007/s00338-013-1111-4.

———. 2014b. "Formalising a mechanistic linkage between heterotrophic feeding and thermal bleaching resistance." *Coral Reefs*. Springer Berlin Heidelberg, 1–6. doi:10.1007/s00338-014-1193-7.

Yellowlees, David, T A V Rees, and William Leggat. 2008. "Metabolic interactions between algal symbionts and invertebrate hosts." *Plant, Cell and Environment* 31: 679–94.

List of Figures

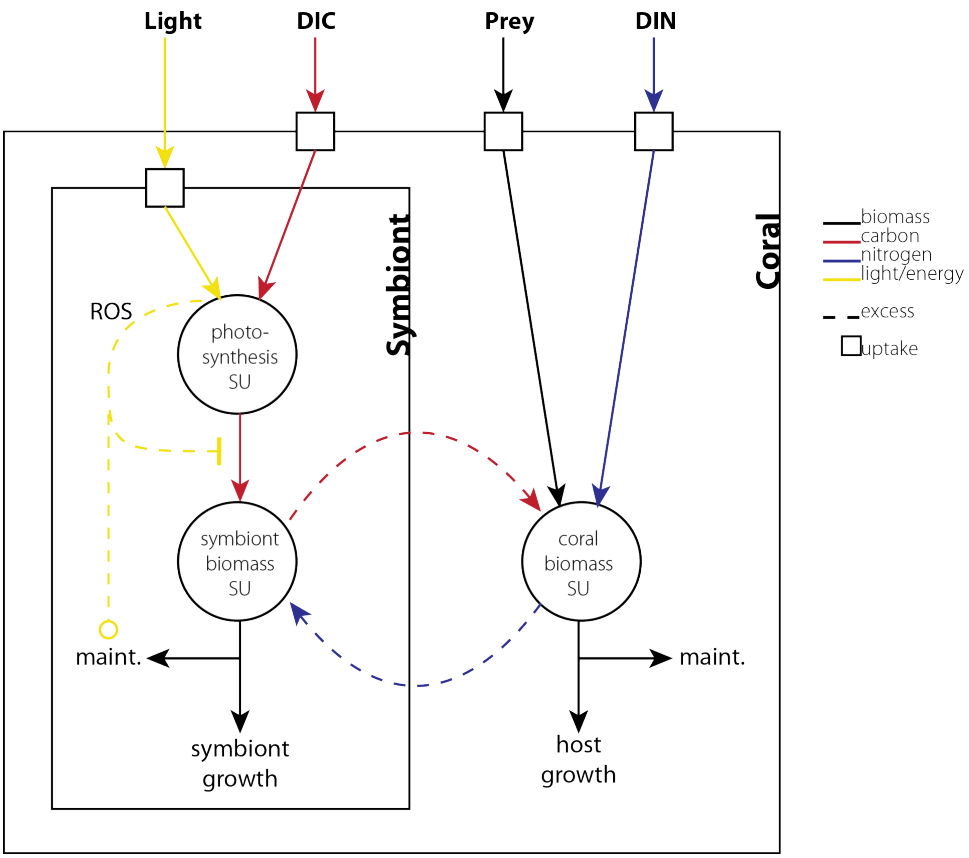

Figure 1: Graphical representation of coral-algal symbiosis model.