

# A simplified dynamic bioenergetic model for coral bleaching

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## Abstract

This is the abstract. Some type of positive feedback is necessary. Compare scenarios of recycling CO<sub>2</sub>, have photodamage increase maintenance that does recycle CO<sub>2</sub>. Compare recycled N to symbiont instead of host How much do you have to reduce the light to get recovery? i.e., magnitude of hysteresis?

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## 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, jeopardizing their future persistence. In order to understand and predict coral responses to complex changes in their 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 performance of reef corals, including responses to environmental stress.

In reef coral symbioses, intracellular *Symbiodinium* translocate photosynthetically fixed carbon to support coral metabolism, while the animal host provides access to inorganic nutrients and carbon dioxide (Muscattine 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 fixed 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 for its own growth. In its simplest form, this principle of sharing the surplus is sufficient to describe the dynamics of diverse syntrophic organs and organisms (e.g., trees, duckweeds, corals), suggesting the mechanism is mathematically and evolutionarily robust (Nisbet et al., in prep.).

While the formal DEB model of Muller et al. (2009) 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

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or severe bleaching can result in mortality, though corals sometimes recover their symbionts. Bleaching susceptibility, severity, and recovery may be influenced by interacting factors such as heterotrophy and 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 (i.e., reproduction, larval stages, and metamorphosis are not considered), 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 further development by the scientific community to include additional complexity and problem-specific components. To widen the audience for this work, we chose the R language because it is freely available and in common use by biologists and ecologists.

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 dynamic bioenergetic 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, and each model flux and parameter are defined in Tables 1 and 2, respectively. 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. Host biomass ( $H$ ), symbiont biomass ( $S$ ), and prey biomass ( $X$ ) have fixed, but different, molar N:C ratios (Table 2). 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 are symbiont biomass and coral biomass; because resources are acquired proportionally to surface area, and surface area is proportional to volume (i.e., corals are “V1-morphs” in DEB terminology (Kooijman 2010)), biomass increases exponentially during growth (indeed, corals grow exponentially (Bak 1976)). The specific growth rate and the ratio of symbiont to host biomass are the responses of interest of the system. Below we describe the formulation of each flux involved in producing these responses.

Table 1. Model fluxes

| Symbol   | Description                          | Units                                    | Eq. no. |
|----------|--------------------------------------|--|---------|
| $j_X$    | Prey uptake rate                     | $\text{molX CmolH}^{-1} \text{ d}^{-1}$  | 3       |
| $j_N$    | Nitrogen uptake rate                 | $\text{molN CmolH}^{-1} \text{ d}^{-1}$  | 4       |
| $j_{HG}$ | Host biomass formation rate          | $\text{CmolH CmolH}^{-1} \text{ d}^{-1}$ | 5       |
| $r_{NH}$ | Recycled nitrogen from host turnover | $\text{molN CmolH}^{-1} \text{ d}^{-1}$  | 6       |
| $\rho_N$ | Nitrogen shared with the symbiont    | $\text{molN CmolH}^{-1} \text{ d}^{-1}$  | 7       |

| Symbol     | Description                                     | Units  | Eq. no. |
|------------|---|--|---------|
| $j_{eC}$   | Excess carbon used to activate host CCMs        | molC CmolH <sup>-1</sup> d <sup>-1</sup>               |         |
| $j_L$      | Light absorption rate                           | molph CmolS <sup>-1</sup> d <sup>-1</sup>              | 9       |
| $j_{CO_2}$ | CO <sub>2</sub> input to photosynthesis         | molCO <sub>2</sub> CmolH <sup>-1</sup> d <sup>-1</sup> | 10      |
| $r_{CH}$   | Recycled CO <sub>2</sub> from host turnover     | molCO <sub>2</sub> CmolH <sup>-1</sup> d <sup>-1</sup> | 11      |
| $r_{CS}$   | Recycled CO <sub>2</sub> from symbiont turnover | molCO <sub>2</sub> CmolS <sup>-1</sup> d <sup>-1</sup> | 12      |
| $j_{CP}$   | Photosynthesis rate                             | molC CmolS <sup>-1</sup> d <sup>-1</sup>               | 13      |
| $j_{eL}$   | Light energy in excess of photochemistry        | molph CmolS <sup>-1</sup> d <sup>-1</sup>              | 14      |
| $j_{NPQ}$  | Total capacity of NPQ                           | molph CmolS <sup>-1</sup> d <sup>-1</sup>              | 15      |
| $c_{ROS}$  | ROS production proportional to baseline         | –  | 16      |
| $r_{NS}$   | Recycled nitrogen from symbiont turnover        | molN CmolS <sup>-1</sup> d <sup>-1</sup>               | 17      |
| $j_{SG}$   | Symbiont biomass formation rate                 | CmolS CmolS <sup>-1</sup> d <sup>-1</sup>              | 18      |
| $\rho_C$   | Fixed carbon shared with host                   | molC CmolS <sup>-1</sup> d <sup>-1</sup>               | 19      |
| $j_{ST}$   | Symbiont turnover rate                          | CmolS CmolS <sup>-1</sup> d <sup>-1</sup>              | 20      |

Table 2. Model parameters

| Symbol        | Description   | Value   | Units                                      |
|---------------|---|---------|--|
| $n_{NH}$      | N:C molar ratio in host biomass   | 0.19    | –  |
| $n_{NS}$      | N:C molar ratio in symbiont biomass   | 0.2     | –  |
| $n_{NX}$      | N:C molar ratio in prey biomass   | 0.13    | –  |
| $j_{HT}^0$    | Specific turnover rate of host biomass  | 0.03    | CmolH CmolH <sup>-1</sup> d <sup>-1</sup>  |
| $j_{ST}^0$    | Specific turnover rate of symbiont biomass                                    | 0.03    | CmolS CmolS <sup>-1</sup> d <sup>-1</sup>  |
| $\sigma_{NH}$ | Proportion host nitrogen turnover recycled                                    | 0.9     | –  |
| $\sigma_{CH}$ | Proportion host carbon turnover recycled                                      | 0.9     | –  |
| $\sigma_{NS}$ | Proportion symbiont nitrogen turnover recycled                                | 0.9     | –  |
| $\sigma_{CS}$ | Proportion symbiont carbon turnover recycled                                  | 0.9     | –  |
| $j_{Xm}$      | Maximum specific feeding rate of host   | 0.1292  | molX CmolH <sup>-1</sup> d <sup>-1</sup>   |
| $K_X$         | Half-saturation constant for prey uptake by host                              | 20e-6   | molX L <sup>-1</sup>                       |
| $j_{Nm}$      | Maximum specific DIN uptake rate by host                                      | 0.048   | molN CmolH <sup>-1</sup> d <sup>-1</sup>   |
| $K_N$         | Half-saturation constant for DIN uptake by host                               | 0.46e-6 | molN L <sup>-1</sup>                       |
| $k_{CO_2}$    | Efficacy of CO <sub>2</sub> delivery by host CCMs                             | 5       | molCO <sub>2</sub> molC <sup>-1</sup>      |
| $j_{HGm}$     | Maximum specific growth rate of host  | 1       | CmolH CmolH <sup>-1</sup> d <sup>-1</sup>  |
| $y_{CL}$      | Quantum yield of photosynthesis   | 0.1     | molC mol ph <sup>-1</sup>                  |
| $\bar{a}^*$   | Effective light-absorbing cross-section of symbiont                           | 1.34    | m <sup>2</sup> CmolS <sup>-1</sup>         |
| $k_{NPQ}$     | NPQ capacity of symbiont, relative to C-fixation                              | 4       | –  |
| $k_{ROS}$     | Excess photon energy that doubles ROS production, relative to baseline levels | 40-80   | mol ph CmolS <sup>-1</sup> d <sup>-1</sup> |
| $k$           | Exponent on ROS production rate   | 1       | –  |
| $j_{CPm}$     | Maximum specific photosynthesis rate of symbiont                              | 2.8     | molC CmolS <sup>-1</sup> d <sup>-1</sup>   |
| $j_{SGm}$     | Maximum specific growth rate of symbiont                                      | 0.25    | CmolS CmolS <sup>-1</sup> d <sup>-1</sup>  |
| $b$           | Scaling parameter for strength of bleaching response                          | 5       | –  |

### State equations

The balance equations for symbiont and host biomass are expressed as:

$$\frac{dS}{Sdt} = j_{SG} - j_{ST} \quad (1)$$

$$\frac{dH}{Hdt} = j_{HG} - j_{HT}^0 \quad (2)$$

These are expressed per unit of symbiont and host biomass, respectively. The specific biomass growth and turnover rates that define these balance equations are produced by combinations of the individual model fluxes (see Table 1 for definitions and units), which are each expressed as mass-specific rates (e.g., per C-mole of symbiont or host biomass). When necessary, conversions between symbiont-mass-specific and host-mass-specific rates are accomplished by multiplying or dividing by the symbiont:host biomass ratio.

### *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 (i.e., a Holling type II function) with a maximum feeding rate  $j_{Xm}$  and half-saturation constant  $K_X$ :

$$j_X = \frac{j_{Xm} \cdot X}{X + K_X} \quad (3)$$

Additionally, the coral animal acquires nitrogen dissolved in the surrounding seawater, which is assumed to represent ammonium, the primary form utilized by corals (Yellowlees, Rees, and Leggat 2008). This gives the host (rather than the symbiont) priority in nitrogen utilization; this capacity is supported by experimental evidence (Wang and Douglas 1998) and is consistent with the physical arrangement of the partners, where the host is in direct contact with the external environment. The uptake of nitrogen from the environment is thus specified by Michaelis-Menten kinetics using a maximum uptake rate  $j_{Nm}$  and half-saturation constant  $K_N$ :

$$j_N = \frac{j_{Nm} \cdot N}{N + K_N} \quad (4)$$

Coral biomass formation is then specified by a parallel complementary SU that combines carbon and nitrogen, according to:

$$j_{HG} = \left( \frac{1}{j_{HGm}} + \frac{1}{\rho_C \frac{S}{H} + j_X} + \frac{1}{(j_N + n_{NX}j_X + r_{NH})/n_{NH}} - \frac{1}{\rho_C \frac{S}{H} + j_X + (j_N + n_{NX}j_X + r_{NH})/n_{NH}} \right)^{-1} \quad (5)$$

where  $\rho_C$  is the surplus fixed carbon shared by the symbiont (see below), and  $r_{NH}$  is the recycled portion of the nitrogen liberated by host biomass turnover:

$$r_{NH} = \sigma_{NH} n_{NH} j_{HT}^0 \quad (6)$$

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<sup>1</sup> of the SU) is then made available to the symbiont:

$$\rho_N = (j_N + n_{NX}j_X + r_{NH} - n_{NH}j_{HG})_+ \quad (7)$$

The carbon rejected from this SU reflects the amount of excess fixed carbon available to the host that is not used in biomass formation:

$$j_{eC} = (j_X + \rho_C \frac{S}{H} - j_{HG})_+ \quad (8)$$

This flux,  $j_{eC}$ , is assumed to be available as a respiratory substrate to support various energetically-demanding processes; of particular importance is the host's active supply of CO<sub>2</sub> for symbiont photosynthesis (Wooldridge 2013; Hopkinson, Tansik, and Fitt 2015) (see below).

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<sup>1</sup>Rejection fluxes must always be positive, and hence are specified with the notation  $(x)_+$ , which means  $\max(x, 0)$ .

Due to the inherent inefficiency of the parallel complementary SU formulation, there is always 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 excess carbon from the coral biomass SU.

#### 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 ( $\text{CO}_2$ ). 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; Marcelino et al. 2013). We used data from Marcelino et al. (2013) to empirically derive an “amplification factor”  $A$  (the ratio of internal scalar irradiance to external downwelling irradiance) as a function of symbiont density (expressed as symbiont to host biomass ratio), which is specified as:

$$A = 1.26 + 1.39 \cdot \exp(-6.48 \cdot \frac{S}{H}) \quad (9)$$

This amplification factor is then multiplied by the external downwelling irradiance  $L$  and the effective light-absorbing surface area of symbiont biomass  $\bar{a}^*$  to specify the total amount of light absorbed:

$$j_L = A \cdot L \cdot \bar{a}^* \quad (10)$$

We then specify the input of  $\text{CO}_2$  to photosynthesis as  $j_{\text{CO}_2}$ , which is mediated by the host. This encompasses potentially diverse mechanisms by which the host may enhance  $\text{CO}_2$  availability for photosynthesis (i.e., carbon-concentrating mechanisms (CCMs)), including active transport of bicarbonate, carbonic anhydrase-catalyzed conversion of bicarbonate to  $\text{CO}_2$  to promote diffusion toward the symbiont (Tansik, Fitt, and Hopkinson 2015), and acidification of the symbiosome to increase localized  $\text{CO}_2$  concentrations around the symbiont (Barott et al. 2014). Since these mechanisms require energetic input by the host, the magnitude of  $\text{CO}_2$  delivery is set proportional to  $j_{eC}$ , the amount of excess carbon from the host biomass SU, assuming that some of this carbon is respired to energize these CCMs. This formulation means that the symbiont indirectly ensures its own  $\text{CO}_2$  supply by providing the host with fixed carbon (Wooldridge 2013), which establishes a positive feedback in the model that proves to be essential in simulating the phenomenon of coral bleaching. The parameter  $k_{\text{CO}_2}$  is included to scale the efficacy of host CCMs, i.e., how many moles of  $\text{CO}_2$  can be delivered from the environment to the symbiont per mole of fixed carbon. Adjusting this parameter offers the user the opportunity to compare different rates of  $\text{CO}_2$  delivery that may characterize different coral species (Wooldridge 2014a). The input of  $\text{CO}_2$  to the photosynthesis SU is therefore specified as:

$$j_{\text{CO}_2} = k_{\text{CO}_2} j_{eC} \quad (11)$$

Additional metabolic  $\text{CO}_2$  recycled from both the host and symbiont biomass turnover is also made available to the photosynthesis SU, according to:

$$r_{CH} = \sigma_{CH} j_{HT}^0 \quad (12)$$

$$r_{CS} = \sigma_{CS} j_{ST}^0 \quad (13)$$

Fixed carbon is then produced by the photosynthesis SU according to:

$$j_{CP} = \left( \frac{1}{j_{CPm}} + \frac{1}{y_{CL} j_L} + \frac{1}{(j_{\text{CO}_2} + r_{CH}) \frac{H}{S}} + r_{CS} - \frac{1}{y_{CL} j_L + (j_{\text{CO}_2} + r_{CH}) \frac{H}{S} + r_{CS}} \right)^{-1} \cdot c_{ROS}^{-1} \quad (14)$$

where  $j_{CPm}$  is the maximum specific rate of photosynthesis, and  $c_{ROS}$  is the relative rate of reactive oxygen species production (see below). Dividing the photosynthetic rate by  $c_{ROS}$  causes a decline in response to photooxidative stress (i.e., photoinhibition).

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

$$j_{eL} = (j_L - j_{CP}/y_{CL})_+ \quad (15)$$

This excess light energy must be quenched by alternative pathways in order to prevent photooxidative damage (Powles 1984). *Symbiodinium* utilize a variety of pathways for non-photochemical quenching (NPQ; Roth 2014), which we collect in a relative NPQ capacity specified as a parameter of the symbiont ( $k_{NPQ}$ ). The total NPQ flux is specified as a single-substrate SU formula:

$$j_{NPQ} = \left( \frac{1}{k_{NPQ}} + \frac{1}{j_{eL}} \right)^{-1} \quad (16)$$

If light energy further exceeds the total capacity of both carbon fixation and NPQ, then reactive oxygen species (ROS) are produced. We represent this as a relative quantity  $c_{ROS}$ , which takes a value of 1 when all light absorbed can be quenched by photochemistry and NPQ, and increases as the amount of excess excitation energy further increases:

$$c_{ROS} = 1 + \left( \frac{(j_{eL} - j_{NPQ})_+}{k_{ROS}} \right)^k \quad (17)$$

where  $k_{NPQ}$ ,  $k_{ROS}$ , and  $k$  are parameters of the symbiont that determine the onset and rate of ROS production. Importantly,  $c_{ROS}$  as specified here is not a function of absolute light absorption, but rather the amount of excess light energy,  $j_{eL}$ , after accounting for carbon fixation and NPQ. A direct consequence of this formulation is that CO<sub>2</sub>-limitation of photosynthesis can lead to ROS production, an important mechanism (Wooldridge 2009) that was not captured by previous representations of photooxidative stress (Eynaud, Nisbet, and Muller 2011). Moreover, this formulation allows functional diversity among symbiont types to be explored by changing the parameters  $k_{NPQ}$ ,  $k_{ROS}$ , and  $k$ .

Carbon fixed by photosynthesis ( $j_{CP}$ ) is then combined with nitrogen shared by the host ( $\rho_N$ ) and nitrogen recycled from symbiont biomass turnover

$$r_{NS} = \sigma_{NS} n_{NS} j_{ST}^0 \quad (18)$$

to build new symbiont biomass, following the SU equation:

$$j_{SG} = \left( \frac{1}{j_{SGm}} + \frac{1}{j_{CP}} + \frac{1}{(\rho_N \frac{H}{S} + r_{NS})/n_{NH}} - \frac{1}{j_{CP} + (\rho_N \frac{H}{S} + r_{NS})/n_{NH}} \right)^{-1} \quad (19)$$

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,  $\rho_C$ , is translocated to the coral host:

$$\rho_C = (j_{CP} - j_{SG})_+ \quad (20)$$

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

Symbiont biomass turnover includes a component of constant turnover specified by the parameter  $j_{ST}^0$ , representing fixed maintenance costs, plus a component that scales with the magnitude of ROS production.

$$j_{ST} = j_{ST}^0 (1 + b(c_{ROS} - 1)) \quad (21)$$

This second component of symbiont biomass loss can represent both photodamage and/or symbiont expulsion (i.e., bleaching), both of which occur in response to high levels of ROS production. The parameter  $b$  is included to scale biomass loss due to bleaching in response to ROS. (Note that recycling of symbiont biomass turnover ( $rNS$  and  $rCS$ ) only occurs based on the maintenance component of turnover (i.e.,  $j_{ST}^0$ ), and not the bleaching-related component, as this loss represents biomass that is damaged or expelled from the host).

### *Numerical analysis*

A time-stepping Euler method was used to solve the state equations since the production and rejection fluxes of the SUs are implicitly defined. Specifically, the rejection fluxes of carbon and nitrogen from the symbiont and host biomass SUs act as reciprocal input fluxes to the other SU. In addition, the rejection flux of excitation energy from the photosynthesis SU acts to reduce its own production flux (i.e., photoinhibition), and hence a discretized time-stepping procedure was necessary. A vector of time values was created for each simulation run, along which dynamic environmental forcing functions (irradiance, DIN, and prey abundance) can be designed. These vectors, along with initial values of symbiont and host biomass, then serve as input to the time-stepping function, which solves for the current system state using values of the previous system state where necessary. A time step of 0.1 days was used for all simulations, which were performed using R code that is available in the data repository accompanying this article: [github.com/jrcunning/Rcoral](https://github.com/jrcunning/Rcoral).

To aid in visualizing model results, we calculated values to indicate the degree to which product formation at an SU was limited by availability of either of its two substrates:

$$\log \left( \frac{\min(j_{S1}, j_{Pm})}{\min(j_{S2}, j_{Pm})} \right) \quad (22)$$

where  $j_{S1}$  and  $j_{S2}$  are the specific input fluxes of the two substrates and  $j_{Pm}$  is the maximum specific product formation rate, all with units of  $\text{Cmol Cmol}^{-1} \text{d}^{-1}$ .

## **Results**

### *Qualitative dynamics*

simulations in constant environs show either positive or negative exponential growth. some environments show two steady states, one with positive and one with negative growth, depending on initial conditions. based on numerical analysis, we see ultimate exponential growth or decline. the mechanism that produces these alternate steady states is: . . . . for practical purposes, we are interested in the positive growth steady states and their properties and how they change across environmental gradients (see section X). but we are also interested in the possibility for flips to the alternate steady states (see section Y).

### *Steady state behavior*

*emphasize that steady state is exponential growth, and fluxes are per unit biomass/specific rates* To analyze qualitative behavior, we ran the model to steady state across gradients of external irradiance and nutrients (Fig. 2), which revealed patterns consistent with observed phenomena in corals. Predicted growth rates are low at low light and DIN, and begin increasing as both of these factors increase (Fig. 2A). Low light is limiting to photosynthesis (Fig. 2D), which leads to carbon-limitation of host growth (Fig. 2B) and an associated increase in the symbiont to host biomass ratio (Fig. 2C). In agreement with this trend are many observations of negative correlation between irradiance and symbiont density (Stimson 1997; Brown et al. 1999; Fitt et al. 2000; Titlyanov et al. 2001). As higher light alleviates light-limitation of photosynthesis, growth becomes less carbon-limited. Similarly, elevating DIN up to  $\sim 2 \mu\text{M}$  alleviates nitrogen-limitation (Fig. 2B). Increased growth at higher DIN is predicted by the DEB model of Muller et al. (2009), and has also been observed experimentally (Muller-Parker et al. 1994; Tanaka et al. 2007; Tanaka et al. 2013). However, DIN elevation beyond a certain point (e.g.,  $2\text{--}3 \mu\text{M}$  in these simulations) has little effect on growth as carbon becomes limiting (Fig. 2B). Very high nutrient levels

may even reduce growth (Shantz, Lemoine, and Burkepille 2015), although these impacts are not likely to occur within the range of concentrations considered here ( $<4 \mu\text{M}$ ) (Ferrier-Pagès et al. 2000).

In addition to increasing growth, DIN also increases the symbiont to host biomass ratio, a phenomenon also observed in reef corals (Marubini and Davies 1996). S:H ratios also increase under low light (Stimson 1997; Fitt et al. 2000; Anthony and Hoegh-Guldberg 2003). At low DIN and intermediate light, more typical of coral reef environments, symbiont to host biomass ratios are around  $\sim 0.1$ - $0.3$ , which is consistent with values reported in the literature (Muscattine, R McCloskey, and E Marian 1981; Edmunds et al. 2011).

The maximum predicted growth rates of  $\sim 0.1 \text{ d}^{-1}$ , occurring between  $\sim 10$ - $15 \text{ mol photons m}^{-2} \text{ s}^{-1}$  light and  $>3 \mu\text{M}$  DIN (Fig. 2A), are comparable to the rate of  $0.07 \text{ d}^{-1}$  measured by Tanaka et al. (2007) under similar N-enriched conditions. Growth under conditions more typical of reef environments ( $<0.5 \mu\text{M}$  DIN) are within the range of  $\sim 0.01$ - $0.05 \text{ d}^{-1}$ ; however, these values are still higher than most specific growth rates reported in the literature, which are typically based on skeletal mass, and fall near or below  $0.01 \text{ d}^{-1}$  (Osinga et al. 2011; Osinga et al. 2012) (though values as high as  $0.025 \text{ d}^{-1}$  have been reported (Schutter et al. 2010)). These generally low skeletal growth rates relative to predicted biomass growth may be explained by differential substrate-limitation (i.e.,  $\text{CO}_2$  may limit calcification, which is not present in the model); indeed, tissue and skeletal growth may not always be well correlated (Anthony 2002). Furthermore, bioerosion may reduce net skeletal growth, especially in the field (Bak 1976). Nevertheless, when rates of increase in coral tissue biomass have been directly measured over short periods, values are consistent with model predictions (e.g.,  $0.07 \text{ d}^{-1}$  in Tanaka et al. (2007)), and similar rates ( $0.04 \text{ d}^{-1}$ ) have been measured in *Aiptasia diaphana*, a non-calcifying symbiotic anemone (Armoza-Zvuloni et al. 2014).

As irradiance continues to increase above  $\sim 15$ - $20 \text{ mol photons m}^{-2} \text{ d}^{-1}$ , growth rates decline until positive growth ceases above  $\sim 30 \mu\text{mol photons m}^{-2} \text{ d}^{-1}$ . The mechanism underlying this decline is the increase in light energy beyond the capacity of photosynthesis and non-photochemical quenching: excess excitation energy generates reactive oxygen species (ROS) (Weis 2008; Roth 2014), which, in this model, have the phenomenological consequences of reducing the photosynthetic rate (representing photoinhibition) and increasing the symbiont biomass loss rate (representing photodamage and/or symbiont expulsion) (see Eynaud, Nisbet, and Muller 2011). Together, these impacts reduce the symbiont to host biomass ratio (Fig. 2C), as occurs during coral bleaching. This reduction in symbionts consequently reduces the flux of fixed carbon to the host, resulting in increasing carbon-limitation (Fig. 2B) and eventual cessation of growth (Fig. 2A). Importantly, these consequences arise in the present model only when light energy exceeds the capacity of photochemistry and NPQ, which in turn depends on  $\text{CO}_2$  availability. While previous models framed photophysiological stress as a fixed response to absolute irradiance levels (Eynaud, Nisbet, and Muller 2011), the current implementation considers the dynamic balance of multiple energy sinks in the causation of stress, which is more consistent with current understanding of symbiosis dysfunction (Wooldridge 2013), and establishes an important role of the host in providing  $\text{CO}_2$  for symbiont photosynthesis (Tansik, Fitt, and Hopkinson 2015; Hopkinson, Tansik, and Fitt 2015).

While bleaching in response to high light alone has been observed experimentally (Schutter et al. 2011; Downs et al. 2013), mass coral bleaching events occur in response to high temperature (Hoegh-Guldberg 1999); thus, it is important to justify our consideration of light as the primary stressor in the model. In reality, light and temperature interact synergistically (Coles and Jokiel 1978; Jones et al. 1998), and in fact, any stressor that disrupts the quenching of light energy may lead to bleaching (Wooldridge 2010; Baker and Cuning 2015). This is because the proximate cause of coral bleaching is excess excitation energy, but the upstream events that lead to this situation may be diverse: indeed, elevated temperature inhibits Rubisco functioning (Jones et al. 1998) and repair of the D1 protein in photosystem II (Warner, Fitt, and Schmidt 1999), which reduces the capacity of photochemical quenching and leads to an excess of light energy. In this way, elevated temperature serves to reduce the threshold above which light causes stress to the system (Hoegh-Guldberg 1999); importantly, light is still the proximate stressor. Therefore, we omitted temperature from the model, which serves to maintain a desired level of simplicity, while still allowing photophysiological stress and bleaching to be simulated with biological realism in response to light. Thus, the specific light levels that cause stress here should be interpreted in this context, and the effects of high light are analogous to the effects of high temperature.

The incorporation of light stress in the model sets an upper limit to the amount of light at which a stable symbiotic interaction can be maintained, but even below this threshold of breakdown, negative effects of high light reduce steady state growth and symbiont:host biomass (Fig. 2A,C). This gradual decline is consistent with



experimental results showing that high light levels decrease growth (Schutter et al. 2011), and field studies documenting optimum growth rates at intermediate depths (Baker and Weber 1975; Huston 1985). Consequently, the model predicts greater variation in state variables across light gradients than was predicted by the model of Muller et al. (2009), which did not include photoinhibition and photodamage. It is important to recognize that these are steady state values predicted under a constant environment at the given light and nutrient levels; a dynamic system may temporarily cross this threshold and experience a period of symbiont loss (bleaching) and reduced growth, after which a return to benign conditions may restore symbiont biomass and positive growth. To explore this further and illustrate the behavior of the model in more detail, we evaluate a number of dynamic simulations below.

*Sensitivity analysis – should come after the steady states bc describes changes in steady states*

Each default parameter value used in the model (Table 2) is based on carefully selected relevant literature. A supplementary document detailing the derivations of each of these default parameter values is provided. Nevertheless, it is important to evaluate the sensitivity of the model to changes in these parameter values. We measured fractional change in steady state values in response to fractional change in parameter values, relative to their default values (Table 2).

*Dynamic behavior*

*varying light: consequences of excess light and light-limitation*

*varying DIN: role of N-limitation and consequences of elevated N*

*elevated nutrients cause system to become C-limited (photo: CO<sub>2</sub> limited; host: fixed-C limited)*

*C-limitation increases susceptibility to bleaching*

*consequences of a less efficient but more tolerant symbiont*

*Rate of symbiont repopulation (Berner et al. 1993)*

*Bicarbonate addition promotes coral growth (Marubini and Thake 1999)*

*Seasonal change in sym. density is larger when nutrients are elevated (Stimson 1997). Such a phenomenon was predicted by Fitt et al. 2000.*

*Death rule: negative growth for a certain amount of time should be defensible.*

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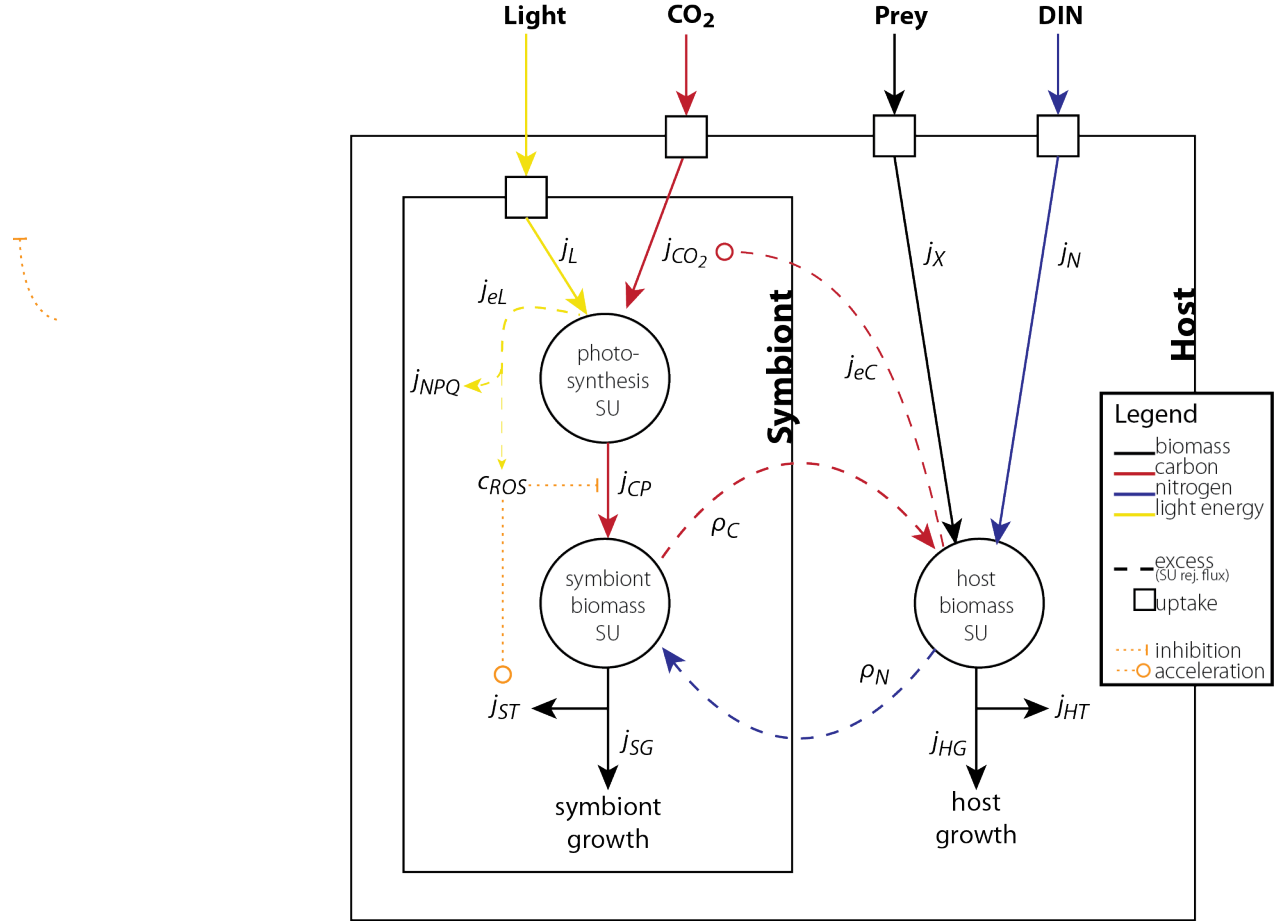
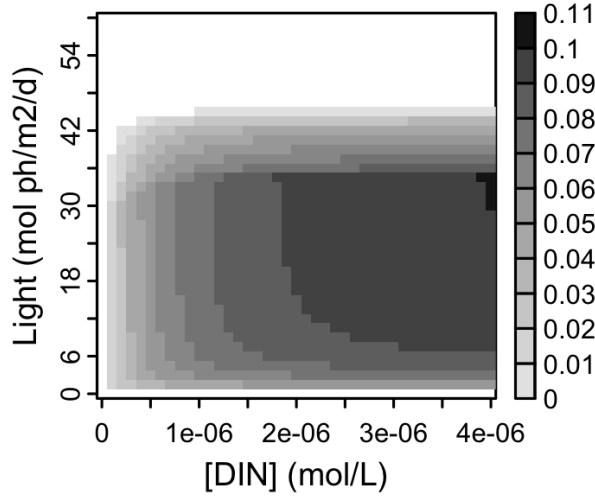
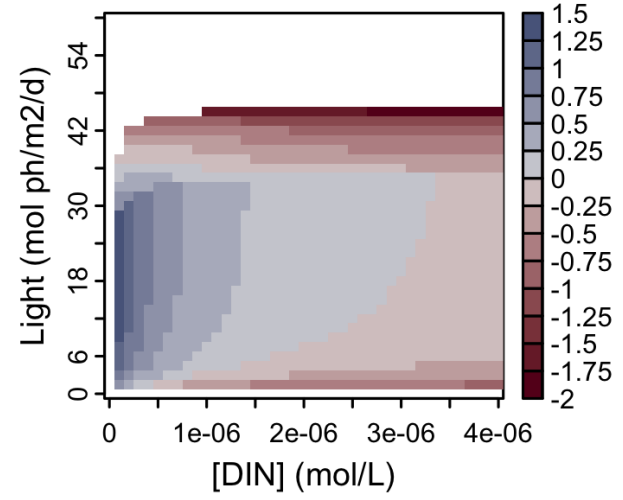


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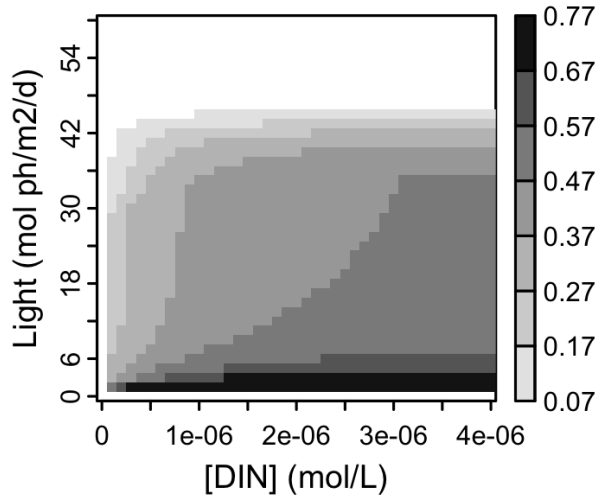
### A. Specific growth



### B. Host growth limitation



### C. Symbiont:host biomass



### D. Photosynthesis limitation

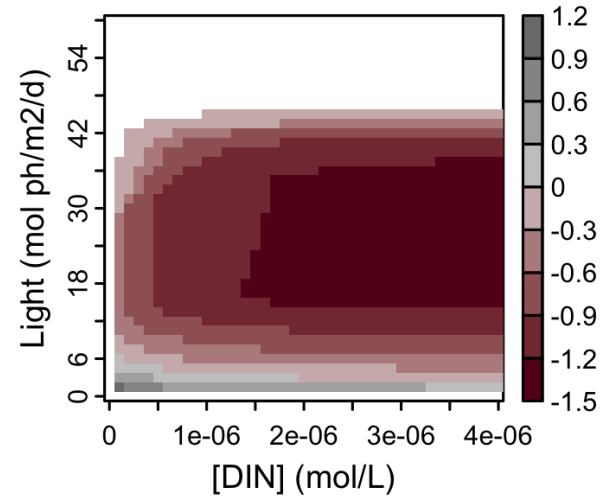


Figure 2: Steady state values of **A**) specific growth (Cmol Cmol<sup>-1</sup> d<sup>-1</sup>), **B**) the symbiont to host biomass ratio (CmolS CmolH<sup>-1</sup>), **C**) relative C- or N-limitation of host biomass formation, and **D**) relative CO<sub>2</sub>- or light-limitation of symbiont photosynthesis, across gradients of external irradiance and dissolved inorganic nitrogen. Note that typical conditions for reefs are ~1e-7 M DIN and 10-20 mol photons m<sup>-2</sup> d<sup>-1</sup>. Simulations for each combination of light and nutrients (41 points along each axis) were run for 100 days with a time step of 1 day. Negative steady state growth rates, and corresponding S:H ratios, were set to zero.



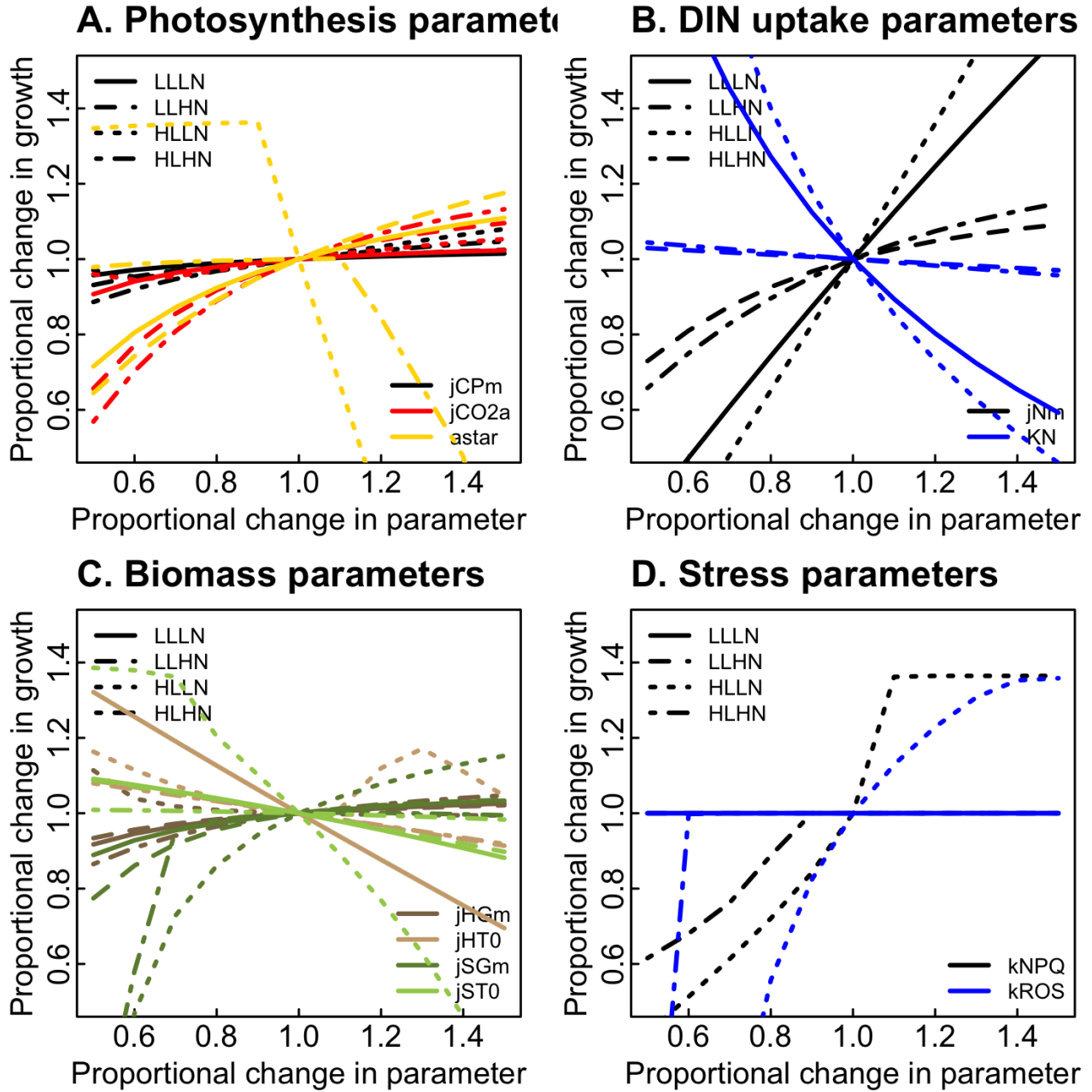


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