

A simplified dynamic bioenergetic model for coral-algal symbiosis and coral bleaching

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Abstract

This is the abstract. Some type of positive feedback is necessary. Compare scenarios of recycling CO₂, have photodamage increase maintenance that does recycle CO₂. 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?

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

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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 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

Symbol	Description	Units	Eq. no.
ρ_N	Nitrogen shared with the symbiont	molN CmolH ⁻¹ d ⁻¹	7
j_{eC}	Excess carbon used to activate host CCMs	molC CmolH ⁻¹ d ⁻¹	
j_L	Light absorption rate	molph CmolS ⁻¹ d ⁻¹	9
j_{CO_2}	CO ₂ input to photosynthesis	molCO ₂ CmolH ⁻¹ d ⁻¹	10
r_{CH}	Recycled CO ₂ from host turnover	molCO ₂ CmolH ⁻¹ d ⁻¹	11
r_{CS}	Recycled CO ₂ from symbiont turnover	molCO ₂ CmolS ⁻¹ d ⁻¹	12
j_{CP}	Photosynthesis rate	molC CmolS ⁻¹ d ⁻¹	13
j_{eL}	Light energy in excess of photochemistry	molph CmolS ⁻¹ d ⁻¹	14
j_{NPQ}	Total capacity of NPQ	molph CmolS ⁻¹ d ⁻¹	15
c_{ROS}	ROS production proportional to baseline	–	16
r_{NS}	Recycled nitrogen from symbiont turnover	molN CmolS ⁻¹ d ⁻¹	17
j_{SG}	Symbiont biomass formation rate	CmolS CmolS ⁻¹ d ⁻¹	18
ρ_C	Fixed carbon shared with host	molC CmolS ⁻¹ d ⁻¹	19
j_{ST}	Symbiont turnover rate	CmolS CmolS ⁻¹ d ⁻¹	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 ⁻¹ d ⁻¹
j_{ST}^0	Specific turnover rate of symbiont biomass	0.03	CmolS CmolS ⁻¹ d ⁻¹
σ_{NH}	Proportion host nitrogen turnover recycled	0.9	–
σ_{CH}	Proportion host carbon turnover recycled	0.9	–
σ_{NS}	Proportion symbiont nitrogen turnover recycled	0.9	–
σ_{CS}	Proportion symbiont carbon turnover recycled	0.9	–
j_{Xm}	Maximum specific feeding rate of host	0.1292	molX CmolH ⁻¹ d ⁻¹
K_X	Half-saturation constant for prey uptake by host	20e-6	molX L ⁻¹
j_{Nm}	Maximum specific DIN uptake rate by host	0.048	molN CmolH ⁻¹ d ⁻¹
K_N	Half-saturation constant for DIN uptake by host	0.46e-6	molN L ⁻¹
k_{CO_2}	Efficacy of CO ₂ delivery by host CCMs	10	molCO ₂ molC ⁻¹
j_{HGm}	Maximum specific growth rate of host	1	CmolH CmolH ⁻¹ d ⁻¹
y_{CL}	Quantum yield of photosynthesis	0.1	molC mol ph ⁻¹
\bar{a}^*	Effective light-absorbing cross-section of symbiont	1.34	m ² CmolS ⁻¹
k_{NPQ}	NPQ capacity of symbiont	112	mol ph CmolS ⁻¹ d ⁻¹
k_{ROS}	Excess photon energy that doubles ROS production, relative to baseline levels	40-80	mol ph CmolS ⁻¹ d ⁻¹
j_{CPm}	Maximum specific photosynthesis rate of symbiont	2.8	molC CmolS ⁻¹ d ⁻¹
j_{SGm}	Maximum specific growth rate of symbiont	0.25	CmolS CmolS ⁻¹ d ⁻¹
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 ρ_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 flux¹ 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 CO₂ for symbiont photosynthesis (Wooldridge 2013; Hopkinson, Tansik, and Fitt 2015) (see below).

¹Rejection 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 (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 , indicating the ratio of internal scalar irradiance to external downwelling irradiance as a function of symbiont density (S:H biomass), 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 light absorption:

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

We then specify the input of CO_2 to photosynthesis as j_{CO_2} , a flux mediated by the host that encompasses potentially diverse carbon-concentrating mechanisms (CCMs), including active transport of bicarbonate, carbonic anhydrase-catalyzed conversion of bicarbonate to CO_2 to promote diffusion toward the symbiont (Tansik, Fitt, and Hopkinson 2015), and acidification of the symbiosome to increase localized CO_2 concentrations around the symbiont (Barott et al. 2014). Since these mechanisms require energetic input by the host, the magnitude of CO_2 delivery is proportional to the host's excess carbon, j_{eC} , assuming that some of this carbon is respired to energize these CCMs. This formulation means that the symbiont indirectly ensures its own CO_2 supply by providing fixed carbon to the host (Wooldridge 2013), which establishes a positive feedback in the model that leads to the existence of multiple stable states, which we discuss below in the context of coral bleaching. The parameter k_{CO_2} scales the efficacy of host CCMs, which enables the comparison of 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:

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

Additional metabolic 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 at high light levels, and the emergent outcome of this SU formulation demonstrates a classic photoinhibition response (see Fig. S1).

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 capacity of both photochemistry and NPQ, then reactive oxygen species (ROS) are produced. We represent this as a relative quantity c_{ROS} , taking a value of 1 when all light energy is quenched by photochemistry and NPQ, and increasing as the amount of excess excitation energy increases:

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

where k_{ROS} is a parameter of the symbiont that determines the rate of ROS production (specifically, the amount of excess excitation energy that doubles ROS production relative to baseline levels). Importantly, c_{ROS} is specified here not as a function of absolute external light, but rather the amount of excess light, j_{eL} , after accounting for quenching by carbon fixation and NPQ. A direct consequence of this formulation is that CO₂-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).

Carbon fixed by photosynthesis (j_{CP}) is then combined with nitrogen shared by the host (ρ_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, ρ_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 represents 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 (r_{NS} and r_{CS}) 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 due to feedbacks present in the model. 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 photosynthesis SU receives CO_2 proportional to the carbon rejection flux from the host biomass SU, and the rejection flux of excitation energy from the photosynthesis SU acts to reduce its own production (i.e., photoinhibition). A vector of time steps is used for each simulation, 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.

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, in units of $\text{Cmol Cmol}^{-1} \text{d}^{-1}$.

Results

Qualitative dynamics

In a constant environment, the system ultimately reaches a steady state of exponential growth or decline. Under some conditions, alternate steady states can be reached depending on initial values of symbiont and host biomass. The mechanism that produces these alternate steady states is the positive feedback between carbon-limitation of the host and CO_2 -limitation of photosynthesis. If the host becomes carbon-limited, the efficacy of its CCMs are reduced and photosynthesis becomes progressively more CO_2 -limited. In turn, less photosynthate is translocated to the host, causing further carbon-limitation and an ultimate decline in biomass; this steady state represents a dysfunctional symbiosis. However, if the host is not carbon-limited, it effectively delivers CO_2 to photosynthesis and ensures its continued receipt of fixed carbon from the symbiont; this system is nitrogen-limited and represents a functional symbiosis with positive exponential growth. Either of these stable states may be reached under (some sets of) constant environmental conditions, depending on the initial values of symbiont and host biomass: if symbiont biomass is initially very low (i.e., a “bleached” coral), the system cannot escape the carbon-limited state and cannot grow. However, if symbiont biomass is initially high (i.e., a healthy coral), then the system maintains positive growth in a nitrogen-limited state. For practical purposes, we consider only positive growth steady states in the “steady state behavior” section below. In the subsequent “dynamic behavior” section, we explore more thoroughly the conditions that cause the system to switch between alternate stable states, and interpret these dynamics in the context of coral bleaching.

Steady state behavior

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 ($\sim 0.01 \text{d}^{-1}$), 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., $\sim 3\text{--}4\ \mu\text{M}$ 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 Burkepile 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 $\sim 0.1\text{--}0.3$, which is consistent with values reported in the literature (Muscantine, R McCloskey, and E Marian 1981; Edmunds et al. 2011).

The maximum predicted growth rates of $\sim 0.1\ \text{d}^{-1}$, occurring between $\sim 10\text{--}20\ \text{mol photons m}^{-2}\ \text{s}^{-1}$ light and $\sim 4\ \mu\text{M}$ 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 $\sim 0.01\text{--}0.03\ \text{d}^{-1}$; these values are slightly 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., 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 $\sim 20\ \text{mol photons m}^{-2}\ \text{d}^{-1}$, growth rates decline until positive growth ceases above $\sim 35\ \mu\text{mol photons m}^{-2}\ \text{d}^{-1}$. 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 symbiont biomass loss (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 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 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 analagous 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

Therefore, we are highly interested in the conditions under which the system switches from one state to another, representing the conditions under which corals “bleach” due to progressive, reinforcing carbon-limitation. Interestingly, this state can be reached in multiple ways, by the acceleration of photoinhibition and photodamage, or by high external DIN, which causes the symbiont to share less carbon, subsequently causing its own CO₂-limitation, and progressive C-limitation of the system. ## 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: CO₂ 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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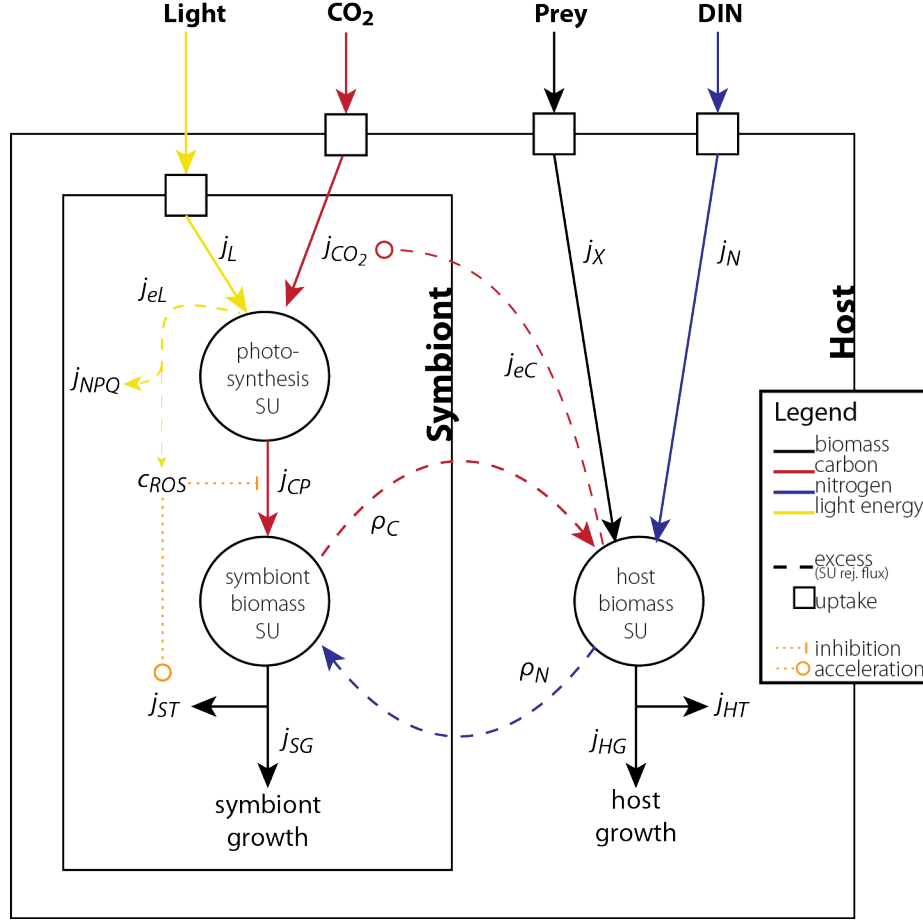


Figure 1: Graphical representation of coral-algal symbiosis model. Light, CO₂, prey, and DIN are acquired from the external environment proportional to the biomass of the partner indicated by the black box for uptake. Mass fluxes (see Table 1 for definitions) are represented by j 's with subscripts indicating the type of mass, and in some cases the process (e.g., j_{CP} is the flux of carbon produced by photosynthesis), and ρ 's indicate fluxes that are shared by one partner with the other. Parallel complementary synthesizing units (SUs) are represented by large circles, and rejection fluxes from these SUs are indicated by dashed lines. c_{ROS} is a proportional rate that impacts other model fluxes by inhibition or acceleration; likewise, j_{eC} accelerates the rate of j_{CO_2} . Recycled mass fluxes from biomass turnover are not shown for clarity (but see Table 1 for definitions).

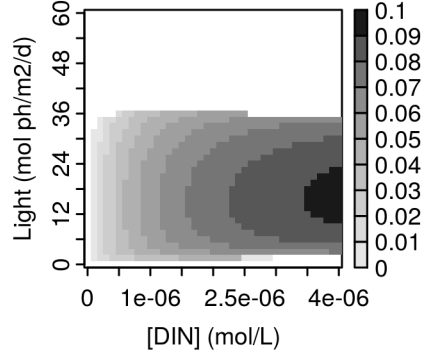
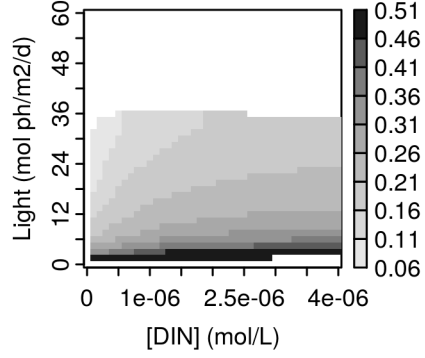
A. Specific growth**B. Symbiont:host biomass**

Figure 2: Steady state values of **A)** specific growth (Cmol Cmol⁻¹ d⁻¹), **B)** the symbiont to host biomass ratio (CmolS CmolH⁻¹), **C)** relative C- or N-limitation of host biomass formation, and **D)** relative CO₂- or light-limitation of symbiont photosynthesis, across gradients of external irradiance and dissolved inorganic nitrogen. Note that typical conditions for reefs are $\sim 10^{-7}$ M DIN and 10-20 mol photons m⁻² d⁻¹. 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.

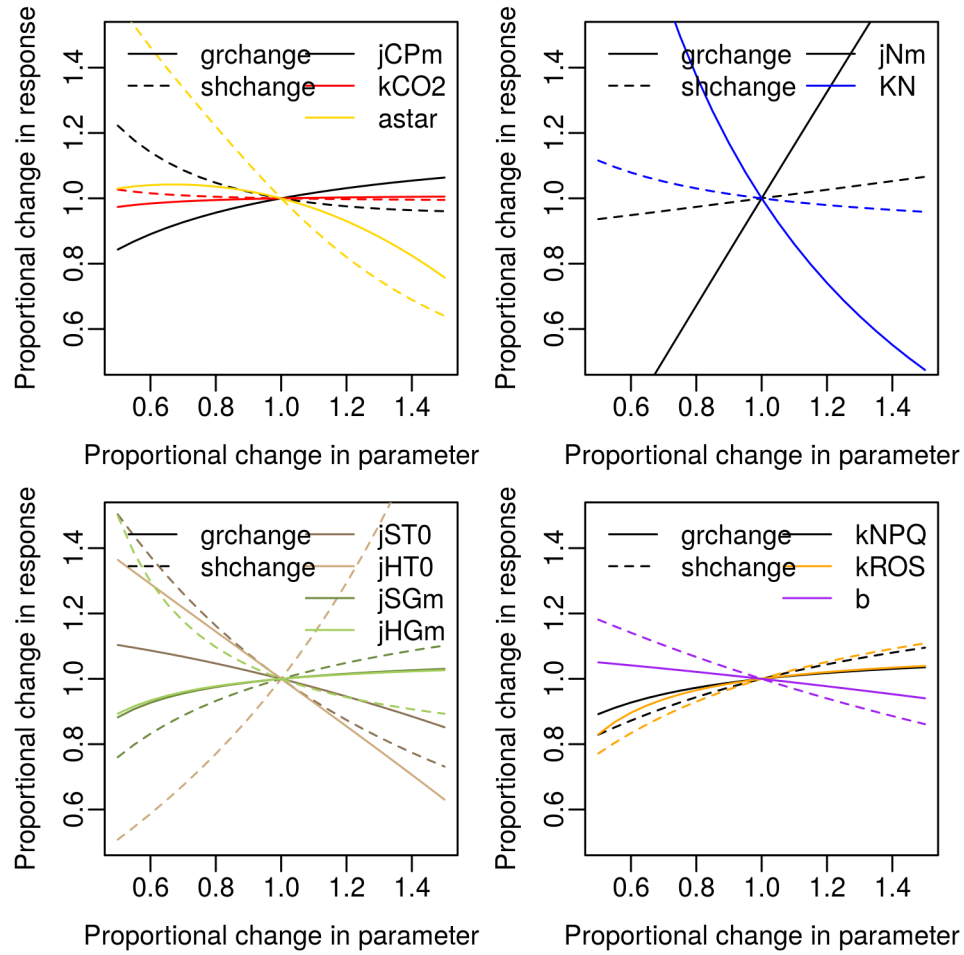


Figure 3: Sensitivity analysis. Plots show the fractional change in steady state values of growth (solid lines) and S:H biomass (dashed lines) in response to fractional changes in default parameter values (see Table 2 for default values). Parameters are grouped by which processes they are involved in. This sensitivity analysis was conducted at conditions typical for coral reef environments: low DIN ($1\text{e-}7\text{ M}$) and intermediate light ($15\text{ mol m}^{-2}\text{ d}^{-2}$). Sensitivity analyses conducted other environmental conditions are presented in the Supplementary Information.