A simplified dynamic bioenergetic model for coral-*Symbiodinium* symbioses and coral bleaching as an alternate stable state

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Abstract

Coral reef ecosystems owe their ecological success–and vulnerability to climate change–to the symbiotic metabolism of corals and *Symbiodinium* spp. The urgency to understand and predict the stability and breakdown of these symbioses (i.e., coral 'bleaching') demands the development and application of theoretical tools; however, the complexity of some approaches may limit their potential application and utility. Here, we develop a simplified dynamic bioenergetic model of coral-*Symbiodinium* symbioses that demonstrates realistic steady-state patterns in coral growth and symbiont abundance across gradients of light, nutrients, and feeding. Furthermore, through a mechanistic treatment of photo-oxidative stress, the model displays dynamic behaviors of bleaching and recovery, and suggests that these phenomena represent transitions between alternate stable states. A suite of complex responses to multiple, interacting environmental factors reproduced by the model suggests it unifyingly captures many important attributes of the system; meanwhile, its modular framework and open source R code are designed to facilitate expansion and problem-specific applications. We see significant potential applications for this modeling framework in generating testable hypotheses and predicting integrated, mechanistic responses of corals to environmental change.

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 responses of corals 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 (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 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

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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 module of photooxidative 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 be influenced by interacting factors such as heterotrophy and nutrient availability (Wooldridge 2014b). To simulate these events and interactions, we develop a photooxidative stress module 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 theory 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 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 model as a resource for futher development by the scientific community to include additional complexity and problem-specific components. We chose the R language, which is freely available and in common use by biologists and ecologists, to reach the widest possible audience with this work.

With these as our primary motivations, we describe a simplified approach to dynamic bioenergetic modeling of coral-*Symbiodinium* symbioses that 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 and provide rationale for the model structure, and demonstrate a range of steady state and dynamic behaviors that are consistent with observed phenomena.

Model description

In this dynamical system, both partners acquire and use carbon and nitrogen to construct biomass: the symbiont fixes carbon through photosynthesis, and receives nitrogen shared by the host, while the host acquires nitrogen from the environment and receives carbon shared by the symbiont. A graphical representation of the model is presented in Fig. 1, and each model flux and parameter is 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). Biomass is produced from carbon and nitrogen 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 of this system 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)).

Environmental stress is implemented in the form of photooxidative stress, which is thought to be the primary trigger of coral bleaching (Lesser 1997; Weis 2008; Wooldridge 2009). To simulate these events, we model the absorption and quenching of light energy by photochemistry and non-photochemical quenching, and the phenomenological responses that occur when these capacities are overwhelmed (i.e., photoinhibition, photodamage, and symbiont loss). 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 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 Cunning 2015). This is because the proximate cause of photo-oxidative stress is excess excitation energy, but the upstream events that lead to this situation may be diverse: indeed, elevated temperature may inhibit Rubisco functioning (Jones et al. 1998) and the 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 stresses the system (Hoegh-Guldberg 1999); importantly, light is still the proximate stressor. Therefore, we omitted temperature from the model to maintain a desired level of simplicity, while still allowing photooxidative stress and bleaching to be simulated with biological realism in response to light.

Below we describe the formulation of each flux in the model.

Table 1. Model fluxes (mass-specific)

Symbol	Description	Units	Eq. no.
j_X	Prey uptake rate	molX $CmolH^{-1}$ d^{-1}	3
j_N	Nitrogen uptake rate	molN $CmolH^{-1}$ d^{-1}	4
j_{HG}	Host biomass formation rate	CmolH $CmolH^{-1}$ d^{-1}	5
r_{NH}	Recycled nitrogen from host turnover	molN $CmolH^{-1}$ d^{-1}	6
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}	8
j_{CO_2}	CO_2 input to photosynthesis	molCO_2 $CmolH^{-1}$ d^{-1}	9
j_L	Light absorption rate	molph $CmolS^{-1}$ d^{-1}	11
r_{CH}	Recycled CO_2 from host turnover	molCO_2 $CmolH^{-1}$ d^{-1}	12
r_{CS}	Recycled CO_2 from symbiont turnover	molCO_2 $CmolS^{-1}$ d^{-1}	13
j_{CP}	Photosynthesis rate	molC $CmolS^{-1}$ d^{-1}	14
j_{eL}	Light energy in excess of photochemistry	molph $CmolS^{-1}$ d^{-1}	15
j_{NPQ}	Total capacity of NPQ	molph $CmolS^{-1}$ d^{-1}	16
c_{ROS}	ROS production proportional to baseline	–	17
r_{NS}	Recycled nitrogen from symbiont turnover	molN $CmolS^{-1}$ d^{-1}	18
j_{SG}	Symbiont biomass formation rate	CmolS $CmolS^{-1}$ d^{-1}	19
ρ_C	Fixed carbon shared with host	molC $CmolS^{-1}$ d^{-1}	20
j_{ST}	Symbiont turnover rate	CmolS $CmolS^{-1}$ d^{-1}	21

Table 2. Model parameters. Derivations of each parameter value along with supporting references are provided in the Supplementary Information.

Symbol	Description	Units	Value
n_{NH}	N:C molar ratio in host biomass	–	0.18
n_{NS}	N:C molar ratio in symbiont biomass	–	0.13
n_{NX}	N:C molar ratio in prey biomass	–	0.2
j^0_{HT}	Specific turnover rate of host biomass	CmolH $CmolH^{-1}$ d^{-1}	0.03
j^0_{ST}	Specific turnover rate of symbiont biomass	CmolS $CmolS^{-1}$ d^{-1}	0.03

Symbol	Description	Units	Value
σ_{NH}	Proportion host N-turnover recycled to host	–	0.9
σ_{CH}	Proportion host C-turnover recycled to photosynthesis	–	0.1
σ_{NS}	Proportion symbiont N-turnover recycled to symbiont	–	0.9
σ_{CS}	Proportion symbiont C-turnover recycled to photosynthesis	–	0.9
j_{Xm}	Maximum specific feeding rate of host	molX CmolH^{-1} d^{-1}	0.13
K_X	Half-saturation constant for prey uptake by host	molX L^{-1}	1.95×10^{-5}
j_{Nm}	Maximum specific DIN uptake rate by host	molN CmolH^{-1} d^{-1}	0.035
K_N	Half-saturation constant for DIN uptake by host	molN L^{-1}	1.5×10^{-6}
k_{CO_2}	Efficacy of CO_2 delivery by host CCMs	molCO$_2$ molC^{-1}	10
j_{HGm}	Maximum specific growth rate of host	CmolH CmolH^{-1} d^{-1}	1
y_{CL}	Quantum yield of photosynthesis	molC mol ph^{-1}	0.1
$\bar{a}^*$	Effective light-absorbing cross-section of symbiont	m^2 CmolS^{-1}	1.34
k_{NPQ}	NPQ capacity of symbiont	mol ph CmolS^{-1} d^{-1}	112
k_{ROS}	Excess photon energy that doubles ROS production, relative to baseline levels	mol ph CmolS^{-1} d^{-1}	80
j_{CPm}	Maximum specific photosynthesis rate of symbiont	molC CmolS^{-1} d^{-1}	2.8
j_{SGm}	Maximum specific growth rate of symbiont	CmolS CmolS^{-1} d^{-1}	0.25
b	Scaling parameter for strength of bleaching response	–	5

State equations

The balance equations for symbiont (S) and host (H) biomass are expressed as:

$$\frac{dS}{Sdt} = j_{SG} - j_{ST} \tag{1}$$

$$\frac{dH}{Hdt} = j_{HG} - j^0_{HT} \tag{2}$$

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 per day). 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:

$$j_X = \frac{j_{Xm} \cdot X}{X + K_X} \tag{3}$$

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 arrangment 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:

$$j_N = \frac{j_{Nm} \cdot N}{N + K_N} \tag{4}$$

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

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

where ρ_C is fixed carbon shared by the symbiont (see Eq. 20), and r_{NH} is recycled nitrogen liberated by host biomass turnover:

$$r_{NH} = \sigma_{NH} n_{NH} j^0_{HT} \tag{6}$$

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[1] of the SU) is then made available to the symbiont:

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

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

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

This flux, j_{eC}, is assumed to be available to the host as a respiratory substrate to support various energetically-demanding processes; of particular importance is the host's active carbon concentrating mechanisms (CCMs) that supply CO_2 for symbiont photosynthesis (Wooldridge 2013; Hopkinson, Tansik, and Fitt 2015). We therefore specify j_{CO_2} as the host-mediated delivery of CO_2 to photosynthesis 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 active CCMs require energetic input by the host, we define j_{CO_2} as proportional to j_{eC}, assuming that some of this carbon is respired to energize the CCMs. This formulation means that the symbiont indirectly ensures its own CO_2 supply by providing fixed carbon (=energy) 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 active input of CO_2 to the photosynthesis SU is therefore specified as:

$$j_{CO_2} = k_{CO_2} j_{eC} \tag{9}$$

[1] Rejection fluxes must always be positive, and hence are specified with the notation $(x)_+$, which means $max(x, 0)$.

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:

$$A = 1.26 + 1.39 \cdot \exp(-6.48 \cdot \frac{S}{H}) \tag{10}$$

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:

$$j_L = A \cdot L \cdot \bar{a}^* \tag{11}$$

CO_2 arrives at the photosynthesis SU from multiple sources: in addition to the CO_2 actively supplied by the host through its CCMs (j_{CO_2}; Eq. 9), a fixed proportion of metabolic CO_2 generated by host biomass turnover is passively available to the photosynthesis SU, according to:

$$r_{CH} = \sigma_{CH} j^0_{HT} \tag{12}$$

along with a fixed proportion of CO_2 generated by symbiont biomass turnover:

$$r_{CS} = \sigma_{CS} j^0_{ST} \tag{13}$$

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

$$j_{CP} = \left(\frac{1}{j_{CPm}} + \frac{1}{y_{CL} j_L} + \frac{1}{(j_{CO_2} + r_{CH})\frac{H}{S} + r_{CS}} - \frac{1}{y_{CL} j_L + (j_{CO_2} + r_{CH})\frac{H}{S} + r_{CS}} \right)^{-1} \cdot c^{-1}_{ROS} \tag{14}$$

where j_{CPm} is the maximum specific rate of photosynthesis, and c_{ROS} is the relative rate of reactive oxygen species production (see Eq. 17). 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 (Fig. S2).

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

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

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 total NPQ capacity specified as a parameter of the symbiont (k_{NPQ}). The NPQ flux j_{NPQ} is then specified as a single-substrate SU formula with a maximum of k_{NPQ}:

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

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}, which takes a value of 1 when all light energy

is quenched by photochemistry and NPQ, and increases as the amount of excess excitation energy increases, specified as:

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

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 after accounting for quenching by carbon fixation and NPQ. A direct consequence of this formulation is that CO_2-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}; Eq. 14) is then combined with nitrogen shared by the host (ρ_N; Eq. 7) and nitrogen recycled from symbiont biomass turnover

$$r_{NS} = \sigma_{NS} n_{NS} j^0_{ST} \tag{18}$$

to build new symbiont biomass, following the SU equation:

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

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:

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

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^0_{ST}, representing fixed maintenance costs, plus a component that scales with the magnitude of ROS production.

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

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 (rNS and rCS) only occurs based on the maintenance component of turnover (i.e., j^0_{ST}), and not the photodamage/bleaching component, as this loss represents biomass that is damaged or expelled from the host.)

Numerical analysis

The model dynamics are specified by the differential equations (1-2) that impose biomass balance for host and symbiont and by a set of coupled non-linear algebraic equations (3-21) that define fluxes. Several of these fluxes are defined *implicitly*; for example, the rejection fluxes of carbon and nitrogen from the symbiont and host biomass SUs, respectively, act as reciprocal input fluxes to the other SU. Similarly, the photosynthesis SU receives CO_2 at a rate 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 through photoinhibition. Without further assumptions, however, the dynamical system is not always unambiguously defined because for some combinations of parameters and environmental forcing functions the system of algebraic equations has more than one solution with all fluxes non-negative (see results below). In such circumstances, the right hand side of the differential equations (1) and (2) is not uniquely defined even when S and H are specified. We resolved this problem by

defining the dynamical system as the limit as a time step $\Delta t \to 0$ of a discretized system corresponding to Euler integration of the differential equations, with those fluxes that represent flows of elemental matter implemented by assuming that transfer of material between components of the system takes one time step. Thus, for example, CO_2 rejected from the host SU at time t arrives at the photosynthesis SU at time $t + \Delta t$.

Simulations using the discretized scheme were performed using R code that is available in the data repository accompanying this article: github.com/jrcunning/Rcoral. By experimentation, we found that a time step of 0.1 days gave adequate precision for most simulations (including used to generate Figs. 2-8 in this paper). For steady state estimations, simulations were run until the change in specific growth rate of host and symbiont and the S:H biomass ratio was less than 1e-5 per time step. In regions of state space where very slow transient dynamics could be expected (i.e. near bifurcation points), sample steady state calculations were verified using MATHEMATICA code for numerical root finding (function FindRoot) with the code written independently by a coauthor without reference to the R code.

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 using the formula

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

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 Cmol Cmol^{-1} d^{-1}.

Steady state behavior

In a constant environment, the system ultimately reaches a steady state of exponential growth or decline. However, under some conditions, either of these outcomes may occur depending on initial values of symbiont and host biomass, indicating the presence of alternate stable states, corresponding to either positive or negative growth (Fig. 2). The mechanism that produces these alternate stable states is the positive feedback between carbon-limitation of the host and CO_2-limitation of photosynthesis: if symbiont biomass is initially very low (i.e., a "bleached" coral), the system cannot escape this positive feedback and cannot grow. However, if symbiont biomass is initially high (i.e., a "healthy" coral), then the system remains in a nitrogen-limited state with positive growth. For practical purposes, this section of the manuscript considers only positive growth steady states under constant environments; subsequently, we explore how environmental forcing may cause the system to switch between alternate stable states, which we interpret in the context of coral bleaching (see "Coral Bleaching and Recovery", below).

To analyze positive-growth steady state behavior, we ran the model to steady state across gradients of external irradiance and nutrients (Fig. 3), which revealed patterns consistent with observed phenomena in corals. Predicted growth rates are low at low light and DIN (~0.01 d^{-1}), and begin increasing as both of these factors increase (Fig. 3A). Low light limits photosynthetic rates, resulting in less fixed carbon shared with the host and an associated increase in the symbiont to host biomass ratio (Fig. 3B). 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, host growth becomes less carbon-limited.

Similarly, increasing DIN alleviates nitrogen-limitation (Fig. 3A). 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., ~3-4 µM in these simulations) has little effect on growth as carbon becomes limiting. 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 µM) (Ferrier-Pagès et al. 2000). In addition to increasing growth, DIN also increases the symbiont to host biomass ratio (Fig. 3B), a phenomenon also observed in reef corals (Marubini and Davies 1996). At low DIN and intermediate light, more typical of coral reef environments, symbiont to host

biomass ratios are around ~0.06-0.21, which is consistent with values reported in the literature (Muscatine, R McCloskey, and E Marian 1981; Edmunds et al. 2011; Hawkins et al. 2016).

The maximum predicted growth rates of ~0.1 d^{-1}, occurring between ~10-25 mol photons m^{-2} s^{-1} light and ~4 µM DIN (Fig. 3A), are comparable to the rate of 0.07 d^{-1} measured by Tanaka et al. (2007) under similar N-enriched conditions. Predicted growth rates under conditions more typical of reef environments (<0.5 µM DIN) are ~0.01-0.03 d^{-1}. Observed specific growth rates, which are typically based on skeletal mass, fall near or below 0.01 d^{-1} (Osinga et al. 2011; Osinga et al. 2012), though values as high as 0.025 d^{-1} have been reported (Schutter et al. 2010). It is not surprising that predicted growth rates are slightly higher than most observations, as the model does not account for external ecological factors that may reduce growth, such as competition, predation, and bioerosion. Furthermore, the model does not explicitly account for skeletal formation, which may not always correlate with biomass growth, potentially due to differential substrate-limitation (Anthony 2002). Nevertheless, when growth of coral tissue biomass has been directly measured over short periods, values are consistent with model predictions (e.g., 0.07 d^{-1} in Tanaka et al. (2007)), and similar rates (0.04 d^{-1}) have been measured in *Aiptasia diaphana*, a non-calcifying symbiotic anemone (Armoza-Zvuloni et al. 2014).

As irradiance continues to increase above ~25 mol photons m^{-2} d^{-1}, growth rates decline until positive growth ceases above ~40 µmol photons m^{-2} d^{-1} (Fig. 3A). The mechanism underlying this decline is the increase in light energy beyond the capacities 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. 3B), 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. 3B) and eventual cessation of growth (Fig. 3A).

The incorporation of photooxidative 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. 3). 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). By incorporating these impacts of light stress, the model predicts greater, and more realistic, 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 the boundary set by photooxidative stress on a stable symbiosis under steady state conditions (Fig. 3) may be temporarily crossed by a dynamic system, which may 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 (see "Dynamic behavior").

Sensitivity analysis

The values used for each parameter in the model (Table 2) are derived from relevant literature; these derivations are described in the Supplementary Information. Here we evaluate the sensitivity of the model to changes in these parameter values, which also serves to demonstrate the behavior of the dynamical system. We measured fractional change in steady state values in response to fractional changes in parameter values, relative to their default values, under environmental conditions typical of coral reefs.

Overall, relative changes in the steady state of the system are less than the equivalent relative change in parameter value, indicating that the system maintains internal stability. However, changes in certain parameter values have more significant impacts: increasing j_{Nm} or decreasing K_N both dramatically increase host growth (Fig. 4), demonstrating the strong nitrogen-limitation that characterizes these symbioses. The parameter $\bar{a}^*$ has a strong impact on S:H biomass ratios (Fig. 4) since this parameter determines the amount of light absorbed by symbionts, with lower values increasing light-limitation. Increasing the maximum growth and turnover rates have the expected effects of increasing and decreasing growth, respectively. Parameters relating to photooxidative stress and bleaching have little impact under these environmental conditions (Fig. 4), but have larger impacts

under higher light (e.g., Fig. S6). Sensitivity analyses conducted under different combinations of external light and nutrients are presented in Figs. S3-S7.

Dynamic behavior

The dynamic behavior of the model demonstrates its power to integrate multiple environmental forcings simultaneously. Here we present several scenarios that demonstrate the model's ability to reproduce complex phenomena that have been observed in corals.

Seasonal variability

Symbiont densities and coral growth rates are known to vary seasonally, representing an integrated response to changes in a suite of environmental factors. Light in particular is a strong driver of these trends (Stimson 1997; Brown et al. 1999; Fagoonee et al. 1999; Fitt et al. 2000), with high light associated with lower symbiont abundance and reduced tissue biomass. The role of light in driving seasonal changes in symbiont density was demonstrated nicely by Stimson (1997), who also found that experimental nutrient-enrichment amplified the light-driven seasonal oscillation. Using the levels of light and nutrients from this study as inputs, the model reproduces this observed interaction among environmental factors (Fig. 5), and also provides the mechanism: under high light in summer, photooxidative stress decreases symbiont biomass and increases carbon-limitation of host growth regardless of nutrient status; when light is reduced in winter, growth and symbiont biomass become constrained instead by nitrogen, and therefore increase more when DIN is enriched (Fig. S8).

The prediction of higher growth when light is reduced indicates that growth is not limited by low light in winter, but is actually reduced by excess light in summer, consistent with the experimental findings of Schutter et al. (2011). Seasonal summertime reductions in tissue biomass have also been well-documented in the field (Fitt et al. 2000), along with reductions in net photosynthetic capacity (Muller-Parker 1987). Importantly, while light alone (at these levels) may drive seasonal dynamics in the ways discussed, temperature fluctuations may attenuate or even reverse the effect of light as cooler winters depress metabolism; thus, the relative magnitude of fluctuation in temperature, light, and other factors may produce wide variability in the direction and magnitude of seasonal changes in growth and symbiont abundance, depending on location and microhabitat. Nevertheless, the seasonal variability predicted here (Fig. 5) is consistent with experimental and field observations for corals, and demonstrates the power of this model to predict dynamic behavior that mechanistically integrates multiple environmental drivers.

Coral bleaching and recovery

Coral bleaching is the stress-induced loss of symbiotic algae from coral tissues, which can occur in response to a variety of environmental stressors. In most cases, coral bleaching is thought to begin with photooxidative stress in symbiont photosynthesis (Lesser 1997), which triggers a cascade of events leading to symbiont expulsion (Weis 2008). As symbionts are expelled, the host receives less fixed carbon, which may then compromise its ability to activate CCMs that deliver CO_2 to photosynthesis (Wooldridge 2013). Increasing CO_2-limitation for remaining symbionts, along with an amplified internal light environment due to reduced self-shading (Enríquez, Méndez, and Iglesias-Prieto 2005), may further exacerbate photooxidative stress and accelerate symbiont expulsion, driving the coral into a bleached state.

While these positive feedbacks have been discussed previously in the literature, this is the first attempt to implement and explore their properties within a dynamical model. Interestingly, these feedbacks lead to alternate stable states in the symbiotic system. The 'healthy' state is characterized by nitrogen-limitation of both symbiont and host: under these conditions, the symbiont translocates sufficient carbon to support host growth and CCMs, which ensures that photosynthesis does not become CO_2-limited. However, if carbon translocation is disrupted (and light is sufficiently high), then the system is driven into the 'bleached' state by photooxidative stress and positively reinforcing carbon- and CO_2-limitation. In this context, coral bleaching can be understood as a transition from one stable state to another, and bleaching thresholds are sets of environmental conditions that push a healthy-state coral onto a trajectory leading to a bleached state.

We are highly interested in the conditions under which the system switches from a healthy to a bleached state, and can use this model as a tool to explore this dynamic behavior. Most straightforwardly, this switch occurs when increasing external irradiance (Fig. 6A) causes sufficient ROS production (Fig. 6B) and photoinhibition (Fig. 6C) such that the positive feedbacks between host carbon-limitation (Fig. 6D) and CO_2-limitation of photosynthesis (Fig. 6E) are rapidly engaged, leading to even greater photooxidative stress and a rapid decline in S:H biomass (Fig. 6F), characteristic of coral bleaching. However, the positive feedbacks involved in bleaching are not engaged only in response to high external irradiance alone; in fact, they depend on the relative balance of light energy absorption and quenching, which in turn depends on the availability of CO_2 for photosynthesis. While previous models framed photooxidative stress as a fixed response to absolute external irradiance (Eynaud, Nisbet, and Muller 2011), our 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 a critical role of host CCMs in providing CO_2 for photosynthesis (Tansik, Fitt, and Hopkinson 2015; Hopkinson, Tansik, and Fitt 2015).

The importance of host CCM activity establishes significant interactive roles for other factors in influencing coral bleaching responses. For example, simulations of high light stress (Fig. 7) demonstrate that bleaching can be attenuated by heterotrophic feeding, a phenomenon which has been observed experimentally (Borell et al. 2008). The mechanism underlying this prediction is that feeding by the host increases host CCM activity, which delays the onset of CO_2-limitation of photosynthesis and reduces bleaching severity. On the other hand, elevated nutrients exacerbate bleaching (Fig. 7), since higher symbiont densities are more susceptible to CO_2-limitation (Wooldridge 2009). Several experimental (Wiedenmann et al. 2013; Cunning and Baker 2013; Vega Thurber et al. 2014) and correlational studies (Wooldridge and Done 2009) are consistent with this mechanistic link between high nutrients and bleaching.

Since bleaching can be understood as a transition from a nitrogen-limited state with high S:H biomass to a carbon-limited state with low S:H biomass, induced by an external stressor, recovery can be understood as a switch back to the nitrogen-limited state once the external stressor is alleviated. In natural settings, this typically occurs through seasonal declines in temperature and light. However, hysteresis associated with the system's alternate stable states indicates that the symbiosis cannot recover along the same trajectory it followed during bleaching; indeed, the stressor must be alleviated *below* the threshold that initially caused bleaching in order for the system to recover (Fig. 2). This is because under the same external conditions, a bleached coral with low S:H biomass (relative to a healthy coral with high S:H biomass) is characterized by greater light amplification and weaker CCM activity, which enhance photooxidative stress and serve to maintain the carbon-limited state. In order for the system to recover, the stressor must be reduced enough such that photooxidative stress ceases and translocation of carbon from symbiont to host is resumed. Once this occurs, the host can energize its CCMs, which further enhances carbon fixation and accelerates the system back toward a nitrogen-limited state, indicative of recovery. The conditions under which recovery can occur – which determine the magnitude of hysteresis (Fig. S9) – depend on the relative abundance of nitrogen and carbon in the environment. Higher food levels, representing a non-autotrophic carbon source for the host, make it easier for the host to overcome carbon-limitation, thus providing a potential mechanism underlying observations that feeding aids recovery from bleaching (Grottoli, Rodrigues, and Palardy 2006; Connolly, Lopez-Yglesias, and Anthony 2012). Conversely, high external DIN impedes the re-establishment of nitrogen-limitation, making recovery from bleaching more difficult (i.e., narrowing the sets of conditions under which recovery is possible).

Dynamic simulations of recovery reveal another interesting behavior of the system: under some conditions, an 'overshoot' occurs in which S:H biomass temporarily increases beyond the ratio maintained in the 'healthy' state, before returning to stabilize at this value (Fig. 8). In fact, unusually high symbiont densities have been observed following bleaching in both experimental (Cunning, Silverstein, and Baker 2015) and field studies (Kemp et al. 2014), and have been interpreted as a potential 'disequilibrium in host-symbiont regulation' (Kemp et al. 2014). The model reveals the dynamics of this 'overshoot' as follows: as symbionts repopulate the host, photosynthesis becomes increasingly CO_2-limited due to weak CCM activity of the carbon-limited host. Thus, although symbiont growth is not yet carbon-limited, a growing symbiont population has less and less excess carbon (per symbiont) to share, and is thus moving toward carbon-limitation. Meanwhile, because S:H biomass is increasing, the host receives more and more carbon per unit host biomass, and is thus moving away from carbon-limitation. If the host overcomes carbon-limitation *before* the symbiont reaches it, then the system rapidly transitions to the nitrogen-limited state and the S:H ratio stabilizes without an overshoot (Fig. 8A). However, if

the symbiont becomes carbon-limited first (Fig. 8B, 8C), then carbon translocation per symbiont declines further and photosynthesis becomes more CO_2-limited, which maintains carbon-limitation of the host. In this situation, continued growth of less and less productive symbionts drives S:H biomass to a much higher level before the host finally overcomes carbon-limitation. At this point, representing the peak of the overshoot, the transition to nitrogen-limitation finally takes place and the S:H biomass ratio declines and stabilizes as positive growth is resumed.

Whether this 'overshoot' occurs or not represents a bifurcation point in the dynamical system that is defined by the relative availability of carbon and nitrogen to the host – any factor that enhances carbon-limitation of host growth (e.g. high DIN and/or low feeding) therefore magnifies the overshoot and prolongs the dysfunctional, carbon-limited state of the symbiosis (Fig. 8). On the other hand, factors that favor nitrogen-limitation, such as low external DIN and/or high feeding rates, will accelerate the re-establishment of nitrogen-limitation and prevent an overshoot from occurring at all. While many scenarios are possible under different environmental conditions, we illustrate the general effects of varying N and C availability on recovery from bleaching with a series of simulations that vary the N:C ratio of host's heterotrophic food source (Fig. 8A-C): lower N:C ratios (effectively representing lower DIN and/or higher heterotrophy) favor nitrogen-limitation and more rapid recovery, while higher N:C ratios (effectively representing higher DIN and/or lower heterotrophy) favor carbon-limitation and prolonged recovery with a larger overshoot in S:H biomass.

These dynamics reveal that the re-establishment of nitrogen-limitation is the most important diagnostic of recovery to a 'healthy' state, as this is when positive growth rates are resumed. A high S:H biomass ratio alone does not necessarily indicate that a 'healthy' state has been reached, since the C-limited state may still persist (e.g., Fig. 8B, 8C). This could explain why corals that have recovered their symbiont populations after bleaching may still exhibit energetic deficits and physiological impacts for much longer periods of time (Levitan et al. 2014, Hughes and Grottoli (2013)). Therefore, host acquisition of carbon from a source other than the symbiont may be extremely important for the system to recover from bleaching. Indeed, host feeding has been shown to promote a more rapid return to pre-bleaching levels of key physiological parameters in recovering corals (Connolly, Lopez-Yglesias, and Anthony 2012). The model predicts that acquisition of carbon from other sources, such as direct uptake of DOC (Levas et al. 2015), may also promote more rapid recovery from a bleached state.

Conclusions

This simplified dynamic bioenergetic model of coral-*Symbiodinium* symbioses mechanistically reproduces patterns in steady-state coral growth and symbiont abundance commonly observed in corals, including higher symbiont abundance with higher nutrients and feeding, lower symbiont abundance with increasing light, and optimal growth at intermediate light levels. Moreover, the model reproduces complex dynamic behaviors including seasonal changes in symbiont density at different nutrient levels, rapid bleaching above a threshold of high light, mitigation of bleaching by heterotrophic feeding, exacerbation of bleaching by elevated nutrients, and an overshoot of symbiont density during recovery from bleaching. These examples demonstrate the model's ability to integrate multiple environmental forcing functions to reproduce complex responses; meanwhile, the diversity of these phenomena suggest the model has captured many of the important features of the system in a unifying mechanistic framework. This model also provides a new conceptual framework for considering coral bleaching as a transition to an alternate stable state, which has important implications for understanding the performance and maintenance of symbiotic interactions. In this context, the 'healthy' stable state represents a scenario in which nitrogen-limitation stabilizes the symbiont to host biomass ratio and maintains positive growth. Conversely, carbon-limitation represents a dysfunctional state wherein positive feedbacks result in a loss of photosynthetic capacity and negative growth. Importantly, these 'control' mechanisms arise entirely passively through feedbacks present in the system.

In addition to the suite of specific examples presented here, the model can be used to explore many different dynamic environmental scenarios, and represents a tool that biologists and ecologists can use to generate hypotheses and make predictions in both experimental and natural settings. Moreover, parameter values can be modified to correspond to different genetic or functional types of coral hosts and *Symbiodinium* partners in order to evaluate variability in system responses. Thus, the diversity of potential applications for this model is high, and

we envision this work as a foundation for continued development, which may include more detailed treatments of specific modules (e.g., DIC processing), and the incorporation of more external forcing capabilities (e.g., external DIC, temperature). Importantly, this effort may be undertaken by the scientific community at large, including those with theoretical and empirical backgrounds, which is why the code for this model has been developed openly using the R language. Ultimately, the continued refinement of these tools is fundamental in elucidating the mechanisms of symbiosis function and dysfunction, and in predicting coral responses to environmental change.

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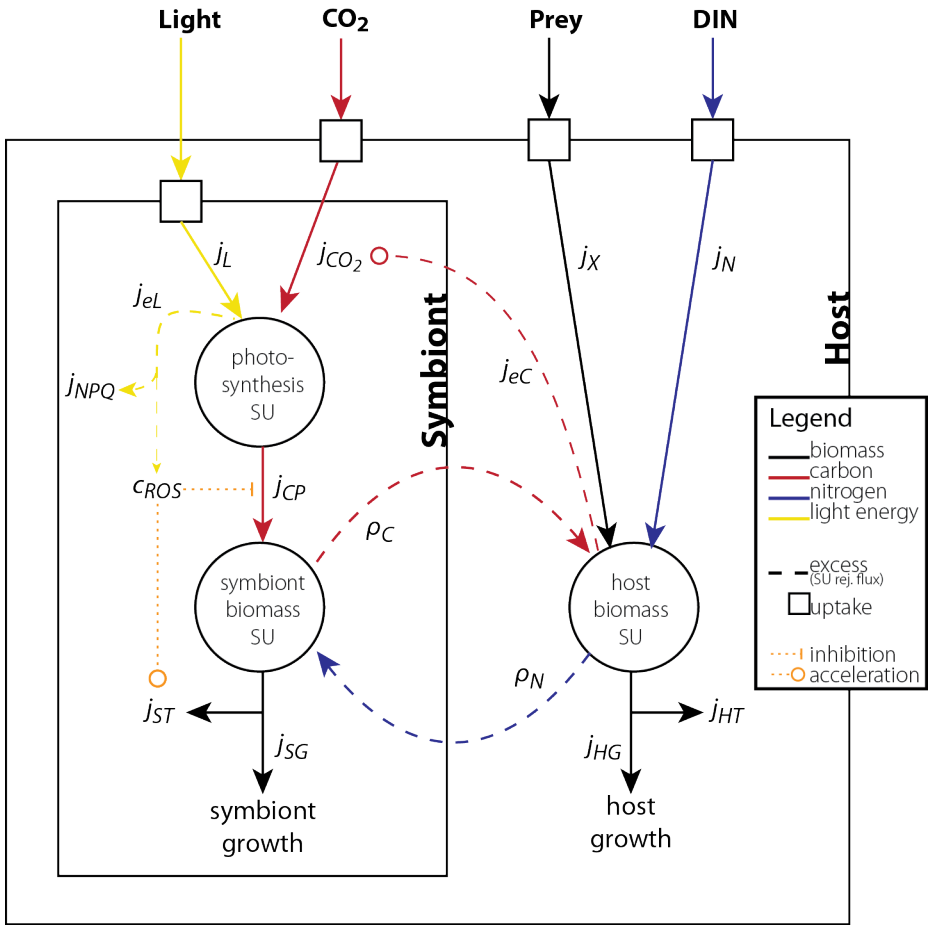

Figure 1: Graphical representation of coral-algal symbiosis model. Light, CO_2, prey, and DIN are acquired from the external environment proportional to the biomass of the partner indicated by the black box for uptake. Mass fluxes (see Table 1 for definitions) are represented by j's with subscripts indicating 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).

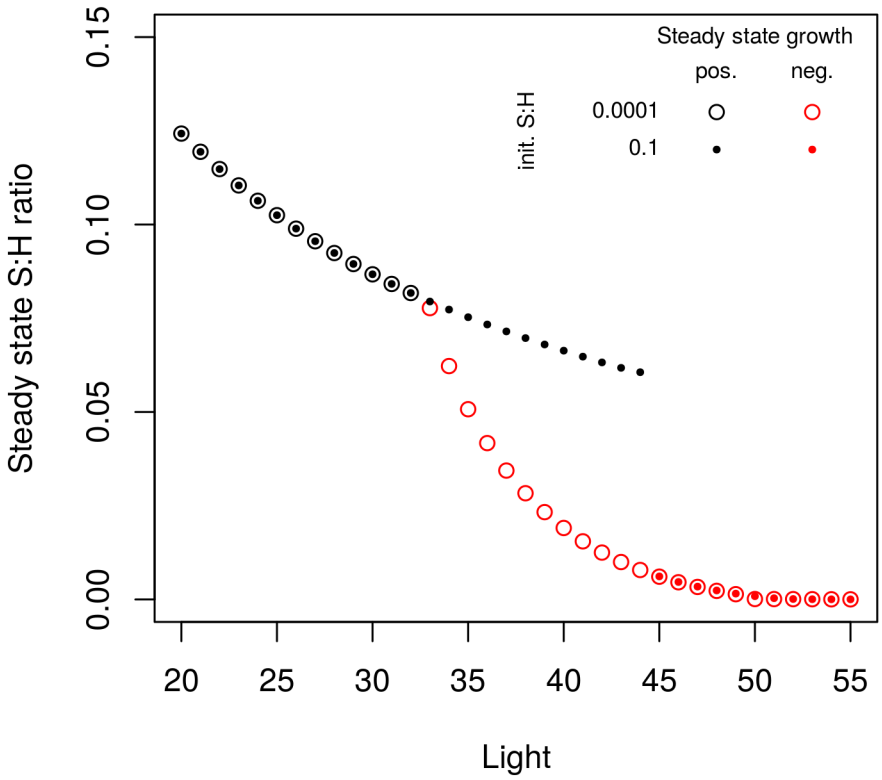

Figure 2: Alternate stable states

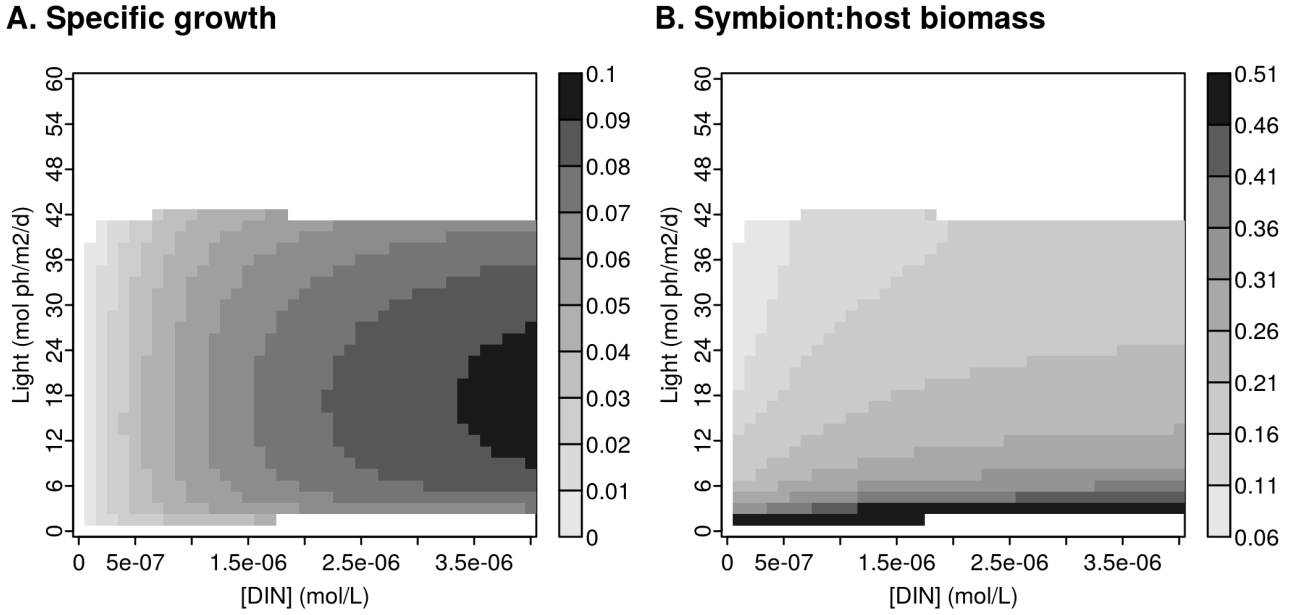

Figure 3: Steady state values of (A) specific growth (Cmol Cmol^{-1} d^{-1}) and (B) the symbiont to host biomass ratio (CmolS CmolH^{-1}) across gradients of external irradiance and dissolved inorganic nitrogen. Note that typical conditions for reefs are ~1e-7 M DIN and 10-20 mol photons m^{-2} d^{-1}. 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. All parameters were set to default values and prey density set to zero. Negative steady state growth rates, and corresponding S:H ratios, were set to zero.

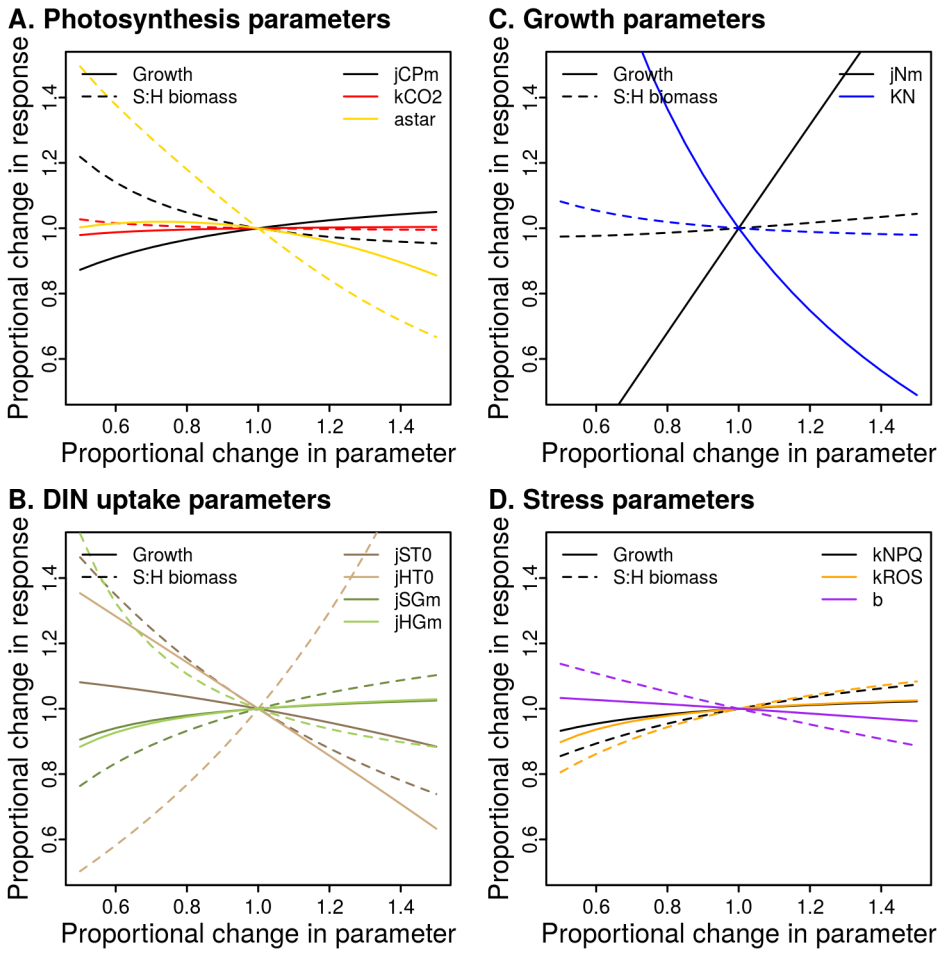

Figure 4: Sensitivity analysis. Plots show the fractional change in steady state values of growth (solid lines) and S:H biomass (dashed lines) in response to fractional changes in default parameter values (see Table 2 for default values). Parameters are grouped by which processes they are involved in. This sensitivity analysis was conducted at conditions typical for coral reef environments: low DIN (1e-7 M) and intermediate light (15 mol m^{-2} d^{-2}). Sensitivity analyses conducted other environmental conditions are presented in Figs S3-S7.

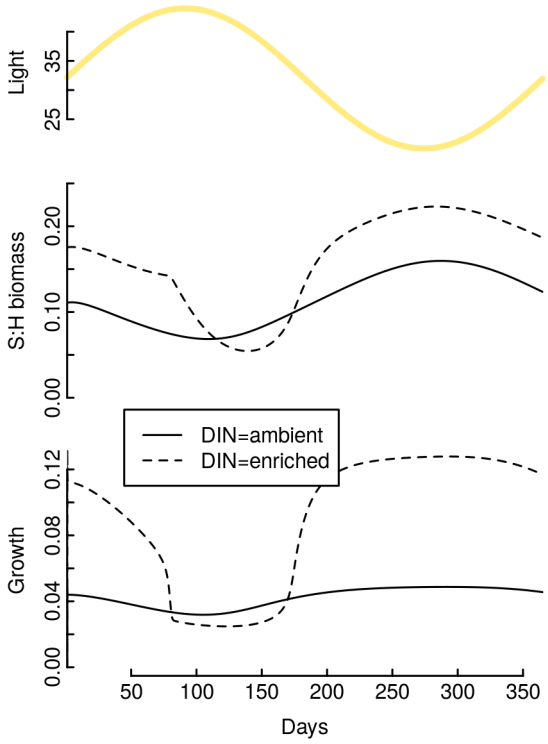

Figure 5: Light-driven seasonal dynamics of symbiont abundance and coral growth. Light input (upper panel) was designed as a sinusoidal curve with a period of one year, with maximum and minimum values of 44 and 22 mol photons m^{-2} d^{-1}, based on Stimson (1997). The dynamic behavior of symbiont to host biomass ratio (middle panel) and the specific growth rate of host biomass (lower panel) show seasonal oscillations that are greater in magnitude under higher nutrients (1e-5 molN L^{-1}; dashed lines) relative to lower nutrients (1e-7 molN L^{-1}; solid lines), consistent with the findings of Stimson (1997). Prey density was set at 1e-5 CmolX L^{-1}.

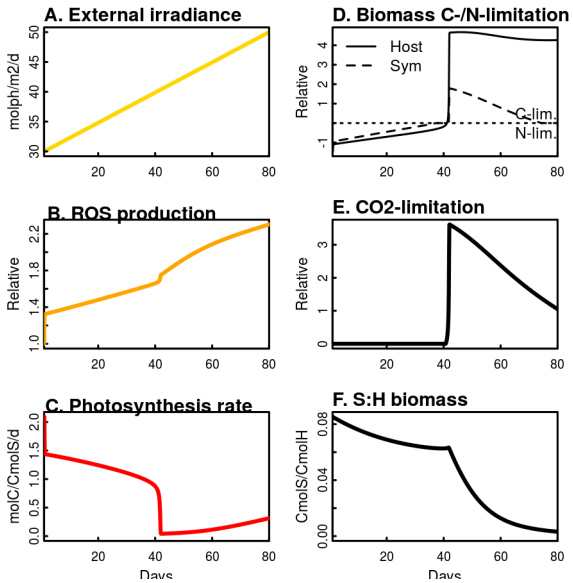

Figure 6: Coral bleaching as a switch from a nitrogen- to carbon-limited alternative stable state. This transition is demonstrated in response to gradually increasing external light (A), which causes an increase in production of ROS (B) that reduces the photosynthetic rate through photoinhibition (C). Decreasing photosynthesis moves the system from overall nitrogen-limitation toward carbon-limitation (D); when this threshold is crossed, the system rapidly becomes highly carbon-limited as photosynthesis becomes CO_2-limited (E) and symbiont densities rapidly decline (F) into a bleached state. Substrate limitation coefficients were calculated using Eq. 22. All parameters were set at default values with external DIN=1e-7 molN/L and prey density=0).

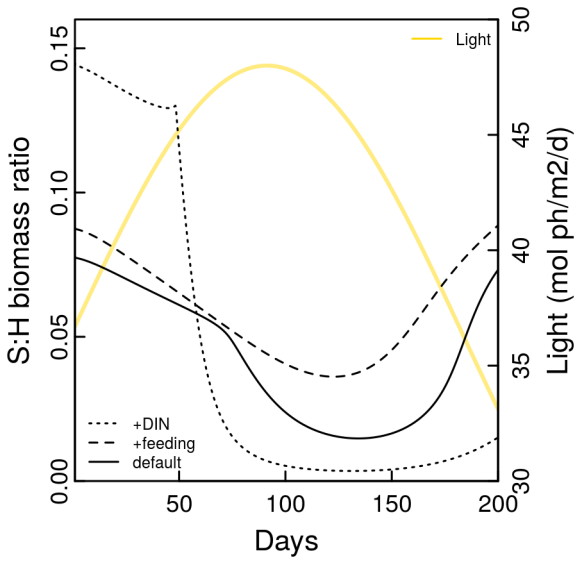

Figure 7: Bleaching with interactive factors. Simulations of high light stress (sinusoid with maximum=48 mol ph m^{-2} d^{-1}) under default environmental conditions (solid line; DIN=1e-7 molN L^{-1}; prey=3e-6 CmolX L^{-1}), or with elevated feeding (dashed line; prey=6e-6 CmolX L^{-1}), or elevated nutrients (dotted line; DIN=1e-6 molN L^{-1}). Initial symbiont biomass was set to the steady state for each set of starting conditions, respectively. (All parameters set to default values).

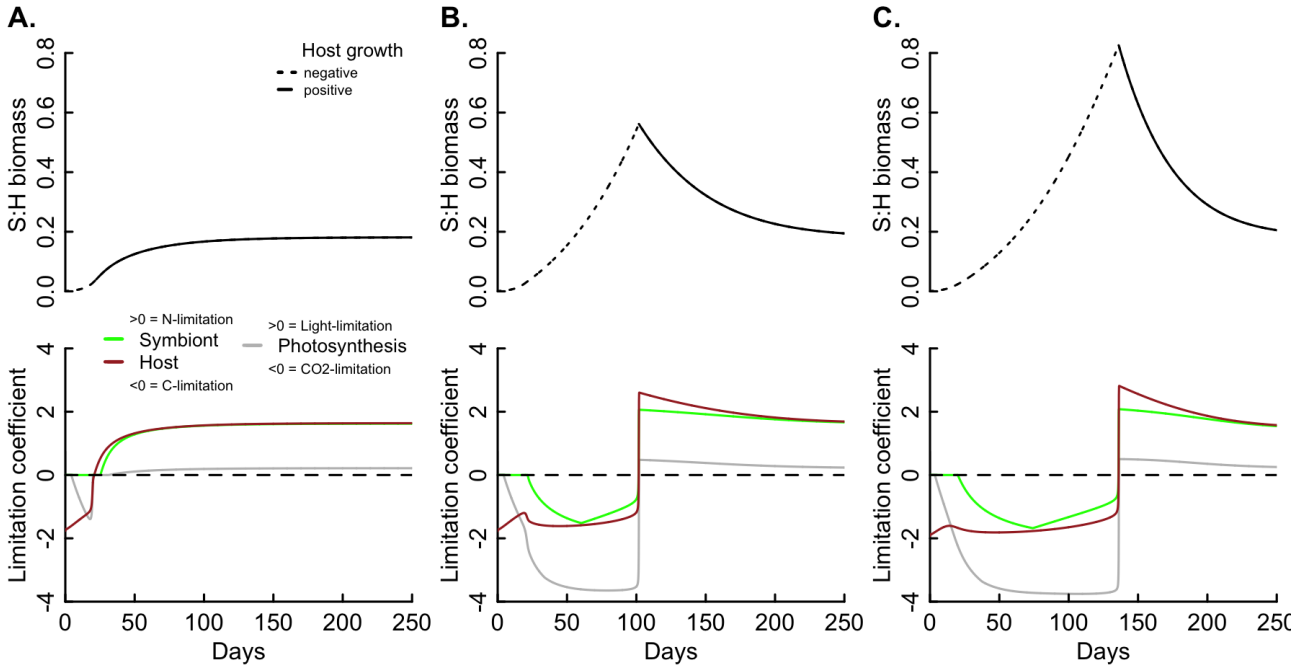

Figure 8: Recovery from bleaching with varying N:C availability (A: N:C=0.09; B: N:C=0.10; C: N:C=0.30). Higher N:C ratios in a heterotrophic food source (effectively representing higher external DIN and/or lower feeding rates) cause a larger overshoot in the S:H biomass ratio, and prolong the duration of time until the system 'recovers' by re-establishing nitrogen-limitation. Substrate limitation coefficients were calculated using Eq. 22. All simulations were run with default parameters (except varying n_{NX}), with L=10 mol photons m^2 d^{-1}, DIN=1e-7 molN L^{-1}, prey=1e-6 CmolX L^{-1}, and initial S:H biomass=0.001.