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

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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') calls for the development and application of theoretical tools. While the biological complexity of the symbiosis is well-suited to dynamical modeling, the theoretical complexity of certain approaches makes them inaccessible to many biologists, thus limiting their potential application and utility. Here, we develop a simplified dynamic bioenergetic model of coral-algal symbiosis that demonstrates realistic steady-state behavior across gradients of light, nutrients, and feeding. Furthermore, through a mechanistic treatment of photo-oxidative stress, the model displays dynamic responses of bleaching and recovery, and suggests that these phenomena represent transitions between alternative stable states. A suite of complex observed behaviors reproduced by this model suggests it has captured 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 high utility for this model in elucidating the mechanistic underpinnings of complex responses, generating testable hypotheses, and predicting integrated responses to simultaneous changes in multiple environmental inputs.

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

Environmental stress is implemented in the form of photo-oxidative 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 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 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 photophysiological stress and bleaching to be simulated with biological realism in response to light.

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

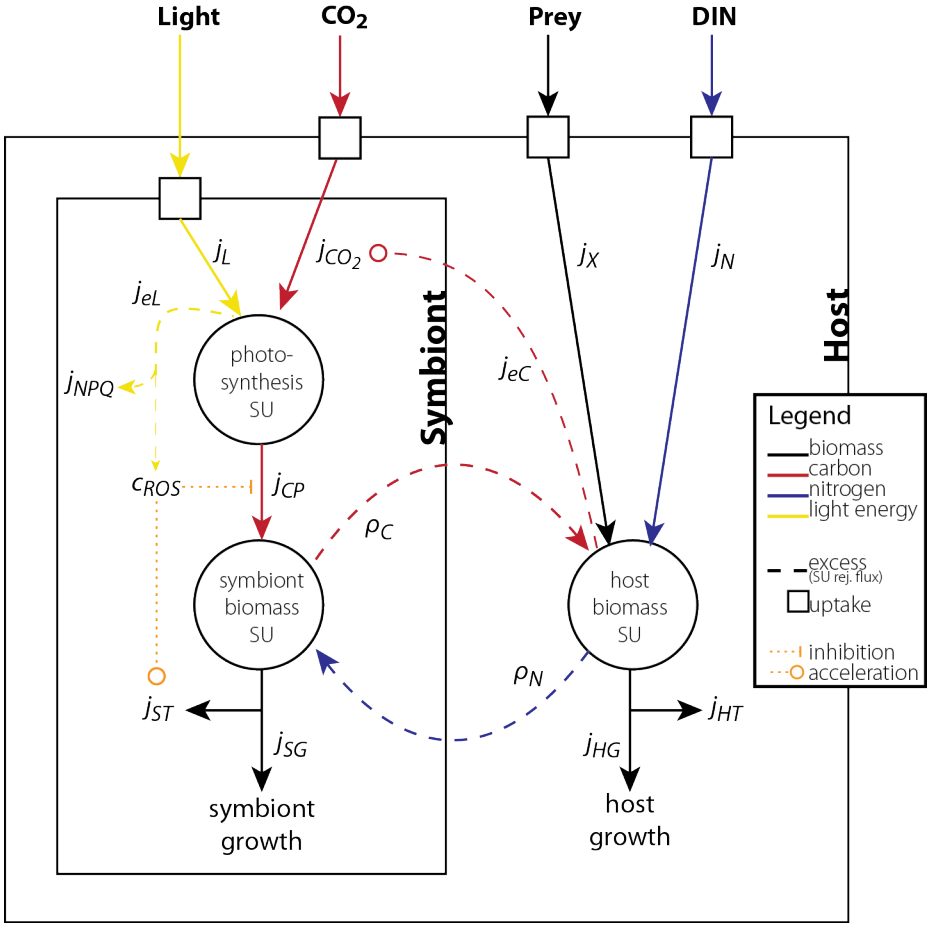
Table 1. Model fluxes

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}	
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	Units	Value
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^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
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

Symbol	Description	Units	Value
σ_{CS}	Proportion symbiont carbon turnover recycled	–	0.9
j_{Xm}	Maximum specific feeding rate of host	molX CmolH^{-1} d^{-1}	0.1292
K_X	Half-saturation constant for prey uptake by host	molX L^{-1}	20e-6
j_{Nm}	Maximum specific DIN uptake rate by host	molN CmolH^{-1} d^{-1}	0.048
K_N	Half-saturation constant for DIN uptake by host	molN L^{-1}	0.46e-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}	40-80
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 and host 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). 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 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:

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

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:

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

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

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

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

This flux, j_{eC}, is assumed to be available as a respiratory substrate to support various energetically-demanding processes; of particular importance is the host's active supply of CO_2 for symbiont photosynthesis (Wooldridge 2013; Hopkinson, Tansik, and Fitt 2015) (see below).

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:

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

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:

$$j_L = A \cdot L \cdot \bar{a}^* \tag{10}$$

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 active CCMs require energetic input by the host, the magnitude of CO_2 delivery is proportional to the amount of fixed carbon available to the host after satisfying its growth demands, 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 (=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 input of CO_2 to the photosynthesis SU is therefore specified as:

$$j_{CO_2} = k_{CO_2} j_{eC} \tag{11}$$

Additional metabolic CO_2 recycled from both the host and symbiont biomass turnover is also made available to the photosynthesis SU, according to:

$$r_{CH} = j^0_{HT} \cdot \frac{S}{H} \tag{12}$$

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

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 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:

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

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

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

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}, 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:

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

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, j_{eL}, 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}) is then combined with nitrogen shared by the host (ρ_N) and nitrogen recycled from symbiont biomass turnover

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

to build new symbiont biomass, following the SU equation:

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

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 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 imiplicitly 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:

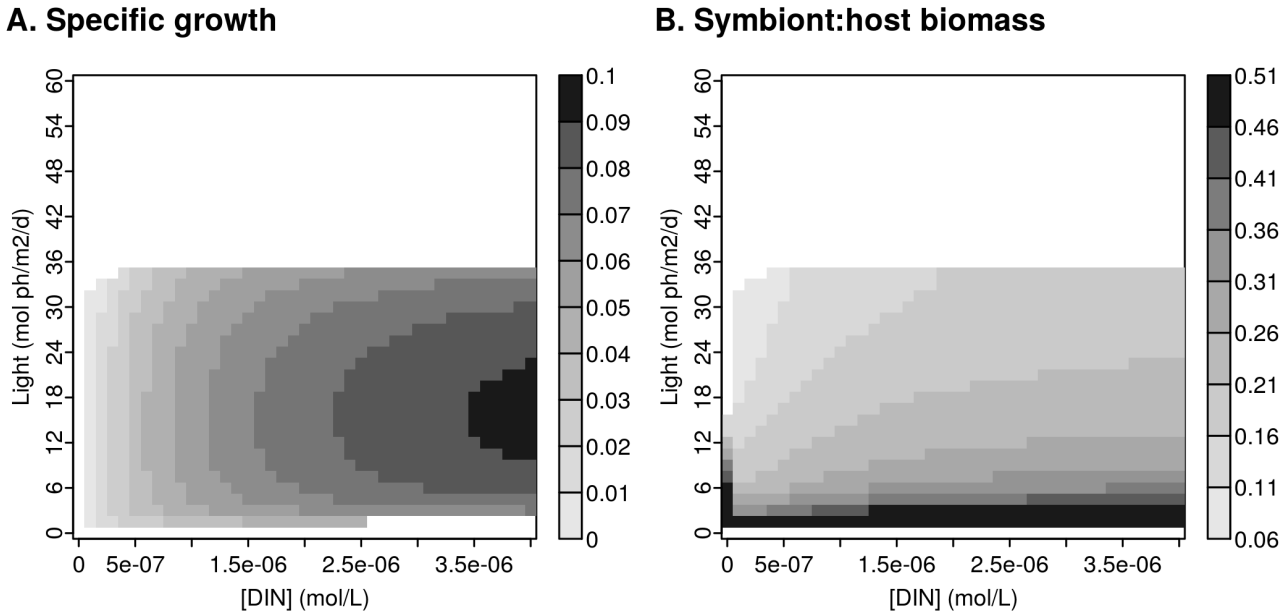
$$\log\left(\frac{\min(j_{S1}, j_{Pm})}{\min(j_{S2}, j_{Pm})}\right) \tag{22}$$

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. 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 positively reinforcing carbon-limitation 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, this section of the manuscript considers only positive growth steady states under constant environments; the subsequent "dynamic behavior" section explores how changing environments may cause the system to switch between alternate stable states, which we interpret in the context of coral bleaching.

To analyze qualitative patterns in steady state 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 (~0.01 d^{-1}), and begin increasing as both of these factors increase (Fig. 2A). 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. 2B). 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, increasing DIN up to ~2 µM alleviates nitrogen-limitation (Fig. 2A). 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. 2B), 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 ~0.1-0.3, 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 ~10-20 mol photons m^{-2} s^{-1} light and ~4 µM DIN (Fig. 2A), 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 ~20 mol photons m^{-2} d^{-1}, growth rates decline until positive growth ceases above ~35 µmol photons m^{-2} d^{-1} (Fig. 2A). 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. 2B), 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).

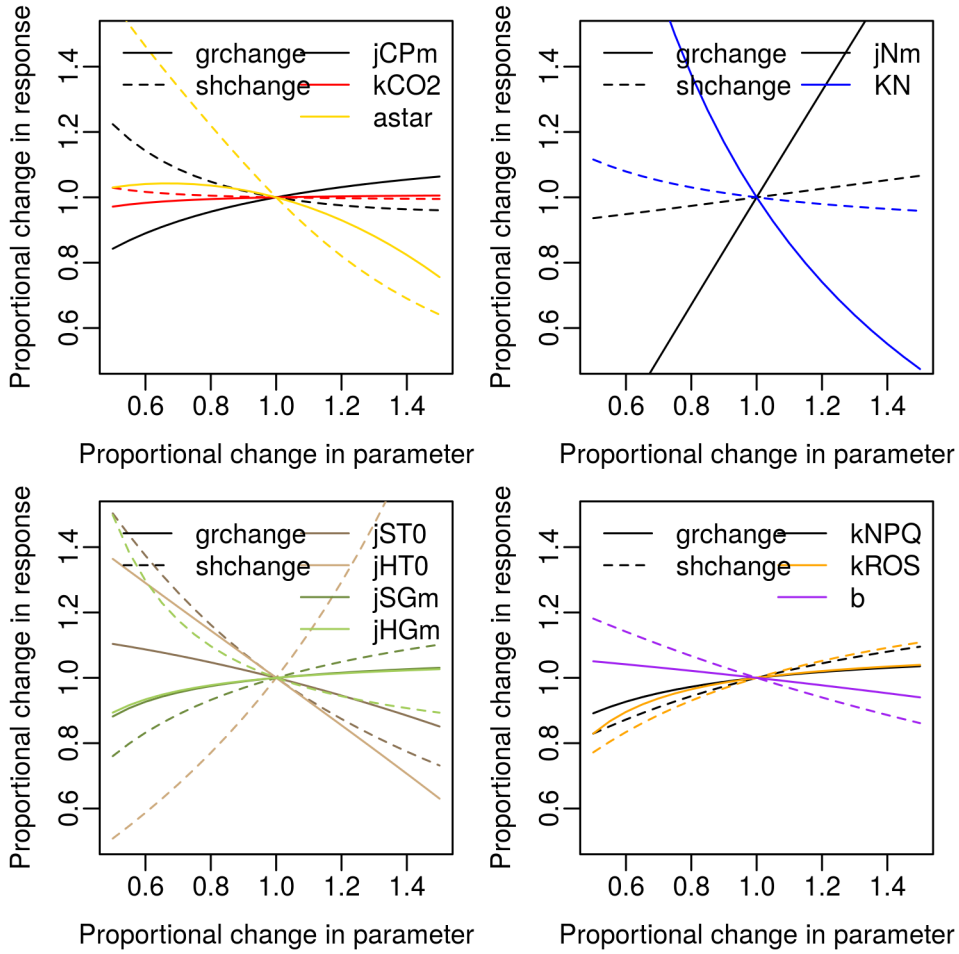
The incorporation of light stress in the model sets an upper limit to the amount of light at which a stable symbiotic

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. 2). 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 photo-oxidative stress on a stable symbiosis under steady state conditions (Fig. 2) 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

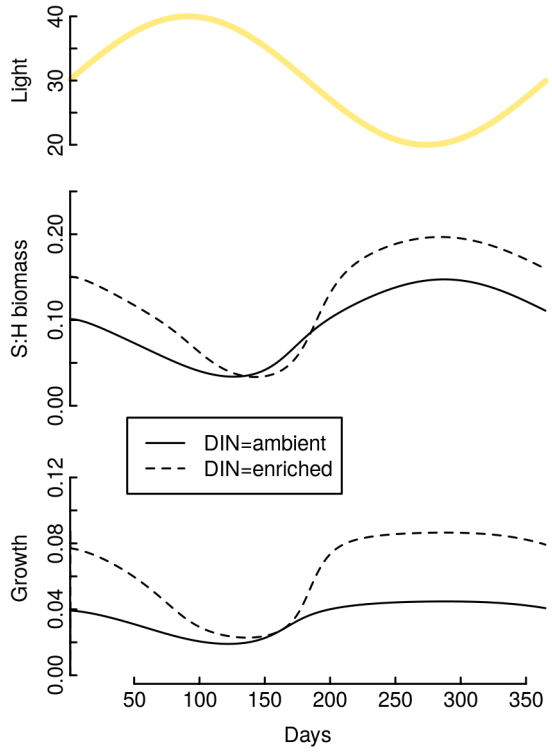
more significant impacts: increasing j_{Nm} or decreasing K_N both dramatically increase host growth (Fig. 3), demonstrating the strong nitrogen-limitation that characterizes these symbioses (REF). The parameter $\bar{a}^*$ has a strong impact on S:H biomass ratios (Fig. 3) since this parameter determines the amount of light absorbed by symbionts, with lower values increasing light-limitation. Altering maximum growth and turnover rates of symbiont and host also have expected impacts on steady states (Fig. 3). Parameters relating to photooxidative stress and bleaching have little impact under these environmental conditions (Fig. 3), but of course have larger impacts under higher light (e.g., Fig. S6). Sensitivity analyses conducted under different combinations of external light and nutrients are presented in the Supplementary Information (Figs. S3-S7)

Dynamic behavior

The dynamic behavior of the model demonstrates its power to integrate multiple environmental forcings simultaneously to produced integrated responses of the system. The potential applications of this are wide-ranging, and so the model may be highly useful for generating hypotheses about the way the system will respond to complex sets of environmental dynamics. Here we present several scenarios to highlight the power of the model and demonstrate that it can also reproduce more 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:1997p3837; 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. 4), and also provides the mechanism: under high light in summer, photoinhibition reduces symbiont biomass and leads to carbon-limitation of host growth regardless of nutrient status; when light is reduced in winter, these responses become constrained instead by nitrogen, and therefore increase more when DIN is enriched (Fig. S8).



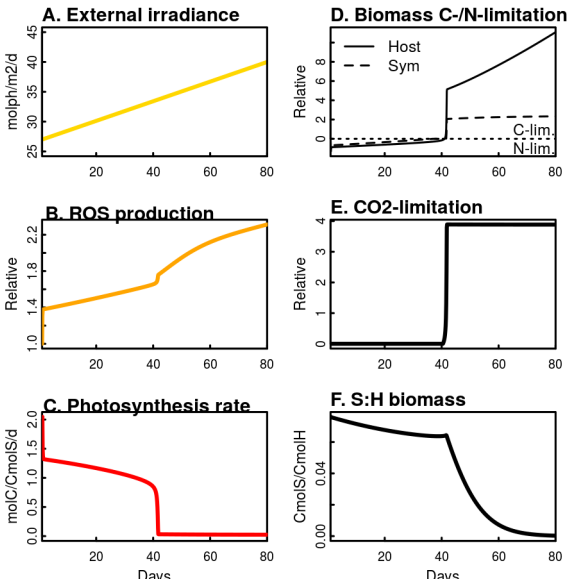
The prediction of higher growth when light is reduced indicates that growth is not limited by low light in winter, but is actually reduced by excess light in summer, consistent with the experimental findings of Schutter et al. (2011). Seasonal summertime reductions in tissue biomass have also been well-documented in the field (Fitt et al. 2000), along with reductions in net photosynthetic capacity (**???**). 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. 4) is consistent with experimental and field observations for corals, and demonstrates the power of this model to predict dynamic behavior that mechanistically integrate the impacts of multiple environmental drivers.

Coral bleaching

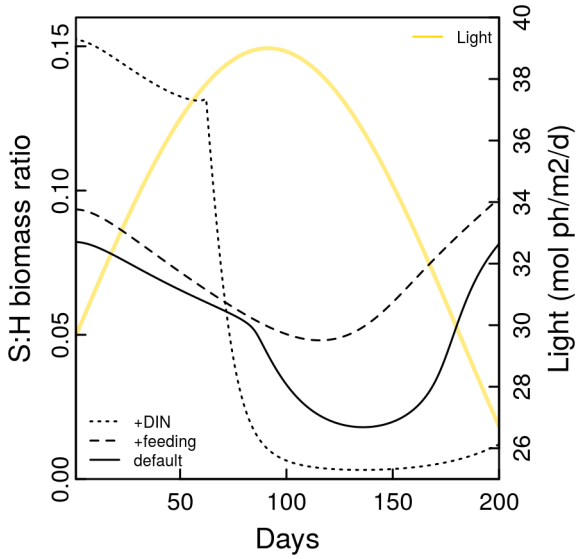
Coral bleaching is the stress-induced loss of symbiotic algae from coral tissues, which can occur in response to a variety of environmental stressors. In most cases, coral bleaching is thought to begin with photo-oxidative stress in symbiont photosynthesis (Lesser 1997), which triggers a cascade of events leading to symbiont expulsion (Weis 2008). As symbionts are expelled, the host receives less fixed carbon, which may then compromise its ability to 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 photo-oxidative 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. 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 photo-oxidative 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 stable 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 irradiance exceeds the capacity of photochemistry and NPQ, causing the production of ROS that leads to photoinhibition, photodamage, and symbiont expulsion, thereby engaging the positive feedbacks that lead to a bleached state (Fig. 5). However, the positive feedbacks involved in bleaching are not engaged only in response to high external irradiance; 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 photo-oxidative 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).

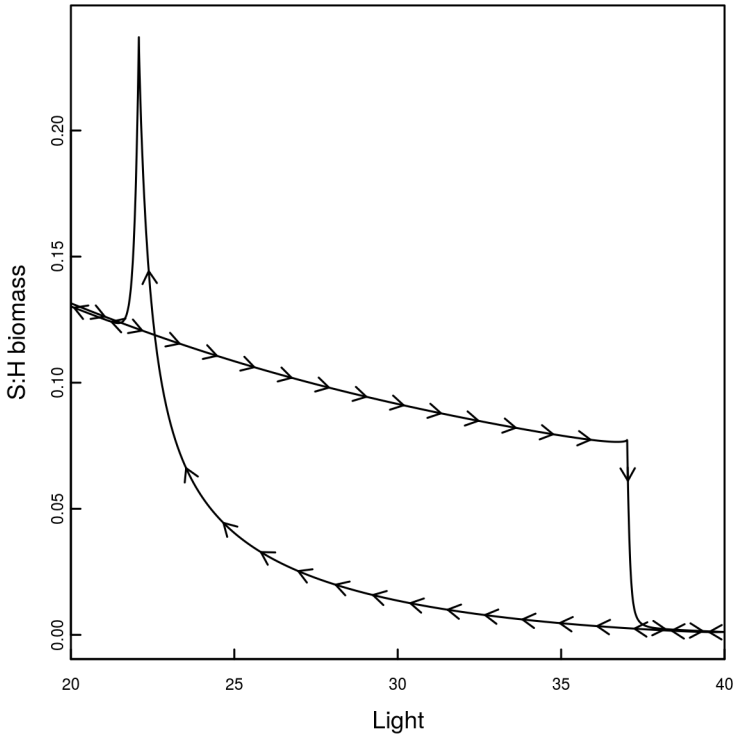


The importance of host CCM activity establishes significant interactive roles for other factors in influencing coral bleaching responses. For example, simulations of high light stress (Fig. 6) demonstrate that bleaching can be attenuated by heterotrophic feeding, a phenomenon which has been observed 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. 6), since higher symbiont densities are more susceptible to CO_2-limitation (Wooldridge 2009). Several experimental (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 represents an alternative stable state, it follows that a bleached coral cannot recover unless the external condition that induced bleaching is alleviated. In natural settings, this typically occurs by seasonal declines in temperature and light. However, due to hysteresis, a coral cannot recover along the same trajectory it followed during bleaching; indeed, the stressor must be alleviated well *below* the threshold that initially caused bleaching in order for the system to recover (Fig. 7). This is because under the same external conditions, a bleached coral (relative to a healthy one) is characterized by greater light amplification and weaker CCM activity, which serve to maintain the bleached state. The magnitude of hysteresis will depend on external nutrients and prey availability, as well as model parameters, yet the fundamental concept demonstrates a core behavior of the

system.



The hysteresis demonstrated in Fig. 7 reveals another interesting behavior of the system: during recovery from bleaching, the S:H biomass ratio reaches a higher value that 'overshoots' the level maintained in the healthy stable state. In fact, such a phenomenon has been observed in both experimental (Cunning, Silverstein, and Baker 2015) and field studies (Kemp et al. 2014) documenting recovery from bleaching, and has been interpreted as a potential 'disequilibrium in host-symbiont regulation' (Kemp et al. 2014). The model explains this 'overshoot' as an approach to a bifurcation point in the dynamical system: during recovery from the 'bleached' state, host growth is more strongly carbon-limited than symbiont growth (since the symbiont has priority access to carbon), so S:H biomass increases. S:H biomass will continue to increase beyond the alternative steady state levels as long as the symbiont remains carbon-limited; not until nitrogen becomes more strongly limiting to symbiont growth (hence forcing the symbiont to share fixed carbon with the host) will the system 'flip' back to a state of high carbon fixation and overall nitrogen-limitation that characterize a 'healthy' symbiosis. Of course, the magnitude of this 'overshoot' will depend on external nutrient concentrations and the rate of change in the stressor during recovery, though simulations predict similar magnitudes to what was observed by Kemp et al. (supp fig?).

Conclusions

The dynamic behavior of the model demonstrates its ability to mechanistically integrate multiple forcing functions, and the degree to which the system state depends not only on external forcing, but also the past history of the system. The model represents a unifying mechanistic framework that reproduces many phenomena observed in corals, suggesting it has captured many of the important features of the system in a relatively simple formulation. Furthermore, it allows the model to be used to predict responses of the system to multiple dynamic environmental forcing functions in a way that incorporates all positive and negative feedbacks. This makes the model potentially highly useful as a tool for generating hypotheses. make N, L, and X go up and down. For example, the model demonstrates and provides a mechanistic explanation for: an increase in symbiont abundance with nutrients (REF), an increase in symbiont abundance with heterotrophic feeding (refs), decrease in symbiont abundance with light (ref), optimal growth at intermediate light, rapid 'bleaching' above threshold of high light (ref) along with positive feedbacks (wooldridge, enriquez), mitigation of bleaching by heterotrophic feeding, exacerbation of

bleaching by elevated nutrients, higher standing stocks of less productive symbionts, greater seasonal change in symbiont density with elevated nutrients, overshoot of symbiont density after recovery from bleaching.

"host control"=>N-limitation. C-limitation=host has lost control of symbiosis: either bleaches or symbiont "overgrows" host with net negative growth. (when does this occur?)

In this context, nitrogen-limitation represents a scenario in which the host is 'in control' of the system: negative feedbacks stabilize the symbiont to host biomass ratio and the system maintains positive growth. Carbon-limitation represents a loss of 'control', wherein positive feedbacks result in a loss of capacity for carbon fixation and positive growth. Importantly, these 'control' mechanisms arise entirely passively through the feedbacks present in the system.

(Very low light also causes the symbiont to not share any carbon, resulting in very high S:H ratios and negative growth of the coral, which we interpret as a dysfunctional (and impossible) condition.)

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