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A mechanistic model of coral bleaching due to temperature-mediated light-driven reactive oxygen build-up in zooxanthellae

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ABSTRACT

Mass coral bleaching has emerged in the 21st century as the greatest threat to the health of the world's reefs. A sophisticated process understanding of bleaching at the polyp scale has now been achieved through laboratory and field studies, but this knowledge is yet to be applied in mechanistic models of shelf-scale reef systems. In this study we develop a mechanistic model of the coral-symbiont relationship that considers temperature-mediated build-up of reactive oxygen species due to excess light, leading to zooxanthellae expulsion. The model explicitly represents the coral host biomass, as well as zooxanthellae biomass, intracellular pigment concentration, nutrient status, and the state of reaction centres and the xanthophyll cycle. Photophysiological processes represented include photoadaptation, xanthophyll cycle dynamics, and reaction centre state transitions. The mechanistic model of the coral-symbiont relationship is incorporated into a ~1 km resolution coupled hydrodynamic – biogeochemical model that encompasses the entire ~2000 km length of the Great Barrier Reef. A simulation of the 2016 bleaching event shows the model is able to capture the broadscale features of the observed bleaching, but fails to capture bleaching on offshore reefs due to the model's grid being unable to resolve the bathymetry of shallow platforms surrounded by deep water. To further analyse the model behaviour, a ~200 m resolution nested simulation of Davies Reef (18°49′ S, 147°38′ E) is undertaken. We use this nested model to demonstrate the depth gradient in zooxanthellae response to thermal stress. Finally, we discuss the uncertainties in the bleaching model, which lie primarily in quantifying the link between reactive oxygen build-up and the expulsion process. Through the mechanistic representation of environmental forcing, this model of coral bleaching applied in realistic environmental conditions has the potential to generate more detailed predictions than the presently-available satellite-based coral bleaching metrics, and can be used to evaluate proposed management strategies.

1. Introduction

Coral bleaching is the expulsion of the unicellular zooxanthellae symbionts from the coral host, often leading to mortality. The link between a warming surface ocean and mass bleaching events had became obvious after the 1998 global event. It was possible in 1999 to predict from climate model simulations that the thermal tolerances of reef-building corals were likely to be exceeded every year within a few decades, and that events as severe as the 1998 event would likely become commonplace within 20 years (Hoegh-Guldberg, 1999). This 1999 prediction of an unprecedented future has eventuated in the late 2010s (Hughes et al., 2017). Thus the broadscale patterns of mass bleaching are predictable on decadal scales.

New management strategies under consideration for coral reef protection include prioritising those individual reefs that are more resilient to future threats (Hock et al., 2017). Thus it is urgent that we are able to identify reefs with lower thermal stress, or other environmental conditions such as good water clarity, that lead to greater resilience. Furthermore, active intervention strategies are being considered that include the introduction of temperature-tolerant individuals or species (Anthony et al., 2017; van Oppen et al., 2017). To predict the success of these interventions requires models of coral-symbiont bleaching dynamics that explicitly consider the tolerance-enabling trait, such as sensitivity to reactive oxygen concentration. Further these bleaching models must be applied in a realistic, spatially-resolved environmental setting to optimise deployment.

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Historically, process-based modelling of the coral-symbiont relationship has received relatively little attention compared to other aquatic ecosystem-building functional groups such as seagrass or phytoplankton (e.g. Madden and Kemp (1996), Baird et al. (2003)). This oversight is being addressed with the increasing awareness of the impacts of climate change on the coral-symbiont relationship. The coral-symbiont relationship was first modelled using a dynamic energy budget approach (Muller et al., 2009; Eynaud et al., 2011). Gustafsson et al. (2013) also explicitly modelled the coral-symbiont relationship, and included some more mechanistic process description such as diffusive limitation of nutrient uptake. Gustafsson et al. (2014) added photo-oxidative stress, and in particular the xanthophyll cycle, reaction centre dynamics and reactive oxygen build-up, to their earlier work, showing that heterotrophic feeding provided protection from temperature-enhanced photo-oxidative stress. Most recently, Cunning et al. (2017) have also shown that the balance of autotrophic and heterotrophic nitrogen sources influences the steady-state of the coral-symbiont system, where bleached or unbleached are two final states.

The process-based models of the coral-symbiont relationship cited above have been undertaken by considering one polyp in isolation, allowing comparison to laboratory experiments, but the output of these one polyp simulations are not easily compared to observations from natural coral reefs. A simplified form of the Gustafsson et al. (2013) model has been implemented in a Great Barrier Reef (GBR) scale model (Baird et al., 2016b; Mongin et al., 2016), but the dynamics of the coral themselves in this complex biogeochemical model has only been briefly analysed (Herzfeld et al., 2016). In order to understand the mass bleaching occurring on reefs around the world, and to support a range of management actions, it is necessary to apply process-based coral-symbiont models that consider temperature-mediated light-driven oxidative stress within biogeochemical/ecosystem models that are capable of predicting the time-varying light, nutrient and prey conditions of natural reef environments.

A large, multi-agency collaboration has developed the eReefs coupled hydrodynamic, sediment and biogeochemical model that simulates at multiple scales the environmental conditions of the Great Barrier Reef (Schiller et al., 2014). The project provides ~1 and ~4 km resolution hindcast and near real time simulations of hydrodynamic and biogeochemical quantities (www.ereefs.info). The models provides skilful predictions of the drivers of coral processes such as temperature, spectrally-resolved bottom light, and water column concentrations of dissolved inorganic nutrients and particulate organic matter across the entire length of the Great Barrier Reef from 2011-present (Skerratt et al., 2018). Furthermore, the eReefs project includes bespoke model generation that allows high-resolution models to be nested within the 1 km regional hindcast (RECOM - RElocatable Coastal Ocean Model).

In this paper, we develop a process-based model of the coral-symbiont relationship that considers temperature-mediated light-driven oxidative stress resulting in zooxanthellae expulsion. The model explicitly represents the coral host and the zooxanthellae biomass, pigment concentration, nutrient status, as well as the reaction centre and xanthophyll cycle dynamics. The process-based model of the coral-symbiont relationship is incorporated into the eReefs 3D coupled hydrodynamic – biogeochemical model of the Great Barrier Reef, and a simulation run of the 2016 bleaching event in the ~1 km configuration and a ~200 m Davies Reef configuration. The model behaviour is analysed at both scales, and model uncertainty discussed. Finally, with a model that captures the impact of temperature, solar radiation and water column inorganic and particulate nutrients on coral bleaching, we consider future applications in the management of the Great Barrier Reef.

2. Model description

The ultimate purpose of the mechanistic model of coral bleaching developed in this paper is to be able to predict bleaching in natural environments, and to explore the impact of interventions to reduce bleaching. This requires a model that responds to water column conditions such as nutrients, light and temperature, and produces metrics of stress such as concentration of reactive oxygen species and zooxanthellae expulsion rates.

The coral-symbiont model developed here is an extension of the coral polyp model of Gustafsson et al. (2013) and the photosystem bleaching model of Gustafsson et al. (2014). Further we have included the photoadaption model of Baird et al. (2013) and the multiple nutrient limitation microalgae model of Baird et al. (2016b). This combination of process descriptions is applied in a complex biogeochemical model of the Great Barrier Reef that has been described elsewhere (Mongin et al., 2016), and was developed in the eReefs Project (Schiller et al., 2014).

The following description of the coral-symbiont model is split into three sections: (1) the interactions between the coral host, the symbiont and the environment; (2) photoadaptation through pigment synthesis and the xanthophyll cycle; and (3) photosynthesis, reaction centre dynamics and reactive oxygen production leading to zooxanthellae expulsion.

2.1. Coral host, symbiont and the environment

The state variables for the coral polyp model (Table A.1) include the biomass of coral tissue, CH (g N m^{-2}), and the structurial material of the zooxanthellae cells, CS (mg N m^{-2}). The structurial material of the zooxanthellae, CS, in addition to nitrogen, contains carbon and phosphorus at the Redfield ratio. The zooxanthellae cells also contain reserves of nitrogen, R_N (mg N m^{-2}), phosphorus, R_P (mg P m^{-2}), and carbon, R_C (mg C m^{-2}).

The zooxanthellae light absorption capability is resolved by considering the time-varying concentrations of pigments chlorophyll a, Chl, diadinoxanthin, X_p, and diatoxanthin X_h, for which the state variable represents the areal concentration. A further three pigments, chlorophyll c_2, peridinin, and β-carotene are considered in the absorption calculations, but their concentrations are in fixed ratios to chlorophyll a. Exchanges between the coral community and the overlying water can alter the water column concentrations of dissolved inorganic carbon, DIC, nitrogen, N, and phosphorus, P, as well as particulate phytoplankton, B, zooplankton, Z, and detritus, D, where multiple nitrogen, plankton and detritus types are resolved (Table A.1).

The coral host is able to assimilate organic nitrogen either through translocation from the zooxanthellae cells or through the capture of water column organic detritus and/or plankton (Fig. 1). The zooxanthellae varies its intracellular pigment content depending on potential light limitation of growth, and the incremental benefit of adding pigment, allowing for the package effect (Baird et al., 2013). The coral tissue is assumed to have a Redfield C:N:P stoichiometry (Redfield et al., 1963), as shown by Muller-Parker et al. (1994). The

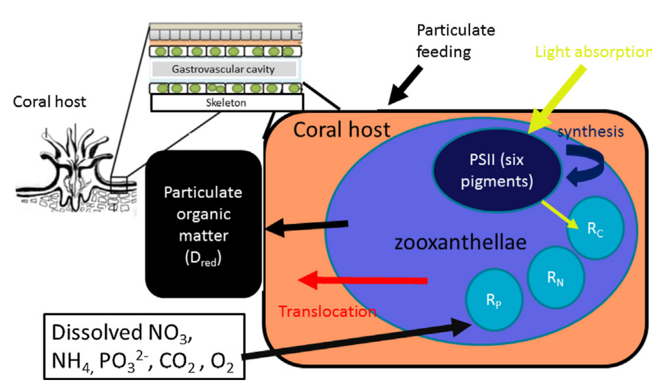

Fig. 1. Schematic showing the coral-symbiont relationship and its interaction with the overlying water column.