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Evolution of symbiosis in hermatypic corals: A model of the past, present, and future

Peter L. Antonelli[a,*], Solange F. Rutz[b], Paul W. Sammarco[c], Kevin B. Strychar[d]

[a] *Department of Mathematical Sciences, University of Alberta, Edmonton, AB, Canada*
[b] *Federal University of Pernambuco — UFPE, Mathematics Department, Recife, PE, Brazil*
[c] *Louisiana Universities Marine Consortium — LUMCON, Chauvin, LA, USA*
[d] *Annis Water Resources Institute, Grand Valley State University, Muskegon, MI, USA*

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ABSTRACT

This work can be considered a prequel to our previous paper on coral bleaching induced by global warming. We once again investigate, using Finsler geometry, dynamical energy budget theory and nonlinear modular mechanics, the origin of endosymbiosis, between reef-building corals and the algae. We assume their relationship starts out as entosymbiosis, with the algal organism living on the external surfaces of host coral exoskeleton, but with both gradually adapting to each other over evolutionary time-scales. Our main conclusion is that such an evolutionary conversion is possible and indeed is quite likely.

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0. Introduction

Coral reefs have been severely negatively affected by climate change over the past 30 years or more [1–3]. In particular, global warming has caused mass mortalities of zooxanthellate (zooxanthellae-bearing) hermatypic (reef-building) corals on reefs around the world [4,5]. This was first reported to occur in the Eastern Pacific [6,7] and later throughout the world's tropical and sub-tropical seas [8–11]. The cause of coral death in these cases was due to increases in both local and regional seawater temperatures which stress the symbiotic relationship between the coral animal and its endosymbiotic alga, the dinoflagellate *Symbiodinium microadriaticum* [12,13] (commonly called zooxanthellae). This effect (i.e., bleaching) is due to the inability of the zooxanthellae to tolerate increasing seawater temperatures, which in turn causes a breakdown in the symbiotic relationship between the coral animal and the zooxanthellae, and the expulsion of necrotic and apoptotic zooxanthellar cells from the holobiont [14,15]. This eviction of zooxthanthellae

* Corresponding author.
E-mail address: peter.antonelli@gmail.com (P.L. Antonelli).

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causes "bleaching" of the coral holobiont because pigmentation in hermatypic corals is generally derived from the zooxanthellae, not pigment in the coral tissue. *Symbiodinium* is the weaker of the two partners in terms of temperature tolerance [16–18], and there has been wide-scale loss of zooxanthellae from the corals on a global scale which has caused coral mortality [19–21]. The loss of zooxanthellae causes the tissue of the coral to become transparent, allowing its white calcium carbonate skeleton to be readily viewed through the transparent coral tissue, causing the coral to appear white or "bleached" [22,16].

Zooxanthellae are highly specialized endosymbionts of scleractinian corals and some other reef organisms (e.g., *Cassiopaea xamachana* [23]; *Aiptasia patella*, *Anthozoa, Actinaria* [24,25]; and other zooxanthellate symbiotic relationships not unique to the Cnidaria [4]; e.g., *Amphiscolops langerhansi* Platyhelminthes [26], *Tridacna gigas*, *T. maxima*, *T. crocea*, and other *Tridacna* spp Mollusca [27,28]. Most of these are known to bleach under high temperature conditions [29–31]). Endosymbiosis as described by Margulis [32] and Margulis and Fester [33] are interactions taking place within a host and includes intracellular (integration at the cellular level) and/or extracellular (association between the host's cells). They were, however, initially autonomous free-living organisms similar to *Gymnodinium* sp. and other closely related dinoflagellates. It is believed that early in the evolution of *Symbiodinium*, they were motile, planktonic, and autotrophic [34]. Thus, the change from free-living dinoflagellates to symbiotic zooxanthellae required adjustments within the immune systems of both the anthozoan and the dinoflagellate [35]. We hypothesize that zooxanthellae evolved first from free-living forms, then to entosymbiosis. Heyword and Hichodzijewski (2010) describe entosymbiosis as symbiosis that can occur as (1) "attachment symbiosis" as observed, for instance, when sea anemones ride hermit crab shells and (2) "behavioural symbiosis" where communication is quintessential to making this relationship possible, (e.g. birds cleaning between the teeth of a crocodile) outside a host's body existing as a permanent/semi-permanent association. Daida [36] describes entosymbiosis as it is possible that the alga started on the surface of a coral but gained a selective advantage by being protected from grazing once inside the anthozoan. This probably ignited the entocommensal relationship. Through time, the complexity of the symbiotic relationship continued to evolve between the coral and the dinoflagellate. The dinoflagellate would have evolved into a sufficiently different organism from its free-living ancestor to become a new and separate genus *Symbiodinium*. The symbiosis became characterized by an obligate inter-dependence between the coral and the zooxanthella, involving an exchange of nitrogenous waste compounds/nutrients and CO_2 from the coral to the endosymbiont, and oxygen and sugars from the alga to the coral.

1. The model basics

We represent this situation with classical ecological equations starting with essentially an arbitrary 2-species system, where species #1 is the host (coral polyp) population of size, N^1, which contributes nitrogenous wastes to #2, the commensal (zooxanthella), in the amount x^1, at rate per polyp k_1, so that

$$k_1 N^1 = \frac{dx^1}{dt}, \qquad \frac{dN^1}{dt} = r_1 N^1 - a_1 (N^1)^2 + a_2 (N^2)^2 - a_3 N^1 N^2. \tag{1.1}$$

Likewise, x^2 denotes the amount of photosynthate passed along to #1 (coral) by species #2 (zooxanthella) at rate k_2, so that

$$k_2 N^2 = \frac{dx^2}{dt}, \qquad \frac{dN^2}{dt} = r_2 N^2 - b_1 (N^2)^2 + b_2 (N^1)^2 - b_3 N^1 N^2. \tag{1.2}$$

Here, a's and b's are all positive and approximately constant (over some pre-assigned time interval of observation) with $(x_1, x_2) \in \mathbb{R}^2$, $(N_1, N_2) \in \mathbb{R}^2$. It is permitted to have the coefficients dependent on the x's, provided they are slowly varying. In this case, the coefficients would be approximately constant in some time

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