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Dynamics of Coral-Algae Phase Shifts via Ecological Stoichiometric Approach

Xin Zhao[1], Na Tian[2], Shiyang Yu[2,3] and Meng Fan[2,*]

[1] *Department of Mathematics, Harbin Institute of Technology (Weihai), Weihai 264209, P.R. China.*
[2] *Center for Mathematical Biosciences, School of Mathematics and Statistics, Northeast Normal University, Changchun 130024, P.R. China.*
[3] *College of Mathematics Science, Bohai University, Jinzhou 121013, P.R. China.*

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On the auspicious occasion of celebrating the ninetieth birthday of Professor Zhien Ma, we extend our heartfelt congratulations and exporess our sincere gratitude for his profound contributions to the academic community.

Abstract. Coral reefs have evolved over hundreds of millions of years and are now considered one of the most critical yet vulnerable ecosystem on earth. Environmental changes, including variations in light availability, nutrient levels, and fishing pressure, can significantly impact the health of coral reefs, potentially leading to ecosystem degradation. A coral-macroalgae-herbivorous fish model is developed based on ecological stoichiometry to investigate the dynamics of coral-algae phase shifts. The positivity, invariance, and dissipativity of the model are carefully established, the existence and stability of equilibria are rigorously demonstrated, and rich dynamics such as bistability and various types of periodic oscillations are numerically explored. Furthermore, the effects of environmental factors (e.g., light intensity, nutrient levels, and fishing pressure) on the system's dynamics are investigated. The main findings highlight that environmental variations are key drivers of ecological phase transitions in coral reef ecosystems, providing more insights into the mechanisms underlying coral-algae dynamics and offering implications for the sustainable management of coral reefs.

AMS subject classifications: 92D25, 34F05, 92B05

Key words: Dynamic model, coral reef degradation, phase shifts, stability analysis, asymmetric dispersal.

1 Introduction

Coral reefs provide significant ecological and economic value, including sustaining marine biodiversity, protecting coastlines, and regulating the environment. In coral reef

*Corresponding author. *Email address:* `mfan@nenu.edu.cn` (M. Fan)

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ecosystems, predation and competition are common ecological interactions that shape reef communities. Macroalgae and coral compete for essential resources such as light and space. Specifically, macroalgae form dense canopies that can shade the light required for photosynthesis, and their exudates can reduce coral calcification, thereby inhibiting coral growth [26, 31]. Corals can suppress macroalgae growth through mechanisms such as physical stimulation, chemical defense, and mucus secretion [34]. Moreover, macroalgae are grazed by herbivorous fish (e.g., parrotfish), a critical determinant of macroalgae biomass regulation in coral reef ecosystems [8, 12, 41]. The interspecific interactions among coral, macroalgae, and herbivorous fish are schematically illustrated in Fig. 1.

However, in recent decades, coral reefs have faced severe threats to their biodiversity, structure, and functionality, which is the result of the combined effects of human activities [57]. It is observed that coral reef degradation typically entails a phase shift in community structure, termed as a coral-algal phase shift, characterized by a decline in coral abundance corresponding to an increase in macroalgal abundance [9, 10, 27]. Ample evidence suggests that overfishing of herbivorous fish promotes the rapid growth of macroalgae [28, 42]. The expansion of macroalgae also suppresses coral settlement, disrupting the symbiotic relationship between coral polyps and their symbiotic algae. If such stress persists for an extended period, corals may experience large-scale mortality and eventual bleaching [32].

Many studies have developed dynamical models to understand the mechanisms driving coral-algae phase shifts. Early work by Mumby *et al.* [35] introduced a simplified model showing how reduced grazing could cause a loss of coral resilience and a shift to macroalgae dominance. Follow-up studies by Li *et al.* [25] and others [4,6,16,47,50,55,58, 59] further explored how overfishing, competition, and habitat degradation affect coral resilience. These models, however, primarily focus on trophic interactions without considering nutrient constraints. In addition, the combined effects of factors such as storm frequency, other physical disturbances, ocean warming, and acidification on coral-algae interactions have been investigated [1, 5, 14]. Sarkar *et al.* [41] utilized the continuous-time food chain models to study the impact of herbivorous fish harvesting on coral-algae phase shifts. Their findings suggest that reducing the harvesting rate of herbivorous fish

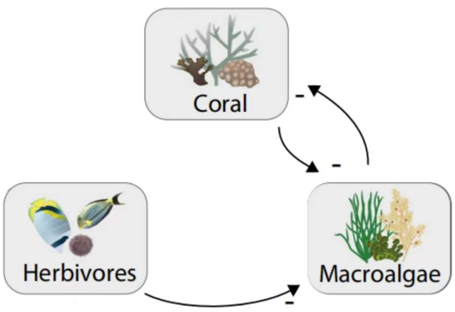

Figure 1: Schematic diagram illustrating the interactions among corals, macroalgae, and herbivorous fish [48].