Consequences of morphological plasticity and fragmentation on space occupation of coral reef macroalgae

Aletta T. Yñiguez [a,b,*], John W. McManus [b], Ligia Collado-Vides [c]

[a] Division of Marine Biology and Fisheries, Rosenstiel School of Marine and Atmospheric Science, University of Miami, 4600 Rickenbacker Causeway, Key Biscayne, 33149, FL, U.S.A.
[b] Marine Science Institute, University of the Philippines, Velasquez St., Diliman, Quezon City, 1101, Philippines
[c] Florida International University, Department of Biology, and Southeast Environmental Research Center, 11200 SW 8th Street, OE 167, Miami, 33199, U.S.A.

ABSTRACT

The macroalgal species, *Halimeda tuna*, *Halimeda opuntia*, and *Dictyota* sp., are modular and clonal organisms that have the capability for morphological plasticity and asexual reproduction through fragmentation. Growth and disturbance factors affect these characteristics and consequently their rate and amount of space capture. A three-dimensional agent-based model SPREAD (Spatially-explicit Reef Algae Dynamics) was used to explore these potential consequences under a range of growth and disturbance conditions, and to investigate the particular conditions leading to variations of these macroalgae in the inshore patch and offshore reefs in the Florida Reef Tract. The morphology of macroalgae, particularly for *H. tuna*, had an effect on the rate and amount of space occupation, where larger and more upright forms were able to attain greater cover. Even with the more prolific growth forms, space occupation was still limited. Inclusion of fragmentation was needed for greater expansion and to obtain abundances comparable to field observations. Disturbance, whether through herbivory or stronger forces like storms, interacts with fragmentation in determining space occupation patterns of the macroalgae species. High disturbance levels can promote increased fragmentation and spatial cover. However, this appears to be only true for *H. opuntia* and *Dictyota* sp., species with relatively high fragment survival capacity. *H. tuna* achieved higher cover at low disturbances. Strong disturbances leading to larger fragment sizes were detrimental to the spatial spread for all species. Temporally, these macroalgal populations in the studied reefs appeared to be stable overall with seasonal increases and decreases, as was shown possible in the model, observed in the field, and supported in the literature. Based on SPREAD and corroborated with field observations, the combined inherent growth requirements, capability for fragment success, and disturbance through fragment generation influenced the abundance of these macroalgae in inshore patch and offshore reefs which experienced different growth and disturbance conditions. The overall stable macroalgal cover in the observed and simulated Florida Keys reefs permits other organisms, particularly hard corals, to capture space on the reef. Nonetheless, specific local conditions and the timing of macroalgae seasonal increases can impact the spatial spread of other benthic organisms.

© 2015 Elsevier B.V. All rights reserved.

1. Introduction

Clonal organisms have at their disposal a substantial array of means to grow and sustain their populations. They are capable of indeterminate growth that enables them to expand their "territories" through primary growth, usually through the iteration of modular units (Harper, 1985; Jackson and Coates, 1986; Hutchings and Wijesinghe, 1997). They also have the ability to occupy new space through asexual processes such as budding and fragmentation (Jackson and Coates, 1986; Collado-Vides, 2002). Clonal benthic species abound in coral reefs where space is an important and potentially limiting resource (Jackson, 1977). The reef-building hermatypic corals display a plethora of growth patterns that have different growth rates and consequences for three-dimensional space capture, even within the same species (Graus and MacIntyre, 1982; Done, 1983; Kaandorp et al., 2005).

* Corresponding author at: Marine Science Institute, University of the Philippines, Velasquez St., Diliman, Quezon City 1101, Philippines. Tel.: +63 22617701.
E-mail addresses: atyniguez@msi.upd.edu.ph, atyniguez@gmail.com (A.T. Yñiguez).

A common means of asexual reproduction in clonal organisms is fragmentation, in which parts of the individual break off and are able to produce a new individual known as a ramet, defined as a physiologically independent individual that belongs to the same clone. Studies on corals (Highsmith, 1982; Lirman, 2000; Foster et al., 2007) and gorgonians (Lasker, 1990; Coffroth and Lasker, 1998) have shown that ramets can represent a major proportion of their populations and that fragmentation is an important process in producing these ramets.

In coral reefs in the Caribbean, clonal macroalgal species are playing a larger role within the ecosystem as their abundances have increased. The role of top-down (herbivory) versus bottom-up (eutrophication) factors in the increase in macroalgal cover in coral reefs has been heavily debated in the past few decades (Hughes, 1994; Lapointe, 1997; Hughes et al., 1999; Lapointe, 1999; McCook, 1999; Miller et al., 1999; Szmant, 2002; McClanahan et al., 2003; McManus and Polsenberg, 2004; Sandin and McNamara, 2012). The roles of disease and bleaching have also been recognized in causing drastic and/or increased coral mortality (Goldberg and Wilkinson, 2004; Hughes et al., 2010; Schutte et al., 2010), which consequently opens up space for other organisms such as macroalgae. Given appropriate light, nutrient and herbivory levels, macroalgae can expand into these open (and possibly even already occupied) spaces through primary growth and asexual reproduction. Different macroalgal species have differing capabilities for space occupation depending on their rates and patterns of vegetative growth or asexual propagation as they experience particular growth (e.g., light, nutrients) and disturbance (e.g., currents) conditions (Santelices, 2004). Vegetative primary growth and fragmentation can have important implications for the rate of space capture and the maintenance of space. For example, fragmentation in the highly invasive *Caulerpa taxifolia* (M.Vahl) C.Agardh appears to be a very successful strategy for rapidly increasing its spatial coverage (Ruesink and Collado-Vides, 2006). The importance of fragmentation as a life history strategy of the red macroalga *Laurencia poiteaui* enabling its dominance in seagrass beds in Florida Bay, USA was observed by Herren et al. (2013). These characteristics of space occupation (rate and persistence) by macroalgae can significantly affect coral reef resilience or the ability to recover to a previous coral-dominated state. More stable macroalgal patches can lead to higher interaction frequencies with corals (Jompa and McCook, 2002a,b; Jompa and McCook, 2003b; Nugues et al., 2004; Mumby et al., 2005) compared to ephemeral macroalgal patches. The nature and frequencies of these interactions can impact corals through direct mortality of adults (Jompa and McCook, 2003a; Nugues and Bak, 2006; Ferrari et al., 2012), space pre-emption and inhibition of recruitment (Nugues and Roberts, 2003; Maypa and Raymundo, 2004; Kuffner et al., 2006; Nugues and Szmant, 2006).

In Yñiguez et al. (2010), the influence of varying conditions of light, nutrients and disturbance on the primary growth form of *Halimeda tuna, Halimeda opuntia*, and *Dictyota* sp. were investigated. They showed that the morphology of successful fragmenters such as *H. opuntia* and *Dictyota* spp. were more influenced by disturbance compared to the less fragmenting *H. tuna*, whose morphologies were more affected by the growth requirements of light and nutrients. The capacity of these macroalgae to sequester space on coral reefs could be determined by factors affecting horizontal spread such as morphological variability.

The overall objective of this study was to investigate how the horizontal spread of macroalgae on a reef substrate is affected by primary growth and fragmentation under various environmental conditions using a small-scale agent-based model approach. It focuses on *H. tuna* (Ellis and Solander) Lamouroux, *H. opuntia* (Linnaeus) Lamouroux and *Dictyota* spp., the dominant macroalgae in the Florida Reef Tract (Fig. 1) and many other Caribbean reefs (Chiappone and Sullivan, 1997; Lirman and Biber, 2000; Williams and Polunin, 2001). Specifically, this paper aims to answer the following questions:

(1) Do the different growth forms within a species affect their rate of space occupation and stability of the occupied space?
(2) How important is fragmentation relative to purely primary growth in the horizontal spread of the macroalgal species being studied?
(3) How does disturbance affect space occupation success?
(4) Can the variations in abundances of these species observed in the reefs be explained through inter-specific differences in responses to growth and disturbance factors?

2. Materials and methods

2.1. Model description

SPREAD is a spatially-explicit agent-based model wherein the basic agent is a macroalgal module. It was developed in order to explore the ecological implications of the inherent morphological plasticity of macroalgae. Details on the formulation and implementation of the model have been described and discussed in Yñiguez et al. (2008, 2010). In the model, a fundamental premise is that the production of modules (the iterative units) by other modules is affected by the external conditions of light, temperature, nutrients and availability of space. For each time step, environmental conditions are updated (see Supplementary Material for model process details). These environmental conditions together with the species' branching rules determine the potential production of a new module by the algae. The last process that occurs for the modules is fragmentation.

Each macroalgal species has particular branching rules that have been derived from previous studies and as observed by the authors' work in the laboratory and field (Yñiguez et al., 2008, 2010; Yñiguez, 2007). For the two *Halimeda* species, the production of a new module depends on where it (the mother module) is located within the thallus of the individual alga (its branch order). If a new module is produced, its location depends on the availability of their preferred space where each species has a hierarchy of choices for where a new module will grow (which leads to the formation of their characteristic branching pattern). *Dictyota* always follows dichotomous branching but the location of these two modules again follows a certain spatial preference. The Supplementary Material contains details on the module production and branching rules.

SPREAD makes use of a three-dimensional grid (3D) in which one cell is equivalent to one square centimeter area. The bottom of this grid is the substrate and each cell row is assigned a particular depth in 1 cm increments. Irradiance or PAR (Photosynthetically Active Radiation) at depth is represented using the Lambert-Beer Law, parameterized with field measurements. Modules within a particular distance directly above can also "shade" the growing module by decreasing the amount of light getting through. *H. tuna* and *H. opuntia* are considered opaque while *Dicyota* is translucent. Temperature and nutrients do not vary spatially within the 3D grid, but can vary temporally depending on the scenario being run. The growth probability functions in response to light for each species of macroalgae are derived from laboratory studies (Yñiguez, 2007). Normal probability distributions are used to represent their response to temperature, based on mean and variance values in the literature. The production of modules by each species of macroalgae in response to various nutrient levels is coarsely represented by a probability value for each of the three nutrient levels (low, medium, high). The parameters used for this study are found in Tables 1 and 2.