2007-12-12

Spatial Dynamics in the Growth and Spread of Halimeda and Dictyota in Florida reefs: A Simulation Modeling Approach

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SPATIAL DYNAMICS IN THE GROWTH AND SPREAD OF *HALIMEDA* AND *DICTYOTA* IN FLORIDA REEFS: A SIMULATION MODELING APPROACH

By

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A DISSERTATION

Submitted to the Faculty
of the University of Miami
in partial fulfillment of the requirements for
the degree of Doctor of Philosophy

Coral Gables, Florida

December 2007

UNIVERSITY OF MIAMI

A dissertation submitted in partial fulfillment of
the requirements for the degree of
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Spatial dynamics in the growth and spread of *Halimeda* and *Dictyota* in Florida reefs: a simulation modeling approach (December 2007)

Abstract of a dissertation at the University of Miami.

Dissertation supervised by Professor John W. McManus.
No. of pages in text. (159)

Macroalgae are an important part of the coral reef ecosystem that has largely been overlooked. However, in the past few decades their abundances have increased and this has been attributed to combinations of coral mortality opening up space in the reef, decreased grazing and increased nutrient load in reefs. This dissertation illustrates a novel means of investigating the effect of various growth and disturbance factors on the dynamics of macroalgae at three different levels (individual, population and 3-species community). Macroalgae are modular and clonal organisms that have differing morphologies depending on the environment to which they are exposed. These traits were exploited in order to understand the factors that were acting on the dominant and common macroalgae in the Florida Reef Tract: *Halimeda tuna, Halimeda opuntia* and *Dictyota* sp. The agent-based model SPREAD (SPatially-explicit REef Algae Dynamics) was developed to incorporate the key morphogenetic characteristics of clonality and morphological plasticity. It revolves around the iteration of macroalgal module production in response to light, temperature, nutrients, and space availability, while fragmentation is the source for mortality or new individuals. These processes build the individual algae then the population. The model was parameterized through laboratory

experiments, existing literature and databases and results were compared to independently collected field data from four study sites in the Florida Keys.

SPREAD was run using a large range of light, temperature, nutrient and disturbance (fragmentation without survival) levels and yielded six morphological types for *Halimeda tuna*, and two each for *Halimeda opuntia* and *Dictyota* sp. The model morphological types that matched those measured in two inshore patch reefs (Cheeca Patch and Coral Gardens) and two offshore spur and groove reefs (Little Grecian and French Reef), were formed in conditions that were similar to the environmental (light, nutrient and disturbance) conditions in the field sites. There were also differences between species in the important factors that influenced their morphologies, wherein *H. opuntia* and *Dictyota* were more affected by disturbance than growth factors, while *H. tuna* morphology was affected by both.

Allowing for fragmentation with survival in the model resulted in significantly higher population abundances (percent cover and density). The highest abundances were achieved under high fragment survival probabilities and a high disturbance level (but not large fragment sizes). Incorporating fragmentation with survival and simulating the variations in light, nutrients and disturbance between the inshore patch reefs and offshore spur and groove reefs in SPREAD led to comparable abundances of *Halimeda* in the virtual reef sites. Adding competition for space and light and epiphytism by *Dictyota* on the two *Halimeda* species suggests that it can regulate the populations of the three macroalgae. However, comparing model abundances to the field, competition may not be a strong regulating force for *H. tuna* in all the sites and *H. opuntia* in the patch reefs. *H. opuntia* in the offshore reefs is possibly competitively regulated. Although SPREAD was

not able to capture the patterns in the population abundance of *Dictyota*, this points to the potential importance of other morphometrics not captured by the model, a variation in growth curves between reef habitats, or the differential contribution of sexual reproduction.

DEDICATIONS

Mama:
striking rocks light up
can burn yet also give warmth
blazing through the night

Daddy:
flow and waterfall
spray glisten on the deep pool
I wish I'd been there

ACKNOWLEDGMENTS

Six years and four months after I first stepped onto the shores of the U.S.A., I go back to the Philippines so much richer, not only from the learning gained through graduate school, but from the people I have had the joy to encounter and learn from as well. Without the multitude of support from many people and institutions, I would most definitely have not made it through the obstacle course that is graduate school!

My committee members, John McManus, Diego Lirman, Ligia Collado, Donald DeAngelis, Larry Brand and Peter Glynn, have been invaluable in providing both insights and much-needed equipment, and guidance on the direction and development of my dissertation. I especially thank Ligia Collado for infusing me with many exciting ideas yet making sure my feet were on the ground. I profusely thank my adviser, John McManus, for so many things: inspiring me to think broadly and creatively, for his generous financial support not only for my research but also to open up wonderful professional opportunities, and for the never flagging belief and positivity.

The Fulbright-Philippine Agriculture Scholarship Program was instrumental in getting me into RSMAS as well as providing financial support together with the University of Miami Maytag Fellowship. Thank you very much to the Philippine-American Education Foundation staff particularly Esmeralda Cunanan, Angela Dizon, Marjorie Tolentino, Yolanda Casas and former executive director Alex Calata. The International Society for Reef Studies-Ocean Conservancy Fellowship, and Project Aware provided much-needed research grants. Thank you to the Santa Fe Institute – Complex Systems Summer School 2004 and 2005 for an eye-opening and wonderful learning experience that has most certainly impacted my scientific perspective.

My fieldwork would not have been possible without the inexpensive and capable services of the Keys Marine Laboratory. Special thanks to Lisa, Lonny, Todd and Chris for being so accommodating. Setting-up laboratory experiments were much faster and fun with the help of John Parkinson. Thank you very much to Susan MacMahon, Maggie Evans, and Marilyn Greene for their patience and guidance through the RSMAS protocol quagmire. The services of B Sapphire are much appreciated as well.

Essential to the completion of this project were my past and present lab-mates: Marilyn Brandt, Felimon Gayanilo, Johnathan Kool, Cara Cooper, Wade Cooper, and Robin Fortuna. They have been the sounding-boards, helping hands, and punching bags through which many details of my dissertation were hashed out. I have to thank Marilyn Brandt especially for withstanding me as a housemate, officemate, dive buddy, and coffee buddy all these years. She is an amazing scientist, friend and person who gives so much to others.

Thank you very much to the wonderful people who have helped fuel me up whether in terms of science and/or simple but essential support: Erica Key, Kirsten and Ethan Colvert, Alison Moulding, and Michelle Paddack. A special thank you to Barbie Ramos, Jennifer Tierro and Cookee Belen who have been constant sources of support through decades and distance.

A heartfelt thank you to the Filipino mafia at RSMAS for making me feel like I was home: Liana McManus, Maria Villanueva, Viva Banzon, Bob Evans (honorary member), Mang Vic, and Wilson Mendoza. A very special thanks goes out to my "godmothers" Liana, Maria and Viva who are amazing women scientists and have inspired and supported me in every possible way.

Thank you to Tito Ding, Tita Neddie, Kuya Boyette, Mireya, Tati and Tyler, who have made me feel part of their family and provided me with many weekends of relaxation and delicious Filipino food that helped re-energize me.

And, of course, thank you and much love to my family, Ate Gi, Ate Nette and Mama and Daddy. Your love and support, in so many ways through all that has happened, is most earnestly appreciated.

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The Two Faces of Macroalgae in Coral Reefs

Macroalgae are important components of the coral reef ecosystem. They play their own roles in coral reefs, ranging from providing the base of the trophic chain to giving settlement cues to coral larvae (Morse et al. 1988, Heyward and Negri 1999) and even helping cement the reef framework (Littler and Littler 1994). Monitoring efforts around the Caribbean in the past decade show that macroalgae occupy a significant portion (average of 45% from 1993-2002) of the reef benthos (Linton and Fisher 2004). In the Florida Keys, Chiappone and Sullivan (1997) found that the cover of macroalgae ranged from 48-84% in the offshore bank-barrier reefs. The long-term monitoring program of the Environmental Protection Agency (EPA) also showed that macroalgae was the second most abundant benthic form in the Keys next to octocorals (Beaver et al. 2006). These values are most likely higher than what would have been found several decades ago. Long term data in the Caribbean (Hughes 1994, McClanahan and Muthiga 1998, Edmunds 2002) and central and western Pacific reefs (Done 1992, Stimson et al. 2001) have documented increased cover of macroalgae that have been linked to anthropogenic activities leading to overfishing and eutrophication.

Currently, the increasing abundance of fleshy macroalgae on reefs has been a cause of much concern. This has been called a "phase-shift," wherein coral abundance has declined and given way to macroalgae (Done 1992, Hughes 1994). This is of great concern regarding ecosystem health and function that could cascade up and affect social and economic systems dependent on coral reefs. Large fleshy macroalgae can directly

overgrow corals and/or affect their growth rates (Lirman 2001, McCook et al. 2001, Jompa and McCook 2002a, 2003a), as well as, pre-empt space for coral recruitment and expansion (Kuffner et al. 2006) and thus drive the system further away from a coral-dominated state (McManus et al. 2000). This could lead to lower abundance and diversity not only for corals but also for higher trophic levels such as fishes (McClanahan et al. 2001). However, surprisingly little is known about the basic population and community ecology of these coral reef macroalgae (Littler and Littler 1994) especially compared to the well-studied species from temperate systems such as kelp beds and rocky intertidal zones (e.g., Dayton 1975, Ang and de Wreede 1992, Airoldi 1998, 2000a, 2000b). Research on this phase shift has focused on the effects of herbivory and nutrients on macroalgal species composition and abundances (e.g., Hughes 1994, Lapointe 1997, 1999, Miller et al. 1999, Szmant 2002) and how the results coincide with the Relative Dominance Model (Littler and Littler 1984) which forecasts what form of algae or if coral will predominate in a reef depending on the level of herbivory and nutrients. Most of these studies have shown that herbivory strongly affects macroalgal biomass or cover and species composition (e.g., Miller et al. 1999, Smith et al. 2001, Thacker et al. 2001, e.g., McClanahan et al. 2003), while nutrients have tended to have a more equivocal effect on these same metrics (Miller et al. 1999, Koop et al. 2001, Thacker et al. 2001, Szmant 2002, McClanahan et al. 2003). Although Bell (2007) and Lapointe et al. (2004) have argued that the latter results were due to ineffective fertilization and/or the sites were already above nutrient threshold concentrations that would give rise to further changes in macroalgal growth rates and biomass from enrichment. The competitive dynamics of macroalgae with other reef organisms, particularly coral, also need to be

taken into account (Lirman 2001, McCook et al. 2001). To facilitate a phase shift in the coral reef, macroalgae need to increase the space they occupy in the reef. This entails directly overgrowing corals or utilizing substrate that has been opened up through, for example, coral mortality.

The dynamics of macroalgae are obviously driven by many factors (Lobban and Harrison 1994). Intrinsically, various species can have different life history strategies that respond in diverse ways to environmental conditions. Extrinsically, light, temperature, nutrients, competition, grazing and other sources of disturbances are major factors influencing their abundance and distribution. The complexity of the system makes it hard to determine the mechanisms leading to changes in the system, moreover, to be able to predict the spatial and temporal variations in the reef macroalgae community in response to differing conditions. Thus, this dissertation, through a 3-D agent-based model, investigates not only herbivory and nutrients, but other growth factors and disturbance factors in general. This dissertation also utilizes a spatial perspective similar to macroalgal invasive species studies (e.g., Hill et al. 1998, e.g., Ruesink and Collado-Vides 2006), and focus on how these indigenous macroalgae grow and occupy space explicitly on the reef and the factors affecting these processes.

Morphological Plasticity and the Use of Space

Space to grow, live and feed is of primary importance to organisms, and this is especially true for sessile species such as macroalgae and benthic invertebrates in reefs (Paine 1984, Connell and Keough 1985). From our perspective, quantifying and potentially forecasting the amount of space taken up by certain organisms is of

importance. However, instead of just asking *how much* space is occupied by which organisms, we can also ask *how* is space occupied by these organisms? Getting at the *how* allows us to explore structural properties that can have consequences for biotic and abiotic interactions and provides the potential for distinguishing characteristics of the organism that can help forecast its space utilization over time.

Investigating *how* macroalgae occupy space is important because of a key characteristic that most of them (and many benthic organisms) possess: morphological plasticity. A large number of macroalgae exhibit non-deterministic phenotypically plastic growth that enable them to have different morphologies under different conditions (Lobban and Harrison 1994, Collado-Vides 2002a). Knowledge of the variety of forms macroalgae have under varying conditions can give us information about the environment they are experiencing, potential effects on other organisms and the environment itself, and trajectory of growth.

Different macroalgal species have varying capacities for morphological plasticity. On one extreme are those that have radically dissimilar morphologies under different conditions or ontogenetic stages. For example, certain species belonging to the genera *Ulothrix, Urospora, Petalonia, Scytosiphon, Bangia* and *Porphyra* exhibit heteromorphic life stages (upright macroscopic filamentous, tube or blade morphologies versus non-upright or boring state) hypothesized to have evolved due to grazing pressure (Lubchenco and Cubit 1980). On the more subtle side, *Caulerpa prolifera* found in high light environments exhibited a more compact and branched form compared to those in the shade (Collado-Vides 2002b). Variation in a species' growth form can consequently lead to variation in the way it occupies space. More spatially separated "individual" growth

forms can potentially spread to larger areas faster, while a clumped form would tend to be denser and could interfere more with settlement of other organisms such as coral larvae (Hay 1981a).

Morphological Characteristics of the Dominant Macroalgae in the Florida Reef Tract: *Halimeda* and *Dictyota*

Species belonging to the genera *Halimeda* (Chlorophyta) and *Dictyota* (Phaeophyta) are two of the dominant macroalgae found in the Florida Reef Tract (Chiappone and Sullivan 1997, Hanisak and Overdorf 1998, Lirman and Biber 2000) as well as many reefs around the Caribbean (Shulman and Robertson 1996, McClanahan and Muthiga 1998, Williams and Polunin 2001).They can represent 77-99% of the macroalgal biomass in the Northern Florida Reef Tract (Lirman and Biber 2000).

The morphologies of these two genera are each composed of two primary structures: a rhizoidal cluster or attachment structure and the thallus (Table 1.1). Both also exhibit modular and clonal growth. Their rhizoids and thalli grow through the iteration of fundamental units -- hence their modularity. The iterating units of the thalli are the calcified segments for *Halimeda* and linear segments for *Dictyota* (Table 1.1). *Halimeda tuna* (Ellis and Solander) Lamouroux and *Halimeda opuntia* (Linnaeus) Lamouroux, two common species in the Florida Reef Tract, grow on hard substrate. *Dictyota* spp. can use pavement, coarse sand and other living organisms (epiphytism) as substrate. The morphological plasticity in these *Halimeda* and *Dictyota* species lean towards the more subtle end of the spectrum rather than dramatic differences in form. The most plastic of these species is *Halimeda opuntia* which has two recognized forms (Littler and Littler 2000). One form is composed of oval segments that grow into a highly

compact shape. The second form (*f. triloba*) has trilobed segments and longer inter-segment distances which result in loose clumps. For *Halimeda tuna*, morphological plasticity has been quantitatively recorded by Vroom et al. (2003), where populations found at 21 meters were taller and had more abundant and bigger segments compared to those at 7 m. *Dictyota* spp. can grow both in an upright and prostrate manner with growth forms ranging from upright compact to horizontal sparse ones (Hay 1981a). These *Halimeda* and *Dictyota* species also produce fragments which survive and reattach to produce ramets (potentially physiologically independent units) (Tuomi and Vuorisalo 1989). This clonality is an important part of their life histories, allowing them to persist and disperse (Vroom 2001, Walters et al. 2002). These macroalgae also undergo sexual reproduction. The two *Halimeda* species have separate male and female individuals which produce the gametes. A special characteristic of *Halimeda* is that production of gametes uses up an individual's protoplasmic content and after release of gametes, the individual dies (Hillis-Colinvaux 1980, Drew and Abel 1988). This is termed holocarpy. *Dictyota* exhibits an isomorphic alternation of generations, and gametophytes and sporophytes can co-exist in the population although the latter are the more commonly (Hoyt 1927, Foster et al. 1972, Phillips 1988). The relative importance of asexual versus sexual reproduction in contributing to the populations of these macroalgae have not been explored.

In the Florida Reef Tract, differences in the abundances of *Halimeda* and *Dictyota* are apparent between some inshore patch reefs (e.g., Cheeca Patch and Coral Gardens) and the offshore spur and groove reefs (e.g., French Reef and Little Grecian) (Figure 1.1). The environments in these patch reefs have larger ranges in temperature, are more turbid,

and have higher nutrient concentrations (Boyer and Jones 2002) than the offshore spur and groove reefs. Collado-Vides et al. (2005) found a correlation between the faster increase in abundance of the seagrass dweller *Halimeda incrassata* at nearshore seagrass beds and higher nutrient concentrations. Nutrient availability, light and temperature are most probably the important factors influencing the growth and spread of these macroalgae in these reefs. However, as mentioned previously, little is known about the biology of these macroalgae and the effect of these factors on their growth and consequent spread through the reef substrate.

The clonality and plasticity of growth in many macroalgae and plants have important implications for their ability to occupy and spread across substrate. Lovett-Doust (1981) coined the terms "guerilla" and "phalanx" growth strategies to describe the two extremes in the continuum of clonal plant growth and space exploration. Species with a guerilla growth form, as the name implies, have widely spaced and scattered ramets. On the other hand, the ramets of phalanx species grow closely together and advance through space like a front. There exists a rich literature on the relation of plant/invertebrate clonal morphology and growth to their ecology and evolution (e.g., Cook 1985, Jackson and Coates 1986, Hutchings and Wijesinghe 1997). However, apart from a few studies (e.g., Collado-Vides et al. 1997, Collado-Vides 2002b) this approach has not been adapted and fully taken advantage of to investigate the growth and spread of macroalgae.

Importance of Modeling and the Approach to be Used

The process and output of modeling have played important roles in helping to increase our understanding of complex systems (Jørgensen et al. 1996). Modeling enables the synthesis of knowledge of complex ecological systems. With an appropriately parameterized and well-validated model, we can "manipulate" parameters in ways that cannot be done in the field. This then allows a more thorough study of the system and can give rise to better understanding of causal mechanisms. Scenario-testing, or using the model to answer "what-if" situations, is also an important use of validated models. Such models can contribute much to education and management of resources. The complex dynamics of macroalgae on coral reefs make the exercise of modeling them an important and instructive one.

During the late 1970s a modeling approach was developed where the characteristics of individuals within populations are tracked during simulation (see DeAngelis and Mooij 2005, Grimm and Railsback 2005 for reviews). This was called individual-based modeling (also agent-based modeling). It is now widely used in fields such as economics (Arthur 1999), social sciences (Axelrod 1997, Kohler and Gumerman 2000, Tillman et al. 2001), ecology (DeAngelis et al. 2002, Grimm and Uchmanski 2002, Railsback and Harvey 2002) and evolution (Holland 1975, Pepper and Smuts 2002). The strength of this approach is its incorporation of variation at the individual (or agent) level as well as allowing for localized interactions. In terms of plant and macroalgae biology, it has been recognized that the non-homogeneous spatial environment is an important component in intra- and inter-specific interactions (Ford and Sorrensen 1992). Space is

an important resource for plants, and they can also change their environment and the availability of resources as they grow and interact.

There has been a long history of simulating terrestrial plants at the morphological level (some examples are Bell 1976, Cain and Cook 1988, Callaghan et al. 1990, Room et al. 1996). Recent advances in computation have allowed simulation models to expand into the 3D morphological realm, scale up to community dynamics using the agent-based modeling approach to represent real space utilization, as well as to facilitate the role of visualization in both research and management. One of the more successful vegetation models is SORTIE (Pacala et al. 1996), which simulated forest community dynamics in the Northeastern United States. These models kept track of different individual parameters of each tree (e.g., growth, mortality, seed dispersal) as well as their spatial location. They made use of a simplified 3-D representation of the crown and trunk of different species (Figure 1.2). This model is being adapted by other countries to help in their own forest management initiatives (e.g., Waititu Forest, New Zealand; Luquillo, Puerto Rico).

Models of plants (Cain et al. 1995) and seagrass (Sintes et al. 2005) that incorporate spatially-explicit local interactions as well as morphology have proven to be successful in understanding mechanisms and factors influencing the spatial occupation and distribution of clonal species.

Objectives

Overall objective: Determine how and what factors affect the growth, morphology and space utilization of the dominant benthic reef macroalgae (i.e., *Halimeda* spp. and *Dictyota* spp.) in the Upper Florida Keys.

Specific objectives:

1) Develop a flexible spatially-explicit growth model of macroalgae, focused on *Halimeda* and *Dictyota* spp., the dominant/representative macroalgal species found in the Florida reef tract, and use this model to:
2) Determine how the growth patterns of *Halimeda* spp. and *Dictyota* spp. and the way they occupy space change under varying light, temperature, nutrient, and disturbance regimes;
3) Determine how different growth patterns and environmental conditions affect the rate of spatial spread of *Halimeda* spp. and *Dictyota* spp. populations; and,
4) Determine how indirect interspecific competition (through resource competition) and epiphytism of *Dictyota* spp. on *Halimeda* spp. affect the growth and spatial spread of these macroalgae under varying environmental conditions.

This dissertation is subdivided into four Chapters, excluding Chapter 1 and 6. Chapter 2 describes the model conceptualization and parameterization, and uses a case study for one species *H. tuna* to investigate its performance. Chapter 3 tackles how the growth and morphology of *H. tuna, H. opuntia* and *Dictyota* vary under changing environmental conditions. Chapter 4 scales up to the population level and investigates the

consequences of these varying morphologies and clonality through fragmentation on horizontal space occupation. Chapter 5 scales up another level and explores how interspecific interactions affect spatial dynamics. The last chapter (Chapter 6) provides a summary of the overall dissertation results and ties together the ensuing conclusions, as well as discusses the gaps that can be filled by future research.

Significance of dissertation research

Despite macroalgae being an important part of the coral reef ecosystem, as well as having a central role in the changes occurring in coral reefs, it is surprising how little is known about the ecology of macroalgae. Experimental and laboratory studies have looked at one or a few factors to determine what is causing the spread of macroalgae. Unfortunately, this is a complex adaptive system where many factors play a part and interact in non-linear ways. This makes it difficult to look at their spatial and temporal variations considering more than two of these factors. This dissertation helps to fill in this gap in knowledge through the investigation of the growth and death of important reef macroalgal species using a spatially-explicit agent-based model. This combined modeling and experimental approach allowed for the exploration and elucidation of growth patterns at the individual and population levels under a large range of varying factors.

Table 1.1. Morphological features of *Halimeda* and *Dictyota* species.

	Halimeda tuna	***Halimeda opuntia***	***Dictyota menstrualis/ cervicornis***
Attachment structure	Holdfast	Rhizoidal clusters, rhizoid formation in segments in contact with substrate	Fibrous holdfast and rhizoid formation in segments in contact with substrate
Thallus structure iterating unit branching	Calcified triangular segments Initially branches in one plane; Can have 2-4 branches at one level	Calcified oval or trilobed segments Branching direction random and irregular	Linear segments Dichotomous branching

Figure 1.1. Percent cover of *Dictyota* spp., *Halimeda* spp. and crustose coralline algae in inshore patch and offshore spur and groove reefs.

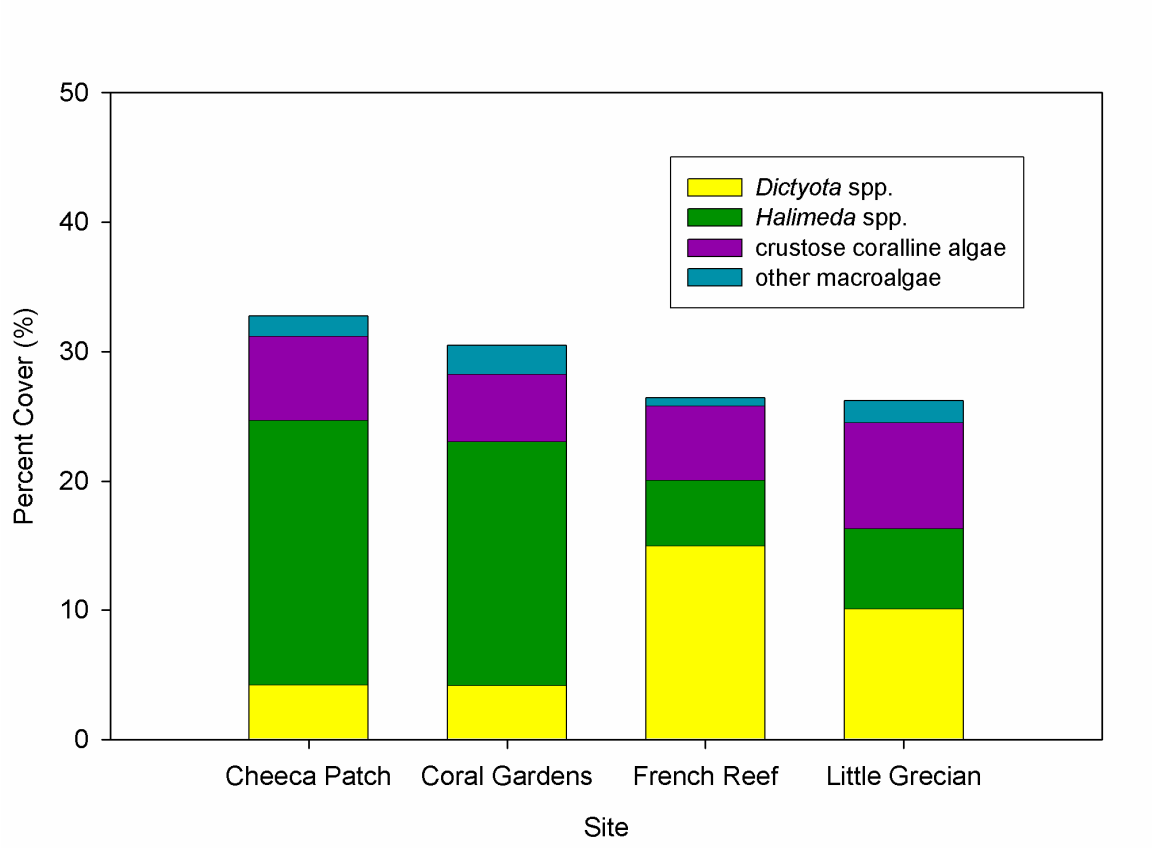
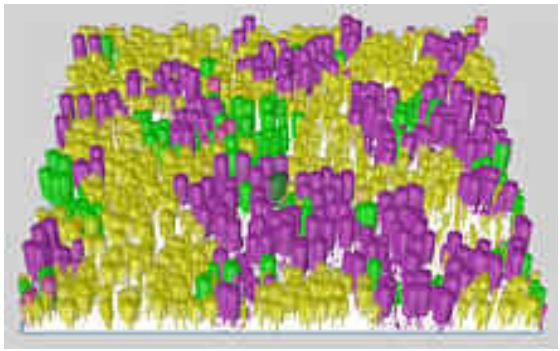


Figure 1.2. The SORTIE model (Deutschman et al. 1997). A 3-D representation of tree species (a) and a snapshot of a sample simulation run (b).

a



b

II. ALLOWING MACROALGAE GROWTH FORMS TO EMERGE: USE OF AN AGENT-BASED MODEL TO UNDERSTAND THE GROWTH AND SPREAD OF MACROALGAE IN FLORIDA CORAL REEFS

Introduction

Macroalgae are important yet largely overlooked components of coral reef ecosystems. They play significant roles in coral reefs, ranging from providing the base of the trophic chain to giving settlement cues to coral larvae (Morse et al. 1988, Heyward and Negri 1999); and even helping to cement the reef framework (Littler and Littler 1994). Currently, the increasing abundance of fleshy macroalgae on reefs has been a cause of much concern. This has been termed a "phase-shift" (also known as "regime-shift"), where coral abundance has declined and given way to macroalgae (Hughes 1994, Gardner et al. 2003). This can have large impacts on ecosystem health and function, as well as on the socio-economics of coral reefs (McManus et al. 2000, McClanahan et al. 2001). However, surprisingly little known about the basic population and community biology of these coral reef macroalgae (Littler and Littler 1994). Research on macroalgae have primarily focused on the effect of the two factors, herbivory and nutrients, on macroalgal biomass or cover and species composition using experimental manipulative techniques or correlative studies (e.g., Hughes 1994, Lapointe 1997, 1999, Miller et al. 1999, Koop et al. 2001, McClanahan et al. 2001, Smith et al. 2001, Thacker et al. 2001) Information on their basic population and community dynamics is important in understanding the mechanisms of their spread on coral reefs, especially considering their potential to inhibit coral recruitment onto reef substrates (Kuffner et al. 2006). To investigate these mechanisms, it is potentially instructive to borrow the perspective of macroalgal invasive species studies (Hill et al. 1998, Ruesink and Collado-Vides 2006)

and focus on how these indigenous macroalgae grow and occupy space explicitly on the reef and on the factors affecting these processes.

Space in which to live, grow, and reproduce is of primary importance to organisms. For sessile species such as macroalgae and many benthic invertebrates in reefs, space is an especially crucial resource (Paine 1984, Connell and Keough 1985). For this reason, quantifying and potentially forecasting the amount of space taken up by certain organisms is of importance. However, instead of just asking *how much* space is occupied by which organisms, we can also ask *how* is space occupied by these organisms? Getting at the *how* allows us to explore structural properties that can have consequences for biotic and abiotic interactions and provides the potential for distinguishing characteristics of the organism that can help forecast its space utilization, from which one can then scale up to the spatio-temporal distribution on larger spatial scales.

Investigating *how* macroalgae occupy space is relevant because of a key characteristic that most of them possess: morphological plasticity through modular and clonal growth. A large number of macroalgae exhibit non-deterministic phenotypically plastic growth that enables them to have different morphologies under different environmental conditions (Lewis et al. 1987, Collado-Vides 2002b). Knowledge regarding the variety of forms that macroalgae have under varying conditions can give us information about the environment they are experiencing, their potential effect on other organisms and environment itself, and their trajectories of growth.

The clonality and plasticity of growth in many macroalgae and plants have important implications for their ability to occupy and spread through substrate. Clonal

organisms are constructed through the iteration of modules, and give rise to ramets, potentially physiologically independent units that can act as ecological individuals (Tuomi and Vuorisalo 1989). These ramets all belong to one genetic individual or genet. Lovett-Doust (1981) coined the terms "guerilla" and "phalanx" growth strategies to describe the two extremes in the continuum of clonal plant growth and space exploration. Species with a guerilla growth form, as the name implies, have widely spaced and scattered ramets. On the other hand, the ramets of phalanx species grow closely together and advance through space like a front. There exists a rich literature on the relationships of plant/invertebrate clonal morphology and growth to their ecology and evolution (Cook 1985, Jackson and Coates 1986, Hutchings and Wijesinghe 1997). However, apart from a few studies (Collado-Vides et al. 1997, Collado-Vides 2002b) this approach has not been adapted in the marine realm.

This study presents a combined modeling and experimental approach in order to investigate the three-dimensional growth of dominant macroalgae in the Florida Reef Tract. The individual-based (or agent-based) model SPREAD (*SP*atially-explicit *RE*ef *A*lgae *D*ynamics), was developed to investigate the influences of growth factors (light, temperature, nutrients), and disturbance leading to fragmentation on macroalgal growth and occupation of space. The objective was to help understand the role of these factors on the growth, persistence and spread of these macroalgae in coral reefs. The key characteristics of clonality and morphological plasticity of these species are incorporated in the model, and specific growth patterns emerge, depending on the environmental conditions. Our premise is that, if we have an understanding of the responses of macroalgae to environmental conditions, the growth and morphology of these macroalgae

in given locations can give important insights into the environmental conditions affecting them. In addition, such information can allow us to estimate potential space occupation patterns (Cain et al. 1995, Sintes et al. 2005).

The primary purpose of this study is to present a novel and important approach to modeling macroalgae growth and compare the model-derived results to independent field measurements on one species for which detailed growth data could be obtained. We first introduce SPREAD using Grimm et al.'s (2006) ODD (Overview, Design concepts, and Details) protocol; then we investigate model performance by comparing growth patterns (individual number of segments, growth and mortality rates in terms of number of segments produced or lost per day) derived from the model to those observed for one species, *H. tuna*, in four sites in the Florida Keys. The relatively untangled growth form of this species facilitates detailed comparisons with field data. The similarities and differences between model and field results are discussed. Detailed investigation of the results of interspecies interactions and other factors on morphologies and horizontal spread of *H. tuna*, *H. opuntia* and *Dictyota* spp. will be tackled in the subsequent chapters.

Methods

Model description

Overview

State variables and scales

The basic unit of SPREAD is the particular species' module, which occupies a location on a three-dimensional spatial grid. A module is defined as the iterating building

block of the macroalgae form, and is either a thallus module or an attachment structure module. The production of new modules by an existing module is what is deemed as growth and this is affected by space availability, light, temperature and nutrient levels (Figure 2.1). The production of new modules constitutes the growth of each individual alga, and many individuals form the populations of algae that compose the three-species community being investigated in the model. SPREAD looks at the dynamics of these species within a local three-dimensional patch (Figure 2.2).

Process overview and scheduling

The model uses discrete daily time steps. Figure 2.3 is a flow chart of the events that occur within one time step. All the environmental parameters of light, temperature and nutrients are calculated first. The modules then undergo growth (or production of new modules), as affected by the environmental conditions within their growth search area. New modules are immediately placed into the grid. After this growth process, modules are removed or rearranged due to death/transport of fragments or survival of fragments, respectively. The calculation of morphometrics (e.g., total number of modules, individual algae width and height, growth rates) are scheduled next. The very last process scheduled is the transformation of the 3-D grid into a 2-D grid from which the percentage cover of each macroalgal species is calculated by simulating a "virtual diver" conducting a percent cover survey using a quadrat.

Design Concepts

Emergence

The growth patterns of individual algae emerge from the "decisions" of each module. It follows that the population and community properties of the macroalgae are

also emergent. The decision of the modules to grow or not and where to grow are represented by rules that are contingent on current conditions, which are embodied in empirically derived regression curves. Fragmentation processes are modeled using empirical rules as well. Adaptation and fitness seeking behavior are implicitly represented through these empirical rules for module production.

Sensing

Each module "knows" its species, type (attachment structure or thallus), which modules it has produced, and its location (x, y, z coordinates). It can also "sense" the light, temperature and nutrient levels in cells adjacent to it.

Interaction

Indirect exploitative interaction, defined as a species using a resource and causes its shortage for the other species (Birch 1957), occurs between modules through competition for space and shading effects that depend on tissue transparency. The model permits direct interaction between *Dictyota* and *H. tuna* or *H. opuntia*, although this option was not used in the current analysis. *Dictyota* modules can overgrow *Halimeda* modules and thus directly affect their growth (Beach et al. 2003b).

Stochasticity

The growth parameters that the modules use in their decisions to grow in response to their environment are probabilities that are drawn from empirical probability distributions. This approach was used because the purpose of this model is to explore the variation in the potential growth patterns of these macroalgae at the higher individual, population and community levels, as well as to reflect the inherent stochasticity in module production of these macroalgae, wherein they grow in unpredictable spurts

(Hillis-Colinvaux 1980, Multer and Clavijo 2004). Fragmentation parameters are drawn from normal probability distributions based on empirical data where available. This also applies to the environmental parameters of light and temperature, but not nutrients, which are not represented as continuous variables, but instead are coarsely represented using three nutrient levels.

Collectives

Modules are grouped into species-specific individual macroalgae.

Observation

The model produces, as output, metrics that are similar to those obtained from real life studies. The main data used for testing and analyses are at the individual level: number of modules (segments) per individual, module production rate (or individual growth rate), individual algal width and height. At the higher levels, the number of individual algae per species, percent cover and absolute area occupied can be calculated.

Details

Initialization

At the start of a model run, the number of base modules per species of macroalgae and the factors and particular settings to be included are set. Light, temperature and nutrients can each be turned on or off. The model can be run using, alternatively, one season, or two seasons; fragmentation or no fragmentation; fragment survival or the lack thereof; and *Dictyota* overgrowth of *Halimeda* or not.

Input

Space and Depth. The 3-D grid is divided into cells that have a one centimeter by one centimeter dimension. The substrate is represented as the bottom of the 3-D grid. The top

of the 3-D grid, however, is not necessarily the water's surface and is truncated here since the macroalgae being studied do not grow tall like kelp species, as well as to conserve computational resources. Cells occupying the same horizontal plane within the 3-D grid have the same depth value.

Light. Irradiance was modeled using the Beer-Lambert law:

$$I_{depth} = I_0 e^{-k(depth)}$$

where,

I_{depth} = irradiance at depth

I_0 = surface irradiance

k = attenuation coefficient

depth = depth of cell

The irradiance a cell receives is modified by shading due to the presence of macroalgae modules within three cells above it; representing shading effects. *Halimeda tuna* modules are considered opaque.

Irradiance data are in Photosynthetically Active Radiation or PAR (μmol quanta m^{-2} s^{-1}). The average surface irradiances with standard deviations from each field site were used. These PAR values were taken using a LI-COR LI-193 Spherical Underwater Quantum Sensor. The attenuation coefficients for each season and habitat type (patch reef and offshore spur and groove reefs) were obtained from the long-term monitoring

database of the Southeast Environmental Research Center (SERC) at Florida International University (http://serc.fiu.edu/wqmnetwork/).

Temperature. Temperature is uniform for all cells within the 3-D grid, but can be varied temporally. The average temperatures for each season and habitat type were obtained from the SERC database as well.

Nutrients. Similar to temperature, nutrient level is uniform for all cells within the 3-D grid, but can be varied temporally. This factor is only coarsely represented using three generalized exploratory probabilities: low, ambient and high.

Submodels

Growth. *H. tuna* tends to grow using only one plane or in a flat manner (Littler and Littler 2000). In the simulations, the search area of a module potentially producing a new module includes only the three spatial cells directly above and the two cells to the sides in the x-y plane. If conditions allow for it, the priority is for a given module to produce a new module in the spatial cell directly above it. The next most likely options are any of the two cells to the sides but still above it, and the least likely options are the cells immediately to its sides. For the last two options, the specific choice depends on availability or is randomly chosen if the two cells for each option are available.

The overall growth probability of *H. tuna* is specified by:

$$P(growth) = P(growth_{light}) \times P(growth_{temperature}) \times P(growth_{nutrients})$$

H. tuna's modeled response to light is based on laboratory growth experiments (Appendix A) where specimens collected from the field sites were subjected to varying

light regimes and segment production rates were measured. The results in terms of the probability of producing a new segment per day were fit to the Platt et al. (1980) curve using least squares nonlinear regression. This particular equation was used because Beach et al. (2003) found a good fit with this equation and the photosynthesis-irradiance curve of *H. tuna*, and because photosynthesis was highly linearly correlated with growth. The data points obtained in the growth experiments showed a similar trend of increasing growth as irradiance increased initially then sloped downwards at higher irradiance values.

$P\ (growth_{light})$ = probability of producing a new module given the light level

$$= a(1 - e^{-bI/a})\ e^{-cI/a}$$

where,

I = irradiance in PAR or μmol m^{-2} s^{-1}

The probabilities obtained from the experiments were very low, and therefore the parameters were scaled up to allow growth to occur in the model. The original values of the scaling parameters *a* and *b* (0.0003 and 0.08, respectively) in the fitted equation, yielded virtually no growth since the peak growth probability was at 0.01, these were shifted to 0.01 and 0.04 to allow for a higher peak growth probability where qualitatively more sensible growth rates were observed. As much as it would be desirable to have the exact same conditions in the aquaria as that found in the field, this is impossible; thus a parameter correction was necessary. Water motion simulating surge and currents could not be replicated in the aquaria. This could have potentially lowered growth rates by

decreasing boundary layer fluxes (Hurd 2000), however, this effect should be uniform across the light treatments.

A normal probability distribution was used to represent the response of *H. tuna* to different temperature levels, with the optimal temperature within 27-29^{o}C (Hillis-Colinvaux 1980).

$P\ (growth_{temperature})$ =probability of growing given the temperature level

$$= \frac{1}{\sqrt{2\Pi\sigma}} e^{-\left(\frac{(t-\bar{t})^2}{2\sigma^2}\right)}$$

where,

t = temperature in degrees Celsius

$\bar{t}$ = mean optimum growth temperature

σ = standard deviation

Nutrients are the most coarsely represented of the modeled factors. Growth probabilities for the macroalgae are assigned to the three categories of low, average and high nutrient conditions. These can be changed depending on the hypothesis to be tested. For example, scenarios can be constructed such that high nutrient conditions have higher growth probabilities and the results compared to observed data to test the hypothesis that increased growth and cover of macroalgae are due to increased nutrient availability (Littler 1980).

$$P(growth_{nutrients}) = \text{probability of growing given the nutrient conditions}$$
$$= \begin{cases} x_{low} & \text{for low nutrient conditions} \\ x_{average} & \text{for ambient nutrient conditions} \\ x_{high} & \text{for high nutrient conditions} \end{cases}$$

Branching. A module producing a new module depends on where it is located within the thallus of the individual alga. This is modeled using a gamma curve to simulate higher probability of producing new segments if the "mother" segment is lower within the thallus. This allows *H. tuna* to maintain an upright and biomechanically stable form by preventing the higher portions from overwhelming the lower portions in weight. Production of a new module is additionally dependent on the number of "offspring" modules that the module has already produced. This is modeled using a negative linear model to represent the limit in producing modules as the number of offspring modules increases. *H. tuna* in the field has been seen to have a maximum of five branches or offspring modules.

Fragmentation. Fragmentation is a process in which algal modules are severed from the attached individual alga. These fragments are formed through breakage due to herbivores or hydrodynamic forces, and they subsequently can survive and reattach to form new individuals. Fragmentation in SPREAD occurs only at the edges. Modules with no offspring modules are considered "edge" modules. A percentage of these edge modules is chosen randomly to start the fragmentation process. The sizes of the fragments are randomly drawn from a normal distribution parameterized with the mean of fragment sizes and standard deviation based on a study of *H. tuna* fragment pool by Walters et al.

(2002). Fragmentation can lead to mortality if fragments are not allowed to survive, or if the fragments are allowed to survive, the probability of surviving is based on estimates from the field study of Vroom et al. (2003). The locations of the newly settled fragments within the grid are randomly assigned.

Measuring *Halimeda tuna* morphometrics in the Florida Keys

The model-derived results were compared with morphometrics and growth data of *H. tuna* in the Florida Reef Tract. The growth pattern of *H. tuna* allowed for detailed tracking of the growth of the segments through time, which could not be done with *H. opuntia* and *Dictyota* due to their highly clumped and fragile (for *Dictyota)* morphologies.

Study site

This study used two inshore patch reefs (Coral Gardens and Cheeca Patch), and two offshore spur and groove reefs (Little Grecian and French Reef) in the Florida Keys National Marine Sanctuary (Figure 2.4).

Model species

H. tuna is a calcareous alga belonging to the Order Chlorophyta. It attaches onto the reefs using filamentous holdfasts. The segments are green, lightly calcified, disc-like and roughly triangular in shape (Littler and Littler 2000). They can reproduce sexually through the synchronous release of gametes typically several times in the summer months (Clifton 1997, Vroom et al. 2003). Sexual reproduction leads to the death of the entire thallus, which is termed as holocarpic reproduction. Asexual reproduction via fragmentation is an important component of their life history (Walters et al. 2002).

Measuring Halimeda tuna

H. tuna were tagged and monitored for growth rates and patterns during Fall 2004, Winter and Summer 2005. At the beginning of the sampling season, 15-20 macroalgae were randomly tagged using haphazardly deployed transects. Tagging consisted of securing a twist tie around the base of the macroalgae and hammering a masonry nail beside it with a unique number. The individuals were relocated every week for at least four weeks per season and digital photographs were taken against a white scaled background. These photos were subsequently analyzed for various morphometrics (Haddad and Ormond 1994, Kaandorp and Kubler 2001, Vroom et al. 2003): number of segments, number of new segments, and number of segments lost.

Statistical analyses

Repeated measures ANOVA was used to analyze the data on growth rates and patterns of tagged *H. tuna*. Data were transformed as necessary to conform to assumptions of normality and homogeneity of variances. Tukey's Honest Significant Difference was used for multiple comparisons between means. If the data did not meet parametric test assumptions, the non-parametric Kruskal-Wallis was used to compare means and Dunn's Test to carry out multiple comparisons.

Results

Model results: running SPREAD using site-specific scenarios

SPREAD was run using growth parameters for *H. tuna* that were held constant (Table 2.1), while the environmental parameters were different for each site (Table 2.2).

The differences between the sites were depths and light levels, while attenuation coefficients and seasonal temperatures varied only between the two habitat types. Nutrient and fragmentation values were equal. A model run was initialized with ten individuals of *H. tuna* in a 30 cm x 30 cm x 30cm grid and allowed to run for 1000 days. Each scenario was run 30 times and the averages obtained.

The average number of segments, or modules, that *H. tuna* individuals varied between the simulated sites (Figure 2.5). French Reef had the highest number of segments per individual, while Little Grecian had the lowest (Kruskal-Wallis test, $p = 1.283 \times 10^{-263}$, Dunn's multiple comparison test). The numbers of segments at the two inshore patch reefs, Cheeca Patch and Coral Gardens, were situated in the middle of these two extremes and were not significantly different from each other. The segment production rate per individual algae followed the same trend as the number of segments: French had the highest segment production rate, while Little Grecian the lowest and the two patch reefs were in the middle (Kruskal-Wallis test, $p = 7.89 \times 10^{-92}$, Dunn's multiple comparison test).

In situ differences in Halimeda tuna growth patterns between habitat types

There was a significant difference in the number of segments an individual *H. tuna* had between sites (Repeated Measures ANOVA, natural log transformed, $p = 0.025$, Tukey's HSD test). Similar to the model results, individuals at French Reef had the most segments, while individuals at Little Grecian had the fewest. The two inshore patch reefs, Cheeca and Coral Gardens, were again located in the middle (Figure 2.5).

When growth rates between sites were compared, they were only weakly different (Repeated Measures ANOVA, Box-Cox transformed $\lambda = -0.95$, $p = 0.06$). However, the pattern was similar to that of the number of segments/individual, with French Reef tending to have high growth rates, and Little Grecian tending to have low growth rates. Cheeca Patch was also more similar to French Reef, while Coral Gardens tended to have low values like Little Grecian.

Looking at mortality rates, there was no difference observed between sites (Repeated Measures ANOVA, Box-Cox transformed $\lambda = 2.1$, $p = 0.169$).

Discussion

SPREAD results comparable to independently observed data: pattern-oriented approach to evaluate SPREAD performance

A focal point in the formulation of SPREAD was to capture the essential characteristics of the target macroalgae that led to realistic growth patterns. Thus, an important part of this modeling project was obtaining data that could be independently compared to the model results and allow us to have confidence in model performance. Grimm et al. (2005) advocated the use of what they term 'pattern-oriented modeling' (or POM) as a means of testing, calibrating and validating agent-based models. POM fundamentally follows the scientific method of using observed patterns in nature to generate questions and hypotheses and, of course, to test these. In the present case, parameters for the model were derived from literature and laboratory experiments, rather than being calibrated with the field data. This completely independently parameterized SPREAD was able to reproduce the general growth patterns (number of

segments/individual and segment production rates) of *H. tuna* as observed in four reef sites in the Florida Keys.

Using SPREAD to investigate potential factors influencing H. tuna growth pattern variations

The primary difference between the sites in the model runs was the light regime. Based on the comparable model results and field data, light seems to play a major role in shaping the growth rates and patterns of *H. tuna* in these reefs. The French Reef populations exhibited the highest number of segments and growth rates, while the shallowest site, Little Grecian, had the lowest values. Vroom et al. (2003) also found differences between the shallow and deep *H. tuna* populations in another Florida Keys reef, Conch Reef. Similarly, they found that the deeper population had more segments, as well as higher growth rates. Beach et al. (2003b), who conducted a study on the ecophysiology of *H. tuna* in the same site as Vroom et al. (2003), provides a potential explanation. This species' photosynthetic saturation point is well below the light that it experiences in the shallow site and can become photoinhibited under high light conditions. The model results lend support to this photo-inhibition hypothesis since the light growth curve of *Halimeda tuna* allows for photo-inhibition to occur. In this study, the Little Grecian *H. tuna* were receiving approximately three times as much light as those in French Reef. The two inshore patch reefs (Coral Gardens and Cheeca Patch) are interesting because, if we only considered depth and surface irradiance, they would not be different from Little Grecian. However, they were significantly more turbid (Boyer and Jones 2004) than the offshore reefs, which is reflected in their attenuation coefficients in the model. This amounted to Little Grecian receiving about one and a half

times more light than these patch reefs and making them intermediate between the two spur and groove sites in their light regimes. The growth patterns seen in the field and model follow this variation in light quantity reasonably well.

There were some differences between the model and observed results. The model values were quantitatively lower compared to the field measurements. This is most likely due to the parameters being derived from laboratory experiments, even though these parameters were scaled up, as discussed in the Methods (Submodel) section of this paper. However, even with this discrepancy, the magnitudes are similar and the inter-site patterns were produced by the model.

Another difference between the model and observed results is that in the real reefs, the number of segments per individual of the patch reefs, particularly Cheeca Patch, tended to be closer to those of French Reef. The segment production rate of Cheeca Patch was also indistinguishable from French Reef. The model results did not show those patterns. However, if nutrient levels differed between sites in the model, with the patch reefs experiencing higher nutrient levels and the *H. tuna* being able to assimilate the higher nutrients, the patch reef populations would be expected to be closer to that of French Reef (Figure 2.5). The long-term monitoring data of the SERC-FIU on water quality has documented the significantly higher Dissolved Inorganic Nitrogen (DIN) found in inshore reefs (Boyer and Jones 2004) and has classified sites close to Cheeca and Coral Gardens as having relatively elevated DIN. Smith et al. (2004) suggest that differences between shallow and deep populations of *H. tuna* in Conch Reef, as well, could also be due to higher nutrient concentrations in the deeper site. They documented

that the deeper populations were less nutrient limited, potentially due to the influx of deep-water nutrients from upwelling events that did not reach the shallow back-reef area.

Conclusions

The use of a spatially-explicit agent-based model enabled us to the capture the emergence of macroalgal growth forms that can have important implications in terms of spatial occupation and spread in the coral reef substrate. The model SPREAD allows incorporation of the modularity, clonality and morphological plasticity of *Halimeda* and *Dictyota* spp., the dominant macroalgae in the Florida Keys. It revolves around the iteration of macroalgal module production in response to light, temperature, nutrients, and space availability, and this process builds the individual algae then the population in a patch of reef substrate.

The SPREAD model was used to simulate the growth of *Halimeda tuna* based on literature and laboratory-derived values for growth factors. The results from the model show that it can reproduce general growth patterns of *H. tuna* in Florida reefs. Explorations with the model in conjunction with field measurements also illustrate its use in potentially teasing out mechanisms and factors responsible for the growth patterns observed. The number of segments an individual macroalga has seems highly influenced by the growth requirements of light and nutrients rather than mortality through fragmentation. Such a mosaic of experiments and scenario-running in models can be instructive in discerning patterns and the potential causes of these patterns.

Table 2.1. Parameters in SPREAD that are held constant in all the scenario runs.

Parameter	Description	Unit	Value	Source
Season	One static or two seasons; make use of seasonal values where specified	-	2	
Light				
Allow shading?	If shading will occur or not	Boolean	true	
Tissue transparency	Amount of light that a module will allow through to the cells below it	Fraction	0	*H. tuna* segments are solid and opaque
# cells affected by shading	Number of cells below module that will be affected by its shade	Cells	3	Estimated*
Branching (*Halimeda tuna)*				
branch order	Curve for effect of branch order on producing a new module			
a		-	0.2	Estimated*
b		-	0.5	Estimated*
c		-	0.3	Estimated*
branch present	Line for effect of number of modules already produced on producing a new one			
slope		-	-0.14	Estimated*
intercept		-	0.7	Estimated*
Mortality				
fragments		Fraction	0.01	Option**
Light curve (*Halimeda tuna)*				
a		-	0.01	Laboratory observations (Chapter 3 – Figure 3.4, Appendix A)
b		-	0.04	Laboratory observations (Chapter 3 – Figure 3.4, Appendix A)
c		-	8	Laboratory observations (Chapter 3 – Figure 3.4, Appendix A)
Temperature curve (*Halimeda tuna)*				
Mean growth temperature		^{o}C	29	Beach et al. (2003b), Biber (2002), Hillis-Colinvaux (1980), Lirman and Biber (2000)
Standard deviation		^{o}C	2	Beach et al. (2003b), Biber (2002), Hillis-Colinvaux (1980), Lirman and Biber (2000)

*These were used to best represent the taxonomic descriptions of the species (see text for discussion).

**This value was set at a relatively low percentage and the same for all scenario runs since no differences were seen in the segment mortality rates of *H. tuna* individuals between sites.

Table 2.2. Parameters in SPREAD that vary for site-specific scenario runs.

Parameter	Description	Unit	Site/Scenarios						Source
			French Reef	Little Grecian	Cheeca Patch	Coral Gardens	Cheeca Patch (high nutrients)	Coral Gardens (high nutrients)	
Depth		m	7	3.2	3.7	3.7	3.7	3.7	Field observation
Irradiance									
Mean	Surface irradiance	µmol m^{-2} s^{-1}	1942	2102	2167	2076	2167	2076	Field observation
standard deviation	Surface irradiance standard deviation	µmol m^{-2} s^{-1}	577	646	740	547	740	547	Field observation
Attenuation coefficient	Irradiance attenuation coefficient	-	Summer: 0.26 Winter: 0.14	Summer: 0.26 Winter: 0.14	Summer: 0.34 Winter: 0.23	Summer: 0.34 Winter: 0.23	Summer: 0.34 Winter: 0.23	Summer: 0.34 Winter: 0.23	SERC-FIU
Temperature									
Mean		°C	Summer: 28 Winter: 24	Summer: 28 Winter: 24	Summer: 29 Winter: 22.3	Summer: 29 Winter: 22.3	Summer: 29 Winter: 22.3	Summer: 29 Winter: 22.3	SERC-FIU
standard deviation		°C	Summer: 1.4 Winter: 3	Summer: 1.4 Winter: 3	Summer: 1.8 Winter: 5.7	Summer: 1.8 Winter: 5.7	Summer: 1.8 Winter: 5.7	Summer: 1.8 Winter: 5.7	SERC-FIU
Nutrients level		1 – low 2 – medium 3 – high	2	2	2	2	3	3	Exploratory and SERC-FIU (relative)
Nutrient growth probabilities									
average		fraction	0.4	0.4	0.4	0.4			Exploratory
high		fraction					0.6	0.6	Exploratory

Figure 2.1. Conceptual diagram of the agent-based model for reef macroalgae dynamics. Pictures of *Halimeda tuna* and *Dictyota menstrualis* illustrate their respective thallus modules.

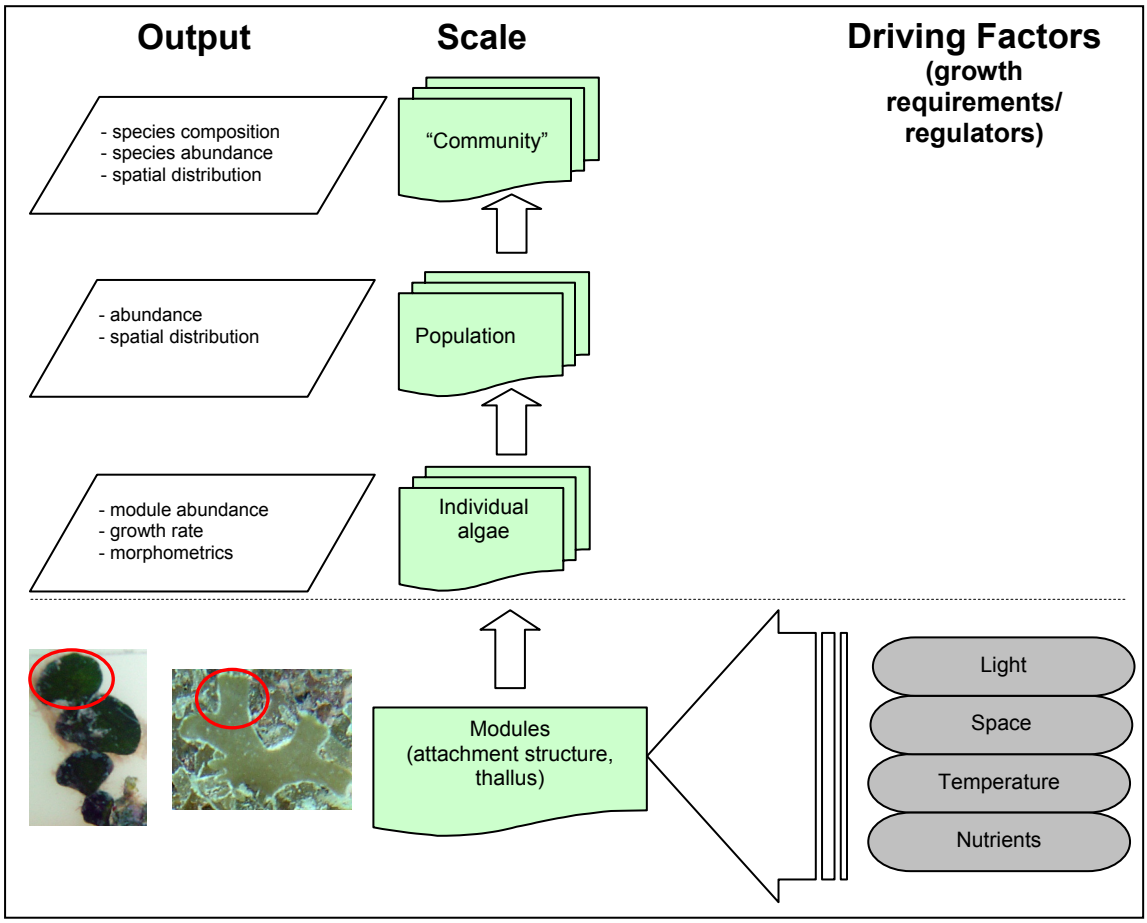


Figure 2.2. Visual output of SPREAD showing representations of *Halimeda tuna* (Base: Thallus:), *Halimeda opuntia* (Base: Thallus:), *Dictyota* sp. (Base: Thallus:) growing in a 3D grid.

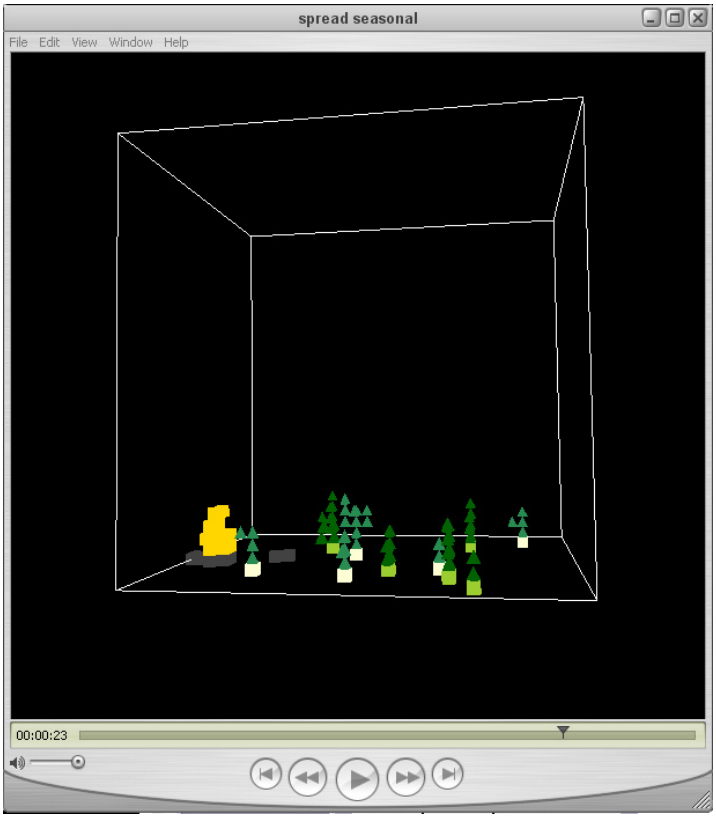


Figure 2.3.Flow chart of elements and processes occurring at each time step (one day) in SPREAD. 1 – Environmental values are set first that affect the decision of a module to produce a new module 2 – Module decides to produce a new module based on the environmental conditions in the cells around it and the species' branching rules. 3 – Modules at the edges can be randomly picked to fragment. These fragments may or may not survive. The accumulation of a string of modules forms the individual macroalgae.

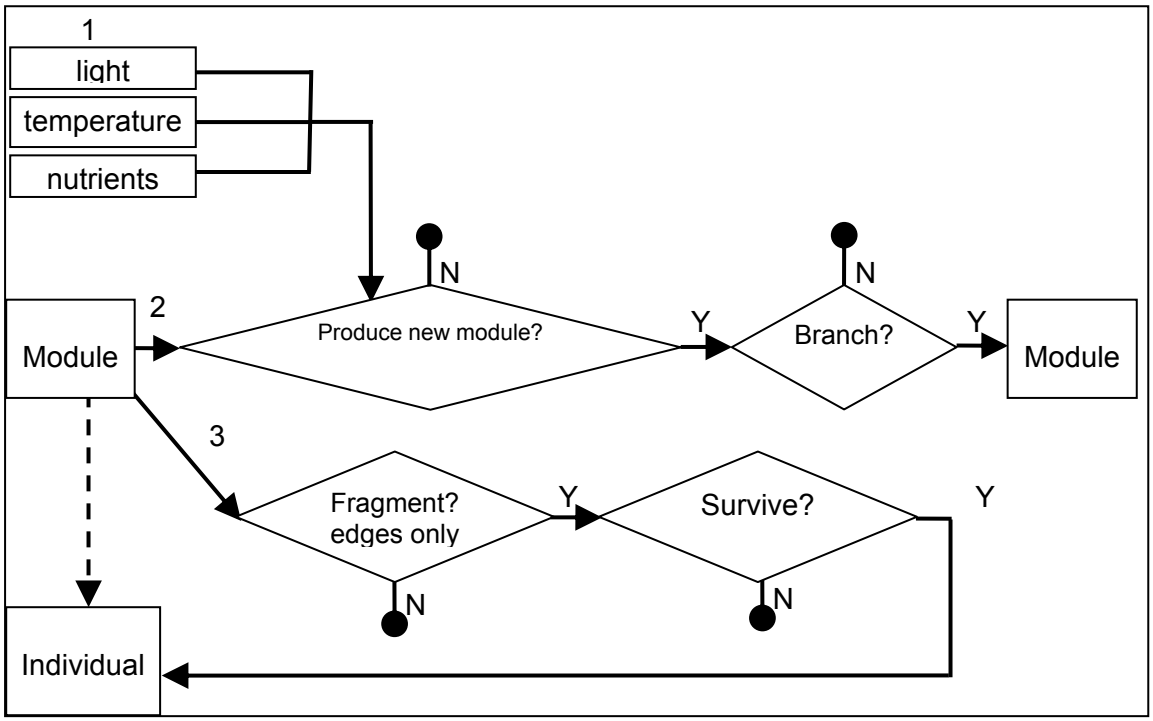


Figure 2.4. Map of study sites in the Florida Keys Reef Tract.

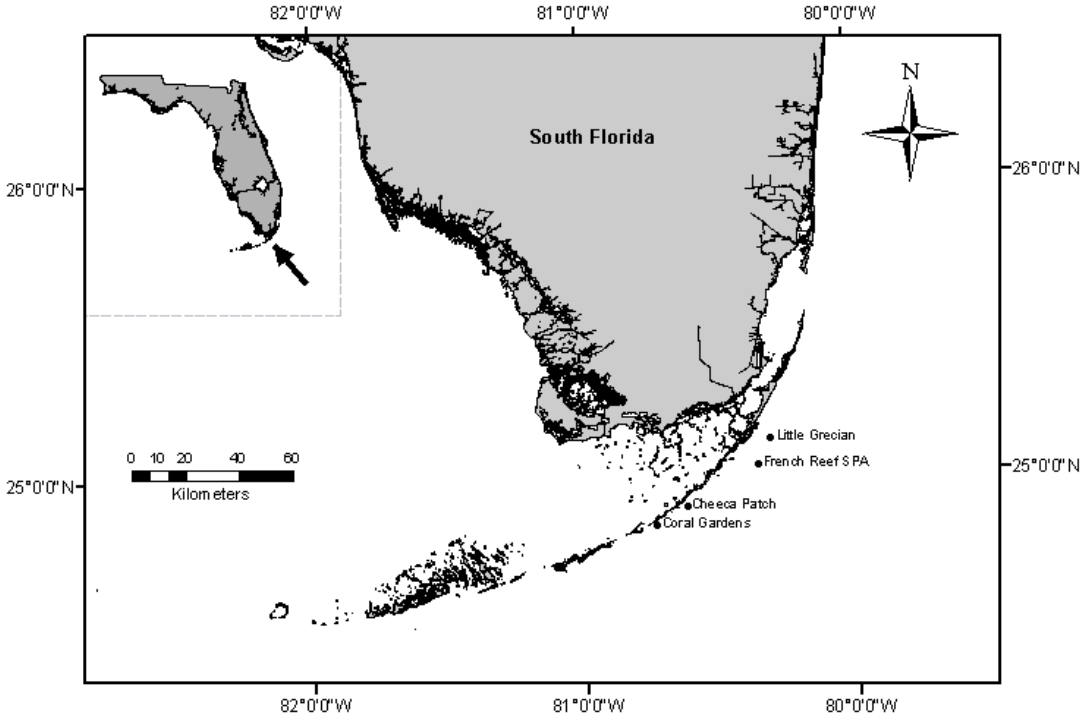
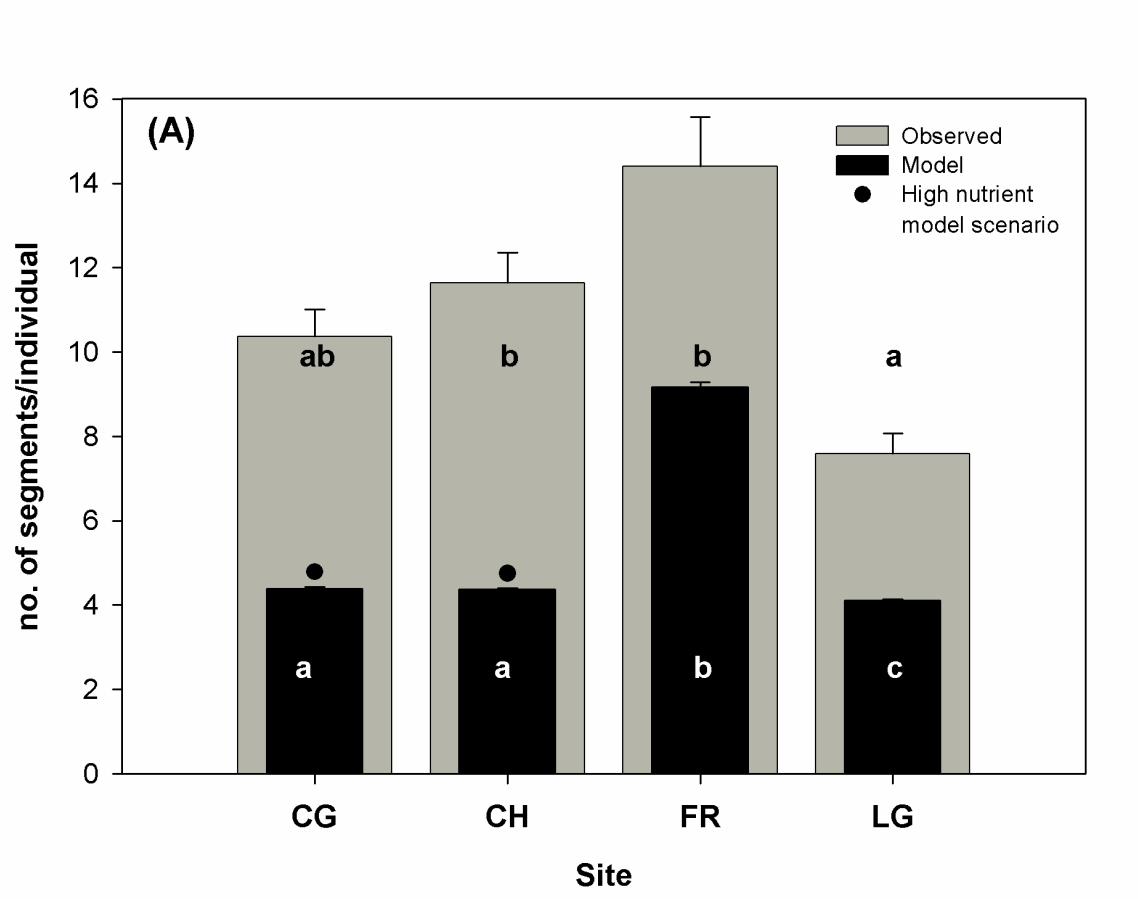
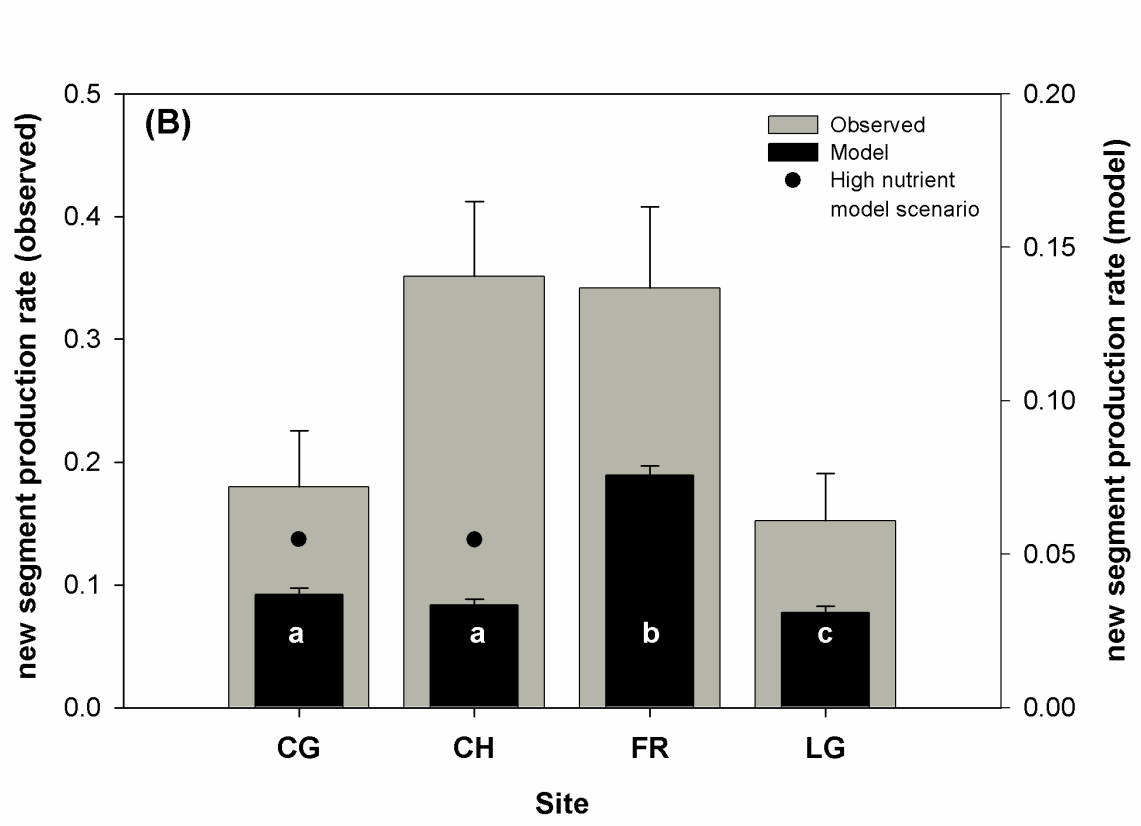


Figure 2.5. Results from simulated site-specific runs of SPREAD and measurements from actual field sites in the Florida Keys. (A) Number of segments per individual *Halimeda tuna*. (B) New segments produced per individual per day. Model values are averages of 30 model runs. Error bars represent the standard errors. Sites with different letters are significantly different from each other ($p < 0.01$). The lower row of letters corresponds to the model data, while the upper row is for the field data. These graphs also show the results from simulated high nutrient conditions in Coral Gardens and Cheeca Patch as points (high nutrient model scenario). CG=Coral Gardens, CH=Cheeca Patch, FR=French Reef, LG=Little Grecian. Note different axes used in (B) in order to better illustrate comparison of patterns.




(B)
Observed
Model
High nutrient model scenario
new segment production rate (observed)
new segment production rate (model)
0.5
0.4
0.3
0.2
0.1
0.0
0.20
0.15
0.10
0.05
0.00
a
a
b
c
CG
CH
FR
LG
Site

III. WHAT'S IN A FORM? DECIPHERING MESSAGES FROM THE MORPHOLOGIES OF *HALIMEDA* AND *DICTYOTA*

Introduction

In general, marine macroalgae found in coral reefs display plasticity in their morphologies. Their modular construction is one source of their morphological plasticity (Halle 1986), where a modular organism's body is built up by the iteration of one or more distinct units, i.e., modules. A large body of literature exists on the dynamics of these modules in terrestrial plants (Bell and Tomlinson 1980, Lovett-Doust 1981, Harper 1985, Hutchings 1988, Hutchings and Wijesinghe 1997, de Kroon et al. 2005). It has been shown that these modules in various plants are able to react, independently of the "whole" plant, to their local environment (Sutherland and Stillman 1988, de Kroon et al. 2005). In terrestrial plants, these modules consist of leaves, stems, and roots. Roots, for example have been found to "forage" for nutrients. For example in low nutrient patches, the filamentous roots lengthen, whereas under high nutrient conditions, they branch more in order to exploit this "good" patch (de Kroons and Hutchings 1995).

For macroalgae, an ideal world would be where the water temperature is just right, the light is good without photo-inhibition, and there is enough water movement to allow for the proper amount of nutrients to be taken in, but not strong enough to cause damage or uprooting. There should also be nothing around that eats it or grows on it. Of course, no such conditions exist and like all other organisms, there are trade-offs to be made between growing and reproducing vs. avoiding injury and death. For modular organisms, such trade-offs can be deciphered from their growth form in conjunction with knowledge about the environment they live in. It has been proposed that to maximize

productivity, thin and wide thallus forms that have high surface area to volume ratio are preferred (Littler and Littler 1980, Hay 1986). However, this growth preference is constrained by forces that detach parts or the whole alga (Lubchenco and Gaines 1981, Koehl 1986). There have been a relatively large number of studies investigating the effect of a trade-off between obtaining light and the potential damage that water motion can cause. In temperate species such as kelp, many morphological traits seem to be strongly affected by these two factors (Koehl and Wainwright 1977, Koehl and Alberte 1988, Carrington 1990). There are only a few studies that have looked at macroalgae in tropical ecosystems. For example, Collado-Vides (2002b) demonstrated differences in the morphology of *Caulerpa prolifera* in a coral reef lagoon in Puerto Morelos, Mexico, related to light and possibly water motion variation. On the disturbance or mortality side, decreased herbivory was shown by Lewis et al. (1987) to lead to a drastic change in the morphology of *Padina jamaicensis* from a prostrate turf growth form to a foliose upright one. A study by Hay (1981a) illustrated the shift from individual and upright growth forms to compact ones of several macroalgal species, including *Halimeda opuntia* and *Dictyota bartayresi*, due to trade-offs between obtaining light and avoiding grazing or desiccation.

Similar to many other coral reef ecosystems in the Caribbean, the Florida Reef Tract has experienced a drastic decline in the cover of reef-building corals within the last three decades (Porter et al. 2002, Gardner et al. 2003, Beaver et al. 2006). These reefs have high cover of macroalgae (Chiappone and Sullivan 1997, Lirman and Biber 2000). The dominant species belong to two genera: *Halimeda* (Chlorophyta) and *Dictyota* (Phaeophyta) (Lirman and Biber 2000, Lirman et al. unpublished manuscript). However,

despite the large body of literature investigating aspects of the phase-shift in coral reefs, little is still known about the dynamics of the macroalgae themselves whether at the individual, population or community level. The objectives of this study were to determine the 1) potential (using a model) and 2) realized (model results compared to the field) morphological variations in three dominant species of macroalgae in the Florida Keys, *H. tuna* (Ellis and Solander) Lamouroux*, H. opuntia* (Linnaeus) Lamouroux*,* and *D. menstrualis* (Hoyt) Schetter, Hörnig and Weber-Peukert; and, 3) factors contributing to these morphologies.

Methods

SPREAD formulation

SPREAD is a spatially-explicit agent-based model constructed by the author, wherein the basic agent is a macroalgal module. It was developed in order to capture the morphological plasticity and modularity of macroalgae. Details on the formulation and implementation of the model were discussed in Chapter 2 and the parameters used for this study are in Table 3.1. In the model, the production of modules by other modules is affected by the external conditions of light, temperature, nutrients and availability of space. Internally, species-specific branching rules are used (Figures 3.1 to 3.3). 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 was represented using the Lambert-Beer Law, parameterized with field measurements. Temperature and nutrients do not vary spatially within the 3D grid,

but can vary temporally or depending on the scenario being run. The probability distributions that each species of macroalgae uses in their decisions to grow in response to light were derived from laboratory studies (Table 3.1 and Figure 3.4, Appendix A). Normal probability distributions were used to represent their response to temperature, based on literature. The production of modules by each species of macroalgae in response to nutrient was coarsely represented by one probability value for each of the three nutrient levels (low, medium, high).

Disturbance in SPREAD occurs through fragmentation of the modules of all the macroalgal species. Fragmentation occurs when algal modules are severed from the attached individual alga. It only occurs from the edges and once fragmented, modules are considered lost or dead (i.e., no fragment survival and settlement) in this study since only the morphology of the individual macroalgae is of concern. Disturbance was distinguished into two types: herbivory and high water motion. Large herbivores such as fish mainly pick on macroalgae from the top and thus from the edges. High water motion from surge or currents can either uproot the whole alga or tear off more and larger fragments from the individual.

Dictyota in the model is a generic species since the light curve was obtained from *Dictyota cervicornis* (Appendix A), while the other parameter values were obtained from literature values for *Dictyota* spp. (Table 3.1).

Morphometrics such as number of segments, height, and width, were obtained from the virtual macroalgae in SPREAD. These are the same as those measured in the field and thus allow for direct comparison.

SPREAD is a Java program incorporating components from the Mason Multiagent Simulation Toolkit (Luke et al. 2005, http://cs.gmu.edu/~eclab/projects/mason/).

Model scenarios

SPREAD was parameterized with various light, temperature and nutrient values. Ten irradiance levels were used, ranging from 100 to 3100 PAR. The minimum value was based on PAR data from the SEAKEYS Fowey Rock and Molasses Reef stations in the Florida Reef Tract, and the maximum value was based on PAR data obtained by A. Yñiguez using a LI-COR LI-193 Spherical Underwater Quantum Sensor at the four study sites discussed below. A 30% standard deviation was used for each level which was also based on the variance observed by the author at the four study sites.

The two seasons of summer and winter were represented in all of the scenarios run. The range of temperatures for the summer season was 24.5 to 32.3 ^{o}C, and for the winter season it was 6.6 to 27.9 ^{o}C. These ranges were based on the Southeast Environmental Research Center 1995-2004 dataset for their sites closest to the four study sites, as well as temperature data obtained directly using a YSI multi-parameter probe. During each discrete time step in the model (equivalent to a day), a temperature value was uniformly randomly chosen from the appropriate seasonal range.

Each irradiance level was crossed with each of the three nutrient levels and three disturbance regimes of 0.01% and 0.05% fragmentation, and 0.05% fragmentation with larger fragment sizes. All of these scenarios were run for the three macroalgal species separately. Ten individuals of a species were randomly distributed in the grid, and the

model was run for 1000 days. Data from the average of 50 runs were used and the same morphometrics obtained from the field were also gathered from the model.

Fieldwork

Study sites and their environmental variability

Four sites in the Florida Keys were used for this study (Figure 3.5). Two inshore patch reefs, Coral Gardens (24^{o} 50.157'N, 80^{o} 43.657'W) and Cheeca Patch 24^{o}53.826'N, 80^{o}36.948'W), and two offshore bank reefs, Little Grecian (25^{o}07.140'N, 80^{o}18.020'W) and French Reef (25^{o}02.022'N, 80^{o}20.997'W). The latter sites were located seaward and were more exposed to the predominantly ESE winds, as well as influenced by the Florida Current (Haus et al. 2004), while the inshore sites are more protected by the outer reef tract. A study by Paddack (2005) compared grazing intensity of herbivores on macroalgae in the inshore versus offshore reefs in the Florida Keys and showed that it was higher in the offshore reef tracts. However, her inshore reef sites in the Upper Keys differed from the ones in this study.

The four sites did not vary in the surface irradiance at noon that they received (One-way ANOVA, $F = 0.265$, $p = 0.850$) (Table 3.2). However, irradiance at substrate level varied when this was calculated using overall average surface irradiance (2071.8910 μmol quanta m^{-2} s^{-1}), site-specific depths and average attenuation coefficients (0.26 for the offshore reef area and 0.34 for the inshore reef areas close to Hawk Channel). The latter were obtained from the long-term water quality monitoring data of the Southeast Environmental Research Center (SERC) at Florida International University. The two inshore patch reefs in the present study, on average, experience lower light conditions at

depth compared to the offshore bank reef sites including French Reef (Figure 3.6) which was deeper than the inshore reefs. This is due to these patch reefs being significantly more turbid (Boyer and Jones 2004). In terms of nutrient conditions, SERC obtained distinct water quality clusters out of their extensive sites throughout the Florida Keys National Marine Sanctuary (Boyer and Jones 2004). Based on their classification, Coral Gardens and Cheeca Patch are included in either cluster 5 or 6 which have relatively higher nutrients, particularly Dissolved Inorganic Nitrogen (DIN), compared to the offshore reef sites, which were all included in cluster 3, which had the lowest nutrient concentrations.

Morphometric surveys

The sites were surveyed during the summer days of September 18-19, 2006 when growth is highest for all three macroalgal species. For each site, the morphometrics of *H. tuna, H. opuntia,* and *D. menstrualis* were obtained. Separate surveys were done for each species, where 0.5 m^2 quadrats were haphazardly deployed, taking care not to sample close to each other, and ten individuals or patches at most of the species currently being surveyed were haphazardly chosen and measured. The depth for each quadrat was noted. For *H. tuna*, data included the 'number of segments' category (categories in bins of five were used, e.g., 1 = 1-5 segments, 2 = 6-10 segments, and so on), number of axes (defined as the number of branches within 3 segments of the bottom-most segment), height, width, substrate it was growing on, percent epiphyte cover, as well as the main epiphytes growing on the individual identified to species level if possible. It was difficult to determine individuals for *H. opuntia* and *D. menstrualis*, both of which grew in tangled clumps. For these two species, patches were distinguished by following what

appeared to be individual boundaries. The following data were measured: height, width, density category (1 – sparse, 2 – lightly packed, 3 – moderately packed, 4 – dense), percent epiphyte cover and main epiphytes identified to species level if possible. Epiphyte cover was not measured for *D. menstrualis* because this species does not commonly have epiphytes, and is itself usually epiphytic on *Halimeda* spp.

Statistical analysis

Model results: Cluster analysis and non-parametric tests

K-means cluster analysis in SPSS was used to differentiate distinct morphological forms that resulted from the various scenarios runs with SPREAD. This method minimizes the variation within a cluster and maximizes variation between clusters. Cluster analyses were run using standardized values of the number of segments, height, width and height: width ratio from all the scenarios. The height:width ratio was used to give an indication of the shape of the macroalgae. A value of one is equivalent to a hemispherical shape, values > 1 point to uprightness and values < 1 indicate a flat form. Separate cluster analyses were conducted for each species. The analysis was run using from two to eight as the number of clusters for each species, and the number of clusters that resulted in distinct, non-redundant forms was utilized.

The Kruskal-Wallis multiple comparison test in Minitab was used to test the differences of irradiance and nutrient levels between clusters for *H. tuna*, while the Mann-Whitney U-test (for two independent samples) was employed for *H. opuntia* and *Dictyota*.

Field data: Principal Components Analysis and MANOVA

The morphometrics gathered from the field study were analyzed using Principal Components Analysis (PCA) in order to condense the information in these morphometrics and the expected co-variances. The data were first transformed to natural logs in order to conform to the assumptions of PCA. Eigenvalues that were greater than or equal to 0.32 were extracted, following Haring and Carpenter (2007). The components were rotated to simplify interpretation using the varimax method which orthogonally rotates the components to minimize the number of variables with high loadings for each component (SPSS 15.0 for Windows). The first two Principal Components were then subjected to MANOVA to determine differences between the study sites. If there was a difference, Tukey's post-hoc test was employed to determine the specific site differences.

Results

Model results

Halimeda tuna

Six clusters yielded distinguishable morphologies (Table 3.3, Figure 3.7 and Figure 3.8a). Table 3.3 lists the detailed clusters, their forms and the conditions under which each is found, while Figure 3.7 are the actual model representations. Four were relatively small with shapes ranging from very flat to very upright. Two morphologies were larger, where one was more hemispherical than the other. The largest and most upright morphology of cluster 1 was found only under low light, high nutrient and low fragmentation conditions (Figures 3.8b, c, d). The other large cluster (2) was formed under high light but mainly under higher nutrient levels. The four clusters which contained the smaller-sized morphologies were found under varying light conditions, but

mainly mid- to high nutrient and higher fragmentation conditions. The upright forms were found more under lower irradiance levels compared to the hemispherical and wide forms, and also under high fragmentation (smaller fragments) conditions.

Halimeda opuntia

The morphological clusters for this species were not as varied as *Halimeda tuna* and the differences between clusters were mainly due to size rather than size and shape. Two clusters were used to represent the main forms observed: small and upright, and large and less upright (Table 3.3, Figure 3.7 and Figure 3.9a). The larger from was tending towards the hemispherical shape, but was still taller than wide.

Both clusters were found under similarly wide irradiance levels and all the nutrient levels (Mann-Whitney U-test, light: $p = 0.074$, nutrients: $p = 0.694$) (Figures 3.9c, d). The primary factor distinguishing the two is the fragmentation level, wherein the small and upright form was found under the extremes of low fragmentation and high fragmentation with large fragments, while the large and upright form was seen primarily under high fragmentation but smaller fragment sizes (Figures 3.9b).

Dictyota

There were three distinct morphological clusters observed for *Dictyota* sp. Two clusters were small and either upright or hemispherical in shape, while the third cluster was large and hemispherical (Table 3.3, Figure 3.7 and Figure 3.10a).

The small and very upright form, Cluster 1, was very restricted, and was only seen under nutrient level two at a mid-irradiance level and high fragmentation (larger fragments) (Figures 3.10 b, c, d). The hemispherical forms occurred under different but higher levels of irradiance (Mann-Whitney U-test, $p = 0.0000$), and different nutrient

levels (Mann-Whitney U-test, p=0.0000). The smaller form was found under relatively lower but still high light levels, lower nutrient and higher fragmentation conditions (both normal and larger fragment sizes).

Field results

There were distinct differences in the size and shape of the three macroalgal species among the four sites, particularly between the offshore spur and groove and inshore patch reef sites.

Halimeda tuna

The first two principal components explained 42% and 21% of the variation in the morphometrics of *H. tuna* from the four sites, respectively. The first principal component (PC1) was strongly correlated to width, height and number of segments, while the second principal component (PC2) was strongly correlated to the height:width ratio (Table 3.4). PC1 seems to differentiate based on size, while PC2 is related more to the shape. MANOVA and post-hoc tests showed that there was a significant difference between inshore and offshore sites in the two component loadings (Tables 3.5 and 3.6). *H. tuna* in the two inshore patch reef sites (Coral Gardens and Cheeca Patch) were larger (had more segments, were taller and wider) and more upright in form than the populations found in the offshore spur and groove sites (French Reef and Little Grecian). The *H. tuna* populations in the offshore spur and groove reefs had height: width ratios closer to one and were more hemispherical in shape.

Halimeda opuntia

Seventy-four percent of the variation in the morphometrics of *H. opuntia* was explained by PC1 (38%) and PC2 (36%). PC1 was highly correlated to the height: width ratio or the shape of the macroalgae, while PC2 was correlated to the size metrics, height and width (Table 3.4). MANOVA and post-hoc tests separated out differences in the morphologies between sites (Tables 3.5 and 3.6). The *H. opuntia* in the two patch reefs had significantly flatter shapes (low height: width) compared to those in French Reef. Little Grecian was in the middle of these two extremes. However, the inshore patch reefs had significantly larger *H. opuntia* than the offshore spur and groove reefs.

Dictyota

The first two principal components accounted for 44% and 30% of the variation in the morphometrics of *D. menstrualis*. PC1 was highly correlated to the shape metrics of height: width, as well as width, while PC2 was highly correlated with height (Table 3.4). Once again, MANOVA and post-hoc tests of PC1 and PC2 highlighted the site differences (Tables 3.5 and 3.6). Coral Gardens and Cheeca Patch had populations of *D. menstrualis* that differed significantly from French Reef and Little Grecian in their shape-related PC1 values. *D. menstrualis* in the two patch reefs were very wide and flat. For PC2, height or size-related, Cheeca was on one side of the spectrum as the largest and Little Grecian on the opposite side. French Reef and Coral Gardens were in the middle.

Model vs. field

The distinct morphologies of the three species in the real world study sites could be matched to the independently-derived morphological clusters in SPREAD (Figures

3.8a, 3.9a, 3.10a). The environments where these clusters occurred in the model also paralleled the inferred environments in the actual reefs. *H. tuna* in the patch reefs were most similar in size and shape to Cluster 1, while the offshore reefs populations were most similar to Cluster 3. Cluster 1 occurred in lower light, high nutrients and low fragmentation conditions. Cluster 3 morphs occurred in high light, low nutrients and high fragmentation conditions. For *H. opuntia*, Cluster 1 corresponded to the inshore reef morphs, and the other cluster (Cluster 2) was the most similar to the offshore reef morphs. These two clusters were differentiated only by fragmentation level and occurred under the same range of light and nutrient levels. Cluster 2 in *Dictyota* was the most similar to the offshore reef morphs, and Cluster 3 with Cheeca Patch and Coral Garden morphs. Although Cluster 2 was found under lower light levels compared to Cluster 3, their average values were both on the higher end and both clusters also encompassed a similar light range. The distinct differences between the two clusters were due to nutrients and fragmentation levels. Cluster 2 occurred in lower nutrient and high fragmentation conditions and Cluster 3 the opposite.

Discussion

The morphological plasticity of organisms provides a unique opportunity to observe and understand the factors influencing their growth and mortality. This is especially true in modular and/or clonal immobile organisms that leave tangible evidence of the production and death of their iterating units. Distinguishable changes in the morphologies of three macroalgal species were observed through SPREAD as they experienced varying light, nutrient and disturbance levels. However, the amount of

morphological variation differed between the three species and the convergence of forms made it difficult to tease out the effects of the growth from the mortality factors in detail. *H. tuna* had the most distinct number of categories, which also allowed for some separation of the factors responsible for them, while the morphological clusters of *H. opuntia* and *Dictyota* converged into two and three clusters, respectively, that differed primarily only in size under a variety of scenarios.

Morphological changes under the ideal to not so ideal growth conditions

SPREAD showed that under low fragmentation or mortality conditions, optimum light and nutrient conditions, all three species, as would be expected, tended to be larger. For *H. tuna*, it also grew in a more upright habit (Cluster 1) and when light and nutrients were higher, it became more hemispherical (Cluster 2). Hay (1981a) proposed that at lower light levels, mono-layered thalli will predominate, while at higher light levels, multilayered ones will be more abundant. Studies on the effect of light on the morphology of macroalgae have shown that if light is limiting, as light decreases, the thallus module units themselves can become wider and/or the spacing of the modular units becomes more sparse (less compact) (Collado-Vides 2002b, Haring and Carpenter 2007). *H. tuna* follows a similar pattern such that there was increased compactness in shape under higher light conditions. However, this is probably not because of their freedom from light limitation, because they have a relatively low light requirement (Beach et al. 2003b) compared to the light conditions in Cluster 2. More likely this form is due to the photo-inhibitory effect of high light that has been shown to affect their morphology (Hader et al. 1996, Beach et al. 2003b, Vroom et al. 2003).

H. opuntia and *Dictyota* did not exhibit any similar shift in shape as *H. tuna* when light or nutrients changed. This could be explained by the larger ranges of optimum light conditions to which they respond to similarly. Growth experiments controlling for light in aquaria that were used to parameterize SPREAD did exhibit similar growth rates under low to high irradiance levels for these two species (Figure 3.4). *Dictyota,* however, changed in size under higher light and nutrient conditions, although this effect co-varied with decreased fragmentation. Beach et al. (2006) did observe that lower light decreased primary productivity in *D. menstrualis* and *D. pulchella* in Conch Reef, Florida Key, and that they can also be nutrient-limited and respond physiologically to nutrient-enrichment.

Effects of mortality through fragmentation on morphology

Mortality, through herbivory and water motion, has long been recognized as a strong factor influencing macroalgae population and evolutionary dynamics (Lubchenco and Gaines 1981, Carpenter 1986, Koehl 1986). On an individual level, these are also important factors affecting the morphology of macroalgae. *H. tuna* did exhibit a shift in shape under increased mortality levels. Higher mortality simulating increased herbivory (high fragment pool but relatively smaller fragment sizes) resulted in smaller sizes and hemispherical shapes (Cluster 3). Lewis et al. (1987) showed that the brown algae, *Padina jamaicensis*, changed from a foliose form to a prostrate turf alga when herbivore intensity increased. Hay (1986) illustrated the role of herbivory and desiccation in favoring clumped and more hemispherical forms versus upright individuals in various macroalgal species including *H. opuntia* and *D. bartayresii*. Under the fragmentation conditions simulating increased disturbance, presumably from water motion, its shape

became small and wider or more prostrate. Studies on macroalgae have shown that they can change their shape to smaller, more compact or prostrate forms when water motion is high (Carrington 1990, Blanchette 1997, Boller and Carrington 2006) . This shape enables them to experience less drag and thus lower probability of being torn off from the substrate. Damage can potentially induce increased branching and/or affect directionality of growth and branching (Hay 1981a, Van Alstyne 1989). Interestingly, although module mortality in SPREAD is only through fragmentation as an external force that does not induce any sort of response from the macroalgae (e.g., re-direction of growth), it is still able to reproduce known patterns in morphology attributable to mortality.

Halimeda opuntia actually grew larger, though relatively less upright, with higher fragmentation levels associated with large fragment sizes (Cluster 1). However, the growth rate for this cluster was higher than Cluster 2's. This is possibly due to the decrease in self-shading that can limit growth of modules in the "understory" (Monsi et al. 1973, Harper 1985). *H. opuntia* is a highly branching species and its lower portions can stop growth and/or die while the upper portion continues growing (Hay 1981a). As large fragments are broken off, the lower segments are then able to sequester light, grow and branch. This is akin to pruning in terrestrial plants, wherein higher growth rates are achieved when pruning is regular. Fragmentation with smaller fragment sizes did not have a similar effect and resulted in smaller, slower growing forms.

Fragmentation, whether with small or larger fragments, affected *Dictyota* only by decreasing its size. The small and upright morphology under high fragmentation level and small fragment sizes (Cluster 1), rarely occurred.

The concept of a trade-off in the morphology of macroalgae implies a response (at the ecological scale) to the forces acting on an individual. One of the common examples for this trade-off is the variation in the blade width of temperate macroalgae between depths and different wave exposures (Koehl and Wainwright 1977, Koehl and Alberte 1988, Carrington 1990, Haring and Carpenter 2007). These studies have shown that not only can the macroalgae actively respond to light availability but also to hydrodynamics as a disturbance factor. In SPREAD, responsiveness is through amount of module production and directionality of module production as affected by light and space availability, while disturbance through fragmentation is an external and random process that does not affect any response. Other mechanisms for responding to light and nutrients that can influence morphology of the three macroalgae studied are size of segments (Beach et al. 2003b, Vroom et al. 2003, Smith et al. 2004) and intersegment distances (Littler and Littler 2000 for Halimeda opuntia). Damage to the macroalgae thallus has been shown to potentially cause the growth of adventitious branches on *Dictyota* (Gaillard et al. 1986, Cronin and Hay 1996). Even though SPREAD does not incorporate these other potential mechanisms for morphological plasticity, it was able to capture realistic variations in the three species because the morphometrics used were generalized enough.

Differential strength of factors influencing morphologies: a sign of differences in life-history strategies?

The three species had varying morphological plasticity and responses to the growth and mortality factors. *H. tuna* could be said to have the most plastic morphology, relative to *H. opuntia* and *Dictyota* spp., in terms of the morphometrics that were

included in this study. This could be due to the larger range of *H. opuntia* and *Dictyota* spp. light requirements, allowing them to grow similarly whether at lower or higher irradiance levels (Beach et al. 2006). An alternative explanation is that other morphometrics that were not used in SPREAD give rise to other morphologies in these two species. Segment size can vary for both, as well as segment shape and intersegment distances for *H. opuntia*. *H. opuntia* with higher intersegment distances, smaller and tri-partite segments that grow up and loosely are known to occur in lower light levels (Kooistra and Verbruggen 2005). For these two species, measuring density could also provide increased distinction of morphologies.

Halimeda tuna was strongly affected by both growth (light and nutrients) and mortality or disturbance factors compared to *H. opuntia* and *Dictyota* that seemed more strongly influenced by disturbance forces. Previous studies on *H. tuna* have shown similar shifts in morphology due to differing light and nutrient conditions (Beach et al. 1997, Beach et al. 2003b, Vroom et al. 2003, Smith et al. 2004) but no observed variation in grazing pressure (i.e., mortality). This species appears to be sensitive not only to limited light but also high light conditions that cause photo-inhibition (Beach et al. 2003b). Increased nutrient levels have also resulted in larger more upright morphologies (Smith et al. 2004). *H. opuntia* and *Dictyota* variation in size and (slightly) in shape was strongly influenced by disturbance rather than light, and for *Dictyota*, nutrients as well. Both of these species are relatively "good" fragmenters compared to *H. tuna*. This mechanism potentially allows these species to persist and even spread under high disturbance conditions. *H. opuntia* produces large fragments that can have high survival probabilities (up to 93%) (Walters et al. 2002). Various *Dictyota* species are the

dominant macroalgae in the offshore reefs despite being in a high disturbance environment. Their morphology in these sites indicates a low nutrient and high disturbance environment, yet they are successful in persisting and occupying the reef substrate. This is probably due to their capacity to easily produce fragments, which have almost a 100% survival probability even with small fragment sizes (Vroom 2001, Herren et al. 2006).

Macroalgae morphology as indicators of environmental conditions

At the cross-genera level, the morphologies of macroalgae can provide information about the environments in which they are found (Littler and Littler 1980, Steneck and Dethier 1994). These generalized groupings tend to be useful when investigating large-scale patterns, although the large variations in life histories of these different groups can obscure this information (Padilla and Allen 2000). Focusing on certain species can help give a clearer picture on the environmental factors influencing macroalgal morphologies (e.g., Hanisak et al. 1988, Benedetti-Cecchi et al. 2006). The concurrence of the morphologies derived from SPREAD with those found in the study sites provided information on the environmental conditions these macroalgae were experiencing where they were located. The conditions under which the particular morphologies were found in the model provided insight into the environmental variation between the inshore and offshore study sites.

Conclusions

SPREAD incorporates only light and spatial competition as the primary factors influencing directionality of module production. These factors, combined with random mortality through fragmentation and varying production rates under different nutrient and temperature levels were able to capture identifiable and realistic forms. The three species had varying morphological responses to growth and mortality or disturbance factors which could be due to their differing life-history strategies. These morphologies also followed known environmental gradients in the real world study sites. Morphometrics can thus be a helpful way of teasing out factors influencing the growth and spread of macroalgae in reefs, particularly if different species with distinct growth requirements and life histories are used.

Table 3.1. Description of SPREAD parameters used in simulations exploring the potential morphological clusters of the three macroalgae.

Parameter	Description	Unit	Species			Source
			Halimeda tuna	Halimeda opuntia	Dictyota sp.	
Season	One static or two seasons; make use of seasonal values where specified	-	2			
Depth		m	7			
Light						
Irradiance	Surface irradiance	μmol m^{-2} s^{-1}	100, 500, 700, 900, 1300, 1700, 2100, 2500, 2900, 3100			Sea Keys and field observations
Irradiance standard deviation	Surface irradiance standard deviation	μmol m^{-2} s^{-1}	30% of surface irradiance			Field observations
Attenuation coefficient	Irradiance attenuation coefficient	-	0.26			SERC-FIU
Allow shading?	If shading will occur or not	Boolean	true			
Tissue transparency	Amount of light that a module will allow through to the cells below it	Fraction	0	0	0.6	*Halimeda* segments are solid and opaque; Dictyota (Hay 1986)
# cells affected by shading	Number of cells below module that will be affected by its shade	Cells	3	3	3	Calibrated
Temperature						
Mean temperature		°C	Summer: 24.5 – 32.3 °C Winter: 6.6 – 27.9 °C			SERC-FIU and Field observations
Temperature standard deviation		°C	Summer: 5.5% Winter: 18.90%			SERC-FIU and Field observations
Nutrients level		1 – low 2 – medium 3 – high	1, 2, 3			Exploratory
Branching					Always dichotomous	
branch order	Curve for effect of branch order on producing a new module					
A		-	0.2	0.2	n/a	Estimated
B		-	0.5	0.5	n/a	Estimated
C		-	0.3	0.3	n/a	Estimated
branch present	Line for effect of number of modules already produced on producing a new one				n/a	
Slope		-	-0.14	-0.05	n/a	Estimated
Intercept		-	0.7	1	n/a	Estimated
Mortality						
Fragments		Fraction	0.01, 0.05			Exploratory
Fragment size ± std. deviation			3 ±1, 6 ±1	22 ±7, 44 ±7	4 ±1, 8 ±1,	Walters et al. 2002, Herren et al. 2006
Light curve			Exponential	Normal	Exponential	
a		-	0.01	0.4	0.003	Laboratory observations (Figure 3.4, Appendix A)
b		-	0.04	0.4	1	Laboratory

Parameter	Description	Unit	Species			Source
			Halimeda tuna	Halimeda opuntia	Dictyota sp.	
						observations (Figure 3.4, Appendix A)
c		-	8			Laboratory observations (Figure 3.4, Appendix A)
Temperature curve						
Mean growth temperature		°C	29	29	28	Beach et al. 2003, Biber 2002, Hillis-Colinvaux 1980, Lirman and Biber 2000
Standard deviation		°C	2	2	2	Beach et al. 2003, Biber 2002, Hillis-Colinvaux 1980, Lirman and Biber 2000
Nutrient probabilities						
low		Fraction	0.2			Exploratory
average		Fraction	0.4			Exploratory
high		Fraction	0.6			Exploratory

Table 3.2. Surface irradiance (Photosynthetically Active Radiation) collected from the four study sites during the sampling period of October 2004 through November 2005. Surface irradiance at noon was calculated using the formula $I_n = I / \sin (\Pi T/D)$ where I_n = irradiance at noon, I = irradiance at sampling time, T = time since sunrise, D = daylength.

Site	Date	Time	Surface irradiance (µmol quanta m^{-2} s^{-1})	Surface irradiance at noon (µmol quanta m^{-2} s^{-1})
French Reef	10/29/2004	1100	952.2	1139.7
	11/4/2004	1200	2271.0	2271.6
	1/31/2005	1230	2402.0	2520.3
	2/1/2005	1200	2251.0	2282.8
	2/9/2005	1200	1269.8	1407.5
	2/16/2005	1100	2026.0	2238.0
	2/23/2005	1130	733.6	765.9
	3/29/2005	1230	2515.0	2515.4
	8/9/2005	1105	1320.7	1559.5
	8/23/2005	1024	1682.0	2252.9
	9/2/2005	1109	1949.8	2281.6
	9/7/2005	1225	2020.0	2072.7
			Site average	1942.3
			Site standard deviation	577.1
Little Grecian	10/29/2004	1315	2353.0	2816.3
	11/4/2004	1520	1719.8	1720.2
	2/9/2005	1230	2116.0	2345.5
	2/16/2005	1255	2574.0	2843.3
	2/23/2005	1215	978.7	1021.7
	3/29/2005	1255	1957.4	1957.7
	8/9/2005	1325	992.4	1171.8
	8/23/2005	1150	1965.9	2633.1
	9/2/2005	1146	2123.0	2484.2
	9/7/2005	1347	1979.0	2030.6
			Site average	2102.5
			Site standard deviation	645.6
Cheeca	10/28/2004	1120	1977.7	2236.6
	2/2/2005	1245	2710	2713.2
	2/3/2005	1230	1080.7	1081.0
	2/7/2005	1130	1045.7	1096.4
	2/14/2005	1000	2288	3048.0
	2/15/2005	1220	2617	2623.6
	2/21/2005	1240	2856	2856.9
	4/5/2005	1100	2406	2917.7

Site	Date	Time	Surface irradiance (µmol quanta m^{-2} s^{-1})	Surface irradiance at noon (µmol quanta m^{-2} s^{-1})
	8/10/2005	1120	1893.8	2161.9
	8/24/2005	1130	1894.4	2115.4
	9/1/2005	1150	2006	2155.0
	9/6/2005	1059	831.5	996.7
			Site average	2166.9
			Site standard deviation	740.1
Coral Gardens	10/28/2004	1320	2162.0	2445.0
	2/2/2005	1030	2540.0	2543.0
	2/3/2005	1030	1034.3	1034.6
	2/7/2005	1045	2506.0	2627.4
	2/15/2005	1015	2236.0	2241.6
	2/21/2005	1045	2366.0	2366.7
	4/5/2005	1000	969.4	1175.6
	8/10/2005	1100	1829.1	2088.1
	8/24/2005	1200	2139.0	2388.5
	9/1/2005	1336	2124.0	2281.8
	9/6/2005	1253	1370.2	1642.5
			Site average	2075.9
			Site standard deviation	547.2
			Overall Average	2071.9
			Overall standard deviation	627.5

Table 3.3. Morphological clusters derived from the model for the three macroalgal species, their morphological description and the conditions where they formed.

Species	Cluster	Morphology	Conditions Found
Halimeda tuna	1	Large and upright	Only at low light levels Higher nutrient levels Only at low mortality
	2	Large and hemispherical	Higher light Higher nutrients levels Low mortality
	3	Small and hemispherical	Mid-light levels Lower nutrient levels High mortality levels primarily with small fragments especially at nutrient levels 2 and 3
	4	Small and upright	Low light Middle nutrient levels High mortality (both small and large fragments)
	5	Small and highly upright	Mid-light levels Lower nutrient levels High mortality (small fragments mainly)
	6	Small and wide	High light Mid-nutrient levels High mortality with large fragments
Halimeda opuntia	1	Large and less upright	All light and nutrient levels Low mortality or high mortality with large fragments
	2	Small and upright	All light and nutrient levels High mortality
Dictyota	1	Small and upright	Mid-level light and nutrients Only at high mortality
	2	Small and hemispherical	Mid-level light Low nutrients High mortality (small and large fragments)
	3	Large and hemispherical	Mid-to high light High nutrient levels Low mortality

Table 3.4. Summary of the two primary Principal Components loading scores for the morphometrics of the three species measured in the four field sites. These were all natural log-transformed to conform to assumptions of Principal Components Analysis.

Species	Morphometric	Principal Component 1	Principal Component 2
Halimeda tuna	No. of segments	.898	-.114
	Height	.910	.355
	Width	.912	-.333
	Number of axes	.211	-.098
	Height / Width	-.058	.992
	Epiphyte load	.170	.037
Halimeda opuntia	Height	.078	.996
	Width	-.742	.671
	Height / Width	.991	.126
	Density	-.030	-.037
Dictyota menstrualis	Height	-.027	.980
	Width	.882	.323
	Height / Width	-.926	.304
	Density	.338	.215

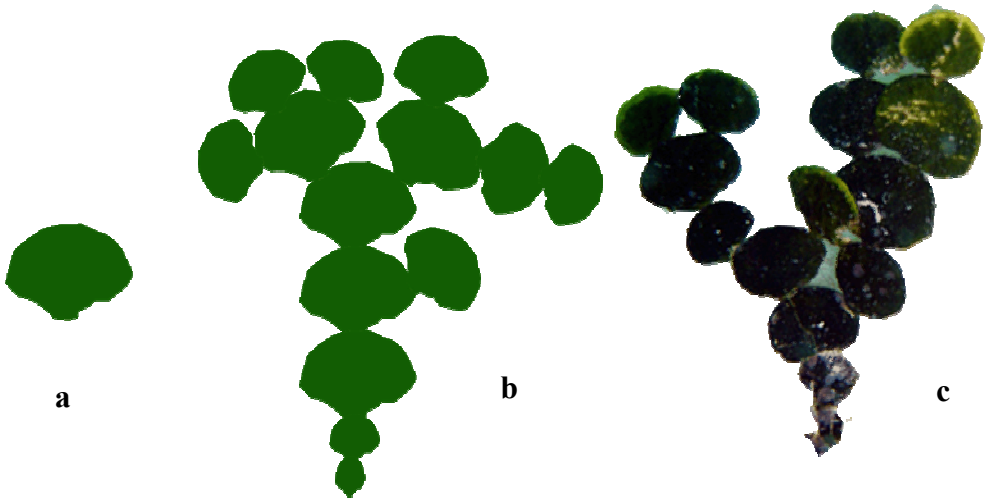
Table 3.5. Summary of the results from MANOVA of Principal Components 1 and 2 with site as treatment factor. Degrees of freedom for all was three since there were four sites. An asterisk on the probability denotes a p-value < 0.01.

Species	Principal Component	F-ratio	Probability
Halimeda tuna	PC 1 (size)	18.899	0.00000*
	PC2 (shape)	9.931	0.00000*
Halimeda opuntia	PC 1 (shape)	6.462	0.00029*
	PC2 (size)	23.142	0.00000*
Dictyota menstrualis	PC 1 (shape)	19.596	0.00000
	PC2 (size)	5.200	0.00157*

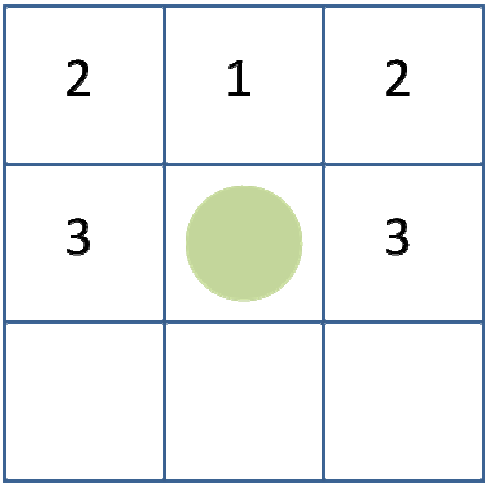
Table 3.6. Summary of the results from Tukey's B post-hoc tests between sites for Principal Components 1 and 2 after being run through a MANOVA. Sites with the same letter for a Principal Component (within a column) are considered similar.

	Halimeda tuna		***Halimeda opuntia***		***Dictyota menstrualis***	
	PC1	PC2	PC1	PC2	PC1	PC2
Little Grecian	A	A	AB	A	A	A
French Reef	A	A	A	A	A	AB
Coral Gardens	B	B	B	B	B	AB
Cheeca Patch	B	B	B	B	B	B

Figure 3.1. *Halimeda tuna* form and branching rules. One module is illustrated in a) and its general form is illustrated in b) while an actual photo is seen in c). The box diagram is a two-dimensional front view perspective of where new modules are produced. The module that will produce another module is represented by the olive circle. The numbers represent preference for where the new module will be placed. Thus, if it is available and the growth probability as influenced by light, temperature and nutrients allows for it, a new module will preferably be produced directly on top of the mother module. The next preferences are the two cells above and to the sides, and the last are the ones immediately to the sides.

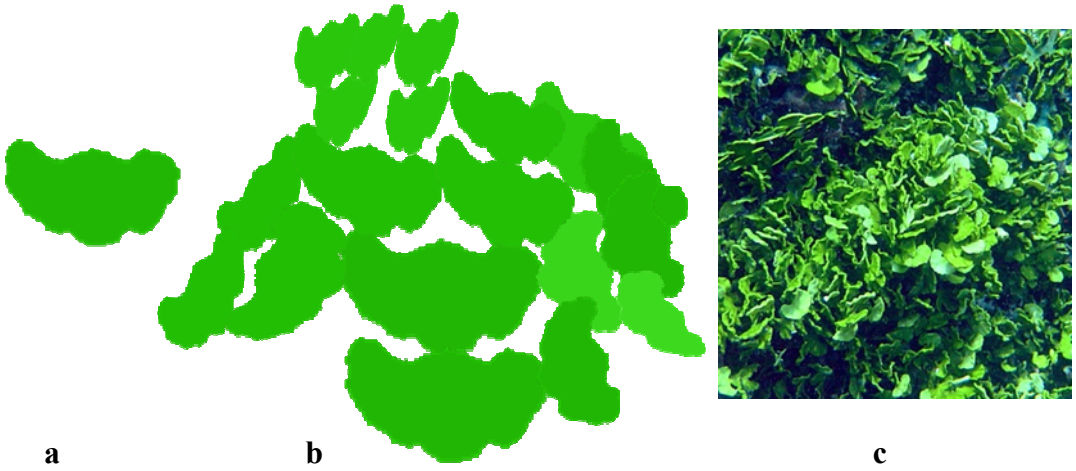


a **b** **c**

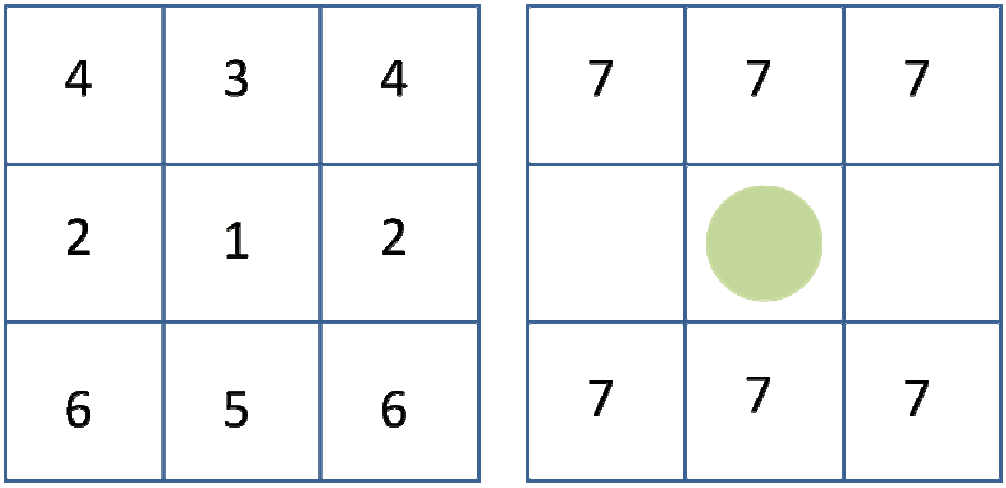


d

Figure 3.2. *Halimeda opuntia* form and branching rules. One module is illustrated in a) and its general form is illustrated in b) while an actual photo from top view is seen in c). The box diagrams are two-dimensional top view perspectives of where new modules can be produced. The module that will produce another module is represented by the olive circle. The numbers represent preference for where the new module will be placed. The plane or cross-section directly above the mother module is shown in d). Thus, if it is available and the growth probability as influenced by light, temperature and nutrients allows for it, a new module will preferably be produced directly on top of the mother module (number 1). The next preferences are the two cells above and to the sides (number 2), then the cells above and back (number 3 middle first), followed by the cells above and front (number 5 middle first). The last preference are the ones immediately to the sides (e).

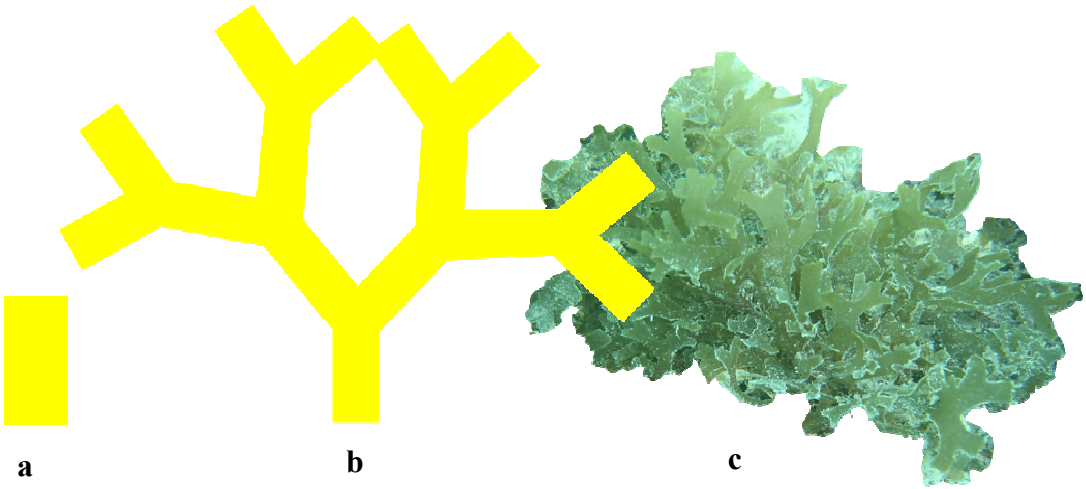


a **b** **c**

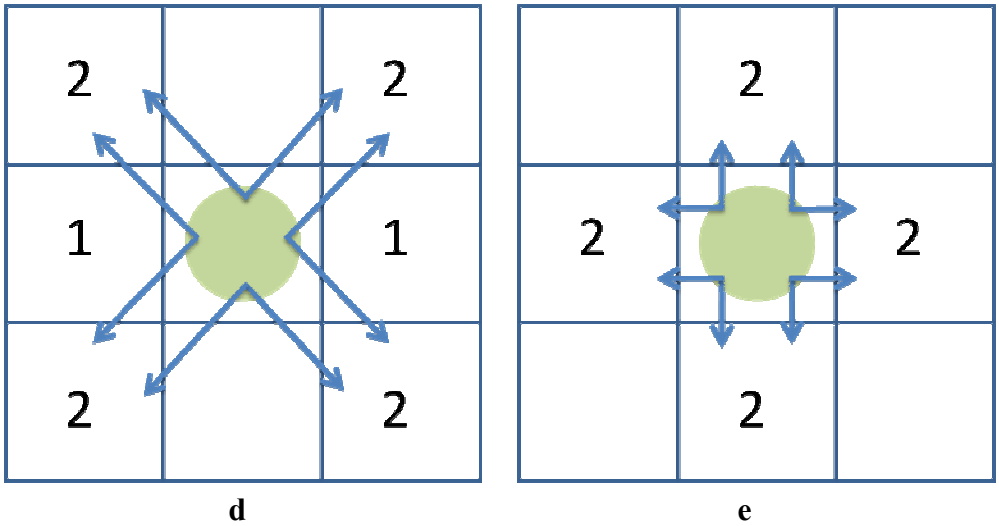


d **e**

Figure 3.3. *Dictyota* sp. form and branching rules. One module is illustrated in a) and its general form is illustrated in b) while an actual photo is seen in c). The box diagrams (d and e) are two-dimensional top view perspectives of where new modules can be produced. Two new modules will always be produced by the "mother" module (represented by the olive circle). The numbers represent preference for where the two new modules will be placed. Cells labeled "1" in d) are located above mother module and are the preferred locations. If the cells directly above and to the sides are not available and/or the growth probability does not allow for it, then the location of the two new modules are randomly chosen between the options (all numbered 2) pointed out by the arrows. In d), the corner locations are shown while in e) the non-corner right-angle options are illustrated. These cross-sections represent both the planes where the mother module belongs to and the one directly above it.



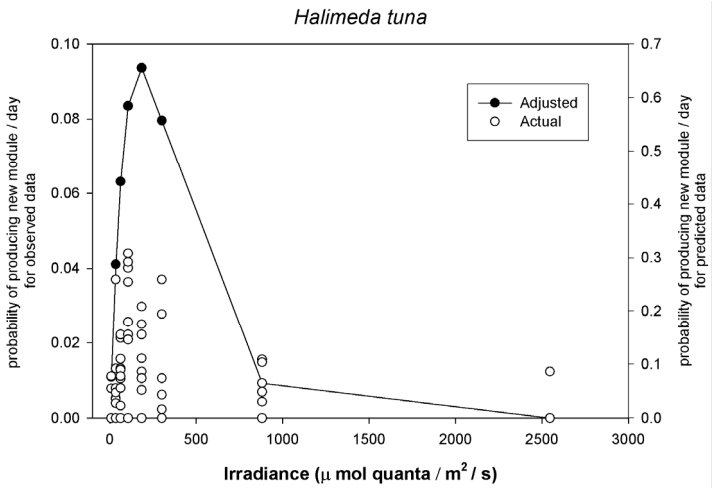
a **b** **c**



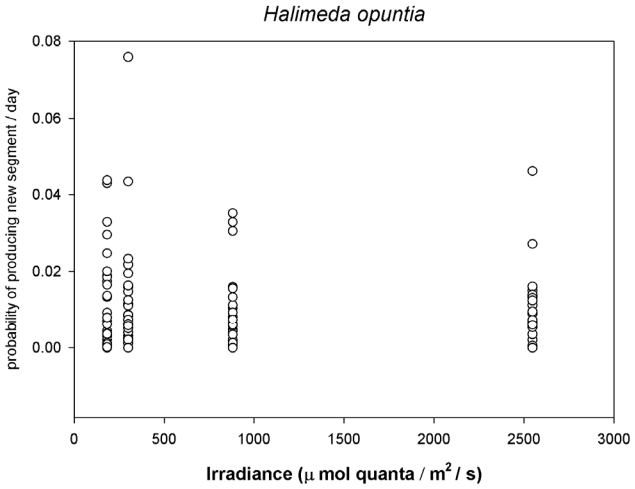
d **e**

Figure 3.4 Module production (growth) curves of a) *Halimeda tuna* b) *Halimeda opuntia* and c) *Dictyota cervicornis* in response to light based on laboratory experiments using four light levels. The Platt et al. (1980) equation was used to fit *Halimeda tuna* as explained in Chapter 2. *Halimeda opuntia* probabilities were uniform across light levels and thus the average ± standard deviation was used in SPREAD. However, the equation was scaled up in order to allow growth to occur since probabilities from the laboratory experiments were very low. An exponential curve provided the best fit to *Dictyota*. For all three macroalgae, the growth equations were scaled up in order to allow growth to occur since probabilities from the laboratory experiments were very low and these are represented by the Adjusted line. See Table 3.1 for values of the equation parameters.

a


Halimeda tuna
probability of producing new module / day for observed data
probability of producing new module / day for predicted data
Adjusted
Actual
Irradiance (μ mol quanta / m² / s)

b


Halimeda opuntia
probability of producing new segment / day
Irradiance (μ mol quanta / m² / s)

c

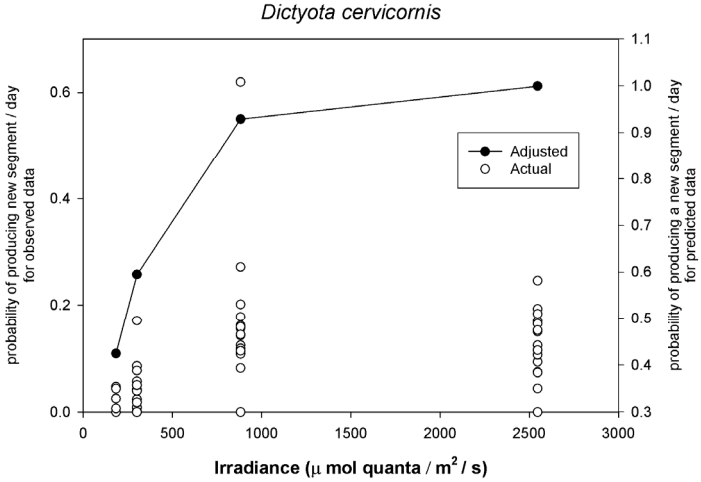

Dictyota cervicornis
probability of producing new segment / day for observed data
probability of producing a new segment / day for predicted data
Adjusted
Actual
Irradiance (μ mol quanta / m² / s)

Figure 3.5. Map of study sites in the Florida Keys Reef Tract.

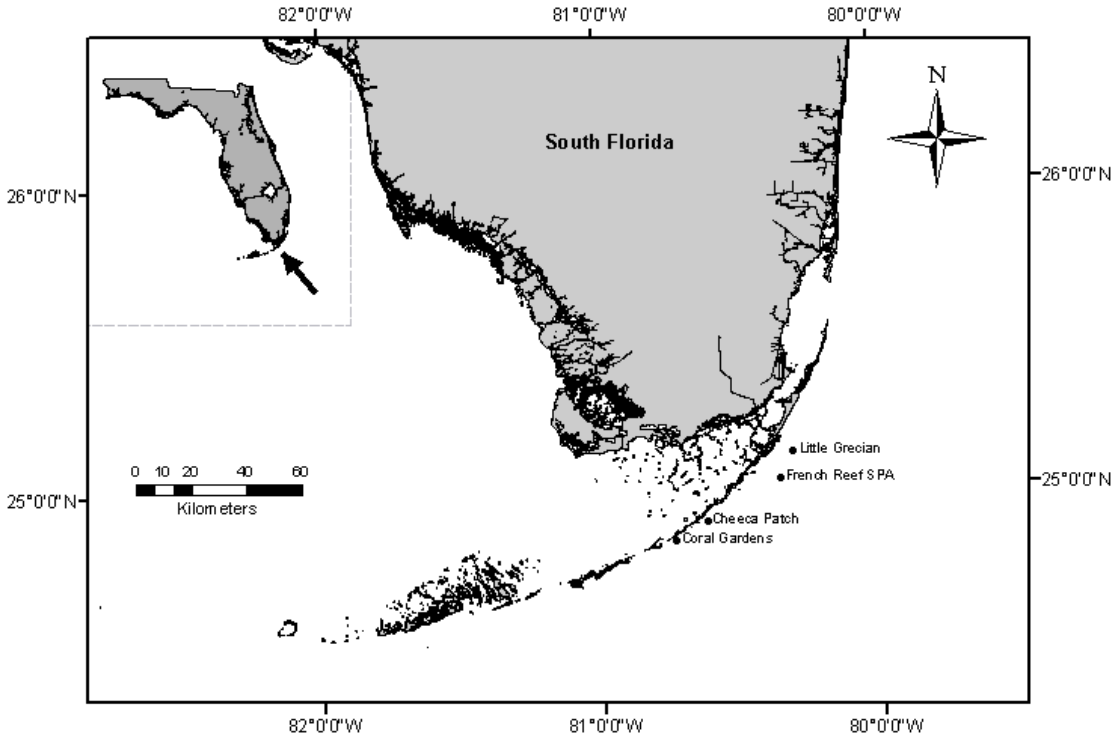
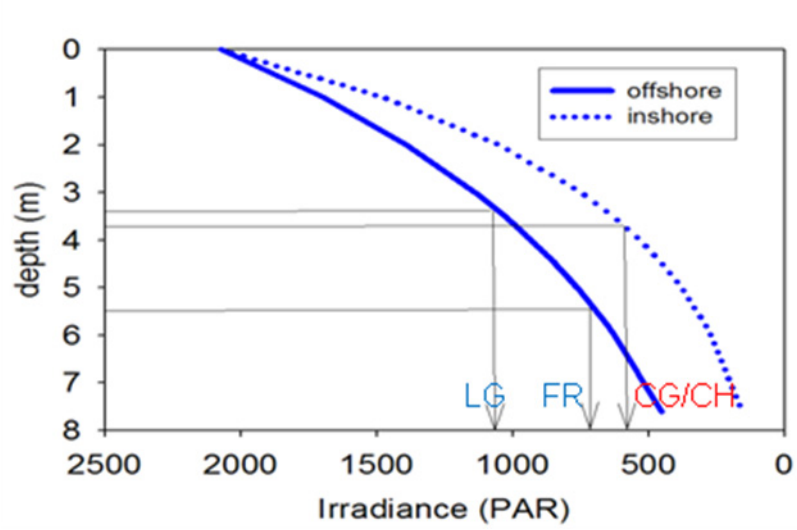
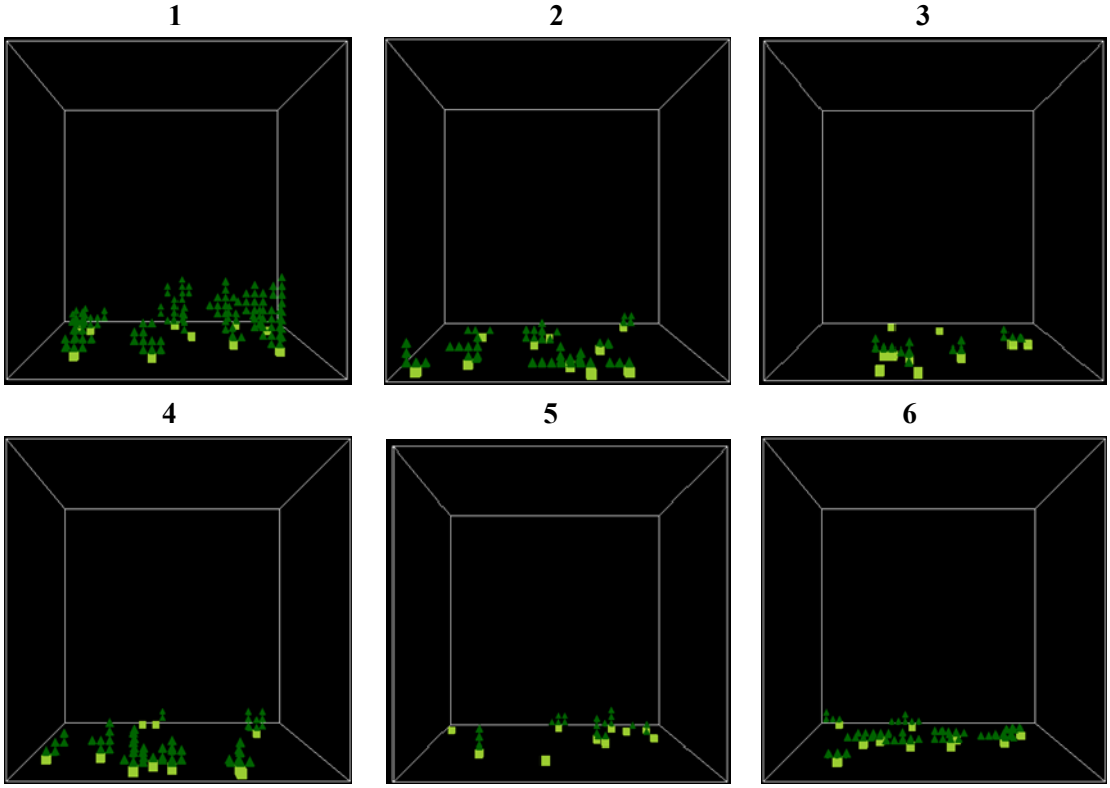


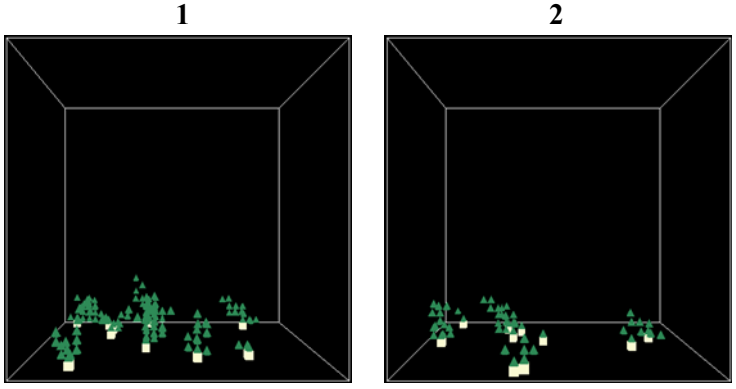
Figure 3.6. Irradiance levels at the four study sites (LG = Little Grecian, FR = French Reef, CG = Coral Gardens, CH = Cheeca Patch) at the depths sampled for the morphometric surveys. Irradiance at depth was calculated using Lambert-Beer law. Surface irradiance did not differ between the sites. Average attenuation coefficients for inshore and offshore sites were used.



Halimeda tuna morphological clusters:



Halimeda opuntia morphological clusters:



Dictyota morphological clusters:

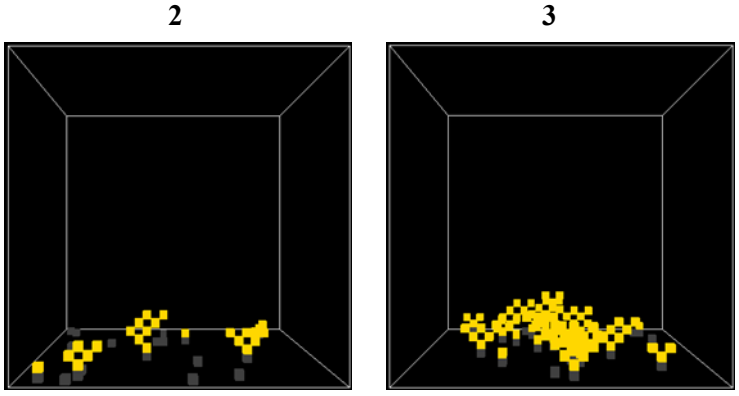


Figure 3.7. Morphological clusters of *Halimeda tuna, Halimeda* opuntia and *Dictyota* derived from SPREAD. *H. tuna* had six clusters, while *H. opuntia* had two. Only the two main clusters of *Dictyota* are shown here.

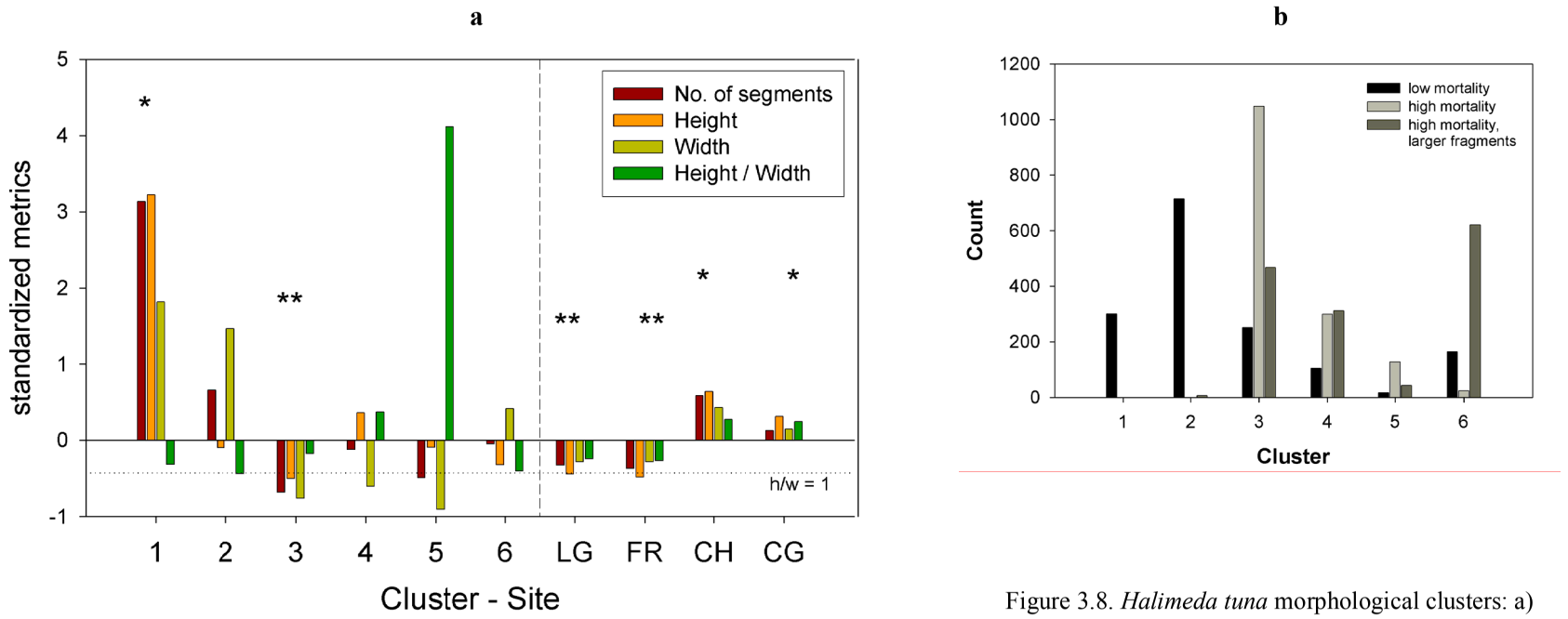


Figure 3.8. *Halimeda tuna* morphological clusters: a) standardized morphometrics for the model-derived clusters and the study sites (LG = Little Grecian, FR = French Reef, CH = Cheeca, CG = Coral Gardens); dotted line denotes the height: width ratio equivalent to 1; similar asterisk labels denote similar morphologies between the model and field results; b) frequencies of mortality scenarios for each cluster from SPREAD; c) average irradiance values where each model cluster was observed; and, d) average nutrient level where each model cluster was observed. Bars denote standard errors and clusters labeled with different letters denotes significant differences for c) and d).

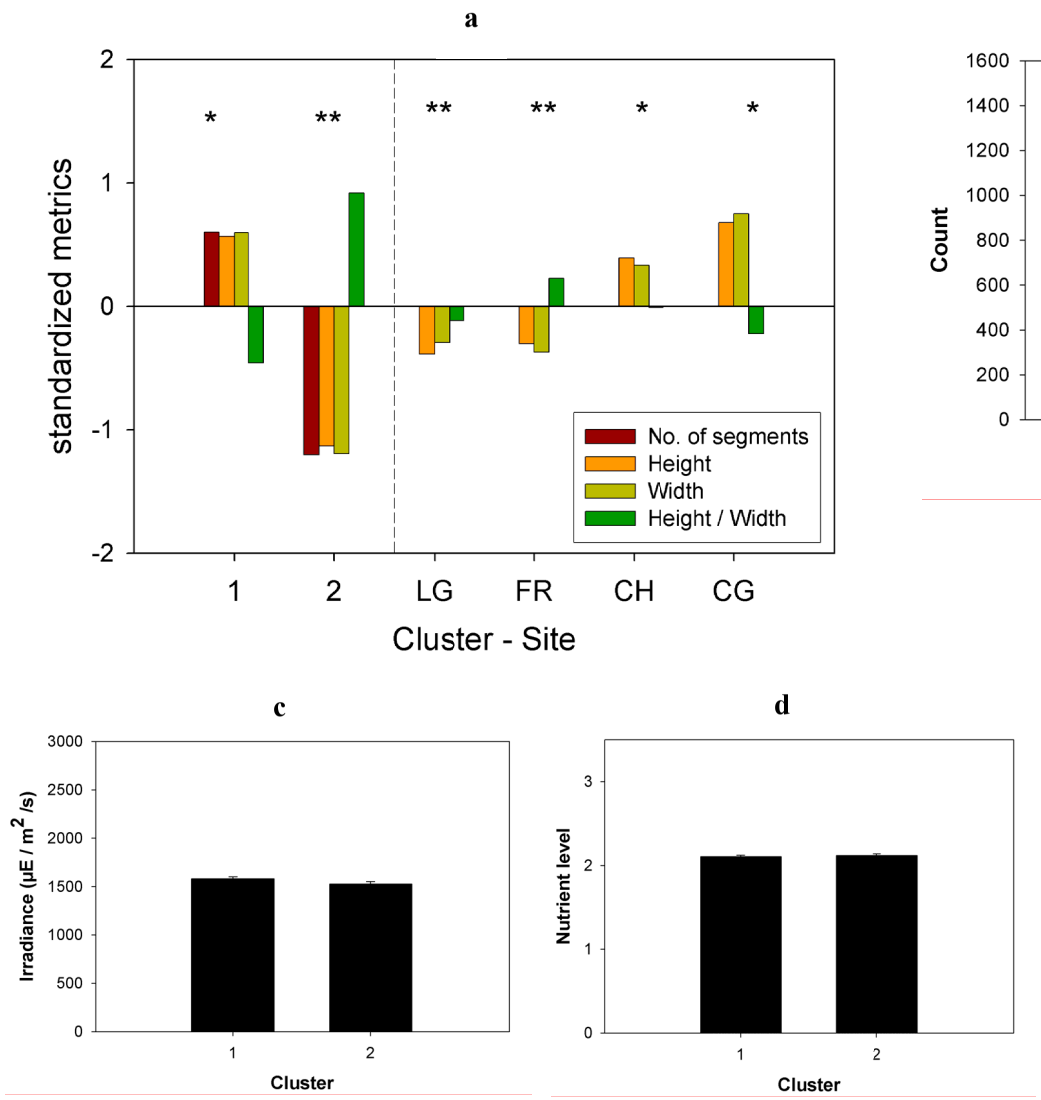


Figure 3.9. *Halimeda opuntia* morphological clusters: a) standardized morphometrics for the model-derived clusters and the study sites (LG = Little Grecian, FR = French Reef, CH = Cheeca, CG = Coral Gardens); dotted line denotes the height: width ratio equivalent to 1; similar asterisk labels denote similar morphologies between the model and field results; b) frequencies of mortality scenarios for each cluster from SPREAD; c) average irradiance values where each model cluster was observed; and, d) average nutrient level where each model cluster was observed. Bars denote standard errors and clusters labeled with different letters denotes significant differences for c) and d).

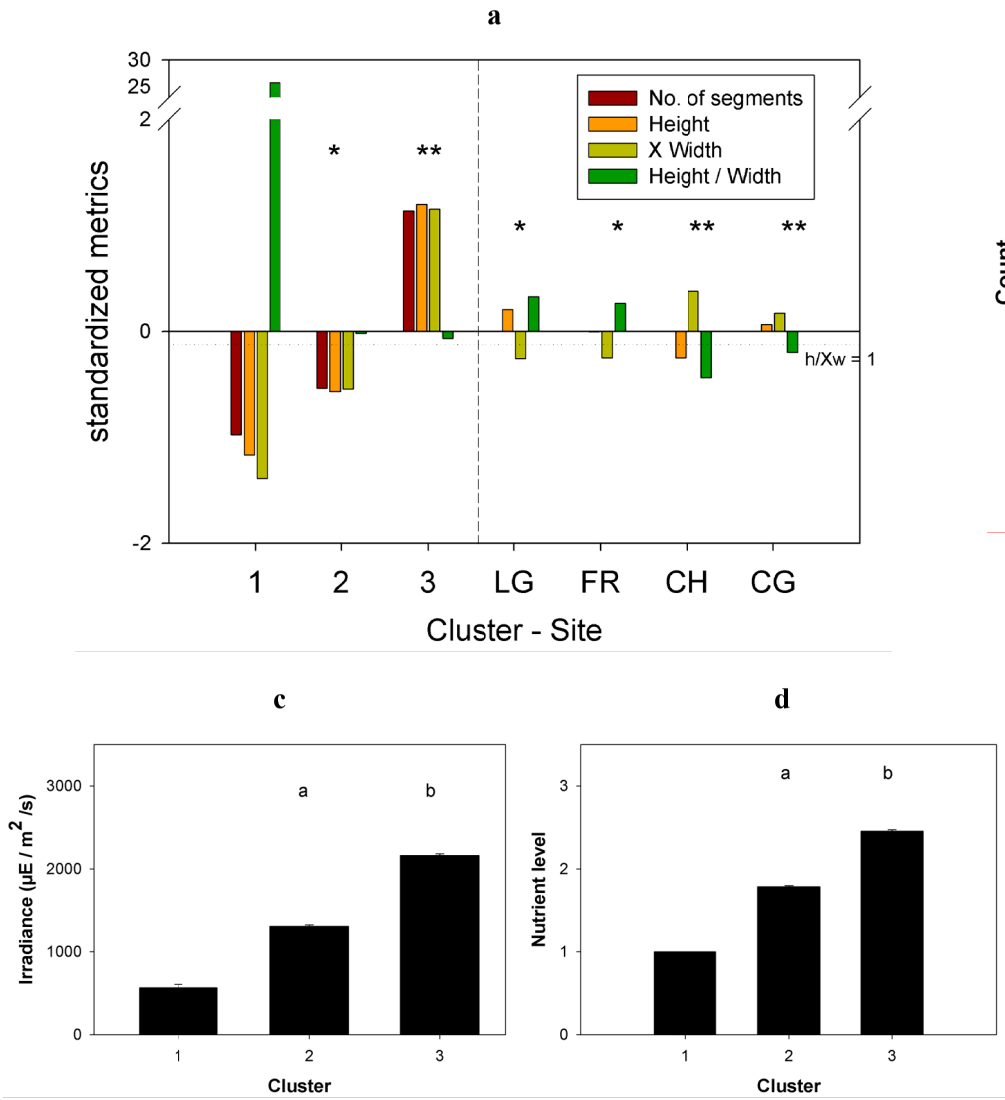


Figure 3.10. *Dictyota* sp. morphological clusters: a) standardized morphometrics for the model-derived clusters and the study sites (LG = Little Grecian, FR = French Reef, CH = Cheeca, CG = Coral Gardens); dotted line denotes the height: width ratio equivalent to 1; similar asterisk labels denote similar morphologies between the model and field results; b) frequencies of mortality scenarios for each cluster from SPREAD; c) average irradiance values where each model cluster was observed (bars represent 95% CI); and, d) average nutrient level where each model cluster was observed. Bars denote standard errors and clusters labeled with different letters denotes significant differences for c) and d).

IV. CONSEQUENCES OF MORPHOLOGY AND FRAGMENTATION ON TWO-DIMENSIONAL SPACE OCCUPATION OF CORAL REEF MACROALGAE

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 2002a). Clonal benthic species abound in coral reefs where space is an important and potentially limiting resource (Jackson 1977). The reef-building species, 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). 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 that is a clone (the ramet). Studies on corals (Highsmith 1982, Lirman 2000, Foster et al. 2007) and gorgonians (Lasker 1990, Coffroth and Lasker 1998) have shown that clones can represent a major proportion of their populations and that fragmentation is an important process in producing these clones.

In coral reefs in the Caribbean, clonal macroalgal species have recently begun to play 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 hotly 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). In addition to these, disease and bleaching are causing increased coral mortality (Goldberg and Wilkinson 2004), which consequently opens up space for other organisms such as macroalgae. Different macroalgal species have different capabilities for primary growth and asexual reproduction under varying conditions of growth factors and disturbances (Santelices 2004). Vegetative primary growth and fragmentation can have different implications for rate of space capture and maintenance of space. For example, fragmentation in the highly invasive *Caulerpa taxifolia* appears to be a very successful strategy for rapidly increasing its spatial coverage (Ruesink and Collado-Vides 2006). In turn, these characteristics of space occupation (rate and persistence) can significantly affect coral reef resilience or the ability to recover to its previous coral-dominated state. More stable macroalgal patches can lead to higher interaction frequencies with corals (Jompa and McCook 2002a, Jompa and McCook 2002b, 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), space pre-emption and inhibition of recruitment (Nugues and Roberts 2003, Maypa and Raymundo 2004, Kuffner et al. 2006, Nugues and Szmant 2006).

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 conditions using a small-scale agent-based model approach. This focuses on *Halimeda tuna* (Ellis and Solander) Lamouroux*, Halimeda opuntia* (Linnaeus)

Lamouroux and *Dictyota* spp., the dominant macroalgae in the Florida Reef Tract and 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 or vegetative growth in the horizontal spread of the macroalgal species being studied?
3) Are there differences in space occupation between primary growth and fragmentation?
4) Are there variations in space occupation under different disturbance conditions and fragment survival probabilities?
5) Are there differences in space occupation patterns between species in the model and as observed in the field? Can the variations in the real study sites be explained through inter-specific differences in responses to growth and disturbance factors?

Methods

Model scenarios: parameter exploration

The first question for this study was concerned only with primary growth of the macroalgal thalli. In Chapter 2, the morphologies of the *H. tuna, H. opuntia* and *Dictyota* sp. varied under different levels of light, nutrients and disturbance. A subset of the Chapter 2 light levels, but similar nutrient and fragmentation without survival (mortality) conditions were used for the model scenarios in this Chapter (Table 4.1). Mortality here

refers to macroalgae modules fragmenting without survival and settling. The two-dimensional (horizontal) percent covers attained under these primary growth scenarios were obtained. With the same set of parameters, the three-dimensional agent-based model SPREAD was run allowing fragments to survive using varying survival probabilities in order to address the second question. Parameters for these were obtained from the extensive studies conducted at Conch Reef on *Halimeda* and *Dictyota* fragmentation (Vroom 2001, Walters et al. 2002, Vroom et al. 2003, Herren et al. 2006). The fragment survival probabilities used for *H. tuna* and *H. opuntia* were based on a 14-day experiment accounting for the percentage of fragments that had pigmentation (Walters et al. 2002). SPREAD was run with a 100cm x 100cm x 30cm grid initially seeded with 10 randomly located individuals of one species (species were run separately). Each run consisted of 1000 time steps (days). Each scenario was run 30 times and the average metrics from these were used for subsequent analyses. The data obtained from the model were percent cover and density (number of individuals per m^2). These were programmed in the model to simulate the way an observer in the field obtains such data, wherein quadrats are placed onto the reef substrate and estimates percent cover or counts of the number of the species/group in question are made from a top-view perspective. In SPREAD, the original three-dimensional grid was first transformed into a two-dimensional one, by using the top-most object in the y-axis as the visible object in the 2-D grid with the same x and z-coordinates. One hundred random points in the 2-D grid were subsequently surveyed for presence of macroalgae. Percent cover was derived as number of points present divided by 100. Density was obtained by counting the number of unique (not connected) individuals within an area equivalent to $0.25m^2$ within the 2-D grid.

Similar to the previous chapter, *Dictyota* in the model is a generic species since the light curve was obtained from *Dictyota cervicornis* (Appendix A), while the other parameter values were obtained from literature values for *Dictyota* spp. (Table 4.1).

Model scenarios: site-specific

SPREAD was also run using parameters that were specific to or were hypothesized to be applicable to the four study sites (Figure 3.1 and see Chapter 3 site descriptions) in order to investigate how these affect the cover of macroalgae and if they can replicate what is observed in the actual sites (Table 4.3). The values for the depth, light and temperature parameters were derived from field data. Model nutrient levels were varied between offshore and patch reef sites, where the former was given a lower level. The offshore reefs' disturbance levels were set to high fragmentation with large fragment sizes and low probability of fragment survival to simulate effects of increased disturbance through water motion and herbivory, while the patch reefs had a low fragmentation level and high fragment survival probability. *Dictyota* fragment survival probability was the same in all reef sites (0.933) since the difference between this and 100% probability observed for *D. menstrualis* (Herren et al. 2006) was not large and this slightly lower probability was probably more realistic than fragments always surviving. This probability was also representative for more than one *Dictyota* (Vroom 2001, Herren et al. 2006). Ten individuals for each species (separately) were randomly located at the start and the model was run for 3000 time steps, and each scenario was replicated 30 times.

Fieldwork

Study sites

The same four sites, Coral Gardens, Cheeca Patch, French Reef and Little Grecian, were used for this study (Figure 3.1). See Chapter 3 for detailed site descriptions.

Abundance assessments

Two methods, permanent plots and random quadrats, were used to document spatial and temporal changes in the cover and numbers of the three macroalgal species being studied within the four study sites. Eight $0.22m^2$ plots were randomly located at each site on September 21, 2004 for the two offshore sites, and October 12 and 28, 2004 for Cheeca Patch and Coral Gardens, respectively. The corners were marked using masonry nails and surveyor tapes and re-located using known heading and distance information from a particular starting point. The plots were monitored four to five times from September 2004 through November 2005 using digital photographs following the method of Preskitt et al. (2004). Photographs were cleaned and cropped to show the same areas then analyzed using the software Coral Point Count with Excel extensions (CPCe, Kohler and Gill 2006). Photos were magnified and the areas of distinct *H. tuna, H. opuntia* and *Dictyota* spp. individuals or patches were delineated. Absolute area, percent and relative cover of the three species were obtained for each plot.

The random quadrats were deployed at each study site in three to four sampling periods (November 2004, March 2005, September 2005 and November 2005). A table of random numbers and an underwater compass with a rotating bezel was used to randomly select the number of fin kicks and direction, respectively. The quadrat was then placed as

evenly as possible on the substrate where the direction and distance of the fin kicks pointed to. The percent cover of the major benthic groups (including zoanthids, sponges and gorgonians), as well as substrate (sand, rubble, silt, bare limestone substrate, sparse turf on substrate), were assessed. Macroalgae and hard corals were identified to the species level as best as possible. Twenty replicates were obtained in each site and sampling period.

Statistical analysis

Model data

To determine differences in the percent cover between the morphological types of each species in the scenarios with no fragmentation, the data from the model were analyzed using appropriate non-parametric tests.

Comparing scenarios with and without fragmentation, Two-way ANOVA was used to investigate the differences in percent covers and densities between mortality (fragmentation without survival) and fragment survival levels for each macroalgae species. Data were transformed to conform to the appropriate assumptions.

Field data

The percent covers, number of fragments/patches per m^2 and relative cover of the three species within replicate plots at the four sites were analyzed using Repeated Measures ANOVA. These metrics were natural log transformed to conform to assumptions of normality and homoscedasticity. If there was a difference between subjects (sites), Tukey's B post-hoc test was used to examine this further. Due to the small sample size (a plot was the experimental unit), it was necessary to analyze the data

in two ways to extract the most information and the most number of replicates possible. There were differences in the sampling periods between the habitat types, thus in order to get the most information about the differences between times two separate analyses were performed for patch reefs and offshore reefs since the Repeated Measures ANOVA with all sites combined required leaving out several sampling periods. An analysis was also performed for all four sites together to investigate site differences with only two sampling periods included. For *H. opuntia*, only Coral Gardens and Cheeca Patch were considered, because there was barely any found in the offshore site plots.

The percent covers for *H. tuna*, *H. opuntia*, *Dictyota* spp. were analyzed separately to distinguish differences between the study sites and sampling periods using Two-Way ANOVA.

Results

Space occupied by the primary growth of different morphologies as simulated

For *H. tuna,* different morphologies also resulted in differences in the amount of horizontal space occupied (Figure 4.1a). The larger morphologies obtained the highest percent cover values, while the upright morphotypes covered more horizontal space compared to the hemispherical forms (Kruskal-Wallis test, $p = 2.801 \times 10^{-128}$, Dunn's multiple comparison test). The large and upright morphology (Cluster 1) had the highest percent absolute area cover, while the small and hemispherical form (Cluster 3) had the lowest. For both *H. opuntia* and *Dictyota*, the larger morphologies also obtained the higher percent covers (Figures 4.1b and 4.1c). Cluster 1, the large and upright morphology of *H. opuntia*, and Cluster 2, the large and hemispherical form of *Dictyota,*

occupied more space at the end of the simulation compared to their smaller and similarly-shaped forms (*H. opuntia*: t-test, $p = 1.436 \times 10^{-112}$; *Dictyota*: Mann-Whitney test, $p = 1.322 \times 10^{-141}$).

Simulated space occupation with fragmentation included

For all three species, there was a clear difference in the amount of space attained due to purely primary growth and that attained when fragmentation was allowed to occur (Figures 4.2 – 4.4). The highest cover and density attained were under the highest probability for fragment survival and high fragmentation (smaller fragment size). After the initial year, the effect of seasonality can be seen in the percent cover, where during the warm months representing spring and summer, cover increases, then declines during the cool months. This oscillation was dampened under the high fragmentation and large fragment sizes scenarios. The rate of increase of cover and density generally abated as time passed and were eventually stabilizing at the end of the model runs. The percent cover and density obtained under the three levels of mortality (fragmentation without survival) and four levels of fragment survival probabilities were all significantly different from each other for *H. tuna* (Tables 4.3 and 4.4 and Figure 4.2). An increase in cover and density was achieved with increasing probability of fragment survival, although the difference between no fragmentation and low probability of survival was relatively small. The interaction between mortality and fragmentation levels was significant which can be attributed to the different behavior of the medium and high fragment survival scenarios compared to the no fragment and low fragment survival ones. In the former, the percent covers and densities dipped under the high and large fragment size scenario, but this was

not seen in the latter. Under the medium and high fragment survival probabilities, cover and densities were smaller when fragmentation was high and fragment sizes were large, but these increased from the low to high fragmentation scenarios.

Percent covers and densities of *H. opuntia* also increased significantly from none to low to high fragment survival probabilities (Tables 4.3 and 4.4 and Figure 4.3). Once again, interaction between mortality and fragmentation levels was significant, and similar to *H. tuna*, this was due to the high fragment survival probability scenario (as well as the low fragment survival scenario for density) showing a decrease in cover and density under the high fragmentation and large fragment size scenario relative to the lower and/or no fragment survival scenarios. The percent cover and density of *H. opuntia* in the low, and high and large fragment size scenarios were significantly lower than under high fragmentation level only.

Similar to the two *Halimeda* species, *Dictyota* cover and density increased with higher fragment survival probabilities (Tables 4.3 and 4.4 and Figure 4.4). Interaction between mortality and fragmentation was significant because of the different behavior of the no fragment survival scenarios compared to the low and high fragment survival ones. The percent cover of the no fragment survival scenario was high under low fragmentation, while it was similar across fragmentation scenarios for density. Under the low and high fragmentation scenarios, percent cover was again highest under high fragmentation and lowest under high fragmentation and large fragment sizes. For density, the low fragmentation and high and large fragmentation scenarios were similar to each other and were lower than the high fragmentation scenario.

Field observations

There were no significant differences in the percent cover, relative cover and number of fragments with time or among the four study sites for *H. tuna* (Table 4.5 and Figures 4.5 – 4.7). The space occupied and dominance of this species was relatively stable and not significantly affected by seasonality.

The only significant difference observed for *H. opuntia* was in the number of fragments among the different sampling periods, where density increased during the summer months (Table 4.5 and Figure 4.6). There was no overall trend for with time. There also was no difference between Coral Gardens and Cheeca Patch. In terms of percent and relative cover, these remained the same between sampling periods and the two sites where *H. opuntia* was found (Figures 4.5 and 4.7).

Dictyota spp. showed the most variation in space occupied among the three species investigated. There were significant differences in percent cover and number of fragments between sampling periods and sites (Table 4.5 and Figures 4.5 and 4.6). The two inshore patch reefs had lower cover and densities compared to the two offshore sites. In terms of trends with time, both cover and density varied due to the season. In the patch reefs, there was an increase in cover and density during the summer, particularly June 2005. The highest percent cover for French Reef in January 2005 was actually not included in the statistical analysis since this time period needed to be removed to facilitate the statistical analyses (Repeated Measures ANOVA), but there was still a significant effect from the three times included, which is most likely due to the higher cover in August 2005, particularly in Little Grecian. Once again, variation in time seems

to be due to seasonality and, overall, cover and density were stable (no increasing and decreasing trend) within the time period sampled.

There were differences in the percent cover results from the random quadrat method compared to those from the permanent plots (Table 4.5). The quadrat surveys documented a significant variation between the inshore and patch reefs for all three macroalgae (Figures 4.8 and 4.9). *H. tuna* cover was significantly higher in the patch reefs; however, interaction between the time and site was also significant. In the offshore reefs, there was a slight decrease in *H. tuna* cover in November 2005, while this did not occur in the patch reefs and here cover was stable during the sampling period. This method showed that *H. opuntia* cover was significantly higher in the patch reefs compared to the offshore reefs. That could not be tested in the permanent plot method due to the rarity of this species in the offshore reef plots. Similar to the permanent plots, the quadrats did not show any difference between sampling periods. *Dictyota* spp. cover was different not only between sites as shown by the permanent plots, but also between sampling periods with the random quadrat method. Cover was significantly higher at the offshore reefs (Figure 4.8). An increase during the warm spring sampling period was observed in all sites, but this declined in September 2005 though this did not occur in Little Grecian. Overall, the random quadrat method highlighted the variation of the cover of the three species between reef habitats, but remained similar through the sampling period except for declines in particular sites either during November 2005 for *H. tuna* or September 2005 for *Dictyota* spp. This method gives a better picture of the spatial variation in percent cover compared to the field plot results since it covers more area and has more replicates.

Comparisons of macroalgal cover and density between SPREAD and what was observed

The model-derived percent covers for *H. tuna* and *H. opuntia* in the site-specific scenarios were similar to the patterns in the actual sites (Figure 4.8). For both species, the variations set in the model resulted in higher percent covers in Cheeca Patch and Coral Gardens relative to French Reef and Little Grecian. For *H. opuntia*, the quantitative values were very close, however, for *H. tuna*, the model values were slightly lower than the observed ones, which is what was also seen in Chapter 2. SPREAD was not able to capture the variation between sites for the percent cover of *Dictyota* spp. The patch reef values were very similar to what was observed in the field; however, the simulated offshore values were lower than the observed values. When the fragmentation scenario was changed to high (rather than high and large fragments), percent cover was similar across the sites.

Once again, for *H. tuna* and *H. opuntia*, the model sites were able to capture the pattern observed in the study sites, although Little Grecian and French Reef had much higher *H. tuna* densities compared to the real reefs (Figure 4.9). There was also a discrepancy in the density of *Dictyota* between the field and the model result. In this case, the modeled patch reef sites had higher values compared to the simulated offshore, as well as the actual sites. However, under the high fragmentation scenario, density was higher in the offshore reefs compared to the patch reefs.

Discussion

Exploration with SPREAD showed that fragmentation can contribute significantly to the populations of *Halimeda* and *Dictyota* spp., and comparison of the model-derived

abundances to those actually seen in the field bears this out. The inclusion of both fragment survival in the model and the variations in growth and disturbance conditions between sites, resulted in the emergence of patterns of abundances similar to that found across the four study sites, at least for the two *Halimeda* species, highlighting the important roles of these processes in generating these observed patterns.

Fragmentation contributes significantly to the potential to occupy space

The ability to fragment and produce clones appears to be a successful strategy in order to grow and persist in many terrestrial and marine clonal organisms despite potential costs associated with the process. Lirman (2000) found that for the coral *Acropora palmata*, fragmentation can lead to high initial fragment mortality, reduced growth rates, and loss of reproductive potential. Several other studies on different coral species have found similar detrimental effects of fragmentation on growth, survival or fecundity (e.g., Smith and Hughes 1999, Nagelkerken et al. 2000). When *H. tuna* segments are cut off, its cytoplasm can ooze out and potentially cause mortality (Walters et al. 2002). The survivorship of the fragments of *H. tuna*, *H. opuntia*, and *Dictyota* spp. run the gamut, wherein *H. tuna* fragments have the lowest survival probabilities while almost all *Dictyota* spp. can survive if they manage to land on suitable substrate (Walters and Beach 2000, Herren et al. 2006). This implies variation in life-history strategies and the role of fragmentation in those strategies. Unfortunately, the costs of fragmentation for coral reef macroalgal species such as *Halimeda* and *Dictyota*, are not known. However, this study does show that if there are minimal costs relative to the benefits, then

fragmentation can be an effective means for these three macroalgal species to obtain space rapidly (increase abundance) and maintain it.

Variation in morphology also plays a role in space occupation and maintenance through vegetative growth. In conditions that permit a particular type of growth form, there would be a corresponding potential for the spread of the macroalgae through the substrate. Upright *H. tuna* could occupy space faster and also more of it compared to its hemispherical types. Environments that allow for large forms of *H. opuntia* and *Dictyota* spp. would also more likely allow for more rapid and more substrate utilized. Patch size has been found to impact the persistence of macroalgae in its space as well (McDermid 1985, Mumby et al. 2005). In a simulation of clonal seagrass growth, Sintes et al. (2006) illustrated how the older and more compact patches had slower growth and expansion rates compared to the younger, smaller and looser patches.

Disturbance and spatial spread

Disturbance affects the generation of fragments and the ability of the fragments to find and settle on a suitable substrate. In SPREAD, the fragmentation levels represent disturbance affecting the fragment pool, while the fragment survival probabilities can be seen as either the inherent capability of the macroalgae to survive, or disturbance that prevents settlement and survival in the patch, or a combination of both. Increasing the disturbance level from low to high yielded the highest amount of horizontal space occupation and densities for all three species. Inclusion of fragmentation also yielded cover and densities that were comparable to the real study sites. In the Florida Keys, storms, an intense form of disturbance, are common occurrences and have been found to

affect macroalgae populations. Vroom (2001) showed the importance of fragmentation in the space utilization of *Dictyota* spp. He was able to survey the cover of *Dictyota* before and after the Category I Hurricane Irene in 1999, and found that the hurricane reduced *Dictyota* spp. cover to 1/6 of its original abundance, but also generated 4-fold the amount of fragments under non-hurricane conditions. A month after the hurricane, it had recovered to half pre-hurricane densities while the densities of other organism were still low. Mumby et al. (2005) found a similar behavior for *Dictyota pulchella* in Belize. Re-colonization and recovery after a hurricane was fast and comprehensive, most likely due to fragments created by the hurricane.

H. tuna and *H. opuntia* on the other hand do not produce fragments that are as successful as those of *Dictyota* species'. This could partly explain why these species are more abundant in the inshore patch reefs that are more protected compared to the offshore reefs. In addition to the good conditions for the growth of these two species in the patch reefs (Chapter 2), more fragments are surviving due to lower water motion energy that moves and disperses them into unsuitable habitat and preventing attachment. Walters et al. (2002) did find more fragments, higher fragment survival and larger dispersal shadows for *H. tuna and H. opuntia* at their calmer deep site (21 m) compared to the more energetic shallow site (7 m) at Conch Reef in the Florida Keys. SPREAD was able to show the difference in abundances between the inshore and offshore sites in *Halimeda* and density in *Dictyota* spp. The discrepancies in the percent cover of *Dictyota* between the model and the field data could be due to competitive effects or varying growth rates and contribution of sexual reproduction that were not included in the model. This discrepancy is further explored and explained in Chapter 5.

Turnover of space in reefs by macroalgae: implications for coral-algal interactions and reef resilience

The simulated macroalgal populations stabilized through time and exhibited small oscillations in cover and density that were primarily due to seasonality. The field data gathered through both methods behaved similarly, with macroalgal cover and densities generally exhibiting no net change in time apart from seasonal variation. The main exception comes from *Dictyota* spp. and *H. tuna* in certain sites which did show a decline late in the year 2005. These are most likely due to the effect of the active hurricane season that year. Although this dataset is only for one year, macroalgae abundance in the Florida Keys seems to be generally stable through time with seasonal increases and decreases (Lirman and Biber 2000, Vroom et al. 2003, Collado-Vides et al. 2005, Beaver et al. 2006). This can be a testament to their capability to grow fast and occupy space through vegetative and asexual means. At the smaller patch scales, the processes of growth and mortality are much more dynamic especially for *Dictyota* spp. However, for *H. tuna* and *H. opuntia*, in the plots observed, there was no instance where they completely disappeared if they were already in the plot, and most especially in Coral Gardens and Cheeca where they were abundant, once the water was warm new green growth was observed from old patches or new fragments. Similarly for *Dictyota* spp. in the offshore reefs, all the plots with the macroalgae (which was all of them) exhibited contraction and expansion of cover but never extinction.

The regulation of the abundances of these three dominant macroalgae by growth and disturbance factors is a promising sign that reef space can still be available for coral recruitment and growth, for as long as other benthic organisms do not take over. However, these macroalgal patches tend to bloom during the season when hard corals

reproduce. Coral planulae could have a difficult time finding suitable substrate for settlement due to space pre-emption, or could even fatally settle on these relatively ephemeral macroalgal patches (Nugues and Szmant 2006).

Conclusions

Although morphological variations in the three macroalgal species, *H. tuna*, *H. opuntia* and *Dictyota* spp., can lead to increased extent of horizontal vegetative growth, fragmentation leads to even higher capacities to capture space. Increasing disturbance such that the fragment pool is increased, but not enough so that fragments cannot survive, leads to the highest potential for fast capture of and larger horizontal spatial spread. Enabling fragmentation in SPREAD, allowed for comparable values in percent cover and densities in the three species between the model and as observed in the actual study sites. Both model and field data showed some seasonal variation but generally stable abundances in time. Spatially, SPREAD was generally able to capture the observed disparity in abundances between the sites. The variation in growth and disturbance conditions, as well as each species' capacity for success with fragmentation, seems to play a strong role in the distinct differences in macroalgal abundances between inshore patch and offshore reef study sites.

Table 4.1. Parameters for model scenarios exploring effects of different fragmentation levels and fragment survival scenarios.

Parameter	Description	Unit	Species			Source
			Halimeda tuna	Halimeda opuntia	Dictyota sp.	
Season	One static or two seasons; make use of seasonal values where specified	-		2		
Depth		m		7		
Light						
Irradiance	Surface irradiance	μmol m^{-2} s^{-1}		100, 700, 1700, 2200		Sea Keys and Field observations
Irradiance standard deviation	Surface irradiance standard deviation	μmol m^{-2} s^{-1}		30% of surface irradiance		Field observations
Attenuation coefficient	Irradiance attenuation coefficient	-		0.26		SERC-FIU
Allow shading?	If shading will occur or not	Boolean		true		
Tissue transparency	Amount of light that a module will allow through to the cells below it	Fraction	0	0	0.6	*Halimeda* segments are solid and opaque; Dictyota (Hay 1986)
# cells affected by shading	Number of cells below module that will be affected by its shade	Cells		3		Assumed
Temperature						
Mean temperature		°C		Summer: 29 °C Winter: 22.3 °C		SERC-FIU and Field observations
Temperature standard deviation		°C		Summer: 1.8% Winter: 5.7%		SERC-FIU and Field observations
Nutrients level		1 – low 2 – medium 3 – high		1, 2, 3		Exploratory
Branching					Always dichotomous	
branch order	Curve for effect of branch order on producing a new module					
A		-	0.2	0.2	n/a	Estimated
B		-	0.5	0.5	n/a	Estimated
C		-	0.3	0.3	n/a	Estimated
branch present	Line for effect of number of modules already produced on producing a new one				n/a	
Slope		-	-0.14	-0.05	n/a	Estimated
Intercept		-	0.7	1	n/a	Estimated
Mortality						
fragments		Fraction		0.01, 0.05		Exploratory
Fragment size ± std. deviation			Small: 3 ±1, Large: 6 ±1	Small: 22 ±7 Large: 44 ±7	Small: 4 ±1 Large: 8 ±1,	Walters et al. 2002, Herren et al. 2006
Fragment survival probability	Probability that a fragment will settle and grow on available space					Walters et al. 2002, Herren et al. 2006

Parameter	Description	Unit	Species			Source
			Halimeda tuna	Halimeda opuntia	Dictyota sp.	
Low		Fraction	0.133	0.333	0.93	
Medium		Fraction	0.333			
High		Fraction	0.5	0.933	1	
Light curve			Exponential	Normal	Exponential	
A		-	0.01	0.4	0.003	Laboratory observations (Chapter 3 – Figure 3.4, Appendix A)
B		-	0.04	0.4	1	Laboratory observations (Chapter 3 – Figure 3.4, Appendix A)
C		-	8			Laboratory observations (Chapter 3 – Figure 3.4, Appendix A)
Temperature curve						
Mean growth temperature		°C	29	29	28	Beach et al. 2003, Biber 2002, Hillis-Colinvaux 1980, Lirman and Biber 2000
Standard deviation		°C	2	2	2	Beach et al. 2003, Biber 2002, Hillis-Colinvaux 1980, Lirman and Biber 2000
Nutrient probabilities						
Low		Fraction		0.2		Exploratory
Average		Fraction		0.4		Exploratory
High		Fraction		0.6		Exploratory

Table 4.2. Parameters for site-specific model scenarios.

Parameter	Site/Scenarios			
	French Reef	Little Grecian	Cheeca Patch	Coral Gardens
Depth	7	3.2	3.7	3.7
Light				
Irradiance	1942	2102	2167	2076
Irradiance standard deviation	577	646	740	547
Attenuation coefficient	Summer: 0.26	Summer: 0.26	Summer: 0.34	Summer: 0.34
	Winter: 0.14	Winter: 0.14	Winter: 0.23	Winter: 0.23
Temperature				
Mean temperature	Summer: 28 Winter: 24	Summer: 28 Winter: 24	Summer: 29 Winter: 22.3	Summer: 29 Winter: 22.3
Temperature standard deviation	Summer: 1.4	Summer: 1.4	Summer: 1.8	Summer: 1.8
	Winter: 3	Winter: 3	Winter: 5.7	Winter: 5.7
Nutrients level	2	2	3	3
Nutrient growth probabilities				
Average	0.4	0.4	0.6	0.6
Mortality				
Fragments	0.05	0.05	0.01	0.01
Fragment size	Small and large	Small and large	small	Small
Fragment survival probability	Low	low	high	High

Table 4.3. Summary of Two-Way ANOVA on model results exploring the effects of fragmentation with and without (mortality) survival on percent cover and density for each species.

	df	SS	MS	F	p
Halimeda tuna					
Percent cover					
Mortality	2	166.958	83.479	174.892	<0.0001
Fragmentation	3	3031.754	1010.585	2117.212	<0.0001
Mortality x Fragmentation	6	238.246	39.708	83.189	<0.0001
Residuals	90795	43338.143	0.477		
Density					
Mortality	2	87.119	43.560	557.562	<0.0001
Fragmentation	3	1238.623	412.874	5284.782	<0.0001
Mortality x Fragmentation	6	82.866	13.811	176.781	<0.0001
Residuals	90795	7093.372	0.078		
Halimeda opuntia					
Percent cover					
Mortality	2	36.401	18.201	18.451	<0.0001
Fragmentation	2	21638.000	10819.000	10967.62	<0.0001
Mortality x Fragmentation	3	759.328	189.832	192.440	<0.0001
Residuals	69434	68493.100	0.986		
Density					
Mortality	2	15678.168	7839.084	2574.758	<0.0001
Fragmentation	2	145401.389	72700.694	23878.64	<0.0001
Mortality x Fragmentation	4	14076.009	3519.002	1155.821	<0.0001
Residuals	69434	211398.137	3.045		
***Dictyota* spp.**					
Percent cover					
Mortality	2	1121.080	560.540	612.154	<0.0001
Fragmentation	2	11806.992	5903.496	6447.080	<0.0001
Mortality x Fragmentation	4	737.629	184.407	201.387	<0.0001
Residuals	69173	63340.694	0.916		
Density					
Mortality	2	9604.961	4802.480	1940.361	<0.0001
Fragmentation	2	65005.138	32502.569	13132.11	<0.0001
Mortality x Fragmentation	4	5098.694	1274.674	515.010	<0.0001
Residuals	69173	171206.258	2.475		

Table 4.4. Summary of Tukey's B post-hoc tests on model results exploring the effects of fragmentation without survival of fragments (mortality) and fragmentation with survival on percent cover and density for each species. Dissimilar letters in a row represent differences between the scenario levels within the scenario grouping only (fragmentation without survival and fragmentation with survival).

Species	**Fragmentation without survival scenarios**			**Fragmentation with survival scenarios**			
	Low	High	High and large fragments	None	Low	Me-dium	High
Halimeda tuna							
Percent cover	A	B	C	A	B	C	D
Density	A	B	C	A	B	C	D
Halimeda opuntia							
Percent cover	A	B	A	A	B	n/a	C
Density	A	B	C	A	B		C
Dictyota spp.							
Percent cover	A	B	C	A	B	n/a	C
Density	A	B	A	A	B		C

Table 4.5. Summary of statistical analyses results on the permanent plots and random quadrat data showing which factors were significant (Site, Time or Site x Time).

Species	Included Factor Levels		Permanent plots results			Random Quadrats results
	Sites	Times	Percent cover	Density (no. of fragments)	Relative cover	Percent cover
Halimeda tuna	CG and CH	Sept-Oct 2004, Jan 2005, June 2005, August 2005	None	None	None	
	FR and LG	Sept-Oct 2004, Jan 2005, August 2005, November 2005	None	None	None	
	All four sites	Sep-Oct 2004, August 2005	Time	Site x Time	None	Time and Site and Site x Time
Halimeda opuntia	CG and CH	Sept-Oct 2004, Jan 2005, June 2005, August 2005	None	Time	None	Site
Dictyota spp.	CG and CH	Sept-Oct 2004, Jan 2005, June 2005	Time and Site	Time	Site	
	FR and LG	Sept-Oct 2004, August 2005, November 2005	Time	Time almost significant (p=0.053)	None	Time and Site
	All four sites	Sep-Oct 2004, August 2005	Site (CG/CH ≠FR/LG)	Time and Site (CG/CH ≠FR/LG)	None	

Figure 4.1. Percentage cover of the different morphologies of (a) *Halimeda tuna*, (b) *Halimeda opuntia* and (c) *Dictyota* sp. in SPREAD. Vertical bars represent the standard error.

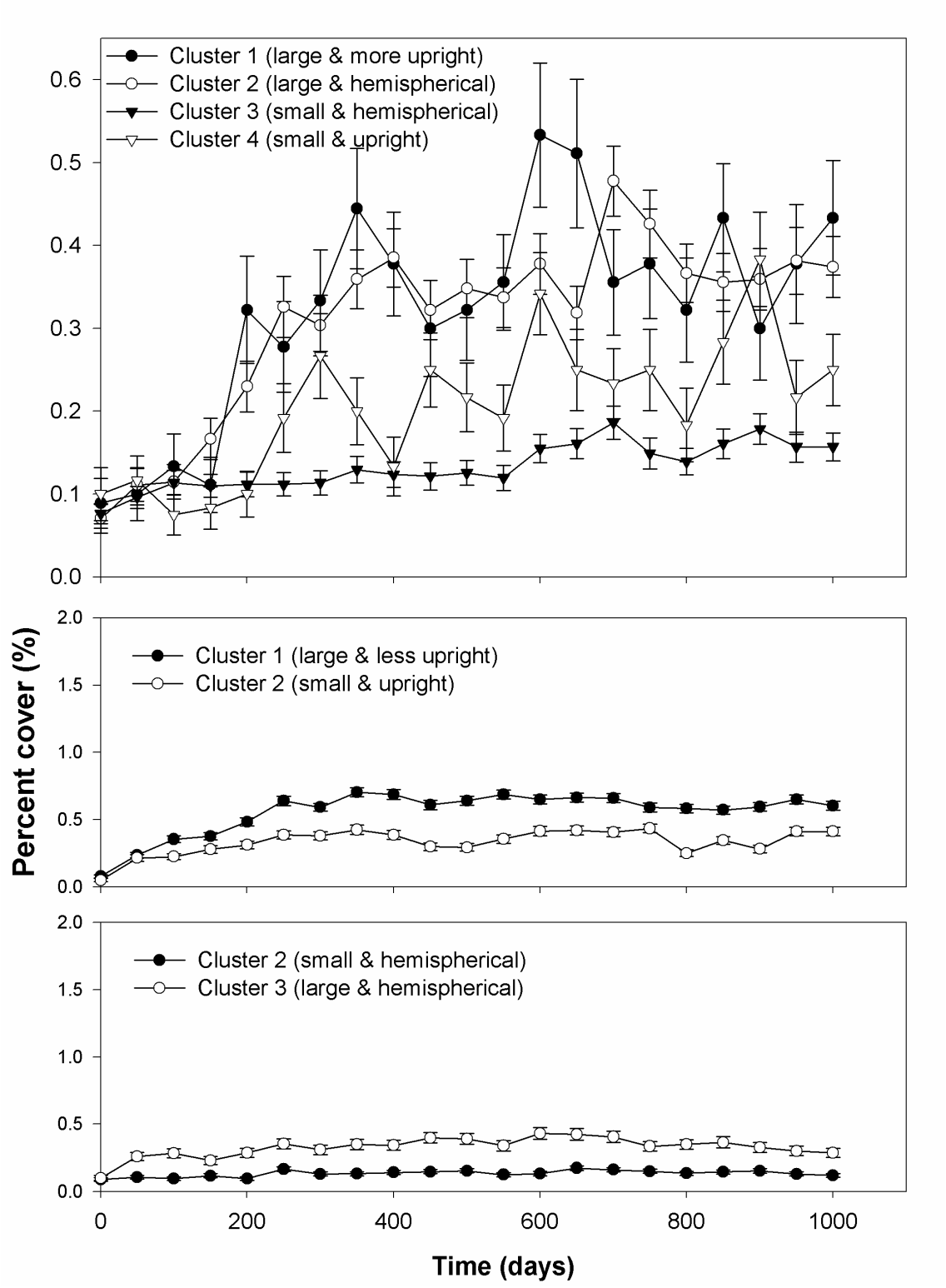


Figure 4.2. Percent cover and density of *Halimeda tuna* under different fragmentation (low, high and high and large fragments) and fragment survival probability levels dervied from SPREAD. Lines represent fragment surival probabilites, which are none (only vegetative growth), low, medium and high.Vertical bars represent the standard error

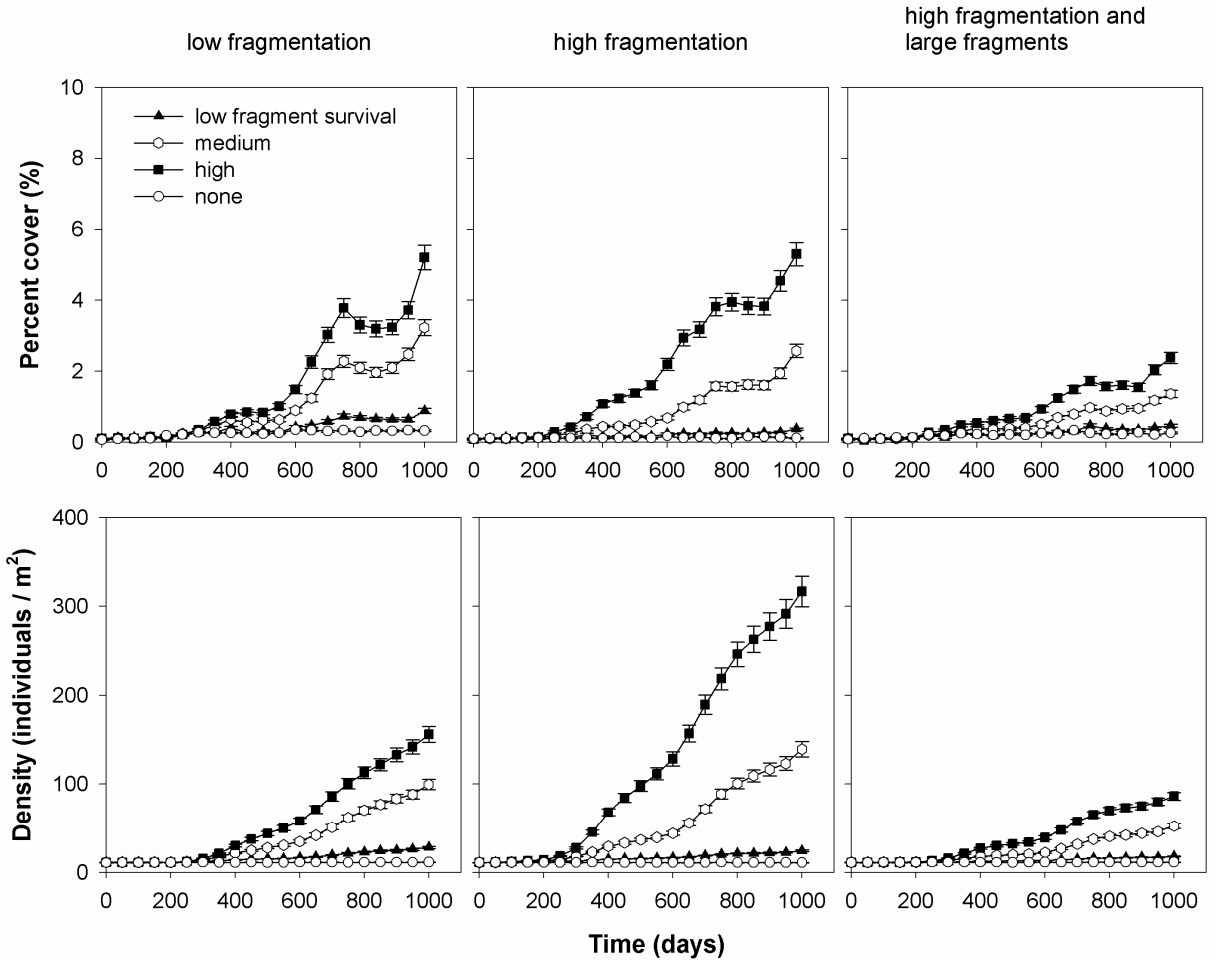


Figure 4.3. Percent cover and density of *Halimeda opuntia* under different fragmentation (low, high and high and large fragments) and fragment survival probability levels derived from SPREAD. Lines represent fragment surival probabilites, which are none (only vegetative growth), low and high. Vertical bars represent the standard error.

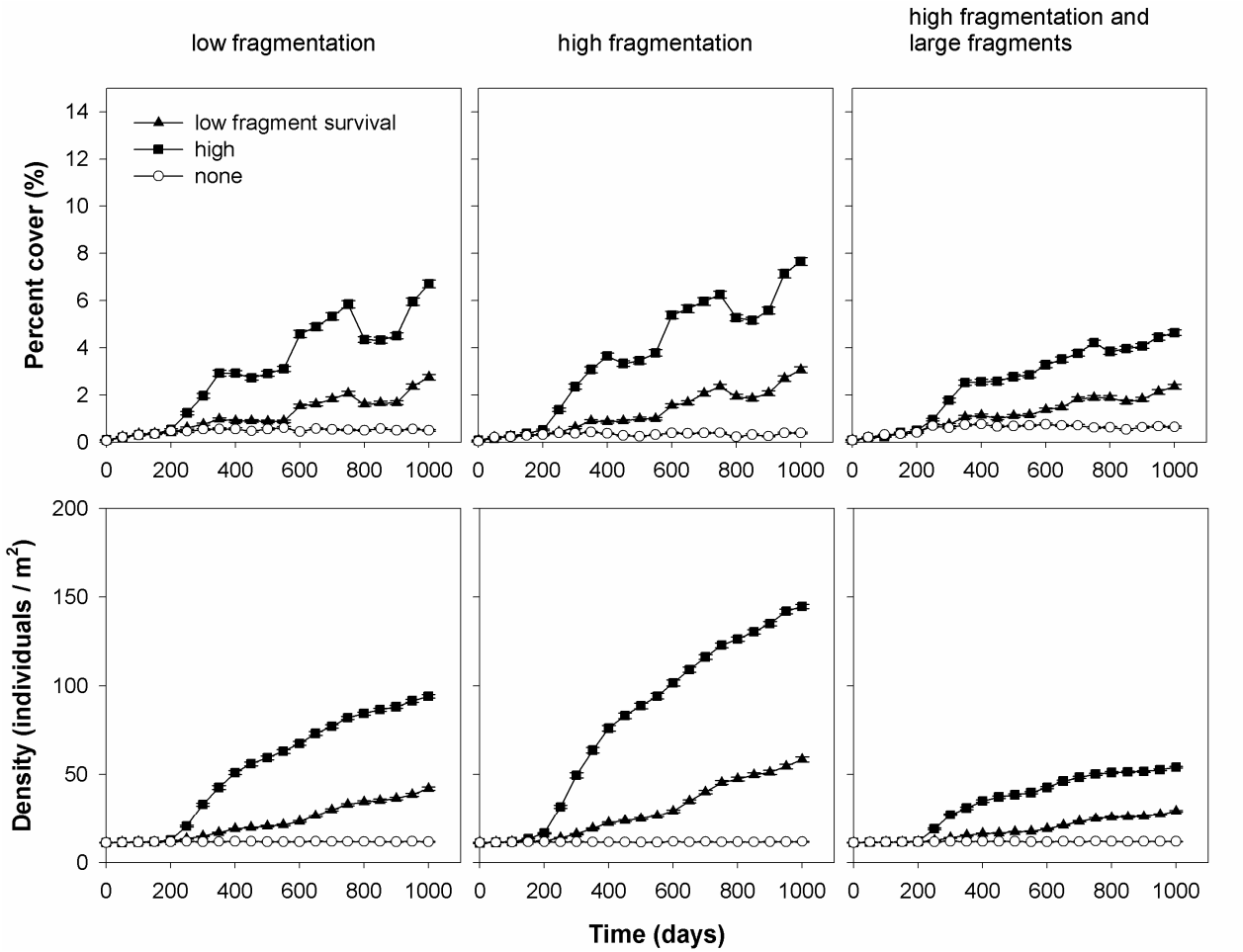


Figure 4.4. Percent cover and density of *Dictyota* sp. under different fragmentation (low, high and high and large fragments) and fragment survival probability levels derived from SPREAD. Lines represent fragment surival probabilites, which are none (only vegetative growth), low and high.Vertical bars represent the standard error.

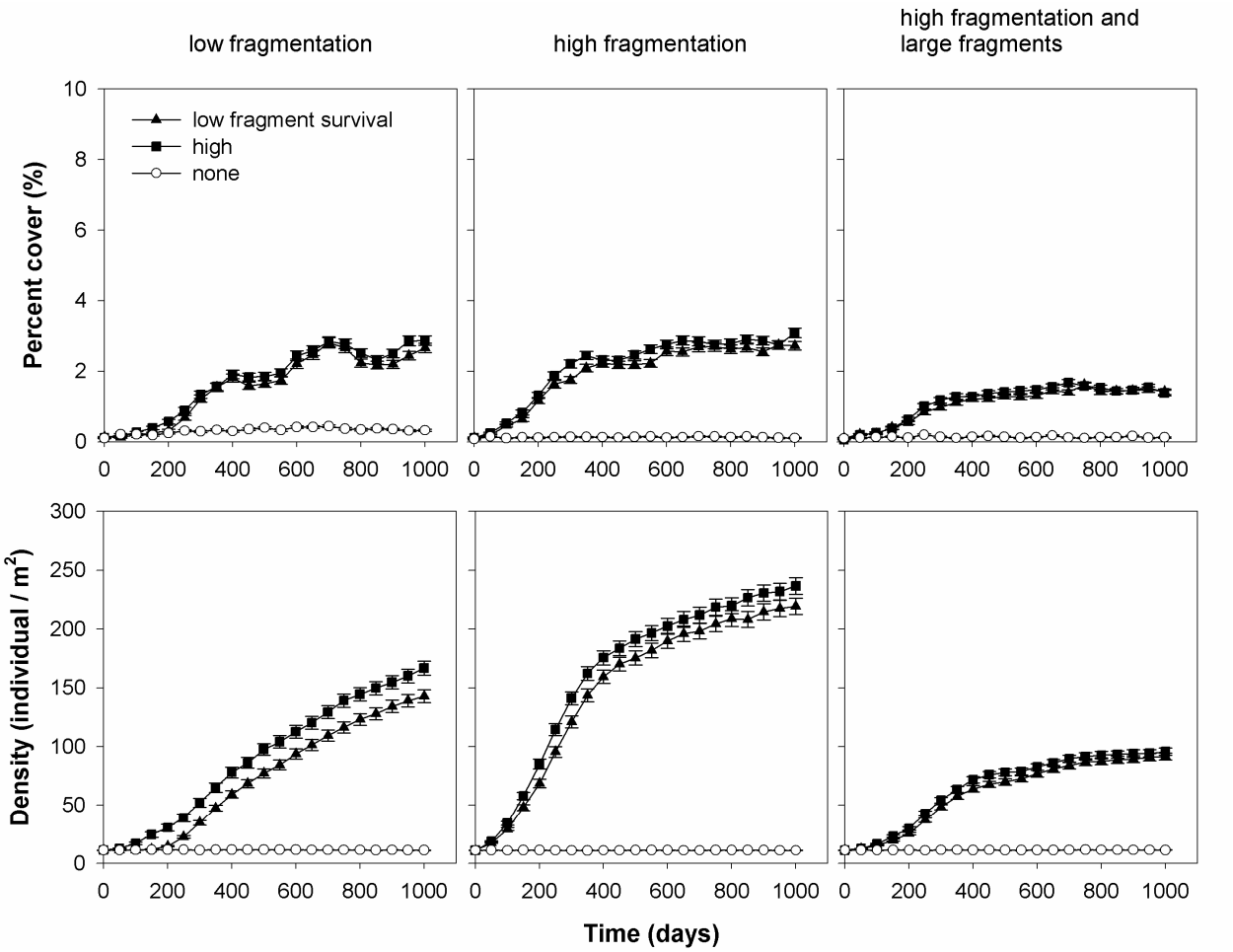


Figure 4.5. Percent cover of the three macroalgae species from permanent plots monitored in the four field sites. Lines represent these four sites and data are the mean ± SE.

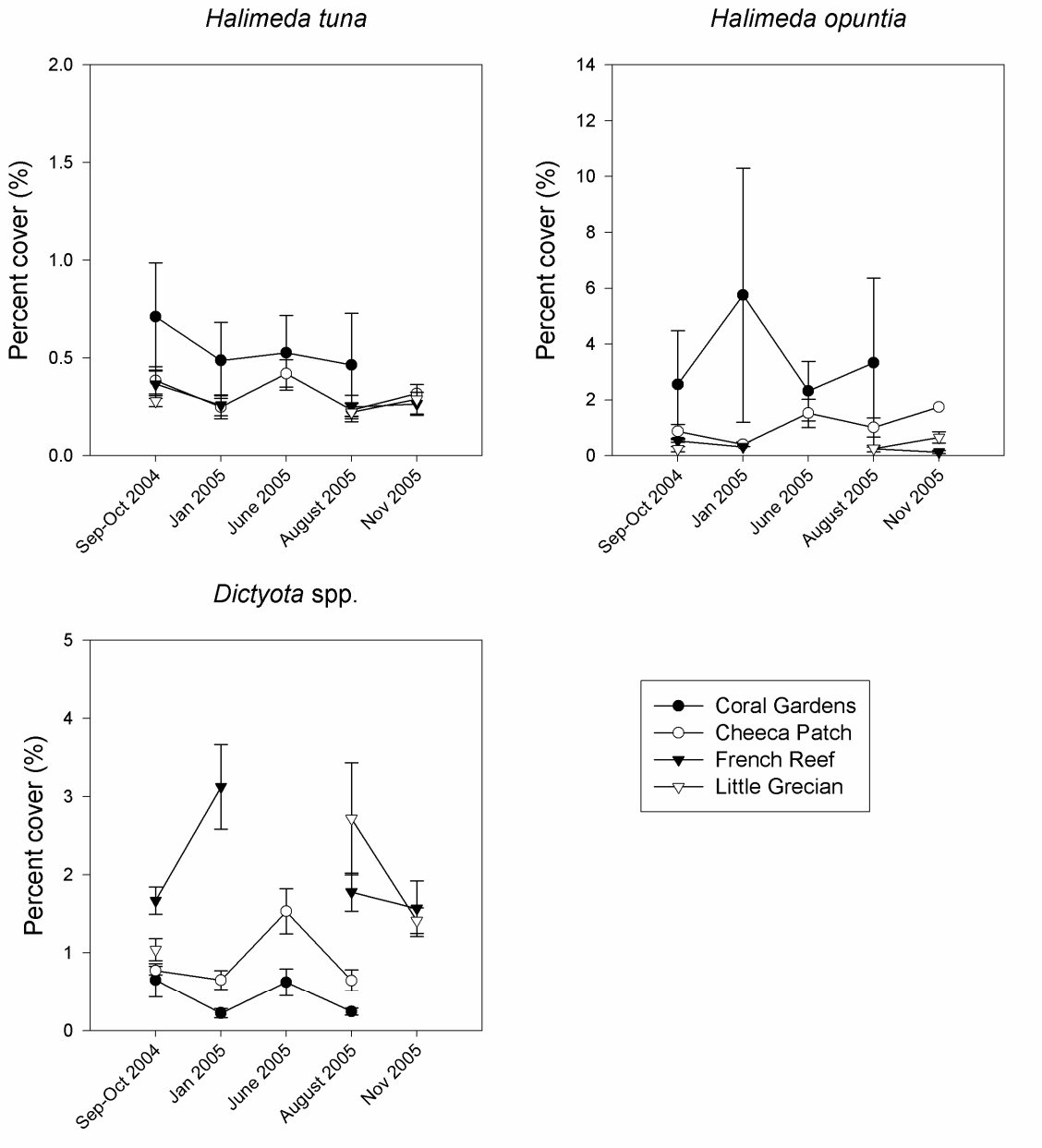


Figure 4.6. Densities of the three macroalgae species from permanent plots monitored in the four field sites. Lines represent these four sites and data are the mean ± SE.

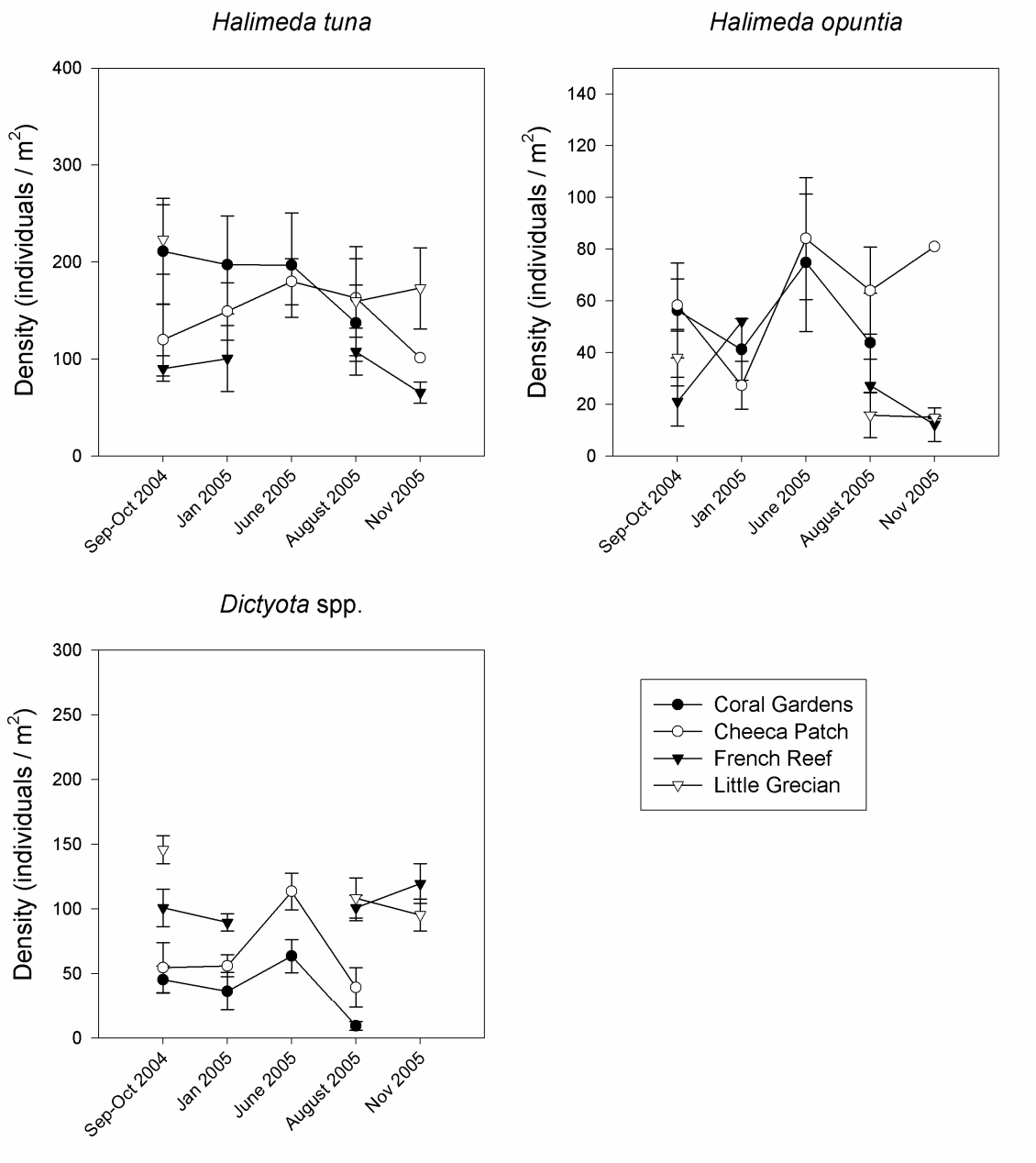


Figure 4.7. Relative cover of the three macroalgae species from permanent plots monitored in the four field sites. Lines represent these four sites and data are the mean ± SE.

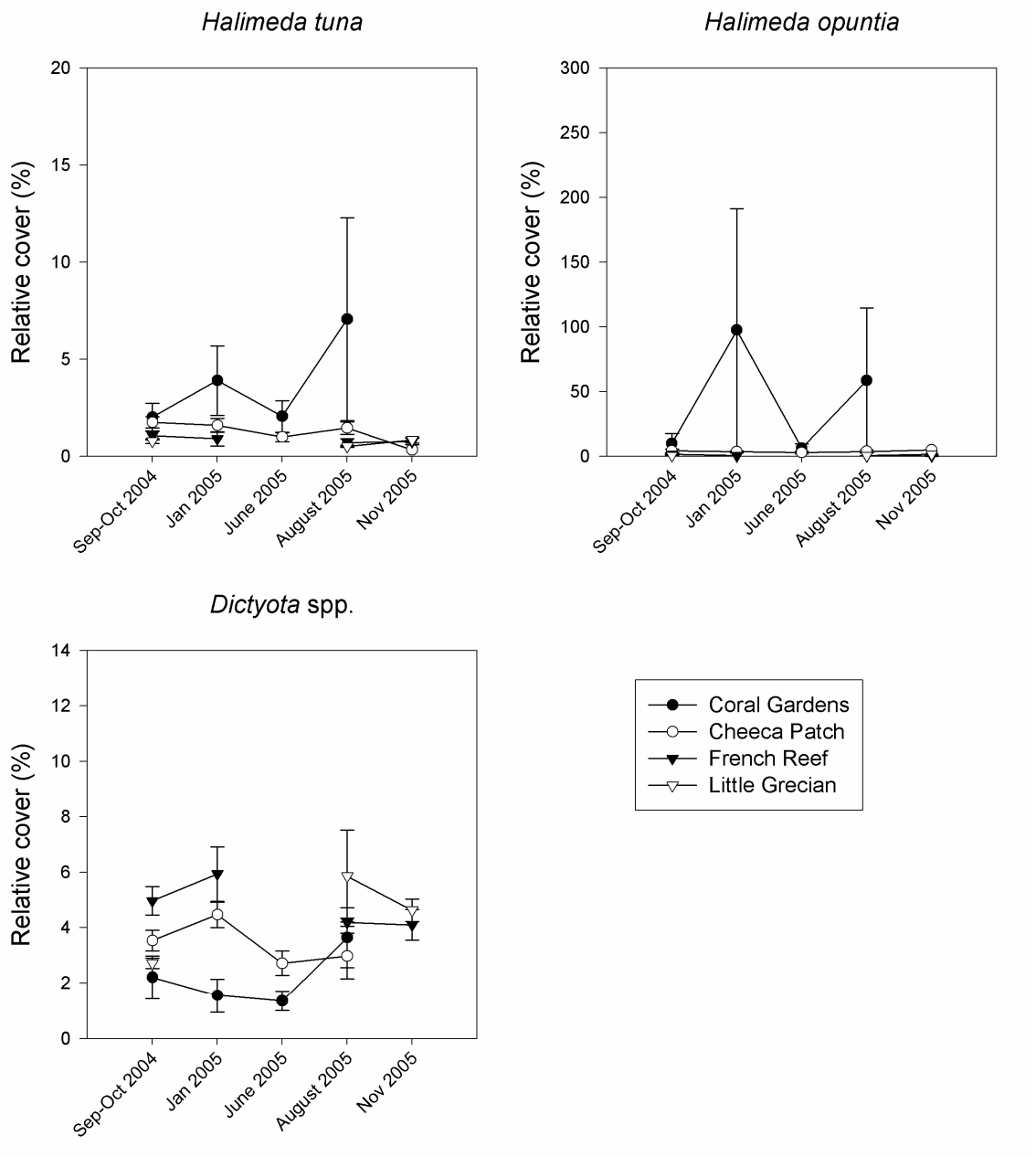


Figure 4.8. Percent cover of the three macroalgae comparing model-derived and field results from the permanent plots and random quadrats. Both the high mortality and large fragments ("Model"), and only high mortality scenarios for French and Little Grecian ("Model FR/LG high") are shown. Cheeca and Coral Gardens were set only at low mortality. Note that *H. tuna* has two y-axes. Data are presented as mean ± SE.

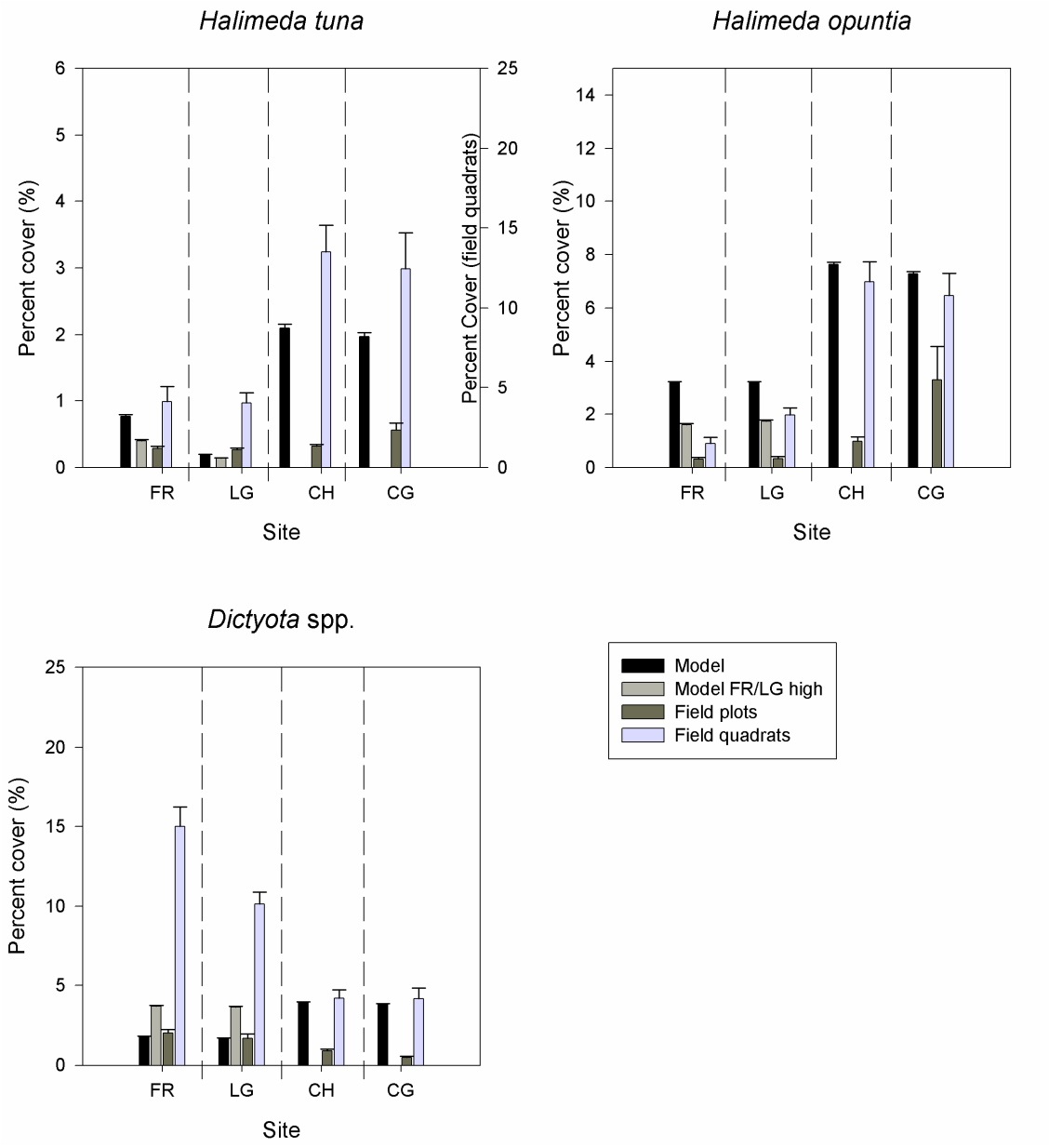
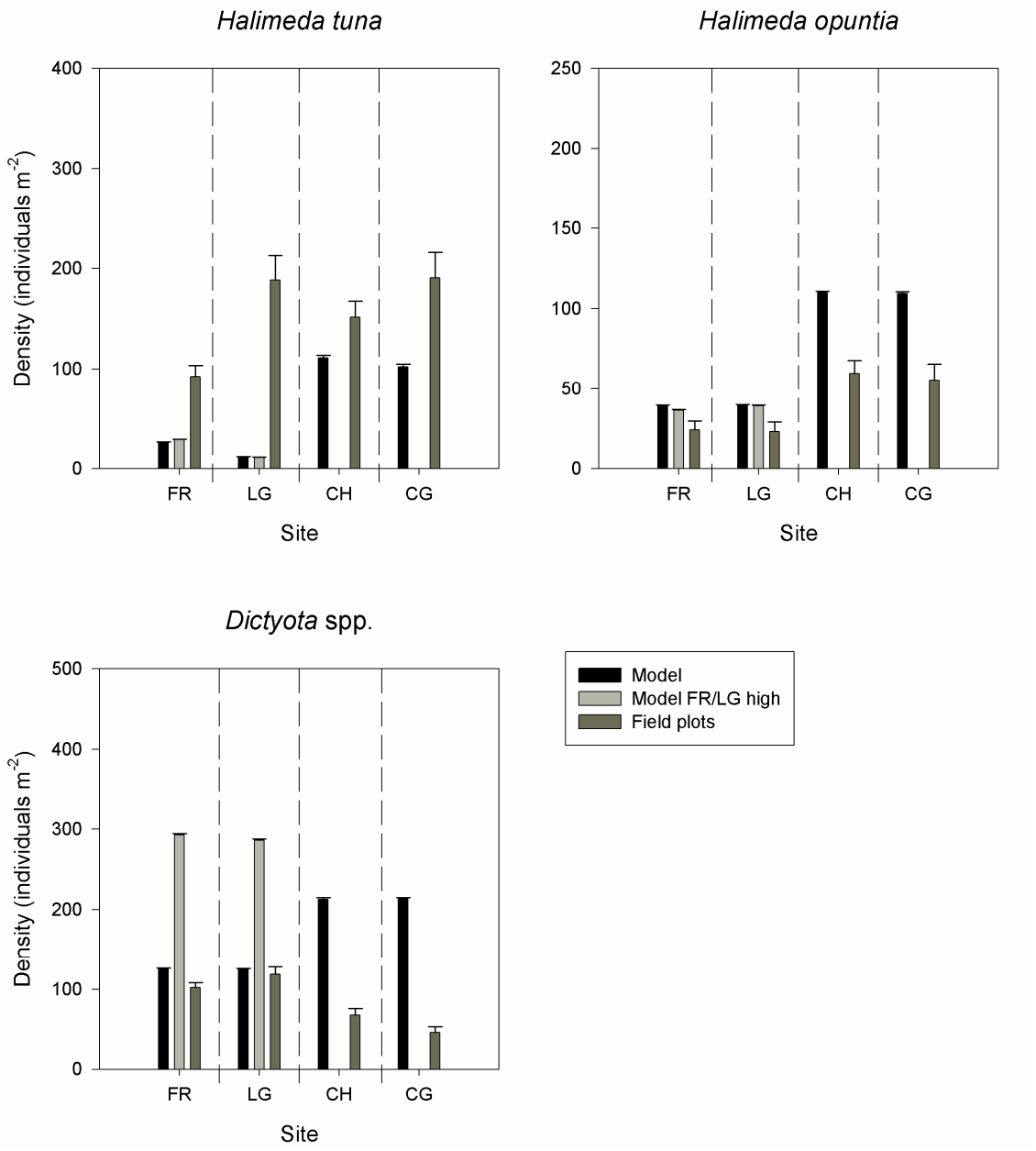


Figure 4.9. Densities of the three macroalgae comparing model-derived and field results from the permanent plots and random quadrats. Both the high mortality and large fragments ("Model"), and only high mortality scenarios for French and Little Grecian ("Model FR/LG high") are shown. Cheeca and Coral Gardens were set only at low mortality. Data are presented as mean ± SE.



V. INTERSPECIFIC COMPETITION FOR SPACE: A MEANS OF POPULATION REGULATION FOR *HALIMEDA* AND *DICTYOTA*?

Introduction

Space is one resource that can be in limited supply for sessile organisms in coral reefs and other benthic systems. Competition for this resource can strongly influence the abundance and distribution of species in these ecosystems (Buss 1979, Buss and Jackson 1979, Connell and Keough 1985, Carpenter 1990, Johnson and Seinen 2002). Competitive interactions can be direct (physical interference) or indirect (exploitative). When one species uses a resource and causes its shortage for the other species, exploitative competition results. Interference competition occurs when one species directly intervenes with the other species' use of a resource. The outcomes of competition range from a hierarchical or transitive structure (species A>B,B>C,A>C), where competitive ability is linear (Lang 1973), and non-transitive networks (Buss and Jackson 1979, Connell and Keough 1985), where species can be competitively equivalent or loops occur in competitive rankings (e.g., A>B,B>C, but C>A).

However, competition is also affected by physical and biological disturbances. In Paine's (1974) classic paper on competition in the western North American intertidal shores, he showed how the mussel, *Mytilus californianus*, can competitively exclude 25 species of benthic invertebrates and benthic algae but only if it is free from predation by the starfish *Pisaster ochraceus*. Disturbances can allow for increased diversity by promoting the co-existence of species (Connell 1978, Russ 1982, Chornesky 1989, Connell et al. 2004) or reversals of the dominant species depending on the characteristics of the organisms involved (Steneck et al. 1991).

The previous chapters have focused on the potential of *H. tuna, H. opuntia,* and *Dictyota* to grow free from competition with other species. However, these algae are exposed to direct and indirect competition with other benthos such as corals (Lirman 2001, Jompa and McCook 2003b, Nugues et al. 2004) and other macroalgae (Lubchenco 1978, Hay 1981b, Beach et al. 2003a, Herren et al. 2006). These three species have a great potential for competitive interaction since they are the dominant macroalgae in the Florida Reef Tract and Beach et al. (2003a) showed that more than 50% of the *Halimeda tuna* and *opuntia* they surveyed in Conch Reef were heavily epiphytized (> 50% covered) by *Dictyota* spp. Their study demonstrated that *Dictyota* could negatively impact the growth of *Halimeda* and correlated the decline in the cover of *Halimeda* in Conch Reef with *Dictyota*'s increase. In this chapter I investigated how interspecific competition for space between the two species of *Halimeda* and *Dictyota* spp. affect their abundances. Once again, the three-dimensional agent-based model SPREAD (Spatially-explicit Reef Algae Dynamics) in conjunction with field data was used to answer the following specific questions:

1) Does interspecific competition between *Halimeda* and *Dictyota* affect their abundances? Is there a difference in their abundances compared to what they achieve under purely intra-specific competition?
2) Does interspecific competition help explain the abundances of these macroalgal species in the patch and offshore reefs that have differing growth and disturbance factors?

Methods

Model scenarios

Two sets of scenarios were run in SPREAD (see Chapter 2 and 3 for details on model formulation and parameterization): one where each species was alone and another where all three species were grown together. The parameters run for all the simulations are documented in Table 5.1. Each set of scenarios was run using site-specific parameters corresponding to the four study sites of French Reef, Little Grecian, Cheeca Patch and Coral Gardens (Table 5.2). The distinctions between the sites were based on field data and literature as described in the Chapter 3 Methods section. The initial numbers of individuals per m^2 were approximated based on the densities obtained from the permanent plots for each site as described in Chapter 4. The same initial numbers were used for the two sets of scenarios for each species. In the second set of scenarios, the three species were all present and allowed to interact. Competition between the two *Halimeda* species consisted only of space pre-emption and shading. There was no direct overgrowth between them. For the *Dictyota*-*Halimeda* interactions, in addition to space pre-emption and shading, *Dictyota* could directly overgrow *Halimeda*. Overgrowth occurred either through modules of *Dictyota* using *Halimeda* modules as substrate for growth if a *Dictyota* module is considering producing a new module into a cell occupied by *Halimeda,* or *Dictyota* fragments settling on *Halimeda* modules. The probability that a *Halimeda* module would be overgrown (71%) was based on the data of Herren et al. (2006) on the incidence of *Dictyota* epiphytizing *Halimeda* in Conch Reef, Florida Keys. Overgrowth did not result in mortality of the affected *Halimeda* module, but in a 60% reduction in probability of growth (Beach et al. 2003a). There was no direct overgrowth

between *H. tuna* and *H. opuntia* and competition between these two SPREAD was run using a 100cm x 100cm x 30cm grid for 3000 time steps (days) and each scenario was run 30 times and the average metrics from these were used for subsequent analyses. The data obtained from the model are percent cover and density (number of individuals per m^2).

Fieldwork

The absolute and relative covers of the three macroalgal species in the four study sites were obtained using random quadrats as described in Chapter 4 Methods section. These data was compared to the abundances of macroalgae in the model with the three species competing.

Model-field comparison

The results from the monospecific and multispecific scenarios were compared to the field data using qualitative and quantitative criteria. The qualitative criteria determined which scenarios were able to simulate the overall patterns in the real reefs. The quantitative comparison determined the scenarios which resulted in cover and density values closest to field values.

Results

Interspecific effects on macroalgal abundances as simulated

In general, for all three macroalgal species, interspecific competition decreased their potential abundances (Figures 5.1 -5.3); however, the strength of the effect varied.

H. opuntia appeared to be the most affected by competition (Figure 5.2), followed by *H. tuna*. The exception was for *H. tuna* in Little Grecian, where percent cover and densities were similar between the multispecies and one species scenarios (Figure 5.1). Decreased abundances in *Halimeda* under the competition scenarios were expected since *Dictyota* was capable of overgrowing them and affecting the production of new segments, however, despite this ability, *Dictyota* abundances were still slightly negatively impacted by spatial competition with these two *Halimeda* species (Figure 5.3).

Comparison of model to field

The qualitative pattern that was strongly observed in the study sites was the difference in the covers of the three macroalgal species between inshore patch and offshore spur and groove reefs (Chapter 4). Inshore patch reefs were characterized by high cover of *Halimeda* spp. and low cover of *Dictyota* spp., while it was opposite for the offshore reefs. For both species of *Halimeda*, the multispecies and one species (no interspecific competition) scenarios were able to simulate the qualitative patterns in abundances (Table 5.3 and Figure 5.4). Quantitatively, there was a difference in which scenarios fit the field data for each species. The closest fit for *H. tuna* percentage cover was with the one species scenarios for all sites except for Little Grecian. Quantitative comparison for density results in a pattern similar to that of the cover pattern for the offshore reefs (Figure 5.4). However, for the offshore patch reefs the observed values were much lower than the model scenarios. None of the model scenarios were able to replicate the higher densities in Little Grecian as well. Unlike the case of *H. tuna,* the multispecies scenarios were the ones that were quantitatively similar to the field values

for *H. opuntia* percentage cover in the offshore reefs. However, for the patch reefs, the higher observed values corresponded more to the one species scenarios. Observed density values for the offshore reefs were also similar to the multispecies scenarios; however, again the inshore patch reefs differed from the pattern in percentage cover, where the patch reefs were also more similar to the multispecies scenarios.

Even when the ability to overgrow *Halimeda* was enabled for *Dictyota*, SPREAD could not replicate the qualitative pattern found in the study sites for both *Dictyota* cover and density (Figure 5.4). Values derived from the model were very much lower than the observed percent cover values in French and Little Grecian. The patch reefs did exhibit values that were most quantitatively similar to the one species scenarios. Comparison of model and field density values were the opposite: the offshore reefs did have values that were comparable to model results (multispecies scenarios), but none were comparable for the patch reefs.

In terms of reliability of measurement and more accurate representation of abundances for the three macroalgae being investigated, percent cover would be a better metric than density. It was difficult to determine the boundaries of the individual patches in the photos, most especially in the sites where the species' cover was high, and this could have led to underestimation of the number of individuals and the discrepancies in the comparisons of the observed cover and density to the model-derived data.

Discussion

Variable population regulation by interspecific competition

Interspecific competition has the capacity to limit the population abundances of *H. tuna*, *H. opuntia* and *Dictyota* spp. Indirect competition through pre-emption of space is a mechanism in this interaction, while for *Halimeda* an added mechanism was the overgrowth of *Dictyota*. The effect of interspecific competition varied with species and site-specific conditions. For *H. tuna*, under conditions that were relatively suboptimal (higher mortality and photo-inhibiting light levels in French and Little Grecian), the effect of competition appeared to decrease. This corresponds to the hypothesis that competition would be a more important factor under low stress and disturbance conditions (Grime 1977, Hay 1981b, Connell et al. 2004). The marked decrease in *H. opuntia* abundances due to competition is most likely because of its larger-sized fragments (that can survive and recruit), which correspondingly require a larger space compared to the two other macroalgae in this model. The effect on *H. opuntia* could be an artifact of the model, but this could also occur in reality, particularly in substrate with minimal space available.

Influence of competition in the real study sites

Based on the comparison of the model results to the observed patterns in the four sites, it appears that *H. tuna* populations were not regulated or at least were less regulated by spatial competition with other benthic organisms. The abundance of this species seemed to be controlled more by the growth (light, temperature, nutrients) and disturbance factors leading to mortality or fragmentation. Thus, the optimal growth

conditions and relatively low disturbance levels that are hypothetically found in the inshore patch reefs potentially explains why they were abundant there. The discrepancy between SPREAD and the Little Grecian *H. tuna* abundances was most likely due to the more heterogeneous area (i.e., depth) surveyed in this site compared to French Reef and the patch reefs). In the model, the depth I used represented only the shallow spurs.

H. opuntia was also abundant in these inshore patch reefs and appeared to be also not regulated by interspecific competition for space, although this was not the case in the offshore spur and groove sites. In French and Little Grecian, their abundances correspond more to the competitively regulated model abundances. This could be due to inability of their larger fragments to find available and suitable space (hard substrate for rhizome attachment) compared to the smaller fragments of *H. tuna* and *Dictyota* (which of course can also epiphytize other organisms). The fact that observed abundances were lower than what could potentially be realized if competition was not an influencing factor could also have been due to much higher mortality in the offshore reefs. *H. opuntia* on these offshore reefs was more frequently found at the edges of the spurs or in areas of the spur with crevices. Such positioning could have led to fragments being lost in the sandy grooves or under the spurs. Alternatively, herbivores, such as juvenile parrotfish could have been targeting this species more than other *Halimeda* species. For example, Overholtzer and Motta (1999) found that *H. opuntia* comprised more than 50% of the diet of three juvenile parrotfishes in Coral Gardens. Paddack (2005) found that *Halimeda* spp. were the most targeted and consumed macroalgae by *Scarus viride* in her offshore reef sites, although she did not distinguish between species of *Halimeda*. These offshore sites could also have experienced more intense water motion during storms and hurricanes,

which led to higher loss of fragments (Walters et al. 2002). Under more optimal growth conditions and relatively lower disturbance, although the fragment pool is smaller, the higher fragment survival probabilities may be able to ameliorate competition effects in the patch reefs.

SPREAD was not able to reproduce the qualitative pattern of *Dictyota* abundances between the offshore and inshore patch reefs, although the inshore patch reef model results were comparable to the actual values. This discrepancy could have been due to different module production rates (thus, different growth parameters) between the inshore patch and offshore spur and groove reefs. *Dictyota* spp. in the offshore reefs could have been thriving because of much higher growth rates that were not captured in SPREAD. Another possible explanation is the unknown contribution of sexual reproduction and asexual reproduction through spores to its population. Compared to the semelparous *H. tuna* and *H. opuntia* (Drew and Abel 1988, Clifton 1997), the spores and sexual recruits of *Dictyota* spp. has more potential to add to the population, however not much is known about how much and when production occurs. Release of gametes and spores possibly occurs periodically over the span of the warm season (Hoyt 1927, Foster et al. 1972). These could then be contributing significantly to the population.

Conclusions

Although interspecific competition could decrease the overall abundances achieved by all three macroalgal species, its effect was variable, depending on the species and the conditions in which they were growing. *H. tuna* was not as sensitive to competition for space relative to *H. opuntia*. However, it was the only species that

exhibited a variation in the strength of the effect depending on the growth and disturbance factors it was experiencing. The less optimal conditions for growth were, the less competition affected its population. For *H. opuntia,* fragment size and survival appeared to mediate the effect of competition, and it was also the species most strongly affected by spatial competition. Even though *Dictyota* could overgrow *Halimeda*, it still exhibited decreased abundances due to competition. For the two *Halimeda*, SPREAD seems to be able to reproduce the patterns that were found in the study sites. Comparison of the model to the field results suggests that *H. tuna* populations in the four reefs and *H. opuntia* in the patch reefs were limited more by the growth and other disturbance factors rather than spatial competition and overgrowth from *Dictyota* spp. However, *H. opuntia* found in the offshore sites could be experiencing interspecific competition or higher mortality levels. The model patterns though deviated from the observed *Dictyota* abundances, which could be due to non-varying growth responses and/or non-inclusion of sporulation and sexual reproduction.

Table 5.1. Description and values of the parameters used in SPREAD for simulations with and without competition.

Parameter	Description	Unit	Species			Source
			Halimeda tuna	Halimeda opuntia	Dictyota sp.	
Season	One static or two seasons; make use of seasonal values where specified	-		2		
Depth		m		7		
Light						
Irradiance	Surface irradiance	μmol m^{-2} s^{-1}		100, 700, 1700, 2200		SeaKeys and Field observations
Irradiance standard deviation	Surface irradiance standard deviation	μmol m^{-2} s^{-1}		30% of surface irradiance		Field observations
Attenuation coefficient	Irradiance attenuation coefficient	-		0.26		SERC-FIU
Allow shading?	If shading will occur or not	Boolean		true		
Tissue transparency	Amount of light that a module will allow through to the cells below it	Fraction	0	0	0.6	*Halimeda* segments are solid and opaque; Dictyota (Hay 1986)
# cells affected by shading	Number of cells below module that will be affected by its shade	Cells		3		Assumed
Temperature						
Mean temperature		°C		Summer: 29 °C Winter: 22.3 °C		SERC-FIU and Field observations
Temperature standard deviation		°C		Summer: 1.8% Winter: 5.7%		SERC-FIU and Field observations
Nutrients level		1 – low 2 – medium 3 – high		1, 2, 3		Exploratory
Branching					Always dichotomous	
branch order	Curve for effect of branch order on producing a new module					
a		-	0.2	0.2	n/a	Estimated
b		-	0.5	0.5	n/a	Estimated
c		-	0.3	0.3	n/a	Estimated
branch present	Line for effect of number of modules already produced on producing a new one				n/a	
slope		-	-0.14	-0.05	n/a	Estimated
intercept		-	0.7	1	n/a	Estimated
Mortality						
fragments		Fraction		0.01, 0.05		Exploratory
Fragment size ± std. deviation			Small: 3 ±1, Large: 6 ±1	Small: 22 ±7 Large: 44 ±7	Small: 4 ±1 Large: 8 ±1,	Walters et al. 2002, Herren et al. 2006
Fragment survival probability	Probability that a fragment will settle and grow on available space					Walters et al. 2002, Herren et al. 2006
Low		Fraction	0.133	0.333	0.93	
Medium		Fraction	0.333			
High		Fraction	0.5	0.933	1	
Overgrowth						
Probability of overgrowing	Probability that a *Dictyota* module would overgrow a *Halimeda* module if it expands to a		0.71	0.71	n/a	Beach et al. 2003, Herren et al. 2006

Parameter	Description	Unit	Species			Source
			Halimeda tuna	Halimeda opuntia	Dictyota sp.	
	cell occupied by a *Halimeda* module					
Effect of overgrowth	Depression of growth of overgrown *Halimeda* module	Percent	40	40	n/a	
Light curve			Exponential	Normal	Exponential	
a		-	0.01	0.4	0.0003	Laboratory observations (Chapter 3 – Figure 3.4, Appendix A)
b		-	0.04	0.2	0.1579	Laboratory observations (Chapter 3 – Figure 3.4, Appendix A)
c		-	8			Laboratory observations (Chapter 3 – Figure 3.4, Appendix A)
Temperature curve						
Mean growth temperature		°C	29	29	28	Beach et al. 2003, Biber 2002, Hillis-Colinvaux 1980, Lirman and Biber 2000
Standard deviation		°C	2	2	2	Beach et al. 2003, Biber 2002, Hillis-Colinvaux 1980, Lirman and Biber 2000
Nutrient probabilities						
low		Fraction		0.2		Exploratory
average		Fraction		0.4		Exploratory
high		Fraction		0.6		Exploratory

Table 5.2 Parameters for site-specific model scenarios.

Parameter	Site/Scenarios			
	French Reef	Little Grecian	Cheeca Patch	Coral Gardens
Depth	7	3.2	3.7	3.7
Light				
Irradiance	1942	2102	2167	2076
Irradiance standard deviation	577	646	740	547
Attenuation coefficient	Summer: 0.26 Winter: 0.14	Summer: 0.26 Winter: 0.14	Summer: 0.34 Winter: 0.23	Summer: 0.34 Winter: 0.23
Temperature				
Mean temperature	Summer: 28 Winter: 24	Summer: 28 Winter: 24	Summer: 29 Winter: 22.3	Summer: 29 Winter: 22.3
Temperature standard deviation	Summer: 1.4 Winter: 3	Summer: 1.4 Winter: 3	Summer: 1.8 Winter: 5.7	Summer: 1.8 Winter: 5.7
Nutrients level	2	2	3	3
Nutrient growth probabilities average	0.4	0.4	0.6	0.6
Mortality				
Fragments	0.05	0.05	0.01	0.01
Fragment size	large	large	small	Small
Fragment survival probability	Low	low	high	High

Table 5.3. Results of the qualitative and quantitative comparison of model and observed percent cover and density for each species in the four field sites. They refer to which model scenarios were comparable to what was observed in the four study sites (FR : French Reef, LG: Little Grecian, CH: Cheeca Patch, CG: Coral Gardens). One or one species are the scenarios where one macroalgal species was used in model runs. Multispecies are the scenarios where all three macroalgae species were used in the model runs. None means there were no similarities in the model and observed measure.

	Percent Cover		Density	
	Qualitative	Quantitative	Qualitative	Quantitative
Halimeda tuna	Both multispecies and one species	FR: One LG: None CH/CG: One	Both multispecies and one species	FR: One LG: None CH/CG: Multispecies
Halimeda opuntia	Both multispecies and one species	FR/LG: Multispecies CH/CG: One	Both multispecies and one species	Multispecies
Dictyota	None	FR/LG: None CH/CG: One	None	FR/LG: Multispecies CH/CG: None

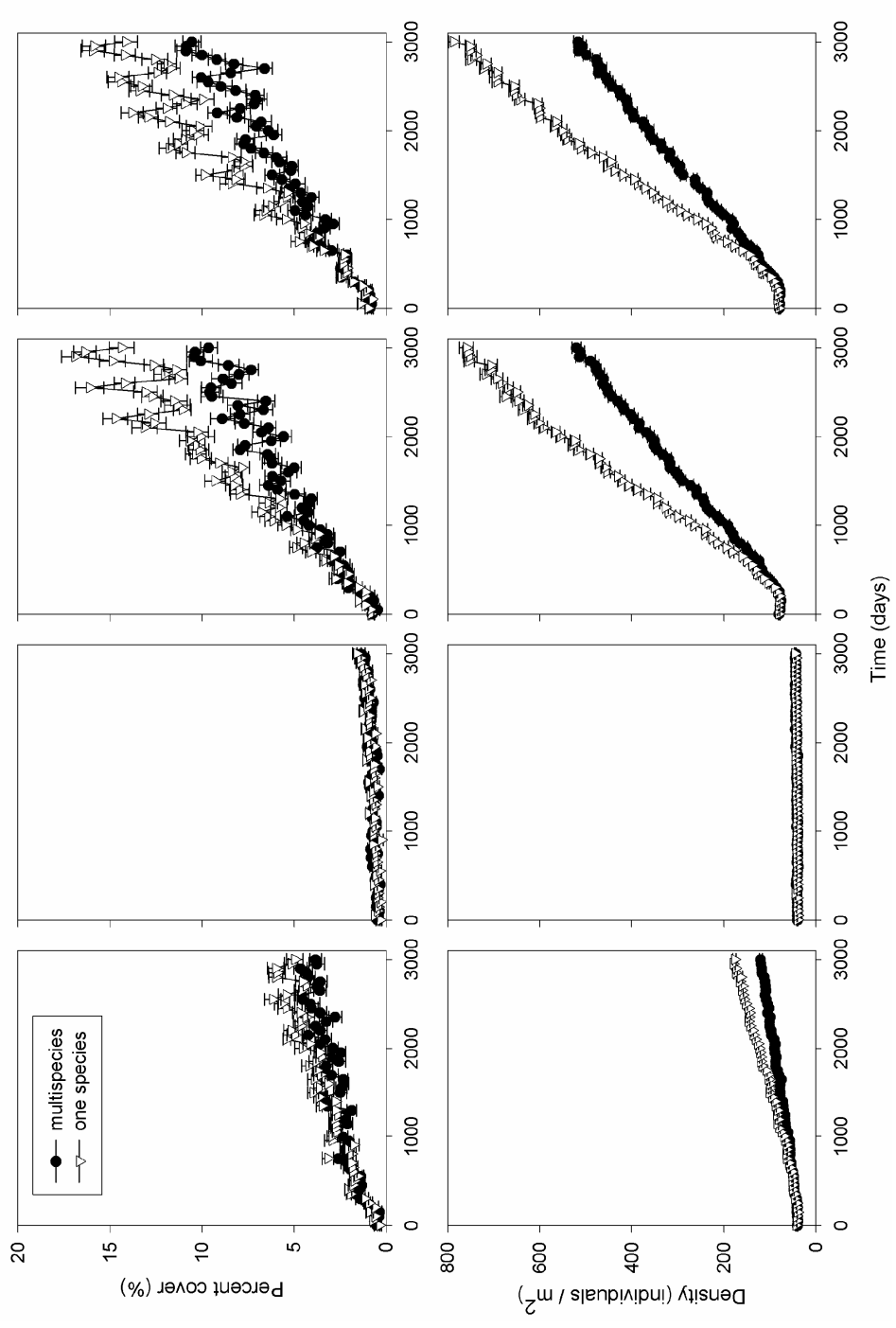


Figure 5.1. Trajectory of the percent cover and density of *Halimeda tuna* when competing with *H. opuntia* and *Dictyota* sp. (multispecies) in SPREAD and on its own (one species), as simulated using site-specific parameters.

Figure 5.2. Trajectory of the percent cover and density of *Halimeda opuntia* when competing with *H. tuna* and *Dictyota* sp. (multispecies) in SPREAD and on its own (one species), as simulated using site-specific parameters.

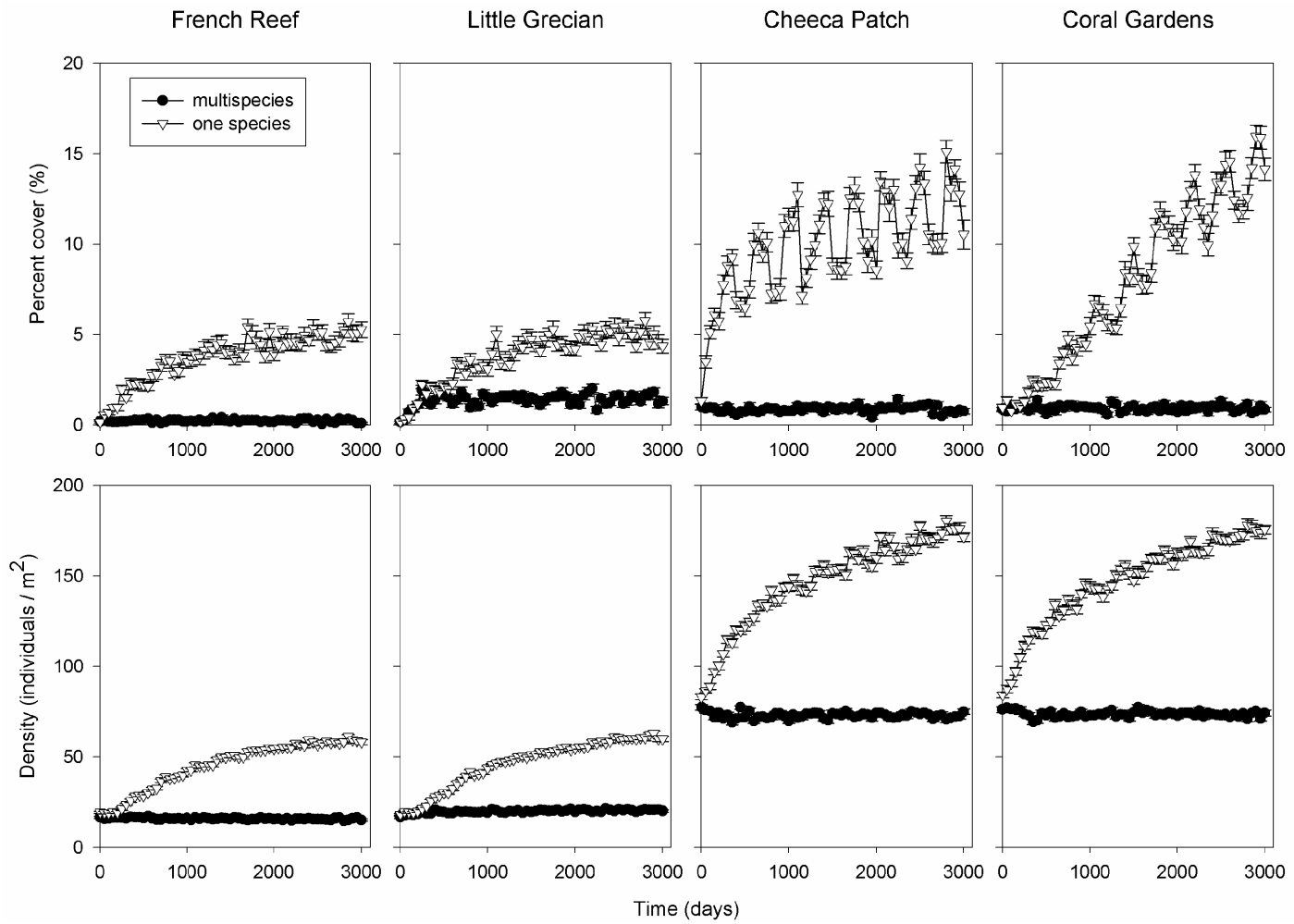
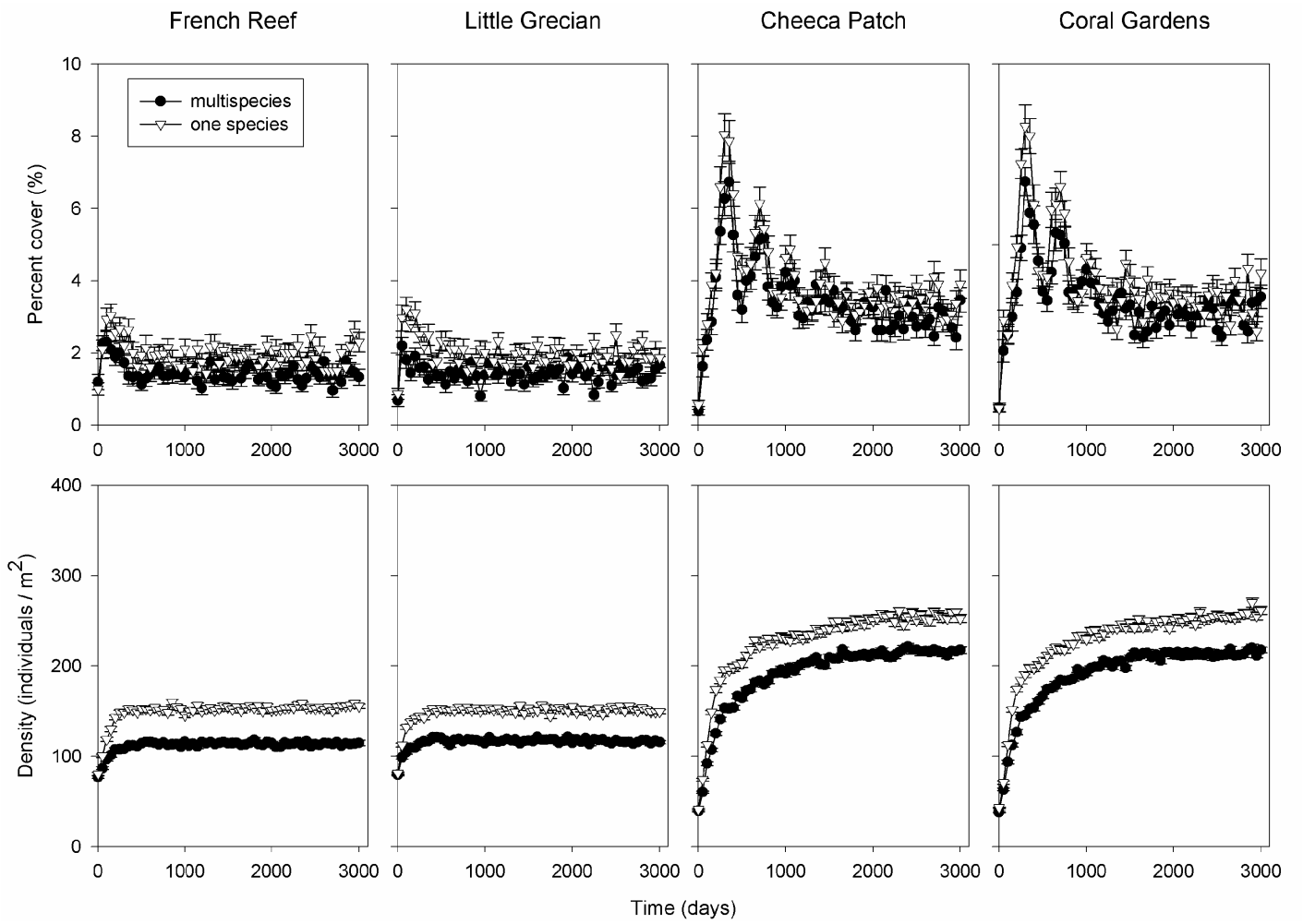


Figure 5.3. Trajectory of the percent cover and density of *Dictyota* sp. when competing with *H. tuna* and *H. opuntia* (multispecies) in SPREAD and on its own (one species), as simulated using site-specific parameters.



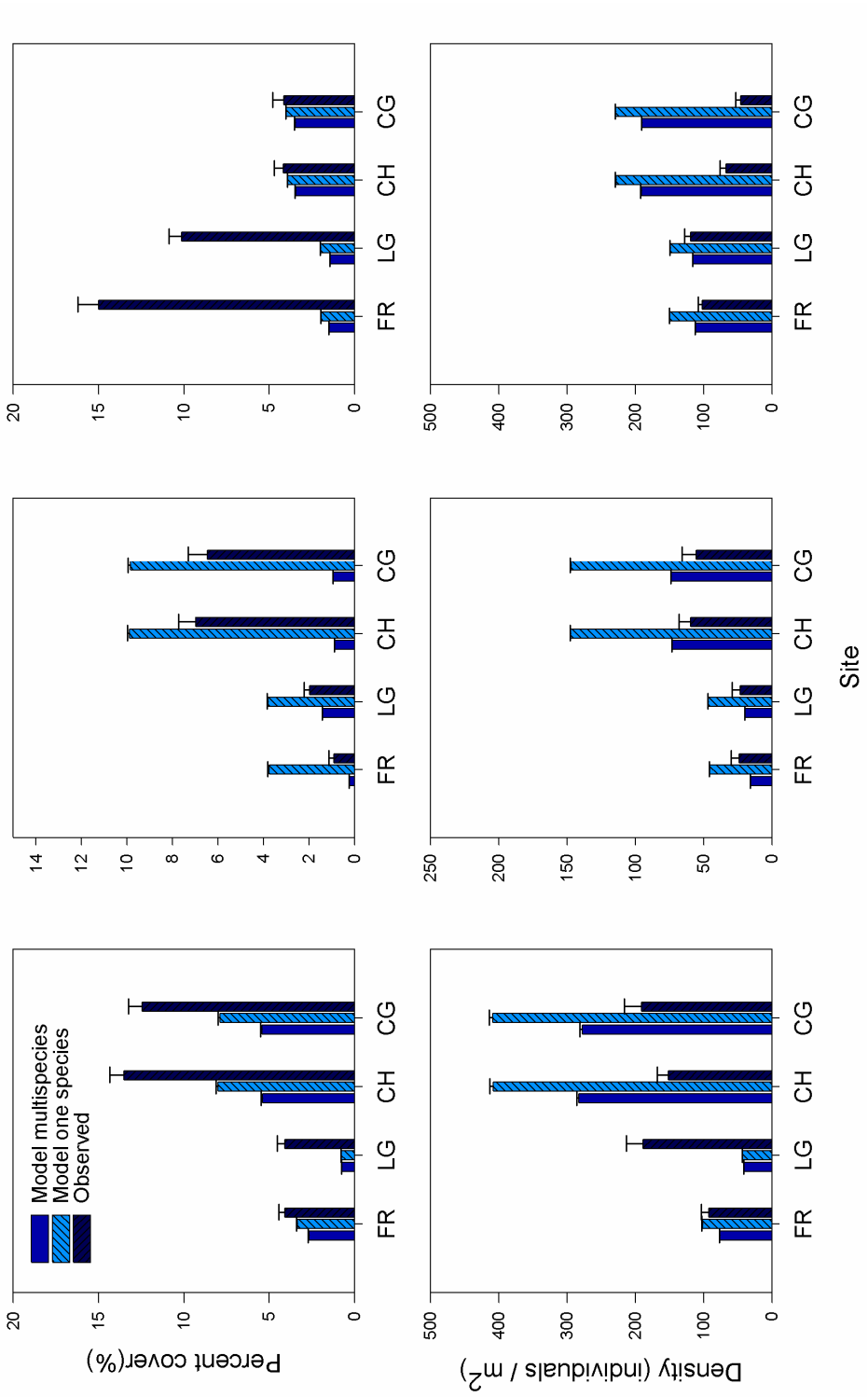


Figure 5.4. Comparison of the model-derived percent covers and densities with observed values in the four study sites (FR: French Reef, LG: Little Grecian, CH: Cheeca Patch, CG: Coral Gardens) for each species. Both multispecies and one species model results are shown.

VI. OVERALL SUMMARY, CONCLUSIONS, AND RECOMMENDATIONS FOR FUTURE RESEARCH

Morphology, space and agent-based modeling

Many ecological concepts, like life-history theory, were developed with an eye towards the unitary perspective and do not take into account the special characteristics of clonal organisms that allow them to be highly abundant and successful in their ecosystems (de Kroons and Hutchings 1995). Such characteristics are their potentially highly plastic morphologies, indeterminate growth, greater importance of size than age in their life histories, and capacity for asexual reproduction (Jackson and Coates 1986). These characteristics have been investigated primarily in terrestrial plants and corals within the past several decades, and have shown that the modules making up the bodies of these organisms, and the ramets that can break off to form new individuals, have their own dynamics analogous to the population dynamics of individuals, and that these strongly influence the pattern of vertical and horizontal capture of space (Bell and Tomlinson 1980, Harper 1985, Halle 1986, Cain et al. 1996).

Modeling the growth and form of modular and clonal organisms, particularly plants, is included in an active field known as morphogenesis. One of the common methods used to model the morphogenesis of plants is the Lindenmayer-system (L-system), which makes use of formal rules which are iterated to create the growth form (Lindenmayer 1968, Prusinkiewicz et al. 1996). The L-system is focused on capturing the general morphology of biological organisms using intrinsic growth rules (e.g., branching angle, node and internode arrangement, inflorescence) and as such is primarily deterministic and does not easily allow for morphogenesis under highly stochastic or

many variable conditions. On the other side of the spectrum is morphogenetic modeling that focuses specifically on growth as a response to exogenous factors (Kaandorp 1995, Kaandorp and Kubler 2001, Merks et al. 2003). For example, in the Laplacian branching growth model, the linear branching growth pattern is set and growth of the tips is controlled by external stimuli in the form of a concentration gradient (Kaandorp and Kubler 2001). The main intent of this dissertation was to highlight and make full use of the modular and clonal characteristics of two genera of coral reef macroalgae in order to discern the factors that were controlling their growth, morphologies, and abundances in the reefs of the Florida Keys. In order to achieve this, a three-dimensional agent-based modeling approach was adapted. This framework can easily integrate both environmental (exogenous) and internal control in the morphogenesis of the macroalgae.

Chapter 2 described the formulation of this model for *H. tuna, H. opuntia* and *Dictyota* spp., the three dominant macroalgal species in the Florida Keys and many parts of the Caribbean. The agent-based model, SPREAD or Spatially-explicit Reef Algae Dynamics, focuses on the growth of the iterating units of the macroalgae (i.e., the modules) in three-dimensional space in response to different levels of light, temperature, nutrients and availability of space. Mortality occurred only through fragmentation of these modules, and fragments can be set to survive depending on a certain probability, or actually "die" (i.e., the fragmented modules are removed from the model). Overgrowth by *Dictyota* on the two *Halimeda* spp. could also be enabled to investigate how interspecific competition in the form of this particular type of epiphytism, as well as space pre-emption between the three species could affect the dynamics of growth and spread of the macroalgae. Modeling at this level (and using the agent-based approach)

enabled the growth form of the macroalgae to emerge rather than being imposed and consequently allowed for the testing of hypotheses on factors that controlled the species' individual morphologies and population abundances. Subsequent comparisons of the more detailed growth data obtained for *H. tuna* in two inshore patch reefs and offshore bank reefs in the Florida Keys yielded a good fit with the model results. The growth parameters were derived from literature and laboratory experiments. Therefore, the model is based on data that is entirely independent from the field data gathered, but it was able to generally simulate patterns observed in the real study sites, generate potential explanations for these patterns, as well as hypotheses that could account for discrepancies.

Controlling factors in the growth and spread of macroalgae

Individual morphology

The individual morphologies of *H. tuna*, *H. opuntia*, and *Dictyota* spp. derived from SPREAD yielded information on the factors leading to these growth forms. All three macroalgal morphologies were influenced by the strength of disturbance, tending to grow smaller and more hemispherical under higher disturbance conditions. However, the form of *H. tuna* was distinctly strongly influenced by the growth factors of light and nutrients (Chapter 2, Beach et al. 2003b, Vroom et al. 2003, Smith et al. 2004), while the imprints of these factors on the other two macroalgae were not as apparent. The model-derived morphologies also corresponded with those found in the real reefs, and the conditions which led to these forms in SPREAD also corresponded with the conditions most likely acting upon these sites.

The two inshore patch reefs were characterized by intermediate light levels, higher DIN concentrations, and calmer conditions, while the offshore bank reefs have higher light levels, lower DIN concentrations and stronger water motion through wave action and currents. It appears that the morphometrics of *H. tuna* can be good indicators of the conditions under which they are found: larger and more upright forms tend to be in lower light (i.e., non-photo-inhibiting), higher nutrient and calmer environs (Chapter 3, Beach et al. 2003b, Vroom et al. 2003, Smith et al. 2004). *H. opuntia* and *Dictyota* morphologies were more indicative of the disturbance conditions, whether herbivory or hydrodynamics, of their habitats. Inclusion of other morphological characteristics such as segment size, branching angles and intersegment distances for *H. opuntia* would probably give more information (Hillis-Colinvaux 1974, 1985, Littler and Littler 2000).

Scaling up to the population and multi-specific patch dynamics

Purely vegetative growth can only result in limited spatial (horizontal) coverage, as was shown in Chapter 4. Different growth forms, though, varied in their capacity for horizontal spread, wherein the hemispherical forms occupied space slower and less in amount compared to the larger upright ones. These are comparable, though not as extreme in distinction, to the theoretical phalanx and guerilla forms described by Lovett-Doust (1981) that lead to potential variation in amount and rate of space occupation in plants. Although investigating the vegetative growth forms of the three macroalgae helped to understand the factors that were important in shaping these forms, primary growth was not enough to explain their abundances in the inshore and offshore reefs (Chapter 4). When the survival of fragments was allowed to occur in SPREAD, the cover

and densities achieved by the three macroalgae were significantly much higher. The site-specific simulations were also able to generate the qualitative patterns observed in the field for the two species of *Halimeda,* as well as the values for percent cover and densities. The model, though, could not simulate the higher cover of *Dictyota* spp. in the offshore reefs and explanations for this were explored in Chapter 5. Fragmentation can be a highly effective means of rapidly increasing spatial coverage (Ceccherelli and Cinelli 1999, Ruesink and Collado-Vides 2006) and this appears to be the case for these three species. However, it can have trade-offs, such that fragment generation can compromise one or more life history parameters such as growth or fecundity (Smith and Hughes 1999, Lirman 2000, Nagelkerken et al. 2000, Walters et al. 2002). *H. tuna* and *H. opuntia* are relatively not as successful as fragmenters compared to *Dictyota*. The two calcareous species produce fragments with much lower survival probabilities than *Dictyota* spp. (Walters et al. 2002, Vroom et al. 2003, Herren et al. 2006). In conjunction with the possibly better growing conditions (optimum light, higher nitrogen), the more protected nature of the inshore patch reefs that allows for higher probabilities of survival of fragments could explain why *H. tuna* and *H. opuntia* are more abundant in these reefs, while *Dictyota*, can thrive in the more disturbed offshore reefs.

Temporally, both the model and observed data from the four study sites show that the populations of these three macroalgae (at least on a patch scale) are stable overall with seasonal variation, which has also been seen in other studies (Lirman and Biber 2000, Beaver et al. 2006). This natural regulation can allow other benthic organisms such as hard corals to make use of available substrate for settlement in these reefs. However, the seasonal increases of these macroalgae also correspond with the reproductive season

of these corals and thus could still impact larvae settlement whether through pre-emption or direct interaction (McCook et al. 2001, Nugues and Szmant 2006, Titlyanov et al. 2007).

Competition can be an important regulating force in the abundances of organisms (Paine 1984, Carpenter 1990, Johnson and Seinen 2002). In Chapter 5, competition between the three-species of macroalgae was simulated in SPREAD in order to investigate its role in regulating their populations. Competition between the two *Halimeda* represent pure space pre-emption as the mechanism, while *Dictyota* can overgrowth both and dampen their growth (Beach et al. 2003a, Herren et al. 2006). The model results showed that competition has the capacity to decrease the abundances of the three macroalgae, but the strength of the effect differed between species and for *H. tuna,* between simulated reefs (differing growth and mortality conditions) as well. *H. opuntia* was the most strongly affected and was hypothesized to be due to the need of its larger fragments for correspondingly larger space. Comparing the site-specific simulations to the observed covers in the study sites, *H. tuna* in all sites and *H. opuntia* in the patch reefs were potentially not regulated by competition for space through pre-emption or *Dictyota* epiphytism. *H. opuntia* in the offshore sites could be competitively regulated or alternatively, higher mortality conditions that the model scenarios did not capture could also be lowering their abundances to levels below what the population could potentially attain based on the non-competition model scenarios. SPREAD results also differed from the observed *Dictyota* patterns of abundance. This could be due to variation in growth curves between inshore and offshore reef populations, where the latter have higher

growth rates, or alternatively, the unknown contribution of spores and sexual reproduction.

Recommendations for future research

Role of asexual reproduction through fragmentation and sexual reproduction in Halimeda and Dictyota population dynamics

Fragmentation is an important process in the spatio-temporal dynamics not only of macroalgae but also of many other reef benthos. The results from this dissertation illustrate the variation in fragmentation capabilities of these three species that represent potential variation in life-history strategies and consequently how successful they can be in different habitats. However, the trade-offs of fragmenting and the relative roles and effects of herbivory and hydrodynamics in generating fragments are unknown.

Although asexual reproduction appears to be an important part in the life history of *H. tuna*, *H. opuntia*, and *Dictyota* spp., they also undergo sexual reproduction. *Halimeda* are dioecious broadcast spawners that release anisogamous gametes in the summer (Drew and Abel 1988, Clifton 1997, Vroom et al. 2003). A special part of the life-cycle of *Halimeda* is holocarpy. This is when an individual releases all the segments' protoplasmic contents through the gametes, and afterwards, the individual alga disintegrates (Hillis-Colinvaux 1980, Drew and Abel 1988). *Dictyota* on the other hand, exhibits an isomorphic alternation of generation. However, populations in the wild are dominated by the sporophytes (Hoyt 1927, Agardh et al. 1972, Foster et al. 1972) that might be producing asexual spores depending on the season (Ateweberhan et al. 2005). Gametophytes are rarely seen but have been found to reproduce periodically possibly with the tides (Hoyt 1927, Phillips 1988) . The contribution to the population of these

sexual recruits from *Halimeda* and *Dictyota*, as well as haploid spores from the former, is a large unknown. These could thus help to increase abundances and distribution more since these are additional sources of individuals. In the case of *Halimeda,* the death and disintegration of the adult might neutralize any increases in abundance from sexual reproduction.

Exploiting the morphological perspective on clonal organisms as indicators of site-specific factors and processes

As has been illustrated in this dissertation as well as other studies, the morphology of modular and/or clonal organisms can be an important source of information on the conditions that are relevant to them, as well as, the conditions that are actually affecting them wherever they are located (Hay 1986, Collado-Vides 2002b, Benedetti-Cecchi et al. 2006, Haring and Carpenter 2007). Given that many relevant questions in coral reef ecology and conservation are concerned with what factors affect the abundance and distribution of benthic clonal organisms, the capacity for inferring such factors and processes using these organisms' morphological plasticity has not been exploited. Unlike the functional form models (Littler 1980, Steneck and Dethier 1994), adapting a growth form model also helps to understand potential for space occupation. Most studies in the past have focused on zonation of coral morphologies, however, the faster growing organisms that are becoming more abundant in reefs nowadays have been ignored. Little is known about how the morphologies of macroalgae, sponges and gorgonians vary in coral reefs. Another macroalgal species that could provide important information on the factors affecting itself and the reef it is located in through morphology is *Lobophora variegata.* This species is found in both the Caribbean and Pacific and can exhibit three

forms (decumbent, encrusting and ruffled) (Littler and Littler 2000). It is a competitively aggressive species that can affect coral growth (Jompa and McCook 2002a), and is also abundant in many Caribbean reefs (Williams and Polunin 2001, Jompa and McCook 2002a). Studying macroalgae and other benthic organisms with differing requirements and life histories can help further understand the environment where they live and their capacity to capture and maintain space.

Modeling macroalgal communities using 3-D agent-based simulations

SPREAD provides an important agent-based modeling framework for simulating macroalgal growth not only for the three species studied in this dissertation, but potentially for expansion into a generalized model that represents a more realistic macroalgae community or ecosystem. This could be achieved by specifically representing the dominant species within a system (similar to what I have done here) or possibly use general classifications of macroalgae forms such as architectural models (Collado-Vides 1993, 2002a).

The challenge to generalizing SPREAD is still similar to the challenges faced even with the current three species system multiplied by however many groups will be included. The appropriate modules to be used for the different architectural growth plans need to be determined to enact the growth rules, then parameterizing the appropriate growth rules, both static and particularly the dynamic rules in response to various environments, needs to be addressed. The primary revision of SPREAD would be a switch to a continuous space rather than a grid. This would enable incorporation of different module types and sizes, and their accompanying growth rules.

APPENDIX A. LABORATORY EXPERIMENTS TO OBTAIN MODULE PRODUCTION CURVES IN RESPONSE TO LIGHT FOR *HALIMEDA* AND *DICTYOTA*

Laboratory experiments were used in order to obtain the probabilities of growth of *Halimeda tuna* (Ellis and Solander) Lamouroux*, Halimeda opuntia* (Linnaeus) Lamouroux, *Dictyota menstrualis* (Hoyt) Schetter, Hörnig and Weber-Peukert, and *Dictyota cervicornis* (Kützing) under different light conditions. Samples of these macroalgae were obtained from the four study sites French Reef, Little Grecian, Coral Gardens and Cheeca Patch. These were allowed to acclimate to laboratory conditions for a week before being placed (ten replicates each) in ten gallon aquaria (Figure A.1a). The two *Halimeda* species were planted on Geo-Marine Florida Crushed Coral substrate in the aquaria. In the summer of 2005, the experiment was run inside a laboratory where light was supplied using two VHO AquaSun 110 Watts Bulbs. Light levels inside the aquaria in terms of Photosynthetic Active Radiation or μmol quanta m^{-2} s^{-1} were measured using a LI-COR LI-193 Spherical Underwater Quantum Sensor. Table A.1 lists the light levels used for the experiments. The different light levels were achieved by covering the aquaria with neutral-density filters and there were two aquaria for each light treatment. Flowing coarsely filtered sea water was supplied to all the tanks via hoses, and pumps were also used to circulate water. In the winter and summer of 2006, the experiments were moved outdoors (Figure A.1b). The same sized aquaria were used with flowing sea water and neutral-density filters to vary light levels (Table A.1). No pumps were used in these set-ups and light came from natural light. Light, temperature and salinity data were obtained each week from the aquaria. The light data were transformed into irradiance at noon values.

H. tuna growth was monitored weekly for four weeks by taking photographs of each individual. The total number of potentially growing segments (i.e., segments with less than five segments already produced) and the number of new segments produced per week were analyzed from the photographs. The average for all weeks of the number of new segments divided by the total number of potentially growing segments represented the growth probability (i.e., the probability of producing a new segment) for a light treatment. The data for all three experiments (summer 2005, winter and summer 2006) were combined to obtain a larger light range for this species.

The wet weights (after careful cleaning, spinning and blotting) of *H. opuntia* and *Dictyota* clumps of approximately the same size were measured at the start and end of the experiment. *Dictyota* clumps were tied to wires hanging in the upper portion of the water column of the aquaria. *D. menstrualis* was used for the winter 2006 experiments, however these did not survive well and thus these data were not used. The summer 2006 experiments made use of *D. cervicornis*. In order to obtain the equivalent number of segments from the wet weights of *H. opuntia* and *D. cervicornis*, the wet weights of known numbers of segments were obtained (120 samples for the former and 100 for the latter). The average weight of one segment for each species (0.016137 g for *H. opuntia* and 0.003425 g for *D. cervicornis*) were used to convert the wet weights in the experiments into number of segments. The average value of the number of new segments divided by the total number of segments represented the growth probability for a light treatment.

Linear and non-linear regression were used to analyze the relationship between light and the probability of producing a new segment as discussed in Chapter 3 in Figure 3.4.

Table A.1. Average irradiances for the summer 2005 indoor laboratory and winter and summer 2006 outdoor experiments for each light treatment level.

Experiment	Average Irradiance (µmol quanta m^{-2} s^{-1})
Summer 2005 (laboratory)	
1	105.6
2	63.1
3	35.4
4	8.1
Winter and Summer 2006 (outdoor)	
1	2547.3
2	881.9
3	301.3
4	183.7

Figure A.1. Photographs of experiments set-up inside the laboratory (a) during summer 2005 and outdoors during winter and summer 2006 (b). The outdoor set-up photo was taken before the neutral sheets were placed on the aquaria while the indoor laboratory photo shows the screens.

a **b**

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