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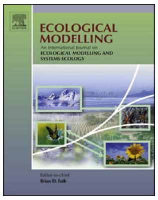

Consequences of morphological plasticity and fragmentation on space occupation of coral reef macroalgae

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ABSTRACT

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

1. Introduction

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

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

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

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

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

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

2. Materials and methods

2.1. Model description

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

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

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

Table 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 (for all)			
Depth		m	7 (for all)			
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 (for all)			SERC-FIU
Allow shading?	If shading will occur or not	Boolean	True (for all)			
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)
No. of cells affected by shading	Number of cells below module that will be affected by its shade	Cells	3 (for all)			Assumed
Temperature			(for all)			
Mean temperature		°C	Summer: 29 °CWinter: 22.3 °C			SERC-FIU and Field observations
Temperature standard deviation		°C	Summer: 1.8%Winter: 5.7%			SERC-FIU and Field observations
Nutrient level		1—low2—medium3—high	1, 2, 3 (for all)			Exploratory
Branching					Always dichotomous	
Branch order	Curve for effect of branch order on producing a new module					See Yñiguez et al. (2008) for details
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	See Yñiguez et al. (2008) for details
Slope		–	−0.14	−0.05	n/a	Estimated
Intercept		–	0.7	1	n/a	Estimated
MORTALITY/FRAGMENTATION						
Fragmentation probability		Fraction	0.01, 0.05 (for all)			Exploratory
Fragment size ± std. deviation			Small: 3 ± 1, Large: 6 ± 1	Small: 22 ± 7Large: 44 ± 7	Small: 4 ± 1Large: 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	n/a	n/a	
High		Fraction	0.5	0.933	1	
Light curve			Exponential	Normal	Exponential	
A		–	0.01	0.4	0.003	Laboratory observations; see Yñiguez (2007) and Yñiguez et al. (2008) for detail
B		–	0.04	0.4	1	Laboratory observations see Yñiguez (2007) and Yñiguez et al. (2008) for details
C		–	8	n/a	n/a	Laboratory observations see Yñiguez (2007) and Yñiguez et al. (2008) for details

Table 1 (*Continued*)

Parameter	Description	Unit	Species			Source
			Halimeda tuna	*Halimeda opuntia*	Dictyota sp.	
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 (for all)			Exploratory
Average		Fraction	0.4 (for all)			Exploratory
High		Fraction	0.6 (for all)			Exploratory

Disturbance in SPREAD is represented through fragmentation of the macroalgal modules. Simulated fragmentation occurs when algal modules are severed from the attached individual alga. This can only occur beginning from modules located at the edges defined as modules with no offspring modules (Fig. 2). A percentage of these edge modules (the fragmentation probability parameter) are chosen randomly to start the fragments with. The sizes of the fragments can be either small or large and are randomly drawn from a normal distribution parameterized with the mean of fragment size and standard deviation based on previous studies (Herren et al., 2006; Walters et al., 2002). If the fragments are not allowed to survive, this is considered mortality, and they are removed from the model. However, if the fragments are allowed to survive, the probability of surviving has three levels (low, medium and high). The locations of the new fragments within the grid are randomly assigned. Disturbance was distinguished into two types: herbivory and high water motion. Large herbivores such as fish mainly pick on macroalgae from the edges, and so herbivory effects in SPREAD were simulated via losses of edge modules at two levels (low and high fragmentation). High water motion from surge or currents can either uproot the whole alga or tear off more and larger fragments from the individual. SPREAD captures this through detachment of larger and more fragments or of whole individuals. Estimates on the parameters for fragmentation at low and high disturbance levels were based on studies conducted by Walters et al. (2002) on *Halimeda* species and Herren et al. (2006) on *Dictyota* species.

Dictyota in the model does not refer to a particular species since the light response curve was obtained from *Dictyota cervicornis* (Yñiguez, 2007), while the other parameter values were obtained from literature values for various *Dictyota* spp. as available.

Morphometrics such as number of segments, height, width, and the height:width ratio were obtained from the virtual macroalgae in SPREAD. Fig. 2 shows examples of these morphometrics. Number of segments represents the number of modules per individual, while height and width refers to the maximum height and width attained by an individual macroalgae. The use of these morphometrics emulates how they were measured in the field, thus allowing for direct comparisons between field characteristics and those resulting from the simulations.

SPREAD was implemented using the object-oriented programming language Java, and the Mason Multiagent Simulation Toolkit (Luke et al., 2005, http://cs.gmu.edu/~eclab/projects/mason/) served as the backbone.

2.2. Model scenarios: spread due to primary growth and fragmentation

In Yñiguez et al. (2010), combinations of the environmental factors were explored in the field to investigate the range of potential growth forms of the three macroalgae. They came up with six, two and three potential morphological types for *H. tuna*, *H. opuntia* and *Dictyota* spp., respectively. For the present study, a subset of those environmental conditions were used. This subset allowed for the common realized morphological types in the model to emerge as observed in the field.

Table 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: 0.26Winter: 0.14	Summer: 0.26Winter: 0.14	Summer: 0.34Winter: 0.23	Summer: 0.34Winter: 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: 1.4Winter: 3	Summer: 1.4Winter: 3	Summer: 1.8Winter: 5.7	Summer: 1.8Winter: 5.7
Nutrients				
Nutrients level	2	2	3	3
Nutrient growth probabilities	0.4	0.4	0.6	0.6
Mortality				
Fragmentation probability	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

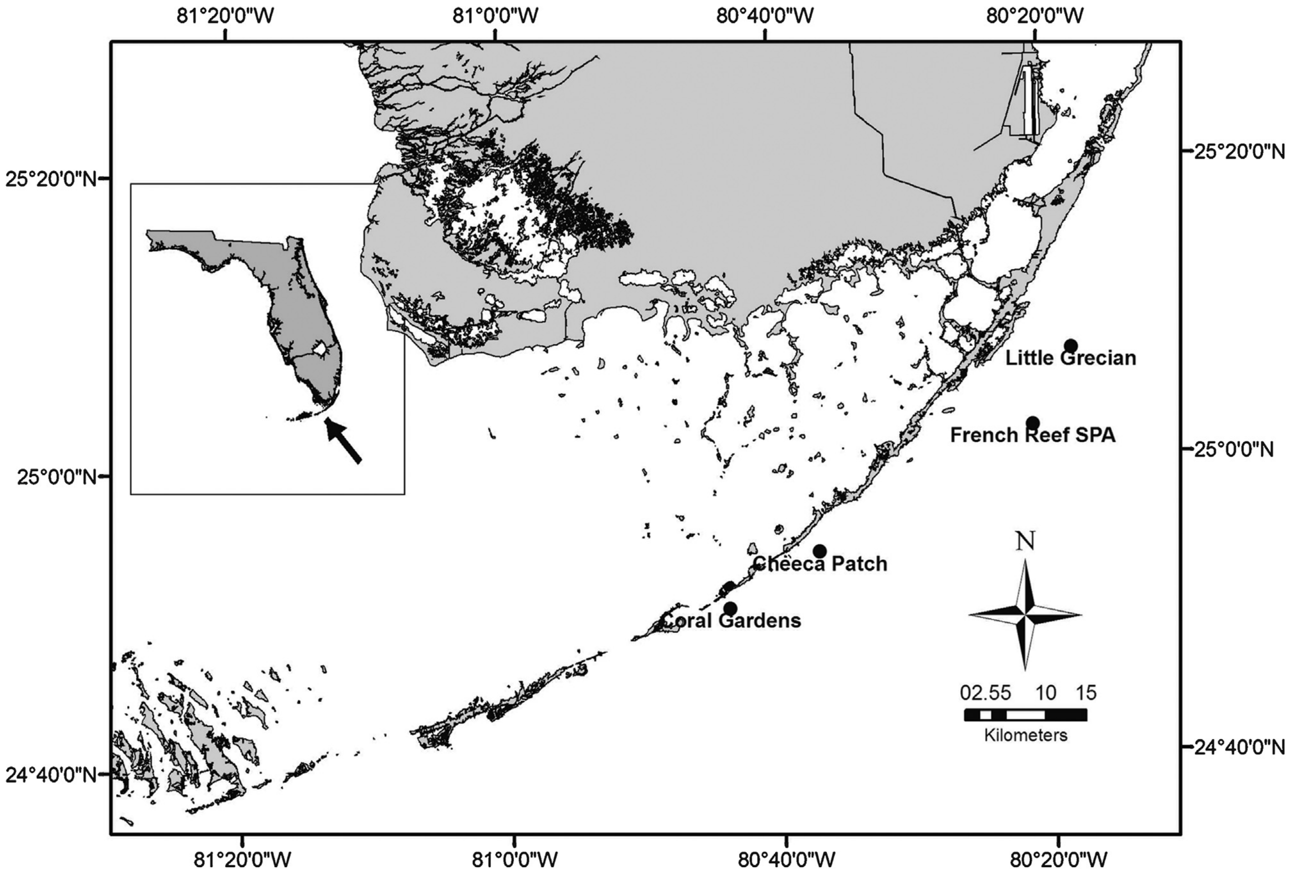

Fig. 1. Map of study sites in the Florida Keys Reef Tract.

To address the first question, the derived subset of conditions for light (100, 700, 1700, 2200 μmol m^{-2} s^{-1}), nutrient levels and growth probabilities (low, medium, high) (Table 1), as well as fragmentation without survival (mortality), were used to investigate the effect of the different growth forms on two-dimensional (horizontal) spread. The importance of fragmentation relative to purely vegetative or primary growth in horizontal spread (second question) was investigated by running SPREAD with this same set of parameters, but this time allowing fragments to survive using varying survival probabilities. Parameters for fragmentation were obtained from the extensive set of published studies conducted at Conch Reef on *Halimeda* and *Dictyota* spp. (Vroom, 2001; Walters et al., 2002; Vroom et al., 2003; Herren et al., 2006). Results from these runs, together with those simulating specific sites (described below), were used to determine the influence of disturbance on space-occupation patterns (third question).

SPREAD was run with a 100 cm × 100 cm × 30 cm grid initially seeded with 10 randomly located individuals of one species (species were run separately). Each run consisted of 5000 time steps (days) equivalent to about 13 years. 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 made of percent cover or counts of the number of the species/group in question from a top-view perspective. In SPREAD, the original three-dimensional grid was first transformed into a

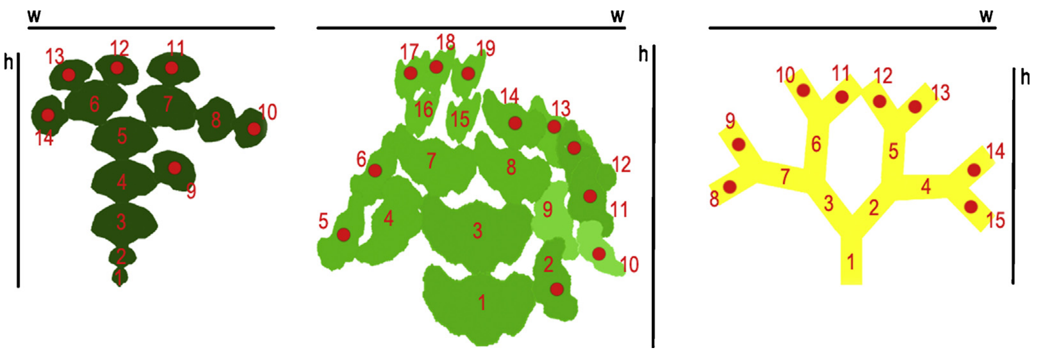

Fig. 2. Diagrams of individuals of the three macroalgae. The modules with red dots are examples of edge modules that can potentially initiate the fragmentation process. The morphometrics used to characterize the growth forms are shown: (1) numbers illustrate the number of modules/segments; (2) width (w); and, (3) height (h) (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.).

two-dimensional (2D) one, by using the top-most object in the Y-axis as the visible object in the 2D grid with the same X and Z-coordinates. One hundred random points in the 2D grid were subsequently surveyed for presence of macroalgae. Percent cover was derived as number of points present.

2.3. Model scenarios: site-specific

SPREAD was also run using parameters and factors that represented four study sites (Fig. 1 and see next section for site descriptions) in orderto investigate how these particular conditions affect the cover of macroalgae, to determine if the model runs would replicate what is observed in the actual sites (Table 2) and ultimately, to investigate variability in responses to actual growth and disturbance conditions. 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 were given a lower level and the latter a high level, in accordance with empirical measurements (Boyer and Jones, 2004). 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. Patch reefs were set to have a low fragmentation level, small fragment sizes and high fragment survival probabilities. *Dictyota* fragment survival probability was the same in all reef sites (0.933), because the difference between this and 100% probability of fragment survival observed in the limited field study of *Dictyota menstrualis* (Herren et al., 2006) was not large and this slightly lower probability was more realistic than fragments always surviving. Ten individuals for each species (separately run) were randomly located at the start, and the model was run for 3000 time steps (equivalent to about 8 years). Each scenario was replicated 30 times. Percent cover and density were tracked per time step to determine the trajectory through time. Density was obtained by counting the number of unique (not connected) individuals (ramets) within an area equivalent to 0.25 m^2 within the 2D grid. The average percent cover and density within the last one thousand days (time steps 2000 to 3000) was used to compare results with field observations per site.

2.4. Field observations

2.4.1. Study sites

Four sites in the Florida Keys were used for this study (Fig. 1), representing distinct environmental conditions. They included two inshore patch reefs, Coral Gardens (24°50.157′N, 80°43.657′W) and Cheeca Patch 24°53.826′N, 80°36.948′W), and two offshore bank reefs, Little Grecian (25°07.140′N, 80°18.020′W) and French Reef (25°02.022′N, 80°20.997′W). The latter two 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 were 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 tract. The inshore sites thus appear to be less exposed to the two types of disturbances (wave motion and herbivory) relative to the offshore ones.

The four sites did not vary in the surface irradiance that they received at noon. 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). These values 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 (both 3.7 m in depth), on average, experienced lower light conditions at depth compared to the offshore bank reef sites Little Grecian (3.2 m deep) and French Reef (5.7 m deep), which was deeper than the inshore reefs. The lower light values were due to these patch reefs being significantly more turbid (Boyer and Jones, 2004). In terms of nutrient conditions, SERC determined that there were several distinct water quality clusters among 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 high nutrient levels, particularly for Dissolved Inorganic Nitrogen (DIN). In contrast, the offshore reef sites, which were all included in Cluster 3, had the lowest nutrient concentrations.

2.4.2. 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 0.22 m^2 plots were randomly located at each site on 21 September 2004 for the two offshore sites, and 12 and 28 October 2004 for Cheeca Patch and Coral Gardens, respectively. The corners were marked using masonry nails and surveyor tapes, and located for each sampling period 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 cropped to show the same areas, and 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 was used to select the number of fin kicks and direction to swim. Each quadrat was then placed at that end point as evenly as possible on the substrate. 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.

2.4.3. Field data analysis

The percent covers and the number of fragments/patches per m^2 (density) 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, and so the Repeated Measures ANOVA with all sites combined required leaving out several sampling periods. Thus, in order to get the most information about the differences between times, two separate analyses were performed for patch reefs and offshore reefs. 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 were very few individuals of this species found in the offshore site plots.

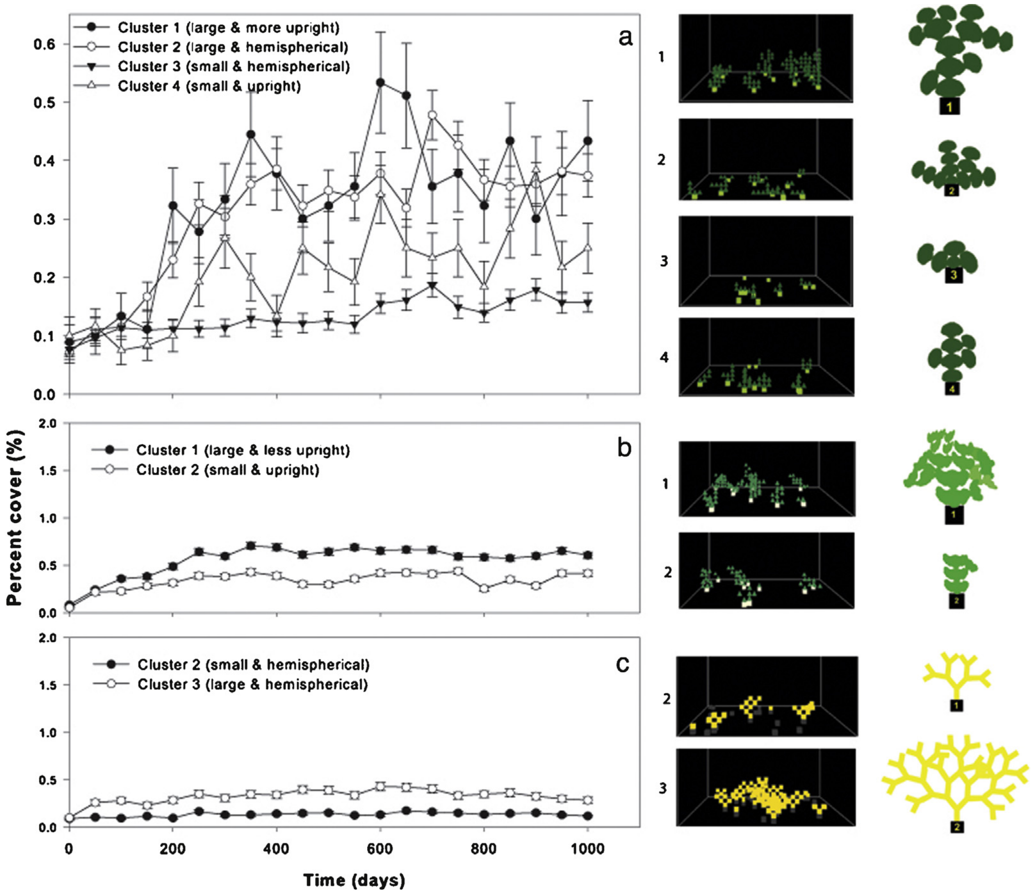

Fig. 3. Percentage cover of the different morphologies of (a) *Halimeda tuna*, (b) *Halimeda opuntia*, and (c) *Dictyota* sp. in SPREAD. Vertical bars represent the standard error. Images are representation of their growth forms in actual model runs and as individual diagrams. Corresponding cluster numbers are to the left of the images.

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

3. Results

3.1. Space occupied by different simulated growth forms

For *H. tuna*, different morphologies resulted in differences in the amount of horizontal space occupied (Fig. 3a). The larger morphologies obtained the highest percent cover values, and the upright morphotypes covered more horizontal space compared to the equivalent-sized hemispherical forms. 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 (Fig. 3b and c). 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 similarly-shaped but smaller forms.

3.2. Space occupation when fragment survival is allowed in the simulation

For all three species, there was a clear difference in the amount of space attained due to purely primary growth and that attained when fragments were allowed to survive (Fig. 4). However, there were differences between species. For *H. tuna*, the highest cover attained was under the highest probability for fragment survival, low fragmentation and small fragment size. For *H. opuntia* and *Dictyota*, highest covers attained were under the highest probability for fragment survival, but high fragmentation rate and small 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 (Figs. 5–7). This oscillation was dampened under the high fragmentation and large fragment sizes scenarios for all three macroalgae species. The rate of increase of cover generally abated as time passed and was eventually stable at the end of the model runs. For all three species, generally, an increase in cover was achieved with increasing probability of fragment survival, although this distinction was not too evident for *Dictyota* due to its high fragment survival probabilities (Figs. 4 and 7). For *H. opuntia* and *Dictyota*, high fragmentation rates enabled higher cover, which was not observed in *H. tuna*. For all three species though, large fragment size was detrimental to spatial spread and led to lowest values of cover. Cover of *H. tuna*, *H. opuntia* and *Dictyota* decreased by 39%, 59%, and 75%, respectively when large instead of small fragment sizes were used in the high fragmentation rate (0.05) and high fragment survival probabilities scenarios (Fig. 4).

3.3. Field observations

There is an indication of seasonality in the observed percent cover and density of the three macroalgae in the different study sites where there tended to be slightly higher cover and density during the spring/summer times compared to winter months. However, there were no statistically significant differences found

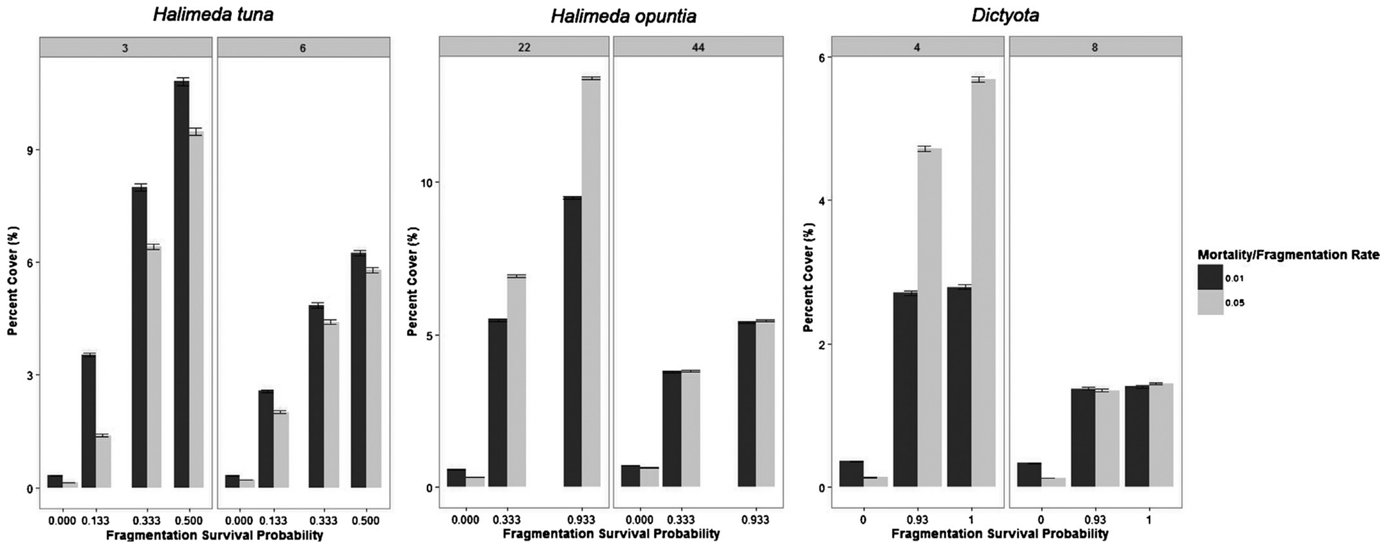

Fig. 4. Percent cover attained under various fragmentation rates, fragment sizes, and fragmentation survival probabilities for the three macroalgae.

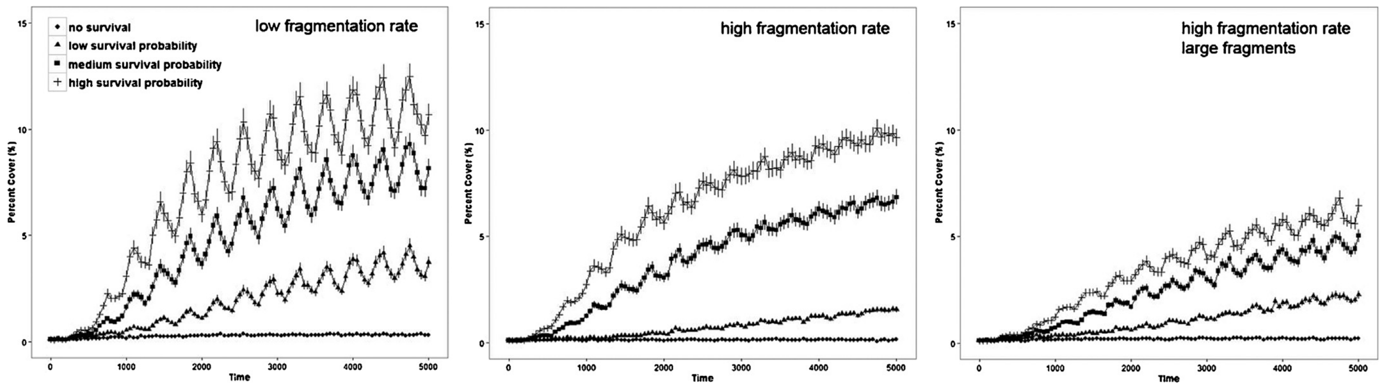

Fig. 5. Percent cover of *Halimeda tuna* under different fragmentation (low, high, and high and large fragments) and fragment survival probability levels (low, medium, high, none) derived from SPREAD. Vertical bars represent the standard error.

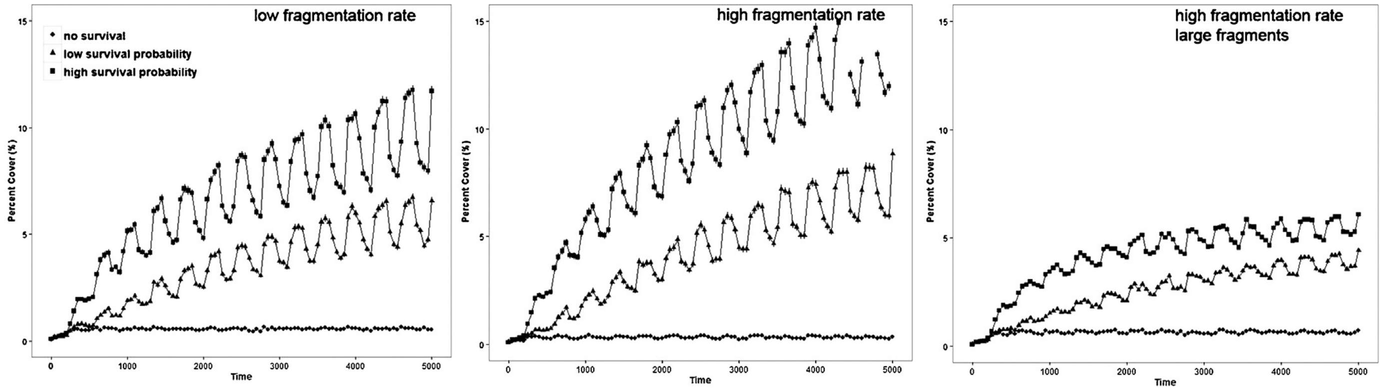

Fig. 6. Percent cover of *Halimeda opuntia* under different fragmentation (low, high, and high and large fragments) and fragment survival probability levels (low, high, none) derived from SPREAD. Vertical bars represent the standard error.

in the percent cover, and number of fragments with time or among the four study sites for *H. tuna* (Table 3 and Figs. 8–9). The space occupied and dominance of this species was relatively stable.

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 3 and Fig. 9). There was no overall trend through the sampling duration. There also was no difference between Coral Gardens and Cheeca Patch. In terms of percent cover, these remained the same between sampling periods and the two sites where *H. opuntia* was found (Fig. 8).

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 3 and Figs. 8 and 9). 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

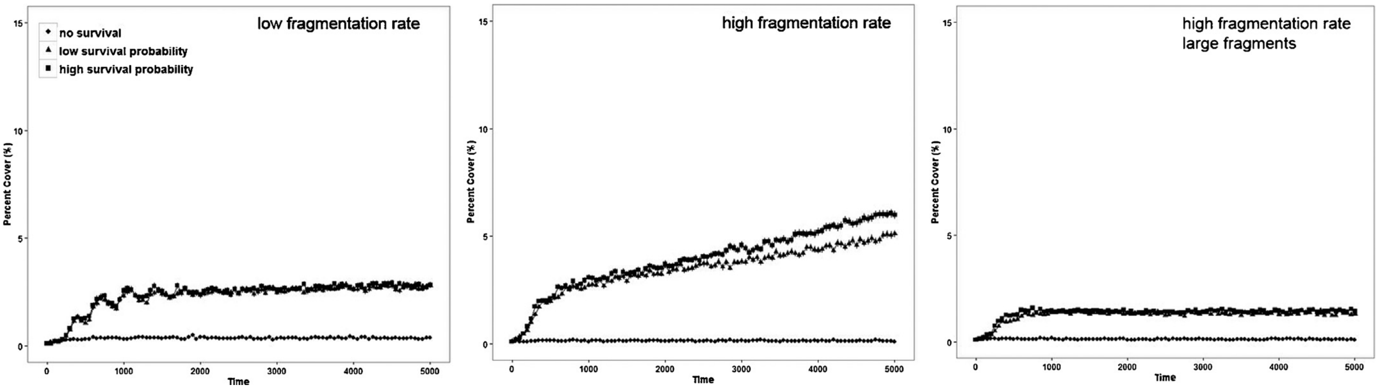

Fig. 7. Percent cover of *Dictyota* sp. under different fragmentation (low, high, and high and large fragments) and fragment survival probability levels (low, high, none) derived from SPREAD. Vertical bars represent the standard error.

seasonally. 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 not included in the statistical analysis because this time period needed to be removed to facilitate the statistical analyses (Repeated Measures ANOVA). However, there was still a significant effect from the three sampling periods included, with higher cover in August 2005—particularly in Little Grecian. Overall, cover and density showed no increasing or decreasing trend within the sampling duration.

There were differences in the percent cover results from the random quadrat method compared to those from the permanent plots (Table 3). The quadrat surveys documented a significant variation between the inshore and patch reefs for all three macroalgae species (Figs. 10 and 11). *H. tuna* cover was significantly higher in the patch reefs. Furthermore, 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 wherein cover was stable during the sampling period. This permanent plot method showed that *H. opuntia* cover was significantly higher in the patch reefs compared to the offshore reefs. This 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 among 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 (Fig. 10). An increase during the warm spring sampling period was observed in all sites, but this declined in September 2005 with the exception of 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

3.4. Comparing macroalgal cover and density under variable conditions in SPREAD and the field sites

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 (Fig. 10). 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, while, for *H. tuna*, the model values were slightly lower than the observed ones. This may be due to the underestimation of the growth parameters which were derived from laboratory experiments. SPREAD was not able to capture the variation between sites for the percent cover of *Dictyota* spp. when the fragmentation scenario used was high fragmentation rate and large fragments. The patch reef values were very similar to what was observed in the field, although the simulated offshore values were lower than the observed values. However, when the fragmentation scenario was changed to high fragmentation rate and small fragments, the offshore reefs' percent covers became slightly higher than the patch reef sites, which is more similar to the observed variation.

In terms of densities, for *H. tuna* and *H. opuntia*, the model sites were able to capture the patterns observed in the study sites, although modelled Little Grecian and French Reef had lower *H. tuna* densities compared to the real reefs (Fig. 11). For *Dictyota*, results

Table 3
Summary of statistical analyses results on the permanent plots and random quadrat data showing which factors were significant (Site, Time, or Site × 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 × Time	None	Time and Site and Site × 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	

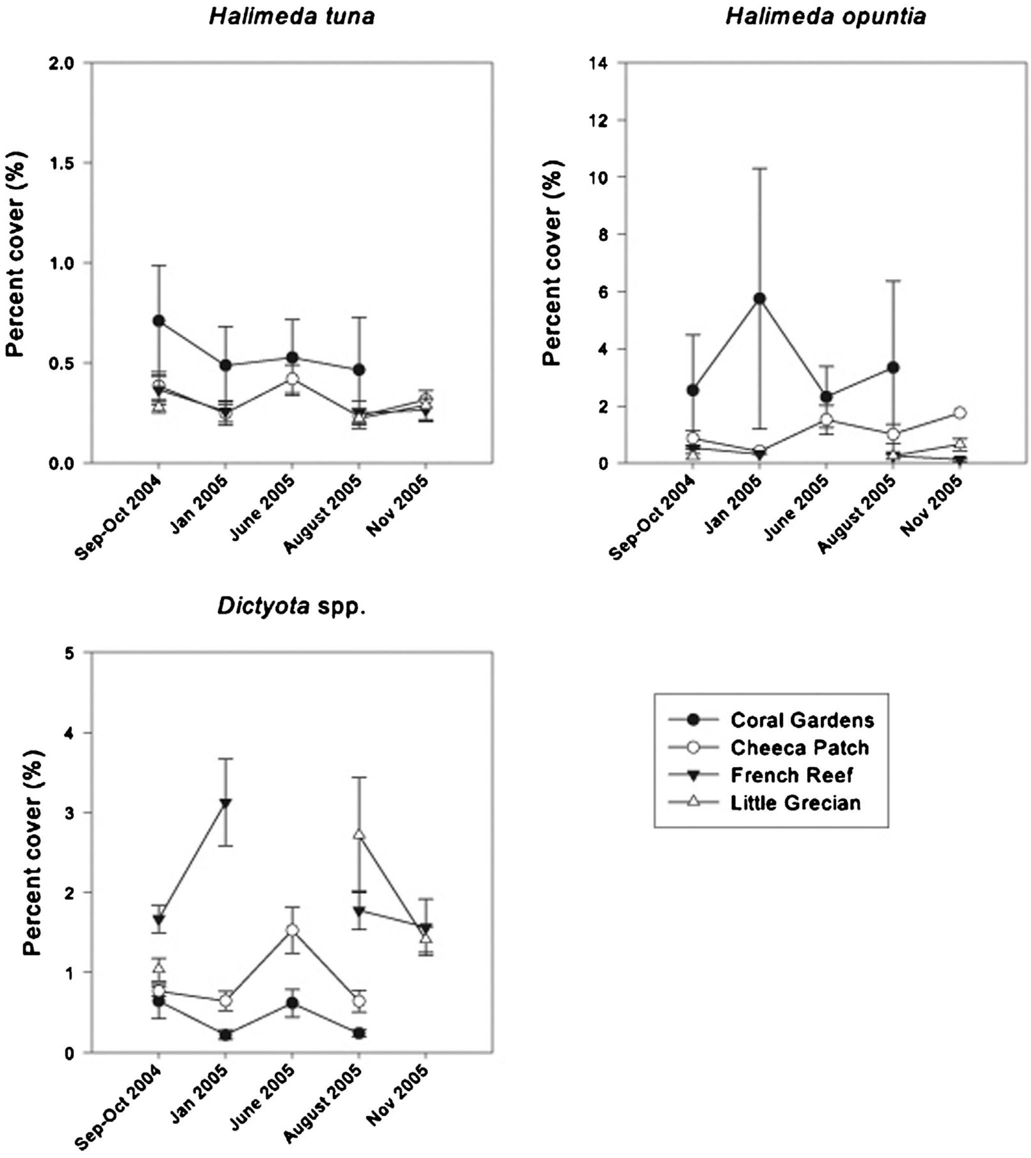

Fig. 8. Percent cover of the three macroalgae species from monitored permanent plots monitored in four sites. Data are the mean ± SE.

were similar to those of percent cover where the modelled patch reef sites had higher *Dictyota* densities compared to the simulated offshore. This was the opposite of the observed field patterns. However, when the high fragmentation and small fragments setting was used, density came out distinctly higher in the offshore reefs compared to the patch reefs, which was more similar to what is observed in the actual sites. The reasons for these variations are detailed in Section 4.

The percent covers and densities of the three macroalgae simulated through time for each study site (Fig. 12) illustrates the seasonality in their abundances in all sites, and the eventual slowing and steadying of growth/spatial spread. The variations between sites as discussed above are also seen immediately for *H. tuna* and *H. opuntia*, while for *Dictyota*, the cover at the offshore reefs under the high fragmentation and small fragment size scenario eventually became higher compared to the modelled patch reefs.

4. Discussion

Exploration of space colonization and retention with SPREAD showed that fragmentation can contribute significantly to *Halimeda* and *Dictyota* spp. dominance and persistence, and comparison of the model-derived abundances to those observed in the field bears this out. The inclusion of both fragment survival in the model and the variations in growth forms 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 importance of clonal characteristics (i.e., plastic morphology and fragmentation) in the process of space occupancy in generating the observed patterns.

4.1. Growth form and fragmentation contribute significantly to the potential to occupy space

Purely vegetative growth can only result in limited spatial (horizontal) coverage. However, different growth forms varied in their capacity for horizontal spread. In conditions that permit a particular type of growth form, there would be a corresponding potential for its spread through the substrate. Upright *H. tuna* could occupy space faster and more of it compared to its hemispherical types. Environments that allow for large forms of *H. opuntia* and *Dictyota* spp. would also likely allow for more rapid utilization and more

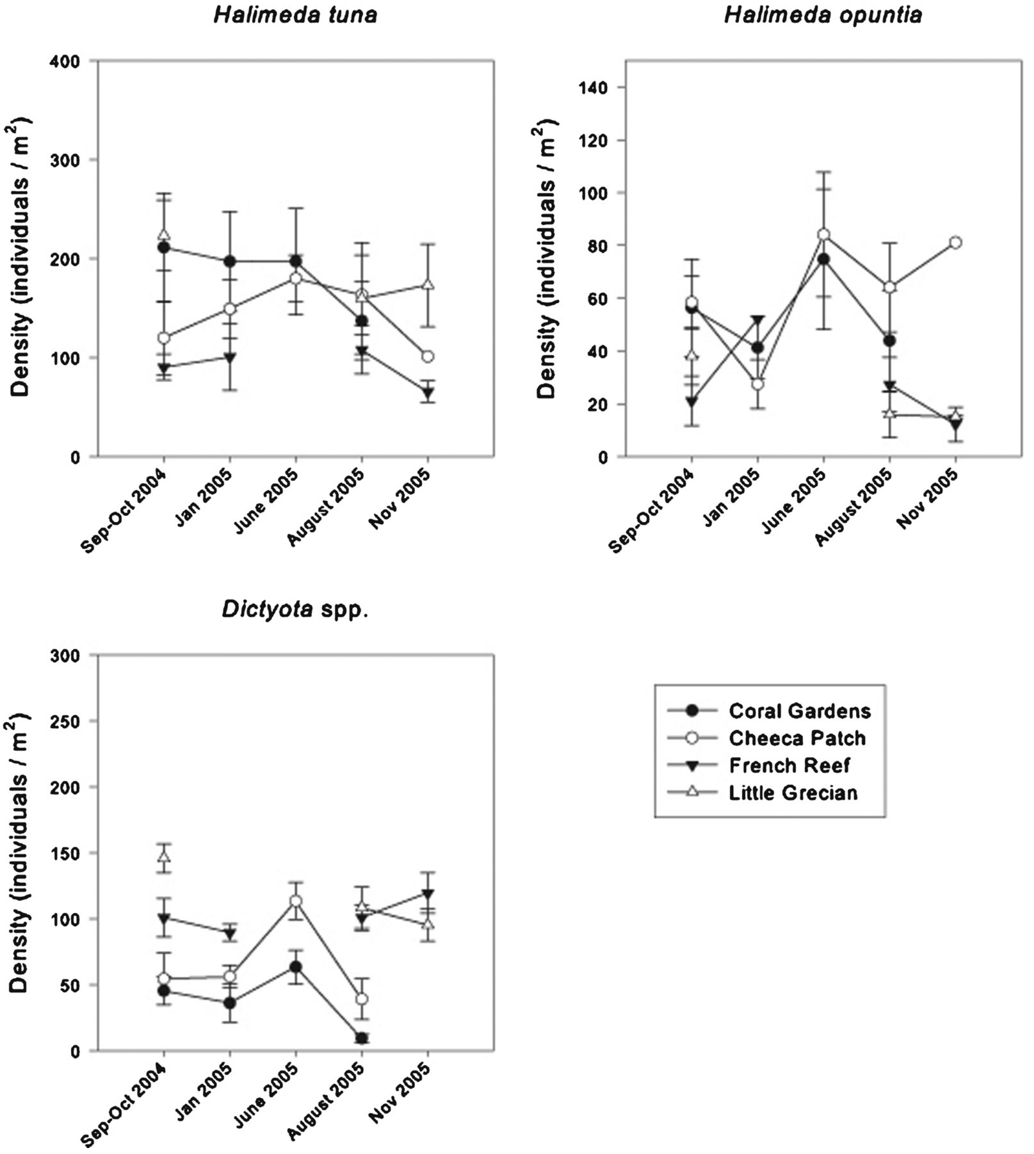

Fig. 9. Densities of the three macroalgae species from monitored permanent plots in four sites. Data are the mean ± SE.

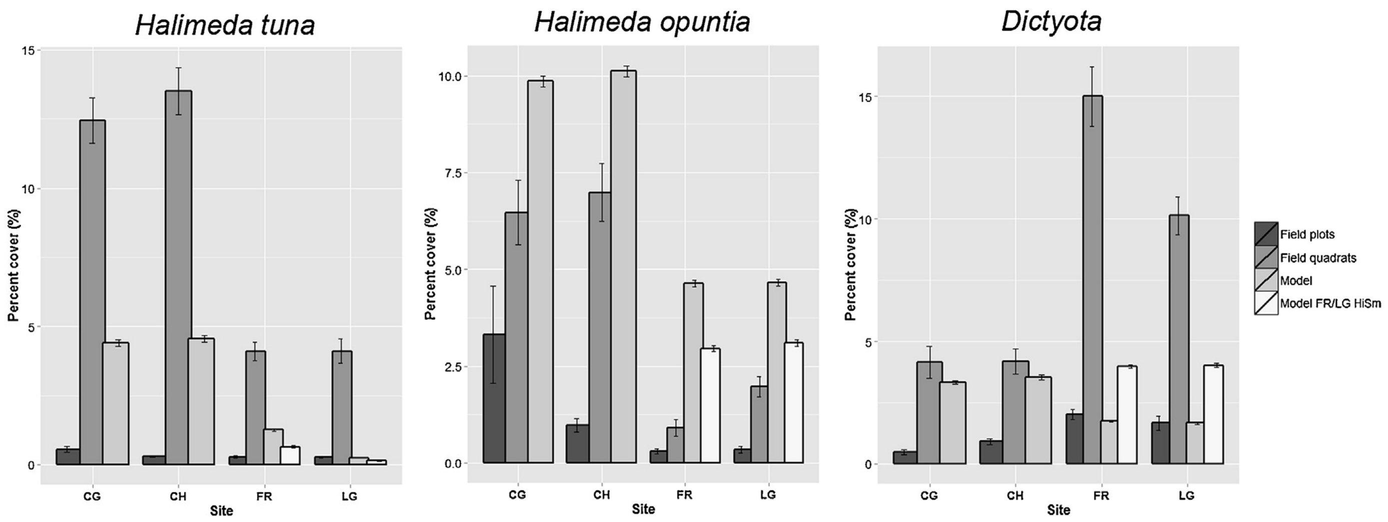

Fig. 10. Percent cover of the three macroalgae comparing model-derived and field results from permanent plots and random quadrats. The high mortality and large fragments ("Model"), and only high mortality and small fragments scenarios for French and Little Grecian ("Model FR/LG HiSm") are shown. Cheeca and Coral Gardens were set only at low mortality. Data are presented as mean ± SE.

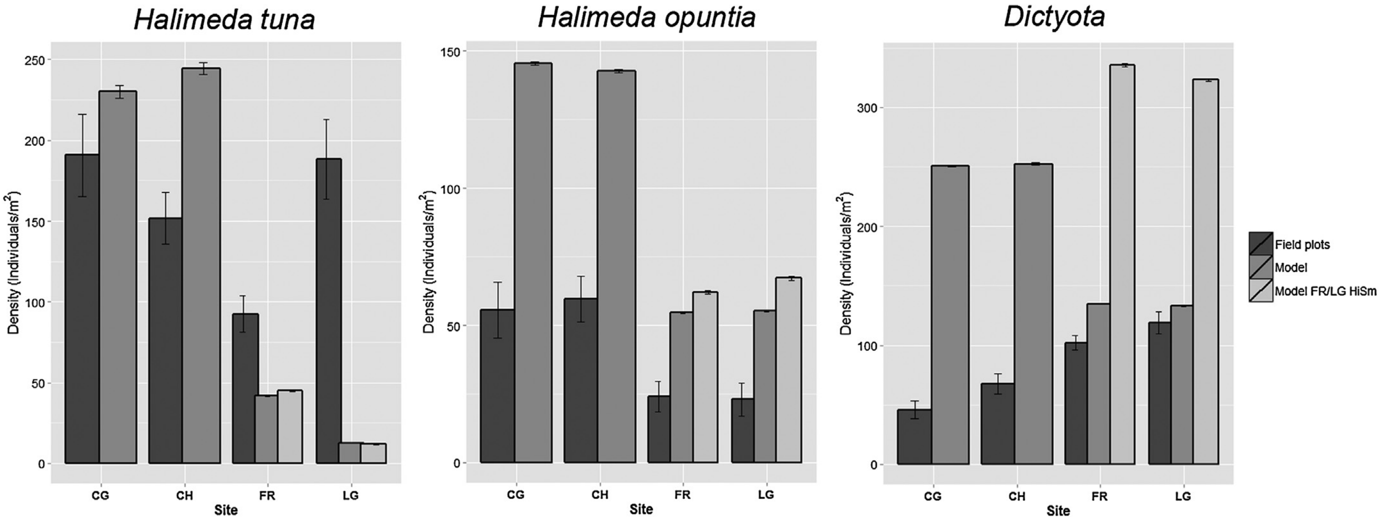

Fig. 11. Densities of three macroalgae comparing model-derived and field results from permanent plots and random quadrats. The high mortality and large fragments ("Model"), and only high mortality and small fragments scenarios for French and Little Grecian ("Model FR/LG HiSm") are shown. Cheeca and Coral Gardens were set only at low mortality. Data are presented as mean ± SE.

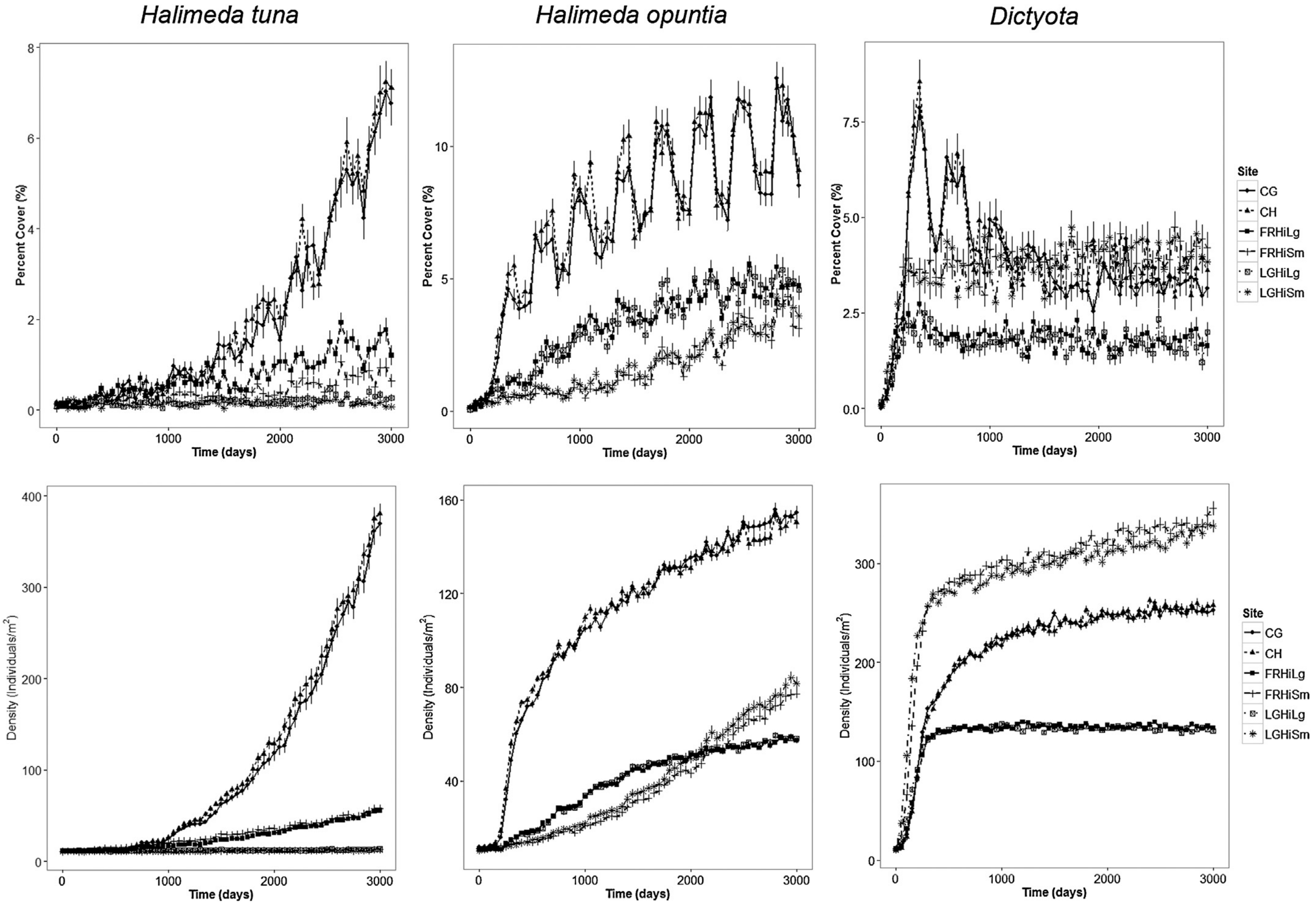

Fig. 12. Simulated percent cover and density through time per study site (Coral Gardens: CG, Cheeca: CH, French Reef: FRHiLg—FR high fragmentation, large fragments; FRHiSm—FR high fragmentation, small fragments; Little Grecian: LGHiLg—LG high fragmentation, large fragments; LGHiSm—LG high fragmentation, small fragments) for the three macroalgae.

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.

However, purely vegetative growth was not enough to explain their abundances in the inshore and offshore reefs. When the survival of fragments was allowed to occur in SPREAD, the percent covers achieved by the three macroalgae were significantly higher and more realistic. The ability to fragment and produce ramets/clones can be a successful strategy in order to grow and persist in many terrestrial and marine clonal organisms (Ceccherelli and Cinelli, 1999; Ruesink and Collado-Vides, 2006; Herren et al., 2006, 2013). However, it can have trade-offs wherein 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). 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. 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 between these species and the important 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 macroalgae to increase, obtain space rapidly and maintain it.

4.2. Spatial spread under modelled and actual disturbance conditions

Disturbance affects the generation of fragments and the ability of the fragments to find and settle on a suitable substrate. In SPREAD, the fragmentation rates and fragment sizes 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. *H. tuna* attains its largest spatial spread under relatively low disturbance conditions (low fragmentation rate, small fragment size and high fragment survival probability). In contrast, for *H. opuntia* and *Dictyota*, an intermediate disturbance level (high fragmentation rate, small fragment size and high fragment survival probability) yielded the highest amount of horizontal space occupation. 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 found that Hurricane Irene in 1999 had reduced *Dictyota* spp. cover to 1/6 of its original abundance, but also generated four-fold higher fragments compared to non-hurricane conditions. *Dictyota* spp. recovered to half pre-hurricane densities a month after 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. Fragmentation success of *Dictyota* is also important in light of disturbance in the form of herbivory in these reefs, particularly higher herbivore pressure on the offshore reefs (Paddack, 2005).

H. tuna and *H. opuntia* on the other hand do not produce fragments that are as successful (with high survival probabilities) as those of *Dictyota*. This could partly explain why these species are more abundant in the inshore patch reefs that are more protected and with lower herbivore pressure (one type of disturbance) compared to the offshore reefs. In addition to having enough light and relatively higher nutrient conditions for the growth of these two species in the patch reefs, more fragments are surviving due to lower water motion energy that could move and disperse them into unsuitable habitat and prevent 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 field data could be due to competitive effects or spatially variable growth rates and contribution of sexual reproduction that were not included in the model. Compared to the semelparous *H. tuna* and *H. opuntia* (Drew and Abel, 1988; Clifton, 1997), the spores and sexual recruits of *Dictyota* spp. have more potential to add to the population. However there is little 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.

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

The simulated macroalgal populations generally stabilized through time and exhibited small oscillations in cover and density 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). A meta-analysis of the long-term trends of macroalgal cover among different Caribbean regions showed that since about 1987 macroalgal cover has remained stable through to 2006 (Schutte et al., 2010). The ability of these macroalgae to recover after periodic declines can be a testament to their capability to grow fast and occupy space through vegetative and asexual means, as well as their ability to save space through survival of vegetative parts. At the smaller patch scales, the processes of growth and mortality are much more dynamic, especially for *Dictyota* spp. Renken et al. (2010) observed high variability in *Dictyota pulchella* patches on Glovers Reef within about a year's sampling period. They attribute this to the decline in patch sizes at a particular time of the year because of a reproductive event. These macroalgae seem to have intrinsic cycles (i.e., sexual reproduction) that can explain the variability in their abundances independent of changes in environmental factors such as temperature. Sexual reproduction events can be influencing these observed seasonalities in the Florida reefs. In the plots observed for *H. tuna* and *H. opuntia*, there were no instances where they completely disappeared if they were already in the plot. In Coral Gardens and Cheeca, in particular, 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).

5. 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. This is similar to the finding of Ruesink and Collado-Vides (2006) in their model of the growth of *C. taxifolia*. 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. Clonal characteristics of macroalgae, such as the ability to fragment and vegetative growth, enable them to maintain and capture space rapidly and thus makes them more resilient to environmental fluctuations. Both model and field data showed some seasonal variation but overall stable abundances in time. This bodes well for the potential recovery of hermatypic corals in Florida reefs, at least in terms of the dominant macroalgae not pre-empting more space on the reefs.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.ecolmodel.2015.04.024

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