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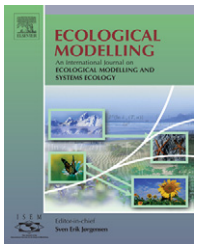

# Allowing macroalgae growth forms to emerge: Use of an agent-based model to understand the growth and spread of macroalgae in Florida coral reefs, with emphasis on *Halimeda tuna*

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ABSTRACT

The growth patterns of macroalgae in three-dimensional space can provide important information regarding the environments in which they live, and insights into changes that may occur when those environments change due to anthropogenic and/or natural causes. To decipher these patterns and their attendant mechanisms and influencing factors, a spatially explicit model has been developed. The model SPREAD (SPatially-explicit Reef Algae Dynamics), which incorporates the key morphogenetic characteristics of clonality and morphological plasticity, is used to investigate the influences of light, temperature, nutrients and disturbance on the growth and spatial occupancy of dominant macroalgae in the Florida Reef Tract. The model species, *Halimeda* and *Dictyota* spp., are modular organisms, with an "individual" being made up of repeating structures. These species can also propagate asexually through clonal fragmentation. These traits lead to potentially indefinite growth and plastic morphology that can respond to environmental conditions in various ways. The growth of an individual is modeled as the iteration of discrete macroalgal modules whose dynamics are affected by the light, temperature, and nutrient regimes. Fragmentation is included as a source of asexual reproduction and/or mortality. Model outputs are the same metrics that are obtained in the field, thus allowing for easy comparison. The performance of SPREAD was tested through sensitivity analysis and comparison with independent field data from four study sites in the Florida Reef Tract. *Halimeda tuna* was selected for initial model comparisons because the relatively untangled growth form permits detailed characterization in the field. Differences in the growth patterns of *H. tuna* were observed among these reefs. SPREAD was able to closely reproduce these variations, and indicate the potential importance of light and nutrient variations in producing these patterns.



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## 1. 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"), wherein 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, there is surprisingly little known about the basic population and community biology of these coral reef macroalgae (Littler and Littler, 1994). This information 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 (and many reef benthos) possess: morphological plasticity. A large number of macroalgae exhibit non-deterministic phenotypically plastic growth that enables them to have different morphologies under different environmental conditions (Lubchenco and Cubit, 1980; Lewis et al., 1987; Collado-Vides, 2002). 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. 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, 2002) this approach has not been adapted in the marine realm.

This paper 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 (Spatially explicit Reef Algae Dynamics) was used to investigate the influences of growth factors (light, temperature, nutrients), mortality, and disturbance 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 paper is to present a novel 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) 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 subsequent papers (Yñiguez et al., in preparation-a,b; Yñiguez, in preparation).

## 2. Methods

### 2.1. Model description

#### 2.1.1. Overview

*2.1.1.1. 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. There are two types of modules: a thallus module and 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 (Fig. 1). The production of new modules constitutes the

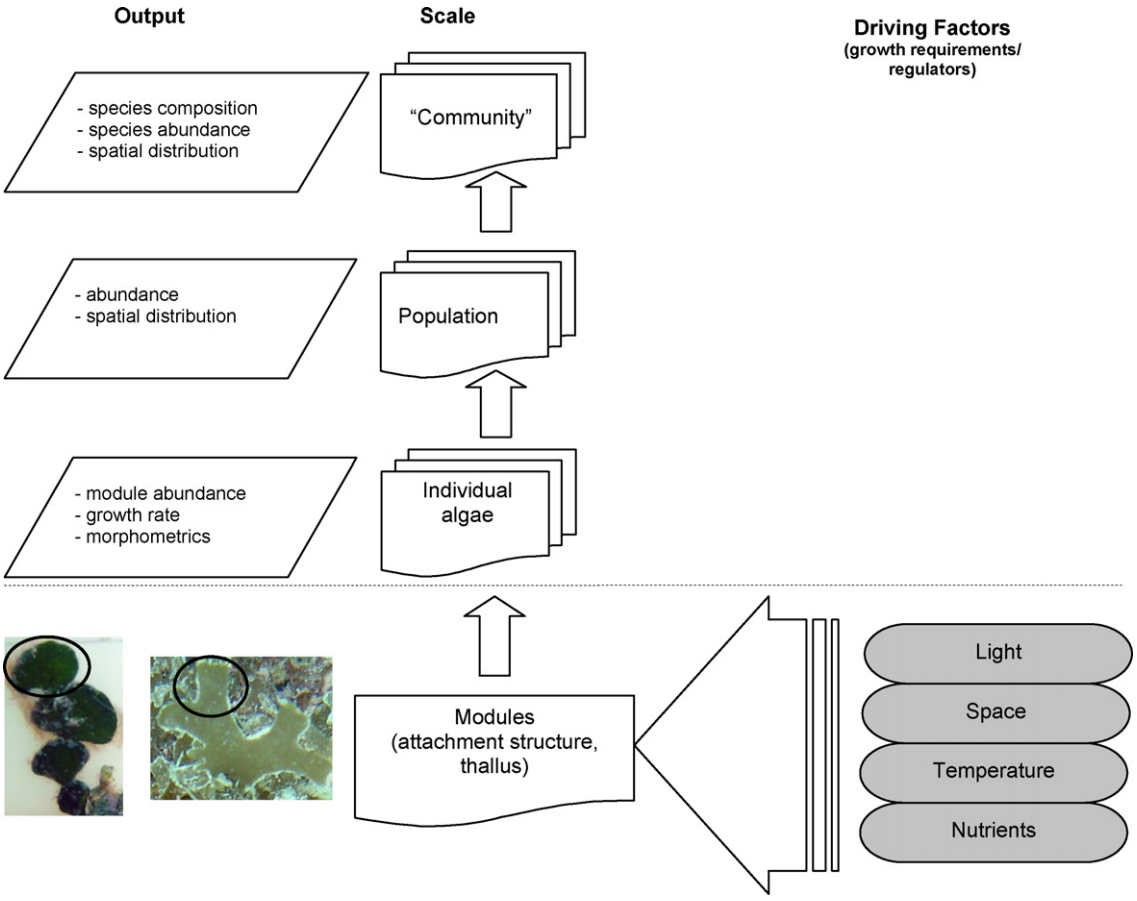


**Fig. 1 – Conceptual diagram of the agent-based model for reef macroalgae dynamics. Pictures of *Halimeda tuna* and *Dictyota menstrualis* illustrate their respective thallus modules.**

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 only looks at the dynamics of these species within a local three-dimensional patch (Fig. 2).

2.1.1.2. *Process overview and scheduling*. The model uses discrete daily time steps. Fig. 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.

2.1.2. *Design concepts*

2.1.2.1. *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. Mortality and fragmentation processes are modeled using empirical rules as well. Adaptation and fitness seeking behavior are only implicitly represented through these empirical rules for module production.

2.1.2.2. *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.

2.1.2.3. *Interaction*. Indirect exploitative interaction 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., 2003).

2.1.2.4. *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

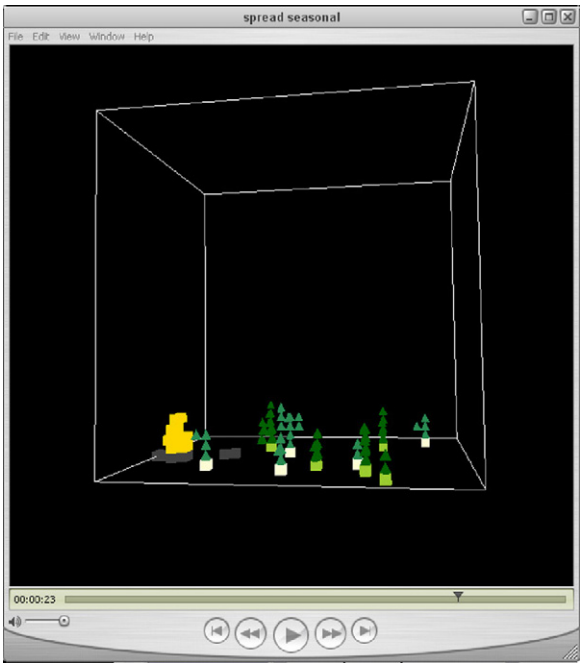


**Fig. 2 – Visual output of SPREAD showing representations of *Halimeda tuna* (base: light green square; thallus: dark green triangle), *Halimeda opuntia* (base: white square; thallus: blue-green triangle), *Dictyota* sp. (base: grey square; thallus: yellow square) growing in a 3D grid. Visual output of SPREAD showing representations of *Halimeda tuna* (base: medium gray square; thallus: dark gray triangle), *Halimeda opuntia* (base: white square; thallus: medium gray triangle), *Dictyota* sp. (base: dark gray square; thallus: light gray square) growing in a 3D grid. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of the article.).**

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). Mortality and 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.

2.1.2.5. *Collectives*. Modules are grouped into species-specific individual macroalgae.

2.1.2.6. *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.

2.1.3. *Details*

2.1.3.1. *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.

2.1.3.2. *Input. Space and depth*. The 3-D grid is divided into cells that have a 1 cm × 1 cm dimension. The substrate is represented as the bottom of the 3-D grid. The top of the 3-D grid,

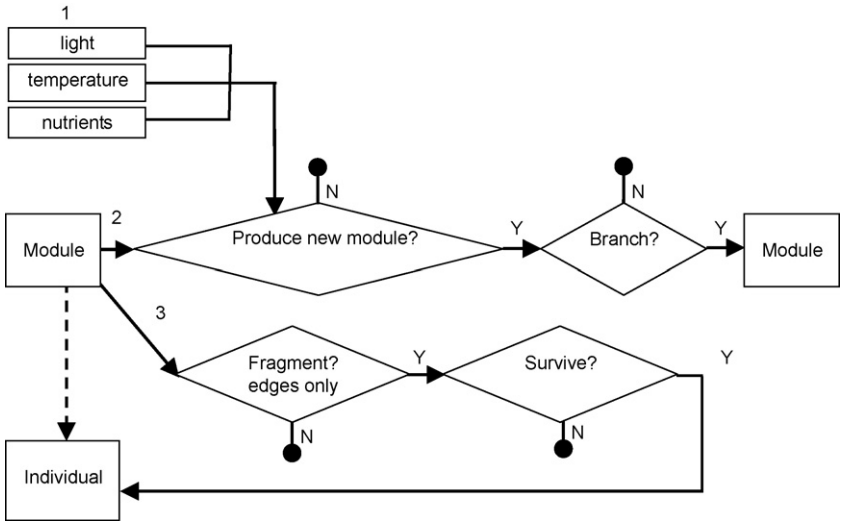


**Fig. 3 – Flow chart of elements and processes occurring at each time step (1 day) in SPREAD. (1) Environmental values are set first that affect the decision of a module to produce a new module. (2) Module decides to produce a new module based on the environmental conditions in the cells around it and 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.**

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:

$$I_{\text{depth}} = I_0\, e^{-k(\text{depth})} \quad (1)$$

where,

$I_{\text{depth}}$ = 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 ($\mu$mol 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 categories: low, ambient and high.

*2.1.3.3. Submodels. Growth. H. tuna* tends to grow using only one plane or in a flat manner (Littler and Littler, 2000). In the simulations, the mother module (i.e., the module potentially producing a new module), considers only the three spatial cells directly above it and the two cells to the sides in the $x$–$y$ plane. If conditions allow for it, the cell directly above it is the first priority in the location of a newly produced module. The next most likely options are any of the four cells to the sides but still above the mother module and the least likely options are the cells immediately to its sides. For these last two options, the specific choice depends on availability or is randomly chosen if the cells are available. The decision on the location of the new modules produced is discussed more under the *Branching* subsection below.

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

$$P(\text{growth}) = P(\text{growth}_{\text{light}}) \times P(\text{growth}_{\text{temperature}}) \times P(\text{growth}_{\text{nutrients}}) \quad (2)$$

*H. tuna*'s modeled response to light is based on laboratory growth experiments 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 non-linear 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.

$P(\text{growth}_{\text{light}})$
= probability of producing a new module given the light level
$$= a(1 - e^{-bI/a})\, e^{-cI/a} \quad (3)$$

where,

$I$ = irradiance in PAR or $\mu$mol $m^{-2}\,s^{-1}$.

The probabilities obtained from the experiments were very low, and therefore the parameters were scaled up to allow reasonable growth rates 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, wherein the optimal temperature lies within 27–29 °C (Hillis-Colinvaux, 1980).

$P(\text{growth}_{\text{temperature}})$
= probability of growing given the temperature level
$$= \frac{1}{\sqrt{2\Pi\sigma}}\, e^{-((t-\bar{t})^2/2\sigma^2)} \quad (4)$$

where,

$t$ = temperature in degree Celsius (°C);
$\bar{t}$ = mean optimum growth temperature;
$\sigma$ = 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 hypoth-

esis that increased growth and cover of macroalgae is due to overcoming nutrient limitation (Littler, 1980).

$$P(\text{growth}_{\text{nutrients}}) = \text{probability of growing given the nutrient conditions} = \begin{cases} x_{\text{low}}, & \text{for low nutrient conditions} \\ x_{\text{average}}, & \text{for ambient nutrient conditions} \\ x_{\text{high}}, & \text{for high nutrient conditions} \end{cases} \quad (5)$$

*Branching*. The decision of a module to produce a new module also depends on where it (the mother module) is located within the thallus of the individual alga (its branch order). This is modeled using a gamma curve to simulate higher probability of producing new segments if the mother segment is situated lower (towards the substrate and lower branch order) within the body of the macroalga:

$$P(\text{branching}_{\text{order}}) = \text{probability of producing a new module based on branch order} = Oab\,e^{-Oc} \quad (6)$$

where,

$O$ = branch order of mother module;
$a$ = parameter for first slope shape;
$b$ = scaling parameter;
$c$ = parameter for second slope shape.

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:

$$P(\text{branching}_{\text{branches present}}) = \text{probability of producing a new module given number of previous modules produced} = m\,\text{numbranches} + b \quad (7)$$

where,

$m$ = slope;
numbranches = number of modules previously produced by mother module;
$b$ = intercept.

*H. tuna* in the field have been seen to have a maximum of five branches or offspring modules. Fig. 4 illustrates the rules governing the potential location of the modules produced.

*Fragmentation and mortality*. 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 from the edges. Modules with no offspring modules are considered "edge" modules. A percentage of these edge modules is chosen randomly to start the fragments with. 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 the *H. tuna* fragment pool at Conch Reef by 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 is based on estimates from the field study of Vroom et al. (2003). The locations of the newly settled fragments within the grid are then randomly assigned.

### 2.2. Sensitivity analysis

Parameters were varied 10 or 20% below and above the default values (Table 1) and one parameter was varied at a time while holding the rest at the default values. The equations were plotted based on the parameters varied. These were visually inspected, and 20% variation was used when the differences in the plotted curves were very slight at 10% (i.e., the curves still overlapped and were similar to the default and each other). The effect of varying the parameters in the equations governing branching (branch order and branch present), light, and nutrients were investigated (Table 2). For the light parameters, $a$ was also adjusted while $c$ was changed in order to preserve the general shape of the curve. The number of modules per individual and the new segment production rates were used as model outputs in the sensitivity analysis. In order to obtain a sensitivity index, the values for each parameter were scaled, and their relationships to the two morphometrics were analyzed separately using linear regression (Cunningham, 2007; Railsback et al., submitted for publication) after initially verifying that no non-linear relationships existed, and that appropriate assumptions were met. The slope of the derived line is the sensitivity index, which gives quantitative information on the magnitude of the effect of a parameter on model results.

### 2.3. Measuring *H. tuna* morphometrics in the Florida Keys

The model-derived results were compared with morphometrics and growth data only 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.

#### 2.3.1. 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 (Fig. 5).

#### 2.3.2. 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 tri-

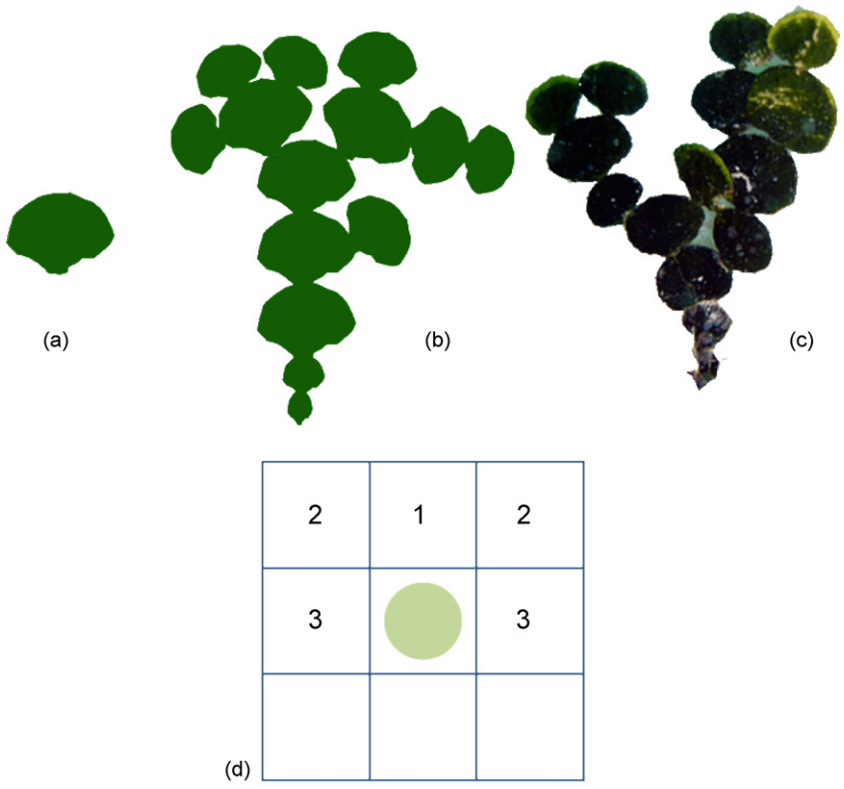


**Fig. 4 – *Halimeda tuna* form and branching rules. One module is illustrated in (a) and its general form is illustrated in (b) while an actual photo is seen in (c). The box diagram is a two-dimensional front view perspective of where new modules are produced. The module that will produce another module 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. *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 gray 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. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of the article.).**

angular 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).

#### 2.3.3. *Measuring H. 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 4 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.

### 2.4. *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. The specific transformations are defined as the results are elaborated. 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.

**Table 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 |
| Number of cells affected by shading | Number of cells below module that will be affected by its shade | Cells | 3 | Estimated[a] |
| Branching (*Halimeda tuna*) | | | | |
| Branch order | Curve for effect of branch order on producing a new module | | | |
| *a* | | – | 0.2 | Estimated[a] |
| *b* | | – | 0.5 | Estimated[a] |
| *c* | | – | 0.3 | Estimated[a] |
| Branch present | Line for effect of number of modules already produced on producing a new one | | | |
| Slope | | – | −0.14 | Estimated[a] |
| Intercept | | – | 0.7 | Estimated[a] |
| Mortality | | | | |
| Fragments | | Fraction | 0.01 | Option[b] |
| Light curve (*Halimeda tuna*) | | | | |
| *a* | | – | 0.01 | Yñiguez (2007) |
| *b* | | – | 0.04 | Yñiguez (2007) |
| *c* | | – | 8 | Yñiguez (2007) |
| Temperature curve (*Halimeda tuna*) | | | | |
| Mean growth temperature | | °C | 29 | Beach et al. (2003), Biber (2002), Hillis-Colinvaux (1980), Lirman and Biber (2000) |
| Standard deviation | | °C | 2 | Beach et al. (2003), Biber (2002), Hillis-Colinvaux (1980), Lirman and Biber (2000) |

[a] These were used to best represent the taxonomic descriptions of the species (see text for discussion).
[b] 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.

## 3. Results

### 3.1. *Robust morphometric results in response to varying parameters*

The sensitivity analysis was accomplished by using site-specific values for the environmental variables depth, light, temperature and nutrients (Table 3). Since outcomes for Coral Gardens were found to be similar to those for Cheeca Patch, only the latter was simulated as a representative for the patch reefs. The analysis showed that the outputs obtained from SPREAD were generally robust to uncertainty in the parameters (Fig. 6). The sensitivity indices were low and the regressions quite weak overall. The parameters that did show some effect on the average number of modules per individual

**Table 2 – Values of parameters used for sensitivity analysis of SPREAD**

| Factor | Parameter | Percent variation from default | Values used |
|---|---|---|---|
| Branch order | *a* | 20 | 0.16, 0.2, 0.24 |
| | *b* | 10 | 0.45, 0.5, 0.55 |
| Branch present | Slope | 20 | 0.13, 0.14, 0.15 |
| | Intercept | 20 | 0.6, 0.7, 0.8 |
| Light | *a* | 10 | 0.009, 0.01, 0.011 |
| | *c* | 20 | 6, 8, 10 (with *a* set to 0.008, 0.01, 0.014, respectively) |
| Nutrients | | 10 | 0.36, 0.44, 0.54, 0.66 |

**Table 3 – 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 | $\mu mol\, m^{-2}\, s^{-1}$ | 1942 | 2102 | 2167 | 2076 | 2167 | 2076 | Field observation |
| Standard deviation | Surface irradiance standard deviation | $\mu mol\, m^{-2}\, s^{-1}$ | 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<br>2—medium<br>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 |

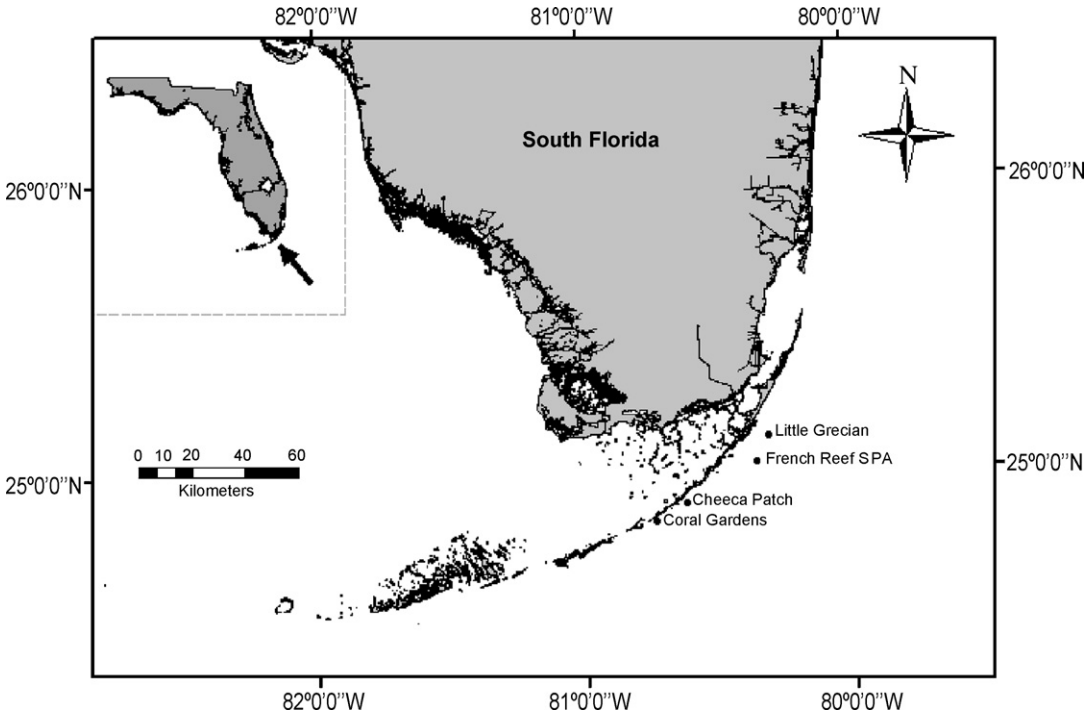


**Fig. 5 – Map of study sites in the Florida Keys Reef Tract.**

and new module production rates were the variables that were of interest: the shape parameter $c$ for the light growth curve (Eq. (3)), and the nutrient growth probability (Eq. (5)). Widening the light growth curve (i.e., increasing the light levels at which growth is not photo-inhibited), and increased nutrient growth probabilities led to higher number of modules and increased growth rates.

### 3.2. *Model results: running SPREAD using site-specific scenarios*

SPREAD was run using growth parameters for *H. tuna* that were held constant (Table 1), while the environmental parameters were different for each site (Table 3). 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 mortality values were equal. A model run was initialized with ten individuals of *H. tuna* in a 30 cm × 30 cm × 30 cm 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, of *H. tuna* individuals varied between the simulated sites (Fig. 7). French Reef had the highest number of segments per individual, while Little Grecian had the lowest (Table 4). 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, wherein French had the highest segment production rate, Little Grecian the lowest and the two patch reefs were in the middle (Table 4).

### 3.3. *In situ differences in H. tuna growth patterns between habitat types*

There was a significant difference in the number of segments an individual *H. tuna* had between sites (Table 4). 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 (Fig. 7).

When growth rates between sites were compared, they were only weakly different (Table 4). 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 (Table 4).

## 4. Discussion

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

The sensitivity analysis showed that SPREAD was generally robust to uncertainty in the parameters. Changes in the parameters would primarily affect the magnitudes of the morphometrics; however, the relative patterns obtained for the simulated sites would not be different. The similarity in the model and field morphometric patterns cannot be ascribed to parameter fitting since these were independently obtained and are likely a product of the importance of light varia-

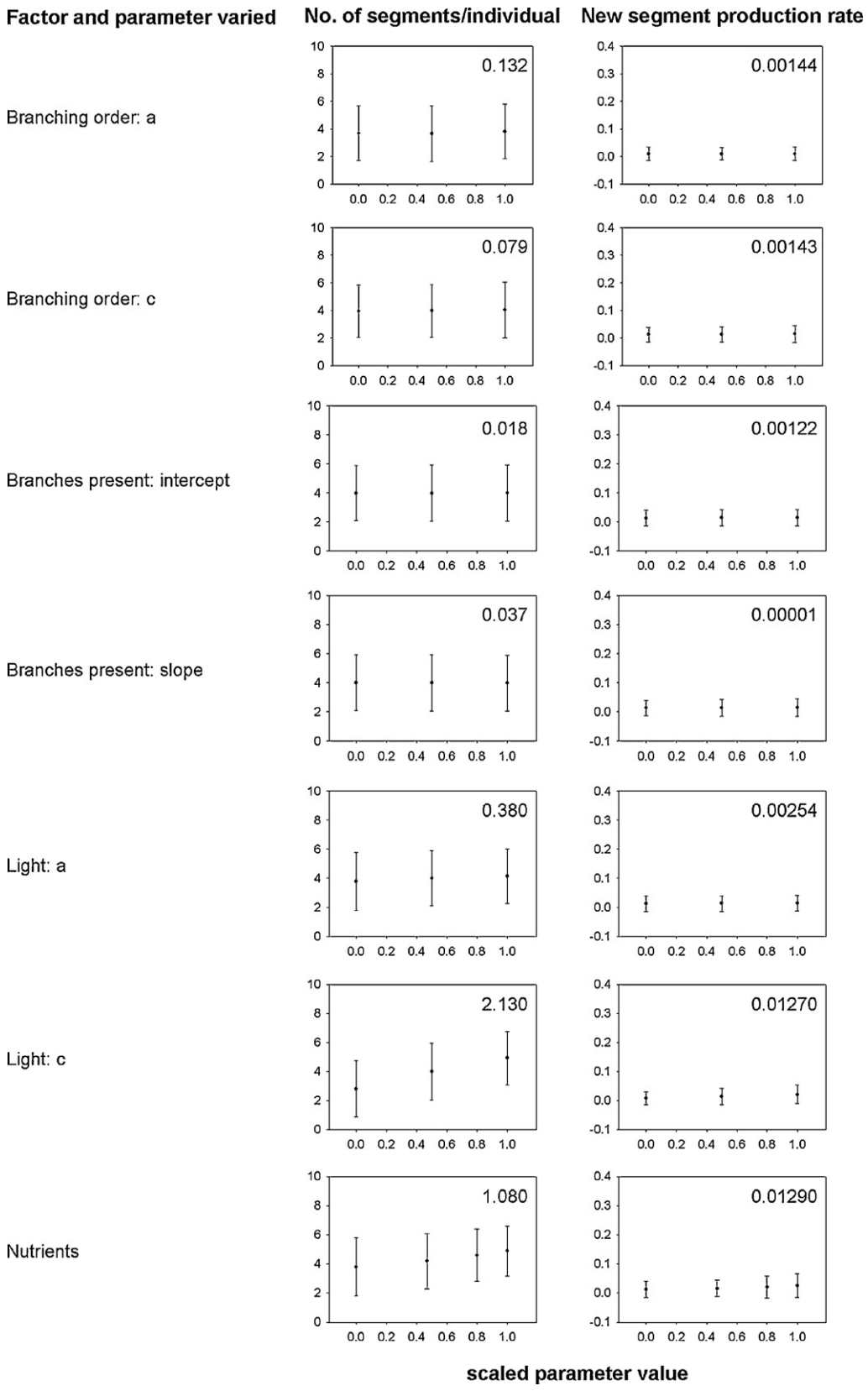


**Fig. 6 – Plots of mean with standard deviation of the number of segments per individual and new segment production rate using different parameter values of different factors. The *x*-axis represent the scaled values of the parameters. Numbers at the upper right-hand corner of each plot are the sensitivity indices for the particular parameter.**

**Table 4 – Summary of statistical analyses of model and field data**

| Metric and factors tested | Statistical test used | Results of analysis |
|---|---|---|
| SPREAD | | |
| Average number of segments per individual between sites | Kruskal–Wallis followed by Dunn's multiple comparison post hoc test | $p = 1.283 \times 10^{-263}$ |
| Average segment production rate per individual per day between sites | Kruskal–Wallis followed by Dunn's multiple comparison post hoc test | $p = 7.89 \times 10^{-92}$ |
| Field | | |
| Average number of segments per individual between sites | Repeated measures ANOVA (natural log transformed) followed by Tukey's HSD post hoc test | $p = 0.025$ |
| Average segment production rate per individual per day between sites | Repeated measures ANOVA (Box–Cox transformed, $\lambda = -0.95$) | $p = 0.06$ |
| Average loss of segments per individual per day (mortality rate) between sites | Repeated measures ANOVA (Box–Cox transformed, $\lambda = 2.1$) | $p = 0.169$ |

tion in *H. tuna* growth dynamics. The slight discrepancies between the model and field results highlights the potential importance of either nutrient levels and/or variation in growth parameters between populations as illustrated by some sensitivity of the model to these parameters.

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. In both the model and observed data, 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. (2003), 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 photo-inhibited under high light conditions. The model results lend support to this photo-inhibition hypothesis since the light growth curve of *H. 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.

Mortality through fragmentation without survival does not appear to affect the variation in the morphometrics of the *H. tuna* populations in the field sites, and as also shown in the model scenarios. This is in spite of potential differences in the intensities of the cause of mortality between the patch and offshore reefs. The inshore patch reefs are protected and calmer sites, whereas the spur and groove offshore reefs are much more exposed to waves and currents that cause *H. tuna* fragmentation. In the SPREAD site-specific scenarios, equal mortality levels were also used and still led to the previously discussed comparable growth patterns between simulated sites.

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 not hugely different (particularly for number of segments/individual while new segment production rate exhibited a one order difference) and the inter-site patterns were generally 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 (Fig. 7). 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 one offshore site, Conch Reef, could also be due to higher nutrient concentrations in the deeper area of the 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.

An assumption so far in the previous discussions has been that the *H. tuna* populations in both the offshore and patch reefs have similar growth curves. However, it is possible that these are different. Beach et al. (2003) saw differences in the photosynthetic performance (i.e., parameters in the photosynthesis–irradiance curves) of shallow (7 m) versus

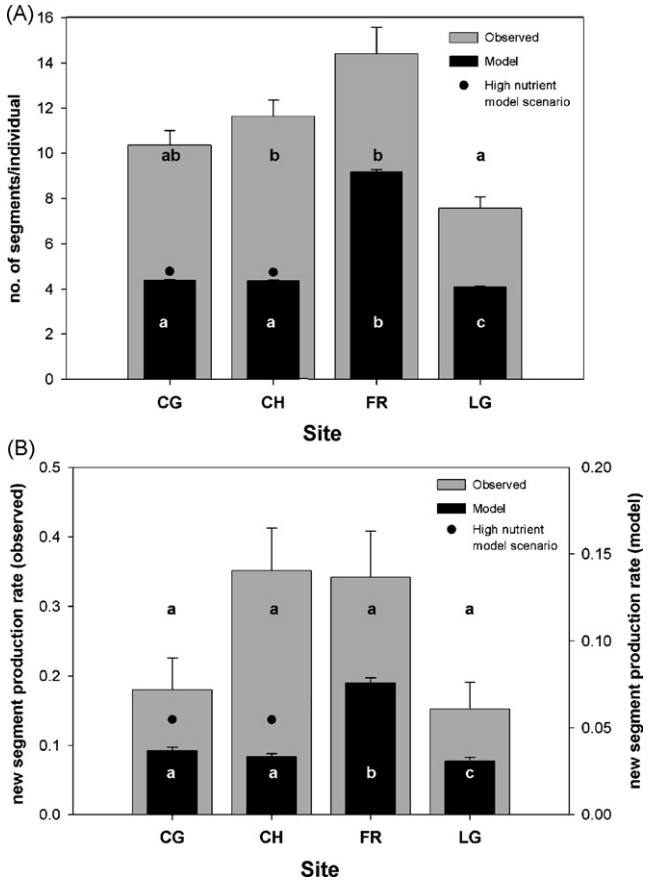


**Fig. 7 – Results from simulated site-specific runs of SPREAD and measurements from actual field sites in the Florida Keys. (A) Number of segments per individual *Halimeda tuna*. (B) New segments produced per individual per day. Model values are averages of 30 model runs. Error bars represent the standard 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.**

deep (21 m) populations; thus, similar variations in growth responses are potentially present between patch and offshore reef populations. Based on the results of the sensitivity analysis, such differences in the shape of the light growth curve can affect the model morphometrics. A comparable effect can also result from discrepancies in nutrient growth probabilities between populations. Although the authors know of no studies that have contrasted growth patterns between populations due to heterogeneous responses to the same nutrient levels, such differences could exist in nutrient uptake rates or the physiological process of converting these nutrients into growth. Variations in the light growth curve parameters (particularly c, which controls the decline due to photo-inhibition) and nutrient growth probabilities could be alternative explanations for the discrepancy between the model and field results, and point to parameters that need to be circumspectly set.

### 4.2. *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.

## 5. 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.

SPREAD was used to simulate the growth of *H. tuna* based on literature and laboratory-derived values for growth factors. 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. When model and field results were qualitatively compared, SPREAD showed that it can reproduce general growth patterns of *H. tuna* in contrasting reef sites. Explorations with the model in conjunction with the field measurements illustrated its use in potentially teasing out mechanisms and factors responsible for the growth patterns observed. The differences in the morphometrics of *H. tuna* between these reefs seem highly influenced by the growth requirements of light and nutrients, rather than mortality, and follow the observed variations in these environmental conditions. However, the potential that inherent differences in growth responses (thus, differences

in growth curve and probabilities parameterization) are also contributing to the observed variations cannot be ruled out.

This study shows that mosaics of experiments and scenario running in models can be instructive in discerning patterns and the potential causes of these patterns.

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