

Capturing the dynamics in benthic structures: environmental effects on morphology in the macroalgal genera *Halimeda* and *Dictyota*

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ABSTRACT: Macroalgae are modular organisms that can express different morphologies depending on the environment to which they are exposed. Their growth under varying light, temperature, and nutrient regimes, interacting with disturbance factors such as herbivory and hydrodynamics, leads to particular morphological types. The present study illustrates the potential of using morphological variations of benthic modular and/or clonal organisms as indicators of the factors and processes influencing them in their particular location. The morphogenetic agent-based model SPREAD (spatially explicit reef algae dynamics) was used to determine the range of potential morphological types in 3 dominant macroalgal species (*Halimeda tuna*, *H. opuntia*, and a species of *Dictyota*) in the Florida Reef Tract. Simulations of growth under a range of light, nutrient, and disturbance conditions similarly found at inshore patch and offshore bank reefs led to 6 potential morphological types for *H. tuna*, 2 for *H. opuntia*, and 3 for a species of *Dictyota*. From these potential sets derived from the model, we observed that particular morphological types corresponded to the morphologies found in the 2 reef habitat types. The simulated conditions that led to the formation of these morphologies in the model were similar to the environmental conditions at these sites. In addition to relating combinations of environmental and disturbance factors to macroalgal growth morphologies, the present study provides insights into the differing life-history strategies among the species, and the adaptive value of plasticity expressed by these macroalgae. The morphologies of the successful fragmenters *H. opuntia* and a generalized species of *Dictyota* were more influenced by disturbance. On the other hand, the morphology of the less successful fragmenter *H. tuna* was strongly influenced by the growth factors of light and nutrients.

KEY WORDS: Agent-based modeling · Macroalgae · Coral reef · Florida Keys · Morphology · *Halimeda* spp. · *Dictyota*

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INTRODUCTION

Modular and/or clonal organisms, such as macroalgae, can have highly plastic morphologies, indeterminate growth, greater importance of size than age in their life histories, and capacity for asexual reproduction (Jackson & Coates 1986). These characteristics have been investigated primarily in terrestrial plants and corals within the past several decades. These stud-

ies have shown that the modules making up the bodies of these organisms, and the ramets that can break off to form new individuals, have their own dynamics analogous to the population dynamics of individuals, and that these strongly influence the pattern of vertical and horizontal capture of space (Bell & Tomlinson 1980, Harper 1985, Halle 1986, Cain et al. 1996). Many species of marine macroalgae found in coral reefs display differential levels of plasticity in their morpholo-

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gies, similar to many other plants and macroalgae in other systems (Bradshaw 1965, Monro et al. 2007). Their modular construction is one source of their morphological phenotypic plasticity (Halle 1986). A modular organism's body is built up by the iteration of 1 or more distinct units, i.e. modules (Tuomi & Vuorisalo 1989). In terrestrial plants, these modules generally consist of leaves, stems, and roots. It has been shown that these plant modules are able to react, independently of the whole plant, to their local environment (Sutherland & Stillman 1988, de Kroon et al. 2005). Roots, for example can 'forage' for nutrients: in low-nutrient patches, the filamentous roots lengthen, whereas under high-nutrient conditions, they branch more in order to exploit the good patch (Lovett-Doust 1981, de Kroon & Hutchings 1995). A continuum of forms can thus be found between 2 extreme strategies: the 'phalanx' or consolidating compact strategy and the 'guerilla' or explorer spreading strategy (sensu Lovett-Doust 1981). Aquatic flora are just as capable of such variations in form. By adjusting size, shape, and resource allocation, macroalgae have a distinctive response to light quality and quantity in which elongated forms (guerilla growth form) are present in low-light environments contrasting with compact forms (phalanx-type) (Lovett-Doust 1981, Collado-Vides 2002, Monro & Poore 2004, 2005, Monro et al. 2007). In these modular organisms, the ability to modify their morphology may function as a mechanism to respond to a changing environment; therefore, plasticity has been considered an important adaptive mechanism by which organisms deal with the environmental challenges to their survival (Bradshaw 1965, Bell & Tomlinson 1980, Lovett-Doust 1981, Harper 1985, Hutchings 1988, Hutchings & Wijesinghe 1997, de Kroon et al. 2005, Monro & Poore 2005).

Macroalgae need certain water temperatures for rapid growth and reproduction, sufficient light for high levels of photosynthesis without photo-inhibition, and enough water movement to allow for an optimal amount of nutrients to be taken in, but not strong enough to cause damage or uprooting. There should also be nothing around that eats it or grows on it. However, it is quite rare that all those conditions exist at one time and area, and like all other organisms, there are trade-offs to be made between growing and reproducing versus avoiding injury and death. For modular organisms, such trade-offs can be deciphered from their growth form in conjunction with knowledge about the environment they live in. It has been proposed that to maximize productivity, thin and wide thallus forms that have high surface area to volume ratio are preferred (Littler & Littler 1980, Hay 1986). However, this growth preference is constrained by forces that detach parts or the whole alga (Lubchenco

& Gaines 1981, Koehl 1986). There have been a relatively large number of studies investigating the effect of the trade-off between obtaining light and the potential damage that water motion can cause. In temperate species such as kelp, many morphological traits seem to be strongly affected by these 2 factors (Koehl & Wainwright 1977, Koehl & Alberte 1988, Carrington 1990). There are only a few studies that have looked at these aspects of macroalgal growth in tropical ecosystems. For example, Collado-Vides (2002) demonstrated that differences in the morphology of *Caulerpa prolifera* in a coral reef lagoon in Puerto Morelos, Mexico, were related to light and possibly variation in water motion. On the disturbance or mortality side, decreased herbivory was shown by Lewis et al. (1987) to lead to a drastic change in the morphology of *Padina jamaicensis* from a prostrate turf growth form to a foliose upright one. A study by Hay (1981) illustrated that trade-offs between obtaining light and avoiding grazing led to shifts between upright and compact growth forms among several macroalgal species, including *Halimeda opuntia* and *Dictyota bartayresii*.

Our study area, the Florida Reef Tract, has a high cover of macroalgae (Chiappone & Sullivan 1997, Lirman & Biber 2000), and similar to many other coral reef ecosystems in the Caribbean, this reef system has experienced a drastic decline in the cover of reef-building corals within the last 3 decades (Porter et al. 2002, Gardner et al. 2003, Beaver et al. 2006, but see Bruno et al. 2009). The dominant macroalgal species belong to 2 genera: *Halimeda* (Chlorophyta) and *Dictyota* (Heterokontophyta) (Lirman & Biber 2000). In these reefs, macroalgae are exposed not only to 1 or 2 factors, but to a set of factors that could be playing important roles in their morphological responses, which ultimately scale up to larger scale patterns and processes (e.g. distributions and rates of spread).

Typically, studies on macroalgal morphology, as well as population and community dynamics, have investigated the effects of only 1 or 2 factors. Understanding of the complex interactions among a larger number of important growth and mortality factors with macroalgae morphologies and the potential underlying mechanisms remains a gap in our knowledge. The present study aimed to help fill in this gap by investigating the responses of the modules making up the individuals of these macroalgae to a combination of factors present in a coral reef environment, and evaluating the role of plasticity as a mechanism to balance the effects of these factors. To meet this overall goal, we wanted to determine (1) the potential (using a model) and (2) the realized (model results compared to the field) morphological plasticity in 3 dominant species of macroalgae in the Florida Keys — *Halimeda tuna* (Ellis and Solander) Lamouroux, *H. opuntia* (Linnaeus) Lamouroux, and *Dictyota men-*

strualis (Hoyt) Schetter, Hörnig and Weber-Peukert — and (3) the factors (light, temperature, nutrients, and disturbance) contributing to these morphologies.

MATERIALS AND METHODS

SPREAD formulation. SPREAD (spatially explicit reef algae dynamics) 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. More details on the formulation and implementation of the model are found in Yñiguez et al. (2008). 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. Internally, species-specific branching rules are used to capture branching characteristics (Figs. S1, S2 & S3 in Supplement 1 available at www.int-res.com/articles/suppl/m411p017_supp.pdf). SPREAD makes use of a

3-dimensional (3D) grid in which 1 cell is equivalent to 1 cm² area. The bottom of this grid is the substrate and each cell row is assigned a particular depth in 1 cm increments. Irradiance or photosynthetically active radiation (PAR) at depth is represented using the Lambert-Beer law, parameterized with field measurements (Table 1). Modules within a particular distance can also ‘shade’ the growing module by decreasing the amount of light getting through. 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 (Table 2) (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 3 nutrient levels (low, medium, high). The parameters used for the present study are found in Tables 1 & 2.

Table 1. *Halimeda tuna*, *H. opuntia* and *Dictyota* sp. SPREAD environmental parameters used in simulations exploring the potential morphological clusters of the 3 macroalgae. SD = standard deviation; SERC-FIU = Southeast Environmental Research Center at Florida International University; na = not applicable

Main factor	Parameters within factor	Description	Unit	Values used	Source
Season		1 static or 2 seasons; make use of seasonal values where specified	na	2	
Depth		Bottom depth	m	7	
Light	Irradiance	Surface irradiance	$\mu\text{mol m}^{-2} \text{s}^{-1}$	100, 500, 700, 900, 1300, 1700, 2100, 2500, 2900, 3100	SEAKEYS and field observations
	Irradiance SD	Surface irradiance SD	$\mu\text{mol m}^{-2} \text{s}^{-1}$	30 % of surface irradiance	Field observations
	Attenuation coefficient	Irradiance attenuation coefficient	na	0.26	SERC-FIU
	Allow shading	If shading will occur or not	Boolean	True	
	No. of cells affected by shading	No. of cells below module that will be affected by its shade	Cells	3	Calibrated
Temperature	Mean temperature		°C	Summer: 24.5–32.3°C; Winter: 6.6–27.9°C	SERC-FIU and field observations
	Temperature SD		°C	Summer: 5.5 %; Winter: 18.90 %	SERC-FIU and field observations
Nutrient levels		Coarse nutrient levels	na	1: low 2: medium 3: high	Exploratory

Table 2. *Halimeda tuna*, *H. opuntia* and *Dictyota* sp. SPREAD species-specific parameters used in simulations exploring the potential morphological clusters of the 3 macroalgae. SD = standard deviation; a,b,c: unitless coefficients used in the branching and growth equations; na: not applicable

Main factor	Parameters within a factor	Description	Unit	<i>Halimeda tuna</i>	<i>Halimeda opuntia</i>	<i>Dictyota</i> sp.	Source
Tissue transparency		Amount of light that a module will allow through to the cells below it	Fraction	0 (opaque)	0 (opaque)	0.6	<i>Halimeda</i> segments are solid and opaque; <i>Dictyota</i> sp. (Hay 1986)
Branching (branch order)		Curve for the effect of branch order on producing a new module				Always dichotomous	
	a		na	0.2	0.2	na	Estimated
	b		na	0.5	0.5	na	Estimated
	c		na	0.3	0.3	na	Estimated
Branching (branches present)		Line for effect of no. of modules already produced on producing a new one				Always dichotomous	
	Slope		na	-0.14	-0.05	na	Estimated
	Intercept		na	0.7	1	na	Estimated
Fragments		Percent of edge modules that will fragment	Fraction	0.01, 0.05	0.01, 0.05	0.01, 0.05	Exploratory
Fragment size \pm SD		Average no. of modules in 1 fragment and SD	No. of modules	3 \pm 1, 6 \pm 1	22 \pm 7, 44 \pm 7	4 \pm 1, 8 \pm 1,	Walters et al. (2002), Herren et al. (2006)
Light response		Growth response of modules to different light levels					
	a		na	0.01	0.4	0.003	Laboratory observations (Yñiguez 2007)
	b		na	0.04	0.4	1	Laboratory observations (Yñiguez 2007)
	c		na	8			Laboratory observations (Yñiguez 2007)
Temperature response		Growth response of modules to different temperature levels					
	Mean growth temperature		°C	29	29	28	Hillis-Colinvaux (1980), Lirman & Biber (2000), Biber (2002), Beach et al. (2003)
	SD		°C	2	2	2	Hillis-Colinvaux (1980), Lirman & Biber (2000), Biber (2002), Beach et al. (2003)
Nutrient response probabilities		Growth response of modules to 3 nutrient levels					
	Low		Fraction	0.2	0.2	0.2	Exploratory
	Average		Fraction	0.4	0.4	0.4	Exploratory
	High		Fraction	0.6	0.6	0.6	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. It only occurs from the edges and once fragmented modules are considered lost or dead (i.e. no fragment survival and settlement). This is appropriate in the present study because only the morphology of the individual macroalga is of concern. Disturbance was distinguished into 2 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 2 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.

Dictyota sp. in the model does not refer to a particular species since the light-response curve was obtained from *D. cervicornis* (Yñiguez 2007), while the other parameter values were obtained from literature values for various *Dictyota* spp. as available (Table 2).

Morphometrics such as number of segments, height, and width were obtained from the virtual macroalgae in SPREAD so as to emulate 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 multi-agent simulation toolkit (Luke et al. 2005, <http://cs.gmu.edu/~eclab/projects/mason/>) as the backbone.

Model scenarios. SPREAD was parameterized with various light, temperature, and nutrient values and disturbance regimes in order to explore the space of potential morphological responses. Ten irradiance levels were used, ranging from 100 to 3100 PAR. The minimum value was based on PAR data from the SEAKEYS Fowey Rock and Molasses Reef stations in the Florida Reef Tract. The maximum value was based on PAR data obtained using a LI-COR LI-193 Spherical Underwater Quantum Sensor at the 4 study sites discussed in the section 'Fieldwork study sites and their environmental variability'. A 30% standard deviation was used for each level, based on the variance observed empirically at the 4 study sites.

The 2 seasons of summer and winter were represented in all of the scenarios run. The range of temperatures for the summer season was 24.5 to 32.3°C, and for the winter season it was 6.6 to 27.9°C. These ranges were based on the 1995 to 2004 data set by the Southeast Environmental Research Center (SERC) at Florida International University for their sites closest to the 4 study sites, as well as temperature data obtained

directly using a YSI multi-parameter probe. During each discrete time step in the model (equivalent to a day), a temperature value was randomly chosen from the appropriate seasonal range, using a uniform distribution.

In the simulations, each irradiance level was crossed with each of the 3 nutrient levels and 3 disturbance regimes of 0.01 and 0.05% fragmentation, and 0.05% fragmentation with larger fragment sizes. Disturbance regimes represent low (0.01%) and high (0.05%) disturbance that simulates more of an herbivory effect because fragments are taken only from edges. The higher disturbance with larger fragment sizes simulates more of the effect of high water motion. All of these scenarios were run for the 3 macroalgal species separately. Ten individuals of a species were randomly distributed in the grid, and the model was run for 1000 d. Data from the average of 50 runs were used and the same morphometrics obtained from the field were also gathered from the model.

Fieldwork study sites and their environmental variability. Four sites in the Florida Keys were used for the present study (Fig. 1), which represented distinct environmental conditions. They included 2 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 2 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 2 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. Paddock (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 2 types of disturbances considered here relative to the offshore ones.

The 4 sites did not vary in the surface irradiance at noon that they received. However, irradiance at substrate level varied when this was calculated using overall average surface irradiance (2071.8910 $\mu\text{mol quanta m}^{-2} \text{ s}^{-1}$), 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 SERC. The 2 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) (Fig. 2), which was much deeper than the inshore reefs. The lower light values were due to these patch reefs being significantly more turbid (Boyer & Jones 2004). In terms of nutrient conditions, SERC obtained distinct water

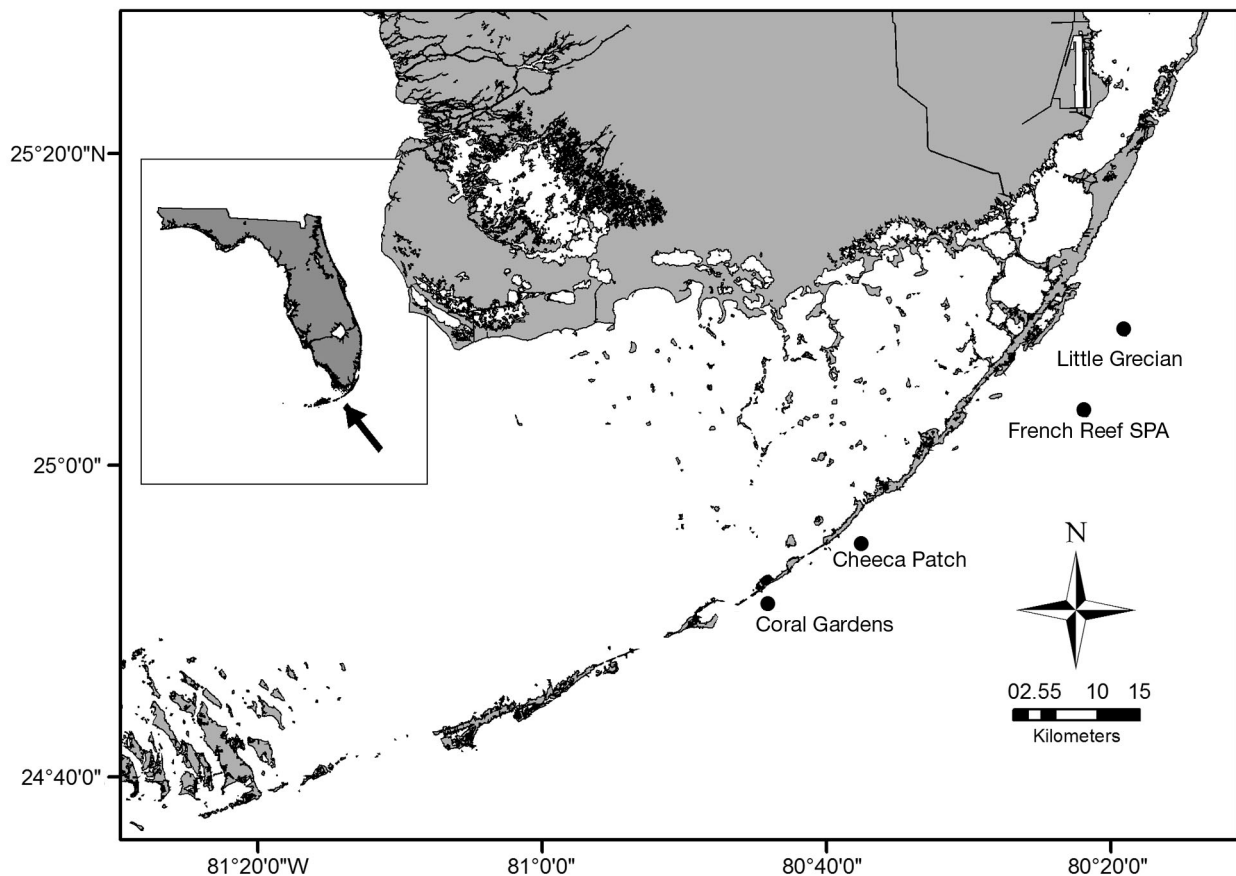


Fig. 1. Study sites in the Florida Keys Reef Tract

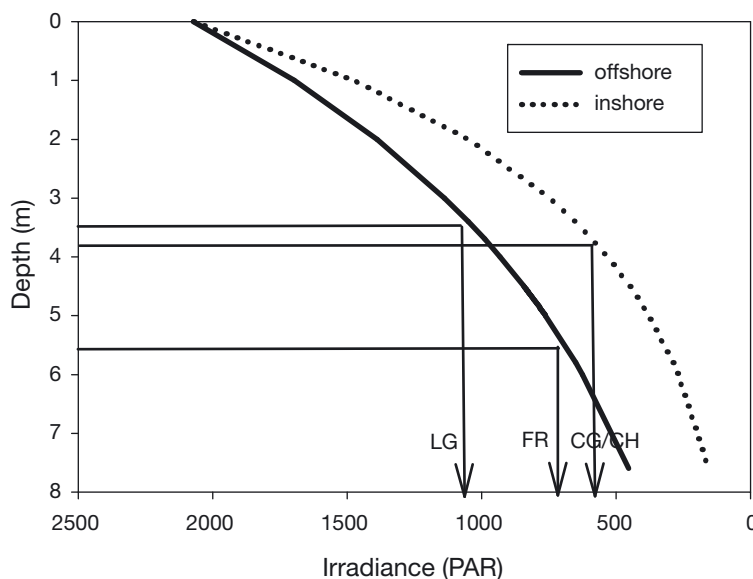


Fig. 2. Irradiance levels at the 4 study sites at the depths sampled for the morphometric surveys. Irradiance at depth was calculated using the Lambert-Beer law, applying attenuation coefficients from SERC data. Surface irradiance did not differ between the sites. Average attenuation coefficients for inshore and offshore sites were used. LG = Little Grecian, FR = French Reef, CG = Coral Gardens, CH = Cheeca Patch

quality clusters out of their extensive sites throughout the Florida Keys National Marine Sanctuary (Boyer & 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.

Morphometric surveys. The sites were surveyed during the summer days of September 18 and 19, 2006 when growth is highest for all 3 macroalgal species. For each site, the morphometrics of *Halimeda tuna*, *H. opuntia*, and *Dictyota menstrualis* were obtained. Separate surveys were done for each species where 0.5 m² quadrats were haphazardly deployed, taking care not to include closely adjacent quadrats. Up to 10 individuals or patches of the species being surveyed were randomly chosen and measured. For *H. tuna*, data included the 'number of segments' category

(categories in bins of 5 were used, e.g. 1 = 1 to 5 segments, 2 = 6 to 10 segments, and so on), number of axes (defined as the number of branches within 3 segments of the bottom-most segment), height, and width. It was difficult to determine individuals for *H. opuntia* and *D. menstrualis*, both of which grew in tangled clumps. For these 2 species, patches were delineated by following distinguishable boundaries. The following data were measured: height, width, and density category (1: sparse, 2: low density, 3: moderately dense, 4: very dense).

Statistical analysis. Model results — cluster analysis and canonical correspondence analysis (CCA): K-means cluster analysis in SPSS was used to differentiate distinct morphological forms that resulted from the various scenarios run with SPREAD. This method minimizes the variation within a cluster and maximizes variation between clusters. Cluster analyses were run using standardized values of the number of segments, height, width, and height:width ratio from all the scenarios. The height:width ratio was used to give an indication of the shape of the macroalgae. A value of 1 is equivalent to a hemispherical shape, values > 1 point to uprightness, and values < 1 indicate a flat form. Separate cluster analyses were conducted for each species using from 2 to 8 as the number of clusters, and the number of clusters that resulted in distinct, non-redundant forms was utilized.

CCA using the Vegan package in R was employed to distinguish the environmental conditions influencing the variation in morphologies emerging from the simulations.

Field data — principal components analysis (PCA) and multivariate analysis of variance (MANOVA): The morphometrics gathered from the field study were analyzed using PCA in order to condense the information in these morphometrics and their co-variances. The data were first transformed to natural logs in order to conform to the assumptions of PCA. Eigenvalues that were ≥ 0.32 were extracted, following Haring & Carpenter (2007). The components were rotated to simplify interpretation using the varimax method, which orthogonally rotates the components to minimize the number of variables with high loadings for each component (SPSS 15.0 for Windows). The first 2 principal components representing the condensed morphometric information were then subjected to MANOVA to determine differences between the study sites. If there was a difference, Tukey's post hoc test was employed to determine the specific site differences. Details of the statistical results from these analyses can be found in Tables S1 & S2 in Supplement 1.

Comparison of model and field results: The morphometrics of the clusters derived from the model and the same metrics from each of the study sites were

compared both visually and using PCA in order to qualitatively determine the similarities of the model and field morphological forms.

RESULTS

Model results

In order to obtain the potential morphologies of the 3 macroalgal species, we ran the model SPREAD using a range of realistic environmental conditions. Next, we used cluster analysis on the resulting morphometrics to distinguish between the morphological types. The effect of environmental conditions on the morphometrics were then investigated using CCA.

Halimeda tuna

There were 6 distinct clusters or morphological types for this species (Table 3, Fig. 3). Table 3 lists the detailed types, their forms and the conditions under which each is found, while Fig. 3 shows the actual model representations. Four were relatively small with shapes ranging from very flat to very upright. Two morphologies were larger, where 1 was more hemispherical than the other. Based on the results of the CCA (Fig. 4A), irradiance had the largest influence on the morphological clusters formed, followed by mortality (through fragmentation) and nutrient levels. The largest and most upright morphology of Cluster 1 (HtLU) was found only under low-light, high-nutrient, and low-fragmentation conditions. The other large cluster (Cluster 2, HtLH) was formed under high-light and relatively higher nutrient levels. The 4 clusters which contained the smaller-sized morphologies were found under varying light conditions, but mainly low to mid-level nutrient and higher fragmentation conditions. The upright forms were found more under lower irradiance levels compared to the hemispherical and wide forms, and also varying fragmentation conditions.

The larger morphologies (Clusters 1 and 2) were formed under relatively higher nutrient and low fragmentation conditions. The shapes of *Halimeda tuna* appeared to be controlled more by light: more upright forms were seen in lower-light conditions, shifting to hemispherical and wider shapes under higher irradiances.

Halimeda opuntia

The morphological clusters for this species were not as varied as for *Halimeda tuna* and the differences

Table 3. *Halimeda tuna*, *H. opuntia* and *Dictyota* sp. Morphological clusters derived from the model for the 3 macroalgal species, their morphological description, and the conditions where they formed. The 'Cluster' column includes the acronym for the particular cluster (e.g. *Halimeda tuna* Cluster 1 large and upright is 1: HtLU)

Species	Cluster	Morphology	Conditions found
<i>Halimeda tuna</i>	1: HtLU	Large and upright	Only at low light levels; higher nutrient levels; only at low mortality
	2: HtLH	Large and hemispherical	Higher light; higher nutrients levels; low mortality
	3: HtSH	Small and hemispherical	Mid-light levels; lower nutrient levels; high mortality levels primarily with small fragments especially at nutrient levels 2 and 3
	4: HtSU	Small and upright	Low light; middle nutrient levels; high mortality (both small and large fragments)
	5: HtSVU	Small and very upright	Mid-light levels; lower nutrient levels; high mortality (small fragments mainly)
	6: HtSW	Small and wide	High light; mid-nutrient levels; high mortality with large fragments
<i>Halimeda opuntia</i>	1: HoLLU	Large and less upright	All light and nutrient levels; low mortality or high mortality with large fragments
	2: HoSU	Small and upright	All light and nutrient levels; high mortality
<i>Dictyota</i> sp.	1: DSU	Small and upright	Mid-level light and nutrients; only at high mortality
	2: DSH	Small and hemispherical	Mid-level light; low nutrients; high mortality (small and large fragments)
	3: DLH	Large and hemispherical	Mid-to high light; high nutrient levels; low mortality

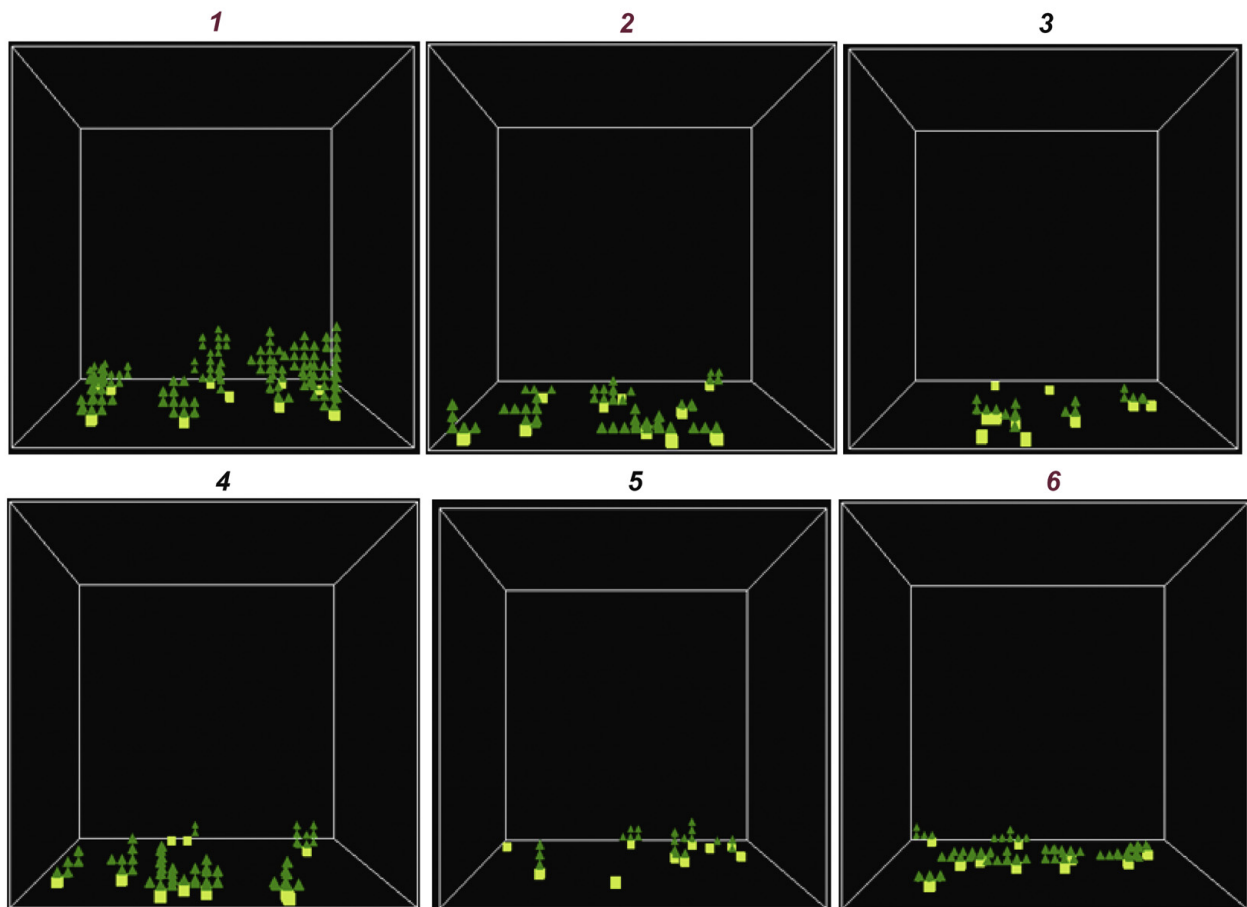


Fig. 3. *Halimeda tuna*. Morphological clusters derived from SPREAD. Table 3 details the characteristics of these clusters. Illustrations of the 2 other macroalgae can be found in Fig. S4 in Supplement 1

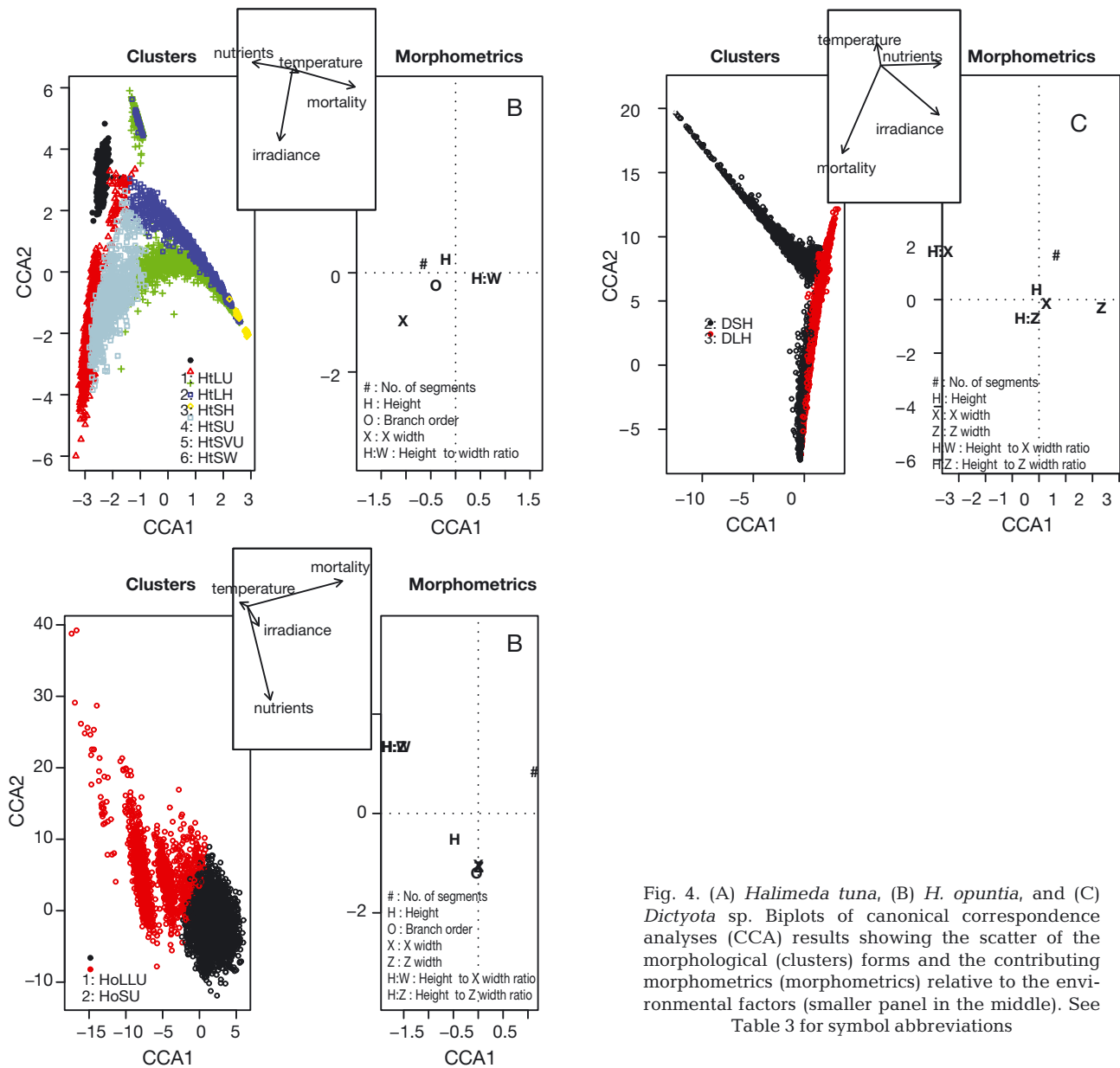


Fig. 4. (A) *Halimeda tuna*, (B) *H. opuntia*, and (C) *Dictyota* sp. Biplots of canonical correspondence analyses (CCA) results showing the scatter of the morphological (clusters) forms and the contributing morphometrics (morphometrics) relative to the environmental factors (smaller panel in the middle). See Table 3 for symbol abbreviations

between clusters were mainly due to size rather than size and shape. Two clusters were used to represent the main forms observed: small and upright, and large and less upright (Table 3, Fig. S4 in Supplement 1). The larger form was tending towards the hemispherical shape, but was still taller than wide.

The primary factor distinguishing the 2 clusters was the fragmentation level (Fig. 4B), wherein the small and upright form was found under the extremes of low fragmentation and high fragmentation with large fragments, while the large and upright form was seen primarily under high fragmentation but smaller fragment sizes. Cluster 1 tended to form in higher light and nutrient conditions compared to Cluster 2.

Dictyota sp.

There were 3 distinct morphological clusters observed for *Dictyota* sp. Two clusters were small and either upright or hemispherical in shape, while the third cluster was large and hemispherical (Table 3, Fig. S4 in Supplement 1).

The small and very upright form, Cluster 1 or DSU, was very restricted (seen only 6 times out of 4503 model runs), and was only found under nutrient level 2 at a mid-irradiance level and high fragmentation (larger fragments). The hemispherical forms (DSH and DLH) occurred under different but higher levels of irradiance, and different nutrient levels (Fig. 4C). The

smaller form (DSH) was found under relatively lower light levels and lower nutrient and higher fragmentation conditions (both normal and larger fragment sizes) compared to the larger form (DLH).

Field results

We also obtained real morphometrics of the 3 macroalgal species from actual reefs in the Florida Keys. Using PCA, we found that there were distinct differences in the size and shape of the 3 macroalgal species among the 4 sites, particularly between the offshore bank and inshore patch reef sites.

Halimeda tuna

The first 2 principal components explained 42 and 21 % of the variation in the morphometrics of *Halimeda tuna* from the 4 sites, respectively. The first principal component (PC1) was strongly correlated to width, height, and number of segments, while the second (PC2) was strongly correlated to the height:width ratio (Table 4). PC1 seems to differentiate based on size, while PC2 is related more to the shape. MANOVA and post hoc tests showed that there was a significant difference between inshore and offshore sites in the 2 component loadings. *H. tuna* in the 2 inshore patch reef sites (Coral Gardens and Cheeca Patch) were larger (had more segments, were taller and wider) and more upright in form than the populations found in the offshore spur and groove sites (French Reef and Little Grecian). The *H. tuna* populations in the offshore spur and groove reefs had height:width ratios closer to 1 and were more hemispherical in shape.

Table 4. *Halimeda tuna*, *H. opuntia* and *Dictyota menstrualis*. Summary of the 2 primary principal component loading scores for the morphometrics of the 3 species measured at the 4 field sites

Species	Morphometric	Principal component 1	Principal component 2
<i>Halimeda tuna</i>	No. of segments	0.898	-0.114
	Height	0.910	0.355
	Width	0.912	-0.333
	Number of axes	0.211	-0.098
	Height:width ratio	-0.058	0.992
	Epiphyte load	0.170	0.037
<i>Halimeda opuntia</i>	Height	0.078	0.996
	Width	-0.742	0.671
	Height:width ratio	0.991	0.126
	Density	-0.030	-0.037
<i>Dictyota menstrualis</i>	Height	-0.027	0.980
	Width	0.882	0.323
	Height:width ratio	-0.926	0.304
	Density	0.338	0.215

Halimeda opuntia

In total, 74 % of the variation in the morphometrics of *Halimeda opuntia* was explained by PC1 (38%) and PC2 (36%). PC1 was highly correlated to the height:width ratio or the shape of the macroalgae, while PC2 was correlated to the size metrics, height, and width (Table 4). MANOVA and post hoc tests separated out differences in the morphologies between sites. The *H. opuntia* in the 2 patch reefs had significantly flatter shapes (low height:width) compared to those in French Reef. Little Grecian was in the middle of these 2 extremes. However, the inshore patch reefs had significantly larger *H. opuntia* than the offshore spur and groove reefs.

Dictyota menstrualis

The first 2 principal components accounted for 44 and 30 % of the variation in the morphometrics of *Dictyota menstrualis*. PC1 was highly correlated to the shape metrics of height:width, as well as width, while PC2 was highly correlated with height (Table 4). Once again, MANOVA and post hoc tests of PC1 and PC2 highlighted the site differences. Coral Gardens and Cheeca Patch had populations of *D. menstrualis* that differed significantly from those at French Reef and Little Grecian in their shape-related PC1 values. *D. menstrualis* in the 2 patch reefs were very wide and flat. For the height- or size-related second PC, Cheeca Patch was on one side of the spectrum as the largest and Little Grecian on the opposite side. French Reef and Coral Gardens were in the middle.

Comparing model-derived and observed results

The distinct morphologies of the 3 species in the real-world study sites could be matched to the independently-derived morphological clusters in SPREAD (Figs. 5, 6 & 7). The environments where these clusters occurred in the model (Table 3) also paralleled the observed environments in the actual reefs. PCA illustrated that the macroalgae model morphologies coincided with their real-world analogues (Figs. 5B, 6B & 7B). However, the variations of the latter were quite large and could not be precisely ascribed to particular clusters just by this analysis. The plots of the morpho-

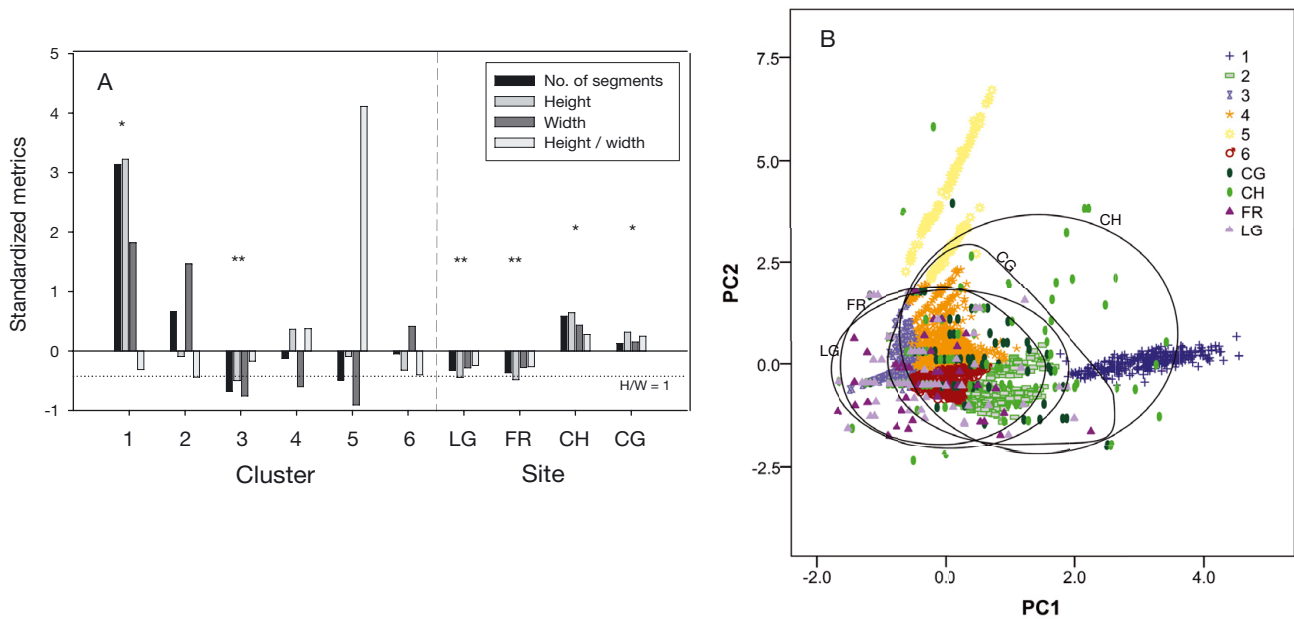


Fig. 5. *Halimeda tuna*. (A) Standardized morphometrics for the model-derived clusters and the study sites; (B) principal components (PC) analysis of model and field morphometrics. In (A), the dotted line denotes height:width ratio = 1. Similar asterisks denote qualitatively similar morphologies between the model and field results. LG = Little Grecian, FR = French Reef, CH = Cheeca Patch, CG = Coral Gardens

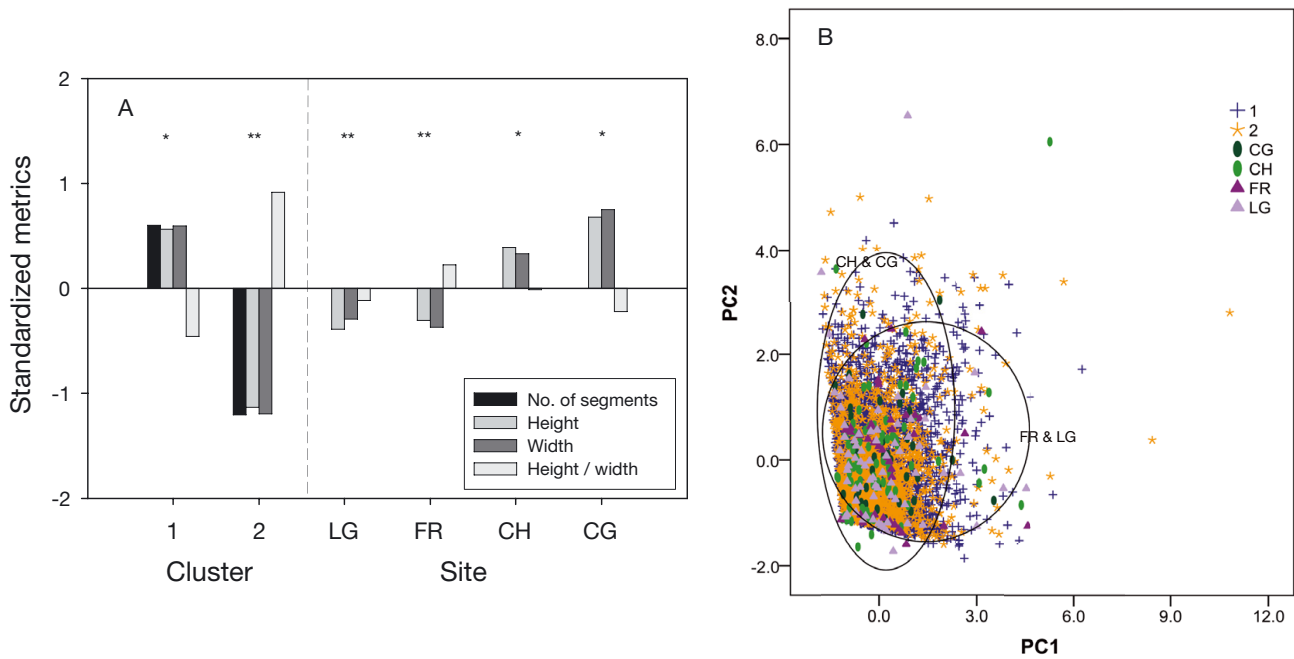


Fig. 6. *Halimeda opuntia*. (A) Standardized morphometrics for the model-derived clusters and the study sites; (B) principal components (PC) analysis of model and field morphometrics. In (A), similar asterisks denote qualitatively similar morphologies between the model and field results. LG = Little Grecian, FR = French Reef, CH = Cheeca Patch, CG = Coral Gardens

metrics from the model and field sites more clearly distinguished the similarities between particular model-derived morphological clusters and observed forms in study sites (Figs. 5A, 6A & 7A).

Halimeda tuna in the patch reefs were most similar in size and shape to Cluster 1 (HtLU), while the populations of the offshore reefs were most similar to Cluster 3 (HtSH). Cluster 1 (HtLU) occurred in lower-light,

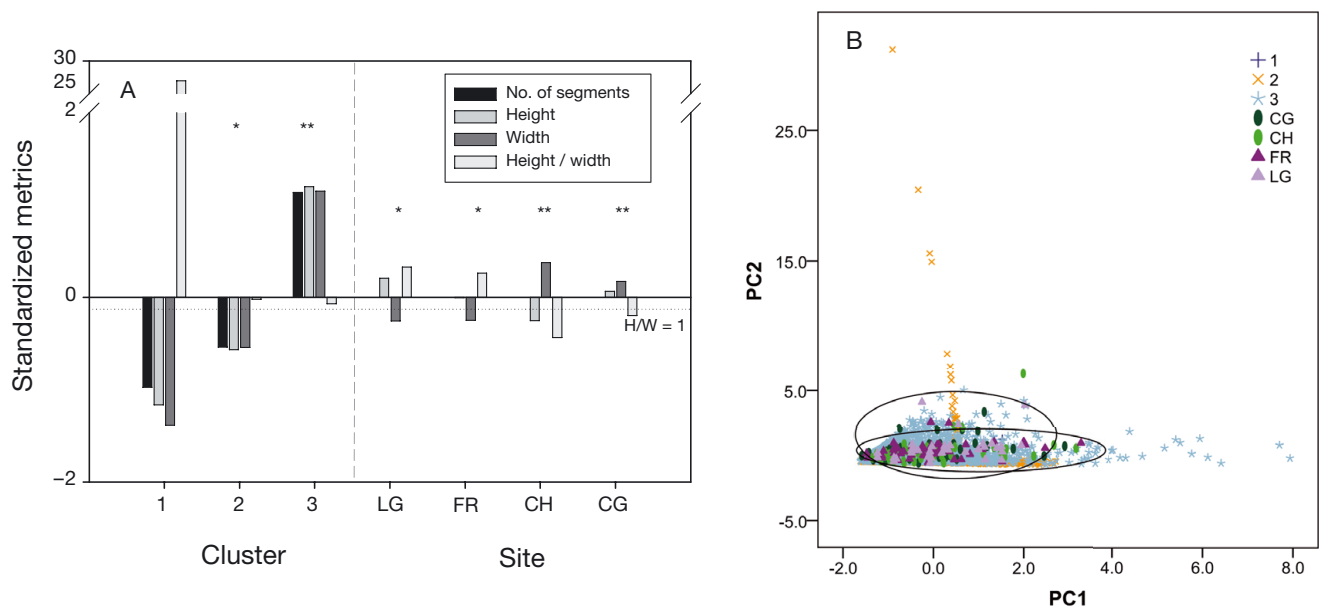


Fig. 7. *Dictyota* sp. (A) Standardized morphometrics for the model-derived clusters and the study sites; (B) principal components (PC) analysis of model and field morphometrics. In (A), the dotted line denotes height:width ratio = 1. Similar asterisks denote qualitatively similar morphologies between the model and field results. LG = Little Grecian, FR = French Reef, CH = Cheeca Patch, CG = Coral Gardens

high-nutrient, and low-fragmentation conditions. Cluster 3 (HtSH) morphs occurred in high-light, low-nutrient, and high-fragmentation conditions. For *H. opuntia*, Cluster 1 (HoLLU) corresponded to the inshore reef morphs, and the other cluster (Cluster 2, HoSU) was the most similar to the offshore reef morphs. These 2 clusters were differentiated only by fragmentation level and occurred under the same range of light and nutrient levels. Cluster 2 (DSH) in *Dictyota* sp. was the most similar to the offshore reef morphs, and Cluster 3 (DLH) with Cheeca Patch and Coral Garden morphs. Although DSH was found under lower light levels compared to DLH, their average values were both on the higher end and both clusters also encompassed a similar light range. The distinct differences between the 2 clusters were due to nutrients and fragmentation levels. DSH occurred in lower-nutrient and high-fragmentation conditions and DLH the opposite.

DISCUSSION

The morphological plasticity of organisms provides a unique opportunity to observe and understand the factors influencing their growth, mortality, and comparative ability to adapt to variable environments. This is especially true in modular and/or clonal immobile organisms that leave tangible evidence of the produc-

tion and death of their iterating units. Distinguishable changes in the morphologies of 3 macroalgal species were observed through SPREAD as they experienced varying light, nutrient, and disturbance (through varying fragmentation effects) levels. However, the amount of morphological variation differed between the 3 species and the convergence of forms made it difficult to tease out the effects of the growth from the mortality factors in detail. *Halimeda tuna* had the most distinct number of categories, which also allowed for some separation of the factors responsible for them, while the morphological clusters of *H. opuntia* and *Dictyota* sp. converged into 2 and 3 clusters, respectively, that differed primarily only in size under a variety of scenarios.

Morphological changes under ideal and less-than-ideal growth conditions

SPREAD showed that under low fragmentation (i.e. low mortality/disturbance conditions) and optimum light and nutrient conditions, all 3 species tended to be larger—as one might expect. *Halimeda tuna* also grew in a more upright form under ideal conditions (Cluster 1), and when light and nutrients were higher, it became more hemispherical (Cluster 2). Hay (1981) proposed that at lower light levels, mono-layered thalli will predominate, while at higher light levels, multilay-

ered (more upright) ones will be more abundant. Studies on the effect of light on the morphology of macroalgae also show that if light is limiting, as light decreases, the thallus module units themselves can become wider and/or the spacing between modular units becomes larger (less compact), leading to a guerilla growth form (Collado-Vides 2002, Monro & Poore 2005, Haring & Carpenter 2007, Monro et al. 2007). *H. tuna* follows a similar pattern such that there is increased compactness in shape (phalanx growth form) under higher light conditions. However, this is probably not because of their freedom from light limitation, because they have a relatively low light requirement (Beach et al. 2003) compared to the light conditions in Cluster 2 (HtLH). More likely this form is due to the photo-inhibitory effect of high light that has been shown to affect their morphology (Hader et al. 1996, Beach et al. 2003, Vroom et al. 2003).

Halimeda opuntia and *Dictyota* sp. did not exhibit any shift in shape similar to those of *H. tuna* when light or nutrients changed. This could be explained by the larger ranges of optimum light conditions to which *H. opuntia* and *Dictyota* sp. respond similarly. Growth experiments controlling for light in aquaria that were used to parameterize SPREAD did exhibit similar growth rates under low to high irradiance levels for these 2 species (Yñiguez 2007). The simulated *Dictyota* sp. did change in size under higher light and nutrient conditions, although this effect co-varied with decreased fragmentation. Beach et al. (2006) have previously observed that lower light decreased primary productivity in *D. menstrualis* and *D. pulchella* in Conch Reef, Florida Key, and that they can also be nutrient-limited and respond physiologically to nutrient enrichment. These productivity responses most likely translate to parallel increased or decreased growth.

Effects of mortality through fragmentation on morphology

Mortality, through disturbances such as herbivory and water motion, has long been recognized as a strong factor influencing macroalgal population and evolutionary dynamics (Lubchenco & Gaines 1981, Carpenter 1986, Koehl 1986). On an individual level, these are also important factors affecting the morphology of macroalgae. *Halimeda tuna* did exhibit a shift in shape under increased mortality levels. Higher mortality simulating increased herbivory (high fragment pool but relatively smaller fragment sizes) resulted in smaller sizes and hemispherical shapes, leading to a phalanx growth form (Cluster 3). Lewis et al. (1987) and Diaz-Pulido et al. (2007) have shown that the brown algae *Padina jamaicensis* and *P. boergerensis*,

respectively, changed from a foliose form to a prostrate turf alga when herbivore intensity increased. Hay (1986) illustrated the role of both herbivory and desiccation in favoring clumped and more hemispherical forms versus upright individuals in various macroalgal species including *H. opuntia* and *Dictyota bartayresii*.

Under the fragmentation conditions simulating increased disturbance, such as that from water motion, the shape of *Halimeda tuna* became small and wider or more prostrate. Studies on macroalgae (e.g. *Mastocarpus papillatus*, *Fucus gardneri*, *Chondrus crispus*) have shown that they can change their shape to smaller, more compact or prostrate forms when water motion is high (Carrington 1990, Blanchette 1997, Boller & Carrington 2006). This shape enables them to experience less drag and thus lower the probability of being torn off from the substrate. Damage can potentially induce increased branching and/or affect directionality of growth and branching (Hay 1981, Van Alstyne 1989). Interestingly, although module mortality in SPREAD is only through fragmentation as an external force that does not induce any sort of response from the macroalgae (e.g. re-direction of growth), it is still able to reproduce known patterns in morphology attributable to mortality. Thus, it is not necessary to infer that these macroalgae respond to module mortality in any active way beyond continued growth.

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

The concept of a trade-off in the morphology of macroalgae implies a response (at the ecological scale) to the forces acting on an individual. One of the common examples for this trade-off is the variation in the blade width of temperate macroalgae among depths and different wave exposures (Koehl & Wainwright 1977, Koehl & Alberte 1988, Carrington 1990, Haring & Carpenter 2007). These studies have shown that the

macroalgae can not only actively respond to light availability but also to hydrodynamics as a disturbance factor. In SPREAD, responsiveness is through amount of module production and directionality of module production as affected by light, temperature, nutrients, and space availability, while disturbance through fragmentation is an external and random process that does not directly effect any response. Other mechanisms for responding to light and nutrients that can influence morphology of the 3 macroalgae studied are size of segments (Beach et al. 2003, Vroom et al. 2003, Smith et al. 2004) and intersegment distances (Littler & Littler 2000 for *Halimeda opuntia*). Damage to the macroalgal thallus has been shown to potentially cause the growth of adventitious branches on *Dictyota* spp. (Gaillard et al. 1986, Cronin & Hay 1996). Even though SPREAD does not incorporate these other potential mechanisms for morphological plasticity, it was able to capture realistic variations in the 3 species because the morphometrics used were generalized enough.

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

The 3 species had varying morphological plasticity and responses to the growth and mortality factors. *Halimeda tuna* could be said to have the most plastic morphology, relative to *H. opuntia* and *Dictyota* sp., in terms of the morphometrics that were included in the present study. This could be due to the larger range of *H. opuntia* and *Dictyota* spp. light requirements, allowing them to grow similarly whether at lower or higher irradiance levels (Beach et al. 2006) leading to a lower plasticity response and limiting their morphological spectrum as compared with *H. tuna*. An alternative explanation is that other morphometrics that were not used in SPREAD give rise to other morphologies in these 2 species. Segment size can vary for both, as well as segment shape and intersegment distances for *H. opuntia*. *H. opuntia* are known to exhibit higher intersegment distances and smaller and tri-partite segments that grow up loosely in lower light levels (Kooistra & Verbruggen 2005). For these 2 species, measuring density could have also provided increased distinction of morphologies.

Halimeda tuna was strongly affected by both growth (light and nutrients) and mortality or disturbance factors. This is in contrast to *H. opuntia* and *Dictyota* sp., which were more strongly influenced by disturbance (fragmentation leading to mortality) forces. Previous studies on *H. tuna* have shown similar shifts in morphology due to differing light and nutrient conditions (Beach et al. 1997, 2003, Vroom et al. 2003, Smith et al.

2004) but no observed variation in grazing pressure (i.e. mortality). This species appears to be sensitive not only to limited light but also high light conditions that cause photo-inhibition (Beach et al. 2003). Increased nutrient levels have also resulted in larger, more upright morphologies (Smith et al. 2004). *H. opuntia* and *Dictyota* sp. variation in size and (slightly) in shape was strongly influenced by disturbance rather than light, and for *Dictyota* sp. nutrients as well. Both of these species are relatively 'good' fragmenters compared to *H. tuna*. This mechanism potentially allows these species to persist and even spread under high disturbance conditions. *H. opuntia* produces large fragments that can have high survival probabilities (up to 93 %) (Walters et al. 2002). Various *Dictyota* species are the dominant macroalgae in the offshore reefs of the Florida Keys despite being in a high-disturbance environment. Their morphology in these sites indicates a low-nutrient and high-disturbance environment, yet they are successful in persisting and occupying the reef substrate. This is probably due to their capacity to easily produce fragments, which have almost a 100 % survival probability even with small fragment sizes (Vroom 2001, Herren et al. 2006).

Macroalgal morphology as indicators of environmental conditions

At the cross-genus level, the morphologies of macroalgae can provide information about the environments in which they are found (Littler & Littler 1980, Steneck & Dethier 1994). These generalized groupings tend to be useful when investigating large-scale patterns, although the large variations in life histories of these different groups can obscure this information (Padilla & Allen 2000). Focusing on certain species can help give a clearer picture on the environmental factors influencing macroalgal morphologies (e.g. Hanisak et al. 1988, Benedetti-Cecchi et al. 2006).

The morphologies derived from SPREAD corresponding with those found in the study sites provided information on the gradient of environmental conditions these macroalgae were experiencing where they were located. The 2 inshore patch reefs were characterized by intermediate light levels, higher DIN concentrations, and calmer conditions (less disturbance), while the offshore bank reefs have higher light levels, lower DIN concentrations, and stronger water motion through wave action and currents. It appears that the morphometrics of *Halimeda tuna* can be good indicators of the conditions under which they are found: larger and more upright forms tend to be in lower-light (i.e. non-photo-inhibiting), higher-nutrient, and calmer environments (Beach et al. 2003, Vroom et al. 2003,

Smith et al. 2004). *H. opuntia* and *Dictyota* sp. morphologies were more indicative of the disturbance conditions, whether herbivory or hydrodynamics, of their habitats.

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