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REPORT

Interaction of herbivory and seasonality on the dynamics of Caribbean macroalgae

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Abstract Many Caribbean coral reefs are undergoing a phase shift from coral to macroalgal dominance. Understanding the processes driving changes in algal abundance and community structure requires clarification of the relative effects of top-down (e.g., herbivory) and bottom-up processes (e.g., light, temperature, and nutrients). To date, a number of studies have examined the relative effects of grazing versus nutrification but interactions between herbivory and natural, seasonal fluctuations in temperature and light have not been investigated. This study considered the dynamics of three Caribbean macroalgal species [*Lobophora variegata* (Lamouroux), *Dictyota pulchella* (Hörnig and Schnetter), and *Halimeda opuntia* (Linnaeus)] and algal turf. A field experiment was established to measure species-specific algal dynamics (changes in abundance) over 13 months in the presence and absence of herbivory. Both herbivory and seasonal changes were important processes controlling macroalgal and turf abundance. Water temperature and light had a key role on *D. pulchella*; this species' abundance significantly increased in the summer, when water temperature and light were the highest, and decreased during winter. Surprisingly, herbivory did not seem to control *D. pulchella* directly. However, herbivory was the most important process controlling the abundance of *L. variegata, H. opuntia,* and turf. The abundance of both algal species was correlated with seasonal changes in the environment, but was depleted outside cages throughout the year. The abundance of *H. opuntia* was positively correlated with temperature and light, but there was no statistical interaction between drivers. The statistical interaction between temperature and light was significant for the abundance of *L. variegata* and turf, but algal abundance declined as both factors increased. Overall, macroalgal and turf cover were mainly controlled by herbivory, while community structure (which species contributed to the overall cover) was largely influenced by seasonal changes in temperature and light.

Keywords *Dictyota pulchella* · *Lobophora variegata* · *Halimeda opuntia* · Macroalgal dynamics · Herbivory · Seasonality

Introduction

Many coral reefs are facing unprecedented levels of disturbance, leading to declines of hard coral cover and a shift toward an increase in macroalgal (Done 1992; Hughes 1994; Shulman and Robertson 1996; McClanahan et al. 1999; Ostrander et al. 2000; Edmunds 2002; Hughes et al. 2010; but see Bruno et al. 2009). The increased incidence of coral–algal interactions (Lirman 2001; River and Edmunds 2001) and growing evidence that scleractinian corals and macroalgae compete for space (Tanner 1995; Jompa and McCook 2002; Nugues and Bak 2006; Rasher and Hay

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2010) support the idea that such interactions have a key role in structuring the benthic community of coral reefs (Burkepile and Hay 2008; Hughes et al. 2007). Coral–algal phase shifts have been studied for many years (Hatcher and Larkum 1983; Done 1992; Hughes 1994; Miller and Hay 1998; McCook et al. 2001; Diaz-Pulido and McCook 2003; Jompa and McCook 2003; Mumby 2006; Hughes et al. 2007; Diaz-Pulido et al. 2009), but the relative importance of top-down (e.g., herbivory) versus bottom-up processes (e.g., nutrification) has been controversial (Lapointe 1997, 1999; Hughes et al. 1999; Burkepile and Hay 2006; Mumby and Steneck 2008). While experimental studies have generally found stronger effects of herbivory over nutrient concentration (Hughes et al. 2004, 2007; Burkepile and Hay 2009), the wider importance of productivity potential (Steneck and Dethier 1994), which includes flow, temperature, and light, has received far less attention (Mumby and Steneck 2008).

In addition to relatively long-term shifts toward reef dominance, macroalgae often exhibit seasonal fluctuations (Hoyt 1907, 1927; Lirman and Biber 2000; Hwang et al. 2005; Ateweberhan et al. 2006; Diaz-Pulido et al. 2009; Mumby 2009; Renken et al. 2010). Such patterns may arise purely because of seasonal solar cycles or more complex changes in physical conditions brought on by upwelling or monsoons (Diaz-Pulido and Garzon-Ferreira 2002). The proximate causes of such patterns, however, may include changes in nutrient concentration, light penetration, temperature, and grazing regime. For example, in the Red Sea, temperature was the fundamental factor controlling the seasonal cycle of the algal community structure and dynamics (Ateweberhan et al. 2005, 2006). Similarly, Diaz-Pulido and Garzon-Ferreira (2002) looked at the seasonality of algal assemblages in upwelling-influenced coral reefs and found that macroalgal abundance, especially *Dictyota* spp., had a significant inverse correlation with water temperature. However, Diaz-Pulido and Garzon-Ferreira (2002) also hypothesized that the negative correlation with water temperature arose because of the increased availability of nutrients during upwelling. While these processes and water temperature are clearly important for reef algal dynamics, a few studies have considered explicitly how herbivory impacts reef algae in different seasons. Carpenter (1986) found that the abundance of herbivorous fishes on an exposed back reef in St. Croix was greater during the summer and varied seasonally. Lefèvre and Bellwood (2010) found that herbivores preferred consuming *Sargassum* when it blooms in summer rather than when it dies back in winter. Recently, Afeworki et al. (2011) looked at the feeding ecology of a parrotfish in relation to seasonal changes in algal functional groups in the southern Red Sea; they found significant seasonal differences in feeding preferences by this herbivore, the studied species specifically targeted turf in the cool season, when this alga was less abundant. However, a direct analysis of the impact of herbivory in different seasons is lacking for most Caribbean reef flora.

Here, we use a field experiment to study seasonal trends in the abundance of three dominant macroalgal species and algal turf (filamentous and fleshy algae <1 cm in size) under manipulated levels of herbivory. The three algal species used were *Lobophora variegata* (Lamouroux), *Dictyota pulchella* (Hörnig and Schnetter), and *Halimeda opuntia* (Linnaeus).

Materials and methods

Study site and species

The study was conducted on Glovers Reef Atoll (87°48′W, 16°50′N), located 32 km offshore from the mainland and 15 km east from the Mesoamerican Barrier Reef off Belize, Central America. The area was declared a no-fishing reserve in 1993 (Carter and Sedberry 1997) and has relatively high levels of fish grazing for the present-day Caribbean (Mumby 2006). The experiment was conducted on the forereef (depth of 7–9 m) on the eastern side of the atoll at Long Caye. The forereef is dominated by colonies of *Montastraea annularis* (Ellis and Solander). The horizontal visibility is approximately 25 m along a transect line at a depth of 8 m. The system has high wave energy and water flow due to its windward orientation (McClanahan and Muthiga 1998; Renken and Mumby 2009).

We focused on three different species of macroalgae, which represent different functional groups. Steneck and Dethier (1994) convincingly assert that a functional group approach can be useful to understand algal dynamics across systems and processes. For example, the different morphologies of these algae species affect their susceptibility to fragmentation (Herren et al. 2006), predation by large sparisomids (Mumby et al. 2006), and potentially their response to temperature and light (Duffy and Hay 1990; Steneck and Dethier 1994). *D. pulchella* has a creeping interwoven to bushy growth form, with dichotomous branching up to 10 cm in height (Littler and Littler 2000). *L. variegata* has three life forms: decumbent, crust, and ruffled (Lewis et al. 1987). This study focused on the decumbent form, which has flat blades up to 15 cm in diameter (Littler and Littler 2000). *H. opuntia* attaches to the substratum from its holdfast and has dense, overlapping, irregular clumps and has *thalli* that calcify in segments up to 20 cm tall (Duffy and Hay 1990). Hereafter, these species will be referred to as *Dictyota*, *Lobophora*, and *Halimeda,* respectively.

Experimental design

A year-long experiment was established to study the effect of herbivory, light, and temperature on macroalgae community structure and abundance. Eighteen permanent quadrates (50×50 cm) were randomly placed over patches of dead *M. annularis* colonies. Three treatments were allocated randomly to the 18 quadrates, providing six replicates per treatment: cages (excluding herbivore fish), cage controls (controls for the cages where two lateral opposite mesh panels were removed to allow grazing in the plots), and uncaged plots (no cage structure and access for herbivores). These controls allowed herbivory while controlling for the structural effect of the cages (water flow and light reduction). The meshed side of the cage controls was oriented toward the prevailing water flow (northeast). We focused on manipulating herbivorous fishes because the density of *Diadema antillarum* is extremely low on the eastern side of Glovers Reef (<0.01 m^2). Cages (50 cm $\times$ 50 cm $\times$ 50 cm) were constructed using polyvinyl chloride (PVC) and plastic mesh (5 cm mesh) to avoid metal contamination that might influence algal growth. Each cage was attached to the reef using zip ties and two re-bars covered with PVC pipe. Preexisting macroalgae were initially cleared using wire brushes and scouring pads to standardize the benthic community at the start of the experiment.

Data collection

Percent cover of benthic components was estimated monthly from December 2008 to December 2009. Each quadrat was filmed using a high-definition Sanyo Xacti video camera held perpendicular to the substratum at a height of 50 cm. Each 25 cm^2 of the quadrat was then photographed separately by placing a smaller fine quadrat immediately over the substratum and slowly sweeping the camera 10 cm above the substratum. Benthic components were recorded in seven species or functional categories: (a) *Lobophora*, (b) *Dictyota*, (c) *Halimeda*, (d) other macroalgae, (e) algal turf (filamentous and fleshy algae <1 cm in size), (f) a category combining bare substrate and calcareous coralline algae (hereafter BS), and (g) ungrazable, a category combining sand, other invertebrates, and live coral (hereafter UNGZ). Here, we focus our results and discussion solely on the three macroalgal species and algal turf, but we present the results for the seven categories. The total percent cover of each benthic category was calculated for every sub-quadrat using the image analysis software VidAna [available from http://www.marinespatialecologylab.org]. Initially (January 2009), the number of times that each algal species was the first colonizer of bare substratum in the caged quadrates was counted in order to assess the potential of colonization without herbivory, then the probability of colonization for each algal species was calculated.

Permanently fixed video cameras were used to evaluate herbivory in the cage controls and uncaged plots (no fish grazing was observed in the caged plots). A total of 395 min of video was recorded for the uncaged plots and 285 min for the cage controls. For parrotfishes, the number of bites per species, life phase, and fish size were quantified, while in the case of acanthurids, only the number of bites per fish was recorded.

Temperature was measured every 30 min during the experimental period, using HOBO temperature sensors (UA-001-64, Onset Computer Corporation, USA). Photosynthetic active radiation (PAR, 400–700 nm) was measured every 30 min during 42 consecutive days inside and outside the cages, using Odyssey loggers (ODYPHOTO, Dataflow Systems 2008), in order to quantify the effect of the cages and cage controls on light attenuation. Additionally, to assess seasonal variation in light, we used solar insolation (W m^{-2}) data collected hourly throughout 2009, 15 km away from the study site by the Smithsonian Institute. Experiment maintenance was executed every 2 weeks and included cleaning the cages, as well as cleaning data loggers and downloading data.

Statistical analyses

Light, temperature, and herbivory in the study area

PAR attenuation inside cages was calculated by comparing the total PAR per day inside and outside cages using a paired one-tailed t test. Normality of data distribution was tested using the Shapiro–Wilks test ($p = 0.05$ for inside and $p = 0.73$ for outside the cage). Monthly averages of daily sums were calculated for light (solar insolation). Temperature was averaged per month, and maximum and minimum values for each month were obtained.

To assess the difference in grazing (G) between herbivory treatments (cage controls and uncaged plots), we calculated the percentage of the reef (two-dimensional area) grazed per hour using the grazing model in Mumby (2006). Observed grazing rate was converted to area grazed per unit time by using the allometric scaling relationships between fork length (in centimeters FL) and bite size, m (in square centimeters) (Bruggemann et al. 1994; Mumby 2006):

$$m = M \times 0.001(\mathrm{FL})^2 \tag{1}$$

where M is the constant that takes the value 4.013 in *Scarus* and 5.839 in *Sparisoma.*

Then, total grazing intensity (TG) is calculated as:

$$\mathrm{TG} = \sum_{s=1}^{S} \sum_{l=1}^{Fs} \sum_{p=1}^{\mathrm{NP}} r_{s,l,p}\, m_{s,l,p} \tag{2}$$

where r is the bite rate, S is the number of species, F_S is the number of size categories for species s, and NP is the number of life phases. Equations 1 and 2 then are combined to convert bite rate to the percentage of the reef grazed per hour, G:

$$G = \left(\frac{\mathrm{TG}}{10000}\right)\left(\frac{1}{\mathrm{ta}}\right) \tag{3}$$

where ta is the total area of sampling unit (in square meters), which was 1.5 m^2 for the uncaged plots and 1.25 m^2 for the cage controls in our experiment. Hence, G is the percentage of reef grazed in 1 h.

In order to consider the difference in acanthurid grazing between the uncaged plots and the cage controls, we calculated the number of bites per square meter per minute, where the total observation time was 6.58 h for the uncaged plots and 4.75 h for the cage controls.

Differences in parrotfish grazing among treatments were examined using a permutation multivariate analysis of variance (PERMANOVA), with the Bray-Curtis similarity coefficient, while a univariate PERMANOVA was used for the surgeonfish (Euclidian similarity coefficient). We ran separate PERMANOVAS for parrotfishes and surgeonfishes, G was the dependent variable in the parrotfish model, while the number of bites per area and unit of time was the dependent variable in the surgeonfish model. A distance-based test for homogeneity of multivariate dispersions (PERMDISP) was used to determine whether the multivariate dispersion was homogeneous among the levels of the fixed factor (quadrats per treatment) and a non-metric Multi-dimensional scaling (MDS) was used to visualize the results. We also used a Similarity of percentages routine (SIMPER accounting to both 90 and 100% contributions) to identify the grazer categories of the parrotfishes [*Sparisoma* terminal (T), initial (I) and juvenile (J), and Scarus terminal (T), initial (I) and juvenile (J)] that contributed most to total grazing (TG) in each treatment.

Effect of light, temperature, and herbivory on macroalgal abundance

The significance of herbivory, temperature, and light (solar insolation) on the change of macroalgal abundance over time was evaluated using PERMANOVA. Euclidean similarity was used to obtain the resemblance matrix. Herbivory was treated as a categorical fixed factor with 3 levels (cage, cage control, and uncaged), and quadrat was included as an un-replicated random factor (included to account for the spatial correlation of the dataset). Monthly average temperature, monthly average of daily sums of solar insolation and time were included as continuous predictors (covariates). To account for temporal autocorrelation of repeated measures, a type-1 decomposition (sequential, SS) was used to calculate the sum of squares blocking the effect of the covariates on the fixed factor (herbivory). The models were run alternating the order of the two explanatory variables (temperature and light), and then models were compared using the cumulative value of the standardized square root of the estimates of variation. The model with the highest value was then chosen. The interactions between the covariates and the fixed factor were included in the model for two reasons. Firstly, it provided a measure of the equality of the slopes of each covariate for each level of the fixed factor (shedding light on how efficiently the model would be able to block the effect of each covariate on the other factors). Secondly, in the case of temperature and light, their effect on macroalgal abundance was of interest for the study, and therefore the interpretation of their interaction with herbivory is relevant. Thus, the interactions between time and any of the other factors were included, although they are not discussed since the only reason to include them is to take into account temporal autocorrelation. When an interaction including any of the covariates was not significant ($p \geq 0.05$), it was removed from the model and the analysis was re-run following the parsimony principle. When the interaction between temperature or light and herbivory was significant, a separate Distance-based linear model (DistLim) analysis was run between temperature or light and each level of herbivory, to determine whether the relationship was consistent across levels. Consequently, we could determine which of the two explanatory factors, herbivory, temperature, or light, had a bigger influence on the macroalgal abundance. Finally, pair wise tests were run for each variable in order to compare their abundance in each treatment (uncaged plot, cage control, and cage).

The presence of a lag effect in macroalgal growth is expected because macroalgae often have rapid responses in growth at the start and end of a growing season. Thus, we have also analyzed the response of macroalgal cover to temperature and light values using a lag of 1 month.

Results

Effect of herbivory, light, and temperature on macroalgal abundance

Herbivory

Herbivory was a major driver of macroalgal abundance in two of the three species of macroalgae and algal turf (Fig. 1). Herbivory had a significant negative effect on the abundance of *Lobophora*, *Halimeda,* and turf ($p \leq 0.001$, see Table 1 for F statistics). The abundance of *Lobophora* was significantly ($p = 0.002$) higher in caged versus uncaged treatments (Table 2). Cover in the cage controls

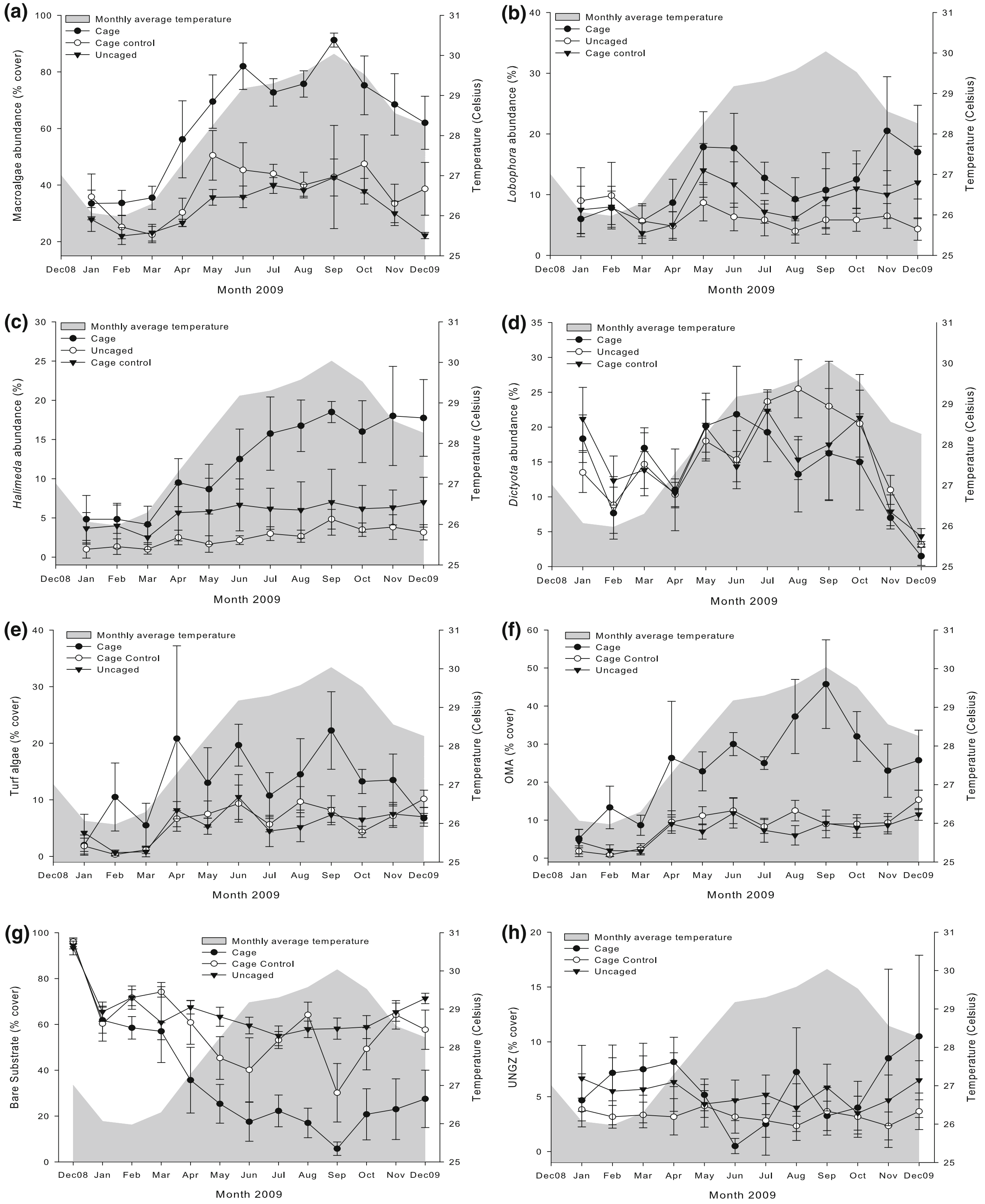

Fig. 1 Benthic category abundance by treatment from January to December of 2009: **a** overall macroalgae, **b** *Lobophora*, **c** *Halimeda,* **d** *Dictyota*, **e** algal turf, **f** other macroalgae (OMA), **g** bare substrate (BS), and **h** ungrazable (UNGZ). The *gray shadow* shows the temperature fluctuations, while the *three lines* show the change in abundance in each of the herbivory treatments throughout the year. *Error bars* depict confidence intervals (95%)

Table 1 Univariate analyses: significance of explanatory variables for the abundance of macroalgae at Glovers Reef Atoll

Fixed effect	DF	*Lob* (*p*)	Pseudo-*F*	*Dic* (*p*)	Pseudo-*F*	*Hal* (*p*)	Pseudo-*F*	Turf (*p*)	Pseudo-*F*
Quadrat	17	0.001**	14.356	0.06	1.6274	0.001**	50.469	0.001**	6.8753
Time (D)	1	0.003**	10.662	0.099	2.9894	0.001**	113.06	0.001**	28.949
Temperature (T)	*1*	*0.045**	*3.9839*	*0.001***	*46.535*	*0.001***	*16.637*	*0.001***	*22.332*
Solar radiation (L)	*1*	*0.657*	*0.2163*	*0.029**	*5.4137*	*0.185*	*1.7406*	*0.023**	*5.1593*
Herbivory (H)	*2*	*0.001***	*9.0583*	*0.748*	*0.28384*	*0.001***	*43.779*	*0.001***	*15.777*
D × T	1	0.039*	4.2308	0.001**	26.503	0.17	ns	ns	ns
D × H	2	0.001**	13.938	0.125	ns	0.001**	33.872	ns	ns
D × L	1	ns	ns	ns	ns	ns	ns	ns	ns
T × L	*1*	*0.006***	*8.6479*	*0.011**	*6.279*	*ns*	*ns*	*0.025**	*4.997*
T × H	*2*	*ns*	*ns*	*ns*	*ns*	*ns*	*ns*	***ns***	*ns*
L × H	*2*	*ns*	*ns*	*ns*	*ns*	*ns*	*ns*	***ns***	*ns*
D × T × H	2	ns	ns	ns	ns	ns	ns	ns	ns

Fixed effect	OMA (*p*)	Pseudo-*F*	BS (*p*)	Pseudo-*F*	UNGZ (*p*)	Pseudo-*F*
Quadrat	0.001**	13.998	0.001**	12.912	0.001**	12.206
Time (D)	0.001**	34.713	0.001**	39.082	0.58	0.34845
Temperature (T)	*0.011**	*6.0443*	*0.002***	*18.398*	***0.248***	*1.3134*
Solar radiation (L)	*0.267*	*1.1881*	*0.001***	*30.923*	*0.041**	*4.5679*
Herbivory (H)	*0.001**	*44.059*	*0.001***	*48.972*	*0.004**	*6.3606*
D × T	ns	ns	ns	ns	ns	ns
D × H	0.001*	15.672	0.001**	19.172	ns	ns
D × L	ns	ns	0.011*	6.1174	ns	ns
T × L	*ns*	*ns*	*ns*	*ns*	*ns*	*ns*
T × H	*0.01**	*4.5763*	*0.015**	*4.4626*	*ns*	*ns*
L × H	*ns*	*ns*	*ns*	*ns*	*ns*	*ns*
D × T × H	0.001**	7.411	ns	ns	ns	ns

Fixed factors are highlighted in italics, random factors were included in the analyses to take into account spatial (quadrat) and temporal (time) autocorrelation, and are in upright. Variables and interactions that gain/lost significance in the lagged analysis (compared to the non-lagged analysis) are shown and those discussed in the paper are highlighted in bold italicized. *, ** denote significant ($p < 0.05$) and very significant ($p < 0.01$) p values. *Lob*, *Lobophora variegata*; *Dic*, *Dictyota pulchella*; *Hal*, *Halimeda opuntia*; *OMA*, other macroalagae; *BS*, bare substrate, *UNGZ*, ungrazable

Table 2 PERMANOVA post hoc multiple comparison between the different herbivory treatments for the abundance of macroalgae at Long Caye Wall, Glovers Reef, for three macroalgal speces, algal turf, and a general class of other macroalgae (OMA)

Comparison	*Lobophora variegata*	*Dictyota pulchella*	*Halimeda opuntia*	*Turf*	*OMA*
Cage versus uncaged	0.002**	0.518	0.001**	0.001**	0.001**
Cage control versus uncaged	0.01*	0.89	0.001**	0.666	0.005**
Cage control versus cage	0.061^{+}	0.575	0.001**	0.001**	0.001**

$^{+}$ denote marginally significant ($p < 0.065$), * denote significant ($p < 0.05$), and ** denote very significant ($p < 0.01$) results

was intermediate between that of cages and uncaged plots (Fig. 1). The abundance of *Halimeda* was significantly different ($p \leq 0.001$) among all treatments (cages > cage controls > uncaged plots) (Table 2). This implies that the cage controls did not work effectively for *Lobophora* or *Halimeda*. Turf abundance was significantly different between caged and uncaged plots, as well as between caged and cage controls ($p \leq 0.001$). Turf abundance did not differ significantly between uncaged and cage controls, implying that the cage controls were effective for algal turf (Table 2). While herbivory affected the abundance of most algae, it did not have a significant effect on the abundance of *Dictyota* ($p = 0.748$). The apparent increase of *Dictyota* abundance in uncaged plots, compared to that in the cages, from July to November was found to be non-significant, even after replacing time as a categorical predictor (per month) and removing the effects of temperature and light from the model.

Light (solar insolation) and temperature

Dictyota was more abundant during the summer regardless of the treatment ($p \leq 0.001$, Table 1; Fig. 1). The interaction between temperature and solar insolation was significantly and positively associated with the abundance of *Dictyota*. The interaction between temperature and solar insolation was positively correlated, temperature being the most significant factor; in other words, the solar insolation effect strengthened at high temperature levels and vice versa. In addition to herbivory, the interaction between temperature and solar insolation was also important for the abundance of *Lobophora* ($p = 0.006$, $F = 8.6479$) and its abundance was lower during the summer (contrasting with *Dictyota*). The interaction was also positively correlated (the effect of one factor strengthening when the other increased); however, an increase in either temperature and/or solar insolation was negatively correlated with the abundance of *Lobophora*. The effect of the interaction between solar insolation and temperature on the abundance of *Halimeda* was not significant. Nevertheless, temperature was found to have a significant positive effect on the abundance of this calcified alga (Fig. 1), while herbivory acted to constrain its abundance. The abundance of turf varied negatively with herbivory ($p = 0.001$, $F = 15.777$). The interaction between temperature and solar insolation varied significantly with turf in a positive way ($p = 0.025$, $F = 4.997$, Fig. 1). In summary, the interaction between solar insolation and temperature was significant in influencing the abundance of two of our three studied macroalgal species and turf, while temperature was significant for all four benthic categories (three macroalgal species and turf). Also, when the interaction between solar insolation and temperature had a significant effect, temperature was more important (Table 1). Hence, while our findings for macroalgal and turf abundance show a correlation between herbivory and seasonal changes in temperature and solar insolation, this seasonal variation was better described by the seasonal change in water temperature than by solar insolation (Fig. 1).

In conclusion, the abundance of *Dictyota* varied with season while the abundance of *Lobophora, Halimeda,* and turf varied with herbivory throughout the year. However, when herbivory was absent, *Lobophora* and *Halimeda* were highly susceptible to seasonal changes. These relationships did not change when we conducted the lagged analysis (please see Electronic Supplementary Material (ESM) Tables 2, 3 and 4 for details on the lagged analysis).

Light, temperature, and herbivory in the study area

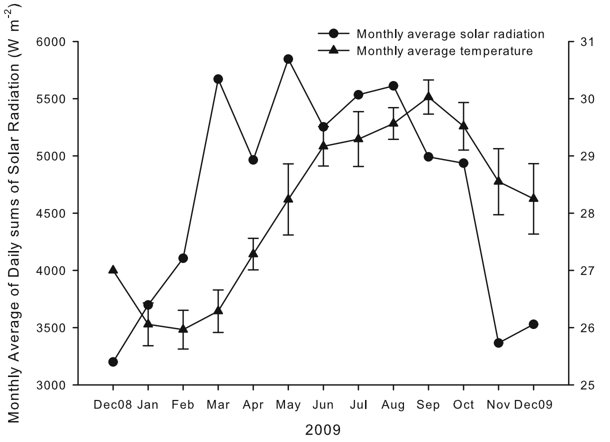

Fig. 2 Monthly average temperature (Celsius degrees) and monthly average of daily sums of solar insolation (W m^{-2}) at Glovers Reef from December 2008 to December 2009

Mean monthly seawater temperatures on the forereef ranged from 26.1°C in winter (January) to 30.0°C in summer (September) (Fig. 2). The highest temperature in 2009 was 31.8°C, while the lowest temperature was 24.2°C. Mean monthly solar insolation throughout 2009 varied following a seasonal pattern, from 5,846.01 W m^{-2} in the beginning of summer (May) to 3,365.4 W m^{-2} in the beginning of winter (November) (Fig. 2 of ESM). Light in cages was significantly attenuated by 18.06 ± 2.40% [size effect ± SE (%)] of ambient levels when comparing the total PAR inside and outside cages (one-tail paired t test, p value < 0.001).

No parrotfish or acanthurid grazing was observed inside cages, and neither the total grazing by parrotfish (TG) nor the standardized grazing of acanthurids were found to differ significantly between cage controls and uncaged plots (parrotfish PERMANOVA $p = 0.133$, Pseudo-$F = 1.9358$; acanthurids: $p = 0.715$, Pseudo-$F = 0.69119$).

Discussion

The abundance of *Dictyota* varied with season while the abundance of algal turf, *Lobophora,* and *Halimeda* mainly varied with herbivory. However, when herbivory was absent, *Lobophora* and *Halimeda* were susceptible to seasonal fluctuations in their abundance. For example, inside the cages, *Lobophora* dominated during the winter while *Dictyota* was the most abundant species during the summer.

Finding that herbivory had a significant negative influence on the abundance of *Halimeda* and *Lobophora* is consistent with previous studies (Hay 1981; Littler et al. 1983a; Mumby 2006; Diaz-Pulido et al. 2007; Fox and Bellwood 2008; Renken and Mumby 2009; Burkepile and Hay 2010). Our results provide additional insight into the effects of seasonality on these algae in Central America. *Halimeda* was significantly and positively influenced by water temperature, its abundance increasing with rising temperature, reaching a maximum in September. This is congruent with other studies (Ballesteros 1991; Lirman and Biber 2000) on macroalgal growth, which found that *Halimeda* growth was greater during the summer when water temperature was the highest.

Lobophora was negatively correlated with water temperature, being more abundant when the water was colder. The disparity in abundance of *Lobophora* between caged and uncaged plots was greatest in winter, implying that herbivory exerts its greatest limitation during this season. It is unlikely that the efficacy of herbivory increases in winter because reef fish are ectothermic and grazing rates tend to decline in winter (Floeter et al. 2005; Afeworki et al. 2011). Furthermore, the abundance of this species in the uncaged plots did not change among seasons, while it increased inside cages (Fig. 1 of ESM). Thus, our results imply that the "bloom" of *Lobophora* in winter most likely represents a relative increase in growth rate rather than a decrease in herbivory. Solar insolation was the lowest in winter; hence, an increase in growth cannot be explained by light. Again, an increase in growth rate would not be expected in winter without an increase in nutrients (Diaz-Pulido and Garzon-Ferreira 2002), but it is possible that the growth constitutes a relaxation of competition with *Dictyota* as the branching alga dies back.

While seasonal fluctuations in temperature and light appear to be important drivers of the dynamics of *Dictyota*, it was surprising to find no overall effect of herbivory. While species of the genus *Dictyota* have been previously reported in the low to intermediate range of herbivore consumption among other algal and sea grass species (Hay 1984; Paul and Hay 1986); *Dictyota* has also been described as a palatable macroalgal species in the region (Littler et al. 1983a, b, 2006; Burkepile and Hay 2010), and high consumption by parrotfish has been reported (Bruggemann et al. 1994; Mumby 2006; Fox and Bellwood 2007). Seasonality in this genus has been previously documented (Hoyt 1927; Bruggemann et al. 1994; Lirman and Biber 2000; Ateweberhan et al. 2005; Ateweberhan et al. 2006; Renken et al. 2010) but its overwhelming effect, relative to that of fish herbivory, has not previously been described. Herren et al. (2006) have shown that grazing activities might actually cause *thallus* fragmentation and exacerbate local blooms of the species. This might partially account for the apparent increase in *Dictyota* in uncaged plots, although this pattern requires further testing to verify whether it is significant or not.

In our experiment, *Dictyota* was the most common macrolga to colonize bare substratum and/or algal turf (85 ± 0.261% (mean ± SD). Hence, we hypothesize that *Dictyota* could take advantage of other competitor macroalgae being grazed upon to colonize the substratum made available by grazers. If herbivory is high, as in Long Caye Wall ($\sim$20 g m^{-2} from (Mumby 2006) and $\sim$42.62 bites m^{-2} m^{-1} from our video data), grazers may reduce the abundance of susceptible macroalgae (for example, *Lobophora* or *Halimeda*), while liberating space where *Dictyota* could settle. In our uncaged plots, *Dictyota* took over the available substratum overgrowing other benthic components during the summer, but during the winter, *Dictyota* was only able to colonize the available substratum and did not overgrow other benthic components, such as *Lobophora*. Lirman and Biber (2000) also found that the abundance of other algae, in their case *Halimeda* spp. and turf, was negatively correlated with the abundance of *Dictyota*. We did not look at the specific mechanisms by which *Dictyota* may outcompete other benthic components. The simplest explanation is that *Dictyota* can grow and colonize substratum faster than other benthic organisms, partly because it could take advantage of fragmentation (Herren et al. 2006) and partly because its branching growth form allows it to grow and proliferate on top of potential competitors (Beach et al. 2003). Further research is required to explore these hypotheses.

PAR was significantly lower (18%) in the cage and cage control treatments than the uncaged plots. A depletion of PAR would tend to deplete the scope for algal growth in cage treatments unless algae were light saturated in cages, in which case, differences in light would not be expected to influence growth. Nonetheless, if light was a limiting factor, then our estimates of the importance of herbivory are likely to be conservative because the disparity in algal growth between uncaged plots and cages might have been even larger had PAR been identical among treatments.

The absence of a significant difference in herbivory conflicts with the response of two algal species (*Lobophora* and *Halimeda*), which showed clear differences in abundance between uncaged and cage control treatments. We hypothesize that the discrepancy likely occurs because the grazing data were highly variable and that such variability may have masked the magnitude and detectability of a real difference among treatments. This seems plausible given that the probability of obtaining the PERMANOVA result by chance was moderately low at 0.13. Future studies will increase the duration of the video surveys (see ESM for PERMANOVA and SIMPER tables and MDS plot).

While temperature and light exhibit some inevitable correlation, their relationships with algal growth are sufficiently different that significant impacts were distinguished. A more mechanistic insight into the relative importance of temperature and light is planned using factorial experiments under laboratory conditions. We also point out that this study was conducted over a single year, and while the thermal and radiative trends were typical of previous years, it would be instructive to examine the robustness of these results over longer time periods, in part to highlight the impact of short-term differences in weather.

We studied the response of three morphologically different species of algae to variable herbivory and seasonal fluctuations of temperature and light. Each species differed in its response with one showing no clear response to herbivory. However, the abundance of all three species varied differently with physical conditions, which underscores the need to consider physical environment explicitly when comparing the results of experiments or monitoring data among studies. Our study site is located on the windward side of Glovers Reef and, being fetch unlimited, has high wave exposure and high levels of light penetration (Renken and Mumby 2009). Thus, our study was carried out in an exceptionally productive environment and this may influence our conclusions. For example, herbivory might have a stronger effect on *Dictyota* in areas where its growth rate is lower. In a previous study, we found that the growth rate of *Dictyota* was considerably higher on the windward forereef used here than in the less productive, leeward side of Glovers Reef (Renken et al. 2010). This might also explain why herbivory was found to have such a strong negative and linear effect on macroalgal cover (including *Dictyota*) across Bahamian reefs in the Exuma Cays (Mumby and Harborne 2010), which are likely to be less productive on account of lower temperatures and higher turbidity (Mumby pers. obs.). In short, it would be highly desirable to repeat this experiment throughout several years and under a gradient of productivity potential (Steneck and Dethier 1994) in order to generalize the relative importance of top-down and bottom-up controls of algal growth.

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