

Calcareous green algae standing stock in a tropical sedimentary coast

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Abstract Calcareous green algae (CGA) are important producers of carbonaceous sediments in coastal environments; they fix carbon producing CaCO_3 and organic compounds through photosynthesis contributing to the carbon budget of these ecosystems. In this study, the CGA standing stock (as dry weight) and its organic matter (OM) and inorganic carbon (CaCO_3) were estimated along the north coast of Yucatan at two sampling sites (Cerritos 1 and Cerritos 2), five times between summer 2014 and summer 2015. The standing stock annual average of three CGA species: *Halimeda incrassata*, *Halimeda opuntia*, and *Penicillus dumetosus* was 1214.8 g m^{-2} , of which 89% corresponded to CaCO_3 and 11% to OM. Significant seasonal differences were found ($p < 0.05$) with a maximum of 1335.5 g m^{-2} , CaCO_3 1178.1 g m^{-2} , OM 156.4 g m^{-2} in summer time in Cerritos 2. From the three species present, the largest standing stock was from *H. opuntia* (annual average 1142.9 g m^{-2}). Seasonal changes were significant correlated with changes in temperature (Kendall Tau_b correlation 0.161, $p < 0.0001$); which is consistent with several studies that demonstrate that calcification is regulated by temperature. The CGA annual average standing stock found in this study is above the values reported for the Caribbean side of the peninsula. In our study sites *H. opuntia* is dominant and its high values are consistent with

the “weedy” behavior reported in reef sites, making this species an important contribution of OM and CaCO_3 into the local system. This study provides the baseline for future estimation of carbonate production of CGA and the role of CGA in the carbon budget of Yucatan.

Keywords Green calcareous algae · Standing stock · Organic and inorganic carbon · Calcium carbonate, Yucatan Peninsula

Introduction

Carbonated sedimentary coasts are ecosystems characterized by the presence of large amounts of carbon in the form of calcium carbonate (CaCO_3) (Granier 2012) these coasts are inhabited by extensive seagrass beds that can store carbon in greater quantities than terrestrial forests (Chmura et al. 2003; Bouillon et al. 2008, Fourqurean et al. 2012). Calcareous green algae (CGA) which are a polyphyletic group of species belonging to Bryopsidales (*Halimeda*, *Penicillus*, *Rhipocephalus*, and *Udotea*) and Dasycladales (*Acetabularia*, *Cymopolia*, and *Neomeris*) are known to be important producers of CaCO_3 through biomineralization in shallow tropical waters (Wilkinson 1979; Granier 2012); and deep waters (Littler et al. 1986).

The process of calcification results in a deposition of calcium carbonate that will be stored as sediments for long periods acting as a rich carbonate source and making significant contributions in the form of karstic sedimentary habitats (Hill et al. 2015). *Halimeda* contributes to mass of carbonate sediment in many reefs (Hillis-Colinvaux 1980; Beach et al. 2003; van Tussenbroek and van Dijk 2007; Mayakun et al. 2014), and it is estimated that *Halimeda* species have contributed to 8% of the total world production of carbonates (Hillis 1997).

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Local production of CaCO_3 may vary depending on species dominance and geographic regions, for example, annual production of *Halimeda* in Puerto Morelos, Quintana Roo, México, is reported as $815 \text{ g CaCO}_3 \text{ m}^{-2} \text{ y}^{-1}$ (van Tussenbroek and van Dijk 2007), while in Panama production may reach $2323 \text{ g CaCO}_3 \text{ m}^{-2} \text{ y}^{-1}$, (Freile and Hillis 1997). Studies in South Florida have a range of values depending on the locality $23 \text{ g CaCO}_3 \text{ m}^{-2} \text{ y}^{-1}$ on a backreef in the Florida Keys (Bosence 1989), compared with $1000 \text{ g CaCO}_3 \text{ m}^{-2} \text{ y}^{-1}$ in the Marquesas Keys (Hudson 1985) or $225 \text{ g CaCO}_3 \text{ m}^{-2} \text{ y}^{-1}$ 200 km from Marquesas Keys (Davis and Fourqurean 2001). Therefore, calcareous green macroalgae can create new sediments that can affect or modify directly or indirectly the distribution and abundance of other species (Granier 2012); in addition, it has been demonstrated that calcareous green algae facilitate the arrival and establishment of seagrass in sedimentary soils by increasing nutrient availability as they decompose (Williams 1990). These ecological roles place calcareous green algae in the category of engineering species (Jones et al. 1994, 1997; van der Heide et al. 2012), and therefore quantifying their sediment contribution is relevant for the understanding of the system.

Yucatan has 378 km of coastline with large seagrass and CGA meadows that provide important services to the region (Herrera-Silveira et al. 2010). However, little is known of their actual CaCO_3 , and organic matter (OM) contribution and seasonal dynamics. Considering the significant contribution of macroalgal calcification to global carbonate budgets, and the importance of these sediments to coastal seagrass ecosystems, we quantified the standing stock of CGA of the genera *Halimeda* and *Penicillus* and the proportion of sediments of the northern coast of the Yucatan Peninsula. Furthermore, we investigated abiotic factors potentially regulating their contribution at two sites. The aim of this study was to create a baseline of the standing stock and CaCO_3 content of CGA across a gradient of environmental regimes, and provide a perspective of the potential role of these algae in the calcium carbonate stocks of the region.

Materials and methods

Study area

This study was conducted near “Isla Cerritos” ($21^\circ 34' 02'' \text{ N}$, $88^\circ 15' 52'' \text{ W}$), a 10.8 km long and 2.8 km wide island, located 5.5 km east of San Felipe’s port, in the eastern region of the coastline of Yucatan state in southeastern Mexico (Aguilar et al. 2012) (Fig. 1). The large extension of the platform of the Yucatan Peninsula, has a slight slope, producing shallow areas (average 150 cm deep) with sand, silt, clay, and limestone bottoms (Robledo and Freile-Pelegrin 1998).

Methods

Two sampling sites were selected: Cerritos 1 ($21^\circ 34' 30.52'' \text{ N}$, $88^\circ 17' 37.14'' \text{ W}$), which is an area composed of seagrass and green calcareous algae such as *Halimeda* and *Penicillus*, with an average depth of 60 cm and silty-sandy bottom, and Cerritos 2 ($21^\circ 33' 30.15'' \text{ N}$, $88^\circ 17' 24.9'' \text{ W}$) which is an area dominated by the green macroalgae *Avrainvillea*, along with calcareous green algae such as *Halimeda*, *Penicillus*, *Udotea* and *Rhizocephalus*, the average depth is 150 cm with sandy and muddy bottom (Fig. 1).

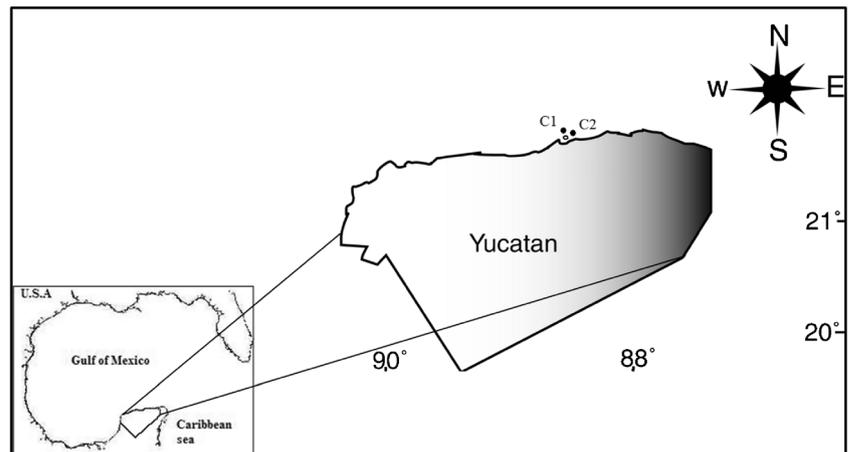
Each site was visited five times (June, September, December, March, and June) between summer 2014 and summer 2015. Salinity, pH, and dissolved oxygen were recorded in situ using a handheld multiparameter YSI 556 (YSI Integrated Systems and Services). Temperature and irradiance were measured continuously throughout the year with a data logger (ua-002-64) HOBO pendant ONSET (Onset Computer Corporation); sensors were clean and changed each sampling season to avoid fouling.

The abundances of seagrass and algal taxa were recorded using a modified Braun-Blanquet method (Fourqurean and Rutten 2003). At each site, the abundance of taxa was recorded as percentage cover in 10 randomly located 0.25 m^2 quadrats along a 100 m permanent transect. Excel (Microsoft) random number generator was used to select at what distance within the 100 m each quadrat should be located. This method was selected following the seagrass and algal monitoring methods used for similar ecosystems (Fourqurean et al. 2002, Fourqurean and Rutten 2003; Collado-Vides et al. 2005). The taxonomic determination was done for algal and seagrass species present to the lowest taxonomic level. The percentage of each taxon observed in each quadrat was assigned a score between 0 and 5. A score of 1 indicates individuals covering <5%, 2 indicates 5–25% cover, 3 indicates 25–50% cover, 4 indicates 50–75% cover, and 5 indicates 75–100% cover.

Total standing stock, equivalent to total dry weight including inorganic and organic matter, was estimated by destructively collecting all *Halimeda* spp. and *Penicillus* spp. individuals present in three randomly selected 0.25 m^2 quadrats; collected material was labeled and stored in plastic bags and transported in a cooler to the laboratory at the Department of Marine Biology at the Autonomous University of Yucatan.

Samples were separated, cleaned to remove organic matter and epibionts and identified to the species level following Littler and Littler (2000), and Dawes and Mathieson (2008). The samples were dried in an oven at 70° C for 48 h to constant weight to obtain the total dry weight; samples were then ignited at 500° C for 4 h, following the procedure for determining the CaCO_3 content of the sediments (Davis and Fourqurean 2001; Barry et al. 2013).

Fig. 1 Sampling sites in Isla Cerritos, San Felipe, Yucatán sampling sites: Cerritos 1 (C1) and Cerritos 2 (C2)



Ash was weighed and recorded as a proxy for CaCO_3 , and organic matter (OM) was calculated by subtracting the ash weight from the total dry weight; therefore, OM is what was lost in the ignition process. To calculate the carbon contribution of the algae to the ecosystem, the following calculations were applied. Carbon is 12% of the molecular weight of CaCO_3 ; the inorganic carbon of the collected algae was estimated by multiplying the CaCO_3 weight (ash) by 0.12, this calculation presumes that only CaCO_3 composes the ash. To estimate the organic carbon content from OM, we used the generalization proposed by Fourqurean et al. (2014); the authors suggest that approximately 4% of the OM in marine plants is carbon. The organic carbon produced in the study sites was estimated by multiplying the OM (Total Dry Weight – ash) by 0.04.

Analysis of variance (ANOVA), and Tukey's posthoc test were applied to environmental factors, percentage of cover, total dry weight, inorganic, and organic carbon across species, to compare their values across sites and season; homogeneity of variance was estimated with the Levene's test. Kruskal-Wallis non-parametric test was applied when the data had no homogeneity of variance, even after the transformation. Kendall Tau b bivariate correlations were applied to detect interactions between standing stock as total dry weight, and abundance as a percentage of the cover of *Halimeda* and *Pencililus* with environmental factors, and with other SAV species. Statistical analyzes were conducted using SPSS version 23.

Results

General overview

Three species of calcareous green algae were found in the study sites: *Halimeda incrassata* (J. Ellis) J. V. Lamouroux, *Halimeda opuntia* (Linnaeus) J. V. Lamouroux, and *Penicillus dumetosus* (J. V. Lamouroux) Blainville.

The average annual standing stock of all CGA species combined was 1214.8 g m^{-2} , of which 89% (1085.9 g m^{-2}) corresponded to CaCO_3 and 11% (128.5 g m^{-2}) to OM. In average, CaCO_3 at both sites ranged between 88 and 91% of the total mass. Following the molecular composition and weight of CaCO_3 , from the 1085.9 g m^{-2} of CaCO_3 , 130 g m^{-2} are estimated to be inorganic carbon; and following the 4% estimated carbon content in marine plants, from the 128.5 g m^{-2} OM, 0.5 g m^{-2} are estimated to be organic carbon.

From all species, the standing stock of *H. opuntia*, with an annual average of 1142.9 g m^{-2} , was significantly higher (Kruskal Wallis $p < 0.0001$) than the standing stock of the other two species: *H. incrassata* (34.03 g m^{-2}) and *P. dumetosus* (37.83 g m^{-2}) (Fig. 2).

Of the two sites studied, Cerritos 2, with an overall average standing stock of 1335.56 g m^{-2} was higher than Cerritos 1, which had an overall average standing stock of 1094.1 g m^{-2} .

Comparing species standing stock by seasons and sites

Species standing stock varied significantly between species and across season. *H. opuntia* standing stock was up to 96% of the total average for all three species. Significant seasonal variability was found for all three species, *H. opuntia* ($F = 6.2$, $p = 0.000$) (Fig. 3); *H. incrassata* (Kruskal Wallis $p < 0.0001$) and *P. dumetosus* (Kruskal Wallis $p = 0.002$). However, the season with the highest values differs between sites; Cerritos 1 maximum standing stock (2125.6 g m^{-2}) was found in summer 2015, while Cerritos 2 maximum (1861.3 g m^{-2}) was recorded in fall. In contrast, the lowest standing stock found in Cerritos 1 was in the winter (287.9 g m^{-2}) (Fig. 3). The lowest value for Cerritos 2 was in the spring (774.1 g m^{-2}) (Fig. 4).

CaCO_3 : OM ratio varied between species, sampling seasons and sites. The CaCO_3 : OM ratio was significantly different between species (Kruskal-Wallis $p < 0.0001$) with

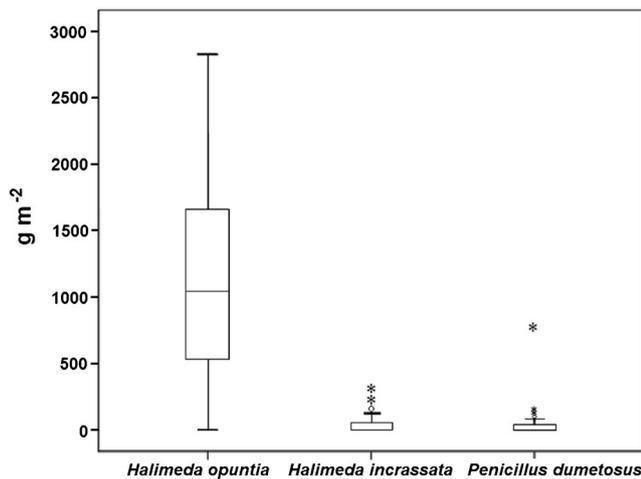


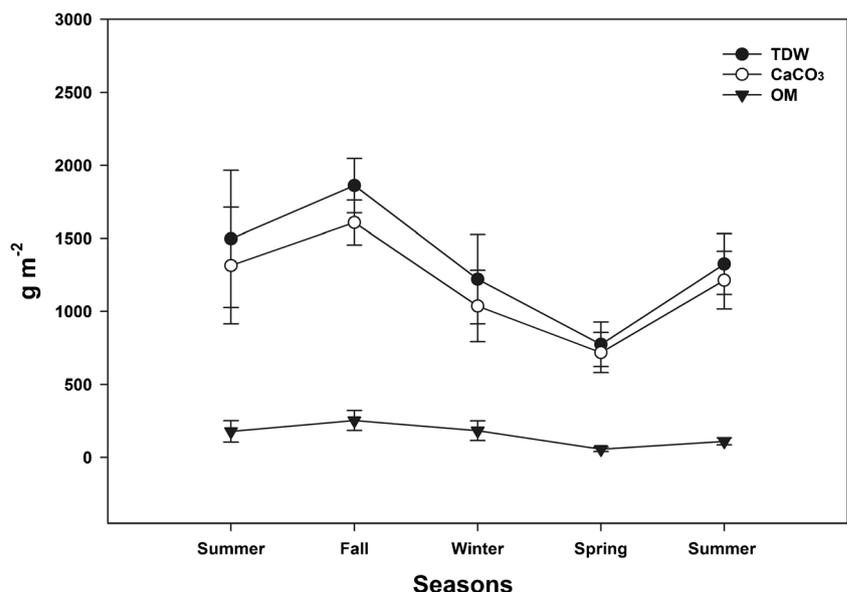
Fig. 2 Box plot of species overall standing stock average by taxa. The horizontal bar within the box represents the median, the upper and lower boundaries of the box represent the lower and upper quartile, and the whiskers represent the extreme values; circles are the outliers and asterisk the maximum extreme case

H. opuntia. CaCO₃: OM ratio average of 90:10, while *H. incrassata* 80:20 and *P. dumetosus* 61:39.

CaCO₃: OM in *H. opuntia*, the species with the highest overall standing stock, varied across seasons (Kruskall Wallis $p < 0.003$) with the extremes, showing a difference of 17% between the minimum (79.96% CaCO₃) and maximum (96.89% CaCO₃) values recorded.

In Cerritos 1, *H. opuntia* had the highest standing stock in summer 2014 (1591.81 g m⁻²) and 2015 (1921.6 g m⁻²) with 89% of CaCO₃ and 11% of OM. *H. incrassata*, was not found in summer 2014, however, its mass increased from September 2014 to a maximum value (157.5 g m⁻²) in summer 2015,

Fig. 3 Total dry weight, CaCO₃, and OM by month and standard error in Cerritos 1



with no signs of decrease in winter. The CaCO₃: OM increased from 67% in fall 2014 to 94% in summer 2015. *P. dumetosus* was not found in along the year, until spring 2015 (67% CaCO₃) reaching the highest mass (46.5 g m⁻²) in summer with lower values of CaCO₃ (64%) (Fig. 5).

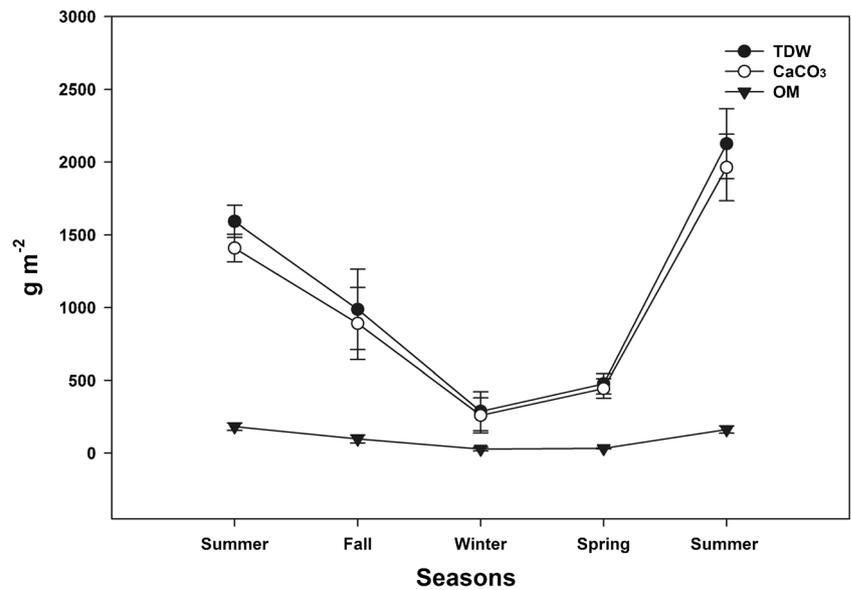
In Cerritos 2, *H. opuntia* had the highest standing stock in fall (1750.5 g m⁻²) but its CaCO₃: OM decreased through winter, while *H. incrassata* standing stock increased from summer (26 g m⁻²) to fall (34.3 g m⁻²) and the CaCO₃:OM increase from 72% in summer to 78% in fall, and a clear decrease in winter 2015, with the lowest CaCO₃:OM of 66%. *Penicillus dumetosus* highest standing stock (173.5 g m⁻²) was found in summer 2014 with the lowest values in summer 2015 (28.3 g m⁻²), similarly CaCO₃:OM was higher in summer 2014 (81%) than summer 2015 (56%) (Fig. 6).

Composition and abundance of submersed aquatic vegetation

A total of 17 algae taxa and 3 species of seagrass was recorded in the study sites, *Halimeda incrassata*, *Halimeda opuntia*, *Penicillus dumetosus*, *Penicillus capitatus* Lamarck, *Rhizocephalus phoenix* (J. Ellis and Solander) Kützing, *Canistrocarpus cervicornis* (Kützing) De Paula and De Clerck, *Caulerpa ashmeadi* Harvey, *Caulerpa prolifera* (Forsskal) J. V. Lamouroux, *Caulerpa racemosa* (Forsskal) J. Agardh, *Acetabularia crenulata* J. V. Lamouroux, *Avrainvillea* spp., *Ceramium* sp., *Hypnea* sp., *Jania* sp., *Laurencia* sp., *Udotea* sp., *Ulva* sp., and three seagrass species: *Halodule wrightii* Ascherson, *Syringodium filiforme* Kützing, and *Thalassia testudinum* Banks ex König.

Not all the species were found at both sites, Cerritos 1, had 12 algal taxa and three seagrasses; this site was dominated by

Fig. 4 Total dry weight, CaCO₃, and OM by month and standard error in Cerritos 2



H. opuntia (25.82% s.e. 1.9), followed by *T. testudinum* (12.65%, s.e. 1.87) and *S. filiforme* (19.92%, s.e. 3.03) while Cerritos 2, had 16 algal taxa and two seagrasses, this site was dominated by *Avrainvillea* spp. (21.78%, s.e. 2.13), followed by *H. opuntia* (18.08%, s.e. 2.12), *T. testudinum* (11.96%, s.e. 1.95), and *S. filiforme* (11.32%, s.e. 1.08).

In Cerritos 1, all *Halimeda* species and *T. testudinum* increased their abundance during the year opposite to *S. filiforme* that had its peak in summer 2014 and decrease through the rest of the study. Meanwhile Cerritos 2, showed a different pattern, *Halimeda* spp. and *Penicillus* spp. increased their abundance from summer 2014 to summer 2015 with no signs of decrease during winter, while *Avrainvillea* spp., had its maximum in the fall and *T. testudinum* and *S. filiforme* had

the highest abundance in summer and fall 2014 decreasing through spring and summer. (Fig. 7).

Halimeda opuntia, the most abundant species in Cerritos 1, had a significant positive correlation with *T. testudinum* (0.309, $p < 0.006$); while *S. filiforme* had a significant negative correlation with *H. incrassata*, ($-0.609, p < 0.001$) and *P. dumetosus* ($-0.475, p < 0.001$), the two species with lower abundance. In contrast, in Cerritos 2, the dominant species was *Avrainvillea* and had a significant negative correlation with *H. opuntia* ($-0.453, p < 0.0001$), *H. incrassata* ($-0.514, p < 0.0001$), and *P. dumetosus* ($-0.216 p < 0.024$), but significant positive correlation with *S. filiforme* (0.243, $p < 0.0001$). *H. opuntia*, had a significant negative correlation with *T. testudinum* ($-0.576, p < 0.0001$).

Fig. 5 Percentage of CaCO₃ and OM (CaCO₃: OM) of H1: *Halimeda opuntia*, H2: *Halimeda incrassata*, and P: *Penicillus dumetosus* in Cerritos1 by seasons

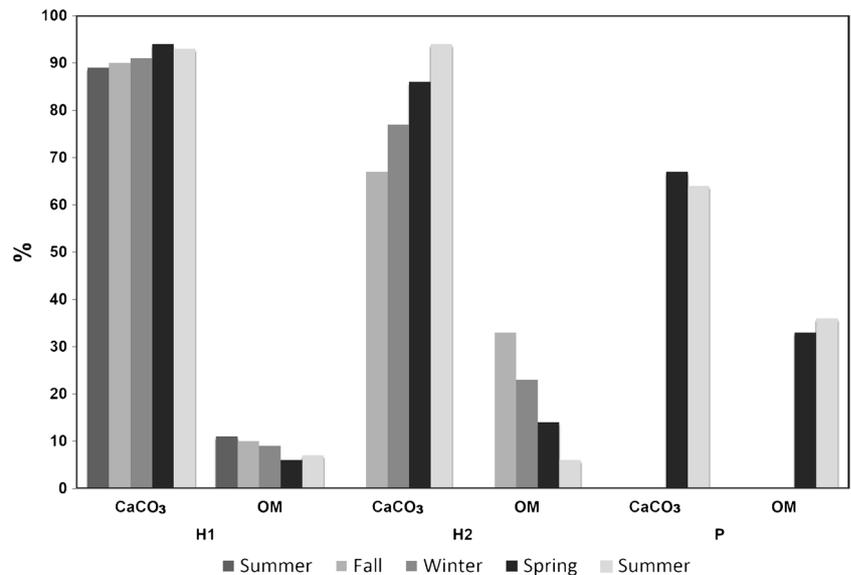
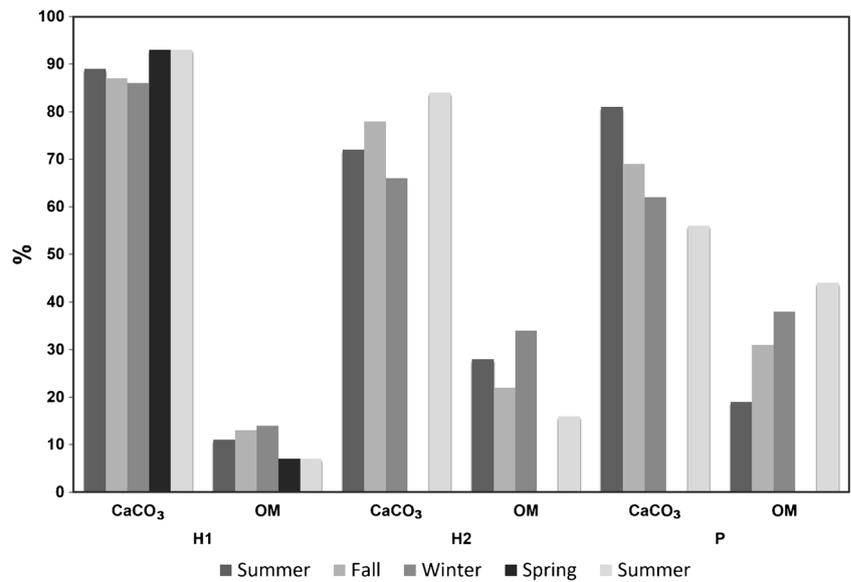


Fig. 6 Percentage of CaCO₃ and OM (CaCO₃: OM) of H1: *Halimeda opuntia*, H2: *Halimeda incrassata*, and P: *Penicillus dumetosus* in Cerritos 2 by seasons



Environmental parameters

Light and temperature had similar values across sites; furthermore, the temperature was higher during summers and fall. The temperature was significantly different between seasons (Kruskal Wallis $p < 0.0001$), but not between sites (Kruskal Wallis $p < 0.0001$). The annual average temperature was 27 °C in the area. The highest recorded temperature (37.8 °C) was in summer 2014 and the lowest (20.6 °C) in winter (Table 1). The light was significantly different across seasons (Kruskal Wallis, $p < 0.0001$) but not between sites (Kruskal Wallis $p < 0.0001$). The high light intensity in average (755.2 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$) was in the spring and the lowest in winter (179.4 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$) (Table.1).

Interactions between standing stock and light and temperature were significant only for temperature, (Kendall Tau_b correlation 0.161 $p < 0.0001$). Higher temperatures were correlated with higher standing stock. CaCO₃ stocks were significant correlated with temperature (Kendall Tau_b correlation 0.161 $p < 0.0001$, Fig. 8).

Discussion

The annual stock of CaCO₃ of *Halimeda* and *Penicillus* species in the study sites was 1085.8 g m^{-2} , from which the total carbon content is 130 g m^{-2} representing the 10.7% of the stock in the study area; at this moment, we do not have

Fig. 7 Percentage of cover by season of the most abundant species in Cerritos 1 and Cerritos 2. *H.inc*: *Halimeda incrassata*, *H.opun*: *Halimeda opuntia*, *Pdum*: *Penicillus dumetosus*, *Avran*: *Avrainvillea*, *Thal*: *Thalassia testudinum*, *Syr*: *Syngodium filiforme*, and *Hal*: *Halodule wrightii*

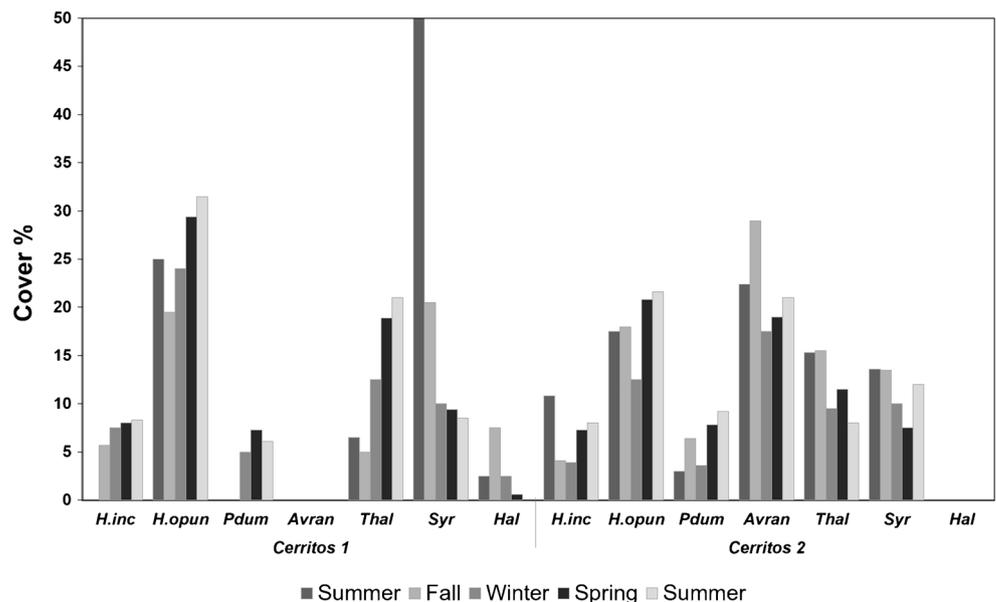


Table 1 Environmental parameters recorded in the collecting sites by season and by site

	Season	Temperature (°C)				Light ($\mu\text{mol photons m}^{-2} \text{s}^{-1}$)			
		Aver	Max	Min	SD	Aver	Max	Min	SD
Cerritos 2	Summer 2014	30.1	32.2	28.2	1.05	234	561	95.7	129
	Fall	27.1	31.9	21.3	2.53	435	2551	217	477
	Winter	24.3	27.5	20.6	1.56	222	867	98.9	159
	Spring	26.9	30.8	22.3	1.73	914	3878	510	681
	Summer 2015	29.4	32.6	26.8	1.28	298	1633	95.7	328
Cerritos 1	Summer 2014	28.8	37.8	24.4	2.15	187	791	95.7	150
	Fall	28.6	34.1	24.9	2.26	355	1276	159	245
	Winter	24.3	26.9	21.6	1.37	137	242	102	36.5
	Spring	27	33.5	22.7	1.92	597	1072	383	208
	Summer 2015	29.2	32.7	25.5	1.53	281	689	134	160

Aver average, Max maximum value, Min minimum value, SD standard deviation

production data, but it is a valuable information about how much carbon the green calcareous algae can provide to the carbonate budget of the study site.

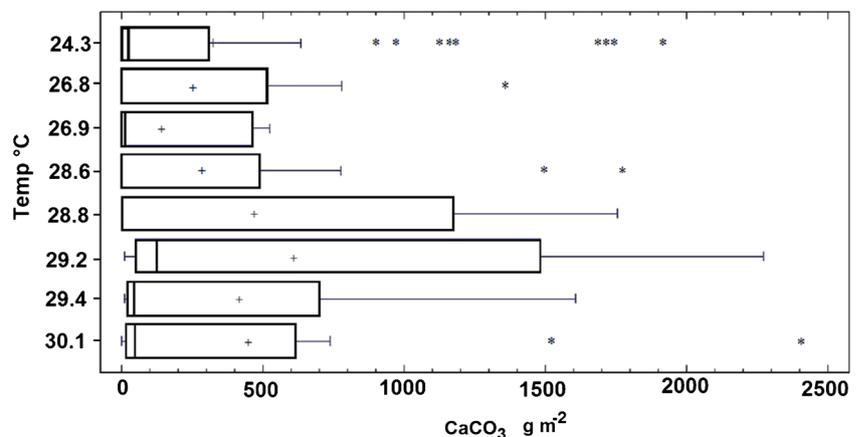
The amount of CaCO_3 in this study was higher than the values reported in the Mexican Caribbean, $815 \text{ g m}^{-2} \text{CaCO}_3$, (van Tussenbroek and van Dijk 2007), and lower than in Panama, $2323 \text{ g m}^{-2} \text{CaCO}_3$ (Freile and Hillis 1997). Global variability of CaCO_3 stocks has been related to species specific calcification rates (Stark et al. 1969); and can be attributed to either taxonomic distinction (Ries 2005, 2009; Kroeker et al. 2010), or the interactive effects of other environmental parameters such as temperature, irradiance, water flow, and/or nutrient regimes (Harborne et al. 2006; Campbell et al. 2015).

While in the Mexican Caribbean, the main species contributing to CaCO_3 stocks is *H. incrassata* (van Tussenbroek and van Dijk 2007); in our study, *H. opuntia* was the dominant species. Differences in standing stock between species found in this study are consistent with the findings of Payri (1988) that demonstrate that *H. opuntia* is nine times more productive than *H. incrassata*. *Halimeda opuntia* is a species from the Indo-Pacific dispersed to the Atlantic after the closure of the Panama strait (Kooistra et al. 2002), and its high mass is

consistent with the “weedy” behavior reported in reef sites having a rapid growth rate compared with other *Halimeda* species (Stark et al. 1969), similar to introduced successful species. In contrast standing stock of *Penicillus* was comparatively smaller and CO_3 : OM ratios lower than *Halimeda* (Böhm 1972, 1973; Liebezeit and Dawson 1982). It is possible to conclude that standing stock and CO_3 : OM is species dependent, with *H. opuntia*, a possible introduced species, having the larger CaCO_3 stocks.

Standing stock and CaCO_3 :OM ratio variability was found to be correlated with temperature, a relationships explained by the fact that growth and calcification are related to photosynthesis, which is light, and temperature dependent (Borowitzka and Larkum 1976), in addition the highest CaCO_3 :OM (94% CaCO_3) was found in warmer months, showing that CaCO_3 stocks are strongly related with temperature (Stark et al. 1969; Borowitzka and Larkum 1976; Littler et al. 1983; Campbell et al. 2015). Interaction of temperature and seagrasses and algal growth are widespread demonstrating that temperature is a major factor affecting seasonal variability of these organisms (Bulthuis 1987; Kun-Seop and Dunton 1996; Kun-Seop et al. 2007).

Fig. 8 Box plot of CaCO_3 in relation with the temperature. The upper and lower boundaries of the box represent the lower and upper quartile, and the whiskers represent the extreme values; and the asterisk the maximum extreme case



Difference across sites might be explained as a function of subaquatic vegetation characteristics such as composition of seagrass and algae and the physical conditions such as depth and wave current.

Cerritos 1, the site with the lowest standing stock, was dominated by *H. opuntia*, intermixed with seagrasses *T. testudinum*, and *S. filiforme*; and Cerritos 2, the site with the highest standing stock was dominated by the green algae *Avrainvillea* followed by *H. opuntia* and seagrasses. The correlation between *Avrainvillea* and *H. opuntia* need to be explored and test for competition for nutrients as a possible mechanism responsible for this negative interaction (Williams 1990), same possible interaction might happen with *T. testudinum* and *H. opuntia* in Cerritos1, for example the negative effects found by Davis and Fourqurean (2001) of *T. testudinum* on *H. incrassata* was the result of competition for nutrients. However, in some places *T. testudinum* beds often support a dense understory of the calcareous alga *Halimeda*, for example in Puerto Rico, *T. testudinum* associated with *Halimeda* mounds was denser with higher biomass and productivity, than meadows lacking *Halimeda* (Duffy 2006). In addition, the interaction of *H. opuntia* with seagrasses could be mediated by the competition of *S. filiforme* with *T. testudinum*; it is known that meadows of *S. filiforme* are replaced by *T. testudinum* (Gallegos et al. 1994), eventually affecting CGA dominance. It is possible that the differences found are related with the nutrient availability, determining the composition of species in seagrass beds (Fourqurean et al. 2003), resulting in a differential standing stock of CGA.

Further *Avrainvillea* spp. prefer shallow open areas with relatively low current and wave energy (Birch and Birch 1984; Kirkman 1985, Littler and Littler 1999, Littler et al. 2004), similar conditions are found, in Cerritos 2 where species of this genus are dominant above seagrasses and *H. opuntia*. These conditions might result in a disadvantage for seagrass (Binning et al. 2007).

The standing stock and contribution of CGA to carbon budgets and sand production in coastal waters are species dependent, based on species specific calcification characteristics and temperature. In turn, the dominance of species will depend on local conditions, and subaquatic vegetation assemblages and their spatial and temporal dynamics. Particularly, the 378 km of coastline in Yucatan with a diverse range of environments (mangroves, seagrass beds, and coral reefs), where *Halimeda* is a major group of species in the region within shallow waters, is expected to be an important player in the carbon budget of the region. The findings of this study demonstrate that not only species evaluations are necessary but the type of vegetation will determine their local standing stock (Payri 1988; Duarte et al. 2005), therefore generalization will require careful evaluations of the environmental context of each study.

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