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Modeling temporal variations of *Gracilaria* Greville and *Hypnea* J.V. Lamouroux (Rhodophyta) assemblages on a midlittoral reef platform at Piedade Beach, Pernambuco State, Brazil

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ABSTRACT – (Modeling temporal variations of *Gracilaria* Greville and *Hypnea* J.V. Lamouroux (Rhodophyta) assemblages on a midlittoral reef platform at Piedade Beach, Pernambuco State, Brazil). The diversity of algal banks composed of species out the genera *Gracilaria* Greville and *Hypnea* J.V. Lamouroux have been impacted by commercial exploitation and coastal eutrophication. The present study sought to construct dynamic models based on algal physiology to simulate seasonal variations in the biomasses of *Gracilaria* and *Hypnea* an intertidal reef at Piedade Beach in Jaboatão dos Guararapes, Pernambuco State, Brazil. Five 20 × 20 cm plots in a reef pool on a midlittoral reef platform were randomly sampled during April, June, August, October, and December/2009 and in January and March/2010. Water temperature, pH, irradiance, oxygen and salinity levels as well as the concentrations of ammonia, nitrate and phosphate were measured at the sampling site. Forcing functions were employed in the model to represent abiotic factors, and algal decay was simulated with a dispersal function. Algal growth was modeled using a logistic function and was found to be sensitive to temperature and salinity. Maximum absorption rates of ammonia and phosphate were higher in *Hypnea* than in *Gracilaria,* indicating that the former takes up nutrients more efficiently at higher concentrations. *Gracilaria* biomass peaked at approximately 120 g (dry weight m^{-2}) in March/2010 and was significantly lower in August/2009; *Hypnea* biomasses, on the other hand, did not show any significant variations among the different months, indicating that resource competition may influence the productivity of these algae.

Keywords - algal biomass, eutrophication, sandstone reefs, trophic models

INTRODUCTION

The red algae *Gracilaria* Greville and *Hypnea* J.V. Lamouroux are widely distributed along the Brazilian coast, but their stocks have been reduced in some coastal areas due to industrial harvesting for agar and carrageenan production respectively (Oliveira Filho 1998, Miranda 2010). Among the dominant algae at the sampling site on Piedade Reef were *Gracilaria caudata* J. Agardh and *Hypnea musciformis* (Wulfen) J.V. Lamouroux, which could be found directly attached to the reef substrate or living as epiphytes (Guimaraens et al. 1996). Due to the economic importance of *Hypnea musciformis* and certain species of the *Gracilaria* genus, several laboratory and field cultivation studies have been undertaken to examine the effects of abiotic factors (salinity, nutrient concentrations, temperature, and irradiance), and the interactions between them, on algal growth (Yokoya & Oliveira 1993, Marinho-Soriano et al. 2002, Bravin & Yoneshigue-Valentin 2002, Miranda 2010).

The sandstone reefs along the southern coast of Pernambuco State extend seaward, forming marine ridges parallel to the coast that are composed mainly of quartz and bioclasts that become partially exposed during low tides. These reefs serve as attachment substrates for benthic algae, harbor diverse faunas, and are hotspots for biological interactions with the environment (Pereira et al. 2002, Simões et al. 2009). Mansilla & Pereira (2001) observed significant reductions in red algae biomasses and lower algal diversity during the rainy season on a reef off the southern coast of Pernambuco state that were found to be related to rainfall, temperature, and salinity. Abiotic factors (such as temperature, nutrient concentrations and salinity) together with biological interactions have been shown to control the spatial-temporal distributions of benthic algae (Sauer-Machado et al. 1992, Guimaraens & Coutinho 1996), which in turn affects macroalgal abundance and hydrodynamic transport (Biber et al. 2004). The Piedade reefs have been impacted by human use, organic pollution, and industrial wastes (Pereira et al. 2002), so that studies on algal populations in this

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environment could aid in establishing policies designed to preserve and manage reef ecosystems.

Nonlinear models that simulate variations in biomass of single species have been developed (Guimaraens et al. 2005, 2008) wich can describe the trophic structures of reef environments that include algae as primary producers (McClanahan 1995). Models of tropical benthic communities still require greater refinement, however, especially in terms of parameters such as recruitment and interspecific competition (Biber et al. 2004) between algae and invertebrates (Vinueza et al. 2006, Guimaraens et al. 2011a). The model described here considers physiological processes that mimic competitive interactions (Fong et al. 1994, Guimaraens et al. 1996, 2005) and their effects on temporal variations of *Gracilaria* and *Hypnea* assemblages through the use of different nutrient absorption curves (Fong et al. 1994, Biber et al. 2004) and different photosynthesis rates for these genera. The present study therefore sought to evaluate the seasonal variations of both environmental factors and *Gracilaria* and *Hypnea* assemblages on the reef platforms of Piedade Beach (Pernambuco State) and use ecological modeling to test the hypothesis that model parameters (representing abiotic factors) affect the temporal abundances of these algae to different degrees.

MATERIAL AND METHODS

Study Area

Piedade Beach is approximately 9.8 km long and is located within the Jaboatão dos Guararapes District on the southern coast of Pernambuco State, Brazil (08°11’08” S and 34°55’04” W-08°11’03” S and 34°55’03” W). The coastline there is composed of a coastal plain formed by fluvial and marine deposits, and originally included a strip of sand dune vegetation that has now been built over (Pereira et al. 2002). The regional climate is tropical, with an average annual temperature of 26 °C and a distinct rainfall pattern composed of a dry season (September-February) with rainfall below 100 mm, and a rainy season (March-August) with rainfall above 100 mm (Cavalcanti & Kempf 1967-69). Piedade Beach is also impacted by the Jaboatão River that delivers upstream pollution from industrial sites and urban areas (Pereira et al. 2002), and by direct physical damage due to trampling (tourism/leisure).

Field and Laboratory Work

Algae samples were collected randomly from five 20 × 20 cm plots in a reef pool in the midlittoral zone during low tide periods in April, June, August, October, and December/2009 and in January and March/2010. The collected algae were removed to the Phycology Laboratory of the Federal Rural University of Pernambuco where they were sorted and identified. Algal dry weights were obtained by drying each sample (in foil bags) in an oven at 60 °C for 72 hours, and then weighing them on an analytical balance. Water temperatures and irradiance levels were measured *in situ* near the sampling plots. Water samples were collected on a monthly basis near the outer edge of the reef (where the ocean water penetrates into the reef platform) to determine the water temperature, pH, and oxygen and salinity levels, as well as the concentrations of ammonia, nitrate, and phosphate. The temperature, salinity, irradiance and nutrients values were incorporated into the biomass simulation model as empirical forcing functions.

Water samples were transferred to 300 mL plastic bottles and frozen for transport to the Chemistry Laboratory of the Oceanography Department at the Federal University of Pernambuco. The techniques used for determining salinity and nutrient levels were based on the methods described by Strickland & Parsons (1972) and Grasshoff et al. (1983): N-ammonia nitrogen (hereafter referred to as N-ammonia; NH_3-+NH_4-N), N-nitrate (NO_3-N), and P-phosphate (PO_4-P).

Statistical Analyses

Principal Component Analyses were performed on the biomass measurements and the salinity, temperature, irradiance, pH, and nutrient values. One-way ANOVAs were used to determine seasonal variations in algal biomass. The algal dry weight data (x) was log (x + 1) transformed before statistical testing. The Tukey test was used to examine differences between monthly biomass averages ($P < 0.05$). The temporal variations in algal dry weights were used to calibrate the model. Simulation results were compared with the field data for *Gracilaria* and *Hypnea* using linear regression analyses. Irradiance measured at the reef pool varied between 27.33 and 169.8 μmol photons m^{-2} s^{-1}, and this data was also interpolated and included in the model to simulate algal biomass. Algal dispersion coefficient values ranged from 0.348 to 0.002 in the model and were correlated with the rainfall data for Jaboatão dos Guararapes ($r = 0.75$, $P < 0.05$). Rainfall (as measured at the local ITEP/LAMEPE government weather station) was highest in April/2009 (268.9 mm) and lowest in October/2009 (6.0 mm). Sensitivity analyses were conducted using initial algal biomass conditions and model parameters.

Biomass Model

The simulation model for algal populations was developed using the Ithink^{TM} software package; model parameter values were obtained by manual calibration with the end ranges cited in the literature (table 2) and validated by sensitivity analyses. The basic simulation equation for algal biomass (*B* in g d wt m^{-2}) at each daily time step was (1):

$$\frac{dB}{dt} = (\mu - \Omega)\,B - \alpha \qquad (1)$$

where the μ and Ω coefficients represent growth and loss respectively. The two algal populations were simulated separately using two groups of equations that differed with respect to the parameter values used. The forcing data in the model were temperature and salinity, with the time series representing irradiance and nutrient resources utilized by both *Gracilaria* and *Hypnea* populations. The alpha (α) coefficient in equation (1) represents algal dispersion (Zoffoli 2009). The dispersion functions were obtained by calibration, and represent the effects of wind and rain; the same dispersion time series was used for both algae

$$\mu = \mu max\, f(T)\, f(S)\, f(I)\, f(N)\, f(P)\, f(K) \qquad (2)$$

The parameter μmax represents the optimal algal growth rate obtained by calibrations based on the range of values cited in the literature. The $f(T)$ function represents the effect of temperature on algal development; the other functions in Equation 2 simulate interactions between salinity, irradiance, nitrogen, and phosphorus parameters, respectively, as well as the carrying capacity function ($f(K)$) (Guimaraens et al. 2005).

Algal loss and senescence, represented by the term Ω, are proportional to algal biomass and the incorporated field temperature values (*temp*, table 1). The mortality rate is inversely proportional to the growth functions from Equation 2.

$$\Omega = \frac{\Omega max\; 0.1^{(temp - \theta)}\, B}{B + Kd f(T)\, f(S)\, f(I)\, f(N)\, f(P)\, f(K)} \qquad (3)$$

In Equation 3, *Kd* represents the half saturation constant for mortality. The temperature coefficient θ, obtained by calibration, was 32 for *Hypnea* and 33 for *Gracilaria* (which may reflect algal acclimation). Equation 4 represents an exponential relationship governed by the difference between field data (*temp*) and the optimal temperature for the algae (*top*). The lambda coefficient was obtained through model calibration.

$$f(T) = exp^{-\lambda(temp - top)^2} \qquad (4)$$

The photosynthetic saturation function in the model represents algal photosynthetic efficiency (5), where *Io* is the daily irradiance based on interpolated field data (table 1). The light extinction coefficients (*Ci*) were 0.7 for *Gracilaria* and 0.8 for *Hypnea* and represent average light extinctions as a function of turbidity, depth, and competition among the algae. In equation (5) *Ki* is the photosynthetic half-saturation constant.

$$f(I) = \frac{CiIo}{CiIo + Ki} \qquad (5)$$

Equation (6) represents the limiting effect of salinity on the species studied in relation to optimal salinity (*sopt*) for algal development. Salinity values measured in the field served as inputs for the model (*sal*, table 1). The *λs* coefficients were obtained through model calibration.

$$f(S) = exp^{-\lambda s\,(sal - sopt)^2} \qquad (6)$$

The algal biomass model also considers growth as a function of an internal nutrient quota within the algal thallus (Droop 1983, Guimaraens et al. 2005), with the absorption of nitrogen and phosphorus being represented as a function of their seawater concentrations. Thus, the internal nutrient quotas were also considered state variables in the model.

$$\frac{dN}{dt} = NHupt - NOupt - \mu N \qquad (7)$$

$$\frac{dP}{dt} = POupt - \mu P \qquad (8)$$

The variables *N* and *P* represent the internal concentrations quotas of nitrogen and phosphorus (mg g^{-1} d wt), and *Nupt*, *NOupt*, and *POupt* are the absorption rates for ammonia, nitrate, and phosphate respectively. The equations presented below represent the absorption of ammonia, nitrate, and phosphate, and are functions of their maximum absorption speeds and half saturation constants

Table 1. Hydrological parameters of the study area.

Data	Salinity ‰	pH	NH_3-N µmol L^{-1}	NO_3-N µmol L^{-1}	PO_4-P µmol L^{-1}	Temperature °C	Irradiance µmol photons m^{-2}
4/20/2009	20.18	8.64	0.01	2.00	0.44	33.7	27.33
6/5/2009	15.26	8.69	0.26	3.70	0.91	28	93.71
7/23/2009	16.20	8.92	0.23	3.60	1.00	30.6	149.42
8/20/2009	20.45	8.94	0.01	2.60	0.64	28.7	20.93
9/20/2009	30.53	8.27	0.01	1.30	0.12	31.5	65.66
10/19/2009	24.29	8.63	0.07	1.60	0.74	33.7	94.89
11/13/2010	28.07	8.38	0.18	0.50	0.07	30	16.20
12/14/2010	27.53	8.45	0.15	0.30	0.30	30.8	169.80
1/29/2010	26.73	8.41	0.49	2.90	0.35	32.5	145.99
3/2/2010	31.54	8.64	0.31	1.10	0.23	33.9	74.33

(table 2), with the time series being based on interpolated field data of nutrient concentrations (*NHconc*, *NOconc*, and *POconc*).

$$NHupt = \frac{VNHmax\ \ NHconc}{KmNH + NHconc} \qquad (9)$$

$$NOupt = \frac{VNOmax\ \ NOconc}{KmNO + NOconc} \qquad (10)$$

$$POupt = \frac{VPOmax\ \ POconc}{KmPO + POconc} \qquad (11)$$

The nutrient limitation functions *f*(*N*) and *f*(*P*) assume that algal growth decreases as internal nutrient concentrations approach minimum nitrogen and phosphorus values (table 2).

$$f(N) = 1 - \frac{QNmin}{N} \qquad (12)$$

$$f(P) = 1 - \frac{QPmin}{P} \qquad (13)$$

The model also assumes that *Gracilaria* and *Hypnea* growth is limited by intraspecific competition based on carrying capacity (*K*) values that reflect biomass values observed in the field during the growing season (Guimaraens et al. 2005, 2008, table 2).

$$f(K) = 1 - \frac{B}{K} \qquad (14)$$

Sensitivity analyses for model outputs were performed using equation (15), varying the initial biomass conditions and each parameter by ±10% to calculate percentage changes in relation to baseline runs (Guimaraens et al. 2008, 2011a).

$$Percent\ Change = \frac{(100)}{N\ Savg}\ (\Sigma(|S1 - S2|)) \qquad (15)$$

Where *N* is the total simulation in days, *Savg* the average biomass value for the baseline run for each algal genus, *S1* the baseline biomass value, and *S2* the biomass value for each sensitivity run.

RESULTS

The first two components of the PCA explained 67.44% of the data variance and indicated that *Gracilaria*

Table 2. Model parameters for algal biomass simulations.

Symbol	Description	Units	Values for *Gracilaria*	Sources	Values for *Hypnea*	Sources
IC	Model initial condition	g d wt m^{-2}	100	field	46	field
K	Carrying capacity	g d wt m^{-2}	500	field	200	field
Kd	Half-saturation constant for mortality	g d wt m^{-2}	50	Calibration	20	Calibration
µmax	Maximum growth rate	Day^{-1}	0.8	Biber et al. 2004	0.6	Rosenberg et al. 1995
Ω*max*	Maximum death rate	Day^{-1}	0.00015	Calibration	0.0001	Calibration
Top	Optimun temperature	°C	30	Miranda 2010	25	Biber et al. 2004
Ki	Half-saturation constant for photosyntesis	µmol photons m^{-2}	40	Miranda 2010	30	Yokoya et al. 2007
Sopt	Optimun salinity	Adimensional	37	Biber et al. 2004	39	Biber et al. 2004
VNHmax	Maximum uptake rate for ammonium	mg L^{-1}	35	Carneiro 2007	55	Calibration
VNOmax	Maximum uptake rate for nitrate	mg L^{-1}	40	Carneiro 2007	30	Hanisak 1983
VPOmax	Maximum uptake rate for phosphate	mg L^{-1}	10	Carneiro 2007	20	Calibration
KMNH	Half-saturation constant for ammonium	mg L^{-1}	3	Biber et al. 2004	16.6	Hanisak 1983
KMNO	Half-saturation constant for nitrate	mg L^{-1}	3	Biber et al. 2004	5	Hanisak 1983
KMPO	Half-saturation constant for phosphate	mg L^{-1}	1	Biber et al. 2004	4.9	Calibration
QNmin	Minimum quota for nitrogen	mg g d wt^{-1}	5	Calibration	5	Calibration
QPmin	Minimum quota for phosphorus	mg g d wt^{-1}	1	Calibration	0.5	Calibration

biomass was positively correlated with temperature and salinity. Additionally, algal biomass was negatively correlated with irradiance and pH, as *Gracilaria* is not characteristic of estuarine environments and can be limited by low irradiance levels (table 1, figure 1). *Hypnea* biomass was negatively correlated with irradiance levels and with ammonia concentrations in the reef pool samples (figure 1). *Gracilaria caudata* and *Hypnea musciformis* were the most abundant components of the algal community in the study area, and their opposing abundance patterns in our samples suggest that competition is an important structuring factor in these populations.

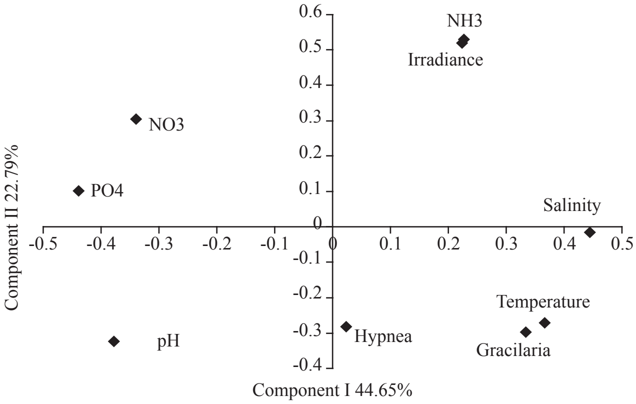

Figure 1. Principal Component Analysis of the environmental data collected at the Reef Pool.

Salinity values at the sampling site were lower during the rainy season (between 20.45 and 15.26 units), indicating a strong influence of the estuarine environment (table 1). Water temperatures at the sampling site ranged between 28 °C and 33.9 °C, but it did not show any clear seasonal pattern. Dissolved oxygen values ranged from 9.2 to 18.1 mg L^{-1}, characteristic of sites having intense photosynthetic activities. Nitrate showed the highest concentration of all of the nutrients in water samples, ranging between 3.7 and 2 µmol L^{-1} during the rainy season; the highest phosphate values were measured in June and July/2009 (0.91 and 1 µmol L^{-1} respectively). In the present study, using calibration experiments, an optimal water temperature of approximately 30 °C was observed for *Gracilaria*, which presumably reflects the acclimation of this alga to this tropical intertidal habitat. The optimal water temperature for *Hypnea* growth in the model was 25 °C (table 2).

The average biomass of *Gracilaria* in August/2009 was different from those of April/2009 and March/2010 ($P < 0.05$), and its dry weight peaked at approximately 120 g d wt m^{-2} in the reef pool (figure 2, table 3). The average biomass of *Hypnea*, on the other hand, was always below 50 g d wt m^{-2} and did not vary significantly during the study period (table 4). The fit between the simulated algal biomass values and the field data using linear regression was statistically significant (r = 0.79, $P < 0.01$), suggesting that the abiotic parameters included in the model, in addition to competition, serve to regulate

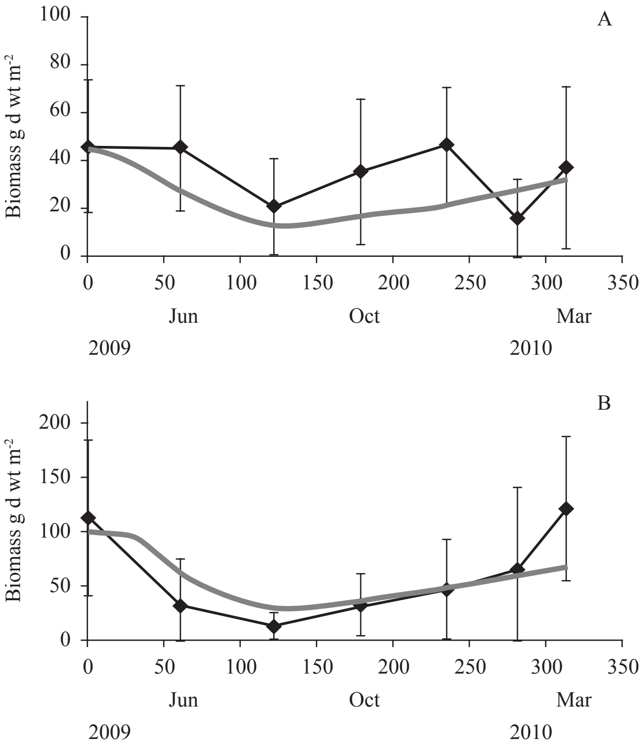

Figure 2. Algal simulations and average biomasses of *Hypnea* (A) and *Gracilaria* (B) (± standard deviations) collected at the Reef Pool.

Table 3. One-Way ANOVA of *Gracilaria* biomass.

Source of variation	Degrees of freedom	SS	MS	F	*P*-level	F crit
Between Groups	6	1.4026	0.2338	3.2873	0.0147	2.4591
Within Groups	27	1.9201	0.0711			
Total	33	3.3227				

Table 4. One-Way ANOVA of *Hypnea* biomass.

Source of variation	Degrees of freedom	SS	MS	F	*P*-level	F crit
Between Groups	6	0.2117	0.0353	0.6216	0.7113	2.4741
Within Groups	26	1.4754	0.0567			
Total	32	1.6871				

populations of these algae. The model was sensitive to initial biomass conditions, however, which had values that varied between 15 and 20% from the baseline runs for both algae. Sensitivity analyses of model parameters yielded values that generally varied less than 10% from the baseline and sensitivity run biomass values (table 5). Model simulations for both algae showed biomass variations greater than 10% in terms of the optimum salinity parameters (table 5), confirming the importance of the dispersion functions affecting temporal variations in *Gracilaria* and *Hypnea* biomasses.

Table 5. Sensitivity analyses of *Gracilaria* and *Hypnea* to initial conditions and model parameters.

	Gracilaria model parameters		*Hypnea* model parameters	
	+ 10%	- 10%	+ 10%	- 10%
IC	**17.19**	**16.80**	**18.13**	**18.08**
K	0.49	0.59	0.68	0.83
Kd	0.47	0.48	0.06	0.06
μmax	3.71	3.80	5.06	5.19
Ω*max*	6.32	6.45	1.00	1.00
Top	0.48	2.87	9.56	12.21
Ki	1.55	1.67	1.50	1.59
Sopt	**17.01**	**18.72**	**21.26**	**24.26**
VNHmax	0.03	0.03	0.02	0.02
VNOmax	0.22	0.26	0.31	0.37
VPOmax	0.22	0.26	0.15	0.18
KMNH	0.02	0.03	0.02	0.02
KMNO	0.15	0.15	0.25	0.25
KMPO	0.16	0.16	0.15	0.15
QNmin	0.26	0.28	0.38	0.39
QPmin	0.24	0.25	0.18	0.18

DISCUSSION

In their study of algal communities at Itamaracá, PE Silva et al. (1987) reported lower *Gracilaria* biomass values during the rainy season than during the dry summer season that could be related to water turbidity, rainfall, and wind dispersion. Principal Component Analyses showed negative correlations between algal biomasses and nutrients, as reef community eutrophication is greater during the rainy season. Bezerra & Marinho-Soriano (2010), however, reported a positive correlation between NH_4^+ and *Gracilaria birdiae* Plastino & EC Oliveira biomass during the dry season, while Marinho-Soriano et al. (2001) observed higher biomass and agar production by *Gracilaria cervicornis* (Turner) J. Agardh during the dry season in northeastern Brazil, with peak biomass values near 400 g m^{-2} during the summer/dry season. Both the growth rate and carrying capacity (K) of *Gracilaria* were higher than those of *Hypnea* in the simulation model despite the presence of epiphytes such as *Hypnea* growing on *Gracilaria*. These interactions may affect the carrying capacities of dominant algae populations in reef and rocky-shore communities (Guimaraens et al. 1996).

Developmental experiments testing *Gracilaria caudata* growth in the laboratory have indicated that this species is euryhaline and has an optimal salinity of 35 ppt in Brazil (Miranda 2010), although Carneiro (2007) reported that low salinity can limit the growth of *G. cervicornis*. Optimal temperatures for laboratory cultivation of *Gracilaria* specimens from the Brazilian coast ranged from 25 °C to 30 °C (Yokoya & Oliveira 1993, Miranda 2010), while measurements of the photosynthetic output of *Gracilaria cornea* J. Agardh in the Florida Keys identified an optimal temperature range between 25 °C and 35 °C (Dawes et al. 1999). Coastal productivity at Piedade Beach may also be limited by the presence of suspended solids during the rainy season (Passavante & Feitosa 1995), so that more frequent measurements of abiotic parameters and *in situ* irradiance levels in the water column (Brush & Nixon 2010) could improve model forecasting in that region. Model forecasting could also be improved by laboratory cultivation experiments that evaluated the sensitivities of local species to a wide spectrum of environmental factors (including salinity and temperature) and determine their nutrient uptake curves and light requirements. Biomass simulation experiments that did not include dispersion coefficients (alpha) did not generate seasonal patterns for the algae and could only qualitatively represent competition.

Hypnea biomass was sensitive to a 10% decrease in its optimum temperature in the models. Experimental calibrations of the biomass model indicated an optimal temperature of 25 °C for *Hypnea*, confirming the findings of Bravin and Yoneshigue-Valentin (2002) for optimal growth under nutrient-enriched conditions. The maximum absorption rates of ammonia and phosphate related to *Hypnea* biomass accumulation in the model suggest that this alga absorbs nutrients more efficiently at higher concentrations than does *Gracilaria* (which is known to absorb nutrients more effectively than *Hypnea*) (Chow et al. 2007). *Gracilaria* has also been described as an alga adapted to low irradiance levels (Dawes et al. 1999, Miranda 2010), as it was encountered under conditions of partial submersion on the Piedade Reef platform, particularly during the rainy season.

Hypnea also has a competitive advantage over *Gracilaria* in relation to environmental light availability – due to its lower half-saturation photosynthetic coefficient (*Ki*) (Biber et al. 2004). This at least partially explains the greater abundance of *Hypnea* in the reef pool as compared to other more exposed regions of the intertidal zone. It should also be noted that benthic algal community structures can be maintained by the occurrence of species with different ecological characteristics during the different seasons of the year and this occupation of different reef micro-habitats, as blooms of ephemeral Chlorophyta have been observed during the rainy season at Piedade Reef (Guimaraens et al. 2011b). In spite of relatively recent environmental impacts such as pollution and trampling, rapid recycling of chemical and biological resources was observed as indicated by high levels of dissolved oxygen, an alkaline pH throughout the study area, and the significant recovery of *Gracilaria* biomass after the rainy season.

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