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METABOLIC BALANCE OF THE POLYP-ALGAE MUTUALISTIC SYMBIOSIS IN THE HERMATYPIC CORAL *Porites panamensis* IN LA PAZ, BAJA CALIFORNIA SUR, MÉXICO

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ABSTRACT: Studies on metabolic balance in hermatypic corals have been unable to separate the analysis of animal's respiration from that of plant. The objective of this research was to determine the metabolic balance in the mutualistic symbiosis polyp-algae through incubations in respirometric chambers of twelve fragments of coral. The species studied *Porites panamensis* (Scleractinia: Poritidae), Verrill, 1866 was collected near La Paz, Baja California Sur, México. Experiments were performed during fall 2009 and winter 2010. Water temperature, salinity, dissolved oxygen, pH, irradiance and photosynthetic pigments were measured every two hours during the incubation times. The concentration of pigments was determined through spectrophotometry. The maximum primary production was at 12:00 h, with 3.80 mg $O_2 \cdot l^{-1} \cdot h^{-1}$ for fall and 4.92 mg $O_2 \cdot l^{-1} \cdot h^{-1}$ for winter. According to the *P : R (Production : Respiration)* ratio of 1.90 for fall and 2.07 for winter, the mutualistic symbiosis in *P. panamensis* showed a predominantly autotrophic behavior. The relative quotients of chlorophyll concentrations (mg·polyp-1), Chl *a* : Chl c_2, were 1.0 : 0.69 for fall and 1.0 : 1.22 for winter; while ratio of concentrations chlorophyll *a* : carotenes , Chl *a* : carotenes (both in mg·polyp-1), were 1.0 : 2.13 for fall and 1.0 : 1.88 for winter. The high relative concentrations of Chl c_2 and carotenes with respect to Chl *a* is explained as an adaptive response to high irradiance.

Keywords: Metabolic balance, hermatypic coral, respiration, mutualistic symbiosis, primary production.

Balance metabólico en la simbiosis mutualista pólipo-alga en el coral hermatípico *Porites panamensis* en La Paz, Baja California Sur, México

RESUMEN: Estudios del balance metabólico en corales hermatípicos han sido incapaces de separar el análisis de la respiración animal y vegetal. El objetivo en este trabajo fue determinar el balance metabólico en la simbiosis mutualista alga-pólipo a través de incubaciones en cámaras respirométricas en doce fragmentos de coral. Los experimentos se realizaron en otoño del 2009 e invierno del 2010. La especie estudiada fue *Porites panamensis* (Scleractinia: Poritidae), Verrill, 1866, recolectada en La Paz, Baja California Sur, México. La temperatura del agua, salinidad, oxígeno disuelto, pH, irradiación y pigmentos fotosintéticos fueron registrados cada dos horas durante los tiempos de incubación. Los pigmentos fotosintéticos se determinaron mediante espectrofotometría. La producción primaria máxima fue a las 12:00 h, con 3.80 mg $O_2 \cdot l^{-1} \cdot h^{-1} \cdot$ para otoño y 4.92 mg $O_2 \cdot l^{-1} \cdot h^{-1} \cdot$ para invierno. De acuerdo con el cociente *P : R* (*Producción : Respiración*) con valor de 1.90 para el otoño, y 2.07 para el invierno, la simbiosis mutualista en *P. panamensis* muestra un comportamiento predominantemente autótrofo. Los cocientes relativos de concentración de clorofilas (mg ·polyp^{-1}), Cl *a* : Cl c_2, fueron 1.0 : 0.69 para otoño y 1.0 : 1.22 para invierno, mientras que la relación de clorofila *a* : carotenos, Cl *a* : carotenos (ambos en mg·polyp^{-1}), fueron de 1.0 : 2.13 para otoño y 1.0 : 1.88 para invierno. Las altas concentraciones relativas de Cl c_2 y carotenos con respecto a Cl *a* se explican como una respuesta adaptativa a una mayor irradiancia.

Palabras clave: Balance metabólico, coral hermatípico, respiración, simbiosis mutualista, producción primaria.

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INTRODUCTION

Hermatypic corals harbor in their tissues microalgae of the genus *Symbiodinum*. The photosynthetic products of the algal cells consist of short-chain carbohydrates that the algae metabolize for their own growth. Parts of these carbohydrates are translocated to the host coral and represent essential nutrients (McCloskey *et al*., 1978; Muscatine *et al.,* 1981; Jesser *et al*., 2000; Apprill *et al*., 2007). Carbon distribution is determined by the polyp-algae mutualistic symbiosis; however, there is an incomplete understanding of how environmental factors affect these organisms (López-Pérez, 2005). Studies of metabolic balance in hermatypic corals have been unable to separate the analysis of animal's respiration from that of the plant. This demands an analysis of the metabolic process in the symbiotic relationship as a system with its own energy flux.

The existence of corals under stress conditions generated by temperature change is an adaptive feature of high-latitude coralline formations (Riegl & Piller, 2003; LaJeunesse *et al*., 2008). The study of coral symbiosis in mid-latitude regions of the eastern Pacific provides important ecological and biogeographic perspectives on the stability and variability of polyp algae mutualistic symbiosis (LaJeunesse *et al*. 2008). Understanding the natural

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variability of photosynthetic pigment ranges and distributions in healthy corals is central to the evaluation of the usefulness of the measurements in assessing the health and status of endosymbiotic reef-building corals (Apprill *et al*., 2007). In the Californian coral patches the species *P. panamensis* is one of the most abundant.

The metabolic balance in mutualistic symbiosis, such as primary production in reef corals, can be estimated from oxygen yield and carbon dioxide (CO_2) incorporation, or indirectly from the organic matter input to the surrounding water (Hatcher, 1990). Despite some uncertain respiration measurements, net primary production values pose a good indicator of the metabolic process.

The polyp-algae mutualistic symbiosis forms part of a highly efficient system for recycling matter and energy that is considered a nutritive advantage in hermatypic corals. The coral polyps may be reasoned in literature as herbivores. However, they may present alternative breeding forms. The coral–algae complex can be thought of as a unique entity, like the fungi-algae lichen complex, establishing the coral concept to refer both elements.

The mutualistic algae are dinoflagellates. The most conspicuous pigments in this algae are chlorophylls (Chl) *a*, c_2 and beta-carotenes. Nevertheless, other pigments have been considered in the literature such as diadinoxanthin, dinoxanthin, neo-dinoxanthin, peridin, neoperidin and three unidentified pigments (Jeffrey & Haxo, 1968; Hochberg *et al*., 2006). The shallowest hermatypic corals may present an unidentified pigment of high absorption at short wavelength; this pigment can function as a protection against high irradiances.

The transfer of photosynthetic products from the algae to the polyp can supply its metabolic requirements and promote rapid calcification (Goreau & Goreau, 1959; Osinga *et al.*, 2011). The photosynthetic fixation of CO_2 and the subsequent calcium carbonate ($CaCO_3$) precipitation are intimately linked on both spatial (cell to ecosystem) and temporal (day–night) scales (Gattuso *et al*., 1999; Falter *et al.*, 2011).

Metabolic balance can be expressed by the quotient between the photosynthetic rate during the daylight (P) divided by the daylight respiration rate (*R*). Several studies involving metabolic measurements in *Porites* (Table 1) have been used to infer that the coral is self-sustaining with respect to carbon.

The aim of this study was to determine the metabolic balance of the polyp-algae mutualistic symbiosis of *P. panamensis* in the reef area of Pichilingue, Baja California Sur, México. This was done through (1) estimations of primary production by changes in dissolved oxygen (DO) on incubations of *P. panamensis* fragments, (2) estimations of the algal biomass through photosynthetic pigments, and (3) the determination of the autotrophy - heterotrophy conditions in the mutualistic association.

Table 1. P: R quotient values for *Porites* spp., date of determination, bioma location, and author reference. (n/d = not dated).

Species	P:R	Month	Location	Authors
P. divaricata	3.4	n/d	Florida, USA	Kanishwer & Wainwright (1967)
P. sp.	2.9	n/d	Enewetak Atoll, Marshal Islands	Roffman (1968)
P. monticulosa	2.9	n/d		
P. compressa	2.1	n /d	Hawai, USA	Coles & Jokiel (1977)
P. porites	2.8	May	Veracruz, México	Signoret *et al*. (1987)
	1.4	Sep.		
P. lutea	2.3	Nov.	Sichang, Thailand	Moberg *et al*. (1997)
P. furcata	1.5	May	Florida, USA	Manzanello & Lirman (2003)

MATERIALS AND METHODS

Collection area: Coral samples were obtained at 24° 17'08" N, 110° 19'50" E, near Pichilingue beach and 2 km north of Unidad de Investigación Pichilingue of the Universidad Autónoma de Baja California Sur. There is an approximately 500m strip of coral to the north side of the beach in which *P. panamensis* is the predominant form. The specimens were collected manually at 1 m depth; they were selected with a similar size and good polyp health (no observable whitening presence). Twelve pieces of coral per season (fall of 2009 and winter of 2010) were collected and moved to the laboratory in marine water containers. To allow acclimation to laboratory conditions, pieces were deposited before the experiment in the experimental pool for 24 hours (h).

Physicochemical variables: Water temperature, salinity and dissolved oxygen (DO) in the experimental pool were registered with a multiprobe hand oxymeter YSI-85. The pH was measured with a Conductronic potentiometer, and irradiance with a LI-Cor 9901-sha220 underwater radiation sensor. The precision for water temperature measurements was ±0.05°C, for salinity ±0.01 psu, for DO 0.5 $mg \cdot l^{-1}$, for pH ±0.1 pH units and for irradiance ±0.01 $\mu mol \cdot s^{-1} \cdot m^{-2}$. Data were tested for normality by the Chi-square test and the null hypothesis as normality; null hypothesis was not rejected in any case (Daniel &Terrel, 1983). Homoscedasticity was

assumed because the data were grouped (low scatter in Figure 2) and in all cases the ratio of the largest sample variance to the smallest variance did not exceed 1.5. Analysis of variance (ANOVA) was applied for each parameter to evaluate the difference between replicates.

Primary production: Primary production was estimated under laboratory conditions for collected fragments of each season (fall of 2009 and winter of 2010). Each coral fragment collected was placed in a respirometric glass chamber, 20 cm diameter and 20 cm height with removable cover. The respirometric chambers were placed on a circular pond of 1.3 m diameter and 50 cm depth with a continuous flow of sea water provided by the pumping-filtering system; this system has a set of filters capable of eliminating 70% of the organic sediment and particulate matter.

The 24 h experiment consisted of three incubations of 2 h during the day and four during the night for three consecutive days in fall and one day in winter; in both cases a rest of 1 h between incubations was allowed. During the resting time each chamber was opened to permit water exchange and reduce stress to the coral.

The dissolved oxygen concentrations (DO) were measured with a YSI-85 oxygen meter, calibrated with the Winkler method at the start and end of each incubation. Also, water variables were measured from a control chamber (without coral). With the discrete dissolved oxygen values, a best fit fourth degree polynomial graph (Fig. 2a, 2b) provided a daily oxygen release curve and the estimation of the primary gross production in the mutualistic symbiosis for each season.

Metabolic balance determination: The dissolved O_2 curve obtained from incubations gave rise to a mathematical model that explains the autotrophic-heterotrophic periods. The range of production periods was determined by the change (increase or decrease) of the initial dissolved O_2 values from each incubator. Inflection points of the oxygen curve were determined to verify correspondence of the model with the metabolic balance. A best fit oxygen concentration hourly curve was built by the evaluation of the polynomial function obtained.

Net production was obtained from the daily photosynthetic and daily respiratory rates calculated from the dissolved oxygen produced or consumed in a given time by a given biomass, according to the following equations (Barreiro & Signoret, 1999):

Biomass estimation and photosyn-

$$P=(O_c - O_0) / t\ N \quad (1)$$

$$R=(O_0 - O_c) / t\ N \quad (2)$$

Where: P= Photosynthetic rate (mg O_2•polyp^{-1}•day^{-1}); R = Respiratory rate (mg O_2•polyp^{-1}•day^{-1}); O_c = O_2 released diurnal values (mg O_2•L^{-1}•day^{-1}); O_0 = O_2 consumed nocturnal values (mg O_2•L^{-1}•day^{-1}), t = Incubation time (hr) and N = Number of polyps per cm^2 of living surface.

thetic pigments: Once incubations had been achieved, the living surface of the coral was estimated from an impression on aluminum foil (Marsh, 1970). Ten 1 cm^2 fragments of each coral were obtained with a Mototool DREMEL-770. Polyps were counted on each 1cm^2 while being shield from direct sun-light. Each sample was macerated with a pestle and mortar with 10ml (90%) acetone and centrifuged at 4000 rpm and 4.0°C for 15 minutes. The supernatant was analyzed in a Thermo Scientific Multiskan Spectrum, with wavelengths ranging from 400 to 750nm. Pigment concentration for chlorophylls *a* and c_2 were determined with the spectrophotometric formulas proposed by Jeffrey & Humphrey (1975); for carotenes concentration the formula proposed by Strickland & Parsons (1972) for dinoflagellate carotenes was used:

$$\text{mg Cl}a \cdot \text{total polyps}\cdot\text{cm}^{-2}=(11.85\ A_{664}-1.54\ A_{647}-0.08\ A_{630})V/P\ l \quad (3)$$

$$\text{mg Cl}b \cdot \text{total polyps}\cdot\text{cm}^{-2}=(-5.43\ A_{664}+21.03\ A_{647}-2.66\ A_{630})V/P\ l \quad (4)$$

$$\text{mg Cl } c1 \text{ y } c2 \cdot \text{total polyps}\cdot\text{cm}^{-2}=(-1.67\ A_{664}-7.60\ A_{647}+24.52\ A_{630})V/P\ l \quad (5)$$

$$\text{mg carotenes} \cdot \text{total polyps}\cdot\text{cm}^{-2}=(10.0\ A480)\ V/P\ l \quad (6)$$

Where: A=Optical density read at the wavelength indicated as subscript; V=Acetone volume (ml); l=Length size of the cell where the light beam passed through (1.0 cm), P=Total polyps per cm^{-2} and Cl=Chlorophyll.

RESULTS

Physicochemical parameters: The abiotic parameters (water temperature, salinity, pH, irradiance and DO) did not differ significantly between specimens or between days of incubation (ANOVA, p>0.5). Water temperature inside the respiratory chamber differed between day and night (Table 2); the average temperatures were 22.50°C for fall (range between 19.74°C at 21:00 h to 26.71°C at 15:00 h) and 17.51°C for winter (range 14.05°C at 07:00 h to 22.06 °C at 16:00 h). Average salinity was 36.7 for fall and 37.4 for winter.

Table 2. Season of incubation, time of the day, average values of irradiance, temperature, salinity, and pH.

Season	Hour	Irradiance ($\mu mol \cdot s^{-1} \cdot m^{-2}$)	Temperature (°C)	Salinity (psu)	pH
	1-3	0	22.32	36.39	8.54
	6-8	1315.62	24.03	36.34	8.51
	9-12	1482.78	25.75	36.47	8.42
Fall	13-15	448.95	25.03	36.43	8.28
	16-18	0	21.26	36.60	8.29
	19-21	0	20.95	36.47	8.41
	22-00	0	21.19	36.85	8.50
	1-3	0	16.00	36.20	7.97
	6-8	1447.3	14.30	38.60	7.88
	9-12	1584.0	15.80	39.50	7.96
Winter	13-15	492.7	18.40	39.20	7.95
	16-18	0	20.40	37.70	7.95
	19-21	0	19.60	35.30	8.11
	22-00	0	18.10	35.30	7.99

Water pH increased during daylight and decreased at sunset. Although differences were not significant ($p>0.05$); pH variation was different in the chambers with corals than in the control chamber (Fig. 1).

Primary production: The first increase in the DO values with sunlight was registered from 06:00 to 8:00 h, with a primary gross production peaking at 12:00 - 14:00 h. DO values began to fall at 16:00 and were stable since the 18:00 h (Table 3).

The lowest average of DO value fell between 22:00 and 03:00 h. Minimum DO values were of 0.5 mg $O_2 \cdot l^{-1}$ in the fall (Fig. 1a) and 1.2 mg $O_2 \cdot l^{-1}$ in winter (Fig. 1b), recorded at dawn (06:00 h) and sunset (18:00 h), under the respiratory effect of the mutualistic symbiosis. The DO curve for each season showed a maximum value of 3.1 mg $O_2 \cdot l^{-1}$ for 12:00 h in the fall and 3.5 mg $O_2 \cdot l^{-1}$ in the winter (Fig. 2A and 2B). Best fit equations of each drawn curve were computed to elaborate the metabolic balance model for each season. Measurement of irradiance started at dawn around 06:30 h and ended with sunset at 17:30 h. Maximum irradiance was between 09:00 and 15:00 h (around 1500 $\mu mol \cdot s^{-1} \cdot m^{-2}$).

M**abolic balance:** The metabolic balance models assume a constant respiratory rate per hour (*r*) for the heterotrophic period. A value of 0.8 $mgO_2 \cdot l^{-1} \cdot h^{-1}$ was determined for fall and 1.5 $mgO_2 \cdot l^{-1} \cdot h^{-1}$ for winter. Because the nocturnal values did not differ significantly between each hour, and in view of other research on corals metabolism (Muscatine *et al*., 1981; Signoret *et al*., 1987) respiratory rates were based on constant values for each hour of the heterotrophic period. Only a best fit straight line was drawn for each season, fall and winter (Fig. 3).

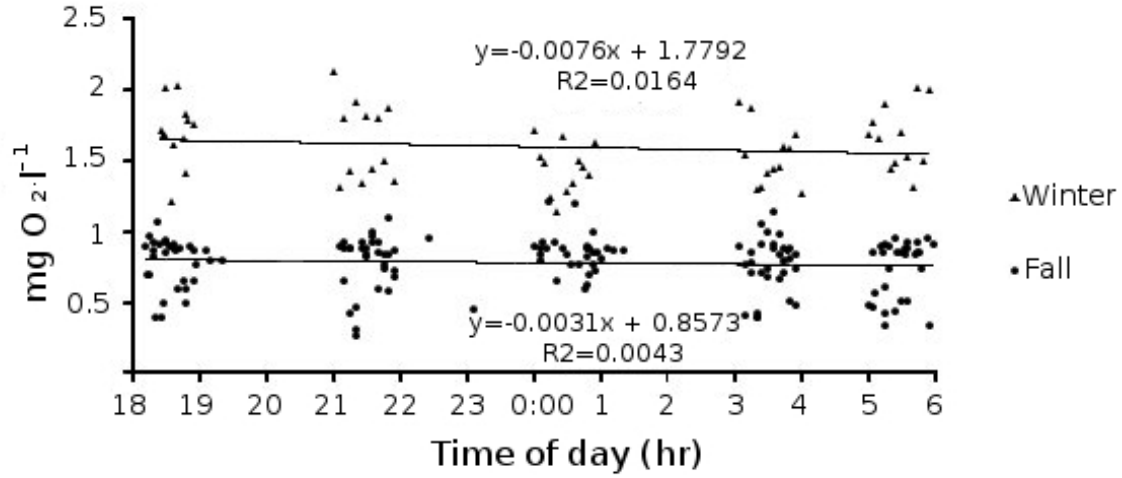

Figure 1. **Dissolved Oxygen during the heterotrophic period** in the incubation chambers

Table 3. Season of incubation, time and average dissolved oxygen concentration (mg $O^2 \cdot L^{-1}$) for different specimens incubation. Bold numbers indicate the time of 6-8 and 16-18 hours for values at dawn and sunset.

Season	Hour	Specimen										
		1	2	3	4	5	6	7	8	9	10	11
	1-3	0.82	0.75	0.69	0.72	0.81	0.73	0.75	0.91	0.84	0.82	0.89
	6-8	2.85	2.60	3.52	2.7	3.00	2.85	2.69	2.50	2.12	3.18	2.97
	9-12	2.71	2.37	3.80	3.2	3.01	3.22	3.14	3.19	2.38	3.70	3.42
Fall	13-15	2.84	2.03	2.76	2.7	2.45	2.30	2.99	2.55	2.34	3.00	2.92
	16-18	0.98	1.00	0.77	0.9	0.91	0.99	1.10	1.09	1.15	0.92	0.87
	19-21	0.91	0.82	0.35	0.9	0.79	0.84	0.73	0.92	0.96	0.78	0.76
	22-00	0.95	0.69	0.41	0.8	0.83	0.74	0.79	0.89	0.98	0.80	0.69
	1-3	1.27	1.54	1.30	1.41	1.45	1.59	1.92	1.87	1.31	1.44	1.60
	6-8	3.25	2.31	3.56	3.24	3.62	3.42	2.93	2.98	3.43	3.46	3.47
	9-12	3.32	2.47	3.97	3.51	3.84	3.53	3.99	3.32	4.92	4.69	4.34
Winter	13-15	3.13	2.06	3.11	3.37	3.15	2.93	3.92	3.35	3.89	3.20	3.65
	16-18	1.67	1.68	1.83	2.01	2.03	1.78	1.61	1.61	1.61	1.61	1.61
	19-21	2.13	1.80	1.91	1.81	1.80	1.87	1.32	1.42	1.34	1.45	1.49
	22-00	1.71	1.49	1.14	1.28	1.50	1.39	1.53	1.24	1.66	1.34	1.46

The metabolic balance models were built by the hourly evaluations of the polynomial equation (obtained from the DO curve) for each hour of the autotrophic period, and with the hourly respiratory rate (*r*) determined for the heterotrophic period. This model shows the metabolic balance between heterotrophic and autotrophic periods.

Photosynthetic rate (*P*) was 0.045 mg $O_2 \cdot l^{-1} \cdot day^{-1} \cdot polyp^{-1}$ for fall and 0.072 mg $O_2 \cdot l^{-1} \cdot day^{1} \cdot polyp^{-1}$ for winter; while the respiratory rate (*R*) was 0.023 mg $O_2 \cdot l^{-1} \cdot day^{-1} \cdot polyp^{-1}$ for fall and 0.034 mg $O_2 \cdot l^{-1} \cdot day^{-1} \cdot polyp^{-1}$ for winter. The *P : R* ratio was 1.977 for fall and 2.047 for winter.

Biomass and photosynthetic pigments: The average animal biomass was 36 (±6.0 SD) polyps·cm^{-2} for fall in a living surface of 2476 cm^2 and 46 (±4.0 SD) polyps·cm^2 in 2066 cm^2 of living surface for winter. This contrasts with Glynn *et al*. (1994) who reported 53 (±2.6 SD) polyps·cm^{-2}.

Measurements of the photosynthetic pigments (Fig. 4) for fall showed an average content of 0.57 (±0.13 SD) mg Chl *a*·$polyp^{-1}$, 0.40 (±0.13 SD) mg Chl c_2·$polyp^{-1}$ and 1.23 (±0.31 SD) mg carotenes·$polyp^{-1}$. In winter the average contents were 0.86 (±0.18 SD) mg Chl *a*·$polyp^{-1}$, 1.05 (±0.14 SD) mg Chl c_2·$polyp^{-1}$, and 1.61 (±0.28 SD) mg carotenes·$polyp^{-1}$. The

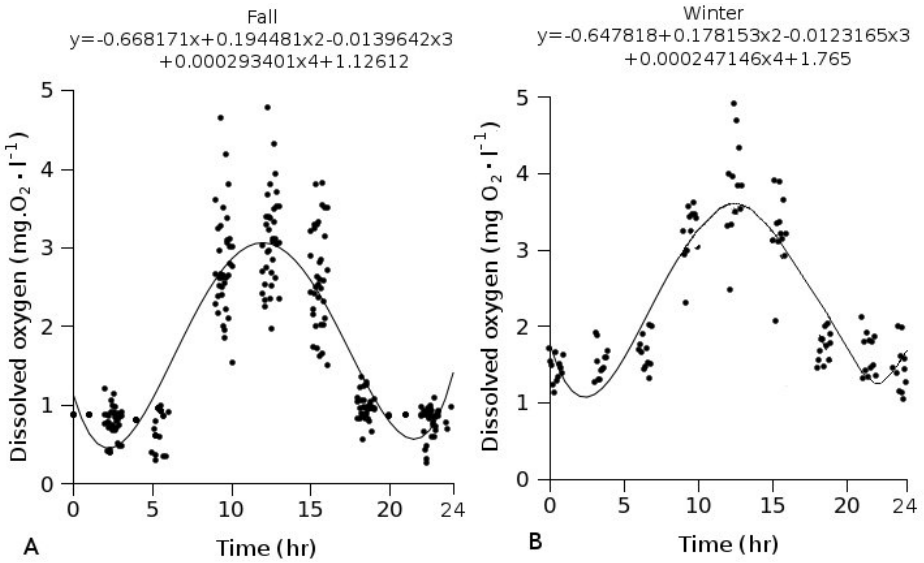

Figure 2. Hourly dissolved oxygen curves and polynomial best fit equations for each season for incubations of *P. panamensis* (1A for winter and 1B for fall).

Table 4. Specimen number, their living surface biomass and average polyps per cm² for fragment of *P. porites* utilized in each chamber. Specimen 3 and 10 showed a relation between increased number of polyps per living surface and maximum GP values.

Specimen	Fall				Winter			
	Live surface (cm^2)	Average polyps per cm^2	GP(mg $O_2 \cdot L^{-1} \cdot h^{-1}$) Max.	Min.	Live Surface (cm^2)	Average polyps per cm^2	GP(mg $O_2 \cdot L^{-1} \cdot h^{-1}$) Max.	Min.
1	248.2	31.4	3.6	0.76	255.0	51.3	1.52	1.05
2	158.0	29.8	3.24	0.41	149.5	42.5	0.39	0.14
3	194.1	47.4	4.78	0.27	156.9	46.9	1.59	0.89
4	193.3	38.9	3.80	0.68	231.7	49.3	1.8	0.58
5	241.0	35.4	4.18	0.6	129.2	41.2	1.6	0.89
6	137.5	34.3	3.93	0.51	148.7	36.7	1.37	0.75
7	220.4	28.7	3.39	0.42	132.5	45.3	1.65	0.53
8	319.0	42.2	3.22	0.91	104.2	45.6	1.00	0.42
9	156.8	34.0	2.81	0.88	260.7	51.2	2.22	0.81
10	289.0	44.1	4.31	0.48	196.2	44.1	2.20	0.46
11	129.2	27.9	3.17	0.70	173.5	40.5	1.59	0.78
12	191.2	33.4	3.06	0.86	127.5	45.4	1.45	0.37

relative quotients of chlorophyll concentrations (mg·polyp^{-1}) (Chl *a* : Chl c_2) were 1.0 : 0.69 for fall and 1.0 : 1.22 for winter. Meanwhile chlorophyll *a* : carotenes concentrations (mg·polyp^{-1}) ratio (Chl *a* : carotenes) were 1.0 : 2.13 for fall and 1.0 : 1.88 for winter.

DISCUSSION

Primary production was higher in winter and this difference could be the result of many factors. One is the limitation of light inasmuch irradiance in the fall was lower than normal because the 2009 hurricane season, that generally ends in September, extended until November, bringing cloudy days. Another factor was the high water temperatures in the fall that increased respiratory rates. A comparison of metabolic balance of field observations with laboratory measurements has a strong correlation of a decrease in respiration rates with a decrease in photosynthetic rates on cloudy days and is related to a regulation of the whole system.

Although DO curves did not differ significantly between specimens, there was some relation between the maximum production values and the number of polyps per cm². Specimens 3 and 10 in the fall, and 9 and 10 in the winter, showed both the highest production levels and the highest number of polyps per living surface (Table 4). This relation did not apply for minimum values because the biomass of polychaetes and other organisms of the association were not considered in this study. As there is no relationship between the size of the polyps and the chlorophyll concentration, animal biomass data were considered in terms of living surface areas.

The metabolic balance determined by *P : R* ratios is consistent with data for other species of the same genus (Table 1). *P. panamensis* maintain a high metabolic efficiency that can even maintain the metabolic requirements of other integral members of the association such as shrimp larvae, polychaetes, ophiuroids and sea cucumbers which live within the coral

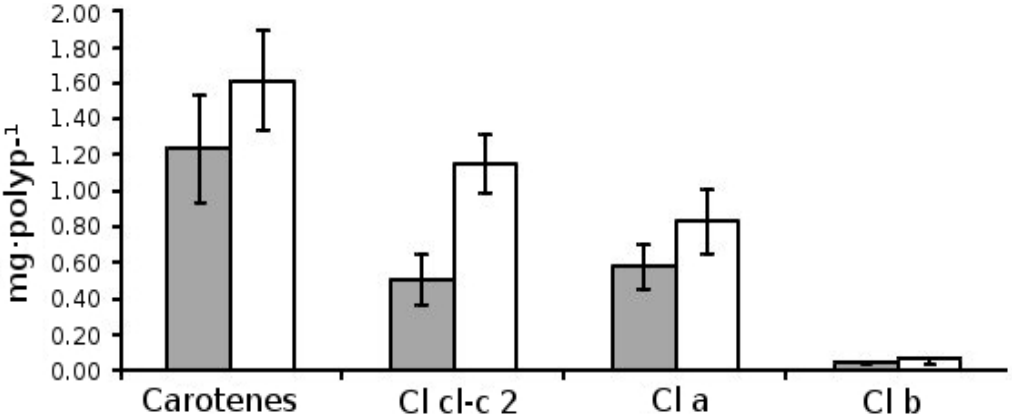

Figure 3. Average concentration (mg) of photosynthetic pigments per polyp in *P. panamensis* for each season.

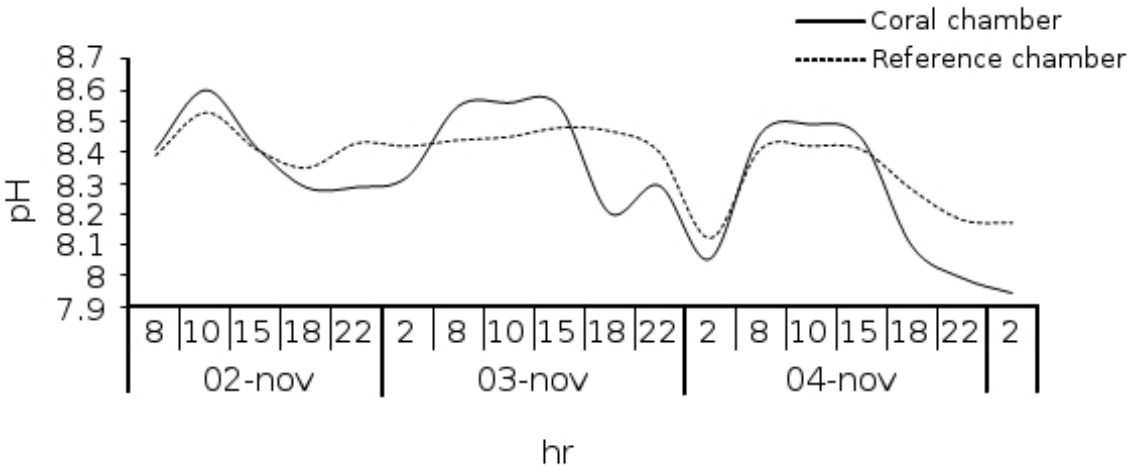

Figure 4. Mesured pH values for the reference and coral chambers in fall season.

framework.

The higher concentration of photosynthetic pigments in the winter than in fall suggests that the *Symbiodinium* population was affected by high irradiance and temperatures in fall. Previous studies have demonstrated that the concentrations of these pigments, as well as symbiont densities, vary in relation to environmental factors. During winter conditions of low temperature and solar irradiance, increased pigments concentrations and symbiont densities are frequently observed (Brown *et al*., 1999; Fagoonee *et al*., 1999; Fitt *et al*., 2000; Apprill *et al*., 2007). Many studies have shown some variability in pigment concentrations between seasons (Brown *et al.,* 1999; Fitt *et al*., 2000; Costa *et al*., 2005); these changes represent some adjustments by mutualistic algae to optimize physiological activity to the environmental changes (Sunagawa *et al*., 2008).

The relative high concentration of carotenes (Fig. 4) is representative of shallow-water corals, because these pigments fulfill a double function, as accessory pigments to absorb light and as a protection for the Chl *a* at high irradiances. Carotenes are related with the survival of the mutualistic algae; elevated concentrations of Chl c_2 and carotenes are indicators of mature and stable communities of dinoflagellates.

The mutualistic relationship in the pH behavior can be explained by the marine carbon dynamics. In marine ecosystems pH is regulated by the carbonate synthesis that changes the water alkalinity. This process is thermodynamically regulated and includes a series of substitutive reactions to transform CO_2 molecules into H_2CO_3 and then HCO_3 (Millero, 1995). Many marine organisms including corals, can use this HCO^-_3 to synthesize $CaCO_3$ by the reaction $Ca^{2+} + HCO_3 \rightarrow CaCO_3 + H_2O$. These changes are controlled by chemical factors more than by physical conditions (Gattuso *et al*., 1999). Both CO_2 decrease due to photosynthesis as well as precipitation of $CaCO_3$ contribute in rising the pH values during light periods, and the increase of CO_2 by respiration acidifies during darkness (Bold & Winne, 1985) (Fig. 1). The mutualistic associations in hermatypic corals are determinants in this control; investigations related to changes in pH and the supply or access to dissolved inorganic carbon might provide further mechanistic explanation for the host role in protecting its symbionts from environmental stresses (Bahgoli *et al.*, 2008). The light intensity and wavelength reaching the symbiotic algae, and the solute exchange between the coral and the surrounding water are the most important external regulators of photosynthesis in reef corals (Ulstrup, 2006).

The metabolic balance in the mutualistic association polyp-algae of *Porites panamensis* had a predominantly autotrophic behavior in both seasons (fall and winter). The presented results show that the mutualistic association consumes in respiration one third of the total carbon fixed by its own primary production. The relative proportions of photosynthetic pigments suggest an adaptive feature of the species, that allows high-quality photosynthetic material (Chl *a*) in low proportions, protected by the high presence of accessory pigments (Chl c_2 and carotenes); these last pigments increase in fall and protect Chl *a* at high irradiances. This coral species has shown a high photosynthetic efficiency in the mutualistic association and can regulate the metabolic balance. This efficiency is higher in the winter than in the fall and is de-

termined by irradiance

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