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Effect of temperature on two reef-building corals *Pocillopora damicornis* and *P. verrucosa* in the Red Sea

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Abstract

The effects of temperature on two reef building corals *Pocillopora damicornis* and *P. verrucosa* inhabiting the Obhur Creek, a small embayment on the western, Red Sea coast of Saudi Arabia, was studied from December 2009 to November 2010. The overall annual range of seawater temperature in Obhur Creek was between 24.5°C and 33°C. Zooxanthellae abundance and diversity showed seasonal variations: the number of zooxanthellae in *P. damicornis* was slightly higher than in *P. verrucosa*, and the abundance of zooxanthellae of both species was low in summer and high during winter. The respiration rate of *P. verrucosa* did not vary between summer and winter, suggesting compensatory acclimation. In contrast, the respiratory rate in *P. damicornis* was lower in winter than in summer. During the

winter season the metabolic rate was higher in both species owing to the optimum seawater temperature (30°C). As a result of the abundance of zooxanthellae and the optimum seawater temperature, the growth rates of the skeletons of the two coral species were higher in winter and lower in summer. In general, the results showed that *P. verrucosa* is more flexible with respect to temperature than *P. damicornis*. The difference in zooxanthellae thermal tolerances at 35°C may be due to the algal genotypes between the two species, resulting in *P. damicornis* becoming bleached as the rate of metabolism exceeds the rate of photosynthesis with increasing temperature.

1. Introduction

Environmental factors such as global warming, ozone depletion, increase in coral diseases (Hallock 2001, Nguyen 2009) and natural events such as hurricanes, earthquakes, predator outbreaks and periods of high temperature (Nguyen 2009) may threaten the health and existence of coral reefs. Coral reefs are among the ecosystems most endangered by climate change and associated effects as corals live near their upper thermal limits and are sensitive to modest increases in background seasonal seawater temperatures (Kleypas et al. 2001, McClanahan et al. 2007).

Stony corals of the order Scleractinia have a symbiotic relationship with the zooxanthellae species *Symbiodinium microadriaticum* that lives within their endoderm layer, providing up to 90% of assimilated carbon to corals as food (Al-Sofyani 1991, Davies 1991, Papina et al. 2003) and enhancing the growth of coral (Goreau 1959). Upon exposure of coral to abnormal environmental conditions such as variations in physical and chemical parameters as well as anthropogenic threats, the spectacular symbiotic relationship between them breaks down, with the zooxanthellae being expelled from the coral tissues, a phenomenon called coral bleaching (Calvin & Muscatine 1997, Downs et al. 2002, Coles & Brown 2003). Shallow coral species have more resistant clade A and B zooxanthellae than the less resistant, deeper coral species, which have clade C zooxanthellae (Rowan et al. 1997), while clade D zooxanthellae have been reported to be the most heat resistant (Baker et al. 2004, Fabricius et al. 2004).

Many reports link coral bleaching to high sea surface temperature (Dunne & Brown 2001), solar radiation (Hoegh-Guldberg 1999, Fitt et al. 2001) and differences in the zooxanthellae clades (Brown et al. 2002, Lewis & Coffroth 2004). Field studies have indicated that some species of corals offer greater resistance to bleaching when subjected to unusual environmental factors, compared to other vulnerable species. Some studies

refer the resistance of corals to bleaching to colony morphology and tissue thickness (Loya et al. 2001). Generally, fast-growing species suffer higher bleaching mortality than slow-growing massive species probably because of the higher respiration rate and protein metabolism that eliminate harmful oxygen, or as a result of their thick tissue, which protects the zooxanthellae from UV-radiation in massive corals (Floros et al. 2004, McClanahan et al. 2004).

The objective of this study was to assess the bleaching tolerance between two coral species *Pocillopora damicornis* and *P. verrucosa*, the respiration and growth rates of which are likely to respond differently to temperature changes. The results obtained in this study will expand our current knowledge on the effect of rising seawater temperature on coral reefs in the Red Sea.

2. Material and methods

The study was carried out at Obhur Creek, which is situated 35 km to the north of Jeddah City (Figure 1). The study site was located at the mouth of the creek on its northern shore at a water depth of

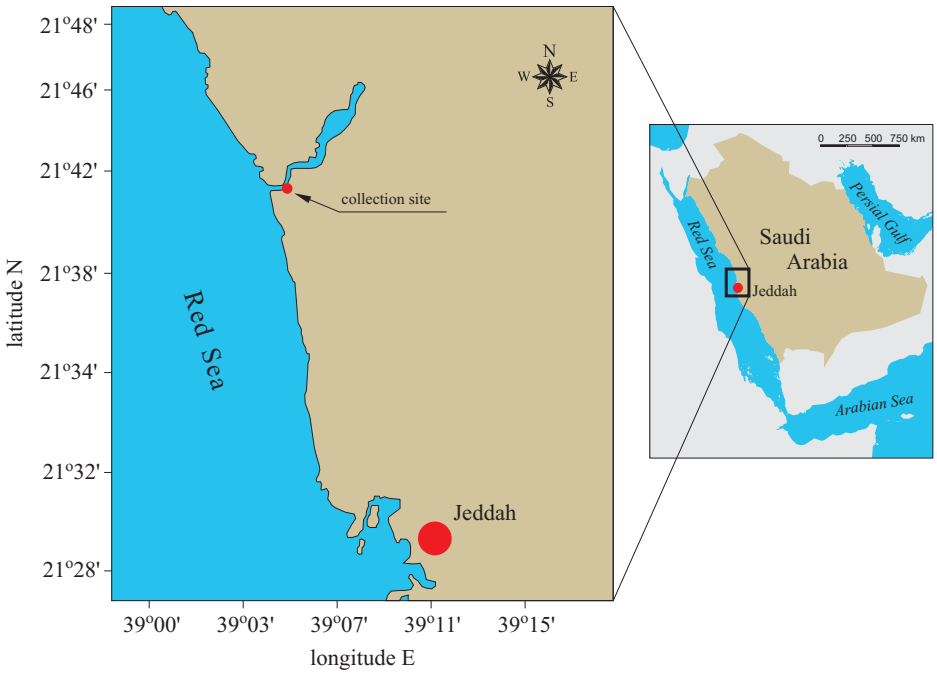

Figure 1. Map of the Red Sea showing the location of the study site at the entrance of Obhur Creek

3 m, from which specimens of *P. damicornis* and *P. verrucosa* were collected.

2.1. Environmental measurements

Water temperature was measured in situ with two maximum/minimum mercury-in-glass thermometers attached to the reef in a shady spot at a depth of 3 m. They were read at monthly intervals from December 2009 to November 2010. The mean temperature for two readings was calculated as the average between the mean maximum and minimum temperature.

2.2. Specimen preparation

Freshly collected colonies of the two species were used to make coral nubbins (Al-Sofyani 1992). Similar-sized regularly shaped branch tips of *P. damicornis* and *P. verrucosa* were broken off and the surfaces ground flat to yield tips of 2.5–3 cm height. These were attached to pre-weighted 3×3 cm acrylic tiles using a small quantity of cyanoacrylate adhesive. They were then placed on racks and returned to the reef to recover for at least 3 days.

2.3. Respiration

Nubbins were placed singly in a water-jacketed, clear, acrylic, closed respirometer cell, filled with 0.45 μm-filtered seawater (110 ml). Respiratory oxygen uptake was detected by a Strathkelvin Instruments 1302 polarographic oxygen electrode connected to a 780 oxygen meter, whose output was displayed on a $10''$ flatbed chart record. Respiratory oxygen uptake of nubbins was measured in darkness in the respirometer cell. The respiration rate was linear with PO_2 over the 90 to 100% saturation levels. The respiration rates were normalized to mg/dry weight of tissue by decalcifying in 10% nitric acid and then drying the resultant tissue to constant weight at 60°C.

Respiration rates of zooxanthellae were estimated using freshly isolated samples from nubbins that had been maintained in darkness for 12 hours. Coral tissue was removed with a water pick, and the slurry centrifuged at $2000 \times$ g for 1 min. Further separation was achieved with a hand-held potter homogenizer, after which the suspension was centrifuged and washed with seawater three times. The pellets were then re-suspended in 1 ml of filtered seawater (0.45 μm), and the rate of oxygen uptake was measured in darkness in an RC 300 respirometer cell (Strathkelvin Instruments) with a 1302 polar graphic oxygen electrode. Zooxanthellae concentrations within the respirometer cell were measured on a sub-sample

using a haemocytometer. Respiration measurements were made in winter (March 2009) (25°C and 30°C) and in summer (August 2010) (35°C and 40°C) ($n = 10$ for *P. damicornis*; $n = 10$ for *P. verrucosa*). The data were subjected to t-test analysis to discover the variations in respiration rate.

2.4. Growth

Nubbins of *P. damicornis* and *P. verrucosa* were placed on racks at the experimental sites at 3 m depth on the fringing reef at Obhur Creek after buoyant weighing in the laboratory with a Precia 120a balance (Al-Sofyani & Davies 1992). They were returned to the laboratory for reweighing after intervals of approximately 10 days. Growth rates were determined in winter and summer ($n = 10$) and expressed as mg skeleton d^{-1}. The appropriate data were analysed by Student's t-test (Tables 1 and 2).

Table 1. The mean skeletal and tissue characteristics of *Pocillopora damicornis* and *P. verrucosa* at the study site. The mean values were compared by Student's t-test. The standard deviation (SD ±) and the number of measurements (n) are given in parentheses

Characteristic	*P. damicornis*	*P. verrucosa*	t-test	p-value
Skeletal density g cm^{-3}	2.78 ± 0.018 (12)	2.77 ± 0.026 (11)	1.50	0.148
mg d.t. g^{-1} skeleton	28.10 ± 13.43 (9)	24.92 ± 5.70 (10)	0.69	0.50
cm^{-2} g skeleton	5.36 ± 0.93 (9)	3.76 ± 0.66 (10)	4.42*	0.001
mg d.t. cm^{-2}	5.33 ± 2.74 (9)	6.92 ± 2.59 (10)	1.30	0.21
No. of poly cm^{-2}	80.40 ± 2.30 (5)	84.40 ± 2.88 (5)	2.43*	0.04
No. 10^6 g^{-1} skeleton (in winter)	2.40 ± 0.57 (10)	2.70 ± 1.07 (10)	0.84	0.41
No. 10^6 g^{-1} skeleton (in summer)	1.49 ± 0.47 (10)	1.78 ± 0.34 (10)	1.57	0.13
No. 10^5 mg^{-1} d.t. (in winter)	1.73 ± 0.23 (9)	1.50 ± 0.52 (10)	2.28*	0.038
No. 10^5 mg^{-1} d (in summer)	0.76 ± 0.50 (9)	0.74 ± 0.17 (10)	0.79	0.44
No. 10^5 cm^{-2} (in winter)	4.76 ± 1.68 (10)	7.85 ± 4.10 (10)	2.21*	0.04
No. 10^5 cm^{-2} (in summer)	2.78 ± 0.73 (10)	4.87 ± 1.23 (10)	1.25	0.23

*significance ($p \leq 0.05$).

Table 2. The mean dark respiration of the colony and freshly isolated zooxanthellae of *Pocillopora damicornis* and *P. verrucosa* at different seawater temperatures. The standard deviation (SD) and number of measurements (n) are given

	P. damicornis				*P. damicornis*				*P. verrucosa*				*P. verrucosa*			
	25°C	30°C	t-test	p-value	25°C	35°C	t-test	p-value	25°C	30°C	t-test	p-value	25°C	35°C	t-test	p-value
Respiration colony																
μl O_2 mg^{-1} d.t. h^{-1}	1.196	1.59			1.196	1.19			1.04	1.42			1.04	1.37		
SD ±	0.56	0.44	1.76	0.09	0.56	0.39	0.12	0.91	0.29	0.35	2.67*	0.016	0.29	0.36	2.29*	0.03
n	10	10			10	10			10	10			10	10		
μl O_2 cm^{-2} h^{-1}	6.49	8.34			6.49	6.46			6.87	9.38			6.87	9.14		
SD ±	3.03	2.28	1.53	0.14	3.03	2.15	0.02	0.98	1.92	2.28	2.67*	0.016	1.92	2.4	2.34*	0.03
n	10	10			10	10			10	10			10	10		
Zooxanthellae																
μl O_2 mg^{-1} d.t. h^{-1}	0.24	0.26			0.24	0.47			0.26	0.27			0.26	0.34		
SD ±	0.1	0.15	0.28	0.78	0.1	0.11	4.73*	0.001	0.14	0.13	0.13	0.89	0.14	0.13	1.39	0.183
n	10	10			10	10			10	10			10	10		
μl O_2 10^{-6} h^{-1}	2.84	3.03			2.84	7.46			2.39	2.48			2.39	5.78		
SD ±	1.10	1.87	0.27	0.79	1.1	1.83	6.67*	0.001	1.3	1.25	0.144	0.89	1.3	2.25	4.12*	0.001
n	10	10			10	10			10	10			10	10		

*significance ($p \leq 0.05$).

3. Results

3.1. Temperature

The seasonal minimum temperature was recorded in March 2009 with a monthly average of 24.5°C, while the maximum was during August 2010 with a monthly average of 33.0°C (Figure 2). The determined mean dry tissue weight per g skeleton was higher for *P. damicornis* (28.1 ± 13.34) than for *P. verrucosa* (24.92 ± 5.7) with no significant differences in relative biomass between the two species (Table 1). The values are significantly different, however, when they are expressed on a surface area basis, i.e. 6.92 ± 2.59 (10) mg d.t. cm^{-2}, (*P. verrucosa*) vs. 5.33 ± 2.74 (9) mg d.t. cm^{-2} (*P. damicornis*) (Table 1).

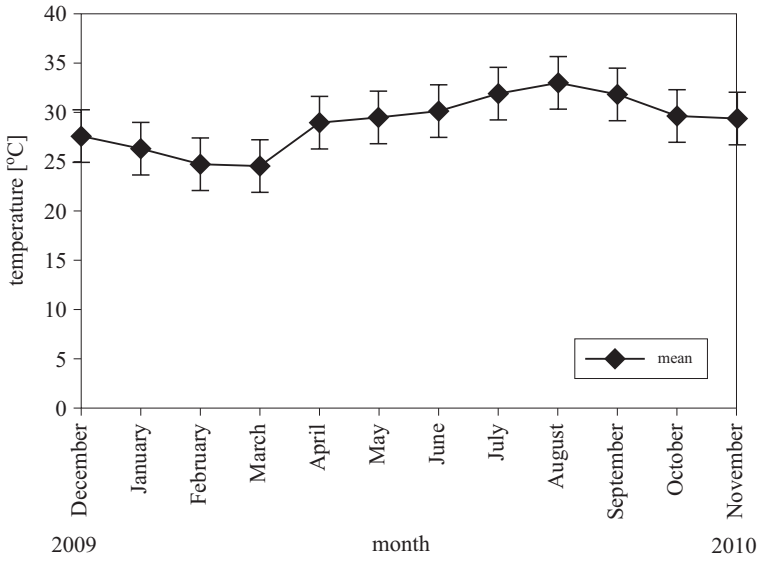

Figure 2. Monthly variation of seawater temperature [°C] at the Obhur Creek study site at 3 m depth from December 2009 to November 2010. Error bars indicate the standard deviation of two values in a month

The difference in the number of zooxanthellae between the two species on the basis of biomass and surface area (t-test $p < 0.004$) was highly significant during winter but not significant during summer. In winter a smaller number of zooxanthellae (1.5×10^5 and 0.74×10^5 mg^{-1} dry tissue wt.) is associated with *P. verrucosa*, whereas in summer it is *P. damicornis* (1.73×10^5 and 0.76×10^5 mg^{-1} dry tissue wt.) that has the smaller number of zooxanthellae. However, on the basis of surface area

the situation was reversed: *P. verrucosa* had more zooxanthellae (7.85×10^5 and 4.87×10^5 cm^{-2}) than *P. damicornis* (4.76×10^5 and 2.78×10^5 cm^{-2}) in winter and summer respectively. Significantly, both species were present in smaller numbers in summer than in winter (Table 1).

3.2. Respiration

The mean values of dark coral respiration for *P. damicornis* and *P. verrucosa* are expressed on the basis of tissue biomass and surface area. The relevant data are given in Tables 2 and 3 and in Figure 3. The average rate of dark respiration in *P. damicornis* was slightly higher during winter at 25°C than in summer at 35°C. However, the values at 25°C and 35°C were lower than at 30°C during winter, with no significant difference, as indicated in Table 2 and Figure 3. The mean rate of dark respiration in *P. verrucosa* was significantly lower during winter at 25°C than during summer at 35°C. It was also significantly higher at 30°C than at 25°C (Table 2, Figure 3). The mean respiration rate per tissue biomass of *P. damicornis* was higher than that of *P. verrucosa* when compared at 25°C and 30°C. At 35°C, the respiration rate of *P. verrucosa* was high with no great differences across the range of all seawater temperatures. With regard to respiration per surface area, *P. verrucosa* had a higher rate of respiration than *P. damicornis*, with a significant difference only at 35°C (Table 3).

3.3. Zooxanthellae

The mean rate of dark respiration of zooxanthellae on the basis of tissue biomass and number of zooxanthellae is given in Tables 2 and 3 and Figure 3. Different patterns were observed in the respiration rates of freshly isolated zooxanthellae. The average respiration rate in *P. damicornis* was lower in winter at 25°C than in summer at 35°C – this difference was significant (Table 2). The value at 30°C was higher than at 25°C, but the difference in this case was not significant (Table 2, Figure 3). Similarly, in *P. verrucosa* the average rate of respiration at 25°C is lower than summer at 35°C, the difference being significant.

The mean rate of dark respiration of zooxanthellae in *P. verrucosa* was higher than in *P. damicornis* on the basis of tissue biomass when compared at 25°C and 30°C, the difference at 30°C being significant, but at 35°C, the rate of zooxanthellae respiration in *P. damicornis* was significantly higher than in *P. verrucosa* (Table 3).

Table 3. Comparison between species of mean dark respiration of the colony and freshly isolated zooxanthellae of *Pocillopora damicornis* and *P. verrucosa* at different seawater temperatures. The standard deviation (SD) and number of measurements (n) are given

	P. damicornis				*P. damicornis*				*P. verrucosa*			
	25°C	30°C	t-test	p-value	25°C	35°C	t-test	p-value	25°C	30°C	t	p-value
Respiration colony												
μl O_2 mg^{-1} d.t. h^{-1}	1.196	1.04			1.59	1.42			1.19	1.37		
SD ±	0.56	0.29			0.44	0.35	0.97	0.34	0.39	0.36	0.84	0.410
n	10	10	0.79	0.43	10	10			10	10		
μl O_2 cm^{-2} h^{-1}	6.49	6.87			8.34	9.38			6.46	9.14		
SD ±	3.03	1.92	0.33	0.75	2.28	2.28	1.02	0.32	2.15	2.4	10.0*	0.001
n	10	10			10	10			10	10		
Zooxanthellae												
μl O_2 mg^{-1} d.t h^{-1}	0.24	0.26			0.26	0.27			0.47	0.34		
SD ±	0.1	0.14	0.34	0.74	0.15	0.13	0.15	0.89	0.11	0.13	2.26*	0.037
n	10	10			10	10			10	10		
μl O_2 10^{-6} h^{-1}	2.84	2.39			1.87	1.25			7.46	5.78		
SD ±	1.1	1.3	0.79	0.44	3.03	2.48	0.77	0.45	1.83	2.25	1.83	0.084
n	10	10			10	10			10	10		

*significance ($p \leq 0.05$).

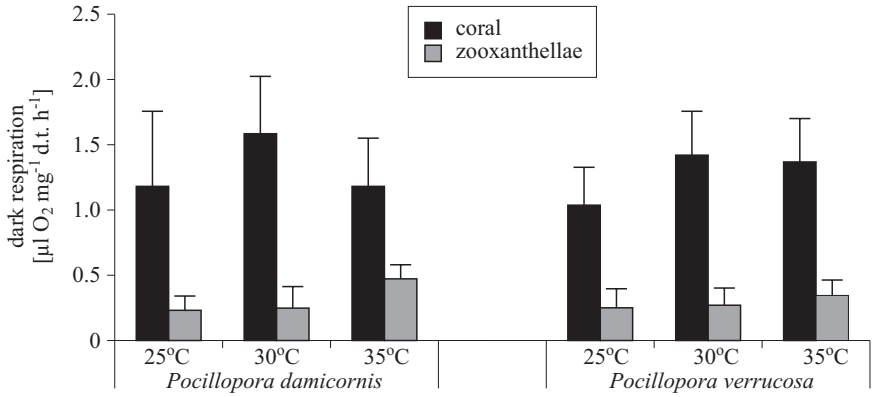

Figure 3. Comparison between the mean dark respiration of *Pocillopora damicornis* and *P. verrucosa* and their freshly isolated zooxanthellae at different temperatures during summer and winter

3.4. Growth rates

The growth rate of *P. damicornis* and *P. verrucosa* was approximately linear during each period of measurement (Figures 4, 5). The highest

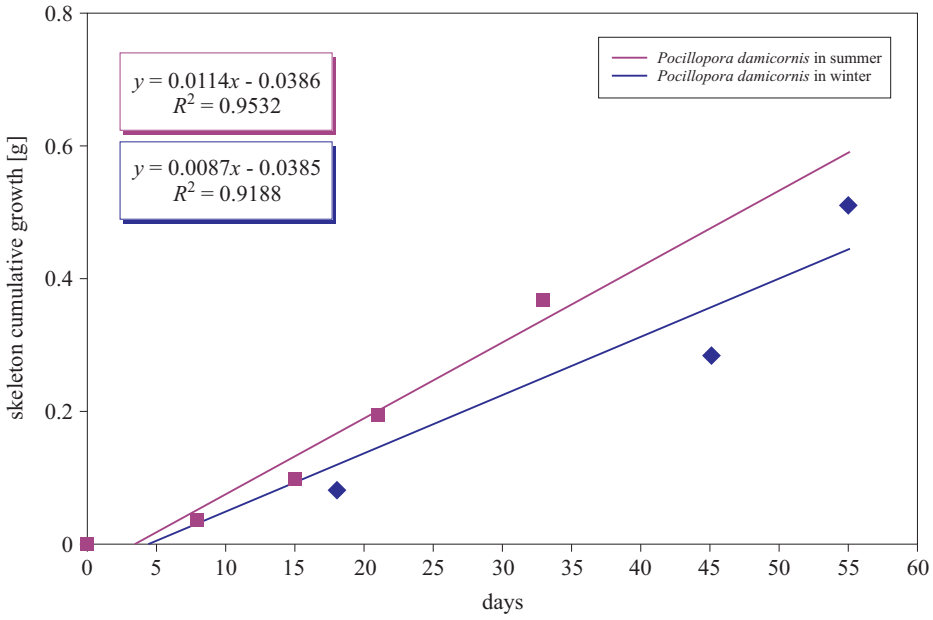

Figure 4. Cumulative growth of the skeleton of *Pocillopora damicornis* growing at a depth of 3 m during summer and winter 2010

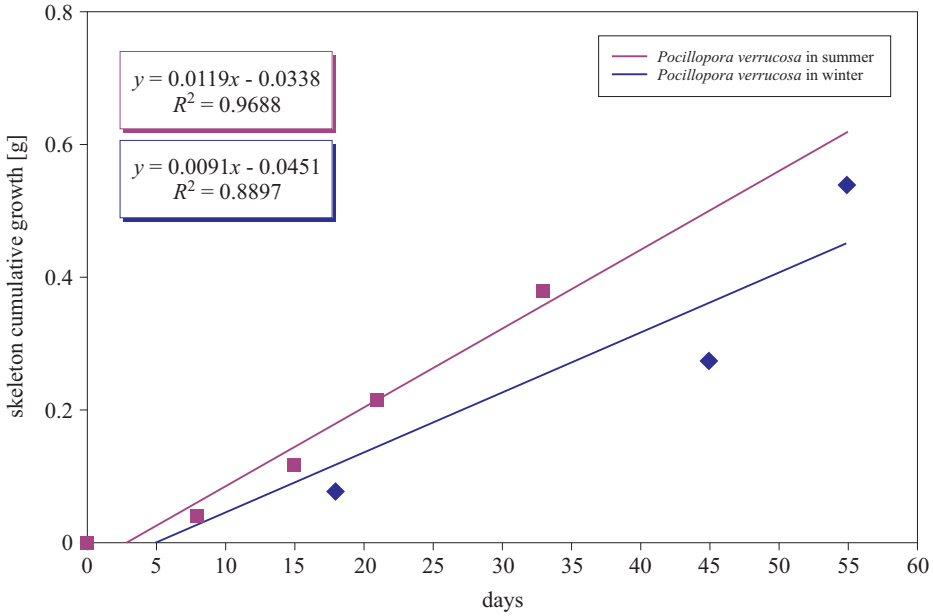

Figure 5. Cumulative growth of the skeleton of *Pocillopora verrucosa* growing at a depth of 3 m during summer and winter 2010

mean daily skeletal growth rate of *P. damicornis* at 3 m was 6.08 ± 0.77 (10) mg skel. d^{-1} during winter whilst the lowest value was 3.90 ± 1.16 (10) mg skel. d^{-1} during summer; the difference was not significant, however. The growth rate of *P. verrucosa* was also lower (5.40 ± 2.00 (10) mg skel. d^{-1}) in summer than during winter (7.44 ± 1.69 (10) mg skel. d^{-1}) at the same depth; this difference was significant. In general, *P. verrucosa* had a higher mean daily skeleton growth rate than *P. damicornis* during

Table 4. Seasonal variation in the mean daily skeleton growth rate of *Pocillopora damicornis* and *P. verrucosa*. The mean growth for each species was compared using Student's *t*-test. The standard deviation (SD) and number of measurements (n) are given

Growth rate	*P. damicornis*				*P. verrucosa*			
	winter	summer	*t*-test	*p*-value	winter	summer	*t*-test	*p*-value
Skeleton								
mg skeleton d^{-1}	6.08	3.90			7.44	5.40		
SD	0.77	1.16	4.94	0.001*	1.69	2.00	2.44	0.025*
n	10	10			10	10		

*significance ($p \leq 0.05$).

winter and summer 2005, the differences between the species being considerable (Table 4, Figure 6).

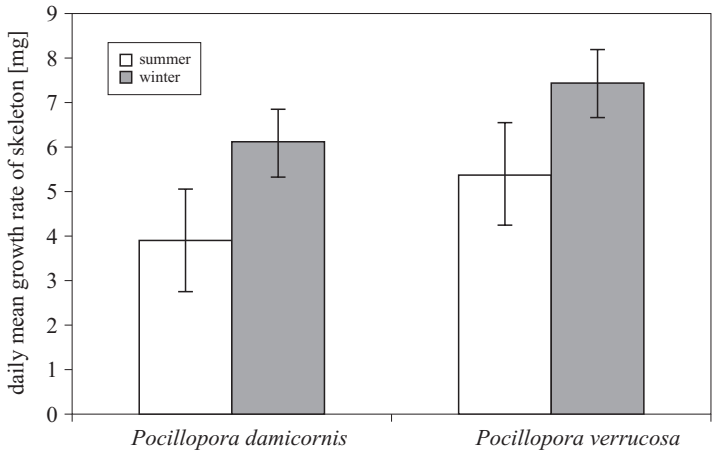

Figure 6. Comparison of the mean daily skeleton growth rate between two species during winter and summer 2010

4. Discussion

The seawater temperature exhibits seasonal variation at Jeddah. During 2005, the seawater temperature ranged from 24.5 to 33.0°C at 3 m depth. These temperature changes had an influence on zooxanthellae respiration rates as well as on the coral growth rate. A previous study by Al-Sofyani & Davies (1992) showed a seawater temperature range between 25 and 32°C at 3 m depth in Obhur Creek, whereas the range in the northern part of the Gulf of Aqaba was from 21 to 27°C (Edward 1987). In general, the main feature of seawater temperature along the Saudi Arabian Red Sea coast is that it generally decreases with distance from the equator (Al-Sofyani 1987, 2002).

It was found that *P. verrucosa* has a lower tissue biomass (11.32%) when compared with *P. damicornis*, but *P. damicornis* has a lower biomass (22.98%) of tissue per surface area than *P. verrucosa*. This is probably due to the differences in the growth form of the two species or to the tissue location within the skeleton (Al-Sofyani 1991, Davies 1991). The tissue biomass, equal to 28.1 mg d.t. g^{-1} skel. in *P. damicornis* and 24.92 mg d.t. g^{-1} skel. in *P. verrucosa* at 3 m depth, is higher than the values reported for *Pocillopora eydouxi* and lower than those for *Montipora verrucosa* and *Porites lobata* (Davies 1984, 1991). The respective tissue biomasses [mg d.t. g^{-1} skel.], reported by Al-Sofyani (1991) for *Stylophora*

pistillata and *Echinopora gemmacea*, were 10.30 and 12.86 mg d.t. g^{-1} skel. from the Red Sea. However, on a unit area basis [mg d.t. cm^{-2}], the values of 5.33 mg for *P. damicornis* and 6.92 mg for *P. verrucosa* were close to the range reported for *Montastrea annularis* at 2 m and 10 m depth respectively (Davies 1980) and for six species at 2.5 m depth from Barbados, West Indies (Lewis & Post 1982). Al-Sofyani (1991) reported low values of 3.52 mg for *S. pistillata* and 4.91 mg for *E. gemmacea* at 1 m and 3 m depth respectively from the Red Sea. The differences between these values may be due to the different growth forms of these species or to the methods used for measuring surface area (Al-Sofyani 1991).

The densities of zooxanthellae at 3 m depth were approximately 13.3% on *P. damicornis* and 2.63% on *P. verrucosa*. The respective zooxanthellae densities at 3 m depth for *P. damicornis* and *P. verrucosa* were $2.40 \times 10^6 \pm 0.57$ and $2.7 \times 10^6 \pm 1.07$ g^{-1} skel.; these values are similar to the value of 2.87×10^6 g^{-1} skel. for *S. pistillata* but higher than the 1.63×10^6 g^{-1} skel. for *E. gemmacea* and the 1.5×10^6 g^{-1} skel. for *Fungia fungites* (Al-Sofyani 1991, Jan 2001). On the basis of dry tissue weight, the density of zooxanthellae was $1.73 \times 10^5 \pm 0.23$ for *P. damicornis* and $1.5 \times 10^5 \pm 0.52$ mg for *P. verrucosa*. These values were lower than that of *S. pistillata*, but is similar to the one reported for *E. gemmacea* (Al-Sofyani 1991). However, the number of zooxanthellae per area unit of 4.76×10^5 cm^{-2} for *P. damicornis* and 7.85×10^5 cm^{-2} for *P. verrucosa* were lower than the values reported for *S. pistillata* (Falkowski & Dubinsky 1981, Porter et al. 1984, Al-Sofyani 1991). Stimson (1997) reported a high variability in algal densities within coral species. Drew (1972) and Porter et al. (1984) reported that the density of zooxanthellae per unit area are the same at different depths and among coral genera, while Dustan (1979, 1982) showed that the number of zooxanthellae in *M. annularis* decreases with increasing depth and that the zooxanthellae appear to photo-adapt to low light intensities by increasing the size of the photosynthetic units.

Both species exhibited an annual cycle in zooxanthellae density, which was lower in summer (Table 1). *P. damicornis* has a lower density (66%) of zooxanthellae in summer than in winter. Likewise, *P. verrucosa* has a lower density (62.08%) in summer than in winter. Previous studies reported that the annual cycle in the number of zooxanthellae of corals was due to changes in shallow water environments in factors such as irradiance, UV radiation, nutrients and temperature (Stimson 1997). The density of zooxanthellae decreased in response to increased irradiance (Stimson & Kinzie 1991, Thinh 1991). In the present study, the seawater temperature showed elevated values during the summer months while Al-Sofyani (1991) reported that the photosynthetically active radiation (PAR μE m^{-2} s^{-1}) in Obhur Creek

at 3 m depth was maximum in June (1212 μE m^{-2} s^{-1}) and minimum at the end of November (727 μE m^{-2} s^{-1}).

The mean dark respiration rates were slightly inconsistent between the two species on the basis of milligram dry tissue weight [mg d.t. wt. h^{-1}]. The respiration rate of *P. damicornis* was higher at 30°C in winter than at 25°C and 35°C in winter and in summer respectively. Conversely, in *P. verrucosa* it was significantly higher at 30°C in winter and 35°C in summer than at 25°C in winter. In *P. damicornis* zooxanthellae respiration was significantly higher in summer with acute responses at 35°C than in winter at 25°C and 30°C. However, the respiration of zooxanthellae on *P. verrucosa* did not show any significant variation between summer and winter, with no acute responses at 35°C. Since the respiration of zooxanthellae contributes only about 10–29% of the colony respiration (Davies 1991, Al-Sofyani & Davies 1992), the difference in the respiration of zooxanthellae in response to experimental temperatures in the present study may be due to the variable thermal tolerances of the symbionts. Unlike the zooxanthellae of *P. verrucosa* at 35°C, which account for only 25% of the colony respiration, those of *P. damicornis* contributed 39% at the same temperature. It is suggested that in both species the difference in zooxanthellae thermal tolerances at 35°C may correspond to differences in tolerance of algal genotypes between *P. damicornis* and *P. verrucosa* (Brown et al. 2000). This view was further supported by the grouping of zooxanthellae of scleractinian corals into different clades. For example, clade D was found in *P. verrucosa* from eastern Pacific reefs (Coffroth & Santos 2005), while clade C was found in *P. damicornis* (Karako-Lampert et al. 2004). The work of Baker et al. (2004) suggests that members of clade D may have greater thermal tolerances than clade C in their zooxanthid samples of *Palythoa caribaeorum*. Further, clades A and B inhabit shallow water colonies, while clade C zooxanthellae are found in deeper water colonies, or in shaded areas of the same individual coral colony (Rowan & Knowlton 1995, Toller et al. 2001).

During the bleaching event in August 1998, some coral species such as *P. damicornis* displayed less resistance to bleaching than *P. verrucosa* owing to the unusually high seawater temperature and the calm sea (Al-Sofyani 2000, Ralph et al. 2005). Nakamura et al. (2004) reported that the dark respiration rate of the coral species *Acropora pruinosa* was higher in winter than in summer, especially in the 20–30°C temperature range. Moreover, Coles & Jokiel (1977) demonstrated a very high response of metabolic rate to temperature change in the corals *P. damicornis*, *Montipora verrucosa*, *Porites compressa* and *Fungia scutaria* over the range 19–31°C in Hawaii and Enewetak.

Respiration rate was inversely correlated with the ambient temperature at which the corals were living (24°C for Hawaii and 28°C for Enewetak), which is strongly indicative of compensatory acclimation to temperature (Hochachka & Somero 1984). Acclimation has the effect of increasing metabolic rate during long-term exposure to reduced temperature. If acclimation is complete, the metabolic rates when measured at the temperature at which the animals are living are identical. This may therefore explain the similarity of respiration rates in summer and winter in *P. verrucosa*. Conversely, the lower rate of zooxanthellae respiration in winter at 25°C and 30°C demonstrated by *P. damicornis* is indicative of the normal acute temperature response at 35°C, and compensatory acclimation does not appear to have occurred.

Linear growth rates can be interpreted as suggesting that growth increases rapidly at the tip of the nubbin rather than laterally (Davies 1984, Al-Sofyani 1991). The results of the present study indicate that in both species the growth rate of the skeleton in winter is twice that in summer. Moreover, there is a very close correlation with the higher rate of metabolism during spring, which may be linked to the suitable experimental temperature at 30°C where the maximum metabolic rate occurred. Coles & Jokiel (1977) demonstrated that maximum skeletal growth occurred at an experimental temperature corresponding to ambient reef temperature, but was slower at both higher and lower temperatures. *P. damicornis* displayed lower rates of skeletal growth than *P. verrucosa* in both summer and winter. Light quality and intensity, as well as seawater temperature during summer may affect the growth rates of *P. damicornis* and *P. verrucosa*, since the mean respiration rate of zooxanthellae increases dramatically with increasing temperature at 35°C, especially in *P. damicornis*. However, the growth rate of hermatypic corals is influenced by external factors such as light quality and intensity, temperature and sedimentation, and also by internal factors such as reproduction, genetics, colony growth form and the number or type of zooxanthellae (Al-Sofyani & Davies 1992, Atkinson et al. 1995).

It is concluded that in both species the difference in zooxanthellae thermal tolerances at 35°C could be due to differences in tolerance of the algal genotypes between the two species. *P. verrucosa* is more flexible to temperature than *P. damicornis*. *P. verrucosa* exhibited a significantly higher mean daily skeletal growth rate than *P. damicornis* during both winter and summer. The zooxanthellae density was slightly higher in *P. damicornis* than in *P. verrucosa*. As a result of the zooxanthellae density and optimum SST, the growth rates of these two coral species were almost twice as fast in winter than in summer.

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