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Variation in photosynthesis and respiration in geographically distinct populations of two reef-building coral species

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ABSTRACT: Studies of the regulation and importance of physiological processes such as coral photosynthesis and respiration on coral reefs require knowledge of spatio-temporal patterns of variability at different scales. Oxygen microelectrodes were used to measure photosynthesis and dark respiration of 2 corals, *Pocillopora damicornis* and *Turbinaria reniformis*, in the northern (Lizard Island) and central (Davies and Broadhurst Reefs) regions of the Great Barrier Reef (GBR) in winter and summer. Genetic characterisation of *Symbiodinium* revealed that *P. damicornis* hosted a single symbiont type (*Symbiodinium* C1) in both regions, whereas *T. reniformis* harboured 2 types, dependent on location. Colonies at Lizard Island harboured *Symbiodinium* D, whereas colonies at Davies Reef harboured *Symbiodinium* C2. Rates of gross photosynthesis were greater in the central than in the northern GBR in summer. A similar pattern was detected for dark respiration rates in *T. reniformis*. No seasonal change in either photosynthesis or dark respiration was evident in the northern GBR, possibly due to less annual variability in light conditions, and for *T. reniformis*, additionally the presence of *Symbiodinium* D. These results highlight that environmental conditions coupled with regional-scale distribution of *Symbiodinium* are likely to exert important influences on respiration and photosynthetic performance of reef-building corals.

KEY WORDS: Gross photosynthesis rate · O_2 microelectrode · *Symbiodinium* · Great Barrier Reef

INTRODUCTION

The obligate association between *Symbiodinium* dinoflagellates and reef-building corals is maintained within a narrow temperature range (Hoegh-Guldberg 1999), where the productivity of *Symbiodinium* results in a net translocation of photosynthates to the host at irradiances higher than the compensation irradiance (E_c) (Muscatine 1990). At irradiances below E_c, respiration exceeds production from photosynthesis, and light is, therefore, insufficient to cover the energetic demands of the holobiont. In highly oligotrophic environments, heterotrophic carbon and nutrient acquisition is considered limited for corals, which are likely to be adapted to a diet based mainly on the translocation of photosynthates from *Symbiodinium*. Environmental changes that cause increased metabolic demands, therefore, need to be paralleled by an increase in *Symbiodinium* production capacity to avoid constraining coral fitness.

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Photosynthesis and respiration, as measured by gas exchange, is, surprisingly, rarely measured for coral systems, despite the importance of understanding their metabolism. Further, we still know little in regards to how the photosynthesis:respiration ratio is regulated in reef systems on seasonal and large spatial scales. Photosynthesis and respiration quantified by O_2 evolution of a coral community (Kayanne et al. 2005) as well as for individual coral species (Al-Sofyani & Davies 1992, Nakamura et al. 2004) have previously been documented over seasonal scales. However, the findings in these studies were not consistent, suggesting that local environmental conditions, and possibly adaptive traits of the investigated holobionts, can exert important influences on metabolic processes.

Specific adaptive traits affecting metabolic processes, such as increased thermal tolerance, could arise from the type of *Symbiodinium* hosted by corals. Partitioning of genetically distinct *Symbiodinium* communities in conspecific coral populations has been found to correlate with latitude (Loh et al. 2001, Rodriguez-Lanetty et al. 2001, Savage et al. 2002, Ulstrup et al. 2006a) as well as with coral bleaching susceptibilities (Glynn et al. 2001, Berkelmans & van Oppen 2006, Ulstrup et al. 2006a). This suggests that thermal tolerance is controlled by local environmental conditions that corals have adapted to (West & Salm 2003) or that have caused the expression of distinct phenotypes. For instance, Ulstrup et al. (2006a) found that *Turbinaria reniformis* in the central region of the Great Barrier Reef (GBR) harboured predominantly *Symbiodinium* C, whereas conspecifics in the northern region of the GBR harboured predominantly *Symbiodinium* D. Although this pattern is specific to the type of coral examined, the occurrence of *Symbiodinium* D in this instance may provide a selective advantage for *T. reniformis* in the relatively warmer environment of the northern GBR.

While the interaction between *Symbiodinium* type and patterns of photosynthesis and respiration activity has been investigated over local-scale depth gradients (Mass et al. 2007), our understanding of such patterns of variation at larger spatial scales is currently limited. However, a recent study by Hennige et al. (2010) of the photosynthesis and respiration activity of corals across an environmental gradient of temperature, light and turbidity confirmed that metabolic rates were governed by acclimatisation to the local environment coupled with adaptation, which was manifested through a shift in *Symbiodinium* clade for one of their study species.

Winter and summer patterns of photosynthesis and dark respiration of geographically distinct coral populations that form symbiotic relationships with different *Symbiodinium* types have yet to be described. In the present study, we examined 2 species of reef-building corals with contrasting thermal tolerances and *Symbiodinium* type, *Pocillopora damicornis* (sensitive, *Symbiodinium* C1-specific) and *Turbinaria reniformis* (tolerant, spatial variation in *Symbiodinium* type harboured), during the austral summer and winter.

MATERIALS AND METHODS

Study area and sampling design. Photosynthesis and dark respiration were examined in *Pocillopora damicornis* and *Turbinaria reniformis* from mid-shelf reefs within the northern and central region of the GBR, Australia. In the northern region, colonies were collected at Lizard Island (14° 40.00′ S, 145° 27.48′ E) in late July 2005 (winter) and January 2006 (summer). In the central region, *T. reniformis* was sampled at Davies Reef (18° 49.57′ S, 147° 37.76′ E) in August 2005 (winter) and February 2006 (summer). *P. damicornis* was sampled at Broadhurst Reef (18° 52.27′ S, 147° 42.35′ E) in winter and at the adjacent Davies Reef during the summer sampling. Lizard Island is located approximately 500 km north of Davies and Broadhurst Reefs, which are about 10 km apart (Fig. 1a).

Corals were sampled between 2 and 4 m below lowest astronomical tide (LAT) on each of 2 occasions spanning 2 wk: July or August 2005 and January or February 2006. Care was taken in targeting upright surfaces exposed to full ambient light and flow conditions, thereby minimising possible effects of microenvironmental gradients among the samples. Secchi depth data for the 2 locations were derived from a spatial model based on a comprehensive dataset comprising >2000 observations across the GBR (http://eatlas.org.au). The daily photoperiod (sunrise to sunset) at Lizard Island and Davies Reef was obtained between May 2005 and April 2006 from Geoscience Australia (www.ga.gov.au) and used to determine the mean monthly photoperiod (Fig. 1b). Sea surface temperatures (SST) were obtained from the Australian Institute of Marine Science long-term temperature monitoring program (www.aims.gov.au/docs/data-centre/seatemperatures.html). Average daily SST was acquired by temperature loggers (Dataflow Systems) deployed at 6 to 9 m depth on the reef slope at Lizard Island (14° 41.3′ S, 145° 26.6′ E) and Davies Reef (18° 48.4′ S, 147° 40.1′ E) (Fig. 1c).

Genetic characterisation of *Symbiodinium*. *Symbiodinium* in 4 colonies from each of the populations of *Pocillopora damicornis* and *Turbinaria reniformis* collected in winter were genetically characterised using the PCR-single stranded conformation polymorphism (SSCP) assay for the internal transcribed spacer region 1 (ITS1) as described in van Oppen et al. (2001). PCR products that resulted in different SSCP profiles

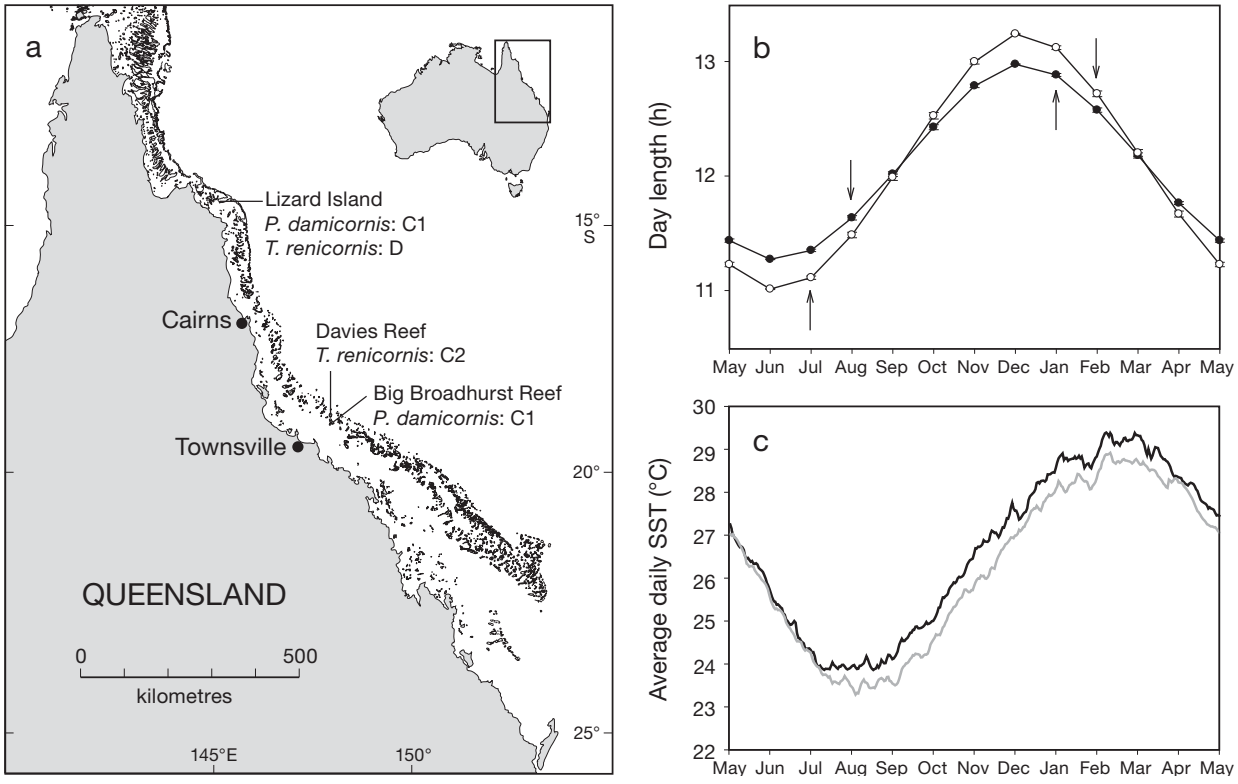

Fig. 1. (a) Map of the northeastern Australian coast showing sampling locations of *Pocillopora damicornis* and *Turbinaria reniformis* and their associated symbiont (*Symbiodinium*) type. (b) Annual variation in day length at Lizard Island (●) and Davies Reef (○) between May 2005 and April 2006. The data is derived from Geoscience Australia (www.ga.gov.au) and represents monthly averages (±SE). Arrows indicate time of sampling at Lizard Island (upward-pointing arrows) and Davies Reef (downward-pointing arrows). (c) Average daily sea surface temperature (SST) for the reef slope (6 to 9 m depth) for each day (48 measurements per day) at Lizard Island (black) and Davies Reef (grey) between May 2005 and April 2006

were sequenced (Macrogen) and compared to existing sequences stored in GenBank (www.ncbi.nlm.nih.gov).

Photophysiological measurements. At each location, fragments of 4 (n = 4) colonies of both species were collected in the afternoon and placed at ambient seawater temperature (winter: ~24.0 ± 0.5°C, summer: ~28.5 ± 0.5°C) in a flow-through seawater tank overnight. During measurements conducted the following morning, the corals were held within a custom-built flow chamber (25 × 10 × 10 cm) at a controlled flow velocity of ~1 cm s^{-1}. O_2 microelectrodes (Unisense) with a tip diameter of 25 to 50 µm were linearly calibrated at experimental temperature and salinity from readings in air-saturated and O_2-free seawater, respectively. The microsensor tip was positioned on the coenosarc surface of the coral through the centre of an LED ring which provided actinic light from oblique angles, thus minimising any self-shadowing effects on the measurements (Ulstrup et al. 2006b). Positioning of the microsensor was done while observing the sample with a dissecting microscope (Leica). Each of 8 actinic irradiances (0, 20, 41, 82, 139, 196, 385, 900 µmol photons m^{-2} s^{-1}) were applied for 10 min. This was sufficient to reach steady-state O_2 conditions, which is assumed for the photophysiological measurements (Ulstrup et al. 2006b).

A vertical microprofile of the O_2 concentration gradient across the diffusive boundary layer was performed at stepwise increments of 10 to 20 µm following incubation at each irradiance level. Area-specific net photosynthesis (P_n, nmol O_2 cm^{-2} s^{-1}) was calculated from the linear slope of the O_2 concentration gradient in the diffusive boundary layer (DBL) using Fick's 1st law assuming a 1-dimensional diffusion geometry (Kühl et al. 1995, 1996). The dark microprofile conducted initially yielded a measure of area-specific respiration, R_D, of the holobiont. Net photosynthesis measured at the maximum irradiance (900 µmol photons m^{-2} s^{-1}, P_{n900}) was chosen to calculate the photosynthesis:respiration ratio, P_{n900}:R_D, as this represented an irradiance level where all samples were light saturated.

Upon completion of microprofile measurements at each irradiance level, the microsensor tip was repositioned at the coenosarc surface and a brief experimental light–dark shift was applied to allow calculation of the local volume-specific gross photosynthesis

rate (P_g, nmol O_2 cm^{-3} s^{-1}). The light-dark shift technique is based on the assumption that the immediate O_2 depletion following the light–dark shift is equal to the gross photosynthetic O_2 production during the previous light period (e.g. Kühl et al. 1996) in the measuring spot. The method yields the local volume-specific gross photosynthesis rate at a spatial resolution of ~100 µm and is independent of respiration (Revsbech & Jørgensen 1983). This approach thus avoids problems associated with using dark respiration to calculate P_g, given the effects of light on respiration rates (Edmunds & Davies 1988, Kühl et al. 1996, Cooper et al. 2011). The light–dark shift technique seems to include O_2 consumed by photorespiration, but not the Mehler reaction, which is tightly coupled to photosynthetic electron transport (Glud et al. 1992).

In principle, net fluxes of O_2 can be subtracted from depth-integrated rates of gross-photosynthesis measurements done throughout the photic zone, yielding a measure of respiration in the light (Kühl et al. 1996). However, we only measured gross photosynthesis at the coenosarc tissue surface and could thus not do such calculations. The whole measuring sequence for each replicate took ~2 h to complete. Collection of coral fragments was staggered such that the difference in acclimatisation period between replicates was no more than 2 h. This was also done to minimise any potential effects of hysteresis and acclimation to the holding facility conditions (Anthony & Hoegh-Guldberg 2003).

Statistical analysis. Changes in symbiont photosynthesis and holobiont dark respiration as a result of sampling time and differences in latitude were assessed by 2-way ANOVA. The factors were Time and Location, with each considered as random and orthogonal. For all ANOVAs, Cochran's *C*-test was used to test for homogeneity of variances and data was transformed if necessary. Pooling procedures involving elimination of terms from the mean square estimates were done if a term was non-significant at $p > 0.25$ (Underwood 1997). Means for significant factors in the ANOVAs were compared using Student-Newman-Keuls (SNK) tests.

RESULTS

Genotyping analysis revealed that *Pocillopora damicornis* harboured *Symbiodinium* C1 irrespective of sampling location. In contrast, *Turbinaria reniformis* collected at Davies Reef harboured *Symbiodinium* C2 and at Lizard Island *Symbiodinium* D (Fig. 1a) sensu Ulstrup et al. (2006a). Light data for Lizard Island and Davies Reef showed that the optical properties of the column were comparable between the 2 locations with Secchi depths ranging from 13 to 16 m and 16 to 21 m, respectively. The annual range in photoperiod was

Table 1. ANOVAs comparing photo-physiological parameters of *Pocillopora damicornis* and *Turbinaria reniformis* between times of sampling and location on the Great Barrier Reef (GBR). * term eliminated at $p > 0.25$. Abbreviations: P_{g900} = gross photosynthesis rate (nmol O_2 cm^{-3} s^{-1}), P_{n900} = net photosynthesis rate (nmol O_2 cm^{-2} s^{-1}) at 900 µmol photons m^{-2} s^{-1}, R_D = dark respiration rate (nmol O_2 cm^{-2} s^{-1}), NR = northern region, CR = central region of the GBR

Variate	Source of variation	df	MS	*F*	p	Post-hoc tests	
P. damicornis							
P_{g900}	Time	1	40.8	0.17	0.7523		
	Location	1	228.09	0.94	0.5099		
	Time × Loc.	1	242.66	5.79	0.0331	Summer	NR < CR
	Residual	12	41.91			Winter	NR = CR
P_{n900}	Time	1	0.8789	3.95	0.0703		
	Location	1	0.3053	1.37	0.2644		
	*Time × Loc.	1	0.0105	0.05	0.8317		
	Residual	12	0.2227				
R_D	Time	1	0.0176	0.15	0.7053		
	Location	1	0.1828	1.56	0.2357		
	*Time × Loc.	1	0.077	0.66	0.4336		
	Residual	12	0.1173				
P_{n900}:R_D	Time	1	4.5382	4.23	0.0622		
	Location	1	0.4774	0.44	0.5175		
	*Time × Loc.	1	0.0513	0.05	0.8306		
	Residual	12	1.0737				
T. reniformis							
P_{g900}	Time	1	133.29	0.42	0.6352		
	Location	1	141.13	0.44	0.6269		
	Time × Loc.	1	320.23	6.54	0.0251	Summer	NR < CR
	Residual	12	48.94			Winter	NR = CR
P_{n900}	Time	1	2.5213	0.97	0.5056		
	Location	1	0.5105	0.2	0.735		
	Time × Loc.	1	2.6117	4.52	0.0549		
	Residual	12	0.5778				
R_D	Time	1	0.6683	2.19	0.3784		
	Location	1	0.0663	0.22	0.7223		
	Time × Loc.	1	0.3053	9.21	0.0104	Summer	NR < CR
	Residual	12	0.0332			Winter	NR = CR
P_{n900}:R_D	Time	1	0.0086	0.01	0.9301		
	Location	1	0.3164	0.3	0.5968		
	*Time × Loc.	1	0.273	0.25	0.6229		
	Residual	12	1.0715				

31 min greater at Davies Reef than at Lizard Island (Fig. 1b). The annual range in SST at Lizard Island was ~5.5°C (23.9 to 29.4°C) and ~5.6°C (23.3 to 28.9°C) at Davies Reef. Ambient average daily winter and summer SST at the time of measurements in both regions were ~24°C and ~28.5°C, respectively (Fig. 1c).

The patterns of variation for gross photosynthesis rate at an irradiance of 900 µmol photons m^{-2} s^{-1} (P_{g900}) were dominated by inconsistent variability between times of sampling and location for both species (Time × Location, Table 1). For example, in summer, the P_{g900} of *Pocillopora damicornis* was higher at Davies Reef (23.92 ± 3.53 nmol O_2 cm^{-3} s^{-1}) than at Lizard Island (8.58 ± 2.99 nmol O_2 cm^{-3} s^{-1}), while there were no differences between regions in winter (Tables 1 & 2, Fig. 2). A similar pattern for P_{g900} occurred in *Turbinaria reniformis* (Tables 1 & 2, Fig. 2). Rates of dark respiration in *T. reniformis* also varied inconsistently between times of sampling and locations (Time × Location, Table 1). In summer, the R_D of *T. reniformis* was higher at Davies Reef (0.91 ± 0.12 nmol O_2 cm^{-2} s^{-1}) than at Lizard Island (0.51 ± 0.12 nmol O_2 cm^{-2} s^{-1}) but there were no differences between regions in winter (Fig. 3, Table 2). Although *P. damicornis* showed a trend for increased P_{n900} during summer in the central region of the GBR (Fig. 3) the P_{n900}:R_D ratio did not differ significantly between times of sampling or locations for either species (Tables 1 & 2). From Fig. 3, it is also apparent that the change in E_c is greater between seasons for the central than for the northern region of the GBR.

DISCUSSION

Measurements of net photosynthesis and dark respiration measured *in hospite* are influenced by an unknown contribution of host respiration as well as the respiration of other organisms associated with the coral colony, such as bacteria as well as *Symbiodinium*. Therefore, our results from O_2 microprofiling at the coral surface reflect the net production and dark respiration of the holobiont and not *Symbiodinium* alone. In

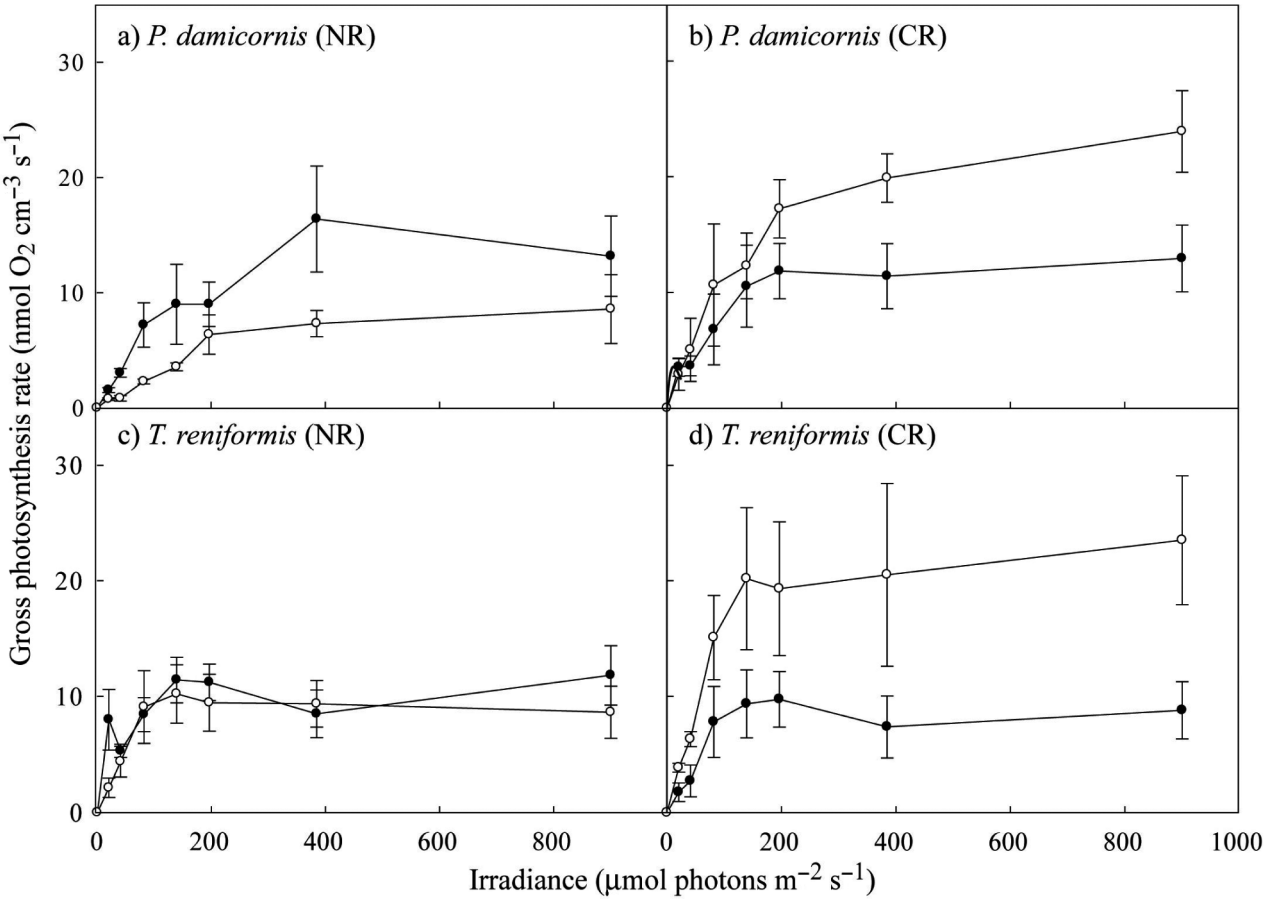

Fig. 2. *Pocillopora damicornis* and *Turbinaria reniformis*. Measurements of gross photosynthesis, P_g, using the light–dark shift method at the coenosarc tissue surface of (a,b) *P. damicornis* and (c,d) *T. reniformis* in summer (○) and winter (●) in (a,c) the northern (NR) and (b,d) central regions (CR) of the Great Barrier Reef. Values are mean ± SE (n = 4)

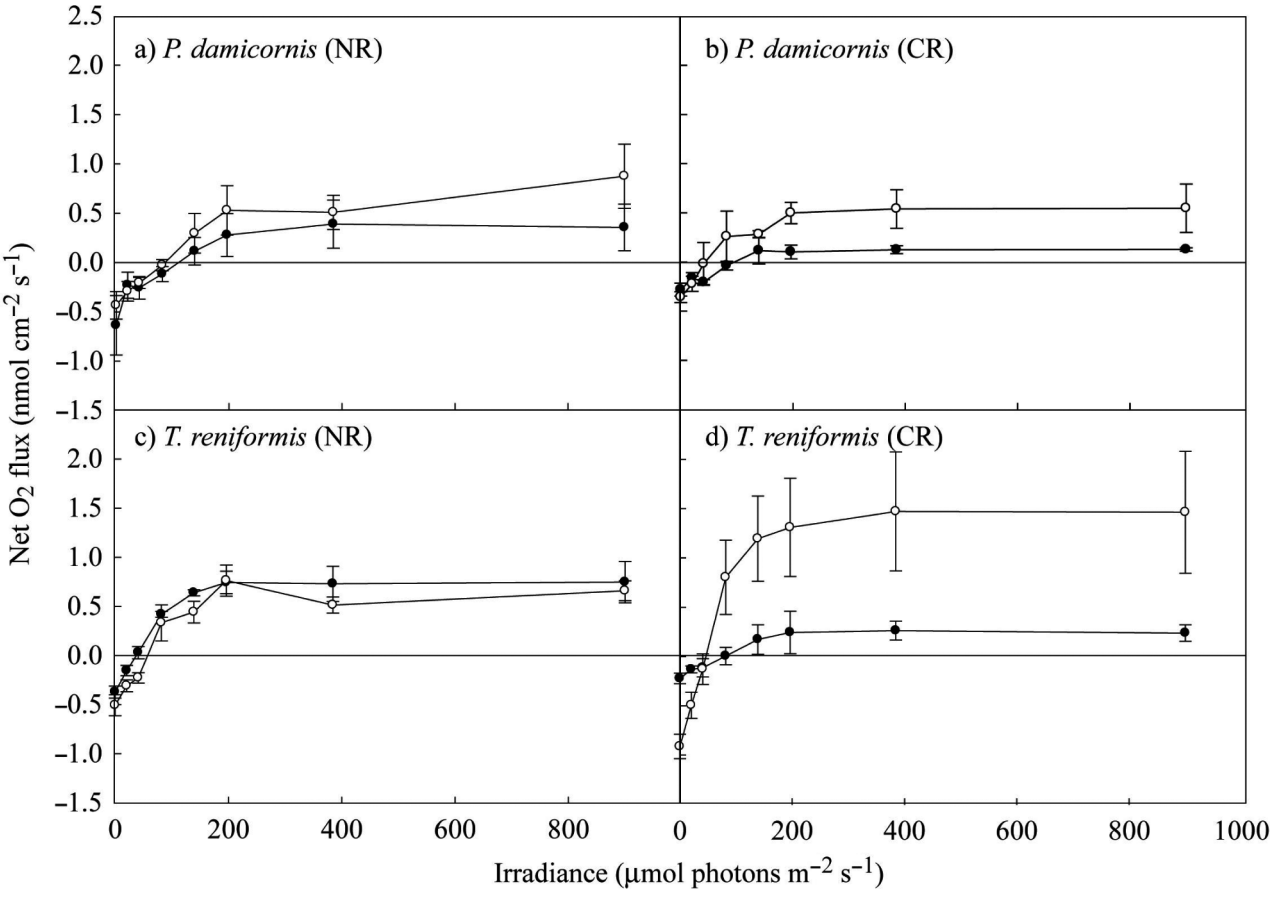

Fig. 3. *Pocillopora damicornis* and *Turbinaria reniformis*. Measurements of net photosynthesis, P_n, as calculated from O_2 microprofile measurements over the coenosarc tissue of (a,b) *P. damicornis* and (c,d) *T. reniformis* in summer (○) and winter (●) in (a,c) the northern and (b,d) central region of the Great Barrier Reef. Values are mean ± SE (n = 4). The horizontal line indicates O_2 flux and the irradiance at which the curve intersects the line is the compensation irradiance, E_c

contrast, measurements of gross photosynthesis rates obtained from the light-dark shift method in this study relate to *Symbiodinium* production *in hospite* and are achieved independently of holobiont respiration measurements. This constitutes a technical advantage of microsensor measurements over the more conventional approach of using respirometry chambers, which does not allow the measurement of P_n and P_g independently (Kühl et al. 1995, Ulstrup et al. 2006b). As a result, we found significant results for P_{g900} and not P_{n900}, which is only possible if respiration rates differ with differing illumination intensities (Table 1, Cooper et al. 2011).

Our results suggest that photosynthesis and dark respiration of corals are influenced by a combination of environmental conditions as well as adaptive traits of the holobiont such as the *Symbiodinium* type hosted. Although beyond the scope of this study, host charac-

Table 2. *Pocillopora damicornis* and *Turbinaria reniformis*. P_{g900}, P_{n900}, R_D and P_{n900}:R_D from the northern and central region of the Great Barrier Reef in summer and winter. See Table 1 for abbreviations. Values are mean ± SE (n = 4)

	P_{g900}		P_{n900}		R_D		P_{n900}:R_D	
	CR	NR	CR	NR	CR	NR	CR	NR
P. damicornis								
Summer	23.92 ± 3.53	8.58 ± 2.99	0.55 ± 0.25	0.88 ± 0.32	0.36 ± 0.05	0.43 ± 0.14	1.79 ± 0.99	4.36 ± 1.79
Winter	12.94 ± 2.89	13.17 ± 3.49	0.13 ± 0.02	0.36 ± 0.24	0.28 ± 0.07	0.64 ± 0.30	0.54 ± 0.16	0.87 ± 0.40
T. reniformis								
Summer	23.52 ± 5.59	8.63 ± 2.24	1.46 ± 0.62	0.66 ± 0.10	0.91 ± 0.12	0.51 ± 0.11	1.57 ± 0.69	1.58 ± 0.47
Winter	8.80 ± 2.46	11.80 ± 2.56	0.24 ± 0.08	0.75 ± 0.21	0.22 ± 0.05	0.37 ± 0.06	1.35 ± 0.53	1.89 ± 0.31

teristics such as pigmentation and anti-oxidative enzymatic activity may also influence the photophysiological responses of *Symbiodinium* (Lesser et al. 1990, Gates & Edmunds 1999, Salih et al. 2000). However, to our knowledge no regional-scale information on these host characteristics is available and this therefore warrants further investigation.

While corals in this study did not show any regional-scale differences in photosynthesis and dark respiration in winter, the differences observed in summer are likely to be affected by the contrasting environmental conditions between regions during this season. Lizard Island was ~0.5°C warmer but had a shorter photoperiod during summer than coral reefs in our central study region. Although photophysiological responses to experimental changes in temperature are well known (e.g. Coles & Jokiel 1977), the effect of spatial differences in irradiance are not. However, Mass et al. (2007) found that rates of photosynthesis and dark respiration decreased with increasing depth (and decreasing irradiance) over a 70 m depth gradient. A study by Cooper et al. (2011) confirmed this pattern but also found that a depth-related shift in *Symbiodinium* type in the coral *Seriatopora hystrix* over similar depths correlated with a non-linear response in the photosynthesis:respiration ratio. In addition to this, *Symbiodinium* cell densities may be dynamic over seasonal timescales, where densities are lower in summer than in winter (e.g. Fagoonee et al. 1999, Fitt et al. 2000). The effects of this on photosynthesis and dark respiration are, however, not easily interpreted as lowered densities may be paralleled by an increase in chlorophyll content per *Symbiodinium* cell (Brown et al. 1999, Cooper et al. 2008) as well as changes in host tissue biomass (Fitt et al. 2000), and are also likely to depend on the relative difference in environmental conditions among seasons.

The distribution pattern of *Symbiodinium* is likely to also influence the differences in photosynthesis and dark respiration observed between species, as *Symbiodinium* D in some associations has shown improved thermal tolerance compared to *Symbiodinium* C (e.g. Glynn et al. 2001, Berkelmans & van Oppen 2006). We hypothesize that the occurrence of *Symbiodinium* D in *Turbinaria reniformis* at Lizard Island is an adaptive response to the higher temperature regime at this site compared with Davies Reef (Ulstrup et al. 2006a). In contrast, the summer increase in dark respiration, and hence higher metabolic cost, of *T. reniformis* in the central region could reflect lower tolerance to increased temperature (Coles & Jokiel 1977), and possibly irradiance, of the association with *Symbiodinium* C2. The association between *Pocillopora damicornis* and *Symbiodinium* C1 was stable with respect to dark respiration across both spatial and temporal scales under non-bleaching conditions. The specificity of the association may, however, come at a cost during bleaching conditions, as a previous study demonstrated greater bleaching sensitivity of *P. damicornis* compared to *T. reniformis* irrespective of location (Ulstrup et al. 2006a).

In summary, these results suggest that local environmental conditions, as well as the *Symbiodinium* type involved in the coral-algal symbiosis are likely to exert important influences on photosynthetic performance and dark respiration of reef-building corals. We showed that temporal changes in photosynthesis and dark respiration were most pronounced in the central GBR. This is possibly due to greater seasonal variability in irradiance as well as adaptive traits of the holobionts investigated, such as the sensitivity of the association between *Turbinaria reniformis* and *Symbiodinium* C2 to summer conditions. Future studies should aim to determine the relative contribution of environmental controls, such as irradiance and temperature, and the effects of different *Symbiodinium* genotypes, on rates of photosynthesis and respiration.

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