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PHOTOSYNTHETIC PRODUCTION OF FOUR SCLERACTINIAN CORALS FROM SINGAPORE

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ABSTRACT

Singaporean reefs are characterised by highly turbid waters, which limit the depth distribution of corals to shallow waters. To investigate the relationship between phototrophic production and distribution, the productivity of four genera of hard corals was determined *in situ* using an automated respirometer. This respirometer measured changes in oxygen concentration in perspex chambers enclosing the experimental organisms. Four samples were obtained for each genus from a reef-flat west of Pulau Hantu, an island south of mainland Singapore. Measurements were taken concurrently with light intensity (irradiance) readings every 20 seconds over 24 hour periods. Photokinetic parameters ($Pm_{(gross)}$, Rd and Ik) were estimated for each sample by fitting a non-linear (hyperbolic tangent function) to the photosynthesis - irradiance curves. Instantaneous photosynthesis to respiration ($Pm_{(gross)}$/Rd) ratios were used to assign species to trophic categories. Estimates of net 24 h production were positive for all genera on both the reef-edge (depth 3.4 m) and the reef-flat (1.4 m). The depth at which net 24 hour compensation occurs for these genera is around 4 m which is close to the limit of their distribution on these reefs. This result suggests that these genera are largely dependant on photosynthesis by their symbionts for a major portion of their carbon requirements, but that they may also feed heterotrophically.

INTRODUCTION

Many aquatic invertebrates, including hermatypic scleractinian corals, are known to live in mutualistic symbioses with photosynthetic endosymbiotic algae commonly called zooxanthellae (Droop, 1963; Goreau, 1961; Odum & Odum, 1955; Taylor, 1973). The permanent nature of these associations enables the invertebrate host to exhibit a polytrophic feeding capacity (Johannes, 1974). Translocation of photosynthetic products from the endosymbiont enables the host to feed autotrophically (Lewis & Smith, 1971; Muscatine & Hand, 1958), while heterotrophic inputs can be obtained from suspension-feeding, tentactular-feeding, ciliary mucoid feeding and absorption of dissolved organic matter (Muscatine, 1973). The importance of this association is that it allows coral reef ecosystems to exist and thrive in the nutrient poor waters characteristic of the tropics.

Photophysiological studies aim to quantify the balance between photosynthesis and respiration in order to determine the relative importance of the autotrophic inputs. When gross 24 hour production exceeds the total respiration (ie net 24 hour production is positive) then the organism is capable of surviving entirely autotrophically. When the gross 24 hour production is less than the total respiration then a level of heterotrophy exists (McCloskey *et al.*, 1978) and is in fact necessary to support the respiratory demand of the organism.

Productivity by reef organisms is best measured *in situ*, where specimens experience a minimum of disturbance and are subjected to ambient conditions of light, temperature, salinity and nutrient availability. Over the past two decades, many automated systems have been developed for measuring the metabolic rates of marine organisms and communities *in situ*. These systems are generally known as respirometers and have been designed to monitor and record data such as O_2 concentration, temperature, light intensities and a variety of other physiological parameters of benthic invertebrates and turf algal communities (Wethey & Porter, 1976a; Svoboda, 1978; Barnes, 1983; Person *et al.*, 1984; Chalker *et al.*, 1985a; Klumpp *et al.*, 1987).

MATERIALS AND METHODS

Photosynthesis and respiration rates were determined *in-situ* for four genera of scleractinian coral (*Heliofungia*, *Goniopora*, *Fungia* and *Platygyra*) using an automated respirometer (designed and constructed at The University of Adelaide). The respirometer has a light sensor (Li-cor), a temperature probe and five chambers for the incubation of specimens. Each chamber was fitted with a stirrer, an O_2 electrode and is connected to a flushing pump. The chambers have an internal volume of 13.4 l (when empty) and a basal area of 0.086 m^2

(diameter of 33 cm). This respirometer is essentially similar to the one described by Chalker *et al.* (1985b) and a detailed description of the composition of the major sub-systems is given in their communication.

The coral genera were selected from a reef-flat west of Pulau Hantu after it was surveyed using the line-intercept-transect method (Dartnall & Jones, 1986). As far as possible within each genera, the organisms chosen were of the same species, but in some instances it was impossible to identify the organisms to species level in the field (specific identification of many hard corals requires the inspection of the $CaCO_3$ skeleton, which is only examinable after the organism is killed). As a consequence, the results presented below are specified at the generic level.

The respirometer was deployed *in-situ* on the edge of the reef-flat at Pulau Hantu at a depth of 3.4 m (at mean low tide - tidal range over the period of the study was around 2-2.5 m). For each deployment replicates of a given species were placed in four of the chambers; the fifth chamber remained empty as a control. Each deployment lasted for 24 hours and comprised a series of 72, 20 minute cycles. A battery powered pump flushed each chamber with seawater for 3 minutes at the start of each 20 minute cycle. Following this the water was circulated within the chamber for a period of 17 minutes during which time the oxygen concentration in the chamber was recorded at 20 second intervals. Over the 24 hour period a total of 4,320 records were obtained per sample per day. The rate of oxygen consumption or production within each chamber was evaluated by a determining the slope of the line relating oxygen concentration in the chamber to time for each 17 minute period. Similarly, the average light intensity was calculated over each 17 minute period. Photosynthetic rate for each period was then plotted against average light intensity to provide a PI (photosynthesis/irradiance) curve for each specimen.

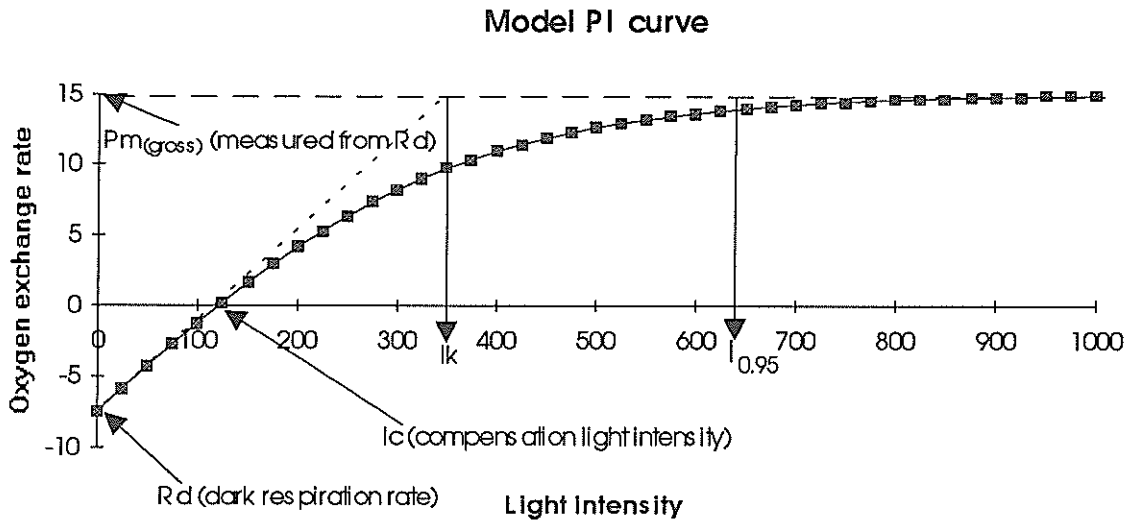

Figure 1 - PI (photosynthesis/irradiance) curve showing the major photokinetic parameters used to define the curve. In this example $Pm_{(gross)}$ = 22.5, Rd = -7.5 and Ik = 350. Additional parameters which may be evaluated include Ic = 115, alpha = $Pm_{(gross)}$/Ik = 0.064 and $I_{0.95}$ = 1.832*Ik = 641.

The photokinetic parameters ($Pm_{(gross)}$, Rd, Ik; Fig. 1) were evaluated by fitting a hyperbolic tangent function (Chalker 1980, 1981) to the data comprising the PI curve. The goodness of fit for the function was assessed using a least squares regression of predicted vs observed values (r^2). Comparisons of the photokinetic parameters, between species, were made using one way analyses of variance followed by *post-hoc* Tukey tests for pairwise comparisons. $Pm_{(gross)}$ (often referred to as Pmax) is the maximal rate of gross photosynthetic production at saturating light intensities and is a measure of the photosynthetic capacity of the organism while Rd is the dark respiration rate. Ik is the light intensity at which the initial slope of the PI curve intersects the $Pm_{(gross)}$ value (Talling, 1957) and is usually used to describe the adaptation of an organism to the irradiance regime it experiences. Once the PI curve has been fitted, a number of additional parameters can be defined including Ic (the compensation light intensity), $I_{0.95}$ is presumed to be the irradiance at which photosynthesis is 95% of $Pm_{(gross)}$ (which is an estimate of the saturation light intensity), it was calculated as 1.832 multiplied by Ik (Chalker *et al.*,1983). Alpha (defined as $Pm_{(gross)}$/Ik) is a measure of the slope of the initial portion of PI

curve and provides a measure of the relative efficiency of photosynthesis at lower light intensities. Net and gross 24 h production and the total 24 h respiration were determined for each species by integrating the PI function over seven days of light data collected during the period of these studies. This calculation involved a correction for the volume of each sample, its surface area and the activity of the water body (determined from the control chambers). The average gross production for each species was obtained by taking the summation of net 24 h production and total dark respiration. The final units obtained for 24 hour production and consumption were expressed as $\mu MolO_2.cm^{-2}.day^{-1}$ (oxygen production per unit surface area of the coral per day).

After each deployment, the experimental organisms were taken back to the laboratory and kept frozen at -20°C. Following all the field work, the organisms were thawed and their volume and surface area determined in litres and cm^2 respectively.

A total of seven sets of 24 h light regimes were obtained (including light data from deployments of species not discussed in this communication). Each set was divided into 12 daylight hours (0700 to 1900) and 12 non-daylight hours (1900 to 0700). For each species the percentage of time the irradiance was above and below the Ik, $I_{0.95}$ and Ic values was determined.

RESULTS

All specimens illustrate clearly defined PI responses (Fig. 2) with relatively high $Pm_{(gross)}$/Rd ratios (4.1-5.1; Table 1) and are therefore classed as phototrophs ($Pm_{(gross)}$/Rd > 1.5; Wilkinson and Trott 1985). All four genera were net producers on a net 24 h basis (Table 2) with instantaneous photosynthetic rates remaining above compensation levels during most of the day (Table 3). On those days where monsoonal rains were experienced, specimens illustrated a significant depression in photosynthetic rates (Fig. 3), but these periods of low light were not sufficient to create a net 24 h deficit.

Table 1. Estimates of the photokinetic parameters (averaged within species; with standard deviation (SD)). Units of measure are; $Pm_{(gross)}$ and Rd ($\mu Mol\ O_2.cm^{-2}.h^{-1}$), Ik, Ic and $I_{0.95}$ ($\mu E.\ m^{-2}.\ s^{-1}$), Alpha {($\mu Mol\ O_2.cm^{-2}.\ h^{-1}$)/($\mu E.\ m^{-2}.\ s^{-1}$)} and $Pm_{(gross)}$/Rd.

Genera	$Pm_{(gross)}$	Rd	Ik	Ic	$I_{0.95}$	Alpha	$Pm_{(gross)}$/Rd
Fungia	5.2	-1.0	337	67.9	617	0.015	5.1
	(1.00)	(0.15)	(64.3)	(5.8)			(0.2)
Goniopora	6.6	-1.3	467	96.8	856	0.014	5.1
	(2.64)	(0.23)	(28.8)	(11.1)			(0.6)
Heliofungia	13.8	-3.0	267	73.5	489	0.052	4.4
	(6.6)	(0.40)	(32.1)	(13.4)			(0.7)
Platygyra	3.3	-0.8	326	80.8	597	0.010	4.1
	(0.66)	(0.10)	(34.0)	(1.2)			(0.3)

The four genera show different photokinetic responses (Table 1) particularly in terms of their photosynthetic efficiency at lower light intensities. The average Ik values for individual species ranged from 267 $\mu E.\ m^{-2}.\ s^{-1}$ for *Heliofungia* to 467 $\mu E.\ m^{-2}.\ s^{-1}$ for *Goniopora* (significantly different P=0.000). In all cases these Ik values were above the average daytime irradiances experienced over the seven days of this study (220 $\mu E.\ m^{-2}.\ s^{-1}$; Table 3).

Heliofungia has a higher $Pm_{(gross)}$ than either *Fungia* or *Platygyra* (P<0.02) but was not significantly different to *Goniopora* (which was intermediate and in turn not different to any other species). *Fungia* and *Heliofungia* have the highest production efficiencies (128-132%; defined as the ratio of gross 24 h production to total 24 h respiration) whilst *Platygyra* and *Goniopora* have the lowest (105-107%; Table 2). *Heliofungia* has a significantly higher alpha (0.05) compared to all other species (alpha=0.010-0.015; P=0.021). This means that *Heliofungia* photosynthesises more efficiently at lower light intensities (alpha is a measure of the initial slope

of the PI curve and higher values indicate a steeper slope and consequently greater rates of photosynthesis at sub-saturating light intensities). Alpha values need to be considered in conjunction with the $Pm_{(gross)}/Rd$ ratios which indicate the extent to which maximal instantaneous photosynthesis exceeds the underlying respiration rate (at saturating light intensities). For *Fungia*, $Pm_{(gross)}/Rd$ was 5.1 (cf *Heliofungia* 4.1). This difference in $Pm_{(gross)}/Rd$ makes up for the reduced alpha in *Fungia* and results in both *Fungia* and *Heliofungia* having the same overall production efficiency (Table 2).

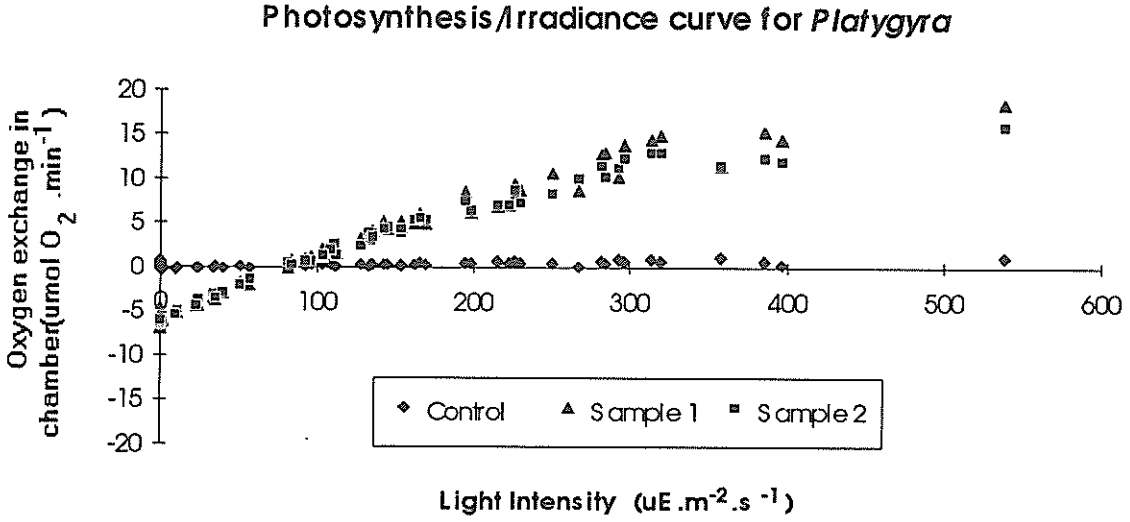

Fig. 2 - Photosynthesis/Irradiance curve for *Platygyra*. Samples 1 and 2 show similar PI responses with the control chamber showing almost no activity.

Table 2. Estimated 24 hour production and respiration. Estimates were obtained by integrating the photokinetic parameters obtained for individual specimens over the 7 days of light data. Values shown are average rates for all specimens at two different depths 3.4 m and 1.4 m. These depths represent the edge of the reef-flat and the reef-flat respectively. Units of measures for Net24, Rd24 and Pg24 are $\mu MolO_2.cm^{-2}.day^{-1}$.

Genera	Net 24 h production (Net24)	Total respiration (Rd24)	Gross 24 h production (Pg24)	Production efficiency %; Pg24/(Rd24)	Depth[1]
Fungia	7	25	32	128	3.40
Goniopora	2	30	32	107	3.40
Heliofungia	23	73	96	132	3.40
Platygyra	1	19	20	105	3.40
Fungia	23	25	48	192	1.40
Goniopora	24	30	54	180	1.40
Heliofungia	60	73	133	182	1.40
Platygyra	11	19	30	158	1.40

[1]Specimens were logged at 3.4 m. Estimates for 1.4 m were obtained by integrating the PI curves against a set of light data obtained over two days at 1.4 m (from deployments of other specimens not detailed in this communication).

All four genera maintained positive production on the reef-flat at a depth of 3.4m. The net 24 h production ranged from 1 $\mu MolO_2.cm^{-2}.day^{-1}$ for *Platygyra* to 23 $\mu MolO_2.cm^{-2}.day^{-1}$ for *Heliofungia* which comprises 105-132% of daily carbon requirements (assuming a respiratory quotient of 1.0; Table 2). If we assume that the photokinetic parameters don't change between the reef-edge (depth 3.4 m) and the reef-flat (1.4 m) we would predict that all four genera would be net producers on the reef-flat (obtaining 158-192% of daily carbon requirements; Table 2). Total respiration averaged between 19 $\mu MolO_2.cm^{-2}.day^{-1}$ for *Platygyra* to 73 $\mu MolO_2.cm^{-2}.day^{-1}$ for *Heliofungia*.

In general, light intensities were above the compensation point but below saturating levels for all genera for the major portion of the daylight hours. Compensation light intensities (Ic), ranged from 68 to 97 $\mu E.\ m^{-2}.\ s^{-1}$ and were lower than the average daytime irradiance. The $I_{0.95}$ values were always greater than the average daytime irradiance (220 $\mu E.\ m^{-2}.\ s^{-1}$; Table 2, Table 3).

Table 3 - Summary of the light environment at a depth of 3.4 m over a 7 day period. Average of seven days of daylight irradiance was 220 $\mu E.\ m^{-2}.\ s^{-1}$, average daytime maximum irradiance was 552 $\mu E.\ m^{-2}.\ s^{-1}$ maximum irradiance on any day was 682 $\mu E.\ m^{-2}.\ s^{-1}$.

Genera	% of daylight hours >Ik	% of daylight hours > $I_{0.95}$	% of daylight hours > Ic
Fungia	26	0.4	77
Goniopora	8	0.0	71
Heliofungia	35	6.6	80
Platygyra	28	1.9	78

DISCUSSION

In Singapore, where coastal waters are highly turbid, there is a sharp decline in light with increasing depth resulting in a marked decrease in photosynthetic activity of benthic organisms. Corals on Pulau Hantu obtain between 150-190% of their daily carbon from photosynthesis on the reef-flat (at 1.4 m) but this decreases to 105-130% at a depth of 3.4 m on the reef-edge. This decrease in production (30%) over a depth of 2 m is caused by the very high attenuation of light on these reefs (attenuation coefficient of 0.4-0.5) and contrasts dramatically with studies undertaken elsewhere. Cheshire and Wilkinson (1991), for example, showed that phototrophic sponges on the Great Barrier Reef had a 25% reduction in production efficiency over a depth of 20 m. In their study the attenuation coefficient of the water body was determined as 0.08 whilst the attenuation coefficient of the water column at Pulau Hantu was measured at 0.47.

On the basis of these studies we would predict that hard corals on Pulau Hantu would be net consumers below a depth of about 4 m and would obtain less than 50% of their daily carbon requirements from photosynthesis at 6 m. This prediction correlates well with the observed distribution of hard corals on this reef where few are found at depths greater than 6 m (below mean low tide). The rapid attenuation of light means that corals will have to rely more upon heterotrophic inputs to satisfy their carbon requirements as depth increases.

The trophic versatility exhibited by coral reef organisms enables them to feed autotrophically as well as function as heterotrophs feeding on detritus, dissolved organic matter, bacteria and/or animal prey (Porter, 1974). Therefore, although symbiotic reef dwellers may be theoretically capable of nearly complete dependence on heterotrophy, this is rare in nature. Zooplankton is generally unavailable as food in concentrations great enough to satisfy this demand (Muscatine & Porter, 1977). Experiments by Johannes and Tepley (1974) showed that zooplankton accounted for less than 10% of the daily energy requirement of the coral over a 24 h period. Lang *et al.* (1975) used indirect evidence to suggest that plankton feeding may not be as important as other forms of energy procurement and all field studies to date agree that zooplankton feeding is not a major contributor of either the calories or carbon required daily by most symbiotic reef organisms, especially hard corals (Muscatine & Porter, 1977). Thus, carbon derived from photosynthetic symbionts and translocated to the host is of major energetic significance to coral reef ecosystems.

Singapore experiences diurnal variations in rainfall, characterised by maximum rainfall in the afternoon (Nieuwolt, 1973). This pattern of rainfall has an effect on the irradiance regimes; due to the accompanying cloud cover irradiance is reduced with a corresponding decrease in photosynthetic rates (Fig. 3). This diurnal variation in rainfall has important implications for reef organisms - during the afternoon period, when irradiance should be at its greatest, reef organisms are getting lower irradiances due to cloud cover. Reef-flat organisms may benefit from this diurnal variation since, being in the shallow part of the reef they may otherwise be subjected to irradiances which would cause photoinhibition.

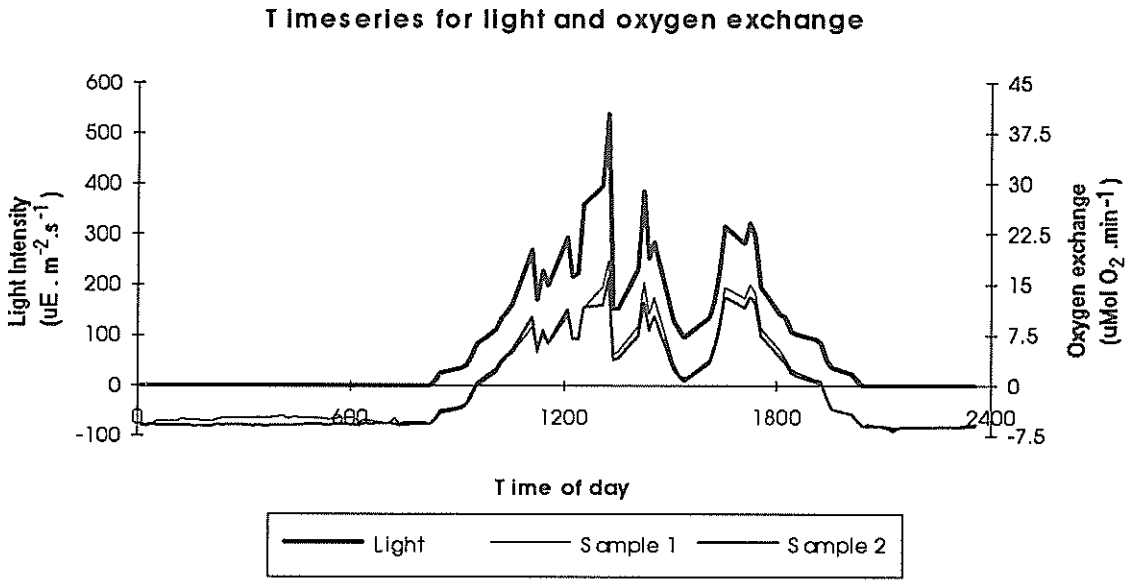

Fig. 3 - Time series showing changes in light intensity (left hand axis) and oxygen exchange (right hand axis). The data are for the same samples as shown in Fig. 2. Note the major fluctuations in light during the afternoon with two major rain periods causing significant depression in both light and consequently photosynthetic rates for the experimental organisms.

The percentage of time that the daylight irradiances exceeded the I_{095} for any of the genera was very low (0-6.6%; Table 3). This implies that these corals are only able to photosynthesis at maximum rates for very short periods during the daylight hours. Therefore, even if the $Pm_{(gross)}$ quoted for any given genus is high, it may not result in increased production because this maximal rate is not realised for prolonged periods.

The light compensation point, Ic, is the irradiance at which production (photosynthesis) is balanced by consumption (respiration). Thus, a species with a lower Ic would be able to start producing in excess earlier in the day than another with higher Ic. Though Ic determines how long after dawn an organism starts to produce in excess, it does not seem to be an important factor in determining the net productivity of any of these four genera. In all cases, Ic was reached within minutes (at most 1 hr) of daybreak.

In tropical climates, it is not surprising to receive sea-surface maximum irradiances in excess of 2300 $\mu E.m^{-2}.s^{-1}$ but in the case of Singapore, the diurnal rainfall variation it experiences effectively reduces the irradiance that it gets for most parts of the year. On average, Singapore experiences a diurnal rainfall pattern for seven months a year (Nieuwolt, 1973). During these times the reef-edge species are unable to photosynthesize at maximal rates.

Light regimes taken over seven days within the same month are not intended to reflect the average light regime over the year. Even in a tropical country like Singapore, where the weather remains almost constant throughout the year, there are some seasonal patterns in the light regime. It is likely however, that while absolute rates of photosynthesis and respiration may change, the relativities defined in this study will hold throughout the year.

Heliofungia and *Goniopora* had the highest rates of instantaneous photosynthesis ($Pm_{(gross)}$). This is probably due to the fact that, in daylight, individual polyps of *Heliofungia* and *Goniopora* are extended which results in

an overall increase in photosynthetically active surface area of the whole colony. In contrast, the polyp extension of *Platygyra* and *Fungia* is nowhere near as extensive. Since symbiotic zooxanthellae in scleractinians are found in the endoderm of coral polyps, especially in the tentacles and oral endoderm (Vandermeulen *et al.*, 1972), it is not surprising that *Heliofungia* and *Goniopora*, with the greatest exposed surface area during daytime, registered the highest $Pm_{(gross)}$. It should be recognised that the surface area determination for the four genera provided a measure of the surface area of the living coral head (with polyps and tentacles unextended). The surface area projected by the extended polyps or tentacles is likely to be much higher for *Goniopora* and *Heliofungia* compared with *Fungia* and *Platygyra*.

Respiration rates measured during the deployments are night-time respiration rates only. Daytime respiration rates were assumed to be the same as the night-time rates, and the total respiration of each genera was calculated by multiplying their night-time hourly rate by 24. The high respiration registered by *Heliofungia* is likely to be due to the greater availability of metabolic substrates associated with the higher rate of photosynthesis in this genera. It may also be that *Heliofungia* has a greater biomass to surface area ratio when compared to the other three species. Since biomass measurements were not done, this hypothesis cannot be verified.

The ratios of gross 24 hour photosynthesis to total 24 hour respiration (production efficiency; 1.0-1.9) obtained in this study are comparable to those reported in the literature for other *in situ* productivity measurements (reported as 0.7 - 1.8 for most reef corals; McCloskey *et al.*, 1978). Species may be classified into a trophic category based on the ratio for instantaneous maximal gross production to dark respiration ($Pm_{(gross)}/Rd$) using the criteria described by Wilkinson and Trott (1985).

Phototrophs = organisms for which $Pm_{(gross)}/Rd > 1.5$
Mixotrophs = organisms for which $1 < Pm_{(gross)}/Rd < 1.5$
Heterotrophs = organisms for which $Pm_{(gross)}/Rd < 1$

All four species were categorised as phototrophs as their ratios were greater than 4. It is likely that at greater depth or during periods of the year when demands for carbon are higher (eg. during reproduction) heterotrophic inputs would become more important (or even essential).

A polytrophic mode of nutrition is a common strategy amongst invertebrates found in reef ecosystems. The fact that reef ecosystems are able to sustain very high productivity in nutrient poor waters attests to the success of the symbiotic associations in reef invertebrates and the trophic versatility exhibited by them. It is doubtful however, whether this trophic versatility is sufficient to provide for the continued growth and development of reefs in the turbid conditions of Singapore's coastal waters. In the longer term reef-growth and survival is dependant upon calcification processes (Chalker 1985b) which in turn are linked to light availability. Whereas growth and development in shallow reefal environments is possible the rates of both biological and physical erosion at depths > 6m (where coral growth is no longer occurring) are likely to determine the long-term fate of these valuable reef systems.

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