

## An energy budget for *Porites porites* (Scleractinia), growing in a stressed environment

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**Abstract.** An energy budget was determined for the coral *Porites porites* living in a stressed environment for comparison of the energy inputs and expenditure with those of the same species living in an adjacent clear water fore reef environment. The stressed site was characterised by higher sedimentation and lower irradiances than at the fore reef site. Zooplankton ingestion was found to be an insignificant component of the energy intake: the coral is fully autotrophic under stress conditions. The integrated 24 h rate of photosynthetic energy production on a clear sunny day was 20% higher for stressed corals compared to fore reef corals. This was largely the result of photoadaptation which resulted in increased values for  $\alpha$  and decreased values for  $I_k$  in the hyperbolic tangent function equation for the photosynthesis versus irradiance curve. The energy investment in growth of animal tissue was lower in stressed corals. The percentage translocation of photosynthate to the animal tissue remained at about 78%, but the respiration rate of the animal tissue was reduced by 3 fold. These data combined with the high rate of photosynthetic production predict a net daily energy surplus of 67% in stressed corals compared with the 45% surplus in unstressed corals. Scope for growth is reduced under stress conditions.

### Introduction

Both anthropogenic and natural stress can lead to the destruction of coral reefs (Johannes 1975). Corals respond to stress events by changes in growth rates, loss of zooxanthellae, aberrant fecundity and reduced planula larval survival, and changes in metabolism (Brown and Howard 1985). All of these responses involve changes in energy allocation, and Brown and Howard (1985) conclude that, by extrapolation of the approach of Bayne and Wid-

dows (1978) with other marine invertebrates, determination of energy budgets may give early indications of environmental stress in corals.

Both carbon and energy budgets have already been calculated for a variety of scleractinians (Muscatine et al. 1984; Porter et al. 1984; Edmunds and Davies 1986). However, the only attempts at comparing carbon or energy budgets between sites have been those of Muscatine et al. (1984) for the coral *Stylophora pistillata* growing in shade and light conditions and Zamer and Shick (1987) for the temperate anemone *Anthopleura elegantissima* from high- and low-intertidal locations. In the present study we have determined an energy budget for *Porites porites* from 10 m depth in a sediment stressed environment for comparison with the budget previously determined (Edmunds and Davies 1986) for *P. porites* at 10 m depth in an adjacent clear water fore reef environment. The purpose of the study was to determine whether environmental stress would have a measurable effect on one or more components of the energy budget of the coral *P. porites*.

### Methods

#### *Environmental features*

The stressed site was at 10 m depth at Columbus Park (CP) on the west side of Discovery Bay, Jamaica. This was approximately 1 km from the fore reef (FR) site. The percentage transmission of surface photosynthetically active radiation (PAR) to 10 m depth was measured close to midday on 38 days between May and July 1985 using a LiCor LI 185-B meter and LI 192-SB sensor. Seawater temperature was measured at 10 m depth. The sedimentation rate was measured 15 cm above the substrate using 27 × 98 mm traps placed for 7 day periods at each site.

#### *Energy budget*

All of the methods used in the determination of the energy budget followed those reported in our earlier paper (Edmunds and Davies 1986). The methods are presented only where modifications were made.

All experimental corals were collected from 10 m depth at the CP site. Branch tips of *Porites porites* were prepared as nubbins (Davies 1984) and used for experiments between September 1984 and September 1985. Each nubbin contained approximately 200 mg of dry tissue and

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was about 2 cm in height. Their photosynthesis/irradiance (P/I) curves were used in conjunction with the predicted irradiance levels at 10 m depth to determine the integrated net photosynthesis over a whole day. Integrated gross photosynthesis values were calculated as net photosynthesis plus dark respiration. In situ irradiances were predicted from the mean transmission of surface PAR to 10 m depth together with the continuous PAR recording made on 16 June 1985 which was a 14 h cloudless day with a maximum irradiance of  $2015 \mu\text{E m}^{-2} \text{s}^{-1}$ . The same surface PAR recordings were used to determine the energy budget in our previous study (Edmunds and Davies 1986). Gross photosynthetic oxygen values were converted to energy units by assuming that the primary product of photosynthesis was glucose.

The respiration rate of zooxanthellae isolated from CP specimens by centrifugation of "water piked" (Johannes and Wiebe 1970) and homogenised coral tissue, was measured with an oxygen electrode. This value was used to estimate the respiration rate of the known zooxanthellae population in a symbiotic nubbin which was then used to predict the host respiration by subtraction. To test the validity of this method the predicted value was compared with the measured respiration rate of aposymbiotic nubbins. These were prepared by maintaining nubbins from the FR site under continuous high irradiance. Nubbins were supplied with a high flow of unfiltered seawater and were exposed to direct sunlight and a 500 W quartz halogen lamp fitted with an infra-red filter at night. The respiration rates of aposymbionts were normalised to predicted surface area using the previously determined regression of surface area on skeletal weight (Edmunds and Davies 1986).

### Scope for growth

Scope for growth, the energy available for growth and reproduction (Bayne and Widdows 1978), was determined as the difference between the total daily assimilated energy and the daily respiratory requirements.

## Results

### Habitat characteristics

The transmission of surface PAR to 10 m depth at the CP site was 20.4% (95% range, 19.1% to 21.7%,  $n=38$ ). This was significantly lower than 26.2% transmission to 10 m depth recorded at the FR site over the same period ( $t=6.5159$ ,  $df=66$ ,  $P<0.001$ ; Edmunds and Davies 1986). Sedimentation rates were significantly higher (Mann-Whitney  $U$  test,  $U=38$ ,  $n_1=n_2=7$ ,  $P<0.05$ ) at the CP site than at the FR site (Table 1). The seawater

**Table 1.** Sedimentation rates at 10 m depth for the fore reef (FR) and Columbus Park (CP) sites between 18 November 1985 and 27 March 1986. Each value is the mean for three traps unless marked with \* when only two traps were analysed. Data could not be collected on 2 days (-)

Trap placement		Sedimentation $\text{g m}^{-2} \text{d}^{-1}$	
Date down	Date up	CP	FR
18-11-85	25-11-85	62.38	39.71*
02-12-85	09-12-85	33.94	24.59
16-12-85	23-12-85	29.86	25.52
23-12-85	30-12-85	50.37	122.93
06-01-86	13-01-86	29.90	15.14
06-03-86	13-03-86	-	14.09*
13-03-86	20-03-86	30.86*	20.08*
20-03-86	27-03-86	42.49	-
Median		24.59	33.94

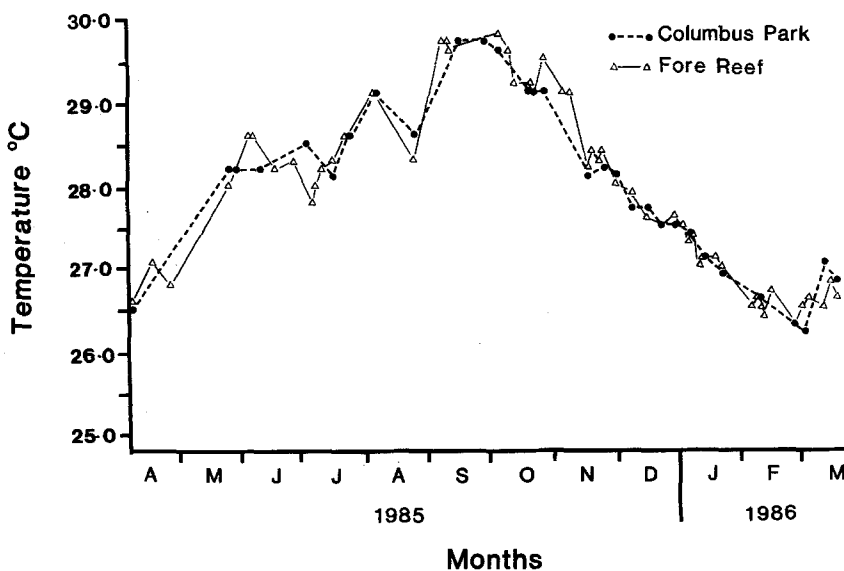
temperature at 10 m depth at both sites ranged from  $26.6^\circ\text{C}$  to  $29.8^\circ\text{C}$  and showed almost no between-site variation throughout 1985-1986 (Fig. 1).

### Coral characteristics

Nubbins prepared from CP *P. porites* had similar physical sizes to those prepared at the FR site (Table 2). *P. porites* at the CP site had a significantly lower dry tissue content, ash content of tissue, tissue energy and energy content of zooxanthellae compared to FR specimens.

### Respiration

The colony dark respiration rates normalised to dry tissue content were not significantly different between sites, but when expressed on a unit area basis the respiration rate of CP nubbins was significantly lower than for FR nubbins (Table 3). The dark respiration rate of isolated zooxanthellae was not significantly different from the value previously recorded for zooxanthellae from FR corals (Table 3).



**Fig. 1.** Sea water temperatures at 10 m depth throughout 1985-1986 at the Columbus Park and fore reef sites, Discovery Bay, Jamaica

**Table 2.** *Porites porites* at the Columbus Park (CP) and fore reef (FR) sites: specimen characteristics. All values are mean  $\pm$  95% confidence limits or means with the 95% ranges in the case of percentage data (calculated as arcsine transformed data: Sokal and Rohlf 1969), sample size in parenthesis. Data were compared between sites by the *t*-test where appropriate. The *t* values are shown together with the probability (*P*) for a significant difference. In the case of the percentage data, *t*-tests were carried out on arcsine transformed data. ns=not significantly different at *P*=0.05. Data for the FR site from Edmunds and Davies (1986)

Characteristic	CP site	FR site	<i>t</i>	Significance
Skeletal density g cm <sup>-3</sup>	2.683 $\pm$ 0.317 (20)	2.822 $\pm$ 0.190 (21)	0.7853	ns
Dry tissue content mg dry tissue cm <sup>-2</sup>	15.51 $\pm$ 1.14 (16)	18.59 $\pm$ 0.99 (22)	4.2502	<i>P</i> < 0.001
Regression of dry tissue on skeletal weight <i>x</i> = log <sub>10</sub> (g skeleton) <i>y</i> = log <sub>10</sub> (mg dry tissue)	<i>y</i> = 1.1145 <i>x</i> + 1.5547 <i>r</i> = 0.9246 (16)	<i>y</i> = 0.7437 <i>x</i> + 1.9034 <i>r</i> = 0.8471 (21)		
Ash content of tissue % dry tissue	12.1% (15) (9.6% to 14.8%)	22.0% (12) (17.2% to 27.2%)	4.0226	<i>P</i> < 0.001
Tissue energy content J mg <sup>-1</sup> dry tissue	14.40 $\pm$ 1.43 (18)	16.18 $\pm$ 1.05 (21)	2.1085	<i>P</i> < 0.05
Tissue protein content % of dry tissue	24.40% (7) (21.28% to 27.66%)	23.30 (10) (20.64% to 26.07%)	0.6207	ns
Number of polyps Polyps cm <sup>-2</sup>	22.6 $\pm$ 1.7 (10)	25.0 $\pm$ 2.4 (8)	1.9427	ns
Zooxanthellae content $\times 10^7$ zoox g <sup>-1</sup> dry tissue $\times 10^6$ zoox cm <sup>-2</sup>	18.97 $\pm$ 4.54 (11) 3.16 $\pm$ 0.77 (11)	15.52 $\pm$ 1.78 (18) 3.13 $\pm$ 0.53 (18)	1.5656 0.0656	ns ns
Zooxanthellae energy content J $\times 10^6$ zoox <sup>-1</sup>	7.76 $\pm$ 0.73 (8)	11.69 $\pm$ 2.41 (10)	3.2017	<i>P</i> < 0.01

**Table 3.** *Porites porites* at the Columbus Park (CP) and the fore reef (FR) sites: mean photosynthetic characteristics taken from individual curves for each of 10 nubbins at each site. All units as shown, values given as mean  $\pm$  95% confidence limits, sample size in parenthesis, dt = dry tissue. Statistical comparisons were carried out by the *t*-test and the *t* values and the probability (*P*) for a significant difference are shown. ns = not significantly different at *P* = 0.05. Data for FR site from Edmunds and Davies (1986)

Characteristic	CP site	FR site	<i>t</i>	Significance
Colony respiration $\mu\text{O}_2$ mg <sup>-1</sup> (dt) h <sup>-1</sup> $\mu\text{O}_2$ cm <sup>-2</sup> h <sup>-1</sup> <sup>a</sup>	0.45 $\pm$ 0.11 (10) 7.01 $\pm$ 1.70 (10)	0.64 $\pm$ 0.21 (10) 11.91 $\pm$ 4.00 (10)	1.7914 2.5482	ns <i>P</i> < 0.05
Maximum gross photosynthesis $\mu\text{O}_2$ mg <sup>-1</sup> (dt) h <sup>-1</sup> $\mu\text{O}_2 \times 10^6$ zoox <sup>-1</sup> h <sup>-1</sup> $\mu\text{O}_2$ cm <sup>-2</sup> h <sup>-1</sup> <sup>a</sup>	4.13 $\pm$ 1.25 (10) 21.78 $\pm$ 6.60 (10) 64.08 $\pm$ 19.40 (10)	4.43 $\pm$ 1.87 (10) 28.53 $\pm$ 12.07 (10) 82.34 $\pm$ 34.82 (10)	0.3011 1.1118 1.0365	ns ns ns
<i>I</i> <sub>k</sub> $\mu\text{E m}^{-2} \text{ s}^{-1}$	215 $\pm$ 39 (10)	456 $\pm$ 250 (10)	2.1510	<i>P</i> < 0.05
95% irradiance: ( <i>I</i> <sub>0.95</sub> ) $\mu\text{E m}^{-2} \text{ s}^{-1}$	393 $\pm$ 71 (10)	835 $\pm$ 459 (10)	2.1197	<i>P</i> < 0.05
Alpha ( $\alpha$ ) $\mu\text{O}_2$ mg <sup>-1</sup> (dt) h <sup>-1</sup> $\mu\text{E}^{-1} \text{ m}^{-2} \text{ s}$	0.019 $\pm$ 0.004 (10)	0.011 $\pm$ 0.003 (10)	3.8520	<i>P</i> < 0.01
Zooxanthellae respiration $\mu\text{O}_2 \times 10^6$ zoox <sup>-1</sup> h <sup>-1</sup>	1.82 $\pm$ 0.33 (16)	1.84 $\pm$ 0.34 (19)	0.0630	ns

<sup>a</sup> Calculated using dry tissue content of 18.59 mg cm<sup>-2</sup> (FR site) and 15.51 mg cm<sup>-2</sup> (CP site)

When symbiotic *P. porites* were exposed to a high irradiance zooxanthellae were expelled in large numbers over the first 2 weeks. The residual zooxanthellae population then decreased slowly over the following 3–8 weeks. After 10 weeks, respiration measurements were

made on white aposymbionts with expanded polyps. Aposymbionts contained a mean of 7.4% (*n* = 4) of the zooxanthellae of a symbiotic nubbin of equivalent size and from the same location. The mean respiration rate of the aposymbionts was 7.2  $\pm$  1.5  $\mu\text{O}_2$  cm<sup>-2</sup> h<sup>-1</sup> (*n* = 5).

The predicted rate of respiration of the zooxanthellae (using data from Tables 2 and 3) equals  $5.8 \mu\text{O}_2 \text{ cm}^{-2}\text{h}^{-1}$ . The sum of the aposymbiont and zooxanthellae rate of respiration  $7.2 + 5.8 = 13.0 \mu\text{O}_2 \text{ cm}^{-2}\text{h}^{-1}$  gives a value which is very similar to that of  $11.9 \mu\text{O}_2 \text{ cm}^{-2}\text{h}^{-1}$  for a complete symbiont from the FR site (Table 3).

### Photosynthesis

Best fit hyperbolic tangent functions were fitted to net photosynthesis versus irradiance data for 10 nubbins of CP *P. porites*. The mean photosynthetic characteristics derived from individual P/I curves for both CP and FR (Edmunds and Davies 1986) corals are shown in Table 3. All the  $I_k$  values were attained at irradiances less than the maximum experimental light intensity. Both  $I_k$  and  $I_{0.95}$  were significantly lower in CP *P. porites*, but there were no significant differences in  $P_{\text{max gross}}$  irrespective of the method of normalising.

### Growth

The growth rate of CP *P. porites* measured every 3 weeks for 14 weeks was almost linear (Fig. 2). The mean tissue-specific skeletogenesis was  $47.1 \pm 7.3 \text{ mg g}^{-1}$  dry tissue  $\text{d}^{-1}$  ( $n=48$ ) and the mean tissue-specific tissue growth was  $2.3 \pm 0.4 \text{ mg g}^{-1}$  dry tissue  $\text{d}^{-1}$  ( $n=48$ ). These are both significantly lower than the equivalent figures of  $81.7 \pm 7.3 \text{ mg g}^{-1}$  dry tissue  $\text{d}^{-1}$  ( $n=41$ ) and  $2.8 \pm 0.2 \text{ mg g}^{-1}$  dry tissue  $\text{d}^{-1}$  ( $n=41$ ) ( $t$ -test,  $t=7.8326$ ,  $df=87$ ,  $P<0.001$ ) respectively, recorded for FR *P. porites* (Edmunds and Davies 1986).

With a constant zooxanthellae to coral-tissue biomass ratio (Patton and Burris 1983),  $4.36 \times 10^5$  zooxanthellae were added each day to a CP nubbin with 1 g of dry tissue. This is equivalent to an algal-specific growth rate ( $\mu_z$ ) of  $0.0023 \text{ d}^{-1}$ .

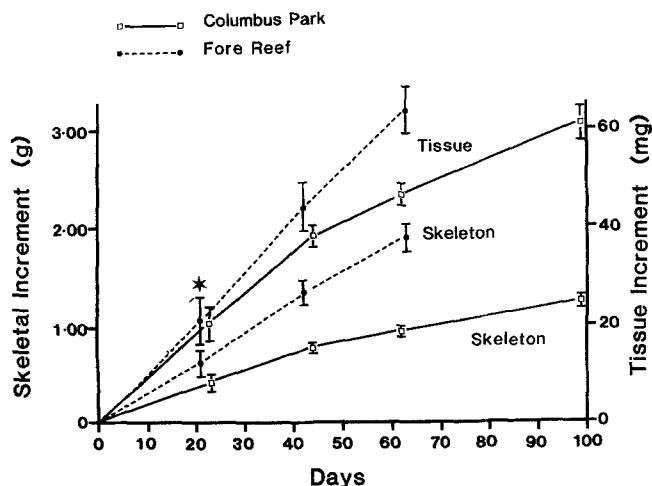


Fig. 2. Cumulative growth increments of skeleton for *P. porites* and predicted cumulative growth increments of tissue at the Columbus Park (CP) and fore reef sites. Means and 95% confidence intervals shown (at the CP site  $n=12$ , at the FR site  $n=14$  except at \* where  $n=13$ ). Fore reef data from Edmunds and Davies (1986)

### Reproduction and heterotrophy

Colonies of CP *P. porites* were considered fecund if some of their polyps contained combinations of mature planulae, immature planulae and gonads. Mature planulae were free in the coelenteron and contained zooxanthellae, mesenteries and sometimes an oral aperture. Their mean maximum diameter was  $0.463 \pm 0.013 \text{ mm}$  ( $n=190$ , preserved samples) which was not significantly different from  $0.455 \pm 0.014 \text{ mm}$  ( $n=205$ , preserved samples;  $t$ -test,  $t=0.8237$ ,  $P<0.05$ ) for FR *P. porites* (this was mistakenly printed as  $0.014 \pm 0.041 \text{ mm}$  in our previous paper, Edmunds and Davies 1986).

Mean data for all colonies and polyps of CP *P. porites* showed that each week 13.1% (95% range 3.4% to 27.7%,  $n=18$ ) of the polyps each contained  $1.7 \pm 0.2$  mature planulae ( $n=105$ ). These data were not significantly different from the equivalent figures for FR *P. porites* (Edmunds and Davies 1986) ( $t$ -test,  $t=0.3975$ ,  $df=34$ , percentage data arcsine transformed;  $t=1.7241$ ,  $df=227$  respectively,  $P>0.05$  for each). Neither the number of fecund polyps, the number of polyps containing mature planulae or the proportion of fecund polyps containing mature planulae in CP *P. porites* showed any significant trend with time (runs test,  $n=18$ ,  $8 \leq r \leq 12$ ,  $P>0.05$ ). However, there was some evidence of a monthly cycle in the proportion of fecund polyps containing mature planulae (Fig. 3). These data give an approximation to the time between initiation and release of planulae.

While determining the reproductive expenditure of CP *P. porites* more than 650 polyps were dissected. None of these contained zooplankton.

### The 24 h energy budget

All energy values are calculated for a nubbin with 300 mg dry tissue as this is similar to the mean size used and is

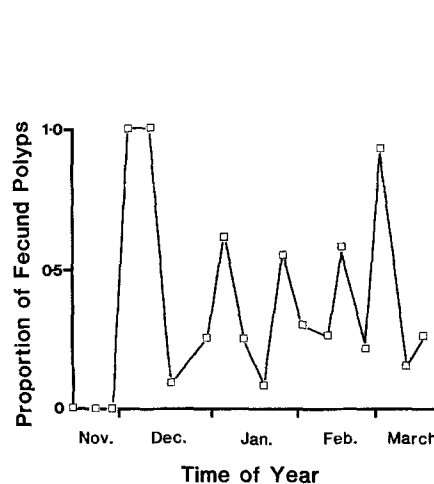


Fig. 3. *P. porites* at the Columbus Park (CP) site: proportion of fecund polyps containing mature planulae from approximately weekly samples between November 1984 and March 1985

consistent with our previous energy budget (Edmunds and Davies 1986).

### Respiration

Assuming that the respiration rate of symbiotic colonies measured in the darkness is the same as their respiration rate in the light, the 24 h respiratory demand of the whole colony (zooxanthellae plus host) is  $0.45 \times 0.3 \times 24 = 3.25 \text{ mlO}_2$ . Assuming that the respiratory substrate is lipid (Patton et al. 1977), and using the lipid oxyjoule coefficient of  $19.63 \text{ J mlO}_2^{-1}$  (Elliott and Davison 1975) this is equivalent to 63.86 J. The dark respiration rate of zooxanthellae isolated from CP *P. porites* ( $1.82 \mu\text{O}_2 \times 10^6 \text{ zoox h}^{-1}$ ) is equivalent to a zooxanthellae respiratory energy expenditure of  $48.80 \text{ J 24h}^{-1}$  per nubbin, leaving 15.06 J by subtraction for the respiratory energy consumption due to the animal tissue alone.

### Gross photosynthesis

On a 14 h sunny day the predicted integrated net photosynthetic oxygen production was  $30.0 \text{ ml g}^{-1}$  dry tissue. The net photosynthesis of nubbins is therefore  $9.0 \text{ ml O}_2$  and the gross photosynthesis is  $9.00 + (0.45 \times 0.3 \times 14) = 10.90 \text{ mlO}_2$ . Assuming that 6 mol of oxygen results in the formation of 1 mol of glucose with an energy content of 2817 kJ (Lehninger 1973), this is equivalent to 228.32 J.

### Growth

Over a 24 h period, 0.69 mg of coral dry tissue is added to each nubbin, equivalent to  $9.94 \text{ J d}^{-1}$  (tissue energy content =  $14.40 \text{ J mg}^{-1}$  from Table 2). With a constant zooxanthellae number to coral tissue biomass ratio, growth adds  $1.3 \times 10^5 \text{ zoox d}^{-1}$  (with  $18.97 \times 10^7 \text{ zoox g}^{-1}$  dry tissue). Zooxanthellae from CP *P. porites* contain  $7.76 \pm 0.73 \text{ J } 10^6 \text{ zoox}^{-1}$ , and the daily zooxanthellae growth increment is, therefore,  $7.76 \times 0.13 = 1.01 \text{ J d}^{-1}$ , leaving  $8.93 \text{ J d}^{-1}$  for animal tissue growth.

### Reproductive expenditure

There are a mean of 437 polyps on a CP nubbin with 300 mg of dry tissue ( $15.51 \text{ mg dry tissue} = 1 \text{ cm}^2 = 22.6$  polyps) of which, in any one week, 13.1% will each contain 1.7 mature planulae (total 97 planulae). Using the energy content of larvae from FR *P. porites* ( $0.27 \text{ J planula}^{-1}$ , Edmunds and Davies 1986), these 97 planulae represent 26.19 J. If the 97 planulae in a nubbin represents 1 month's (30 d) reproductive effort, the reproductive expenditure is  $0.87 \text{ J d}^{-1}$ .

### Losses from zooxanthellae

Assuming that there is no expulsion of excess zooxanthellae from the colony, the energy unrequired for zooxanthellae growth or respiration will be assumed to be translocated to the animal tissue. This amounts to 178.51 J.

<u>COLUMBUS PARK SITE</u>				
<u>ZOOXANTHELLAE</u>				
Photosynthesis	=	Respiration + Growth + Losses		
228.32J		48.80J	1.01J	178.51J
100%		21.4%	0.4%	78.2%
<u>ANIMAL TISSUE</u>				
Photosynthetically Fixed Excess Energy	=	Respiration + Growth + Reproduction + Losses		
178.51J		15.06J	8.93J	0.87J
<b>a</b>		6.6%	3.9%	0.4%
<u>FORE REEF SITE</u>				
<u>ZOOXANTHELLAE</u>				
Photosynthesis	=	Respiration + Growth + Losses		
190.62J		40.36J	1.52J	148.74J
100%		21.2%	0.8%	78.0%
<u>ANIMAL TISSUE</u>				
Photosynthetically Fixed Excess Energy	=	Respiration + Growth + Reproduction + Losses		
148.74J		50.14J	12.07J	0.77J
<b>b</b>		26.3%	6.3%	0.4%

Fig. 4. Partitioning of the 24 h energy budget into zooxanthellae and animal components for *P. porites* from 10 m depth at **a** the Columbus Park site and **b** the fore reef sites. The budgets are calculated for specimens with 300 mg of dry tissue for a clear sunny day as recorded on 16 June 1985. Absolute Joule values and percentage of the gross photosynthetic input are shown. Budget from the fore reef site from Edmunds and Davies (1986)

### Scope for growth

The assimilated energy was taken as the total photosynthetically fixed energy as there was no evidence for significant zooplankton feeding. The apparent scope for growth is therefore  $228.32 - (48.80 + 15.06) = 164.46 \text{ J}$  (CP) and  $190.62 - (40.36 + 50.14) = 100.12 \text{ J}$  (FR). These are equivalent to 72% (CP) and 53% (FR) of the assimilated energy.

The complete energy budget for CP corals is shown in Fig. 4a and the comparable budget for FR corals is shown in Fig. 4b.

### Discussion

The main between site differences in the energy budgets for *Porites porites* are the higher photosynthetic productivity, the lower growth rates and animal respiration rate and the higher losses of energy at the CP site compared to the FR site. These differences are probably the result of the 6% reduction of in situ PAR and the higher sedimentation rates recorded at the CP site compared to the FR site.

### Photosynthesis

The P/I curves for CP *P. porites* have significantly lower values for  $I_k$  and  $I_{0.95}$  in the equation for the hyperbolic tangent and a significantly higher value of  $\alpha$  compared to FR corals. These photoadaptive responses are typical of corals exposed to low irradiances (Chalker et al. 1983) and allow the CP corals to be more efficient at using PAR in photosynthesis. As a result of these changes, CP *P. porites* are only exposed to subsaturating irradiances for 42% instead of 70% (FR site) of a 14 h sunny day such as 16 June 1985 (with mean transmission of light to 10 m depth at each site). Lengthy periods of saturating irradiances result in a higher integrated photosynthesis of the CP nubbins (228.32J) compared to the FR nubbins (190.62J).

### Respiration

The reduced unit area respiration rate of CP *P. porites* compared to FR corals is probably due to the decreased dry tissue content of CP nubbins, as neither the zooxanthellae abundance nor their respiration rates were significantly different between sites. A similar effect is suggested for *Montastrea annularis* which shows a depth dependent reduction in colony respiration rate (Davies 1980), while the zooxanthellae respiration rate remains almost constant with depth (Dustan 1982). The host respiration rate in CP *P. porites* is low compared to other corals (e.g. Muscatine et al. 1984). However, the respiration rates of CP corals were measured in clear water in the lab and it is possible that under in situ conditions the high respiration rates associated with sediment shedding (Dallmeyer et al. 1982) would be observed.

The respiration rates of zooxanthellae from *P. porites* are the same order of magnitude as measured values previously recorded (Dustan 1982). However, zooxanthellae respiration in *P. porites* accounts for 21.4% (CP site) and 21.2% (FR site) of the gross photosynthetic input which are greater than the equivalent values of 9.8% in *Pocillopora eydouxi* (Davies 1984) or 2.5% in *Stylophora pistillata* (Muscatine et al. 1984). This discrepancy may result from the different species of coral involved or from the different methodologies used.

### Growth

The high sedimentation rate and low irradiances at the CP site may have depressed the growth rates of *P. porites* compared to the FR specimens. Similar responses for other species have been reported (Dodge and Vaisnys 1977; Barnes 1982). The lower expenditure in biosynthesis and calcification with the lower growth rate of CP nubbins may partly explain the low host respiration rate at this site.

The algal specific growth rates ( $\mu_z$ ) for CP nubbins ( $0.0023 \text{ d}^{-1}$ ) are similar to those for FR nubbins ( $0.0028 \text{ d}^{-1}$ ). These estimates are lower than the mea-

sured values of  $\mu_z$  for other Caribbean corals (Muscatine et al. 1985). A higher  $\mu_z$  for *P. porites* would produce an excess of zooxanthellae, necessitating a regulatory mechanism to prevent overpopulation of host cells.  $\mu_z$  values were more than 3-fold greater than host specific growth rates in *Stylophora pistillata* (Muscatine et al. 1985) but regulation by expulsion of zooxanthellae occurred at less than 4% of the rate at which new cells were added (Hoegh-Guldberg et al. 1987). Muscatine et al. (1985) suggested that regulation might be achieved by host digestion of zooxanthellae. This potential source of energy needs to be further studied in *P. porites*.

### Excess energy

The "losses" in the energy budget for CP nubbins have been calculated by subtraction and are assumed to represent a surplus of energy which is lost from the colony. This amounts to 67% of the photosynthetically fixed energy, which is greater than the 45% surplus from FR nubbins due to the increased photosynthetic productivity and the lower host respiration rate in CP corals. There is no energetic need for zooplankton capture in either CP or FR *P. porites*.

Some corals lose significant amounts of energy in the form of mucus and lipid (Crossland 1987). We were unable to measure an oxidisable component released into the sea water during in situ experiments with *P. porites* from the FR site (Edmunds and Davies 1986). However, *P. porites* also produces mucus tunics (Coffroth 1984) at a frequency of 2–3 per month which have an energy content of  $6.88 \pm 2.86 \text{ J } 10 \text{ cm}^{-2}$  ( $n=6$ ) (Edmunds unpublished). For a nubbin with 300 mg of dry tissue and a surface area of  $16.1 \text{ cm}^2$ , the tunic would contain 11.1 J equivalent to  $1.1 \text{ J d}^{-1}$  if three are formed each month. It, therefore, seems unlikely that mucus tunics represents an important route for energy loss in *P. porites*.

### Scope for growth

The apparent scope for growth is greater for stressed CP corals than for unstressed FR corals. Both values exceed the measured growth rate. Zamer and Shick (1987) found a similar discrepancy between scope for growth and measured growth in high versus low-intertidal *Anthopleura elegantissima* which they attributed to unmeasured additional costs. The same reasoning applies to *P. porites* in the present study where the energy budgets were balanced by subtraction. If the "losses" in the energy budgets are subtracted from the apparent scope for growth, the scope for growth for stressed CP corals becomes 4.7% compared to 7.5% for FR corals. Clearly the next step is to determine the "losses" by direct measurement.

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