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Shifting roles of heterotrophy and autotrophy in coral energetics under varying turbidity

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Abstract

Suspended particulate matter (SPM) strongly alters the trophic environment of photosymbiotic aquatic organisms. At high particles loads, phototrophic energy gains can be diminished due to light absorption by suspended particles, and stress from particle abrasion or deposition on tissues. However, energy gains are enhanced if organisms are able to use SPM as a food source. For photosymbiotic benthic suspension feeders, increases in SPM concentrations may require both phototrophic and heterotrophic acclimation to sustain a positive energy balance. This study provides an experimental analysis of the effects of contrasting light and SPM regimes on the energy budget (scope for growth) of two zooxanthellate corals (*Goniastrea retiformis* and *Porites cylindrica*). Using a factorial design in a flow-through tank system, corals were exposed for 2 months to shaded and unshaded conditions (equivalent to 3–4 m depth at 4 and 16 mg dry weight SPM l^{-1}, respectively) and a range of controlled SPM loads with a natural organic content (~3% w/w). In *G. retiformis*, rates of particle ingestion were a linear function of SPM concentration within a broad range (1–30 mg dry weight l^{-1}). After 2 months of shading, photosynthetic acclimation was significant in *G. retiformis*, but did not compensate for the reduced light level, as daily respiration exceeded daily photosynthesis. However, in response to the prolonged shading, *G. retiformis* more than doubled its rate of particle feeding. At high SPM treatments (16 mg dw l^{-1}), sediment feeding by this species compensated fully for the 35–47% lower phototrophy in the shaded treatment. Due to both photo- and heterotrophic plasticity, *G. retiformis* gained tissue and skeletal mass at all experimental levels of light and SPM. In contrast, rates of particle intake by *P. cylindrica* contributed $<10\%$ to the energy budget in shaded and $<3\%$ in unshaded conditions. Feeding rates of *P. cylindrica* were half-saturated at ~3 mg dry weight l^{-1}, and four- to eight-fold lower than those of *G. retiformis*. Skeletal growth was sustained, but tissue mass and lipid contents declined in shaded and high-SPM treatments, and carbon loss due to shading by SPM was not

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compensated for by particle feeding. Thus, due to a lack of photo- and heterotrophic plasticity, periods of high turbidity resulted in energy deficiency in *P. cylindrica*, and high turbidity conditions appeared physiologically unsustainable for this species. This study is the first to show heterotrophic plasticity in a symbiotic coral, and to show that such plasticity can offset stress from high particle loads. It demonstrates that changes in the trophic mode of some coral species are a mechanism for sustaining a positive energy balance in turbid environments, thereby broadening their physiological niche.

Keywords: Energy budget; Heterotrophy; Autotrophy; Turbidity; Sediment; Diet theory; Trophic plasticity; Symbiotic cnidarian; Scleractinian coral; *Goniastrea*; *Porites*

1. Introduction

Substantive growth of scleractinian reef corals is assumed to depend primarily on high light availability for their symbiotic unicellular algae (zooxanthellae, reviewed by Buddemeier and Kinzie, 1976; Barnes and Chalker, 1990; Muscatine, 1990). In many coastal areas, frequent resuspension events (e.g., Larcombe et al., 1995) result in high concentrations of suspended particulate matter (SPM), which can strongly reduce light levels even in shallow water (see Kirk, 1994, for a general description of the relationship between particle concentration, depth and light). Rates of photosynthesis are expected to decrease in such turbid habitats, unless corals are able to fully photoacclimate to low light (e.g., Falkowski et al., 1990). Furthermore, high SPM loading may cause sediment accumulation on coral tissues and thereby stress and reduced growth (review by Rogers, 1990). However, besides their phototrophic dependence, corals are also heterotrophs and have been shown to feed on a range of food types, e.g. zooplankton (Porter, 1974; Sebens et al., 1996), microzooplankton (Ferrier-Pages et al., 1998a), bacteria (Bak et al., 1998), sediment (Stafford Smith and Ormond, 1992) and suspended particulate matter (Anthony, 1999a, 2000), the latter comprising components from all particle types. Thus, in habitats where the rate of photosynthesis is compromised by high SPM concentrations, heterotrophy may be favoured if the SPM represents a significant nutritional value. It has previously been suggested that corals in turbid water are more dependent on heterotrophy than in clear water (Tomascik and Sander, 1985; Ayling and Ayling, 1991; Anthony, 2000, Fabricius and Dommisse, 2000), but the hypothesis that sediment feeding can offset the stress effects of turbidity and sediment loading in corals has not been tested experimentally.

Relative to zooplankton, SPM is a poor-quality food source (Corner and Davies, 1971; Anthony, 1999a) but may constitute the most abundant source of nutrition in the water column of some areas (e.g., Roman et al., 1990; Hansen et al., 1992). According to the predictions of optimal diet theory (reviewed by Hughes, 1980) such an abundant, although low-quality, food source should be incorporated in the diet of suspension feeders as its rejection may be costly. The recent findings that some coral species on inshore, turbid reefs have higher sediment clearance rates than their conspecifics on offshore, clear-water reefs (Anthony, 2000) supports this hypothesis. Since coral photosynthesis is a negative function of SPM concentration (because SPM attenuates

light) and particle ingestion is a positive function of SPM concentration, species with different phototrophic and heterotrophic capacities are likely to have differing thresholds at which turbidity and sediment become stress factors. The relative contributions from phototrophy and heterotrophy to the coral energy balance in turbid environments will therefore depend on the efficiency with which light and particle availabilities are utilised, and the capacity by which nutritional modes can acclimatise to changing conditions.

In this study, we demonstrate for the first time by experimental analysis that feeding rates on natural suspended particulate matter (SPM) can compensate for reduced phototrophy in symbiotic scleractinian corals in turbid environments, in effect converting a stress factor into a resource. Specifically, we test the hypotheses that corals with differing phototrophic–heterotrophic capacities show stress responses or growth optima at differing combinations of light and SPM.

To provide a framework for testing these hypotheses, we compiled a model carbon budget for symbiotic cnidarians based on a range of environmental and physiological parameters. For this purpose we used the model of Scope for Growth (*SfG*) which is defined as the difference between energy acquisition and that lost via metabolism and excretion (Warren and Davis, 1967). *SfG* provides a convenient quantitative measure of physiological stress (e.g., Calow and Sibly, 1990; Maltby, 1999), the term 'stress factor' thus referring to a cause of reduced *SfG*. For corals and other organisms that are capable of both phototrophy and heterotrophy (mixotrophs), *SfG* with respect to carbon is given by

$$SfG = P_g + A + R - EX \quad (1)$$

where P_g is gross phototrophic carbon assimilation, A is assimilation of carbon from ingested food particles, R is the amount of carbon respired (negative by convention, Barnes and Chalker, 1990), and EX is the excretion of, for example, dissolved organic carbon or mucus (Crossland, 1987). A positive *SfG* indicates surplus carbon that can be allocated to somatic growth, gonads, and/or energy reserves (lipids), whereas a negative *SfG* implies that more carbon is allocated to catabolic processes (i.e. respiration) or lost via excretion than is acquired. Assimilated organic carbon is not directly allocated to calcification (except for the organic matrix), but is linked to processes driving the calcification process (Barnes and Chalker, 1990; McConnaghey and Whelan, 1997, see below). At high particle loads, energy costly processes such as active sediment rejection may lead to an increase in both R (Dallmeyer et al., 1982; Telesnicki and Goldberg, 1995) and EX through the production of mucus (e.g., Dallmeyer et al., 1982; Riegl and Branch, 1995), and consequently a decrease in *SfG*. Accurate measurements of excretions of mucus and dissolved organic carbon are notoriously difficult (Krupp, 1985), and are further complicated by turbidity treatments due to contamination by particulate carbon. For operational reasons we therefore rearrange Eq. (1) so that daily energy acquisition through feeding and photosynthesis is balanced by scope for growth plus excretory losses:

$$SfG + EX = SfG' = P_g + A + R \quad (2)$$

The hourly, net photosynthetic rate (P_n, μg C cm^{-2} h^{-1}) can be expressed as an

exponentially saturating function of light availability (I, μmol quanta m^{-2} s^{-1}) composed of wavelengths in the range of photosynthetically active radiation (PAR, see review by Falkowski and Raven, 1997):

$$P_n = P_{g,max}(1 - e^{-I/I_k}) + R_t \quad (3)$$

where $P_{g,max}$ (μg C cm^{-2} h^{-1}) is the maximum rate of gross photosynthesis, I_k (μmol quanta m^{-2} s^{-1}) is the light level at which P_g is 63% saturated, and R_t (μg C cm^{-2} h^{-1}) is the rate of respiration. Corals exposed to a low-light environment photoacclimate by developing greater photosynthetic efficiency, i.e. $P_{g,max}$ and I_k are reached at a lower light level (Chalker et al., 1983). The amount of light reaching the organism depends on both the water depth (z, m) and the extinction coefficient for light within the PAR range (k_{PAR}, m^{-1}) as determined by the optical properties of the water column (e.g., Kirk, 1994):

$$I_{z,t} = I_{0,t}\, e^{-zk_{PAR}} \quad (4)$$

where $I_{0,t}$ is the light level immediately below the water surface at time t. Importantly, k_{PAR} increases in direct proportion to particle concentration (c_{sp}), their ratio being dependent on the nature of the particulate matter (e.g., Te, 1997). Light availability at a given depth and time of day can thus be estimated as a function of particle availability:

$$I_{z,t} = I_{0,t}\, e^{-z\psi c_{sp}} \quad (5)$$

where ψ (m·l mg^{-1}) is a coefficient relating k_{PAR} to c_{sp}. The daily rate of net photosynthesis can thus be expressed as

$$P_g + R = \int_{t=0}^{24} (P_{g,max}[1 - e^{-I_{z,t}/I_k}] + R_t)\, dt \quad (6)$$

Daily rates of heterotrophic carbon assimilation (A, μg C cm^{-2} d^{-1}) depend on the rate of particle ingestion ($IN_{c_{sp},t}$, μg dw cm^{-2} h^{-1}), relative organic carbon content (C_{org}, dimensionless), the efficiency by which the ingested carbon is assimilated (AE, dimensionless), and the number of hours spent feeding daily (T, h). Rate of particle encounter and capture by passive suspension feeders is a function of particle flux, which is the product of particle concentration (c_{sp}, mg dw l^{-1}) and the rate of water flow (Shimeta and Jumars, 1991). Other factors such as particle size and flow-related efficiency of capture, handling and retention (Shimeta and Koehl, 1997) will govern how much material is eventually ingested. Over a broad range of particle concentrations, the rate of ingestion is predicted to follow a curvilinear (Type II) functional response (e.g., Ruxton and Gurney, 1994), for example the Michaelis–Menten model:

$$IN_{c_{sp},t} = \frac{IN_{max} \cdot c_{sp}}{c_{sp} + K} \quad (7)$$

where IN_{max} is the maximum rate of ingestion and K (mg dw l^{-1}) is the particle concentration at which the ingestion rate is half of maximum. The hourly ingestion rate

is here rendered a variable of time of day to accommodate for species with diel variation in feeding activity (e.g., Porter, 1974; Sebens and Deriemer, 1977). Over concentration ranges where saturation is absent (K large), however, $IN_{c_{sp},t}$ is a linear function of c_{sp}, the slope representing the particle clearance rate (Anthony, 2000). The assimilation efficiency (AE) generally correlates negatively with $IN_{c_{sp},t}$ (Szmant-Froelich and Pilson, 1984; Zamer, 1986), but is assumed here to be independent of C_{org}. Thus,

$$A = \int_{t=0}^{T} (IN_{c_{sp},t})\, dt\ AE_{IN_{c_{sp},t}} C_{org} \tag{8}$$

The 24-h carbon budget based on contributions from photosynthesis and particle feeding hence becomes

$$SfG' = \int_{t=0}^{24} (P_{g,max}[1 - e^{-I_{z,t}/I_k}] + R_t)\, dt + \int_{t=0}^{T} (IN_{c_{sp},t})\, dt\ AE_{IN_{c_{sp},t}} C_{org} \tag{9}$$

In summary, gross daily photosynthesis ($P_{g,d}$, left-most term) will decrease with particle concentration, depth, and surface irradiance, as these variables govern light availability (assuming a constant ψ, Eq. (5)), as well as changes in photo-kinetic parameters of the P–I curve in response to lowered light levels. Heterotrophy (right-most term) will increase (linearly or curvilinearly) with particle concentration (Eq. (7)), depending on the variation in assimilation efficiency, food quality, diel pattern of expansion, and adaptive changes in feeding ability to changes in turbidity. The daily rate of respiration (R) may be affected by light level as well as feeding rate; and where $P_g \leq R$, SfG' will be fully dependent upon heterotrophy to remain positive.

2. Materials and methods

2.1. Study species

To analyse experimentally the effects of particle heterotrophy on coral energy budgets at different levels of turbidity, we used two common species of zooxanthellate scleractinian coral with contrasting SPM feeding capacities. *Goniastrea retiformis* (family Faviidae) forms encrusting to dome-shaped colonies with large polyps (up to 5 mm diameter, Fig. 1A) that are highly efficient in particle capture (Anthony, unpublished). Conversely, *Porites cylindrica* (family Poritidae) has a digitate to branching growth form and small polyps (~1 mm diameter, Fig. 1B) with poor particle-feeding abilities (Anthony, 1999a). *G. retiformis* occurs on intertidal reef flats as well as subtidally in most reef habitats of the Great Barrier Reef, and *P. cylindrica* is found in the subtidal of fore reefs and lagoonal areas (e.g., Veron, 1986).

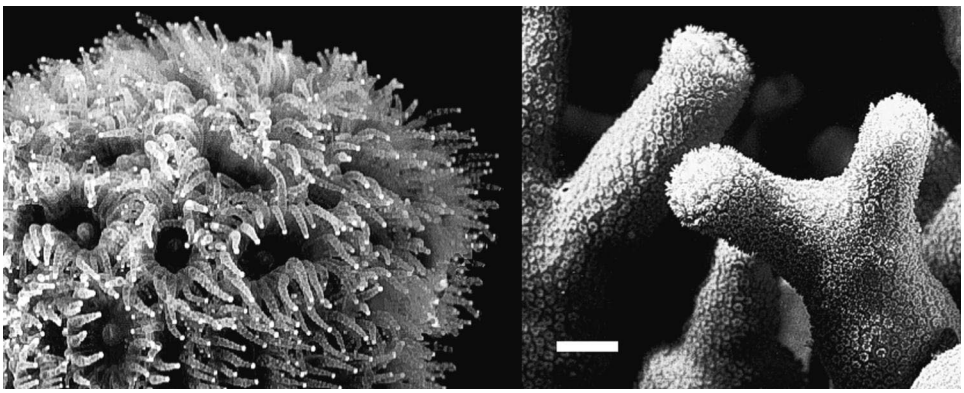

Fig. 1. Comparative size of expanded polyps of the study species *Goniastra retiformis* (A) and *Porites cylindrica* (B). The scale bar is 5 mm and applies to both panels.

2.2. Experimental framework

To quantify effects of particle concentration and shading on all components of the coral energy budgets, the investigation was composed of three main studies.

2.2.1. Study 1: growth experiment

Effects of two contrasting light regimes and four concentrations of suspended particulate matter (SPM) on tissue and skeletal growth rates were determined for 250–300 coral colonies (or branches) of each species to investigate long-term bioenergetics at contrasting environmental conditions. To test for effects of treatments on energetic status, subsets of the experimental coral populations were sampled both at the beginning and after the growth experiment to compare changes in tissue mass, energy reserves in the form of lipids, and energy investment into growth in response to the various treatment levels.

2.2.2. Study 2: photosynthesis and respiration

At conclusion of the growth experiment, rates of respiration and photosynthesis were determined to estimate daily carbon requirements and the contribution of phototrophy to the carbon balance, and to determine to what extent photoacclimation can compensate for the reduction in light level.

2.2.3. Study 3: feeding experiments

To determine and compare general SPM-feeding capacities and the contribution of heterotrophy to energy budgets, rates of particle ingestion were determined as a function of particle concentration. Also, particle-feeding capacities before and after the prolonged exposure to differing light and particle regimes were compared to determine the significance of heterotrophic plasticity in meeting energy demands.

The results of all studies were combined to construct a predictive energy model for each coral species over a range of light levels, SPM concentrations, and depths.

2.3. Experimental tank system

The growth experiment was conducted in a large flow-through tank system at Orpheus Island Research Station (18°35′S, 146°20′E, ~15 km off the coast of North Queensland, Australia). The system consisted of 32 tanks (46 l each) placed in a shallow pool under a Solarweave roof. Seawater flowing through the pool buffered temperature fluctuations, and the roof allowed 40% penetration of sunlight within the photosynthetically active range as measured with a LI-192SA irradiance sensor. In each tank, a rack for mounting groups of corals was suspended ~15 cm below the water surface and above a pump that generated water circulation. To keep the majority of particles in suspension, a turbulent flow speed averaging 15–17 cm s^{-1} was used. A detailed description of the setup is given elsewhere (Anthony, 1999b).

We performed the experiment using a 2 by 4 factorial design with light and SPM as the experimental factors. Each treatment combination was replicated by four tanks, and additional racks with corals were deployed in the field to control for tank artefacts (see also Section 2.4). Treatments were assigned randomly to individual tanks to control for heterogeneity in light regime, temperature or water supply among positions within the pool. The 16 tanks in the Shaded treatment were covered with screens that allowed 25% light penetration (mean subsurface I at noon ~140 μmol quanta m^{-2} s^{-1}), whereas the 16 tanks in the Unshaded treatment were left without additional shading under the tent (mean subsurface I at noon ~600 μmol quanta m^{-2} s^{-1}). The two light levels simulated light conditions at 3–4 m depth at particle concentrations of 4 and 16 mg dry weight (dw) l^{-1}, respectively. The four water-quality treatments consisted of tanks with a continuous supply of (1) filtered seawater (<1 μm) to provide a treatment that was largely deprived of particulate food (Filtered), (2) untreated seawater directly from the reef which served as a control for water treatment (Raw), (3) seawater with a low addition of SPM (Low), and (4) seawater with a high addition of particles (High SPM).

Using the methods described by Anthony (1999b), particles from a stock suspension of natural SPM (collected daily by filtration of water pumped from the reef) were dispensed by an automated system to each of the eight Low and eight High SPM treatment tanks such that final concentrations were 3.9 ± 0.5 and 15.8 ± 1.4 mg dw l^{-1}, respectively. Briefly, particle concentrations in the treatment tanks were determined based on those of stock suspensions (subsamples determined gravimetrically on GF/F filters), volumetric rates of dispensation, tank volumes and rates of seawater flow-through. In the filtered treatment, particles smaller than 1 μm and autochthonous material from algal growth resulted in particle concentrations of 0.5–0.7 mg dw l^{-1}. Concentrations of SPM in the different treatment groups, tank controls and in the field are given in Table 1. Coral growth was measured for all treatments. However, particle feeding, photosynthesis and respiration were measured for the four extreme treatment groups only: Filtered/Shaded, High SPM/Shaded, Filtered/Unshaded, and High SPM/Unshaded (henceforth referred to as the 'main treatments').

The light regime in the tent was monitored continuously using a LI-COR quantum sensor (LI-192SA with datalogger LI-1000) positioned 2 m above the tanks in the centre of the pool. At 2–4 day intervals, light was also measured underwater inside all treatment tanks and compared with concurrent readings from the overhead sensor. Ratios

Table 1
Concentrations and quality of suspended particulate matter in the tank system and in the field at different sampling occasions during the 2-month growth experiment[a]

Tank setup	Particle concentrations (mg dw l^{-1})								
	Mean	S.E.	*N*	Field controls			Mean	S.E.	*N*
Filtered	0.68	0.07	10	Reef slope			1.30	0.11	15
Raw (tank controls)	1.85	0.10	12	Reef flat			1.49	0.14	12
Low	3.95	0.35	25						
High	15.79	1.40	25						
	Particle quality (% of dw)								
	Tank setup			Reef slope			Reef flat		
	Mean	S.E.	*N*	Mean	S.E.	*N*	Mean	S.E.	*N*
Total carbon	5.23	0.15	25	4.65	0.38	25	5.29	0.34	25
Organic carbon	2.62	0.09	10	4.30	0.46	10	3.91	0.06	10
Nitrogen	0.42	0.01	13	0.41	0.05	11	0.41	0.05	11
Phosphorus	0.095	0.003	23	0.090	0.007	14	nd		

[a] Values are mean weight percentages±standard error or samples from *N* days during the experimental period. nd, not determined.

of within-tank and overhead measurements were used to estimate light regimes inside the treatment tanks at all times during the experiment. Because the water column above corals in the tanks was <10 cm (and tank walls and bottoms were cleaned weekly) light regimes in the High SPM treatments were not significantly lower than those in the Filtered treatments (two-way ANOVA, $F_{(1,10)} = 1.88$, $P = 0.200$). The daily-integrated light per day was 2.5–4.0 mol quanta m^{-2} d^{-1} for Shaded and 8.1–12.8 E m^{-2} d^{-1} for Unshaded treatments (the range being 25 and 75% quartiles). Water temperature in the tanks, recorded continuously during the experiment, ranged from 25.5 to 28°C.

To monitor the carbon and nutrient contents of the suspended particles, water samples were taken every 2–3 days from the different treatments, and from the field sites at high tide. The samples were filtered through precombusted Whatman GF/F filters for gravimetric analysis of particulate dry weight. Organic carbon was determined on a Shimadzu 5000 C analyser, total nitrogen was assayed on an Antek 720 C/N analyser, and reactive particulate phosphorus was determined by persulphate digestion using a technique modified from Parsons et al. (1984). A summary of the carbon and nutrient contents of both experimental and ambient SPM is given in Table 1. The weight-specific content of particulate organic carbon in the tank system was 32–39% lower than at the reef slope and reef flat (*t*-test for tanks vs. slope assuming unequal variances: $t_{(7)} = 3.6$, $P_{(\text{two-tailed})} = 0.01$), presumably due to the filtration and short-term storage (see Anthony, 1999b). However, relative contents of particulate nitrogen and phosphorus in the tanks were almost identical to those in the field.

2.4. Collection of coral colonies

Coral colonies were collected from fringing reefs on the western (coastal) side of

Orpheus Island. Approximately 250 small encrusting to dome-shaped colonies of *G. retiformis* of 5–8 cm diameter were chiselled from the reef flat in Pioneer Bay, and transferred to a large holding tank at Orpheus Island Research Station. The undersides of the colonies were cleaned of epibionts and tagged. About 300 terminal branches of *P. cylindrica* (6–8 cm long) were collected from the reef slopes in Pioneer Bay and adjacent bays and mounted vertically on numbered stands as described in Anthony (1999b). The majority of branches carried two branchlets distally (1–3 cm long) which is the typical morphology of the local population. Only fragments with a broken edge of less than 5% of the total surface area were used. The corals were placed on racks and left to recover from handling in the field for 6–8 weeks.

Immediately prior to the growth experiment, all corals were transported from the reef site to the tank setup and distributed randomly among tanks. Each tank held six to seven colonies of *G. retiformis* (total of 24–28 replicate colonies per treatment group) and seven to eight branches of *P. cylindrica* (28–32 per treatment group). To control for tank artefacts, groups of corals were also transferred back to racks on the reef. Shading of the field controls was accomplished by shade frames mounted over the racks. Sixty colonies of *G. retiformis* and 80 branches of *P. cylindrica* were distributed among four Shaded and four Unshaded racks (10 and seven colonies per rack, respectively) on the reef slope at ~3 m below datum. Since *G. retiformis* was collected intertidally, ~60 additional colonies of this species were distributed among four Shaded and four Unshaded racks on the reef flat (~0.3 m above datum). Light levels (measured weekly using the LI-COR system above) for Shaded and Unshaded corals of both species on the reef slope corresponded to those in the tanks, whereas Shaded and Unshaded *G. retiformis* on the reef flat experienced light levels two- to three-fold those in the tanks and on the slope, depending on the tide.

2.5. Study 1: effects of turbidity on coral growth

2.5.1. Growth of tissue mass

To estimate changes in tissue dry weight per cm^2 surface area (Δw_{Tis}, mg cm^{-2}) under the different turbidity regimes, 15 corals of each species were collected in the field prior to the 2-month growth experiment, and three to four corals were sampled from each tank at completion of the experiment (Table 2). Surface areas (S) of these colonies were measured by foil wrapping before they were preserved in 7% formalin in freshwater for 24 h, decalcified in 2–4% HCl, and the tissue dried at 50°C until constant weight ($W_{Tis1}$and W_{Tis2}). Δw_{Tis} was determined by subtracting pre-experimental from post-experimental area-specific tissue mass and normalising to 1 month ($\Delta w_{Tis} = (w_{Tis2} - w_{Tis1})/2$, see also Table 2). Due to the relatively narrow size range used, tissue growth rates were not adjusted for differences in colony (or branch) size. Also, because the growth experiment was relatively short, tissue growth attributable to increases in surface area was less than 5% for both species, and therefore considered negligible.

2.5.2. Changes in lipid stores

To determine storage or exhaustion of energy stores, lipid contents were assayed for 12 freshly collected colonies (or branches) of each species prior to the growth

Table 2
Summary of measured and derived variables and number of samples (N) associated with each variable[a]

Measurements and derived variables	Symbol and equations	Sampling regime per species	
		N at Day 0–2	N at Day 60–62
Tissue surface area (cm^2)	S	6–8 per rack	6–8 per rack
Colony (or branch) buoyant weight (mg)	W_B	6–8 per rack	6–8 per rack
Buoyant weight (mg cm^{-2})	$w_B = W_B/S$	6–8 per rack	6–8 per rack
Skeletal dry weight standard (mg)	$W_{Sk} = bW_B + c$	15 from reef	nd
Skeletal growth (mg cm^{-2} $month^{-1}$)	$\Delta w_{Sk} = b(w_{B2} - w_{B1})/2$		
Tissue mass (mg cm^{-2})	$w_{Tis} = W_{Tis}/S$	15 from reef	3–4 per rack
Tissue growth (mg cm^{-2} $month^{-1}$)	$\Delta w_{Tis} = (w_{Tis2} - w_{Tis1})/2$		
Lipid content (mg cm^{-2})	$w_{Lip} = W_{Lip}/S$	12 from reef	3–4 per rack
Lipid build-up or exhaustion (mg cm^{-2} $month^{-1}$)	$\Delta w_{Lip} = (w_{Lip2} - w_{Lip1})/2$		
Photosynthesis and respiration (μg C cm^{-2} 24 h^{-1})	$P_{net} = P_{gross} + R$	nd	2 per rack[b]
Feeding rate, concentration-dependent (μg C cm^{-2} h^{-1})	$IN_{c_{sp}}$	16–20 from reef	nd
Feeding rate at 16 mg l^{-1} (μg C cm^{-2} h^{-1})	IN_{16}	nd	2 per rack[b]
Feeding period (% of 24 h)	T	nd	6–8 per rack[b]

[a] All except colony buoyant weight are normalised to tissue surface area. Tissue mass and lipid content are given as dry weight. nd, not determined.

[b] Corals used in respirometry and feeding trials were taken from the following treatments only: Shaded/Filtered, Shaded High SPM, Unshaded/Filtered/Unshaded/High SPM.

experiment, and for three to four conspecifics from each tank at the conclusion of the experiment. The corals were frozen at −20°C, and while frozen, a fragment was cut from each colony and freeze-dried immediately. The tissue surface area of each dried fragment was measured by foil wrapping before grinding the fragment (tissue and skeleton) to a powder. Lipids were extracted from the powder with chloroform/methanol (2:1, v/v) using techniques described by Folch et al. (1957) and Harland et al. (1992b). After drying of the extracts, total lipid content (W_{Lip}, mg) was determined gravimetrically to the nearest 0.1 mg and then normalised to unit surface area of tissue (w_{Lip}, mg cm^{-2}). Analogous to Δw_{Tis}, rates of lipid storage (Δw_{Lip}, mg cm^{-2}) were estimated as the difference in lipid content between pre- and post-experimental corals (Table 2).

2.5.3. Skeletal growth

Changes in skeletal dry weight (Δw_{Sk}, mg) were derived from changes in buoyant weighing (ΔW_B, mg) using the technique described by Spencer Davies (1989). To enable the conversion of W_B to W_{Sk}, 14–16 coral colonies (or branches) with known W_B were bleached in chlorine to remove tissues, and dried at 50°C until constant weight. The

Table 3
Summary of regressions used to convert buoyant weight (W_B, g) to skeletal dry weight (W_{Sk}, g)

Species	Relationship	S.E. of coefficient	P	R^2	N
G. retiformis	$W_{Sk} = 1.576W_B + 353$ mg	0.021	<0.001***	>0.99	14
P. cylindrica	$W_{Sk} = 1.693W_B + 87$ mg	0.029	<0.001***	>0.99	16

relationship $W_{Sk} = a \cdot W_B + c$ was determined for both species using linear regression (Table 3).

To standardise skeletal growth to tissue surface, the latter was measured at Day 1–2 and 60–62 (Table 2). For *Goniastrea retiformis*, S was modelled as a sphere cap based on the mean of largest and smallest diameter and the height of the live part of the colony. For *Porites cylindrica*, S was determined based on combinations of basic geometrical shapes of individual branchlets (cones, cylinders, and hemispheres). Geometric modelling was chosen over the more accurate foil-wrap technique (Marsh, 1970) to avoid stressing the live corals at the onset of the experiment. Based on a subset of 14 corals per species, S determined geometrically was ~2% (*G. retiformis*) and ~10% (*P. cylindrica*) lower than that determined by foil wrapping. However, S determined by the two methods did not differ significantly by a t-test for paired comparisons (*G. retiformis*, $t_{(13)} = 1.45$, $P_{(\text{two-tailed})} = 0.17$; *P. cylindrica*, $t_{(13)} = 0.58$, $P_{(\text{two-tailed})} = 0.57$).

2.5.4. Estimating energy and carbon investment into growth

Energy investment into growth was calculated for all treatment groups based on estimated costs of tissue growth and skeletal growth. The allocation of energy into tissue growth was estimated based on the ratio of lipid storage (Δw_{Lip}) to total tissue growth (Δw_{Tis}). This method was preferred over calorimetric analyses of tissue samples, since the energetic properties of tissues are likely to be altered by formalin fixation and decalcification (Kathy Burns, personal communication). We assumed that tissue mass other than lipids was comprised of proteins and carbohydrates in the ratio 1:2 as reported for sea anemone tissue (Zamer and Shick, 1989). Energy allocation to tissue growth (ΔE_{Tis}, J cm^{-2}) was then calculated from enthalpies of combustion based on values by Gnaiger and Bitterlich (1984): lipid (−39.5 J mg^{-1}), protein (−23.9 J mg^{-1}) and carbohydrates (−17.5 J mg^{-1}). Non-lipid tissues ($\Delta w_{Tis} - \Delta w_{Lip}$) were therefore assumed to have an enthalpy of combustion of $-2/3 \cdot 17.5$ J mg^{-1} $-1/3 \cdot 23.9$ J mg^{-1} $= -19.6$ J mg^{-1}. Energy investment into tissue (positive) was thus estimated as

$$\Delta E_{Tis} = 39.5 \text{ J mg}^{-1}\, \Delta W_{Lip} + 19.6 \text{ J mg}^{-1}\, (\Delta W_{Tis} - \Delta W_{Lip}) \quad (10)$$

Analogously, carbon investment into tissue was estimated based on standard mass fractions of carbon in lipid (0.776), carbohydrate (0.444) and protein (0.529, Gnaiger and Bitterlich, 1984), and using the above ratio of carbohydrate to protein for non-lipid tissues ($2/3 \cdot 0.444 + 1/3 \cdot 0.529 = 0.472$). Thus,

$$\Delta C_{Tis} = 0.776\Delta W_{Lip} + 0.472(\Delta W_{Tis} - \Delta W_{Lip}) \quad (11)$$

Energy equivalents of skeletal growth (Δw_{Sk}) were estimated based on the model that 1 mol of ATP is used for energising the uptake of 2 mol of Ca^{2+} ion by the site of calcification in exchange of 4 mol of protons (McConnaghey and Whelan, 1997). Assuming that this exchange is the only energetic expense of skeletal growth, the precipitation of 1 mg dw of $CaCO_3$ (100.2 g mol^{-1}) requires 5 μmol of ATP, which equates to 0.152 J (Zubay, 1983). Energy investment into skeletal growth (ΔE_{Sk}, J cm^{-2}) was thus estimated as

$$\Delta E_{Sk} = 0.152 \text{ J mg}^{-1} \Delta w_{Sk} \quad (12)$$

Carbon equivalents of skeletal growth (for comparison with photosynthesis and feeding) were estimated from Eq. (12) by assuming that ATP used in the Ca^{2+} transport is generated from the catabolism of carbohydrates (ΔE_{Sk}/39.4 J mg C^{-1}).

2.6. Study 2: effects of turbidity on photosynthesis and respiration

At completion of the growth experiment, we measured photosynthesis and respiration of corals from the four main treatment groups. Two coral colonies (or branches) of each species were taken from each of the four tanks in each of the four treatment groups. Net photosynthesis (P_n) was measured as the sum of gross production and respiration (negative) (McCloskey et al., 1978) using a respirometer with four 2.5-l chambers with individual oxygen probes connected to a central logger unit (setup described in Fabricius and Klumpp, 1995). Each colony was deployed in an individual chamber over a 12-h period starting at 12:00 or 24:00 h to construct photosynthesis–light (P–I) curves for the four treatment groups. The chambers were continuously stirred and automatically flushed every 15 min for 3 min. Concentrations of dissolved O_2, as well as light and temperature, were logged at 1-min intervals. To standardise light conditions among trials, an artificial light source with a spectral composition resembling natural sunlight was used (two metal-halide lamps, each 400 W). Light intensity was adjusted by elevating or lowering the lamps over the incubation chambers, exposing the corals to four discrete light levels for 1.5 h each (80, 160, 320 and 640 μmol quanta m^{-2} s^{-1}) during the day, and to complete darkness during the night to measure dark respiration. Control incubations without corals in both light and darkness showed that background oxygen production/consumption of the incubation water was negligible. After each run, the corals were frozen immediately and stored (−20°C) for later analysis of tissue dry weight and surface area. Hourly rates of oxygen produced by photosynthesis (P_g) and consumed by respiration (R_t) were converted to carbon equivalents ($P_{g,C}$ and $R_{t,C}$) based on molar weights, hence $P_{g,C}$ = μg O_2 produced · 12/32/PQ and $R_{t,C}$ = μg O_2 consumed · 12/32 · RQ, where PQ and RQ are the photosynthetic and respiratory quotients assumed to be 1.1 and 0.8, respectively (Muscatine et al., 1981). R_t was measured as dark respiration ($R_{t,dark}$), and was assumed to be representative of daytime rates.

2.7. Study 3: effects of turbidity on particle feeding

Two sets of experiments were conducted to evaluate the adaptive significance of SPM

feeding in the different environments. Firstly, to compare the general suspension-feeding capacities of the two species, the concentration-dependent rates of particle ingestion (feeding responses) were determined for 16–20 freshly collected colonies (or branches) prior to the growth experiment. Feeding trials were conducted using the setup and protocol described by Anthony (1999a). Briefly, individual specimens were incubated in a suspension of ^{14}C-labelled natural particulate matter for 1 h using 2-l recirculating flow chambers. Feeding experiments were run at night (~19:00–22:00), during which all *Goniastrea retiformis* had their polyps extended (*Porites cylindrica* does not have a distinct diel cycle). The incubations were run in darkness to minimise photosynthetic uptake of $^{14}CO_2$. Four colonies were incubated at each of five different particle concentrations (1, 4, 8, 16 and 30 mg dw l^{-1}) to model feeding responses. In the second set of experiments, we tested whether prolonged exposure to different sediment and light regimes during the growth experiment produced changes in rates of particle intake (heterotrophic plasticity). Here, feeding trials were run with eight corals from each of the four main treatments (Shaded/Filtered, Shaded/High SPM, Unshaded/Filtered, and Unshaded/High SPM) after completion of the growth experiment. These corals were incubated using a protocol similar to the above, but at a particle concentration of ~16 mg dw l^{-1} only (corresponding to the High SPM treatment level). The tissues containing the ingested, ^{14}C-labelled material were subsequently digested from their skeletons (using 1 M KOH, Anthony, 2000) and the radioactivity determined in a scintillation counter. Radioactivity per sample (dpm) was converted to particle intake (μg dw cm^{-2} h^{-1}) based on a specific radioactivity of 750 dpm (mg dw)$^{-1}$ of sediment used in the feeding trials (Anthony, 1999a).

2.8. Data analysis and modelling

2.8.1. Measured growth data: tissue, lipids and skeleton

Effects of shading and SPM concentration on rates of tissue growth, lipid storage and skeletal growth were tested for each species separately using two-way ANOVAs based on means for each tank within a treatment, the latter to avoid pseudoreplication (Hurlbert, 1984). Field controls were excluded from the ANOVAs since their exclusion enabled a stronger interpretation of treatment effects in the tank design. Only corals that survived and displayed no partial mortality (intact tissue surface) until completion of the experiment were used. The added variance from before versus after comparisons of tissue mass and lipid content, and from the regression of skeletal dry weight on buoyant weight, were included in the analysis. We used the conservative Tukey's HSD test to locate significant differences between individual treatment groups.

2.8.2. Derived growth variables: energy investment

Analogous to the measured growth variables, effects of shading and SPM concentration on energy investment into tissues (ΔE_{Tis}, including lipids), skeletal growth (ΔE_{Sk}) and total energy investment ($\Delta E_{Tis} + \Delta E_{Sk}$) were tested for each species separately using two-way ANOVAs based on the means for each tank within a treatment and variances among treatments. Variances were calculated based on variance contributions from all variables involved using the method of Travis (1982). Briefly, the variance

V of product X_1X_2 was obtained as $V = V_1/n \cdot X_2^2 + V_2/n \cdot X_1^2 + V_1/n_1 \cdot V_2/n_2$, where V_1 and V_2 are variances and n_1 and n_2 are sample sizes associated with the means X_1 and X_2, respectively. The variance of the product of a constant and a variable (Xc) was calculated as Vc^2.

2.8.3. Carbon budgets: heterotrophy versus autotrophy

Changes in saturation light level (I_k), maximum hourly rate of photosynthesis ($P_{g,max}$) and rate of dark respiration ($R_{t,dark}$) in response to treatment history were tested using two-way ANOVAs for the two species separately (using tank means), followed by Tukey's HSD test. Daily carbon budgets with respect to photosynthesis and respiration were constructed based on Eq. (6) for corals from the main treatments.

The relationship between ingestion and particle concentration of pre-experimental corals was modelled using linear or non-linear regression analysis (the latter based on Eq. (7), STATISTICA, 1997). Differences in feeding capacity at 16 mg dw l^{-1} of corals from the four main treatments were tested using one-way ANOVAs using tank means. Feeding budgets for all treatments were based on post-experimental feeding rates at 16 mg dw l^{-1} and interpolated (using linear curves or saturation characteristics determined previously) to feeding rates at lower (Filtered, Raw and Low) particle concentrations. The contributions from particle feeding to the carbon budget were calculated using Eq. (8). We assumed an assimilation efficiency (AE) of 50%, which represents a conservative estimate (Anthony, 1999a, 2000). Using data on phototrophy and heterotrophy, predicted coral carbon budgets were also modelled over a range of turbidity regimes and depths (Eq. (9)). The aim was two-fold: first, to estimate in situ light and turbidity threshold levels, where the energy balance shifts from positive to negative due to reduced photosynthesis. Second, to determine the extent to which heterotrophy can offset these thresholds. Light level as a function of depth was predicted from SPM concentration (c_{sp}) according to Eq. (5), integrated over the light profile of an average day to produce daily estimates, and assuming that $\psi = 0.035$ m·l mg^{-1} (Te, 1997) and $I_0 = 1200$ μmol quanta m^{-2} h^{-1} at noon.

3. Results

3.1. Survivorship and general observations

Survivorship of *Goniastrea retiformis* in the tank system was 100%. Judging from the lack of tissue bleaching and partial mortality, and nightly expansion of all polyps, all colonies of this species appeared healthy in all treatments throughout the experiment. Shaded *G. retiformis* generally had their polyps expanded 16 h per day (~17:00 to ~09:00), whereas conspecifics in the Unshaded treatment were expanded for less than 12 h per day (~19:00 to ~05:00). Colonies of *Porites cylindrica* in the tanks showed 7% mortality, and an additional 20% displayed some partial mortality from algal overgrowth despite regular cleaning of stands and racks. However, mortality and partial mortality of *P. cylindrica* were not related to treatment ($\chi^2_{(4)} = 3.73$, $P = 0.44$). The polyps of *P. cylindrica* were generally extended during day and night, except during occasional 2–3 d periods of mucus-sheath production.

3.2. Study 1: effects of prolonged turbidity on coral growth rates

3.2.1. Tissue growth

Tissue growth rates of *Goniastrea retiformis* were significantly enhanced at High SPM concentrations (~16 mg dw l^{-1}). For example, tissue growth rates of Shaded and Unshaded corals in the High SPM treatment were twice those of colonies in the Filtered and Raw treatments (Fig. 2). Although shading caused more than a 40% decrease in the tissue mass of *G. retiformis*, this decrease was not significant by the ANOVA due to the large within-treatment variation (Table 4). Tissue growth rates of Unshaded corals of this species in the Low treatment were also significantly higher than rates in the Filtered and Raw treatments, suggesting a nutritional significance of intermediate particle concentrations in well-lit conditions. The rates of tissue growth of *G. retiformis* on the reef slope did not differ significantly from those of conspecifics on the reef flat or in the control tanks (Raw), despite that corals on the reef flat experienced two- to three-fold higher light levels (1000–1500 μmol quanta m^{-2} s^{-1} for Unshaded groups at noon) than corresponding groups on the slope and in the tanks.

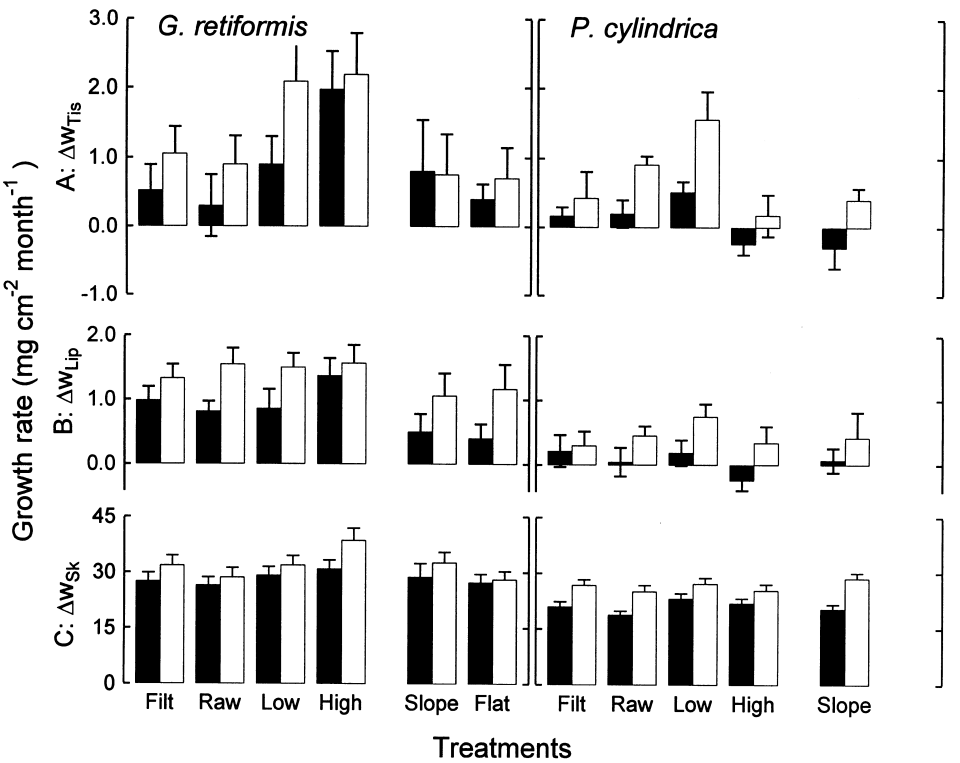

Fig. 2. Summary of changes in (A) tissue mass (Δw_{Tis}), (B) lipid content (Δw_{Lip}), and (C) skeletal growth (Δw_{Sk}) in corals exposed to different light and SPM treatments. All data are in units of mg cm^{-2} $month^{-1}$ (mean±1 S.E. of $N = 4$ tanks). Solid and open bars represent Shaded and Unshaded treatments, respectively. Treatments were: Filt, filtered seawater; Raw, unfiltered seawater; Low, low particle addition; High, high particle addition. Field controls: Slope, reef slope; Flat, reef flat. See Table 4 for ANOVA results.

Table 4
Summary of two-way ANOVA results for tissue growth, change in lipid contents and skeletal growth (all in mg dw cm^{-2} $month^{-1}$) for corals in the eight tank treatments (see also Fig. 2)[a]

	Shading		SPM		Shading×SPM		Post hoc
Response variable:	*F*	*P*	*F*	*P*	*F*	*P*	
G. retiformis							
Tissue growth (Δw_{Tis})	3.50 (1, 24)	0.074 ns	4.03 (3, 24)	**0.019***	0.36 (3, 24)	0.781 ns	Hi>Fi, Hi>R
Change in lipid content (Δw_{Lip})	7.69 (1, 24)	**0.011***	0.73 (3, 24)	0.544 ns	0.53 (3, 24)	0.667 ns	US>SH
Skeletal growth (Δw_{Sk})	5.15 (1, 24)	**0.033***	2.66 (3, 24)	0.071 ns	0.46 (3, 24)	0.714 ns	US>SH
P. cylindrica							
Tissue growth (Δw_{Tis})	12.67 (1, 24)	**0.002****	5.69 (3, 24)	**0.004****	0.83 (3, 24)	0.490 ns	US>SH, L>Hi, L>Fi
Change in lipid content (Δw_{Lip})	7.71 (1, 24)	**0.010***	1.34 (3, 24)	0.286 ns	0.60 (3, 24)	0.618 ns	US>SH
Skeletal growth (Δw_{Sk})	21.92 (1, 24)	<**0.001*****	1.60 (3, 24)	0.216 ns	0.42 (3, 24)	0.741 ns	US>SH

[a] The analysis was performed using untransformed means and composite variances with tanks as replicates. Numbers in parentheses are degrees of freedom. Key to symbols: SH, Shaded; US, Unshaded; Fi, Filtered; R, Raw; L, Low SPM; Hi, High SPM. *$P<0.05$, **$P<0.01$, ***$P<0.001$; ns, non-significant.

In contrast, tissue growth rates of *Porites cylindrica* were strongly affected by both shading (about 80% decrease relative to Unshaded) and SPM concentrations (Table 4). Maximum tissue growth rates of *P. cylindrica* occurred in the Unshaded/Low treatment (Fig. 2) and were four-fold those of conspecifics in the Unshaded/Filtered treatment. Contrary to the pattern for *G. retiformis*, tissue growth rates of *P. cylindrica* in the Shaded or Unshaded High SPM treatments were negative or zero, suggesting stress effects at high SPM loads. Control corals on the reef slope showed lower tissue growth rates than corresponding groups in the control tanks, particularly for corals on the Shaded racks. This was consistent with decreasing light levels for Shaded corals on the reef slope during the experiment due to fouling of the shade screens by sediment and algae (65–90 μmol quanta m^{-2} s^{-1} compared to 100–135 μmol quanta m^{-2} s^{-1} in the tanks at noon in the last 2 weeks of the experiment). The generally higher rates of tissue growth in *G. retiformis* compared with *P. cylindrica* paralleled an almost two-fold difference in tissue mass per unit surface area at Day 1 (*G. retiformis*, 15.1±0.5 (S.E.) mg dw cm^{-2}; *P. cylindrica*, 7.5±0.4 (S.E.) mg dw cm^{-2}).

3.2.2. Lipid storage

In both species, changes in lipid content were significantly reduced by shading but were unaffected by SPM treatments (Table 4). Lipid storage in Shaded *Goniastrea*

retiformis was 30% reduced and that in Shaded *Porites cylindrica* almost 90% reduced relative to Unshaded corals. Lipids comprised a significant proportion of the tissue growth in both species; more than half for *G. retiformis* (Shaded, 56±15%; Unshaded, 57±12%) and almost half for *P. cylindrica* (Shaded, 43±31%; Unshaded, 52±14%). In the Shaded/High SPM treatment, the reduction in lipid contents of *P. cylindrica* fully accounted for the reduction in tissue mass in this treatment. Higher rates of lipid accumulation in *G. retiformis* than in *P. cylindrica* paralleled differences in their initial lipid contents (*G. retiformis*, 3.9±0.3 mg cm^{-2}; *P. cylindrica*, 1.8±0.2 mg cm^{-2}).

3.2.3. Skeletal growth

Analogous to the changes in lipid storage, skeletal growth rates of both species were negatively affected by shading but unaffected by SPM treatments (Table 4). Skeletal growth in *Goniastrea retiformis* was marginally affected by SPM ($P = 0.071$), as skeletal growth rates were relatively high in the Unshaded/High SPM treatment (Fig. 2). Importantly, skeletal growth in *Porites cylindrica* from the Shaded/High SPM treatments was not significantly lower than in conspecifics from other treatment groups, despite loss in tissue mass and lipid contents. Coefficients of variation for skeletal growth among SPM treatments (9 and 5%, in *G. retiformis* and *P. cylindrica*, respectively) were only a tenth to a fifth those of tissue growth (44 and 54%, respectively) (Table 3). Skeletal growth rates of Shaded and Unshaded field controls did not differ significantly from those of the tank controls (Raw, Fig. 2).

3.2.4. Energy investment

In *Goniastrea retiformis*, effects of shading and SPM concentrations on energy investment into tissue growth (ΔE_{Tis}, derived from the energetics of non-lipid tissue and lipids) were strong (Fig. 3, Table 5), due to general agreement between patterns in tissue growth rates and lipid storage (Fig. 3). Most importantly, the reduction in energy investment into tissue growth in Shaded compared with Unshaded *G. retiformis* was highly significant (tissue growth rates per se were not affected by shading; Table 4). In *Porites cylindrica*, the pattern of tissue energetics was analogous to that of tissue growth.

Energy investment into tissue growth (ΔE_{Tis}) constituted on average ~88% of the total energy investment (ΔE) in *G. retiformis* and ~77% in *P. cylindrica*. Also, ΔE_{Tis} varied dramatically across treatments in both species (about 9 to 66 J cm^{-2} $month^{-1}$ for *G. retiformis* and about −9 to 42 J cm^{-2} $month^{-1}$ for *P. cylindrica*, Fig. 3C), whereas energy investment into skeletal growth (ΔE_{Sk}) varied within a narrow range (about 3.5–5.0 J cm^{-2} $month^{-1}$, Fig. 3B). Consequently, the patterns of total energy investment across SPM treatments were, in both species, largely a function of their tissue energetics. Most notable was the contrast between energy loss of tissue (−8.8±4.1 J cm^{-2} $month^{-1}$) and energy investment into skeleton (3.3±0.2 J cm^{-2} $month^{-1}$) for *P. cylindrica* in the Shaded/High SPM treatment. Using a more conservative estimate of skeletal energetics, by assuming that 1 (rather than 2) mol of Ca^{2+} is transported per mole of ATP, still rendered skeletal growth less energy costly than tissue growth (*G. retiformis*, ~23%; *P. cylindrica*, ~40%).

Table 5
Summary of two-way ANOVA results for energy investment into tissue (including lipids) and calcification (both in J cm^{-2} $month^{-1}$) for corals in the main treatments (see also Fig. 3)[a]

	Shading		SPM		Shading × SPM		Post hoc
Response variable:	*F*	*P*	*F*	*P*	*F*	*P*	
G. retiformis							
Tissues (ΔE_{Tis})	15.00 (1, 24)	**0.001****	11.99 (3, 24)	<**0.001*****	0.76 (3, 24)	0.529 ns	US>SH, Hi>Fi, Hi>R
Skeleton (ΔE_{Sk})	5.01 (1, 24)	**0.035***	2.58 (3, 24)	0.077 ns	0.45 (3, 24)	0.723 ns	US>SH
Total ($\Delta E_{Tis} + \Delta E_{Sk}$)	15.90 (1, 24)	<**0.001*****	12.54 (3, 24)	<**0.001*****	0.71 (3, 24)	0.557 ns	US>SH, Hi>Fi, Hi>R
P. cylindrica							
Tissues (ΔE_{Tis})	11.98 (1, 24)	**0.002****	5.38 (3, 24)	**0.006****	0.84 (3, 24)	0.486 ns	US>SH, L>Hi, L>Fi
Skeleton (ΔE_{Sk})	21.45 (1, 24)	<**0.001*****	1.56 (3, 24)	0.224 ns	0.41 (3, 24)	0.748 ns	US>SH
Total ($\Delta E_{Tis} + \Delta E_{Sk}$)	12.97 (1, 24)	**0.001****	5.44 (3, 24)	**0.005****	0.83 (3, 24)	0.492 ns	US>SH, L>Fi, L>Hi

[a] The analysis was performed using untransformed means and composite variances with tanks as replicates. Numbers in parentheses are degrees of freedom. Symbols are as in Table 4.

3.3. Study 2: effects of prolonged turbidity on photosynthesis and respiration

The tissue of Shaded colonies of both species showed conspicuous darkening within the first month of the growth experiment, indicating that photoacclimation was occurring. After completion of the growth experiment, the average light level at which *Goniastrea retiformis* was 63% photo-saturated (I_k) was 20% lower in shade-acclimated corals, compared to light-acclimated conspecifics (Tables 6 and 7). The maximum rate of photosynthesis ($P_{g,max}$) of *G. retiformis* was 28±15% higher in shade-acclimated colonies. In *Porites cylindrica*, in contrast, neither I_k nor $P_{g,max}$ differed significantly between shade- and light-acclimated branches. In both species, I_k and $P_{g,max}$ were unaffected by particle treatments (Tables 6 and 7). Furthermore, dark respiration ($R_{t,dark}$) did not change in response to the experimental history of shading or particle concentration in either species.

3.4. Study 3: effects of prolonged turbidity on particle feeding

In freshly collected colonies of *Goniastrea retiformis*, particle ingestion rates increased almost linearly as a function of SPM concentration over the range 1 to 30 mg dw l^{-1} (Fig. 4). The estimate of half-saturation concentration (K, Eq. (3)) was 52.6±18.6 mg dw l^{-1}, i.e. above the maximum experimental concentration. In contrast, *Porites cylindrica* was half-saturated at low particle concentrations ($K = 2.7 \pm 1.0$ mg dw

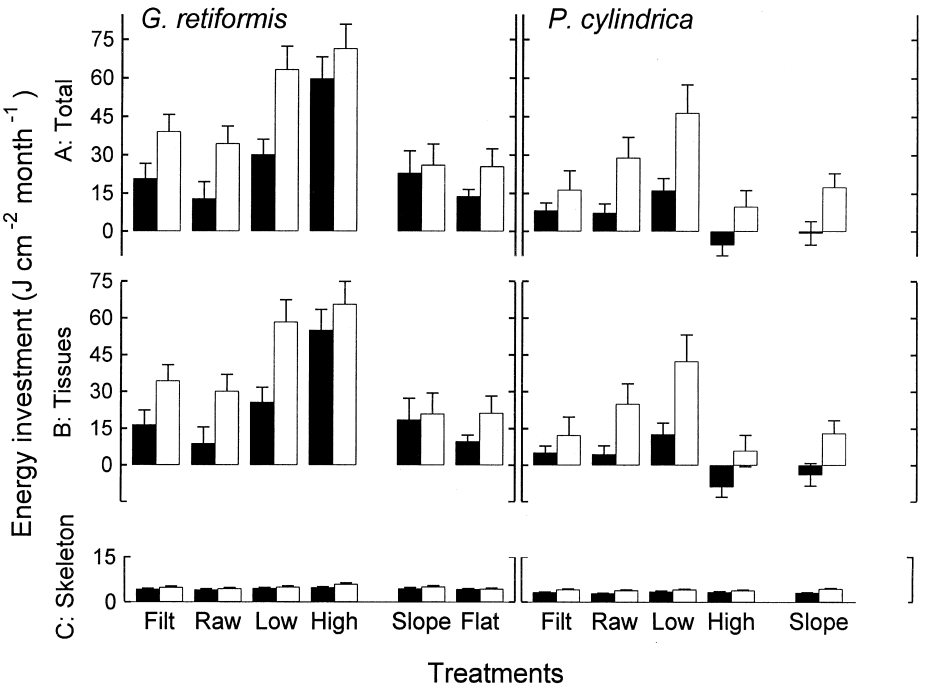

Fig. 3. Energy investment (J cm^{-2} $month^{-1}$) into (A) total growth, (B) tissue growth, and (C) skeletal growth by corals with different histories of light conditions and particle concentrations. Data are mean±S.E., the latter based on composite variances. Solid and open bars represent Shaded and Unshaded treatments, respectively. See Fig. 2 for abbreviations, and Table 5 for results of ANOVAs.

l^{-1}). At particle concentrations corresponding to the High SPM treatment (15.8±1.4 mg dw l^{-1}), the ingestion rate of *G. retiformis* (41±8 μg dw cm^{-2} h^{-1}) was one order of magnitude higher than that of *P. cylindrica* (4.2±0.9 μg dw cm^{-2} h^{-1}).

After the 2-month growth experiment, the rate of particle ingestion by *G. retiformis* had doubled as a result of shading, but was unaffected by prolonged exposure to different particle concentrations (Fig. 5, Table 8). In contrast, the rate of particle ingestion by *P. cylindrica* did not differ in response to shading, but was marginally higher for conspecifics from the High SPM treatment compared with those from the Filtered treatment.

The estimated daily rates of heterotrophic carbon intake (Eq. (8)) by Shaded *G. retiformis* were almost three-fold those of Unshaded conspecifics (Table 9). This was due to a 30% longer feeding period of Shaded (~16 h d^{-1}) compared to Unshaded corals of *G. retiformis* (~12 h d^{-1}) and the two-fold higher feeding rate of shade-acclimated colonies of this species. The feeding behaviour of *P. cylindrica* did not change in response to shading, and hourly feeding rates were used to produce 24-h estimates.

Table 6
Response parameters of photosynthesis–irradiance (P–I) curves estimated after 3 months of exposure to four contrasting treatments in the tank system. Numbers in parentheses are standard errors

Response parameter	*Goniastrea retiformis*				*Porites cylindrica*			
	Shaded		Unshaded		Shaded		Unshaded	
	Filtered	High SPM	Filtered	High SPM	Filtered	High SPM	Filtered	High SPM
Saturation irradiance (I_k, μmol quanta m^{-2} s^{-1})	263.4 (29.7)	261.4 (33.1)	310.6 (13.8)	321.2 (18.7)	350.3 (19.8)	306.8 (35.5)	390.7 (10.7)	334.0 (18.7)
Max photosynthesis ($P_{g,max}$, μg O_2 cm^{-2} h^{-1})	127.6 (7.6)	137.6 (12.1)	105.7 (7.9)	101.4 (11.0)	141.4 (19.6)	130.6 (29.6)	130.0 (13.2)	92.2 (14.4)
Respiration ($R_{r,dark}$, μg O_2 cm^{-2} h^{-1})	−25.9 (2.8)	−29.4 (2.4)	−25.1 (3.0)	−22.3 (3.7)	−22.3 (2.4)	−21.1 (2.7)	−21.4 (4.9)	−23.0 (3.5)

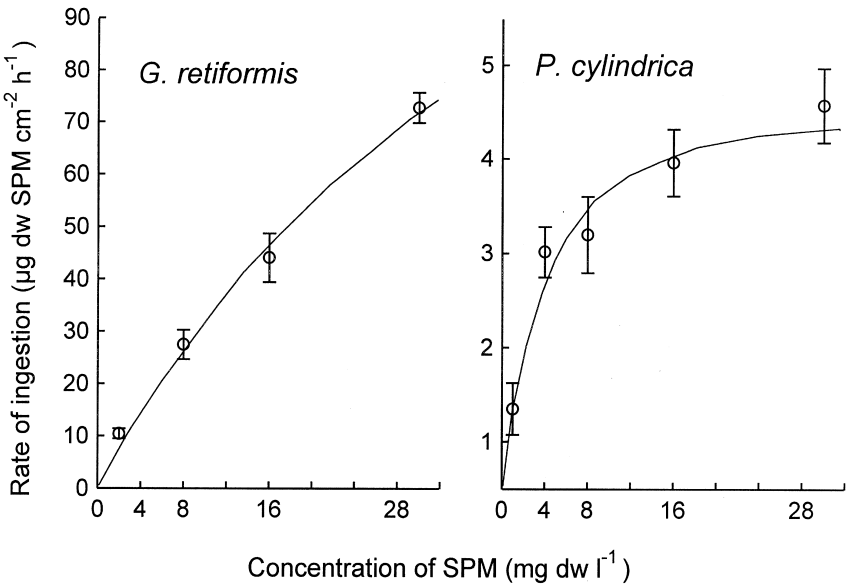

Fig. 4. Rate of particle ingestion as a function of particle concentration for freshly collected corals from the field. Data are mean±S.E. of four to eight colonies (*G. retiformis*) or branches (*P. cylindrica*). The Michaelis–Menten saturation model is fitted to the datasets (see Eq. (3)). Note different scales on *y*-axes.

3.5. Contributions of phototrophy and heterotrophy to the carbon budget

Photosynthesis exceeded respiration by 23–26% in Unshaded *G. retiformis* and 22–45% in Unshaded *P. cylindrica* (calculated by integrating hourly rates of photo-

Table 7
Summary of two-way ANOVA results for effects of environmental history on response parameters of the *P–I* curves[a]

Response parameter	df_1, df_2	Shading		SPM		Shading×SPM		Post hoc
		F	*P*	*F*	*P*	*F*	*P*	
Goniastrea retiformis								
Saturation irradiance (I_k)	1, 12	5.74	**0.034***	0.04	0.851 ns	0.08	0.783 ns	US>SH
Maximum photosynthesis ($P_{g,max}$)	1, 12	8.70	**0.012***	0.09	0.776 ns	0.52	0.484 ns	SH>US
Respiration ($R_{t,dark}$)	1, 12	1.74	0.206 ns	0.01	0.916 ns	1.11	0.313 ns	
Porites cylindrica								
Saturation irradiance (I_k)	1, 12	1.07	0.322 ns	0.43	0.525 ns	1.42	0.257 ns	
Maximum photosynthesis ($P_{g,max}$)	1, 12	1.34	0.269 ns	1.28	0.280 ns	0.39	0.542 ns	
Respiration ($R_{t,dark}$)	1, 12	0.02	0.886 ns	0.01	0.922 ns	0.17	0.687 ns	

[a] Data were analysed untransformed. Symbols are as in Table 4.

Table 8
Summary of two-way ANOVA results for effects of environmental history on particle ingestion[a]

Source of variation (history)	*Goniastrea retiformis*				*Porites cylindrica*			
	df	*F*	*P*	Post hoc	df	*F*	*P*	Post hoc
Shading	1	20.98	<**0.001*****	SH>US	1	2.51	0.139 ns	
Particle concentration (SPM)	1	0.39	0.544 ns		1	7.16	**0.020***	Hi>Fi
SPM×Shading	1	1.04	0.328 ns		1	2.91	0.114 ns	
Error (tanks)	12				12			

[a] Corals from four treatment groups in the tank setup (Shaded/Filtered, Shaded/High SPM, Unshaded/Filtered and Unshaded/High SPM) were incubated in flow chambers containing ^{14}C-labelled particle suspensions at concentrations corresponding to the High-particle treatment (~16 mg l^{-1}) at conclusion of the growth experiment. See Fig. 5 for means±standard errors. Symbols are as in Table 4.

synthesis and respiration over 24 h, using a typical light-time profile as encountered during the growth experiment; Eq. (6)). In contrast, Shaded corals were phototrophically deficient (i.e. $R > P_g$) by 14–22% in *Goniastrea retiformis* and 34–38% in *Porites cylindrica* (Table 9). Shade-acclimation (increased P_{max} and reduced I_k) compensated for 45% of the predicted reduction in photosynthesis in Shaded *G. retiformis*. Interestingly, the daily phototrophic surplus of *P. cylindrica* in the Unshaded/Filtered treatment was more than twice that of conspecifics from the Unshaded/High SPM treatment, and twice that of Unshaded *G. retiformis* at all particle treatments.

Daily rates of particle feeding in *G. retiformis* in the High SPM treatments corresponded to ~29% of its daily rates of gross photosynthesis in Shaded and 7% in Unshaded conditions (Table 9), despite the low organic carbon content of suspended

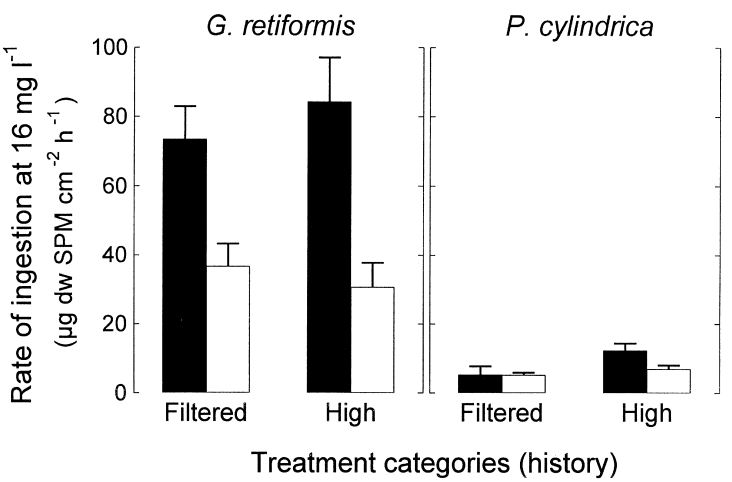

Fig. 5. Effects of particle and light history on rate of particle feeding by corals from the tank setup assayed at completion of the growth experiment. Corals were incubated in a particle concentration corresponding to that of the High SPM treatment in the tank setup (16 mg dw l^{-1}). Solid and open bars denote Shaded and Unshaded treatments, respectively.

particles (~3%, Table 1). Importantly, feeding rates of *G. retiformis* at the High SPM concentration could compensate fully for its 35–47% lower rates of gross photosynthesis in the Shaded compared with Unshaded treatments (Table 9). For instance, the daily carbon budget of Shaded *G. retiformis* in the Filtered treatment was in deficit by 30.6 ± 13.5 μg C cm^{-2} d^{-1}, whereas Shaded conspecifics in the High SPM treatment sustained a carbon surplus of 19.8 ± 14.9 μg C cm^{-2} d^{-1}. In contrast, feeding by *P. cylindrica* compensated for less than 20% of the carbon deficit in turbid conditions (-58.0 ± 19.7 to -43.4 ± 17.6 μg C cm^{-2} d^{-1}), rendering its carbon surplus highly dependent upon phototrophy.

Particle feeding by *G. retiformis* at high particle concentrations accounted for all of its carbon investment into tissue and skeletal growth in Shaded conditions, and more than 30% in Unshaded conditions (Table 9). Also, feeding by *P. cylindrica* in the Unshaded/High SPM treatment accounted for ~60% of its total carbon investment. Due to the loss in tissue mass in Shaded *P. cylindrica* at high particle concentrations, a comparison with heterotrophy was not meaningful. Assuming that respiration and photosynthesis of corals from Low SPM treatments were intermediate of those from Filtered and High SPM treatments, feeding by *P. cylindrica* in the Shaded/Low and Unshaded/Low treatments accounted for only 16 and 8% of its energy investment, respectively.

Scope for growth and excretion (*SfG′*, given by the sum of observed rates of

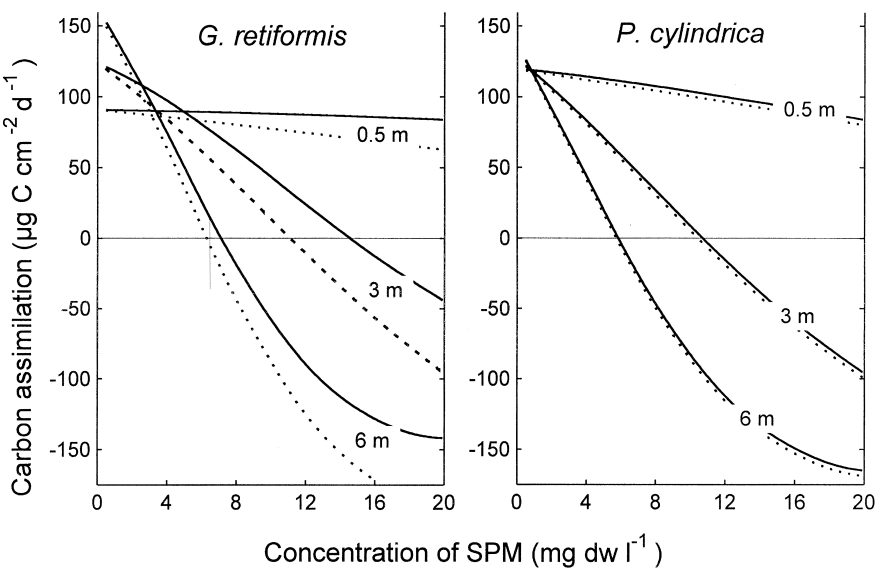

Fig. 6. Predicted total daily carbon budget including particle feeding (———) and excluding particle feeding (- - -) as a function of particle concentration at three depths. Corals in shallow (≤0.5 m) and deep (≥3 m) water were assumed to have feeding rates and feeding cycles similar to conspecifics from Unshaded and Shaded treatments, respectively. Also, we assumed a 3% organic carbon content and 50% assimilation efficiency of the ingested organic carbon. Light level as a function of depth was calculated based on particle concentrations using Eq. (5), assuming that $\psi = 0.035$ m·l mg^{-1} and $I_0 = 1200$ μmol quanta m^{-2} s^{-1} at noon. Photosynthesis, feeding (assimilation) and respiration were integrated over the day using Eq. (9).

Table 9
Summary of total daily carbon budget (*Sfg′*, see Eq. (2)) for the corals *G. retiformis* and *P. cylindrica* with a history of contrasting light and particle treatments in the tank system[a]

Treatment	*Goniastrea retiformis*							*Porites cylindrica*						
	Estimated carbon budget					Growth		Estimated carbon budget					Growth	
	P_g	+ A	+ R	= SfG'		Tissue	Skel.	P_g	+ A	+ R	= SfG'		Tissue	Skel.
Shaded														
Filtered	132.4	6.1	−169.1	−30.6		11.4	3.5	95.4	1.0	−154.4	−58.0		3.5	2.7
	(5.2)	(0.6)	(12.4)	(13.5)		(4.2)	(0.3)	(5.7)	(0.3)	(18.8)	(19.6)		(2.1)	(0.2)
High SPM	152.9	44.5	−177.6	19.8		43.4	4.0	100.4	8.3	−152.1	−43.4		−5.9	2.8
	(7.8)	(5.8)	(11.3)	(14.9)		(6.0)	(0.3)	(12.5)	(1.5)	(12.3)	(17.6)		(2.8)	(0.2)
Unshaded														
Filtered	248.8	3.0	−192.0	59.8		23.5	3.5	292.1	0.7	−160.7	132.1		8.6	3.4
	(7.3)	(0.5)	(11.8)	(13.9)		(4.6)	(0.3)	(17.3)	(0.1)	(13.9)	(22.2)		(5.5)	(0.2)
High SPM	236.1	16.2	−175.8	76.5		46.0	4.0	212.2	4.6	−165.4	51.4		4.0	3.3
	(13.3)	(1.9)	(12.5)	(18.4)		(6.6)	(0.3)	(12.9)	(1.5)	(16.1)	(20.7)		(4.4)	(0.2)

[a] Data are mean±1 S.E. (in parentheses) and are in units of μg C cm^{-2} d^{-1}. Daily rates of photosynthesis (P_g) were obtained by integrating hourly rates of photosynthesis over an average day. Daily rates of feeding (A, carbon assimilation) assume 3% organic carbon content of the SPM and 50% assimilation efficiency. Daily rates of respiration (R) were based on nightly rates. Feeding rates by corals in the High-particle treatment were based on post-experimental feeding rates (Fig. 5), and feeding rates in the Filtered treatment were estimated by interpolation using the functional response curves (Fig. 4) adjusted for differences in feeding rates between shade- and light-acclimated corals (Fig. 5). Rates of carbon investment into growth were converted from standard mass-specific carbon contents of lipids, carbohydrates and protein using Eq. (11). Carbon equivalents of skeletal growth were estimated by assuming that ATP used in the Ca^{2+} transport is driven by the catabolism of carbohydrates (see Eqs. (11) and (12)).

photosynthesis feeding and respiration, Eq. (2)) showed large deviations from the rates of carbon investment (estimated from rates of tissue growth, lipid storage and skeletal growth converted to carbon investment, Table 9). For example, in both species a negative *SfG′* was calculated for the Shaded/Filtered treatment but positive growth rates were observed. Also, in the Shaded/High SPM treatment, *SfG′* of *G. retiformis* was less than 50% of the estimated carbon investment, suggesting that rates of photosynthesis or feeding were underestimated. At the other extreme, the *SfG′* for *P. cylindrica* in the Unshaded treatments were an order of magnitude higher than observed growth rates, suggesting high rates of carbon loss (excretion).

3.6. Predicted carbon balance as a function of depth and turbidity

Modelling net photosynthesis ($P_n = P_g + R$) as a function of SPM concentration and depth (Eq. (6)) indicated that both factors act synergistically in reducing the daily phototrophic carbon budget (Fig. 6). For example, at 6 m depth the $P_{g,d}$:R_d ratio declined below unity in both species at a particle concentration of only 7–8 mg dw l^{-1}. The pattern of predicted P_d:R_d ratios along the SPM concentration×depth gradient differed marginally for the two species. The different intercepts of corals from different depths indicated a greater ability of *Goniastrea retiformis* to photo-acclimate (Fig. 6). Including estimated heterotrophic assimilation in the model showed that the high rates of particle feeding by *G. retiformis* can broaden its physiological (resource) niche, i.e. it can maintain a positive carbon budget over a wider range of environmental conditions with heterotrophic contribution than in a fully autotrophic mode (Fig. 6). Heterotrophy becomes an increasingly important carbon source for *G. retiformis* towards intermediate depths and particle concentrations, as the daily net photosynthesis approaches zero (P_g:R ratio=1). *G. retiformis* reaches this threshold at 12 mg dw l^{-1} at 3 m depth, but if feeding on SPM is considered, the total daily C budget remains positive until SPM concentrations of 16 mg dw l^{-1} are encountered. These model predictions agree with the results of the growth study, in that Shaded *G. retiformis* at high particle concentrations (~4 m depth at 16 mg dw l^{-1}) showed high rates of energy investment, whereas Shaded conspecifics from filtered treatments showed significantly lower energy investment. In *Porites cylindrica*, however, the low rates of particle feeding barely influence the carbon balance at any depth and particle concentration. Also, the low or negative energy investment in tissue growth in Shaded *P. cylindrica* are in accordance with the predicted negative carbon budget of this species at 3 m depth and at 16 mg dw l^{-1}.

4. Discussion

4.1. Effects of shading and sediment load on coral growth rates

This study is the first to analyse experimentally on the relationship between concentrations of suspended particulate matter (SPM) and rates of energy investment in symbiotic corals. Energy investment of both coral species was reduced by shading, in

agreement with the results of other studies of bioenergetics in photo-symbiotic organisms (e.g., Frost and Williamson, 1980; Spencer Davies, 1991; Klumpp and Griffiths, 1994). However, for both shaded and unshaded colonies, maximum rates of energy investment into growth occurred at the High (~16 mg dw l^{-1}) and Low (~3–4 mg dw l^{-1}) SPM concentrations (*Goniastrea retiformis* and *Porites cylindrica*, respectively), despite a low organic content of the particles (~3% w/w). These results were corroborated by the shapes of the feeding-response curves for both species. The findings support the hypothesis that SPM represent a resource as well as a stress factor for corals, depending on the SPM concentrations, and the feeding physiology of the species. While *G. retiformis* showed high rates of particle feeding and addition of tissue mass at high particle concentrations, *P. cylindrica* displayed a stress response (evident as the loss of tissue mass) at the High SPM concentration. The feeding saturation of *P. cylindrica* at only 4–8 mg l^{-1} may, in part, explain this pattern, since increases in particle concentration above the level of saturation represent intensified physical disturbance and energy loss (e.g., through respiration and excretion; Telesnicki and Goldberg, 1995) without increasing the energy intake (see also Anthony, 1999a).

The negative effect of shading on skeletal growth rates in both species was in agreement with coral calcification models (reviewed by Barnes and Chalker, 1990). However, the low variation in skeletal growth (a tenth of the variation in tissue growth) across SPM treatments in both species was surprising. Importantly, skeletal growth in *P. cylindrica* remained positive in conditions where tissue growth was negative. These results suggest that skeletal growth rate is relatively insensitive to high sediment loads per se, thereby providing a poorer indication of sediment stress and nutritional status in corals than previously assumed (e.g., Dodge et al., 1974; Gladfelter et al., 1978; Spencer Davies, 1990; Vago et al., 1997). In support of the findings of this study, Barnes and Lough (1999) found that annual skeletal growth rates of massive *Porites* colonies were uninfluenced by sediment discharge, whereas tissue thickness decreased significantly with increasing rates of sedimentation. Similarly, Brown et al. (1990) observed only marginal effects of high-sediment regimes on skeletal growth rates of intertidal (high-light) colonies of *Porites* sp. Net reef building may therefore in the short term be more robust to variation in turbidity than the physiological energetics of corals suggest.

The effects of particle concentrations on growth rates observed in this study are in contrast to the results of previous experimental studies of coral growth. According to Johannes (1974) and Wellington (1982), growth of hermatypic corals is not significantly reduced by the deprivation of particulate food at shallow-water light levels. Johannes (1974) found that three coral species grew equally fast in 1 μm filtered seawater as they did in unfiltered seawater. However, particle concentrations in the unfiltered treatments were not quantified by Johannes (1974), precluding comparison of food availabilities between treatments. In the present study, particles smaller than 1 μm as well as autochthonous material from algal growth inside the tanks in the Filtered treatment resulted in particle concentrations of 0.5–0.7 mg dw l^{-1}, similar to those recorded on mid-shelf reefs in the Great Barrier Reef lagoon (Devlin et al., 1997). Wellington (1982) showed that growth rates in two out of three coral species were independent of zooplankton >95 μm in shallow-water light conditions. However, suspended particles <95 μm which predominate the biomass in oligotrophic tropical waters (e.g., Ayukai,

1991) were still available to the 'starved' treatments of Wellington (1982) and could explain similarity of growth rates.

4.2. Effects of treatment history on rates of photo- and heterotrophy

The increase in heterotrophic capacity in *G. retiformis* in response to a history of prolonged shading represents a new layer of complexity to the nutritional biology of symbiotic cnidarians. Whereas shade-acclimated photosynthesis is well documented for corals (reviewed by Falkowski et al., 1990), heterotrophic plasticity has previously been demonstrated mainly for mixotrophic microorganisms (e.g., Sanders et al., 1990; Berk et al., 1991; Jones et al., 1995). The doubling of the feeding rate and longer periods of expansion in *Goniastrea retiformis*, in concert with photoacclimation, resulted in a positive energy balance in the Shaded/High SPM treatment. The data indicate that phototrophic and heterotrophic acclimation (or plasticity) contributed equally to maintaining a positive energy balance in *G. retiformis* in Shaded and High SPM conditions. The positive rates of energy investment in the Shaded/Filtered treatments in both species despite significantly negative scope for growth and excretion (*SfG′*) suggest either that *P:R* ratios were underestimated or that uptake rates of dissolved organic carbon were significant. Since corals generally excrete net amounts of dissolved material (e.g., Ferrier-Pages et al., 1998a,b), the former is the most likely, for example through elevated rates of respiration upon handling and transfer to the respirometer.

The higher sediment-feeding rates of shade-acclimated *G. retiformis*, and to some extent the SPM-acclimated *P. cylindrica*, corroborate the results of Anthony (2000) who found that two species of coral from nearshore, turbid habitats had higher particle-clearance rates than their offshore, clear-water conspecifics. Sediment feeding by corals may therefore be an example of optimal foraging (e.g., Hughes, 1980) by two mechanisms: (1) inclusion of sediment in the diet which counteracts immediate short-term reductions in scope for growth, and (2) enhanced sediment-feeding capacity in response to prolonged turbidity (heterotrophic plasticity) which counteracts, either fully or in part, long-term reductions in scope for growth. The adaptive significance of both mechanisms is obvious in habitats with fluctuating turbidity and hence alternating resources (food and light), and during longer periods of high turbidity. Species with low heterotrophic capacity and generally low trophic plasticity (*P. cylindrica*), on the other hand, may only maintain growth in low-turbidity regimes. In support of this, *G. retiformis* prospers in extremely turbid inshore environments as well as on clear-water reefs in the Great Barrier Reef lagoon. In contrast, *P. cylindrica* is found mostly in mid-shelf to offshore locations (Done, 1982) and is absent from the most turbid inshore reefs.

The photoacclimation by *G. retiformis* following prolonged shading (high P_{max}, low I_k) appears to disagree with the predictions of Dustan (1982) that shallow-water zooxanthellae function poorly when transplanted to low light intensities. Since all colonies of *G. retiformis* were collected from the reef flat, the light regime in the shaded treatment (in the tanks and on the reef slope) was one order of magnitude lower than that experienced naturally prior to the experiment. A proportion of the population of *G. retiformis* found on the reef flats of inshore fringing reefs, however, is shaded by

macroalgae (e.g., *Sargassum* spp.) to an extent that exceeds the levels of shading used in this experiment (Anthony, unpublished). Despite its predominantly shallow-water distribution, *G. retiformis* may occur naturally in a wide range of light and sediment regimes, necessitating a high capacity for trophic plasticity in response to shifting environments.

4.3. The role of phototrophy and heterotrophy on scope for growth

The model of scope for growth and excretion (*SfG′*, synthesised based on data for photosynthesis, respiration and feeding) showed that relatively small increases in particle concentration and depth led to large shifts in the contributions of phototrophy and heterotrophy to the carbon budget of *Goniastrea retiformis*. The enhanced feeding rate in concert with shade-acclimated photosynthesis in *G. retiformis* effectively elevated the threshold turbidity level (or depth) at which *SfG′* was positive. *Porites cylindrica*, on the other hand, did not acclimate to reduced light levels and could not compensate heterotrophically for reduced rates of photosynthesis. Since nutrient limitation was not included in the model for *SfG′*, the high energy investment of *P. cylindrica* in Unshaded/Low SPM conditions was not accounted for. Nevertheless, these results demonstrate that particle feeding and plasticity of phototrophy and heterotrophy may dictate the location of a species' habitat optimum and the width of its physiological (resource) niche, which has implications for its potential distribution. The patterns of *SfG′* indicate advantages of particulate matter as a complementary resource to light in both species, but the utilisation of different ranges of particle loads (concentration as well as composition) and the onset of stress responses at different levels of turbidity and sedimentation (see below) contribute to niche differentiation with respect to particulate matter.

The patterns of total tissue growth and lipid storage suggested that growth of matrix tissue is stimulated by the availability of both food (particulate carbon and nutrients) and light, whereas the build-up of lipids is primarily stimulated by light (photosynthesis). According to the nutrient-limitation hypothesis (e.g. Muscatine, 1990; Dubinsky and Jokiel, 1994), the likely explanation for this is the dependence of protein synthesis on the supply of essential nutrients (e.g., N and P; Zubay, 1983), whereas the carbon-rich lipids can be derived largely from photosynthesis (Crossland et al., 1980). The observed negative effect of shading on lipid contents were in accordance with those observed by Stimson (1987). Nutrient limitation was also supported by the data on photosynthesis, feeding and the nutrient content of SPM, which further suggested that tissue growth patterns were to a varying degree explained by differences in SPM feeding (Table 9). Based on the N and P contents of the SPM (and assuming that heterotrophic assimilation efficiencies of N and P are similar to that of C), SPM feeding by *G. retiformis* accounted for ~60% of its difference in tissue growth between Unshaded/Filtered and Unshaded/High SPM treatments. As a result, the ratio of predicted (*SfG′*) to observed (derived) carbon investment into tissue increased from ~30 to ~60% between these treatments (Table 9), signifying a reduced excretory loss at high rates of SPM feeding. By contrast, feeding by *P. cylindrica* could only account for ~25% of the difference in tissue growth between Unshaded/Filtered and Unshaded/Low treatments. However, the ratio of

predicted to observed tissue carbon investment in this species (the latter based on interpolated rates of photosynthesis and respiration) increased from ~7 to ~32%, suggesting a significant uptake of dissolved nutrients in the Low treatment (e.g., Muscatine and D'Elia, 1978).

4.4. Suspended sediment: stress factor of food source?

Although suspended sediment has a lower food value than zooplankton or phytoplankton (Corner and Davies, 1971), it constitutes an often more abundant component of the seston in aquatic environments (reviewed by Wotton, 1994). It may be the predominant food source for suspension feeders, especially in turbid nearshore habitats (e.g., Blanchot et al., 1989; Barille et al., 1997). Importantly, the large surface-to-volume ratio of fine suspended particles (as used in this study) provides substrate for colonisation by microorganisms (Almeida and Alcantara, 1992; Crump and Baross, 1996), which account for a significant proportion of the food value (see also Ward and Cummins, 1979).

Due to the greater tendency for massive growth forms to trap sediment on their surfaces (e.g., Abelson et al., 1993), stress effects of sedimentation (manifest as reduced energy investment) would have been expected to be more severe for the massive to encrusting *G. retiformis* rather than for the tall, branching *P. cylindrica*. However, flow regimes in the growth and feeding tanks were more turbulent than expected for most field situations (Anthony, 1999b), therefore the ratio of vertical to horizontal particle fluxes in the tanks was likely to be lower than in situ. The turbulent flow rates may have alleviated sediment stresses for *G. retiformis*, and exacerbated the physical disturbance of high SPM loads on *P. cylindrica*. Indeed, the suppressed growth rates of *P. cylindrica* at high SPM concentrations indicated that SPM became a stress factor at high concentrations. By analogy, the turbulent flow in the tanks resulted in relatively low rates of food encounter for the massive *G. retiformis* but relatively high rates of encounter for the branching *P. cylindrica*.

4.5. Conclusion

This study documents contrasting energetic responses of two symbiotic coral species (*Goniastrea retiformis* and *Porites cylindrica*) to different combinations of light levels and particle concentrations. Differences in energy budgets between the two species were largely explained by the higher capacity of *G. retiformis* to photoacclimate and to utilise suspended sediment as a food source. Although full heterotrophic compensation for reduced photosynthesis in turbid environments could occur in shallow water only for *G. retiformis*, its two-fold increase in rates of particle feeding rates in response to shading could significantly reduce energy loss during periods of high turbidity. This combination of photoacclimation and heterotrophic plasticity enables *G. retiformis* to occupy a relatively broad physiological niche.

The energy budget of *P. cylindrica* was dictated to a larger extent by light availability. However, this species showed maximum tissue growth rates at intermediate SPM concentrations, indicating some energetic gains by feeding on SPM. High SPM

concentrations and low light levels resulted in severely suppressed rates of tissue growth (even loss of tissue mass), thus high turbidity appears physiologically unsustainable for this coral species. The lower capacity of *P. cylindrica* to utilise suspended particles, and its lower capacity to photoacclimate, potentially confines this species to a more narrow physiological niche.

Thus, the energetics of corals and their ability to sustain growth in differing turbidity regimes are functions of their ability to tolerate as well as utilise sediment, and shift their relative dependence from phototrophy to heterotrophy, potentially confining different strategists to different light–turbidity niches. Enhanced feeding rate in response to shading, in concert with photo-acclimation, is an effective mechanism for optimising the use of two inversely related resources. Although the food value of suspended and settling sediment is generally too low to constitute a fully alternative source of energy for photosynthetic corals, its role as a complementary resource is likely to be important during periods of high turbidity and low light.

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References

Abelson, A., Miloh, T., Loya, Y., 1993. Flow patterns induced by substrata and body morphologies of benthic organisms, and their roles in determining availability of food particles. Limnol. Oceanogr. 38, 1116–1124.

Almeida, M.A., Alcantara, F., 1992. Bacterial colonization of seston particles in brackish waters (Ria de Aveiro, Portugal). Mar. Ecol. Prog. Ser. 89, 165–173.

Anthony, K.R.N., 1999a. Coral suspension feeding on fine particulate matter. J. Exp. Mar. Biol. Ecol. 232, 85–106.

Anthony, K.R.N., 1999b. A tank system for studying benthic aquatic organisms at predictable levels of turbidity and sedimentation: case study examining coral growth. Limnol. Oceanogr. 44, 1415–1422.

Anthony, K.R.N., 2000. Enhanced particle-feeding capacity of corals on turbid reefs (Great Barrier Reef, Australia). Coral Reefs 19, 59–67.

Ayling, A.M., Ayling, A.L., 1991. The effect of sediment run-off on the coral populations of fringing reefs at Cape Tribulation. Research Publication No. 6, Great Barrier Reef Marine Park Authority, Townsville

Ayukai, T., 1991. Standing stock of microzooplankton on coral reefs: a preliminary study. J. Plankton Res. 13, 895–899.

Bak, R.P.M., Joenje, M., de Jong, I., Lambrechts, D.Y.M., Nieuwland, G., 1998. Bacterial suspension feeding by coral reef benthic organisms. Mar. Ecol. Prog. Ser. 175, 285–288.

Barille, L., Prou, J., Heral, M., Razet, D., 1997. Effects of high natural seston concentrations on the feeding, selection, and absorption of the oyster *Crassostrea gigas* (Thunberg). J. Exp. Mar. Biol. Ecol. 212, 149–172.

Barnes, D.J., Chalker, B.E., 1990. Calcification and photosynthesis in reef-building corals and algae. In: Dubinsky, Z. (Ed.), Ecosystems of the World: Coral Reefs. Elsevier, Amsterdam, pp. 109–131.

Barnes, D.J., Lough, J.M., 1999. *Porites* growth characteristics in a changed environment: Misima Island, Papua New Guinea. Coral Reefs 18, 213–218.

Berk, S.G., Parks, L.H., Ting, R.S., 1991. Photoadaptation alters the ingestion rate of *Paramecium bursaria* a mixotrophic ciliate. Appl. Environ. Microbiol. 57, 2312–2316.

Blanchot, J., Charpy, L., Le Borgne, R., 1989. Size composition of particulate organic matter in the lagoon of Tikehau atoll (Tuamotu archipelago). Mar. Biol. 102, 329–340.

Brown, B.E., Le, T.M.D.A., Scoffin, T.P., Tudhope, A.W., 1990. Evaluation of the environmental impact of dredging on intertidal coral reefs at Ko Phuket, Thailand, using ecological and physiological parameters. Mar. Ecol. Prog. Ser. 65, 273–281.

Buddemeier, R.W., Kinzie, R.A., 1976. Coral growth. Oceanogr. Mar. Biol. Annu. Rev. 14, 183–225.

Calow, P., Sibly, R.M., 1990. A physiological basis of population processes: ecotoxicological implications. Funct. Ecol. 4, 283–288.

Chalker, B.E., Dunlap, W.E., Oliver, J.K., 1983. Bathymetric adaptations of reef-building corals at Davies Reef, Great Barrier Reef, Australia. II. Light saturation curves for photosynthesis and respiration. J. Exp. Mar. Biol. Ecol. 73, 37–56.

Corner, E.D.S., Davies, A.G., 1971. Plankton as a factor in the nitrogen and phosphorus cycles in the sea. Adv. Mar. Biol. 9, 101–204.

Crossland, C.J., 1987. In situ release of mucus and DOC-lipid from the coral *Acropora variabilis* and *Stylophora pistillata*. Coral Reefs 6, 35–42.

Crossland, C.J., Barnes, D.J., Borowitzka, M.A., 1980. Diurnal lipid and mucus production in the staghorn coral *Acropora acuminata*. Mar. Biol. 60, 81–90.

Crump, B.C., Baross, J.A., 1996. Particle-attached bacteria and heterotrophic plankton associated with the Columbia River estuarine turbidity maxima. Mar. Ecol. Prog. Ser. 138, 265–273.

Dallmeyer, D.G., Porter, J.W., Smith, G.J., 1982. Effects of particulate peat on the behavior and physiology of the Jamaican West-Indies reef building coral *Montastrea annularis*. Mar. Biol. 68, 229–234.

Devlin, M., Lourey, M., Sweatman, H., Ryan, D., 1997. Water quality. In: Sweatman, H. (Ed.), Long-term Monitoring of the Great Barrier Reef. Status Report, Vol. No. 2. Australian Institute of Marine Science, Townsville, Australia.

Dodge, R.E., Aller, R.C., Thompson, J., 1974. Coral growth related to resuspension of bottom sediments. Nature 247, 574–577.

Done, T.J., 1982. Patterns in the distribution of coral communities across the central Great Barrier Reef. Coral Reefs 1, 95–107.

Dubinsky, Z., Jokiel, P.L., 1994. Ratio of energy and nutrient fluxes regulates symbiosis between zooxanthellae and corals. Pac. Sci. 48, 313–324.

Dustan, P., 1982. Depth-dependent photoadaptation by zooxanthellae of the reef coral *Montastrea annularis*. Mar. Biol. 68, 253–264.

Fabricius, K.E., Dommisse, M., 2000. Depletion of suspended particulate matter over coastal reef communities dominated by zooxanthellate soft corals. Mar. Ecol. Prog. Ser. 196, 157–167.

Fabricius, K.E., Klumpp, D.W., 1995. Widespread mixotrophy in reef-inhabiting soft corals: the influence of depth, and colony expansion and contraction on photosynthesis. Mar. Ecol. Prog. Ser. 125, 195–204.

Falkowski, P.G., Jokiel, P.L., Kinzie, III R.A., 1990. Irradiance and corals. In: Dubinsky, Z. (Ed.), Ecosystems of the World: Coral Reefs. Elsevier, Amsterdam, pp. 89–107.

Falkowski, P.G., Raven, J.A., 1997. Aquatic Photosynthesis. Blackwell Science, Malden, MA.

Ferrier-Pages, C., Allemand, D., Gattuso, J.P., Jaubert, J., Rassoulzadegan, R., 1998a. Microheterotrophy in the zooxanthellate coral *Stylophora pistillata*: effects of light and ciliate density. Limnol. Oceanogr. 43, 1639–1648.

Ferrier-Pages, C., Gattuso, J.P., Cauwet, G., Jaubert, J., Allemand, D., 1998b. Release of dissolved organic carbon and nitrogen by the zooxanthellate coral *Galaxea fascicularis*. Mar. Ecol. Prog. Ser. 172, 265–274.

Folch, J., Lees, M., Sloane Stanley, G.H., 1957. A simple method for the isolation and purification of total lipids from animal tissues. J. Biol. Chem. 226, 497–509.

Frost, T.M., Williamson, C.E., 1980. In-situ determination of the effect of symbiotic algae on the growth of the freshwater sponge *Spongilla lacustris*. Ecology 61, 1361–1370.

Gladfelter, E.H., Monahan, R.K., Gladfelter, W.B., 1978. Growth rates of five reef-building corals in the northeastern Caribbean. Bull. Mar. Sci. 28, 728–734.

Gnaiger, E., Bitterlich, G., 1984. Proximate biochemical composition and calorific content calculated from elemental CHN analysis: a stoichiometric concept. Oecologia 62, 289–298.

Hansen, J.A., Klumpp, D.W., Alongi, D.M., Dayton, P.K., Riddle, M.J., 1992. Detrital pathways in a coral reef lagoon: II. Detritus deposition, benthic microbial biomass and production. Mar. Biol. 113, 363–372.

Harland, A.D., Spencer Davies, P., Fixter, L.M., 1992. Lipid content of some Caribbean corals in relation to depth and light. Mar. Biol. 113, 357–361.

Hughes, R.N., 1980. Optimal foraging theory in the marine context. Oceanogr. Mar. Biol. Annu. Rev. 18, 423–481.

Hurlbert, S.H., 1984. Pseudoreplication and the design of ecological field experiments. Ecol. Monogr. 54, 187–211.

Johannes, R.E., 1974. Sources of nutritional energy for reef corals. Proc. 2nd Int. Coral Reef Symp., Brisbane 1, pp. 133–137.

Jones, H.L.J., Durjun, P., Leadbeater, B.S.C., Green, J.C., 1995. The relationship between photoacclimation and phagotrophy with respect to chlorophyll a, carbon and nitrogen content, and cell size of *Chrysochromulina brevifilum* (Prymnesiophyceae). Phycologia 34, 128–134.

Kirk, J.T.O., 1994. Light and Photosynthesis in Aquatic Ecosystems, 2nd Edition. Cambridge University Press, Cambridge, UK.

Klumpp, D.W., Griffiths, C.L., 1994. Contributions of phototrophic and heterotrophic nutrition to the metabolic and growth requirements of four species of giant clam (Tridacnidae). Mar. Ecol. Prog. Ser. 115, 103–115.

Krupp, D.A., 1985. An immunochemical study of the mucus from the solitary coral *Fungia scutaria* (Scleractinia, Fungiidae). Bull. Mar. Sci. 36, 163–176.

Larcombe, P., Ridd, P.V., Prytz, A., Wilson, B., 1995. Factors controlling suspended sediment on inner-shelf coral reefs, Townsville, Australia. Coral Reefs 14, 163–171.

Maltby, L., 1999. Studying stress: the importance of organism-level responses. Ecol. Applic. 9 (2), 431–440.

Marsh, J.A., 1970. Primary productivity of reef-building calcareous red algae. Ecology 51, 255–263.

McCloskey, L.R., Wethey, D.S., Porter, J.W., 1978. The measurement and interpretation of photosynthesis and respiration in reef corals. Monogr. Oceanogr. Methodol. (SCOR-UNESCO) 4, 379–396.

McConnaghey, T.A., Whelan, J.F., 1997. Calcification generates protons for nutrient and bicarbonate uptake. Earth-Sci. Rev. 967, 95–117.

Muscatine, L., 1990. The role of symbiotic algae in carbon and energy flux in reef corals. In: Dubinsky, Z. (Ed.), Ecosystems of the World: Coral Reefs. Elsevier, Amsterdam, pp. 75–87.

Muscatine, L., D'Elia, C.F., 1978. The uptake, retention and release of ammonium by reef corals. Limnol. Oceanogr. 23, 725–734.

Muscatine, L., McCloskey, L.R., Marian, R.E., 1981. Estimating the daily contribution of carbon from zooxanthellae to coral animal respiration. Limnol. Oceanogr. 26, 601–611.

Parsons, T.R., Maita, Y., Lalli, C.M., 1984. A Manual of Chemical and Biological Methods For Seawater Analysis. Pergamon Press, Oxford.

Porter, J.L., 1974. Zooplankton feeding by the Caribbean reef-building coral, *Montastrea cavernosa*. In: Proc. 2nd Int. Coral Reef Symp., Brisbane 1, pp. 111–125.

Riegl, B., Branch, G., 1995. Effects of sediment on the energy budgets of four scleractinian (Bourne 1900) and five alcyonacean (Lamouroux 1816) corals. J. Exp. Mar. Biol. Ecol. 186, 259–275.

Rogers, C.S., 1990. Responses of coral reefs and reef organisms to sedimentation. Mar. Ecol. Prog. Ser. 62, 185–202.

Roman, M.R., Furnas, M.J., Mullin, M.M., 1990. Zooplankton abundance and grazing at Davies Reef, Great Barrier Reef, Australia. Mar. Biol. 105, 73–82.

Ruxton, G.D., Gurney, W.S.C., 1994. Deriving the functional response without assuming homogeneity. Am. Nat. 144, 537–541.

Sanders, R.W., Porter, K.G., Caron, D.A., 1990. Relationship between phototrophy and phagotrophy in the mixotrophic chrysophyte *Poteriochromonas malhamensis*. Microb. Ecol. 19, 97–110.

Sebens, K.P., Deriemer, K., 1977. Diel cycles of expansion and contraction in coral reef anthozoans. Mar. Biol. 43, 247–256.

Sebens, K.P., Vandersall, K.S., Savina, L.A., Graham, K.R., 1996. Zooplankton capture by two scleractinian corals, *Madracis mirabilis* and *Montastrea cavernosa*, in a field enclosure. Mar. Biol. 127, 303–317.

Shimeta, J., Jumars, P.A., 1991. Physical mechanisms and rates of particle capture by suspension feeders. Oceanogr. Mar. Biol. Annu. Rev. 29, 191–257.

Shimeta, J., Koehl, M.A.R., 1997. Mechanisms of particle selection by tentaculate suspension feeders during encounter, retention, and handling. J. Exp. Mar. Biol. Ecol. 209, 47–73.

Spencer Davies, P., 1989. Short-term growth measurements of corals using an accurate buoyant weighing technique. Mar. Biol. 101, 389–395.

Spencer Davies, P., 1990. A rapid method for assessing growth rates of corals in relation to water pollution. Mar. Pollut. Bull. 21, 346–348.

Spencer Davies, P., 1991. Effect of daylight variations on the energy budget of shallow-water corals. Mar. Biol. 108, 137–144.

Stafford Smith, M.G., Ormond, R.F.G., 1992. Sediment-rejection mechanisms of 42 species of Australian scleractinian corals. Aust. J. Mar. Freshwater Res. 43, 683–705.

STATISTICA, 1997. Release 5.1. StatSoft Inc., Tulsa, OK.

Stimson, J.S., 1987. Location, quantity and rate of change in quantity of lipids in tissue of Hawaiian hermatypic corals. Bull. Mar. Sci. 41, 889–904.

Szmant-Froelich, A., Pilson, M.E.Q., 1984. Effects of feeding frequency and symbiosis with zooxanthellae on nitrogen metabolism and respiration of the coral *Astrangia danae*. Mar. Biol. 81, 153–162.

Te, F.T., 1997. Turbidity and its effects on corals: a model using the extinction coefficient (k) of photosynthetic active radiance (PAR). In: Proc. 8th Int. Coral Reef Symp., Panama 2, pp. 1899–1904.

Telesnicki, G.J., Goldberg, W.M., 1995. Effects of turbidity on the photosynthesis and respiration of two South Florida reef coral species. Bull. Mar. Sci. 57, 527–539.

Tomascik, T., Sander, F., 1985. Effects of eutrophication on reef-building corals 1. Growth rate of the reef-building coral *Montastrea annularis*. Mar. Biol. 87, 143–156.

Travis, J., 1982. A method for the statistical analysis of time-energy budgets. Ecology 63, 19–25.

Vago, R.G., Gill, E., Collingwood, J.C., 1997. Laser measurements of coral growth. Nature 386, 30–31.

Veron, J.E.N., 1986. Corals of Australia and the Indo-Pacific, 2nd Edition. University of Hawaii Press, Honolulu, HI.

Ward, G.M., Cummins, K.W., 1979. Effects of food quality on growth of a stream detritivore, *Paratendipes albimanus* (Meigne) (Diptera: Chironomidae). Ecology 60, 57–64.

Warren, C.E., Davis, G.E., 1967. Laboratory studies on the feeding, bioenergetics and growth of fish. In: Gerking, S.D. (Ed.), The Biological Basis For Freshwater Fish Production. Blackwell Scientific, Oxford, pp. 175–214.

Wellington, G.R., 1982. An experimental analysis of the effects of light and zooplankton on coral zonation. Oecologia 52, 311–320.

Wotton, R.S., 1994. Particulate and dissolved organic matter as food. In: Wotton, R.S. (Ed.), The Biology of Particles in Aquatic Systems, 2nd Edition. CRC Press, Boca Raton, FL, pp. 235–288.

Zamer, W.E., 1986. Physiological energetics of the intertidal sea anemone *Anthopleura elegantissima*. I. Prey capture, absorption efficiency and growth. Mar. Biol. 92, 299–314.

Zamer, W.E., Shick, J.M., 1989. Physiological energetics of the intertidal sea anemone *Anthopleura elegantissima*. III. Biochemical composition of body tissues, substrate-specific absorption, and carbon and nitrogen budgets. Oecologia 79, 117–127.

Zubay, G., 1983. Biochemistry, 2nd Edition. Addison-Wesley, Reading, MA.