Sediment: stress factor or food source for reef corals?

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Abstract

Nearshore reefs in many parts of the tropics are subject to high concentrations of suspended sediment, conditions that impose stress on symbiotic reef organisms by reducing light for photosynthesis and smothering of tissues. The formation of extensive fringing reefs in many nearshore turbid areas, however, challenges the dogma that reef corals need clear water and bright light for survival and substantive growth. The central hypothesis of this thesis is that suspended sediment is also a food source for corals. Specifically, I test the hypotheses that (1) corals ingest and assimilate suspended sediment in proportion to availability, (2) that corals from nearshore turbid habitats have higher sediment-feeding capacities than corals from offshore oligotrophic habitats in accordance with optimal diet theory, and (3) that high rates of sediment feeding by some species may energetically offset effects of reduced photosynthesis and sediment stress. The implications of these hypotheses are that sediment feeding may provide an energetic explanation for the presence of coral reefs in turbid environments.

To investigate the capacity of corals to utilise suspended particulate matter (SPM) as a food and energy source in different sediment regimes, I quantified ingestion and assimilation of ^{14}C-labelled SPM for four common species of scleractinian coral on the Great Barrier Reef (GBR) over a wide range of SPM concentrations (1-30 mg dry weight [dw]/L). Ingestion rates of three species (*Pocillopora damicornis*, *Montipora digitata*, and *Acropora millepora*) increased linearly over the full range of SPM concentrations. Only one species (*Porites cylindrica*) conformed to traditional saturation-kinetic models (Michaelis-Menten) with ingestion rates reaching maximum at moderate SPM concentrations (4-8 mg dw/L). All study species assimilated a major proportion of the ingested label, but assimilation efficiency was inversely related to SPM concentration in agreement with the findings of previous studies. At low SPM concentration (1 mg dw/L), assimilation efficiencies ranged from 89 to 95% of the ingested SPM, which are among the highest reported for suspension feeders, decreasing to 40-50% at the highest concentration.

The maximum rate of carbon assimilated from SPM can cover less than 5% of basic metabolic costs, which is not significantly different from reported contributions of

zooplankton feeding to coral energy budgets. More importantly, SPM feeding at high particle concentrations may cover up to half of the carbon and a third of the nitrogen used in tissue growth.

In order to test the hypothesis that corals from turbid nearshore areas have greater capacity to utilise sediment as a food source than conspecifics from less turbid midshelf areas I used two common species with a widespread distribution across the GBR lagoon (*P. damicornis* and *A. millepora)*. Samples from turbid reefs of both coral species fed 1-3 times more efficiently on SPM than did conspecifics from midshelf reefs. Rates of particle ingestion were a linear function of particle load for both inshore and offshore groups, indicating no significant saturation within the concentration range 1-30 mg dw/L. Assimilation efficiency of particulate ^{14}C was maximised for midshelf *A. millepora* at the lowest sediment concentration, suggesting a more efficient heterotrophy in oligotrophic habitats. Based on feeding-response curves, assimilation efficiencies, and published records of ambient particle concentrations, representatives of these species on turbid inshore reefs are 10-20 times more heterotrophic on suspended sediment than their conspecifics on less turbid midshelf reefs.

In a two-month experiment involving manipulated sediment and light treatments, I analysed experimentally the effects of different light and SPM regimes on the growth rates of two species of scleractinian coral. A ten-fold higher sediment-feeding capacity of *G. retiformis* compared to *P. cylindrica* provided an excellent opportunity to test the ecological and physiological implications of sediment feeding for the energy budgets of symbiotic cnidarians in turbid environments. To provide an energetic analysis of growth patterns across treatments, I quantified changes in the energetics of total tissue mass, lipid contents, and skeletal mass.

Shading corresponding to 16 mg dw SPM/L at 3-4 m depth resulted in reduced growth rates in both species. However, the two species showed contrasting patterns of energy investment across SPM treatments (<1, ~4, ~16 mg dw/L and controls ~2 mg dw/L). Growth rates of *G. retiformis* increased monotonically with SPM concentration, and growth rates at the maximum particle load were almost twice those of conspecifics in filtered seawater. Importantly, growth rates of shaded and unshaded *G. retiformis* did not differ significantly at high SPM concentrations, but growth rates of corals from both these treatment groups were significantly higher than those of shaded and unshaded

corals in particle-depleted treatments. Conversely, *P. cylindrica* showed maximum growth rates at the intermediate SPM concentration (~4 mg/L), and the combination of shading and maximum particle load resulted in negative tissue growth in this species. Energy investment was strongly partitioned between tissue and skeletal growth in both species, with preference given to tissue growth in corals with high overall rates of energy investment. Minor differences in skeletal growth were primarily explained by differences in light level.

The results of this study indicate that high turbidity enhances growth in *G. retiformis* to the extent that it compensates for reduced light, whereas a similar high-turbidity regime causes stress in *P. cylindrica*. At intermediate sediment concentrations, however, the nutritional effect of sediment is greater than its stress effect on *P. cylindrica*.

As a corollary to the growth study, I investigated the physiological processes underlying the different growth patterns displayed by the two species. Specifically, I quantified the relative contributions of sediment feeding and photosynthesis to the energy budget in the range of turbidity regimes used in the growth study. Further, I analysed the importance of heterotrophic plasticity of corals in adapting to prevailing turbidity regimes with implications for the width of physiological niches.

In *G. retiformis*, sediment feeding more than compensated for the reduction in photosynthesis and sediment removal at high sediment concentrations (~16 mg dw/L), resulting in a positive total carbon balance despite shading (corresponding to 16 mg dw/L at 3-4 m depth). Part of this compensation was enabled by a doubling of the feeding capacity at a given particle availability in response to a history of shading, a mechanism not previously reported for symbiotic invertebrates. In contrast, the feeding capacity of *P. cylindrica* increased only marginally in response to high sediment loads and its total carbon budget remained in deficit in shaded treatments.

Multiple regression analysis indicated that > 85% of the variation in energy investment into growth of *G. retiformis* was explained jointly by the variation in energy acquisition through sediment feeding (r-part = 72%) and photosynthesis (r-part = 92%). A similar analysis for *P. cylindrica* indicated an almost exclusive dependence on phototrophy. Using the data from the prolonged turbidity experiment, a predictive model of energy budgets as a function of SPM concentration and depth indicated that

particle feeding by *G. retiformis* can effectively increase the depth at which the energy balance remains positive in a turbid environment.

In summary, SPM represents a quantitatively important food source for most coral species, but concentration thresholds at which SPM becomes a stress factor varies among species. Enhanced rates of sediment feeding in response to prolonged increased turbidity in some species suggest that corals are able to alter their trophic strategies to optimise the nutritional potential of their habitat. Heterotrophic plasticity of *G. retiformis*, *P. damicornis* and *A. millepora* may be important for maintaining the energy balance of corals on reefs that are subject to high or seasonally fluctuating sediment loads. Given that coral species with high sediment-feeding capacity should have selective advantage over poor sediment feeders in muddy environments, species-specific variation in heterotrophic plasticity undoubtedly contributes to inshore-offshore patterns in the composition of coral communities and may alter community structure if sedimentation regimes increase.

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Chapter 1

General Introduction

1.1. The general role of suspended particles in aquatic systems

Suspended particulate matter (SPM) is a universal component of all aquatic systems, and its ecological role in both pelagic and benthic communities has received increasing attention over the past three decades (e.g. Riley 1963, Pomeroy 1974, reviewed by Parsons et al. 1984 and Wotton 1994b). In both temperate and tropical regions, SPM plays an important role in the energy flow of food webs in which it is used at both low and high trophic levels, for example by zooplankton (Parsons et al. 1984, Ayukai 1987, Roman et al. 1990), by benthic suspension and deposit feeders (Jumars & Nowell 1984, Seiderer & Newell 1985, Taghon & Greene 1992, Navarro & Widdows 1997) and by fish (Lemke & Bowen 1998). Fluxes of SPM may be the primary source of food for some temperate benthic communities (Mann 1982), in particular in the deep-sea (e.g. Tyler et al. 1990, Rosenberg 1995, Witte et al. 1997).

Despite its obvious role as a resource in most aquatic systems, SPM is also receiving growing attention through its role as a disturbance, in particular on tropical coral reefs (Grigg & Dollar 1990, Ginsburg & Glynn 1993, Zann 1995). One reason for this disparity of roles is that the productivity of most benthic invertebrate communities in temperate waters is based on heterotrophy (e.g. Widdows & Johnson 1988, Petersen & Riisgård 1992, Lesser et al. 1994, Taylor 1998), whereas the high productivity of tropical coral reefs (e.g. Crossland et al. 1991) is attributed mainly to the photosynthesis of endosymbiotic algae, in particular those hosted by scleractinian corals (reviewed by Muscatine 1990). Although there are several examples of zooxanthellate invertebrates in temperate waters (e.g. Sutton & Hoegh-Guldberg 1990, Shick 1991), they may rely more on heterotrophy than on phototrophy (e.g. Farrant et al. 1987, Davy et al. 1996). Since SPM acts as a light filter and potentially reduces primary productivity, its property as a food source on tropical reefs is often masked by its property as a disturbance. As a result, most studies of suspended and settling particles on coral-reef

organisms have focussed mainly on the stress effects of high particle loads. This study is the first to investigate in-depth the combined resource and stress effects of SPM on the physiological energetics of corals.

1.2. Some definitions and properties of particles

The definition of particulate matter differs among studies and mainly reflects the aspect from which the particles are studied. Suspended particulate matter (SPM) is commonly referred to as the broad category of fine particles (< 1mm) that are retained on a filter with 0.45µm pore size (reviewed by Wotton 1994a). Hence, SPM generally includes micro-zooplankton, phytoplankton, plant material (detritus), animal products and excretions (faeces, mucus), as well as inorganic material such as resuspended silt and sand. Traditionally, live zooplankton and phytoplankton are not considered part of SPM (Parsons et al. 1984), but a separation of these components for analytical purposes is difficult in practice. Larger, non-living and non-zooplanktonic particles in suspension, formed, for example, by diatoms (e.g. Jackson 1990, Kiørboe et al. 1990), are usually referred to as flocs or aggregates, and may carry large quantities of bacteria which potentially increases their food value (Ward & Cummins 1979, Simon et al. 1990).

An important functional categorisation of particle types distinguishes between suspended and sedimenting particles because of the different effects of horizontal and vertical fluxes on benthic organisms. Both types of fluxes will affect capture probability by benthic feeders (Shimeta & Jumars 1991, Abelson et al. 1993, Abelson & Loya 1995), and vertical flux (sedimentation) may cause organism smothering (Rogers 1983, Rice & Hunter 1992). The combination of particle size, particle density and the flow environment are useful predictors of suspension versus settling (Jumars & Nowell 1984, Riebesell & Wolf Gladrow 1992) and the probability of resuspension of bedload particles (Allen 1997, Clarke & Elliott 1998). A more important categorisation of particles in a biological context is based on food value (i.e. organic content). In the case of non-living particles, relative food value is often inversely related to particle size (e.g. Johnstone et al. 1990), in part due to the proportionately larger surface area of small particles for colonisation by bacteria (Novitsky 1990, Almeida & Alcantara 1992, Crump & Baross 1996). Organic content is generally higher for suspended compared to sedimented particles due to mineralisation in the water column (e.g. Clavier et al. 1995,

Hata et al. 1998), which, in combination with size distributions (Shimeta & Koehl 1997), has implications for the ecology of benthic suspension and deposit feeders.

1.3 Particulate matter and the problem of coral reef degradation

On tropical coral reefs, high concentrations of suspended particles are generally assumed to indicate poor water quality (e.g. Grigg & Dollar 1990), somewhat the inverse of the SPM/water-quality relationship generally assumed in temperate benthic communities (Mann 1982). Thus, stipulated increases in sediment concentrations in tropical nearshore environments resulting from coastal development and increased land use in river catchments (e.g. Moss et al. 1992, Wasson 1997) are considered a threat to nearshore coral reefs on a global scale (e.g. UNEP/IUCN 1988, Rogers 1990, Ginsburg & Glynn 1993, Richmond 1993, Brown 1997). In the Great Barrier Reef (GBR) lagoon, in which more than 10% of the GBR reef area of the Cairns and Far Northern sections is located within 20 km from the Queensland coast (GBRMPA unpublished data), sedimentation has become a topic of central importance for the sustainability of nearshore reefs (e.g. Zann 1995). A recent synthesis of data from studies of sediment dynamics and terrestrial input to the inshore part of the GBR lagoon, however, suggests that resuspension of existing sediment deposits contribute substantially more to turbidity levels and sedimentation rates than do terrestrial inputs (Larcombe & Woolfe 1999), in turn suggesting that nearshore reefs have developed under high natural turbidity (see also Woolfe & Larcombe 1998).

At least two processes drive the perception that corals are stressed by high SPM concentrations. Firstly, normal growth of most tropical reef-building corals depends on energy (in the form of carbon) from photosynthesis of their endosymbiotic algae (zooxanthellae, see reviews by Falkowski et al. 1990 and Muscatine 1990). Since light transmission through the water column is an inverse function of particle concentration (turbidity, McCarthy et al. 1973, Kirk 1994), high particle loads may impair photosynthesis of symbiotic algae, and hence the energy balance of the coral (see also Section 1.5 below). Secondly, high particle concentrations, whether they be the direct result of terrestrial run-off (Acevedo et al. 1989, Ayling & Ayling 1991, Hopley et al. 1993), enhanced production in the water column (Brodie 1995, Arias Gonzalez et al. 1997, McEwan et al. 1998) or from wave-induced resuspension of sediment (Larcombe

et al. 1995, Kleypas 1996), result in a rain of particles potentially smothering or burying coral colonies (Cortés & Risk 1985, Rice & Hunter 1992). The relationship between particle concentration (turbidity) and rate of sedimentation is complex, however, and depends on local hydrodynamics as well as characteristics (size distribution, density) of the particulate matter (e.g. Clarke & Elliott 1998, reviewed by Allen 1997). Therefore, the relative importance of turbidity and sedimentation for the biology of corals will depend on the habitat. In her review, Rogers (1990) referred mainly to sedimentation (i.e. sediment accumulation) as the primary cause of reef degradation, but no experimental evidence exists in the literature that enables a general ranking of turbidity and sedimentation in terms of their adverse effects on corals. Also, reported effects of high sediment loads on corals are inconsistent on a global scale, ranging from high mortality (Dodge & Vaisnys 1977, Acevedo et al. 1989, Stafford-Smith 1992) and reduced species diversity and community complexity (van Katwijk et al. 1993) to no discernible effect (Dollar & Grigg 1981, Brown & Howard 1985, McClanahan & Obura 1997). Furthermore, many nearshore reefs in the GBR lagoon sustain high coral cover and high-diversity assemblages (e.g. Done 1982, Veron 1986a, Ayling & Ayling 1991, 1995), and may have developed over millennia under high turbidity levels (Woolfe & Larcombe 1998). Such inconsistencies call for a broadening of the paradigm that turbidity and sedimentation exclusively represent stress factors for reef corals. Also, it raises the hypothesis that nearshore corals have adapted to high turbidity levels, either through sediment tolerance or through the ability to use high particle loads as a resource.

1.4. The alternative view on suspended sediment: a food source for reef corals?

Apart from their dependence on phototrophy by zooxanthellae, cnidarians, and especially benthic anthozoans, are traditionally referred to as zooplanktivores (Yonge 1930, Stephenson 1935, Muscatine 1973, Porter 1974, Porter 1976, Shick 1991). The more omnivorous nature of anthozoan feeding has, however, gradually become accepted (review by Sebens 1987). Several studies have documented feeding by cnidarians on a variety of non-zooplanktonic food sources, including bacteria and dissolved organic matter by corals (Sorokin 1973, Bak et al. 1998), phytoplankton by octocorals (Fabricius et al. 1995), detritus by sea anemones (Zamer et al. 1987), fine inorganic particles by corals (Lewis 1977), and coarse sediment by corals (Stafford

Smith & Ormond 1992, Mills & Sebens 1997). Most studies of coral bioenergetics have focused on phototrophy (reviewed by Muscatine 1990) whereas the quantitative (and qualitative) role of heterotrophy has generally been assumed or inferred when balancing the energy budget (e.g. Falkowski et al. 1984, Spencer Davies 1984, Bythell 1988, Edmunds & Davies 1989, Spencer Davies 1991). In Chapter 2 of this thesis I quantify the extent to which corals can utilise suspended sediment, the first attempt to rigorously evaluate the role of particulate matter in coral energetics.

Under normal shallow-water conditions in the tropics, photosynthesis by endosymbiotic unicellular algae (zooxanthellae) provides corals with excess carbon for respiration and growth (e.g. Muscatine et al. 1981, Spencer Davies 1984). Photosynthesis almost exclusively delivers carbon to the animal host (Muscatine et al. 1984) and tissue synthesis (which requires, for example, nitrogen, phosphorus and other essential nutrients) will be limited by the availability of a nutrient source under high light conditions (Dubinsky & Jokiel 1994). Although corals are efficient at taking up dissolved inorganic (e.g. D'Elia 1977, Muscatine & D'Elia 1978) and organic compounds (Schlichter 1982), a large proportion of the phototrophically fixed carbon is consequently lost from the association in oligotrophic, high-light conditions because of this lack of other compounds/nutrients required for tissue synthesis (Crossland et al. 1980a,b, Muscatine et al. 1984, Spencer Davies 1984). On shallow-water reefs where photosynthesis is saturated and produces carbon in great excess of nutrient uptake, coral heterotrophy on suspended matter may enhance tissue growth by reducing such nutrient limitation. Since capture and ingestion rate by most feeders increases with particle flux (Lehman 1976, Parsons et al. 1984, Balczon & Pratt 1996, Hansen et al. 1997, Kiflawi & Genin 1997), whereas rate of photosynthesis may be significantly impaired at high particle concentrations (e.g. Te 1997), heterotrophy and phototrophy in corals are likely to show opposite responses to increasing levels of turbidity. The degree to which corals can sustain a positive energy balance in turbid subtidal habitats may therefore depend on their ability to utilise suspended particles as an alternative carbon source. Optimal diet theory for filter feeders (Lehman 1976, reviewed by Hughes 1980) predicts that an abundant, although poor, food source should be included in the diet if its rejection becomes too costly. Based on this prediction, corals on nearshore turbid reefs would be expected to have higher sediment-feeding capacity than their conspecifics on offshore more oligotrophic reefs. Resource partitioning and changing capacities to utilise low-

quality (or non-preferred) diets in response to variation in abundance has been demonstrated for obligate heterotrophs (e.g. Calow 1981, Demott 1998), but may have even greater significance for mixotrophs in which an increased abundance of a low-quality food source may be directly linked to a reduction in photosynthesis. Zooxanthellate reef corals represent an ideal model organism with which to test this hypothesis. Accordingly, in Chapter 3, I test for the presence of heterotrophic plasticity in corals across a range of turbidity regimes. Further, in Chapter 5 and 6 I provide an experimental analysis of the role of heterotrophic as well as phototrophic plasticity in maintaining a positive energy balance in corals.

1.5. Implications of sediment regimes for coral energy budgets and niches

Effects of sediment stress on coral reefs have been investigated mainly at the community level, for example by analysing species-diversity indices (Tomascik & Sander 1987, McClanahan & Obura 1997, Edinger et al. 1998) and changes in species abundances (Acevedo et al. 1989, van Katwijk et al. 1993). Community-level studies of stress, however, provide limited knowledge of the mechanisms underlying the observed community responses and long-term studies are required to improve the understanding of the underlying processes (Hughes & Connell 1999). Organism-level responses to stressors, on the other hand, may provide insight into mechanisms of community changes, and can form an important basis for predicting community-level responses (Calow & Sibly 1990, Maltby 1999). Coral growth is one such organism response, and is a function of energy and nutrient acquisition (heterotrophy and phototrophy) as well as energy-consuming processes (respiration, excretion). In Chapter 5, I provide an experimental analysis of sediment and light effects on both energy acquisition and investment in corals using two phototrophic species with contrasting heterotrophic capacities. To investigate further the role of trophic strategies and physiological stress in defining the physiological niches of corals, I develop a model in Chapter 6 that integrates energy acquisition and expenditure as a function of particle concentration, particle quality, depth and light availability. This integrated, ecophysiological approach enables an evaluation of the role of sediment feeding in maintaining the energy balance of some coral species on reefs that are subject to high or seasonally fluctuating sediment loads, and can provide predictions about community responses if turbidity regimes increase.

Chapter 2

Coral suspension feeding on fine particulate matter

This chapter forms the basis for the publication:

- Anthony, K.R.N. 1999. Coral suspension feeding on fine particulate matter. *J. Exp. Mar Biol. Ecol.* **232:** 85-106 (see Appendix).

2.1 SYNOPSIS

High concentrations of fine suspended particulate matter (SPM) on nearshore coral reefs are generally assumed to be a stress factor for corals. However, the extent to which SPM serves as a food source for corals has not previously been quantified. Using ^{14}C-labelled natural particulate matter, this study investigates the relationship between concentration and suspension feeding on fine SPM by four common species of scleractinian coral on the Great Barrier Reef (GBR), Australia.

In ingestion trials, only one species (*Porites cylindrica* Dana) conformed to traditional saturation-kinetic models (Michaelis-Menten, Hollings type I) with ingestion rates reaching maximum at low to moderate SPM concentrations (4-8 mg dw/L). For the remaining three species (*Pocillopora damicornis* Linnaeus, *Montipora digitata* Dana, and *Acropora millepora* Ehrenberg) ingestion rates increased linearly over the full range of SPM concentrations (1-30 mg dw/L).

All study species assimilated a major proportion of the ingested label, but assimilation efficiency was inversely related to SPM concentration in agreement with the findings of other studies. At low concentrations (1 mg dw/L), estimates of assimilation efficiency ranged from 89 to 95% of the ingested SPM, decreasing to 40-50% at the highest concentrations (30 mg dw/L). Although the labelling with ^{14}C was mainly concentrated in the organic coating of particles, which would tend to produce overestimates of assimilation efficiencies for the bulk of the particle, these estimates are among the highest reported for suspension feeders, even at high particle concentrations.

The maximum rate of carbon assimilated from SPM can cover less than 5% of basic metabolic costs, which is not significantly different from reported contributions of zooplankton feeding to coral energy budgets. More importantly, SPM feeding at high particle concentrations may cover up to half of the carbon and a third of the nitrogen required for tissue growth.

2.2. INTRODUCTION

High concentrations of suspended particulate matter (SPM) in waters over nearshore coral reefs are considered to be a stress factor for coral assemblages, mainly by reducing light for photosynthesis and smothering coral tissues (reviewed by Rogers 1990). Nevertheless, many reefs with high coral cover are found in relatively turbid conditions, such as fringing reefs around inshore continental islands in the Great Barrier Reef Lagoon (Done 1982, Veron 1986b), suggesting that turbid conditions are not necessarily detrimental to corals. On coral reefs, SPM constitutes a diverse food source derived from a variety of sources including detrital matter (Marshall 1965, Roman et al. 1990), resuspended sediment (Larcombe et al. 1995), coral mucus (Coffroth 1990), and excretory products from other animals (e.g. from fish, Meyer & Schultz 1985). In addition, such particles are subject to colonisation by bacteria and microalgae, which increases the organic value of this food package (Riley 1963, Wotton 1988, Almeida & Alcantara 1992, Crump & Baross 1996).

Although hermatypic corals gain the majority of their carbon requirement through their symbiotic association with unicellular algae (zooxanthellae, Falkowski et al. 1984, Muscatine 1990), they are also passive suspension feeders with a potential for utilising a range of food sources (reviewed by Sebens 1987). Corals on nearshore reefs in the GBR lagoon often experience high concentrations of fine SPM for extended periods of time (up to 20 mg dw/L, Larcombe et al. (1995), see also Chapter 1) which raises the hypothesis that SPM is potentially a more important food source in nearshore habitats than in oligotrophic (offshore) environments. Although heterotrophy has been recognised as an important function of hermatypic scleractinian corals for half a century (e.g. Yonge 1930, Goreau et al. 1971, Erez 1990), no studies have quantified the importance of SPM for the energy budget and nutrition of corals. Stafford-Smith & Ormond (1992) reported that several coral species ingest large particles settled on their tissues. The organic content of large bedload particles, however, may be less than 0.3% on coral reefs (Johnstone et al. 1990), whereas that of fine suspended particles is typically above 3% (M. Dommisse, pers. comm.). In a recent study, Mills & Sebens 1997) showed that corals could sort heavy sediments and remove large particles such as *Artemia* cysts, suggesting a preference for the finer and more nutritious material.

Numerous early studies documented the ability of hermatypic corals to capture and ingest various sources of particulate food, including zooplankton, phytoplankton and bacteria (reviewed by Muscatine 1973). Only a few studies, however, have tested the capacity of corals to utilise SPM (as defined above) as a food source, despite its abundance in many nearshore waters. Attempts to quantify feeding on SPM by corals have mainly used artificial food substrates, including colloidal graphite (Lewis 1977), plastic beads (Clayton & Lasker 1982), and *Artemia* cysts (Clayton & Lasker 1982, Sebens & Johnson 1991, Helmuth & Sebens 1993, Johnson & Sebens 1993) which have little resemblance to natural SPM. Important shortfalls in most early studies on suspension feeding in corals (or by suspension feeders in general) are that the experimental flow regime and particle concentration were often not characterised. Both parameters govern the rate of delivery to the feeding structures of passive suspension feeders (particle flux, Shimeta & Jumars 1991, Abelson et al. 1993). Recent studies of suspension feeding have focused on hydro-mechanical aspects of particle capture (e.g. Helmuth & Sebens 1993, Sebens et al. 1997, Shimeta & Koehl 1997) rather than on the energetic importance of particle capture. Due to this variation in objectives and experimental protocols among previous studies, the energetic importance of suspension feeding on particulate matter, especially for corals, is still uncertain.

The purpose of this study is to quantify particulate feeding for four species of hermatypic, scleractinian coral as functions of SPM concentrations typical of those found across the GBR lagoon. I test whether ingestion as a function of SPM concentration for these species conforms to traditional models of functional responses (rectilinear: Type 1, Holling (1959); curvilinear: e.g. Michaelis-Menten, Parsons et al. (1984), Fig. 2.1) to be able to identify what particle loads cause feeding saturation. Furthermore, I estimate what proportion of the ingested material is assimilated by corals at different SPM concentrations to assess the energetic importance of particulate matter as a food source for corals in different turbidity regimes.

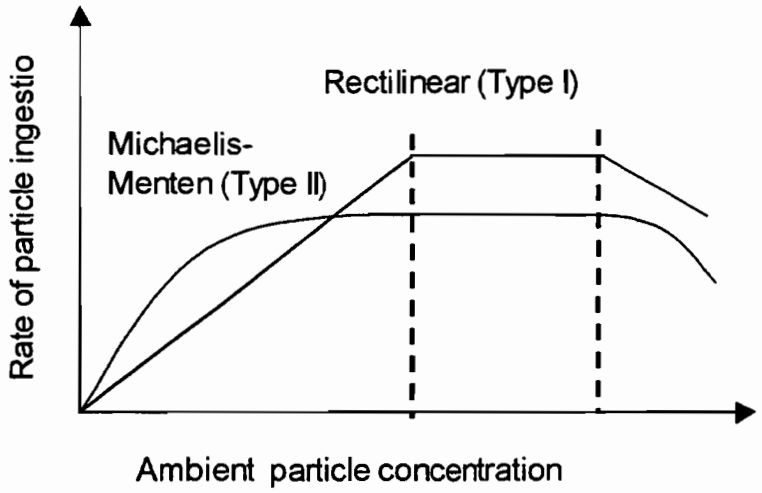

Fig. 2.1. Predictive models of particle feeding as a function of ambient particle regime. The rectilinear (type I) model has been applied to early studies of both filter (Rigler 1961) and raptorial (Holling 1959) feeders. Curvilinear saturation models (e.g. the M-M model) have become more generally applied to various groups of feeders and have a stronger theoretical basis (Lehman 1976, Ruxton & Gurney 1994), especially over a broad range of food concentrations (Currie 1982). With increasing food concentrations, both models are predicted to reach a plateau of maximum feeding rate (left dashed line). In this study, I hypothesise that at some threshold concentration (right dashed line), feeding rate will decrease as the feeding apparatus becomes stressed by high particle concentrations (dotted curves).

MATERIALS AND METHODS

2.3.1. Study species

Four coral species from three families commonly dominating coral assemblages in the Great Barrier Reef (GBR) region were chosen for this study: *Pocillopora damicornis, Montipora digitata, Acropora millepora,* and *Porites cylindrica.* The choice of coral species was mainly based on two morphological and behavioural properties. Firstly, all species have a digitate to branching growth form and comparable polyp sizes (1-2 mm diameter, Fig. 2.2) which minimise potential effects of geometry on local flow patterns and thus flux of particles and rate of encounter with tentacles (Rubenstein & Koehl 1977, Shimeta & Jumars 1991). The use of branching rather than massive growth forms maximises the ratio of suspension feeding to feeding by gravitational deposition (Abelson et al. 1993, Johnson & Sebens 1993). Secondly, all species generally have their polyps extended during both day and night, which allows a direct comparison of diel SPM consumption among species.

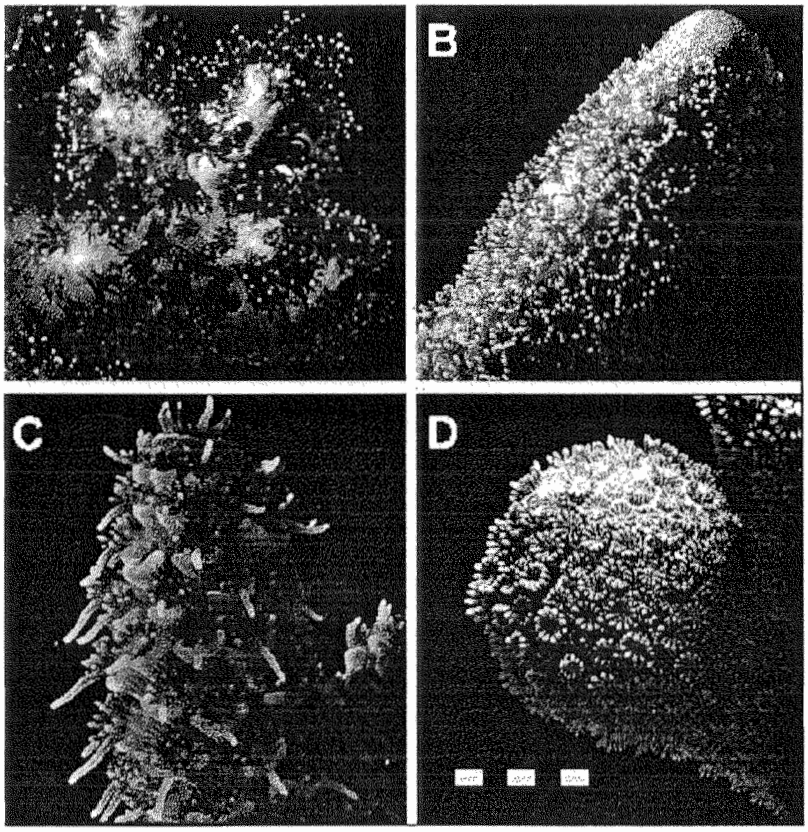

Fig. 2.2. Fine-scale morphology of the four study species. **A:** *Pocillopora damicornis;* **B:** *Montipora digitata;* **C:** *Acropora millepora;* and **D:** *Porites cylindrica*. The scale is 5 mm and applies to all panels.

2.3.2. Collecting and maintaining corals

All corals were collected from fringing reefs in Pioneer Bay and Cattle Bay on the inshore side of Orpheus Island in the central region of the GBR. Turbidity regimes in these areas range from 1-8 mg dw suspended particulate matter (SPM) per liter. *Montipora digitata* is an intertidal species (Veron 1986b, Stobart 1994) and was collected from less than one meter depth below datum. All other species were collected from a narrow subtidal depth range (3-4 m below datum) to minimise potential differences in heterotrophic capacity which could arise through differences in feeding strategies in different light regimes. Coral samples consisted of 4-6 cm long terminal branches, cut from the colony with bone cutters. Only one branch was sampled per coral colony, and only widely spaced colonies were sampled to maximise the number of clones in the analysis. Each branch was mounted on a stand consisting of a PVC cup (16 mm high by 16 mm wide) with a vertical stalk for attachment to racks and to the bottom of flow tanks (Fig. 2.3A). The base of each branch was embedded in non-toxic wax to keep

the coral firmly attached to its stand, and all mounted branches were placed on racks and transported while submerged to holding tanks with running seawater. Corals were held in the tanks for a maximum of one week prior to experimentation to allow acclimatisation but avoid stress from prolonged exposure to laboratory conditions.

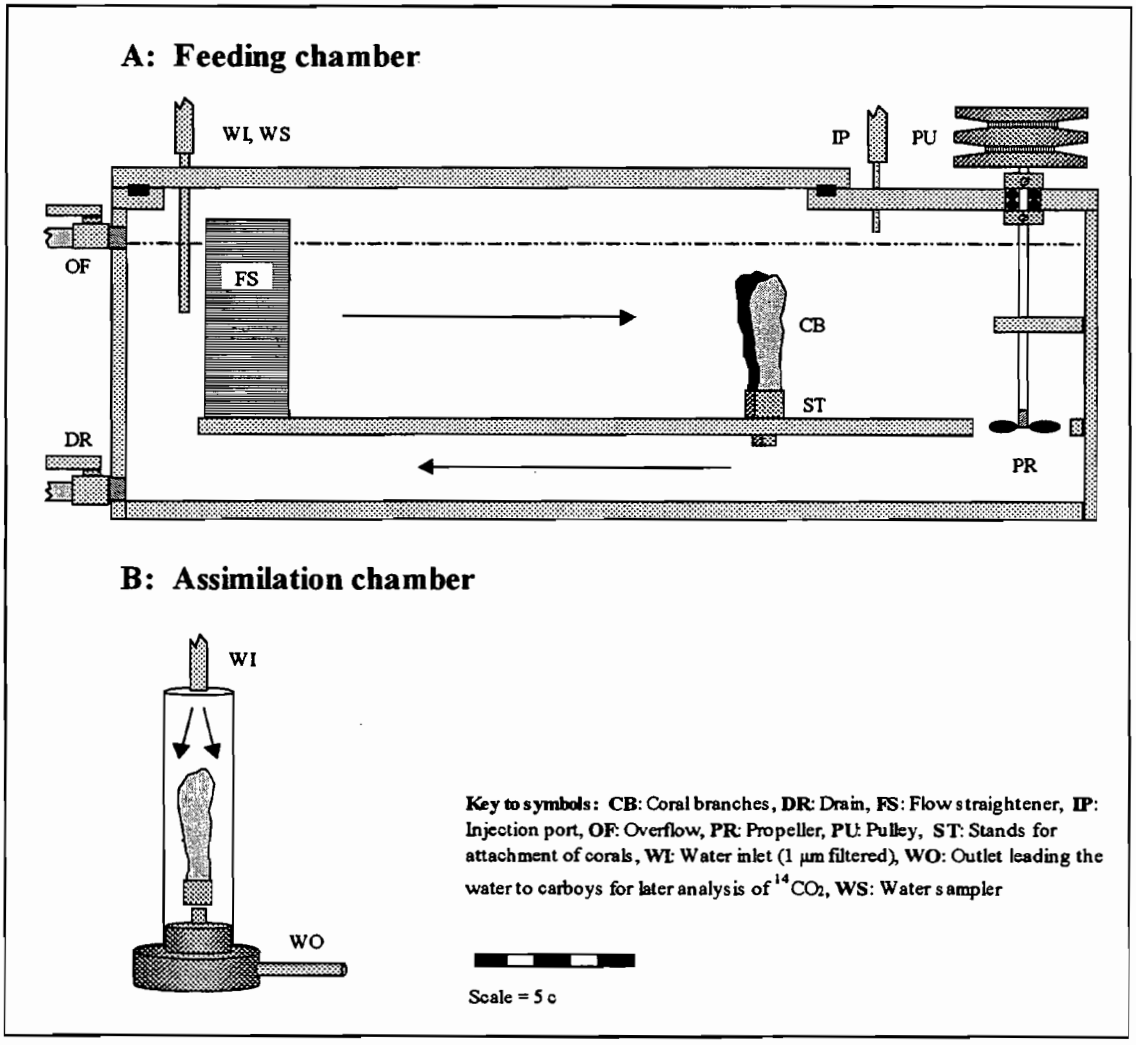

Fig. 2.3. Diagram of (**A**) feeding chamber and (**B**) assimilation chamber. Two coral branches were incubated in each feeding chamber, from which one branch was subsequently transferred to an assimilation chamber. The propellers of the four feeding chambers were driven by one motor through belts and pulleys to assure a constant flow speed for all incubations.

2.3.3. Collecting and labelling of suspended particulate matter (SPM)

To provide a suspension of particulate matter which closely resembles that experienced by corals in situ, all experiments used natural suspended particulate matter

(SPM) collected by filtration of seawater (10 µm) pumped from 3-5 meter depth, immediately above the reef crest in Pioneer Bay, Orpheus Island. The composition of the material with respect organic carbon and total nitrogen is given in Table 4.2. Particulate matter resulting from 24 hours of filtration was resuspended in 10 litres of seawater and strained through a 100 µm mesh to remove large zooplankters. A one-litre subsample was taken from the suspension and used to determine the weight-specific concentration (~ 300 mg dw/L), and the remainder (8 litres) incubated with ^{14}C in a 20-l transparent carboy. The particle suspension was labelled with a mixture of ^{14}C-glucose and ^{14}C-$NaHCO_3$, targeting surface bacteria and microalgae, respectively (Carman 1990).

Although only part of the organic fraction is labelled by this method, it was preferred over the use of artificial substrates such as diatom cultures or labelling with ^{14}C-formaldehyde (Lopez & Crenshaw 1982). The suspension was placed on a magnetic stirrer, sealed, and incubated for 48 hours under constant illumination (four 18 Watt True-Lite tubes, 80 µmol/m²/s) with 500 µCi ^{14}C-glucose (bacteria) and 1 mCi $NaH^{14}CO_3$ (microalgae). After labelling, the suspension was centrifuged twice for 10 min at 3500 rpm, divided into 4-ml portions, and stored in the freezer (-70°C) until used. By subsampling from a frozen stock suspension rather than preparing new stocks prior to incubation, identical substrates were used for all feeding trials and consisted of dead particulate matter with minimum microbial activity during incubations. Results of pilot studies showed that material from frozen aliquots is ingested by corals as readily as live material (Anthony, unpublished). Previously, Nygaard & Hessen (1990) have shown that ^{14}C-labelled bacteria lose < 20% of their activity after freezing and thawing.

To standardise feeding to µg SPM, the radioactivity (dpm) per ml labelled SPM stock suspension was determined for five randomly chosen samples. Aliquots (200 µl) were solubilised in 1 ml Soluene-350 (Packard) for 24 hrs, and bleached in 100 µl H_2O_2 to reduce colour quenching before 10 ml of scintillation cocktail was added (Hionic Fluor, Packard). Radioactivity of samples was determined in an LKB Wallac (Rackbeta) scintillation counter, and corrected for quenching using external standard ratios. Volume-specific activity of the SPM stock was 1.5×10^6 ($\pm$ SE 1.0×10^4) dpm/ml. Five 1-ml aliquots from the labelled stock suspension were filtered (0.7 µm) through Whatman GF/F filters, and dried for 72 h at 55°C to obtain weight-specific concentration, which was 1.9 ($\pm$ SE 0.1) mg dw SPM/ml . Weight-specific radioactivity of the labelled SPM stock was thus 750 dpm/µg SPM and was used to convert dpm data to µg SPM.

2.3.4. Experimental design

Experiments were divided into (1) a 1-hour feeding phase followed by (2) an assimilation phase in which half of the fed coral population was allowed to digest and assimilate the ingested ration as well as egest unincorporated label. A conceptual model describing the flux and compartmentalisation of ^{14}C in the coral during ingestion and assimilation phases is depicted in Fig. 2.4, and the experimental protocol for both phases is outlined in Fig. 2.5. The feeding trials consisted of one-hour incubations during which pairs of coral branches (one analysed for ingestion and one for assimilation) were allowed to feed on a ration of ^{14}C-labelled SPM. To determine the relationship between SPM concentration and rates of feeding (the functional response) and assimilation for all study species, feeding trials were replicated with five different loads of suspended particulate matter (treatment levels: 1, 4, 8, 16, and 30 mg dw/L). Coral branches were assigned randomly to these five treatment levels, and each level was replicated with four-to-eight branches per feeding and assimilation phase. Replication was intensified at the high SPM concentrations (16-30 mg dw/L) to reduce bias of parameter estimates for the Michaelis-Menten model (Currie 1982).

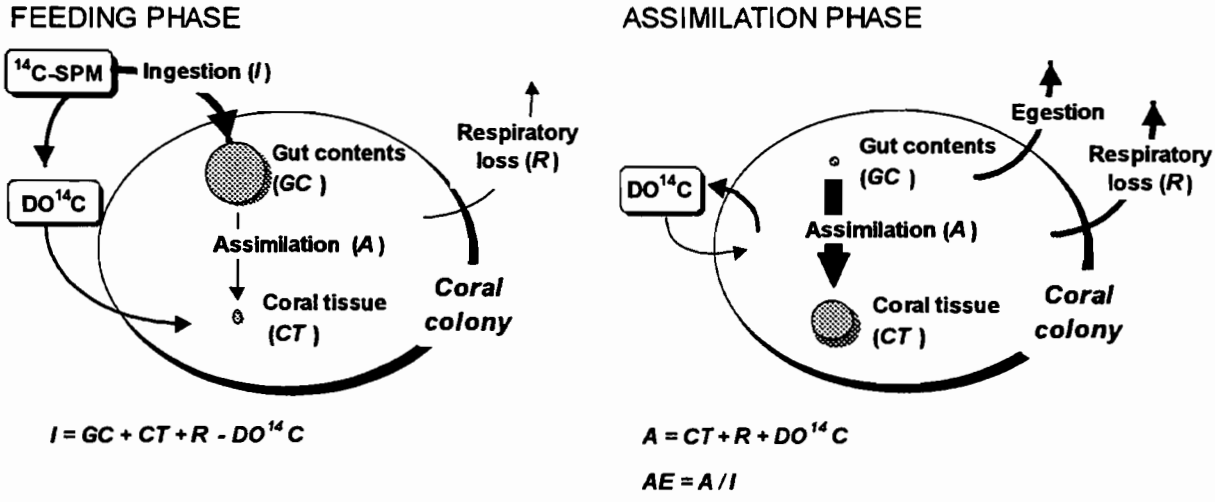

Fig. 2.4. Conceptual model of carbon fluxes and compartmentalisation of the ingested and assimilated ^{14}C within a coral colony during the two experimental phases. The derivation of assimilation efficiency (AE) is shown. In the ingestion phase, $DO^{14}C$ leaching from SPM and subsequently taken up by the coral causes overestimates of ingestion and is therefore subtracted. In the assimilation phase, on the other hand, $DO^{14}C$ lost from ingested and assimilated SPM will cause underestimates of assimilation and is added (see also section 2.3.9).

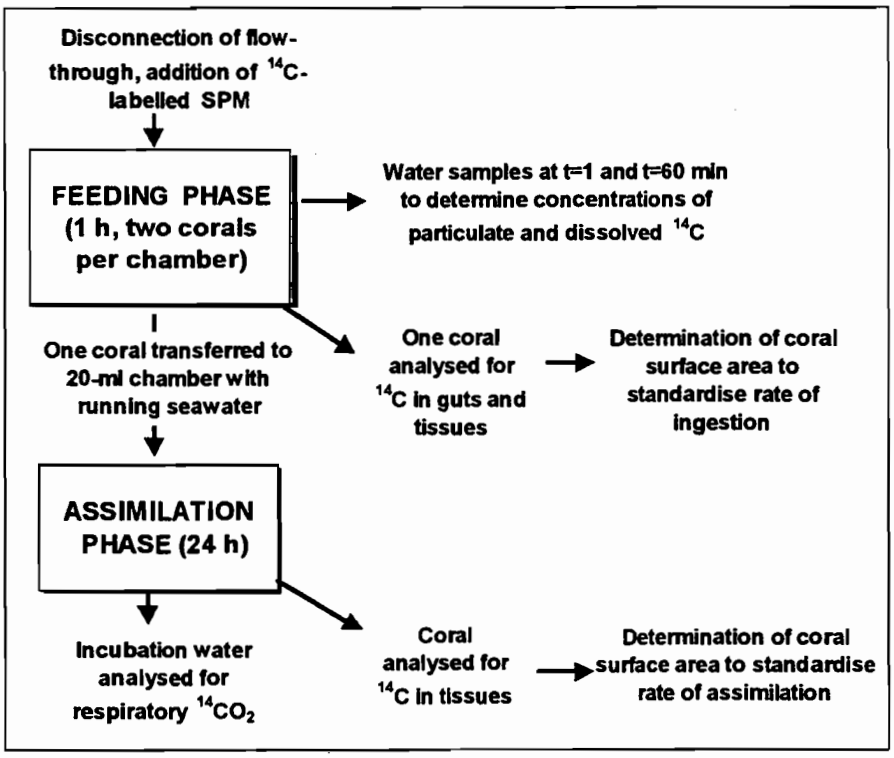

Fig. 2.5. Flow chart outlining the experimental protocol for one feeding incubation comprising two coral branches. This procedure was replicated with 4-8 pairs of corals per SPM level and per coral species (total of 120 runs).

2.3.5. Feeding experiments

All feeding trials were run using four 2-litre acrylic incubation chambers constructed as mini-flumes (30 cm long, 8 cm wide, and 8 cm high) in which a constant, unidirectional flux of SPM was established (Fig. 2.3). The flow in each flume was generated by a propeller driven by a 24 V DC motor (Electro Craft, Minneapolis) with a solid state speed control. One motor drove the propellers of all four chambers through a series of belts and pulleys to assure similar flow speeds in all tanks. A moderate, constant flow speed of 5-7 cm/s was used in all incubations, which maintained > 80% of the particles in suspension and hence available for capture, and is representative of the flow regime at 3-5 m depth in wind-protected lagoonal reefs on the GBR (Sebens & Done 1992, Fabricius & Dommisse 1999). Flow rates in the chambers were estimated by repetitive trackings of neutrally buoyant particles (hydrated *Artemia* cysts) over an 8-cm part of the downstream section of one chamber. The flow was smoothed by flow straighteners in the

upstream end of each chamber. Two 6-mm diameter holes in the floor of the chamber in the working section (20 cm downstream) functioned as attachments for the coral stands (Fig. 2.3 A).

All feeding trials were run at night and in darkness to minimise uptake of $^{14}CO_2$ through photosynthesis of zooxanthellae. Corals were allowed to acclimate to chamber conditions for 2-4 hrs prior to the experiments, during which period the chambers received a constant flow of seawater directly from the reef. The feeding phase was initiated when the polyps of all corals were fully extended, typically at 20:00 hrs. Immediately prior to a feeding trial, the ^{14}C-labelled SPM suspension was rinsed three times by centrifugation (3500 rpm for 10 min) to minimise dissolved organic label and added to each chamber through the injection port. Although, rinsing and centrifugation is likely to cause loss of labelled surface bacteria and organic films, the weight-specific radioactivity of the experimental SPM did not vary from that of the stock samples determined by filtration (750 dpm/µg SPM, see above).

After 60-min of incubation, one coral was removed from each chamber, briefly submerged in seawater to remove uningested adhering label, and cut from its base directly into a 20-ml glass scintillation vial with 2 ml tissue solubiliser (Soluene-350, Packard). The samples were incubated at 55°C until all tissues were digested (48-72 hours), and bleached in 200 µl H_2O_2 to reduce colour quenching. Ten ml scintillation fluid (Hionic Fluor, Packard) was added to each sample and left for 24 hours to allow solubilised tissue inside the skeleton to become extracted. Each piece of skeleton was transferred to an empty vial, washed, dried, and analysed for surface area (see Section 2.3.7). Less than 2% of the sample radioactivity was lost when removing the coral skeleton from the scintillation vial (estimated by subsequent transfers to new vials).

Ingestion of particulate matter was determined from the amount of radioactivity in coral tissues, controlled for uptake of dissolved organic label evolving during incubations. Uptake of dissolved label was determined from the tissue-radioactivity of corals incubated in filtered (0.45 µm) water to which a labelled filtrate (0.2 µm) was added. This method was preferred over using corals with contracted polyps (non-feeding) as controls, since the latter have a reduced surface for uptake of dissolved matter and thereby produce underestimates of dissolved uptake by feeding corals. The amount of dissolved label added to these control chambers was based on the mean concentration of dissolved label during control runs without corals (sets of four

chambers) using two different SPM concentrations (1 and 30 mg dw/L). To quantify this evolution of dissolved ^{14}C, four 2-ml water samples were taken at t = 1, 15, 30, 45 and 60 min, filtered 0.2 µm through 13 mm Nucleopore membranes, fixed in 1% formalin to prevent microbial activity and consequent loss of $^{14}CO_2$, and the radioactivity determined by liquid scintillation counting. Based on this assay, control corals were incubated in water with a concentration of dissolved ^{14}C corresponding to 15% of the mean concentration of particulate ^{14}C (Fig. 2.6).

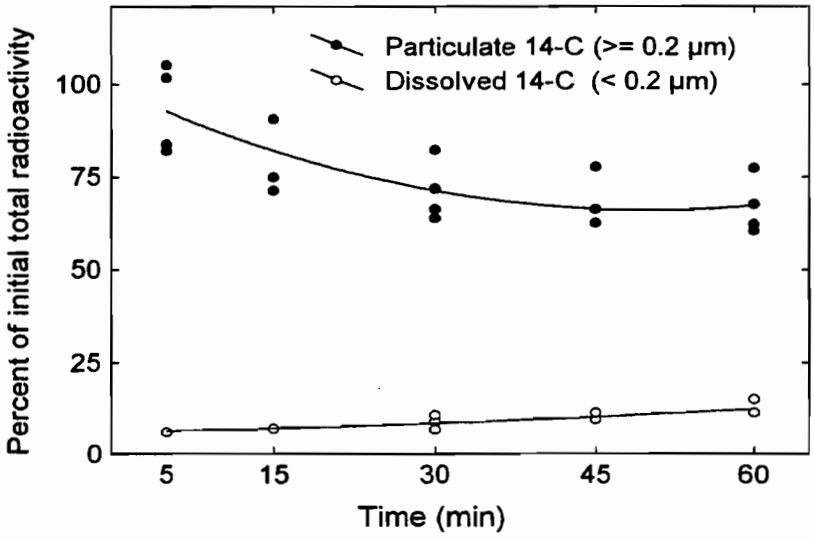

Fig. 2.6. Proportions of particulate and dissolved ^{14}C in an empty feeding chamber during a 60 min control run. Data are given as percent of the total initial radioactivity. The concentration of particulate label declined ~25% as a result of sedimentation on the chamber floor and the concomitant evolution of dissolved ^{14}C. The average concentrations of dissolved ^{14}C measured during such control runs were reproduced in a series of incubations with corals to control for the uptake of dissolved label. A negative exponential (particulate) and a linear (dissolved) function provided the best fits to the datasets.

2.3.6. Determination of the duration of the egestion phase

To determine experimentally the time when corals should be sampled to provide estimates of assimilation, a set of feeding and egestion experiments were run using a mixture of natural, unlabelled particles and inert markers which could be traced over the course of egestion. Fluorescent latex beads (Polysciences Inc.) with a diameter of 6 µm were used as markers, representative of the lower size range of the natural particles. By using a low concentration of small inert beads (3×10^6 beads/L, corresponding to ~0.03 mg dw/L) together with a relatively high concentration of natural particles (~8 mg dw/L),

possibility that corals showed selective egestion of the inert beads was assumed to be minimal. Inert particles have previously been used successfully as markers of particle retention time in, for example, bivalves (Decho & Luoma 1991). Eight coral branches of each coral species were fed the mixture of natural particles and beads for 1 h, and subsequently transferred to individual assimilation chambers consisting of 20-ml syringes (20-mm diameter) with flow-through seawater. Each branch (and stand) was mounted on a modified piston, and inserted into the syringe without the coral touching the inside of the syringe. Filtered (1 µm pore) seawater entered through the top of the syringe and left through an outlet below the coral, and was led into a 10-litre container. The small chamber volume and downward unidirectional waterflow served to minimize recapture of egested beads. The outlet water was collected every 2 h during the first 6 h, and thereafter every 4-6 h for a total of 26-28 h. To enable enumeration of the egested markers, the water from each chamber during each time interval was filtered through a GF/C filter (0.7 µm pore), mounted on a glass slide, and the beads counted under an epifluorescence microscope. Based on the asymptotic decline in egestion rate (Fig. 2.7), egestion was assumed to be complete for all species (except *P. cylindrica*) 24 hours after termination of the ingestion phase.

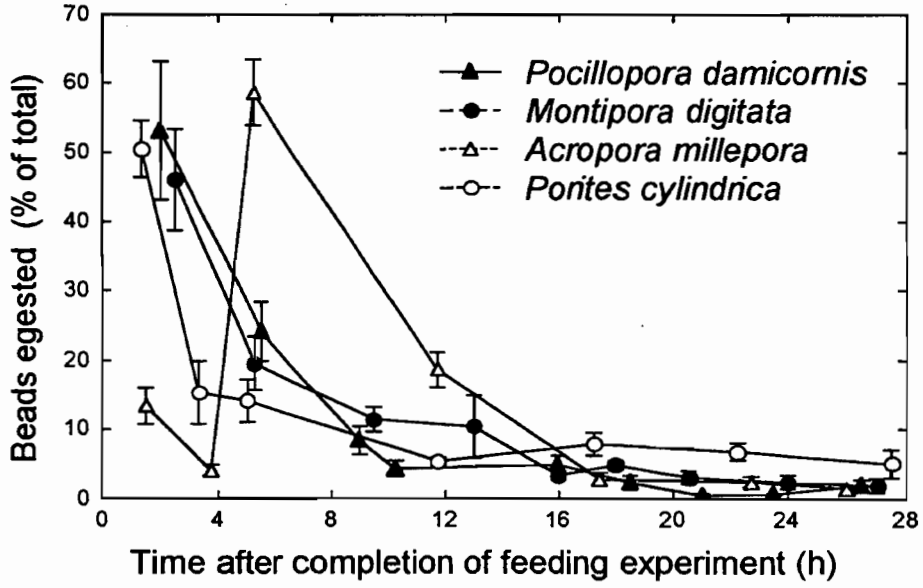

Fig. 2.7. Egestion of unincorporated fine particulate matter as traced by inert beads (6 µm diameter). Data are means ± 1 SE of 4 coral branches.

2.3.7. Assimilation of SPM

The second coral branch from each feeding chamber was transferred to a smaller chamber (Fig. 2.3 B) with a flow-through of filtered (1 μm) unlabelled seawater in which the coral was allowed to digest and assimilate the ingested particulate matter, and egest any unincorporated material. The duration of this phase was kept at 24 h based on the egestion trials in Section 2.3.6. The assimilation phase was typically initiated at 21:00, and the corals were exposed to a natural light regime corresponding to 5 m depth during the following day to allow natural metabolism. Respiratory loss of $^{14}CO_2$ from the corals during the assimilation phase was determined using a technique modified from that of Crosby et al. (1989). The filtered water from each egestion chamber was collected in 25-l carboys with formalin (1% final solution) to prevent the evolution of $^{14}CO_2$ from microbial activity. To trap any gaseous $^{14}CO_2$, air displaced from each carboy while filling and during subsequent treatment was bubbled through a series of four 25-ml sealed centrifuge vials with 10 ml 2 M NaOH which functioned as $^{14}CO_2$ traps. At conclusion of the assimilation phase, 100 ml 1M citric acid was injected into the carboys (pH 1-2) to stimulate release of $^{14}CO_2$ from solution, and the water was ventilated with N_2 for 48 hrs. A 2-ml subsample from each vial in the CO_2 traps was added to 10 ml StarScint (Packard) and the radioactivity determined by scintillation counting. The decline in radioactivity over the series of vials provided an effective means of monitoring the efficiency (~ 98%) of $^{14}CO_2$ retention by the traps. After completion of the assimilation phase, each coral fragment was cut from its base and treated as described for the feeding phase.

2.3.8. Normalisation of ingestion data

Feeding data were standardised to μg SPM ingested per cm² surface area per h. Based on the mass-transfer model of Patterson (1992), metabolic and photosynthetic rates are likely to be more dependent on colony and polyp morphology (via effects on flow patterns) than on tissue thickness. For *Montipora digitata*, *Acropora millepora* and *Porites cylindrica*, branch surface area was calculated based on the simple geometrical shapes and dimensions of coral branches. For *Pocillopora damicornis*, which has a more irregular surface, total number of corallites (polyps) were counted and converted to surface area from the number of corallites per cm² (67±5 SE for N=10 9-mm² quadrats).

2.3.9. Data analysis of ingestion rates and feeding responses

The Hollings type I and Michaelis Menten models were fitted to the datasets (ingestion rate vs SPM concentration) using piecewise-linear and non-linear least squares regression, respectively (Simplex and Quasi-Newton iterative methods, STATISTICA 1997). The Hollings type I (piecewise-linear) model was of the form

$$I_C = b_o + a \times C \ (for\ C < C_{saturation}) + I_{max} \ (for\ C \geq C_{saturation}) \quad (1)$$

where I_C is ingestion rate as a function of SPM concentration (C), b_0 is the intercept, a is the slope of the feeding response below the SPM concentration at which the coral becomes saturated ($C_{saturation}$), and I_{max} is the maximum rate of ingestion. In the absence of saturation over the range of concentrations used, the model becomes a simple linear regression.

The curvilinear Michaelis-Menten model was used here in the form

$$I_C = (I_{max} \times C) / (K + C) \quad (2)$$

where K is the SPM concentration at which half-saturation occurs. The conformity of the data to these two models was evaluated based on the percentage of explained variance (R^2). Coral species displaying a similar type of relationship between SPM concentration and ingestion were compared using an analysis of covariance (ANCOVA) followed by Tukey's HSD test.

2.3.10. Data analysis of assimilation efficiencies.

The amount of label assimilated by the corals (A) was the radioactivity in coral tissues after egestion was complete (CT_A), corrected for label remaining from uptake of dissolved organic matter during the ingestion phase ($DO^{14}C_I$), and respiratory loss of $^{14}CO_2$ (R). Dissolved organic carbon released by the corals during the assimilation phase ($DO^{14}C_A$) could not be determined since the label was too diluted in the carboys and would have included label leaching from egested particles. Also, incorporation of label into the skeleton was not quantified since a significant incorporation of skeletal $Ca^{14}CO_3$ is expected through passive ion exchange with the incubation water (Barnes & Crossland 1977). The amount of label assimilated by the coral was thus determined as

$$A = CT_A - DO^{14}C_I + R \quad (3)$$

and the efficiency (*AE*) by which the species assimilated label from the ingested SPM at different SPM concentrations was determined as

$$AE = A / I \quad (4)$$

obtained for pairs of branches from each feeding chamber. Effects of coral species and SPM concentration on assimilation efficiency were tested using a two-factor ANOVA followed by a Tukey's HSD multiple comparisons test (Sokal & Rohlf 1995). The raw data conformed to ANOVA assumptions, and were analysed untransformed.

2.4. RESULTS

2.4.1. Feeding responses to concentrations of fine SPM

All four species demonstrated a capacity to feed on fine suspended particulate matter (SPM), and their rates of ingestion increased markedly with increasing particle concentration (Fig. 2.8). Ingestion rates were relatively low for all species, however, with maxima of less than 5 µg SPM per square cm coral surface area per hour. For three of the four species, rate of ingestion increased five to ten fold as a function of SPM concentrations between 1 and 30 mg dw/L. These three species (*Pocillopora damicornis*, *Montipora digitata*, and *Acropora millepora*) showed simple linear feeding responses (R^2 from 0.82 to 0.96) over the wide range of SPM concentrations. *P. damicornis* showed a tendency to become saturated at high SPM concentrations as indicated by a significant fit to both the piece-wise linear and curvilinear models, as well as to the simple linear model (Table 2.1). However, estimates of the saturation ($C_{saturation}$, Hollings type 1) and half-saturation (K, Michaelis-Menten) constants (20 and 28 mg dw/L , respectively) for *P. damicornis* were located in the upper range of the SPM concentrations used, which renders the non-linear models inappropriate for representing the feeding response of *P. damicornis* within this range of concentrations (see also Currie 1982). Only *Porites cylindrica* showed convincing saturation as the feeding rate did not increase significantly over the concentration range 4-30 mg dw/L. The feeding response of *P. cylindrica* could be explained equally well by the piecewise-linear- and the Michaelis-Menten models as indicated by similar R^2-values (0.67 and 0.66, respectively; Table 2.1). According to the Michaelis-Menten model, half-saturation of *P. cylindrica*

occurred at SPM concentrations as low as 2.7 ± SE 1.1 mg dw/L , approximately an order of magnitude lower than that estimated for *P. damicornis* (27.5 ± 2.0 mg dw/L).

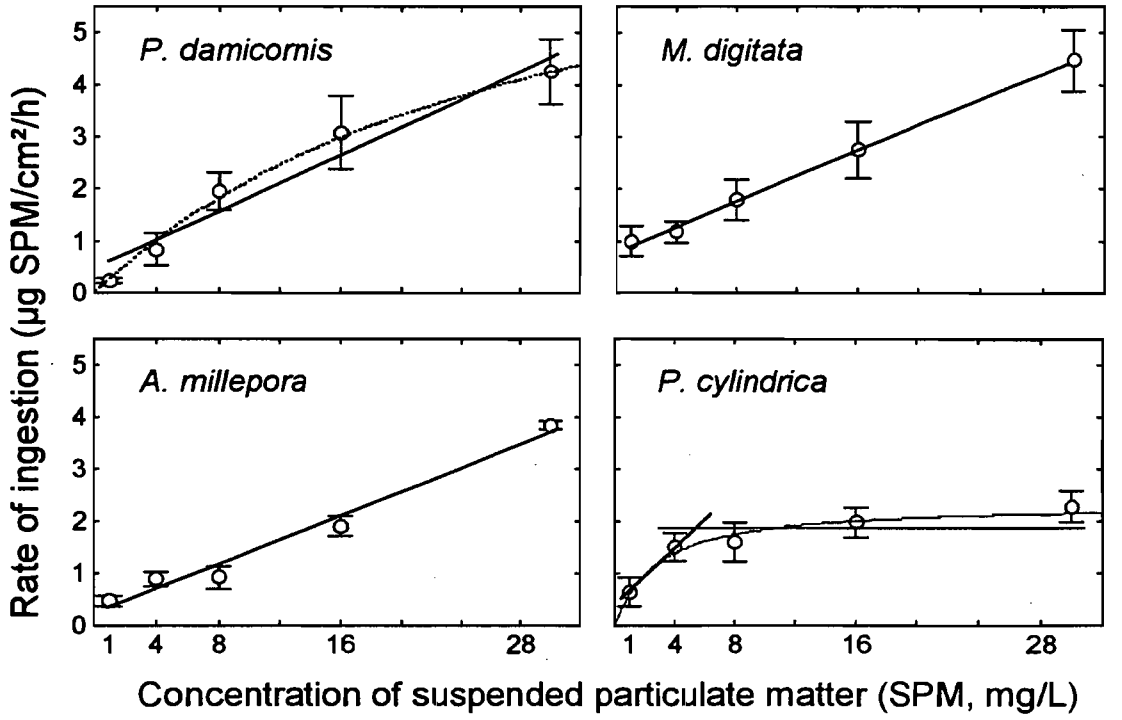

Fig. 2.8. Ingestion rates as a function of SPM concentration (functional response) for the four coral species. Data are means ± 95% confidence limits of N = 4 to 8 incubations. Piecewise linear (Holling's type 1, solid lines) and curvilinear (Michaelis-Menten, dashed lines) models are fitted to the data normalised to units of tissue surface area using iterative non-linear regression, whereas simple linear models are fitted by linear regression. For clarification, only the models with the best fit are shown. Results of all regressions are presented in Table 2.1.

Of the three linear feeding responses, ingestion rates of *P. damicornis* and *M. digitata* were generally higher compared to that of *A. millepora* as indicated by the results of the ANCOVA (Table 2.2). Interestingly, the slopes of the linear feeding responses (and thus particle clearance rates, ml/cm²/h) for *P. damicornis*, *M. digitata*, and *A. millepora* were almost identical (0.12 - 0.13 ± SE 0.01, $F_{2,71}$ = 0.85, P = 0.43, Table 2.1). Below the level of saturation, the clearance rate for *P. cylindrica* (0.29) was three-fold those of the three simple linear responses.

Table 2.1. Summary of regressions for feeding responses of the four coral species depicted in Fig. 2.8. Parameters for the piece-wise linear model (I_{max} = maximum rate of ingestion, and C_{sat} = concentration at which saturation occurs) and the Michaelis-Menten model (I_{max} and K = half-saturation constant) were calculated using iterative least-squares regression.

Simple Linear (SL) and Piecewise Linear (PL) models: $I = b_0 + a \times C$ (for $C < C_{sat}$) + I_{Max} (for $C > C_{sat}$)

Parameter estimates (SE in parentheses)

Species	N	Model	R^2	b_0 (intercept) µg SPM/cm²/h	a (slope) ml/cm²/h	I_{Max} µg SPM/cm²/h	C_{sat} mg SPM/L
P. damicornis	30	SL	0.82	0.49 (0.19)	0.13 (0.01)	4.51 (0.24)*	nd
	30	PL	0.86	0.15 (0.22)	0.19 (0.02)	4.25 (0.23)	20 **
M. digitata	27	SL	0.86	0.80 (0.16)	0.12 (0.01)	4.46 (0.23)*	nd
A. millepora	24	SL	0.95	0.23 (0.08)	0.12 (0.01)	3.70 (0.12)*	nd
P. cylindrica	25	SL	0.47	1.11 (0.14)	0.04 (0.01)	2.25 (0.20)*	nd
	25	PL	0.67	0.36 (0.30)	0.29 (0.09)	1.90 (0.12)	5**

* *Imax* of simple linear relationship is the predicted feeding rate at C_{SPM} = 30 mg DW/L

** C_{sat} is determined empirically, and the set of parameters shown is that which provided the best fit to the data.

nd = not determined

Curvilinear Michaelis-Menten (M-M) model: $I = Imax \times C / (K + C)$

Parameter estimates (SE in parentheses)

Species	N	Model	R^2	*Imax* µg SPM/cm²/h	K (half-saturation const) mg SPM/L
P. damicornis	30	M-M	0.85	8.22 (0.33)	27.5 (2.0)
P. cylindrica	25	M-M	0.66	2.36 (0.24)	2.7 (1.1)

Table 2.2. Analysis of covariance for rates of ingestion for three coral species with linear feeding responses to increasing concentrations of suspended particulate matter (SPM, covariate). Data are untransformed (µg dw SPM/(cm² coral surface area)/h). Horizontal lines join ingestion rates which are not significantly different by the Tukey's HSD test.

Source of variation	df	MS	F	p-level
Effect	2	2.56	8.97	0.0003
Error	73	0.29		

	M. dig.	*P. dam.*	*A. mil.*
Ingestion rates, adjusted means	2.19	1.99	1.55
Tukey HSD test ($p < 0.05$)			

Based on the control incubations, approximately 25% of the radioactivity in coral tissues after the feeding phase could be attributed to uptake of dissolved ^{14}C. This ratio of dissolved to particulate uptake remained constant (26 ± 3%) across species and between lowest and highest SPM concentrations used. A factor of 0.75 was thus used to correct all ingestion data for uptake of dissolved label. Interestingly, only a maximum of 15% of the total label added to chambers was in dissolved form (at t = 45 and 60 min, Fig. 2.6), suggesting that dissolved label is more readily taken up than particulates.

2.4.2. Effects of SPM concentration on assimilation efficiency

The four coral species assimilated between 91 and 100% of the ingested label at the lowest SPM concentration (1 mg dw/L), decreasing to 45 - 80% at the highest SPM concentration (30 mg dw/L, Fig. 2.9). The decline in assimilation efficiency (*AE*) as a function of SPM concentration was significant (P = 0.027, Table 2.3) attributable only to differences in *AE* between highest and lowest SPM concentration (Tukeys test, Table 2.3). The two-way ANOVA also showed an effect of species on *AE* governed by contrasts between two species. The mean *AE* of *M. digitata* (89.4%) was significantly higher than that of *A. millepora* (62.2%) but neither species differed significantly from *P. damicornis* (75.4%) or *P. cylindrica* (77.4%, Tukeys test, Table 2.3). Surprisingly, the slopes of *AE*s as a function SPM concentration were similar for all species (Fig. 2.9, test of parallelism, $F_{[3,114]}$, P = 0.57) despite differences in the amount of material ingested and hence processed.

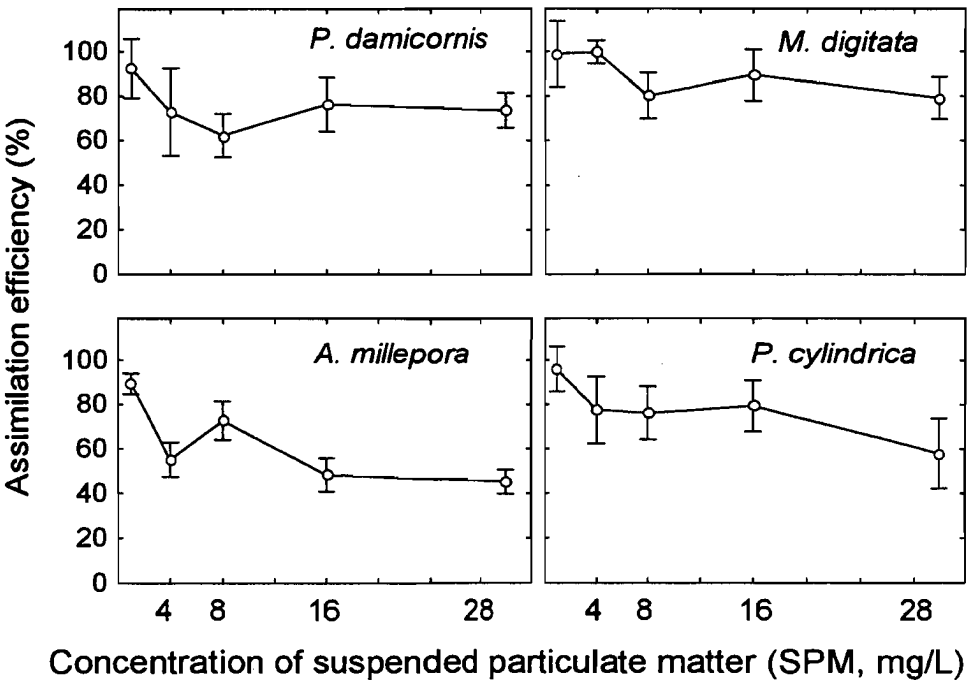

Fig. 2.9. Effects of SPM concentration on assimilation efficiency for the four corals species. Assimilation efficiency was estimated as the sum of radioactivity in coral tissues 24 h after the feeding phase and respiratory loss of $^{14}CO_2$ during this period, relative to the radioactivity in coral tissues immediately after the feeding phase. Data are means ± SE of N = 4 to 8 coral branches.

Only 13 - 34% of the estimated assimilated label was lost as respiratory $^{14}CO_2$ during the 24-h assimilation phase (Fig. 2.10). Interestingly, this ratio did not differ significantly between high and low SPM concentrations (ANOVA, $F_{[1,44]} = 1.24$, $P = 0.27$), suggesting that larger food rations are metabolised as readily as small rations. *P. cylindrica* showed a tendency to respire the greatest proportion of the retained label (31 - 34%, Fig. 2.10), although this tendency was significant only when compared to *A. millepora* (ANOVA, $F_{[3,44]} = 6.18$, $P = 0.0013$).

Table 2.3. Comparison of assimilation efficiencies (*AE*) for the four coral species at five different SPM concentrations using two-way ANOVA. Data are untransformed. Horizontal lines join assimilation efficiencies which are not significantly different by the Tukeys HSD test.

Two-factor ANOVA

Source of variation	df	MS	F	P-value	
SPM concentration	4	2726	2.86	0.027	*
Species	3	2893	3.04	0.032	*
SPM concentration x Species	12	528	0.55	0.874	NS
Error	106	953			

Effect of SPM concentration on assimilation efficiency (AE

SPM concentration (mg/L)	1	4	8	16	30
Mean AE (%)	94.1	76.4	72.7	73.4	64.0
Tukey HSD test ($p < 0.05$)					

Effect of coral species on assimilation efficiency (AE)

Coral species	*M. dig.*	*P.cyl.*	*P.dam.*	*A. mil*
Mean AE (%)	89.4	77.4	75.4	62.2
Tukey HSD test ($p < 0.05$)				

* P<0.05, ns not significant

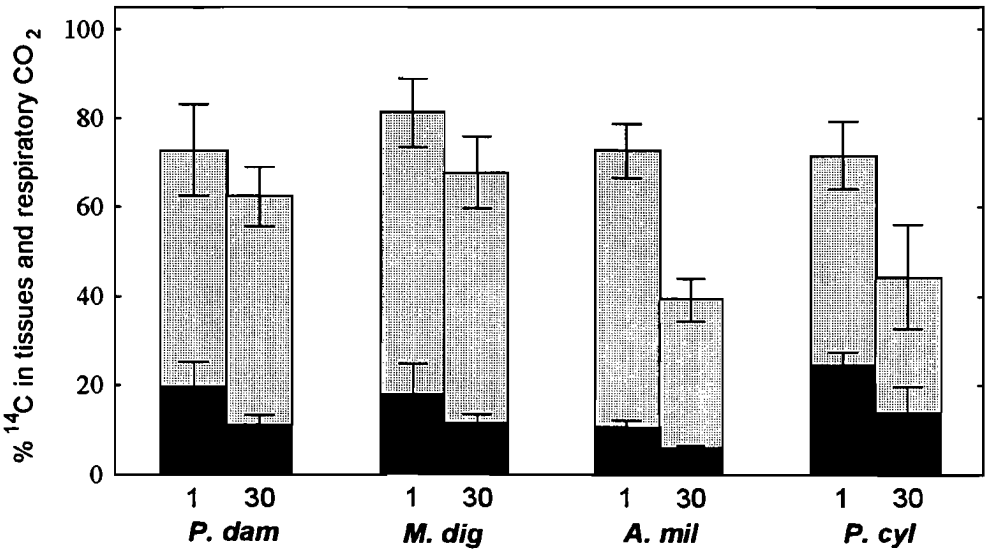

Fig. 2.10. Percent of ingested ^{14}C incorporated into coral tissues (light-shaded) and lost as respiratory CO_2 (dark-shaded) during the 24-h assimilation phase following feeding trials with SPM concentrations of 1 and 30 mg SPM/L. Data are means ± SE of N = 4 to 8 coral branches. Tissue label was determined for all SPM concentrations, whereas loss of respiratory $^{14}CO_2$ was only determined for corals incubated at 1 and 30 mg dw/L. Respiratory $^{14}CO_2$ for corals feeding at intermediate concentrations was estimated by interpolation.

2.5. DISCUSSION

2.5.1. Ingestion rate as a function of particle concentration

All four species demonstrated a capacity to feed on fine suspended particulate matter, a capacity that was positively correlated with particle availability. Surprisingly, the relationship between particle concentration and rate of ingestion was a simple linear function of concentration rather than a traditional saturation curve for three out of the four species (*P. damicornis, M. digitata,* and *A. millepora*). Even particle concentrations mimicking observed peak turbidity regimes in some nearshore coral reefs in the Great Barrier Reef Lagoon (16 and 30 mg dw/L, e.g. Brodie et al. 1989, Larcombe et al. 1995), did not cause significantly lower rates of ingestion than expected from the linear model. Interestingly, since particle concentrations at the study sites rarely exceed 8 mg dw/L, maximum experimental concentrations were at least three times higher than those normally experienced by these corals. Only *P. cylindrica* conformed convincingly to traditional saturation-kinetic models by reaching maximum rate of ingestion at low-to-moderate particle concentrations (4-8 mg dw/L). *P. damicornis* showed a tendency to become saturated at concentrations > 16 mg dw/L, and would most likely saturate at lower concentrations than both *M. digitata* and *A. millepora* over a broader range of concentrations. However, constructing feeding response curves based on higher particle concentration would not reflect the conditions under which these species naturally feed.

According to Rigler (1961) and Holling (1959), a rectilinear functional response is expected for filter feeders, i.e. feeding rate is a linear function of prey concentration until it reaches a plateau. For three of the four species (*P. damicornis*, *M. digitata*, and *A. millepora*) such a plateau was not reached within the range of particle concentrations used in this study. The feeding responses for *P. cylindrica*, however, was equally well modelled by the rectilinear (Hollings type I) and curvilinear (Michaelis-Menten) relationships. Tentatively, feeding by coral polyps can be modelled analogous to active sites in enzyme kinetics, showing increasing levels of saturation with increasing substrate concentration (curvilinear response) rather than a linear increase up to a certain plateau (rectilinear response). My conclusion is supported by theoretical models of shapes of feeding responses for filter feeders that predict curvilinear rather than rectilinear responses (Lehman 1976). For passive suspension feeders the shape of the feeding

response curve is likely to be governed by morphological, physiological and behavioural characteristics of the organism (Hart & Latta 1986, Leonard 1989), however, an explanation as to why only *P. cylindrica* showed saturation is not apparent from the results of this study. A number of hypotheses appear plausible. Firstly, a lower tentacle cleaning rate as determined by the velocity of ciliary feeding currents (Muscatine 1973) may be a limiting factor at high particle concentrations. The low cleaning rate of the congeneric *Porites lutea* in sediment-rejection experiments (Stafford Smith 1993) adds support to this hypothesis. Secondly, space-limitations of polyp coelenterons may define a limit to ingestion (Lehman 1976, Taghon & Jumars 1984) and will be relatively more important for small-polyped species such as *P. cylindrica* and *M. digitata*. The maximum SPM ingestion rate for *P. cylindrica* of 2 µg/(cm² colony surface)/h (Fig. 2.8) corresponds to a volumetric intake of 2 µl/(cm² colony surface)/h, assuming neutral buoyancy of the particles. Since *P. cylindrica* carries approximately 65 polyps per cm² colony surface (Anthony, unpublished), each polyp would ingest a volume of the order 0.03 µl which corresponds to one spherical particle of 400 µm diameter per hour, which suggests that space could be restricting ingestion. These results support previous assumptions that members of the genus *Porites* rely mainly on autotrophy (Johannes & Tepley 1974, Edmunds & Davies 1989). Thirdly, high particle concentrations may elicit a stress response and stimulate the coral to stop feeding. However, the tentacles of all corals exposed to maximum particle loads (30 mg dw/L) remained expanded during the full length of the incubations suggesting that the feeding behaviour of the corals was not adversely affected by high particle concentrations. Fourthly, Lewis & Price (1975) noted for Atlantic corals that poritids and pocilloporids only employed tentacular feeding whereas acroporids showed both tentacular and mucus feeding. Whether such differences in feeding behaviours and mechanisms are responsible for the different kinetics observed in, for example *P. cylindrica* and *A. millepora*, is unclear and deserves further study.

Based on absolute values of the maximum feeding rates in this study (less than 5 µg per cm² per h), all four coral species showed low affinity for fine particulate matter, which would tend to prevent feeding saturation. Furthermore, only one-hour incubations were used in this study (to minimise the build-up and uptake of dissolved label) which may be insufficient time to accumulate enough material to cause saturation (Patterson 1991). Periods of high turbidity over reefs are often of the scale of days to weeks (Larcombe et al. 1995) rather than of hours.

The generally low feeding rates and low slope (clearance rates) observed in this study may be related to the small particle size as suggested by aerosol-filtration theory (Rubenstein & Koehl 1977, Shimeta & Jumars 1991). The spacing between tentacle tips for the coral species used in this study was of the order 500 - 2000 µm whereas the range of particle sizes was 10 - 100 µm, thereby excluding sieving as a likely mode of capture for corals feeding on fine SPM. Sieving is suggested to be an important mechanism in the capture of zooplankton for both octocorals (Sebens & Koehl 1984) and scleractinian corals (Sebens et al. 1996). For particles with diameters only 1/20 to 1/5 of the spacings between coral tentacles, and at flow velocities typical of lagoonal coral reefs (5 - 10 cm/s) the predominant mode of capture is most likely direct interception, i.e. the particle follows a streamline that brings it within one particle radius of a tentacle (Rubenstein & Koehl 1977). In order for such small particles to be intercepted by a tentacle they must travel in streamlines closer to the tentacles than large particles, and thus have a lower probability of capture than larger particles of similar abundance. For spionid polychaetes, Shimeta & Koehl (1997) found that the probability of encounter increased as the square of the particle diameter, corresponding to an almost 100-fold increase in capture probability with an increase in particle size from 10 to 100 µm.

Only coral species with a branching/digitate growth form and small polyps were used in this study, as this morphology is expected to facilitate higher capture rate of small prey items than that of massive large-polyped species, in part due to a larger area of contact (projected tentacle surface) with the flowing water. According to the model by Abelson et al. (1993), coral species with a high ratio of body height to basal width encounter high fluxes of small suspended particles, whereas massive and encrusting forms encounter fluxes of predominantly heavier, resuspended material. Also, Sebens et al. (1996) found that *Madracis mirabilis* (small polyps, branching) captured > 36 times more plankton per unit of biomass than *Montastrea cavernosa* (large polyps, massive). The use of individual coral branches rather than whole colonies in this study, however, may overestimate in situ feeding rates due to partial depletion of the water by polyps upstream, especially in large clones (Anthony 1997, Sebens et al. 1997).

2.5.2. Feeding responses as a proxy of tolerance to turbidity regimes?

The low saturation constant ($C_{saturation}$ *or* K) of *P. cylindrica* in contrast to the absence of saturation for the other three species may suggest that *P. cylindrica* performs poorly in high-turbidity habitats. Moreover, it raises the hypothesis that the suitability of a high-turbidity regime to a given coral species may be indicated by the saturation characteristics (parameters $C_{saturation}$ or K) of that species. However, the relative abundances of the four study species in habitats of different turbidity levels along an inshore-offshore transect across the Great Barrier Reef lagoon (Done 1982), does not add convincing support to this hypothesis. For example, *P. damicornis* is abundant in most coral reef habitats across the GBR lagoon from extreme inshore to exposed offshore reefs. Interestingly, however, *M. digitata* (the best SPM feeder) is often the dominant coral species on shallow mudflats where it is periodically exposed to extremely turbid conditions, whereas *P. cylindrica* (the poorest SPM feeder) is generally absent from the most turbid inshore habitats (Stafford-Smith et al. 1993), somewhat in agreement with its complete saturation of feeding rates at concentrations as low as 4-8 mg dw/L. The extent to which saturation parameters of feeding response curves can be used to predict sediment stress in corals needs further study, however, and I will in this study limit their use to predictive modeling of particle heterotrophy across turbidity regimes.

2.5.3. Effects of SPM concentration on assimilation efficiency

The estimates of assimilation efficiency were high for all species. At low particle concentrations, almost the total consumption of particulate matter was assimilated (mean 94%), and an average of 64% of the ingested matter was utilised at the highest SPM concentration (30 mg dw/L). This inverse relationship between assimilation efficiency and rate of ingestion corroborates the pattern found for other marine invertebrates (see Szmant-Froelich & Pilson (1984), Zamer (1986), and references therein). Sorokin (1973) also reported high rates of assimilation for corals feeding on planktonic bacteria (and lower rates for phytoplankton); but his data are not readily comparable to this study, mainly due to different methods of standardisation. Zamer (1986) found that the temperate symbiotic sea anemone *Anthopleura elegantissima* assimilated between 68% and 95% of the ingested carbon (based on gravimetric methods), assimilation efficiencies

that are not significantly different from those found in this study.

Assimilation efficiency as estimated in this study, however, must be interpreted with caution due to shortfalls of the labelling method, since only the live portion of the organic fraction (mainly bacteria and microalgae) was labelled with ^{14}C. Although this labelling method is satisfactory to provide a marker for ingestion, assuming that the label is homogenously distributed among particles, it will almost certainly overestimate assimilation efficiency (Lopez et al. 1989). Since most suspension and deposit feeders will readily digest and assimilate the live organic coating and reject/egest the less labelled refractory matrix (see review by Wotton 1994), assimilation will reflect the utilisation of the more intensely labelled live organic matter rather than the whole particles. Notwithstanding this source of error, the community of microorganisms coating the fine particles (which are targeted in the labelling process) presumably constitute the most nutritionally important component of suspended particulate matter. The results of this study demonstrate that the major proportion of this organic component is utilised by suspension feeding corals, even at concentrations up to 30 mg/L.

2.5.4. Importance of fine SPM as a food source for corals

The maximum feeding rates on fine SPM observed in this study (5 µg SPM/(cm² colony surface area)/h) are low compared with data on suspension feeding by corals in other studies. For example, Clayton & Lasker (1982) found that in concentrations corresponding to 30 mg dw of *Artemia* nauplii/L, *P. damicornis* ingested approximately 40 µg nauplii per cm² colony surface per h (based on a polyp density of 67 per cm², this study). This value is approximately eight times the feeding rate found in this study. However, the feeding rates of *P. damicornis* as found by Clayton & Lasker (1982) are not readily comparable to those in this study due to differences in experimental protocol and types of food. The mean size of *Artemia* nauplii is 600 µm compared to a particle size range of 10 -100 µm in this study, resulting in a several-fold higher capture probability of nauplii due to size per se (see Shimeta & Koehl 1997), and even more so if capture of nauplii is aided by sieving (see above) and gravitational deposition.

Relative to daily respiratory and photosynthetic carbon fluxes, the contribution of carbon from SPM appears to be insignificant. For example, using an organic carbon content of 5% for fine SPM in the study area (M. Dommisse, pers. comm., see also

Chapters 4 & 5) and an assimilation efficiency of 79% (Fig. 2.9), *P. damicornis* would be assimilating 4.75 µg C/(cm² surface area)/d at the highest particle concentration (30 mg dw/L). For comparison, Muscatine et al. (1984) reported rates of respiration and gross photosynthesis in *Stylophora pistillata* of 125 and 138 µg C/(cm² surface area)/d, respectively. Despite a small contribution to daily energy budgets, feeding on SPM may, however, be important for coral growth. It is well documented that most of the carbon translocated from zooxanthellae is lost as respiration or excretion (e.g. Falkowski et al. 1984, Spencer Davies 1984), in part due to low contents of N and P limiting tissue synthesis (for review, see Muscatine 1990). Assuming a 1 to 5% daily increase in tissue mass in *P. damicornis* (Spencer Davies 1991) and an animal carbon content of 0.94 mg per cm² surface area (Muller et al. 1994), the carbon-specific growth rate of this species ranges from 9 to 46 µg C per cm² per day (24 h). At high particle concentrations (30 mg dw/L), the daily assimilation of 4.75 µg organic carbon per cm² from SPM can thus potentially account for 10 - 52% of the growth needs in *P. damicornis*. The low respiratory loss of ^{14}C assimilated from SPM (13 - 34%, Fig. 2.10) supports the hypothesis that a large proportion of the heterotrophic carbon is channelled into growth. Applying similar calculations and assumptions to assimilation of nitrogen suggests that particle feeding can account for 7 - 33% of the tissue growth, given an organic C:N ratio of 6.4 for coral animal tissue (Muller et al. 1994) and 10 for fine SPM (see Chapter 4).

Numerous studies have addressed the hypothesis that coral-algae associations may be nutrient limited and depend on an external supply of nutrients in either dissolved or particulate form (e.g. Falkowski et al. 1984, Spencer Davies 1984, Atkinson 1988, Hoegh-Guldberg & Smith 1989, Stambler et al. 1994). Based on a mass-balance estimate for *Acropora palmata*, Bythell (1988) suggested that 70% of the required nitrogen intake came from particulate feeding. Although zooplankton is an essential food source for corals (Sebens 1987, Sebens et al. 1996) that contains high contents of N and P (e.g. Corner & Davies 1971), the low abundance of zooplankton in reef waters (Johannes et al. 1970, Roman et al. 1990) is unlikely to meet all the nutrient demands of corals. In nearshore turbid regions, SPM is likely to occur in higher concentrations (dw/L) than both phyto- and zooplankton. Also, fine SPM provides a large surface area for colonisation by microorganisms and hence a coating with organic nutrients (Almeida & Alcantara 1992, Wotton 1994, Crump & Baross 1996, Crump et al. 1998). Further, concentrations of particulate relative to dissolved macronutrients (N and P) may be

highly elevated in coastal areas (e.g. Lebo 1991). In the Great Barrier Reef lagoon, N and P bound up with fine SPM are almost two orders of magnitude higher than concentrations of dissolved macronutrients (M. Dommisse, pers. com), rendering fine SPM a potentially important vehicle for nutrient delivery to corals, even at low rates of consumption.

The results of this study support previous suggestions that suspended particulate matter occurring over lagoonal or inshore reefs may be an important food source for corals (e.g. Goreau et al. 1971, Lewis 1977), even relative to other food sources. Daily intakes of SPM in this study are not significantly different from estimated feeding rates on zooplankton by scleractinian corals in situ. For example, Porter (1974) found that zooplankton feeding by *Montastrea cavernosa* could account for only between 0.2 and 11% of the coral's daily energy requirements. Furthermore, Johannes et al. (1970) estimated that the availability of zooplankton in coral-reef waters is sufficient to cover only 5.4% of the coral's dark respiration. Due to a high content of N and P in zooplankton (Corner & Davies 1971), however, this food source is likely to be more efficient than SPM in delivering nutrients to corals. Also, results of recent studies (e.g. Sebens et al. 1998) suggest that, under high zooplankton abundances and high flow speeds, zooplankton feeding may be an important source of energy. Nevertheless, contrary to nocturnal zooplanktivores, the polyps of species such as *P. damicornis*, *M. digitata*, *A. millepora* and *P. cylindrica* are also expanded during the day, and thus have the potential for sustaining their heterotrophy full time. Furthermore, concentrations of fine SPM on inshore reefs do not show the diel patterns characteristic of zooplankton (Porter 1974, Ohlhorst 1982) and may stay high for extended periods of time, maintained mostly by wind and swell (Larcombe et al. 1995). *P. damicornis*, *M. digitata* and *A. millepora*, which all ingest SPM as a linear function of concentration, may thus have higher daily heterotrophic intakes than nocturnal zooplanktivores in lagoonal, high-turbidity habitats.

Chapter 3

Cross-shelf comparison of particle-feeding capacities of corals

This chapter forms the basis for the publication:

- **Anthony, K.R.N.** 2000. Enhanced particle-feeding capacity in nearshore reef corals on the Great Barrier Reef, Australia. *Coral Reefs* **19** (in press).

3.1. SYNOPSIS

Reef corals occur across a wide range of habitats, from offshore clear waters to nearshore sediment-laden environments. This study tests the hypothesis that corals from turbid nearshore areas have greater capacity to utilise suspended sediment as a food source than conspecifics from less turbid inshore and midshelf areas. The hypothesis was tested on two common and widespread coral species on the Great Barrier Reef (*Pocillopora damicornis* and *Acropora millepora*).

The particle clearance rates of samples from more turbid reefs were 2-4-fold those of conspecifics from less turbid reefs. Rates of sediment ingestion were generally a linear function of sediment load indicating no significant saturation within the concentration range 1-30 mg dry weight/L. Estimated assimilation efficiency of particulate ^{14}C varied between 50% and 80%, and was maximised for midshelf *A. millepora* at the lowest sediment concentration, suggesting that heterotrophy is more efficient in oligotrophic habitats. Based on feeding-response curves, assimilation efficiencies, and published records of ambient particle concentrations, representatives of these species on turbid inshore reefs are 10-20 times more heterotrophic on suspended sediment than their conspecifics on less turbid midshelf reefs. These results agree with optimal foraging theory for filter feeders which predicts that a poor food source should be included in the diet when it becomes abundant as its rejection may be too costly .

3.2. INTRODUCTION

Tropical corals form reefs in a wide range of sediment regimes, from oceanic waters characterised by low particle concentrations to turbid nearshore waters along coastlines of major landmasses. The nearshore part of the Great Barrier Reef (GBR) lagoon receive a substantial input of terrigenous material (Mitchell & Furnas 1997), and frequent resuspension of sediment deposits result in elevated concentrations of suspended sediment (e.g. Larcombe et al. 1995), thereby reducing light availability for photosynthesising organisms (Kirk 1994). Despite high turbidity levels and sedimentation rates, which often exceed those described as lethal for corals on Caribbean reefs (reviewed by Pastorok & Bilyard 1985), inshore reefs in the GBR lagoon generally sustain high coral cover and diversity (e.g. Ayling & Ayling 1991) suggesting that local adaptation to intense sediment regimes has occured. Numerous studies have focussed on the adverse effects of sedimentation and turbidity on survival and performance of reef corals (reviewed by Rogers 1990). Only a few studies, however, have addressed the hypothesis that variable sediment regimes also represent variation in heterotrophic resources (Mills & Sebens 1997), see also Chapters 2). To date, no studies have examined whether corals can optimise their use of suspended sediment as a source of food in different environments.

Although phototrophy by reef corals may be impaired by shading associated with elevated particle concentrations (Dallmeyer et al. 1982, Te 1997) and respiration tends to increase with turbidity (Telesnicki & Goldberg 1995), heterotrophy may be enhanced by increased availability of particulate food. In Chapter 2 (see also Anthony 1999a) I showed that corals may achieve up to 50 % of their predicted carbon growth by feeding on fine suspended sediment at high concentrations (30 mg dry weight [dw]/L). Particle concentrations may reach 40 mg dw/L for extended periods of time on inshore reefs in the central GBR, (Larcombe et al. 1995, Woolfe & Larcombe 1998) whereas offshore locations rarely experience concentrations higher than 0.5 mg dw/L (Devlin et al. 1997). Coral communities inshore are therefore often exposed to particle concentrations about two orders of magnitude higher than offshore communities, conditions which also represent a shift from high to low light availability. Optimal foraging theory for filter feeders (reviewed by Hughes 1980) predicts that corals in highly turbid conditions should

make optimal use of the high particle availability despite its relatively low food value. The basis for this prediction is that the rejection of an abundant, albeit low quality, food source is costly (see also Lehman 1976). Under extremely turbid conditions, enhanced particle feeding may be necessary to counteract reduction in phototrophy and to maintain a positive energy budget. The expected responses for corals from turbid reefs is therefore a steep near-linear function over a broad range of particle loads, which eventually saturates at extremely high loads (Fig. 3.1). In contrast, corals in offshore oligotrophic conditions can be expected to be poor at handling high particle concentrations given their environmental history, and are likely to saturate at lower concentrations than inshore corals (Fig. 3.1). However, offshore corals should make more efficient use of the low particle (food) availability to supplement their phototrophic carbon fixation with a maximum supply of nutrients to enable tissue synthesis (see also Bythell 1988, Dubinsky & Jokiel 1994).

The purpose of this study was to provide a test of the hypothesis that corals from turbid inshore reefs in the GBR lagoon have developed a greater capacity to feed on suspended sediment than conspecifics from less turbid nearshore areas and offshore (midshelf) reefs. Also, I address the hypothesis that inshore corals are more efficient at utilising SPM as a food source at low concentrations. These hypothesised differences in feeding responses curves between corals from contrasting habitats are in accordance with the adaptive variation in consumer's functional responses predicted by Abrams (1990). To provide a general example, I selected two common species of scleractinian coral that occur in a wide range of habitats across the Indo-Pacific. *Acropora millepora* occurs commonly on inshore fringing reefs as well as at offshore locations, predominantly from 1-8 m below datum. *Pocillopora damicornis* is a habitat-generalist on the GBR (Done 1982) and may be found in all habitats where hard substratum allows colonisation (Veron & Pichon 1976). Both species have their polyps extended both day and night, a behaviour that enables extrapolation of sediment-feeding rates to 24-h estimates.

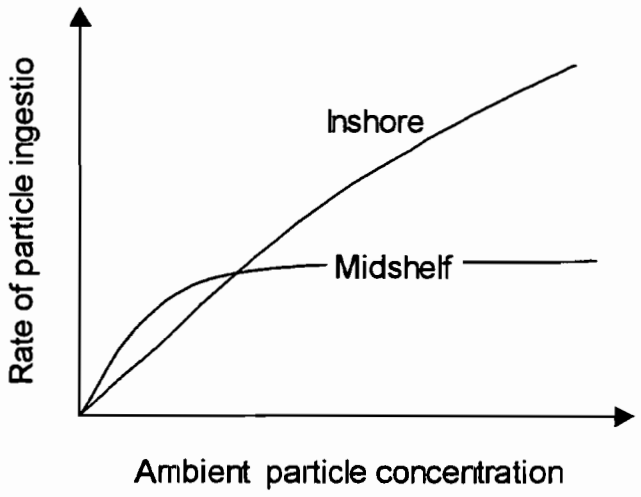

Fig. 3.1. Predictive model of particle feeding as a function of ambient particle regime for corals from turbid inshore and less turbid midshelf locations in the GBR lagoon.

3.3. MATERIALS AND METHODS

3.3.1. Study sites

To address the hypothesis that inshore corals have higher particle-feeding capacity than their offshore conspecifics, five reef sites were selected along an inshore-offshore transect in the central section of the Great Barrier Reef lagoon (Fig. 3.2). Two sites constitute true inshore reefs (Nelly Bay and Pandora Reef) as they are located within the boundary of the terrigenous sediment wedge (Woolfe & Larcombe 1998, Fig. 3.2), two sites are located midshelf (Britomart Reef and Kelso Reef), and one site is located nearshore, but outside of the terrigenous sediment wedge (Pioneer Bay, Orpheus Island).

Because concentrations of suspended solids show notoriously high temporal variation, water samples were not taken in conjunction with coral collecting. Instead, data on suspended particle concentrations were compiled from several water-quality studies undertaken both previously and concurrently in the region (Table 3.1). While no data on suspended solids were available for Kelso Reef and Britomart Reef, long-term datasets for nearby mid-shelf reefs (Rib Reef and John Brewer Reef (Fig. 3.2) were used to describe the inshore-midshelf turbidity profile.

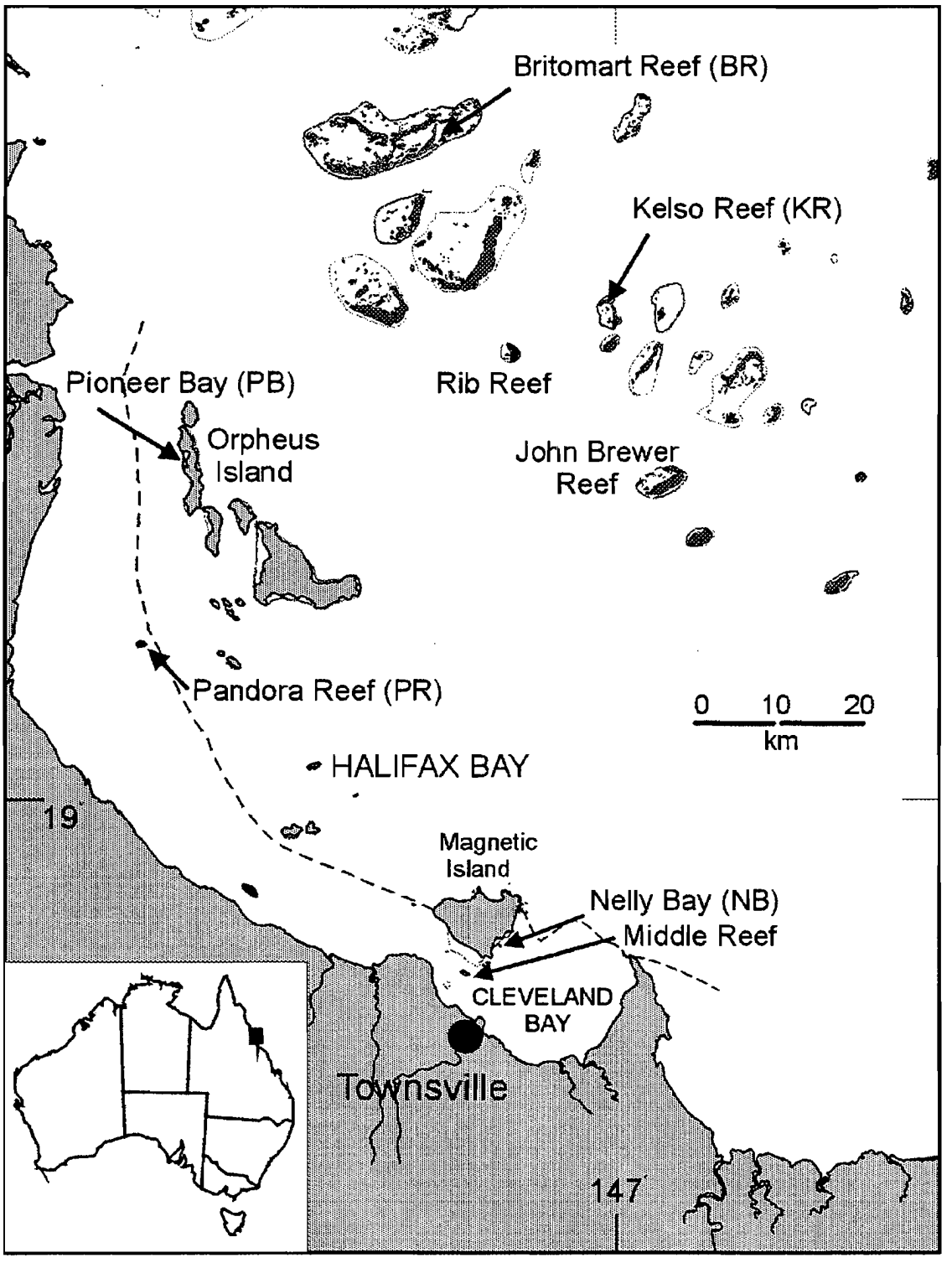

Fig. 3.2. Map of central area of the Great Barrier Reef showing the five reef sites **(bold)** from which corals were collected. Nelly Bay (Magnetic Island) and Pandora Reef are true inshore sites as they are located within the terrigenous sediment wedge (dashed line), Pioneer Bay (Orpheus Island) is located inshore but outside the sediment wedge, whereas Kelso and Britomart Reef are located on the mid-shelf. See Table 3.1 for data on ambient concentrations of suspended solids at the different locations. Graphics courtesy of AIMS.

Table 3.1. Concentrations of suspended particles in the Townsville section of the Great Barrier Reef. Data were bsed on water sampling and filtration in all studies except Larcombe et al. (1995) which used backscatter nephelometers. Sampling locations are depicted in Fig. 3.2. N = number of samples, na: not available.

	Particle concentration (mg DW l^{-1})						
Reef (location)	Median	Min	Max	N	Time frame	Weather conditions	Source
High-turbidity sites							
Magnetic Island (Cleveland Bay)							
Nelly Bay	3.3	0.4	12.9	30	13 Dec 88 - 16 Feb 89	Variable	Brodie et al. (1992)
-	9.3	9.0	9.4	4	23 Jan 98	Following flood event	Devlin et al. (in press)
Middle Reef	3.0	1.2	4.7	32	10 Aug 92 - 17 Apr 96	Generally calm	Devlin et al. (1997)
-	na	<5	>40	>1000	Jan 93 - Apr 93	Variable	Larcombe et al. (1995)
Pandora Reef (Halifax Bay)	1.7	0.5	8.7	39	11 Aug 92 - 8 Apr 96	Generally calm	Devlin et al. (1997)
-	4.2	3.3	5.8	12	15 - 22 Jan 98	Following flood event	Devlin et al. (in press)
Moderate-turbidity site							
Pioneer Bay (Orpheus Island)	1.3	0.6	2.4	23	2 May 97 - 27 Jun 97	Variable	Anthony (1999a)
Low-turbidity sites							
Midshelf GBR (Townsville section)							
Rib Reef	0.5	0.2	3.0	32	13 Dec 93 - 21 Apr 96	Variable	Devlin et al. (1997)
John Brewer Reef	0.4	0.1	1.6	55	12 Aug 92 - 22 Apr 96	Variable	Devlin et al. (1997)

3.3.2. Coral collecting and maintenance

Samples of *Pocillopora damicornis* and *Acropora millepora* were collected from a narrow subtidal depth range (3-5 m below datum). Due to the greater light extinction in turbid water, light availability is likely to be lower inshore than offshore, resulting in potential differences in photo-physiology of corals between sites. However, depth of collection was fixed so that comparisons could be made between conspecifics experiencing different light environments caused by the local sediment regimes. Also, to reduce the likelihood of sampling corals that are adapted to different flow regimes, midshelf corals were collected from sheltered back-reef margins only.

Coral samples consisted of 5-7 cm long terminal branches, cut from the branching colonies with bone cutters. A total of 50-60 branches were sampled at each site with a maximum of three branches originating from a single colony. Only widely separated (> 10 m) colonies were sampled to maximise the number of clones in the analysis. To

minimise potentially confounding effects of polymorphism on feeding capacities, corals with intermediate branch thickness of corresponding to one of the reproductively isolated morphs of *A. millepora* (Willis et al. 1997) were used. Also, both the brown and pink morphs of *P. damicornis* were sampled since these have previously been shown to differ physiologically and ecologically (Takabayashi & Hoegh-Guldberg 1995).

Individual branches were mounted on stands for ease of attachment to racks in holding tanks and to the bottom of flow chambers (see Chapter 2). Corals were held in tanks for a maximum of 5 days prior to experimentation and were not fed during the maintenance period. Since water temperature potentially affects anthozoan metabolism and activity (e.g. Shick 1991), temperatures in the holding tank and incubation chambers were recorded regularly. Also, sea temperatures at the sites and times of collection were obtained from the Sea Temperature Monitoring Program of the Great Barrier Reef Marine Park Authority (GBRMPA 1999, Table 3.2).

To reduce the risk of differential experimental conditions (e.g. temperature) confounding the effects of location on feeding responses, corals from one inshore and one midshelf reef were sampled and assayed within a one-week window (Table 3.2). Corals from Pandora Reef, however, could not be sampled until June 1998, and were assayed together with corals from Pioneer Bay. The sampling of both species from Pioneer Bay during different times of year enabled testing for effects of season on feeding responses.

Table 3.2. Time table for coral collection from the different reefs and subsequent feeding trials at Orpheus Island. Also shown are the sea temperatures at each site (~3-5 m below datum) during one week prior to collection (source: GBRMPA 1999), and the temperatures in the feeding chambers during acclimation and incubation. Temperatures for Britomart Reef (†) were represented by data from Kelso Reef, and temperatures for Pandora Reef (*) were estimated by interpolation between concurrent measurements in Nelly Bay and Pioneer Bay (see Fig. 1 for details of site location). Relative turbidity categories: H = high; M = moderate; L= low based on Table 3.1.

Location	Relative turbidity	Time window of collection and incubation	Temperature (°C) on reef		Temperature (°C) in chambers / tanks	
			min	max	min	max
Pioneer Bay	M	11-14 Nov 96	25.7	27.3	26.5	27.5
Kelso Reef	L	13-15 Nov 96	25.8	27.2	27.0	28.0
Pioneer Bay	M	15-16 Dec 96	27.3	29.0	27.0	27.5
Britomart Reef †	L	10-15 Jan 97	28.0	28.8	28.5	29.0
Nelly Bay Reef	H	14-17 Jan 97	28.4	30.1	28.0	28.5
Pioneer Bay	M	20-22 May 97	24.1	24.7	24.0	25.5
Pioneer Bay	M	17-20 Jun 98	24.4	24.9	24.0	25.0
Pandora Reef *	H	23-24 Jun 98	23.5	24.7	24.5	25.0

3.3.3. Feeding experiments

To determine rates of particle ingestion as well as to provide estimates of carbon assimilation, corals were fed suspensions of natural particles labelled with ^{14}C according to the protocol described in Chapter 2. Feeding experiments were conducted on seawater tables using the four 2-litre recirculating flow chambers described in Chapter 2. To determine feeding response as a function of particle concentration, groups of corals from each species and each site were fed five different particle concentrations: 1, 4, 8, 16, and 30 mg dw/L. This encompassed the broad range of concentrations encountered along offshore-inshore transects in the GBR lagoon (e.g. Brodie et al. 1989, Brady et al. 1991, Larcombe et al. 1995, Devlin et al. 1997). The ^{14}C-labelled sediment used in these experiments was from the same frozen stock as that used in Chapter 2, which had a weight-specific radioactivity of 750 dpm/μg dw particles. This standardisation of food

substrate improved the ability to reproduce particle concentrations and specific radioactivity of incubations in this study, as well as enabled comparison with experiments in Chapter 2.

Analogous to procedures used in Chapter 2, experiments were run at night and in darkness to minimise photosynthetic uptake of $^{14}CO_2$ produced during incubations. When all corals had their polyps fully extended, the seawater supply was disconnected and a suspension of ^{14}C-labelled particles was added. Particle concentrations were assigned randomly to the chambers to control for potential effects of chamber heterogeneity, and 2-3 incubations were run per night. A total of 3-4 chambers (6-8 corals) were run per concentration per species. Since each pair of coral branches were aligned perpendicular to the flow, and the branches were well separated in the relatively large chambers (> 4 cm apart), coral samples were considered to be independent.

After one hour of feeding, the corals were removed from the chambers, briefly rinsed in seawater to remove uningested adhering label, and transferred to a 50-ml vial together with 30 ml KOH (1 M) to solubilise coral tissues. KOH was used as an alternative to Soluene 350 (Chapter 2), since the inexpensive KOH proved to be an equally efficient digesting agent, and showed equally low quenching. Analogous to the procedures in Chapter 2, external standard ratios were constructed for KOH/coral-tissue solutions at concentrations corresponding to those of experimental samples. Experiments in Chapter 2 indicated that 25 ± 4% of the ^{14}C taken up by these two coral species during 1-h incubations is from uptake of dissolved label leaking from the suspended particles. A correction factor of 0.75 was therefore used with raw ingestion rates in this study to account for the uptake of dissolved label.

3.3.4. Estimates of assimilation

To test whether inshore and offshore corals utilise (assimilate) ingested particles with different efficiencies over the range of particle concentrations offered, half the corals from one series of feeding experiments (one branch of each pair in each feeding chamber) were allowed to digest and assimilate the ingested material, and to egest unincorporated matter prior to sampling. For the purpose of this comparison, assimilation was estimated as the amount of radioactivity in coral tissues after complete egestion, relative to that ingested by the other branch in the pair (both normalised to cm^2

surface area). This analysis was limited to a comparison between corals at two extremes of turbidity (Nelly Bay and Britomart Reef). To avoid effects of differential morphometrics and fragment size on ingestion and assimilation, pairs were selected to be as similar as possible, and the branch sampled for ingestion from each pair was selected at random. Since part of the assimilated label is respired before egestion is complete (e.g. Sorokin 1973, Crosby et al. 1989, Gremare et al. 1989, Gremare et al. 1991), tissue radioactivity provides an underestimate of true assimilation. However, assuming that effects of meal size on respiratory loss of label does not vary between conspecifics from different locations, tissue label after egestion is a valid approach for measuring assimilation rates. To allow complete egestion of any unincorporated material, corals to be assayed for ^{14}C assimilation were kept in running, unlabelled seawater for 24 hours before sampling. Based on previous trials (Chapter 2), > 95% of any unassimilable material is egested within this time frame.

3.3.5. Data analyses

To test the hypothesis that feeding rates of midshelf corals become saturated at lower concentrations than inshore conspecifics, the Michaelis-Menten saturation model was fitted to the feeding rates vs particle concentrations for each group. Corals from midshelf reefs were thus expected to have lower K values than offshore corals. The model was fitted using non-linear least-squares regression (Quasi-Newton and Simplex iterative methods, STATISTICA 1997). Initial analyses using this model, however, showed that ingestion curves did not saturate within the range of particle concentrations used for any of the groups (indicated by the half-saturation constant, $K > 30$). Therefore, particle ingestion rates were instead modelled as linear functions of particle concentrations for all location- and species-specific datasets. The linearity of feeding-response curves enabled calculation of particle clearance rates as the slope of the response curves (regression coefficients, ml/cm²/h). To test the hypothesis that corals from inshore turbid reefs have higher sediment clearance rates than conspecifics from more oligotrophic habitats, slopes of feeding- response curves were compared among locations using one-way ANOVAs (Model 1), followed by Tukey's unplanned comparison (HSD test, Sokal & Rohlf 1995) to identify significant differences among clearance rates at individual locations.

Two analyses were conducted to explore effects of location and particle concentration on estimated assimilation. Firstly, effects of reef of collection and experimental particle concentration on assimilation efficiency (determined for pairs of branches from the same feeding chamber) were tested for each species separately using two-way ANOVAs (Model 1), followed by Tukey's HSD test. Secondly, the relationship between estimates of assimilation and rate of ingestion was explored using linear regression on log-log transformed data, the latter being necessary to produce linearity and normality. To test whether in- and offshore corals utilise the ingested particles with different efficiency, regression slopes were compared among locations (Nelly Bay vs Britomart Reef) for each species using one-way ANOVAs for slope equality (Sokal & Rohlf 1995). The first analysis enables comparison of assimilation efficiencies among habitats (particle concentrations), whereas the second analysis compares the efficiency by which corals from different habitats utilise the ingested ration independent of the experimental particle concentrations.

3.4. RESULTS

3.4.1. General observations on polyp behaviour

Overall, there were no apparent differences in feeding or expansion-contraction behaviour of corals from different locations at most particle concentrations, as all corals remained expanded throughout the day (and night) and during the course of the feeding experiments. Corals from midshelf locations, however, showed a tendency to contract their polyps when exposed to maximum particle concentrations (30 mg dw/L) which undoubtedly contributed to their reduced feeding rate at high particle concentrations.

3.4.2. Feeding responses and particle clearance rates

Linear feeding-response curves (Fig. 3.3) indicated that corals from the more turbid inshore reefs (Nelly Bay and Pandora Reef) had a much higher sediment-feeding capacity than corals from Pioneer Bay and the midshelf reefs (Kelso Reef and Britomart Reef, Fig. 2). Feeding rates at maximum particle concentration were double for *Pocillopora damicornis* from turbid reefs compared to less turbid reefs, and more than 3

times greater for *Acropora millepora*. All regressions were highly significant, with 70% - 96 % of the variation in ingestion rates explained by the variation in particle concentrations (Table 3.3A). Due to this linearity of feeding responses for groups from all sites, clearance rates (calculated from the slopes of the feeding-response curves) could be compared among and within inshore/midshelf locations. Also, the ANOVA for effects of season (November/December and May/June) on clearance rate of corals from Pioneer Bay (Fig. 3.4) was not significant in either species (Table 3.4), despite 4-5°C differences in temperature (Table 3.2), suggesting a minimal variation in feeding-response curves (and clearance rates) over the year.

Particle clearance rates were significantly greater on inshore turbid reefs compared to less turbid reefs in both species (Table 3.3AB, Fig. 3.5). The cross-shelf difference in clearance rates was most pronounced for *A. millepora*: the clearance rates of corals from Nelly Bay and Pandora Reef were both significantly different from conspecifics from Kelso Reef, Britomart Reef and Pioneer Bay (see Table 3.3B). Clearance rates of conspecifics from the three latter reefs did not differ significantly. This pattern was generally repeated in *P. damicornis*. The higher clearance rates of *A. millepora* at turbid and less turbid reefs reefs suggested some correlation between clearance rate and median particle concentrations recorded at the sites of collection (Spearman R = 0.70, Fig. 3.5).

Particle concentrations recorded by different sampling programs vary markedly along the inshore-offshore transect, and median particle concentrations at the most inshore reefs (e.g. Nelly Bay) are almost one order of magnitude higher than at the midshelf reefs (exemplified by John Brewer Reef and Rib Reef, Table 3.1, Fig. 3.2). Multiplying the median recorded sediment concentrations in Nelly Bay (~ 3.3 mg dw /L, excluding periods of flood plumes) and at the outer midshelf reefs (~ 0.5 mg dw /L, Table 3.1) by the clearance rates of resident corals (Table 3.3), predicts that *P. damicornis* and *A. millepora* in Nelly Bay are 11- and 21-fold (respectively) more heterotrophic than their conspecifics at Britomart Reef.

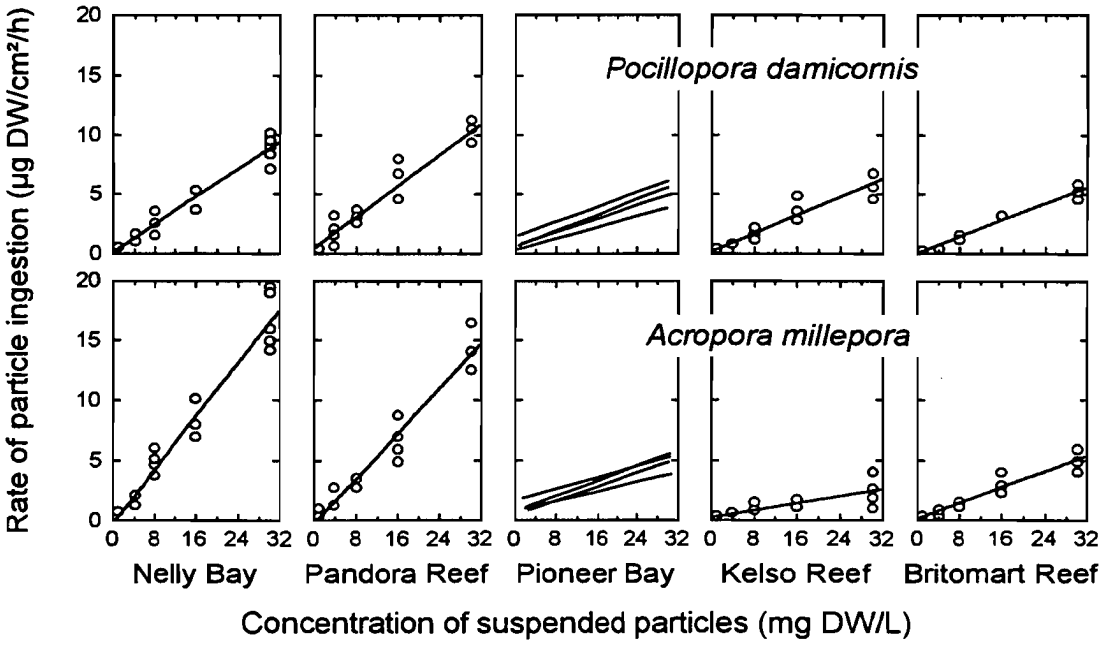

Fig. 3.3. Ingestion rates as a function of concentration of suspended particles. Sites are arranged according to increasing distance from shore (left to right). Regression lines only are shown for four feeding trials at Pioneer Bay in different seasons, see Fig. 3.4 for datapoints.

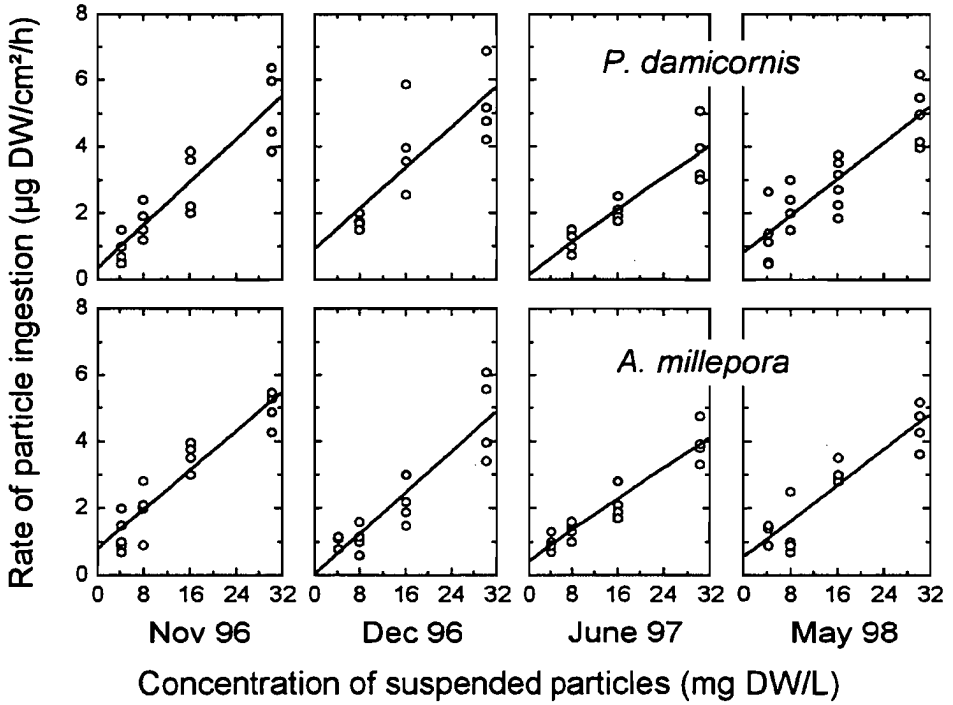

Fig. 3.4. Feeding responses for the two coral species collected from Pioneer Bay (and subsequently assayed at Orpheus Island Research Station) at different times over the year. See Table 3.2 for experimental time table and water temperatures, and Table 3.3 for regression results.

Table 3.3. **A.** Linear regression analyses of feeding-response curves for two coral species from five reef sites. CR is the clearance rate (ml/cm²/h) calculated as the slope of the linear regression. See Fig. 3.2 for details on reef location, Fig. 3.3 and Fig. 3.4 for regressions, and Table 3.2 for dates of incubation and water temperatures. **B.** Results of the ANOVA for homogeneity of slopes (CRs) among sites. To render the analyses conservative with respect to the comparison between corals from turbid inshore reef sites and the less turbid Pioneer Bay (inner midshelf), only the December 1996 dataset was used for Pioneer Bay. Horizontal bars underline means that are not significantly different by the Tukey's (HSD) test. **C.** Results of the ANOVA for homogeneity of CRs among seasons in Pioneer Bay. N is number of samples, df is degrees of freedom, and *** denotes significance at P = 0.001.

A.

Reef (location)	*Pocillopora damicomis* CR (ml cm^{-2} h^{-1})	SE	R^2	N	*Acropora millepora* CR (ml cm^{-2} h^{-1})	SE	R^2	N
Nelly Bay Reef (NB)	0.29	0.02	0.94	27	0.56	0.03	0.95	24
Pandora Reef (PR)	0.32	0.02	0.92	19	0.43	0.04	0.88	19
Pioneer Bay (PB)								
11-14 Nov 96	0.16	0.02	0.83	16	0.15	0.01	0.87	17
15-16 Dec 96	0.15	0.04	0.65	12	0.14	0.02	0.82	16
20-22 May 97	0.12	0.02	0.80	12	0.12	0.01	0.90	16
17-20 Jun 98	0.14	0.02	0.76	20	0.13	0.02	0.84	14
Kelso Reef (KR)	0.19	0.02	0.92	29	0.07	0.01	0.70	32
Britomart Reef (BR)	0.17	0.01	0.96	20	0.16	0.02	0.90	19

B. Test of slope (CR) equality among sites

Source of variation	*Pocillopora damicomis* df	MS	F	P	*Acropora millepora* df	MS	F	P
Among slopes	4	16.50	32.60	<0.001 ***	4	128.62	147.00	<0.001 ***
Error	112	0.51			114	0.88		
Tukey's test	PR	NB	KR	BR PB	NB	PR	BR	PB KR

C. Test of slope (CR) equality for measurement series at Pioneer Bay

Source of variation	df	MS	F	P	df	MS	F	P
Among slopes	3	0.39	0.59	0.626 ns	3	0.43	1.16	0.334 ns
Error	52	0.67			55	0.37		

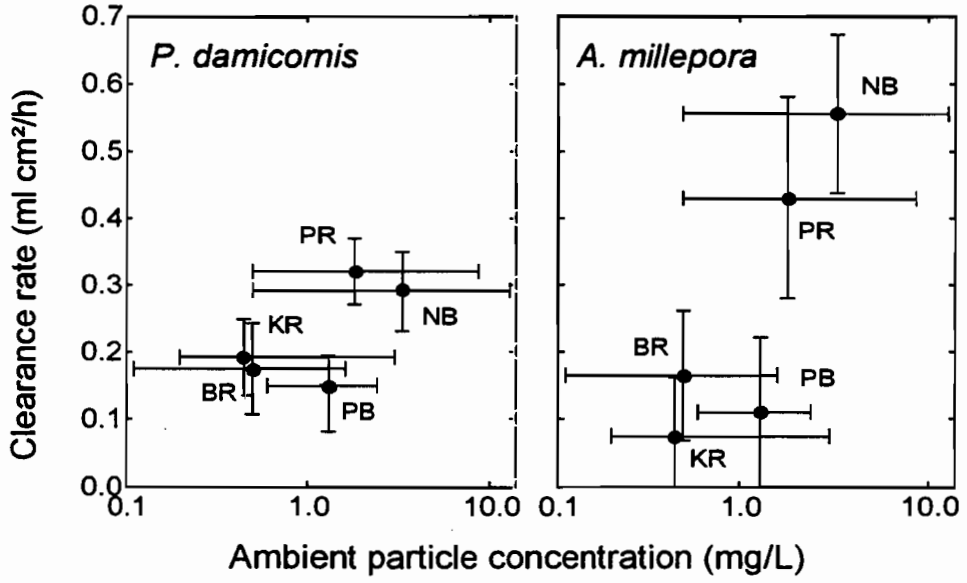

Fig. 3.5. Clearance rate as a function of ambient (published) particle concentrations recorded at the sites of collection. Labels are the initials of each site of collection as given in Fig. 3.2. The mean clearance rate of each experimental group is determined by the slope of the linear regression (feeding response, see also Table 3.3). Vertical error bars are 95 % comparison limits as determined by the Tukey's unplanned comparison, ie. groups with overlapping bars are not significantly different. Median ambient particle concentrations are from the AIMS long-term monitoring program (Devlin et al. 1997), except for Orpheus Island (Chapter 4, Anthony 1999b). Horizontal error bars describe the ranges of particle concentrations recorded at each location.

3.4.3. Estimates of assimilation

The estimated rates of assimilation did not differ significantly between turbid inshore and less turbid midshelf corals in *Pocillopora damicornis* (ANOVA, Fig. 3.6, Table 3.4). However, for *Acropora millepora* there was a significant interaction between location and experimental particle concentration, attributable to the higher assimilation efficiencies by midshelf conspecifics at the low particle concentrations (1 and 4 mg dw/L, Fig. 3.6). Assimilation efficiencies of *P. damicornis* showed a somewhat similar pattern, but the interaction between location and particle concentration was not significant, mainly due to the greater within-concentration variability of assimilation efficiencies in this species. Including estimated assimilation efficiencies in the above comparison of heterotrophy across the shelf (using clearance rates and data on particle concentrations in Table 3.1) still render inshore *A. millepora* ~17 times more heterotrophic than midshelf conspecifics, despite higher assimilation efficiencies on the midshelf.

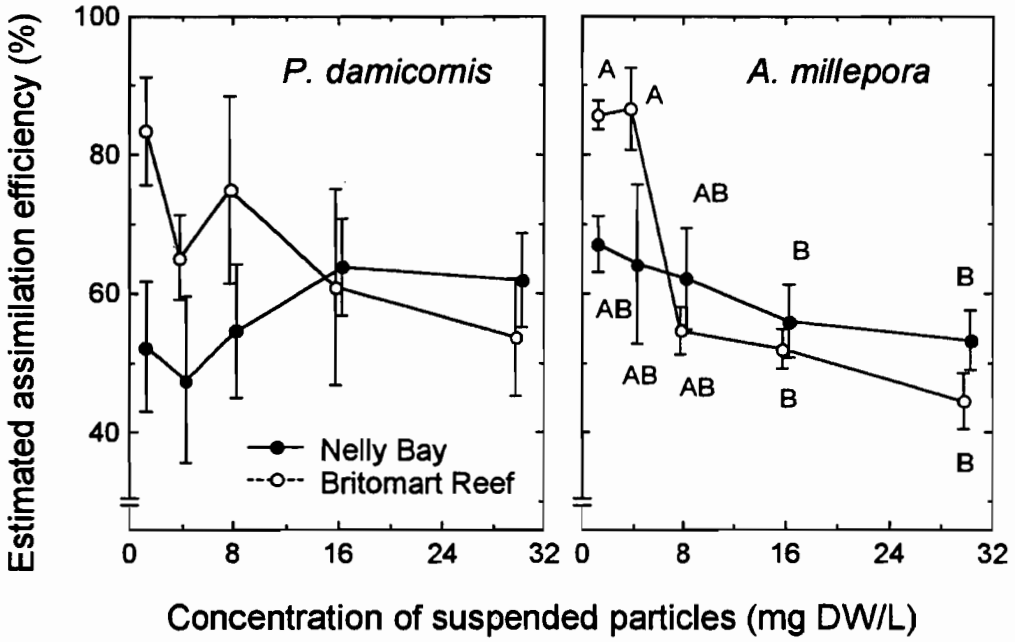

Fig. 3.6. Estimates of assimilation efficiency (ratio of assimilation to ingestion) as a function of location and particle concentration for the two coral species. Mean assimilation efficiencies of *Acropora millepora* that are significantly different by Tukey's (HSD) test have different labels (A or B).

Table 3.4. Summary results of two-way ANOVA for effects of reef of origin (location) and experimental concentration of suspended particles (CSP) on estimates of assimilation efficiency. Data were analysed untransformed. ** denotes significance at P = 0.01, other symbols as in Table 3.3. See Fig. 3.6 for means and standard errors.

	Pocillopora damicornis				*Acropora millepora*			
Source of variation	df	MS	F	P	df	MS	F	P
Location	1	1444.1	3.57	0.067 ns	1	349.3	2.88	0.098 ns
Particle concentration (CSP)	4	180.7	0.45	0.774 ns	4	1300.5	10.72	<0.001 ***
Location X CSP	4	591.2	1.46	0.234 ns	4	605.8	4.99	0.002 **
Error	35	404.0			38	121.3		

The slope of the assimilation rate vs ingestion rate function for inshore *Pocillopora damicornis* from Nelly Bay was marginally greater (P = 0.050, Table 3.5) (Fig. 3.7) than that of conspecifics from Britomart Reef, suggesting that inshore and midshelf corals are marginally better at utilising large and small ingested rations, respectively. The same

comparison for *Acropora millepora* produced a non-significant result (P = 0.116). Since only ingestion data within the range common for both inshore and midshelf corals (Fig. 3.7) were included in this analysis to avoid extrapolation, however, cross-shelf comparisons were likely to be conservative for both species.

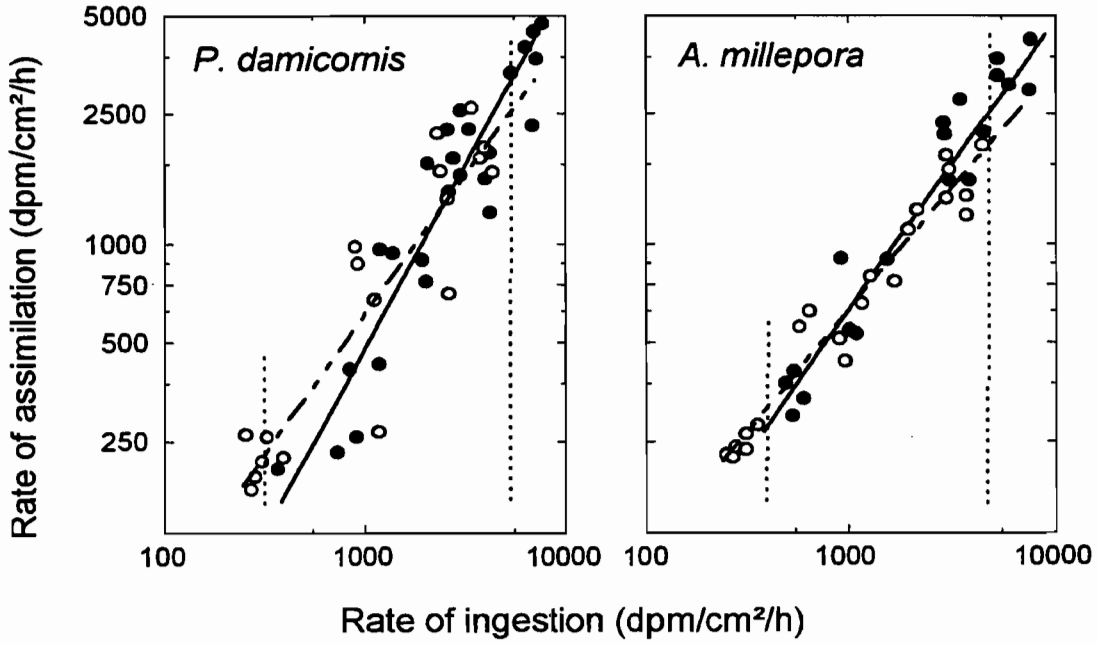

Fig. 3.7. Log-log plots of estimates of assimilation rate vs particle ingestion rate in corals from a turbid inshore (Nelly Bay) and a less turbid midshelf (Britomart) reef. Assimilation is estimated from the amount of ^{14}C in coral tissues after complete egestion of unincorporated material (~24-h, see Chapter 2). See Table 3.5 for tests of slope equality. Dashed vertical lines mark data interval used in the analyses.

Table 3.5. Summary results of tests for slope equality of regressions of log assimilation rate on log ingestion rate for corals from Nelly Bay (NB, inshore) and Britomart Reef (BR, midshelf), see also Fig. 3.7

	Pocillopora damicornis				*Acropora millepora*			
Source of variation	df	MS	F	P	df	MS	F	P
Location (among slopes)	1	0.111	4.11	0.050	1	0.021	2.61	0.116
Error	36	0.027			31	0.008		

3.5. DISCUSSION

3.5.1. Functional responses in particle use

This study demonstrates that representatives of *Pocillopora damicornis* and especially *Acropora millepora* from inshore turbid environments have a greater capacity to feed on suspended sediment than conspecifics from midshelf oligotrophic environments. Particle ingestion did not saturate over the broad range of particle concentrations used in this study, even though corals from midshelf locations most likely seldom experience concentrations above 10 mg dw/L. Any curvature of the feeding response of offshore representatives of *Acropora millepora* may have been due to the partial polyp contraction observed at maximum particle concentrations. The general lack of saturation corroborates the findings of Clayton & Lasker (1982) for feeding by *P. damicornis* on *Artemia* nauplii and the results of Ferrier-Pages et al. (1998) for microzooplankton feeding by *Stylophora pistillata*. According to Lehman (1976), partial filling of the gut is an important determinant of maximum ingestion rate. For example, the highest observed ingestion rate for *A. millepora* in Nelly Bay was of the order 0.5 µg polyp/h (assuming ~ 30 polyps per cm^2 surface area, Chapter 2). Disregarding effects of hydration on particle volume and assuming neutral buoyancy, such a feeding rate would equate to an hourly intake of a 1-mm diameter spherical particle. Given that the average polyp diameter of *A. millepora* is not significantly greater than 1 mm (Chapter 2, Anthony 1999a), gut saturation is indeed possible at high feeding rates, and might have been observed if longer feeding periods were used.

The high sustained ^{14}C assimilation efficiencies (> 50%) across all particle concentrations, despite 10-fold differences in ingestion rates, suggests that the utilisation of heterotrophic carbon is maximised across a broad range of turbidity regimes. Although the ingested label represents only a small fraction of the total ingested material (because most of the label was in the live organic coating), assimilation efficiencies reported here are high and comparable to maximum efficiencies reported for other suspension feeders (e.g. Szmant-Froelich & Pilson 1984, Zamer 1986, for review see Wotton 1994).

The 2-3 times higher particle clearance rates by representatives of *A. millepora* from turbid inshore reefs found in this study despite the relatively low organic carbon

content of suspended sediment (e.g. 3-5%, see Chapter 4, 5, and Anthony 1999b, Anthony & Fabricius in review) support predictions of optimal diet theory for filter feeders (Lehman 1976, reviewed by Hughes 1980). Briefly, when a low-quality food source becomes abundant, it may be energetically favourable to include it in the diet because its rejection would become too costly. Also, the tendency for midshelf corals to have higher assimilation efficiencies suggests optimal foraging offshore given the potential for nutrient limited growth. Functional response curves of both ingestion rate and assimilation efficiency may thus change adaptively to maximise the trophic potential of the habitat (see also Abrams 1990).

Importantly, since inshore and midshelf conspecifics were incubated under similar experimental conditions, enhanced feeding rates by inshore corals are attributable to their different environmental histories, suggesting a heterotrophic preadaptation (or plasticity) to turbid conditions. This study is the first to demonstrate such heterotrophic plasticity in symbiotic cnidarians, a finding that is likely to have major implications for the energy balance of corals on inshore reefs where high turbididity may impair photosynthesis periodically. Previous studies have shown differences in feeding rates in response to experimental conditions, but mainly as a behavioural reduction in feeding activity in direct response to increasing light levels (Ferrier-Pages et al. 1998), or reduced feeding capacity as a stress response to prolonged darkness (Clayton & Lasker 1982).

The comparisons of heterotrophy across habitats assumes that particle quality is constant, an assumption that is unlikely to be true. Factors such as input of terrestrial organic matter may increase the nutritional value of inshore particles. Also, concentrations of phytoplankton are generally higher inshore in the GBR lagoon (Brodie et al. 1997), and the consequent production of detrital flocs (e.g. Jackson 1990) may increase effective particle size and thereby the probability of capture by suspension feeders (Shimeta & Koehl 1997). Upwelling of nutrients at the shelfbreak (Furnas & Mitchell 1996), however, may elevate primary production offshore and, in turn, enhance the availability and food quality of the suspended particulate matter.

The above discussion assumes that particle availability is strictly a function of concentration and disregards effects of flow regimes on particle delivery. Although midshelf corals were sampled from sheltered backreef margins to reduce effects of preadaptations to different flow regimes, mishelf reefs in the GBR lagoon are generally

more wave and flow exposed than inshore reefs (Done 1982, Veron 1986b, Sebens & Done 1992, Wolanski 1994). The potential flux of particles past coral tentacles is therefore also higher on midshelf reefs, which may to some extent reduce the difference in particle availability for suspension feeders across the shelf.

3.5.2. Implication of clearance rates for particle depletion

One obvious question arising as a result of the relatively high clearance rates of inshore corals is their implications for particle depletion. Tentatively, using clearance rates of 0.3 and 0.5 ml per cm^2 of colony surface area per hour for inshore *P. damicornis* and *A. millepora*, and assuming that the colony surface area is 5 times the area of substrate that it covers (Vytopil 1997), a 1-m^2 patch of reef may potentially deplete a 0.4-0.6-m tall water column daily. At peak turbidity levels of 30 mg dw/L, such depletion rates would correspond to an import of 11-18 g dw sediment/m^2/d, which in the case of 5 % organic carbon content (Chapter 4 & 5) would translate to 0.6 – 0.9 gC/m^2/d. Compared to estimates of gross community production rates of 3 gC/m^2/d for lagoonal reefs (Crossland et al. 1991), the heterotrophy on suspended sediment by the two study species inshore is small but significant. In offshore conditions, the depletion rates by *A. millepora* and *P. damicornis* lead to predicted retention rates of about 0.1 gC m^2/d, a rate similar to that found by (Ayukai 1995) for depletion of phytoplankton and planktonic microbes by coral assemblages on another GBR midshelf reef (Davies Reef, 0.1 gC/m^2/d). Interestingly, this value corresponds closely to estimates of net community production (Crossland et al. 1991). It is important to note, however, that whole-colony depletion rates may be lower than those estimated here, due to reduced particle fluxes between branches in colony centres (Sebens et al. 1997) and downstream depletion (Anthony 1997, Fabricius et al. 1998).

3.5.3. Energetic significance of enhanced sediment feeding inshore

Reductions in light, for example caused by increases in particle concentration, may have adverse effects on a coral's carbon balance (e.g. Te 1997) unless prevented by shade-adaptation or by enhanced feeding. Based on the light-extinction data of Te (1997) for mixed carbonate silt and terrigenous sediment, an increase in particle concentration

from 2 to 10 mg dw/L at 4-m water depth would cause a 75% decline in light availability. For perspective, the light level at 4 m depth in this turbidity regime (10 mg dw/L) corresponds to the light availability at 60 m depth in particle concentrations typical of offshore locations (0.5 mg dw/L). According to Larcombe et al. (1995), concentrations of suspended solids on reefs around Magnetic Island may exceed 20 mg dw/L for 3-9% of the time and 10 mg dw/L for 15-24% of the time. Since elevated turbidity levels mostly occur as periodic events among longer periods of low turbidity (Larcombe et al. 1995), it is unlikely that inshore shallow-water corals are sufficiently shade-adapted to maintain an autotrophic carbon balance at high turbidity. With photosynthesis potentially reduced for days, the up to 3 fold higher particle clearance rates of corals from Nelly Bay (*A. millepora*) may be necessary to ensure a positive energy balance in periodically turbid and shaded environments.

My results suggest that particle feeding in turbid and dark habitats could counteract a significant part of the carbon deficit. For example, under highly turbid conditions of 20 mg dw/L, a particle ingestion rate of 10 µg/cm²/h with a 4% organic carbon content (see Chapter 4 & 5, Anthony 1999b) that is assimilated with 60% efficiency would result in a daily carbon assimilation of ~6 µgC/cm²/d. For comparison, Muscatine et al. (1984) estimated that the carbon budget for *Stylophora pistillata* in highly shaded habitats (2% light availability compared to unshaded) is in deficit by ~ 28 µgC/cm²/d, and a further ~14 µgC/cm²/d was lost as mucus or dissolved organic material (see also Falkowski et al. 1984). At similar turbidity, but in less light-limited conditions (e.g. in shallow water) where the phototrophic deficit is smaller, feeding by inshore corals may fully compensate for phototrophic deficits. Further, during periods where the phototrophic carbon balance is in surplus inshore, enhanced rates of particle feeding will potentially increase the supply of particulate nutrients, and thereby promote tissue growth (e.g. Bythell 1988, Dubinsky & Jokiel 1994).

3.5.4. Adaptive significance of sediment feeding

Two mechanisms may be driving the observed disparity in feeding responses between turbid inshore and less turbid midshelf reefs: (1) selection of more heterotrophic genotypes inshore, and (2) switching to sediment feeding as a physiological response to high particle concentrations. The first hypothesis, that corals have adapted to local

sediment regimes, appears likely given the low predicted degree of cross-shelf larval dispersal (Dight et al. 1988, 1990). The alternative explanation, that the enhanced clearance rates of *P. damicornis* and *A. millepora* from inshore turbid reefs represent a physiological response (phenotypic plasticity), is equally likely in the context of optimal foraging. According to the model of (Robinson & Sloan Wilson 1998), optimally foraging consumers may evolve phenotypic specializations on nonpreferred (low-quality) resources (e.g. sediment in this study) without greatly compromising their ability to use preferred (high-quality) resources, such as zooplankton for corals. To determine which mechanism is the cause of the observed cross-shelf differences in feeding rates and assimilation efficiencies for *P. damicornis* and *A. millepora* would require long-term reciprocal transplantation experiments, which was beyond the scope of this study. Regardless of genetic or physiological mechanisms, the observed heterotrophic plasticity may be important for maintaining the energy balance of corals on reefs that are subject to increasing or seasonally fluctuating sediment loads.

3.5.5. Conclusion

The two common species of coral, *Pocillopora damicornis* and in particular *Acropora millepora*, from inshore turbid reefs showed significantly higher sediment clearance rates than their conspecifics from offshore, suggesting adaptive changes or phenotypic plasticity in trophic modes across these environments. Despite 2-3 fold higher particle clearance rates of inshore corals, particle feeding is unlikely to provide a dominant and alternative carbon source under high turbidity, but may significantly reduce temporary energy deficits. Assuming these results are representative of the pattern of heterotrophic capacities of other corals across the GBR shelf, they have major implications for the current perception of the role of particulate matter as a stress factor in coral ecology. Enhanced heterotrophic capacity inshore may provide a partial physiological explanation for the success of reef corals in high-turbidity nearshore habitats.

Chapter 4

Effects of turbidity and sedimentation on coral energetics: system development and pilot study

This chapter forms the basis for the publication:

- Anthony, K.R.N. 1999. 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 (see Appendix).

4.1. SYNOPSIS

A tank system and experimental design is described for long-term exposure of corals to well-defined ranges of particle loads on a background of natural flowing seawater. Using low technology and a simple mathematical model, the concentration of suspended particulate matter (SPM) and the rate of sedimentation could be predicted and sustained with high precision. The system and operational procedures were tested in a 1-month experiment investigating the effect of SPM concentrations on the skeletal growth rates of the symbiotic scleractinian coral *Porites cylindrica*.

Corals showed low rates of mortality and minimal apparent stress from containment in the tank system. Also, growth rates of tank controls did not differ significantly from those of conspecific field controls, indicating that the system satisfied basic experimental requirements. Rates of skeletal growth of *P. cylindrica* were significantly reduced at the High (10-12 mg/L) relative to the Low (3-4 mg/L) sediment concentration, but did not differ significantly between Filtered (0.8-1.0 mg/L), Low and Moderate (4.5-7.0 mg/L) concentrations. Since the shading effect of high turbidity was not included in the experimental design of this pilot study, differences in growth pattern in response to treatment are the results of differing ability to utilise SPM as a food source or differing susceptibility to SPM as a mechanical stress factor.

Processing and short-term storage of the experimental particulate matter significantly reduced the content of organic carbon (~3%) relative to that of field samples (~5-6%). The contents of nitrogen and phosphorus in the experimental SPM, however, did not differ from levels in the field. The heterotrophic potential of the particle concentrations in the tank system, and the implications for scope for growth, was therefore conservative with respect to carbon.

The high level of environmental control and the constancy of SPM treatment levels was reflected in the absence of tank effects on growth rates, and provided sufficient statistical power to detect relatively small differences in growth rates between corals from different treatments.

4.2. INTRODUCTION

Numerous field studies have addressed the problems presented by turbidity and sedimentation for coral assemblages, but their findings have been generally inconsistent (Chapter 1). Most studies have been conducted in environments of high spatial and temporal variability, potentially precluding the identification of turbidity and sedimentation as the primary factors of stress or reduced growth in corals. For example, van Katwijk et al. (1993) showed that nearshore coral reefs in Kenya were severely affected by high sediment loads from the Sabaki River, whereas the community study by McClanahan and Obura (1997) using the same reefs found only minor effects of high sediment loads. Importantly, increased particle fluxes are often associated with other factors which affect coral physiology (Brown & Howard 1985), e.g. freshwater run-off from land (e.g Sakai and Nishihira 1991, Porter et al. 1999), wave action (Larcombe et al. 1995), reduced light (Dallmeyer et al. 1982, Te 1997), and high nutrient loads (Mitchell & Furnas 1997). To enable hypothesis testing of the effect of sediment concentrations on aspects of the biology of corals (and benthic organisms in general), a higher degree of environmental control is necessary than can be obtained from field studies.

In this chapter, I describe and test a flow-through tank system that enables exposure of corals (and benthic organisms in general) to highly predictable concentrations of SPM and rates of sedimentation. This chapter forms the experimental basis for studies of coral energetics in different turbidity regimes which are presented in Chapters 5 and 6. I have devoted a full chapter to describing the methods, experimental system and results of an associated pilot study, as the understanding of how the physical regime is controlled is critical for interpretation of the results of the growth study (Chapter 5) and the subsequent feeding, respirometry, and energetic modelling study (Chapter 6). The development and design of this system was based on three requirements of the studies described in Chapters 5 and 6. Firstly, a background of ambient water was required to allow control groups to be established within the set-up. Secondly, to enable interpretation of physiological responses (e.g. growth) with respect to particle loads, it was necessary to obtain ample stocks of fresh, natural SPM. The latter is especially important in experiments involving heterotrophic species in which growth may be strongly related to particle quality. Lastly, to allow hypotheses to be developed on physiological responses to specific particle loads, a method was required for predicting

and adjusting SPM concentrations within distinct, narrow ranges. I tested the operation and efficacy of the system in a four-week growth experiment in 1996 using one species of scleractinian coral.

4.3. MATERIALS AND METHODS

4.3.1. Description and design of the experimental set-up

This study was conducted at Orpheus Island Research Station (OIRS), located 15 km off the North Queensland coast, Australia (18° 35' S, 146° 20' E, see Fig 3.2). The aquarium system on the station is supplied continuously with large quanitites of seawater pumped directly from the reef front of the adjacent Pioneer Bay, rendering the station an ideal setting for long-term tank experiments. The experimental system consisted of 20 white plastic tanks (46 litres: 56 cm long, 37 cm wide, 22 cm deep) arranged in a 4.2-m diameter shallow seawater pool that was protected from rainwater dilution by a solarweave roof. The water in the pool buffered spatial and temporal temperature variation, and the roof allowed ~40% penetration of natural sunlight. Each of the 20 tanks received a constant supply of seawater (0.60 ± 0.03 L/min). For the purpose of establishing five different water qualities (filtered, low SPM, moderate SPM, high SPM, and control), three pipelines supplied seawater with different levels of filtration to different tanks. One line of water was rigorously filtered (~ 1 μm) to provide particle–depleted water (4 tanks), the second was coarsely filtered (~15 μm) for use in the low, moderate and high SPM treatments (three levels, 12 tanks) and the third supplied unfiltered water directly from the reef to function as a control for particle depletion and addition (4 tanks). Two 50-litre drums functioned as sediment reservoirs and were connected to the three sets of tanks that were supplied with particles to produce the low, moderate and high treatments. The spatial arrangement of tanks with differing levels of filtration and particle addition was randomised to control for the effect of tank position. To provide convection and near-bottom water flow, thereby reducing sedimentation of added particles, a circulation pump (Aquaclear 401) fitted with spray bars was installed inside each tank (Fig. 4.1). The pumps generated an evenly distributed, but turbulent, flow of 10-15 cm/s as determined by erosion of plaster blocks (Jokiel & Morrissey 1993, Thompson & Glenn 1994). Briefly, 20 hemispherical plaster blocks (7 cm diameter, 3 cm high) glued to individual PVC panels (10 cm by 10 cm) were distributed among five

randomly chosen tanks and incubated during 24 hours at the experimental flow regime. The blocks were preweighed dry before and after deployment. Two blocks in each tank were positioned in tank corners and two were positioned towards the centre to test for differences in flow regimes within tanks. The % weight loss during incubation was converted to flow rate using the following relationship determined for 80 flume-calibrated blocks with similar properties: % weight loss = $-0.025\ U^2 + 1.70\ U + 3.59$ ($R^2 = 0.83$). Results of a nested ANOVA showed that flow rates were homogenous within ($F_{1,10} = 0.93$, $P = 0.358$) and among tanks ($F_{4,10} = 0.443$, $P = 0.443$).

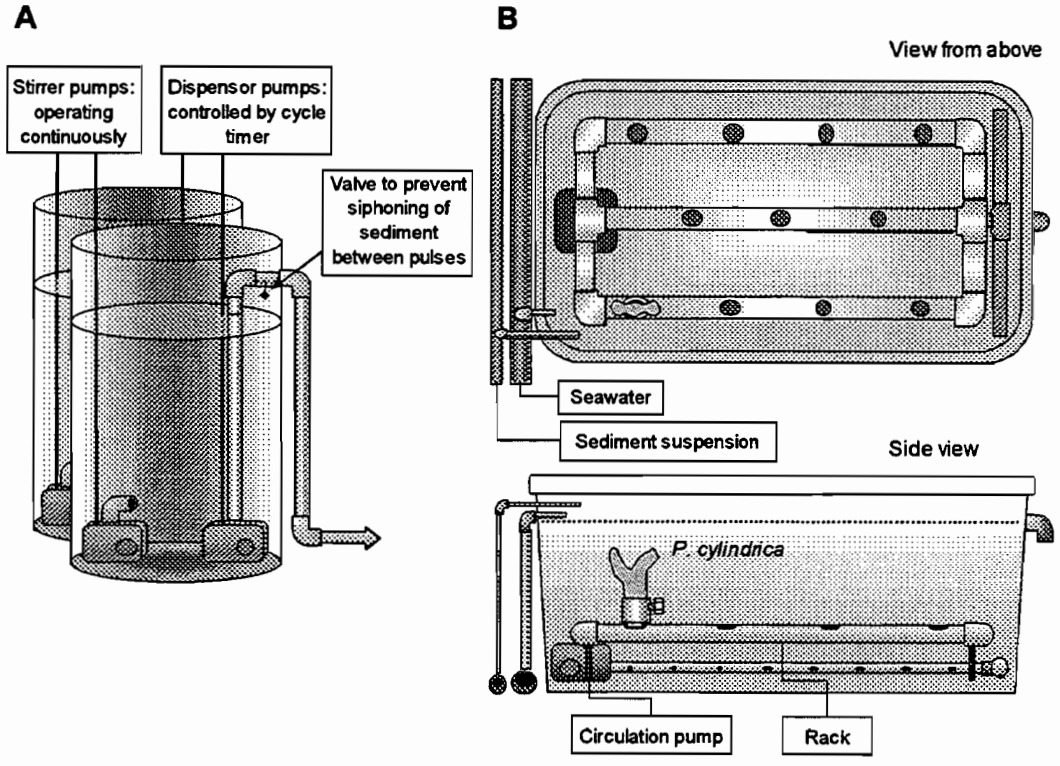

Fig. 4.1. Design and operation of (A) dispenser drums with sediment stock suspensions and (B) coral treatments tanks. Corals in all tanks were held in flow-through seawater, and in two treatments levels, tanks received frequent pulses of sediment suspensions of a known volume to establish two stable SPM treatment levels. Most of the added particulate matter was kept in suspension by a circulation pump under the coral rack in each tank.

4.3.2. Collection and quantification of particulate matter

Particulate matter similar to that found naturally was obtained by using the seston accumulated in a 500-litre sandfilter connected to the main seawater intake of the Research Station. The filter processed >400,000 litres of seawater per day. The

particulate matter was retrieved by backwashing the sandfilter daily into two 1500-litre tanks, in which the particulates were allowed to settle over a 3-4 h period before transfer to a 25-litre carboy for further sedimentation. To enable instantaneous measurement and adjustment of the sediment concentration in the reservoirs, the relationship between light absorbance and SPM concentration was determined. Briefly, a subsample of sediment suspension was divided into two series of 20 aliquots diluted between 1 and 40 times. The first series was analysed spectrophotometrically at a wavelength of 325 nm. The second series was filtered through GF/F filters (0.5-µm pore), rinsed with distilled water, and dried at 50°C for 24 h to obtain volume-specific dry weight (dw). Within the range of sediment concentrations of 0.05 to 2 mg dw/ml, a second-order equation showed sediment concentration (C) to explain more than 99.9% of the variation in light absorbance ($Abs = -0.20\,C^2 + 1.47\,C + 0.02$, Fig. 4.2).

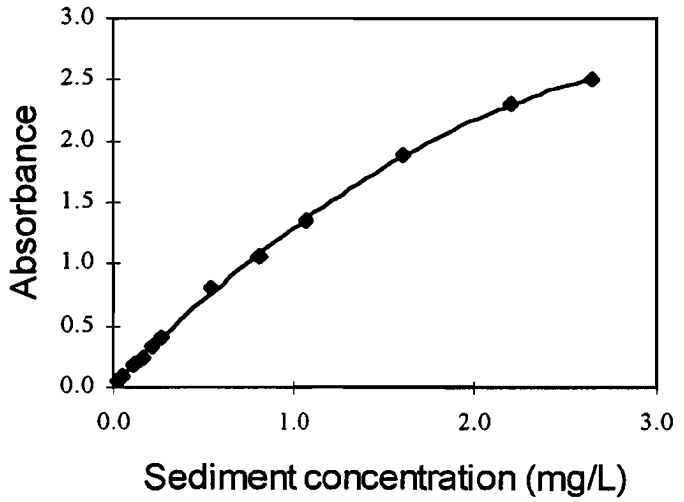

Fig. 4.2. Relationship between light absorbance and sediment concentration used to enable instantaneous measurements of particle concentrations of stock suspensions. A second order polynomial provided the best fit to the data ($R^2 > 0.99$).

4.3.3. Dispensation of SPM

The SPM was dispensed to the treatment tanks from two 50-litre drums holding stock suspensions of different concentrations (see below). The particulates were kept in constant suspension and circulation by a pump (Aquaclear 801) at the bottom of each drum (Fig. 4.1). Delivery of sediment to the coral tanks within each treatment was administered by a second pump connected to eight lines of 4-mm-diameter polypropylene tubing leading to the eight replicate tanks in each SPM treatment. A

standard length of dispenser tubing assured equal flow resistance and hence equal suspension flow rate to all tanks within a treatment level. Sediment was dispensed in discrete pulses of 15-s duration at fixed time intervals (10 min in the growth study), controlled by an unequal-cycle timer (Rhomberg Bräsler). Discrete pulses were preferred over continuous particle supply, as the former prevents sediment accumulation and anoxic residues inside the tubing. Each pulse delivered 80 ± 2 ml of stock suspension to each of the eight tanks, resulting in an ~12 h lifetime for each 50-l drum in the case of 10-min pulse intervals.

4.3.4. Modelling concentrations of SPM over time

The concentration of suspended particles in an experimental tank (C_t, mg dw/L) at time t (min) was a function of at least six parameters: tank volume (V, litres), particle concentration of the stock suspension (C_{st}, mg dw/L), volume of stock suspension added per pulse (V_{st}, litres), flow rate of seawater to each tank (FR, L/min), sedimentation rate of particles escaping resuspension (SR, expressed as a clearance rate, L/min), and time interval between pulses (T, min). For simplicity, I will express particle delivery (PD) at each pulse as $PD = C_{st}V_{st}$ (mg dw) in the following discussion.

After a sediment pulse, the depletion of particles over time (dC_t/dt, mg dw/L/min) will be a function of particle concentration in the tank at time t (C_t), and the rates at which particles are removed from the water due to seawater flow-through (FR) and sedimentation (SR), hence

$$\frac{dC_t}{dt} = -C_t \frac{FR + SR}{V} \tag{4.1}$$

Through separation of variables and subsequent integration, the SPM concentration in the tank is given by

$$C_t = C_0 e^{-\frac{t(FR+SR)}{V}} \tag{4.2}$$

where C_0 is the SPM concentration at the beginning of the pulse cycle. The model assumes complete mixing immediately after particle addition, which was verified in the experiment as sediment suspensions were generally homogenous within 10 seconds after

each pulse. The particle concentration immediately after the subsequent pulse ($C_{T+\delta}$) is then given by

$$C_{T+\delta} = C_0 e^{TK} + \Delta C_p \tag{4.3}$$

where $K = -(FR+SR)/V$ and ΔC_p is the increase in particle concentration due to the pulse (PD/V). Immediately prior to the next pulse (at $2T-\delta$), the particle concentration is then

$$C_{2T-\delta} = (C_0 e^{TK} + \Delta C_p) e^{TK} \tag{4.4}$$

Continuing this argument for a sequence of N pulse cycles at their start and end phases, respectively, the upper (C_U) and lower (C_L) limits of the concentration range are given by the geometric series:

$$C_U = \Delta C_p (1 + e^{TK} + e^{2TK} + ... + e^{NTK}) \tag{4.5.1}$$

$$= \Delta C_p (1-e^{NTK})/(1-e^{TK}), \tag{4.5.2}$$

which at steady state (high N) approaches

$$\Delta C_p / (1-e^{TK}) \tag{4.5.3}$$

Analogously

$$C_L = \Delta C_p (e^{TK} + e^{2TK} + ... + e^{NTK}) \tag{4.6.1}$$

$$= \Delta C_p e^{TK} (1-e^{NTK}) / (1-e^{TK}), \tag{4.6.2}$$

at steady state approaching

$$\Delta C_p e^{TK} / (1-e^{TK}) \tag{4.6.3}$$

The difference between C_U and C_L at steady state is therefore given by ΔC_p; i.e., the amount of sediment delivery per pulse relative to tank size governs the experimental range of particle concentrations. To maximise the precision of steady-state particle concentrations at a given tank volume, ΔC_p should be minimized, for example by using low values for T and FR. Furthermore, the number of pulse cycles needed to reach 95 % of C_U (an indication of system resilience) is predicted by

$$N_{0.95} = ln(1\text{-}0.95) / TK \sim 3V / [T(FR+SR)] \quad (4.7)$$

Depending on the application, optimal system performance will be a compromise between high precision (e.g. short T, low FR) and high resilience (e.g. long T, high FR). An example with two different settings of parameters ΔC_p and T is depicted in Fig. 4.3.

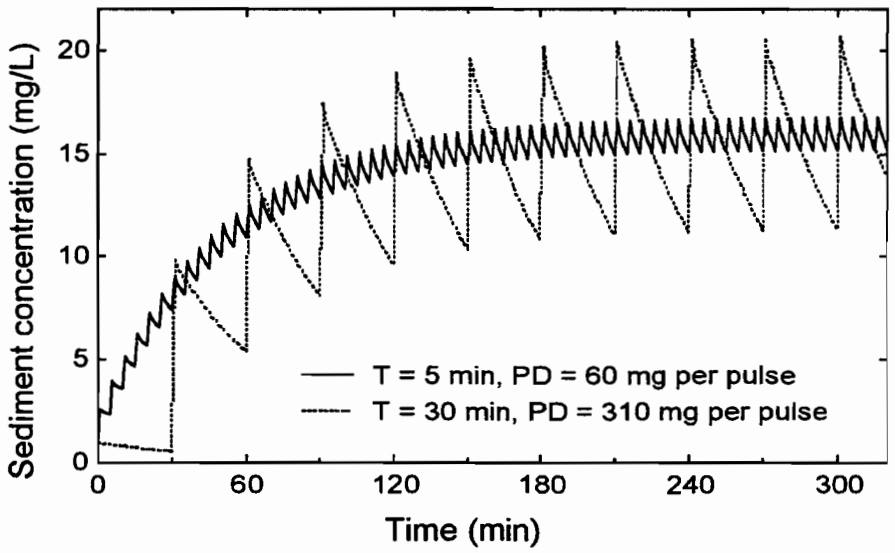

Fig. 4.3. Predicted concentration of suspended sediment in a coral growth tank as a function of time using two different combinations of particle delivery (PD) and intervals between pulses (T). The graph shows that a narrow, stable range of particle concentrations is obtained by short pulse cycles. The two systems stabilise within the same time frame, independently of PD. Tank volume (V) was 46 liters, flow rate of background seawater (FR) was 0.6 L/min and the sedimentation rate (SR) was here assumed to be negligible.

4.3.5. Determination of sedimentation rate and test of model predictions.

Before the prediction of C_U (or C_L) by the model could be validated, SR was determined empirically. Sedimentation was measured indirectly by monitoring particle concentrations in two tanks without a flow-through of seawater (FR = 0), but with water recirculation and racks identical to that of all other tanks in the system. After initial addition of ~1.3 g sediment suspension per tank (C_0 ~28 mg dw/L), duplicate 50-ml samples were taken from each tank every 15 min for 1.5 h and filtered immediately through preweighed GF/F filters for gravimetric analyses. SR was hence calculated by fitting the model

$$C_t = C_0 e^{-t\ SR/V} \quad (3.8)$$

to the datasets using non-linear estimation (Quasi-Newton and Simplex iterative models, STATISTICA 1997). The prediction of an exponential decline in the particle concentration over time due to sedimentation is consistent with that of Reynolds et al. (1990) in flow channels.

To validate the prediction of C_U based on system parameters (including measured *SR*), C_t was monitored over a 16-h period in duplicate tanks identical to those above, however with a flow-through rate (*FR*) of 0.60 ± 0.03 L/min. Every 1-2 h, duplicate 50-ml water samples were taken from each tank ~20 s after a sediment pulse, and filtered immediately. In both of the above tests, sampling volume was < 2% of tank volume, and was replaced by normal supply of seawater. The level of agreement between predicted and observed C_U was validated by fitting Eq. 4.5.2 to the datasets by non-linear estimation. *SR* was entered as an unknown parameter in the model to compare predicted with measured sedimentation. The error range for predicted C_U was determined by varying the input variables *FR*, *SR*, and *PD* in Eq. 4.5.3 ± SE of their means.

4.3.6. Effects of particle processing on particle quality

To test the effect of the processing procedure on the quality of SPM, the weight-specific contents of organic carbon, total nitrogen and reactive phosphorus were compared between SPM from the tank system and from the field. Concurrent sampling from both tank system and field was carried out regularly over a two-month period to account for temporal variability in water quality. Samples from the tank system were taken as duplicate 50-ml aliquots of the stock suspension. Water samples in the field were taken adjacent to the seawater intake in Pioneer Bay using a 2.5-litre Niskin bottle. All samples were filtered immediately through precombusted Whatman GF/F filters for gravimetric analysis of particulate dry weight. Organic carbon was determined with a Shimadzu 5000 carbon analyser, and total nitrogen was determined with an Antek 720 C/N analyser.

4.3.7. Pilot growth study

A one-month experiment was conducted in the tank system in 1996 to test: (1) the overall efficacy and performance of the tank set-up and methods for producing and dispensing natural suspended particles; (2) survival, apparent health, and growth rates of corals in the set-up compared to in the field; and (3) the number of replicate corals and tanks needed to obtain sufficient statistical power to examine the effects of turbidity on

coral growth rates. To maximise replication within particle treatments, only one light level corresponding to 4 mg/L at 3-4 m depth was used in this design.

Porites cylindrica was chosen for the pilot study since this species occurs in high abundance in Pioneer Bay and neighbouring bays. Further, its digitate growth form and high powers of regeneration of terminal branches enables a high level of replication with minimal damage to the reef. Based on growth form, *P. cylindrica* was expected to be fast growing as is generally the case for branching corals with a large surface-to-volume ratio (Wellington 1982, Oliver 1984), rendering it particularly suitable for testing effects of environmental variables in relatively short-term growth experiments.

One month prior to initiation of the pilot study, ~200 terminal branches of *P. cylindrica* were collected from the reef in Pioneer Bay. The branches (7-8 cm length) were broken off from their colonies and attached to numbered stands (PVC tubes, 15 mm inner diameter, 50 mm long) and mounted onto racks (Fig. 4.1B). The base of each coral branch was fixed inside one end of the tube by a nylon bolt. To allow the corals to recover from handling they were left for one month at the site of collection. On the day prior to initiation of the growth experiment, all corals were transferred to the tank system and distributed haphazardly among treatments. Twelve to thirteen branches were assigned to each tank. After initial measurement of size (see below), eight racks with corals were transferred back to the reef to control for tank artifacts. Four of the field racks were deployed in the southern end of Pioneer Bay, and the remaining four in the northern end (~ 2 km apart) to control for heterogeneity in the field. Both groups of field controls were placed on the reef slope, ~ 3 m below datum.

Table 4.1. Experimental design for the four-week pilot growth study with *P. cylindrica* in the tank system and in the field. See Table 4.2 for details of particle concentrations used in the different treatments and recorded in Pioneer Bay South and North. The control sites were approximately 2 km apart.

	TANK DESIGN					FIELD CONTROLS	
Treatment group	Filtered	Low	Moderate	High	Raw	Pioneer Bay S	Pioneer Bay N
Tanks per treatment		1 2 3 4				1 2 3 4	
Colonies / branches		9 - 11				9 - 11	

Coral growth was measured as the increase in buoyant weight over the two-month experiment using the technique described by Spencer Davies (1989). Corals were weighed in a constant-temperature room (25°C) using a digital balance (Sartorius, ± 1 mg) placed over a seawater bath. During weighings, the corals were suspended in the waterbath by their stands from a hook underneath the balance. The coral branches were manipulated by their stands only to minimise handling stress, and holes in the stands functioned as sites of attachment during weighings. All corals were weighed within 12 hrs on day 1 and day 30, following a consistent order, to ensure that growth intervals were of similar length for all corals. To enable conversion of buoyant weight (W_B) to skeletal dry weight (W_{Sk}), a W_{Sk} vs W_B standard was constructed based on coral branches sampled from the experimental population at conclusion of the growth experiment. Briefly, 15 coral branches covering the full size range of the experimental population were sequentially buoyant weighed, their tissues removed from the skeleton by digestion in 10% chlorine (sodium hypochlorite), the skeleton rinsed in freshwater, and dried at 50°C until constant weight. A simple linear function showed skeletal dry weight to explain > 99% of the variation in buoyant weight ($W_{Sk} = 1.69 \cdot W_B + 0.09$, see Fig. 4.4).

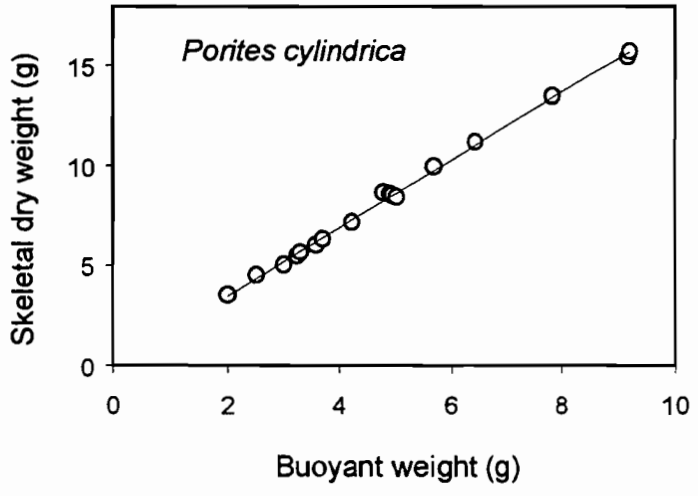

Fig. 4.4. Relationship between skeletal dry weight and buoyant weight for branches of *Porites cylindrica* used in the growth study. The linear function $W_{Sk} = 1.69 \cdot W_B + 0.09$ provided a good fit to the data ($R^2 > 0.99$, N = 14) and was used to convert changes in W_B to changes in W_{Sk}.

Tank system settings. For the growth study, system parameters *T* (10 min), *FR* (0.60 ±0.03 L/min), and *PD* (High: 80 ± 4 mg dw/pulse; Moderate: 41 ± 3 mg dw/pulse, Low: 23 ± 2 mg dw/pulse) were adjusted so that the range of particle concentrations at

steady state ($C_{L,obs}$ - $C_{U,obs}$) was 10.2 - 12.0 mg dw/L for the High-particle treatment, 5.2 - 6.1 mg dw/L for the Moderate treatment, and 2.9 - 3.5 mg dw/L for the Low treatment (see also Table 4.2 for empirical values). The low *FR* was sufficient to maintain a high turnover of tank volume (> once every h) and yet allow an economical use of added particles. The system reached steady state, as governed by *V*, *T*, and *FR*, within ~3 h (Eq. 4.7, see also Fig. 4.3).

Table 4.2. Concentrations and quality of suspended particulate matter in the tank system and in the field at different sampling occasions during the pilot growth experiment. Samples for particle quality analyses in the tank system were taken from the stock suspensions. Values are mean weight percentages ± SE of samples from N days during the experimental period.

Particle concentrations (mg DW/L)

Tank system	Mean	SE	N	Field controls	Mean	SE	N
Filtered	0.85	0.09	8	Pioneer Bay South (PB-S)	2.40	0.40	12
Raw (tank controls)	2.10	0.27	8	Pioneer Bay North (PB-N)	1.80	0.25	9
Low	3.20	0.41	10				
Moderate	5.65	1.10	10				
High	10.95	0.18	10				

	Tank system			Pioneer Bay South			Pioneer Bay North		
Particle quality (% of DW)	Mean	SE	N	Mean	SE	N	Mean	SE	N
Total carbon	4.60	0.25	12	5.40	0.52	10	5.15	0.45	9
Organic carbon	3.37	0.43	11	3.10	0.46	10	2.91	0.12	8
Nitrogen	0.46	0.07	13	0.44	0.13	7	0.42	0.17	8

4.3.8. Data analysis of coral growth

Effects of SPM treatments and Tanks on log-transformed growth rates (ΔW_{SK}) were tested using a two-way ANCOVA with the factor Tanks nested within SPM treatment, and initial (day 1) buoyant weight (W_{B0}) as the covariate. Due to the relatively narrow size range of coral branches used (1.8 g < W_{B0} ≤ 4.3 g), and the consequently weak correlation between growth and initial size, data were also analysed using ANOVA on percentage change in branch weight ($\Delta W_{SK} / W_{B0}$). Data conformed to ANOVA/

ANCOVA assumptions without transformation, in part due to the narrow size range. Field controls were included in the analyses to enable comparison of tank controls (Raw) with field analogues (PB-S and PB-N). The factor Tank (parallelled by racks in the field) was important for the analysis as it enabled the assessment of environmental homogeneity in the tank system (or among racks in the field). Tukey's HSD test was used to identify significant differences among individual group means.

For the purpose of designing and scaling the growth experiment in 1997, *a posteriori* power analyses were conducted based on the results of the pilot study to identify the minimum design that provides an observed power (ϕ) $\geq$ 0.80. Observed powers were calculated using SPSS (Release 8.0) for both the factors SPM and Tank (nested within SPM) to determine the combination of minimum tank and coral replication necessary to satisfy $\phi \geq 0.8$. Subsets of the *P. cylindrica* growth data with N = {4, 3, 2} for tanks and with N = {10, 7, 5, 4} for coral replicates were obtained by random sampling using random number generation in SPSS. Between 2 and 5 repeated samplings and subsequent power analyses were conducted for each combination of tank N and coral N.

4.4. RESULTS AND DISCUSSION

4.4.1. Validation of sediment concentration model

The ranges of SPM and rates of sedimentation in the tanks were highly predictable over time. Measured SPM concentrations at steady state were well within the confidence band of the predicted C_U (Fig. 4.5). The latter was determined using a sedimentation rate of 0.12 ($\pm$ 0.01, SE) L/min estimated in tanks without flow-through of seawater (Fig. 4.6). Conversely, fitting Eq. 5.2 to the observed C_U's with unknown *SR* explained 93% of the variation in SPM concentration, and *SR* estimated by this model (0.10 $\pm$ 0.01 L/min) was almost identical to that determined in tanks without flow-through. These rates of sedimentation corresponded to the deposition of 2.2 - 2.8 mg dw sediment/cm^2/d (mean C_t = 30 mg dw/L, area of tank floor ~ 2,000 cm^2) which are trivial compared to those measured in turbid, nearshore environments (Cortés & Risk 1985, Woolfe & Larcombe 1998). By minimising sedimentation through high near-bottom convection, the system enabled examination of the effects of high particle concentrations without

confounding effects of sedimentation. Conversely, regulating intensity of convection (resuspension) would enable testing effects and interactions of specific levels of sedimentation and particle concentration.

4.4.2. Effects of filtration procedure and storage on particle quality

The organic carbon content of the SPM in the stock suspensions was only 50% to 75% that of seston filtered from natural water (Table 4.2). This suggests that a significant proportion of the live material, e.g. microorganisms coating the particle surfaces, was removed during the filtration procedure and short-term storage, and/or that organic contents were metabolised by non-attached bacteria. The low carbon content of the experimental relative to ambient SPM may have reduced the likelihood that heterotrophy on suspended particles may have contributed to growth. However, the weight-specific N content of stock suspensions did not differ significantly from that in field samples (t test , $t_{26} = 0.21$, $P = 0.42$), in agreement with the often higher N content of aged detrital material (Rice 1982). In high-light conditions where photosynthesis is saturated, the nutrient content of ingested particles is likely to play a more important role for coral growth than organic carbon content (Dubinsky & Jokiel 1994, Muller et al. 1994). Thus it was considered unlikely that the reduced carbon content significantly affected the coral growth rates.

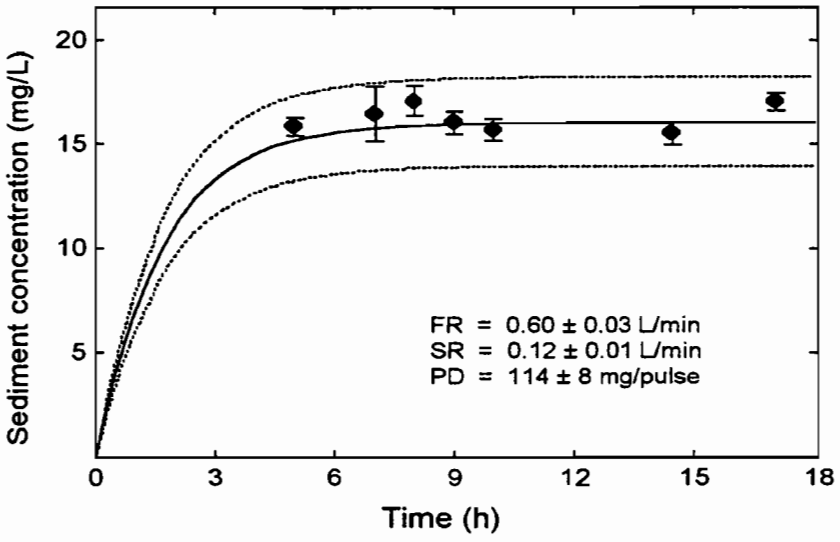

Fig. 4.5. Predicted and observed upper sediment concentration (C_U) at steady state. Observed sediment concentrations are means ± SE of duplicate samples for two tanks. The solid line depicts mean predicted C_U (Eq. 5.2) and dashed lines represent the maximum error range for predicted C_U. Fitting Eq. 3.5.2 to

the observed data with sedimentation rate (*SR*) as a variable explained 94% of the variance, and *SR* was estimated to be 0.10 ± 0.01 (L/min) by this method, not significantly different from the *SR* measured (see Fig. 4.6).

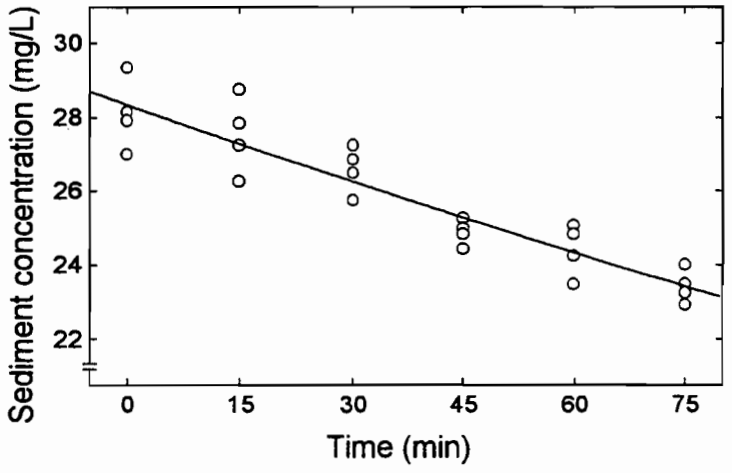

Fig. 4.6. Depletion of suspended particles due to sedimentation in two tanks without flow-through of seawater. Data are duplicate samples from each of two tanks. The function $Ct = 28\ e^{-SR\ t}$ provided a significant fit to the data ($P < 0.001$, $R^2 = 0.86$), and sedimentation rate (*SR*) was estimated as 0.12 ± 0.01 (L/min).

Elaborate artificial and natural flow-through systems have been used to examine organism and community responses to factors such as long-term nutrient enrichment (Larkum & Steven 1994, Stambler et al. 1994) and salinity variation (Cooper & Copeland 1973). However, the system and methods described here represent the first simple and inexpensive means of producing predictable levels of turbidity and sedimentation using natural SPM in long-term experiments. Optimal scaling of system parameters (e.g. *V, T, FR*) produces high stability (resilience) of the steady-state particle concentration. This inherent stability is, in part, explained by the asymptotic way in which injected SPM reaches steady-state concentration in a flow-through tank (Fig. 4.3, Eq. 4.5–4.6). The steady-state concentration is therefore relatively robust to fluctuations in the system parameters, which reduces the need for continuous monitoring or computer control.

4.4.3. Effects of sediment loading on coral survivorship and growth

Coral survivorship and general observations. The growth experiment indicated that the tank system was ideal for testing effects of water-quality treatments on corals. The survivorship of *P. cylindrica* was ~75% in the tanks and ~90% on the field racks.

Mortality and partial mortality of *P. cylindrica* in the tanks were, in part, due to its susceptibility to algal overgrowth around the branch bases. Algal overgrowth was not observed for the field controls of *P. cylindrica*, and was probably prevented by herbivory. Mortality of the field controls was mainly attributable to incidental damage by fish browsing on the racks.

Coral growth rates. The results of the ANCOVA for whole-branch skeletal growth (ΔW_B) showed a significant effect of particle treatment (Table 4.3 A). This effect was attributable to the higher growth rates of corals in the Low SPM treatment relative to the High SPM treatment and the Tank and field controls (Raw, PD-S, PB-N). The adjusted mean growth rate of Low corals was almost 22% higher than that of High corals. Surprisingly, growth rates of corals from the Low treatment were significantly higher than those from the control tanks, but not higher than those from the Filtered tanks (Table 4.3). Growth rates were therefore not a simple function of particle concentration, perhaps confounded by somewhat higher levels of algal overgrowth of the racks in the Raw relative to Filtered tanks. The reduced growth rates at high particle loads could almost conclusively be attributed to suspended particles as a mechanical stress factor, and not to shade effects of high turbidity as light levels in the high particle tanks were only reduced 7-9% as a consequence of lowered reflectance from tank walls. Given that light levels below the water surface inside the tanks at noon were ~600 μE/m²/s, such small reductions in light level are likely to occur over the saturated range of the P-I curve (see also Chapter 6), and hence are predicted to cause insignificant effect on growth.

Importantly, the adjusted mean growth rates of *P. cylindrica* branches in the control tanks (Raw seawater) were not significantly lower than those on racks in the field (Table 4.3), indicating that the tank environment satisfied the basic requirements for experimentation on the time scale of months for this species. Also, there was no effect of the nested factor Tank, indicating a homogeneous environment within the tank system that enabled interpretation of the main effect. The overall regression for the dependent variable ΔW_{Sk} vs the covariate W_{B0} was highly significant (Table 4.3) despite considerable variability in the growth rates around the regression line ($R^2 = 0.09$, Fig. 4.7). The low percentage of explained variation was, in part, attributable to the narrow range of initial buoyant weights (the covariate).

Table 4.3. **A:** Summary results of ANCOVA for effects of SPM treatments and tanks nested within treatments on monthly increase in skeletal growth of *P. cylindrica*. Initial buoyant weight (W_{B0}) was used as the covariate. Data were analysed untransformed (see below). **B:** Results of Tukey's HSD test. Adjusted means of treatment groups with similar subscripts are not significantly different. **C:** Results of within-cell regression for the dependent variable (ΔW_{Sk}) vs the covariate. **D:** Results of the test for slope-equality which is an assumption for the ANCOVA. Untransformed data also conformed to normality and variance homogeneity (not shown). See also Fig. 4.7 for scatterplots of the data.

A. ANCOVA for whole-branch change in W_{Sk} with W_{B0} as the covariate

Source of variation	df	MS	F	p-level
SPM treatments	6	0.032	3.42	0.003 **
Tanks (within SPM treatments)	21	0.011	1.17	0.276 ns
Error	293	0.009		

B. Post-hoc

SPM treatments	Low	Mod	Filt	PB-S	Raw	PB-N	High
Adjusted means (g/branch/month)	0.46	0.43	0.41	0.40	0.39	0.39	0.38
Tukey's (HSD) groups	a	ab	ab	b	b	b	b

C. Regression results

Source of variation	df	MS	F	p-level	R^2
Effect	1	0.277	29.77	<0.001 ***	0.09
Error	293	0.009			

D. Tests of slope equality

Source of variation	df	MS	F	p-level
Among treatments	6	0.010	1.07	0.380 ns
Error	287	0.009		
Among tanks within treatments	3	0.017	1.87	0.135 ns
Error	290	0.009		

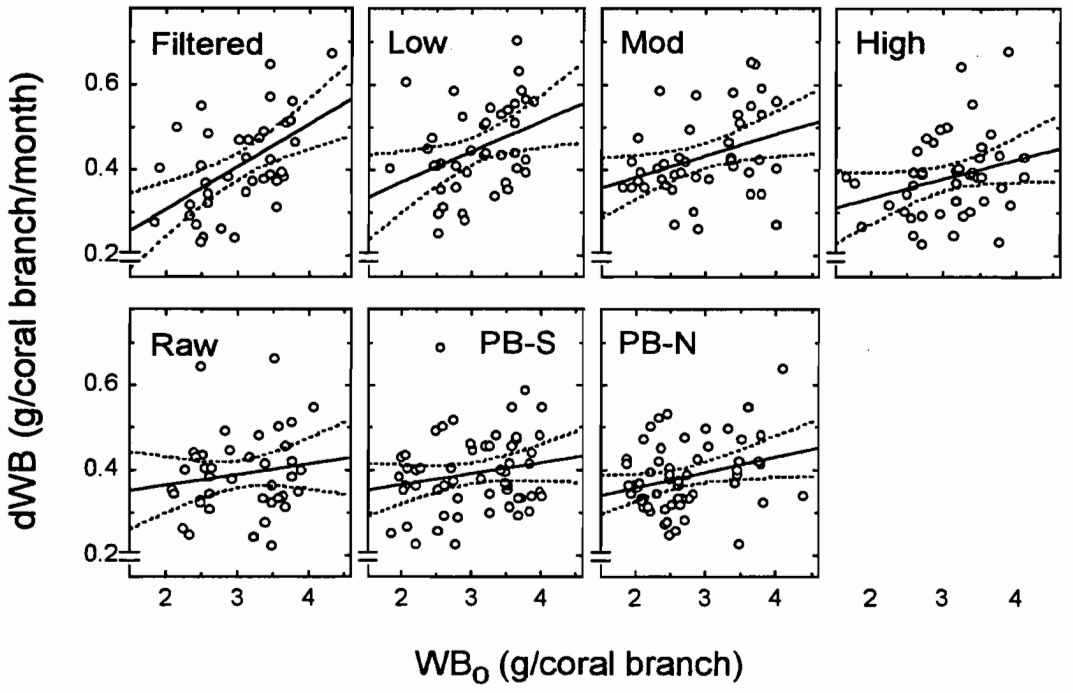

Fig. 4.7. Scatterplot and regressions of branch growth rates (ΔW_B) as a function of initial buoyant weight (W_{B0}) . The overall regression was highly significant despite that < 10 % of the variation in growth was explained by the covariate (see also Table 4.3 C). Slopes were not significantly different among treatments or tanks (Table 4.3 D).

4.4.4. Power analyses and recommendations for growth experiments

The analyses of observed power (ϕ) for growth rates suggested that the optimal design was 10 corals per tank and 4 tanks per treatment (the design already employed), producing a $\phi \geq 0.80$ for both factors (Table 4.4). Reducing the design to 7 corals per tank (and 4 tanks per treatment) produced an observed power of 0.78 for both treatment and tanks, and would thus represent the minimum replication required for studying growth rates of *P. cylindrica* in this tank system. Contrary to expectations, different combinations of tank replication for the ANCOVA design produced observed powers as high as those for percentage growth rates analysed by ANOVA. The above design recommended for the 1997 growth study would therefore apply to both ANCOVA and ANOVA.

Table 4.4. Observed power (ϕ) of the ANCOVA design for testing effects of SPM concentrations and Tanks (nested within SPM treatments) on the growth rates of *Porites cylindrica* during the one-month pilot study. The power analysis was run using different replication levels for tanks per treatment and coral branches per tank to identify the minimum design that has ≥ 80% power to detect an effect of SPM concentration (or Tank) on coral growth rate if such an effect does occur. Subsets of tanks per SPM treatment and corals per tank used in each analysis were chosen randomly, and sampling and subsequent analysis was repeated 2 to 5 times.

Tanks per SPM treatment	Corals per tank	Observed power (ϕ, range for N runs) SPM	Tanks (SPM)	Number of runs (N)
4	10	0.86 - 0.92	0.84 - 0.93	2
4	7	0.78 - 0.86	0.78 - 0.84	4
4	5	0.62 - 0.74	0.72 - 0.81	4
4	4	0.43 0.64	0.55 0.86	4
3	10	0.68 0.84	0.45 0.77	4
2	10	0.36 - 0.70	0.22 - 0.52	5

4.4.5. Relevance of tank studies to sediment effects on corals *in situ*

Previous manipulative studies of sediment effects on coral assemblages have mainly involved spot loads *in situ* (e.g. Rogers 1983) or in aquaria (Stafford-Smith 1992) using sedimented material. Riegl (1995) devised a method for continuous application of sand onto corals in a flow-through aquarium by recirculation of bottom sediments, although with limited control of dispensation over time. While treatments with discrete loads of sand mimic the resuspension and sedimentation resulting from discrete hydrodynamic events, they have no relevance to the often sustained concentrations of fine SPM characteristic of many inshore environments (Cortés & Risk 1985, Woolfe & Larcombe 1998).

The treatment levels used in this study cover a significant part of the range of particle concentrations experienced regularly in the nearshore areas of the GBR lagoon (Brodie et al. 1989, Brady et al. 1991, Devlin et al. 1995, Larcombe et al. 1995). The maximum particle levels used in this study (9.2-12.7 mg/L) occur mainly during flood events and storms (Larcombe et al. 1995), and inshore reefs would rarely experience such high particle loads for as long as one month, as simulated in this study. According

to continuous nephelometer readings by Larcombe et al. (1995) at multiple sites in Cleveland Bay, turbidity levels > 10 mg/L is only experienced ~10% of the time. The High constant sediment treatment in this study therefore represents an extreme situation both in terms of particle level and exposure time. This in concert with the non-significant difference between growth rates of corals in Filtered, Low, and Moderate sediment treatments, and the fact that many shallow, nearshore reefs in the GBR lagoon sustain high coral cover despite high sediment input (Ayling & Ayling 1991, Johnson & Carter 1991, Hopley et al. 1993, Ayling & Ayling 1995), all suggest that reef corals are relatively tolerant to naturally occurring elevations of suspended sediments. If the high particle load used in this study represents a true threshold at which *P. cylindrica* becomes significantly stressed by long-term exposure, habitats with such high chronic particle levels should be expected to be denuded of this species of coral, or replaced by species which have adapted to such conditions. Interestingly, *P. cylindrica* is generally absent from the most turbid inshore reefs in Cleveland Bay (Stafford-Smith et al. 1993) and from the fringing reefs in Daintree (Veron 1986).

The pros and cons of microcosms (e.g. tanks) in experimental ecology have been thoroughly debated (Carpenter 1996, Drake et al. 1996). While this debate has focused on the relevance of "bottle" experiments in community ecology (Peters 1991), the use of tank experiments in ecophysiological studies at the organism level have been less subject to reproach. The combination of flow-through natural seawater and tightly controlled levels of natural particles over a time frame of months makes this system a semi-natural setting with the advantages of laboratory control. Some points, however, may further improve the relevance of tank experiments in studying physiological responses to turbidity in the context of the natural environment. For instance, larger tanks with a flow regime mimicking that on the reef (e.g. waves and tides) would allow incorporation of hydrodynamics into models of particle-organism interactions, especially important for suspension (Shimeta & Jumars 1991) and deposit (Jumars & Nowell 1984) feeders. Also, a wider range of specimen sizes representing those of natural populations would reduce bias due to scaling. Although the advantages of such refinements are obvious, three important objectives for conducting long-term experimentation in tanks are likely to be sacrificed: high replicability, realistic cost and cost effective effort.

Chapter 5

Effects of turbidity on coral growth

This chapter forms part of the publications:

- **Anthony, K.R.N. & K.E. Fabricius.** In review. Shifting roles of heterotrophy and autotrophy in coral energetics under varying turbidity. *J. Exp. Mar. Biol. Ecol.*
- **Anthony, K.R.N.** Submitted. Skeletal growth: a poor indicator of sediment stress in corals? *Coral Reefs.*

5.1. SYNOPSIS

This study provides an experimental analysis of the effects of light and sediment regimes on the growth rates of two species of scleractinian coral with contrasting heterotrophic capacities (*Goniastrea retiformis* and *Porites cylindrica*) to test the hypothesis that high rates of sediment feeding can offset negative effects of shading and sediment stress on the scope for growth. Preliminary feeding trials demonstrated that rates of sediment feeding for *G. retiformis* were more than 10-fold higher than those of *P. cylindrica* at high SPM concentrations (16-30 mg dw/L), providing a valid framework for testing this hypothesis.

Shading corresponding to 16 mg SPM/L at 3-4 m depth resulted in reduced growth rates (as total energy investment) in both species. However, the two species showed contrasting growth patterns as a function of SPM concentrations (1-16 mg dw/L). Growth rates of *G. retiformis* increased monotonically with SPM concentration and were maximised at the highest SPM concentration (~16 mg dw/L). Importantly, growth rates of shaded and unshaded *G. retiformis* did not differ significantly at high SPM concentrations, suggesting that effects of shading were counteracted by photoacclimation and/or sediment feeding. In contrast, *P. cylindrica* showed maximum growth rate at the intermediate SPM concentration (~4 mg dw/L) and the combination of shading and maximum particle load resulted in negative growth.

Patterns of energy investment were almost exclusively explained by variation in tissue growth, with skeletal growth explaining less than 1% of the variation in total energy investment across sediment treatments. This result demonstrates that prevailing sediment regimes are recorded with much higher resolution by the energetics of coral tissues than by the growth rates of coral skeletons. Both tissue and skeletal growth, however, varied significantly with sediment concentration and light level in *G. retiformis*, whereas skeletal growth of *P. cylindrica* varied with light level only. Changes in lipid content accounted for 20%-100% of the total tissue growth, but varied significantly with light level only. Increases in matrix (non-lipid) tissue were relatively greater in corals with high rates of total energy investment.

The contrasting patterns of energy investment for the two species indicate that high sediment loads represent an opportunity for increased growth in one species (the good sediment feeder), yet constitute a stress factor in another (the poor sediment feeder). These

results challenge previous generalisations that sustained sediment loads higher than 10 mg dw/L (midway between the low and high treatments) are detrimental to corals. I hypothesise that the different growth patterns displayed by the two species are produced by a combination of different heterotrophic capacities and different susceptibilities to SPM as a mechanical stress factor.

5.2. INTRODUCTION

Numerous studies have investigated effects of environmental disturbances on coral growth rates (Brown et al. 1990, Rice and Hunter 1992, Guzman et al. 1994, Vago et al. 1994, Miller and Cruise 1995, Heiss 1996, earlier studies reviewed by Brown and Howard 1985), but none of these studies have rigorously determined the energetics of coral growth rates in order to quantify the levels of physiological stress (or nutritional stimulus) imposed by the environment. The term "stress" is referred to in this study as a negative impact on the organism's scope for growth (*SfG*), which is defined as the difference between energy acquisition and that lost via metabolism and excretion (Warren and Davis 1967, see also Widdows and Johnson 1988, Calow and Sibly 1990, Maltby 1999). The term "stress factor" thus refers to an inferred cause of a reduction in *SfG* (see also Rosen 1982).

For mixotrophic corals, scope for growth with respect to carbon is given by

$$SfG = P_g + A + R - EX, \tag{5.1}$$

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 & Chalker 1990), and EX is the excretion of, for example, dissolved organic carbon or mucus (Crossland et al. 1980a, Crossland 1987). In Chapter 6, I will provide a more detailed analysis of the energy acquisition in corals and will limit the introduction here to a focus on energy allocations to growth. 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 skeletal growth, but is linked to processes driving the calcification process (Barnes and Chalker 1990, McConnaghey and Whelan 1997, see below). The uptake of inorganic carbon, however, has recently been shown to enhance skeletal growth (Marubini & Thake 1999).

At high particle loads, energy costly processes such as active sediment rejection would lead to an increase in both *R* (Dallmeyer et al. 1982, Telesnicki & Goldberg 1995) and *EX* through the production of mucus (e.g. Schuhmacher 1979, Dallmeyer et al. 1982, Riegl and Branch 1995), and consequently a decrease in *SfG*. Also, respiration increases with light intensity (Barnes & Chalker 1990), thus presumably with photosynthesis, as well as with rate of feeding (Szmant-Froelich & Pilson 1984), further placing constraints on *SfG*.

The role of nutrients in the synthesis of tissue (e.g. proteins, carbohydrates, and lipids) is perhaps of greater importance than carbon fluxes for the *SfG* of hermatypic corals, and mixotrophic organisms in general. Photosynthesis mainly provides carbon to the symbiosis (e.g. Muscatine et al. 1984, Spencer Davies 1984, reviewed by Muscatine 1990) although the associated uptake and production of essential nutrients are also facilitated by photosynthesis (Hoegh-Guldberg, pers. com.). Particle heterotrophy, on the other hand, provides both carbon and nutrients directly, including essential nutrients that may otherwise limit growth of the symbiosis. Thus, *SfG* relevant to tissue synthesis may be strongly dependent on the uptake rates of particulate (via heterotrophy) or dissolved nutrients. Such nutrient limitation is well demonstrated for phototrophic organisms in general (e.g. phytoplankton: Caperon and Meyer (1972); higher plants: Koerselman and Meuleman (1996); and for the coral-alga symbiosis in particular (e.g. Hoegh-Guldberg & Smith 1989, Dubinsky & Jokiel 1994, Muller et al. 1994) where it may be evident as high excretion rates of mucus in oligotrophic, high-light environments (Crossland 1987)). The scope for energy investment into tissues in such conditions may thus be compromised by high values of *EX*. The use of *SfG* as a measure of stress under high photosynthetic rates and normal nutrient levels, however, is not intuitively meaningful because corals are highly efficient at taking up nutrients at low concentrations (Muscatine & D'Elia 1978) as well as at conserving nutrients (Szmant et al. 1990), but may become relevant at high nutrient levels where toxicity is likely (Butcher 1994, Ward 1994).

Energy investment into skeletal growth is not directly nutrient limited since coral skeletons mainly consist of $CaCO_3$ (Barnes & Chalker 1990), but may indirectly depend on the ability of the tissue surface area to keep pace with skeletal growth rates. Conversely, nutrient enrichment tends to suppress skeletal growth rates (e.g. Marubini & Thake 1999). Most coral growth studies have measured changes in the skeleton exclusively (reviewed by Brown and Howard 1985) and have largely ignored tissue growth. Skeletal growth, as determined by linear extension of especially branching morphologies, may correlate closely with tissue growth due to the concomitant increase in surface area, but skeletal growth may be

a poor indicator of coral energetics if tissue thickness (e.g. lipid contents, carbohydrates, proteins) varies inversely with rates of linear extension. Paradoxically, energy equivalents of calcification *per se* have not previously been attempted, except from estimates by Falkowski et al. (1984) and Muscatine et al. (1984) based on the incorporation of ^{14}C into the skeleton of *Stylophora pistillata*. Unfortunately, energy equivalents of calcification estimated by this method produce spurious results with no relevance to *SfG* because ^{14}C is both precipitated and dissolved from the skeleton during incubation (Barnes & Crossland 1977). Recently, McConnaghey and Whelan (1997) presented an ATP stoichiometry for the exchange of Ca^{2+} ions over the membrane of calicoblastic cells in calcifying organisms such as corals, which enables the energy cost of calcification to be estimated, assuming that this is the only metabolic activity involved in calcification. Thus, using conventional methods of determining tissue enthalpies and the above stoichiometry for estimating energy investment into skeletal mass, this study will for the first time quantify the energetics of skeletal growth rates for corals in controlled sediment and light regimes.

In this study I quantify for the first time the effects of sediment concentration and light regime on the growth energetics of two coral species with contrasting sediment-feeding capacities. My primary objective is to evaluate the significance of particle heterotrophy in offsetting stress effects of high turbidity. As growth integrates over both energy-consuming (catabolic) and energy-producing (anabolic) physiological processes (Buddemeier & Kinzie 1976, Neudecker 1981, Sebens 1982, Widdows et al. 1995), it provides direct insights into the stress versus resource potentials of the environment (see also review by Maltby 1999)

For the purpose of testing the hypothesis that particle heterotrophy can offset stress effects in corals on turbid reefs, I will focus mainly on *SfG* in scenarios where photosynthesis is reduced as a result of light attenuation, and where increased sediment accumulation or abrasion may lead to elevated *R* and *EX*. Further, given that particle concentrations and light availability are inversely related on subtidal inshore reefs (Chapter 1), I test the hypothesis that intermediate particle concentrations are more optimal for growth than extreme low or high concentrations, and that the relative optimum will differ among species with different trophic strategies. This analysis of *SfG* among habitats and nutritional strategies has implications for the physiological niches of corals, and hence the energetic basis for growth and survival in high-turbidity regimes, topics which will be explored further in Chapter 6.

5.3. MATERIALS AND METHODS

5.3.1. Study species

To investigate the significance of high rates of sediment feeding for the energy budgets of corals in turbid habitats, I conducted a pilot study to identify two common species of zooxanthellate scleractinian coral with contrasting heterotrophic capacities. Potential study species were selected based on the following selection criteria: (1) a widespread distribution on inshore or midshelf reefs in the Great Barrier Reef lagoon, (2) high relative abundance on reefs surrounding the Palm Islands to enable high replication, ease of sampling and transport to Orpheus Island Research Station (see Chapters 3 and 4) where the study was to be conducted, and (3) probability that samples would show minimal trauma due to collecting or containment in tanks over the time scale of months. *Porites cylindrica*, used previously in feeding experiments (Chapter 2) and in the pilot growth study (Chapter 4) was selected as an example of a poor sediment feeder. Candidates selected for the good sediment feeder were: *Galaxea fascicularis, Goniastrea retiformis, Goniopora columna, and Turbinaria peltata.* All of these species have large polyp sizes (> 3 mm diameter) and a relative low height-to-width ratio of colonies which were assumed to indicate high probability of particle capture, notably of large sedimenting particles (Abelson et al. 1993, Johnson & Sebens 1993). The sediment-feeding responses of these species were determined and compared using the protocols outlined in Chapters 2 and 3 (i.e. using ^{14}C-labelled SPM at concentration 1, 4, 8, 16, 30 mg dw/L).

The results of the pilot feeding trials showed that *Goniastrea retiformis* and *Porites cylindrica* represented upper and lower extremes in a continuum of SPM-feeding capacities (Fig. 5.1). The rate of sediment ingestion by *G. retiformis* increased linearly by more than 60-fold over the 30-fold increase in sediment concentration and was one order of magnitude higher than the feeding rate of *P. cylindrica*. *G. retiformis* forms encrusting to dome-shaped colonies with large polyps (up to 5 mm diameter), enabling it to utilise the vertical fluxes of sedimenting particles, whereas *P. cylindrica* has a digitate to branching growth form and small polyps (~1 mm diameter) which reduces the likelihood of it using settling sediment (Fig. 5.2). *G. retiformis* occurs on intertidal reef flats as well as subtidally in most reef habitats of the Great Barrier Reef and *P. cylindrica* is confined to subtidal lagoonal areas (Veron 1986b).

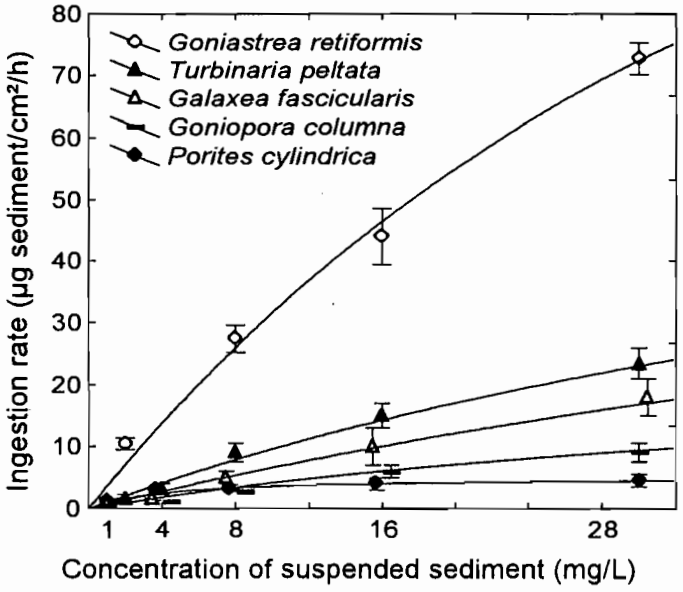

Fig. 5.1. Rate of sediment ingestion as a function of sediment concentration for five common inshore coral species. The comparison was conducted to identify two species with contrasting SPM-feeding capacities for growth (this chapter) and energetics (see Chapter 6) studies. Ingestion was measured as uptake of ^{14}C-labelled particles according to protocols in Chapters 2 and 3.

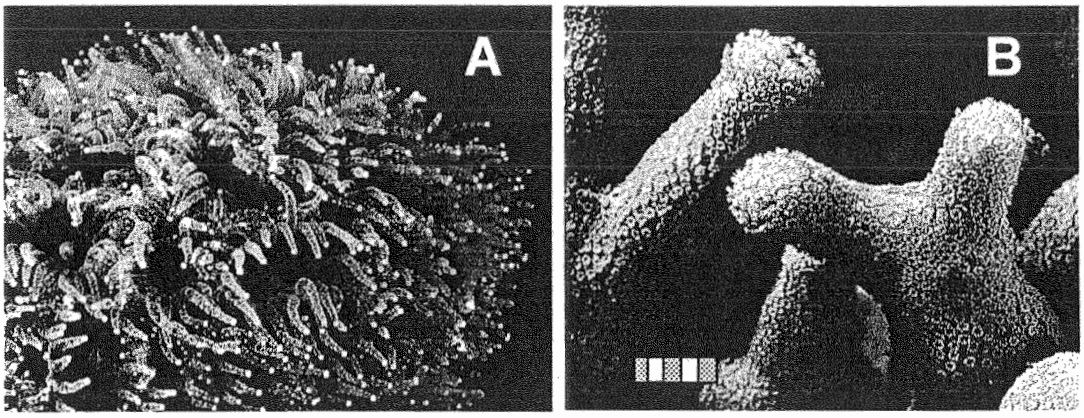

Fig. 5.2. Comparative size of expanded polyps of the study species *Goniastrea retiformis* (A) and *Porites cylindrica* (B). The scale bar is 5 mm and applies to both panels.

5.3.2. Experimental design

To investigate the long-term bioenergetics of corals in contrasting environmental conditions, effects of light/shade and particle treatments on tissue and skeletal growth rates were determined for ~250 colonies of *G. retiformis* and ~300 branches of *P. cylindrica* over an eight-week growth experiment. The study was conducted in the large flow-through tank system at Orpheus Island Research Station described in Chapter 4 (see also Anthony 1999b),

which for the purpose of this study was expanded to 32 tanks (volume of 46 liters each) to accommodate a larger two-factorial experimental design.

Two light regimes and four water-quality treatments were set up within the system. Sixteen tanks were covered with screens that allowed ~20% light penetration (Shaded, maximum subsurface I_{PAR} ~ 120 μE/m^2/s) whereas the remaining 16 tanks were left without additional shading under the solar-weave roof (Unshaded, max subsurface I_{PAR} ~ 600 μE/m²/s). The two light levels mimicked conditions at 3-4 m depth for particle concentrations of 4, and 16 mg dw SPM/L, respectively, and were selected based on the predictive model of Te (1997, see Fig. 5.3). As described for treatments in Chapter 4, each of the 32 tanks received a constant supply of seawater (0.60 ± 0.03 L/min). 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 SPM (High). The Moderate SPM treatment level used in Chapter 4 was omitted from this design to enable high within-level replication for the SPM and light treatments. Each SPM treatment level was replicated in eight tanks, of which four were Shaded and four left Unshaded, and each tank contained 7-9 coral colonies of each species. The levels of replication for tanks and corals within tanks were chosen based on the results of power analyses for growth rates of *P. cylindrica* in Chapter 4. The spatial arrangement of tanks with different light levels, filtration levels and levels of particle addition was randomised to control for the effect of tank position.

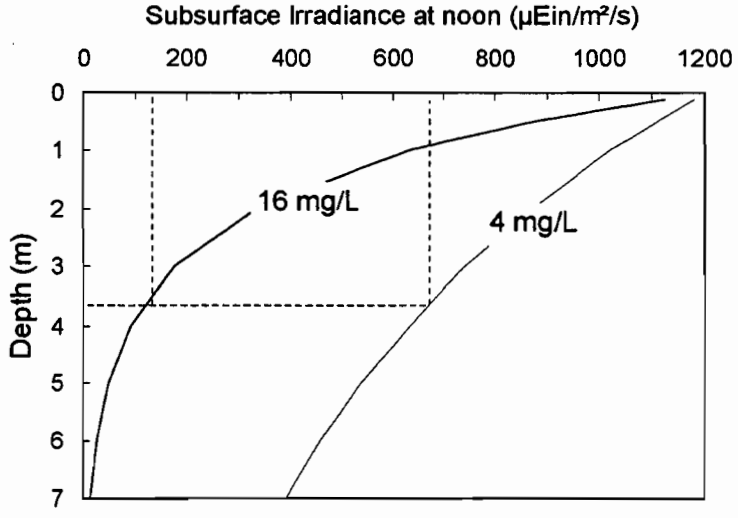

Fig. 5.3. Predicted light profile through the water column at two particle concentrations used to determine corresponding light levels for the growth experiment in the tank system. The light curves were calculated using the relationship $I = Io \cdot exp(-z \cdot \beta Csp)$, where I is irradiance (μE/m²/s), Io is the light level immediately

below the surface (μE/m²/s), z is depth (m), *Csp* is particle concentration (mg dw/L) and β is a proportionality constant (m·L/mg) relating *Csp* to the extinction coefficient (m^{-1}, see Kirk 1994). β was assumed to be 0.04 m L/mg for inshore SPM based on the results of Te (1997). See Chapter 6 for a more detailed description of the light-SPM relationship.

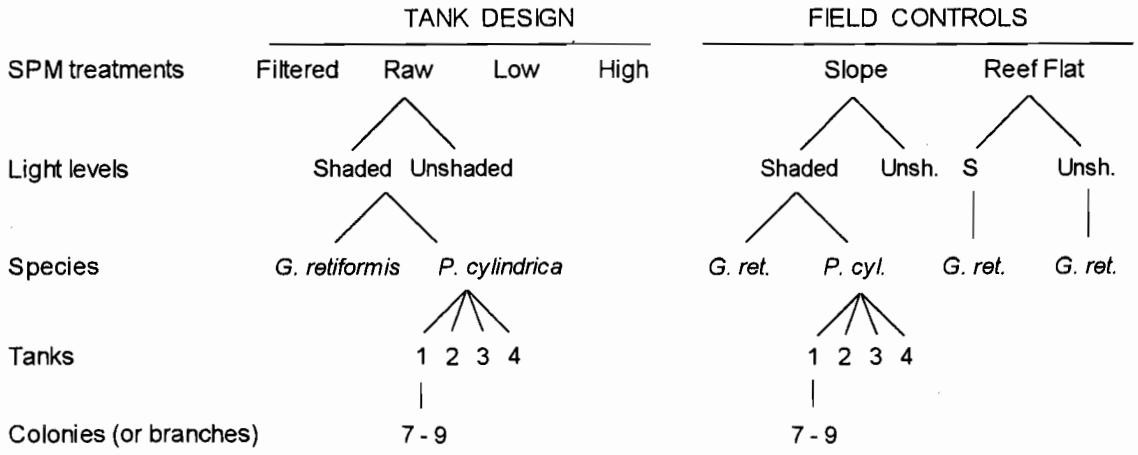

Fig. 5.4. Experimental design for the growth study in 1997. Particle concentrations and light levels were orthogonal fixed factors, and the factor Tanks was nested within the two fixed factors. Species were analysed separately due to within-tank dependence, and the factor species was thus not included in the ANOVA model.

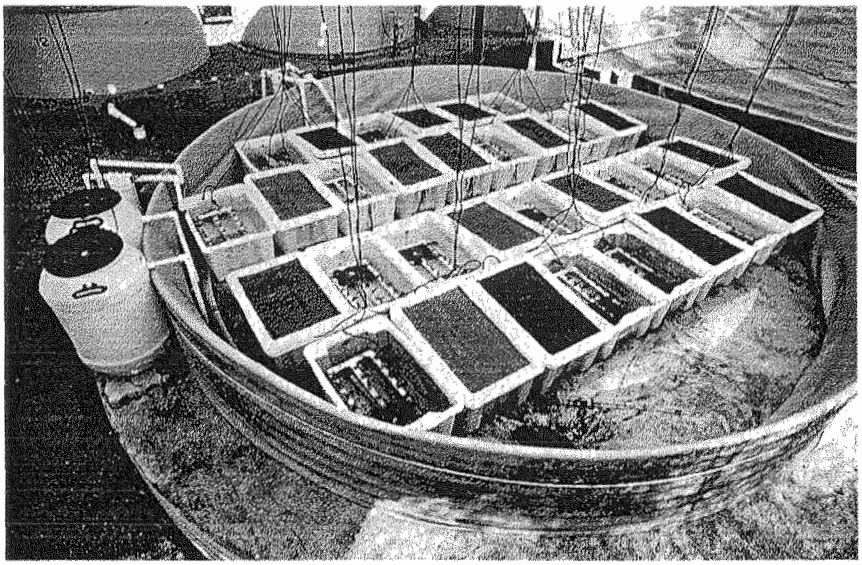

Fig. 5.5. Experimental tank set-up at Orpheus Island Research Station. The four particle treatments and two light levels were randomly interspersed among tanks within the pool to control for environmental heterogeneity. The two drums to the left hold the sediment stock suspensions. Shade-cloth covers are visible on tanks in the shaded treatment.

Particles were dispensed automatically from stock suspensions of natural SPM (collected daily by filtration of water pumped from the reef, see Chapter 4) to each of the eight Low and eight High treatment tanks such that final concentrations were 3.9 ± 0.5 and 15.8 ± 1.4 mg dw/L, respectively. To obtain these ranges, the intervals between sediment pulses were set to T = 10 min, seawater flush rate to FR = 0.60 ± 0.03 L/min, and particle delivery per pulse per tank for high and low treatments to PD_{High} = 115 ± 8 mg dw, and PD_{Low} = 28 ± 2 mg dw, respectively. See Chapter 4 and Anthony (1999b) for details of the adjustment of system parameters. In the filtered treatment, particles smaller than 1µm and autochthonous material from algal growth resulted in particle concentrations of 0.5 - 0.7 mg dw/L. To monitor the carbon and nutrient contents of the suspended particles, water samples were taken every 2-3 days from each treatment, and from the field sites at high tide. The samples were processed as described in Chapter 4, including analyses of organic C and total N. Reactive particulate phosphorus was determined by persulphate digestion using a technique modified from Parsons et al. (1984). SPM concentrations in the treatment groups were maintained well within the predicted range of target concentrations throughout the experimental period Table 5.1).

Counter intuitively, particle concentrations in the control tanks were ~30% higher than those measured at the slope or on the reef flat. As also observed in Chapter 4, autochthonous material in the filtered tanks produced a relatively high particle concentration (~0.7 mg dw/L), but which was less than half that of tank controls (Raw). Furthermore, organic carbon content of the SPM in stock suspensions was significantly lower than that of the SPM at the two field sites (slope and reef flat), suggesting, for example, that mineralisation occurs in the sand filters or in the settling tanks. Nitrogen and phosphorus of the experimental SPM, however, were not significantly lower than that of SPM *in situ* (Table 5.1).

Table 5.1. Concentrations and quality of suspended particulate matter in the tank system (stock suspensions) and in the field at different sampling occasions during the two-month growth experiment. Values are mean weight percentages ± standard error of samples from N days during the experimental period. nd = not determined.

Particle concentrations (mg dw/L)

Tank set-up	Mean	SE	N	Field controls	Mean	SE	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				

	Stock suspensions			Reef slope			Reef flat		
Particle quality (% of dw)	Mean	SE	N	Mean	SE	N	Mean	SE	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	0.01	14	nd		

The light regime under the solar-weave roof was monitored continuously over the eight-week experiment using a quantum sensor (Licor, LI-192S) positioned centrally 2 m above the tanks and coupled to a datalogger (Licor, LI-1000). At 2-4 day intervals, light was also measured underwater in tanks from all treatments and compared with concurrent readings of the overhead sensor. Ratios of within-tank and overhead measurements were used to estimate light regimes in the treatment tanks at all times during the experiment. Water temperature in the tanks, recorded daily during the experiment, ranged from 26.5 to 28°C.

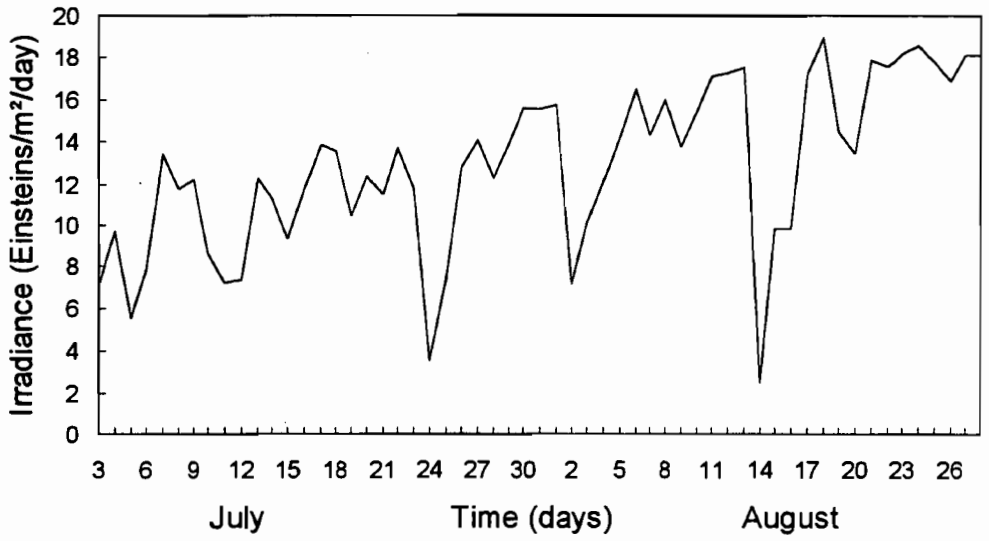

Fig. 5.6. Daily, accumulated light (PAR) levels under the solar-weave roof during the growth experiment as measured half-hourly by an overhead Licor quantum sensor and integrated over each day.

5.3.3. Collection of coral colonies

Coral colonies were collected from fringing reefs on the western (coastal) side of Orpheus Island. Small encrusting to dome-shaped colonies of *Goniastrea 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 all colonies were cleaned of epibionts and tagged. Terminal branches of *Porites cylindrica* (6 - 8 cm long) were collected from the reef slopes in Pioneer Bay and adjacent bays and mounted on numbered stands. 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. For *G. retiformis*, colonies below puberty size (~50 cm², Hall and Hughes 1996) were specifically targeted to ensure that energy investment into tissues were allocated to somatic growth rather than to gonads. Fragments of larger colonies are likely to undergo reversed puberty (Kojis & Quinn 1985, Szmant-Froelich 1985) so the branches of *P. cylindrica* were assumed to invest solely in somatic growth.

Immediately prior to the growth experiment, all corals were transported from the reef site to the tank system and distributed randomly among tanks. Each tank held 6-7 colonies of *G. retiformis* (total of 24-28 replicate colonies per treatment group) and 7-8 branches of *P. cylindrica* (28-32 per treatment group). All corals were mounted on racks suspended 10 - 15 cm below the water surface and above a pump that generated water circulation and

kept particles in suspension. To control for tank artefacts, corals on racks were also transferred back to the reef and exposed to the same light treatments. 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 7 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 experienced by these corals were 2-3 fold those in the tank system and on the reef slope, depending on the tide. It was necessary to cage the field controls of *G. retiformis*, as preliminary observations of colonies transplanted to the slope site indicated that they were prone to predation by fish.

5.3.4. Measurements of colony size and growth rate.

5.3.4.1. Changes in colony surface area and buoyant weight.

Growth rates of coral colonies or branches were determined primarily from changes between days 1 and 60 in their buoyant weight (ΔW_B, mg) using the technique described by Spencer Davies (1989). Changes in tissue surface area (ΔS, cm²) and skeletal dry weight (ΔW_{Sk}, mg) were later derived from ΔW_B. At day 60 of the growth experiment, both W_B and S were determined for all corals, and the relationship $S = a\ W_B{}^C$ was determined for each species using non-linear regression (STATISTICA 1997). For *G. retiformis*, S was modelled as a sphere cap, based on the mean of the largest and smallest diameters, and the height of the live part of the colony. For *P. cylindrica*, S was determined based on combinations of basic geometrical shapes of individual branchlets (cones, cylinders, and hemispheres). Geometric modelling was preferred over the more accurate foil-wrap technique (Marsh 1970), since the latter technique was likely to stress the live corals. Based on a subset of 14 corals per species, however, a t-test for paired comparisons indicated that S determined by both methods did not differ significantly (*G. retiformis*: $t_{(13)} = 1.45$, P (two tailed) = 0.17; *P. cylindrica*: $t_{(13)} = 0.58$, P (two tailed) = 0.57). To enable the conversion of W_B to W_{Sk}, 15 coral colonies (or branches) with known W_B were bleached in 10% chlorine to remove tissues and dried at 50°C until constant weight. The relationship $W_{Sk} = a \cdot W_B + c$ was determined for both species using linear regression and used to convert W_B to W_{Sk}.

5.3.4.2. Growth of tissue mass

To estimate changes in tissue dry weight per cm² surface area (ΔW_{Tis}, mg/cm²) under the different turbidity regimes, 15 corals of each species were collected in the field prior to the growth experiment and 7-8 corals were sampled from each treatment group at completion of the experiment. Surface areas of these colonies were measured by foil wrapping before they were preserved using 7% formalin in freshwater for 24 h, decalcified in sequential solutions of 1-4% HCL, and the tissue samples dried at 50°C until constant weight. Because this fixation and decalcification process may lead to some loss of tissue (Hoegh-Guldberg, pers. com.), the method may have produced underestimates of tissue growth. Also, because determination of tissue dry weight is a destructive technique, it was assumed that the field subsample was representative of the tissue dry weight per unit area of all corals before experimental treatment. ΔW_{Tis} was therefore determined for each experimental coral by subtracting the representative pre-experimental from the measured post-experimental area-specific tissue mass adjusted for changes in tissue surface area, thus

$$\begin{aligned} \Delta W_{Tis} &= (W_{Tis2} \cdot S_2 - W_{Tis1} \cdot S_1)/S_1 \\ &= W_{Tis2} \cdot S_2/S_1 - W_{Tis1}, \end{aligned} \tag{5.2}$$

where W_{Tis1} and W_{Tis2} are tissue masses per unit area (mg/cm²) before and after the experiment, and S_1 and S_2 are colony tissue surface areas (cm²) before and after the experiment (see above).

5.3.4.3. Changes in lipid stores:

To determine build-up or exhaustion of energy stores, lipid contents were assayed for 10 freshly collected colonies (or branches) of each species prior to the growth experiment and for 7-8 conspecifics from each treatment group 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 it to a powder. Lipids were extracted from the powder with chloroform: methanol (2:1, v/v) using the techniques described by Folch et al. (1957) and Harland et al. (1992). Total lipid content was determined gravimetrically to the nearest 0.1 mg after drying the extracts, and lipid content was normalised to unit surface area of tissue (W_{Lip}, mg/cm²). Analogous to ΔW_{Tis}, changes in lipid content (ΔW_{Lip}, mg/cm²) were each calculated as the difference in lipid content between pre- and post-experimental corals, adjusted for difference in colony size.

5.3.4.4. Modelling energy 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 (pers. com. Kathy Burns). Preliminary analyses of tissue energy contents using bomb calorimetry of dried tissue samples produced relatively low values and suspiciously low variability among treatments (see Table 5.2). Instead, using the lipid-tissue ratio method, I assumed that tissue mass other than lipids comprised proteins and carbohydrates in the ratio 1:2 as reported for sea anemone tissue (Zamer & Shick 1989). Energy allocation to tissue growth (ΔE_{Tis}, J/cm²) was then calculated from enthalpies of combustion based on the following values listed by Gnaiger and Bitterlich (1984): -39.5 J/mg for lipid, -23.9 J/mg for protein, and -17.5 J/mg for carbohydrates. Non-lipid tissues ($\Delta W_{Tis} - \Delta W_{Lip}$) were therefore assumed to have an enthalpy of combustion of -(2 × 17.5 + 23.9)/3 J/mg = -19.6 J/mg. Energy investment into tissue (positive) was thus estimated as

$$\Delta E_{Tis} = 39.5\ J/mg \cdot \Delta W_{Lip} + 19.6\ J/mg \cdot (\Delta W_{Tis} - \Delta W_{Lip}) \qquad (5.3)$$

Table 5.2. Energy content of coral tissue samples from four treatment groups assayed by bomb calorimetry at completion of the growth experiment. Data are in Joules per mg of dry tissue weight. Tissue energy content of unshaded corals was slightly, though not significantly, higher than that of shaded corals.(ANOVA, *G. retiformis*: F(1,13) = 1.06, P = 0.32; *P. cylindrica*: F(1,10) = 0.93, P = 0.36). Due to the likelihood that formalin fixation and decalcification affect energetic properties of the tissues resulting in underestimates of enthalpies, energy investment into tissues was instead estimated based on changes in lipid content relative to total tissue mass.

	Shaded			Unshaded		
Treatment group	Mean	SE	N	Mean	SE	N
G. retiformis						
Filtered	20.48	0.61	4	21.52	0.86	4
High particle concentration	20.77	0.74	6	21.33	0.75	5
P. cylindrica						
Filtered	20.44	0.89	3	21.56	1.41	4
High particle concentration	20.79	0.83	4	21.08	1.08	4

Energy equivalents of skeletal growth (ΔW_{Sk}) were estimated based on the model that one ATP is used for energising the uptake of two Ca^{2+} ions by the site of calcification in exchange of four protons (McConnaghey & Whelan 1997). Assuming that this exchange is the only energetic expense of skeletal growth, the precipitation of 1 mg dw of $CaCO_3$ requires 5 µmoles of ATP, which equates to 0.152 J (Zubay 1983). Energy investment into skeletal growth (ΔE_{Sk}, J/cm²) was thus estimated as

$$\Delta E_{Sk} = 0.152\ J/mg \cdot \Delta W_{Sk} \quad (5.4)$$

Based on the results of Allemand et al. (1998) the energy invested into organic matrix compared to that invested into inorganic skeleton is negligible. For example, Allemand et al. (1998) estimated that for every 3.8×10^6 moles of Ca^{2+} incorporated into the skeleton only one mole of aspartic acid was incorporated into the organic matrix (aspartic acid may comprise up to 50% of the organic matrix proteins). Converting this ratio to units of mass and subsequently to energy equivalents for the transport of Ca^{2+} (0.152 J/mg dw $CaCO_3$) and the enthalpy of proteins (23.9 J/mg dw) produces an energy ratio of ~7000. Even by assuming that aspartic acid constitutes a low 10% of the organic matrix, energy invested into the organic matrix is three orders of magnitude less than the energy invested into $CaCO_3$.

The variance and standard errors of energy investment into tissue and skeletal growth of each adjusted group mean were calculated from the composite variances from all variables involved using the method by Travis (1982) in which the variance V of product X_1X_2 is 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 a the product of a constant and a variable (Xc) was calculated as Vc^2.

Effects of shading and SPM concentration on ΔE_{Tis}, ΔE_{Sk} and total energy investment ($\Delta E_{Tis} + \Delta E_{Sk}$) were tested for each species separately using two-way ANOVAs based on means and composite variances for each treatment group. 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 included in the analysis. I used the conservative Tukey's HSD test to locate significant differences between individual treatment groups.

5.4. RESULTS

5.4.1. General observations

Survivorship of *Goniastrea retiformis* in the tank system was 100%, and all colonies of this species appeared healthy in all treatments at conclusion of the experiment. Colony health was inferred from the lack of change in tissue colour and the normal behaviour of polyps, which continued to expand nightly 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* was not related to treatment ($\chi^2_{(4)} = 3.73$, P = 0.44). The polyps of *P. cylindrica* were generally extended day and night, except during occasional 2-3 d periods of mucus-sheath production. The area-specific tissue mass of *G. retiformis* (15-20 mg dry weight/cm²) was almost twofold that of *P. cylindrica* (7-10 mg dry weight/cm²).

5.4.2. Effects of turbidity on total energy investment

Total energy investment into growth ($\Delta E = \Delta E_{Tis} + \Delta E_{Sk}$) was negatively affected by shading in both *G. retiformis* and *P. cylindrica* (Fig. 5.7, Table 5.3). Shading, corresponding to 3-4 m depth *in situ* under high turbidity (~16 mg SPM/L), caused a 37 ± 8% decrease in energy investment in *G. retiformis*, and a 64 ± 7% decrease in that of *P. cylindrica* (Fig. 5.7A). Patterns of energy investment caused by SPM treatments, however, differed between species. In *G. retiformis*, ΔE increased almost monotonically with increasing SPM concentration, especially in the Shaded treatments. For example, ΔE for corals of this species in the High treatments (Shaded and Unshaded combined) was on average 82 ± 9 % greater than that of conspecifics in the Filtered treatments (Fig. 5.7A). Importantly, ΔE of *G. retiformis* in the High treatment did not differ significantly among light levels, whereas ΔE's of corals from the Raw and Low treatments were significantly higher in the Unshaded treatment. For *P. cylindrica*, ΔE of corals in the intermediate SPM treatment (Low, 4 mg dw/L) was more than two-fold that of corals in the Filtered treatments for both shaded and unshaded corals. Also, *P. cylindrica* in the Unshaded/Low

treatment showed 2-fold higher energy investment than corals in the Unshaded/High treatment. The combination of shading and high particle concentration resulted in net energy loss for *P. cylindrica*.

Total energy investment by corals in control tanks (Raw treatments) generally did not differ from that of field controls in either species, except that ΔE_{Tis} of Shaded *G. retiformis* on the reef slope (3-4 m depth) was 2-fold higher than that of corresponding tank controls (Fig. 5.7B). In contrast, Shaded and Unshaded controls of *G. retiformis* on the reef flat (0-1 m depth) were not significantly different from their corresponding tank controls, despite the higher light levels experienced by Unshaded corals on the reef flat (1000-1500 μE/m²/s at noon).

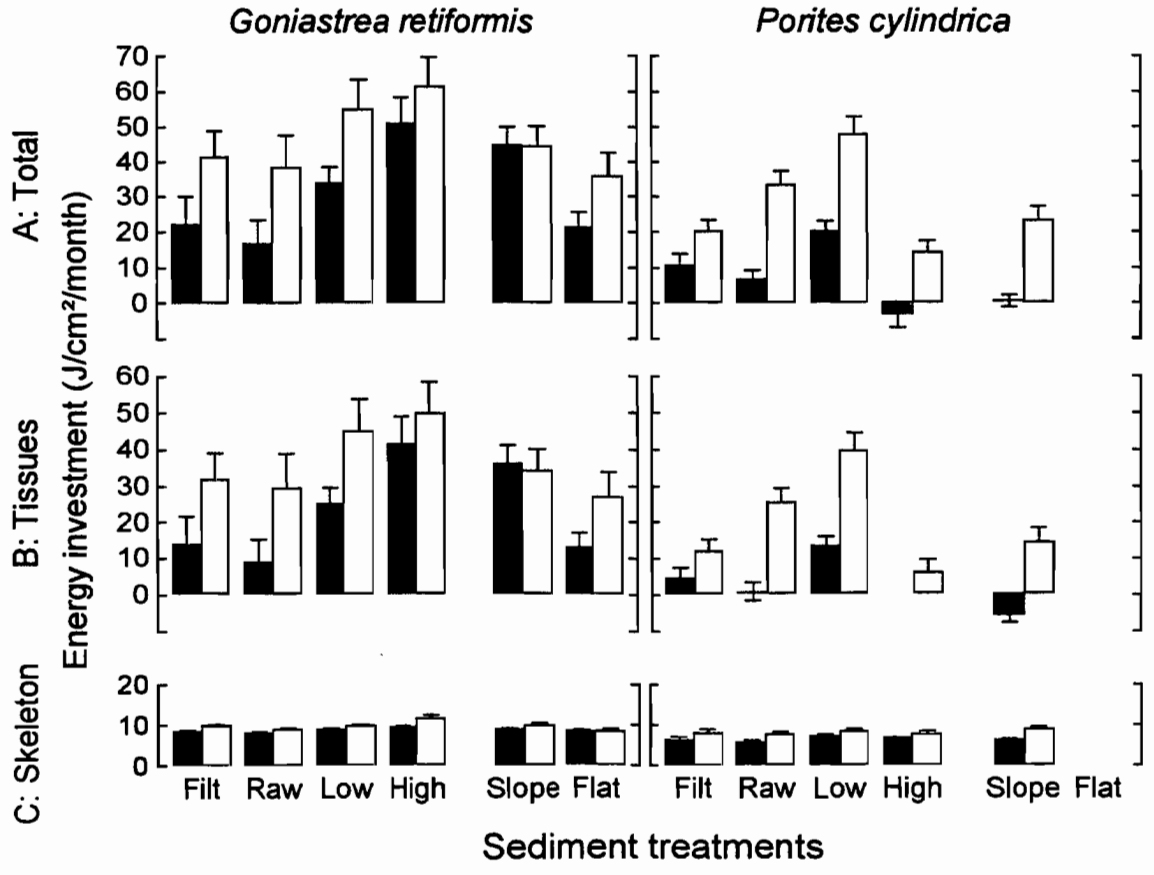

Fig. 5.7. Energy investment (J/cm²/month) into (**A**) total growth, (**B**) tissue growth, and (**C**) skeletal growth by corals exposed to different light and particle treatments. Data are means ± SE, the latter based on composite variances (see Section 5.3.4.4). Solid and open bars represent Shaded and Unshaded treatments, respectively. Tank 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 5.3 for results of ANOVAs.

Table 5.3. Summary of two-way ANOVA results for energy investment into tissues and skeleton (both in J/cm²/month) for corals in the eight main treatments (see also Fig. 5.7). Numbers in parentheses are degrees of freedom (df_1, df_2). * P < 0.05, ** P <0.01, *** P <0.001, ns non-significant.

Response variable	Source of variation	df	MS	F	P	Post Hoc †
Goniastrea retiformis						
Total ($\Delta E_{Tis} + \Delta E_{Sk}$)	Shading	1	4198.7	11.76	**0.001** **	US > SH
	SPM	3	1956.2	5.48	**0.003** **	Hi > Fi, Hi > R
	Shading X SPM	3	100.7	0.28	0.838 ns	
	Error	40	357.1			
Tissues (ΔE_{Tis})	Shading	1	3642.0	10.28	**0.003** **	US > SH
	SPM	3	1692.3	4.78	**0.006** **	Hi > Fi, Hi > R
	Shading X SPM	3	128.0	0.36	0.781 ns	
	Error	40	354.4			
Skeleton (ΔE_{Sk})	Shading	1	39.6	14.50	**0.001** ***	US > SH
	SPM	3	20.4	7.48	**0.001** ***	Hi > R
	Shading X SPM	3	3.5	1.29	0.283 ns	
	Error	88	2.7			
Porites cylindrica						
Total ($\Delta E_{Tis} + \Delta E_{Sk}$)	Shading	1	4918.3	50.05	**0.001** ***	US > SH
	SPM	3	1722.7	17.53	**0.001** ***	L > Fi , L > Hi, Fi > Hi
	Shading X SPM	3	217.1	2.21	0.102 ns	
	Error	40	98.3			
Tissues (ΔE_{Tis})	Shading	1	4224.5	44.35	**0.001** ***	US > SH
	SPM	3	1675.2	17.59	**0.001** ***	L > Hi, L > Fi
	Shading X SPM	3	219.6	2.31	0.091 ns	
	Error	40	95.3			
Skeleton (ΔE_{Sk})	Shading	1	61.5	20.42	**0.001** ***	US > SH
	SPM	3	4.5	1.49	0.222 ns	
	Shading X SPM	3	1.2	0.39	0.761 ns	
	Error	104	3.0			

Notes: The analysis was performed using untransformed means and composite variances.

† SH: Shaded, US: Unshaded, Fi: Filtered, R: Raw, L: Low, Hi: High

5.4.3. Tissue growth versus skeletal growth

Tissue growth. In both species, energy investment into tissue varied dramatically across sediment treatments (-8 to +50 J/cm²/month, Fig. 5.7B), whereas investment into skeleton varied within a relatively narrow range (7 to 10 J/cm²/month, Fig. 5.7C). Interestingly, ΔE_{Sk} remained positive in treatments where ΔE_{Tis} was significantly negative

(e.g. the Shaded/High treatment for *P. cylindrica*). Based on comparisons of mean squares for ΔE_{Tis} and ΔE_{Sk} (Table 5.3) almost 99% of the variation in ΔE among treatments was explained by the variation in ΔE_{Tis} for both species. Consequently, the pattern of total energy investment was mainly a function of tissue (rather than skeletal) growth. In almost all treatments, more energy was invested into tissue compared to skeletal growth in *G. retiformis* (ΔE_{Tis} = 70 ± 8% of ΔE), particularly for the High-SPM treatment groups and in most Unshaded groups. In *P. cylindrica*, ΔE_{Tis} of corals in the Unshaded/Low and Unshaded/Raw treatment groups were almost 4-fold those of ΔE_{Sk} Fig. 5.7A. On average, however, *P. cylindrica* showed equal partitioning between tissues and skeleton (43 ± 18%).

Skeletal growth. Due to low within-treatment variation in ΔE_{Sk} the ANOVA detected effects of both shading and SPM treatments on skeletal growth rate in *G. retiformis* and effects of shading on skeletal growth of *P. cylindrica* (Table 5.3). For example, comparisons of group means showed that ΔE_{Sk} of Shaded *G. retiformis* was ~13% lower than ΔE_{Sk} of Unshaded conspecifics. Similarly, ΔE_{Sk} of the High treatment was ~17% higher than that of the Filtered treatments. Thus, the patterns of skeletal growth among treatments resembled those of tissue growth in *G. retiformis*, but relative differences between group means were far less pronounced than for tissue growth. Compared to the above example, tissue growth of *G. retiformis* decreased ~43% due to shading and increased ~107% between the Filtered and the High treatment. In *P. cylindrica*, ΔE_{Sk} of Unshaded corals was ~19% higher than that of Shaded conspecifics, but varied less than 10% among SPM treatments. Again, in comparison, tissue growth of *P. cylindrica* decreased ~80% due to shading, and decreased >100% between the Filtered and High SPM treatment. However, the low within-treatment variation in ΔE_{Sk} was, in part, attributable to the strong correlation between colony skeletal dry weight (W_{Sk}) and colony buoyant weight in both species (W_B, Table 5.4B), enabling precise estimates of skeletal growth and greater power to detect treatment effects.

Table 5.4. Summary of regressions used to convert buoyant weight data to (A) colony surface area and (B) skeletal dry weight. See also Fig. 5.9 for relationship between buoyant weight and colony surface area.

Conversion	Species	Relationship	SE of exponent	R^2	N
A Colony surface area (S, cm^2)	*G. retiformis*	$S = 5.425\, W_B^{0.669}$	0.097	0.72	219
vs buoyant wt (W_B, g)	*P. cylindrica*	$S = 8.672\, W_B^{0.609}$	0.067	0.61	326
			SE of coefficient		
B Skeletal dry wt (W_{SK}, g)	*G. retiformis*	$W_{SK} = 1.576\, W_B + 0.353$	0.021	>0.99	16
vs buoyant wt (W_B, g)	*P. cylindrica*	$W_{SK} = 1.693\, W_B + 0.087$	0.029	>0.99	16

5.4.4. Effects of turbidity on lipid content relative to total tissue mass

The contributions of changes in lipid content to overall changes in tissue weight were variable in both species (ΔW_{Lip} accounted for 41% and 75% of ΔW_{Tis} in *G. retiformis*, and 13% to 82% of ΔW_{Tis} in *P. cylindrica*). Although ΔW_{Tis} was affected by both Shading and SPM concentration, ΔW_{Lip} was only affected by shading (Table 5.5). The effect of shading on ΔW_{Tis} and ΔW_{Lip} was stronger for *P. cylindrica* than for *G. retiformis* (Fig. 5.8, Table 5.5). Significant effects of shading were detected despite the ANOVA for tissue growth being encumbered with a large error contribution (~80%) from unexplained variation in the regression of S on W_B for both species (Fig. 5.9, Table 5.4A).

Build-up of matrix tissues was relatively greater than, or equal to, changes of lipid mass for some treatment groups . For example, rates of total tissue growth for *G. retiformis* in Low and High treatments at both light levels (as well as Shaded field controls) were 2-3-fold those of corresponding changes in lipid mass (Fig. 5.8AB). Similarly, for *P. cylindrica* growth of non-lipid tissues in the Unshaded/Low treatment was significantly greater than storage of lipids. The almost two-fold greater tissue mass per unit surface area of *G. retiformis* than *P. cylindrica* (see Section 5.4.1.) may explain the higher absolute increments in tissue growth and lipid storage of *G. retiformis*.

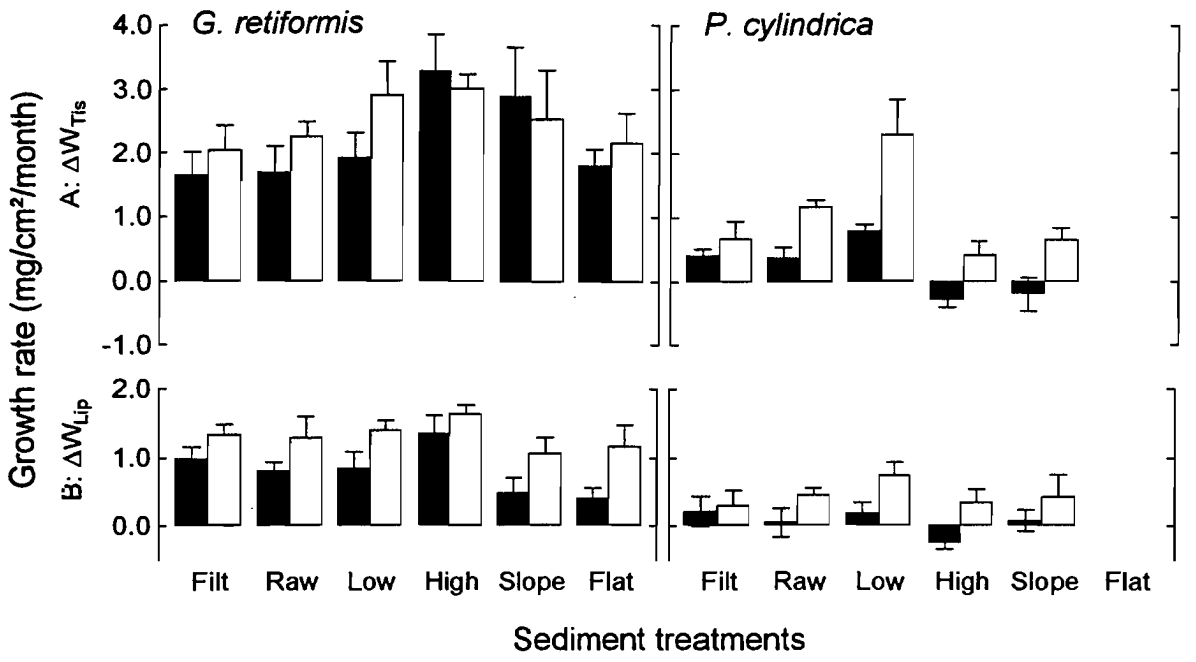

Fig. 5.8. Summary of changes in (A) tissue mass (ΔW_{Tis}) and (B) lipid content (ΔW_{Lip}) in corals exposed to different light and SPM treatments. All data are in units of mg/cm^2/month (adjusted means ± 1 SE of N = 6-9 corals). Symbols are as in Fig. 5.7. See Table 5.5 for ANOVA and ANCOVA results.

Table 5.5. Summary of two-way ANOVA* and ANCOVA** results for tissue growth and changes in lipid content (both in mg dw/cm²/month), respectively, for corals in the eight main treatments (see also Fig. 5.8). Numbers in parentheses are degrees of freedom (df_1, df_2). Symbols are as in Table 5.3.

Response variable	Source of variation	df	MS	F	P	Post Hoc †
Goniastrea retiformis	Shading	1	25.3	5.3	**0.025** *	US > SH
Tissue growth (ΔW_{Tis})	SPM	3	32.8	6.9	< **0.001** ***	Hi > Fi, Hi > R
	Shading X SPM	3	6.1	1.3	0.287 ns	
	Error	59	4.8			
Change in lipid content (ΔW_{Lip})	Shading	1	15877.9	4.9	**0.031** *	US > SH
	SPM	3	3253.0	1.0	0.410 ns	
	Shading X SPM	3	919.9	0.3	0.838 ns	
	Error	56	3262.2			
Porites cylindrica						
Tissue growth (ΔW_{Tis})	Shading	1	13.9	10.3	**0.003** **	US > SH
	SPM	3	6.6	4.9	**0.006** **	L > Hi, L > Fi
	Shading X SPM	3	1.1	0.8	0.513 ns	
	Error	35				
Change in lipid content (ΔW_{Lip})	Shading	1	1423.1	16.7	**0.001** ***	US > SH
	SPM	3	210.2	2.5	0.072 ns	
	Shading X SPM	3	54.2	0.6	0.595 ns	
	Error	54	85.1			

* Data for tissue growth were analysed using ANOVA due to slope heterogeneity of the tissue growth versus colony surface area regressions.

** Change in lipid content (log transformed) was tested using ANCOVA with initial colony surface area as the covariate.

† SH: Shaded, US: Unshaded, Fi: Filtered, R: Raw, L: Low, Hi: High

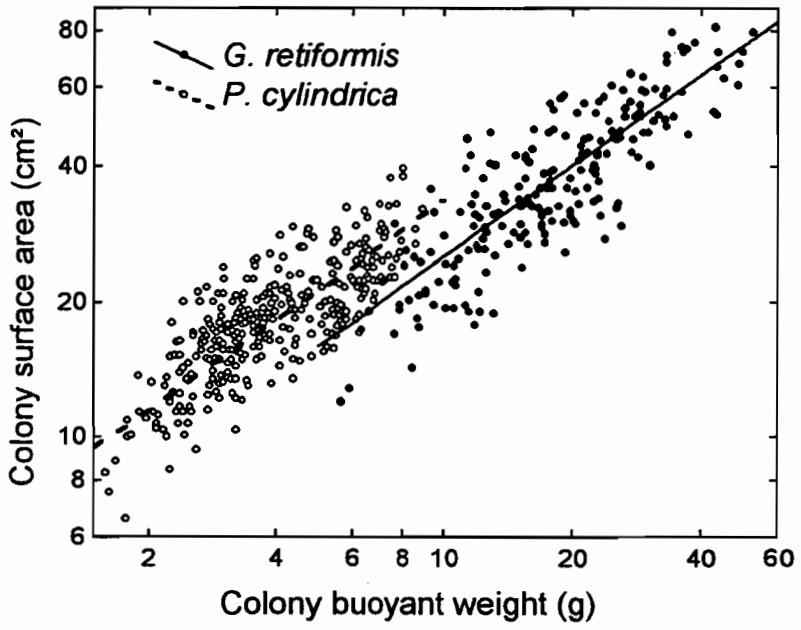

Fig. 5.9. Relationship between buoyant weight and colony surface area based on measurements prior to the growth experiment. The exponents of the power functions were not significantly different from that of a geometric solid (2/3), indicating isometric growth in both species within the experimental size ranges. See Table 5.4 A for details of regressions.

5.4.5. Modelling energy investment into tissue and skeletal growth

To investigate the ability of the general model for *SfG* to explain the observed patterns of energy investment into tissue and skeletal growth, I parameterised Eq. 5.1 (Section 5.2) with respect to daily integrated irradiance (I_d) and experimental particle concentration (C_{sp}) so that

$$SfG = P_{(Id)} + A_{(Csp)} + R_{(Id,Csp)} - EX_{(Id,Csp)}$$

For simplification, the unknown terms respiration (R) and excretion (EX) were reduced to the term total losses (L), with the assumption that rates of losses above basal metabolism and basal excretion are functions of both light and sediment concentrations. I further assumed that high light levels and high particle concentrations induce losses by their interaction rather than by additive effects. Since only two light levels were used in the experiment, $P_{(Id)}$ could in this case be modelled as a linear function of daily integrated light flux. The heterotrophic term, $A_{(Csp)}$ was modelled as a linear function for *G. retiformis* since its feeding did not show saturation over the range of particle concentrations tested (Fig. 5.1). Thus

$$SfG = k_1 \cdot I_d + k_2 \cdot C_{sp} - L_B(1 + k_3 \cdot I_d \cdot C_{sp}),$$

where L_B is baseline losses and k_1, k_2, *and* k_3 are coefficients. The heterotrophic term for *P. cylindrica*, which shows feeding saturation, was modelled using the Michaelis-Menten function with a half-saturation constant (K_m) of 3 mg dw/L (Chapter 2).

Tissue growth. Results of iterative non-linear fitting (STATISTICA, 1997) of the *SfG* models to energy investment into tissue growth produced highly significant coefficients (k_2) for the heterotrophic term in both *G. retiformis* ($A = k_2 \cdot C_{sp}$) and *P. cylindrica* ($A = k_2 \cdot C_{sp}/(C_{sp}$ + 3 mg dw/L, Table 5.6). The model was run for *P. cylindrica* with light level (I_d) omitted from the term enhanced losses as it severely underestimated the growth rate in the Unshaded/High treatment and overestimated that in the Shaded/High treatments, suggesting that losses are mainly governed by sediment rather than light in this species. As predicted from the results of the feeding trials in Chapter 2, the saturation model for the heterotrophic term in *P. cylindrica* explained a greater percentage of the variance than the linear model (89.4% and 78.5% respectively), whereas the linear model was optimal for *G. retiformis* (explaining 88.3 % of the variation, Fig. 5.10, Table 5.6). The light coefficient (k_1) for the autotrophic term ($P_d = k_1 \cdot I_d$) of *SfG* was also significant for both species. The non-significant coefficients for baseline losses and for enhanced losses (caused by increased sediment and light) in both *G. retiformis* and *P. cylindrica* predict non-significant net tissue growth under the conditions $I_d = 0$ and $C_{sp} = 0$ and that losses are not enhanced by high light and/or high sediment concentrations.

Skeletal growth. In *G. retiformis*, the autotrophic and heterotrophic parameters of the model (k_1 and k_2, respectively) were both non-significant (Table 5.6), suggesting that calcification proceeds independently of light level and sediment concentration. Although the ANOVA in Section 5.4.3. detected significant differences in skeletal growth as a consequence of both light and particle concentration, means varied by less than 20%, partially reflecting the apparently invariant nature of calcification in this species. The autotrophic term for skeletal growth in *P. cylindrica*, on the other hand, was significant whereas the heterotrophic term was not, analogous to the pattern for the ANOVAs. Significantly negative baseline losses of skeleton for both species predicted that calcification proceeds at zero light and feeding. This result may to some extent be an artefact of the simplified model and its assumptions, but is consistent with the high and relatively constant calcification rates across treatments, regardless of whether total energy investment was positive or negative (Fig. 5.7).

Table 5.6. Results of non-linear estimations of the coefficients for light (I_d), particle concentration (C_{sp}), and unknown losses (L_{Base} and its coefficient k_3) in the *SfG* model fit to the mean energy investment into tissue and skeletal growth for each treatment group. See also Fig. 5.10. Symbols are as in Table 5.3.

	G. retiformis				*P. cylindrica*			
	Est	SE	P	R^2	Est	SE	P	R^2
Total tissue growth								
k_1 *(Id)*	2.48	± 0.75	**0.030** *	88.3	2.21	± 0.55	**0.016** *	89.4
k_2 *(Csp)*	2.18	± 0.74	**0.042** *		78.16	± 24.48	**0.033** *	
L (baseline losses)	-4.47	± 6.15	0.508 ns		21.25	± 8.82	0.074 ns	
k_3 (loss coefficient)	0.09	± 0.09	0.371 ns		3.87	± 0.96	0.118 ns	
Skeletal growth								
k_1 *(Id)*	0.09	± 0.06	0.194 ns	89.7	0.20	± 0.06	**0.024** *	78.6
k_2 *(Csp)*	0.04	± 0.06	0.492 ns		3.67	± 2.53	0.221 ns	
L (baseline losses)	-8.04	± 0.46	**0.000** ***		-4.57	± 0.91	**0.007** **	
k_3 (loss coefficient)	-0.01	± 0.01	0.167 ns		0.12	± 0.10	0.301 ns	

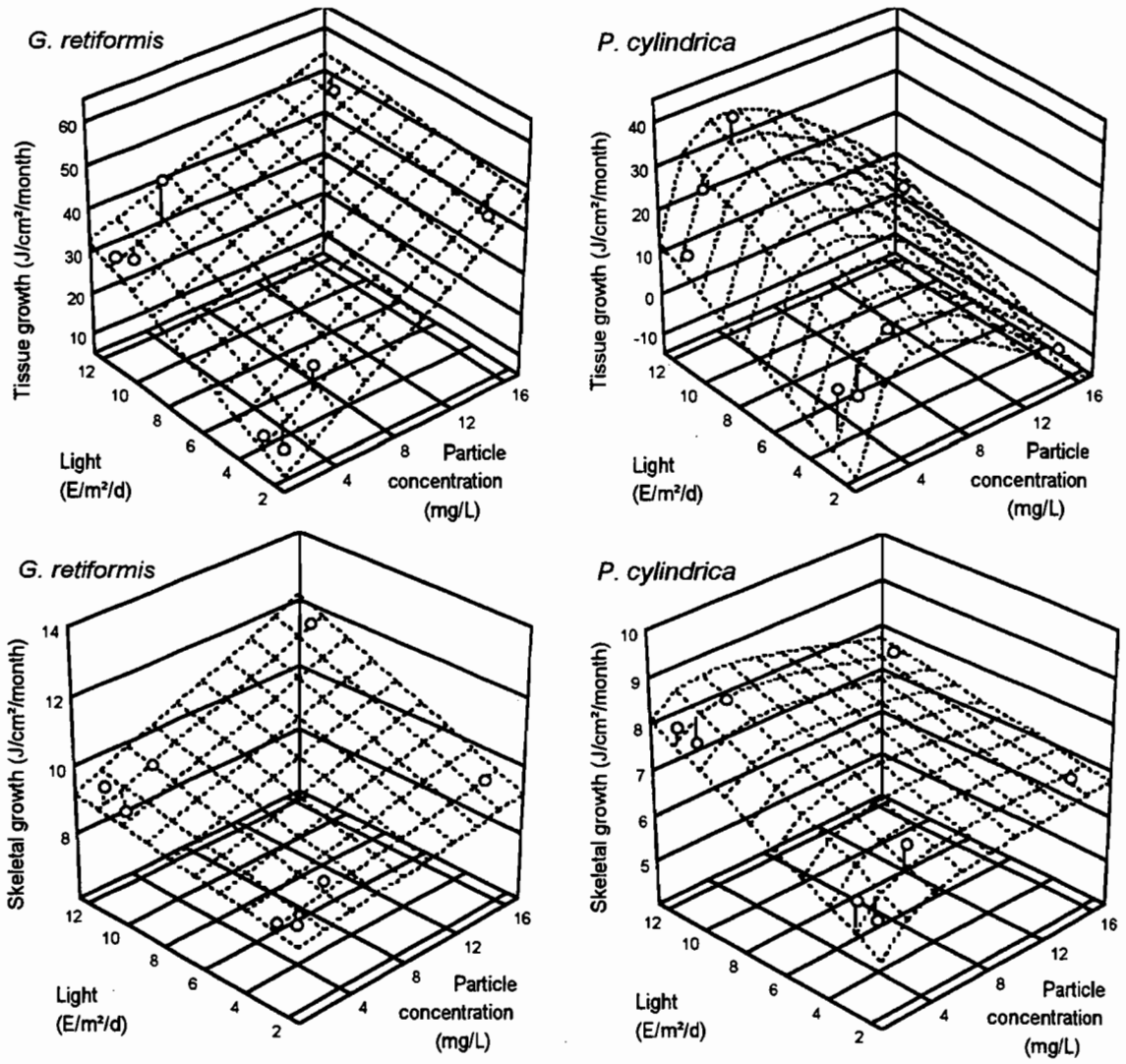

Fig. 5.10. Non-linear estimations of the model for *SfG* fitted to mean observed energy investment into tissue and skeletal growth of *Goniastrea retiformis* and *Porites cylindrica*. Note different scales on z-axes. See Table 5.6 for details of the parameter estimates.

5.5. DISCUSSION

5.5.1. Effects of SPM and shading on total energy investment

This study is the first to report a positive correlation between turbidity and growth in symbiotic corals. The almost two-fold higher energy investment into tissue growth by *Goniastrea retiformis* at High-SPM concentrations compared to conspecifics in particle-

depleted (Filtered) treatments and controls demonstrates that suspended sediment with an organic content as low as ~3% can represent a resource rather than a stress factor. The monotonic increase in growth as a function of sediment concentration in *G. retiformis* was consistent with the linear increase in feeding rates with sediment concentration reported in Chapter 2 for this species. Also, the maximum growth rate of *Porites cylindrica* at intermediate SPM concentrations (~4 mg dw/L) in both Shaded and Unshaded conditions, suggests that the nutrition of this species is improved by moderate increases in food availability. Interestingly, the reduced growth rate of *P. cylindrica* in the High sediment treatment was consistent with the half-saturation of feeding rates at Low sediment concentrations (~3-4 mg dw/L, Chapter 2). The significant suppression of *P. cylindrica's* total energy investment into growth in shaded, high-turbidity treatments, however, is consistent with the general results of previous studies of turbidity effects on coral growth (reviewed by Rogers 1990). For example, Dodge et al. (1974) reported a 30% decrease in the rate of linear extension of *Montastrea annularis* with an increase in rate of sedimentation from 0.5 to 1.1 mg/cm²/d; and Cortés and Risk (1985) predicted a further 30% decrease in this species with an increase in sedimentation rate from 10 to 200 mg/cm²/d. For comparison, sedimentation rate in the tank system was only 2.2-2.8 mg/cm²/d due to maintenance of a turbulent flow (Chapter 4), and therefore in the lower range of these sedimentation regimes (see also Woolfe and Larcombe 1998; Hopley et al. 1993). Direct sediment effects on *P. cylindrica* were therefore likely to result exclusively from mechanical abrasion by particles (or toxicity, see below) resulting in energy loss from increased rates of respiration or excretion. The highly significant coefficient for enhanced losses (attributable to sediment only) in the growth model supports this hypothesis.

Disregarding nutritionally advantagous effects of particle accumulation, any stress effect of sedimentation would have been expected to be found in *G. retiformis* rather than in *P. cylindrica* given the greater tendency of its massive growth form to trap sediment on its tissues. The opposite pattern observed in stress responses, however, can only be explained by a greater ability of *G. retiformis* to utilise sediment fluxes as food, and/or that abrasion by sediment fluxes and low feeding ability imposes stress (negative *SfG*) on *P. cylindrica* in shaded high–particle regimes. The constrast between tissue growth of the Shaded/High (negative by ~8 J/cm²/month) versus the Shaded/Filt (positive by >5 J/cm²/month) groups of *P. cylindrica* demonstrates that high sediment does constitute a stress effect in this species. For *G. retiformis*, this pattern was reversed as the tissue growth of corals in the Shaded/High was 3-fold that of conspecfics in the Shaded/Filtered

treatment. Given that sedimentation rates in the system were low relative to rates reported under corresponding turbidity regimes in other studies (see above), however, it cannot be ruled out that higher rates of sedimentation may cause stress in *G. retiformis*.

5.5.2. Tissue versus skeletal growth

The two orders of magnitude higher variability of energy investment into tissue growth relative to skeletal growth among sediment treatments was surprising, especially in view of the proportion of studies that have focussed entirely on skeletal growth in their assessment of disturbance effects on corals. To further emphasise the problem of such a non-integrated approach in assessing coral stress, skeletal growth of *Porites cylindrica* in the dark and turbid (Shaded/High) treatment proceeded at a rate not significantly lower than that of shaded corals at the other sediment levels, despite the fact that the rate of tissue growth for corals in this treatment was significantly lower and, more importantly, negative. Corals in significant energy deficit may thus sustain skeletal growth rates in the short-term, possibly by catabolising tissue reserves. A portion of the apparent tissue loss can be explained by the thinning of the tissue layer that will occur as skeletal volume increases if a disproportionate amount of energy is channelled into skeletal growth in stressful conditions, especially in branching geometries with high surface-to-volume ratios. Paradoxically, this will further reduce nutritional status per unit area of tissue surface. These findings render skeletal growth a poorer indicator of stress in corals than previously assumed (e.g. Buddemeier and Kinzie 1976, Gladfelter et al. 1978, Brown and Howard 1985, Vago 1997). In agreement with the results of this study, Brown et al. (1990) found that skeletal growth rates of intertidal colonies of *Porites lutea* did not differ significantly over a 9-month period of elevated (10-fold) rates of sedimentation caused by dredging, further questioning the efficacy of using calcification as an index of environmental stress.

Elevated sediment concentrations without the associated light attenuation, for example in intertidal habitats, are therefore less likely to cause adverse effects on calcification rates (see also Brown et al. 1990). Skeletal growth rates of both species in this study were adversely affected by shading as predicted by coral calcification models (reviewed by Barnes & Chalker 1990), indicating that high particle loads may impair skeletal growth of corals in deeper water. The relatively small effect size of shading on skeletal growth (<20%), however, indicates that calcification is relatively more robust to

fluctuating tubidity in deeper water than tissue growth, the latter varying >40% (*G. retiformis*) to 80% (*P. cylindrica*) over the same range of light levels.

The patterns of tissue growth among sediment and light regimes suggest two important roles of sediment feeding in coral nutrition, especially when related to the shapes of the feeding response curves of these two species. Firstly, enhanced growth in bright light and intermediate (or high) sediment loads strongly suggests that sediment feeding alleviates nutrient (e.g. N and P) limitation of the animal-alga symbiosis. Previous studies have shown that the majority of carbon fixed by zooxanthellae at high rates of photosynthesis does not contribute to coral tissue growth (e.g. protein synthesis) unless the carbon is coupled to a nutrient source (Muscatine 1990, Dubinsky & Jokiel 1994). Secondly, the increased tissue growth rate of shaded *G. retiformis* at high sediment concentrations provides evidence that sediment is also a significant source of carbon where light is limiting, even when the sediment contains little organic matter. Although particle feeding by *P. cylindrica* may be insignificant in terms of carbon equivalents (Chapter 2), it may be crucial in supplying essential nutrients to the coral-alga symbiosis at low to moderate SPM concentrations, and thereby increasing the efficiency by which photosynthetically fixed carbon is channelled into growth. The greater ability of the saturating feeding-response curve for *P. cylindrica* to explain its high growth rates at intermediate sediment regimes (in comparison to the linear response curve) adds further support to the nutrient-limitation hypothesis in corals. Despite the low nutrient content of suspended sediment (N ~ 0.5 %) relative to zooplankton (1-12 %, e.g. Corner and Davies 1971), the relatively greater abundance of SPM on inshore reefs is likely to render it the major nutrient supplier for corals. Recently, Schaffelke (in press) found that the growth rates of macroalgae are enhanced under high loads of particulate matter deposited on their thalli, which raises the hypothesis that nutrients leaching from deposited particles enriches the diffusive boundary layer over algal (and coral) tissues, facilitating a greater uptake rate of dissolved nutrients. Tissue growth may therefore be promoted by particle deposition on tissue surfaces in shallow water without high rates of sediment feeding, which could explain why tissue growth rates of unshaded *P. cylindrica* in the Low particle treatment (~4 mg dw/L) were higher than those in filtered, unshaded seawater (<0.7 mg dw/L), and higher than expected from rates of particle feeding.

The comparison of total tissue growth and change in lipid content suggests that the growth of non-lipid tissues is primarily stimulated by the availability of particles (food),

whereas the build-up of lipids is stimulated by light (photosynthesis). The likely explanation for this pattern is the greater dependence of protein synthesis on the supply of, for example, nitrogen (C:N w/w for protein = 7.7, Gnaiger and Bitterlich 1984), whereas storage of an equal amount of lipids requires a lower supply of nitrogen (C:N w/w for lipids = 12.5, Gnaiger and Bitterlich 1984), and may therefore show stronger correlation with photosynthesis.

The increased growth rates of corals in response to increased particle supply, as 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 depriving them of particulate food at shallow-water light levels. Johannes (1974) found that three coral species grew equally fast in 1 µm filtered seawater and in unfiltered seawater. However, particle concentrations in the unfiltered treatments were not quantified by Johannes (1974), precluding comparison of food availabilities between treatments. Also, 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.

5.5.3. Other potential effects of suspended particles

Fine particulate matter in nearshore environments of the GBR lagoon consists of terrigenous material to a large extent (Mitchell & Furnas 1997, Woolfe & Larcombe 1998). Such material, especially fine clays, have the capacity for adsorbing and carrying chemical contaminants to corals. In a comprehensive review of toxicity of marine sediments, Long (1992) found that concentrations of mercury and fluoranthene as low as 1 ppm were associated with adverse biological effects. Pollution effects of particulate matter on corals are probably of greatest significance in areas receiving sewage discharges from urban areas (Pastorok & Bilyard 1985), river run-offs from farmland catchments (Wasson 1997) or in areas where dredging occurs (Brown et al. 1990, Stafford-Smith et al. 1993a). The experimental sediment suspensions were not analysed for potential pollutants in this study, and it cannot be ruled out that the reduced growth in the High treatment was caused by particle-born contaminants if these led to increased metabolic activity or repair mechanisms and hence reduced scope for growth (Calow & Sibly 1990, Widdows et al.

1995, Maltby 1999). However, since the study area (Orpheus Island) is located relatively distant (>15 km) from any sources of pollution, the observed growth response by *P. cylindrica* at high particle concentrations is unlikely to be caused by particulate contaminants.

Chapter 6

The effects of turbidity on coral energy budgets: particle feeding vs photosynthesis and respiration

This chapter forms part of the publications:

- **Anthony, K.R.N. & K.E. Fabricius.** In review. Shifting roles of heterotrophy and autotrophy in coral energetics under varying turbidity. *J. Exp. Mar. Biol. Ecol.*
- **Anthony, K.R.N.** Submitted. Skeletal growth: a poor indicator of sediment stress in corals? *Coral Reefs.*

6.1. SYNOPSIS

In aquatic habitats, concentrations of suspended particulate matter (SPM) and light availability are inversely related. For photosymbiotic and suspension-feeding benthic invertebrates, changes in particle concentrations and sedimentation may thus require heterotrophic and phototrophic adaptations to sustain a positive energy balance, or scope for growth (*SfG*). Also, sediment stress may increase metabolism and further reduce *SfG*. This study provides an experimental analysis of the effects of prolonged (two-month) exposure to contrasting light and sediment regimes on the energy balance of the two coral species (*Goniastrea retiformis* and *Porites cylindrica*) for which I investigated growth responses in Chapter 5. Further, I analyse the importance of heterotrophic plasticity for energy budgets under changing turbidity, and develop a predictive model of habitat optima and physiological niches (with respect to resources) of corals based on environmental parameters and the response variables of particle heterotrophy, phototrophy and metabolism.

After two months of shading (equivalent to 3-4 m water depth at 16 mg/L), photosynthetic adaptation was significant in *G. retiformis*, but did not fully compensate for reduced light. However, in response to the prolonged shading, *G. retiformis* more than doubled its rate of particle feeding, compensating fully for the 50% decline in phototrophy at the high SPM concentration (~16 mg/L). In contrast, rates of particle feeding by *P. cylindrica* contributed < 10% to the scope for growth in shaded and less than 3% in unshaded conditions. Due to a lack of both photo- and heterotrophic plasticity, periods of high SPM concentrations resulted in energy deficit in *P. cylindrica*. This study is the first to show that heterotrophic plasticity is a mechanism for sustaining a positive energy balance in turbid environments.

Integrating data on feeding, photosynthesis and respiration as functions of environmental variables (particle concentration, particle quality, and depth) into the model of *SfG* + excretory losses (*SfG'*) provided a good prediction of the growth data presented in Chapter 5. Also, the contrasting trophic strategies of the two species were reflected in the results of a multiple regression analysis, in which sediment feeding and photosynthesis contributed comparably to the explained variance of growth in *G. retiformis*, whereas photosynthesis was the main descriptor of growth in *P. cylindrica*. A sensitivity analysis of *SfG'* in different turbidity/depth scenarios indicated that SfG' is most sensitive to the photokinetic parameters of the *P-I* curve and to the rate of respiration. The sensitivity of

SfG' to changes in clearance rate, organic carbon content and assimilation efficiency were relatively low, but increased > 5-fold between shallow, clear and deep, turbid water.

6.2. INTRODUCTION

Symbiotic cnidarians possess two mechanisms for obtaining energy from their environment: carbon fixation through photosynthesis by symbiotic unicellular algae (zooxanthellae) and the capture of particulate food by means of tentacles or mucus adhesion (reviewed by Sebens 1987, see also Chapters 1 and 2). As already discussed in Chapter 1, passive suspension feeding and photosynthesis of symbiotic cnidarians are both functions of resource availability in the forms of prey items and irradiance, respectively. Since suspended particles act as a light filter and thus reduce the transmission of light through the water column (Jerlov 1976, Kirk 1994), light availability and the concentration of particulate food are inversely related, a relationship that is enhanced with depth (Fig. 6.1). Symbiotic cnidarians that inhabit contrasting SPM and light conditions (turbidity, see Chapter 1) may therefore rely on different nutritional strategies to meet their energy demands.

The results of the growth study showed that energy investment into tissues by *G. retiformis* increased monotonically as a function of SPM concentration, and tissue growth in *P. cylindrica* was maximised at intermediate concentrations. SPM may therefore confer nutritional advantages as well as cause stress, depending on the coral species, particle load, and light level. In this chapter, I investigate further the role of SPM as an energy and nutrient source as well as a stress factor for these species under different turbidity regimes, by comparing the relative contributions of particle heterotrophy and photosynthesis to the observed energy investments into tissues and skeleton. In particular, I investigate the extent to which SPM feeding and photoadaptation can compensate for suboptimal light availability under high turbidity. Finally, I provide a modelling framework to predict scope for growth *in situ*, habitat optima and the width of the resource dimensions of physiological niches (e.g. see Begon et al. 1986) characterised by *P-I* curves and feeding-response curves for corals with different environmental histories, in terms of ambient SPM concentration, particle quality, and depth. Using this model and experimental data on feeding and photosynthesis, I test the hypotheses that enhanced particle feeding in some

habitats can compensate for reduced phototrophy under high turbidity and that plastic trophic strategies can broaden physiological niches.

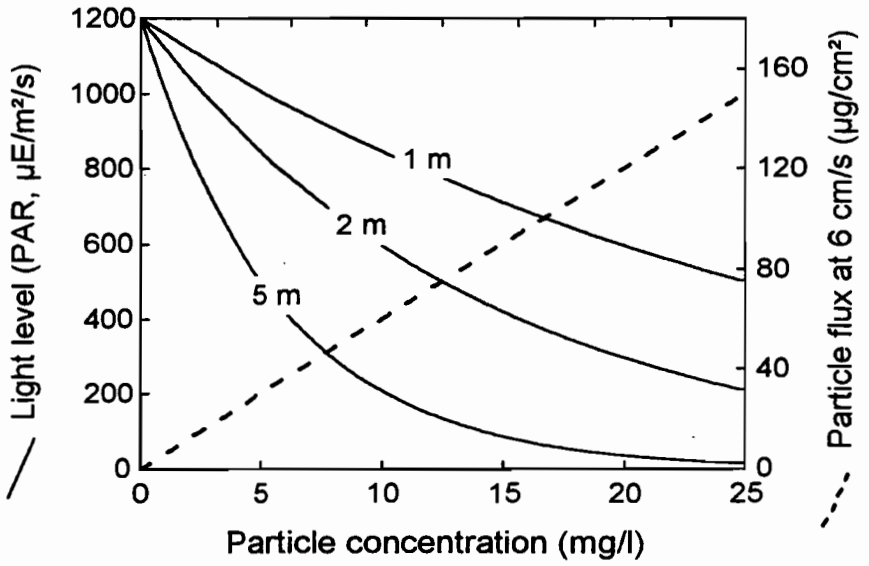

Fig. 6.1. The inverse relationship between light and particle (food) availability over a range of particle concentrations typical for inshore reefs (e.g. Nelly Bay, Magnetic Island). Particle availability is expressed as flux (particle concentration × flow speed), using a flow speed typical for back-reef environments (Sebens & Done 1992). Light at 1, 2 and 5 m depth are calculated from particle concentrations based on the light-extinction coefficient from Te (1997, see also Eq. 6.5 - 6.8).

As already outlined in Chapter 5, the energy balance (or scope for growth, *SfG*) is a function of energy acquisition, metabolic cost and excretory losses. In the following I will provide a more detailed modelling framework for the contributions of coral heterotrophy and autotrophy, based on the general model described by Eq 5.1 although I will not quantify the term for excretion (EX). Accurate measurements of excretions of mucus and dissolved organic carbon are notoriously difficult (Krupp 1985), and would be further complicated by turbidity treatments due to contamination by particulate carbon. Therefore, for the purpose of this study, I rearrange Eq. 5.1 so that daily energy acquisition through feeding and photosynthesis is balanced by scope for growth plus excretory losses.

$$SfG + EX = SfG' = P_g + A + R \qquad (6.1)$$

where Pg = gross photosynthesis, A = heterotrophic assimilation of particulate carbon and R = respiration (see also Section 5.2). Given that the production of mucus and dissolved organic matter is the result of assimilated carbon (photo- or heterotrophically), it is convenient in this study to consider such excretions as part of the energy budget available for growth. A

conceptual model of the effects of turbidity and sedimentation is outlined in Fig. 6.2. The sizes of the fluxes between factors and responses, and their interaction, determine how much energy is available for energy investment (and excretion).

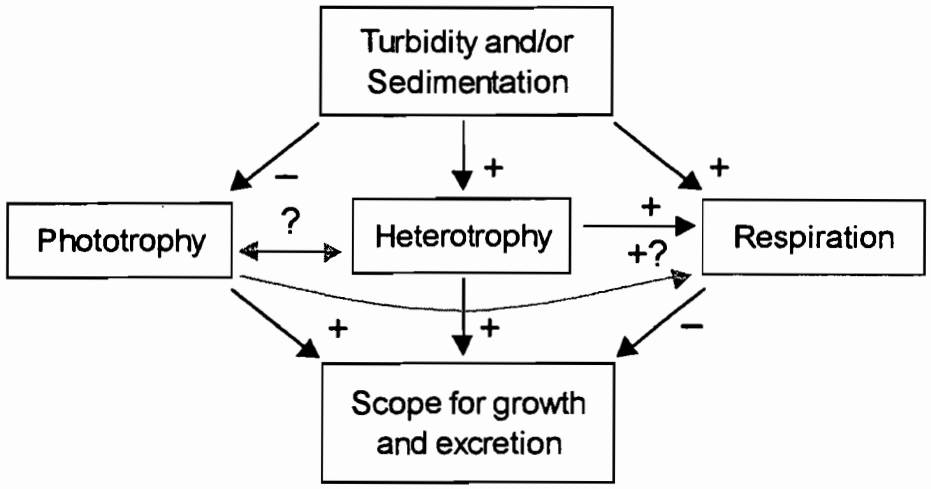

Fig. 6.2. Conceptual model depicting the predicted positive and negative relationships between sediment regimes, energy acquisition, and scope for growth and excretion (SfG', see also Eq. 6.1). An increase in respiration may be expected at high rates of phototrophy through high light levels (Barnes & Chalker 1990). Also, the relationship between photo- and heterotrophy is uncertain, but plasticity of both trophic modes under varying turbidity may maximise SfG'.

Food encounter by passive suspension feeders is a function of ambient concentration of suspended particulate food (c_{sp}, mg dw/L) and the rate by which the food is transported within reach of the feeding apparatus (Shimeta & Jumars 1991). Other factors such as particle size and flow-related efficiency of capture, handling and retention (Shimeta & Koehl 1997) will govern how much material is eventually ingested. Over a broad range of prey concentrations, the hourly rate of ingestion ($IN_{csp,t}$, µg dw/cm²/h) is predicted to follow a curvilinear (Type II) functional response (e.g. Ruxton & Gurney 1994), for example the Michaelis-Menten model (see also Chapter 2):

$$IN_{c_{sp,t}} = \frac{IN_{max} \cdot c_{sp}}{c_{sp} + K} \tag{6.2}$$

where IN_{max} is the maximum rate of ingestion and K (mg dw/L) 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. see Porter 1974, Sebens & Deriemer 1977). Daily carbon assimilation

(A_d, µg C/cm²/24h), however, depends on the 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). Assimilation efficiency is a function of ingestion rate (Szmant-Froelich & Pilson 1984, Zamer 1986), but is assumed here to be independent of C_{org} (see also Barille et al. 1997, Navarro & Widdows 1997). Thus,

$$A_d = \int_{t=0}^{T} (IN_{Csp,t})\,dt\; AE_{IN_{Csp,t}} C_{org} \tag{6.3}$$

Analogous to photosynthesis in plants, photosynthesis in zooxanthellate cnidarians is generally a curvilinear function of light availability (I, µE/m²/ s) composed of wavelengths in the range of photosynthetically active radiation (PAR, e.g. Falkowski et al. 1990). The hourly, net photosynthetic rate (P_n, µg C/cm²/h) can be expressed using the following exponential function (P-I curve, see review by Falkowski & Raven 1997):

$$P_n = P_{g,max}\,(1 - e^{-I/I_k}) + R_t \tag{6.4}$$

where $P_{g,\,max}$ is the maximum rate of gross photosynthesis, I_k is the light level at which P_g is 63% saturated, and R_t (µg C/cm²/h) is the rate of respiration. Corals exposed to a low-light environment photoadapt 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 PAR 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)

$$I_{z,t} = I_{0,t}\; e^{-z\,k_{PAR}} \tag{6.5}$$

where $I_{0,t}$ is the light level immediately below the water surface at the 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), thus

$$k_{par} \propto c_{sp} \qquad \text{or} \qquad k_{par} = \beta\, c_{sp} \tag{6.6}$$

where β (m·L/mg) is a constant relating k_{PAR} to c_{sp}. Light availability at a given depth and time of day can thus be expressed directly as a function of particle availability

$$I_{z,t} = I_{0,t}\; e^{-z\,\beta\,c_{sp}} \tag{6.7}$$

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

$$SfG' = \int_{t=0}^{24} (P_{g,max}[1-e^{-I_{z,t}/I_k}]+R_t)\cdot dt + \int_{t=0}^{T} (IN_{C_{sp,t}})dt\, AE_{IN_{Csp,t}} C_{org} \qquad (6.8)$$

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 β, Eq. 6.7), as well as adaptive changes in photo-kinetic parameters of the *P-I* curve to low light levels. Heterotrophy (right-most term) will increase (linearly or curvilinearly) with particle concentration (Eq. 6.3), 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_d) may be affected by light level as well as feeding rate, and where $P_{g,d} \leq R_d$, *SfG'* will be fully dependent upon heterotrophy to remain positive.

6.3. MATERIALS AND METHODS

6.3.1. Feeding as a function of turbidity, history and particle size

Three sets of experiments were conducted to evaluate the adaptive significance of sediment feeding in different environments and the extent to which the contribution of particle feeding to *SfG'* changes with prolonged exposure to high turbidity. Firstly, to compare the general suspension-feeding capacities of the two species, the concentration-dependent rates of particle ingestion (feeding responses) were determined for freshly collected colonies prior to the growth experiment (see Chapter 5). Feeding trials were conducted using the set-up and protocol described in Chapter 2 (see also Anthony 1999a). Four to six colonies were incubated at each of five different particle concentrations (1, 4, 8, 16 and 30 mg dw/L) to determine feeding responses.

In the second set of experiments, I tested whether prolonged exposure to contrasting sediment and light regimes had altered 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, Unshaded/Filtered, and Unshaded/High) after completion of the growth experiment. These corals were incubated using the same protocol as corals in

the first set of experiments, but at a particle concentration of 16 mg dw/L only (~ High treatment level). The tissues containing the ingested, ^{14}C-labelled material were subsequently digested from their skeletons (using 1 M KOH, Chapter 3) and the radioactivity determined in a scintillation counter. Surface areas of colonies (or branches) were determined using the foil-wrap technique (Marsh 1970), and the radioactivity per sample (dpm) was converted to particle intake (μg dw/cm²/h) based on the specific radioactivity of 750 dpm/mg dw found for sediment used in the feeding trials (Chapter 2).

In the third series of experiments, corals of both species were fed particle suspensions with six discrete size classes of particles to determine whether the two species show differential size-selective feeding. *Goniastrea retiformis* was predicted to feed more on larger and heavier settling particles due to its dome (massive) shape and large polyps, whereas *Porites cylindrica* was expected to feed mainly on the smaller particles that stay in suspension due to its branching morphology and small polyps (see also Abelson et al. 1993). To enable recovery and counting of ingested particles I used fluorescent latex beads (Polysciences, see also Chapter 2) for the sizes 1, 2, 6, 21, and 88 μm diameter, and hydrated *Artemia* cysts for the largest size class (250 μm). The nominal density of the latex beads was 1.05 mg/ml, producing predicted settling rates in non-turbulent conditions from 0.01 to 59 cm/min for the smallest and largest size classes, respectively (for empirical equations see Gibbs et al. 1971). Corals were incubated in three large (12-liter) flow tanks so that water depth would allow particle settling onto corals (mainly *G. retiformis*). Flow speed (~7 cm/sec) and timing of incubation were similar to incubations with ^{14}C (see Section 2.3.5). Since particle concentration was not included in this design, only one overall concentration (<1mg/L) was used, in which the concentrations of individual size classes were an inverse logarithmic function of particle size, providing some representation of size-frequency distributions of suspended particles in situ (Ayukai 1995). Three tanks with four corals (one pair of each species) were used in each of three consecutive experiments, giving a total of 12 corals per species. Duplicate 20-ml water samples were taken 3-4 times from each tank during each experiment to determine bead (and cyst) concentrations. After incubation, each coral was transferred to a 250-ml jar with filtered seawater to allow egestion of beads and cysts. All large (88-μm) beads and *Artemia* cysts were assumed to be egested within this timeframe, whereas smaller beads were likely to be phagocytosed and retained for longer periods of time (Van-Praet 1985). After 24 hrs, the corals were transferred to a 120-ml jar with 50 ml 2M NaOH in which tissues, but not beads, were solubilised within 48-72 hrs. Water subsamples from chambers and post-

incubation jars as well as solubilised tissue samples were filtered through irgalan-black membranes (Millepore, 0.5 µm pore) and analysed for bead counts using an epifluorescence microscope. The non-fluorescent *Artemia* cysts in seawater were counted under a dissecting microscope. Total bead and cyst counts per size class per species were normalised to cm² coral surface area, and averaged for the two corals in each pair so that tanks were replicates in the analysis. The size electivity index (E) was determined as $(IN_i\Sigma c_i/\Sigma IN_i c_i - 1)(IN_i\Sigma c_i/\Sigma IN_i c_i + 1)$ as described by Vanderploeg & Scavia (1979). IN_i and c_i are the ingestion rate and particle concentration, respectively, of the i'th size class. To compare size electivities of corals for the beads to the size-frequency distributions of particles used in feeding and growth studies, three samples from the sediment drums were analysed using a Malvern MasterSizer-X laser particle sizer within the window of 1.2 - 600 µm. Since the experimental sediment used in the growth study was collected from the sand-filters (see also Chapter 4) and further settled out and filtered (<500 µm), the resulting size-frequency was not expected to reflect the natural size-frequency distribution in situ. Rather, it was used to evaluate particle availability for the two species during the growth experiment.

6.3.2. Measurement of photosynthesis and respiration

At completion of the growth experiment, photosynthesis and respiration were measured for corals from the four main treatment groups to determine the relative contribution of phototrophy to scope for growth and basic metabolic costs across treatment groups. Importantly, *a posteriori* sampling from the growth design enabled testing of the extent which the two coral species adapted to different light and turbidity regimes over the two-month period, parameterised by the photokinetic parameters of the *P-I* curve. At least one coral colony (or branch) of each species was taken from each of the four tanks in each of the four treatment groups. Corals remained in the tank system at their growth-experiment treatment level until 2-3 hours prior to being used in a respirometry run. Net photosynthesis (P_n) was measured as production or consumption of oxygen (McCloskey et al. 1978), using a respirometer with four 2.5-L chambers, each with individual oxygen probes connected to a central logger unit (Fig. 6.3). Each colony (or branch) was deployed in a chamber over a 12-h period starting at 12:00 or 24:00 hrs 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 with filtered seawater. Sediment addition

was not included in these incubations due to the added background error of respiration and photosynthesis by microorganisms in the sediment. Concentration of O_2, as well as light and temperature, were determined every second, and the means over a minute of each variable logged in memory. To control light conditions, an artificial light source with a spectral composition resembling natural sunlight was used (two mercury-halide lamps, each 400 W). Light intensity was adjusted by elevating or lowering the lamps over the respirometer, exposing the corals to four discrete light levels for 1.5 h each (80, 160, 320 and 640 $\mu E/m^2/s$) 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. At conclusion of each run, the corals were frozen immediately and stored (-20°C) for later analysis of tissue dry weight and surface area. Oxygen produced by hourly photosynthesis (P) and consumed by respiration (r_t) were converted to carbon equivalents based on molar weights, hence P_C = µg O_2 produced · 12/32 / PQ and r_{Ct} = 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). Carbon values were further converted to energy equivalents (J) based on enthalpies of protein, carbohydrate and lipid in the ratios used for tissue growth (see Section 5.3.4).

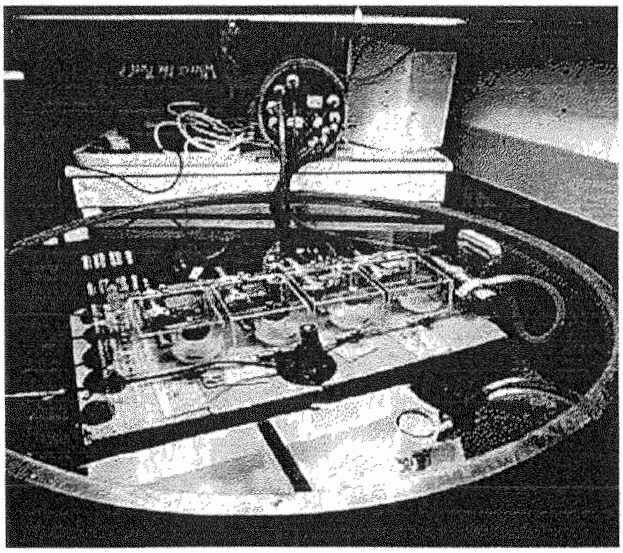

Fig. 6.3. Respirometer used to measure photosynthesis and respiration (courtesy of B. Schaffelke and K. Fabricius, AIMS). Light-level and O_2 concentration were recorded continuously over a 12-24 h period, and photosynthesis or respiration were determined from evolution/depletion profiles of O_2 concentrations over the 15-min incubations between chamber flushings.

6.3.3. Analysis and modelling of energy budgets: Heterotrophy vs autotrophy

The relationship between ingestion and particle concentration of pre-experimental corals was modelled according to Eq. 6.2, using non-linear regression as described in Chapter 2 (section 2.3.9). Differences in feeding capacity at 16 mg/L of corals from the four main treatments were tested using a one-way ANOVA for each species separately. Contributions of particle feeding to *SfG'* at different concentrations were estimated based on post-experimental feeding rates at 16 mg/L, interpolated to feeding rates at lower (Filt, Raw and Low) particle concentrations using a linear function for *Goniastrea retiformis* and the pre-experimental saturation constant for *Porites cylindrica*. For the purpose of constructing energy budgets, I initially assumed an assimilation efficiency of 50% of the ingested organic carbon, which represents a conservative estimate (Chapter 2, Anthony 1999a). However, assimilation efficiency was later varied along with other parameters as part of a sensitivity analysis for *SfG'* (see below). Changes in saturation light level, maximum rate of photosynthesis and respiration in response to the main treatments were tested using two-way ANOVAs for the two species separately, followed by post-hoc tests (Tukey's HSD). Daily carbon budgets were modelled for both species based on feeding-response curves and *P-I* curves. Composite variances and standard errors of variable means for each treatment group were calculated after Travis (1982) as described in Chapter 5 (Section 5.3.4.4).

Using data on heterotrophy and phototrophy, coral carbon budgets were also modelled over a range of turbidity regimes and depths (Eq. 6.8) to estimate thresholds at which the energy balance shifts from positive to negative due to reduced photosynthesis, and the extent to which heterotrophy can offset these thresholds. Light level as a function of depth was predicted from c_{sp} according to Eq. 6.7, and assuming that $\beta = 0.04$ m·L/mg (Te 1997) and $I_0 = 1200$ µE/m²/h at noon. The sensitivity of *SfG'* ($S_{SfG'}$) to 10% changes in all of the above parameters was analysed according to the general model for sensitivity analyses, $S_{SfG'} = (\partial SfG'/SfG')/(\partial X/X)$ (Jørgensen 1986), where X is the parameter analysed. To test whether the sensitivity of *SfG'* to changes in a given parameter differs between scenarios, $S_{SfG'}$ was analysed for four different combinations of depth and SPM.

6.4. RESULTS

6.4.1. Effects of turbidity on heterotrophy

For pre-experimental colonies freshly collected from the field prior to the growth study (Chapter 5), particle ingestion rates in *Goniastrea retiformis* increased almost linearly as a function of particle concentration over the range 1 to 30 mg/L (Fig. 6.4, see also Fig. 5.1). The Michaelis-Menten model indicated that feeding did not show any saturation within the experimental range of particle concentrations (K_m = at 52.6 ± 84.6 mg dw/L). The feeding response of *G. retiformis* was therefore analysed using linear regression, in which it was found that > 90% of the variation in ingestion rate was explained by the variation in particle concentration. In contrast, *Porites cylindrica* was half saturated at low particle concentrations (2.7 ± 1.0 mg/L), conforming closely to the Michaelis-Menten model in agreement with the results of Chapter 2. At particle concentrations corresponding to the High particle treatment (15.8 ± 1.4 mg/L), the ingestion rates of *G. retiformis* (41 ± 8 µg/cm²/h) were one order of magnitude higher than those of *P. cylindrica* (4.2 ± 0.9 µg/cm²/h).

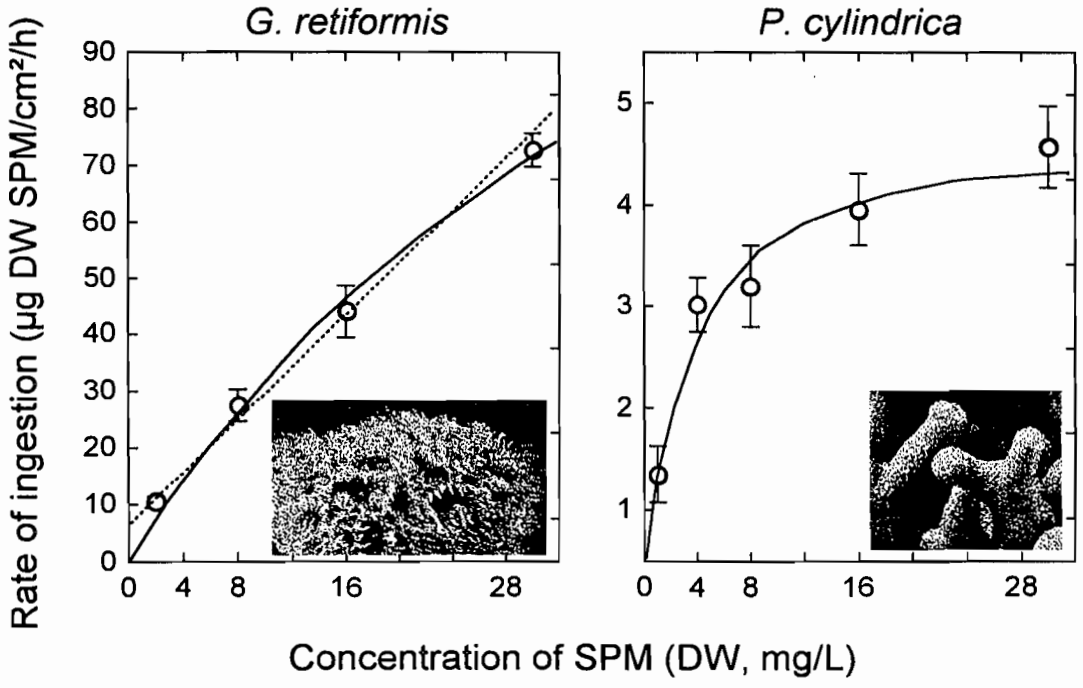

Fig. 6.4. Rate of particle ingestion as a function of particle concentration for newly collected corals prior to the growth experiment. Data are means ± SE of 4-8 colonies (*G. retiformis*) or branches (*P. cylindrica*). Solid lines are fitted using the Michaelis-Menten saturation model (Eq. 6.2), and the dashed line is the result of a linear regression. Note different scales on y-axes.

6.4.2. Particle-size selectivity

The two species showed comparable electivities for particles in the size range 1-20 μm, but contrasting electivities for the two large size classes (Fig. 6.5). These feeding data are consistent with feeding response curves for ^{14}C-labelled particles in that *Goniastrea retiformis* had 1-2 orders of magnitude higher feeding rates than *Porites cylindrica* over most of the particle size spectrum. *P. cylindrica* captured no *Artemia* cysts and only occasionally particles in the 88-μm size class, whereas *G. retiformis* preferred *Artemia* cysts over the smallest size class (1 μm). Also, *P. cylindrica* tended to prefer 6-μm particles over the two smallest size classes, but not over 20-μm particles. Interestingly, the electivity of *G. retiformis* for large particles and that of *P. cylindrica* for small particles matched the bimodal size-frequency distribution of the experimental sediment. Given this pattern of electivities and size-specific particle concentrations, feeding by *G. retiformis* would have been optimised by high exposure to loads of large settling particles during the growth experiment, and feeding by *P. cylindrica* would have been optimised because of high fluxes of fine suspended particles in the range 4 – 20 μm. The large variation in electivity indices were, in part, attributable to the variation in particle concentrations among chambers (Fig. 6.5A), and the variable states of expansion for coral polyps during feeding trials.

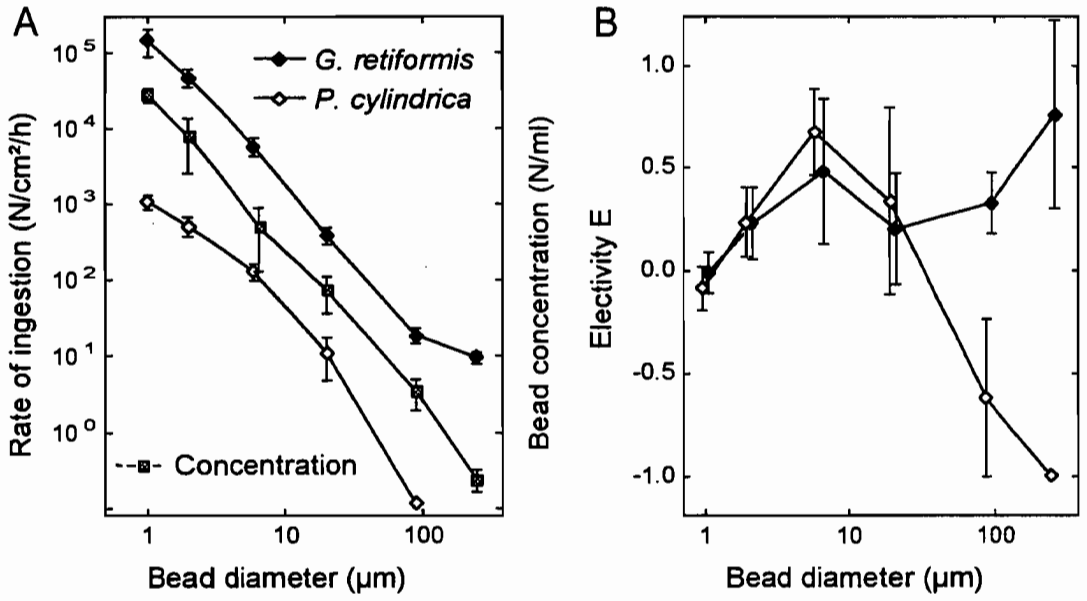

Fig. 6.5. Size-selective feeding by corals incubated in suspensions of fluorescent beads (1-88 μm diameter) and hydrated *Artemia* cysts (~250 μm). **A:** Size-specific ingestion rates and bead concentrations used in incubations. **B:** Electivity index E as described by Vanderploeg & Scavia (1979). *P. cylindrica* did not

ingest any particles ≥ 88 μm (**A**), reflected in a negative E for this size range. Data are means ± SE of three trials and three flow tanks.

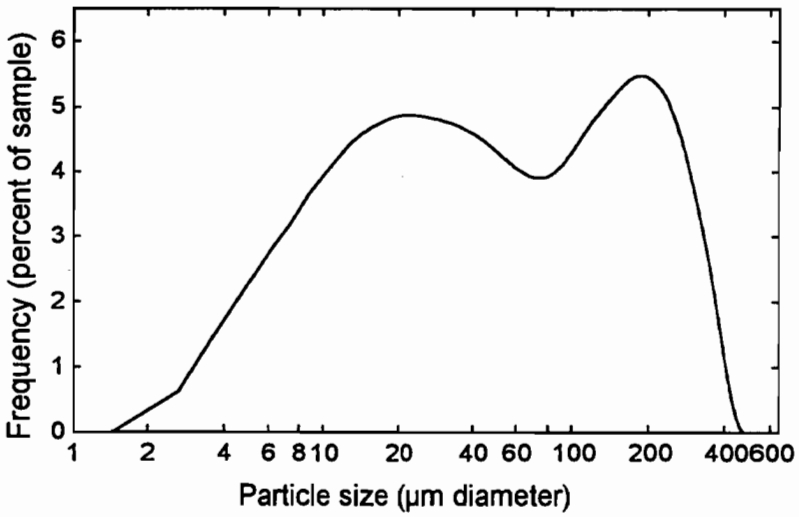

Fig. 6.6. Size-frequency distribution of sediment used in the growth experiment (Chapter 5). The sediment was collected from the sediment drums prior to dispensing to treatment tanks, and thus does not reflect the size-frequency distribution of suspended particles in situ. The peak at 200 μm represents the heavier sediment prone to settling.

6.4.3. Effects of experimental history on feeding capacity

After the eight-week growth experiment (Chapter 5), the rate of particle ingestion by *Goniastrea retiformis* had doubled as a result of shading, but was unaffected by the history of particle load (Fig. 6.7, Table 6.1). In contrast, the rate of particle ingestion by *Porites cylindrica* did not differ in response to shading, but was ~30% higher in the High compared to the Filtered treatment. The difference in feeding rates between *P. cylindrica* from the Filtered and High particle treatments was only marginally significant (Table 6.1), in part due to the large within-treatment variation. The daily heterotrophic carbon intake by Shaded *G. retiformis* was almost three fold that of Unshaded conspecifics, attributable to a ~30% longer feeding period (~16 h/day in Shaded vs ~12 h/day in Unshaded colonies) and a doubling of the concentration-specific feeding capacity. The feeding behaviour of *P. cylindrica* did not apparently change in response to Shading or particle treatment and polyps were generally extended during both day and night, except for occasional 1-2 day periods of mucus-sheath production.

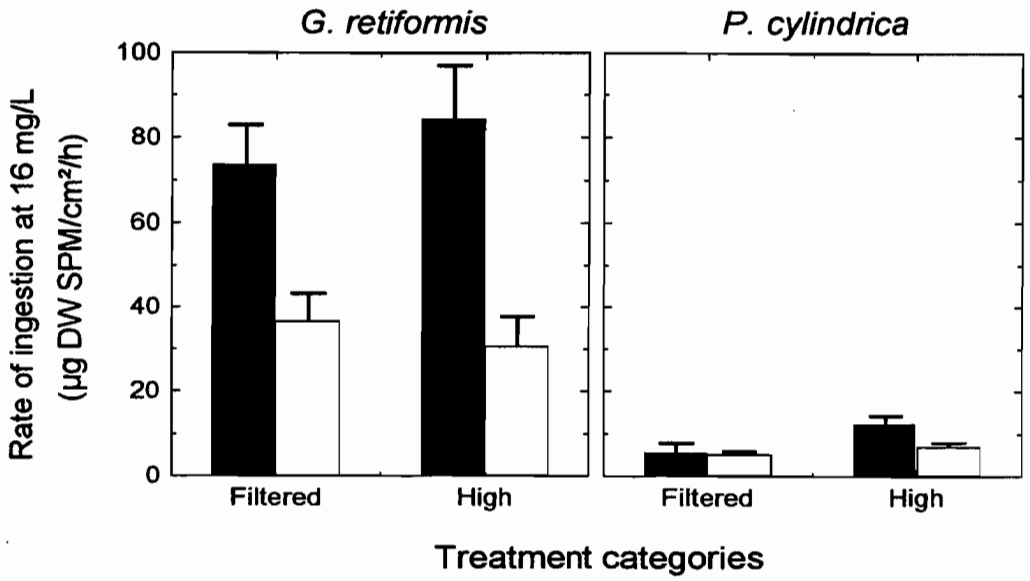

Fig. 6.7. Effects of particle and light history on rate of particle feeding by corals from the tank set-up assayed at completion of the growth experiment (see Chapter 5). Corals were incubated in a particle concentration corresponding to that of the High treatment (16 mg/L). Solid and open bars denote Shaded and Unshaded treatments, respectively.

Table 6.1. Summary of two-way ANOVA results for effects of experimental history on particle ingestion. Corals from four treatment groups (Shaded/Filtered, Shaded/High, Unshaded/Filtered and Unshaded/High) were incubated in ^{14}C-labelled particle suspensions of concentrations corresponding to the High-particle treatment (~16 mg/L) at conclusion of the growth experiment presented in Chapter 5. See Fig. 6.7 for means ± SE.

	Goniastrea retiformis				*Porites cylindrica*			
Source of variation (history)	df	F	P	Post hoc †	df	F	P	Post hoc †
Shading	1	18.13	< 0.001	SH > US	1	2.24	0.172	
Particle concentration	1	0.05	0.830		1	5.93	0.041	Hi > Fi
Shading X Particle conc.	1	0.62	0.440		1	2.12	0.183	
Error	18				12			

† SH: Shaded, US: Unshaded, Fi: Filtered, Hi: High

6.4.4. Effects of light and particle history on photosynthesis and respiration

Shaded groups of both species showed conspicuous darkening within the first month of the growth experiment, indicating that photoadaptation was occurring. After completion of the growth experiment, the average saturation light level (I_k) was ~20% lower and max rate of gross photosynthesis (P_{max}) was ~28% higher for shade-adapted *Goniastrea retiformis* compared to light-adapted conspecifics (Table 6.2). For *Porites cylindrica*, in contrast, I_k or P_{max} did not differ significantly between shade- and light-adapted branches. In both species, dark respiration did not change in response to different histories of shading or particle concentration. Also, I_k and P_{max} were unaffected by history of particle treatments in both species (Table 6.2).

Table 6.2. A: Response parameters of photosynthesis-irradiance (*P-I*) curves estimated after three months of adaptation to four treatment conditions in the tank set-up: Shaded/Filtered, Shaded/High, Unshaded/Filtered and Unshaded/High. B: Summary of ANOVA results for P-I response parameters of corals with different experimental histories. All datasets were analysed untransformed. * $P < 0.05$, ** $P < 0.01$

	Goniastrea retiformis				*Porites cylindrica*			
	Shaded		Unshaded		Shaded		Unshaded	
A. Response parameters	Filtered	High SPM	Filtered	High SPM	Filtered	High SPM	Filtered	High SPM
Saturation irradiance (I_k, µE/m²/s)	263.4 (29.7)	261.4 (33.1)	310.6 (13.8)	321.2 (18.7)	350.3 (19.8)	306.8 (70.5)	390.7 (10.7)	334.0 (18.7)
Max photosynthesis ($P_{g,\,max}$, µgO$_2$/cm²/h)	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_t, µgO$_2$/cm²/h)	-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)

Table continued on next page

Table 6.2. Continued

B. ANOVA results	df_1, df_2 †	Shading F	Shading P	Particle conc. F	Particle conc. P	Shading X Particle conc. F	Shading X Particle conc. P	Post Hoc ‡
Goniastrea retiformis								
Saturation irradiance	1, 16	5.74	**0.029** *	0.04	0.850	0.08	0.782	US > SH
Max photosynthesis	1, 16	8.70	**0.009** **	0.09	0.774	0.52	0.481	SH > US
Respiration	1, 16	1.74	0.206	0.01	0.915	1.11	0.308	
Porites cylindrica								
Saturation	1, 11	1.07	0.324	0.43	0.526	1.42	0.259	
Max photosynthesis	1, 11	1.34	0.271	1.28	0.282	0.39	0.543	
Respiration	1, 11	0.02	0.886	0.00	0.962	0.17	0.688	

Notes: Parameters were determined by non-linear regression using Eq. 6.4. Data are means and standard error (in parentheses) of 5 colonies per treatment for *G. retiformis* and 4 for *P. cylindrica*.

† Since Shading and Particle treatments were represented by two levels each, $df_1 = 1$ for both treatments and the interaction.

‡ SH: Shaded, US: Unshaded

Integrating hourly rates of photosynthesis and respiration over 24 h, using a light - time profile of an average day of the growth experiment (Fig. 6.8), indicated that daily photosynthesis of Unshaded corals (~ 3-4 m depth at 2-4 mg dw/L) exceeded respiration by 30% to 34% in *G. retiformis* and 28% to 81% in *P. cylindrica* (Table 6.3). In contrast, daily respiration in Shaded treatments (3-4m depth at 16 mg dw/L) exceeded photosynthesis by 14% to 22% in *G. retiformis* and 34% to 38% in *P. cylindrica*. Interestingly, the daily phototrophic surplus of Unshaded *P. cylindrica* in the High treatment was less than half that of conspecifics from the Filtered treatment, mainly attributable to the low $P_{g,max}$ (Table 6.2). These estimates, however, do not take into account the variation in daily irradiance, which was substantial during the two-month experiment (Fig. 5.6). Using this longer term variation in the construction of daily *P-I* curves showed that net photosynthesis in Unshaded treatments was negative for 12 to 16 days per month in *G. retiformis* and for 6 to 20 days per month in *P. cylindrica*. Net photosynthesis of Shaded corals was negative every day of the month for both species (data not shown).

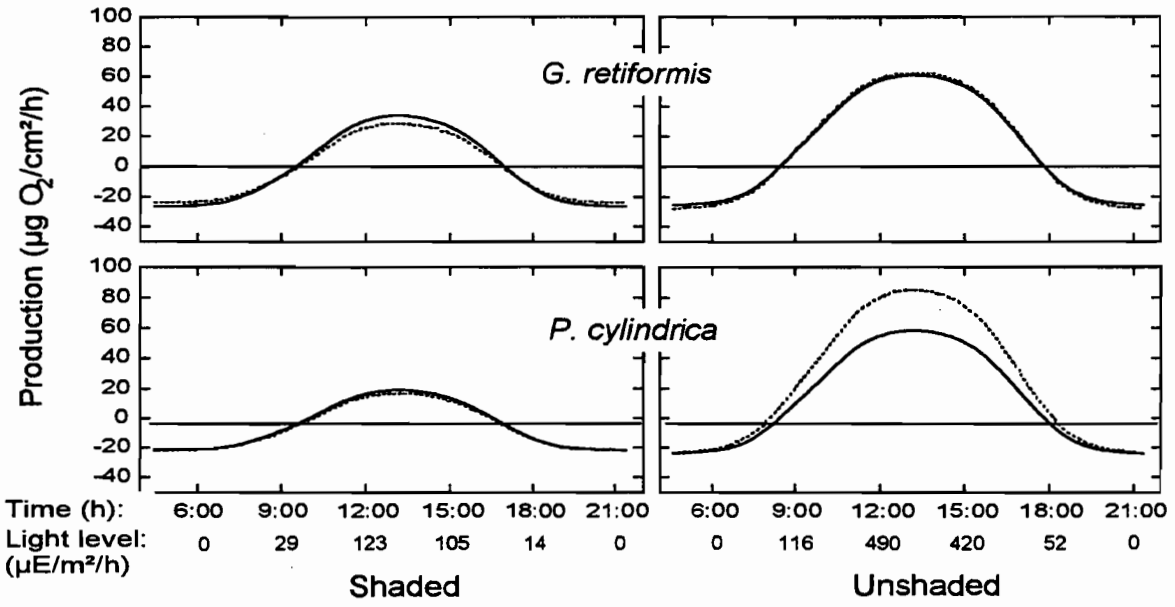

Fig. 6.8. Photosynthesis and respiration integrated over an average day of the growth experiment. The *P-I* curves are constructed using average values for max photosynthesis, saturation irradiance, and respiration (N = 5 for *G. retiformis* and 4 for *P. cylindrica*). Solid curves are the High treatment and dashed curves are the Filtered treatments.

Table 6.3. Summary of total daily carbon budget (µg C/cm²/24h) for the corals *G. retiformis* and *P.cylindrica* adapted to two contrasting light levels and particle treatments in the tank set-up. The column Total is the predicted carbon available for investment and excretion (SfG'), and the column Growth is the energy investment into tissue and skeleton determined empirically in Chapter 5. Data are means ± 1 standard error (in parentheses), the latter calculated using composite variances.

	Goniastrea retiformis					*Porites cylindrica*				
Treatments	Photos. +	Feed. +	Resp. =	Total	Growth	Photos. +	Feed. +	Resp. =	Total	Growth
SHADED										
Filtered	132.4	6.1	-169.1	-30.6	15.0	95.4	1.0	-154.4	-58.0	7.2
	(5.2)	(0.6)	(12.4)	(13.5)	(4.3)	(5.7)	(0.3)	(18.8)	(19.6)	(2.2)
High	152.9	44.5	-177.6	19.8	34.0	100.4	8.3	-152.1	-43.4	-2.3
	(7.8)	(5.8)	(11.3)	(14.9)	(3.9)	(12.5)	(1.5)	(12.3)	(17.6)	(3.2)
UNSHADED										
Filtered	248.8	3.0	-192.0	59.8	27.7	292.1	1.0	-160.7	132.4	13.5
	(7.3)	(0.5)	(11.8)	(13.9)	(4.2)	(17.3)	(0.1)	(13.9)	(22.2)	(2.6)
High	236.1	16.2	-175.8	76.5	41.0	212.2	4.7	-165.4	51.5	9.3
	(13.3)	(1.9)	(12.5)	(18.4)	(4.9)	(12.9)	(1.5)	(16.1)	(20.7)	(3.5)

Notes to Table 6.3: Total photosynthesis was obtained by integrating hourly rates of photosynthesis over an average day of the growth experiment (see Fig. 5.6 and Fig. 6.8). Daily rates of heterotrophic carbon assimilation assumed 3% organic carbon content and 50% assimilation efficiency (see Section 6.3.3). Feeding rates in High-particle treatments (15.8 ± 1.4 mg/L) were based on post-experimental feeding rates (Fig. 6.7), and feeding in Filtered treatments (0.7 ± 0.1 mg/L) was estimated by linear interpolation. Rates of carbon investment into total growth (and excretion) were estimated from Joule equivalents of carbon in protein (45 J/mg C, Gnaiger & Bitterlich 1984).

6.4.5. Contributions of heterotrophy and phototrophy to the carbon budget

Daily particle feeding constituted 4% to 30% of daily gross photosynthesis in Shaded and 1% to 7% in Unshaded *Goniastrea retiformis* (Table 6.3), despite the low organic carbon content of suspended particles (~3%, Table 5.1). At high particle concentrations, feeding by *G. retiformis* could compensate fully for the 35-41% decline in photosynthesis caused by shading. For instance, the daily carbon budget for Shaded *G. retiformis* in the Filtered treatment was in deficit by 30.6 ± 13.5 μgC/cm²/d, whereas Shaded conspecifics in the High-SPM treatment sustained a carbon surplus of 19.8 ± 14.9 μgC/cm²/d due to their 7-fold greater heterotrophic carbon intake. In contrast, feeding by *Porites cylindrica* compensated for less than 20% of the carbon deficit in turbid conditions (-58.0 ± 19.7 to -43.4 ± 17.6 μgC/cm²/d), rendering its carbon surplus highly dependent upon phototrophy.

Particle feeding by *G. retiformis* at high particle concentrations accounted for more than 130% of its investment into tissue growth and calcification in Shaded conditions, and 40% of its growth in Unshaded conditions. Also, feeding by Unshaded *P. cylindrica* in the high treatment accounted for ~-50% of its growth rate. Due to the negative growth rate by Shaded *P. cylindrica* at high particle concentrations, a comparison with its feeding rate was not meaningful. Assuming that respiration and photosynthesis of corals from Low particle treatments were intermediate of those from Filtered and High treatments, feeding by *P. cylindrica* in the Shaded and Unshaded Low treatments accounted for only 16% and 8% of its energy investment, respectively (not shown).

Regressing the mean daily rates of tissue growth (from Chapter 5) on daily rates of feeding and gross photosynthesis demonstrated the contrasting nutritional strategies of the two species (Fig. 6.9). Investment into tissue growth (μgC/cm²/d) in *G. retiformis* was positively correlated with feeding (partial r = 0.90) and phototrophy (partial r = 0.93),

jointly explaining 85% of the variation (R^2 adjusted, Table 6.4). The rate that carbon was allocated to tissue growth relative to the rate it was acquired (i.e. the growth efficiency, indicated by the slope of the partial regression) was two fold higher for feeding than for photosynthesis. The result of the same analysis for *P. cylindrica* was not significant and produced a negative (although non-significant) regression coefficient for feeding, attributable to the reduced growth rates of corals in the Shaded High-particle treatment. Accordingly, photosynthesis and feeding jointly explained only 29% of the tissue growth variation (R^2 adjusted, Table 6.4) in *P. cylindrica*.

The pattern of energy allocation to skeletal growth as a function of feeding and photosynthesis was in contrast to that for tissue growth. The heterotrophic contribution to skeletal growth was non-significant in both species, whereas phototrophy contributed significantly. However, the growth efficiency of skeleton with respect to photosynthesis was only 10-20% that of tissues.

Table 6.4. Results of multivariate regressions showing the relationship between energy investment into tissues and skeleton (the dependent variables) and energy acquisition through particle feeding and net photosynthesis for the two coral species. All variables are in units of µg C/cm²/24h. Regressions are based on group means for the eight main treatments (two light and four SPM treatments), of which net photosynthesis for the groups Low and Raw (see Chapter 5) are obtained by interpolation between Filtered and High. See also Fig. 6.9.

	Feeding			Photosynthesis			Combined	
Species	Slope ± SE	† r-part	P	Slope ± SE	† r-part	P	R^2 adj	P
Tissues								
G. retiformis	0.51 ± 0.11	0.90	0.006 **	0.19 ± 0.03	0.93	0.002 **	0.85	0.004 **
P. cylindrica	-1.78 ± 1.34	-0.51	0.240 ns	0.06 ± 0.04	0.49	0.250 ns	0.29	0.183 ns
Skeleton								
G. retiformis	0.04 ± 0.02	0.68	0.582 ns	0.02 ± 0.01	0.82	0.024 *	0.57	0.004 **
P. cylindrica	0.05 ± 0.08	0.25	0.261 ns	0.01 ± 0.00	0.88	0.010 **	0.68	0.026 *

† r-part is the partial correlation coefficient between the dependent variable and one independent variable, adjusted for the other independent variable.

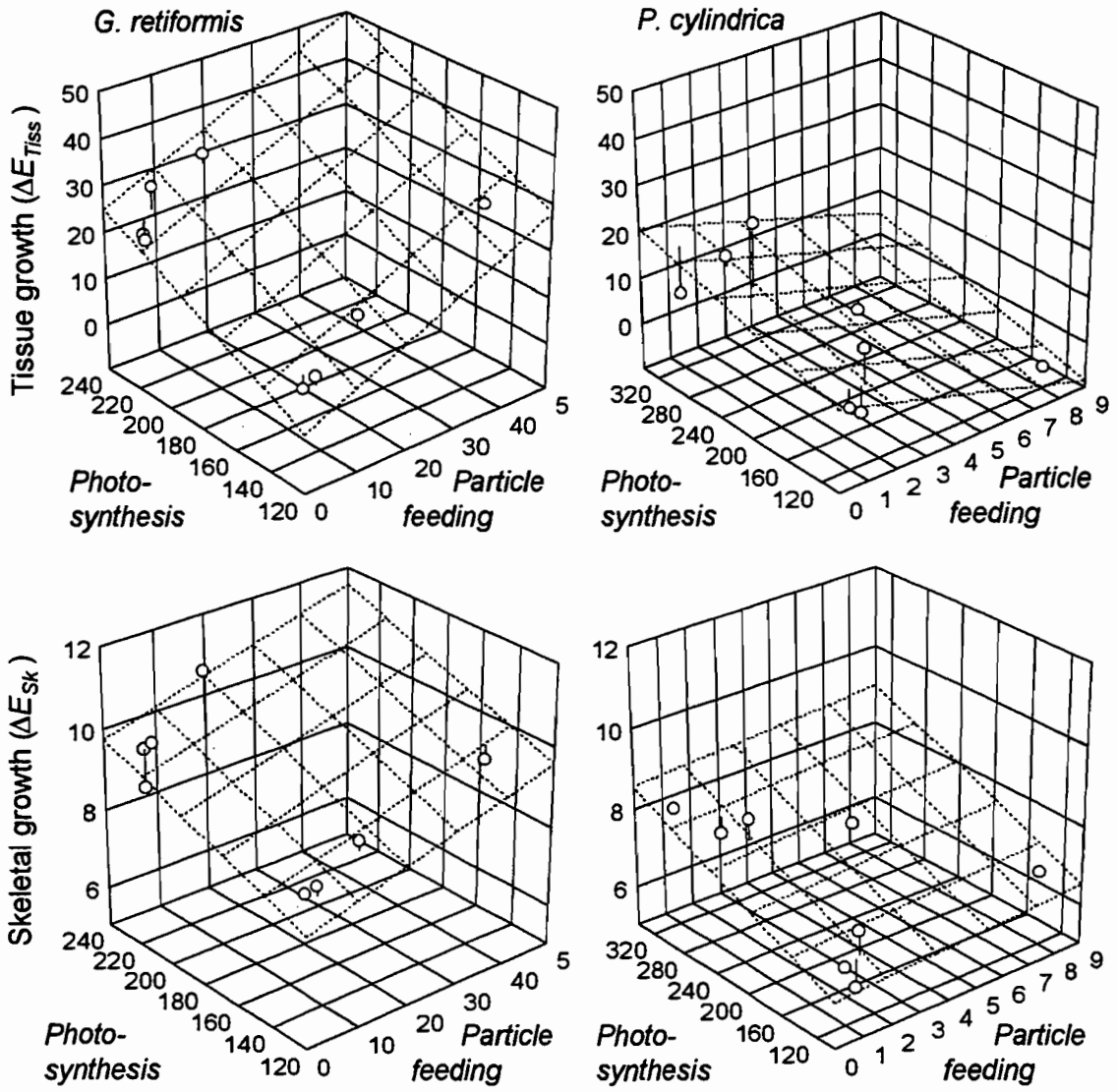

Fig. 6.9. Daily (empirical) carbon investment into tissue growth (including lipids, see Chapter 5) and skeletal growth as functions of particle feeding (assimilation) and gross photosynthesis. Data are group means for conspecific corals from the eight experimental light and SPM treatments (see also Table 6.3). Photosynthesis by corals in the Raw and Low SPM treatments (see Chapter 5) were estimated by interpolation between Filtered and High treatments. Planes are established by multiple regression (Table 6.4).

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

Modelling net photosynthesis ($P_{n,d} = P_{g,d} + R_d$) as a function of particle concentration and depth predicted that both factors act synergistically in reducing the daily phototrophic carbon budget (Fig. 6.10). 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/L. The pattern of P_d:R_d ratios along the particle concentration vs depth profile is comparable for the two species, despite a greater ability of *Goniastrea retiformis* to photo-adapt (indicated by the different

intercepts of corals from different depths (Fig. 6.10). High rates of particle feeding by *G. retiformis* can potentially broaden its physiological (resource) niche, maintaining a positive carbon budget over a wider range of environmental conditions than in a fully autotrophic mode (indicated by the differences between predicted curves for phototrophy and phototrophy+heterotrophy in Fig. 6.10). At intermediate depths and particle concentrations, heterotrophy by *G. retiformis* becomes an increasingly important carbon source as the predicted daily net photosynthesis approaches zero ($P_{g,d}$:R_d ratio = 1). For instance, the model predicts that *G. retiformis* reaches this threshold at 12 mg/L at 3 m depth, but if feeding on SPM is considered, the total daily C budget stays positive until SPM concentrations of 16 mg/L are encountered. The predictions of this model agree with the results of the growth study, in that Shaded *G. retiformis* at high particle concentrations (~4 m depth at 16 mg/L) showed high rates of energy investment into growth, whereas Shaded conspecifics from filtered treatments showed significantly lower growth rates. The low rates of particle feeding by *Porites cylindrica*, however, have a minor influence on its total carbon balance across depths and particle concentrations. Also, the minimal growth rates of Shaded *P. cylindrica* are in accordance with the predicted negative carbon budget of this species at 3-m depth and at 16 mg/L.

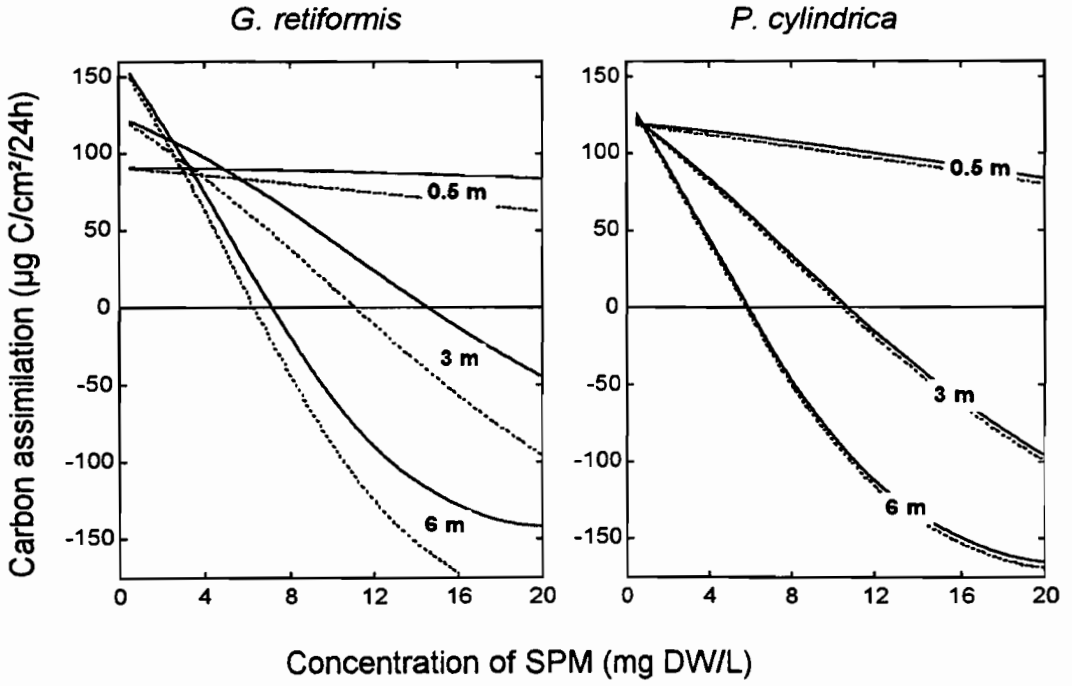

Fig. 6.10. Predicted total daily carbon budgets (as scope for growth plus excretion, *SfG'*) as a function of particle concentration at three depths. Dashed lines are carbon budgets based solely on phototrophic carbon

fixation and solid lines are carbon budgets based on both phototrophic and heterotrophic carbon, the latter assimilated from suspended particles. 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, I assumed a 3% organic carbon content and 50% assimilation efficiency of the ingested organic carbon (see Chapter 5). Light level as a function of depth was calculated based on particle concentrations using Eq. 6.6, assuming that β = 0.035 m·L/mg and I_0 = 1200 μE/m²/s at noon. Photosynthesis, feeding (assimilation) and respiration were integrated over the day using Eq. 6.7.

As expected from Fig. 6.10, scope for growth and excretion (*SfG'*) was strongly sensitive to changes in depth, and more so at high particle concentrations. For example, in deep water (3 m depth) the sensitivity of *SfG'* at 16 mg/L was an order of magnitude higher than at 4 mg/L (Table 6.5). The sensitivity of *SfG'* to changes in depth, particle concentration and the concentration-specific light extinction coefficient (β) were identical given that these form a product in the light-attenuation function (Eq. 6.7). Because predicted *SfG'* was negative in the deep and turbid water, all sensitivities shifted signs when the analysis was run for this scenario (Table 6.5). Ten-percent changes in surface irradiance (I_o) in deep and turbid water caused a four-fold greater change in *SfG'* than in shallow and turbid water, whereas changes in I_0 in shallow water caused only slight decreases in *SfG'* between low and high particle concentrations.

Also as expected, *SfG'* was highly sensitive to changes in the photokinetic parameters of the *P-I* curve (I_k and P_{max}) in deep and turbid water, and also to changes in the rate of respiration. The slightly decreasing sensitivity of *SfG'* to P_{max} and R with increasing particle concentration in shallow water suggest that the increase in the heterotrophic component of *SfG'* more than compensates for light dependent decline in phototrophy in shallow water. The sensitivity of *SfG'* to the heterotrophic parameters particle quality (C_{org}), clearance rate (CR) and assimilation efficiency (AE) increased four-fold as particle concentrations increased from low to high in shallow water, and more than ten-fold from shallow to deep water at high concentrations, reflecting the relatively greater importance of heterotrophic carbon assimilation in shaded (deep) environments. Interestingly, in shallow water the negative sensitivity of *SfG'* to 10% increases in depth, particle concentration and concentration-specific light extinction coefficient were similar to the positive sensitivity of *SfG'* to the 10% increases in each of the heterotrophic parameters.

Table 6.5. Sensitivity analysis of the model for the daily carbon budget (*SfG'*) of corals as depicted in Fig. 6.10. The analysis was run for four combinations of depth and particle concentration relevant to the design of the growth experiment (Chapter 5) and experimental analyses.

Parameters	Range		Sensitivity (∂SfG'/SfG')/(∂Par/Par)			
	Mean	+10%	Shallow Low	Shallow High	Deep Low	Deep High
Depth (z, m) †	-	-	-0.05	-0.23	-0.51	4.93
Particle concentration (c_{sp}, mg dw l^{-1}) ‡	-	-	-0.05	-0.23	-0.51	4.93
ß (k_{PAR}/c_{sp}, m l mg^{-1})	0.04	0.044	-0.05	-0.23	-0.51	4.93
Surface irradiance at noon (I_0, µE m^{-2} s^{-1})	1200	1320	0.56	0.65	0.98	-2.66
Max rate of photosynthesis ($P_{g,max}$, µgC cm^{-2} h^{-}	35	38.5	2.19	2.00	2.64	-3.42
Saturation irradiance (I_k, µE m^{-2} s^{-1})	300	330	-0.66	-0.68	-1.12	2.52
Rate of respiration (R_t, µg C cm^{-2} h^{-1})	-7	-6.3	-1.25	-1.22	-1.72	5.40
Organic carbon content (*Corg* %)	4	4.4	0.06	0.22	0.08	-1.00
Clearance rate (*CR*, ml cm^{-2} h^{-1})	4	4.4	0.06	0.22	0.08	-1.00
Assimilation efficiency (*AE*, %)	50	55	0.06	0.22	0.08	-1.00

† Shallow : 0.5 m, Deep : 3 m

‡ Low : 4 mg l^{-1}, High : 16 mg l^{-1}

6.5. DISCUSSION

6.5.1. Effects of turbidity on rates of photo- and heterotrophy

The enhanced rates of particle feeding by *Goniastrea retiformis* in response to a history of prolonged shading represent an additional layer of complexity to the nutritional biology of symbiotic cnidarians. The results corroborate those of Chapter 3 (see also Anthony 2000) in that corals 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 by two mechanisms: (1) inclusion of sediment in the diet in proportion to availability 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 where periods of high turbidity may last from days to weeks. 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 may be important during periods of high turbidity and low light. These organism-level changes in *SfG* in response to turbidity and sedimentation provide information critical to the modelling of population-level responses, a topic that I discuss further in Chapter 7.

Heterotrophic plasticity has not previously been demonstrated for cnidarians, but has been observed in mixotrophic microorganisms (e.g. Sanders et al. 1990, Berk et al. 1991, Jones et al. 1995) which show variable patterns of heterotrophic capacity in relation to light history. Both morphological and behavioural plasticity have been shown to affect feeding rates in fish (sticklebacks) in short term studies (Day & McPhail 1996). Changes in feeding behaviour were evident for *G. retiformis* in this study in the form of a prolonged diel feeding cycle and could contribute to heterotrophic plasticity, but no morphological changes of polyps or tentacles were observed in response to shading or sediment treatments. It is also likely that an increase in mucus production and/or a change in the composition of cnidae resulting in greater tentacle stickiness contributed to a doubling in capture ability. Telesnicki & Goldberg (1995) observed that the polyps of *Dichocoenia stokesii* and *Meandrina meandrites* changed from predominantly nocturnal activity to full diel activity when exposed to prolonged high turbidity, however, because no feeding experiments were conducted so it is unclear whether this behavioural response was one of feeding or sediment cleaning. Ferrier-Pages et al. (1998) showed that feeding rates of the coral *Stylophora pistillata* on ciliates were enhanced when shaded during feeding trials, but mainly as a behavioural response to reduced light levels.

The adaptive changes in photokinetic parameters of the *P-I* curve were convincing for *G. retiformis* only, and could counteract ~45% of the reduction in photosynthesis that would have occurred without photoadaptation due to the 75% reduction in light between Unshaded and Shaded treatments. This measure is obtained by comparing daily net photosynthesis of light- and shade-adapted corals in the shaded regime. Phenotypic plasticity with respect to both heterotrophy and phototrophy therefore contributes to maintaining a positive energy balance in *G. retiformis*. It is likely that a longer period of shading would have revealed a higher photosynthetic efficiency in *Porites cylindrica* (and *G. retiformis*), but would have been less relevant as a simulation of turbidity-caused

shading since high-turbidity events are usually on the scale of days or weeks rather than months (Larcombe et al. 1995, see also Chapter 3). The increase in the maximum rate of photosynthesis (P_{max}) of Shaded relative to Unshaded *G. retiformis* was surprising given that P_{max} is predicted to decline during photoacclimation to lowered light levels (e.g. Falkowski et al. 1990). Also, the photoadaptation by *G. retiformis* following prolonged shading 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 large 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. Schaffelke & Klumpp 1997) to an extent that exceeds the levels of shading used in this experiment (pers. obs). 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 phenotypic plasticity in response to shifting environments.

6.5.2. Effects of particle size on feeding rate: electivity

As predicted from differences in colony morphology and polyp size, *Goniastrea retiformis* showed electivity for large settling particles, whereas *Porites cylindrica* fed mainly on small suspended particles. Assuming that large and small particles have similar food value (weight-specific), such electivities may render *G. retiformis* the optimal forager where particle fluxes include a significant proportion of large particles. Although the electivities estimated here are likely to be biased by the differential flux types of small suspended and large settling particles, and the contrasting susceptibilities of massive and branching species to encounter such fluxes (e.g. Abelson et al. 1993), the results indicate differences in the food niches of the two species. While the weight-specific food value of live particles may not vary appreciably with size for zoo- or phytoplankton (Corner & Davies 1971), the food value per unit weight (or volume) of suspended and settled sediment generally decreases with grain size (e.g. Taghon 1982, Johnstone et al. 1990), in part due to a higher surface:volume ratio of small particles, and hence greater potential for bacterial colonisation and organic coating per unit weight (see also Chapter 1). The feeding rates by *G. retiformis* may therefore be overestimated in particle concentrations composed mainly of particles < 10 μm diameter, or composed of larger sediment particles with a low

food value. In patches comprising large phytoplankters, zooplankters, or high-energy detrital flocs, on the other hand, its heterotrophy may be severely underestimated. For example, Blanchot et al. (1989) found that particles < 3-μm diameter in Tikehau Atoll had a weight-specific organic carbon content of ~9% (three-fold the content of particles used here), but particles >35 μm (mainly zooplankton) had a weight-specific organic carbon content of 19%-37%. Such a scenario would most likely optimise heterotrophy in coral species such as *G. retiformis*. In contrast, the electivity for small suspended particles by branching, small-polyped species such as *P. cylindrica* enables access to small nutrient-rich particles in turbid water, and also avoids smothering by sedimentation due to its upright digitate morphology. The C:N ratio of suspended sediment may be less than half that of sedimented material (Clavier et al. 1995), rendering suspended particles the better nutrient source. Also, selectivity for smaller suspended particles by organisms with small gut volumes is predicted by optimal diet theory (Taghon 1982), but in the case of *P. cylindrica* may be more a function of its small tentacle and colony morphology which place constraints on particle encounter and capture ability of larger particles. Despite differences in electivity between species, the rates of feeding by *G. retiformis* on 1-6-μm diameter particles were still two orders of magnitude higher than those of *P. cylindrica*, rendering *G. retiformis* the superior heterotroph over the full spectrum of particle sizes.

6.5.3. The role of particle feeding and phototrophy in energy investment

Energy investment by both coral species was enhanced by high rates of phototrophy in agreement with the results of other studies of bioenergetics in symbiotic suspension feeders (e.g. Rogers 1979, Frost & Williamson 1980, Spencer Davies 1991, Klumpp & Griffiths 1994, Tsuchida & Potts 1994). Previous studies of growth in hermatypic corals have focused primarily on the role of phototrophy, in particular the dependence of skeletal growth on photosynthesis (reviewed by Barnes & Chalker 1990). The role of heterotrophy in energy investment by corals has previously been based largely on assumptions and inferences when balancing energy budgets (Falkowski et al. 1984, Muscatine et al. 1984, Bythell 1988, Edmunds & Davies 1989, but see Ferrier-Pages et al. 1998), and has not previously been rigorously partitioned into tissues and skeleton. It is interesting in this context that although only the phototrophic contribution to skeletal growth was significant in this study, the growth efficiency of tissues with respect to photosynthesis was 5-fold that

of skeleton. This highlights the deficiency of skeletal growth as an indicator of stress or nutritional status in corals, especially in massive or encrusting colonies with low surface:volume ratios.

The relative importance of phototrophy and heterotrophy shifted significantly for *Goniastrea retiformis* with relatively small increases in particle concentration and depth, indicated by the predictions of the model for *SfG'*. The enhanced feeding rate in concert with shade-adapted photosynthesis in *G. retiformis* effectively elevated the threshold turbidity level (or depth) at which the energy balance (given by *SfG'*) was positive. *Porites cylindrica* was unable to increase the width of its niche because of low feeding rates and lack of photoadaptation, although it was able to enhance its energy investment in shallow-water conditions at moderate turbidity levels. These results demonstrate that particle feeding and plasticity of phototrophy and heterotrophy may dictate the location of a species' habitat optima and the width of its physiological (resource) niche, which has implications for its potential distribution (e.g. zonation). 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. In comparison, Lemke & Bowen (1998) showed that fish (fathead minnows) feeding exclusively on detrital aggregates lost weight, but fish offered detrital aggregates as a supplement to small rations of invertebrate prey showed significantly higher growth rates than fish feeding on invertebrate prey only. The importance of complementary resources may, however, be substantially higher for mixotrophic organisms than for fully heterotrophic, and especially phototrophic, organisms due to nutrient limited growth (see below), unless tradeoffs in the form of higher metabolic costs are associated with the mixotrophic strategy (Rothhaupt 1996).

The enhanced tissue growth rates of Unshaded *G. retiformis* and *P. cylindrica* at High and Low SPM concentrations, respectively, relative to Unshaded and Filtered treatments, support the hypothesis that reef-building corals are nutrient limited (e.g. Muscatine 1990, Dubinsky & Jokiel 1994, Muller et al. 1994b). For instance, carbon invested into tissue by Unshaded/Filtered *G. retiformis* and *P. cylindrica* constituted only 31% and 13% of the daily photosynthetic carbon fixation, respectively. The latter corroborates the results of studies showing that the majority of the phototrophic carbon is lost from the symbiosis in shallow, unshaded and oligotrophic environments (Falkowski et

al. 1984, Muscatine et al. 1984), presumably through the excretion of dissolved organic matter (Crossland 1987). Also, Meyer et al. (1983) and Meyer & Schultz (1985) showed that corals hosting resident fish schools had higher tissue growth rates and nutritional condition than conspecific corals without fish schools, presumably due to nutrient enrichment of the inter-branch water by fish faeces and excretions. At the intermediate (Low) level of particle availability in this study (~4 mg dw/L), however, carbon investment into tissue growth was 44% of the phototrophic carbon in *G. retiformis* and 27% of that in *P. cylindrica*, the latter suggesting that the increased availability of particulate nutrients induced a doubling of the tissue growth rate in *P. cylindrica*. The ratios of organic carbon (C) to nitrogen (N) to phosphorus (P) of the experimental particulate matter (~70:10:1, on the basis of dry weight) corresponded closely to those reported for coral tissue (Muller et al. 1994a). The heterotrophic uptake of C in this study may thus directly reflect the incorporation of N and P into tissue, assuming that assimilation efficiencies of N and P are similar to that of C. The latter may be a conservative assumption since nutrient-deficient diets may enhance the assimilation efficiencies of nutrients (Demott 1998). Based on the N and P contents of the experimental particles and that of coral tissues as found by Muller et al. (1994a), feeding by Unshaded *G. retiformis* accounted for between 17% and 59% of its tissue growth, whereas feeding by Unshaded *P. cylindrica* covered only 5% to 30% of its tissue growth. These comparisons indicate that particle feeding alone could not supply the entire N and P required. Thus, part of the tissue growth may have been enabled through efficient uptake of dissolved nutrients by zooxanthellae (e.g. Muscatine & D'Elia 1978). In a subsequent experiment using the same tank system and protocol for particle collection and dispension developed here (Chapter 4), Schaffelke (in press) showed that concentrations of dissolved organic nitrogen and phosphorus were significantly greater in the High-particle treatments relative to controls, and marginally higher in the Low treatment. In addition to feeding, the uptake of dissolved nutrients may therefore have been greater in the High and Low treatments. Interestingly, and as predicted by the *SfG'* model and the results of the sensitivity analysis, a higher organic content in the particulate matter would have increased the heterotrophic contribution to energy budgets, and may have implications for corals on reefs frequently subject to high phyto- and zooplankton productivity.

The results of the sensitivity analysis for *SfG'* indicates that variation in the rate of respiration is one of the most important response variables to changing light levels and sediment concentrations. This is in partial agreement with the model analysis of *SfG* (=

SfG'-EX) in Chapter 5, in which the coefficient for sediment-induced losses in *P. cylindrica* was highly significant, but was non-significant for *G. retiformis*. Previous studies have demonstrated an increase in respiration rate in corals in response to elevated particle loads (e.g. Dallmeyer et al. 1982, Abdel-Salam & Porter 1989) as predicted by energy models of responses to stressors (Widdows et al. 1995, Maltby 1999) and/or increased resources (e.g. Fitt et al. 1982, Szmant-Froelich & Pilson 1984). For example, Telesnicki & Goldberg (1995) showed a reduction from 1.5 to 1 in the P:R ratio over a 7-day period for two Caribbean coral species incubated at turbidities similar to the maximum levels used here (14-16 NTU), and attributed this decrease to a doubling of the respiration rate rather than to a reduced rate of photosynthesis. If the respiration rates used in this study are 50% underestimated at the high particle concentrations, the scope for growth with respect to carbon will be severly overestimated. Whereas this may be the case for *P. cylindrica*, and is suggested by the reduced growth rates at high turbidities and the significant coefficient for sediment-induced losses (Chapter 5), respiration rates for *G. retiformis* are unlikely to have been underestimated given the non-significant coefficient for induced losses (Table 5.6). Since corals were transferred directly from their treatment tanks to the respirometer (with filtered water), rates of respiration were likely to have been elevated above baseline due to handling. Also, if High-sediment treatments caused elevated rates of respiration, these were likely to have remained elevated for at least part of the respirometry runs. The observed rates of respiration may thus represent levels intermediate between true baselines and levels expected for high turbidities.

6.5.4. Conclusion.

This study documents contrasting energetics of two symbiotic coral species (*Goniastrea retiformis* and *Porites cylindrica*) exposed 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 utilise suspended sediment as a food source. Enhanced particle feeding by *G. retiformis* in response to shading, in concert with its photo-adaptation, is an effective mechanism for optimising the potential of two inversely related resources, resulting in a broad physiological niche. The energy budget of *P. cylindrica* was dictated to a larger extent by light availability, but showed a growth optimum at intermediate particle regimes, indicating some dependence

on heterotrophy. The lower capacity of *P. cylindrica* to utilise suspended particles, and its lower degree of photoadaptation, potentially confine this species to a more narrow energy optimum in low-turbidity environments. The predicted carbon budget of *G. retiformis* as a function of particle concentration and depth indicates that full heterotrophic compensation for reduced photosynthesis in turbid environments occurs in shallow water only. Its two-fold increase in particle feeding rates in response to shading and at greater depth, however, significantly reduces energy loss during periods of high turbidity.

Chapter 7

General Discussion

7.1. Major findings

The results of this series of experiments support the hypothesis that particle feeding is important for coral energy budgets in turbid habitats, and that high feeding rates of some species offset the stress effects of high particle loads. These results have implications for the development and sustained growth of coral reefs in nearshore environments in general, and in the Great Barrier Reef lagoon in particular. The study highlights the role that optimal balancing of heterotrophy and phototrophy plays in maximising scope for growth and thereby reducing energy deficits under short- and long-term fluctuations in turbidity. In particular, the integrated perspective gained from analysising organism responses within the framework of functional-response models, optimal foraging theory, and the model of scope for growth has revealed novel insights into the importance of trophic strategies of corals in predicting coral energetics across habitats. Although these theories have long been available and frequently used in ecological studies of organisms as well as populations (e.g. Begon et al. 1986, Stephens & Krebs 1986), no studies have previously analysed the effects of variable particle loads on symbiotic cnidarians in the context of this theoretical and conceptual framework.

The linear feeding responses over a broad range of particle concentrations shown for most of the species studied, combined with high assimilation efficiencies (Chapter 2), predict that corals on turbid reefs (e.g. inshore) may be more than one order of magnitude more heterotrophic on suspended particles than corals on oligotrophic reefs (e.g. offshore). These results, in combination with response curves of corals feeding on zooplankters (e.g. Clayton & Lasker 1982, Ferrier-Pages et al. 1998), suggest that corals are generalist feeders (see also Sebens et al. 1996). The efficient use by corals of suspended sediment, which is a relatively poor-quality food source, has adaptive advantages for corals on reefs where zooplankton is sparse or patchy, but where detritus

(e.g. Hansen et al. 1992) or suspended sediment (Larcombe et al. 1995) is temporarily abundant. For example, a comparison of the maximum estimates of zooplankton biomass (~2.2 μgC/L) and organic carbon in detritus (~150 μgC/L) found by Roman et al. (1990) at Davies Reef (midshelf GBR), suggests that detritus may provide >60-fold more organic carbon to coral nutrition than zooplankton. A similar comparison between SPM and zooplankton inshore (using the same estimate of zooplankton biomass and assuming an organic carbon content of 3-5% for SPM) predicts that the organic carbon available as SPM is more than two orders of magnitude greater than that available as zooplankton. Thus, even if large zooplankters are 100-fold easier to capture and digest than fine suspended particles (see discussion in Chapter 2 and 6), sediment feeding would still confer significant energetic and nutritional advantage to corals on turbid reefs. Although the ingestion and assimilation of particulate carbon may be insignificant compared to phototrophic carbon fixation under normal shallow-water conditions for most corals, nevertheless the contribution of nutrients associated with heterotrophic sources of carbon to tissue growth may be highly significant (Chapters 2 and 6).

The enhanced rate of sediment feeding of inshore *Pocillopora damicornis* and *Acropora millepora* relative to their midshelf conspecifics, and the higher assimilation efficiencies of midshelf *A. millepora* at low concentrations (Chapter 3), supports the hypothesis that corals are optimal foragers (Hughes 1980), and suggest that good sediment feeders would have higher fitness than poor sediment feeders in turbid environments (see also p.p. 267 and 484 in Futuyma 1986). Given the ability of corals to feed on particles as well as to photosynthesise, the generally predictable inverse relationship between particle availability and light availability may be a mechanism that drives their trophic plasticity in response to environmental conditions. An important question resulting from the differing heterotrophic capacities within species between inshore and offshore locations is: what is the nature of the underlying mechanisms? Are these mechanisms mainly behavioural, physiological, or morphological? and are they genotypically fixed or phenotypically plastic? If gene flow across the GBR shelf is limited (for example through limited dispersal, (Dight et al. 1988, Black 1993, Ayre & Dufty 1994), selection could favour good sediment feeders on turbid reefs, and the enhanced feeding rates by *P. damicornis*, *A. millepora* inshore may be interpreted as genetic adaptation of local populations. Furthermore, coral species with a predominantly inshore distribution may show even more distinct differences in feeding

capacities than these more widely distributed species. Future studies should therefore focus on population- or species-level comparisons of heterotrophic capacities and the role of phenotypic plasticity. The enhanced feeding capacity of *G. retiformis* in response to prolonged shading (Chapter 6) demonstrated such phenotypic plasticity in addition to a direct behavioural response. Regardless of mechanism, the heterotrophic plasticity demonstrated in both experiments provides new support for the hypothesis that corals are optimal foragers.

The development of the tank system in Chapter 4 for testing effects of particle concentrations and light levels on coral growth enabled quantification and interpretation of patterns of energy investment across habitats in two species (Chapter 5) without the noise from confounding factors characteristic of many previous studies (e.g. van Katwijk et al. 1993, Miller & Cruise 1995, McClanahan & Obura 1997, earlier studies reviewed by Rogers 1990). Importantly, the purpose of this design and type of experimentation, used in conjunction with the feeding and respirometry experiments in Chapter 6, was to develop and parameterise a model of coral energetics, rather than to provide predictions of population changes of corals *in situ*. According to Huston (1999), synthesising the recent debate on the relevance of microcosm experiments in ecology, the studies of Chapters 5 and 6 should be regarded as a reductionistic test of organism responses to specific turbidity and light levels. Although the growth experiments included multiple sets of field controls, the power of the model developed using this experimental and analytical framework require further validation in the field to gain predictive power in nature. Notwithstanding this limitation, the level of insight into the effects of sediment on coral energetics gained through this set of tank experiments are an important step towards a mechanistic understanding of the physiological responses that describe coral niches.

The results of Chapter 5 provided the first empirical evidence that sediment loading can contribute positively to the energy balance of corals. Furthermore, the contrasting growth patterns of the two species with respect to sediment concentrations indicated that growth optima exist between extremely low and high sediment concentrations, and that the location of these optima are influenced by the trophic strategy of the species. The tissue growth optimum of *G. retiformis* at high particle concentrations in both light and shade indicates the significance of SPM as a complementary carbon and nutrient

source, despite the potential stress effect of high sediment loads. The growth optimum of *P. cylindrica* at intermediate (~4 mg/L) particle concentrations in unshaded conditions, however, represents a situation where particulate (and some dissolved) nutrient uptake is high enough to promote growth under saturated photosynthesis. Above this optimum where feeding is saturated, sediment loading becomes a stress factor rather than a food source and suppresses growth. Whereas the importance of dissolved nutrient enrichment in reducing nutrient-limited growth has been demonstrated previously (e.g. Hoegh-Guldberg & Smith 1989, Muller et al. 1994) the role of particle feeding in reducing nutrient limitation has mainly been inferred or assumed.

Another important finding of this growth experiment is that the variation in energy investment into tissues across sediment concentrations is two-fold higher than that of energy investment into skeleton. This result strongly suggests that processes in the tissues should be the primary target for any study attempting to relate coral growth to coral energetics, questioning the conclusions and relevance to physiological stress of the many studies of coral growth that have relied entirely on rates of calcification (e.g. Dodge & Vaisnys 1977, Gladfelter et al. 1978, Hudson 1981, Spencer Davies 1990, Vago 1997).

The result that feeding by *G. retiformis* on sediment with an organic content as low as 3% can fully compensate for reduced phototrophy in shaded conditions has major implications for the energy budget of corals on turbid reefs, potentially explaining the broad physiological niche of this species. Photoadaptation has previously been assumed the only mechanism of maintaining energy balance in corals on turbid reefs (e.g. Edmunds & Davies 1989), but these results demonstrate that the combination of enhanced feeding and an extended diel feeding cycle may be equally important. Numerous factors, however, interact with particle loading in causing stress or growth. The sensitivity analysis of scope for growth in Chapter 6 illustrates that the role of SPM depends strongly on the conditions under which the coral grows, its physiological responses (feeding curves, P-I curves, rate of respiration) and the quality of the particles. This pattern corroborates the results of Fong et al. (1997) who showed that the sensitivity of predicted seagrass productivity is strongly dependent on the nutrient regime.

The trophic and energetic modelling approach to sediment effects on corals in this study is a promising tool for quantitatively describing resource dimensions of coral niches, and may provide a physiological explanation for the success of some coral species in nearshore turbid environments. The concept of resource availability and utilisation in defining niche breadth have been used extensively in ecological studies (e.g. Garbutt & Zangerl 1983, Begon et al. 1986, Rollo & Hawryluk 1988, Leibold 1995). Although the consequences of differential photosynthesis and feeding across habitats for zonation have been inferred for corals (Porter 1976, Wellington 1982), effects of differing particle availability (and consequently light) across habitats has not been formally investigated in the context of niche differentiation. Recent studies of niches in corals (Karlson & Cornell 1998) and softcorals (Fabricius & De'ath 1996) have focused less on the role of resource availability and physiological mechanisms, and more on physical characteristics of habitats and regions.

Species with the ability to shift between phototrophy and heterotrophy would be expected to have a broader physiological niche than species with low heterotrophic capacity and generally low trophic plasticity. 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 less abundant on the most turbid inshore reefs (e.g. Stafford-Smith et al. 1993). The efficacy of the experimental and modelling approach I have taken to predict species niches is also demonstrated by members of the genera *Turbinaria* and *Galaxea* which are good sediment feeders (Chapter 5) and mainly abundant in deeper, turbid inshore environments (Done 1982) suggesting an adaptation to such environments. The fundamental resource niche, however, is larger than the realised ecological niche (Begon et al. 1986, Leibold 1995), and information about organism interactions and environmental variables are necessary to achieve a better prediction of distributions. For example, the results of this study predict an ability of *G. retiformis* to prosper in deeper water than *P. cylindrica*, but the former is mainly found intertidally. Despite the physiological potential of *G. retiformis* to inhabit deep turbid water, factors such as predation by fish (which made caging of *G. retiformis* field controls necessary on the reef slope) may reduce its ecological niche. Therefore, although the agreement between the model of scope for growth (*SfG*) and empirical

growth measurements proposes an important role of *SfG* in predictive models of coral population responses to sediment and turbidity, its efficacy will depend upon the control of, for example, other factors of mortality and survival and effects of differing resources on organism interactions (see also Calow & Sibly 1990).

7.2. Suspended sediment: stress factor of food source?

The problem of high particle loads on coral reefs has given rise to a large number of studies, of which most have addressed one-sided hypotheses aimed at revealing adverse effects (reviews by Pastorok & Bilyard 1985, Grigg & Dollar 1990, Rogers 1990, Richmond 1993). Rogers (1990) proposed that thresholds at which a stress response in corals can be expected are 10 mg/cm²/d for sedimentation rates and 10 mg/L for turbidity. In combination, the contrasting growth responses by *G. retiformis* and *P. cylindrica* to the highest particle load (~16 mg/L), the finding that corals show heterotrophic as well as phototrophic acclimations/plasticity, and the fact that the thresholds proposed by Rogers (1990) are frequently exceeded on inshore reefs in the Great Barrier Reef lagoon (Brady et al. 1991, Hopley et al. 1993, Larcombe et al. 1995, Woolfe & Larcombe 1998), all suggest that generalisations about sediment loads causing stress in corals have limited relevance in nature. High turbidity levels and rates of sedimentation are without doubt detrimental to corals in many circumstances (Rogers 1979, 1983, Stafford-Smith 1992, Riegl 1995), but may not be in others. In order for reef ecologists and managers to successfully predict which combinations of turbidity, depth, and sedimentation are likely to cause stress in a given coral assemblage (and which combinations are not), detailed knowledge is required of at least the handful of biological and environmental parameters studied here, the recent environmental history, the trophic strategy and the general physiology of the most abundant and ecologically important species.

Literature cited

Abdel-Salam, H.A. and J.W. Porter. 1989. Physiological effects of sediment rejection on photosynthesis and respiration in three Caribbean reef corals. *In* JH Choat (ed.), Proc. 6th Int. Coral Reef Symp., Townsville, **2:** 285-292.

Abelson, A., T. Miloh and Y. Loya. 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.

Abelson, A. and Y. Loya. 1995. Cross-scale patterns of particulate food acquisition in marine benthic environments. *Am. Nat.* **145:** 848-854.

Abrams, P.A. 1990. The effects of adaptive behavior on the type-2 functional response. *Ecology* **71:** 877-885.

Acevedo, R., J. Morelock and R.A. Olivieri. 1989. Modification of coral reef zonation by terrigenous sediment stress. *Palaios* **4:** 92-100.

Allemand, D., E. Tambutte, J.-P. Girard and J. Jaubert. 1998. Organic matrix synthesis in the scleractinian coral *Stylophora pistillata*: Role in biomineralization and potential target of the organotin tributyltin. *J. Exp. Biol.* **201:** 2001-2009.

Allen, P.A. 1997. Earth Surface Processes, Blackwell Sciences, Oxford

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

Anthony, K.R.N. 1997. Prey capture by the sea anemone *Metridium senile* (L.): Effects of body size, flow regime, and upstream neighbors. *Biol. Bull.* **192:** 73-86.

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 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* (in press) **19.**

Anthony, K.R.N. and K.E. Fabricius. In review. Shifting roles of heterotrophy and autotrophy in coral energy budgets under varying turbidity. *Ecology.*

Arias Gonzalez, J.E., B. Delesalle, B. Salvat and R. Galzin. 1997. Trophic functioning of the Tiahura reef sector, Moorea Island, French Polynesia. *Coral Reefs* **16:** 231-246.

Atkinson, M.J. 1988. Are coral reefs nutrient-limited? Proc. 6th Int. Coral Reef Symp., Australia, **1:** 157-166.

Ayling, A.M. and A.L. Ayling. 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

Ayling, A. M. and A. L. Ayling. 1995. A preliminary survey of benthic communities in fringing reefs in the middle Cairns section. Unpublished report to the Great Barrier Reef Marine Park Authority, Townsville.

Ayre, D.J. and S. Dufty. 1994. Evidence for restricted gene flow in the viviparous coral *Seriatopora hystrix* on Australia's Great Barrier Reef. *Evolution* **48:** 1183-1201.

Ayukai, T. 1987. Feeding by the calanoid copepod *Acartia clausi* Giesbrecht on natural suspended particulate matter of varying quantity and quality. *J. Exp. Mar. Biol. Ecol.* **106:** 137-149.

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

Ayukai, T. 1995. Retention of phytoplankton and planktonic microbes on coral reefs within the Great Barrier Reef, Australia. *Coral Reefs* **14:** 141-147.

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

Balczon, J.M. and J.R. Pratt. 1996. The functional responses of two benthic algivorous ciliates. *Microb. Ecol.* **31:** 209-224.

Barille, L., J. Prou, M. Heral and D. Razet. 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. and C.J. Crossland. 1977. Coral calcification: sources of error in radioisotope techniques. *Mar. Biol.* **42:** 119-129.

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

Begon, M., J.L. Harper and C.R. Townsend. 1986. Ecology: Inividuals, Populations, and Communities, Blackwell Scientific Publications, Oxford

Berk, S.G., L.H. Parks and R.S. Ting. 1991. Photoadaptation alters the ingestion rate of Paramecium bursaria a mixotrophic ciliate. *Applied Env. Microbiol.* **57:** 2312-2316.

Black, K.P. 1993. The relative importance of local retention and Inter-reef dispersal of neutrally buoyant material on coral reefs. *Coral Reefs* **12:** 43-53.

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

Brady, B.A., F.G. Thomas and D. Yellowlees. 1991. Water quality between the Barron River / Trinity inlet and Green Island, and the effects of seasonal change. Unpublished report to the Great Barrier Reef Marine Park Authority,Townsville

Brodie, J. 1995. Nutrients and the Great Barrier Reef. Report for the Australian Environment Report, Department of Sport & Territories, Canberra

Brodie, J., B.D. Mapstone and R.L. Mitchell. 1989. Magnetic Quay water quality and sediment baseline study. *Research Publication No. 18.* Great Barrier Reef Marine Park Authority,Townsville

Brodie, J.L., M.J. Furnas, A.D.L. Steven, L.A. Trott, F. Pantus, et al. 1997. Monitoring chlorophyl in the Great Barrier Reef lagoon: trends and variability. Proc. 8th Int. Coral Reef Symp., Panama, **1:** 797-802.

Brown, B.E. 1997. Disturbances to reefs in recent times. *In* C Birkeland (ed.), Life and death of coral reefs: Chapman and Hall, Inc., New York. pp. 354-385.

Brown, B.E. and L.S. Howard. 1985. Assessing the effects of "stress" on reef corals. *Adv. Mar. Biol.* **22:** 1-63.

Brown, B.E., T.M.D.A. Le, T.P. Scoffin and A.W. Tudhope. 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. and R.A. Kinzie. 1976. Coral growth. *Oceanogr. Mar. Biol. Ann. Rev.* **14:** 183-225.

Butcher, D.J. 1994. Growth responses of *Acropora longicyathus* to elevated nutrient concentrations (abstract). Proc. Joint Scientific Meeting on Science, Management, and Sustainability of Marine Habitats in the 21st Century, Townsville

Bythell, J.C. 1988. A total nitrogen and carbon budget for the elkhorn coral *Acropora palmata* (Lamarck). Proc. 6th Int. Coral Reef Symp., Australia, **2:** 535-540.

Calow, P. 1981. Invertebrate Biology, Halstead, New York

Calow, P. and R.M. Sibly. 1990. A physiological basis of population processes: ecotoxicological implications. *Func. Ecol.* **4:** 283-288.

Caperon, J. and J. Meyer. 1972. Nutrient-limited growth of marine phytoplankton. II. Uptake kinetics and their role in nutrient-limited growth of phytoplankton. *Deep Sea Res.(A)* **19:** 619-632.

Carman, K.R. 1990. Radioactive labelling of a natural assemblage of marine sedimentary bacteria and microalgae for trophic studies: an autoradiographic study. *Microb. Ecol.* **19:** 279-290.

Carpenter, S. R. 1996. Microcosm experiments have limited relevance for community and ecosystem ecology. *Ecology* 77: 677-680.

Chalker, B.E., W.E. Dunlap and J.K. Oliver. 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.

Clarke, S. and A.J. Elliott. 1998. Modelling suspended sediment concentrations in the Firth of Forth. *Est. Coast. Shelf Sci.* **47:** 235-250.

Clavier, J., P. Chardy and C. Chevillon. 1995. Sedimentation of particulate matter in the South-West lagoon of New Caledonia: Spatial and temporal patterns. *Est. Coast. Shelf Sci.* **40:** 281-294.

Clayton, W.S., Jr. and H.R. Lasker. 1982. Effects of light and dark treatments of feeding by the reef coral *Pocillopora damicornis*. *J. Exp. Mar. Biol. Ecol.* **63:** 269-280.

Coffroth, M.A. 1990. Mucous sheet formation on poritid corals: An evaluation of coral mucus as a nutrient source on reefs. *Mar. Biol.* **105:** 39-49.

Cooper, D. C. and B. J. Copeland. 1973. Responses of continuous-series estuarine microecosystems to point-source input variations. *Ecol. Monogr.* **43:** 213-236.

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

Cortés, N. J. and M. J. Risk. 1985. A reef under siltation stress: Cahuita, Costa-Rica. *Bull. Mar. Sci.* **36:** 339-356.

Crosby, M.P., C.J. Langdon and R.I.E. Newell. 1989. Importance of refractory plant material to the carbon budget of the oyster *Crassostrea virginica*. *Mar. Biol.* **100:** 343-352.

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

Crossland, C.J., D.J. Barnes, T. Cox and M. Devereaux. 1980b. Compartmentation and turnover of organic carbon in the staghorn coral *Acropora formosa*. *Mar. Biol.* **59:** 181-187.

Crossland, C.J., B.G. Hatcher and S.V. Smith. 1991. Role of coral reefs in global ocean production. *Coral Reefs* **10:** 55-64.

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

Crump, B.C., J.A. Baross and C.A. Simenstad. 1998. Dominance of particle-attached bacteria in the Columbia River estuary, USA. *Aquatic Microbial Ecology* **14:** 7-18.

Currie, D.J. 1982. Estimating Michaelis-Menten parameters: bias, variance and experimental design. *Biometrics* **38:** 907-919.

Dallmeyer, D. G., J. W. Porter and G. J. Smith. 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.

Davy, S.K., I.A.N. Lucas and J.R. Turner. 1996. Carbon budgets in temperate anthozoan-dinoflagellate symbioses. *Mar. Biol.* **126:** 773-783.

Day, T. and J.D. McPhail. 1996. The effect of behavioural and morphological plasticity on foraging efficiency in the threespine stickleback (*Gasterosterus* sp.). *Oecologia* **108:** 380-388.

Decho, A.W. and S.N. Luoma. 1991. Time-courses in the retention of food material in the bivalves *Potamocorbula amurensis* and *Macoma balthica*: significance to the absorption of carbon and chromium. *Mar. Ecol. Prog. Ser.* **78:** 303-314.

D'Elia, C.F. 1977. The uptake and release of dissolved phosphorus by corals. *Limnol. Oceanogr.* **22:** 301-315.

Demott, W.R. 1998. Utilization of a cyanobacterium and a phosphorus-deficient green alga as complementary resources by daphnids. *Ecology* **79:** 2463-2481.

Devlin, M., M. Lourey, H. Sweatman and D. Ryan. 1997. Water quality. *In* H Sweatman (ed.), Long-term monitoring of the Great Barrier Reef: Status report number 2. Australian Institute of Marine Science, Townsville, Australia

Devlin, M., M. Lourey, J. Oliver and G. De'ath. 1995. Long-term monitoring of the Great Barrier Reef: Water quality. Status report number 1, Australian Institute of Marine Science, Townsville, Australia

Dight, I.J., L. Bode and M.K. James. 1988. Models of larval dispersal within the central Great Barrier Reef: Patterns of connectivity and their implications for species distributions. *In* JH Choat, D Barnes, MA Borowitzka, JC Coll, PJ Davies, P Flood (eds.), Proc. 6th Int. Coral Reef Symp., Townsville, Australia, **3:** 217-224.

Dight, I.J., L. Bode and M.K. James. 1990. Modelling the larval dispersal of *Acanthaster planci*. 2. Patterns of reef connectivity. *Coral Reefs* **9:** 125-134.

Dodge, R.E. and J.R. Vaisnys. 1977. Coral populations and growth patterns: responses to sedimentation and turbidity associated with dredging. *J. Mar. Res.* **35:** 715-730.

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

Dollar, S.J. and R.W. Grigg. 1981. Impact of a kaolin clay spill on a coral reef in Hawaii. *Mar. Biol.* **65:** 269-276.

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

Drake, J. A., G. R. Huxel and C. L. Hewitt. 1996. Microcosms as models for generating and testing community theory. *Ecology* 77: 670-677.

Dubinsky, Z. and P. L. Jokiel. 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.

Edinger, E.N., J. Jompa, G.V. Limmon, W. Widjatmoko and M.J. Risk. 1998. Reef degradation and coral biodiversity in Indonesia - effects of land-based pollution, destructive fishing practices and changes over time. *Mar. Pollut. Bull.* **36:** 617-630.

Edmunds, P.J. and P.S. Davies. 1989. An energy budget for *Porites porites* (Scleractinia), growing in a stressed environment. *Mar. Biol.* **8:** 37-43.

Erez, J. 1990. On the importance of food sources in coral-reef ecosystems. *In* Z Dubinsky (ed.), Ecosystems of the World: Coral Reefs: Elsevier, Amsterdam, pp. 411-418.

Fabricius, K., G. Yahel and A. Genin. 1998. In situ depletion of phytoplankton by an azooxanthellate soft coral. *Limnol. Oceanogr.* **43:** 354-356.

Fabricius, K.E. and G. De'ath. 1996. Habitat optima of softcorals on the Central Great Barrier Reef: niche characteristics using regression tree analysis. Great Barrier Reef: science, use and management; a national conference: proceedings. Great Barrier Reef Marine Park Authority, Townsville, **2:** 167-174.

Fabricius, K.E. and M. Dommisse. In review. Import of suspended particulate matter into soft-coral dominated nearshore communities. *Limnol. Oceanogr.*

Fabricius, K.E., Y. Benayahu and A. Genin. 1995. Herbivory in asymbiotic soft corals. *Science* **268:** 90-92.

Falkowski, P.G., Z. Dubinsky, L. Muscatine and J. Porter. 1984. Light and the bioenergetics of a symbiotic coral. *BioScience* **34:** 705-709.

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

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

Farrant, P.A., M.A. Borowitzka, R. Hinde and R.J. King. 1987. Nutrition of the temperate Australian soft coral *Capnella gaboensis* 2. The role of zooxanthellae and feeding. *Mar. Biol.* **95:** 575-582.

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

Fitt, W.K., R.L. Pardy and M.M. Littler. 1982. Photosynthesis respiration and contribution to community productivity of the symbiotic sea anemone *Anthopleura elegantissima*. *J. Exp. Mar. Biol. Ecol.* **61:** 213-232.

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

Fong, P., M.E. Jacobson, M.C. Mescher, D. Lirman and M.C. Harwell. 1997. Investigating the management potential of a seagrass model through sensitivity analysis and experiments. *Ecol. Applic.* **7:** 300-315.

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

Furnas, M.J. and A.W. Mitchell. 1996. Nutrient inputs into the central Great Barrier Reef (Australia) from subsurface intrusions of Coral Sea waters - a two-dimensional displacement model. *Continental Shelf Res.* **16:** 1127-1148.

Futuyma, D.J. 1986. Evolutionary Biology, Second edition, Sinauer Associates, Massachusetts, USA

Garbutt, K. and A.R. Zangerl. 1983. Application of genotype-environment interactioin analysis to niche quantification. *Ecology* **64:** 1292-1296.

GBRMPA. 1999. Sea Temperature Monitoring Program. http\\www.gbrmpa.gov.au/seatemp/index.html

Gibbs, R.J., M.D. Matthews and D.A. Link. 1971. The relationship between grain size and settling velocity. *J. Sed. Petrol.* **41:** 7-18.

Ginsburg, R.N. and P.W. Glynn. 1993. Summary of the colloquium and forum on the global aspects of coral reefs: Health, hazards and history. *In* RN Ginsburg (ed.), Proceedings of the Colloquium on Global Aspects of Coral Reefs: Health, Hazards and History: University of Miami, Rosenstiel School of Marine and Atmospheric Science, i-ix.

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

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

Goreau, T.F., N.I. Goreau and C.M. Yonge. 1971. Reef corals: autotrophs or heterotrophs? *Biol. Bull.* **141:** 247-260.

Gremare, A., J.M. Amouroux and J. Amouroux. 1989. Modelling of consumption and assimilation in the deposit feeding polychaete *Eupolymnia nebulosa*. *Mar. Ecol. Prog. Ser.* **54:** 239-248.

Gremare, A., J.M. Amoureaux and F. Charles. 1991. Compartmental analysis and analog modelling, a tool to study consumption of organic matter by benthic invertebrates. *In* PJ Kershaw and DS Woodhead (eds.), Radionuclides in the study of marine processes: Elsevier Applied Sciences, London & New York, pp. 319-328.

Grigg, R.W. and S.J. Dollar. 1990. Natural and anthropogenic disturbance on coral reefs. *In* Z Dubinzky (ed.), Coral Reefs: Elsevier, Amsterdam, pp. 439-452.

Guzman, H.M., K.A. Burns and J.B.C. Jackson. 1994. Injury, regeneration and growth of Caribbean reef corals after a major oil spill in Panama. *Mar. Ecol. Prog. Ser.* **105:** 231-241.

Hall, V.R. and T.P. Hughes. 1996. Reproductive strategies of modular animals: comparative studies of reef-building corals. *Ecology* **77:** 950-963.

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

Hansen, B., T. Wernberg Moller and L. Wittrup. 1997. Particle grazing efficiency and specific growth efficiency of the rotifer *Brachionus plicatilis* (Muller). *J. Exp. Mar. Biol. Ecol.* **215:** 217-233.

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

Hart, D.D. and S.C. Latta. 1986. Determinants of ingestion rates in filter-feeding larval blackflies (Diptera: Simuliidae). *Freshwater Biol.* **16:** 1-14.

Hata, H., A. Suzuki, T. Maruyama, N. Kurano, S. Miyachi, et al. 1998. Carbon flux by suspended and sinking particles around the barrier reef of Palau, western Pacific. *Limnol. Oceanogr.* **43:** 1883-1893.

Heiss, G.A. 1996. Annual band width variation in *Porites* sp. from Aqaba, Gulf of Aqaba, Red Sea. *Bull. Mar. Sci.* **59:** 393-403.

Helmuth, B. and K.P. Sebens. 1993. The influence of colony morphology and orientation to flow on particle capture by the scleractinian coral *Agaricia agaricites* Linnaeus. *J. Exp. Mar. Biol. Ecol.* **165:** 251-278.

Hoegh-Guldberg, O. and G.J. Smith. 1989. Influence of the population density of zooxanthellae and supply of ammonium on the biomass and metabolic characteristics of the reef corals *Seriatopora hystrix* and *Stylophora pistillata*. *Mar. Ecol. Prog. Ser.* **57:** 173-186.

Holling, C.S. 1959. Some characteristics of simple types of predation and parasitism. *Can. Entomol.* **91:** 385-398.

Hopley, D., R. van Woesik, D. C. J. D. Hoyal, C. E. Rasmussen and A. D. L. Steven. 1993. Sedimentation resulting from road development, Cape Tribulation Area. *Technical Memorandum No. 24*, Great Barrier Reef Marine Park Authority, Townsville.

Hudson, J.H. 1981. Growth rates in Montastrea annularis: a record of of environmental change in Key Largo Coral Reef Marine Sanctuary, Florida. *Bull. Mar. Sci.* **31:** 444-459.

Hughes, R.N. 1980. Optimal foraging theory in the marine context. *Oceanogr. Mar. Biol. Ann. Rev.* **18:** 423-481.

Hughes, T.P. and J.H. Connell. 1999. Multiple stressors on coral reefs: A long-term perspective. *Limnol. Oceanogr.* **44:** 932-940.

Huston, M.A. 1999. Microcosm experiments have limited relevance for community and ecosystem ecology: synthesis of comments. *Ecology* **80:** 1088-1089.

Jackson, G.A. 1990. A model of the formation of marine algal flocs by physical coagulation processes. *Deep Sea Res.* (A) **37:** 1197-1212.

Jerlov, N.G. 1976. Marine Optics, Elsevier Scientific Publishing Company, Amsterdam

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

Johannes, R.E., S.L. Coles and N.T. Kuenzel. 1970. The role of zooplankton in the nutrition of some scleractinian corals. *Limnol. Oceanogr.* **15:** 579-586.

Johannes, R.E. and L. Tepley. 1974. Examination of feeding of the reef coral *Porites lobata* in situ using time lapse photography. Proc. 2nd Int. Coral Reef Symp., Great Barrier Reef Commitee, Brisbane, pp. 127-131.

Johnson, A.S. and K.P. Sebens. 1993. Consequences of a flattened morphology: Effects of flow on feeding rates of the scleractinian coral *Meandrina meandrites*. *Mar. Ecol. Prog. Ser.* **99:** 99-114.

Johnson, D. P. and R. M. Carter. 1991. Sedimentary framework of mainland fringing reef development, Cape Tribulation Area. *Technical Memorandum No 14*, Great Barrier Reef Marine Park Authority, Townsville

Johnstone, R.W., K. Koop and A.W.D. Larkum. 1990. Physical aspects of coral-reef lagoon sediments in relation to detritus processing and primary production. *Mar. Ecol. Prog. Ser.* **66:** 273-284.

Jokiel, P. L. and J. I. Morrissey. 1993. Water motion on coral reefs: evaluation of the "clod card" technique. *Mar. Ecol. Prog. Ser.* **93:** 175-181.

Jones, H.L.J., P. Durjun, B.S.C. Leadbeater and J.C. Green. 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.

Jørgensen, S.E. 1986. Fundamentals of Ecological Modelling. Vol. 9, Elsevier, Amsterdam

Jumars, P. A. and A. R. M. N. Nowell. 1984. Fluid and sediment dynamic effects on marine benthic community structure. *Amer. Zool.* **24:** 45-55.

Karlson, R.H. and H.V. Cornell. 1998. Scale-dependent variation in local vs. regional effects on coral species richness. *Ecol. Monogr.* **68:** 259-274.

Kiflawi, M. and A. Genin. 1997. Prey flux manipulation and the feeding rates on reef-dwelling planktivorous fish. *Ecology* **78:** 1062-1077.

Kiørboe, T., K.P. Andersen and H.G. Dam. 1990. Coagulation efficiency and aggregate formation in marine phytoplankton. *Mar. Biol.* **107:** 235-246.

Kirk, J.T.O. 1994. Light and Photosynthesis in Aquatic Ecosystems, Second edition, Cambridge University Press, Cambridge.

Kleypas, J.A. 1996. Coral reef development under naturally turbid conditions: fringing reefs near Broad Sound, Australia. *Coral Reefs* **15:** 153-167.

Klumpp, D.W. and C.L. Griffiths. 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.

Koerselman, W. and A.F.M. Meuleman. 1996. The vegetation N:P ratio: a new tool to detect the nature of nutrient limitation. *J. Applied Ecol.* **33:** 1441-1450.

Kojis, B.L. and N.J. Quinn. 1985. Puberty in *Goniastrea favulus*. Age or size limited? Proc. 5th Int. Coral Reef Congress., Tahiti, pp. 289-293.

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

Larcombe, P. and K.J. Woolfe. 1999. Increased sediment supply to the Great Barrier Reef will not increase sediment accumulation at most coral reefs. *Coral Reefs* **18:** 163-169.

Larkum, A. W. D. and A. D. L. Steven. 1994. ENCORE: The effect of nutrient enrichment on coral reefs. I. Experimental design and research programme. *Mar. Pollut. Bull.* **29:** 112-120.

Lebo, M.E. 1991. Particle-bound phosphorus along an urbanised coastal plain estuary. *Mar. Chem.* **34:** 225-246.

Lehman, J.T. 1976. The filter-feeder as an optimal forager, and the predicted shapes of feeding curves. *Limnol. Oceanogr.* **21:** 501-516.

Leibold, M.A. 1995. The niche concept revisited: Mechanistic models and community context. *Ecology* **76:** 1371-1382.

Lemke, M.J. and S.H. Bowen. 1998. The nutritional value of organic detrital aggregate in the diet of fathead minnows. *Freshw. Biol.* **39:** 447-453.

Leonard, A.B. 1989. Functional response in *Antedon mediterranea* (Lamarck) (Echinodermata: Crinoidea): the interaction of prey concentration and current velocity on a passive suspension feeder. *J. Exp. Mar. Biol. Ecol.* **127:** 81-103.

Lesser, M.P., J.D. Witman and K.P. Sebens. 1994. Effects of flow and seston availability on scope for growth of benthic suspension-feeding invertebrates from the Gulf of Maine. *Biol. Bull.* **187:** 319-335.

Lewis, J.B. and W.S. Price. 1975. Feeding mechanisms and feeding strategies of Atlantic reef corals. *J. Zool. Lond.* **176:** 527-544.

Lewis, J.B. 1977. Suspension feeding in Atlantic reef corals and the importance of suspended particulate matter as a food source. Proc. 3rd Int. Coral Reef Symposium, University of Miami, pp. 405-408.

Long, E.R. 1992. Ranges in chemical concentrations in sediments associated with adverse biological effects. *Mar. Pollut. Bull.* **24:** 38-45.

Lopez, G.R. and M.A. Crenshaw. 1982. Radiolabelling of sedimentary organic matter with ^{14}C-formaldehyde. Preliminary evolution of a new technique for use in deposit-feeding studies. *Mar. Ecol. Prog. Ser.* **8:** 283-289.

Lopez, G.R., P. Tantichodok and I.J. Cheng. 1989. Radiotracer methods for determining utilization of sedimentary matter by deposit feeders. *In* GR Lopez, G Taghon and J Levinton (eds.), Ecology of marine deposit feeders. Lecture notes on coastal and estuarine studies: Springer Verlag, New York, pp. 149-170.

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

Mann, K.H. 1982. Ecology of coastal waters: a systems approach. Vol. 8, Blackwell Scientific Publications, Oxford.

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

Marshall, N. 1965. Detritus over the reef and its potential contribution to adjacent waters of Eniwetok Atoll. *Ecology* **46:** 343-344.

Marubini, F. and B. Thake. 1999. Bicarbonate addition promotes coral growth. *Limnol. Oceanogr.* 44: 716-720.

McCarthy, J.C., T.E. Pyle and G.M. Griffin. 1973. Light transmissivity, suspended sediments, and the legal definition of turbidity. *Est. Coast. Shelf Sci.* **2:** 291-299.

McClanahan, T. R. and D. Obura. 1997. Sedimentation effects on shallow coral communities in Kenya. *J. Exp. Mar. Biol. Ecol.* **209:** 103-122.

McCloskey, L.R., D.S. Wethey and J.W. Porter. 1978. The measurement and interpretation of photosynthesis and respiration in reef corals. *Monographs of Oceanographic Methodology (SCOR-UNESCO)* **4:** 379-396.

McConnaghey, T.A. and J.F. Whelan. 1997. Calcification generates protons for nutrient and bicarbonate uptake. *Earth-Science Reviews* 967: 95-117.

McEwan, J., A.J. Gabric and P.R.F. Bell. 1998. Water quality and phytoplankton dynamics in Moreton Bay, south-eastern Queensland. II. Mathematical modelling. *Mar. Freshwater Res.* 49: 227-239.

Meyer, J.L., E.T. Schultz and G.S. Helfman. 1983. Fish schools: an asset to corals. *Science* **220:** 1047-1049.

Meyer, J.L. and E.T. Schultz. 1985. Migrating haemulid fishes as a source of nutrients and organic matter on coral reefs. *Limnol. Oceanogr.* **30:** 146-156.

Meyer, J.L. and E.T. Schultz. 1985. Tissue condition and growth rate of corals associated with fish schooling. *Limnol. Oceanogr.* **30:** 157-166.

Miller, R.L. and J.F. Cruise. 1995. Effects of suspended sediments on coral growth - evidence from remote sensing and hydrologic modeling. *Remote Sensing of Environment* **53:** 177-187.

Mills, M.M. and K.P. Sebens. 1997. Particle ingestion efficiency of the coral *Siderastrea sidera* and *Agaricia agaricites*: effects of flow speed and sediment loads. Proc. 8th Int. Coral Reef Symp., Panama, **2:** 1059-1064.

Mitchell, A. W. and M. J. Furnas. 1997. Terrestrial inputs of nutrients and suspended sediments to the Great Barrier Reef lagoon. Great Barrier Reef, science, use and management: a national conference: proceedings, Townsville, Conference Great Barrier Reef Marine Park Authority, **1:** 59-71 in

Moss, A.J., G.E. Rayment, N. Reilly and E.K. Best. 1992. A preliminary assessment of sediment and nutrient exports from Queensland coastal catchments. Department of Environment and Heritage Deaprtment of Primary Industries, Queensland Government.

Muller, P. G., L. R. McCloskey, O. Hoegh-Guldberg and P. J. McAuley. 1994. Effect of ammonium enrichment on animal and algal biomass of the coral *Pocillopora damicornis*. *Pac. Sci.* **48:** 273-283.

Muller, P.G., C.B. Cook and C.F. D'Elia. 1994. Elemental composition of the coral *Pocillopora damicornis* exposed to elevated seawater ammonium. *Pac. Sci.* **48:** 234-246.

Muscatine, L. 1973. Nutrition of corals. *In* OA Jones and R Endean (eds.), The Geology and Biology of Coral Reefs: Academic Press, London, pp. 77-115.

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

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

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

Muscatine, L., P.G. Falkowski, J.W. Porter and Z. Dubinsky. 1984. Fate of photosynthetic fixed carbon in light- and shade-adapted colonies of the symbiotic coral *Stylophora pistillata*. *Proc. Royal Soc. London (B)*, **222:** 181-202.

Navarro, J.M. and J. Widdows. 1997. Feeding physiology of *Cerastoderma edule* in response to a wide range of seston concentrations. *Mar. Ecol. Prog. Ser.* **152:** 175-186.

Neudecker, S. 1981. Growth and survival of scleractinian corals exposed to thermal effluents at Guam. Proc. 4th Int. Coral Reef Symp. **1:** 173-180.

Novitsky, J.A. 1990. Evidence for sedimenting particles as the origin of the microbial community in a coastal marine sediment. *Mar. Ecol. Prog. Ser.* **60:** 161-168.

Nygaard, K. and D.O. Hessen. 1990. Use of carbon-14 protein-labelled bacteria for estimating clearance rates by heterotrophic and mixotrophic flagellates. *Mar. Ecol. Prog. Ser.* **68:** 7-14.

Ohlhorst, S.L. 1982. Diel migration patters of demersal reef zooplankton. *J. Exp. Mar. Biol. Ecol.* **60:** 1-15.

Oliver, J. K. 1984. Intra-colony variation in the growth of *Acropora formosa*: Extension rates and skeletal structure of white (zooxanthellae-free) and brown-tipped branches. *Coral Reefs* **3:** 139-147.

Parsons, T.R., M. Takahashi and B. Hargrave. 1984. Biological Oceanographic Processes, Third edition, Pergamon Press, Oxford.

Parsons, T.R., Y. Maita and C.M. Lalli. 1984. A manual of chemical and biological methods for seawater analysis, Pergamon Press, Oxford.

Pastorok, R.A. and G.R. Bilyard. 1985. Effects of sewage pollution on coral-reef communities. *Mar. Ecol. Prog. Ser.* **21:** 175-190.

Patterson, M.R. 1991. Passive suspension feeding by an octocoral in plankton patches: empirical test of a mathematical model. *Biol. Bull.* **180:** 81-92.

Patterson, M.R. 1992. A chemical engineering view of cnidarian symbioses. *Amer. Zool.* **32:** 566-582.

Peters, R. H. 1991. A critique for ecology. Cambridge University Press. Cambridge, England.

Petersen, J.K. and H.U. Riisgård. 1992. Filtration capacity of the ascidian *Ciona intestinalis* and its grazing impact in a shallow fjord. *Mar. Ecol. Prog. Ser.* **88:** 9-17.

Pomeroy, L.R. 1974. The ocean's food web, a changing paradigm. *BioScience* **24:** 499-504.

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

Porter, J.W. 1976. Autotrophy, heterotrophy, and resource partitioning in Caribbean reef-building corals. *Amer. Nat.* **110:** 731-742.

Porter, J. W., S. K. Lewis and K. G. Porter. 1999. The effect of multiple stressors on the Florida Keys coral reef ecosystem: A landscape hypothesis and a physiological test. *Limnol. Oceanogr.* **44:** 941-949.

Reynolds, C. S., M. L. White, R. T. Clarke and A. F. Marker. 1990. Suspension and settlement of particles in flowing water: Comparison of the effects of varying water depth and velocity in circulating channels. *Freshw. Biol.* **24:** 23-34.

Rice, L. R. 1982. The detritus nitrogen problem: new observations and perspectives from organic geochemistry. *Mar. Ecol. Prog. Ser.* **9:** 153-162.

Rice, S.A. and C.L. Hunter. 1992. Effects of suspended sediment and burial on scleractinian corals from West Central Florida patch reefs. *Bull. Mar. Sci.* **51:** 429-442.

Richmond, R.H. 1993. Coral reefs - present problems and future concerns resulting from anthropogenic disturbance. *Amer. Zool.* **33:** 524-536.

Riebesell, U. and D.A. Wolf Gladrow. 1992. The relationship between physical aggregation of phytoplankton and particle flux: A numerical model. *Deep Sea Res.* (A) **39:** 1085-1102.

Riegl, B. 1995. Effects of sand deposition on scleractinian and alcyonacean corals. *Mar. Biol.* **121:** 517-526.

Riegl, B. and G.M. Branch. 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.

Rigler, F.H. 1961. The relationship between concentration of food and feeding rate of *Daphnia magna* Straus. *Can. J. Zool.* **39:** 857-868.

Riley, G.A. 1963. Organic aggregates in seawater and the dynamics of their formation and utilization. *Limnol. Oceanogr.* **8:** 372-381.

Robinson, B.W. and D. Sloan Wilson. 1998. Optimal foraging, specialization, and a solution to Liem's paradox. *Am. Nat.*, **151:** 223-237.

Rogers, C.S. 1979. The effect of shading on coral reef structure and function. *J. Exp. Mar. Biol. Ecol.* **41:** 269-288.

Rogers, C.S. 1983. Sublethal and lethal effects of sediments applied to common Caribbean reef corals in the field. *Mar. Pollut. Bull.* **14:** 378-382.

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

Rollo, C.D. and M.D. Hawryluk. 1988. Compensatory scope and resource allocation in two species of aquatic snails. *Ecology* **69:** 146-156.

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

Rosen, B.R. 1982. The tropical high diversity enigma - the corals eye view. *In* P.L. Forey (ed.), The Evolving Biosphere, Cambridge University Press, London

Rosenberg, R. 1995. Benthic marine fauna structured by hydrodynamic processes and food availability. *Neth. J. Sea Res.* **34:** 303-317.

Rothhaupt, K.O. 1996. Utilization of substitutable carbon and phosphorus sources by the mixotrophic chrysophyte *Ochromonas* sp. *Ecology* 77: 706-715.

Rubenstein, D.I. and M.A.R. Koehl. 1977. The mechanisms of filter feeding: some theoretical considerations. *Am. Nat.* **111:** 981-994.

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

Sakai, K. and M. Nishihira. 1991. Immediate effect of terrestrial runoff on a coral community near a river mouth in Okinawa. *Galaxea* **10:** 125-134.

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

Schaffelke, B. and D.W. Klumpp. 1997. Biomass and productivity of tropical macroalgae on three nearshore fringing reefs in the central Great Barrier Reef, Australia. *Botanica Marina* **40:** 373-383.

Schaffelke, B. In press. Particulate organic matter as an alternative nutrient source for tropical *Sargassum* species (Fucales, Phaeophyceae). *Phycologia.*

Schlichter, D. 1982. Epidermal nutrition of the alcyonarian *Heteroxenia fuscescens* (Ehrb.): absorption of dissolved organic material and lost exogenous photosynthates. *Oecologia* **53:** 40-49.

Schuhmacher, H. 1979. Experiments on adaptations to sedimentation and substrate in fungiid corals (Scleractinia:Fungiidae). *Int. Revue der Gesamten Hydrobiologie* **64:** 207-243.

Sebens, K.P. 1982. Limits to indeterminate growth: an optimal size model applied to passive suspension feeders. *Ecology* **63:** 209-222.

Sebens, K.P. 1987. Coelenterata *In* F.J. Vernberg and TJ Pandian (eds.), Animal Energetics: Academic Press, New York, USA, pp. 55-120.

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

Sebens, K.P. and M.A.R. Koehl. 1984. Predation on zooplankton by the benthic anthozoans *Alcyonium siderium* (Alcyonacea) and *Metridium senile* (Actiniaria) in the New England subtidal. *Mar. Biol.* **81:** 255-272.

Sebens, K.P. and A.S. Johnson. 1991. Effects of water movement on prey capture and distribution of reef corals. *Hydrobiologia* **226:** 91-102.

Sebens, K.P. and T.J. Done. 1992. Water flow, growth form and distribution of scleractinian corals: Davies Reef (GBR), Australia. Proc. 7th Int. Coral Reef Symp., Guam, **1:** 557-568.

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

Sebens, K.P., J. Witting and B. Helmuth. 1997. Effects of water flow and branch spacing on particle capture by the reef coral *Madracis mirabilis* (Duchassaing and Michelotti). *J. Exp. Mar. Biol. Ecol.* **211:** 1-28.

Sebens, K.P., S.P. Grace, B. Helmuth, E.J. Maney and J.S. Miles. 1998. Water flow and prey capture by three scleractinian corals, *Madracis mirabilis*, *Montastrea cavernosa* and *Porites porites*, in a field enclosure. *Mar. Biol.* **131:** 347-360.

Seiderer, L.J. and R.C. Newell. 1985. Relative significance of phytoplankton, bacteria and plant detritus as carbon and nitrogen resources for the kelp bed filter-feeder *Choromytilus meridionalis*. *Mar. Ecol. Prog. Ser.* **22:** 127-139.

Shick, J.M. 1991. A functional biology of sea anemones, Chapman & Hall, London.

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

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

Simon, M., A.L. Alldredge and F. Azam. 1990. Bacterial carbon dynamics on marine snow. *Mar. Ecol. Prog. Ser.* **65:** 205-211.

Sokal, R.R. and F.J. Rohlf. 1995. Biometry, Third edition, W.H. Freeman & Co., New York, USA

Sorokin, Y.I. 1973. On the feeding of some scleractinian corals with bacteria and dissolved organic matter. *Limnol. Oceanogr.* **18:** 380-385.

Spencer Davies, P. 1984. The role of zooxanthellae in the nutritional energy requirements of *Pocillopora eydouxi*. *Coral Reefs* **2:** 181-186.

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. 1992. Mortality of the hard coral *Leptoria phrygia* under persistent sediment influx. Proc. 7th Int. Coral Reef Symp, Guam, **1:** 289-299.

Stafford Smith, M.G. 1993. Sediment-rejection efficiency of 22 species of Australian scleractinian corals. *Mar. Biol.* **115:** 229-243.

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

Stafford-Smith, M.G., U.L. Kaly and J.H. Choat. 1993. Short-term response of corals to dredging of Platypus Channel, Cleveland Bay, Townsville, Queensland. Townsville Port Authority, Townsville

Stambler, N., P. L. Jokiel and Z. Dubinsky. 1994. Nutrient limitation in the symbiotic association between zooxanthellae and reef-building corals: The Experimental design. *Pac. Sci.* **48:** 219-223.

STATISTICA. 1997. Release 5.1, StatSoft Inc., U.S.A.

Stephens, D.W. and J.R. Krebs. 1986. Foraging theory, Princeton University Press, New Jersey.

Stephenson, T.A. 1935. The British Sea Anemones. Vol. II, Ray Society, London

Stobart, B. 1994. Delimiting coral species using alternative techniques: *Montipora digitata* (Dana, 1846), a case study. PhD Thesis, James Cook University, Townsville.

Sutton, D.C. and O. Hoegh-Guldberg. 1990. Host-zooxanthella interactions in four temperate marine invertebrate symbioses: assessment of effect of host extracts on symbiosis. *Biol. Bull.* **178:** 175-186.

Szmant-Froelich, A.M. 1985. The effect of colony size on the reproductive ability of the Caribbean coral *Montastrea annularis* (Ellis and Solander). Proc. 5th Int. Coral Reef Congress, Tahiti, **4:** 295-300.

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

Szmant, A.M., L.M. Ferrer and L.M. Fitzgerald. 1990. Nitrogen excretion and O:N ratios in reef corals: evidence for conservation of nitrogen. *Mar. Biol.* **104:** 119-127.

Taghon, G.L. 1982. Optimal foraging by deposit-feeding invertebrates: roles of particle size and organic coating. *Oecologia* **52:** 295-304.

Taghon, G.L. and P.A. Jumars. 1984. Variable ingestion rates and its role in optimal foraging behavior of marine deposit feeders. *Ecology* **65:** 549-558.

Taghon, G.L. and R.R. Greene. 1992. Utilization of deposited and suspended particulate matter by benthic "interface" feeders. *Limnol. Oceanogr.* **37:** 1370-1391.

Takabayashi, M. and O. Hoegh-Guldberg. 1995. Ecological and physiological differences between two colour morphs of the coral *Pocillopora damicornis*. *Mar. Biol.* **123:** 705-714.

Taylor, R.B. 1998. Density, biomass and productivity of animals in four subtidal rocky reef habitats: the importance of small mobile invertebrates. *Mar. Ecol. Prog. Ser.* **172:** 37-51.

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

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

Thompson, T. L. and E. P. Glenn. 1994. Plaster standards to measure water motion. *Limnol. Oceanogr.* **39:** 1768-1779.

Tomascik, T. and F. Sander. 1987. Effects of eutrophication on reef-building corals. II. Structure of scleractinian coral communities on fringing reefs, Barbados, West Indies. *Mar. Biol.* **94:** 53-75.

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

Tsuchida, C.B. and D.C. Potts. 1994. The effects of illumination, food and symbionts on growth of the sea anemone *Anthopleura elegantissima* (Brandt, 1835). 1. Ramet Growth. *J. Exp. Mar. Biol. Ecol.* **183:** 227-242.

Tyler, P.A., D.S.M. Billett and J.D. Gage. 1990. Seasonal reproduction in the sea star *Dytaster grandis* from 4000 M in the Northeast Atlantic Ocean. *J. Mar. Biol. Assoc. UK* **70:** 173-180.

UNEP/IUCN. 1988. Coral reefs of the world. Vol. 1-3, UNEP/IUCN, Cambridge, and Nairobi.

Vago, R., E. Vago, Y. Achituv, M. Benzion and Z. Dubinsky. 1994. A non-destructive method for monitoring coral growth affected by anthropogenic and natural long term changes. *Bull. Mar. Sci.* **55:** 126-132.

Vago, R.G., E; Collingwood, JC. 1997. Laser measurements of coral growth. *Nature* **386:** 30-31.

van Katwijk, M.M., N.F. Meier, R. Vanloon, E.M. Vanhove, W.B.J.T. Giesen, et al. 1993. Sabaki river sediment load and coral stress: correlation between sediments and condition of the Malindi-Watamu reefs in Kenya (Indian Ocean). *Mar. Biol.* **117:** 675-683.

Vanderploeg, H.A. and D. Scavia. 1979. Two electivity indices for feeding with special reference to zooplankton grazing. *J. Fish. Res. Board. Can.* **36:** 362-365.

Van-Praet, M. 1985. Nutrition of sea anemones. *Adv. Mar. Biol.* **22:** 65-99.

Veron, J.E.N. 1986a. Coral species list for the Cape Tribulation area. Proceedings of the Fringing Reefs Workshop - Science, Industry and Management, Conference, Great Barrier Reef Marine Park Authority, Townsville, pp. 99-103.

Veron, J.E.N. 1986b. Corals of Australia and the Indo-Pacific, Second edition, University of Hawaii Press, Honolulu, Hawaii.

Veron, J.E.N. and M. Pichon. 1976. Scleractinia of Eastern Australia. Part I: Families Thamnastreriidae, Astrocoeniidae, Pocilloporidae. vol. 1, Australian Government Publishing Service, Canberra

Vytopil, E.G. 1997. Coral commensal communities and the nature of the *Tetralia* (Brachyura) - *Acropora* (Scleractinia) symbiosis. Honours Thesis, James Cook University, Townsville.

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

Ward, S. 1994. The effects of the ENCORE (enrichment of nutrients on a coral reef) experiment on the fecundity of the scleractinian coral *Acropora longicyathus* (abstract). Proc Joint Scientific Meeting on Science, Management, and Sustainability of Marine Habitats in the 21st Century.

Warren, C.E. and G.E. Davis. 1967. Laboratory studies on the feeding, bioenergetics and growth of fish. *In* SD Gerking (ed.), The biological basis for freshwater fish production: Blackwell Scientific, Oxford, pp. 175-214.

Wasson, R.J. 1997. Run-off from the land to the rivers and the sea. The Great Barrier Reef, science, use and management: a national conference: proceedings: Great Barrier Reef Marine Park Authority, Townsville, p.p. 23-41.

Wellington, G. M. 1982. An experimental analysis of the effects of light and zooplankton on coral zonation. *Oecologia* **52:** 311-320.

Widdows, J. and D. Johnson. 1988. Physiological energetics of *Mytilus edulis*: scope for growth. *Mar. Ecol. Prog. Ser.* **46:** 113-121.

Widdows, J., P. Donkin, M.D. Brinsley, S.V. Evans, P.N. Salkeld, et al. 1995. Scope for growth and contaminant levels in North Sea mussels *Mytilus edulis*. *Mar. Ecol. Prog. Ser.* **127:** 131-148.

Willis, B.L., R.C. Babcock, P.L. Harrison and C.C. Wallace. 1997. Experimental hybridization and breeding incompatibilities within the mating systems of mass spawning reef corals. Coral Reefs **16** (Suppl S): 53-65.

Witte, U., T. Brattegard, G. Graf and B. Springer. 1997. Particle capture and deposition by deep-sea sponges from the Norwegian-Greenland Sea. *Mar. Ecol. Prog. Ser.* **154:** 241-252.

Wolanski, E. 1994. Physical oceanographic processes of the Great Barrier Reef, CRC Press, Boca Raton.

Woolfe, K.J. and P. Larcombe. 1998. Terrigenous sediment accumulation as a regional control on the distribution of reef carbonates. *Spec. Publs Int. Ass. Sediment.* **25:** 295-310.

Wotton, R.S. 1988. Dissolved organic material and trophic dynamics. *BioScience* **38:** 172-178.

Wotton, R.S. 1994a. Particulate and dissolved organic matter as food. *In* R.S. Wotton (ed.), The biology of particles in aquatic systems: CRC Press, Boca Raton, pp. 235-288.

Wotton, R.S. 1994b. The classification of particulate and dissolved matter *In* R.S. Wotton (ed.), The Biology of Particles in Aquatic Systems: CRC Press, Boca Raton, p.p. 1-6.

Yonge, C.M. 1930. Studies on the physiology of corals. I. Feeding mechanisms and food. British Museum (Natural History)

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., R.E. Robbins and J.M. Shick. 1987. Beta glucuronidase activity and detritus utilization in the sea anemones *Metridium senile* and *Anthopleura elegantissima*. *Comp. Biochem. Physiol.* (B) **87:** 303-308.

Zamer, W.E. and J.M. Shick. 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.

Zann, L.P. 1995. Our Sea, Our Future. Commonwealth of Australia.

Zubay, G. 1983. Biochemistry, Second edition, Addison-Wesley Publishing Company, Reading, Massachusetts

Appendix

Publications resulting from this thesis

The list below summarises the publications arising from this study. Reprints of published papers are included in this section.

PUBLISHED

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

IN PRESS

- **Anthony, K.R.N.** 2000. Enhanced particle-feeding capacity of nearshore reef corals on the Great Barrier Reef, Australia. *Coral Reefs* **19**

IN REVIEW

- **Anthony, K.R.N. & K.E. Fabricius.** Shifting roles of heterotrophy and autotrophy in coral energy budgets under variable turbidity. *J. Exp. Mar. Biol. Ecol.* (submitted June 1999).

CONFERENCE PAPERS

- **Anthony, K.R.N.** 1997. Detrital matter: a food source for corals? (abstract only). *Eighth International Coral Reef Symposium*, Panama 1996.
- **Anthony, K.R.N.** 1999. Skeletal growth rate: a poor indicator of sediment stress in corals? (abstract) NQ Sedimentologists' 1st Annual Workshop, School of Earth Sciences and CRC Reef